v.11.20.09
2009 Revision/Edit
2010 ClassUse Version

The Evolutionary Ecology of Weeds and Invasive Plants

Jack Dekker
Weed Biology Laboratory
Agronomy Department
Iowa State University
Ames, Iowa 50011
USA
EMail: jdekker@iastate.edu
WWW URL: www.public.iastate.edu/~jdekker

Weeds-Я-Us

Book info, formating: custom margins: top = 1” inside = 1.5”
bot = 1” outside = .75”
multiple: mirror margins

2009/10 TABLE OF CONTENTS

FORWARD: 2009-2010

The astute reader will realize principles of weedy invasion and colonization are same as for all plants regardless of the time they appear in a locality during ecological succession. Weeds colonize disturbed unoccupied opportunity spacetime, while later successional species colonize opportunity spacetime created by earlier-appearing species in those same localities. The same underlying processes and locality pertain, only the traits and opportunity change.

Harper's 'Population Biology of Plants' (1977) provided a broad view of plant biology, especially weed biology. It is now out of print. This textbook was the original source I used in developing and teaching Agronomy 517, Weed Biology, since 1992. There is no replacement that provides the scope and detail this classic reference provided. In the intervening years I transferred much of Harper's concepts to the 517 web site. I also relied on Jonathan Silvertown's two demographic-centric textbooks (Silvertown and Doust, 1993; Silvertown and Charlesworth, 2001) to fill out the scope of that course. I have also been strongly influenced by a relatively under-utilized text by Sigurd Hakesson, 2003, a classic comprehensive weed science reference. The influence of all these outstanding books is clear in the development of this text.

The contributions of all past students in Agronomy 517, from 1992 to present, have been a crucial component in the development of this book. Student projects, often focused on a single weed species, as well as student discussions and questions, have strongly influenced the evolution of the course and the book. Organizing crucial traits and qualities of weeds into species guilds, or ecological roles, in plant communities is a central organizing experience of this course. Understanding the role a species plays is the foundation for the consequential agricultural community structure we observe in fields today. It is the foundation for future evolution of the species in these habitats.

Scientific jargon is informative, extensive and can be very confusing. Scientific terminology often has different meanings in different disciplines. Terms are sometimes used promiscuously, causing misunderstanding and incorrect mental models of how systems work. For this reason, definitions of most important concepts are provided, with alternative meanings provided to highlight where confusion and misunderstanding within the sciences arises (e.g. trait; Violee et al., 2007). Discussion of these differing usages can provide much insight in the classroom. Understanding the variety of student perspectives on definitions is gained by this comparative etymology.

The background and experience of the author is centered on the mid-continent North American agricultural areas, including those of the United States 'Corn Belt' and grain producing areas of eastern and western Canada. Extensive Eurasian travel, germplasm collection, research and teaching in areas outside of the U.S. and Canada have enriched this perspective. My research experience with the weedy foxtails, *Setaria* species-group, provides a model system to explain weedy concepts throughout book. Weed Science as a discipline encourages species community understandings, with far less emphasis on the biology of individual species (or closely related species groups), a disciplinary mode more common in Entomology and Plant Pathology. Communities are the emergent behavior arising from individuals. Both perspectives provide insights into the workings of weed communities.

Ecology often utilizes demographic models, while evolutionary models of weed behavior emphasize the central role traits play in community behavior and change. Both perspectives must be understood in depth, and seen as an integrated whole, to fully understand agricultural weed communities. The conceptual limitations and intellectual liberations of both types of models are also a focus in this book.

This new version of the book (2009-2010) is a major reorganization of material strongly guided by evolutionary principles clearly elucidated by Ernst Mayr in “What Evolution Is” (2001), especially his clear presentation of the component processes and conditions by which natural selection operates in biological systems. It is this that has provided the structural organization of this book.

This new version contains a new chapter (chapter 8) on model representations of weed population dynamics, a field dominated by demographic thinking in which numeration of instantaneous states of weed populations are quantified in time as an inferential surrogate for the intervening trait-driven processes that control populations whose composition is constantly changing to fit the demands of natural selection.

This version of the book is incomplete, a work in progress.

INTRODUCTION

This is a book of the ecology and evolutionary biology of weeds and other colonizing and invasive plants. Weed biology is the ecology and evolution of plants in localities influenced by human activity, notably agriculture. The focus is on these big WHY, HOW & WHAT questions of weed biology:

What are weeds?
Why do we have weeds?
Why do we have the weed species that we do? (And not others)
Why do these weeds look and behave as they do?
How did the weeds we have get to be the way they are?
What is the basis of future changes in weeds?

The goal of this book is to provide comprehensive factual information about weed biology in an evolutionary context as the basis for understanding and management of local weed communities of the future. The goal is also to provide the reader with a dynamic framework to guide understanding of new observations in the future: a mental 'toolkit' to focus observations of new weed phenomena, a way to understand the fundamental forces in nature that cause weediness.

Nothing in biology makes sense unless seen in the light of evolution (ref Dobhansky). Weed and crop management is the management of selection and elimination leading inexorably to the weed adaptations that plague our fields and interfere with our crops. To understand what we observe in agriculture and want to manage more wisely and efficiently, we need to understand how the evolutionary process works in weed communities.

The thesis of this book is that human disturbance (e.g. tillage, herbicides, atmospheric pollution) creates opportunity spacetime by leaving unused resources in a local field with few or no plant neighbors. Opportunity spacetime is seized and exploited by heterogeneous plant phenotypes with preadapted life history traits expressed at favorable times as the growing season unfolds. Successful weed populations assemble and interact with crop and other weedy neighbors in their particular locality. The consequences of successful interactions lead to local adaptation maximizing survival and fitness in that plant community.

The first task is to define what weeds are.

CHAPTER 1: THE NATURE OF WEEDS

Summary. The concept of a weed plant is inherently human. Human values related to disturbed and agricultural habitats, appearance, utility and biological traits dominate how we define a plant as weedy.

What is a weed?

Human desires, values, and most importantly economic needs are what drive a plant being defined as a weed. The features by which humans define plants as weeds include disturbed places, aesthetics, utility or biological characteristics. All of these definitions are the consequence of interactions with humans. Many of these definitions are anthropomorphic, plant qualities as perceived by humans. As such they reveal the plants' relationship to us, and tell us much of how we view nature. The nature of weeds and weediness begins by understanding all these types of plants.

weed:
1: a plant is a weed if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed my man (without, of course, being deliberately cultivated plants) (Baker, 1965, p. 147)
2: a plant that grows spontaneously in a habitat greatly modified by human action (Harper, 1944)
3: unsightly (Thomas, 1956)
4: useless, unwanted, undesirable (Bailey, 1941)
5: a plant out of place (as determined by humans) (WSSA, 1956)
6: a plant whose virtues have not yet been discovered (Emerson, 1878)
7: competitive and aggressive behavior (Brenchley, 1920)
8: appearing without being sown or cultivated (Brenchley, 1920)
9: persistance and resistance to control (Gray, 1879)

ruderal: a plant inhabiting a disturbed site (Lincoln et al., 1998)

agrestal: growing on arable land (Lincoln et al., 1998)

feral plants: a plant that has reverted to the wild from a state of cultivation or domestication; wild, not cultivateted or domesticated (Lincoln et al., 1998)

colonizing species: a plant, typically ‘r’-selected, which invades and colonizes a new habitat or territory (Lincoln et al., 1998)

invasive species: organism undergoing a mass movement or encroachment from one area to another (Lincoln et al., 1998)

Collections of traits have also been used to define the nature of weediness.

Table 1.1 Baker's 'ideal weed concept', common biological characteristics of the world's worst weeds (1965, 1974).

Seed Bank	Germination requirements fulfilled in many environments
	Discontinuous germination (internally controlled) and great longevity of seed
Vegetative	Rapid growth through vegetative phase to flowering
	If a perennial, vigorous vegetative reproduction or regeneration from fragments
	If a perennial, brittlenenss so as not to be drawn from ground easily
	Ability to compete interspecifically by special means (e.g. rosette, choking growth, allelochemicals)
Reproductive	Continuous seed production for as long as growing conditions permit
	Self-compatibility but not complete autogamy or apomixy
	Cross-pollination, when it occurs, by unspecialized visitors or wind
	Very high seed output in favorable environmental circumstances
	Production of some seed in wide range of environmental conditions; tolerance and plasticity
	Adaptations for short-distance and long-distance dispersal

Table 1.2 Patterson's (ref) adaptive characteristics of agronomic weeds, common biological characteristics of the world's worst agricultural weeds.

Related to physiology, growth, and competitiveness	High relative growth rates in seedling stage
	High rates of photosynthesis
	Rapid development of exploitative root systems
	Rapid partitioning of photosynthate into new leaf area production
	Rapid vegetative growth to reproductive phase
	Special "weapons" for interference
	Freedom from environmental constraints ("general purpose genotype"); high capacity for acclimation to changing environment
Related to reproductive phase	Breeding systems that provide some outcrossing but also allow self-fertilization
	Copious seed production under favorable conditions with some seed production occurring over a range of favorable and stressful conditions
	Pollination by wind or generalized insect visitors
Related to cultural practices	Morphological and physiological similarity to crop
	Timing of seed maturity to coincide with crop harvest
	Resistance or tolerance to chemical herbicides
	Resistance to mechanical control; regeneration from rhizomes or other vegetative propagules
	Seed dormancy, longevity in soil; discontinuous germination over long periods of time

Chapter 2: Evolution, Natural Selection and Weedy Adaptation

SUMMARY:

2.1 Introduction

The nature of weeds is fully revealed in the story of the evolutionary processes that determine their adaptive form and behavior. The primary character in this story is human, the antagonist. Human activity affects directly or indirectly much of the arable land of the earth. Agricultural fields, forests, residential spaces, urban landscapes, industrial factory tracts, land-air-water transportation systems, golf courses, parks, school yards and amusement parks are all managed habitats disturbed directly and indirectly by human activity, whether these actions are intended or not. The atmosphere is filled with the gases humans generate and the oceans and lakes are home to the waste products humans flush into them. The community structure dominated by herbivores and predators that once balanced the abundant plant life of continental ecosystems are gone. The balance now is the balance of the human omnivore.

In all these changes the human antagonist has become the administrator of natural selection in those habitats. Managed habitats fail to utilize all the resources made available by human disturbance and thereby create opportunities for other organisms to exploit at particular times (opportunity spacetime).

The protagonists of this story are the weedy organisms humans create by their actions to control and manage nature: weeds are us. The weedy organisms that seize and exploit these opportunities do so because their phenotypes possess traits that are well suited to those localities and conditions. Natural selection in, and adaptation to, these opportunity spacetimes are the fundamental means by which weedy plants evolve and exploit the changing conditions they are confronted with in disturbed habitats. This chapter explores the fundamental forces and processes that form weed communities and drive the appearance and changes in the weeds we have created.

The story of weed evolution unfolds in a local setting, the activities of the population lead to adaptive resolutions in future generations. The setting of weed evolution, the stage upon which diversifying evolution takes place, is a local population of variable phenotypes of a weed species in a particular locality. The nature of a particular locality is defined by the opportunity spacetime it affords the weed population to survive and reproduce. Opportunity spacetime of a local habitat for a population is defined by its available resources and conditions, interactions with neighbors, and disturbances: the local niche.

The action and characterization of the weed evolution story is divided into two linked processes. First, the chance production of various heritable traits in combinations within diverse unique individual phenotypes. The second process is the evolutionary plot, the necessary consequences of natural selection and elimination among the excess individual phenotypes of the population in every generation. The plot of the story is the resolution of the central problem, survival and reproduction by a small fraction of the local population in the next generation. The resolution is adaptation and fitness of those favored by natural selection and elimination.

2.2 Evolution

In biology, evolution is the process of change in the inherited traits of a population of organisms from one generation to the next:

evolution:
1: any gradual directional change
2: change in the properties of populations of organisms over time (Mayr, 2001)
3: any cumulative change in characteristics of organisms or populations from generation to generation; descent or development with modification
4: the opportunistic process of change in the characteristics (traits) of individual organisms/phenotypes and their local populations (demes) from generation to generation by the process of natural selection
5: change in the frequency of genes in a population
6: the genetic turnover of the individuals of every population from generation to generation (Mayr, 2001)
7: the gradual process by which the living world has been developing following the origin of life (Mayr, 2001)

variational evolution: a population or species changes through continuous production of new genetic variation and through elimination of most members of each generation because they are less successful either in the process of nonrandom elimination of individuals or in the process of sexual selection (i.e. they have less reproductive success) (Mayr, 2001)

co-evolution:
1: reciprocal evolution as a consequence of two (or more) kinds of organisms interacting with each other such that each exerts a selection pressure on the other; much of the process of evolution occurs through coevolution (Mayr, 2001)
2: parallel evolution of two kinds of organisms that are interdependent, like flowers and their pollinators, or where at least one depends on the other, like predators on prey or parasites and their hosts, and where any change in one will result in an adaptive response in the other (Mayr, 2001)
3: change of a biological object triggered by the change of a related object (Wikepedia, 5.09)

2.2.1 Micro- and macroevolution. Evolutionary phenomena are sometimes categorized as microevolution or macroevolution.

microevolution:
1: minor evolutionary events usually viewed over a short period of time, consisting of changes in gene frequencies, chromosome structure or number within a population over a few generations (Lincoln)
2: the occurrence of small-scale changes in allele frequencies in a population, over a few generations, also known as change at or below the species level (Wikipedia, 5.08)
3: evolution at or below the species level (Mayr, 2001)

macroevolution:
1: major evolutionary events or trends usually viewed through the perspective of geological time; the origin of higher taxonomic categories; transspecific evolution; macrophylogenesis; megaevolution (Lincoln)

2: a scale of analysis of evolution in separated gene pools; change that occurs at or above the level of species; the occurrence of large-scale changes in gene frequencies in a population over a geological time period (Wikipedia, 5.08)
3: evolution above the species level; the evolution of higher taxa and the production of evolutionary novelties, such as new structures

2.2.2 Units of evolution and natural selection. The lowest level of living organization to evolve is the population. Every sexually reproducing species is composed of numerous local populations, within which every individual is uniquely different from every other individual.

population:
1: all individuals of one or more species within a prescribed area;
2: a group of organisms of one species, occupying a defined area and usually isolated to some degree from other similar groups

deme: a local population of potentially interbreeding individuals of a species at a given locality

local community: all the interacting demes in a locality

The variable population of phenotypes in a particular local opportunity spacetime defines the fundamental unit of evolution, the setting of evolution, the stage upon which diversifying evolution occurs.

???:
-The object of evolutionary adaptation: local opportunity spacetime
-Unit of phenotype description = life history; “The life cycle is the fundamental unit of description of the organism.” (Caswell, 2001)

The individual phenotype member of a local population, including its extended phenotype, is the unit of natural selection and elimination, the object of selection, the target of elimination.

phenotype:
1: the sum total of observable structural and functional properties of an organism; the product of the interaction between the genotype and the environment.
2: the total of all observable features of a developing or developed individual (including its anatomical, physiological, biochemical, and behavioral characteristics). The phenotype is the result of interaction between genotype and the environment (Mayr, 2001)
3: the characters of an organism, whether due to the genotype or environment
4: the manifested attributes of an organism, the joint product of its genes and their environment during ontogeny; the conventional phenotype is the special case in which the effects are regarded as being confined to the individual body in which the gene sits (Dawkins,1999), p.299).

Each individual phenotype a sexually reproducing population is unique. This same unique individual changes continuously throughout its lifetime, and when placed into a different environments. Among these heterogeneous members of the population differential survival and reproduction result in adaptation to that local opportunity spacetime.

Richard Dawkin (ref) argues cogently that the allele (within the context of the individual organism's entire genome) may be the unit of natural selection-elimination: the concept of 'selfish genes' or 'selfish DNA'.

2.3 Natural Selection and Elimination

Natural selection is the increase in frequency of the fittest individual phenotypes of a diverse local population relative to less well-adapted individuals. Natural selection is the process of elimination of those less well-adapted phenotypes. The consequences of natural selection is the adaption of certain individual weeds to the local opportunity spacetime they exist in over generations.

natural selection:
1: process by which forms of organisms in a population that are best adapted to the environment increase in frequency relative to less well-adapted forms over a number of generations
2: the process by which phenotypes of individual organisms in a local population that are best adapted to the local opportunity spacetime increase in frequency relative to less well-adapted phenotype neighbors over a number of generations
3: the non-random and differential reproduction of different genotypes acting to preserve favorable variants and to eliminate less favorable variants; viewed as the creative force that directs the course of evolution by preserving those variants or traits best adapted in the face of natural competition
4: essence of theory of evolution by natural selection is that genotypes with higher fitness leave a proportionately greater number of offspring, and consequently their genes will be present in a higher frequency in the next generation

artificial selection: natural selection by humans; domestication; selective breeding.

2.4 The Process of Natural Selection and Elimination

Adaptative evolution results from the virtually simultaneous actions of two seemingly opposed causations, chance (variation) and necessity (elimination). Evolution is characterized by both chance (contingency) in the generation of population variability, and necessity (adaptation) in survival and reproduction of the fittest progeny. All evolutionary phenomena can be assigned to one or the other of two major evolutionary processes: the origin and role of organic diversity, and the acquisition and maintenance of adaptedness.

Natural selection/elimination is a two-step process that requires five conditions to occur, which results in an adapted local population of weed phenotypes (table 2.1).

<table>
<tr><td colspan="2">Precondition 1: Excess local phenotypes compete for limited opportunity spacetime</td></tr>
<tr><td rowspan="2">Process step 1: Produce phenotypic variation</td><td>Condition 1: generate variation in individual traits</td></tr>
<tr><td>Condition 2: generate variation in individual fitness</td></tr>
<tr><td rowspan="2">Process step 2: Survival and reproduction of the fittest phenotypes</td><td>Condition 3: survive to reproduce the fittest offspring, eliminate others</td></tr>
<tr><td>Condition 4: reproduction transmits parental traits to offspring (inheritance)</td></tr>
<tr><td colspan="2">Adaptation arises in the local population of phenotypes</td></tr>
</table>

Table 2.1 The process of natural selection of the fittest phenotypes resulting in an adapted local population of weeds.

2.4.1 Precondition to natural selection.

A necessary precondition to the process of natural selection is the formation of a local population, a deme.

precondition 1: excess individuals in a local deme competing for limited local opportunity spacetime

A weed species invades a susceptible opportunity spacetime with excess numbers of members than the local habitat can support, setting the stage for evolution to occur through the process of natural selection and elimination. These weeds produce many more seed than will survive. Many more seeds germinate and form seedlings than will mature to produce their own seeds. Only the successful competitors will reproduce, mortality is very high.

2.4.2 Process of natural selection, step 1: generation of phenotypic variation.

The first step in the process of natural selection is the production of variation that provides the material for the selection and elimination processes in step two.

step 1: production of phenotypic variation in the local population

New variation is produced in the first step, which consists of all the processes leading to the production of a new zygote, including meiosis, gamete formation and fertilization. Variation arises from several sources in the weed genotype/phenotype: mutation of the zygote (from fertilization to death) caused by errors of replication during cell division; recombination via crossing-over during the first division of meiosis; random movement of homologous chromosomes during the second division of meiosis; and, to random aspects of mate choice and fertilization. The production of variation that provides the material for the selection process is dominated by stochastic processes (chance, contingency, accident) (Mayr, 2001).

The first condition necessary for evolution to occur is that there must be genetic variation in heritable characters (traits) among the excess offspring (phenotypes) produced.

condition 1: generation of variation in individual characters/traits among phenotypes of the local population

trait:
1: a character: any detectable phenotypic property of an organism
2: any character or property of an organism
3: a characteristic feature or quality distinguishing a particular person or thing
4: predictors (proxies) of organismal performance (Darwin, 1859)

functional trait: morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction or survival, the three components of individual performance (Violle et al., 2007)

The second condition in step one of the natural selection process is variation in fitness of the excess phenotypes of the population.

condition 2: variation in fitness of individual phenotypes of the local population

fitness:
1: the average number of offspring produced by individuals with a certain genotype, relative to the numbers produced by individuals with other genotypes
2: the relative competitive ability of a given genotype conferred by adaptive morphological, physiological or behavioral characters, expressed and usually quantified as the average number of surviving progeny of one genotype compared with the average number of surviving progeny of competing genotypes; a measure of the contribution of a given genotype to the subsequent generation relative to that of other genotypes (Lincoln, et al., 1998)
3: the relative ability of an organism to survive and transmit its genes to the next generation (or some defined number of future generations)

Darwinian fitness:
1: the relative probability of survival and reproduction for a genotype
2: a measure of the relative contribution of an individual to the gene pool of the next generation
3: the relative reproductive success of a genotype as measured by survival; fecundity or other life history parameters

Productivity and fecundity are often confused with fitness (e.g. Silvertown and Charlesworth, 2001). This confusion is understandable in crop science where crop yield is directly related to crop fitness.

productivity:
1: the potential rate of incorporation or generation of energy or organic matter by an individual, population or trophic unit per unit time per unit area or volume; rate of carbon fixation;
2: often used loosely for the organic fertility or capacity of a given area or habitat

fecundity:
1: the potential reproductive capacity of an organism or population, measured by the number of gametes or asexual propagules (Lincoln et al., 1998)
2: potential fertility or the capability of repeated fertilization. Specifically the term refers to the quantity of gametes, generally eggs, produced per individual over a defined period of time.

2.4.3 Process of natural selection, step 2: differential survival and reproduction of offspring. The "survival of the fittest" from among the excess, unique and variable phenotypes of the local population is to a large extent determined by genetically based characteristics.

step 2: non-random aspects of survival and reproduction. Specific sets of parental characters/traits are transmitted to the offspring who resemble them by the process of reproduction; and the fittest progeny survive to reproduce themselves:

At the second step of natural selection the quality of the new individual weed phenotype is constantly tested for its entire life history, from embryo to vegetative plant to reproductive plant. Those individuals most capable of coping with the environment, competing with other members of the local community (its species, other species) for opportunity spacetime, will have the best chances to survive to reproduce progeny (Mayr, 2001). During this selection and elimination process certain phenotypes are clearly superior to others: the fittest to survive. This second step is primarily deterministic, but there are also many chance factors of elimination including natural catastrophes (floods, hurricanes and tornados, volcanic eruptions, lightning, blizzards and violent storms) the loss of superior genes in small populations due to sampling errors. The "survival of the fittest" is to a large extent determined by genetically based characteristics.

The third condition necessary for evolution to occur is for the parent plant to survive to reproduction, and then to produce more offspring than can normally survive.

condition 3: reproduction: the act or process of producing offspring/progeny

reproduction: the act or process of producing offspring

The net (average) result of reproduction is that a parent plant leaves one descendant that reproduces, yet many more die than are produced.

The fourth condition necessary for evolution to occur is the transmission of parental traits of the "fittest" phenotypes that survive to the successful progeny.

condition 4: heredity, the transmission of specific characters/traits/genetic information from the ancestral parent to the descendants/offspring/progeny

The offspring must tend to resemble their parents.

heredity: the mechanism of transmission of specific characters or traits from parent to offspring.

inheritance: the transmission of genetic information from ancestors or parents to descendants or offspring.

2.5 Adaptation

Adaptation arises as a consequence of natural selection and elimination among excess phenotypes in a local population as the seize and occupy opportunity spacetime.

adaptation:
1: the process of adjustment of an individual organism to environmental stress; adaptability;
2: process of evolutionary modification which results in improved survival and reproductive efficiency;
3: any morphological, physiological, developmental or behavioral character that enhances survival and reproductive success of an organism
4: a positive characteristic of an organism that has been favored by natural selection and increases the fitness of its possessor (Wikipedia, 5.08)
5: any property of an organism believed to add to its fitness (Mayr, 2001)

Adaptation by elimination of the less fit individuals is dominated by the processes of survival and sexual selection favoring those most successful in seizing and exploiting local opportunity spacetime: superior success of certain phenotypes throughout their life history (survival selection); nonrandom mate choice, and everything that enhances reproductive success of certain phenotypes (sexual selection). A considerable amount of random elimination occurs simultaneously with these non-random processes.

Adaptation is not an active process. Adaptation is a passive consequence of the process of natural selection and elimination. It is a property of the local population of phenotypes favored by non-elimination.

2.6 Conclusion

From J.L. Harper in the conclusion in Population Biology of Plants (1977, pp. 776-778):

> "Adaptation is a word too loosely used in ecological writing. Often to say that a feature of an organism's life or form is adaptive is to say no more than that the feature appears to be a good thing, judged on the basis of an anthropomorphic attitude to the problems that the organism is seen to face. More accurately, adaptations are those features of an organism that in the past improved the fitness of its ancestors and so were transmitted to descendants. Adaptation is always retrospective. Fitness itself is relative - it is defined by the numbers of descendants left by an individual relative to its fellows. An organism will be more fit if its activities reduce the number of descendants left by neighbors, even if the activities do nothing to the number of descendants that it itself leaves. The point is easily made by considering the evolution of height in plants. Within a population of plants growing densely and absorbing the larger part of incident light, success depends on placing leaves high in the canopy and shading and suppressing neighbours. There is no intrinsic advantage to the individual from being high (there are some real disadvantages in the amount of non-reproductive tissue to be supported), only an advantage from being higher than neighbours. It is being higher, not just high, that pays. Similarly a genetic change that gave a plant a larger and earlier root system might bring no advantages to the possessor other than the relative advantage over the neighbors that it is able to deprive. If an activity of an organism brings no direct benefit but hinders the chance the neighbors will leave descendants, the activity will increase fitness - it will be "adaptive".
>
> This argument may be important in understanding evolutionary processes. Often the process is seen as in some way optimizing the behavior of descendants - in some way making them "better" or "adjusted to the environment". There is in fact nothing innate in a process that maximizes evolutionary fitness, that necessarily "optimizes" physiological function. Indeed a genetic change that resulted in an organism immobilizing mineral nutrients in old tissue until it died instead of returning them to the cycle within the ecosystem would almost certainly confer fitness provided that potentially competing neighbors were deprived of needed nutrients by this activity.
>
> A theory of natural selection that is based on the fitness of individuals leaves little room for the evolution of populations or species towards some optimum, such as better use of environmental resources, higher productivity per area of land, more stable ecosystems, or even for the view that plants in some way become more efficient than their ancestors. Instead, both the study of evolutionary processes and of the natural behaviour of populations suggest that the principles of "beggar my neighbor" and "I'm all right Jack" dominate all and every aspect of evolution. Nowhere does this conclusion have more force than

when man takes populations that have evolved in nature under criteria of individual fitness, grows them in culture as populations and then applies quite different criteria of performance - productivity per unit area of land. Natural selection is about individuals and it would be surprising if the behavior that favoured one individual against another was also the behavior that maximized the performance of the population as whole. For this to happen, selection would have to act on groups. It is an interesting thought that group selection which is believed to be extremely rare or absent in nature (Maynard Smith, 1964) may be the most proper type of selection from improving the productivity of crop and forest plants. Plant breeding would then be concerned to undo the results of selection for selfish qualities of individual fitness and focus on the performance of populations."

Chapter 3: Precondition to Natural Selection: Formation of the Local Population (Deme)

Summary. How do weeds assemble in plant communities? What are the functional characteristics they express that result in community structure? To answer these important questions, first there is a need to understand local opportunity that weeds can exploit (Chapter 3). With this foundation, the process of how weeds invade and occupy those opportunities is examined (Chapter 4). With an understanding of opportunity space, and how it is seized, the functional characteristics that those weeds exhibit provides the basis for understanding plant community structure and dynamic change with time (Chapter 5).

3.1 The Nature of Local Oppportunity: Space and Time

A plant succeeds in becoming a member of a plant community by possessing life history traits suitable to exploit an opportunity space in a particular locality. The presence of that species may be dependent on its ability to disperse into the locality, or disturbance at that locality creating opportunity, or both (Dekker, 2005).

Weedy and invasive plants perform the plant colonization niche. Weedy plants are the first to seize and exploit the opportunity spacetime created by human disturbance, notably in resource-rich agricultural cropping systems.

Local opportunity spacetime is the habitable space available to an organism at a particular time which includes its:
-resources (e.g. light, water, nutrients, gases)
-conditions (e.g. heat, climate, location)
-disturbance history (e.g. tillage, herbicides, winter)
-neighboring organisms (e.g. crops, other weed species).

Therefore, it is hypothesized that weedy plant life history behavior in a deme is a consequence of natural selection and reproductive success among excess variable phenotypes (and functional traits) in response to the structure, quality and timing of locally available opportunity spacetime.

Plants will fill any available and habitable growing space, therefore the primary resource limiting plant growth is habitable space. Every potentially habitable space includes the resources (e.g. relative abundance of light, water, nutrients, gases) and conditions (e.g. relative abundance of heat) of that location, its disturbance history, as well as the neighboring organisms that occupy that space. The structure of available and habitable space to an invading plant is also opportunity space at a particular time.

opportunity spacetime: locally habitable space for an organism at a particular time which includes its:
  -resources: light, water, nutrients, gases
  -conditions: heat, terroir
  -disturbance history: e.g. tillage, herbicides
  -neighboring organisms: e.g. crops, other weed species

Opportunity space-time is not general, it is always particular to a locality and time. Opportunity space-time is synomymous with habitat and niche. The more difficult task is to understand the structure of opportunity space-time, a challenge not entirely met. Herein we present an attempt, conceptualizing opportunity or the niche hypervolume as four dimensions: spatial heterogeneity, time, disturbance and differential use of resources and conditions.

Local opportunity space-time can be represented as a weedy habitat, a niche or as a niche hypervolume.

3.1.1 Weedy habitats. Local opportunity space-time can be represented as a weedy habitat. Definitions:

habitat:
1: the locality, site and particular type of local environment occupied by an organism
2: local environment
3: the physical conditions that surround a species, or species population, or assemblage of species, or community (Clements and Shelford, 1939).
4: an ecological or environmental area that is inhabited by a particular species; the natural environment in which an organism lives, or the physical environment that surrounds (influences and is utilized by) a population (Wikipedia, 5.08).

microhabitat:
1: a physical location that is home to very small organisms (e.g. a seed in the soil); microenvironment is the immediate surroundings and other physical factors of an individual plant or animal within its habitat
2: a very localized habitat (e.g. on the size scale of an individual seed in the soil seed bank)

microsite: analogous to a microhabitat; e.g. the immediate site perceived by a seed in the seed bank, or a seedling in a field.

locality: the geographic position of an individual population or collection

Habitats are constructed within the space-time matrix. A habitat is the place, the site, the locality and particular type of local environment occupied by weeds. As an agronomist I think of habitats mostly as crop production fields, like a field of corn early in the growing season. This book discusses weeds in crop fields as well as other disturbed habitats (a residential lawn, a waste field near a factory, a highway roadside, etc.). Weeds are found everywhere, not just in corn fields. Any place weeds thrive is any important habitat, with its own unique set of environmental opportunities and restrictions.

Habitats are also defined by land use factors, the type and level of management of the habitat by humans. These land use factors are closely related to disturbance, which is discussed in more detail in this chapter.

One of the most important characteristics of a habitat is the biological community of the locality. In agroecosystems this is often dominated by the crop and other weeds. This aspect of Habitat will be fully developed in the Life History section.

3.1.2 Niches in the local community. Local opportunity space-time can be represented as a niche. Definitions:

niche:
1: the ecological role of a species in a community; conceptualized as the multidimensional space, of which the coordinates are the various parameters representing the condition of existence of the species, to which it is restricted by the presence of competitor species;
2: loosely as an equivalent of microhabitat
3: the relational position of a species or population in its ecosystem; how an organism makes a living; how an organism or population responds to the distribution of resources and neighbors and how it in turn alters those same factors (Wikipedia, 5.08)

Different weed species can occupy similar niches in different locations and the same species may occupy different niches in different locations. It is this plastic response to opportunity that makes the definition of its structure so complex.

The different dimensions, or plot axes, of a niche represent different biotic and abiotic variables. These factors may include descriptions of the organism's life history, habitat, trophic position (place in the food chain), and geographic range. According to the competitive exclusion principle, no two species can occupy the same niche in the same environment for a long time:

competitive exclusion principle: a theory which states that two species competing for the same resources cannot stably coexist, if the ecological factors are constant. Either of the two competitors will always take over the other, leading to either the extinction of one of the competitors or its evolutionary or behavioural shift towards a different ecological niche (Wikipedia, 5.08).

Ecological factors in this sense are never constant. It is for this reason that opportunity space can be imagined as infinite. The full range of environmental conditions (biological and physical) under which an organism can exist describes its fundamental niche:

fundamental niche: the entire multidimensional space that represents the total range of conditions within which an organism can function and which it could occupy in the absence of competitors or other interacting (neighbor) species

As a result of pressure from, and interactions with, other organisms (e.g. superior competitors), species are usually forced to occupy a niche that is narrower than this, and to which they are mostly highly adapted. This is termed the realized niche:

realized niche: that part of the fundamental niche q.v. actually occupied by a species in the presence of competitive or interactive (neighbor) species

The niche concept is fundamental to understanding the evolutionary ecology of weeds. There exists certain connotations implicit in the term that prevent full understanding of the concept underlying niche. Niche is a passive term, it connotes receptivity, a state, the yin of yin-yang if you will. And of course, it is, afterall, French. Presented next is the concept of opportunity spacetime, conceptually analogous to niche. The word concept ‘opportunity’ contains something not implicit in niche. Opportunity connotes exploitation, an action or process physically seizing something in the habitat, the yang in yin-yang. And of course, it is, after all, very American.

3.1.3 Local opportunity spacetime structure. The structure of local opportunity can be defined by a space-time matrix: the niche hypervolume.

3.1.3.1 The niche hypervolume. Niche differentiation can be formalized as the dimensions of time and space in which resources and conditions are used in a locality. Opportunity space-time can therefore be expressed as an n-dimensional niche hypervolume (Hutchison, 1957):

n-dimensional niche hypervolume:
1: the multi-dimensional space of resources and conditions available to, and specifically used by, organisms in a locality
2: the phenotype is described by the niche hypervolume; phenotype = G x E = realized niche; the selection pressure consequence of the G x E interaction
3: the limits or borders within which which a species has adapted,
4: experimentally defined by the testable parameters (dimensions) one can evaluate; the parameters determining the form of existence of a plant

What is the structure of opportunity space-time that weeds seize and exploit? How do we represent it?

Trewavas (2000) had suggested there are several distinguishable environmental signals to which individual plants are sensitive: 1) water; 2-7) 5-6 primary minerals: N, P, K, etc.; 8) light; 9) gravity; 10) soil structure; 11) neighbor competition; 12) herbivory; 13) disease; 14) allelopathy; 15) wind; 16) gases; oxygen and carbon dioxide. This incomplete list is an alternative way of expressing the dimensions of a niche hypervolume. Is there a better way of expressing this seemingly infinite range of parameters?

Harper (1977) wrote that resource heterogeneity drives niche differentiation. He discussed elements contributing to the diversity of plant populations and to community structure:

> "Specializations that we most commonly see within communities of plants are with respect to the dimensions of time and space in which resources are used."

Weeds specialize their life history traits by adapting to the space-time available in a locality.

> "Most of the niche differentiation that has occurred has been interpreted in relation to heterogenous distribution of resources in space and time."

Different niches in a locality are created by heterogeneous local space-time opportunity.

Harper concluded that plant community diversity is dependent on four dimensions of the niche hypervolume: the lateral heterogeneity of environments, the vertical heterogeneity of environments, the temporal division of the environment, and differential use of resources. His spatial dimensions (patchiness, lateral, vertical) can be conveniently combined, and a fourth, disturbance, included.

The dimensionality or structure of opportunity space-time, the niche hypervolume, can be represented by four aspects of opportunity operating in habitats: spatial heterogeneity, temporal use of environment, the dominant role of local habitat disturbance, and the differental use of resources and conditions.

Natural selective forces guide a weed population in its search for, and exploitation of, opportunity (space-time, disturbance, resources-conditions). It is to these that weeds respond and adapt. The cumulative effect of weed populations interacting within these aspects of opportunity result in the observed local community structure over time.

3.1.3.2 Spatial heterogeneity and patchiness. The niche hypervolume is defined and confined by the spatial dimensionality of the local habitat weeds exploit. The diversity of local community structure is dependent on spatial heterogeneity and patchiness. The diversity of weed populations and plant community structure is a consequence of natural selection and adaptation to heterogeneous local opportunity.

There are many lateral and vertical factors that comprise the spatial diversity of habitats that weeds exploit. The horizontal spatial variability over the landscape is a mosaic. It consists of heterogeneous soil gradients, topography factors and global position, to name but a few. Vertical spatial variability includes the soil below and the atmosphere above. Some few examples are presented in table 3.1.

LOCAL SPATIAL HETEROGENEITY		
HABITAT	Soil	type, structure, tilth, aggregation, fertility, moisture (% moisture/drainage/drought risk) organic matter %, soil pH, depth, sub-soil, geology, age
		seed pool distribution; ground cover
	Topography	slope, gradient, aspect, elevation, landscape-watershed position
	Atmosphere	gases, moisture, pollution
	Location	latitude, longitude, solar exposure
		microsite
DISTURBANCE	Farmer-Land Manager Practices	crop production disturbances such as tillage and planting; combines and harvesting; herbicides and cultivation
	Non-human	cycles, crashes, catastrophes
NEIGHBORS	Seeds	seed heteroblasty; seed dispersal pattern
	Community	competition and interactions with neighbors
		population phenotype diversity
RESOURCES & CONDITIONS	Resources	nutrients: nitrogen; phosphorus; potassium; micronutrients
		light: quality, quantity, plant canopy
		water: quantity, quality (salinity, toxins)
		gases: oxygen, carbon dioxide
	Conditions	temperature

Table 3.1 Habitat-disturbance-neighbor-resource/conditions responsible for setting the scale of local spatial heterogeneity/patchiness to which weed populations adapt and evolve.

An essential part of understanding habitats is the scale at which habitats exist. For example, to a farmer trying to manage a field, there are very big differences between habitats at the microsite scale and the field scale. The farmer is most interested in scale from a practical perspective: tractor scale and field scale. This viewpoint is the essence of site-specific crop and field management. Habitats exist in an ordered spatial hierarchy at many scales: global > continental > regional or State > landscape > farm > field > locality or site > microsite.

Weed populations in local fields and habitats usually exhibit spatial patchiness. Natural selection on patchy and spatially heterogenous weed populations acts in many niches, providing opportunity space-time for a complex community structure. Many factors set the scale of natural selection in a plant population's spatial diversity (e.g. Table 3.1).

Seed dispersal mechanisms, as well as perennial weed ramet foraging, set the scale to a plant populations spatial heterogeneity. They are the means by which the plant "reaches out" to contact neighbors. They determine the selection pressures the plant will meet. This topic will be more fully developed in Chapter 9, the life history of the vegetative plant.

3.1.3.3 Temporal division of the environment. The structure of opportunity space-time, the niche hypervolume, is apparent in the temporal use of the environment made by weed populations. Resources and conditions in a locality are unevenly distributed over time, the basis of differential life histories of weed species and the temporally differential expression of traits during life history development of the individual weed plant. Some few examples are presented in table 3.2. Temporal exploitation of opportunity is fully developed in Unit 4, weed life history.

LOCAL TEMPORAL HETEROGENEITY		
SHORT-TERM	Phenology: timing of development and growth	seedling emergence times; leaf, branch and tiller timing
	Phenology: reproductive timing	flowering timing; seed production periodicity; time to seed maturity; pollenation timing
	Disturbance	tolerance to farming practices: e.g. tillage, herbicides; winter freezing
SEASONAL	Risk of mortality: temporal avoidance of neighbors, disturbance, stress	life cycle time and duration: perennials, biennials, summer annuals, winter annuals
LONG-TERM	Plant ecological succession	annual colonizing species succeeded by herbaceous perennials, by woody perennials
	Environmental adaptation	long-lived species (e.g. perennials) experience full range of yearly climate; annual species experience, and adapt to, seasonal periods of active growth

Table 3.2 Factors responsible for setting the scale of local temporal heterogeneity to which weed populations adapt and evolve.

[ADD: rhythmic plant behaviors; circadian rhythms; diurnal rhythms, temporal adaptations for purposes, etc.]

3.1.4 Disturbance. The dimensionality of opportunity space-time, the niche hypervolume, includes the dominant role of local habitat disturbance. The creation of new, and the destruction of old, opportunity space-time for plant invasion can be a consequence of disturbance, a change in the local space-time matrix, a natural selection pressure fostering invading and colonizing populations.

Changes in plant community structure, and the process of plant invasion, require an appreciation of the broad role disturbance plays in creating and destroying opportunity for new individuals to exploit. Competitive exclusion by extant individuals within a plant community puts invading species at a disadvantage in establishment. The role of disturbance in creating and destroying opportunity is crucial to community structure. It is often not fully considered in the ecology of apparently undisturbed habitats. This is reflected in the definitions provided for disturbance:

disturbance
1: the act of disturbing or the state of being disturbed (Anonymous, 1979, 2001)
2: an interruption or intrusion (Anonymous, 1979, 2001)
3: destruction of biomass by any natural or human agency (Silvertown and Charlesworth, 2001)

Disturbance cannot be avoided in studying agroecosystems, and the profound changes in plant community it causes. Herein a more inclusive definition of disturbance is provided:

disturbance
4: an interruption or intrusion with direct and indirect spatial, temporal, biological or abiological effects that alters or destroys a biological individual or community

Disturbance is more than the direct cause of damage or mortality to a plant. It also includes the indirect effects of the abiotic environment, and the biological community (neighbors), with which the individual phenotype interacts. Disturbance of plant communities can be human-mediated or not.

<u>Disturbance possesses dimensionality</u>. Disturbance can be understood by considering the biological community structure, and the abiotic environment, influencing the community at a locality (the population) and microsite (the individual) (Table 3.3).

DIMENSIONALITY OF DISTURBANCE		
Disturbance Dimension	Disturbance Factor	Examples
SPATIAL	•proximity of effect: direct or indirect •localized or widespread •heterogeneity and fragmentation	•direct, localized: lightning strike spot in field •indirect, widespread: highway corridor effects on adjacent forests •variable erosion and drainage effects with landscape elevation
TEMPORAL	•severity: quantity, frequency and duration •regularity and predictability of patterns	•cycles: annual winter soil freezing •crashes: yearly tillage of crop field •catastrophes: removal of tropical rain forests
BIOLOGICAL COMMUNITY	•competitive neighbor interactions •specificity and vulnerability: sensitivity and resistance •change in biodiversity	•competitive exclusion by earliest emerging seedling in field •response to predators, parasites and diseases •increase in prairie fires with loss of large herbivores
ABIOTIC ENVIRONMENT	•resource availability •inhibitors and stress	•drought •herbicides

	•climate and weather	•winter freezing of soil

Table 3.3. Dimensions of disturbance (spatial, temporal, biological community, abiotic environment), disturbance factors within each dimension, and examples of factors.

Proximity of disturbance. Disturbance can have proximate and distal effects in the creation and elimination of opportunity. Disturbance is more than the direct cause of damage or mortality to a plant. It also includes the indirect effects of the abiotic environment, and the biological community (neighbors), with which the individual phenotype interacts and is affected. Disturbance of plant communities can be human-mediated or not. The scale of the disturbance is also important: local versus widespread.

Vulnerability to disturbance. The susceptibility and sensitivity of a locality or microsite to invasion varies with the robustness and resistance of a local community to the traits possessed by an invading species. The vulnerability of habitats to invasion is often a function of the extent of direct and indirect disturbance by humans. Ironically, many agro-ecosystems have stable weed communities that resist invasion by new species. Weed populations often are stable due to the high, consistent level of disturbance management of these controlled systems. Population shifts are most likely to occur in these agriculture fields when crop management tactics change, e.g. introduction of new herbicides or herbicide resistant crops (Dekker and Comstock, 1992). The disturbances accompanying cropping systems creates very large selection pressures which open and close large amounts of opportunity space depending on the life history traits of crops, control tactics and the temporal sequence of the systems components. The impact of these strong forces of selection are enhanced in annual cropping systems which eliminate above ground vegetation every year, leaving vast open opportunity space-times available to weed infestation and invasion. Less disturbed habitats are often more vulnerable to invasion due to the fact that direct and indirect disturbance can change the ecological balance within these unmanaged biological communities, creating new opportunities (e.g. plant community changes due to the loss of large herbivores with human colonization of North America).

Temporal patterns in disturbance. Harper defined a fifth selection force driving variability in weed population, the evolutionary consequences of disturbance, which included differentiating crashes, cycles, catastrophes (Harper, 1977, pg. 769-774).

Catastrophes are rare, once in a lifetime events:

catastrophes:
1: an event subverting the order or system of things; significant population decrease, possible local extinction
2: disaster, a horrible event (Wikipedia, 5.08)

Of tangential interest, raising the some interesting speculations about disturbance and community structure predicability, is:

catastrophe theory: a field of mathematics that studies how the behaviour of dynamic systems can change drastically with small variations in specific parameters (Wikipedia, 5.08)

In mathematics, catastrophe theory is a branch of bifurcation theory in the study of dynamical systems; it is also a particular special case of more general singularity theory in geometry. *Bifurcation theory studies and classifies phenomena characterized by sudden shifts in behavior arising from small changes in circumstances*, analysing how the qualitative nature of equation solutions depends on the parameters that appear in the equation. This may lead to sudden and dramatic changes, for example the unpredictable timing and magnitude of a landslide. Small changes in certain parameters of a nonlinear system can cause equilibria to appear or disappear, or to change from attracting to repelling and vice versa, leading to large and sudden changes of the behaviour of the system. However, examined in a larger parameter space, *catastrophe theory reveals that such bifurcation points tend to occur as part of well-defined qualitative geometrical structures*. (Wikipedia, 5.08)

Catostrophe examples include the October blizzard of 1947, and the Armistice Day Freeze when 90% of Iowa apple (*Malus* sp.) trees died. Catastrophes are not cyclical, they occur on a time scale such that an organism can't adapt to their unpredictability. They can produce genetic changes that are themselves not adaptive as populations struggle to become re-established (e.g. genetic bottleneck). Catastrophes are outside of the "memory" of organism; events for which no member of the soil seed pool or population has adapted to (no pre-adaptations to prevent local extinction)**.**

Crashes are a decrease in a population, within the time scale of an organism:

crash: [need definit here]

Potentially an organism is pre-adapted to crashes. Crashes are within an organism's evolutionary experience; potentially some variants with pre-adaptations will allow continuation in locality. Examples include tillage, herbicide application, grazing, harvesting; longer or shorter seed rain period, dispersal; drought, flooding, freezing, fire, tornado, lightening; alien landing sites (e.g. crop circles); pathogen attack; diseases (epidemics).

Cycles occur on many time scales: diurnal: daily temperature cycles; seasonal: tillage, planting, cultivating, harvesting; cycles of predator-prey.

cycle:
1: happening at regular intervals
2: an interval of space or time in which one set of events or phenomena is completed
3: a complete rotation of anything
4: a process that returns to its beginning and then repeats itself in the same sequence
(Wikipedia, 5.08)

Cycles are predictable (predictable crashes), therefore weeds and other organisms are well adapted to them. The cycle crucial to weed populations is their life history, developed in detail in the following unit. Another very important cycle in nature is plant community succession, discussed in Chapter 5, community dynamics.

3.1.5 Limiting resources-conditions in local opportunity spacetime

> "Plants interfere with the distribution of neighbors by depleting limited resources. An effect will occur only when the depletion zone created by one plant includes the zone available to another. Resources (or supply factors) are exhaustible and contrast with conditions (quality factors) such as temperature that are not exhaustible. The nature of a resource (light, water, nutrients, O_2, CO_2) determines how a plant may affect a neighbors' growth; the diffusion of light, gases and nutrients are at very different rates and determine how far away from an individual depletion effects are sensed. Light, water and nitrates are probably the three resources most commonly involved but the interaction

> between resource factors makes it unrealistic to isolate any one resource as that for which competition occurs: the extent of interference below ground is not well understood."
>
> -Harper (1977; summary, p. xvii; Ch. 10: pp. 305-345

The fourth dimension of the structure of opportunity space-time, the niche hypervolume, can be represented by the differental use of resources and conditions in local habitats. The diversity of community structure is dependent on their differential use.

Resources and conditions. Plants interfere with neighbors by depleting limited resources available to another. Resources are exhaustible (supply factors) and contrast with pervasive conditions (quality factors) such as temperature (heat) that are not exhaustible.

The presence of a plant changes the resource-condition environment of its neighbor, affecting the growth and form of both. Neighbor interactions can take many modal forms, including competition, interference, coexistence, cohabitation and synergism, topics developed in section 7.5 on neighbor interactions.

Limiting resources in the environment. Seedling plant growth depends on internal resources supplied by parents: stored seed food reserves (e.g. cotyledons, endosperm). Autotrophic growth by the seedling depends on its ability to extract external resources from the environment: consumable supply factors such as light, nutrients, water and gases.

These resources are limited by neighbor effects, competition. It is very difficult to untangle what mechanism is involved when neighbor plants interfere with the growth and development of each other. Relief of density stress by the addition of a resource may not be sufficient evidence that the resource was the limiting factor in the stress. For example, the addition of water may increase nitrate availability and relieve its shortage. Limiting resources are intimately related to each other and act in concert. Light, water and nitrates are the three resources most commonly involved, but it is often impossible to separate the competitive interaction between resource factors. For example, light and heat affect leaf stomatal aperture opening, through which moisture conductance regulates the amount of soil water-disolved nutrient uptake via the xylem from the roots.

3.1.5.1 Light as resource. Supply of light is the most reliable of the environmental resources because of the regularity of diurnal and annual photocycles. Although light may be available above the canopy of leaves of a community, it can be limited below by shading from neighbor plants. Light can not accumulate. Light varies in intensity, duration, quality, direction and angle of incidence both in daily and annual cycles.

Light intercepted by plants can be reflected. It can be absorbed and converted into photosynthetic product or heat. The light profile of the leaf canopy changes as it passes down through the canopy to the soil. The canopy leaves can transmit and filter the light so that the lower leaves receive less quanta, and the light quality or spectra altered (e.g., enriched far red). Canopy shading can occur as self-shading of upper and lower leaves on the same plant, and mutual shading by neighboring plants. The intensity of light under plant vegetation commonly is below the compensation point (photosynthesis is balanced with respiration).

Light passing down throught the canopy is not a continuous gradient but a moving, dappled pattern of direct light added to a background of diffuse light. Leaf morphology varies between species, and on the same plant, in terms of the angle at which they are borne and consequently in the time of day at which they cast the greatest shadow. Leaf movements affect the amount of light that is intercepted. For example there exist diurnal leaf and shoot solar tracking/avoidance movements in *Helianthus* spp. and *Abutilon theophrasti*.

Photosynthesis in the canopy of a population depends on the affects of neighbors. In an isolated, individual leaf that is free of neighbor effects, the rate of photosynthesis increases linearly with increasing light intensity until a maximum value is reached. Beyond this maxima no further photosynthetic productivity increases occur with increasing light. The whole canopy may respond differently. There may occur increased photosynthesis in a population with increasing light intensity over a much wider range of light intensities. In a canopy the upper leaves become saturated more quickly as light intensity increases. The lower leaves in the shade may still respond to increasing light intensity that penetrates through the light-saturated upper canopy. Canopies are a population of leaves, not individuals. The population acquires a holistic physiology within which the individual plant is subordinated to the physiology of the whole. Plant populations adjust their structure and growth rate to the resources available. Perfect adjustment is impossible because the environment changes. Canopies are compromises, balancing respiration and photosynthesis.

The effects of neighbors in light competition occur between individual leaves, not individual plants, permitting individual leaves to act as discrete units often interfering directly with other parts of the same plant. For example, different species may use light quality differently: shade and sun-loving competitors can coexist. For example, *Rosa* sp. (multi-flora rose) can form clumps in a grassy pasture. The rose shades out the grass, and the community structure appears clumpy with both present.

3.1.5.2 Water as resource. The supply of water in a locality is often the least reliable of all the plant growth resources. It can be in excess or in limited supply. Plants draw water primarily from stored moisture, the soil acting as a buffer against the uncertainty of its availability. Plants act as wicks, drawing stored water reserves from the soil into the atmosphere via the xylem and leaf stomates (transpiration). With time and plant growth (leaf area, root system size), the size of this wick increases, increasing water loss rates. Bare soil dries quickly and impedes the continued loss of water from the soil. The dry surface no longer acts as a continuous wick, becoming to some extent self-sealing. Light and water are intimately related. Heat from solar radiation drives transpiration while light quanta drive photosynthesis. Stomatal leaf function links both together: it is impossible to separate the roles of light and water in limitations to plant growth. There exists an intimate role of CO_2 uptake with these phenomena: both pass into, out of, plant through stomates

The amount of water available to a plant is determined by the extensiveness of the root system. Dense plant populations suffer water shortages earlier in life than sparsely dispersed populations. Sparse populations cover the surface later with leaves, and water is conserved in the soil longer. Sparse populations suffer less neighbor stress by shading and nutrient depletion. These widely spaced plants are more vigorous and develop more extensive root systems than densely packed populations.

Variable plant shoot development above ground is reflected in below ground root system growth. Therefore water stress occurs differentially by these different individuals. Greater interference occurs between root systems of different individuals in a population than between parts of one root system, in contrast to the potentially greater interference between leaves on the same plant above ground. Different species develop different root systems at different times. Earlier germinating species (e.g. *Chenopodium album*) can use up water and nutrient resources sooner, depriving later emerging species. Different species may exploit different zones of the soil profile and avoid interference for water.

Water use affects community structure. For example, *Carnegiea gigantea* (sagaro cactus) and *Artimesia tridentata* (sagebrush) have different strategies in storing and seeking out water which determine their community structure. Saguaro holds water in its body and has a shallow root system. Sagebrush doesn't store water but has a deep and extensive root system to find water. Another example is found in wetlands. *Lythrum salicaria* (purple loosestrife) thrives in wetlands in which the water level is lower and dry at certain times of the year. *Typha latifolia* (cattail) can't tolerate periods of no water. Communities that contain both species indicate a response to selection pressure for a dry period tolerant cattail (ecological combining ability).

3.1.5.3 Mineral nutrients as resources. [*needs lots more; list each mineral and its role briefly, especially in context of agriculture and pollution*] Plants obtain mineral resources primarily from the soil (exceptions include atmospheric nitrogen-fixing leguminoseae), and many of the conditions that govern their availability are similar to those affecting water. Soil minerals are held in the soil by physical and chemical linkages with insoluable soil components and are in a rapid, dynamic, equilibrium with ions in the soil water solution. When nutrients are removed by a root, there is a local lowering of its concentration, a diffusion gradient is created, nutrients diffuse along this gradient. Nitrate ions are an exception, not being held to soil colloids and being wholly mobile in the soil solution.

The transpiration stream in plants from the roots absorbing water from the soil, through the vascular system (xylem) to the leaves, creates a mass flow of soil solution towards the absorbing roots. Mass flow and nutrient diffusion in the soil maximize nutrient flow towards plants with the greatest growth: they tap the largest soil volume and they have the greatest transpiration rates. Some plants have "luxury" consumption of nutrients, the excess over immediate needs being absorbed when the plant is young and subsequently redistributed in the plant as it grows. This can occur when a plant takes up larger quantities of nutrients early in the competitive interaction with other species, preventing timely uptake by neighbors. *Chenopodium album* (common lambsquarters) is believed to be such a species. Mycorrhizal associations with plant roots can affect nutrient availability, increasing uptake.

It is very difficult to identify the effects of nutrients as a limiting resource in plant populations. There exists an intimate relationship between water and nutrient availability. Supplying nutrients to plants may just speed up the time that light becomes limiting to growth. Enhanced fertility may result in increased root system size speeding up the time water availability becomes limiting to growth.

Nutrient resource use can affect community structure in many ways. For example, in a legume-grass pasture, leguminous clover fixes atmospheric nitrogen. Excess nitrogen in the soil solution is used by the grassy species. A stable, heterogeneous community structure arises from this differential supply and use of soil nitrogen.

3.1.5.4 Gases as resources. [*list each gas: n, co2, o2, h20*]

Carbon dioxide. The amount of carbon dioxide supplied to a leaf can control the rate of photosynthesis in that leaf, therefore it can be a limiting resource to plant growth. Determining whether CO_2 can be a limiting resource in the plant leaf canopies depends on two factors: evidence that levels of CO_2 fall in photosynthesizing canopies; and evidence that rate of photosynthesis falls in response to these decreased CO_2 levels. These situations are not typical of most terrestial plant communities.

Movement and flux of CO_2 within plant canopies to leaf surfaces occurs by gaseous diffusion and by turbulent transfer (e.g. wind). There can sometimes occur diurnal cycles of measurable zones of CO_2 depletion and enrichment within canopies. Depletion zones are the greatest, and extend deep into canopy. Evening CO_2 levels can rise as respiration exceeds photosynthesis, enriching the local atmosphere. Wind can increase plant assimilation rates in canopies by resupplying depleted CO_2.

Differences in carbon metabolism occur in C3 and C4 plant species. In these species, photosynthetic rates can differ due to the role of the CO_2 compensation point. The compensation point is the CO_2 level below which photosynthesis does not occur. In C3 plants the compensation point is about 30-70 PPM CO_2. In C4 plants it is 5 PPM CO_2 or lower. C3/C4 plants utilize different biochemical pathways to assimilate CO_2. C4 plants can maintain very low CO_2 levels in the intercellular spaces of the leaf, creating a steeper diffusion gradient to the atmosphere which speeds up the movement of carbon to the sites of photosynthesis. The enhanced CO_2 uptake in C4 plants results in a narrower stomatal opening for less time. Smaller stomatal aperture results in more efficient water usage, C4 transpiring less water per unit dry weight gain than C3 plants. C4 plants continue to increase photosynthesis with increasing light beyond the point C3 plants reach a plateau. C4 plants have a higher optimal temperature for photosynthesis than C3 plants. The net effect in plant populations is greater efficiency of C4 plant. This efficiency is reflected not in producing larger plants, but in a more effective water-conserving plant with a greater reproductive efficiency.

Overall, atmospheric CO_2 level is of lesser importance than understanding the factors that influence intercellular CO_2 levels in plants. Photosynthesis proceeds on the basis of carbon availability in the chloroplast in many instances. Intercellular CO_2 is a function of stomatal aperature, which in turn is a function of the plant metabolic system, water availability, transpiration, carbon utilization in the plant, and many more factors. Atmospheric CO_2 probably is relatively unimportant in terms of a limiting resource in most instances. Intercellular CO_2 is a very important limiting resource in plant growth and development; its availability is another excellent example of the dynamic relationship between all the resources in limiting productivity (water, light, nutrients)

<u>Oxygen as resource</u>. It is difficult to imagine oxygen being limiting to above ground plant parts. Oxygen may become limiting to plant growth below ground, in the soil. Diffusion of O_2 in water is 10,000 slower than in air. The presence of water films in soil and on plant roots can slow or stop diffusion pathways in soil, and can hinder O_2 movement in soil. These factors are balanced by the extremely high affinity of plant terminal oxidase systems for oxygen. The net effect is that aerobic respiration in roots unlikely to be hindered unless the O_2 concentration approaches zero near the root. Local zones of O_2 depletion may arise in water-saturated soils. Short (1 day) periods of anaerobiosis can seriously damage roots. Neighbor roots may exaggerate depletion of O_2. Of all the resources needed by plants, oxygen is the least likely to limit growth, the least likely to be limited by neighbors.

3.1.5.5 Pervasive Conditions in the Environment. Heat and terroir.

<u>Heat</u>. The most common condition in the environment is temperature, or the presence of heat to support or hinder growth and development. Heat penetrates soil, plant and air so it is ubiquitous. Heat in the environment can affect the availability of oxygen dissolved in water, and the amount of water in the soil and atmosphere.

<u>Terroir</u>. [local affects of slope, aspect, latitude, longitude, elevation; find definition; concept of relationships of these location conditions to underlying soil matrix substrate]

3.2 Plant Invasions

The structure of opportunity provides the foundation for understanding how it is seized and exploited: the invasion process. The concept of 'invasive species' has broader social, economic and political implications, emphasizing the differences in how humans perceive weedy and colonizing species.

3.2.1 The plant invasion process: seizing, exploiting and occupying opportunity spacetime. Successful plant invasion is the consequence of the presence of a particular species possessing life history traits suitable to exploit an opportunity space in a particular locality. Given these conditions, an individual invading species must successfully survive three processes: dispersal of that species into that locality, followed by colonization and enduring occupation of that habitat. Lastly, the species succeeding in occupying a locality must be perceived by humans as being problematic. Without the occurrence of all three processes, a plant species is not labeled invasive.

Plant invasions are events in the ecology of community assembly and succession, as well as in the evolution of niche differentiation by speciation. There is not meaningful difference between the invasion process and these processes except the scale of attention humans bring to their observations. In all these processes disturbance is a prime motivator of change. Habitat disturbance as a direct or indirect consequence of human activity is of central importance. The scale of habitats in time and space is continuous; and all communities are inter-related.

Plant invasion can be succinctly described by four processes : dispersal, colonization, enduring occupation and extinction:

<table>
<tr><th colspan="3">PLANT INVASION IN A 'NUTSHELL'</th></tr>
<tr><td>OPPORTUNITY CREATION</td><td colspan="2">Individual phenotypes respond to opportunities created by disturbances affecting locally available resource-conditions, to neighbors (or lack thereof), and to mortality</td></tr>
<tr><td>NATURAL SELECTION FAVORS INDIVIDUALS</td><td colspan="2">Natural selection favors individual phenotypes able to preferentially take advantage of these opportunities at the expense of their neighbors</td></tr>
<tr><td rowspan="3">PREADAPTED LIFE HISTORY PHENOTYPES INVADE</td><td rowspan="3">Plants seize local opportunity by timing their life history to optimize the invasion process</td><td>dispersal of propagules into an opportunity</td></tr>
<tr><td>colonization: recruitment and establishment</td></tr>
<tr><td>enduring occupation of that locality for some time</td></tr>
<tr><td>EXTINCTION</td><td colspan="2">Local populations become extinction ultimately from any locality</td></tr>
</table>

Table 3.4 Plant invasion in a nutshell: opportunity, selection, invasion and extinction.

The invasion process specifically consists of three sub-processes. Given a plant species with certain life history traits and a vulnerable local opportunity space, the invasion process is successful only when all of these are accomplished. Most invading species probably fail to complete all three steps, and there is little experimental information estimating the failure rate. All local plant populations become extinct eventually.

INVASION PROCESS	LIFE HISTORY ACTIVITY	Example
Invasion	Dispersal	propagule (e.g. seed, vegetative bud, spore, pollen) movement from one continent (or locality) to another and fails to reproduce

Colonization	All events must occur: a] recruitment b] establishment c] reproduction	volunteer maize (Zea mays L.) lives for only one generation (F2) in a field, failing to colonize due to lack of dormancy
Enduring Occupation	Several modes possible: a] enduring presence for more than one generation b] range expansion c] formation of soil propagule (e.g. seed) pool	successful, long-term, agricultural weeds; e.g. North America: Amarathus spp.-gp.; Setaria spp.-gp
Extinction	Mortality	Population shift from susceptible to resistant weed biotypes with the widespread use a herbicide

Table 3.5 The processes (invasion, colonization, enduring occupation, extinction), life history activities (dispersal, recruitment, establishment including reproduction, and several modes of enduring occupation) and examples

3.2.2 Dispersal. The first activity in invasion is successfully introducing propagules (seeds, vegetative buds, etc.) into a candidate opportunity space. Definition:

dispersal
1: the act of scattering, spreading, separating in different directions (Anonymous, 2001)
2: the spread of animals, plants, or seeds to new areas (Anonymous, 1979)
3: outward spreading of organisms or propagules from their point of origin or release (Lincoln et al., 1998)
4: the outward extension of a species' range, typically by a chance event (Lincoln et al., 1998)

Herein dispersal is defined:

5: the search by plant propagules (e.g. seeds, buds) for opportunity space

3.2.3 Colonization. The process of colonization includes three activities: recruitment, establishment and reproduction at the new locality. Definitions:

colonization
1: (of plants and animals) to become established in (a new environment) (Anonymous, 1979)
2: the successful invasion of a new habitat by a species (Lincoln et al., 1998)
3: the occupation of bare soil by seedlings or sporelings (Lincoln et al., 1998)

recruitment
1: seedling and bud shoot emergence
2: the influx of new members into a population by reproduction or immigration (Lincoln et al., 1998)

establishment: growing and reproducing successfully in a given area (Lincoln et al., 1998)

3.2.4 Enduring occupation of a locality. Several modes of long-term presence at a locality are possible. An invading species can have an enduring presence for more than one generation in the same locality. This long-term presence is often facilitated by plant traits that allow the formation of soil propagule (e.g. seed) pools. A species present in one locality can also expand its range into new localities.

Local selection and adapted phenotypes. Once a species successfully occupies a local site of some time period, the action of selection pressures result in local adaptation in favor of particular genotypes and phenotypes. The selection pressures these populations experience in the invasion and occupation phases derives from both biological, abiotic and human selection pressures. This local selection also acts on the variable phenotypes of that invading species and selects adapted biotypes that occupy that space into the future. Some of the consequences of this local evolution and adaptation include increases in locally-adapted phenotypes, range expansion beyond the locality, and population shifts in the local community as a consequence of altered neighbor interactions.

3.2.5 Extinction. All plant populations go extinct at some time. Definition:

extinction

1: the process of elimination, as of less fit genotypes

2: the disappearance of a species or taxon from a given habitat or biota, not precluding later recolonization from elsewhere

All local populations become extinct. The important considerations for an individual species are on what spatial and time scale these extinction events occur. Many of our most common crop field weeds (e.g. *Setaria*) have been around for thousands of years. But every local population goes extinct at some point. For example, many herbicide susceptible phenotypes have disappeared from local fields and were replaced by either herbicide resistant populations of the same species, or by other species in that locality. Within any field an individual weed species is spatially located in patches. These patches can change from year to year. On this local spatial scale extinction occurs continuously with re-invasion of adjacent areas. Most weed species accomplish this process of patch movement continuously on many spatial and temporal scales. Plant community succession is a series of invasions and extinctions. As the colonizers become established they create opportunity space for later successional plant species. On and on it goes.

3.2.6 The perception of plant invasion. The biology of the invasion process as presented in the section above is rational and experimentally tractable. What is less apparent is the human component of the selection process that creates opportunity spaces into which invasive species disperse (Dekker, 2005). Of critical importance is the role human perception plays in selection and creation of opportunity space for invasive species. There exists a perception that invasive species are increasing of late due to increased global movement of people, trade, and transport of biological and agricultural commodities and novel plant materials. The terminology used by those interested in invasion biology is often defined somewhat differently by these respective groups. The perception of a plant species as invasive by humans is a complex, often highly subjective process. A discussion of this topic can be found in Appendix 1.

Chapter 4: Process of Natural Selection 1: Generation of Genotypic and Phenotypic Variation

[Revisit Mayr and get this summary right. This may lead to reorganization of the chapter which I leave as-is from 2008/9 version. Topics to include:
1. random aspects of variation generation: generation of variable phenotypes as unique combinations of variable traits
2. differentiate sources of random variation in sexual reproduction and non-random sources such as mating systems that conserve and direct variation production
3. genetic foraging: link with competition foraging strategies in old chapter 7.1]

Summary.

4.1 Genotypes and Phenotypes

Individual organisms are the units of natural selection. The diversity found among individual weed plants in populations and agricultural floral communities arises from both genetic, somatic and behavioral variation. This diversity of individual plants and plant characters is revealed in the weed genotype and phenotype.

genotype:
1: the hereditary or genetic constitution of an individual; all the genetic material of a cell, usually referring only to the nuclear material
2: all the individuals sharing the same genetic constitution; biotype
3: the set of genes of an individual (Mayr, 2001)

phenotype:
1: the sum total of observable structural and functional properties of an organism; the product of the interaction between the genotype and the environment.
2: the total of all observable features of a developing or developed individual (including its anatomical, physiological, biochemical, and behavioral characteristics). The phenotype is the result of interaction between genotype and the environment (Mayr, 2001)
3: the characters of an organism, whether due to the genotype or environment
4: the manifested attributes of an organism, the joint product of its genes and their environment during ontogeny; the conventional phenotype is the special case in which the effects are regarded as being confined to the individual body in which the gene sits (Dawkins,1999), p.299).

The relationship between the genotype (G), the phenotype (P) and the environment (E) is expressed as:

$$P = G \times E$$

Genes provide a 'blueprint' for expression as phenotypes. The phenotype that arises from an individual weed genotype is highly variable, or plastic, in many traits. This variable and plastic gene expression is one of the key biological features of weeds. They possess the ability to respond to their local conditions in a very precise and fine-scale manner to maximize their productivity for their given environment.

A much broader view of the phenotype has been expressed by Richard Dawkins (1999), a concept he calls the 'extended phenotype'.

extended phenotype: all effects of a gene upon the world; 'effect' of a gene is understood as meaning in comparison with its alleles; the concept of phenotype is extended to include functionally important consequences of gene differences, outside the bodies in which the genes sit; in practice it is convenient to limit 'extended phenotype' to cases where the effects influence the survival chances of the gene, positively or negatively (Dawkins, 1999, p.293).

<u>Epigenesis and gene expression</u>**.** Genotypes produce phenotypes in their interactions with the environment, and variation in phenotypes is usually associated with concommitant variation in genotype. But this is not always the case, especially in weed species which possess the ability to express phenotypic variation from a single genotype. How does a single genotype produce a wide array of phenotypes?

Each gene does not act independently of other genes, there exist numerous interactions among genes to produce the phenotype Many genes may simultaneously affect several aspects of the phenotype. In other instances a particular aspect of the phenotype my be affected by several different genes. These multiple interactions of genes are called epistasis.

epistasis:
1: a class of interactions between pairs of genes in their phenotypic effects; technically the interactions are non-additive which means, roughly, that the combined effect of the two genes is not the same as the sum of their separate effects; for instance, one gene might mask the effects of the other. The word is mostly used of genes at different loci, but some authors use it to include interactions between genes at the same locus, in which case dominance/recessiveness is a special case (Dawkins,1999)
2: the interaction of non-allelic genes in which one gene (epistatic gene) masks the expression of another at a different locus (Lincoln, et al.)
3: the nonreciprocal interaction of nonallelic genes; the situation in which one gene masks the expression of another
4: interactions between two or more genes (Mayr, 2001)
5: the interaction between genes; the effects of one gene are modified by one or several other genes (modifier genes) (Wikepedia, 5.09)

pleiotropy:
1: pertaining to how a gene may affect several aspects of the phenotype (Mayr, 2001)
2: a single gene influences multiple phenotypic traits; a mutation in a gene may affect some all or all the traits simultaneously; selection on one trait may favors one allele while selection on another trait favors another allele (Wikepedia, 5.09)

polygenic inheritance (polygeny):
1: inheritance of a trait govered by several genes (polygenes or multiple factors); their effect is cumulative (Mayr, 2001)
2: quantitative inheritance; multifactorial inheritance; inheritance of a phenotypic characteristic (trait) that is attributable to two or more genes and their interaction with the

environment; polygenic traits do not follow patterns of Mendelian inheritance (qualitative traits). Instead their phenotypes typically vary along a continuous gradient depicted by a bell curve (?Gaussian frequency distribution?) (Wikepedia, 5.09)

epigenesis:
1: 'in addition to' genetic information encoded in DNA sequence
2: heritable changes in gene function without DNA change

epigenetics:
1: the study of the mechanism that produces phenotypic effects from gene activity, processes involved in the unfolding development of an organism, during differentiation and development, or heritable changes in gene expression that do not involve changes in gene sequence
2: the study of how environmental factors affecting a parent can result in changes in the way genes are expressed in the offspring, heritable changes in gene function without DNA change
3: the study of reversible heritable changes in gene function that occur without a change in the sequence of nuclear DNA: how gene-regulatory information that is not expressed in DNA sequences is transmitted from one generation (of cells or organisms) to the next.

<u>Genome size, weediness and intra-genomic competition</u>. Dawkins (1999; Ch. 9 Selfish DNA, pp.156-164) has hypothesized, based on the work of several others, that weediness is associated with small genome size due to the heightened intra-genomic competition in these aggressive species. The significance of genome size in phylogeny is not understood, the so-called 'C-value paradox' (Orgel and Crick, 1980). Cavalier-Smith (1978) asserts there is a good correlation between low C-values and strong r-selection, selection for weedy qualities. Dawkins (1999) suggests that intragenomic selection pressure may lead to a decrease or elimination of "junk" DNA (untranslated introns) and therefore smaller genome size in colonizing, invasive species like foxtails.
[add: the 'selfish trait' concept of mine about how one trait can drive invasion process, population shifts, etc. E.g. herbicide resistance or seed dormancy; organize and complete this section]

4.2 Generate Genetic Variation

The generation of of new weed genotype-phenotype genetic variation is required for natural selection to drive evolution. The mating system, or mode of fertilization, of a weed species is crucial to the generation of appropriate amounts and types of genotypic variants. The mating system of a plant is the mechanism creating its genetic diversity, and several genetic forces result in increases and decreases in population diversity. Amounts of appropriate generation of genetic variation allow an individual weed species to seize available opportunity space in an efficient manner.

Appropriate generation of genotypic variation by an individual plant, or a population, can be an effect hedge-betting strategy for enhanced fitness of progeny. Evolutionarily, hedge-betting is a strategy of spreading risks to reduce the variance in fitness, even though this reduces intrinsic mean fitness. Hedge-betting is favored in unpredictable environments where the risk of death is high because it allows a species to survive despite recurring, fatal, disturbances. Risks can be spread in time or space by either behavior or physiology. Risk spreading can be conservative (risk avoidance by a single phenotype) or diversified (phenotypic variation within a single genotype) (Jovaag et al., 2008C; Cooper and Kaplan, 1982; Philippi and Segar, 1989; Seger and Brockman, 1987).

[*add stuff from BioD: F/F article and nuggets from Gen of Colon Spp, Allard, etc.*]

4.2.1 Sources of Genetic Diversity. Their exist genomic trade-offs between fidelity and mutability in the generation and loss of genetic diversity in a population or species. The forces in nature that drive genetic diversity can be either from external or internal to the plant. To understand these changes in genetic diversity in a locality the following important concepts are defined:

Hardy-Weinberg equilibrium: the maintenance of more or less constant allele frequencies in a population through successive generations; genetic equilibrium

Hardy-Weinberg law: that allele frequencies will tend to remain constant from generation to generation and that genotypes will reach an equilibrium frequency in one generation of random mating and will remain at that frequency thereafter; demonstrating that meiosis and recombination do not alter gene frequencies

External. Much of the variation in populations and species is retained due to changes in the environment (adaptive traits are only good in some environments, and not in others). Hardy-Weinberg Law above indicates that the original variability in a population will be maintained in the absence of forces that tend to decrease or increase this variability: changes in gene frequencies are brought about by outside forces in the plants' environment.

Internal. The ultimate sources of variation, the source of new heritable characteristics in populations and species, are due to mutation and recombination in chromosomes, genes, DNA. The frequency of a gene, or allele, in a population is due to number of forces: forces increasing variability, and forces decreasing variability.

4.2.1.1 Forces increasing population variability. Four important allelic forces drive population heterogeneity: mutation, recombination, gene flow and segregation distortion.

[*Mayr: recombo by far the most important; add for mayr here*]

mutation:

1: a sudden heritable change in the genetic material, most often an alteration of a single gene by duplication, replacement or deletion of a number of DNA base pairs;

2: an individual that has undergone such a mutational change; mutant

recombination:

1: any process that gives rise to a new combination of hereditary determinants, such as the reassortment of parental genes during meiosis through crossing over; mixing in the offspring of the genes and chromosomes of their parents.

2: event, occurring by crossing over of chromosomes during meiosis, in which DNA is exchanged between a pair of chromosomes of a pair. Thus, two genes that were previously unlinked, being on different chromosomes, can become linked because of recombination, and linked genes may become unlinked.

Recombination doesn't change gene frequency, but it does lead to combinations of different genes that could be better than others. Also, the number of genetic recombinations is infinitely larger than the possible number of mutations. Most new types in populations arise from recombination.

gene flow:
1: the exchange of genetic factors within and between populations by interbreeding or migration; incorporation of characteristics into a population from another population
2: in population genetics, gene flow (also known as gene migration) is the transfer of alleles of genes from one population to another (Wikipedia, 5.08).

Migration of genes into or out of a population may be responsible for a marked change in allele frequencies (the proportion of members carrying a particular variant of a gene). Immigration may also result in the addition of new genetic variants to the established gene pool of a particular species or population. There are a number of factors that affect the rate of gene flow between different populations. One of the most significant factors is mobility, as greater mobility of an individual tends to give it greater migratory potential. Animals tend to be more mobile than plants, although pollen and seeds may be carried great distances by animals or wind. Maintained gene flow between two populations can also lead to a combination of the two gene pools, reducing the genetic variation between the two groups. It is for this reason that gene flow strongly acts against speciation, by recombining the gene pools of the groups, and thus, repairing the developing differences in genetic variation that would have led to full speciation and creation of daughter species. Example: If a field of genetically modified corn is grown alongside a field of non-genetically modified corn, pollen from the former is likely to fertilize the latter (Wikipedia, 5.08).

segregation distortion: the unequal segregation of genes in a heterozygote due to:
1: an aberrant meiotic mechanism; e.g. meiotic drive: any mechanism operating differentially during meiosis in a heterozygote to produce the two kinds of gametes with unequal frequencies;
2: other phenomena that result in altered gametic transmission ratios; e.g. in pollen competition where one allele results in a more slowly growing pollen tube than an alternate allele. Gametes bearing this allele will therefore show up in zygotes at a frequency less than 50%, as will all genes linked to the slow growing pollen tube allele (Wendel, pers. comm., 1998).

Intra-genomic conflict. The selfish gene theory postulates that natural selection will increase the frequency of those genes whose phenotypic effects ensure their successful replication. Generally, a gene achieves this goal by building, in cooperation with other genes, an organism capable of transmitting the gene to descendants. Intragenomic conflict arises when genes inside a genome are not transmitted by the same rules, or when a gene causes its own transmission to the detriment of the rest of the genome. This last kind of gene is usually called selfish genetic element, or ultraselfish gene or parasitic DNA (Wikipedia, 5.08).
Meiotic drive. All nuclear genes in a given diploid genome cooperate because each allele has an equal probability of being present in a gamete. This fairness is guaranteed by meiosis. However, there is one type of gene, called a segregation distorter, that "cheats" during meiosis or gametogenesis and thus is present in more than half of the functional gametes. True meiotic drive is found in other systems that do not involve gamete destruction, but rather use the asymmetry of meiosis in females: the driving allele ends up in the ovocyte instead of in the polar bodies with a probability greater than one half. This is termed true meiotic drive, as it does not rely on a post-meiotic mechanism. The best-studied examples include the neocentromeres (knobs) of maize, as well several chromosomal rearrangements in mammals (Wikipedia, 5.08).

4.2.1.2 Forces decreasing population variability. The phenomena of genetic drift decreases genetic diversity in a population.

genetic drift:
1: the occurrence of random changes in the gene frequencies of small isolated populations, not due to selection, mutation or immigration; drift; Sewall Wright effect; equivalent to static noise in system; adaptive alleles can be lost in process, especially in small populations
2: in population genetics, genetic drift (or more precisely allelic drift) is the evolutionary process of change in the allele frequencies (or gene frequencies) of a population from one generation to the next due to the phenomena of probability in which purely chance events determine which alleles (variants of a gene) within a reproductive population will be carried forward while others disappear (Wikipedia, 5.08).

Genetic drift is especially relevant in the case of small populations. The statistical effect of sampling error during random sampling of certain alleles from the overall population may result in an allele, and the biological traits that it confers, to become more common or rare over successive generations, and result in evolutionary change over time. The concept was first introduced by Sewall Wright in the 1920s, and is now held to be one of the primary mechanisms of biological evolution. It is distinct from natural selection, a non-random evolutionary selection process in which the tendency of alleles to become more or less widespread in a population over time is due to the alleles' effects on adaptive and reproductive success (Wikipedia, 5.08).

[Add: discuss selection as source of increasing or decreasing population diversity; compromise with 2.4.3 selection and biodiversity, Opp space niches Biodiversity; and Neighbors: Harpers 6 forces driving population diversity]

Selection as a source of decreasing genetic diversity.

4.2.2 Speciation. No single weed species dominates a crop production field or an agroecosystem. Usually several weed species coexist in a field to exploit the diverse resources unused by crop plants (inter-specific diversity). Within a single weed species, a diverse population of genotypes and phenotypes interfere with crop production (intra-specific diversity). Given sufficient time and other factors, new species can arise from within current weed populations. Unused resources left by homogeneous crop populations, diverse and fit weed populations, as well as crop management practices, provide ample opportunity for new weeds and the process of speciation.

speciation
1: The formation of new species;
2: the splitting of a phylogenetic lineage;
3: acquistion of reproductive isolating mechanisms producing discontinuities between populations;
4: process by which a species splits into 2 or more species
5: the evolutionary process by which new biological species arise (Wikipedia, 5.08)

species
1: a group of organisms, minerals or other entities formally recognized as distinct from other groups;
2: a taxon of the rank of species; in the hieracrchy of biological classification the category below genus; the basic unit of biological classification; the lowest principal category of zoological classification

3: a group of morphologically similar organisms of common ancestry that under natural conditions are potentially capable of interbreeding
4: a species is a group of interbreeding natural populations that are reproductively isolated from other such groups (Lincoln)
5: the basic units of biological classification and a taxonomic rank; a group of organisms capable of interbreeding and producing fertile offspring (Wikipedia, 5.08)

4.2.2.1 Process of Speciation. The process of speciation is a two stage process in which reproductive isolating mechanisms (RIM's) arise between groups of populations. Reproductive isolation is the condition in which interbreeding between two or more populations is prevented by factors intrinsic to their situation.

Stage 1: Gene flow is interupted between two populations. The absence of gene flow allows two populations to become genetically differentiated as a consequence of their adaptation to different local conditions (genetic drift also can act here too). As the populations differentiate, RIMs appear because different gene pools are not mutually coadapted. Reproductive isolation appears primarily in the form of postzygotic RIMs: hybrid failure. These early RIMs are a byproduct of genetic differentiation, and are not directly promoted by natural selection yet.

Stage 2: Completion of genetic isolation. Reproductive isolation develops mostly in the forms of prezygotic RIMs. The development of prezygotic RIMs is directly promoted by natural selection: alleles favoring intraspecific fertility will be increased over time at the expense of interspecific fertilization alleles.

4.2.2.2 Reproductive isolating mechanisms.

reproductive isolating mechanism: a cytological, anatomical, physiological, behavioral, or ecological difference,or a geographic barrier which prevents successful mating between two or more related groups of organisms.

reproductive isolation
1: the absence of interbreeding between members of different species
2: the condition in which interbreeding between two or more populations is prevented by intrinsic factors

Two types of RIMs facilitate speciation: prezygotic and postzygotic. Natural selection favors development of RIMs, especially prezygotic RIMs. Less favored by natural selection are postzygotic RIMs, which waste more energy.

Prezygotic RIMs prevent the formation of hybrid zygotes	Ecological isolation	populations occupy the same territory but live in different habitats, and thus do not meet
	Temporal isolation	mating or flowering occur at different times, whether in different seasons, time of the year, or different times of the day
	Mechanical isolation	pollen transfer is forestalled by the different size, shape or structure of flowers

	Gametic isolation	female and male gametes fail to attract each other, or the pollen are inviable in the stigmas of flowers
Postzygotic RIMs reduce the viability or fertility of hybrids	Hybrid inviability	hybrid zygotes fail to develop or at least to reach sexual maturity
	Hybrid sterility	hybrids fail to produce functional gametes
	Hybrid breakdown	the progenies of hybrids (F2 or backcross generations) have reduced viability or fertility

Table 4.1 Reproductive isolating mechanisms.

4.2.2.3 Modes of Speciation.

[re-org intro: more than 1 mode here; rewrite for clarity; re-org speciation needed?]

There are four modes of natural speciation, based on the extent to which speciating populations are geographically isolated from one another: allopatric, peripatric, parapatric, and sympatric. Speciation may also be induced artificially, through animal husbandry or laboratory experiments. (Wikipedia, 5.08).

Natural speciation. All forms of natural speciation have taken place over the course of evolution, though it still remains a subject of debate as to the relative importance of each mechanism in driving biodiversity. There is debate as to the rate at which speciation events occur over geologic time. While some evolutionary biologists claim that speciation events have remained relatively constant over time, some palaeontologists such as Niles Eldredge and Stephen Jay Gould have argued that species usually remain unchanged over long stretches of time, and that speciation occurs only over relatively brief intervals, a view known as punctuated equilibrium.

Allopatric speciation. During allopatric speciation, a population splits into two geographically isolated allopatric populations (for example, by habitat fragmentation due to geographical change such as mountain building or social change such as emigration). The isolated populations then undergo genotypic and/or phenotypic divergence as they (a) become subjected to dissimilar selective pressures or (b) they independently undergo genetic drift. When the populations come back into contact, they have evolved such that they are reproductively isolated and are no longer capable of exchanging genes. Observed instances include island genetics, the tendency of small, isolated genetic pools to produce unusual traits. This has been observed in many circumstances, including insular dwarfism and the radical changes among certain famous island chains, like Komodo and Galápagos, the latter having given rise to the modern expression of evolutionary theory, after being observed by Charles Darwin. Perhaps the most famous example of allopatric speciation is Darwin's Galápagos Finches.

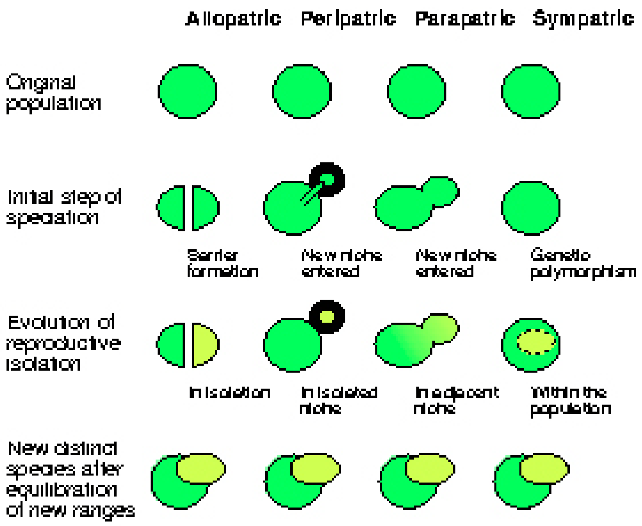


Figure 4.1 Comparison of allopatric, peripatric, parapatric and sympatric speciation (Wikipedia, 5.08).

Peripatric speciation. In peripatric speciation, new species are formed in isolated, small peripheral populations which are prevented from exchanging genes with the main population. It is related to the concept of a founder effect, since small populations often undergo bottlenecks. Genetic drift is often proposed to play a significant role in peripatric speciation. Observed instances include the London Underground mosquito. This is a variant of the mosquito *Culex pipiens* which entered in the London Underground in the nineteenth century. Evidence for its speciation include genetic divergence, behavioral differences, and difficulty in mating.

Parapatric speciation. In parapatric speciation, the zones of two diverging populations are separate but do overlap. There is only partial separation afforded by geography, so individuals of each species may come in contact or cross the barrier from time to time, but reduced fitness of the heterozygote leads to selection for behaviours or mechanisms which prevent breeding between the two species. Ecologists refer to parapatric and peripatric speciation in terms of ecological niches. A niche must be available in order for a new species to be successful. Observed instances include the grass *Anthoxanthum* has been known to undergo parapatric speciation in such cases as mine contamination of an area.

Sympatric speciation. In sympatric speciation, species diverge while inhabiting the same place. Often cited examples of sympatric speciation are found in insects which become dependent on different host plants in the same area. However, the existence of sympatric speciation as a mechanism of speciation is still hotly contested. People have argued that the evidences of sympatric speciation are in fact examples of micro-allopatric, or heteropatric speciation. The most widely accepted example of sympatric speciation is that of the cichlids of Lake Nabugabo in East Africa, which is thought to be due to sexual selection. Sympatric speciation refers to the formation of two or more descendant species from a single ancestral species all occupying the same geographic location. Until recently, there has a been a dearth of hard evidence that supports this form of speciation, with a general feeling that interbreeding would soon eliminate any genetic differences that might appear. Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

Speciation via polyploidization. A new species can arise by means of a polyploidization event.

ploidy: the number of sets of chromosomes present (e.g. haploid, diploid, polyploid)

polyploidy: multiple sets of homologous chromosomes in an organism (e.g. tetraploid, octaploid)

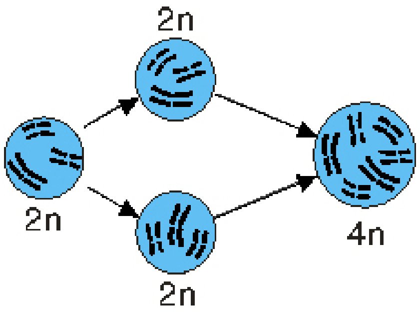


Figure 4.2 Speciation via polyploidy: A parental diploid cell (left cell) undergoes failed meiosis, producing diploid gametes (center 2 cells), which self-fertilize to produce a tetraploid zygote (right cell). (Wikipedia, 5.08)

A diploid cell undergoes failed meiosis, producing diploid gametes, which self-fertilize to produce a tetraploid zygote. Polyploidy is a mechanism often attributed to causing some speciation events in sympatry. Not all polyploids are reproductively isolated from their parental plants, so an increase in chromosome number may not result in the complete cessation of gene flow between the incipient polyploids and their parental diploids. Polyploidy is observed in many species of both plants and animals. In fact, it has been proposed that all of the existing plants and most of the animals are polyploids or have undergone an event of polyploidization in their evolutionary history.

A weed example is the instantaneous formation of giant foxtail, *Setaria faberi*, when two diploid genomes (probably the ancestral *Setaria viridis* and an unknown *Setaria* species) hybridized in a polyploidization event (probably in Southern China) to form the new, fertile and viable, weed species that subsequently found niche not fully exploited by green foxtail. It now is a major weedy pest plaguing the □Midwestern US corn belt.

Reinforcement. Reinforcement is the process by which natural selection increases reproductive isolation. It may occur after two populations of the same species are separated and then come back into contact. If their reproductive isolation was complete, then they will have already developed into two separate incompatible species. If their reproductive isolation is incomplete, then further mating between the populations will produce hybrids, which may or may not be fertile. If the hybrids are infertile, or fertile but less fit than their ancestors, then there will be no further reproductive isolation and speciation has essentially occurred (e.g., as in horses and donkeys.) The reasoning behind this is that if the parents of the hybrid offspring each have naturally selected traits for their own certain environments, the hybrid offspring will bear traits from both, therefore would not fit either ecological niche as well as the parents did. The low fitness of the hybrids would cause selection to favor assortative mating, which would control hybridization. If the hybrid offspring are more fit than their ancestors, then the populations will merge back into the same species within the area they are in contact.

Reinforcement is required for both parapatric and sympatric speciation. Without reinforcement, the geographic area of contact between different forms of the same species, called their "hybrid zone," will not develop into a boundary between the different species. Hybrid zones are regions where diverged populations meet and interbreed. Hybrid offspring are very common in these regions, which are usually created by diverged species coming into secondary contact. Without reinforcement the two species would have uncontrollable inbreeding. Reinforcement may be induced in artificial selection experiments as described below.

Hybrid speciation. Hybridization between two different species sometimes leads to a distinct phenotype. This phenotype can also be fitter than the parental lineage and as such natural selection may then favor these individuals. Eventually, if reproductive isolation is achieved, it may lead to a separate species. However, reproductive isolation between hybrids and their parents is particularly difficult to achieve and thus hybrid speciation is considered an extremely rare event. Hybridization without change in chromosome number is called homoploid hybrid speciation. It is considered very rare but has been shown in sunflowers (*Helianthus* spp.). Polyploid speciation, which involves changes in chromosome number, is a more common phenomena, especially in plant species.

4.3 Generate Phenotypic Variation

Individual weed plants possess a high degree of variability based on both their response to local environment and on their genetic constitution. Two important sources of phenotypic variation in weed plants are phenotypic plasticity and somatic polymorphism.

4.3.1 Phenotypic plasticity. Phenotypic plasticity is the capacity for marked variation in the individual plant phenotype as a result of environmental influences on the genotype during development. An individual plant can grow larger of smaller depending on the resources available to it in its habitat. Phenotypic plasticity can be expressed through epigenetic mechanisms in weed plants.

phenotypic plasticity:

1: The capacity of an organism to vary morphologically, physiologically or behaviorally as a result of environmental flucuations; reaction type
2: the capacity for marked variation in the phenotype as a result of environmental influences on the genotype during development [during the plant's life history]

The ability of an organism with a given genotype to change its phenotype in response to changes in the environment is called phenotypic plasticity. Such plasticity in some cases expresses as several highly morphologically distinct results; in other cases, a continuous norm of reaction describes the functional interrelationship of a range of environments to a range of phenotypes. The term was originally conceived in the context of development, but is now more broadly applied to include changes that occur during the adult life of an organism, such as behavior.

Organisms of fixed genotype may differ in the amount of phenotypic plasticity they display when exposed to the same environmental change. Hence phenotypic plasticity can evolve and be adaptive if fitness is increased by changing phenotype. Immobile organisms such as plants have well developed phenotypic plasticity, giving a clue to the adaptive significance of plasticity.

A highly illustrative example of phenotypic plasticity is found in the social insects, colonies of which depend on the division of their members into distinct castes, such as workers and guards. These two castes differ dramatically in appearance and behaviour. However, while these differences are genetic in basis, they are not inherited; they arise during development and depend on the manner of treatment of the eggs by the queen and the workers, who manipulate such factors as embryonic diet and incubation temperature. The genome of each individual contains all the instructions needed to develop into any one of several 'morphs', but only the genes that form part of one developmental program are activated (Wikipedia, 5.08).

The range of possible phenotypes that a single genotype produces is often expressed experimentally in terms of a 'reaction norm' or 'norms of reaction':

reaction norm:
1: set of phenotypes expressed by a singe genotype, when a trait changes continuously under different environmental and developmental conditions
2: phenotype space; opportunity space; hedge-bet structure
3: a norm of reaction describes the pattern of phenotypic expression of a single genotype across a range of environments (Wikipedia, 5.08)

In ecology and genetics, a norm of reaction describes the pattern of phenotypic expression of a single genotype across a range of environments. One use of norms of reaction is in describing how different species—especially related species—respond to varying environments. But differing genotypes within a single species will also often show differing norms of reaction relative to a particular phenotypic trait and environment variable. For every genotype, phenotypic trait, and environmental variable, a different norm of reaction can exist; in other words, an enormous complexity can exist in the interrelationships between genetic and environmental factors in determining traits.

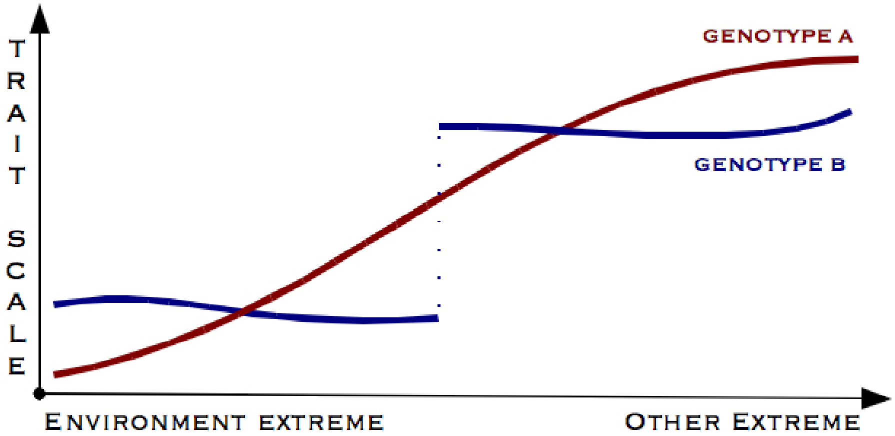


Figure 4.3 Norms of reaction illustrating bimodal distribution for two genotypes. Genotype B shows a strongly bimodal distribution indicating differentiation into distinct phenotypes. Each phenotype is buffered against environmental variation - it is canalised (Wikipedia, 5.08)

A monoclonal example. Scientifically analyzing norms of reaction in natural populations can be very difficult, simply because natural populations of sexually reproductive organisms usually do not have cleanly separated or superficially identifiable genetic distinctions. However, seed crops produced by humans are often engineered to contain specific genes, and in some cases seed stocks consist of clones. Accordingly, distinct seed lines present ideal examples of differentiated norms of reaction. In fact, agricultural companies market seeds for use in particular environments based on exactly this.

Suppose the seed line A contains an allele b, and a seed line B of the same crop species contains an allele B, for the same gene. With these controlled genetic groups, we might cultivate each variety (genotype) in a range of environments. This range might be either natural or controlled variations in environment. For example, an individual plant might receive either more or less water during its growth cycle, or the average temperature the plants are exposed to might vary across a range.

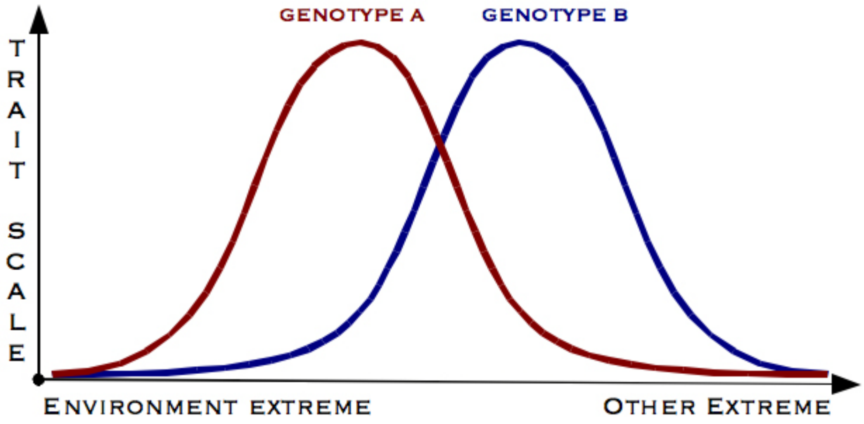


Figure 4.4 Illustration of norm of reaction: different peaks in Gaussian distributions (Wikipedia, 5.08).

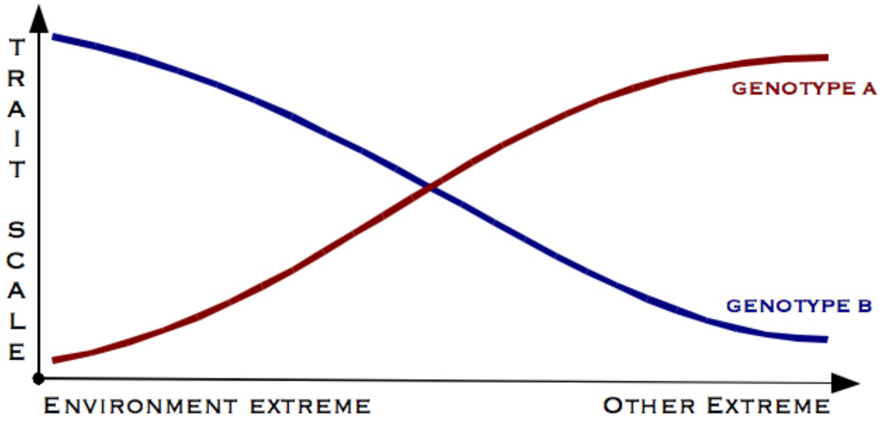


Figure 4.5 Example of norm of reaction: approximately linear norms at opposite slopes (Wikipedia, 5.08)

A simplification of the norm of reaction might state that seed line A is good for "high water conditions" while a seed line B is good for "low water conditions". But the full complexity of the norm of reaction is a function, for each genotype, relating environmental factor to phenotypic trait. By controlling for or measuring actual environments across which monoclonal seeds are cultivated, one can concretely observe norms of reaction. Normal distributions, for example, are common. Of course, the distributions need not be bell-curves.

4.3.2 Somatic Polymorphism. Somatic variation pertains to diversity in the plant body or any non-germinal cell, tissue, structure or process. Somatic polymorphism is the genetically controlled expression of diverse plant parts and processes independent of environment: e.g. cotyledons and true leaves in plants are both leaf tissue.

somatic polymorphism

1: production of different plant parts, or different plant behaviors, within the same individual plant; the expression of somatic polymorphism traits is not much altered by the environmental conditions it encounters (as opposed to phenotypic plasticity)

2: the occurrence of several different forms of a structure-organ of a plant body; distinctively different forms adapted to different conditions.

Somatic (body) polymorphism (many forms) is a type of phenotypic biodiversity. It is the production of different plant parts, or different plant behaviors, within the same individual plant. Somatic diversity is ultimately genetic, it is the product of differential genetic expression due to differential penetrance and expressivity of plant genes. Unlike phenotypic plasticity, somatic polymorphism is always expressed in plants that possess those traits, and is not altered much by the environment conditions it encounters.

Somatic polymorphism can be confused with phenotypic plasticity. The examples and explanations below will help make this concept clearer. Somatic polymorphism is a very important trait for a weed to possess. It provides an individual plant species the ability and flexibility to adapt its plant parts to the changing conditions during development it encounters in agricultural fields. In evolutionary terms, different forms of plant parts are the adaptations natural selection can act on, favoring those giving advantage to that individual if it reproduces better than its neighbor. Somatic diversity can be found in leaves on the same plant, seed from the same plant, and the form of the plant at different times of its life cycle.

Somatic polymorphism in leaves. *Glycine max* (soybeans) provide an example of leaf somatic diversity that most of us have problem seen before. The first set of leaves are the seed leaves (cotyledons), then the unifoliates emerge, then a continuing series of trifoliates. On the top right you can see some soybean seedling with root rot. The cotyledons and unifoliates are visible. The soybean seedlings on the top left are suffering from trifluralin injury. Again the cotyledons and unifoliates are visile. The soybean plant in the center has partially survived a dose of acifluorfen. The damaged cotyledons and unifoliates are visible. Different leaf forms, for different functions, at different times of the life cycle.\

Green foxtails (left), as with most other foxtails, have the ability to tiller. These stem branches allow it to take advantage of opportunities. Each subsequent tiller has a different shape and size. Stem length, panicle size, all seem to get smaller as tillering proceeds.

Somatic Polymorphism in Seed**.** Foxtail plants shed seed with different germination requirements, an important form of seed somatic polymorphism. Most giant foxtail seed shed in the fall is dormant, but some can germinate immediately. Some try to germinate even earlier as can be seen above with the seed that germinated in the pollenation bags that were placed over the panicles before harvest, seed vivipary.

Corn (above), and not just weeds, possess this type of somatic diversity, seed vivipary. In corn, plant breeders have purposefully bred this trait out to the best of their ability. Still, every once in a while some corn will germinate before it should.

Common cocklebur seed capsules contain two seeds inside (above). One can germinate in the first year following dispersal, the other is more dormant and germinates later. This is an important form of seed dormancy somatic polymorphism: different seed dormancy in seeds from the same plant.

Wild oats shed seed with different germination requirements, dormancy, also. Seed from different parts of the panicle (above) possess different levels of dormancy.

Common lambsquarters shed both black and brown seed (above). The darker seed is also more dormant.

Somatic Polymorphism: Seasonal Dimorphism**.** Another form of somatic diversity is seasonal dimorphism: two distinct phases of growth of an individual plant, each adapted to a specific season (seasonally dimorphic phenotype). Below are those two growth, or plant, forms in common burdock. At the top left is the first year form of this biennial. On the top right [*missing*] the taller, more leafy form with seedheads apparent in the second year.

[Add: rhizome buds; flower color on same plant, e.g. sunflower]

Chapter 5: Process of Natural Selection 2: Survival and Reproduction

[Revisit Mayr and get this summary right. This may lead to reorganization of the chapter which I leave as-is from 2008/9 ver4sion. Topics to include:
1. non-random aspects of survival and reproduction and inheritance
2. mortality and death; hedge-betting and risk
3. mating systems: regulation of reproduction and inheritance; conservation of variability]

Summary.

5.1 Survive, Avoid Mortality.

IDEAS:
1. Mortality. Mostly rethinking of mortality as driver of seizing opportunity space of life history; mortality fully developed here;
2. Life history modes. Big here is life history types (annuals, perennials, etc.; this isn't presented anywhere yet! Modes, as all things, are shaped by mortality cycles
3. See all edit notes in 2008 class edit version.
4. Mortality and the risk of mortality as the primary shaper of life history duration and timing (ref: old chapter 11 parts; Silvertown): e.g. annual-perennial, winter vs. summer annual; time of flowering, duration of flowering; etc.
5. mortality and death; hedge-betting and risk

Definitions:

mortality: death rate as a proportion of the population expressed as a percentage or as a fraction; mortality rate; often used in a general sense as equivalent to death

density-dependent mortality: mortality and a decrease in population density (numbers per unit area) due to the effects of population density (self-thinning)

density-independent mortality: mortality and a decrease in population density due to any factor which is independent of population density

5.2 Reproduce the Fittest, Eliminate the Others

[warning: demographic models ahead!]

Two (2) major components of fitness that the life history of a particular plant are correlated with: survival and reproduction. Net reproductive rate: a summation of reproduction and survival/mortality. Fitness includes reproduction and survival which are the consequences of trade-offs of conflicting goals/ends for a plants life history. There is much more to fitness than net reproductive rate discussed here. Using R_o as equaling net reproductive rate, an optimal life history under particular ecological conditions can be defined as one which maximizes (Silvertown & Doust (1993) Ch. 9):

$$\Sigma l_x m_x$$

Components of $\Sigma l_x m_x$:

$\Sigma l_x m_x$ = R_o = net reproductive rate
l_x = proportion of individuals surviving to age x
m_x = fecundity of an individual of age x

5.2.1 Timing of reproduction. Life history features of reproduction and survival that push a plant to precocious reproduction or push it to wait to reproduce in a particular set of ecological conditions

Optimum age of reproduction. Optimum age when individual should begin reproduction depends on how reproduction at a particular age would affect later survival and reproduction. Optimum age of reproduction reached when no further increase in lxmx can be obtained by further delay.

Maximizing $\Sigma l_x m_x$. $l_x m_x$ may be maximized by delaying reproduction until plant reaches a size to be able to survive and complete (1st bout of) reproduction. Survival expectation mitigates otherwise precocious preproduction

Delaying reproduction incurs a demographic penalty when the annual rate of population size is > 1 (demographic penalty is inability to exploit available opportunity space). When the annual rate of population size increasing (is > 1): the greater its value (greater its rate of annual population increase), the greater the demographic penalty against plants which delay, and the more plants with precocious reproduction are favored. When the annual rate of population size decreasing (is < 1): there is an advantage to delaying reproduction. For example, mortality in corn field is greater early as weed seedlings are killed by herbicides, tillage.

Precocious reproduction. If reproduction incurs no costs, and a population is in a phase of increase (annual rate of population size increase is > 1), the earlier reproduction occurs the better for fitness. But reproduction does incur costs. The cost of reproduction may slow its growth and increase its risk of death because small plants are more vulnerable

5.2.2 Reproductive value. Reproductive value and its affect on the time of reproduction for an individual species in its life history . V_x = reproductive value: contribution an average individual aged x will make to the next generation before it dies. V_x has two components: current fecundity (m_x) [= fecundity of an individual of age x]; residual reproductive value ($V_x - m_x$), potential reproductive contribution an individual might yet make; equivalent to the chances that remain to it to produce further offspring in following seasons. The species that uses all the resources available to it over the entire season is the one that will predominate. Precocious growth and quitting early lets those that continue (even with greater hazards of mortality) will ultimately win because there are unused resources.

Think of it from the point of view of two identical plants "deciding" whether to reproduce early or wait until the end of the season. The one that reproduces early shifts its energy to flowers, its vegetative phase neighbor shades it out right away, so the loss to early reproducer happens right away. Larger, waiting, individuals that survive have much increased seed yield from larger vegetative body than earlier reproducers:

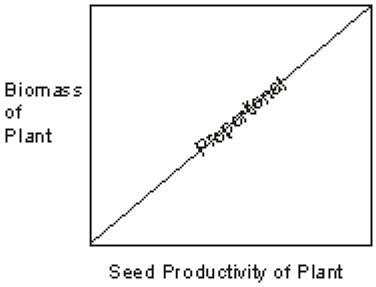


Figure 5.1 Caption

5.2.3 Risk of death determines life history. Key to understanding reproductive precocity: Is the risk of death greater early or late? Mortality from density-independent causes (e.g. tillage, herbicides)? Risk greatest early in crop field. The cost of reproduction may slow early reproducing plants growth and increase its risk of death because small plants are more vulnerable. If you stop in the spring or summer to reproduce while your neighbors are still growing, remaining vegetative, you suffer a penalty while the larger plants shade you out and out-compete you for resources. Precocious get seed production over quick, only advantage in this is if next generation in the same season has a good chance of setting seed, on and on. This is how they exploit new land. But in Iowa corn fields the competitor species will shade you out (competititive exclusion) and later emerging seedling of the precocious species (its 2nd generation of that season) will not do well, or die. So trade-offs shift advantage to the longer vegetative period species and and its big seed rain at end of the season. High adult mortality risk favors earlier reproduction because it lowers the residual reproductive value. A weed in a corn field that can past layby (Iowa: June, early July; the time after which farmers can't get equipment in the field because the crop is too large; they "layby" their equipment) has a low risk of farmer mortality until the time of seed set. Whether to reproduce early in season or wait depends on the particular ecological conditions of a locality: unused late season resources will get grabbed by someone, and the fuller their use in the face of death the more fit the species

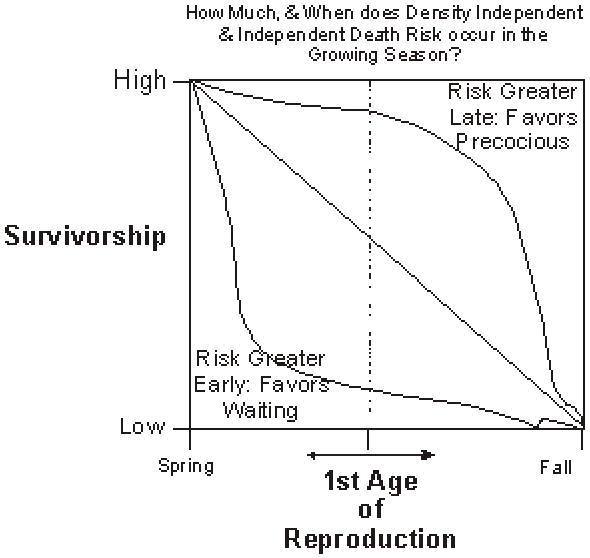


Figure 5.2 Caption

The best time to reproduce for a summer annual if it waits. Environmental causes of mortality (not directly related to cost of repro) may determine where the upper limit of the optimum age of 1st reproduction lies. This environmental cause of mortality is winter for summer annuals. Season length (and winter) is predictable over the time spans of the evolutionary experience in crop fields of America and Eurasia. What varies now is onset of frost (Clay Co., Iowa: fair time, 2nd week of Sept.; Story Co. Iowa: mid-Oct.). Seed set timing hedgebet favors August and September, which clearly before frost. Uncertain time is October and November with chance of frost; don't wait until the autumn and chance of frost and chance of harvest destruction occurs. Winter: time of declining population size (ignoring dormancy). When the annual rate of population size decreasing is < 1, there is

an advantage to delaying reproduction. Exception: The case of the 2 leaf foxtail plant emerging in October and producing one seed: is this precocious is bad? Foxtail has a multiple seedling emergence timing hedgebets, including precocity late in the season
5.2.4 Plant age states. An organisms reproductive value changes with age. Seed from a plant produced at different times in its life cycle differ in their contributions to the future growth of the population**.** This true for successional species (perennial woody plants, trees) and for annual weeds**.** Plants reproductive value changes with age and it depends on the plant's life cycle. Annuals: summer annuals, winter annuals. Biennials. Perennials: herbaceous, woody.

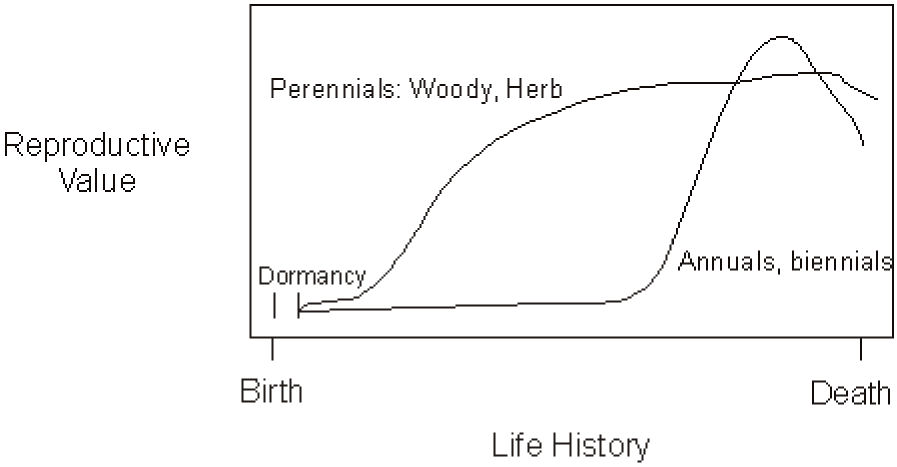


Figure 5.3 Caption

Plant Age. How long does an annual plant live? How old is it when it dies? Annual plants actually can live to very old age, older than mature trees. For example, velvetleaf can live for 20, 50, 100 years in the seed bank, then it germinates and finishes life cycle. Seedbanks are enormously elongated □orpholo periods, providing potentially very old plants as seedlings. What is the oldest plant in nature? Candidates include: bristlecone pine, 2000+ years; olive trees; oak: 200+; Sequoia: ?; lotus seed, 10,000 year old live seed found in dig; aspen as clonal tree colony, forest: distant shoots subject to mutation, is shoot still same genotype as other shoots attached too? The oldest weed from evolutionary perspective might be the primitive *Equisetum*, spores, rhizomes, primitive photosynthetic leaves, scales. Perennial weeds like quackgrass, johnsongrass, hemp dogbane, milkweed, and Canada thistle could be older than mature trees in the later phases of succession. Vegetative clones never die, may be decades, hundreds, thousands of years old since seed production. If very old: somatic mutations affect different parts of plant: plant may be composed of different genotypes in different tissues: evolution of genotype in same individual plant. There exists a twist to natural selection and precocity: "eternal life" of herbaceous perennials favored because plants spend most of their lives in declining populations.

5.3 Inheritance: Transmit Parental Traits to Offspring

[intro]

5.3.1 Inheritance.

Ideas for inheritance section:

1. the objects and targets of natural selection are traits and phenotypes which are inherited with/in the genes]
2. mating systems
3. gene and pollen flow vectors

4. opposed to them: genetic drift

The genes that are passed on to an organism's offspring produce the inherited traits that are the basis of evolution. Mutations in genes can produce new or altered traits in individuals, resulting in the appearance of heritable differences between organisms, but new traits also come from the transfer of genes between populations, as in migration, or between species, in horizontal gene transfer. In species that reproduce sexually, new combinations of genes are produced by genetic recombination, which can increase the variation in traits between organisms. Evolution occurs when these heritable differences become more common or rare in a population.

…

Over many generations, adaptations occur through a combination of successive, small, random changes in traits, and natural selection of those variants best-suited for their environment. In contrast, genetic drift produces random changes in the frequency of traits in a population. Genetic drift results from the role chance plays in whether a given individual will survive and reproduce. Though the changes produced in any one generation by drift and selection are small, differences accumulate with each subsequent generation and can, over time, cause substantial changes in the organisms. (Wikipedia, 5.08)

5.3.2 Mating systems.

[add: source of variation for genetic foraging; also serves to conserve local adaption in the absence of change: a conservative role]

[combine, compromise and clean up two intro sections] [new intro start]

The search for opportunity space is accomplished with genetic variability within populations of a species. Variation in heritable characteristics in populations and species arise from selection, mutation of genetic material, recombination of genes and chromosomes, gene flow by hybridization and migration, segregation distortion of alleles, and genetic drift in small populations.

A plant species particular mating system controls recombination to generate variation which searches opportunity space. Mating systems for colonizing species varies from obligate outcrossing (e.g. monoecy, dioecy) to self-pollinating and apomictic species (Harper, 1977). The spatial structure of opportunity space being explored and exploited favors certain mating systems and [rates of] hybridization. The purpose of a plant species mating system is to generate variation appropriate to a locally available habitable locality. A local population relies on its mating system to adjust genetic recombination to the fabric of the exploited disturbed space: "We would predict on the basis of such work that different genetic strategies of colonization will be evolved depending upon the statistical pattern of the environment. Populations with low genetic variability for a character will more often be successful in environments requiring frequent radical alteration of phenotype, whereas populations with high genetic variability will more often leave successful colonies in environments which, although radically different from the original species range, are in themselves rather stable." (Lewontin, 1965; p. 91).

A genetically plastic mating system has to generate variation sized exactly to the space being searched and seized. If the mating system generates intra-specific variants that unsuited to the breadth and grain of the environment explored they are at a disadvantage in colonizing that space. Even self-pollinated species, and apomictic races within a species, produce a "carefully considered" amount of variation needed for the space searched, seized and occupied. For these reasons, the responses of a plant's mating system to an opportunity space creates the population genetic structure of a locally adapted population.

Mating system control of population genetic structure is a consequence of the exploration for opportunity space, and the degree of variation or no variation generated by a particular species mating system is a strong inference clue to the space being explored. The spatial scale of hybridizing populations, demes and metapopulations spans the globe, continents, regions, landscapes, localities and microsites. Highly successful colonizing plant species also exploit the fragmentary spatial and temporal structures they confront, be it island geography or a landscape of farmlands amidst roads, residences and woodlands: "Colonization can be an effective strategy under the following conditions. If a species is able to populate many semi-isolated regions, such as a system of oceanic islands, its populations will be tested by a variety of physical and biotic environments. Over a period of time, the greater the number of regions colonized, the higher the probability that the species will survive somewhere, so the endemic foci persist out of which colonization can proceed again." (E.O. Wilson, 1965; p. 14)

This experience preadapts a species to colonize neighboring regions. It also reveals a potential answer to the question posed by Lewontin (1965; p.88) concerning: "... what the optimal genetic structure is for a colonizer to maintain a positive rate of increase in a new environment, while at the same time maintaining itself in the original territory of the species. The same question can be asked over time rather than in space. Given a species which is reduced sharply in numbers at more or less regular intervals by unfavorable conditions, what is the optimal genotypic structure of the population which will both guarantee its survival in low numbers during unfavorable times and allow it to maintain very large populations at peak periods?".

Allard has argued (1965, p. 49) that "There is, however, one feature which the great majority of these notably successful colonizers share: a mating system involving predominant self-fertilization." This certainly has been observed amongst weeds of North American agroecosystems (e.g. *Setaria* species-group; Dekker, 2003, 2004b), but in the last half of the 20th century, with the introduction of numerous selective herbicides, a mating system population shift has occurred favoring outbreeding species such as *Lolium* and *Amaranthus* which are highly effective in generating variability in search of rare, yet highly advantageous, biotypes resistant to those chemicals. Mating, or breeding, systems in weed species range from obligate clones (e.g. apomixis in *Taraxicum officinale*, dandelion) to obligate out-crossing species (e.g. dioecy in *Amaranthus* x, tall waterhemp)

A plant's mating system is an important mechanism by which is responds to changes in its locality, and the way it searches for opportunity space in the habitats it lives in. When conditions are within historical experience of the population little new variation is needed for enduring occupation. When changes occur beyond the pre-adapted variation of a population, new genotypes and phenotypes may be better. So, this new variation may increase its fitness in that locality.

A plant's mating system affects its ability to handle changes, crashes, in the environment. Self-pollenation, □orpholo protects against quick change in progeny. Some types of mating system buffers against longer term changes: colonizers more likely to be self-pollenated. Selfers: protect self against effects of large genetic display, big swings in population composition; avoid tracking transient adaptive optima; keep on long term course. Polyploid more likely later successional, diploid more likely colonizers: Why? Phenotypic plasticity enables same genotype capable to form different phenotypes depending on conditions.

[old intro start] Weed species generate a typical amount of variation in each generation. Too many new unsuccessful genotypes/phenotypes can waste precious resources of the parent plant. Too little new variation can lead to competitive disadvantage with neighbors who can seize these new opportunities. As such, almost all weed species generate some degree of variation each generation. Mating systems are a compromise between conflicting ends: the means to control a balance between repetition (selfing) and novel new forms (genotype experiments).

Survival of a local population involves variation in individual genotype-phenotypes as hedge-bets. There is no such thing as a "perfect" weed phenotype. Fitness changes in a locality with changing conditions, environmental as well as community neighbors. All mating systems end up in the same place: provide diversity anticipating change or die.

All mating systems end up in the same place: be diverse or die. Mating systems maintain genetic diversity within populations by different means: co-adapted inbred lines, apomictic races; co-adapted gene complexes (partly inbreeding species), or ecological differentiation between sexes (outbreeding species). Mating systems are a compromise between conflicting ends: control balance between repetition (self) vs. novel new forms (experiments). Gene flow is not critical to maintain or have diversity arise: e.g. apomicts and inbreeders. Diversity is maintained within populations in many different ways, ways that compensate for apparent differences between breeding systems. Natural populations have genetic diversity, even within breeding systems not think of as diverse. Natural selection favors diversity in the long run because so many slightly different niches available to a species at a locality. The net effect of natural selection is to create more variability: survival depends on many hedge-bet "roulette chips" genotype-phenotypes, despite the fact that the immediate effect of selection 'seeks' the "perfect" type for the immediate conditions of that generation.

Several patterns of genotypic novelty generation can be discerned in examples from the mating systems of typical weed species.

[get weed archetype mating systems table and include in this section]

5.3.2.1 Apomictic species. Apomictic species do not utilize sexual reproduction, but populations contain considerable heterogeneity for exploiting opportunity space. They are defined:

apomixis: In botany, apomixis (also called apogamy) is asexual reproduction, without fertilization. In plants with independent gametophytes (notably ferns), apomixis refers to the formation of sporophytes by parthenogenesis of gametophyte cells. Apomixis also occurs in flowering plants, where it is also called agamospermy. Apomixis in flowering plants mainly occurs in two forms:

agamogenesis: (also called gametophytic apomixis), the embryo arises from an unfertilized egg that was produced without meiosis.

adventitious embryony: a nucellar embryo is formed from the surrounding nucellus tissue.

Apomictically produced seeds are genetically identical to the parent plant. As apomictic plants are genetically identical from one generation to the next, each has the characters of a true species, maintaining distinctions from other congeneric apomicts, while having much smaller differences than is normal between species of most genera. They are therefore often called microspecies. In some genera, it is possible to identify and name hundreds or even thousands of microspecies, which may be grouped together as aggregate species, typically listed in Floras with the convention "Genus species agg."

(e.g., the bramble, *Rubus fruticosus* agg.). Examples of apomixis can be found in the genera *Crataegus* (hawthorns), *Amelanchier* (shadbush), *Sorbus* (rowans and whitebeams), *Rubus* (brambles or blackberries), *Hieracium* (hawkweeds) and *Taraxacum* (dandelions). Although the evolutionary advantages of sexual reproduction are lost, apomixis does pass along traits fortuitous for individual evolutionary fitness. A unique example of male apomixis has recently been discovered in the Saharan Cypress, *Cupressus dupreziana*, where the seeds are derived entirely from the pollen with no genetic contribution from the female "parent" (Pichot, et al., 2000, 2001) (Wikipedia, 5.08).

The best example of a weed species that utilizes apomixis for its mating system is *Taraxacum officinale* (dandelion), an aggregate species with many apomictic microspecies with strictly maternal inheritance. One would expect genetically uniform population structure from this species, but this is not so. Natural populations contain an assortment of apomictic races varying from site to site. Races are differentiated on the basis of precocity of flowering, seed output, and longevity. The high apparent genetic homogeneity provides a low-cost (minus the costs of sexual reproduction) generation of successful genotypes. See also apomicts in Baker's Ideal Weed trait list.

Hawkweed refers to any species in the very large genus *Hieracium* and its segregate genus *Pilosella*, in the sunflower family (Asteraceae). They are common perennials, occurring worldwide . They are usually small and weedy. Only a few are ornamental plants. Most are considered to be troublesome weeds. They grow to 5-100 cm tall, and feature clusters of yellow, orange or red flower heads, similar to dandelions, atop a long, fuzzy stalk. Few genera are more complex and have given botanists such a headache due to the great number of apomictic species. Through speciation by rapid evolution, polyploidy, and possibly also hybridisation, this variable genus has given rise to thousands of small variations and more than 10,000 microspecies, each with their own taxonomic name, have been described (Wikipedia, 5.08).

Another example of a plant with this type of reproductive mode is *Rubus fruticosus*, another aggregate species composed of apomictic microspecies. Small populations contain a mixture of several distinct microspecies.

5.3.2.2 Self-pollinating species. Many annual weedy plant species reproduce almost exclusively by inbreeding, self-pollenation. Their anthers rarely emerge, and pollen is shed directly on its own stigmas for self-fertilization. Genetic diversity arises in a local population of a species despite this selfing. There are as many potential adaptive optima (microsites) within a habitat as there are individuals. Therefore there is no perfect phenotype, therefore population variety is maintained. Different optima in the same locality drives different variants needed to exploit those opportunities.

Genetic selection is more complex than selection for individuals. Selection acts to structure the genetic resources of a local population into highly interactive allelic complexes: diversity at the level of co-adapted gene complexes (the 'selfish' trait) rather than strictly at the level of inbred genetic lineages. For example, *Fescue microstachys* is a grass species with almost no outbreeding. Natural populations are as genetically variable as other species. This genetic heterogeneity is explained by supposing nearly as many adaptive optima within a habitat as there are individuals.

Setaria spp.-gp. (foxtails) and *Elymus repens* (quackgrass) self-fertilization mating system affects its population genetic structure. Self-fertilization provides high local population genetic homogeneity; high landscape scale genetic heterogeneity provides rare outcrossing opportunity for inter-locality variation when confronted with environmental change.

Baker (see Baker's Ideal Weed Traits in chapter 1) has argued many of the most successful weed species in the world are self-compatible but not completely autogamous (sexual self-fertilization) or apomictic (asexual reproduction through seeds) (Baker, 1974). When cross-pollinated (out-cross), by unspecialized visitors or wind utilized (Baker, 1974).

Other examples include the early flowers of *Viola* sp. (violet) are cleistogomous that are completely enclosed, sealed and protected from foreign pollen.

5.3.2.3 Out-crossing species. Genetic variation is expected with outbreeding species. Outbreeding provides genetic novelty that explores for subtle differentiation of types to fill different niches. Obligate outcrossing provides continuous genetic novelty from local genotype pool. The cross-pollenating mating system provides maximum variation to searches for highly adapted traits (e.g. herbicide resistance alleles).

In general long-lived plants tend to be outcrossers, and annuals tend to be inbreeders. Out-crossers can have perfect flowers (hermaphrodites), or single sex flowers (dioecy, monoecy). In outcrossing species with perfect flowers some percent of them experience pollen transfer from another individual. The rate of hybridization with pollen from another plant varies from low-to-100%: 1-10% in *Avena fatua* (wild oat), to 100% in obligate outcrossers *Lolium multiflorum* (or *L. perenne*) or *Kochia scoparia*.

Other mating system mechanisms exist to ensure outcrossing. Some obligate out-crossers control hybridization with physical or chemical mechanisms to prevent self-fertilization. Obligate outbreeders also include species with separate male and female flowers and/or plants. Monecious species have their flowers separated on same plant. Dioecious species have separate sex plants.

There are several sexual modes by which weedy plants perform outcrossing. Specific terms are used to describe the sexual expression of individual plants within a population. These definitions will help you understand these fascinating reproductive traits (Wikipedia, 5.08):

hermaphrodite: plant that has only bisexual reproductive units (flowers, conifer cones, or functionally equivalent structures); i.e. perfect flowers. In angiosperm terminology a synonym is monoclinous from the Greek "one bed".

dioecious: having unisexual reproductive units with male and female plants (flowers, conifer cones, or functionally equivalent structures) occurring on different individuals; from Greek for "two households". Individual plants are not called dioecious: they are either gynoecious (female plants) or androecious (male plants).

androecious: plants producing male flowers only, produce pollen but no seeds, the male plants of a dioecious species.

gynoecious: plants producing female flowers only, produces seeds but no pollen, the female of a dioecious species. In some plant species or populations all individuals are gynoecious with non sexual reproduction used to produce the next generation.

monoecious: having separate male and female reproductive units (flowers, conifer cones, or functionally equivalent structures) on the same plant; from Greek for "one household". Individuals bearing separate flowers of both sexes at the same time are called simultaneously or synchronously monoecious. Individuals that bear flowers of one sex at one time are called consecutively monoecious; plants may first have single sexed flowers and then later have flowers of the other sex.

protoandrous: describes individuals that function first as males and then change to females

protogynous: describes individuals that function first as females and then change to males.

subdioecious: a tendency in some dioecious species to produce monoecious plants. The population produces normally male or female plants but some are hermaphroditic, with female plants producing some male or hermaphroditic flowers or vise versa. The condition is thought to represent a transition between hermaphroditism and dioecy. [8].

gynomonoecious: has both hermaphrodite and female structures.

andromonoecious: has both hermaphrodite and male structures.

subandroecious: plant has mostly male flowers, with a few female or hermaphrodite flowers.

subgynoecious: plant has mostly female flowers, with a few male or hermaphrodite flowers.

trimonoecious (polygamous): male, female, and hermaphrodite structures all appear on the same plant.

Dioecy hinders local adaptation, hybridization aways generates new variants. This mode of reproduction demands very high selection pressure to maintain local adaptation. It allows different sex plants to take different ecological roles: different seasonal niches, differential competition, different times of scenescence, and it allows differential exploitation of the light enviroment.

Species examples include *Rumex asetosella*. Like *cannabis sativa*/*indica* (hemp) different sex plants exploit different seasonal and temporal niches. The males arise earlier, die and scenesce earlier, thereby allowing greater light penetration in the canopy as they complete their earlier life cycle. The male plants of *Asparagus officinalis* are utilized for their edible shoots, but they die early and don't compete with females (season niche differentiation). *Mercurialis perennis* is a perennial with male and female plants in different parts of woodlands: those in shaded and open areas exploit different light environments. Other important weedy dioecious species include *Amaranthus tuberculatus* and *A. rudis* (tall and common waterhemp).

5.3.3 Modes of selection and population diversity. Natural selection alters the frequency of phenotypes in a population and species. Because human disturbances in agro-ecosystems are so widespread, variable, direct and indirect, we will use natural selection to cover both natural and artificial. Humans are natural too, aren't they?

Several modes of selection can be discerned in population dynamics:

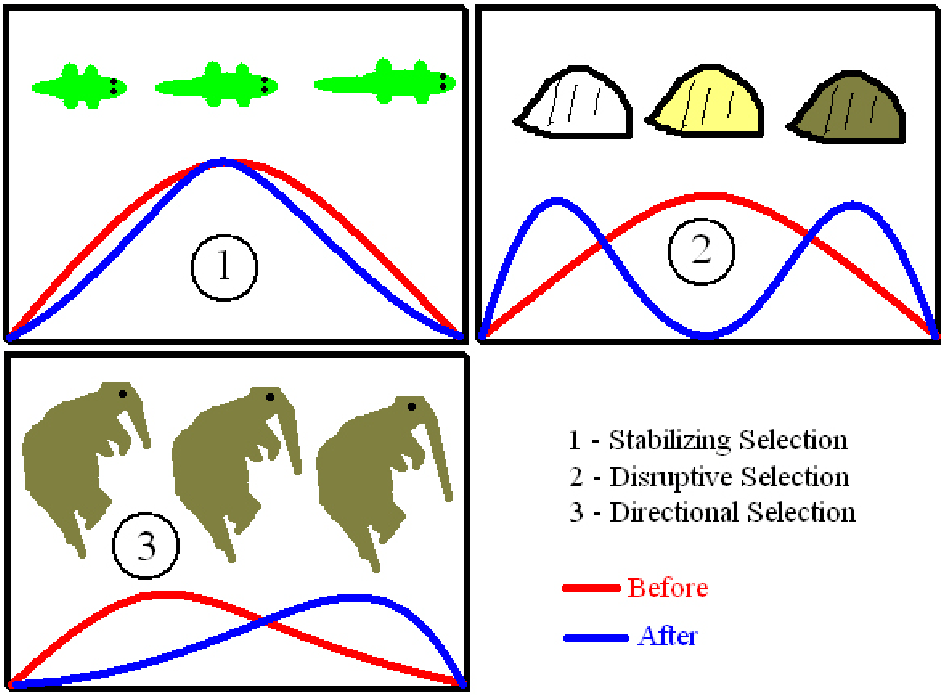


Figure 5.4 Modes of natural selection: stabilizing, disruptive and directional (Wikipedia, 5.08).

> **directional selection**: selection for an optimum phenotype resulting in a directional shift in gene frequencies of the character concerned and leading to a state of adaptation in a progressively changing environment; dynamic selection; progressive selection

In population genetics, directional selection occurs when natural selection favors a single phenotype and therefore allele frequency continuously shifts in one direction. Under directional selection, the advantageous allele will increase in frequency independently of its dominance relative to other alleles (i.e. even if the advantageous allele is recessive, it will eventually become fixed). Directional selection stands in contrast to balancing selection where selection may favor multiple alleles, and is the same as purifying selection which removes deleterious mutations from a population, in other words it is directional selection in favor of the advantageous heterozygote. Directional selection is a particular mode or mechanism of natural selection (Wikipedia, 5.08).

> **disruptive selection**: selection for phenotypic extremes in a polymorphic population, which preserves and accentuates discontinuity; centrifugal selection; diversifying selection.

Disruptive selection, also called diversifying selection, is a descriptive term used to describe changes in population genetics that simultaneously favor individuals at both extremes of the distribution. When disruptive selection operates, individuals at the extremes contribute more offspring than those in the center, producing two peaks in the distribution of a particular trait. (Wikipedia, 5.08)

> **stabilizing selection**: selecting for the mean, mode or intermediate phenotype with the consequent elimination of peripheral variants, maintaining an existing

state of adaptation in a stable environment; centripetal selection; normalizing selection.

Stabilizing selection, also referred to as purifying selection or ambidirectional selection, is a type of natural selection in which genetic diversity decreases as the population stabilizes on a particular trait value. Put another way, extreme values of the character are selected against. This is probably the most common mechanism of action for natural selection. Stabilizing selection operates most of the time in most populations. This type of selection acts to prevent divergence of form and function. In this way, the anatomy of some organisms, such as sharks and ferns, has remained largely unchanged for millions of years (Wikipedia, 5.08)

Chapter 6: Adaptation in the Local Weed Population (Deme)

Topics:
1. Weed biodiversity
2. weed population and community structures

Summary.

6.1 Weed Communities

> "The plant population that is found growing at a point in space and time is the consequence of a catena of past events. The climate and the substrate provide the scenery and the stage for the cast of plant and animal players that come and go. The cast is large and many members play no part, remaining dormant. The remainder act out a tragedy dominated by hazard, struggle and death in which there are few survivors. The appearance of the stage at any moment can only be understood in relation to previous scenes and acts, though it can be described and, like a photograph of a point in the performance of a play, can be compared with points in other plays. Such comparisons are dominated by the scenery, the relative unchanging backcloth of the action. It is not possible to make much sense of the plot or the action as it is seen at such a point in time. Most of our knowledge of the structure and diversity of plant communities comes from describing areas of vegetation at points in time and imposing for the purpose a human value of scale on a system to which this may be irrelevant."
> -J.L. Harper, 1977, Population Biology of Plants, Ch. 23, p.705-706.

Understanding weed communities, the populations that live in them and how they change with time, is one of the most important areas of weed biology. Weed communities are the consequence of particular phenotypes seizing and exploiting opportunity. Much remains to be discovered about how weed populations assemble in communities with crops and how they change over time.

John Harper (1977) highlights an important consideration in the quote above. He uses metaphors from stories, movies, or the theater to point out the difficulty in studing community dynamics, and how as humans we often look at them in an inappropriate way. There is a tendency to set the scale of observation of the community as system at our convenience, missing the action and failing to observe the plot. The plot in communities is acting out a plants' life history to seize and exploit opportunity at a neighbors' expense. The action is the behavior and timing during that life history, as well as the action of neighbors, disturbance and death. The actors in the story of community are the individual plants, their phenotypes, the traits they display, and the roles they play. The actors also include the dormant members in the soil seed pool as well as the dominating crops of the community. The actors in this story play a role in every community, their guild or trade when the species is observed as a whole. The stage and scenery is the environment and the neighbors of a locality, or a microsite in that locality.

The local community population structure at any time is a consequence of past events, and can only be understood in terms of what has happened up until then. In human terms, this history is filled with tragedy, stress and struggle, in which few survive.

Those that do manage to survive are capable of exponential reproductivity. In the study of weed communities it is easy to look at this population structure at times convenient to the observer; e.g. planting, emergence, harvest. But these single 'snapshots' of community tell us little, in the same way that a single frame from a movie reveals little of the story that is unfolding.

All of this raises the question of at what scale (space, time) is it appropriate to describe the system? Based on what? With what criteria? In the Life History unit following, ways to study weed dynamics is discussed: how to formalize what we know about weed communities in models. For now, lets set the stage and try to understand who these interesting actors, the weeds, are and what they do over time.

So, given that community structure and dynamics is complex, what insights have been gained to help us understand the weed biology of agricultural communities?

A primary feature of assembly of weeds and crops in agricultural communities is periodic (annual), severe and widespread disturbance that eliminates above-ground vegetation (e.g. winter kill, tillage including seedbed preparation, early season herbicide use). This annual recommencement of community assembly makes studies of agro-communities experimentally more tractable than in more complex, longer-lived plant communities. Initial plant establishment plays a large role in these annually disturbed agricultural fields (Dekker, 2004).

Weed communities will be revealed in this chapter in several ways. First is a discussion of weed biodiversity at several scales and perspectives. Weed biodiversity is the pool of potential candidate populations that might invade, seize and exploit local agricultural opportunity. Second, weed population structure is discussed. Gene flow over historical time has produced the successful weedy phenotypes that exploit opportunity. Although evolution acts at the level of the individual plant, residual genetic connections between individuals, populations and species still exist and provide an often hidden advantage in the struggle to exploit local opportunity. In the final section of the chapter is discussed community dynamics, changes with time. The source of this change is the evolving phenotypes of the community, constantly struggling with the habitat and neighbors. In this relentless adaptation, weed populations often assume a role, form a guild, based on clusters of interacting traits that allow them to dominate in particular localities. Nothing stays the same, change is constant in weed communities. Plant communities, crops and weeds, are typically removed on a regular basis, usually annually. Weed communities thrive because they begin again every year: they are colonizing species. Against this human managed opportunity space-time are powerful forces leading to ecological community succession, wherein the current community creates new opportunity for the communities of the future.

We begin with definitions:

community

1: any group of organisms belonging to a number of different species that co-occur in the same habitat or area and interact through trophic and spatial relationships; typically characterized by reference to one or more dominant species (Lincoln)

2: in ecology, an assemblage of populations of different species, interacting with one another; sometimes limited to specific places, times, or subsets of organisms; at other times based on evolutionary taxonomy and biogeography; other times based on function and behavior regardless of genetic relationships (Wikipedia, 6.08)

biological community

1: biocoenosis, biocoenose, biocenose

2: all the interacting organisms living together in a specific habitat (or biotope); biotic community, ecological community; the extent or geographical area of a biocenose is limited only by the requirement of a more or less uniform species composition. (Wikipedia, 6.08)

ecosystem
1: a community of organisms and their physical environment interacting as an ecological unit; the entire biological and physical content of a biotope
2: an ecosystem is a natural unit consisting of all plants, animals and micro-organisms (biotic factors) in an area functioning together with all of the non-living physical (abiotic) factors of the environment (Wikipedia, 6.08)
3: a biotic community along with its physical environment (Tansley, 1935)

A biological community is characterized by the interrelationships among species in a geographical area. These interactions are as important as the physical factors to which each species is adapted and responding. It is the specific biological community that is adapted to conditions that prevail in a given place. Biotic communities may be of varying sizes, and larger ones may contain smaller ones. The interactions between species are especially evident in their substrate (resources, food or feeding) relationships. Biotic communities can be better understood by observing the utilization of limiting resources, or for animal populations the food network, to identify how species acquire substrate and then determine the system boundary. (Wikipedia, 6.08)

Agricultural communities consist typically of interacting crop species and the weeds that invade that opportunity. Local opportunity demands exploitation by weedy species. Weed biodiversity and population structure predicate community dynamics. Weed populations are preadapted phenotypes that invade opportunity, and successful populations form communities. The structure of communities provides opportunity for certain roles to be played, and not for others. The functional characteristics of those populations, and the time of their expression, are the basis of plant community dynamics. Community dynamics is an emergent property of interacting phenotypes with successful life history traits. These life history traits allow those populations to play a unique role in exploiting locally available opportunity the community. Local opportunity changes over time as a direct consequence of both disturbance and the current roles played by populations in the community. The behavior of populations in an existing community provides opportunity for new community structure.

6.2 Weed Community Biodiversity

Weed communities are revealed by biodiversity at several scales and perspectives. Weed biodiversity predicates community dynamics. Weed biodiversity is the pool of potential candidate populations that might invade, seize and exploit local agricultural opportunity. The basis of community is the behavior, the life history, of an individual plant. Individuals form local populations in communities. Dispersal of pollen, seeds and other propagules across the landscape link local communities into meta-communities and ecosystems. The behavior at all these scales is an emergent property of the cumulative individual behaviors.

Biodiversity is defined:

biodiversity
1: the variety of organisms considered at all levels, from genetic variants of a single species through arrays of species to arrays of genera, families and still higher taxonomic

levels;
2: includes the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live;
3: the totality of biological diversity

6.2.1 Biodiversity as diversity encountered by an individual interacting with neighbors. Harper (1977; p. 707-8) defines biodiversity in a different, and more comprehensive, way. He describes it in terms of the levels of diversity that an individual plant may meet when it interacts with its neighbors. A more complete development of this broad view of weed biodiversity in found in Dekker, 1997. Harper posits five ways individual plants sense their local biological community, elements contributing to population diversity.

In the first instance, individuals meet neighbors in the somatic polymorphism of their plant parts, shoots or organs occupying space over time that interact directly with both neighbors of other parts of the same individual (e.g. leaves, roots, other shoots on the same plant). In the community this can occur between sexually (plant from a signle seed) or asexually (perennating vegetative meristems) reproduced genets. (parts of the genet).

genet:
1: unit or group derived asexually from a single zygote: seedling, clone.
2: a clonal colony, a group of genetically identical individuals that have grown in a given location, all originating vegetatively (not sexually) from a single ancestor.

ramet: an individual in a plant genet

Clonal colonies are common in many plant species. Although many plants reproduce sexually through the production of seed, some plants reproduce by underground stolons or rhizomes. Above ground these plants appear to be distinct individuals, but underground they remain interconnected and are all clones of the same plant. However, it is not always easy to recognize a clonal colony especially if it spreads underground and is also sexually reproducing. These concepts will be fully developed in the Life History unit on spatial and temporal foraging behavior in competitive interactions with neighbor plants.

The second level of biodiversity that an individual plant may meet when it interacts with its neighbors is the diversity of age-states within the community. In a broader sense, this includes developmental, phenological or life history time. The third level of biodiversity an individual in a community will encounter is the more common expression of biodiversity, the genetic variants (intra-specific, inter-specific) of neighbor species. The fourth expression of biodiversity is that of microsites within the habitat.

The fifth level of biodiversity that an individual in a community may meet in its interactions with neighbors is groupings at a higher level than the species (e.g. species-groups). This interesting, and little studied, topic is developed later in this chapter in the section on weed population structure.

6.2.2 Levels of weedy biodiversity within a habitat. [*review these tables and section carefully for clarity*] At what scale of time and space should we use to describe weedy biodiversity? What biology should these scales act within? Weed genetic biodiversity exists at several levels of organization, each in its own scale. Insight might be gained by using four different criteria of scale diversity: genotype, plant system, spatial (biogeographical) and temporal (Table 5.1):

<table>
<tr><th colspan="2">OPPORTUNITY MAP OF COMMUNITY BIODIVERSITY</th></tr>
<tr><td><i>SCALE</i></td><td><i>LEVEL</i></td></tr>
<tr><td rowspan="4">GENOTYPE</td><td>allele/trait</td></tr>
<tr><td>individual plant phenotype</td></tr>
<tr><td>species</td></tr>
<tr><td>species associations</td></tr>
<tr><td rowspan="3">PLANT SYSTEM</td><td>local community</td></tr>
<tr><td>population</td></tr>
<tr><td>ecosystem</td></tr>
<tr><td rowspan="6">SPATIAL</td><td>molecular</td></tr>
<tr><td>microsite</td></tr>
<tr><td>locality</td></tr>
<tr><td>landscape</td></tr>
<tr><td>continent</td></tr>
<tr><td>global</td></tr>
<tr><td rowspan="5">TEMPORAL</td><td>instantaneous</td></tr>
<tr><td>diurnal</td></tr>
<tr><td>seasonal</td></tr>
<tr><td>ecological succession</td></tr>
<tr><td>long-term</td></tr>
</table>

Table 6.1 Scalar space-time opportunity for genetic and plant system biodiversity as a basis/foundation of local plant community structure.

Of course these are general categories, and much finer or coarser scale divisions can be utilized for many purposes of understanding weedy biodiversity. These scales are overlapping in time and are intimately related. The interrelations between these criteria can be mapped within the following generic, graphical schematic. Examples are provided below (Table 6.2) for genetic (e.g. individual, top) and plant system (e.g. local community, bottom):

<table>
<tr><th colspan="7">SPACE-TIME MAP OF BIODIVERSITY: GENETIC</th></tr>
<tr><td rowspan="6">SPACE</td><td>GLOBAL</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>CONTINENTAL</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>LANDSCAPE</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>LOCALITY</td><td rowspan="3" colspan="3">INDIVIDUAL</td><td></td><td></td></tr>
<tr><td>MICROSITE</td><td></td><td></td></tr>
<tr><td>MOLECULAR</td><td></td><td></td></tr>
<tr><td colspan="2" rowspan="2"></td><td>INSTANT</td><td>DIURNAL</td><td>SEASON</td><td>SUCCESSIONAL</td><td>LONG-TERM</td></tr>
<tr><td colspan="5">TIME</td></tr>
</table>

Example 6.2.1: the individual plant phenotype

<table>
<tr><th colspan="7">SPACE-TIME MAP OF BIODIVERSITY: PLANT SYSTEM</th></tr>
<tr><td rowspan="5">SPACE</td><td>GLOBAL</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>CONTINENTAL</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>LANDSCAPE</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>LOCALITY</td><td rowspan="2" colspan="4">LOCAL COMMUNITY</td><td></td></tr>
<tr><td>MICROSITE</td><td></td></tr>
</table>

	MOLECULAR	▨				
		INSTANT	DIURNAL	SEASON	SUCCESSIONAL	LONG-TERM
		TIME				

Example 6.2.2: the local community

Table 6.2 Generic schematic map of space-time opportunity of genetic and plant system biodiversity.

The exact areas that define each of the spatial and temporal scales of the genetic and plant systems is imprecise, with considerable overlap of levels. Dispersal and gene flow phenomena occur at some rate for each weed species, potentially connecting all world plant populations over time, from the global to the allele. Weedy species are especially effective at crossing continental boundaries and invading localities across continental and regional landscapes.

6.2.3 Stability, sustainability and biodiversity in plant communities.

> "There is no comfortable theorem assuring that increased diversity and complexity beget enhanced community stability; rather, as a mathematical generality, the opposite is true. The task, then, is to elucidate the devious strategies which make for stability in enduring natural systems. There will be no one simple answer to these questions." (May, 1973.)

What is the relationships between biodiversity, ecosystem or community stability and sustainability? These are important questions to human society. It has been argued that agriculture itself is not sustainable and its stability rests on the continuity of human management. Human management is susceptible to human actions and long-term human social stability (Diamond book ref).

It has been conjectured that increased agro-ecosystem biodiversity will result in more stable and sustainable, not to mention more economically viable, crop production systems (Barberi reviews refs; expand section with ideas from B/B review paper started). [Is biodiversity good or bad in cropping systems?]

If Robert May (1973) is correct in the quote above, that it is a mathematical certainty that increased biodiverity will only complexify the issues of community stability, and therefore possibly sustainability, in agroecosystems. Whether this is true or not, the 'devious strategies' which have allowed weed populations to exploit opportunity, and colonize disturbed habitats, will be discussed in detail later in this chapter (traits and guilds) and the unit on weed life history to follow. It is certainly true that weedy populations of several important current weed species and species-groups existed before the advent of agriculture some 10,000 years before present. This long-term stability is most apparent in weed species with crop relatives: *Amaranthus*, *Brassica*, *Chenopodium*, *Setaria*, *Solanum* and *Oryza* to name but a few. Is this not the ultimate form of plant community stability?

Biodiversity, stability and sustainability are viewed from different perspectives, with much opinion and some disagreement. Therefore, first are defined some terms to ensure conceptual clarity:

stability: [dictionary, Lincoln]

ecological stability:

1: connoting a continuum, ranging from resilience (returning quickly to a previous state) to constancy (lack of change) to persistence (simply not going extinct); the precise definition depends on the ecosystem in question, the variable or variables of interest, and the overall context
2: in conservation ecology, populations that do not go extinct; in mathematical models of systems, Lyapunov stability (dynamical system that start out near an equilibrium point stay there forever) (Wikipedia, 6.08)

Due to the inconsistent usage of the term stability in ecological literature, specific terms of the types of ecological stability have been proposed:

ecological stability-constancy and persistence: living systems that can remain unchanged in observational studies of ecosystems (Wikipedia, 6.08)

ecological stability-resistance and inertia (or persistence):
1: a system's response to some perturbation (disturbance; any externally imposed change in conditions, usually happening in a short time period)
2: resistance is a measure of how little the parameter of interest changes in response to external pressures
3: inertia (or persistence) implies that the living system is is able to resist external fluctuations (Wikipedia, 6.08)

ecological stability-resilience, elasticity and amplitude:
1: resilience is the tendency of a system to return to a previous state after a perturbation
2: elasticity and amplitude are measures of resilience; elasticity is the speed with which a system returns; amplitude is a measure of how far a system can be moved from the previous state and still return (Wikipedia, 6.08)

The concept of ecological stability is often associated with that of sustainability:

sustainability:
1: humanity’s investment in a system of living, projected to be viable on an ongoing basis that provides quality of life for all individuals of sentient species and preserves natural ecosystems
2: a characteristic of a process or state that can be maintained at a certain level indefinitely.
3: environmental, the potential longevity of vital human ecological support systems, such as the planet's climatic system, systems of agriculture, industry, forestry, fisheries, and the systems on which they depend
4: how long human ecological systems can be expected to be usefully productive; emphasis on human systems and anthropogenic problems (Wikipedia, 6.08)

On what time and spatial scales do we assess stablility and sustainability? How exactly do ecological stability and sustainability relate to each other?

6.3 Weed Community Structure

[entire section needs to be carefully editted and completed; some blocks may be out of place; compromise when add critical new info from dewet-harlan and erhendorfer.]

Weed communities are populated by individual phenotypes that colonize local agricultural opportunity. What is the population structure of those plant communities?

Weed community population structure is the emergent property of the evolution of those individuals over time. Gene flow over historical time has produced the successful weedy phenotypes that exploit opportunity. Although evolution acts at the level of the individual plant, residual genetic connections between individuals, populations and species exist that provide advantages in the struggle to exploit local opportunity.

Weed community population structure is revealed at several spatial-temporal scales of local opportunity. At the lowest level of plant system organization, qualities from the molecular to the individual plant reveal the basis for community population structure. Larger scale phenomena are an emergent property arising from smaller scale sources of community structure: the traits that determine the behavior of the phenotype in the community. In the relentless evolutionary process of adaptation, weeds assume a role, they form a functional guild. This guild is based on clusters of interacting traits that allow them to dominate local opportunity at their neighbors expense in a very particular and specialized manner.

Community structure is apparent at higher levels of plant system organization: global to local community. Observation of this larger scale structure provides insights of the outcome of long-term weedy adaptation: population genetic structure and species associations.

Weed communities are populated by individual phenotypes that colonize local agricultural opportunity. Weed community population structure is the emergent property of the evolution of those individuals over time. Weed community population structure is revealed at several spatial-temporal scales of local opportunity. Community structure is apparent at higher levels of plant system organization: global to local community. Observation of this larger scale structure provides insights of the outcome of long-term weedy adaptation: population genetic structure and species associations. Gene flow over historical time has produced the successful weedy phenotypes that exploit opportunity. Although evolution acts at the level of the individual plant, residual genetic connections between individuals, populations and species exist that provide advantages in the struggle to exploit local opportunity: weed species associations. In this section we will observe several of these associations between weed species and crops. These include wild-crop-weed complexes, preadaptive colonizing archetypes (generalist-specialist genotypes, reproductive colonizing types) and colonizing species associations (species-groups, polyploid species clusters, aggregate species). All of these ways of looking at associations of different species overlap. Each provides a different insight into the consequences of evolution in the relentless adaptation to local opportunity that results in the population community structure we see in present day communities.
[ADD: These associations can be viewed by the following criteria of relatedness:]

PLANT GENETIC ASSOCIATIONS	
Source	Association Type
Genetic Evolutionary History	wild-crop-weed complex
Genetic Evolutionary History & Biogeographic Distribution	population genetic structure
	species-group
	polyploid cluster
	aggregate species
Genetic Evolutionary History Functionally Preadapted Phenotypes	generalist-specialists
	reproductive colonizing types

Table 6.3 Plant genetic associations of closely related species based on genetic evolutionary history, biogeographic distribution and functionally preadapted phenotypes

Which will lead us logically to traits, roles-guilds of trait clusters to changes in communities including pop shifts and community ecological succession.]

6.3.1 The Origins of Weeds: Wild-Crop-Weed Plant Complexes

Where do weeds come from? How long have we had weeds? Wild colonizing plants existed before agriculture, able to seize opportunity when natural disturbances destroyed or altered exisiting plant communities. It was these wild colonizing species that became weeds with the advent of agriculture. In many cases, it was these vigorous colonizing species that humans gathered and selected among for the very earliest crops.

Weeds started 10,000 B.P., with human agriculture which resulted over time in wild-crop-weed plant complexes (w-c-w).
[says much about gene flow of introduced transgenic species and traits (dekker and comstock ref)]
[get DeWet article and strip of content and add here; try other DeWet-Harlan refs in texts have for more]

PLANT PRE-HISTORY		
Time		
Years B. P.	Period/Epoch	Plants
458 million	Ordovician Period	First land plants
428 million	Silurian Period	*Cooksonia*, one of first land plant species found
60-140 million	Cretaceous Period	First flowering plants, angiosperms
10,000	Recent Epoch	Human agriculture: first weeds

Table 6.4 Plant pre-history in years before present, period or epoch; B.P., before present.

It is certainly true that weedy populations of several important current weed species and species-groups existed before the advent of agriculture some 10,000 years before present. This long-term stability is most apparent in weed species with crop relatives. Is this not the ultimate form of plant community stability?
[get table from dekker and comstock and add to table here]
[a human-sustained crop which acts as genetic reservoir for weedy relatives, and vice-versa; this topic is developed in the section following on weed species associations]

WILD-CROP-WEED COMPLEXES		
Plant Genus	Wild-Weed Species	Crop Species
Amaranthus	pigweeds: water hemps:	amaranth:
Avena	wild oat:	oats:
Brassica	mustards:	oilseed rape: mustards: radishes:
Chenopodium	lambsquarters: goosefoot:	
Helianthus	wild sunflowers:	sunflowers:
Hordeum		
Oryza	red rice:	rice:
Setaria	foxtails:	foxtail millet: korali:

Solanum	nightshades:	potatoes: tomatoes:
Sorghum	johnsongrass: shattercane: almum grass:	sorghum:

Table 6.5 Wild-crop-weed species genetic complexes of some important crop species.

The species lines are fuzzy within a particular w-c-w group due to gene flow and introgression, and this fuzziness varies between different w-c-w groups. Some pre-human wild colonizing species possessed pre-adaptations that made them ideal weeds with the introduction of agriculture. Some other wild colonizing species were not as good as weed colonizers with the advent of agriculture as before. Pre-agriculture wild colonizing plants can be broken into two groups with advent of Ag: wild plants that thrived in human selected disturbed habitats (agriculture) and therefore became successful weeds that we have today; formed wild-crop-weed complexes; wild species whose colonizing pre-adaptatations were not selected for, they were not as fit, and therefore did not thrive in agricultural habitats.

6.3.2 Biogeographic Population Genetic Structure

Population genetic structure is the spatial distribution of genotypes (and phenotypes) across the locality, the landscape and around the world. It is biogeography, and is relevant to what species and intra-specific genetic variants occupy a habitat.

population genetic structure
1: the spatial distribution of genotypes (Jax)
2: [genetics dictionary]
[add to glossary when done]

One of the important aspects of population biology is population genetic structure, which forms the basis of plant spatial and temporal organization. Knowledge of population genetic structure has practical implications (Barrett and Husband, 1990). It can be used to reconstruct the historical process of invasion, migration and colonization, and provide insights into the ecological persistence and evolutionary potential of populations in new habitats, leading to a better understanding of weedy adaptation. It provides a foundation for understanding the spatial structure of individuals within an individual field or local community. Population genetic structure is unique to a species, or species-group. One of the best ways to understand the population genetic structure and opportunity is to observe it in a widely distributed species-group (see appendix 4, the population genetic structure of the weedy *Setaria* species-group).

6.3.3 Genotype structuring: species associations for weedy colonization. Genetic evolutionary history and biogeographic distribution: species-groups, polyploid clusters, aggregate species.

Weed communities are populated by individual phenotypes that colonize local agricultural opportunity. Weed community population structure is the emergent property of the evolution of those individuals over time. Weed community population structure is revealed at several spatial-temporal scales of local opportunity. Community structure is apparent at higher levels of plant system organization: global to local community.

Observation of this larger scale structure provides insights of the outcome of long-term weedy adaptation: population genetic structure and species associations. Gene flow over historical time has produced the successful weedy phenotypes that exploit opportunity. Although evolution acts at the level of the individual plant, residual genetic connections between individuals, populations and species exist that provide advantages in the struggle to exploit local opportunity: weed species associations. In this section we will observe several of these associations between weed species and crops. These include wild-crop-weed complexes, preadaptive colonizing archetypes (generalist-specialist genotypes, reproductive colonizing types) and colonizing species associations (species-groups, polyploid species clusters, aggregate species). All of these ways of looking at associations of different species overlap. Each provides a different insight into the consequences of evolution in the relentless adaptation to local opportunity that results in the population community structure we see in present day communities.

6.3.3.1 Species-groups. Many of the most successful colonizing plant species co-exist together loosely in a species-group. Species-groups provide several advantages in colonization. They provide a more complete exploitation of opportunity niche space and generate variation appropriate to the habitats and landscapes being exploited. Definition:

species-group: a group of closely related species, usually with partially overlapping ranges (Lincoln et al., 1998).

superspecies:

Genus	Weed Species-Group
Amaranthus	*A. retroflexus* *A. common waterhemp?* *A. tall waterhemp?* *A. palmerii?*
Avena	*A.*
Brassica	*B. niger* *B.*
Chenopodium	*C. album* *C.*
Helianthus	*H. annuus?*
Hordeum	
Oryza	*O.*
Setaria	*S. faberi* *S. geniculata* *S. pumila* *S. verticillata* *S. viridis*
Solanum	*S. nigrum* *S. physal?*
Sorghum	*S. almum* *S. shattercane?* *S. johnsongrass?*
Polygonum	*P. pensylvanicum* *P. ladysthumb* *P. prostrate knotweed?*

	P. erectus

Table 6.6 Weed species-groups and their interacting species members.
[go thru NC weed ID and nebraska weeds books for more; euro sources/; get from GMO article table too]

One of the best adapted and known weedy species-groups are the foxtails (*Setaria*). Another related way closely related species group is the polyploid-species cluster (Zohary), which we will discuss later in the course. The pigweeds are another infamous species-group. There is considerable diversity within this superspecies, maybe because promiscuous outcrossing between plants (and maybe species) makes firm species identification problematic. Is it any wonder that most weed management tactics miss at least some of these diverse pests? The smartweed (*Polygonum*) species-group consists of several species, including ladysthumb and Pennsylvania smartweed. Below are a variety of leaf shapes and colors from several plants in this group. They could be from the same or different species, it is hard to tell from just this picture.

6.3.3.2 Polyploid species clusters. Some important colonizing species-groups consist of closely related species consisting of several deriviative polyploids clustered around a diploid ancestor. This species-group/polyploid species cluster is preadapted to exploit opportunity space and is an important type of wild-crop-weed complex, discussed below. The characteristics of a orphologi cluster have had a significant impact on the evolution of colonizer species.

The first feature is the occurrence of a diploid "theme", a "common trend of adaptive specialization" of preadaptation to certain habitats and opportunity spaces (Zohary, 1965; p. 418). This pivotal genome is a conservative gene complex that controls the evolutionary theme with a pool of recombinable material in the orphologi, modified, genomes. Thus a dual system is created wherein "the genes controlling the preadaptive "theme" are held together by one part of the chromosomal complement and where wide "variation in theme" is provided by a second part of the chromosomal complement". The result is a [species?] cluster "designed for "canalization" of the evolving population in its preadaptive, basic "theme"" protecting it from haphazard variation from unrestricted recombination.

The *Aegilops-Triticum* is a species-group of aggressive, genetically linked, polyploids preadapted for rapid colonization (Zohary, 1965). This group is more than its component, independent, allotetraploid (amphidiploid) species. Instead they are a genetically linked species cluster, a "compound, loosely interconnected [?] superstructure". The *Aegilops-Triticum* species-group is a "system of compound amphiploidy in combination with a mating system of predominant self-pollination that have apparently enabled the polyploids to build up genetic variation rapidly and evolve successfully as aggressive weedy annuals." This genetic structure facilitates introgression and the creation of large pool of genetic variation by means of a "specific combination of elements: compound amphidiploidy, buffering pivotal genomes, and predominance of self-pollination."

An important contrast in historical gene flow exists between diploids and polyploids within this species-group. The diploid genomic groups are reproductively isolated from one another as opposed to the loose genetic connections between the polyploids.

From p. 414: "Another striking contrast between diploids and polyploids [here in wheat wild-crop-weed complex historical gene flow] is the reproductive isolation of the diploid genomic groups from one another as compared to loose genetic connections between polyploids. Genetic links and gene flow through occasional spontaneous hybridization and subsequent introgression are apparently a general rule in the case of seven [?] species sharing the pivotal Cu genome."

All this in *Aegilops* is similar to that in the *Setaria* species group: both are searching opportunity space with this type of loosely interrelated and interacting genome systems in the different species. Green as diploid theme, giant, etc. as the □orphologi offshoots

The *Setaria* Species-Group. Several weedy *Setaria* species often coexist in a single field, each exploiting a slightly different opportunity space or niche (Dekker, 2004b). The geographic distribution of the several weedy foxtail species provides an initial insight into the niches they occupy (Dekker, 2004b). More than one *Setaria* species often co-exist together in a field, exploiting resources left available in somewhat different ways and times. *S. viridis* is the most ancient and widespread weedy foxtail species, and is often the most commonly found species when more than one is found in a single field. The □orphologi weedy foxtails are less widely distributed than the diploid *S. viridis,* and are often more specialized. Weedy foxtail biogeographical distribution is associated soils that possess a wide range of moisture, gas, and nutrient regimes with distinctive seasonal and diurnal temperature fluctuations. These seasonal temperature-water cycles are correlated with their cyclical germination behavior (e.g. Dekker et al., 2001; Forcella et al., 1992, 1997). Dekker, 2004b: Speciation by polyploidization (either alloploidy or autoploidy) may be an important means by which new foxtail species were formed. Based on chromosomal data, Khosla and Sharma (1973) speculate polyploidization at various levels has played and active role in speciation and delimiting taxa in *Setaria*. Polyploidization of the more diverse and ancient *S. viridis* may have been the genesis of the specialized and less diverse *Setaria* spp. set (giant, yellow, bristly, knotroot) of specialized and less diverse *Setaria* spp. Allotetraploid forms of S. faberi and S. pumila have been explained as ancient crosses of S. *viridis* with and unknown diploid species (Li, 1942; Kholsa and Singh, 1971; Till-Bottraud et al., 1992). Li et al. (1942) concluded that *S. faberi* is a product of *S. viridis* and an unknown *Setaria* sp., followed by a chromosome doubling (polyploidization) event, forming an alloploid species. Relatively homogeneous population allozyme data suggest this polyploidization event in *S. faberi* was a relatively recent evolutionary event (Wang et al., 1995b). Genetic analysis has suggested that some variants of *S. verticillata* (n=18) may be the product of chromosome doubling of *S. viridis,* autotetraploidy (Till-Bottraud et al., 1992)

6.3.3.3 Aggregate species. Text …

aggregrate species:
1: a group of species that are so closely related that they are regarded as a single species.
2: a named species that represents a range of very closely related organisms; examples include *Limonium binervosum* and *Aspergillus niger*
[*chenopodium album? dandelion? gallium?*]

6.3.4 Genetic structuring: pre-adaptive colonizing archetypes.

[*make this section clearly different than 6.2.3*]
genetic evolutionary history and functionally preadapted phenotypes
    generalist-specialists
    reproductive colonizing types

[these show clear functional, trait, characteristics as the cause of their association, therefore they are the bridge to traits, roles and guilds developed in the following section on community dynamics.]

Another category of weed species associations is based on function within the local community. In both instances these categories are expressions of preadaptation, defined as:

preadaptation: the possession by an organism of characters or traits that would favor its survival in a new or changed environment

6.3.4.1 Generalist-specialist genotypes. The following sections are taken from Wang, et al. (1995) and provide some insight into generalist and specialist genotypes with the *Setaria* species-group.

Genetic variation and the evolutionary success of colonizers. The population genetic structure of many widely distributed, introduced, self-pollinating, weed species clearly indicates that a high level of genetic variation is not a prerequisite for successful colonization and evolutionary success (Allard, 1965; Barrett and Shore, 1989). Two contrasting, adaptive, strategies are hypothesized to explain weedy adaptation and the success of colonizers: genetic polymorphism with the development of locally adapted genotypes ("specialists"), and phenotypic plasticity for the development of "general purpose" genotypes (generalists) adaptable to a wide range of environmental conditions (Baker, 1965, 1974; Bradshaw, 1965; Barrett and Richardson, 1986). *Setaria* population genetic structure itself allows some insight into the dichotomy of generalism versus specialization. *Setaria* possess both generalists and specific strategy types. A key observation is that although a single, multilocus genotype predominates or is fixed in all local populations, not all multilocus genotypes are equally prevalent within individual weedy *Setaria* species (Wang et al., 1995a, 1995b).

The most striking example of this is in *S. pumila*, where the most common multilocus genotype was found in 53 (of 94 evaluated) accessions from widely separated geographic areas in Europe (Belgium, Czech Republic), Asia (Manchuria, China, Turkey), and North America (Ontario, Canada; eastern U.S.: MD, PA; western US: WA, WY; south U.S.: AK; north and midwestern U.S.: IA, IN, KS, MN, ND, WI) (Wang et al., 1995b). Overlaying this pattern of homogeneity were other, less abundant *S. pumila* genotypes, each with a more narrow geographical and ecological distribution.

The population genetic structure of *S. viridis* suggests that this species also possesses both generally adapted and specially adapted genotypes. Many *S. viridis* populations are strongly differentiated genetically (e. g., northern and southern North America), while other populations remain identical. The most widely distributed *S. viridis* genotype (fixed multilocus genotype) occurred in 25 (of 168 evaluated) accessions from six countries, from both the Old World and the New World (Wang et al., 1995a, 1995b). This common *S. viridis* genotype was found in many geographic locations, in very different ecological habitats: the □midwestern U.S. Corn Belt areas of Indiana, Minnesota, and North Dakota; the eastern U.S. Corn Belt of Maryland; the western U.S. agricultural valley of Washington; the highlands of Ontario, Canada; the lowlands of Belgium in northwest Europe; the plains of Bohemia, Czechoslovakia in central Europe; the waste areas interspersed between limestone outcroppings in the Akiyoshi Dai National Park, Honshu, Japan; and between cracks in a cement pier over the bay in Yokohama Harbor, Honshu, Japan. Interestingly, this common genotype has not yet been found in Iowa, despite the diversity of *S. viridis* populations found in this state.

These observations reveal a complex hedge-betting strategy by individual foxtail species, a strategy that balances general adaptation with the additional niche opportunities available with specialization: the ratio of general and special genotypes available in a species for invasion. The ratio of generalist to specialist genotypes was quite different within *S. pumila*, *S. geniculata* and *S. viridis* (Wang et al., 1995a, 1995b).

6.3.4.2 Genetic-reproductive colonizing types. An alternative organization was provided by Ehrendorfer (1965), correlating successful colonizing ability and critical genetic and reproductive characteristics. In some ways like the list of Baker (1965), Ehrendorfer surveyed (interestingly, in the same book as Baker, 1965) a wide range of plant species and collated their traits, looking for patterns of traits in species of particular habitat and behavioral types. This type of analysis is directly relevant to weed roles or guilds in communities, to be discussed later in this chapter.

The traits of interest included life-form (e.g. annual), mode of fertilization (e.g. autogamy), differentiation of seed structure and dispersal mechanism, utilization of vegetative reproduction, and chromosome ploidy condition. Colonizing plant types were also categorized in terms of population structure: mode of reproductive isolation (e.g. floral anatomy), population differentiation (e.g. allopatric), level of hybridization, population variability, and the plant successional habitat colonized.

Three different kinds of plant types were identified, I., II., and III. These types represent variation in genetic and evolutionary strategies of colonization: "The □polyploid perennials (I) are "conservative" types. They draw upon genetic diversity mainly built up on the diploid level. In their ecologically more "centrally" located position they operate successfully by mobilizing and recombining genetic material from ecologically divergent parental races. On their more reticulate course of evolution neither rapid nor very decisive changes have occurred.

GENETIC-REPRODUCTIVE COLONIZING PLANT TYPES			
TYPE	**I.**	**II.**	**III.**
Life-Form	polyploid perennials: -conservative types -ecologically 'central' position	autogamous annuals	dysploid annuals (chromosome number not exact haploid multiple)
Course of Evolution/ Reproductive Stragegy	reticulate (net-like): no rapid or decisive changes have occurred	evolutionary strategy: a. partly that of I.: polyploidy b. partly that of III. occassional aberrant line establishment	evolutionary 'avante-garde': a. carriers of rapid and divergent evolution b. variable, aberrant off-spring are new types: enhanced survival-colonizing ability in 'marginal' habitats
Genetic Flexibility/ Stability	a. genetic diversity from diploids b. successful by	consequence of: a. short sequence of (annual) generations b. maximum exploitation of gametic mutation rates	

	mobilizing and recombining divergent parental races	c. occassional outcrossing and hybridization (including alloploidy) between selfing lines in type II	c. occasional outcrossing and hybridization (including alloploidy) in the high outcrossing rate in type III a. increased mutation rate: gross chromosome structure-number changes b. swamping by hybridization less likely by new, structurally differentiated, genomes

Table 6.7 Genetic-reproductive colonizing species types (I., II., III.) from Ehrendorfer (1965).
[example species/]

The dysploid (aneuploid: chromosome number not exact multiple of haploid) annuals (III), on the other hand, can be regarded as evolutionary "avante-garde". Their increased mutation rate is reflected in gross changes of chromosome structure and chromosome number. Their variable offspring often includes rather aberrant new types and has better chances for survival or even expansive colonization in their ecologically more "marginally" located habitats. The structural differentiation of genomes makes swamping of such new types by hybridization less likely. These types then appear as carriers of rapid and divergent evolution. The evolutionary strategy of the autogamous annuals (II) seems to approach partly more type I (e.g. in respect to the occurance of polyploidy), partly more type III (e.g. in respect to the occasional establishment of quite aberrant new lines."

The genetic systems in all these types of colonizing species optimize modes of balance between genetic flexibility (selection among highly variable progeny) and stability (fixation and multiplication of successful biotypes) (Stebbins, 1958). Genetic flexibility in type II. and III. annuals is a consequence of the short sequence of generations, maximum exploitation of gametic mutation rates, occasional outcrossing and hybridization (including alloploidy) between selfing lines in type II, and the high outcrossing rate in type III. The outcome of these different genetic and reproductive systems is population genetic structure.

6.4 Exploiting Opportunity: Weed Community Dynamics

[reorganize: make clear key linked concepts of community assembly, traits, roles and guilds]

In this final section of the chapter community dynamics, changes with time, is presented. The source of this change is the evolving phenotypes of the community, constantly struggling with the habitat and neighbors. Nothing stays the same, change is constant in weed communities.

Weed community population structure is revealed at several spatial-temporal scales of local opportunity. In the preceding section community structure was apparent at higher levels of plant system organization: global to local community. Observation of this larger scale structure provided insights of the outcome of long-term weedy adaptation: population genetic structure and species associations. At the lowest level of plant system organization, qualities from the molecular to the individual plant reveal the fundamental bases for community population structure. Larger scale phenomena are an emergent property arising from smaller scale sources of community structure: the traits that determine the behavior of the phenotype in the community.

In the relentless evolutionary process of adaptation, weeds assume a role, they form a functional guild. This guild is based on clusters of interacting traits that allow them to dominate local opportunity at their neighbors expense in a very particular and specialized manner.

Agricultural plant communities, crops and weeds, are typically removed on a regular basis, usually annually. Weed communities thrive because they begin again every year, they are colonizing species. Against this human managed opportunity space-time are powerful forces leading to ecological community succession, wherein the current community creates new opportunity for the communities of the future.

6.4.1 Phenotypic life history traits. The expression of genes, alleles, results in the phenotype. The phenotype demonstrates its fitness by means of critical traits, characteristics. The adaptative advantage of these traits is determined by the time they are expressed relative to that of their neighbors behavior and development. Timing is everything. Timing of trait expression defines an individual plants life cycle, its life history.

Phenotypes and traits inevitably fill opportunity spaces in disturbed localities. Selection favors individual phenotypes and traits that preferentially take advantage of these opportunities at the expense of their neighbors. Selected phenotypes dominate their neighbors because the timing of their life history optimizes their relative fitness and minimizes mortality. The character of these opportunity spaces can be deduced by observing the new phenotypes adapted to these new spaces, and what traits they possess allowing such ready invasion.

Definitions:

[*find where traits and functional traits defined, then compromise location with here; make clear this section is only about functional, selectable, adaptable traits*]

functional trait: [see Violle ref]

life cycle
1: the sequence of events from the origin as a zygote, to the death of an individual
2: those stages through which an organism passes between the production of gametes by one generation and the production of gametes by the next

life history: the significant features of the life cycle through which an organism passes, with particular reference to strategies influencing survival and reproduction

Phenotypic life history traits. Given an opportunity in a locality, the second condition necessary for plant invasion is the presence of propagules of a particular species possessing life history traits suitable to exploit that space. A life history perspective provides some advantages in understanding how invasion occurs in a community. Plants experience the same general life history processes (birth, dispersal, recruitment, vegetative and seed reproductive growth). This life cycle can be described by the underlying plant morphological structures, developmental processes and whole plant activities that occur during each of these phases (Table 2). The time a plant performs these developmental processes and activities, relative to that of its neighbors, determines its success in the invasion process: timing is everything. If a particular invading plant is at the right place, at the right time, it is the traits that it expresses at those times that make it a winner or a loser relative to its neighbor. A plant's life cycle is a Markov Chain process in which the state of the plant at any one time is a direct consequence of its state in the previous time period (Dekker, 2004a). Failure at any time in the life history ends the invasion process.

6.4.1.1 Plant morphology and life history behavior. The table below summarizes the plant morphological structures, developmental (physiological, morphogenic) processes and whole plant phenotypic activities that occur during the plant life history processes of birth, dispersal, recruitment, vegetative growth and seed reproductive growth.

PLANT LIFE HISTORY: PROCESS, MORPHOLOGY, DEVELOPMENT & BEHAVIOR			
Process	**Morphology**	**Development**	**Behavior**
BIRTH	flower/meristem; seed/vegetative bud	•fertilization •zygote formation •embryogenesis •bud morphogenesis •dormancy induction	•seed and bud formation
DISPERSAL	seed/vegetative bud (independent ramet; parental ortet)	•dormancy maintenance	•spatial dispersal •spatial foraging (ortet) •seed or bud pool formation (dispersal in time)
RECRUITMENT	seedling/bud shoot (juvenile)	•germination or bud growth •emergence from soil •first leaf greening	•establishment
VEGETATIVE GROWTH	vegetative plant (adult)	•growth •meristem morphogenesis •senescence of some tissues	•interactions with neighbors
SEED REPRODUCTIVE GROWTH	flowering plant (adult)	•flower formation •senescence •meristem morphogenesis	•pollen dispersal

Table 6.8 Plant life history: morphological plant structures, developmental processes and whole plant behaviors.

Rhythmic behaviors. [add here circadian, diurnal rhythms; e.g. velvetleaf leaf movements, triazine resistant brassica photosynthetic activity in R and S; also connections here to TIME; other rhythmic behaviors].

6.4.1.2 Preadaption. Many traits in weed species assume an important role when crop management practices, disturbances or the environment change. A good example would be oxidative-degradative metabolic systems in plants that provide the ability to degrade herbicides, even before they were ever exposed to these chemicals. This is a good example of preadaptation:

preadaptation

the possession by an organism of characters or traits that would favor its survival in a new or changed environment

What phenotypic traits confer weedy success? All traits depend on the context (genotype) within which they are found. All traits in a weed interact with each other, and the norm is that there are trade-offs among them in reaching a balance within an individual plant (homeostasis). Many traits that seem non-weedy can lead to weed success if they are mixed with certain other traits in the same individual.

6.4.1.3 Trait basis of the invasion process. Why study the invasion process in terms of traits? They are identifiable phenotypes, functions and structures. The are selectable and heritable. How should these critical traits best be seen: in isolation or in a broader context? Life history provides some important advantages to organizing morphological traits. "Timing is Everything": when a plant performs important developmental processes and activities, relative to its neighbors, it a key to its success in the invasion process. If a particular invading plant is at the right place at the right time, it is the traits that it expresses at those times that make it a winner or a loser over its neighbor. Trade-offs among these traits that compete within the individual phenotype are apparent when we organize them into similar times in their life history.

6.4.1.4 Functional life history traits. The processes of life history, natural selection and invasion biology underlie functional traits arising from the fulfillment of roles fulfilled during weed life hstory (table 6.9). These general roles and traits can be found in the process and trait tables preceeding each of the life history phases in which weed adaptation occurs (see sections 7.2-7.5).

Table 6.9 Processes of life history, natural selection and invasion biology underlying functional traits of weeds.

PROCESSES		
LIFE HISTORY	NATURAL SELECTION	INVASION BIOLOGY
Propagule reproduction	Condition 3: survive to produce the fittest offspring	Colonization & Extinction
Parental Architecture		
Floral induction		
Anthesis	Condition 1: generate variation in individual traits Condition 4: reproductive transmission of parental traits to offspring	
Fertilization (threshold event)		
Embryogenesis		Enduring occupation
Abscission (threshold event)	Condition 2: generate variation in individual fitness	
Progagule dispersal	Condition 3: survive to produce the fittest offspring	Colonization & Extinction
Spatial dispersal	Pre-Condition 1: excess local phenotypes compete for limited opportunity	Invasion
Temporal dispersal	Enduring occupation	Enduring occupation
Recruitment Seed germination Seedling emergence (threshold event)	Pre-Condition 1: excess local phenotypes compete for limited opportunity Condition 3: survive to produce the fittest offspring	Invasion, Colonization & Extinction

Vegetative growth Neighbor Interactions: Growth-Development Stress Responses	Pre-Condition 1: excess local phenotypes compete for limited opportunity Condition 3: survive to produce the fittest offspring	Colonization & Extinction

6.4.2 Ecological roles-guilds-trades in weed-crop plant communities.

Every species in a weed-crop plant community plays a role, fills a niche, utilizes resources and conditions, has a trade or is a member of a guild that functionally defines the species and provides insight into both the opportunity space available in the locality and the predicates of the neighbor interactions that will ensue over the season and life history of the plants.

The crop is easy to define, its role is to produce biomass or seed for human utilization. Every crop species utilizes opportunity space in a locality and leaves some other part of opportunity space unused. It is this unused opportunity space that determines what roles are left unfilled, or what ecological trade of guild a weed species might occupy that will make it successful in seizing and occupying that opportunity space.

Guilds are defined:

ecological guild
1: a group of species having similar ecological resource requirements and foraging strategies, and therefore having similar roles in the community
2: a group of species that exploit the same class of environmental resources in a similar way (Root, 1967)
3: groups of functionally similar species in a community

6.4.2.1 Guild structure and community organization

Guilds. Root (1967) coined the term "guild" to describe groups of functionally similar species in a community. In competitive communities, guilds would represent arenas with the potential for intense interspecific competition, with strong interactions within guilds but weaker interactions with the remainder of their community. A guild is a group of species separated from all other such clusters by an ecological distance greater than the greatest distance between the two most disparate members of the guild concerned. This conservative definition allows complex hierarchical patterns of nesting of smaller guilds within larger ones.

Another very useful technique that depicts some of a community's "connectedness" involves ranking each species' neighbors in niche space from the nearest to the most distant (Inger and Colwell 1977). When overlap is plotted against such nearness ranks in niche space, very similar species (such as those belonging to the same guild) fall out together, whereas species on the periphery of niche space have low overlap with the remainder of the community and tend to fall well below other species.

Ecological guild. A group of species that exploit the same class of environmental resources in a similar way (Root, 1967); e.g a group of species having similar requirements and foraging habits and so having similar roles in the community. Species that act as herbivores, omnivores, carnivores and detrivores are examples of guilds. The concept's early roots lie in plant and animal ecology, when ecologists recognized the organization of trophic groups called "Genossenschaften" (Schimper, 1903); see guild and "Synthropia" (Balogh & Loksa, 1956). An assumption derived from competition theory is that species within guilds are most likely competitors, therefore guilds are suggested to form the basis of community organization (Uetz, Halaj & Cady, 1999). However, members of guilds often differ in their precise food requirements, thus reducing the

6.4.2.2 Parameters of weed species ecological role and niche. The ecological role of a particular weed species in a particular agro-ecosystem is more problematic. No one has attempted to define ecological guilds of weeds in agriculture, but herein we make a first approximation. What dimensions, or parameters, would define ecological guild/agro-community structure?

The role, trade, guild or ecological niche that a particular weed species plays and occupies is a function, fundamentally, of its developmental life cycle and life history processes and traits.

Individual weed species guilds are the fulfillment of specific roles they play at different times in their life history. These roles are accomplished by means of specific traits expressed during life history. The processes of life history, natural selection and invasion biology underlie functional traits arising from the fulfillment of these roles (see table 6.9). The general roles and traits that form the basis of individual weed guilds can be found in the process and trait tables preceeding each of the life history phases in which weed adaptation occurs (see sections 7.2-7.5).

Certain functional traits have a disproportionate influence on subsequent life history events. For example, the traits responsible for seedling emergence timing relative to other crop and weed species in an agroecosystem has a profound effect on subsequent fitness (see 7.4). The induction of variable dormancy states among individual seeds of a single parent plant (seed heteroblasty) provides the ‘blueprint’ for fine scale seedling emergence timing and pattern to maximize exploitation of local opportunity spacetime. As such, traits responsible for dormancy-germinability regulation can be considered ‘keystone’ traits.

keystone trait:

Expand theoretical basis of community dynamics with expansion of the definition of community:

community: any group of organisms belonging to a number of different species that co-occur in the same habitat or area and interact through trophic and spatial relationships; typically characterized by <u>reference to one or more dominant species</u> (Lincoln)

With reference to one or more "life history defining temporal crossroads" (e.g. emergence) and the associated traits and guilds that define the different pathways taken at this crucial life history junction.

MORPHOLOGY	LIFE HISTORY PROCESS	DEVELOPMENTAL ACTIVITY	ECOLOGICAL TRAIT	ECOLOGICAL, FUNCTIONAL ROLE
seedling	Agro-Community Assembly	seedling recruitment, emergence	•seed dormancy, heteroblasty •seedling emergence time, pattern •relative	•assembly in community with neighbors

			seedling emergence order	
vegetative plant	Neighbor Interactions	opportunity space exploitation:	Spatial foraging: •weed shoot and root architecture and function •vegetative bud: -bud morphogenesis -plant bud architecture -bud foraging from parental ortet	•resource allocation •spatial foraging
flowering plant	Reproduction	•flowering •pollen dispersal and spatial foraging •birth of zygote: -fertilization -embryogenesis -dormancy induction •meristem architecture and morphogenesis •abscission from parent •time of senescence	•mating system •time and duration of reproduction	•multiplication of parent •display of genotypic variation, novelty
seed	Dispersal	Spatial dispersal: •seed movement: local, distant Temporal dispersal: •soil seed pool formation	Propagule qualities: •seed mobility •seed dormancy, heteroblasty	•dispersal in space and time •invasion and colonization •persistence, enduring occupation of locality
all plant forms	Multi-Year Processes: •generation periodicity •ecological succession	life cycle	life cycle timing: annual, biennial, perennial	•multiplication, colonization, persistence, enduring occupation of locality

Table 6.10 Plant morphological structures, developmental (physiological, morphogenic) life history activities, ecological traits and functional roles that occur during the plant life

history processes of agro-community assembly, interactions with neighbors, reproduction and dispersal over generational, and ecological successional, time. See also tables in section 2.3.4.6.3 Phenotypic traits and weed life history.

6.4.2.3 Trait Guild: Relative seedling/bud emergence order. The time and pattern of seedling emergence of a weed relative to that of the crop is the primary determinate of both plant community assembly and structure, and the ultimate fate of that individual. As such, many traits are responsible for controlling the relative emergence time of a species in a locality. It is these traits that determine the ecological role that that species will play in the community in the seizure of opportunity space and its fitness. Relative emergence time is a very good place to start in understanding the ecological role, or guild, that a species occupies in the crop-weed plant community.

Iowa maize and soybean crop production fields may be a good agro-ecosystem to begin this process of identifying the ecological role of a weed species, and the collection of ecological guilds that comprise an agro-community. Iowa is in many ways monolithic and homogeneous: 21 million acres of row crops, a one- (maize) or two-crop (maize, soybeans) crop rotation system is utilized on the vast majority of this land. This simple rotational crop production system has been in use for some decades (e.g. 1950's till now). The communities that are established on these Iowa crop fields can provide our first view of ecological roles filling opportunity space.

[see Appendix 2, p.171]

6.4.3 Changes in plant community structure. [*weed pop shifts; succession*]

6.4.3.1 Weed population shifts. Weedy microevolution includes the occurrence of population shifts in agricultural fields and local adaptation by individuals and populations to those localities. Weed population shifts are the changes in the individual organisms that make up the population of a locality, often caused by changes in weed management practices. The bottom line for a farmer, and an individual field, is that when things change the weeds adapt. Those practices that control weeds in a field this year probably won't provide acceptable weed control in future years. Why? Because what you do today kills those weeds susceptible to your management practices. The few weeds that survive today's management practices are the parents of the weed problems you will have in the future: leaner, meaner, better able to handle what you dish out. This process has been going on for thousands of years. Every crop grown by humans, in every field, in every year for the history of agriculture has resulted in the weeds you have in your field today. Agronomic practices (e.g. mechanization, herbicides, new crops and crop varieties) and an increase in the size and structure of land holdings can change the weed species present in a field (interspecific population shifts), as well as the genotypes of a single species present in a local agroecosystem (intraspecific population shifts).

6.4.3.1.1 Inter-specific Population Shifts. The weed species present in a local weed community can change in response to changes in environment, neighbors, cropping practices and disturbance. Many weed species have undergone very large extensions of the ranges (e.g. *Setaria* spp.-gp.) they thrive in while others formerly widespread have all but disappeared.

Grassy weed tolerance to 2,4-D. Before WWII, the early 1940's, selective herbicides were not used on weeds in Iowa corn fields. The weed communities were different than they are today. At that earlier time broadleaf weeds were considered the major weed problem (farmers often grouped plants in their fields into "weeds" and "grasses"). With the introduction of 2,4-D, this selective weed control killed the broadleaf weeds in most cases, but did little to the grasses. Grassy weed species suddenly became a much larger weed problems than before. *Setaria faberi* (giant foxtail) was largely unknown to midwestern US growers before 1950. Since that time, population shifts have occurred as a response to the introduction of a new herbicide mode of action. For example, in the 1980-1990's the appearance of *Panicum mileaceum* (wild proso millet) and *Eriochloa villosa* (woolly cupgrass), weeds largely unknown previously, have spread across the Midwestern US.

Herbicide-induced life cycle shifts. Populations of summer annuals subjected to herbicide selection pressure has resulted in a population shift to winter annual life cycle or to seed that germinated much later in the season in England.

6.4.3.1.2 Intra-specific Population Shifts. Changes in crop fields can favor particular variants within a species. The selection for new and better adapted genotypes and phenotypes of a species can cause shifts in the composition of a population of an individual species in a field or area. Just as herbicides selected and shifted different species in a fields weed community, herbicides and other disturbance changes have caused shifts within populations of one species to better adapted variants.

Early flowering in *Avena fatua*. Population shifts to early flowering forms of wild oat (*Avena fatua*) and *Arabidopsis thaliani* were selected for by changes in weed seed cleaning and crop harvesting practices.

Crop mimicry in *Echinochloa crus-galli*. Barnyardgrass has a variant (*Echinochloa crus-galli* (L.) Beauv. var. *oryzicola* (Vasing) Ohwi.) that mimics cultivated rice so effectively it escapes handweeding. Its growth habit and appearance are more similar to rice than some of rice's closer relatives. The main selective force favoring this intra-specific variant has been intensive handweeding in Asian rice crops.

Dwarf variants in cereal crops. Dwarf populations of *Aethusa cynapium* and *Torilis japonicum* in English cereal crops were selected by the introduction of harvesting equipment. The equipment selected against the taller variants, but the dwarf variants thrived.

Shift to lower biodiversity. Herbicide use led to a decrease in the diversity of genotypes present in a weed species population in California.

6.3.3.1.3 Herbicide Induced Population Shifts. Some of the most dramatic and widespread population shifts in agricultural communities occurs in response to the introduction of herbicide use in a crop. Natural selection quickly selects for resistance, whether caused by alterations to the molecular target site in the plant or by altered metabolism and detoxification of the herbicide. Survivors rapidly exploit the opportunity space left by their dead neighbors.

Herbicide resistance genotype shifts: altered herbicide target variants. Herbicide resistance can be conferred in a plant by many mechanisms. These resistance mechanisms include a change in the target site (usually a protein) that the herbicide binds to, causing death or injury. Below is a partial list of some of these types of population shifts caused by herbicide use that kills the susceptible variants and allows the resistant survivor variants to thrive. Altered herbicide binding (target) site variants include atrazine-resistant *Chenopodium album* biotypes (altered psbA chloroplast gene product and binding site); ALSase-inhibitor resistance (altered acetolactate synthase gene in *Amaranthus rudis* (common waterhemp) and *Kochia scoparia*); ACCase inhibitor resistance (altered acetyl CoA carboxylase gene in *Avena fatua* (wild oat) and *Setaria viridis* (green foxtail)).

Herbicide resistance genotype shifts: enhanced herbicide metabolism variants. Herbicide resistance can also be conferred on variants within a species that detoxify herbicides more rapidly than susceptible genotypes. Repeated herbicide applications kill off the more susceptible and leave the enhanced detoxifying variants to thrive.

Selection for variants of *Tripleurospermum inodorum* (scentless mayweed) with incrementally enhanced herbicide metabolism resulted from repeated applications of several herbicides, including simazine. *Avena fatua* (wild oat) herbicides (barban, difenzaquat) led to an increase in variants with better metabolic detoxification systems. Populations of *Alopecurus myosuroides* Huds. (slender foxtail or blackgrass) in the UK, and *Lolium rigidum* (rigid ryegrass) populations in Australia, have been identified in agricultural fields with high levels of metabolic cross-resistance to several different chemical families of herbicides. In the later instance in Australia, some populations were found to be resistant to all herbicides available for weed control in those crops in which it appears. Several populations of *Abutilon theophrastiI* (velvetleaf) in Maryland and Wisconsin in the US have been identified as resistant to s-triazine herbicides. Resistance was not due to altered triazine binding (psbA gene mutants), but due to enhanced metabolism in those biotypes.

6.4.3.2 Plant community ecological succession. [text]

[begins with seizing unoccupied opp space, then neighbor competition for occupied space; each community is the opportunity space of the next successional community, with the wild card of disturbance to reset the community structural sequence again in patchy spatial patterns]

from chapter 3:

Cycles are predictable (predictable crashes), therefore weeds and other organisms are well adapted to them. The cycle crucial to weed populations is their life history, developed in detail in the following unit. Another very important cycle in nature is plant community succession, discussed in Chapter 5, community dynamics: annual herbaceous colonizers > perennial herbaceous > perennial woody. A sequence of species moving from colonizing to density-stressed conditions. Plant succession changes the fitness of a species: later successional species are adapted to density-dependent competition. Colonizing plants avoid successional changes and disturbances by many of their key life history traits: disperse to, invade, disturbed sites; escape succession and go elsewhere to colonized new area: continuous return to beginning of successional cycle. Seed and bud bank buffer against short term changes. Colonizing "r" selected species takes on traits of "K" species: life cycle: biennial; perennial with early competitive propagules like rhizomes, rootstocks; e.g. knotroot foxtail with rhizomes vs. yellow foxtail; johnsongrass vs. shattercane; bamboo example of plant species with forms in all stages of succession.

Definitions:

ecological succession

1: the chronological distribution of organisms within an area

2: the geological, ecological or seasonal sequence of species within a habitat or community

3: the development of plant communities leading to a climax

4: a process of continuous colonization of and extinction on a site by species populations (Bazzaz, 1979)

successional trajectory

the likely sequence of plant and animal communities predicted to occur in a habitat following a particular type of disturbance

From Wikipedia (http://en.wikipedia.org/wiki/Ecological_succession):

Ecological succession, a fundamental concept in ecology, refers to more-or-less predictable and orderly changes in the composition or structure of an ecological community. Succession may be initiated either by formation of new, unoccupied habitat (e.g., a lava flow or a severe landslide) or by some form of disturbance (e.g. fire, severe windthrow, logging) of an existing community. The former case is often referred to as primary succession, the latter as secondary succession.

The trajectory of ecological change can be influenced by site conditions, by the interactions of the species present, and by more stochastic factors such as availability of colonists or seeds, or weather conditions at the time of disturbance. Some of these factors contribute to predictability of successional dynamics; others add more probabilistic elements. In general, communities in early succession will be dominated by fast-growing, well-dispersed species (opportunist, fugitive, or r-selected life-histories). As succession proceeds, these species will tend to be replaced by more competitive (k-selected) species.

Trends in ecosystem and community properties in succession have been suggested, but few appear to be general. For example, species diversity almost necessarily increases during early succession as new species arrive, but may decline in later succession as competition eliminates opportunistic species and leads to dominance by locally superior competitors. Net Primary Productivity, biomass, and trophic level properties all show variable patterns over succession, depending on the particular system and site.

Ecological succession was formerly seen as having a stable end-stage called the climax (see Frederic Clements), sometimes referred to as the 'potential vegetation' of a site, shaped primarily by the local climate. This idea has been largely abandoned by modern ecologists in favor of non-equilibrium ideas of how ecosystems function. Most natural ecosystems experience disturbance at a rate that makes a "climax" community unattainable. Climate change often occurs at a rate and frequency sufficient to prevent arrival at a climax state. Additions to available species pools through range expansions and introductions can also continually reshape communities.

Many species are specialized to exploit disturbances. In forests of northeastern North America trees such as Betula alleghaniensis (Yellow birch) and Prunus serotina (Black cherry) are particularly well-adapted to exploit large gaps in forest canopies, but are intolerant of shade and are eventually replaced by other (shade-tolerant) species in the absence of disturbances that create such gaps.

The development of some ecosystem attributes, such as pedogenesis and nutrient cycles, are both influenced by community properties, and, in turn, influence further community development. This process may occur only over centuries or millennia. Coupled with the stochastic nature of disturbance events and other long-term (e.g., climatic) changes, such dynamics make it doubtful whether the 'climax' concept ever applies or is particularly useful in considering actual vegetation.

History of the idea. The idea of ecological succession goes back to the 19th Century. In 1860 Henry David Thoreau read an address called "The Succession of Forest Trees" in which he described succession in an Oak-Pine forest.

Henry Chandler Cowles, at the University of Chicago, developed a more formal concept of succession, following his studies of sand dunes on the shores of Lake Michigan (the Indiana Dunes). He recognized that vegetation on sand-dunes of different ages might be interpreted as different stages of a general trend of vegetation development on dunes, and used his observations to propose a particular sequence (sere) and process of primary succession. His paper, "The ecological relations of the vegetation of the sand dunes of Lake Michigan" in 1899 in the Botanical Gazette is one of the classic publications in the history of the field of ecology.

Understanding of succession was long dominated by the theories of Frederic Clements, a contemporary of Cowles, who held that successional sequences of communities (seres), were highly predictable and culminated in a climatically determined stable climax. Clements and his followers developed a complex taxonomy of communities and successional pathways (see article on Clements).

A contrasting view, the Gleasonian framework, is more complex, with three items: invoking interactions between the physical environment, population-level interactions between species, and disturbance regimes, in determining the composition and spatial distribution of species. It differs most fundamentally from the Clementsian view in suggesting a much greater role of chance factors and in denying the existence of coherent, sharply bounded community types. Gleason's ideas, first published in the early 20th century, were more consistent with Cowles' thinking, and were ultimately largely vindicated. However, they were largely ignored from their publication until the 1960s.

Beginning with the work of Robert Whittaker and John Curtis in the 1950s and 1960s, models of succession have gradually changed and become more complex. In modern times, among North American ecologists, less stress has been placed on the idea of a single climax vegetation, and more study has gone into the role of contingency in the actual development of communities.

Chapter 7: Adaptation in Weed Phenotype Life History

Summary. [*text*]

This large chapter encompasses the entire life history of weeds, the traits that have evolved and the adaptations that resulted from the process of natural selection. The life history components of this chapter are organized as:

7.1 Introduction

> "The life cycle is the fundamental unit of description of the organism." (Caswell, 2001)

Adaptation in weed life history consists of three overlapping processes: the plant's life cycle, natural selection and the biological processes of weed invasion and exploitation of local opportunity spacetime (see table 6.9).

The life history of an annual weedy plant consists of several discrete threshold events, events that can provide strong experimental inferences in life history studies: anthesis, fertilization and zygote formation, abscission from the parent plant, seedling emergence time and death.

7.2 Adaptation in Reproduction

Summary. The life history of a weed from floral primordial intiation in the developing parent plant architecture to independent organism crossing the abscission threshold.

A plant is born, and begins its life history, when the egg is fertilized by pollen. Events of critical importance prior to the formation of the zygote include development of the flower primordial inside the plant during the vegetative phase; flowering and seed head formation; mating systems; anthesis and fertilization; embryogenesis; acquisition of germinability competency; dormancy induction during, and just after, embryogenesis; and heterogeneous dormancy states among individual seeds from the same flowering structure (seedhead, panicle). All these processes include parental influences on the developing zygote, developmental influences from two potentially different individual genotypes. This reproductive process ends with the threshold life history event of seed abscission.

Adaptation in propagule reproduction is the consequence of the three overlapping processes of weed life history, natural selection and invasion biology (table 7.1).

Table 7.1 Propagule reproduction: processes of life history, natural selection and invasion biology underlying functional traits of weeds (see table 6.9).

PROCESSES		
LIFE HISTORY	NATURAL SELECTION	INVASION BIOLOGY
Propagule reproduction	Condition 3: survive to produce the fittest offspring	Colonization & Extinction
Parental Architecture		
Floral induction		
Anthesis	Condition 1: generate variation in individual traits Condition 4: reproductive transmission of parental traits to offspring	
Fertilization (threshold event)		
Embryogenesis		Enduring occupation
Abscission (threshold event)	Condition 2: generate variation in individual fitness	

Traits important to reproductive adaptation are those that fulfill roles that generate heritable genotypic, phenotypic and speciation variation in fitness appropriate to the opportunity spacetime being exploited by the weed species (table 7.2). During reproduction morphogenesis of traits whose expression is crucial in subsequent times of life history occurs.

Table 7.2 Weedy life history functional roles and traits for adaptation in reproduction.

TRAIT ROLE	TRAITS
Mating system: control recombination: balance genetic foraging with genetic conservation appropriate to the opportunity being exploited	**Genetic foraging**: outcrossing; monoecy; dioecy; speciation and reproductive isolating mechanisms; external pollination vectors
	Genetic conservation: apomixis; self-pollenation; vegetative reproduction
Floral quality	**Floral morphogenesis**: seedhead architecture and morphogenesis; floral organ expression and anthesis
	Perennial fecundity: balance production of

	vegetative buds and seeds
THRESHOLD EVENT: FERTILIZATION	
Timing of reproduction	**Seasonal timing**: floral induction and morphogenesis; fertilization; plant reproductive period duration and times of abscission **Periodicity**: embryogenic duration; time to embryo germination competence
Embryo-propagule quality	**Propagule morphogenesis**: 1. Seed dormancy and heteroblasty induction 2. Seed size 3. Protective structures enveloping embryo 4. Nutritive tissues supporting embryo 5. Dispersal structures
Propagule fecundity: maximizing/optimizing local opportunity spacetime	**Propagule number**: 1. plastic production of flowers, flowering branches and seed number maximizing/optimizing plant size 2. reallocation of plant food-nutrients to propagules 3. propagule productivity and duration maximizes seasonal conditions-resources 4. propagule number appropriate to future safe sites available in locality
THRESHOLD EVENT: PARENTAL ABSCISSION	

7.2.1 Flowering, anthesis, fertilization and birth. Parental plant architecture and mating systems.

7.2.1.1 Parent plant floral architecture. About tillering, branching and canopy development, floral primordial development, flowering and the development of the seedhead. All these processes in the individual phenotype are strongly influenced by relationships to neighbors at the time they occur. The expression of these functional traits during weed life history determine the above ground form of the plant when it begins reproduction, and is a significant determinate of its subsequent reproductivity.

7.2.1.2 Mating systems. See section 5.3.2, pp. 57-63.

7.2.2 Embryo adaptation: embryogenesis and dormancy induction. Once a weed seed is fertilized it begins the process of embryogenesis, the formation, growth and development of the seed, the propagule. During this critical process the new plant is formed. In many, if not most, weed species this is also the time of seed dormancy induction, a process inseparable from development of the rest of the embryo and seed. In this section seed dormancy-germinability mechanisms are discussed. As such there is overlap with seed dormancy-germinability as a life history mechanism for dispersal in time (section 7.3), and seedling recruitment (section 7.4), following the threshold life history event of abscission from the parent plant.

7.2.2.1 Induction of seed dormancy. Dormancy mechanisms, seed pools and recruitment are of a whole. Dormancy mechanisms are the drivers of, the reasons why, seed pools form in the soil (or not). Much of the material on dormancy mechanisms overlaps with seed pools and recruitment. Soil seed pools are the inevitable consequence of dormancy mechanisms. Recruitment, seed germination and seedling emergence/establishment are also inevitable consequences of dormancy mechanisms.

Some basic seed dormancy definitions include:

seed dormancy (and bud dormancy)
1: a state in which viable seeds (or buds; spores) fail to germinate under conditions of moisture, temperature and oxygen favorable for vegetative growth (Amen, 1968);
2: a state of relative metabolic quiescence; interruption in growth sequences, life cycle (usually in embryonic stages)
3: dispersal in time

seed germinability
the capacity of an seed, bud or spore to germinate under some set of conditions

Primary (1°) dormancy category (arising from the parent) definitions:

innate dormancy
1: the condition of seeds (born with) as they leave the parent plant, and is a viable state but prevented from germinating when exposed to warm, moist aerated conditions by some property of the embryo or the associated endosperm or parental structures (e.g. envelopes) (implies time lag) (after-ripening)
2: characteristic of genotype, species; dormancy when leave parent
3: innate dormancy is caused by: incomplete development; biochemical 'trigger'; removal of an inhibitor; physical restriction of water and/or gas access

vivipary
germinating while still attached to the parent plant; in crops its called pre-harvest sprouting, or precocious germination

viviparous
producing offspring from within the body of the parent

Secondary (2°) dormancy category (arising from environmental conditions) definitions:

induced dormancy
1: is an acquired condition of inability to germinate caused by some experience after abscission
2: acquired dormancy after abscission due to some environmental condition(s)
3: after-ripening different, comes after abscission dormancy inducing experience

enforced dormancy
1: is an inability to germinate due to an environmental restraint: shortage of water, low temperature, poor aeration, etc.
2: unfavorable conditions prevent germination, otherwise the seed would germinate

after-ripening
period after dispersal when the seed, spores and bud cannot germinate, even under favorable conditions, and during which changes occur allowing it to germinate.

7.2.2.2 Life history of a seed. Seed banks formed by individuals with diverse dormancy states (seed heteroblasty) results in several observed behaviors. Seedling emergence occurs during the growing season; summer annuals typically with the majority in the spring and early summer; many with extended emergence for the remainder of the growing season. Seed become after-ripened (AR; environmental experiences in the soil);

typically only a fraction germinate and emerge every year. Seeds can become ready for germination (a germination "candidate") in AR conditions (e.g. cool, moist), but fail to germinate without a change to somewhat different environmental conditions specifically favorable to germination (warm, moist). Higher soil temperatures of summer reverse the earlier AR effects and secondary (2°) dormancy is induced. Taken together these environmental conditions result in an annual cycling between dormant and highly germinable states within the heterogeneous seeds remaining in the soil seed bank (see Baskin and Baskin, 1985.

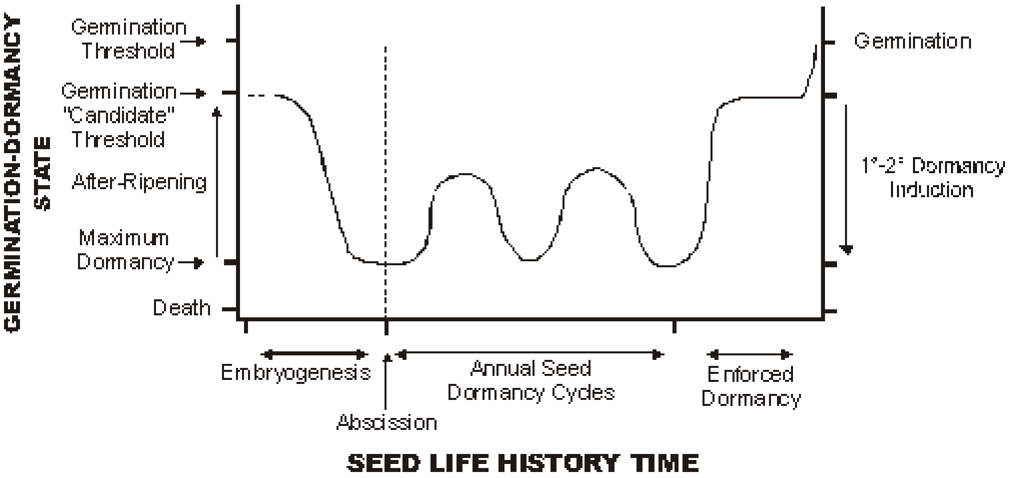


Figure 7.1 Schematic model of life history changes in individual foxtail seed germination-dormancy states with time from embryogenesis to germination or death; dashed (---) vertical lines represent irreversible life history events; axes not to scale.

7.2.2.3 The evolutionary ecology of seed dormancy. Plants have seed (or bud) dormancy because it is a successful, well-adapted strategy. Seed dormancy is dispersal in time to avoid mortality (winter, farming practices), allowing the seed to wait till the right conditions, or until the favorable habitat, reappears. The existence and duration of seed dormancy evolved by adopting one of three (3) high-cost options, or alternative strategies, to survival during unfavorable conditions. They are somewhat similar and overlap: some species have adopted all 3 ecological strategies for survival.

<u>Option 1: seeds or bud dormancy</u>. Annuals produce dormant seed, herbaceous perennial species produce dormant underground rhizome, rootstock, etc., to avoid unfavorable conditions.

<u>Option 2: seasonally dimorphic phenotypes</u>. Perennial and biennial plant species that adopt different vegetative bodies at different times of the year (somatic polymorphism over time). Herbaceous perennials display a dormant underground rhizome, rootstock, etc. in the winter; and shoot and underground organs in summer. Biennial plants display an overwintering rosette; in the spring the shoot elongates.

<u>Option 3: homeostatic growth form that is tolerant of the entire range of environmental conditions in the plant's life cycle</u>. Woody perennials (trees) display a permanent shoot year-round, but in the winter have dormant leaf shoot buds. An exception is found with evergreen, conifer, leaves that don't drop in the autumn (but even their leaves are dormant in cold, dry conditions).

Seed and bud dormancy afford a lowered struggle for existence, low cost, but at expense of fitness). It allows them to survive during, escape from, harsh winters. Seed dormancy is the least stressful form for a plant during harsh times, and is also the smallest. The dormant plant isn't using, demanding, resources when they are unavailable, or at their lowest level. Seed dormancy delays the start in producing progeny to more favorable times. The seed bank is an adaptation that provides a genetic buffer, long-term continuity, for the weed species.

Seed and bud dormancy differ from each other in some ways. The differences are revealed in these roles (see discussion of the 5 roles of seeds in section 7.2.3). Buds have no hulls, protective structures, less tissue differentiation; seeds do. Longevity in seeds is usually greater than that in buds. There exists less spatial movement, dispersal in buds. In terms of genetic novelty of new generation, buds have no genetic novelty (they are clones), while seeds are usually produced with sexual reproduction and therefore are potentially new genotypes.

Seeds and vegetative buds are similar to each other in other ways. The similarities are revealed in these roles (of the 5 roles of seeds). Both seeds and buds are for multiplication or individuals, and for storage of energy for growth. Both are profoundly influenced by their parents until birth-germination. Buds are connected to the parental plant in system, by which they are regulated and dependent. Seeds are usually enclosed by dormancy-inducing parental tissues regulating germination (displaced wombs?).

7.2.2.4 Weed seed dormancy variability and somatic polymorphism. The importance of seed dormancy heterogeneity as a functional trait in weed life history is revealed in several insights:

“The discovery of clines in seed polymorphism in [3 species listed] suggests that seed polymorphism may be a most sensitive indicator of evolution in weedy species.” (Harper, 1964, Genetics of Colonizing Species; p.257)

“There is increasing evidence that specialized properties of the seed, its shape, its size and form, and the nature of its surface determine the type of contact the seed makes with the soil and on this depends the ability of the seed to germinate successfully.” (Harper, 1964, Genetics of Colonizing Species; p.257)

“Present knowledge of the behavior of invading species, both successful and unsuccessful, suggests that it is in phases of germination and seedling establishment that their success or failure is most critically determined and it would seem reasonable therefore, to look particularly closely at seeds and seedlings of invading species. The considerations set out in this paper lead one to expect that it is in properties such as seed number, seed size, seed polymorphisms, and precise germination requirements that the most sensitive reactions of a species to an alien environment are likely to occur.” (Harper, 1964, Genetics of Colonizing Species; p.261)

“Seed polymorphisms seem particularly likely to be sensitive indicators of evolutionary change in alien invaders.” (Harper, 1964, Genetics of Colonizing Species; p.261)

Definitions:

somatic polymorphism of seed dormancy: the occurrence of several different forms (amounts) of seed dormancy produced by an individual plant; distinctively different dormancy forms (amounts) adapted to different conditions

heteroblasty: seed dormancy capacity variability at abscission among individual seeds shed by a single parent plant

seed dormancy capacity: the dormancy state of an individual seed at abscission, as well as the amount of environmental signals (water, heat, oxygen, etc.) required to stimulate a change in state (after-ripening)

Keep in mind that just because the differences in dormancy among seed are often not apparent (biochemical, physiological, etc.).

7.2.2.5 Evolutionary ecology of seed heteroblasty. Why is seed dormancy so variable at so many levels of plant organization? What is the purpose, or selective advantage, of a plant shedding seed with variable dormancy? Seed dormancy polymorphisms can be seen as a hedge betting strategy for an uncertain future. This strategy has a roulette wheel analogy, if you place a bet or chip on every number you can't lose. If you have a means of remembering (winners live, losers die), over time selection occurs for the best number to bet on, or the best combination of numbers. Each winning seed once again produces seeds with same ratio; but over time an mutation/variation ratio can shift to more favorable ratio for local conditions. Selection for dormancy somatic polymorphism, instead of genotype polymorphism, for dormancy allows each different weed genotype to produce an array of dormancy state individuals. The mechanisms by which they are produced can be epigenetic (e.g. weed *Setaria*). More variety and flexibility can be produced with different phenotypes than with different genotypes. A species only needs one genotype at a location to colonize it fully, exploit all good emergence times. Different genotypes would require all of them being there to spread their pollen for full exploitation of that locality.

How variable is seed dormancy in a species, a parent plant, a local population? This is poorly understood, yet the answer for any individual is critical to understanding and predicting it's life history and fitness.

Is variation greater between plants or between habitats? Weed germination variation differences are greater between plants than between habitats (Cavers and Harper, 1966). Why? Wide amount of variation in seed dormancy is necessary at any site it is capable of growing in, in order to take advantage of the variable opportunities, micro-sites in the field.

7.2.2.6 Weed species seed heteroblasty examples. Habitat to habitat variability is less than intra-field variability. (Reference Harper (1977), Ch. 3). [organize by dicots/grasses; families]

***Xanthium*, cocklebur; p.69:**

a. 2 seeded capsule with different dormancy:
    1] 1 germ in year 1, other in year 2;
    2] but is year 1 precocious germination (second generation that year) or is it the first following year?
b. one seed larger than the other; which one goes first?
c. first seed germinates, capsule partially splits, pulls capsule out of soil with emerging cotyledons, re-disperses capsule remnant and second, dormant seed
d. mutant from Mississippi with 5 seed per capsule
e. which seed might be the one with more dormancy, in absence of knowing the answer?:
    1] first more dormant: use large, non-dormant seed first, more food reserve at start; #1 large to break out of capsule
    2] second seed more dormant: small seed goes later, less investment, less bet; first seed larger and gets jump with more food reserves; second smaller and lives longer;
    3] no order to their dormancy: different triggers depend on microsite conditions, could go either way

***Chenopodium album*; *Chenopodiaceae* family**

[Lindsey Iowa seed update]

a. e.g. common lambsquarters: 4 types, two color morphs, two surface morphs:
  1] 2 seed color types have most variation in dormancy
    a] brown, 3% of seed produced, less dormant and larger size; easily germinated, cool temperatures and thin seed coat wall controls germinability; shorter longevity in soil
    b] black, majority, more dormant; germinatation in cooler temperatures plus light stimulation in the presence of nitrate
  2] seed surface: two types: reticulate, smooth
    -smooth and reticulate coat seed; coat differences utility unknown but could be dispersal or signal transduction from soil environment signaling behavior

Foxtails (*Setaria* spp.-gp.)

a. somatic polymorphism of narrow placental pore opening (TACL) restricting water-gas entry into seed: water freely available, oxygen limited
b. somatic polyolymorphism of oxygen sponge peroxidase preventing after-ripening and germination;
c. somatic polyolymorphism of hull rugosity (wrinkles) and shape may affect water accumulation on seed, transport across seed to placental pore, uptake into seed
e. range of dormancy on a single individual plant from viviparous to profoundly dormant
f. different dormancy phenotypes shed during season by different tillers (the "Early-Early" rule):
  -earliest seed on panicle most dormant
  -earliest panicles (primary, August seed) most dormant while later/latest panicles (secondary, tertiary; September, October) relatively less dormant
g. embryo, plus caryopsis, plus hull dormancy: variable seed rain
h. early season dormancy > later season
i. 1° panicle seed dormancy > 2° or 3° panicle seed
j. early seed on a panicle > dormancy than later seed on same panicle

***Rumex crispus*, curly dock**
***Atriplex*, salt-bush genus; (spreading orache in dry US)**
-differences in dormancy
-smaller black seeds earliest produced
-larger brown seed produced later
-environmental conditions during seed formation, embryogenesis, determine the ratio of brown:black produced on parent plant

Poppy, *Papaver somniferum*

a. dormant and non-dormant genotypes: each with 3% minority
b. typical of domestication selection for genotypes expressing less (never lose all) dormancy
c. 2 types of seed dormancy: summer and winter annual life cycle dimorphism
  -non-dormant shed in fall,
  -winter mortality high depending on weather
  -but survivors in spring produce 10X as much seed as other type

***Cruciferae* family**

a. seed dehiscence: dispersal differences
  -indehiscent: closed silique, 1 seed per silique
  -dehiscent: opens, many seed per silique, soil germination quickly
b. dormancy differences

Wild oats, *Avena fatua* and *A. ludoviciana*
a. grains, seeds on spikelet different:
  -seed on end of spikelet lacks dormancy
  -below spikelet end seeds are deeply dormant

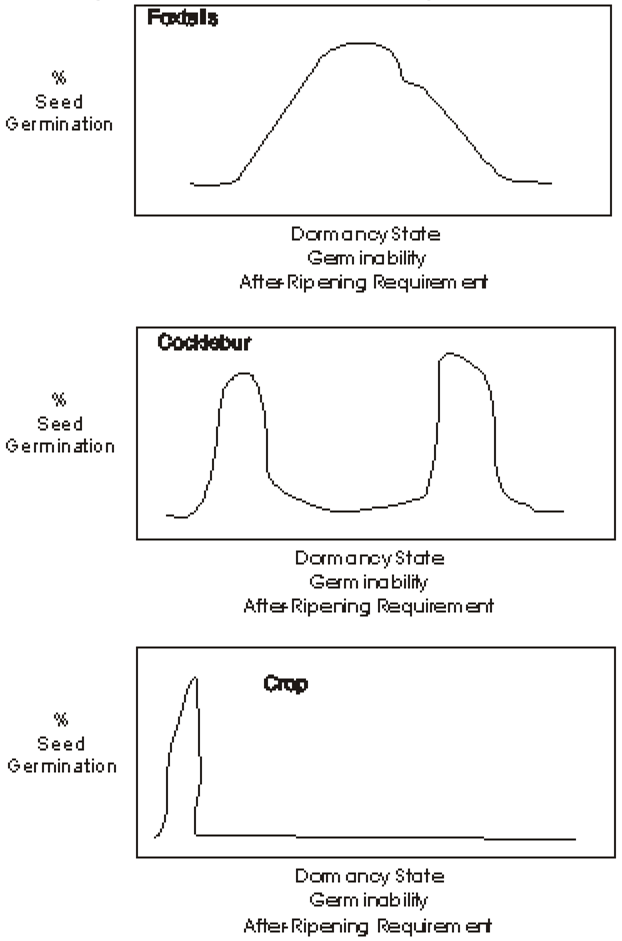
***Dimorphotheca* sp. is like other composite family sunflowers**
a. disk and ray flowers on capitulum are different
b. Gymnarrhena sp. (field marigold) is extreme case, has 2 types of flowers, flowering:
  -open flowers, small; flower when more rain available
  -closed, cleistogamous (flowering inside flower never open to outside, outside pollen) below ground when low rainfall

Velvetleaf, *Abutilon theophrasti*. Differences in seed germination based on subtle differences in weight, presumably in seed coat thickness (DiTomasso, NY)

***Polygonum* spp., smartweeds**: variable dormancy revealed by after-ripening treatment

The consequences of seed dormancy somatic polymorphism from some of these examples can be visualized in figure 7.2: foxtails: continuous dormancy phenotypes from one plant; cocklebur: discontinuous, discrete, dormancy phenotypes from capsules; crop: human selection for no/low dormancy; with consequence of increased vivipary.

Figure 7.2 Hypothetical schematic frequency distribution graphs of seed dormancy state heterogeneity: after-ripening requirement vs. % seed germination.



7.2.2.8 Observable seed dormancy-germinability regulation modes. Weed germination occurs when an individual seed embryo receives the appropriate signal to stimulate the resumption of growth. Dormant seeds require a period before actual germination can occur, after ripening.

after-ripening
1: the poorly understood chemical and/or physical changes which must occur inside the dry seeds of some plants after shedding or harvesting, if germination is to take place after the seeds are moistened (Chambers Scientific and Technology dictionary)
2: the period after a seed has been dispersed when it cannot germinate, even if conditions are favorable, and during which physiological changes occur so that it can germinate (Henderson's Dictionary of Biological Terms).

The environmental signals that stimulate weed seed germination, or any viable seed, are heat, water and oxygen. Some species have specialized physiological and morphological systems that are stimulated by light (e.g. phytochrome; sometimes also requiring nitrogen). Based on this, weed seed dormancy is regulated by the inhibition of these 3 (or 4) requisite factors.

Categories of germinability-dormancy regulation mechanisms in weeds and other plants can be distinguished based on functional, observable qualities that inhibit, modulate or regulate these requisite environmental signals. What are the different types of dormancy patterns, types, observed in weeds? What do the types tell us about the niche they are adapted to?

7.2.2.7.1 Non-dormant: unregulated heat, water and oxygen signal stimulation of germination. Non-dormant seed types, like crop seeds, do not inhibit heat, water or oxygen entry into the seed, and therefore germinate readily when these signals are present for some period of time. Kochia, galinsoga, crops (human selection). Dust-like seed: no reserves; must get to favorable food source quick or die; parasitic plants.

7.2.2.7.2 Vegetative, perinating buds: heat (and intra-plant hormonal apical dominance) signal stimulation of germination. Perennial herbaceous weed species begin growth when sufficient heat is present in the immediate vicinity of the perennating bud (rhizome, rootstock, etc.). Individual buds in an intact plant are also regulated by apical dominance along a gradient from the parent plant by hormonal control. Not shoot buds except maybe stolons. Propagule types: rootstocks (dicot perennials) (Canada thistle, milkweeds); rhizomes (grass perennial) (quackgrass, Johnsongrass); taproots (dandelion); tubers (nutsedge); corms, bulbs (wild onion) and bulblets (wild garlic).

corm: an enlarged solid subterranean stem, rounded in shape, composed of 2 or more internodes, and covered externally by a few thin membranous scales or cataphyllary (rudimentary; scale-like) leaves; not layered like an onion; e.g. crocus, gladioli

Three types of bud dormancy can be discerned.

Apical dominance in intact plant system. Auxin distribution and translocation from crown region (most dormant) to foraging ends (least dormant). For example, quackgrass rhizome basal buds most dormant in crown region which escape herbicides (no accumulation in dormant buds), and herbicide tends to translocate to ends of rhizome system. Inhibition of buds by shoot at one end; germination of tip buds, farther from shoots. Auxin suppression of basal buds while shoot and terminal buds grow. Perennial buds can be dormant while others on same plant at same time are actively growing.

Dormancy of whole system in winter, cold or frozen soil.

Dormancy of fragmented, alive bud piece due to lingering parental apical dormancy, dominance.

7.2.2.7.3 Hard seed coats: water and oxygen inhibition of germination. Gas and water tight inhibition; water entry probably naturally through morphological, chalazal slit, type structures (e.g. the chalazal slit in dicots like *Abutilon theophrasti*). Fire increases germination (see below), as does bird, animal digestion: increases seed germination with chemical action; plus crop/gizzard scarification; also can decrease seed germination, kill seed viability. Examples include:

morningglory (field and hedge bindweeds);

sunflower (Pioneer Seed Co. does commercial scarification to ensure cultivar germ;

velvetleaf (crack seed coat: heat (50°C) or sulfuric acid;

Polygonum: hard coat, scarification; cold temperature treatment requirment too;

tomato: endosperm as hard seed coat; mucilage plug in entry hole inhibits germ; soak and ferment tomato seed to open mucilage plug hard seed coat

nightshade berry, buffalobur with mucilage stickyness around seeds inside; same as tomato?

clover: scarification to increase germination: physically abraid and thin hard seed coat; acid treatment for same; 50° C heat treatment; ants chew hard seed coat.

cherry stone, apple seed, raspberry seeds all hard.

7.2.2.7.4 Light and nitrate stimulated soil surface germination. Light (phytochrome) plus nitrate stimulated, mediated, germination of weed seeds on soil surface or very shallow under dirt, or crop residues. Weed species include pigweed (*Amaranthus*), lambsquarters (*Chenopodium*), many horticultural crops (marigolds, poppies, lettuce cv. Grand Rapids), curled dock. Red, far-red forms of phytochrome; species vary and use phytochrome as switch-inhibitor in both directions. :ight levels often only need to be short duration, but light quality is important: red enriched light under canopy often turns off stimulation of germination. Light plus nitrate N (NO_3^-) often causes big boost in effect, especially in N poor soils; pigweed (*Amaranthus*) germination decreased with ammonia N form (NH_3) but nitrogen N alone has no stimulation effect. Night tillage, tractor headlights in night tillage, stimulate germination. Nightshade (*Solanum*) late season emergence in canopy holes when light strikes mid-season soil surface.

7.2.2.7.5 Oxygen and water signal restriction of after-ripening and germination. Dormancy induction, maintenance, re-induction due to restriction of oxygen (dissolved in water) availability in the seed symplast (living tissue: embryo, endosperm, aleurone layer). Germination when sufficient oxygen (dissolved in water) reaches aleurone layer, which allows respiration, metabolism to proceed in very first events of germination process (e.g. production of α-amylase). May be quite common in weedy annual grasses: interactions with seed envelopes (hulls, caryopses, embryos). Observed with weedy foxtails (*Setaria*), but may fit other species, especially grasses like barnyard grass, wild oat, cheat, jointed goatgrass, etc.

Weedy foxtails (*Setaria*). Clues available in literature before 1990: stratification (4°C, moist, dark) stimulates foxtail to germinate (and many other weedy grasses like barnyard grass). Water freely enters seed, no water imbibition uptake restriction. Therefore heat and water are available for germination, the only essential resource not present is oxygen. Another clue is that germination increased significantly when germinated in alternating temperatures. Another clue is that seed dormancy is maintained or increased with burial deep in soil. Germination increased significantly with puncturing the seed envelopes and allowing free entry of water (and oxygen dissolved in imbibition water).

What is the signal that stimulates the big spring flush of emergence? Germination and seedling emergence patterns are that the first emergence occurs in mid-April in Iowa conditions. This is a delay by several weeks after warm enough soil temperatures occur that could support germination. Why doesn't germination occur earlier, what causes the delay? Only 5-25% of seed bank germinates in any one season. During July-August seed that was ready to germinate earlier now goes completely dormant in response to high temperatures. The global distribution of foxtails around world is in the north temperate regions; in North America in northern Canadian prairies down to Oklahoma-Texas, then decreased markedly going south.

A big insight, clue, was provided by the insight that the foxtail seed is a small 'Thermos Bottle', a hard gas- and water-impereable barrier surrounding a narrow opening (the transfer aleurone cell layer, a membrane regulating water in and out) into the seed interior, the only entrance and exit for water (and oxygen dissolved in water) allowing germination of the interior embryo (T. Rost, 1971 Ph.D., ISU; pubs). Another clue provided by insight that heteroblasty, dormancy variation, arises by about day 7 of embryogenesis (an approximately 12+ day process in giant foxtail (Dekker et al., 1996?). Another clue was provided by the discovery of an oxygen-scavenging, heme peroxidase, in the seed interior.

Current understandings of these clues indicate that weed *Setaria* seed behavior (dormancy induction, after-ripening, germination) are regulated by multiple mechanisms: seed hull oxygenation; transfer aleurone cell layer regulation of water-oxygen diffusion to the symplast, oxygen scavenging protein in the symplast (Dekker, 2004).

7.2.2.7.6 Other seed dormancy mechanisms.

Incomplete embryo development at abscission.

Inhibitors. Questionable, not clearly demonstrated to be operative in experimentation. Not a dynamic mechanism if it does exist; no reversibility or adaptation to changing conditions.

Allelopathic chemicals for dormancy regulation possible, not shown.

Fire increases seed germination in many ways (see overlap with hard seed coat scarification). Pine cones released from dormancy, free seed from cone structure, with fire. Fire increases light penetration to the ground, reduces the plant canopy, makes available for light stimulation. Fire increases soil temperature. Chemicals affecting germination released with fire: fertilize emerged plants with burn products; smoke stimulated seed germination (refs). Fire can physically change seed position, change microsite around seed. Heat of fire can crack hard seed.

Interactions with soil microflora; endophytic fungi could possible affect seed or bud germination.

7.2.2.7.7. Species with multiple interacting dormancy mechanisms. In all probability, if we knew much more about weed species, the successful weed species of the world would all possess several different, interacting, mechanisms controlling seed behavior of all types. Why should a species have more than one mechanism to control dormancy and germination? The more interacting systems a species has the more able it is to respond precisely to new, changing, conditions and avoid false signals that stimulate unfit behaviors. Some examples include:

Foxtails (*Setaria*). See above in somatic polymorphism of seed dormancy and oxygen exclusion dormancy mechanism.

Polygonum, smartweeds. Hard coat, scarification; cold temperature treatment requirment too.

Solanum, nightshade. Temperature plus moisture; phytochrome system?
Amaranthus, pigweeds. Nitrate plus light.
Chenopodium, lambsquarters. Different morphology seeds: black dormant seed: cold temperatures + nitrate + light; brown less dormant seed: cold temperatures only; thinned walled seed
Alpine sp. (Harper, p.81): scarification + cold-moist stratification.
Betula sp. (beech tree): light + temperature; when chill lose light dependence.

7.2.2.8 Conclusions.

Seed dormancy experimental science considerations. An alternate title to this section might be " Beware of the seed dormancy literature" or "Why is seed dormancy science such a confusing mess?". Long experience with seed dormancy literature has left me with a skeptical approach to research. There are many reasons why this is so, but the over-riding consideration is that most of what goes on in dormancy and germination for our major weed species is unknown. The phenomena of dormancy is very complex and difficult to study experimentally. The literature is loaded with articles that make claims, conclusions that are not entirely justified because they are riddled with experimental artifacts.

Some of the compromising types of artifacts in the seed experiments include a lack of seed characterization and description (repeatability) both before and after testing for treatment effects. What was the history of seed storage, conditions, duration, etc. What was the experimental genotype, where was it collected, correct species description. To study dormancy there is a need to collect and document seed immediately after abscission to avoid after-ripening in field (e.g. Kegode and ?, ref). What is the variability of seed used, its heteroblasty, so that variation in phenotype response can be separated from variation in treatment effects. Mean behaviors mask what is going on. For this reason, studies of populations require large numbers of individuals. Germination variability is masked by data presented as bulk means (many plants, etc.) without variances. Often, researchers refuse to embrace variability of weed seed because weeds behave so differently than crop seeds ("if my c.v. is high then I must have been doing things sloppily"). Embracing this heteroblasty will open up what weeds do best, anticipate anything we throw at them, the things they have adapted to so well. Population phenomena is confused with individual behavior, again, means mask the action. Conducting studies with no model or hypothesis of what the dormancy mechanism of the species is before the experiment is designed, conducted to guide you. Germination assays done over and over with no idea what the causation is fill the libraries, what can others learn from them?

Seed dormancy conclusion. There exists no good model of dormancy, because every weed species has potentially a different means of regulating its seed life history. Until we discover those mechanisms we will not understand how weeds assemble in agricultural communities. Seed dormancy is highly variable within an individual plant, within a seed rain season, within an individual seed bank. It is this heteroblasty that makes them so successful, so highly adaptive. Dormancy is a confusing term, it confuses and obscures the mechanisms underlying behavior ("the biology of what isn't happening"). Many dormancy mechanisms in weeds, many weeds have several interacting in combination for more control of behavior. Caution should be exercised in reading the seed dormancy literature: does a study provide information about the seed history, characterization, time zero control, biotype, etc. It is hard to separate dormancy from environment, soil seed bank, recruitment

7.2.3 Propagule adaptation: post-abscission fecundity. One of the most crucial threshold events in weed seed life history is abscission from the parent plant. Prior to this time the traits expressed by the parental genome guide the new offspring's development. That relationship ends with abscission, the seed is an independent organism and important functional traits concerning propagule reproductive fecundity are displayed.

7.2.3.1 Five roles of seeds. The 5 roles that a seed has to accomplish to be fit, but these roles compete and conflict with each other for their parent plants limited resources, resulting in trade-offs:

1. dispersal and colonization [to the "right" place]
2. persistence (seed banks) (avoid mortality, predation) (longevity)
3. food reserves for embryo
4. stage in life cycle in which new genetic recombinant are released (novelty for change)
5. multiplication of parent (continue successful genotype)

Following are trait-strategy examples of how individuals accomplish these compromises among the five roles.

Dispersal and colonization: accomplished by a projectile mechanism, attachment to a vector, hitchhikers (e.g. *Oxalis* sp.); gravity; aerial traits such as wings, pappus; floating coconuts; palatability that encourages them to be eaten, moved by the vector, and excreted intact (the seed coat must be strong; obligate digestion for germination).

Persistence (seed banks): accomplished by a hard seed coat; precocious germination; dormancy; heterogeneous dormancy phenotypes; e.g. cocklebur two seeds with different dormancy; phytochrome stimulated germination.

Food reserves for embryo: accomplished by seed size; food for seedling establishment. Parasitic weeds, and real small seeds, have no endosperm, they require energy from their safe site. Kinds of seed tissues that provide food reserves include the endosperm in monocots, grasses (coconut); cotyledons for dicots. Weeds in general possess relatively small seed size, small seed reserve. Velvetleaf has relatively larger seed size, the food reserves are in cotyledons. Perennial species rhizomes provide the food for growth of the perennial propagule bud.

Stage in life cycle in which new genetic recombinants are released (novelty for change). Sexual reproduction introduces novelty. Mating systems all introduce different levels of novelty, ranging from outcrossing; dioecious and obligate outcrossers; tristylic flowers: 3 partners; gynodioecious (perfect + female flowers on same plant); clonal; self-pollenating; apomictic.

Multiplication of parent (continue successful genotype). The seed numbers produced range from lots to few; the vegetative growth of clones.

The compromises between the five roles of seed of a species involves trade-offs. The differences in fecundity, the numbers produced, is only one component that natural selection acts on. Emphasis on one role is likely to involve compromises in others.

7.2.3.2 Principle of strategic allocation. Variations in fecundity can be seen as a result of a partitioning of resources. Individual plants can't do everything at once. There exists conflicts among three things: limited time, resources, energy.

principle of strategic allocation: organisms under natural selection optimize partitioning of limited resources and time in a way that maximizes fitness: tradeoffs.

Strategic allocation in a plant is the when resources are allocated among alternative demands. These onflicting demands lead to trade-offs between different activities.

Natural selection acts to optimize the form of the compromises in such a way to maximize individual fitness (ref).

7.2.3.3 Trade-off among seed roles. The compromises between the five roles of seed of a species involves trade-offs. The differences in fecundity, the numbers produced, is only one component that natural selection acts on. Emphasis on one role is likely to involve compromises in others. "Natural selection acts to optimize the form of the compromises in such a way to maximize individual fitness". Examples of trade-offs, conflicts and compromises among the five roles of seeds in individual species appear in table 7.4.

Table 7.4 Examples of trade-offs, conflicts and compromises among the five roles of seeds in individual species.

SEED ROLES	SEED ROLE TRADE-OFFS
Multiply-number vs. disperse-colonize	•Size (weight is good for food reserves) vs. dispersal (light is good for distance). •Precocity and all its advantages (short time, less seed #) vs. dispersal timing (before and after harvesting, disperse in combine, by combine) •Seed # vs. seed size vs. dispersal: energy costs: novelty vs. food reserves vs. persistence, envelopes •Example: Kochia: low or no dormancy vs. high seed number, dispersal farther •long distance structure vs. seed #
Multiply-number vs. persistence	•size (large size is good for food) and persistence (big seed more desirable to predators)
Food vs. disperse-colonize	•Energy into dispersal structures vs. embryo or food reserve: burrs, floatation, barbs •Perennial vs annual: rhizome bud vs seed: trade-off in form of propagule and food reserve •reserves vs. #'s, •dispersal vs. ?, reserves vs. dispersal; •quackgrass: separate 2 genetic roles: seed = variability (obligate outcrosser), rhizome for multiplication of parent •perennials in general produce fewer big seeds vs. weeds with more numerous smaller seeds: opportunities and what the seeds confront differ (forest shade vs. tilled field bonanza of sites) •exception: purple loosestrife has very small seed but it is a perennial. Reason: wetland disturbed, changing water level creates new unoccupied space
Multiply-number vs. genetic variation	•seed multiplication of parent (same genotype) and genetic recombination (different genotype) •mating system = variation vs. multiply compromise •seed number (more seed #'s, more probability of new genotypes) vs. recombination ability; clonal vs. dioecious as poles of recombination •vegetative propagules vs. seeds in a perennial weed that can produce both: quackgrass (only viable seed when different genotype around with different pollen; □orpho thistle*; milkweeds*; hemp dogbane; dandelion*; creeping □orphol; johnsongrass: seed vs. rhizome trade-offs: food [*produce lots of seed that move distances in dispersal]

Persistence vs. multiply	•longevity-dormancy-seed size •seed number vs. dispersal structure that is also an anti-predator structure (e.g burr) •palatability for dispersal vs. anti-palatability chemical cost •hard seed coat (increased persistence, gravity dispersal) vs. other dispersal means (non-gravity) •physical damage, dormancy vs. multiply •envelopes at cost of numbers •predation vs. multiply; palatability, spiny stop herbivores
Persistence v. food	•seed coat (protection, dormancy) vs. embryo capital; energy in seed envelopes vs. embryo •big seed, food, attractive to predation vs. persistence
Genetic variation vs. food	•genetic variation novelty tradeoff vs. energy tradeoff
Genetic variation vs. food vs. disperse	•above interaction (variation vs. food) plus disperse: seed size and #: fewer #, less novelty released; smaller seed = more numbers = more released novelty; this relates to mating system too •hard coat for longeveity vs. energy for food •short persistence vs. low dispersal distance •large seed, short persist, low distance disperse (tropical rain forest tree strategy?)
Disperse-colonize vs. food	•energy cost for palatability: + disperse tasty, attractive, edible •predation

The compromises in maize seed show the trade-offs among the five seed roles. Consider a crop, a non-weed, and the compromises reached between the 5 roles of maize seed. Compared to a weed species or its wild ancestor, domesticated maize is less persistent; has less dispersal by itself, but more dispersal considering human actions, which is dispersal at no cost to plant, no energy; less genetic variation, especially at the population level, but variation increased by being a hybrid at each generation; increased food reserves for embryo, human selection; less multiplication of parent or increased multiplication of parent, all used as food.

7.2.3.4 Life history trade-offs. Characteristics of plants that evolution has shaped by means of trade-offs. Each individual weed species has a unique life history which is the evolutionary consequence of trade-offs between these life history characteristics; each component below affects reproduction and survival.

<u>Reproduction</u>: when they reproduce, how often they reproduce seed crops, how large the seeds are (linked to seed numbers).

<u>Birth and growth</u>: when seeds germinate, how plants grow.

<u>Mortality</u>: when plants die.

Trade-offs occur between reproduction and growth-survival, and between early flowering and later growth and reproduction. Key compromises between conflicting life history goals. Fitness tradeoffs: reproduction vs. competition vs. predator avoidance. Flowering vs. vegetative growth (precocity). Seed number vs. seed size (see following unit).

Flowering as an alternative to vegetative growth: seed production at the expense of vigorous vegetative growth. Fitness relies on both survival during vegetative growth (competition) as well as seed production. Allocation of time and energy critical, but limits of one can drive the system. Perennials and annuals can reallocate resources within the plant when changing from vegetative to reproductive: plant stature, size, nutrient and quality. Colonizers allocate more resources to repro vs. veg than those in mature habitats. The amount allocated to reproduction is plastic. Clonal growth in perennials is an alternative to seed production in annuals.

Seed production is an alternative to vegetative vigor and long life. There exists a big trade-off between two contradictory goals in plant's life history: decisions about allocating limited resources between two competing uses: seed products VS. activities that are of selective advantage in competitive environments. Trade-Off: the reproductive regime of a species, its seed production, involves allocation of limited resources between many small seeds versus fewer large seed. It is unrealistic to believe reproductive capacity is an adaptation to the rigors of environment. Strategies of growth and reproduction need to be seen as compromises between conflicting specific adaptabilities toward a general compromise in strategy that maximizes fitness. Sexual/asexual reproduction trade-off also exists (see Mating Systems).

7.2.3.5 Trade-offs between seed number and seed size.

7.2.3.5.1 Seed number. How many offspring does the average plant leave in the course of its life? The answer is one: if it was <1 it would go extinct; if it was >1 it would take over world.

There exists a very large range in the numbers of seeds produced by individual plants. This fantastic variation in the range of reproductive capacities of plants extends from 1 to 10^{10} (infinity for vegetative clone propagule production). Most weed species produce relatively large numbers of seeds. Guess-timates of seed number per plant per year from weed species projects by past student's are listed in table 7.2 below.

Table 7.2 Estimates of seed numbers per plant produced by various weed species.

SPECIES	NUMBER PER PLANT
Purslane	maximum, optimum: +200,000/plant; ave. 175,000/plant; 100 seed per flower
Kochia	12,000-14,000
Fall panicum	2,000
Nightshade	178,000 (800,000 max)
Quackgrass	Seed = 15-400; rhizome buds = 206
ladysthumb (Polygonum)	880-4010; 2898 ave.
Sequoia, redwood	109-110
multi-flora rose	200,000 per season
Amaranthus sp.; water hemp	1,800,000 per season
Ground ivy	perennial, stolons; fruits per ramet, 4 seeds per fruit; 500-900 seeds per year per ramet per plant; gynodioecious (both perfect, bisex, flowers as well as female only flowers)
Thistles	680/plant (Canada thistle) but with experimental collection losses; 4 inflorescences per stalk; 47 seeds per inflorescence; = 1955 achenes/seeds per plant
Purple loosestrife	ave. 2.5 million seeds
Johnsongrass	1 panicle = 400 seed; 2 yrs: 28,000 seeds per plant

7.2.3.5.2 Seed size.

[Add: chart for factors leading to relatively large or small seed size; like seed banks; see old exams for chart]

7.2.3.5.3 Seed size plasticity and stability. Seed size is one of the least plastic organs on a plant (phenotypic plasticity). There is a strong stability to seed size, which is a trade-off with high plasticity of seed #. For example, species with a relatively constant, stable, non-plastic seed size include velvetleaf, cotton, johnsongrass, foxtail, galinsoga, purple loosestrife, ground ivy and shattercane. Species with relatively different seed sizes include curly dock, corn, soybean, sunflower, black jack (Bidens pilosa), multiflora rose hips and seeds size varies, cocklebur and ragweed. Keep in mind though, that seed size stability in a species is scale relative. Some seeds are plastic but within very narrow range of sizes. It is harder for us to see and measure but this range can be very important; e.g. velvetleaf hard seed coat investment results in differences in dormancy (ref di Tomasso articles).

Seed size stability is a consequence of success in habitat adapted to (see below). Changes in seed size are the last, the consequence, of other tradeoffs that occur previously in development: seed number as highly plastic, allows adaptation to particular situation of individual (quantity). Seed size is a matter of scale. Small changes in seed size may not be apparent to us, but to seed small differences can have big implications. For example, in a velvetleaf study from Quebec, very small individual weight differences translated into more seed hull, hard seed coat dormancy mechanism enhanced. Experimentally we miss these fine scale size differences when we characterize seed by 100-seed weight, we miss heterogeneity within those 100 seeds. Seed size may be much more important evolutionarily than seed number. Plants initiate more seeds than they produce, abortion during development is plastic response to stresses of competition. There exists a strong stabilizing selection for one constant size, quality not compromised by quantity.

Size is related to the habitats and time in ecological succession that a species thrives in: colonizer versus stable environment (related to r vs. K selection). Seed size is a heritable trait, unlike many other organs with plastic size. There exists an optimal size for a species. The rules about seed size change with cultivated crops. Human selection can lead to different seed sizes not found in the wild progentor species. For instance, cultivated sunflower has a 6x difference in ray and disk seeds (Harper, p.669.6). Plasticity of parent plant ovary tissue (capsule, silique, etc.) size compared to the size of the seed within reveals that velvetleaf has plastic capsule seed size but little seed size plasticity. Is this plasticity difference related to developmental sequences: capsule first, flower primordial within second, seed fill and or abortion third?

7.2.3.5.4 Variable seed size. Variation can occur in seed size in some species. For example, clover with 17x differences in seed size in seeds from same plant. When seed size does change it is often an adaptive polymorphism (e.g. very small differences in velvetleaf seed weight is correlated with dormancy amount). It indicates a different allocation to both large (high investment category) and small (low investment category) seeds. Variable seed size implies 2 distinct optima (somatic polymorphism), the operation of disruptive selection (unusual for seed size) that allows it to exploit 2 different niches. For example, it is common in Compositae weeds with capitum which possess large disk flowers which disperse their seeds; as well as small ray flowers, seeds that stay with seedhead and do not disperse (also tansy ragwort, knapweed). Another example is the coffee tree with two beans per fruit. These can be 2 half rounds (don't roll, disperse down steep hills), or they can be one round and roll, disperse; or they can be 1/3 and 2/3; never uniform. Seed size not critical at low population density and competition; small and large seed competing together at high population density probably will favor the large seed size in struggle due to greater embryonic capital.

7.2.3.5.5 Relationship of seed size to habitat. There exists a seed size for a particular habitat will allow a plant the best chance for success. For early successional habitats small seed size is best in open colonizable habitats. These species must depend on own independent photosynthesis from early age. They are often more widely dispersed, and the large seed number allows rapid colonization of many available sites. Species that thrive in intermediate successional communities have larger seed size. Later successional species, like thos in woodlands and forests have the largest seeds. The large embryos, food reserves allow emergence from greater depth, survive longer, grow to more aggressive size in environments low on resources. They can devote more resources to maximize individual survival rather than fecundity. For example, Trifolium, clover, has different seed sizes depending on where in succession the plant is establishing itself.

7.2.3.5.6 Small seed size. Why do some species have relatively small seed sizes. There are many reasons, such as "because it works". Orchids, parasites like orobanche, fern species have seeds that "hunt" for place to germinate. They have no need stored energy. They all have anomalous nutrition, food arrives exactly at where they germinate. For example, early mycorrhizal association, parasitic, saprophytes. Many of these are induced to germinate when assured of food supply by germination stimulants. There small size allows them to be compared to viruses, they are just a collection of selfish genes, a bag of DNA not making a complete individual that lets the host do the work. An invalid reason to explain small seed size is that they possess a need to produce large numbers to overcome difficulty in establishing themselves with low food reserves (there is:"no survival value in death").

7.2.3.5.7 Relative weed species seed sizes.

Table 7.3 Estimates of seed size produced by various weed species.

SPECIES	SEED SIZE
perennial species	seeds and vegetative buds like rhizomes are both larger
annual species	seeds are small compared to perennials; small good for dispersal; Iowa corn field summer annuals: smaller: water hemp; larger, medium: foxtails: green, 1.5 mm length; giant, 3 mm length; bigger: sunflower
galinsoga	1.5 mm
ground ivy	1.5 x 1 mm
thistles	achene with one seed + pappus, except plumeless thistle
Circium, Canada thistle	2.5-4 mm L,1-1.5 mm W, 288,254 seeds/lb.
bull thistle	3-4 mm L, 1.3-1.6 mm W; tall thistle, 4.5-6 mm L,1.5-2 mm W;
flodman thistle	3-4 mm L , 1.5-2 mm W; mean, 3.25-4.5mm L, 1.3-1.8 mm W
Carduus, musk thistle	3-4 mm L; plumeless, 2.5-3 L; mean, 2.75-3.5mm L
johnsongrass	3 mm

7.2.3.5.8 Seed weight variation. Seed weight differences between flowering plant species can be as high as 10.5 orders of magnitude (10^{-6} to 10^{-4}; coconut to orobanche). North America weeds can have three orders of magnitude (10-5 to 10-2 g) difference in weight.

7.2.3.5.9 Seed size and number variation trade-offs. We are left with a big question about seeds and reproduction. What is the significance of these size-number combinations? Why are there these variations in reproductive capacity?

Trade-offs among competing seed factors any plant has to confront. The variation in reproductive capacity of different species seeds is a reflection of the trade-offs among different interacting features that conflict, each demanding the same limited resources available to that plant**.**

The allocation of resources between seed numbers and seed size. Three variables that determine seed number production by an individual plant is the product of 3 variables: weight of the plant (#1), multiplied by the proportion allocated to seeds (#2), multiplied by the number of seeds per unit weight (#3). Also must consider the chemical composition of the seed weight: protein, carbohydrate, lipid, other biochemical.

Size-number variation explanations. Three reasons used to explain these wide variation in reproductive capacity among plant species. Wrong: Differences in reproductive capacity reflect differences in hazards of life. Wrong: Differences in reproductive capacity are responsible for the differing abundances of organisms. Right: Variations in reproductive capacity depends on Fisher's "Fundamental theorem of natural selection".

Reason 1 is wrong. Differences in reproductive capacity reflect differences in hazards of life. Aren't there differences in seed production because some plants (weeds) face more hazards and they need to produce more seed to overcome these hazards. For example, the pigweeds produce bazillions of seeds. Most die. Don't they produce extra progeny, so that some will survive? For example, velvetleaf leaves bigger seed (more seed reserves). Don't they do this so not as many die? Darwin thought this was true. Why this is not true: all current weed species had successful ancestors, their reproductive capacity was enough to leave descendants. Seeds of all sizes die; the most numerous surviving individuals are what we have: the winners, the survivors for their particular niches. Dead seed don't contribute to future generations; leaving dead progeny isn't heritable; there is no survival value to death; there is no future in death.

Reason 2 is wrong: Differences in reproductive capacity are responsible for the differing abundances of organisms. Isn't this true? Weeds produce more numerous, small seeds than oak and maple trees do and weeds are more abundant. Darwin didn't think this was true. Seed # doesn't equal seedling #, or fitness. Abundance of a species has more to do with the abundance of habitable sites, and the genotypic and phenotypic [?] that permit a wide range of sites to be occupied. It has nothing directly to do with the reproductive capacity of the plants. Seed # in one place may mean fitness; but seed # in another place may equal death. For example, purple nutsedge is the world's worse weed, producing many nutlets, seeds and rhizomes: that doesn't help it at all in Iowa. For example, kudzu is bad weed down south, doesn't help it here.

Reason 3 is right. Variations in reproductive capacity depends on:

> **R.A. Fisher's Fundamental theorem of natural selection**: the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.

Fitness has to do with and abundance of habitable site interacting with an abundance of genotypic and phenotypic heterogeneity among the individuals of a species, allowing more opportunities for producing progeny. Natural selection leads remorselessly to an increase in the population to those forms (biotypes, variants) that contribute more descendants than their neighbors. Genotypes that produce lots of seed that are less fit will die out. Genotypes that produce seeds in any quantity that are fitter will increase over time. Therefore: the fitter genotypes will be those with the fittest combination of traits; their seed number, seed size, etc. are (by definition, by survival) the fittest traits or combinations of traits, or the fittest trade-off of opposed traits.

Fitness stems from natural selection of many competing seed factors. Those selected are trade-offs of competing factors. Those selected are compromise-collections, not individual features. Abundance (fitness) of a species has more to do with the abundance of habitable sites, and the genotypic and phenotypic heterogeneity that permit a wide range of sites to be occupied, it has nothing directly to do with the reproductive capacity of the plants.

Anecdote from Ames/ISU history: R.A. Fisher spent the summers of 1938 and 1939 here at ISU teaching statistics. He was offered a job, but decided not to make it permanent because the summers were too hot and miserable.

7.2.3.6 Weed seed role trade-off examples. Examples of trade-offs in weed development include those in vegetative versus reproduction: structures not related to reproduction. Trade-offs in perennials: roots as competititive organs as well as reproductive organs. In bamboo: mast year, when it produces lots of seed' synchronized death of parent with this mast high seed output year

Examples involved in predator defense include predation protection at expense of embryo or food reserves: produces spines, allelochemicals, hard seed to survive seed bank. Plant symbiosis: Acacia tree, legume gives energy in form of spines for ants to live in, spine holes; less herbivore attack, less other pests, less neighbor plants, all because of ants action helping tree; ants attack giraffes. Foxtail has neutral or helpful fungi on seed, in seed (endophytic): may prevent bad fungi from colonizing it (my speculation from observations). Corn and endophytic fungi (Beaeuveria ?) that colonizes inside corn seed; when corn borer larvae enters seeds fungi there and attacks, kills larvae; seed provides energy and support to fungi, gets predator protection. Size of seed: changes predator likely to eat it: larger seed easier for macro-predator, small seed easier for micro-predator; predator likely changes with size/ Alfalfa fungus attacks leaf hoppers. Thistle spine: anti-predation but trade-off with other things; spine competition cost: less photosynthetic leaf area, carbon to spine; spine reproduction cost: less photosynthate for rootstocks, propagules. Purple loosestrife has small seed: anti-predation with small seed, harder for birds to find, eat; small seed disperse to new habitat with less competition. Oak trees produce acorns, a large seed: good competitor, lots of food reserve, animals eat, bury seed, disperse to new place, less predation with high tannin, anti-feeding chemicals, hull protection, seed number less with large size, mast year syndrome (one big seed year, other low seed number years). Cacti are good competitors, waxy, drought resistant epidermis; spines for anti-predation, reproduction: waits for years for reproduction, right conditions; reproduction: vegetative and seed reproduction. Foxtail seed dormancy: anti-predation: hide in soil; emergence timing: hedge-bet; dormancy envelopes vs. embryo or more seed numbers.

7.3 Propagule Dispersal in Space and Time

Summary. The life history of a weed from the threshold event of abscission from the parent plant until just prior to seed germination and the end of the seed phase. Dispersal overlaps with recruitment.

7.3.1 Introduction.

Propagule dispersal in space and time is the consequence of the three overlapping processes of weed life history, natural selection and invasion biology (table 7.7).

Table 7.7 Propagule dispersal: processes of life history, natural selection and invasion biology underlying functional traits of weeds (see table 6.9).

PROCESSES		
LIFE HISTORY	NATURAL SELECTION	INVASION BIOLOGY
Progagule dispersal	Condition 3: survive to produce the fittest offspring	Colonization & Extinction
Spatial dispersal	Pre-Condition 1: excess local phenotypes compete for limited opportunity	Invasion
Temporal dispersal	Enduring occupation	Enduring occupation

Traits important to propagule dispersal in space and time are those that fulfill roles of propagule independence from parent plants, exploitation of available establishment sites, structures and mechanisms for spatial dispersal, and temporal dispersal in the soil to escape and exploit appropriate opportunity spacetime by the specific weed species (table 7.8).

Table 7.8 Weedy life history functional roles and traits for propagule dispersal in space and time.

TRAIT ROLES	TRAITS
Propagule independence	**Seed shattering**: commence dispersal soon after abscission
	Perennial ramet formation: ramet bud independence from parent plant; ramet-ortet ratio balance
Seize local opportunity spacetime	**Optimize propagule size and number** appropriate to amount of safe soil microsites available for exploitation
Spatial propagule dispersal: spatial foraging appropriate to opportunity spacetime being exploited	**Structures and mechanisms**: move propagules in space via: 1. Gravity: no structures to ensure local placement 2. Wind-air: pappus; wings 3. Water: flotation 4. Animal: attachment burs; attraction 5. Human: mimic crop seed
	Perennial ramet foraging: underground bud dispersal via parent vegetative tissue spatial foraging
Temporal propagule dispersal: form enduring seed pools in the soil of opportunity spacetime being	**Propagule dormancy-heteroblasty**: Responsiveness to environmental signals stimulating propagule behavior in the soil:

exploited	germinability-dormancy state seasonal cycling; germination
	Escape to survive: soil life: longevity; soil depth tolerance-preference; self-burial
	Escape to exploit: genetic resource reservoir: 1. propagules for future local and distant invasion 2. genetic foraging novelty for future out-crossing, recombination 3. genetic buffering against short-term local environment changes 4. genetic memory of successful past phenotypes

Much of the material in this section was provided by Harper (1977), Ch. 2, The seed rain, pp. 33-60; summary p. XIV. Definition:

dispersal
1: outward spreading of organisms or propagules from their point of origin or release; one-way movement of organisms from one home site to another
2: the outward extension of a species' range, typically by a chance event; accidental migration

7.3.1.1 The evolutionary ecology of dispersal. Evolution favors development of dispersal structures and mechanisms when there is a greater chance of colonizing a site more favorable than the one that is presently inhabited.

The evolution of cocklebur (*Xanthium*) dispersal is interesting. This important weeds species evolved along river banks with two dispersal mechanisms: barbed burrs (the inspiration for Velcro) to snag a macrofaunal vector, and the ability to float and move down river to a favorable establishment site. In recent times cocklebur appears in crop fields where floating (or barb) dispersal may be less important, or not at all. If barbs are not important to dispersal, over time we could predict that crop field biotypes of cocklebur would adapt to the new (non-aquatic) conditions and invest less energy in expensive dispersal mechanisms. Barbs would be reduced, as well as morphology for floating in water. It is interesting to speculate that this might have already occurred to some extent. The are published reports (ref weed sci) from Mississippi of cocklebur with five seeds per capsule. Ordinary cocklebur has two seeds per capsule. This could be evidence of adaptation to crop fields wherein more numbers of seeds (vs. size) are favored because of the many more microsites available in crop fields.

7.3.1.2 Seed dispersal trade-offs. One of the most important trade-offs an individual species makes is the allocation of resources during reproduction between seed number and size: few large or many small? The most important forces of natural selection acting on that individual species are the number of habitable sites and the speed with which they are discovered and colonized. Weeds tend to favor relatively more numbers of relatively smaller sizes because the number of habitable sites in a crop field are very large.

7.3.1.3 Cost of dispersal. Dispersibility has a cost to the plant, but not always. Energy invested in specialized structures cannot be used for more numerous seed production, or for embryo or food reserves in that same seed. The cost of these structures is a measure of the fitness advantage they confer to their ancestors, ancestors who have gained by placing descendants at a distance, rather than close by, parent. Weed species usually have no specialized structures for dispersal because distant dispersal is not the primary force of selection they face in agricultural and disturbed localities. Later succession plants (trees; shrubs; weeds like milkweed, thistles; obligate long distance dispersers: mullein, musk thistle) do invest in distant dispersal mechanisms/structures because they are often in competition with parents at the local site where they are born.

7.3.1.4 Space-time dimensions of dispersal. Dispersal of seeds is a process of discovery of habitable sites with time. Discovery depends on the spatial distribution of habitable areas and on the dispersibility of seeds.

There are the two ways, or contexts, to look at dispersal. The first is dispersal that expands the range a species colonizes and occupies. The second is dispersal that leads to increasing population size of an invading species in an area. They are both part of the process by which an established and stabilized population maintains itself. These two are parts of the same intertwined, inseparable, whole.

Seed are dispersed in four (4) dimensions: surface distance [horizontal], surface width [horizontal], soil depth and air height [vertical], and time.

7.3.2 Dispersal in space. Spatial dispersal is critical to population size and structure of a locality. Dispersal mechanisms of a plant species seed indicate how it seeks habitable sites over a patchy landscape. The numbers of an individual species in a locality are determined by the number and spatial distribution of habitable sites, the dispersibility of seeds, and the speed with which they are discovered and colonized.

Most weed species disperse their seed at the base of the parent plant (gravity), with decreasing numbers with distance from the parent ('if was good for your parents, it will be good for you'). Isolated, widely dispersed, plant populations have a different spatial dispersal structure, their seed is dispersed widely because the spatial structure of favorable sites is widely dispersed. Those species need to send their seed across the landscape to search for those favorable sites.

7.3.2.1 Dipersal and post-dispersal processes. The separate processes of dispersal and post-dispersal overlap. Dispersal clearly begins with physiological independence from the parent plant (abscission), and just as clearly is over when a seed germinates or becomes established and capable of autotrophic growth. Although, the shortest dispersal time imaginable would be vivipary, when the seed germinates while still attached to the parent plant). Seed that are initially dispersed to a location can experience post-dispersal movement, such as that caused by tillage, cropping practices, before they enter the soil seed pool (or die).

Purple loosestrife (*Lythrum*) has a complex dispersal process, complicating the difference between dispersal and post-dispersal processes. In the beginning it disperses from the parent plant and falls to bottom of open water where the parent lives (dispersal event 1). When it germinates it floats to the establishment site (dispersal event 2). *Galinsoga* begins germination on parent plant (pre-abscission, vivipary; dispersal-establishment event 1), then falls to ground with germination already begun (a head start; dispersal-establishment event 2).

7.3.2.2 Seed flux at a locality. The flux of seed into, and out of, a locality determines the potential population size and species composition of the plant community at that site. The flux at a site is a consequence of the number already there, the number that disperse in, the number that leave or die, and the replacement and rearrangement by dispersal of seed within that site. The net flux out for gravity weeds may not be quantitatively significant. The flux out for long distance dispersal mechanism possessing plants may be quantitatively important.

7.3.2.3 Modes of seed and propagule dispersal. There are six (6) modes, or ways, seeds and propagules are dispersed. They are gravity, wind and air, water, animal (non-human), human, other miscellaneous types.

7.3.2.3.1 Gravity. Most seed of our common crop field weed species have no specialized structures and mechanism (e.g velvetleaf (*Abutilon theophrasti*), weedy foxtails (*Setaria*), galinsoga, ground ivy (*Glechoma hederacea*), purple loosestrife (*Lythrum*). As such, seed falls to the ground by gravity, but other modes may act also (e.g. wind, animal, fall into soil cracks and self-plant). Most gravity seed dispersal acts to leave seed at base of parent, with decreasing numbers of seeds with distance. Seeds move as a horizon, a front away from the source. Gravity dispersal is found with weeds that favor their present site, no dispersal structures, mechanisms needed.

7.3.2.3.2 Wind and air. There are four different morphological adaptations, seed structures, for wind dispersal. Three involve an energy cost to the plant, one is for for free.

Dust. Dispersal of dust-like seed is for free, there are no trade-offs in adopting dust as a dispersal mode. Dust seed is so light it can stay up even in still air. Example species include poppies (*Papaver*), fungal spores, ferns, parasitic plants, orchids. See more discussion in later material on very small seed size. Dust seed can dissolve in water, a rain drop, and disperse that way.

Plumes. Plumes are like a feather, or feather-like structure. Examples include thistles (*Circium*, *Carduus*, etc.).

Pappus. A pappus is a circle or tuft of bristles, hairs, or feathery processes (could be plume-like) in place of a calyx. They are typical of the Compositae family (e.g. dandelion (*Taraxacum*), milkweed (*Asclepias*), sowthistles (*Sonchus*)

Wings. Wings with concentrated central mass are adapted to still air, lift and distance. They have stable flight and glide. Examples include the lianes (woody vines) and tropical forest trees

Winged seeds and fruits which rotate when they fall can have a symmetrical and asymmetrical flight which affects where fall (ex. maple (*Acer*) seeds).

Different adaptations in weeds can produce the same wind dispersal effects as these structures. Selective evolutionary pathways producing the same wind dispersal effect include a decrease in weight, and increase in the ratio of pappus to achene, improvement of the drag efficiency of the pappus, and release of the seed from a higher place. Soil surface roughness affects how far the wind can blow a seed. Wind dispersed seed tend to accumulate along fence rows, along furrows: traps. Seed can also move still attached to the parent plant (e.g. tumbleweed or Russian thistle (*Salsola kali*), tumble pigweed (*Amaranthus*), *kochia*. I observed velvetleaf (*Abutilon theophrasti*) capsules with seeds still attached to branches blowing over the snow in a Michigan crop field into the neighbors yard. Wind dispersal. A tornado can move any seed. Specialized wind dispersal mechanisms, structures, don't colonize and move as a front or horizon, but as isolated individuals over a greater distance.

7.3.2.3.3 Water. Seed can be dispersed by water in fou(r) 4 different ways.

Float. Floating seeds are ones that can have a low specific gravity seed (milkweed, *Asclepias*), or a flattened seed shape (e.g. the corky seed wings of curled dock seed, *Rumex*). Floating seed tend to concentrate on edges of water, possibly an ideal establishment site (e.g. cocklebur (*Xanthium*), waterhemps (*Amaranthus*). Coconut is a species that can float in the ocean for long distance movement, it is a heavy seed with low specific gravity.

Movement with surface water, irrigation, rivers, lakes requires a relatively higher specific gravity seed (heavy) to be borne along on fast moving water surfaces.

Flooding can have a similar effect and has a big influence on long distance movement.

Movement over soil surface with surface water (erosion). This can stir and mix seed in soil for germination, which affects formation of seed banks and can shift the distribution of seed in the soil. Slippery seed move easily over soil surfaces. An example is found with mangrove at the mouth of a river. The mangrove propagule is a stick that floats upright. It is held at the right height to germinate when it comes against the land's edge. The seed is at the bottom of the propagule stick at just the right location to germinate at the shore. Mangrove roots breathe air.

7.3.2.3.4 Animal, Non-Human. Non-human animals disperse seed if several ways.

Eating, digestability and viability by means of animal-mediated chemical and physical actions.

A seed eaten by an animal can experience different fates. It can be eaten and disperse as a viable seed, or be eaten and destroyed by digestion. Eating can also remove a dormancy factor (e.g. physical scarification by gut action, acids, abrasion, etc. of hard seed coat dormancy type species). After being eaten a seed can be dispersed with animal feces, the feces can then provide nutrients and/or a favorable microsite for germination and establishment. Some seeds are attractive to animal eating, specialized attraction structures that come at an energy cost; e.g. for pollenation. These species specific feeding patterns affect seed dispersal. Migratory birds (ducks, geese) can vector long distance dispersal. Seeds can accumulate at bird roosting sites (red cedar trees in Oklahoma). Birds sit on fences and defecate out seeds where they germinate in these protected sites. Animals can break open fruit and expose seeds for dispersal without eating the seeds. Plants can possess attractants, fruits and flowers, that draw animals to them that in turn disperse seed (Trilium has eliasomes, which ants eat with the oil body structure and attached seed after collecting).

Animal seed storage. Animals collect and store seeds as food which can affect dispersal distance, the spatial concentration of seed, and its location. Ants cache seed in their nests. When these germinate they move them out of the nest into a more favorable zone of germination. Mice cache seed. A manure pile can be a favorable germination site.

Specialized movement structures of seeds can facilitate their movement by animals. These structures include burrs (cocklebur, sandbur), spines, barbs, hooks (foxtail barley, beggarticks). Seed can become stuck to animals and fur with mud.

These three modes can lead to special spatial patterns of dispersal. These spatial distribution patterns are related to how animals move seed (e.g. clumping at a storage or defecation site such as under a fence row).

7.3.2.3.5 Human. All the dispersal modes of non-human animals above applies to humans. Humans and their technology and restless movement provide many many other ways by which seed are dispersed. Humans are arguably the best weed seed vectors on earth. Just a few examples include local dispersal with far, equipment (cultivators, tillage, combines, planters). Seed are carried along this way with mud, grain or feed on equipment too. Weeds movement as contaminants with irrigation or attached to humans by burrs, barbs, etc.

Long distance dispersal occurs in things moved around the world like in ship ballast, soil and seed, farm equipment, crop seed, grain sales, campers in wilderness areas. Waffle-tread hiking boots pick seeds up easily.

Imported crops that turn to weeds once they are introduced include *Opuntia* cactus in Australia as border plant, aquatic plants, morningglory flowers, kudzu as forage, johnsongrass as forage, hemp and velvetleaf as fiber crops, multiflora rose as border plant or hedge, *Plantana cantaria* is a hedge introduced to Kenya that is now a weed, ground ivy was a cover crop that was introduced and is now a weed. Other species introduced as crops or ornamental plants include butter & eggs (*Linaria* spp.), crown vetch, Japanese honeysuckle, honeysuckle escaped in woods as weed, purple loosestrife was once a horticultural crop, water hyacinth.

Crops with weed seed in it can be dispersed with poor combine separation, poor sieving (e.g. soybeans with nightshade seed stuck it). Weed seed in hay dispersed as it is moved. Commercial seed with weed seed contamination.

Weed seed can mimic crop seeds (crop seed mimicry). It looks like crop seed and is moved with crop seed (e.g. barnyardgrass in rice) The weed seed has the same size and shape as crop seed (e.g nightshade berries in dry beans in Michigan).

Maybe the best way a weed can disperse itself is to become a crop, or a plant that humans like (e.g. medicinal plants, ornamentals, drugs). Look at the success of maize, rice and wheat, all weeds in their day.

7.3.2.3.6 Other modes of dispersal.

Seed ejaculation disperses mistletoe and other parasitic weeds. Some rely on water potential differences in the seed and plant parts. They disperse by explosion (propulsion, click). Milkweed capsules crack and the seeds with pappus are partially ejected because the seeds are highly compressed inside the capsule. Example: fungal puffball.

Sticky seed stick to bird feet on a plant branch. Nightshade berry breaks in the combine with soybeans. The nightshade's sticky juice dries and sticks its seed to the crop seed. Rugose, rough seed sticks to mud easier than smooth seed. Other interactions of seed surfaces and soil roughness create seed aggregation traps.

Hygroscopic awns are a mechanism for a seed to self-plant itself by the twisting of awns (*Avena fatua*; *Erodium* spp.) with areas of differential water and humidity absorption.

Self-burial. The pappus or plume holds a seed in a soil crack and keeps it near the soil surface, a proper planting depth, shallow (dual role with wind dispersal). Chaff of the prairie grass bluestem allow the seed glumes around the seed to hold it in cracks, openings that are good germination positions.

Fire.

Anecdote on Dispersal: Capitalism as dispersal vector**.** In 1992 I visited the Czech Republic along Elbe River collecting weed seed germplasm. This river was a major route of grain traffic from US in the cold war years. The banks of the river and adjacent areas were covered in *Amaranthus* and *Setaria* plants that looked very similar to the biotypes I have seen in the [?] US corn and soybean fields. My host complained bitterly about these "invasive weed species" and how some people felt their introduction was a capitalist-imperialist plot to disperse weed seeds. The irony was missed by me: *Setaria* was introduced to the Americas from the Old World, an Old World invader re-invading the Old World. "What goes around, comes around" or "If you buy your grain from your neighbor you get their weeds."

7.3.3 Dispersal in time: formation of seed pools in the soil.

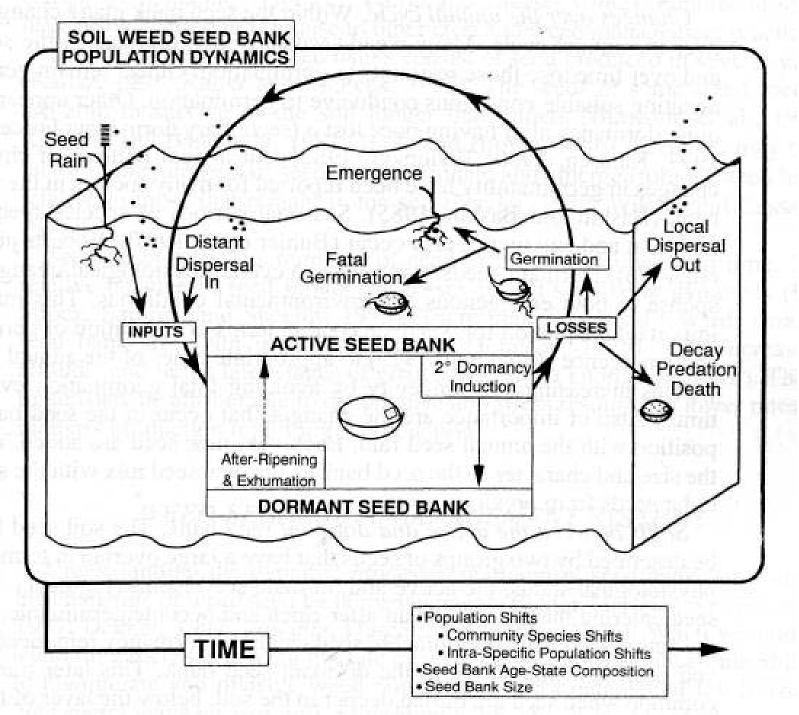
Seed are dispersed in time in several ways. Seed dormancy is dispersal in time, temporal dispersal. It provides an escape until conditions are more favorable to continue growth and development. Seeds, especially in weed species, are dispersed over seasonal time by differential times of shattering (physiological maturity on parent plant, abscission). Perennial species can disperse seed in time over several years. For example, some perennial species have 'mast' years, a year in which seed production is exceptionally high, usually followed by a several years in which production is low. Seed production in a locality varies with plant community succession, variable dispersal by time and species.

Soil seed pools, or seed banks, are seeds in the soil awaiting either death, seedling emergence, or long-term occupancy in the soil. Dormancy mechanisms are the causes, the drivers, the reasons why seed pools form in the soil (or not). The source of all future weed infestation in a locality are soil seed pools (and dispersal in from other seed pool recruits). Much of this material in the dormancy mechanism section overlaps with seed pools and recruitment, they are just different ways at looking at the same phenomena, the seed life history. Seed pools are the inevitable consequence of dormancy mechanisms. Recruitment, seed germination and seedling emergence/establishment are also inevitable consequences of dormancy mechanisms. Dormancy mechanisms, seed pools and recruitment are of a whole.

7.3.3.1 Adaptative roles of soil seed pools. Soil seed pools play five (5) adaptive roles in weed seed survival and colonization. The first role is continuity of a species in that location, a reservoir of seed for future reproduction. Soil seed pools provide a refuge for survival during periods unfavorable for growth (e.g. winter). Soil seed pools buffer the species genotype composition at that site against shorter term (e.g. yearly) changes. This results in the maintenance of successful, locally adapted genotypes and genetic variation when challenged by the vagaries of year-to-year population shifts. They also store the novel genotypes from unusual years in anticipation, pre-adaptation, of the recurrence of those conditions. The seed pool is a memory of past successful genotypes and phenotypes within and among species present in the community of that locality; prevention of genetic "drift". Lastly, seed pools are the source of variable genotypes for outcrossing within a year, a source of new genotype novelty and variability, as well as the source of seeds for invasion of other localities in the range expansion of that species.

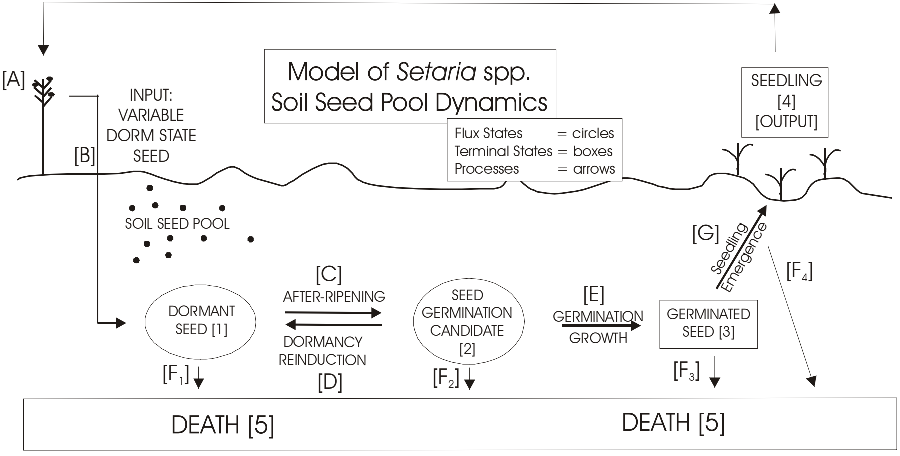
7.3.3.2 Population dynamics in the soil seed pool.

Figure 7.3 The annual life cycle of weed seed in the soil seed pool.



7.3.3.2.1 Seed states and fates.

Figure 7.4 The annual life cycle of weed seed in the soil seed pool: processes causing changes in seed states and fates with time.



[this all needs lots of work; get definitions from glossary and elsewhere]

Dormant (primary) seed: seed with dormancy from primary dormancy induced on the parent plant.

After-ripened seed: environmental signals in the soil decrease or remove primary dormancy in heteroblastic seed. Fully after-ripened seed are considered 'germination candidates', seed ready to germinate given minimum favorable conditions (environmentally enforced dormancy).

Dormant (secondary) seed. Seed that has after-ripened in the soil and then had dormancy re-induced in the soil. For some weed species dormancy reinduction can be caused by hot summer temperatures or light (phytochrome mediated dormancy).

Germinating seed. Seed in the process of germination and emergence from the soil.

Emerged seed. Germinating seed that emerge from the soil. Recruitment begins when the emerged seedling becomes autotrophic (photosynthesizes its own food).

Dead seed. Seed can die at any time, from many types of mortality, including fatal germination (death during the germination process)

7.3.3.2.2 Seed state transition processes.

Induction of heteroblastic dormancy in seed dispersed into soil. Primary, parental, dormancy differentially induced in seeds on the same plant.

Dispersal of heteroblastic seed into the soil. Movement of seed into the soil, either from local or distant sources.

Seed after-ripening. Environmental signals decreasing or removing primary dormancy.

Dormancy re-induction. Environmental signals in the soil that re-induce (secondary) dormancy in after-ripened seed.

Germination. Emergence of the seed axes (shoot and root) from the seed.

Seedling emergence. Emergence of a developing seed organ from the soil.

Dispersal out of the soil. Seed in the soil in any state can be moved physically to a new location.

Death. Mortality can happen at any time. Fatal germination is mortality during the germination process.

Factors that determine the population dynamics of an individual soil seed bank: inputs, losses and continuity.

<u>Additions to the seed pool</u>. seed dispersal into a local seed pool; seasonal seed rain of occupant plants of the community.

<u>Losses from the seed pool</u>.

Germination and seedling emergence. Once a seed germinates it is committed to resuming growth and development. It can proceed and emerge as a seedling (recruitment) or die (fatal germination). Fatal germination can occur for a number of reasons, including insufficient seed energy reserves to grow and emerge from deep in the soil, predation and herbicides (typically a layer incorporated into, or directly on, the soil surface.

Mortality. Death can occur at any time. In addition to fatal germination and herbicidal death, seeds can die from predation, decay (rotting increases with time, moisture, temperature, slow and/or stressed germination), scenscence (bury forever till die, "old age"; mutation), other chemicals (allelopathy, soil fumigants as methyl bromide, and cropping system disturbances (e.g. tillage bring seed to surface, then eaten; physical destruction by tillage equipment, other cropping disturbances).

Dispersal out of the local seed pool.

Speed of seed lost from the seed pool. Seed losses from the seed bank occur at an exponential rate in most instances. This means that when the seed pool is relatively large, large numbers are lost quickly. It also means that when seed pools are relatively small, the losses are small and the last seeds may never disappear due to the low loss rate. The consequence of this is that you never really eliminate entirely the seed pool. All it takes is one patch in a field to escape until harvest and the exponential increase in seed production that weeds possess can quickly fill the seed bank up with high numbers. The germination and recruitment losses every year are a function of the species (recruitment rate is a heritable trait in weeds). Kochia seed are non-dormant and all seeds either germinate, die or are prevented from germination by an unfavorable environment. *Setaria* seed range from 5-50% germination and recruitment depending on environmental conditions during dormancy, heteroblasty, induction and during the growing season.

Continuity in the seed pool with time. Continuity in the seed pool is provided by the dormant seed already in the pool from past seed rains. There exists an age- and dormancy state structure to this diversity.

7.3.3.3 Structure of soil seed pools.

7.3.3.3.1 Spatial distribution in the soil profile.

Depth in the soil profile. Weed seed are located, distributed, in soils horizontally and vertically. Most weed seeds fall on, are dispersed to, the soil surface (e.g. top 10 cm). Predation losses are enormous on the seed surface from macrobiotic predators as mice, beetles (e.g. carabid), earthworms, etc. Some small minority of seed become incorporated into the soil with time. These numbers are greatest when tillage incorporates them, and least in no-till production systems. The density of weed seeds declines exponentially with depth, as does microbial (seed degrading) biomass.

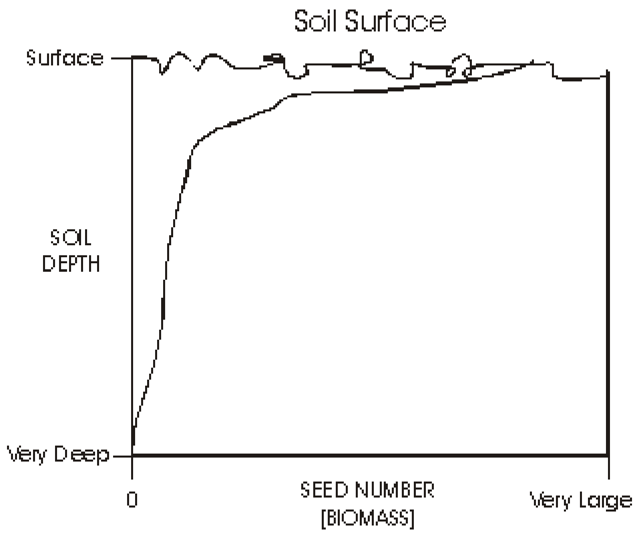


Figure 7.5 Changes in seed numbers with changes in soil depth.

Effects of tillage. The distribution of seed in the soil profile changes when tillage changes from moldboard plowing to no-till. The vertical distribution changes to a shallower seed location. Phytochrome-regulated light/nitrate requiring surface germinators are favored as they remain susceptible to light. Shallower soil depths also favor oxygen stimulated species in zones of moist surface layer soils.

Changes in tillage systems from no-till to moldboard plowed production systems result in deeper seed placement, seed distributed more evenly at many levels in the soil, seed longeveity longer (possibly due to less oxidative stress at depth). It does not favor surface germinators like light-phytochrome-nitrate types (no light signal). It does favor large-seeded dicots able to emerge from depth (more food reserve for deeper emergence), seed with hard coats are protected for soil degradation.

Seed size and depth of burial in the soil. Small seed are more likely to be found at depth. They are more likely to fall into soil cracks and holes. Movement of smaller seeds by worms and animals increase their distribution. These movements are a function of tillage, soil surface crop litter and soil type.

Horizontal seed distribution. The horizontal distribution of seed in the soil is highly variable. *Papaver*, poppy, seed are very small and are distributed fairly evenly throughout the Spanish crop fields they occur in. Most other weed species, with larger seeds, are distributed in a highly patchy and variable distribution. The horizontal distribution of weed seed in the soil may be experimentally intractable, despite numerous reports relying on sub-sampling estimates.

7.3.3.3.2 Floral seed community composition. The floral plant species composition of a seed bank is determined by several inherent biases intrinsic to the locality. It is biased by the history of past vegetation. It is biased by the weed species differences in dispersability, reproductive output (number per plant, numbers of plants), seed longevity and predation. It is biased by the weed species differences in dormancy and dormancy heterogeneity (heteroblasty). It is biased by the effects differences and heterogeneity in environmental-physical qualities of the soil niche and safe microsites of the locality.

Floral composition of soil seed pools in agro- and other eco-systems is typically a community composed of a majority subset of dominant species, and subsets of minority species. This results in a skewed distribution of species, a hierarchy of large numbers of a few dominant species and smaller numbers of other minority species. This observation of skewed distributions consisting of numbers of dominant and minority species is a common theme in the mating systems of weeds, mostly observed in herbaceous annuals, but also in a few perennial species. This theme of skewed distribution in species composition is reflected also in skewed competititive interactions in plant communities that results in skewed distributions of individual plant size within a species in a locality: a few big individuals, and a large number of small individuals.

The species that are dominant or in a minority in any particular soil seed pool varies as function of the qualities and environment of that locality. What is most typical is that this skewed hierarchy of dominant sized and numbers exists across such a wide range of agricultural and disturbed localities. Iowa corn fields dominant grassy weeds include foxtails, bromegrass, woolly cupgrass (moving north), and yellow nutsedge (sandy soils, river bottom soils). Dominant dicot weeds include common lambsquarters, velvetleaf (NE), common cocklebur, smartweeds (seasonal, depends on year), pigweeds (including waterhemp, common north of I-80; tall waterhemp south of I-80), giant ragweed (NE), and common ragweed. Minority species in Iowa are found either low numbers in lots of fields, or dominants in a few number of fields. They include the grassy weeds wild proso millet, panicums, barnyardgrass, shattercane. Minority dicot weeds in

Iowa include prickly sida (sandy soils), shepards purse, mustards, sunflower, milkweed, hemp dogbane, curly dock, nightshades and volunteer corn.

Species composition changes with a changes in tillage from moldboard plowing to no-till favor surface germinating species (light-requiring, light/nitrate requiring, oxygen stimulated), winter annuals (e.g. shepards purse), perennials, common lambsquarters (an early emerger) and the pigweeds.

7.3.3.3.3 Seed pool size. The size of a soil seed pool at a locality is a product of its qualities and environment and the species that occupy it. Seed bank size is a heritable trait of a species. Colonizing species, especially herbaceous annual weeds, thrive in disturbed localities tend to have relatively larger seed pools because there exist so many microsite opportunities to exploit and fill. Sites occupied by grazing animals tends to increases soil pool size size due to the open habitat, manure and seed, and the effects of animal trampling. Forests tend to have small seed pools. Prairies also tend to have relatively smaller seed pools because herbaceous perennials have low seed production investment relative to that invested in vegetative propagules. The common feature in these later two system types is that both are relatively stable and advanced succession communities.

Table 7.6 Qualities of relatively large and small soil seed pools.

Large Seed Pools	Small Seed Pools
annuals	perennials
colonizers	later successional species: forests, prairies
small seeded species	large seeded species
tilled fields	(versus) prairies, forests
tilled fields	(versus) pastures and hay fields
pastures (herbivory, grazing)	(versus) hay fields (biomass harvested)
acidic, poorly drained, water-logged soils	neutral, well drained soils
resource rich	(versus) resource poor

7.3.3.3.4 Seed longevity in the soil. The longevity of seeds in the soil is highly variable. Kochia scoparia is non-dormant and lives typically only one year. Velvetleaf (*Abutilon theophrasti*) can live 50 or more years in the soil. Some examples include *Galinsoga*, 1 year; lambsquarters, 1600 years in archaeological digs; purslane up to 40 years; nightshade up to 30 years, with a mean of 5-10 years; *Polygonum* 5-10 years, usually less than 5 years. Viable seed has been found in the Egyptian pyramids in jars by mummies. Lotus sp. have lasted 1,000 years. Seed longevity increases when interred in a peaty, acidic, anaerobic bog. Biennials species tend to last longer than annuals. Mutagenesis (radon, chemical mutagens, microflora toxins) can harm very old seed in the soil. The Beal experiment at Michigan State University has been measuring seed viability of some common weed seeds buried in glass jars since the 19th century, some species are still viable although the storage method is atypical of crop fields (ref).

Experimentally estimating the longevity of the seed of a species in the soil is difficult, and there are several considerations that arise because of the heterogeneous nature of the seed of a species (including heteroblasty). Although mortality is, in general, exponential with time, three different parameters are needed to characterize longevity of species in a seed pool. The longest time is that taken for the last seed of a cohort to die, this may be an atypical number when compared to the rest of the seeds. The second is the mean half-life, the time when 50% of the seed are gone. The third is how many seeds are left after year 1, year 2, etc.

Some species' soil seed banks are longer-lived than others. Natural selection acts on the longevity of a species seed in unpredictable environment.

Table 7.7 Qualities of relatively long- and short-lived seeds in the soil.

Long-lived	**Short-lived**
seed that thrive in tilled, disturbed habitats	seed that thrive in undisturbed habitats
lower soil oxygen conditions	higher soil oxygen conditions
deeper burial	shallower burial
trapped in soil aggregates	brought up from lower depths
compacted soil	loose, lower specific gravity, soil structure
acidic soil	neutral to basic reaction soil
anaerobic soil	aerated soil
cold soil	warm soil
dry soil (less oxidation, microbial activity)	wet but aerated soil
	soils whose conditions change significantly

Relatively smaller seeds tend to be longer-lived than large in soil seed pools. Most small seeded species are colonizers of disturbed habitats. There is relatively less predation of small seed by macrobiota because it is harder for birds and big animals to get gather. Larger seed size provides more stored food reserve to eat. Small seeds are easier to bury and fall down cracks to soil depth. Small seeds are more likely to be incorporated into soil aggregates, a protective condition.

7.4 Propagule Germination and Recruitment

Summary. The life history of a weed from seed to emergence from the soil and commencement of independent autotrophic growth as a seedling.

7.4.1 Introduction. Seedling emergence is called seedling recruitment.

The single most important determinant of agricultural weed community assembly, and subsequent community structure, is the relative timing of weed seedling emergence relative to that of the crop and related crop management activities (e.g. tillage, herbicide use). Seedling emergence and plant establishment are a direct consequence of the inherent dormancy of individual seeds (heteroblasty) and the environmental conditions that modulate the behavior of those dormant seeds.

Propagule germination and seedling recruitment is the consequence of the three overlapping processes of weed life history, natural selection and invasion biology (table 7.9).

Table 7.9 Propagule recruitment: processes of life history, natural selection and invasion biology underlying functional traits of weeds (see table 6.9).

PROCESSES		
LIFE HISTORY	NATURAL SELECTION	INVASION BIOLOGY
Recruitment Seed germination Seedling emergence (threshold event)	Pre-Condition 1: excess local phenotypes compete for limited opportunity Condition 3: survive to produce the fittest offspring	Invasion, Colonization & Extinction

Traits important to propagule germination and recruitment are those that fulfill roles of timing of emergence and assembly in local agricultural communities (table 7.10).

Table 7.10 Weedy life history functional roles and traits for propagule germination and recruitment.

TRAIT ROLES	TRAITS
Propagule germination timing: in the soil	**Propagule germinability-dormancy**: Responsiveness to seasonal environmental signals stimulating germination in the soil: 1. non-dormant 2. perennial species bud dormancy 3. hard seed coat dormancy 4. light-nitrate stimulation 5. oxygen-water restriction 6. other and multiple control
Seedling emergence & community assembly: number, timing and pattern to maximize subsequent local opportunity spacetime exploitation	**Seed heteroblasty**: fine-scale timing of emergence appropriate to locality
	Emergence ability: 1. horizontal: seed number-size appropriate to exploit all local safe microsites 2. vertical: emergence from depth; soil surface
THRESHOLD EVENT: SEEDLING EMERGENCE	

7.4.2 Process of recruitment.

Seedling recruitment and establishment is characterized by four events.

Loss of dormancy is the widening of the germinability 'window' of individual seeds of a species at particular times of the year, and among years.

Seed germination, once a seed is after-ripened, is determined by conditions, resources and stimuli in immediate environment. The specific environmental signals that stimulate germination in largely unknown for most common weed species, but many clues exist. The minimum requirements for all seeds are moisture, heat and oxygen. Other dormancy regulating mechanisms, signals stimulating germination, may include light-photoperiod-phytochrome, physical factors affecting seed envelopes, carbon dioxide and other soil gases, and microbial activity, depending on the species.

Seedling emergence from the soil.

Photosynthetic independence of the seed from parental seed food reserves for growth and development, autotrophic activity of its leaves.

This characterization of the seedling recruitment can be enhanced by viewing it as an evolutionary process in which disturbance in a locality creates both risk-mortality as well as opportunity space-time. Weed seed traits provide th mechanisms and means by which they can exploit opportunity space-time created by disturbance. As an example, weedy *Setaria* species are stimulated to germinate by oxy-hydro-thermal units over time. The amount of oxygen dissolved in water imbibed into the seed embryo over time determines its behavior. In the spring, cool oxygen-rich water diffuses into the seed and oxygenation of the symplast is at its yearly maxima. These oxygen-rich seeds await warming temperatures that stimulate germination in the most available seed, the numbers precisely determined by local microsite moisture and temperature conditions. As the soil warms, oxygen solubility decreases, resulting in a lessening of germination due to less available oxygen despite the favorably warm soil temperatures. As summer approaches oxygen levels are at their seasonal minima, and secondary dormancy is induced in the previously germinable seed.

7.4.3 Germination microsites. Seed germination and seedling emergence occurs on the scale of the size of the seed. Seed-scale micro-sites in the soil that are favorable are termed 'safe-sites' for germination. Safe micro-sites in the soil are very heterogeneous across a seed pool or field. They are characterized by conditions, resources and stimuli in immediate environment conducive to germination. They are habitable sites that avoid or reduce the risk of predation and decay. The qualities that make a site safe vary by the requirements of each individual species and seed. The qualities safe for a surface germinating species differ from those of deeper germinating species. For example, surface germinators place more reliance on seed shape and seed structures for favorable soil-water contact.

7.4.4 Patterns of seedling emergence. The pattern of seedling recruitment is a heritable, phenotypic, trait: seed dormancy capacity at abscission. Local adaptation of heteroblasty in an individual weed allows that species to maximize its time of emergence for maximum fitness, an ecological hedge-bet.

Several modal patterns of seasonal seedling emergence can be observed among common weed species. The timing of emergence may be over an extended, or in a relatively short, period.

Single 'flush' period. Perennials often have new shoots that appear early in spring. Winter annuals emerge in the fall before they overwinter. Precocious species germinate immediately after leaving parent plant. Seeds without dormancy all germinate soon after shed. They may also be delayed by winter conditions (enforced dormancy), but germinate in a flush when conditions are favorable. Opportunistic emergence occurs when seeds are regulated by enforced dormancy, only awaiting the right conditions to germinate. Some species require a specific event or specific environmental signal for germination to occur. These simple signals may include a fire event, a rainfall event (e.g. desert plants), disturbance, or light (e.g. nightshade germination stimulated by light through an opening in the surrounding leaf canopy). In all these instances of a single germination event, the range of emergence times might be only apparently narrow.

<u>Continuous emergence</u>. *Bidens pilosa* germinates anytime in the tropics. Conditions in some areas are relatively constant all year and may be conducive to continuous emergence. Crabgrass (*Digitaria*) emerges continuous all year in turfgrass and home lawn habitats.

<u>Major period of, followed by an extended period of infrequent, seedling emergence</u>. This may be the most typical pattern of seedling emergence in many temperate region agro-ecosystems. In Iowa, as well as most major grain producing areas of North America, a large number of weed seedlings are recruited in the spring, followed by much smaller numbers of seedlings for the remainder of the season until the soil freezes again. Typical emergence pattern for the foxtails, lambsquarters and shattercane.

<u>Bi-modal recruitment</u>. Dandelion (*Taraxicum officinale*) has two times of seedling emergence, spring and fall flushes.

<u>Relative emergence order</u>. In any particular agricultural area there are certain weed species that appear consistently over time. Their relative abundance, and dominance or minority status, in a field can change but they are present in soil seed pools and compose the weed floral community of that area. There exists a consistent relative order of emergence in the growing season over time, and this emergence sequence is a consequence of the traits these weed species possess. For example, in Iowa the following table has been proposed:

Table 7.9 Relative seedling emergence order for the common weeds of summer annual crops in Iowa and adjacent areas. Source: Buhler and Hartzler, Leopold Center for Sustainable Agriculture.
[add Julian weeks, set up for foxtail and LQ calendars, with disturbance, etc.]

PREVIOUS AUTUMN	**EARLY SPRING**	**< TIME OF SEASON >**					**LATE SPRING**
GROUP 0	**GROUP 1**	**GROUP 2**	**GROUP 3**	**GROUP 4**	**GROUP 5**	**GROUP 6**	**GROUP 7**
horseweed, marestail	foxtail barley	quack-grass	smooth brome	Canada thistle	green foxtail	black nightshade	fall panicum
downy brome	kochia	orchard-grass	common ragweed	giant foxtail	common milkweed	shattercane	crabgrass
field pennycress	prostrate knotweed	giant ragweed	woolly cupgrass	common cocklebur	hemp dogbane	common sunflower	morning-glories
shepard's purse	wild mustard	Penn-sylvania smartweed	velvetleaf	yellow nutsedge	wirestem muhly	□orpho mallow	jimsonweed
biennial thistles	dandelion	ladys-thumb smartweed	wild buckwheat	redroot pigweed	barnyard-grass	waterhemp	witchgrass
wild carrot	Russian thistle	common lambsquarters			yellow foxtail	smooth ground-cherry	
dandelion (from seed)	white cockle	wild oats			wild proso millet	Jerusalem artichoke	
		hairy night-shade					
PREVIOUS AUTUMN	**PRIOR TO PLANTING**		**ABOUT PLANTING TIME**			**AFTER CROP PLANTING**	

These particular species appear when they do for many reasons, some inherent in the species seed in the seed pool (e.g. seed dormancy heteroblasty), others a consequence of the micro-site and environmental qualities of the locality.

Much could be revealed about the process of weed community assembly if this list was analyzed in terms of traits that affected both the relative emergence timing and pattern, but also the traits that made the species at an advantage in emerging when it does relative to the neighbors that had emerged prior, at the same time, and later in the season. For instance, *kochia scoparia*, kochia, has no inherent seed dormancy and emerges very early in the season (group 1). It is apparently cold-tolerant of those early conditions, but does not appear to be display vigorous growth and photosynthesis as species that emerge later. Kochia's growth traits are a trade-off between early emergence stress tolerance and low growth/photosynthetic growth rates.

7.4.5 Relationship between seed heteroblasty and recruitment timing. [glean kari III. for story here]

7.5 Weedy Adaptation to Neighbor Interactions in the Local Community.

Summary. The life history of a weed from seedling to flowering plant.

7.5.1 Introduction.

[Also: this chapter is about the consequences of community assembly begun at planting and weed seedling recruitment times: reap what ye have sown]

Once the weed seeding has emerged from the soil and established itself with photosynthetic, autotrophic, growth and development its life becomes markedly different. Life in the soil is harsh, but relatively interactions with neighbors are few. Once established as a vegetative plant the interactions with neighbors will dominate the life history of a weed plant until it dies or reproduces.

This chapter is divided into four parts to emphasize three different ways of understanding the vegetative plant and its interactions with neighbors. The first is about spatial and temporal foraging beginning with the newly emerged plant. In the second, the influences on the plant population density, morphological form and the diversity within its community are discussed. In the third, the forces of selection that act on community interactions is presented. In the fourth, the mechanisms that operate in neighbor interactions are explored.

Weedy adaptation to neighbor interactions in the local community is the consequence of the three overlapping processes of weed life history, natural selection and invasion biology (table 7.11).

Table 7.11 Neighbor interactions in vegetative growth: processes of life history, natural selection and invasion biology underlying functional traits of weeds (see table 6.9).

PROCESSES		
LIFE HISTORY	NATURAL SELECTION	INVASION BIOLOGY
Vegetative growth Neighbor Interactions: Growth-Development Stress Responses	Pre-Condition 1: excess local phenotypes compete for limited opportunity Condition 3: survive to produce the fittest offspring	Colonization & Extinction

Traits important to weedy interactions in the local community are those that fulfill roles of adaption to resources, conditions, plant structure, life history timing, response to stress and offensive capabilities against those neighbors; considerable overlap exists between these role categories (table 7.12).

Table 7.12 Weedy life history functional roles and traits for weedy adaptation to neighbor interactions in the local community.

TRAIT ROLES	TRAITS
Neighbor adaptation to resources	**Nutrients**: 1. early acquisition 2. luxury consumption **Water**: 1. early acquisition 2. water use efficiency **Light**: 1. canopy, branch and tiller photomorphogenesis **Gases**: 1. C3/C4/CAM leaf physiology

Neighbor adaptation to conditions	**Heat**: 1. cool temperature growth 2. hot temperature growth 3. temperature tolerance **Terroir**: maximize/optimize location conditions
Neighbor adaptation by plant structure: phenotypic plasticity and somatic polymorphism to maximize/optimize exploitation of resources and conditions	**Shoot structure**: 1. shoot architecture; branching and tillering 2. photomorphogenic responses 3. leaf structure and polymorphism; canopy formation **Root structure**: 1. root architecture **Root-shoot partitioning** **Perennating structure**: 1. spatial foraging 2. food reserve accumulation & partitioning 3. bud dormancy **Biennial plant form**: 1. overwinter structure (rosette) 2. spring structure (elongation) **Crop mimicry**
Neighbor adaptation by life history timing	**Early establishment**: 1. rapid acquisition of seedling autotrophic growth 2. rapid early growth **Mid-growth**: 1. high growth rates **Late vegetative/early reproductive**: 1. timing of tillering and branching 2. scenescence timing **Escape neighbors by life history timing**: 1. biennial plant life history
Neighbor adaptation by response to stress	**Poison tolerance to**: 1. herbicides 2. alleochemicals **Environmental tolerance to**: 1. physical injury recovery; regeneration; meristem location 2. grazing 3. salt; minerals 4. resources: drought; shade 6. conditions: heat, cold, freezing
Neighbor adaptation by offensive ability against neighbors	Allelopathy Climbing growth habit Host for neighbor diseases and self-tolerance Anti-grazing

7.5.2 Spatial and temporal foraging.

[Add here: Spatial foraging (ramet vs. genet; height vs. lateral) = phenotypic plasticity: separate topic, mechanism; perennial vs. annual; ??; ramet vs. genet: plasticity of individual parts birth-death, harper p.21]

1. New section somewhere in this reorganized chapter on **spatial and temporal foraging** by annuals and perennials. Begins with ramet extension and foraging, parent as disperser of buds into soil.
2. "Seed dispersal mechanisms, as well as perennial weed ramet foraging, set the scale to a plant populations spatial heterogeneity. They are the means by which the plant "reaches out" to contact neighbors. They determine the selection pressures the plant will meet. This topic will be more fully developed in Chapter 9, the life history of the vegetative plant." [harper page 774-775]
3. <u>Dispersal mechanisms set scale to a plants spatial heterogeneity</u>. These determine the selection pressures they will meet. Dispersal mechanisms sets the scale to the species spatial diversity, these are all about how the plant "reaches out" to contact neighbors. Three (3) ways plants sense the spatial diversity of their environment: how dispersal sets the scale of a species's spatial diversity. [harper page 774-775]
4. Spatial foraging (ramet vs. genet; height vs. lateral) = phenotypic plasticity: separate topic, mechanism; perennial vs. annual; ??; ramet vs. genet: plasticity of individual parts birth-death, harper p.21:

The form of the plant (genet) determines the way in which it meets its neighbor.
Definition:

genet: a unit or group derived from asexual reproduction from a single original zygote, such as a seedling or a clone

ramet:
[add ramet? place to introduce spatial foraging?]

A clonal colony or genet is a group of genetically identical individuals (e. g., plants, fungi, or bacteria) that have grown in a given location, all originating vegetatively (not sexually) from a single ancestor. In plants, an individual in such a population is referred to as a ramet. In fungi, "individuals" typically refers to the visible fruiting bodies or mushrooms that develop from a common mycelium which, although spread over a large area, is otherwise hidden in the soil. Clonal colonies are common in many plant species. Although many plants reproduce sexually through the production of seed, some plants reproduce by underground stolons or rhizomes. Above ground these plants appear to be distinct individuals, but underground they remain interconnected and are all clones of the same plant. However, it is not always easy to recognize a clonal colony especially if it spreads underground and is also sexually reproducing (Wikipedia, 5.08).]

<u>Space</u>. Different plant parts experience different environmental aspects of the habitat; for example, rhizomes and roots vs. lower leaves and stems vs. upper leaves and stems. Seed dispersal mechanism determines range of environmental heterogeneity that is sampled, e.g. most weeds are gravity dispersal; limited dispersal, a narrow range of local dispersal may be appropriate for some plants: why waste seed on exploring variable , unfavorable habitats; long range wind dispersal can allow wide range of habitats. Mechanism of pollen dispersal determines range of environment that is sampled; pollen travels farther, larger spatial genetic spread.

7.5.3 Plant density, plant form and community diversity.

"Neighboring plants interfere with each other's activities according to their age, size and distance apart. Such density stress affects the birth rates and death rates of plant parts. As plants in a population develop, the biomass produced becomes limited by the rate of availability of resources so that yield per unit area becomes independent of density-the carrying capacity of the environment. The stress of density increases the risk of mortality to whole plants as well as their parts and the rate of death becomes a function of the growth rate of the survivors. Self-thinning in populations of single species regularly follows a 3/2 power equation that relates the mean weight per plant to the density of survivors. Density-stressed populations tend to form a hierarchy of dominant and +/- stressed subordinate individuals. The death risk is concentrated within the classes of suppressed individuals." Harper (1977): summary, p. xvi; Ch. 6, pp. 195-235.

"The effects of density do not fall equally on all parts of a plant. In general the size of parts (e.g., leaves or seeds) is much less plastic than the number of parts (e.g., branches). The stress created by the proximity of neighbors may be absorbed in an increased mortality risk for whole plants or their parts, reduced reproductive output, reduced growth rate, delayed maturity and reproduction. The term density is used in a special sense here, to signify the integrated stresses within a community rather than the number of individuals per unit area" Harper (1977): summary, p. xvi; Ch. 7, pp. 195-235.

7.5.3.1 Influences of plant density and growth on yield. Density stress is the integrated stresses within a community produced by neighbors on each other, and includes plastic growth and well as the altered risk of death. The population-like structure of an individual plant also responds to density stress: varied birth and death rate of parts, leaves, branches, flowers, fruits; unlike animals (numbers).

7.5.3.1.1 Density-yield response. There exists a relationship between the yield of dry matter per unit area and the density of plants per unit area (e.g., *Bromus* sp. at 3 levels of N fertilization; Donald 1951). Early in growth, and at low numbers of plants per unit area, the number of plants and yield are directly, linearly related. With time, and/or greater numbers of plants per unit area, the yield per unit area becomes independent of plant number: a saturated yield, the holding capacity of that space ("law of constant yield"; Kira et al., 1953). Variations in sowing density are largely compensated for by the amount of growth made by individual plants. The population's apparent behavior is that of an integrated system, reacting independently of individuals, with individual behavior subordinate to that of the population.

7.5.3.1.2 Plant-to-plant variation. Plants growing under density stress have a skewed distribution of individual plant weights. Skewing of the frequency distribution (numbers of plants versus weight per plant) increases with time and with increasing density (plants per unit area). At harvest a hierarchy of individuals is established: a few large dominants and a large number of suppressed, small, plants. There exists a danger in assuming that the average plant performance represents the commonest type, or most typical, plant performance.

The place an individual occupies within the hierarchy of a plant population is largely determined in the very early stages of plant establishment and development (the critical role of relative time of emergence). The weight of an individual is a function of its starting capital (the embryo plus some part of food reserve weight), the relative growth rate of the genotype in the environment provided, the length of time for which this growth rate is continued, and restrictions on the rate or time of growth imposed by the presence, character or arrangement of neighbors in the population.

The "percentage emergence ranking" is an index of the position in emergence ranking an individual occupies in a population "sown" at the same time. The amount of growth made by an individual is more directly determined by its order in the sequence of emergence than by the actual time at which it emerges, or the relative spatial arrangement of neighbors. The greater time that it has been allowed to grow allows it to capture more opportunity space. The earlier emerger has been able to capture a disproportionate share of environmental resources, with a corresponding deprivation of late emergers. Once a difference between neighbors has been triggered, it becomes progressively exaggerated with time (especially when competition for light is the dominant mode of interaction among neighbors). Pre-emption of space (resources) by developing seedlings is seen below (Ross, 1968).

7.5.3.2 Influences of plant density on mortality. Definitions:

density dependence: a change in the influence of an environmental factor (a density dependent factor) that affects population growth as a population density changes, tending to retard population growth (by increasing mortality or decreasing fecundity) as density increases or to enhance population growth (by decreasing mortality or increasing fecundity) as density increases

density independent factor: any factor affecting population density, the influence of which is independent of population density
There exist two categories of mortality: density-independent and density-dependent:

density-dependent mortality: the increasing risk of death associated with increasing population density

density-independent mortality: the increasing risk of death not associated with population density change

Pre-emption of space (resources) by developing seedlings in a plant population (Ross, 1968), density-dependent mortality, is also called "self-thinning". "Alien-thinning" is density-dependent mortality in one species that can be ascribed to the stress of density of an associated species. An example of density-independent mortality is the risk of death to a seedling from being hit by a raindrop or hailstone.

Population density may act to enhance seedling establishment. The positive effects are usually restricted to early stages of germination and establishment. Most density responses are negative: reduced plant size or increased death risk. There are regulating properties of increasing mortality risk with increasing density, the buffering action against unrestrained population increase.

The risk of death often assumes a slope of -1.5 (the "3/2 power law). This rule says that while the number of individuals is decreasing, the weight of the population as a whole is increasing. The rate of growth of individuals more than compensates for the decrease in numbers. The risk of mortality does not change with age. There is a constant risk of death. This also holds true for plant parts on an individual plant.

Self-thinning is mortality due to density stress of neighbors of the same species. Mortality is greater in high fertility environments. Survival is greater in high light regimes than in low light regimes. The mechanism of self-thinning is not understood. The individuals most likely to die are the smallest and weakest.

Populations derived from large seed suffer more rapid mortality than those derived from small seed. The faster-growing, larger, more vigorous seedlings produce a more intense density stress among themselves than in populations of the same density but from smaller, slower growing, seedlings.

7.5.3.3 Influence of plant density on form and reproduction. Higher plants are plastic in size and form. This plasticity derives from the population-like structure of individuals. The form of repeating units of plant construction (leaves and flowers) is tightly controlled and changes only slightly over a wide range of environments. The number of these units, and thus the size of the whole plant, varies greatly with both age and conditions.

The dry weight of a plant population compensates more or less perfectly with variations in density, but the parts of individuals are not altered to the same extent. The growth of individuals under density stress results in differential allocation of assimilates between different structures, and resulting differences in the size of those parts. For example, the ratio of seed total dry matter changes with density stress. High density results in more reproductively inefficient plants. The optimal density for a particular product (seed, storage root, latex, etc.) may be different than that density for dry matter production. For example, the optimal population size for maize seed yield is less than that for silage.

Density stress is generally expressed in a reduction in number of plant parts produced (branches, flowering nodes) and in part by organ abortion (death of old leaves, abscission of flowers and pods). An example of this density stress is observed in wheat. Stable vegetative parts include height, leaf width, stem diameter, and number of spikelets per spike. Plastic parts include branching (tiller formation). Stable reproductive parts include grains per ear and mean weight per grain. Plastic components include fertile tillers per plant (ears).

There is no reason to believe density stresses resulting in plastic plant responses act any different than those responses to the shortage of supply factors (moisture, nutrients, light, etc.) that exist independent of population size.

7.5.3.3.1 Plant form and diversity of a community. One of the elements contributing to the diversity of plant populations, community structure, includes that that arises from the growth form of the individual plant. Harper (1977) said that the "growth pattern of a genet can itself impose order of diversity on a plant community".

The most likely contact between plants in a field, in a very local community, is among parts of the same individual. Take the individual plant's point of view. The nearest neighbor of a plant part (a leaf) is another such unit on the same plant (another leaf on the same plant). The most contact and interaction is with other parts of same plant self. The next most likely contact is with other plants of same species. This situation is altered in viney, upright, spreading or prostrate plants whose most likely contact is the plant it is climbing over.

Examples of plant form diversity, somatic polymorphisms include mulberry trees with two different types of leaves (somatic polymorphism), co-existence and cooperation amongst different plant parts of the same individual. The upper leaves are smaller and lobed allowing more light penetration. The lower leaves are larger, with no lobes allowing more light capture.

Johnsongrass underground organs are rhizomes that have buds, which allow shoot axis emergence for lateral exploitation and foraging for space. These rhizomes are also the root system for nutrient and water absorption.

Soybeans have three different types of leaves for different functions at different times of its early life history: cotyledons, unifoliates, 1st trifoliate. Weedy grasses typically have several leaf types, beginning with the seed embryo coleoptiles, first true leaf, and the various leaves of the several potential tillers of a plant.

The form of the plant may be such that it avoids contact over time, avoidance of intra-specific competition. For example, winter annuals form rosettes in autumn, then a leafy upright flowering stalk the next spring (e.g. shepard's purse). Biennials act similarly.

Plant community patterns are determined by the morphology of branching in plants. For example, Indian cucumber growth and development gives an intraspecific community (a monoculture) its distinct structure. Rhizome buds emerge at certain angles in the soil, this leads to characteristic, specific patterns of spatial structure and foraging in the field.

7.5.3.3.2 Phenotypic plasticity and somatic polymorphism. [reference earlier discussion] Means plants that are stuck in one location have to change their form, size, to fit local conditions (in real time). Phenotypic plasticity is an immediate, short term response to local conditions. Somatic polymorphism is constitutive, genetic, hence a longer term, non-plastic adaptation.

7.5.4 Forces of selection acting on the plant community. J.L. Harper, Population Biology of Plants (1977) developed the way of understanding plant community dynamics and competition for the point of view of the forces of selection acting on them.

"The study of population biology ought to display those forces that are important at the level of the life of the individual and what sort of variation is important in determining survivorship and reproduction."

"...to pick from knowledge of the population biology of plants those forces that, on a local scale, seem likely to dominate the chance that an individual will leave descendants. The scale is local because natural selection acts on individuals in the context of their immediate experience."

The forces of selection have been described as (i) directional selection ... (ii) stabilizing selection ... and (iii) disruptive selection... These broad categories of selective force are in a sense statistical rather than biological categories; the biological categories need to take into account the nature as well as the direction of selection. A number of generalized biological categories can be recognized."

7.5.4.1 Biological categories of selection. Harper (1977, pp. 753-776) presents several important environmental, community or phenotypic selection forces driving population variability. Each of these is presented elsewhere in this book (Life History, Neighbor Effects). These forces of selection increase population variability. The six categories of selective forces driving diversity are:

1] genetic variation within species with different mating/breeding systems (see Mating Systems);
2] forces of selection acting within populations of plants (speciation, r and K selection);
3] selection for ecological combining ability;
4] selection by the activity of predator and pathogens;
5] evolutionary consequences of crashes, cycles, and catastrophes (disturbance selection); and
6] selection in a patchy environment.

[make this subsection organization clearer; the last 2 or 3 are not developed, so direct reader here to those previous section and drop them from the end of this subsection]

These forces of selection drive population variability. This conflicts with the discussion of selection presented below as a factor decreasing population genetic variability. Can selective forces both increase and decrease genetic variability, depending on the factor and context?

7.5.4.1.1 'r' and 'K' selection.

<u>r-selection</u>. Selection for the qualities needed to succeed in unstable, unpredictable environments, where ability to reproduce rapidly and opportunistically is at a premium, and where there is little value in adaptations to succeed in competition. A variety of qualities are thought to be favoured by r-selection, including high fecundity, small size, and adaptations for long-distance dispersal. Weeds, and their animal equivalents, are

examples. Contrast with K-selection (q.v.). It is customary to emphasize that r-selection and K-selection are the extremes of a continuum, most real cases lying somewhere between. Ecologist enjoy a curious love/hate relationship with the r/K concept, often pretending to disapprove of it while finding it indispensable. Dawkins (1999).

Example: Arabidopsis; "live fast, reproduce quick, die young". Winter annuals are r: the main struggle is with winter survival. Autumn emergence is relatively easy with no competition. In the spring they bolt and set seed before competition starts. Environmental stress is the biggest challenge.

Example: Kochia is first to emerge, and is adapted to more dry areas (environment is the main challenge). It’s a wimpy competitor with subsequent weeds. It's an exception to competitive exclusion where the first seedlings up capture resources preferentially. r selection favors: fecundity, precocity, allocating resources mostly to seed, colonizers after crash or new invasion.

Space-time is key: environmental competition most important; time is key: quick; no premium on competition; poor predator defense.

<u>K-selection</u>: Selection for the qualities needed to succeed in stable, predictable environments where there is likely to be heavy competition for limited resources between individuals well-equipped to compete, at population sizes close to the maximum that the habitat can bear. A variety of qualities are thought to be favored by K-slection, including large size, long life, and small numbers of intensively cared-for offspring. Contrast with r-selection (q.v.). The 'K' and 'r' are symbols in the conventional algebra of population biologists. Dawkins (1999).

K selection: "live slow, reproduce slow, die old"; redwoods; put effort into competitive vegetative body; perennials (veg reproduction + seed reproduction)is more a K strategy; biological, density-dependent, competition is more important than environment; invest in competitive body first, seed investment second; favor competition over precocity & fecundity.

<u>Population biology symbols</u> (Silvertown and Charlesworth, 2001):

r in population biology, the intrinsic rate of increase

K_i the maximum sustainable density of a species in a mixture. Subscripts denote different species.

7.5.4.1.2 Selection for ecological combining ability. Darwin said competition was greatest within a species; because of the similarity in habits, constitution and structure intra-specific struggle is the most intense. Selection and adaptation lead to avoidance of competition between population if enough time elapses. Allard and Adams (ref) indicate that selection in mixed populations favors genotypes with superior ecological combining ability (good neighbors and good competitors). It is exactly this selection pressure for combining ability that makes me feel that niche space for organisms in a habitat is "infinite" (mites feeding on mites on mites, ad infinitum). Biological competition in a locality is what is most important (in the inseparable selection force of biological community and environment). Darwin said that in a new habitat with the same environment the conditions of life are changed in an essential way. Darwin also said that the structure of an organism is related in an essential way (although it may be hidden) to that of the other organisms with which it competes or preys upon (neighbors define what you are).

<u>Ecological combining ability</u>. Selection can lead to a species adaptating to avoid competition. Co-existing forms that are selected together over a long time are less

competitive with each other than they are with new unselected variants entering the locality.

Niche diversification. Selection may favor a divergence in behavior between populations so that each makes less demand on resources needed by the other.

Mechanisms to avoid competition.

Time: different life history timing, resource use. Example: horseweed (*Erigeron*): summer annual and perennial forms. Example: musk thistle: summer annual and biennial forms. Example: dandelion: summer annual, winter annual, biennial, perennial forms.

Space: all these examples are cases in which species avoid direct conflict and competing for the same resources at the same time. In these examples the genus, species does better in mixed stands than if alone.

EX: Dioecious species: the different sexes avoid competing with each other.

EX: erect (Polygonum erectum) and prostrate knotweed (P. aviculare): genus does better in mixed stands than one species alone; edges of high traffic walkways on campus; see seasonal succession: low forms, then high.

EX: giant, green, yellow, knotroot foxtail in Iowa fields. Genus does better in mixed stands than if only on foxtail species alone. It is known that they exist together in same field, presume occupy slightly different niches for greater genus-level exploitation of field.

EX: Velvetleaf in soybeans: velvetleaf does better in soybeans than alone in pure stands; individuals and individual plant parts die readily when shaded (by other velvetleaf plants); soybeans individuals and leaves will not die very readily when shaded (unlike VLF).

EX: Fescue populations, some better in mixtures with barley than alone.

EX: Clover (trifolium): legume-grass associations. Locally adapted populations have evolved with neighbor genotypes. If they are placed in new habitats with new neighbor genotypes of the same species they do not do as well.

7.5.4.1.3 Selection by predator and pathogen activity. Harper (1977; p. 768-9): "An individual plant that is more prone than its neighbor to attack by pathogens and/or predators will almost inevitably have lowered fitness. The variety of ways in which a host may gain resistance, immunity or a degree of tolerance to such an attack immediately defines equivalent ways in which the predator or pathogen might counter the defence. Just as in the coevolution of competing species at the same trophic level, any change in one component immediately changes the selective forces acting on the other."

Susceptibility to predation lowers fitness; resistance to predation increases fitness. There exists a dynamic interaction: changes in R (or S) brings about changes in selection acting on the other. Definitions:

pathogen: parasite which causes disease

pathogenesis : the course or development of a disease disease: any impairment of normal physiological function affecting all or part of an organism, esp. a specific pathological change caused by infection, stress, etc. producing characteristic symptoms

predator

1: the consumption of one animal (the prey) by another animal (the predator) (carnivore)

2: also used to include the consumption of plants by animal (herbivore), and the partial consumption of a large prey organism by a smaller predator (micropredation) (parasites; parasitoids)

Examples of animal predators includes birds eating seeds, grazing on vegetative and seed tissues (cows, insects), tapeworm, lamprey eel .

Examples of pathogens includes soil microorganisms on roots and seeds, aerial shoot attack.

Evolutionary arms race. The Red Queen (Alice in Wonderland, Lewis Carol) needs to keep running just to stay in same place and not fall behind . The evolutionary relationship of neighbors: co-evolution of mechanisms of defense and offense; each elicits response, a new trait to counteract, in neighbor or predator/pathogen. For example, herbicide resistance in weeds.

Corn borer to Bt transgenic corn cultivars, Bt insecticide (lepidopteran) in corn pollen. Monarch butterflies much more prefer milkweed in corn field compared to milkweed in other habitats. Monarch butterflies eat milkweed leaves with Bt pollen on leaves: they eat poisonous Bt pollen. Only the last generation of monarch butterfly is exposed to Bt pollen, previous generations have no exposure; USDA estimates 0.2% of butterfly population exposed. The corn borer (lepidopteran crop pest) can develop resistance to Bt (arms race); can monarch develop R to Bt corn?

Examples of feedback mechanisms (changes in R and S). Feedback from plant to insect:

-plant makes allelochemical to stop insect feeding; insects that survive become resistant to chemical survive. Delayed diapause in corn rootworm result of selection in corn-soybean rotation. Rootworms wait in soil for 2, 3 years until corn replanted in soil, then the larvae hatch and eat corn again. Changes in environment affect seed adaptation in seed bank to fungi and pathogens: seed spend the longest time of their life cycle in the soil. Different soil types, drainage and water availability affect which fungi around, affects favorable microsite for a seed if it is to survive without pathogen attack and death: the pathogen diversity drives weed diversity. Seed bank seed adaptation to birds and predators: they can aid dispersal by passing seed unharmed through their digestive tract; attractiveness of seed to predator may influence this process; bird-seed coevolution.

7.5.4.1.4 The evolutionary consequences of disturbances. See discussion in disturbances and the creation of opportunity space, chapters 5-6.

[these next 2 seem to go together; combine? reorganize whole area?]

7.5.4.1.5 Selection in a patchy environment. See discussion in diversity in community structure, chapter 5.

7.5.4.2 Maximizing fitness in a spatially variable environment.

[add here conventional selection categories: e.g. disruptive; or refer to previous section]

Seven (7) categories of solution to the dilemma of maximizing fitness in an environment (physical-biological) that varies in space and time. Utilize unused resources and fill a niche better. Find and occupy new opportunity space.

Four genetic ways when confronting spatial diversity (4 mechanisms, at 4 increasing levels of variation). Formation of local specialized races: demands inbreeding. Development of genetic polymorphism with large blocks of linked coadapted genes or supergenes. Maintenance of high degree of genetic variance within a population, coupled with longevity or soil seed banks providing memory of past adapted genotypes. Act of speciation and the formation of distinct breeding groups that can evolve independently.

Two phenotypic ways when confronting spatial diversity. Development of somatic polymorphism: not a response to the local environment. Single genotype develops a variety of phenotypes, each adapted to a different time or space phase of community. For example, leaf polymorphisms between seasons or ages of a plant (different times, different needs); cotyledon, unifoliate, trifoliate leaves of soybean. For example, seed polymorphism: different seed germination phenotypes shed by one plant into seed bank; seed dormancy phenotypes of cocklebur seed capsule. Evolution of phenotypic plasticity: changes in response to the local conditions. The individual responds directly to the conditions it experiences; genes triggered directly by environment.

Phenotype-Genotype way (5th genetic way). Evolution of heterozygotic superiority: succeeding generations meet alternating conditions; only heterozygote can produce progeny good in both conditions.

7.5.4.3 Biodiversity, complexity and community stability.

[vs. sustainability]

[compromise with earlier section on stability]

"There is no comfortable theorem assuring that increased diversity and complexity beget enhanced community stability; rather, as a mathematical generality, the opposite is true. The task, then, is to elucidate the devious strategies which make for stability in enduring natural systems. There will be no simple answer to these questions." May, R.M (1973).

Is increasing agroecosystem, cropping system, diversity better, more stable, more sustainable? Does increasing biodiversity inherently lead to a stable agroecosystem, a stable ecosystem?

Counter-arguments to increased biodiversity include: monocultures decrease insect and disease biodiversity, lest substrate is available, reduced choices. Complex, multi-species, cropping systems in turn favor different weed species; the presence of many different weed species provides locally available seeds when an opportunity arises which change; "balanced" seedbanks with many species poised for explosive growth provides this opportunity.

For example, in a North Dakota study (WSSA 2002; abstract 141, p.40-41) when 1964 and 2000 wild oat populations compared from same locations, there was an increase in diversity in time to more herbicide resistant (R) and multi-R wild oat genotypes. 26 years of selection occurred with the introduction and use of many old and new wild oat herbicides in that period. By 2000 the genotype fractions of each R biotype were similar: many different R genotypes were poised for whatever management (herbicide program) the grower would use. Is this biodiversity good?

Stability is illusory in plant communities. Forces driving patchiness and community diversity also make it unstable. Predator-prey relationships go through wild flucuations. Disturbed, agroecosystems, community structures go through big changes.

“It is difficult to give a clear answer to this question. The relationship between species diversity and ecosystem stability seems to be controversial. Some literature says more diverse communities lead to greater stability because they contained a greater abundance of individuals. Relationships between diversity and stability tended to be weak, because more diverse communities contained higher densities of individuals. As diversity increases, population stability is predicted to decline while the stability of aggregate community properties should increase. Anyway, if we consider cropping systems in this point of view, monoculture decreases insect and disease biodiversity, less substrate is available and reduced choices. While complex, multi-species cropping system favor different weed species. Therefore, stability is illusory in plant communities. Forces driving patchiness and community diversity also make it unstable.” (A.Taab, 4.07)

7.5.5 Modes of neighbor interaction in the community.

From ch.3, differential use of resources-conditions: p.61:

The presence of a plant changes the environment of its neighbor, affecting the growth and form of both. Neighbor interactions can take many modal forms, including competition, interference, coexistence and cohabitation and synergism, topics developed in Unit 5 on neighbor interactions.

Such neighbor effects brought about by proximity of individuals is called interference. Interference by neighbor plants causes effects due to consumption of resources in limited supply, allelopathy (production of toxins), and changes in conditions (e.g., protection from wind, behavior of predators). There can also be stimulatory, beneficial, effects of neighbors.

The struggle for existence among weed plants starts at the seedling stage, sometimes earlier, sometimes a little later. Once emerged weed plants grow rapidly and begin to interact with nearby plants (neighbors), either of the same species in the population or with other species (weeds, crops, other plants of the community). As they grow several things happen simultaneously: the compete for limited amounts of resources; their plant number density affects their growth and development; their presence acts as a feedback influence on subsequent seedling recruitment.

The mechanisms of interaction among weeds and crops can be also grouped into several general categories.

7.5.5.1 Preferential tolerance to environmental poisons.

[relative to that of your neighbor]

[add directions to herbicide resistance section]

7.5.5.2 Interference. Competitive ability: superior growth rates; internode elongation for enhanced height. Aggression and offense: nutrient luxury consumption: common lambsquarters; allelopathy; parasitism (e.g. dodder; Orabanche).

7.5.5.3 Coexistence-cohabitation-synergism. Escape and avoidance: ecological combining ability and niche diversification; life history timing (e.g. recruitment timing, seed dormancy); spatial patterning. Tolerance and defense: of stress: crop mimicry; herbicide resistance; shade tolerance; anti-feeding mechanisms: chemical, structural (e.g. spines).

7.5.5.4 Modify the environment. Interactions dominate most field situations, and the search for unique factors of competiton (beyond death or reduced growth) may not be very sensible. Plants modify the environment of their neighbors by changing conditions, reducing the level of available resources or by adding toxins to the environment. These effects can be demonstrated in artificial populations, but demonstrating them in the field has not been successful.

"Plants may modify the environment of their neighbors by changing conditions, reducing the level of available resources or by adding toxins to the environment. All these effects can be shown quite clearly to operate in experiments with artificial populations, but there are probably no examples of plant interactions in the field in which the mechanism has been clearly and unambiguously demonstrated. Interactions dominate most situations that have been analysed in the field and the search for unique factors of competiton may not be very sensible. Death or a reduced growth rate are often attributable to competive interactions, but interpretation of competition in the field may depend on the recognition of much more specific symptoms." (Harper (1977): summary, p.xvii-xviii; Ch. 11: pp. 347-381).

7.5.6 Experimental characterization of weed-crop interactions.

[from p97, ch 7 intro: The life history of an annual weedy plant consists of several discrete threshold events, events that can provide strong experimental inferences in life history studies: anthesis, fertilization and zygote formation, abscission from the parent plant, seedling emergence time and death.]

Attempts to understand the nature of weed-crop interactions is difficult, if not impossible. Experimentally we attempt to ascribe the success of one weed over another, or over a crop, to a particular morphological feature, a particular pattern of life cycle, or a simple physiological trait. The chance that a seed will produce a plant is affected in many ways by the presence of another plant, including the following.

Resource interference; light: reducing light intensity; changing light quality; water: transpiring limited water; changing humidity profile; nutrients: absorbing limited nutrients; providing limited nitrogen; gases: reducing CO2 or O2 levels, or their ratios in the local atmosphere; temperature: altering the temperature of the seed environment.

Predation: sheltering or excluding predators (or sheltering predators of predators); favoring or reducing pathogenic activity; encouraging defecation or urination in the neighborhood; providing rubbing posts or play objects and so encouraging local trampling.

Direct interference, soil activity: raising the soil level (accumulation of organic matter, litter); liberating selective toxins (allelopathy); changing the soil reaction

Predators are influencing the germination of seed in this field. Many other factors are contributing to the interaction of these plants including the rocky soil environment, the soil pH, the soybean plants ([get picture] below, top), the quackgrass plant ([get picture] below, lower left) and atrazine residues around the hole. Determining the exact mechanism of interaction between plants (seeds) in this spot in the field would be very difficult and complex experimentally.

Comparisons of particular factors influencing the interaction of species is very difficult, and will usually not reveal the nature how they affect each other. Correlation between individual factors is the best we often do experimentally. Differences between plants and species include small and large contributions, the size of those factors is often hard to determine. The summation of the contributing factors to a plant-plant interaction is often greater than the individual components: synergistic phenomena emerge as a non-linear consequence of their mutual interaction.

The methodological problems of evaluating the nature of plant-plant interactions is revealed by the problems posed in answering component questions, each themselves involving complex interactions. Does the interaction take place above or below the soil surface? Does the interaction take place because a plant changes the environment of its neighbors? Does the interaction take place because a plant deprives its neighbors of resources? Does the interaction take place because a plant produces toxic chemicals (or toxic chemical conditions) that harm or kill its neighbors? Conversely, does it take place because a plant can resist or tolerate a toxic chemical?

Chapter 8: Model Representation of Weed Life History Behavior

[Add here: Pop growth demography; Silver, Harper p.2-3, 20-29; harper p.25 why demography is doomed; growth vs. reproduction p.26-27]
[LIMITATIONS OF DEMOGRAPHIC MODELS: Harper, 1977; pp. 25-26]
ADD: Develop fully ideas and organization from harper 77, p.1-30
ADD: Notes on Modeling: manuscript started after Denmark Modeling workshop
ADD: describe demographic repro lamda model here, from both harper and silvertown (first book may be better)

Summary.

> "The existence of two levels of population structure in plants makes for difficulties, but the problems are much greater if their existence is ignored. One of the strongest reasons why a population biology of plants failed to develop alongside that of animals was that counting plants gives so much less information than counting animals. A count of the number of rabibits or *Drosophila* or voles or flour beetles gives a lot of information: it permits *rough* predictions of population growth rates, biomass and even productivity. A count of the number of plants in an area gives extraordinarily little information unless we are also told their size. Individual plants are so "plastic" that variations of 50,000-fold in weight or reproductive capacity are easily found in individuals of the same age. Clearly, counting plants is not enough to give a basis for a useful demography. The plasticity of plants lies, howerever, almost entirely in variations of the number of their parts. The other closely related reason why plant demography has been slow to develop is that the clonal spread of plants and the break-up of old clones often makes it impossible to count the number of genetic individuals.
>
> The problems are great: they can be regarded as insoluable and a demography of plants an unattainable ideal, or they can be ignored with a certainty of serious misinterpretation, or they can be grasped and methods, albeit crude, developed to handle the problem.
>
> The way in which the problem can be faced is to accept that there are two levels of population structure in plant communities. One level is described by the number of individuals present that are represented by original zygotes (genets, e.g. seedling, clone; Kays and Harper, 1974). Such units represent independent colonizations. Each genet is composed of modular units of construction – the convenient unit may be a shoot of a tree, a ramet of a clone, the tiller of a grass or the leaf with its bud in an annual."
>
> (Harper, 1977; pp. 25-26)

8.1 Introduction

Weedy and invasive plants perform the plant colonization niche. Weedy plants are the first to seize and exploit the opportunity spacetime created by human disturbance, notably in resource-rich agricultural cropping systems. The urge to understand and predict weed life history behavior with time has provided a strong scientific and practical motivation for the development of these models. Weed models are tools with the potential to provide improved scientific understanding of changing weed populations, including insights into the biological functioning of these plants, and prediction of future life history population dynamics. Weed modeling can also provide practical support for crop management decision making, including evaluation of weed management tactics and strategy, risk, economics and efficacy. Modeling can also be a less expensive means of providing information compared to that of field experimentation. Much progress has been made to realize the potential of weed modeling, but much remains undone.

The basis of most current weed models is quantitative and demographic: comparisons over years of the numbers and sizes of plants per unit area at different times of their life history. The current state of affairs, including limitations of current demographic models, have been featured in two recent reviews in Weed Research (Holst et al., 2007; Freckleton and Stephens, 2009).

The opportunities and limitations of models arise from the manner in which weeds and their life histories are represented, the inferences that can be derived from the informational content of the models, and the consequences of these factors on the ability of the model to predict future behavior. The purpose of this review is to assess the limits and potentials of two different, but compatible, types of weed population dynamics models: demographic, and those based on functional phenotypic traits and the biological processes of natural selection, elimination and evolutionary adaptation. Models of both types are assessed in terms of how they represent weed life histories as well as ability to infer and predict future behavior based on their inherent informational content.

8.1.1 Weed life history models. A model is a representation of reality. It is inherently an abstraction and a simplification. It is a conceptual framework of a system constructed by indicating which elements should be represented and how these elements are interrelated. This conceptual framework then is translated into algorithms, precisely defined step-by-step procedures by which dynamics are carried out. What elements should be represented in a weed population dynamics model? The first, most important element is a group of plants of one weed species occupying a local habitat. This population is usually isolated to some degree from other populations, but local populations over spatial scales of landscape to global interact (e.g. gene flow) with each other to form metapopulations. It is the local population, the deme, that is the unit of evolution. Populations change with time. Population dynamics are changes in the quality and quantity of member phenotypes, as well as the biological and environmental processes influencing those changes.

What conceptual framework can best represent the interrelationships among members of a population? One crucial component of any conceptual framework of weed models is the life history of the weed species: “The life cycle is the fundamental unit of description of the organism.” (Caswell, 2001). Holst et al. (2007) also conclude that “Almost all models consist of a number of life cycle stages, nearly always including at least seeds, seedlings and mature plants.” (figure 1).

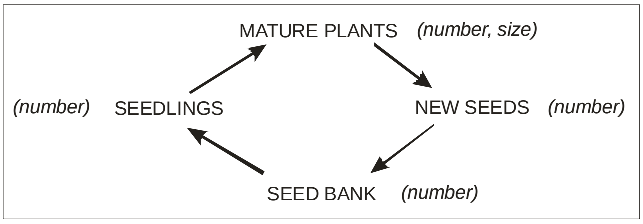


Figure 8.1. Representation of the an annual weed species life history by discrete life history phases, or states (mature plant, new seeds, seed bank, seedlings) and the metrics

used for their measurement (number, size); arrows represent transitions between states; redrawn from Holst, Rasmussen and Bastiaans, 2006.

A weed population dynamics model is a representation of the phenomena of a weed population's life history growth and development, from fertilization to death. The model in figure 1 represents weed life history phases as discrete phenotypic states of the individual organism with growth. The demographic form of a life history model is quantifiable, with measurements of changes in phase state pool number and sizes with time, often expressed on a unit area basis. What this model does not contain are the deterministic biological processes that drive growth and development during life history. These uncharacterized processes are represented as transitions between quantitative state pools (figure 1, arrows).

8.1.2 Demographic weed life history population dynamics models. Representations of weed life history population dynamics have largely been accomplished using demographic models (big refs: FieldWeeds; Intercom; Natalie Colbach models; see papers in Weed Res reviews):

> "The essence of population biology is captured by a simple equation that relates the numbers per unit area of of an organism N_t at some time *t* to the numbers N_{t-1} one year earlier." (Silvertown & Doust, 1993, p.1)

From this perspective, weed population dynamics can be represented in its most essential form by this function describing the interrelationships of elements:

$$N_t = N_{t-1} + \mathrm{B} - \mathrm{D} + \mathrm{I} - \mathrm{E}$$

Where: N_t, number per unit area organisms at time *t;* $N_{t-1,}$ number per unit area organisms one year later; B, number of births; D, number of deaths; I, immigrants in; E, emigrants out. Schematically translating this demographic function onto figure 1 reveals four potential life history state phases, or pools, and the relationship of the life history to its complementary metapopulation (I, E), as well as to mortality (D; figure 2).

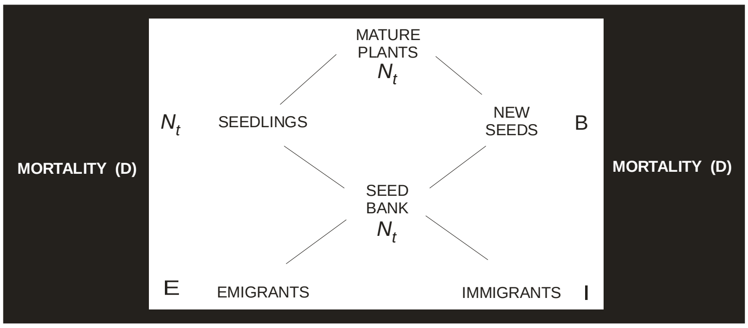


Figure 8.2. Demographic representation of an annual weed species life history by quantification (number, size) of discrete life history states (mature plant, new seeds, seed bank, seedlings); population size influenced by metapopulaton immigration and emigration dispersal events into and out of the soil seed pool; arrows represent transitions between states.

Weed population dynamics are algorithmically represented by the calculation of lambda (λ), the rate of population size change over one generation where: $\lambda = R_0$, net reproductive rate,. rate of population increase over a generation; $\lambda_t = N_t / N_{t-1}$, annual population growth rate, finite rate of increase. The finite rate of increase for a population is also expressed as a measure of *W*, so-called Darwinian fitness. The most common formulation of weed population models is as an iterative equation with next year's population calculated from that of the current year (Holst, et al., 2007). The rate of population change over several generations is schematically represented in figure 3.

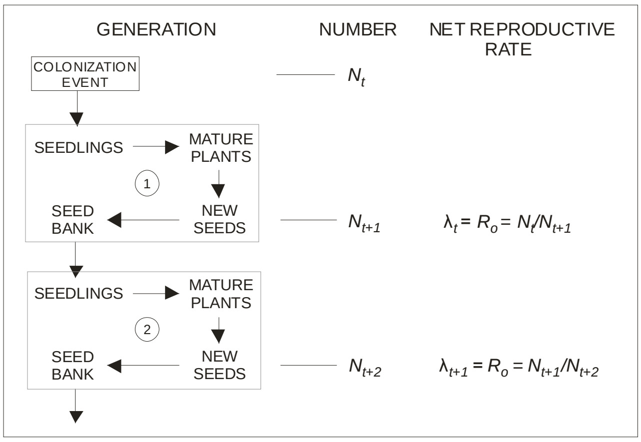


Figure 8. 3 Change in numbers or organisms per unit area (N_t) with life history generation time (N_t, N_{t-1}, etc.) and associated net reproductive rates ($\lambda = R_0$) per generation (1, 2, 3, 4).

The simplest form of demographic models presented above has been refered to as the "standard population model" (Holst et al., 2007; Sagar and Mortimer, 1976). This simple form has been expanded and extended in several ways (Colbach, InterCom, etc,; the big weed model refs here). Variation on this basic theme include genetic or spatial components or aspects. The primary amplification of these demographic models occurs in increased attention to life history states: seedling recruitment, mature plants, new seeds and the soil seed bank. Interactions among plants is typically expressed in terms of final biomass of crop and weeds at harvest, with various shortcuts utilized predict the outcome in terms of yield. In most models the outcome of this process is simply reflected in a single competition parameter, which is kept constant over the years. Stochasticity is introduced in some of the models to generate a more irregular population development. [other uses of stochasticity?] Quantification of new seed is based on fecundity per unit area, and is derived in various ways (Holst et al., 2007). Little is said in Holst, Rasmussen and Bastiaans (2007) about soil seed pools, which appear to be equated with quantities of old and new seeds, immigrant and emigrant seeds, all with similar or uniform qualities.

Given that the current state of the art of weed population dynamics modeling is represented almost entirely with demographic models, what inherent properties of quantitative models provide the ability to predict future weed behavior?

8.2 Representation and Information, Inference and Prediction

The opportunities and limitations of models arise from the manner in which weeds and their life histories are represented, the inferences that can be derived from the informational content of the models, and the consequences of these factors on the ability of the model to predict future behavior.

8.2.1 Representation and information. Information is the meaning given to data (facts, norms) by the way in which it is interpreted. It is a message received and understood.

> "Information is revealed in the correlation between two things that is produced by a lawful process (as opposed to coming about by sheer chance). Information itself is nothing special. It is found wherever causes leave effects. What is special is information processing. We can regard a piece of matter that carries information about some state of affairs as a symbol: it can "stand for" that state of affairs. As a piece of matter, it can do other things as well, physical things, whatever that kind of matter in that kind of state can do according to the laws of physics and chemistry." (Pinker, 1997).

Information can be viewed as a type of input important to the function of the organism (e.g. resources), causal inputs. Information is captured in the physical structure of the organism that symbolize things in nature and that respond to external stimuli allowing causation. Information exists in the physical and physiological structures that capture the way a complex organism can tune itself to unpredictable aspects of the world and take in the kinds of stimuli it needs to function (Pinker, 1997). A good example of biological information taking a physical form is the genome, the informational content of DNA. Closer to home for weed modelers, it is contained in the functional traits of a weed phenotype. Functional traits, such as seed dormancy capacity (e.g. see discussion below on seed heteroblasty), respond to the environment in a particular manner during life history to maximize survival and reproduction. Information can take other forms too.

For weed modelers, what is information? How is information represented in a weed model? Different models contain differing amounts of useful information, the basis of inference and prediction. Inference and prediction are restricted to the informational content of the model.

In the demographic model presented above, the phenotypic identity of weed plants in a local population is represented in their numbers and sizes in spacetime. The informational content derives from the meaning and interpretation given to the numbers and sizes of plants of a particular weed species observed in a particular place, at a particular time (season, life history phase). These metrics provide no information about causation or dynamics. Causation can be inferred indirectly if the same plant in the same location is observed at a later time.

In the evolutionary model presented below, phenotypic identity and informational content are contained in the variation in germination-dormancy capacities induced by a parent plant during embryogenesis, seed heteroblasty. Seed heteroblasty is information physically captured in the structure of the various seeds. It is the behavioral blueprint that responds to specific environmental signals in the soil resulting in seedling emergence carefully timed to the historical occurrence of predictable cropping system disturbances (e.g. herbicide application, tillage, harvesting). Seed heteroblasty is the physical information encoded in the morpho-physiology of the seed, it is the cause and determinant of its subsequent life history. It acquired this preadapted physical information by the processes of natural selection-elimination over time. Causation for its life history can be directly inferred from a seed germination assay at seed abscission.

Evolutionary models represent weed life history dynamics in a local population by capturing the physical and behavior information contained in functional traits of the individual weed phenotype that respond to specific environmental signals, opportunity spacetime, in a manner that optimizes their fitness in terms of survival and reproduction.

A complementary way of measuring informational content of a weed model is provided by algorithmic information theory, which measures the information content of a list of symbols based on how predictable they are, or more specifically how easy it is to compute the list through a program. A symbol is an entity with two properties glued together. This symbol carries information, and it causes things to happen. When the caused things themselves carry information, we call the whole system an information processor, or a computer. The processing of symbols involves arrangements of matter that have both representational and causal properties, they simultaneously carry information about something and take part in a chain of physical events. Those events make up a computation (Pinker, 1997).

[Algorithmically, it is a set of rules that provides an accurate and complete description of a life history capturing its key properties. It provides an algorithmic, or computational, means of forecasting the future behavior of that life history.]

Weed phenotypes contain these 'symbols' in the physical form of the functional traits they possess. For example, the DNA coding for the multiple traits of phenotypic plasticity in a weed species is information. It is a physical algorithm computed by the phenotype at every step of its life history that results in its current form and function closely tracking the environmental signals it receives in the local community. Model representations can contain algorithmic forms of this type of information: step-by-step recipes that will, when given an initial state, proceed through a well-defined series of successive states, eventually terminating in an end-state.

A truly dynamic weed population model then would be one that incorporates model algorithms that specify the life history steps a phenotype will go through given an initial state (e.g. seed heteroblasty; time of emergence), as modulated by the specific environment encountered by the individual phenotype in a local population. The biological foundation of these model algorithms is the manner in which specific functional traits are represented.

Evaluating a weed population dynamics model should include a search for its informational content, specifically its representation of the biological traits of the phenotypes of a local population that determine its life history trajectory to survive and reproduce.

8.2.2 Inference. Inference is the process of reasoning from premises to a conclusion, a deduction. The primary premise, or assumption, of demographic models is that the essence of population biology is captured by a simple equation that relates changes in numbers of organisms per unit area of space with time (Silvertown and Doust, 1993). With this premise, what inferences can, and cannot, be derived from a demographic model of weed population dynamics? A critical review of demographic models reveals a dearth of informational content, flaws in its representation of the deme and life history developmental behavior, and insufficient model formalization.

8.2.2.1 The deme. Several fundamental flaws are associated with the way the local population is represented in demographic models. The first artifact is the confounding effects of plant, as opposed to animal, population structure. The second derives from how unique individual phenotypes in the local population are represented. The third arises from population membership changes with time that compromise assumptions of covariance structure.

8.2.2.1.1 Population structure. The local population, the deme, is the fundamental unit of biological evolution. The deme consists of unique individual phenotypes, the unit of natural selection. Of crucial importance is how these two components of any weed population dynamic model are represented. Plants respond in a highly plastic manner to locally available opportunity. Unlike animals, plant quantification fails to capture the qualities of the population that drive future dynamics. Demographic weed models that fail to represent this structural nature of plant populations are therefore compromised at conception. John Harper (1977, pp. 25-26) warned of this fatal flaw in weed models:

> “The existence of two levels of population structure in plants makes for difficulties, but the problems are much greater if their existence is ignored. One of the strongest reasons why a population biology of plants failed to develop alongside that of animals was that counting plants gives so much less information than counting animals. A count of the number of rabbits or *Drosophila* or voles or flour beetles gives a lot of information: it permits *rough* predictions of population growth rates, biomass and even productivity. A count of the number of plants in an area gives extraordinarily little information unless we are also told their size. Individual plants are so “plastic” that variations of 50,000-fold in weight or reproductive capacity are easily found in individuals of the same age. Clearly, counting plants is not enough to give a basis for a useful demography. The plasticity of plants lies, however, almost entirely in variations of the number of their parts.”

Demographic representation of the structure of a local plant population depends therefore on the specification of the number of individuals (level one), and on the number and variability of parts (e.g. leaves, axes) of each individual (level two).

8.2.2.1.2 Individual phenotypic identity. Natural elimination acts by nonrandomly selecting the fittest individuals in the local population. Changes in demes therefore are an adaptive reflection of the unique biodiverse qualities of those survivors. Weed models are critically evaluated for their ability to represent individual phenotypic identity by means of their functional properties. Weeds assemble in local communities as collections of unique phenotypes. The urge to simplify their representation by categorical or average qualities obscures this biodiversity.

> “The assumptions of population thinking are diametrically opposed to those of the typologist. The populationist stresses the uniqueness of everything in the organic world. What is true for the human species – that no two individuals are alike – is equally true for all other species of animals and plants. Indeed, even the same individual changes continuously throughout its lifetime when placed in different environments. All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and the statistics of variation. Averages are merely statistical abstractions, only the individuals of which the population are composed have reality. The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is the abstraction and only the variation is real. No two ways of looking at nature could be more different.” (Mayr, E. 1959)

Demographic representations of weed populations are limited to the extent that numbers of plants fail to provide information of the qualities of their members. The demographic representation of weed population dynamics is an incomplete abstraction because it ignores the importance of phenotypic variation by averaging behaviors at experimentally convenient times in life history. Measurement of quantities and sizes of uncharacterized phenotypes, and the uncharacterized processes of transitions between life history states, provide little inherent inference of population dynamics.

8.2.2.1.3 Local population dynamics. The third, and possibly the most telling, artifact of demographic representations of populations arises from the changing phenotypic structure of the local community with time. Natural selection eliminates lesser fit individuals to the enrichment of the survivors. As such the phenotypic-genotypic composition of the deme is constantly changing with time. During the growing season mortality alters the composition of the population. The population genetic structure of a local soil seed pool is different every year with the addition of offspring from those favored individuals. As such, demographic models represent populations as constant qualitative entities. Causation cannot be inferred from plant numbers that consist of different individual phenotypes. Inferences derived from them are incomplete as the assumptions underlying population covariance structure are violated. Covariance is a measure of how much two variables change together, for example plant number with time. The phenotypic membership of the local deme and soil seed pool changes as natural selection favors some and eliminates others. Natural selection violates this covariance structure by assuming the individuals are the same at each life history measurement time in the local habitat.

8.2.2.2 Life history development and behavior. Strong inferences of weed population dynamics can be made when the functional traits driving individual phenotypic behavior in local population are represented. Some of the most important functional traits of weeds are found in individual plant polymorphism and plasticity.

8.2.2.2.1 Life history states and processes. Demographic models represent weed populations by quantifying numbers of plants, their sizes and their density per unit area of space at discrete times in their life history. Lacking is a representation of the developmental growth processes that cause transitions between life history states to occur (arrows, figure 1). Demographic models do not embrace the dynamic processes causing weed life history, despite the claim that "Processes governing the transition from one stage to the other, like germination and seed production and processes responsible for the losses that occur throughout, like seed mortality, plant death and seed predation, are included." (Holst et al., 2007). Process is indirectly inferred, a surrogate derived from computational number-size frequency transitions between discrete life history times. Mature plant number and size are not the competitive processes of interaction among neighbors. Soil seed pool numbers are not the motive forces driving the processes of germination, dormancy reinduction and seedling recruitment. New seed numbers do not reveal adaptive changes in these new phenotypes caused by natural selection and elimination: changes in the genetic-phenotypic composition of the local population. Life history developmental behavior is motivated by specific environmental signals stimulating functional traits inherent in the phenotype. Weed population dynamics come about as a direct adaptive consequence of generating phenotypic-trait variation among excess progeny in the deme, followed by the survival and reproduction of the fittest phenotypes among those offspring with time.

8.2.2.2.2 Polymorphism and plasticity. Individual weed phenotypes derive fitness from their heterogeneity by exploiting local opportunity. Weed population structure is difficult to model unless somatic polymorphism and phenotypic plasticity are represented, inherent functional traits that control life history behavior as well as allow the individual to assume a size and function appropriate to its local opportunity spacetime. Somatic polymorphism is the production of different plant parts, or different behaviors, within the individual that is expressed independently of its local environment. Seed heteroblasty is an example of parentally-induced dormancy heterogeneity among offspring that provides strong inferences of future behavior. Phenotypic plasticity is the capacity of a weedy plant to vary morphologically, physiologically or behaviorally as a result of environmental influences on the genotype during the plant's life history. Experimentally capturing this level of population structure entails measuring the population of phenotypes expressed by a single genotype when a trait changes continuously under different environmental and developmental conditions: the reaction norm. The reaction norm in population structure is expressed by number and size of constituent leaf, branch, flower and root modules of the individual plant that vary in response to the locally available opportunity spacetime. This plasticity of form confounds the ability of a purely demographic model to make predictions of population growth rates, biomass and even productivity. The consequence of phenotypic plasticity is that plants growing under density stress typically have a skewed distribution of individual plant weights, especially when they compete for light. Skewing of the frequency distribution (numbers of plants versus weight per plant) increases with time and with increasing density (plants per unit area). Typically at harvest a hierarchy of individuals is established: a few large dominants and a large number of suppressed, smaller, plants. The individual weeds in the hierarchical population structure possess the potential for explosive, nonlinear exponential growth and fecundity. Individual weed plants have the potential to produce a very large range of seed numbers depending on their size. The range in reproductive capacities of plants extends from 1 to 10^{10} (approaching infinity for vegetative clone propagule production; Harper, 1977). There exists a danger in assuming that the average plant performance represents the commonest type, or most typical, plant performance (Dekker, 2009).

8.2.2.3 Model formalization and measurement metrics.

8.2.2.3.1 Hypotheses of local weed population dynamics. Any model of weed behavior must be preceded by an experimental hypothesis of how population dynamics comes about: to what is the deme adapted? It should be a statement of an overarching intuition of how the biological system works, or the primary forces driving its expression. Such a hypothesis should appropriately begin with the intelligent designer of the system: human agricultural activity. Such a hypothesis could provide a tool to realistically guide the mathematical, algorithmic and statistical formalization of model components, metrics and output. No hypothesis of this type has been proposed for demographic models.

8.2.2.3.2 Mathematical, algorithmic, statisitical model formalization and component description. A model is a representation of reality. It is inherently an abstraction and a simplification. It is a conceptual framework of a system constructed by indicating which elements should be represented and how these elements are interrelated. This conceptual framework then is translated into algorithms, precisely defined step-by-step procedures by which dynamics are carried out.

1. Many models are published without "… a complete description of the model logic and mathematics, including the parameter values." Of the 134 papers reviewed, 16-19% were not open for re-use or even critique. (Holst et al., 2007)

-algorithmic content: a smaller list of core truths and a set of rules to deduce their implications

-simplicity that were inherent in the totality of all the elements taken together

-lack of specification of the underlying demographic model structure and its algorithms

2. Inference in simple and complex systems and models: model parameter space

> "An intelligent system, then, cannot be stuffed with trillions of facts. It must be equipped with a smaller list of core truths and a set of rules to deduce their implications." (Pinker, 1997)

> "The real issue here is the apparent reduction in simplicity. A skeptic worries about all the information necessary to specify all the unseen worlds. But an

> entire ensemble is often much simpler than one of its members. The principle can be stated more formally using the notion of algorithmic content."
> "… the whole set is actually simpler than a specific solution …"
> "The lesson is that complexity increases when we restrict our attention to one particular element in an ensemble, thereby losing the symmetry and simplicity that were inherent in the totality of all the elements taken together."
> (Tegmark, M. 2009)

> "Spatially explicit models tend to get complex, or mathematically demanding, like the model of neighbourhood interference between *Abutilon theophrasti* and *Amaranthus retroflexus* (Pacala & Silander, 1990). Another hindrance to fully grasp these models is that they may contain so many details, that it makes a full description of the model in scientific journals impossible, e.g. the within-field model of Richter *et al.* (2000) or the landscape model of Colbach *et al.* (2001b). To counteract this inherent complexity in spatial processes, one can reduce the complexity of the weed model itself. But this makes for very abstract models which can be difficult to relate to real weed population dynamics (e.g. Wang *et al.*, 2003)." (Holst, Rasmussen and Bastiaans. 2006)

> "… the danger that the model develops into a monstrous specimen covering far too many facets and bearing an enormous parameter requirement. Collecting relevant parameters then becomes a time consuming exercise or might even develop into an objective on its own, putting the focus on analysis, rather than on synthesis of knowledge. Additionally, models containing too many parameters are often characterized by enormous error margins, and often lose their robustness." (Holst, Rasmussen and Bastiaans. 2006)

8.2.2.3.3 Measurement metrics. The metrics used to measure weed populations restrict our view of what is happening in the deme. When a demographic model is chosen to represent the essence of population biology certain artifacts inevitably follow. When experimental attention is focused on counting plant numbers to represent a population, certain computational artifacts follow.
Biological variability and population heterogeneity are lost when individuals are homogenized by computational simplification:
-the expedient of mean, average, mean behaviors to represent highly skewed number-size frequency distributions
-the inherently low informational content of demographic parameters
-inappropriate, too few, and inprecise life history times of measurement
-invalid correlations life history state that violate covariance structures by measuring different plant individuals in the population at the various measurement times
Fitness and fecundity**.** Demographic models confuse numerical superiority with fitness. Lambda, the annual population growth rate, and the finite rate of increase ($\lambda_t = N_t / N_{t-1}$), is used as a measure of '*W*', Darwinian fitness (Silvertown and Doust, 1993). This usage confuses fecundity with fitness, an artifact of seeing and evaluating agricultural plant communities in terms of productivity. Fitness is survival and reproduction relative to your neighbors.

Random-nonrandom processes**.** Any model of weed population dynamics must accurately represent both random and nonrandom processes. Holst et al. (2007) indicate that stochastic models can be used to explain past population dynamics. If successful, stochastic models gain credibility as predictive tools of long-term population dynamics. The authors indicate that stochastic models are a tool to handle the uncertainty of future conditions. This review classifies environmental unpredictability, agricultural practice (cropping disturbances) and statistical error in model parameter estimates as random, unpredictable, and stochastic. Classification of some of these experimentally tractable phenomena (e.g. cropping disturbance; survival and reproduction) as random is inappropriate. Significantly for this review of evolutionary weed population dynamic models, they classify natural demographic variation in reproduction and mortality as stochastic. Apparently Charles Darwin's contributions (1859) are underappreciated by demographic weed modelers. Variational evolution of a population or species occurs through changes in its members by natural selection, the processes of nonrandom elimination and nonrandom sexual selection (Mayr, 2001).

8.2.3 Predicting weed population dynamics.

"It's hard to make predictions, especially about the future." (Yogi Berra).

Two recent reviews of weed modeling have come to similar conclusions (Holst et al., 2007; Freckleton and Stephens, 2009). Prediction is an emergent property of the inherent biological information contained within the individual weed phenotype (and its traits) as it accomplishes its life history survival and reproduction. Demographic models inherently do not contain this biological information. Limitations in the inferences that demographic models render them of limited utility in predicting future behavior. The predictability of a model is based in its complexity. The work of nobel laureate F.A. Hayek (1974) is revealing. He distinguished the capacity to predict behavior in simple systems and those in complex systems through modeling. Complex biological phenomenon could not be modeled effectively in the same manner as those that dealt with essentially simple phenomena like physics. Complex phenomena, through modeling, can only allow pattern predictions, compared with precise predictions made of non-complex phenomena. How then is it possible to predict weed population dynamics? What is missing in demographic population models is the biological information contained in weedy traits whose expression drives the missing deterministic processes, processes incorrectly attempted to be replaced by stochastic probabilities of knowable weed phenomena (Holst et al., 2007; ref using stochasticity too). What then are the "…smaller list of core truths and a set of rules to deduce their implications." (Pinker, 1997) that will simplify weed population models and allow strong inference and predictability? Intuitively, these core truths most come from the inherent biological traits of the weeds themselves. It is to this that evolutionary models are directed.

8.3 Evolutionary, Trait-Based, Weed Life History Population Dynamics Models

First, add a clear statement of the weed population dynamics hypothesis:

Weedy and invasive plants perform the plant colonization niche. Weedy plants are the first to seize and exploit the opportunity spacetime created by human disturbance, notably in resource-rich agricultural cropping systems. Local opportunity spacetime is the habitable space available to an organism at a particular time which includes its resources (e.g. light, water, nutrients, gases) and conditions (e.g. heat, climate, location), its disturbance history (e.g. tillage, herbicides, winter), and neighboring organisms (e.g. crops, other weed species). Therefore, it is hypothesized that weedy plant life history behavior in a deme is a consequence of natural selection and reproductive success among excess variable phenotypes (and functional traits) in response to the structure, quality and timing of locally available opportunity spacetime.

The thesis of this paper is that understanding population dynamics in agroecosystems requires a qualitative evolutionary representation of local populations based upon the two component processes of natural selection and elimination resulting in weedy adaptation.

Evolutionary models based on the two component processes of natural selection (generation of variation, selection and elimination) are discussed in terms of these same critical factors. FoxPatch, an evolutionary trait-based model of weed *Setaria* species-group life history is reviewed as an example of an alternate mode of representation providing the predictive ability of seed heterblasty blueprinting the crucial life history threshold events of seedling emergence.

> "Nothing in biology makes sense, except in the light of evolution" (T. Dobzhansky)
>
> "Indeed there is no other natural explanation than evolution for [biological phenomena]" (Mayr, 2001).

What alternative is there to quantitative demographic life history models to represent weed population dynamics? How can the limitations and artifacts of quantitative demographic models be overcome? How is the essence of population biology captured in a life history representation?

8.3.1 Weed population dynamics: the process of natural selection-elimination and its consequences. The essence of population biology is captured by a weed life history representation stated in the form of the processes of natural selection: the fittest parents generate phenotypic variation in their offspring that preferentially survive and reproduce in the local deme. Figure 8.1 can be redrawn to represent this in a much simplified form:

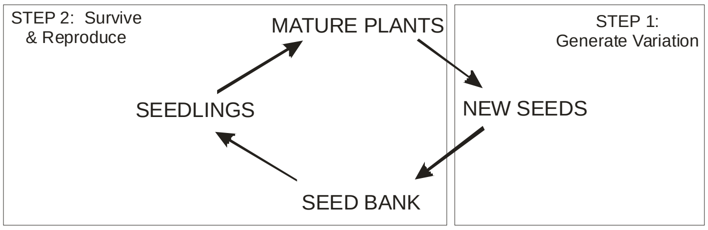


Figure 8.4. Representation of an annual weed species life history in terms of the two component processes of natural selection and elimination: step 1, production of phenotypic variation by the fittest parent plants; step 2, survival and reproduction of the fittest phenotypes, elimination of the others.

In each generation, new seed dispersed into the local deme comes from the fittest parent plants of the previous generation.

deme:	a local population of potentially interbreeding individuals of a species at a given locality

local community: all the interacting demes in a locality

<u>It's not a cycle, it's a spiral</u>. It is not a life cycle that returns to the same starting line, new surviving seed join the preexisting seed bank to form the new local population every winter in a sexually reproducing annual weed species. The local population is dynamic,

its phenotypic composition (the plant communities of the future) changes with new addition and loss.
(Expanding spiral for growing populations; constricting spiral for dying populations)

Therefore both the quantity and quality (traits) of the individual phenotypes in the deme change with time: adaptation to the local habitat. This evolutionary adaptation is the most dynamic element of the weed population that any realistic model must represent.

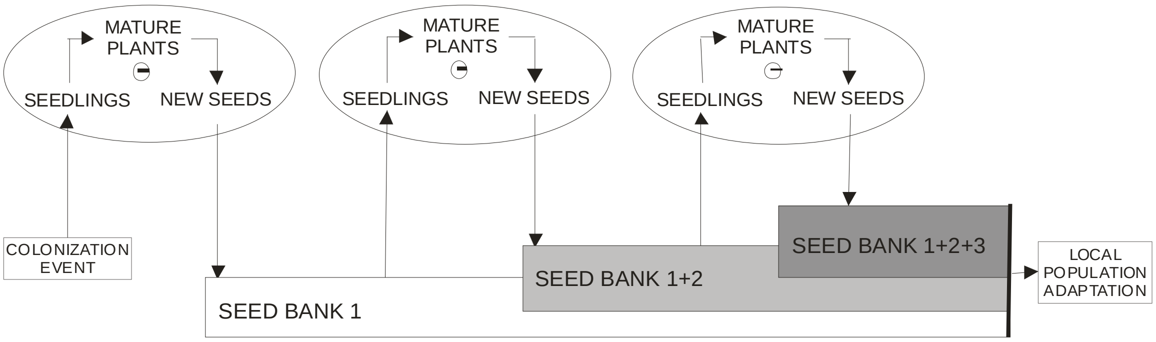


Figure 8.5. Schematic representation of the adaptive changes in the local population of an annual weed species through several generations (life cycles) as a consequence of the two processes of natural selection and elimination.

The phenotypic composition of each new local population changes with the recruitment of seedling from the seed pool. The composition of the seed pool is the dynamic element of local adaptation: the progeny of the fittest individuals selected from the previous generations. The representation of this changing seed pool is most challenging element in the formalization of a realistic life history model.

Sexually reproducing, annual, weed population dynamics are the adaptive consequence of natural selection and elimination of excess individuals in the local deme. This evolutionary process is represented by two processes and 5 conditions (Table 1)

Precondition 1: Excess local phenotypes compete for limited opportunity spacetime	
Process step 1: Produce phenotypic variation	Condition 1: variation in individual traits
	Condition 2: variation in individual fitness
Process step 2: Survival and reproduction of the fittest phenotypes	Condition 3: survive to reproduce the fittest offspring, eliminate the others
	Condition 4: reproductive transmission parental traits to offspring
Adaptation arises in the local population of phenotypes	

Table 8.1 The local adaption of a sexually reproducing weed population by the processes (and component conditions) of natural selection of the fittest phenotypes.

8.3.2 Units and objects of evolution and natural selection.

unit of evolution: local population (deme)

unit of selection: the individual phenotype

phenotype:
1: the sum total of observable structural and functional properties of an organism; the product of the interaction between the genotype and the environment.
2: the total of all observable features of a developing or developed individual (including its anatomical, physiological, biochemical, and behavioral characteristics). The phenotype is the result of interaction between genotype and the environment (Mayr, 2001)
3: the characters of an organism, whether due to the genotype or environment
4: the manifested attributes of an organism, the joint product of its genes and their environment during ontogeny; the conventional phenotype is the special case in which the effects are regarded as being confined to the individual body in which the gene sits (Dawkins,1999), p.299)

extended phenotype:
all effects of a gene upon the world; 'effect' of a gene is understood as meaning in comparison with its alleles; the concept of phenotype is extended to include functionally important consequences of gene differences, outside the bodies in which the genes sit; in practice it is convenient to limit 'extended phenotype' to cases where the effects influence the survival chances of the gene, positively or negatively (Dawkins, 1999, p.293)

trait:
1: a character: any detectable phenotypic property of an organism
2: any character or property of an organism
3: a characteristic feature or quality distinguishing a particular person or thing
4: predictors (proxies) of organismal performance (Darwin, 1859)

functional trait:
morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction or survival, the three components of individual performance (Violle et al., 2007)

8.3.3 The local habitat. Plants will fill any available and habitable growing space, therefore the primary resource limiting plant growth is habitable space. Every potentially habitable space includes the resources (e.g. relative abundance of light, water, nutrients, gases) and conditions (e.g. relative abundance of heat) of that location, its disturbance history, as well as the neighboring organisms that occupy that space. The structure of available and habitable space to an invading plant is also opportunity space at a particular time.

opportunity spacetime: locally habitable space for an organism at a particular time which includes its resources (light, water, nutrients, gases) and conditions (heat, climate, location), [add here and text: climate environment] disturbance history (e.g. tillage, herbicides), and neighboring organisms (e.g. crops, other weed species)

-an integration of the influences directly perceived by the individual phenotype; phenotypic response is also integrated to them as a whole perception, effective signal received;
-habitat: the seed-plant experiences OST as an integrated effective signal: time and place is everything
-OST as the phenotypes viewpoint of experience: they see OST as overlapping succession of integrated effective signals simultaneously from: 1] resources, 2] disturbance, 3] conditions, 4] see foxpatch paper for example of evolutionary model.

8.4 Conclusions

See foxpatch paper for example of evolutionary model.

Combine demographic and evolutionary models to optimize their individual strengths.

Evolutionary models like FoxPatch used for their ability to recognize and elucidate local population pattern (seedling emergence timing hedge-bet structure): model pattern driver. Use demographics for quantification of pools within a year to confirm, calibrate, predictive models (not used as future predictors): enrichment of adaptive phenotypes, recovery of latent seed bank types with changes in cropping systems, etc.

REFERENCES CITED

Baker 1965. In: Genetics of colonizing species; H.G. Baker and G.L Stebbins (Eds.). Academic Press, NY.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. Annual Review of Ecological Systems 10:351-371.

Dawkins, R. 1999. The extended phenotype The long reach of the gene, Ch. 1 Necker cubes and buffaloes, pp.1-8; Ch. 9, Selfish DNA, jumping genes, and a Lamarckian scare, pp.157-164 . Oxford University Press, Oxford.

Dekker, J. 1997. Weed diversity and weed management. Weed Science 45:357-363.

Dekker, J. 2004a. The evolutionary biology of the foxtail (*Setaria*) species-group. In: Weed Biology and Management; Inderjit (Ed.). Kluwer Academic Publishers, The Netherlands. Pp. 65-113.

Dekker, J. 2003. The foxtail (*Setaria*) species-group. Weed Science 51:641-646.

Dekker, J. 2005. Biology and anthropology of plant invasions. In: Invasive plants: Ecological and agricultural aspects; Inderjit (Ed.). Birkhauser Verlag, Switzerland.

Dekker, J. et al. 2001.

DeWet, J.M.J. 1966. The origin of weediness in plants. Proc. of the Okla. Acad. of Sci. 47:14-17.

Ehrendorfer, F. 1965. Dispersal mechanisms, genetic systems, and colonizing abilities in some flowering plant families. In: Genetics of colonizing species; H.G. Baker andG.L Stebbins (Eds.). Academic Press, NY.

Forcella, F. et al 92 and 97: seed bank articles with me

Harper, J. 1977. Population biology of plants. Academic Press, NY.

Hakansson, S. 2003. Weeds and weed management on arable land-An ecological approach. CABI Publishing, Cambridge, MA, USA.

Lincoln et al., 1998. A dictionary of ecology, evolution and systematics. Cambridge Press.

May, R.M. 1973. Stability and complexity in model ecosystems. Princeton Univ. Press, NJ

Silvertown, J. and D. Charlesworth. 2001. Introduction to plant population biology, 4th Edition. Blackwell Science, Oxford, UK.

Silvertown, J.W. and J.L. Doust. 1993. Introduction to plant population biology. Blackwell Science, Oxford, UK.

Trewavas (2000) resource signals in Opp Space

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, E. Garnier. 2007. Let the concept of trait be functional! Oikos xx:xxx-xxx.

Wang, R.L, J. Wendell and J. Dekker. 1995a. Weedy adaptation in *Setaria* spp.: I. Isozyme analysis of the genetic diversity and population genetic structure in *S. viridis*.. American Journal of Botany 82(3):308-317.

Wang, R.L, J. Wendell and J. Dekker. 1995b. Weedy adaptation in *Setaria* spp.: II. Genetic diversity and population genetic structure in *S. glauca*, *S. geniculata* and *S. faberii*. American Journal of Botany 82(8):1031-1039.

Zohary 1965 (Polyploid species clusters) In: Genetics of colonizing species; H.G. Baker and G.L Stebbins (Eds.). Academic Press, NY.

From model paper:

Atchison B., 2001 - Relationships between foxtail (*Setaria* spp.) primary dormancy at abscission and subsequent seedling emergence. M.S. Thesis, Iowa State University, Ames, USA.

Bernoulli, J. 1713. Ars conjectandi, opus posthumum. Accedit Tractus de seriebus infinitis, et epistola gallicé scripta de ludo pilae reticularis. Basel: Thurneysen Brothers.

Colbach, N. [Natalie Colbach models; pushing the envelope with demography; see papers in Weed Research 2006]

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

Dekker J., 2003 - The foxtail (*Setaria*) species-group. *Weed Science*, 51, 641-646.

Dekker J., Atchison B., Jovaag K., 2003 - *Setaria* spp. seed pool formation and initial assembly in agro-communities. *Aspects of Applied Biology*, 69, 247-259.

Dekker J., Dekker B.I., Hilhorst H., Karssen C., 1996 - Weedy adaptation in Setaria spp.: IV. Changes in the germinative capacity of S. faberi embryos with development from anthesis to after abscission. *American Journal of Botany*, 83(8), 979-991.

Dekker J., Hargrove M., 2002 - Weedy adaptation in Setaria spp.: V. Effects of gaseous atmosphere on giant foxtail (*Setaria faberi*) (Gramineae) seed germination. *American Journal of Botany*, 89, 410-416.

Dekker, J., Luschei E.C. 2009 - Water partitioning between environment and *Setaria faberi* seed exterior-interior compartments. *Agriculture Journal*, 4(2), 66-76.

Donnelly J.L., Adams D.C, Dekker J., 2009 – Does phylogeny determine the shape of the outer seed hull in *Setaria* seeds? (Manuscript in preparation).

Freckleton R.P., Stephens P.A., 2009 - Predictive models of weed population dynamics. *Weed Research*, 49, 225-232.

Harper, J, 1977. Population biology of plants. Academic Press, ?? ; pp. 25-26)

Hayek, F.A. 1974. The pretence of knowledge. Nobel Prize in Economics Lecture, Sweden.

Holst, N., Rasmussen I.A, Bastiaans L., 2007 - Field weed population dynamics: a review of model approaches and applications. *Weed Research*, 47, 1-14.

Intercom model: Wageningen

Jovaag K., 2006 - Weedy *Setaria* species-group heteroblasty blueprints seedling recruitment. Ph.D. Thesis, Iowa State University, Ames, USA.

Liebman, M. Agronomy model review; papers with Andy

Mayr, E. 1959. Darwin and the evolutionary theory in biology. In: Evolution and anthropology: a centennial appraisal, pp. 1-10. Washington, D.C.: Anthropological Society of American:

Mayr, E., 2001 – *What Evolution Is*. Basic Books, New York, 318 p.

Pinker, Steven. 1997. How the mind works. Penquin Books, London, UK.

Rost T.L., 1971 - Structural and Histochemical investigations of dormant and non-dormant caryopsis of *Setaria lutescens* (Gramineae). Ph. D. dissertation Iowa State University, Ames, USA.

Rost, T.L., Lersten N.R., 1970 - Transfer aleurone cells in *Setaria lutescens* (Gramineae). *Protoplasma*, 71, 403-408.

Sareini H.T., 2002 - Identification and characterization of the major seed peroxidase in *Setaria faberi*. M.S. Thesis, Iowa State University, Ames, USA.

Silvertown J.W., Doust J.L, 1993 – *Introduction to Plant Biology*. Blackwell Science, Oxford, 210p.

Tegmark, M. 2009. Parallel universes. Scientific American special report SCA45026.

Wang, R.-L., Wendell J., Dekker J., 1995a - Weedy adaptation in Setaria spp.: I. Isozyme analysis of the genetic diversity and population genetic structure in *S. viridis*. *American Journal of Botany*, 82(3), 308-317.

Wang, R.-L., Wendell J., Dekker J., 1995b - Weedy adaptation in *Setaria* spp.: II. Genetic diversity and population genetic structure in *S. glauca*, *S. geniculata* and *S. faberii*. *American Journal of Botany*, 82(8), 1031-1039.

Wikipedia: http://en.wikipedia.org/wiki/Main_Page

From Dijon 2009 FoxPatch Evolutionary Model Paper, Appendix 4:

Atchison B., 2001 - Relationships between foxtail (*Setaria* spp.) primary dormancy at abscission and subsequent seedling emergence. M.S. Thesis, Iowa State University, Ames, USA.

Dekker J., 2003 - The foxtail (*Setaria*) species-group. *Weed Science*, 51, 641-646.

Dekker J., 2009 - *The evolutionary ecology of weeds and invasive plants*. .pdf at: http://www.agron.iastate.edu/~weeds/PDF_Library/Agron_517/EcolEvolWIP_12.12.08.pdf

Dekker J., Atchison B., Jovaag K., 2003 - *Setaria* spp. seed pool formation and initial assembly in agro-communities. *Aspects of Applied Biology*, 69, 247-259.

Dekker J., Dekker B.I., Hilhorst H., Karssen C., 1996 - Weedy adaptation in Setaria spp.: IV. Changes in the germinative capacity of S. faberi embryos with development from anthesis to after abscission. *American Journal of Botany*, 83(8), 979-991.

Dekker J., Hargrove M., 2002 - Weedy adaptation in Setaria spp.: V. Effects of gaseous atmosphere on giant foxtail (*Setaria faberi*) (Gramineae) seed germination. *American Journal of Botany*, 89, 410-416.

Dekker, J., Luschei E.C. 2009 - Water partitioning between environment and *Setaria faberi* seed exterior-interior compartments. *Agriculture Journal*, 4(2), 66-76.

Donnelly J.L., Adams D.C, Dekker J., 2009 – Does phylogeny determine the shape of the outer seed hull in *Setaria* seeds? (Manuscript in preparation).

Freckleton R.P., Stephens P.A., 2009 - Predictive models of weed population dynamics. *Weed Research*, 49, 225-232.

Holst, N., Rasmussen I.A, Bastiaans L., 2007 - Field weed population dynamics: a review of model approaches and applications. *Weed Research*, 47, 1-14.

Jovaag K., 2006 - Weedy *Setaria* species-group heteroblasty blueprints seedling recruitment. Ph.D. Thesis, Iowa State University, Ames, USA.

Mayr, E., 2001 – *What Evolution Is*. Basic Books, New York, 318 p.

Rost T.L., 1971 - Structural and Histochemical investigations of dormant and non-dormant caryopsis of *Setaria lutescens* (Gramineae). Ph. D. dissertation Iowa State University, Ames, USA.

Rost, T.L., Lersten N.R., 1970 - Transfer aleurone cells in *Setaria lutescens* (Gramineae). *Protoplasma*, 71, 403-408.

Sareini H.T., 2002 - Identification and characterization of the major seed peroxidase in *Setaria faberi*. M.S. Thesis, Iowa State University, Ames, USA.

Silvertown J.W., Doust J.L, 1993 – *Introduction to Plant Biology*. Blackwell Science, Oxford, 210p.

Wang, R.-L., Wendell J., Dekker J., 1995a - Weedy adaptation in Setaria spp.: I. Isozyme analysis of the genetic diversity and population genetic structure in *S. viridis*. *American Journal of Botany*, 82(3), 308-317.

Wang, R.-L., Wendell J., Dekker J., 1995b - Weedy adaptation in *Setaria* spp.: II. Genetic diversity and population genetic structure in *S. glauca, S. geniculata* and *S. faberii. American Journal of Botany*, 82(8), 1031-1039.

APPENDICES

Appendix 1: The Perception of Plant Invasion (Dekker, 2005)

> "With the present tremendous population explosion the most common habitat has become man-made, and it may not be many centuries before this will be the only habitat available. With the disappearance of stable habitats, truly wild species will be the first to become extinct. Wild colonizers may survive as long as habitats remain that are only sporadically disturbed by man. Eventually these must also disappear and *Homo sapiens*, the ultimate of all weeds, will lord it over the domain he has created for himself, his companion weeds, his crops and domesticated animals." (J.M.J. de Wet, 1966)

The biology of the invasion process as presented in the section above is rational and experimentally tractable. What is less apparent is the human component of the selection process that creates opportunity spaces into which invasive species disperse (Dekker, 2005). The direct effects of human activity are also more discernable than the indirect effects. Of critical importance is the role human perception plays in selection and creation of opportunity space for invasive species.

Invasive, or colonizing, plants have a significant affect on the biological and human communities in which they appear (Dekker, 2005). These affects include economic, environmental, aesthetic, and biological harm to agriculture, biodiversity, ecosystem function, and human welfare. There exists a perception that invasive species are increasing of late due to increased global movement of people, trade, and transport of biological and agricultural commodities and novel plant materials. Introduced non-native species include useful crop and animal species used for human food consumption, as well as other species used for land restoration, biological pest control, sport, pets and food processing.

To mitigate or ameliorate the harm caused by invasive species, knowledge of their biology and behavior is needed. This management information is often incomplete, especially that concerning behavior in the newly invaded communities and the life history traits they possess allowing invasion. Also of critical importance is consideration of the roles played by human activity, perception, public policy and social values. Management of plant invasions is a complex task, requiring consideration of the roles played by the biological community and humans, both of which must be considered in any rational management system.

A broad perspective is required of everyone involved in the dialogue of invasive species. Those interested and involved in invasion biology are a very diverse range of humans, including citizens, biological and social scientists, and those with governmental, environmental or public policy roles. The terminology used by those interested in invasion biology is often defined somewhat differently by these respective groups.

A species succeeding in occupying a locality must be perceived by humans as being problematic for it to be labeled invasive. The perception of a plant species as invasive by humans is a complex, often highly subjective process. Despite this, there are several systematic ways to understand how human perception and cultural values create selection pressure and opportunity spaces conducive to plant invasions. They include insights gained from public policy and reflection on human values. These social and perceptual factors are inherently anthropological and anthrocentric in nature, and need to be understood in those contexts for a complete understanding of the forces of selection conducive to invasion.

anthropology
1: the scientific study of human beings, their origins, distribution, physical attributes and culture (Anonymous, 2001)
2: the study of man, his origins, physical characteristics, institutions, religious beliefs, social relationships, etc. (Anonymous, 1979)

culture
1: the skills, arts, etc. of a given people in a given period (Anonymous, 2001)
2: the entire range of customs, beliefs, social forms, and material traits of a religious, social, or racial group (Anonymous, 2001)
3: the total of the inherited ideas, beliefs, values, and knowledge, which constitute the shared bases of social action
4: the total range of activities and ideas of a group of people with shared traditions, which are transmitted and reinforced by members of the group (Anonymous, 1979)

antrocentric
1: centering in man (Anonymous, 2001)

anthropocentric
1: regarding man as the most important and central factor in the universe (Anonymous, 1979)

Public policy can provide a starting point to determine human perceptions of invasive species, an expression of human values. Of particular interest is public policy on invasive species promulgated by the U.S. Federal government in Executive Order 13112 of February 3, 1999 (Anonymous, 1999, 2004b). Research, management and dissemination of information about invasive species in the U.S. are funded by government agencies in compliance with this order. The terminology used in this public policy statement reveals how some perceive invasion biology. Therein (Anonymous, 1999, 2004b) they define several terms, below included with definitions from more conventional sources:

invasive species
1: an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health (Anonymous, 1999)
2: a species that is non-native (or alien) to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm human health (Anonymous, 2004)

alien species
1: with respect to a particular ecosystem, any species, including seeds, eggs, spores, or other biological material capable or propagating that species, that is not native to that ecosystem (Anonymous, 1999)
2: non-native; a species occurring in an area to which it is not native (Lincoln et al., 1998)

native species: with respect to a particular ecosystem, a species that, other than as a result of an introduction, historically occurred or currently occurs in an ecosystem (Anonymous, 1999)

native
1: relating to the indigenous inhabitants of a country or area; a local inhabitant; an indigenous plant or animal (Anonymous, 2001)
2: relating or belonging to a person or thing by virtue of conditions existing at the time of birth; born in particular place (Anonymous, 1979)
3: indigenous; living naturally within a given area; used of a plant species that occurs at least partly in natural habitats and is consistently associated with certain other species in these habitats (Lincoln et al., 1998)

nativism
1: the doctrine of innate ideas
2: in U.S., the advocacy of the claim of native as opposed to that of naturalized Americans (Anonymous, 2001)
3: Chiefly U.S. the policy of favouring the natives of a country over the immigrants (Anonymous, 1979)

natural
1: of or produced by nature (Anonymous, 2001)
2: in accordance with human nature (Anonymous, 1979)
3: not affected by man or civilization; uncultivated; wild (Anonymous, 1979)

introduction
1: intentional or unintentional escape, release, dissemination, or placement or a species into an ecosystem as a result of human activity (Anonymous, 1999)

Several aspects of invasion biology are revealed in these definitions. These include the concept of economic, environmental and human harm; the differentiation between alien and native species; the existence of natural conditions; and the purposeful introduction of a plant species to a locality.

The purpose of this section is only to highlight the explicit statements of human goals and values that may influence invasion biology. Of specific importance to public policy is the value placed on nativism, natural conditions and the different categories of harm. How public policy is implemented with these guiding, often subjective, concepts is at the heart of how these species are managed. The management elicited by public policy is the selection pressure these invasive species will respond and adapt to in their subsequent evolution.

The historical expansion of human populations, and their activities, has affected almost every habitat on earth to some extent, either directly or indirectly. Air and water pollution alone have affected much of the surface biology of earth (e.g. CO_2, O_3). Human perception of what is natural and indigenous, what is disturbed and artificial, is therefore compromised to some degree. In one form or another, willingly or not, the earth is the garden of humanity. The equivocal nature of what harm is caused by invasive species is therefore confounded by the heterogeneous array of human viewpoints and aesthetic values of what is desirable in landscapes. This heterogeneity of opinion is not resolvable but remains at the core of invasion biology because values guide activity and management. For better or worse, the actualization of human values creates opportunity space for new species to invade: they are a direct reflection of human activity.

The best expression of human-mediated invasion biology can be found in agriculture. With the advent of agriculture some 10,000 years ago, hunter-gatherer and nomadic peoples were displaced gradually by spatially sedentary agriculturists. The opportunity space for agriculture was vast. Humans imposed disturbance regimes on those spaces (e.g. soil tillage) and favored plant species with desirable phenotypic traits to cultivate and harvest. Evolutionary changes in those cultivated species led to somewhat ironic consequences: the formation of stable, long-lived wild-crop-weed complexes (de Wet, 1966; de Wet and Harlan, 1975). Wild progenitor species were domesticated. Crop phenotypes escaped cultivation and developed weedy habits ideal for infestation with their crop relative, and both shared space with the original wild relatives. Gene flow was continuous between these closely related forms of the same species-group, an ideal genetic situation for the longevity of the species. Archetypical examples of these wild-crop-weed complexes are found in Amarathus (grain amaranth, pigweeds), Setaria (foxtail millet, green foxtail; Dekker, 2003; 2004b), Brassica (rapeseed and wild mustards), Helianthus (sunflowers), Avena (oat), Oryza (rice), sorghum (crop, johnsongrass), Solanum (potatoes, nightshades), and Hordeum (barley, foxtail barley).

The most important current agricultural plant invasion is the introduction of transgenic crops, often on a vast scale (e.g. glyphosate-resistant crops). Introduction of any trans-gene into the crop cultivars of these wild-crop-weed complexes increases the chances of introgression into its related non-cultivated weedy and wild phenotypes (e.g. Dekker and Comstock, 1992). The development of these biotechnologies in wild-crop-weed complexes fulfill the conjecture provided in the introduction: a critical interaction of disturbance, dispersal and plant traits adapted for the resultant opportunity space. The introduction of such biotechnologies as herbicide-resistant crops provides a mixture of environmental and economic benefit and harm which makes implementation of public policy as defined by U.S. Federal policy (Anonymous, 1999, 2004a) somewhat problematic and highlights the complex interaction of biology and human values.

Invasion biology is a reflection of the impact human populations have on the earth's ecology. Public policy is currently focused on management and control of specific species, but at the same time ignoring the fundamental and complex sources of these changes in biological communities. Fundamentally the problem is human: human population size and collateral disturbance, human dispersal of invasive species propagules, heterogeneous human values about the nature of harm and beauty, and the priorities of human scientific endeavors. In all this there may be some benefit to humans by exploiting the very traits we despise most for plant improvement.

There is not a meaningful difference between the invasion process and the processes of ecological community assembly, succession and the evolution of niche differentiation by speciation. Despite this, disciplinary barriers are apparent in the differentiation of invasion biology science in unmanaged and managed habitats: agricultural weed biology and invasive plant biology are often separated in the scientific academy. Both these realms are unified by disturbance as a prime motivator of change in community structure. The scale of habitats in time and space is continuous; and all communities are inter-related and inter-dependent. Agriculturalists often do not completely embrace the invasion process in understanding population shifts, and ecologists studying unmanaged systems often fail to recognize the role of indirect disturbance and dependence on adjacent agricultural habitats in the larger landscape. The science of both will advance when the unifying principles underlying both types of undesirable species are acknowledged in a larger view of invasion biology.

Appendix 2

Weed biology casebook: Relative seedling/bud emergence order

See related material in:
6.4.2.3 Trait guild: relative seedling/bud emergence order; p. 91
7.4.4 Patterns of seedling emergence. Table 7.9; p. 132

Previous Autumn Post-Harvest October JW 40-45 **GROUP 0**	Early Spring Prior to Planting Early April JW 14-15 **GROUP 1**	Early Spring Prior to Planting Late April JW 16-17 **GROUP 2**	Spring Maize Planting Early May JW 18-19 **GROUP 3**	Spring Soybean Planting Late May JW 20-21 **GROUP 4**	Late Spring Planting Time Early June JW 22-23 **GROUP 5**	Late Spring Post- Planting Late June JW 24-25 **GROUP 6**	Early Summer Layby Early July JW 26-27 **GROUP 7**
WINTER ANNUALS: **Cruciferae Family**: •*Capsella bursa-pastoris* (Shepard's purse) •*Thlaspi arvense* (field pennycress) **Poaceae Family:** •*Bromus tectorum* (downy brome)	**SUMMER ANNUALS:** **Chenopodiaceae Family:** •*Kochia scoparia* (kochia) •*Salsola kali* (Russian thistle) **Cruciferae Family**: •*Brassica kaber* (wild mustard) **Polygonaceae Family:** •*Polygonum aviculare* (prostrate knotweed)	**SUMMER ANNUALS:** **Chenopodiaceae Family:** •*Chenopodium album* (common lambsquarters) **Compostitae Family:** •*Ambrosia trifida* (giant ragweed) **Poaceae Family:** •*Avena fatua* (wild oat) **Polygonaceae Family:** •*Polygonum pensylvanicum* (Pennsylvania smartweed) •*Polygonum persicaria* (ladysthumb) **Solanaceae Family:** •*Solanum physalisfolium* (hairy nightshade)	**SUMMER ANNUALS:** **Compositae Family:** •*Ambrosis artemisiifolia* (common ragweed) **Malvaceeae Family:** •*Abutilon theophrasti* (velvetleaf) **Poaceae Family:** •*Eriochloa villosa* (woolly cupgrass) **Polygonaceae Family:** •*Polygonum convolvulus* (wild buckwheat)	**SUMMER ANNUALS:** **Amaranthaceae Family:** •*Amaranthus retroflexus* (redroot pigweed) **Compositae Family:** •*Xanthium strumarium* (common cocklebur) **Poaceae Family:** •*Setaria faberii* (giant foxtail)	**SUMMER ANNUALS:** **Poaceae Family:** •*Echinochloa crus-galli* (barnyardgrass) •*Panicum miliaceum* (wild proso millet) •*Setaria pumila* (yellow foxtail) •*Setaria viridis* (green foxtail)	**SUMMER ANNUALS:** **Amaranthaceae Family:** •*Amaranthus rudis* (common waterhemp) **Compositae Family:** •*Helianthus annuus* (common sunflower) **Malvaceae Family:** •*Hibiscus trionum* (□orpho mallow) **Poaceae Family:** •*Sorghum bicolor* (shattercane) **Solanaceae Family:** •*Solanum ptycanthum* (eastern black nightshade)	**SUMMER ANNUALS:** **Convolvulaceae Family:** •*Ipomoea* spp. (morningglory) (*I. hederacea*, ivyleaf; *I. purpurea*, tall) **Poaceae Family:** •*Digitaria* spp. (crabgrass) (*D. sanguinalis*, large; *D. ischaemum*, smooth) •*Panicum capillare* (witchgrass) •*Panicum dichotomiflorum* (fall panicum) **Solanaceae Family:** •*Datura stramonium* (jimsonweed)
BIENNIALS: **Composite Family:** •*Carduus, Cirsium* (biennial thistles) **Umbelliferae Family**: •*Daucus carota* (wild carrot)	**BIENNIALS:** **Caryophyllaceae Family:** •*Lychnis alba* (white cockle)						
PERENNIALS: **Compositae Family:** •*Conyza □orphologi* (horseweed; marestail) •*Taraxacum officinale* (dandelion); from seed	**PERENNIALS:** **Compositae Family:** •*Taraxacum officinale* (dandelion) **Poacea Family:** •*Hordeum jubatum* (foxtail barley)	**PERENNIALS:** **Poacea Family:** •*Elymus repens* (quackgrass) •*Dactylis glomerata* (orchardgrass)	**PERENNIALS:** **Poacea Family:** •*Bromus inermis* (smooth brome)	**PERENNIALS:** **Compositae Family:** •*Circium arvense* (Canada thistle) **Cyperaceae Family:** •*Cyperus esculentus* (yellow nutsedge)	**PERENNIALS:** **Apocynaceae Family:** •*Apocynum cannabinum* (hemp dogbane) **Asclepiadaceae Family:** •*Asclepias syriaca* (common milkweed) **Poacea Family:** •*Muhlenbergia frondosa* (wirestem muhly)	**PERENNIALS:** **Compositae Family:** •*Helianthus tuberosus* (□orpholog artichoke) **Solanaceae Family:** •*Solanum subglabrata* (smooth groundcherry)	**PERENNIALS:**
Previous Autumn Post-Harvest October JW 40-45 **GROUP 0**	Early Spring Prior to Planting Early April JW 14-15 **GROUP 1**	Early Spring Prior to Planting Late April JW 16-17 **GROUP 2**	Spring Maize Planting Early May JW 18-19 **GROUP 3**	Spring Soybean Planting Late May JW 20-21 **GROUP 4**	Late Spring Planting Time Early June JW 22-23 **GROUP 5**	Late Spring Post- Planting Late June JW 24-25 **GROUP 6**	Early Summer Layby Early July JW 26-27 **GROUP 7**

Table 2. Relative seedling emergence order for the common weeds of summer annual crops in Iowa and adjacent areas; JW, julian week. (based on Buhler and Hartzler).

What first generalizations can be made about the structure and emergence timing of this Iowa corn-soybean crop rotation production system agro-community? Observations include:

1. 14 plant families.
2. 53 species were reported in this agro-community.
    a. 36 annual species: 3 winter annual (early, group 0); 33 summer annuals (groups 1-7)
    b. 3 biennial species: 2 winter annual (early, group 0), 1 summer annual (early, group 1)
    c. 14 perennial species, all but one in Poaceae or Compositae:
        1] Poaceae: 4 species; early, groups 1-3
        2] Compositae: 6 species; early (groups 0-1) and late (groups 4-6)
        3] Solanaceae: 1 species, group 6
3. Compositae and Poaceae were by far the dominant plant families represented in terms of annual and perennial life histories, and in terms of numbers of species:
    a. Poaceae had 19 species represented, the most of any family
    b. Poaceae emerged in all annual emergence groups (except group 1); 19 species, the most of any family
    c. Poaceae perennials emerged relatively early, groups 1-3
    d. Compositae had 11 species represented, the second most of any family
    e. Compositae had species represented in annual (groups 2-4, 6), biennial (group 0) and perennial (groups 0-1, 4-6) life histories
4. Families represented by a single species included:
    a. Biennial species only: Umbelliferae (group 0), Caryophyllaceae (group 1)
    b. Perennial species only: Apocynaceae (group 5), Asclepiadaceae (group 5) and Cyperaceae (group 4)
5. Families with more than one species, whose species all emerged at similar times of the season include:
    a. Early emerging species:
        1] Chenopodiaceae, 2 species both early (groups 1-2)
        2] Cruciferae, 3 species early (groups 0-1)
    b. Late emerging species:
        1] Amaranthaceae, 2 species both relatively late (groups 4 and 6); this number of species may be greater due to the inherent taxonomic uncertainty in this obligate out-crossing weed family.
        2] Convolvulaceae, 2 species both very late (group 7)
        3] Malvaceae, 2 species emerging later (groups 3 and 6)
        4] Solanaceae, 4 species, with 3 annual and perennial species emerging very late (groups 6-7), but one species emerging early (group 2)

<u>Dominant families and species</u>**.** From these observations the following ecological role or guild table can be predicted for Iowa maize-soybean production weed communities.

Table 3.

	ANNUALS	BIENNIALS	PERENNIALS	ECOLOGICAL ROLE
Previous	Winter Annuals:	•Compositae	•Compositae	•Escape neighbors by

Autumn Post-Harvest October JW 40-45 **GROUP 0**	•Cruciferae •Poaceae	(biennial thistles)		early emergence and winter survival
Early Spring Prior to Planting Early April JW 14-15 **GROUP 1**	•Cruciferae •Chenopodiaceae		•Compositae •Poaceae	•Dominate neighbors by early emergence: -light competition -hasten reproduction)
Early Spring Prior to Planting Late April JW 16-17 **GROUP 2**	•Compositae •Poaceae •Chenopodiaceae •Polygonaceae		•Poaceae	Dominate neighbors by early emergence: -light competition -luxury nutrient consumption)
Spring Maize Planting Early May JW 18-19 **GROUP 3**	•Compositae •Poaceae •Malvaceae		•Poaceae	Dominate neighbors by light competition
Spring Soybean Planting Late May JW 20-21 **GROUP 4**	•Compositae •Poaceae •Amaranthaceae		•Compositae	•Dominate neighbors with high growth rates
Late Spring Planting Time Early June JW 22-23 **GROUP 5**	•Poaceae		•Poaceae	
Late Spring Post- Planting Late June JW 24-25 **GROUP 6**	•Compositae •Poaceae •Amaranthaceae •Solanaeceae		•Compositae •Solanaeceae	•Dominate neighbors with high growth rates •Exploit late season light opportunities
Early Summer Layby Early July JW 26-27 **GROUP 7**	•Poaceae •Solanaeceae			•Exploit late season light opportunities

Appendix 4

Weed biology casebook:

XXXIIITH INTERNATIONAL CONFERENCE ON WEED BIOLOGY
DIJON – 8-10 SEPTEMBER 2009

FOXPATCH: AN EVOLUTIONARY MODEL SYSTEM FOR WEEDY *SETARIA* SPP.-GP. SEED LIFE HISTORY DYNAMICS

J. Dekker

Weed Biology Laboratory
Agronomy Department
Iowa State University
Ames, Iowa 50011
jdekker@iastate.edu

SUMMARY: FoxPatch represents weedy *Setaria* seed-seedling life history population dynamics with explicit seed process prediction rules via trait-process-signal modeling. Inherent, trait-based processes are modulated by effective signals (O_2-H_2O -thermal-time) determining soil seed behavior. Phenotypic variation is generated during embryogenesis by induction of variable seed germinability-dormancy capacities among parental offspring, seed heteroblasty. Seed heteroblasty, modulated by O_2-H_2O-thermal-time, thereafter determines reversible seasonal dormancy cycling in the soil as well as irreversible germination leading to seedling emergence. Hedge-bet patterns of seedling emergence exploit predictable local opportunity spacetime (resources, conditions, cropping disturbances, neighbors). Seed heteroblasty blueprints seedling emergence pattern.

Key words: population dynamics models; weedy adaptation; *Setaria*; seedling recruitment

INTRODUCTION

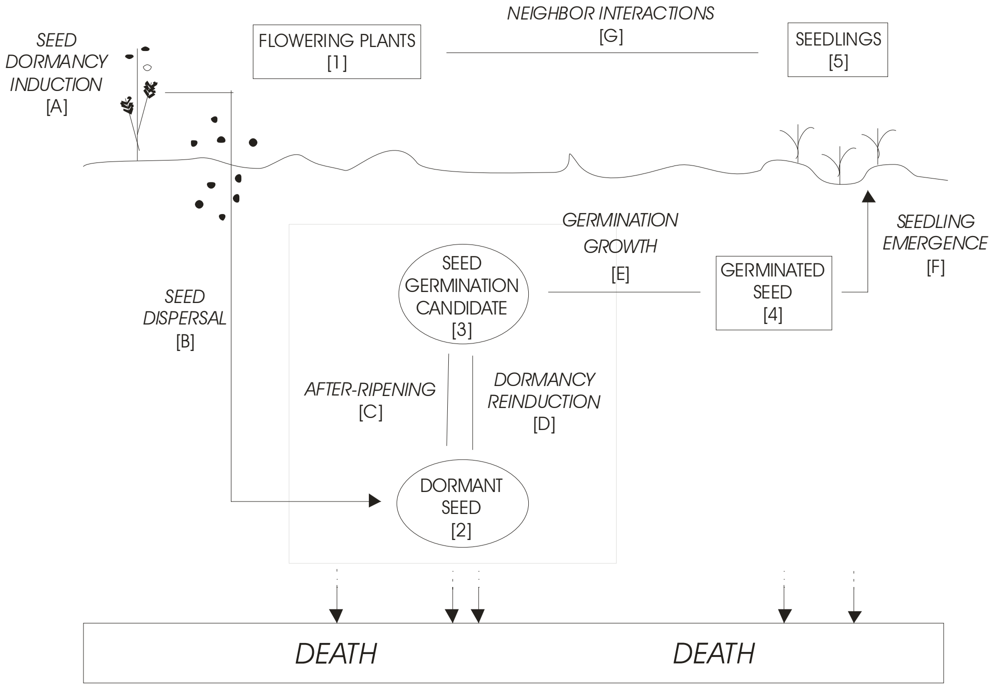
Life history representation. Weed population dynamics models are primarily demographic: "The essence of population biology is captured by a simple equation that relates the numbers per unit area of an organism" with changes in time (Silvertown & Doust, 1993). Two recent reviews have emphasized the limitations of these quantitative models in enabling predictions of future population behavior (Holst et al., 2007; Freckleton and Stephens, 2009). Demographic models are fundamentally limited in their ability to provide inferences (hence prediction) due to their failure to represent explicitly the developmental processes responsible for life history dynamics, processes inherent in the functional traits of weed species. An evolutionary-trait representation of weed population dynamics may provide this needed inference.

FoxPatch Representation of Seed Life History. FoxPatch represents life history dynamics with two nested process models. Overarching natural selection processes (table I; Mayr, 2001) are defined by the functional traits responsible for the processes of seed-seedling life history development (figure 1).

Table I. Local adaption of a sexually reproducing weed population by the processes (and component conditions) of natural selection of the fittest phenotypes.

Precondition 1: excess local phenotypes compete for limited opportunity spacetime	
Process step 1: produce phenotypic variation	**Condition 1**: variation in individual traits
	Condition 2: variation in individual fitness
Process step 2: survival and reproduction of the fittest phenotypes	**Condition 3**: survive to reproduce the fittest offspring, eliminate the others
	Condition 4: reproductive transmission of parental traits to offspring
Adaptation arises in the local population of phenotypes	

Figure 1. Schematic diagram of weedy *Setaria* sp. life history soil seed pool behavior: plant/seed state pools (1-5) and processes (A-F; C-D are reversible).



FoxPatch represents weedy *Setaria* species-group (*S. viridis*, *S. verticillata*, *S. pumila*, *S. geniculata*; Dekker, 2003) life history, but is experimentally focused on *S. faberi*. Annual, self-fertilizing *Setaria* weed life history is represented with five life history states (1-5) and six developmental processes (A-F) (figure 1) (Dekker et al., 2003). The risk of death is constant during life history.

DISCUSSION

Precondition for Natural Selection-Elimination. Excess local *Setaria* phenotypes compete for limited opportunity spacetime in a locality. Opportunity spacetime is the locally habitable space for an organism at a particular time which includes its resources (light, water, nutrients, gases) and conditions (heat, weather), disturbance history (e.g. tillage, herbicides, winter freezing), and neighboring organisms (e.g. crops, other weed species) (Dekker, 2009). The character of local spacetime seized and exploited by local populations of *Setaria* is typified by predictable disturbances in resource-rich cropping systems (e.g. Iowa, USA, maize-soybean fields; table III, top, bottom).

Process of Natural Selection 1: Produce Phenotypic Variation. Variation in individual traits (hence individual fitness) is generated during seed fertilization and embryogenesis, and released at seed abscission. Local adaptation arises from natural selection and elimination among these variable phenotypes. Arguably the most crucial group of functional traits in generating phenotypic diversity induced during embryogenesis are those responsible for germinability-dormancy capacity heterogeneity (seed heteroblasty), the blueprint for seedling emergence timing (Jovaag, 2006). The key traits responsible for seed heteroblasty include differential development of three seed compartments enveloping the embryo (Dekker et al., 1996): seed hull shape (Dekker & Luschei, 2009; Donnelly et al., 2009), placental pore and seed transfer aleurone cell layer (TACL) membrane aperture qualities (Rost, 1971; Rost & Lersten, 1970), and the those of a putative oxygen-scavenging protein in the seed (Dekker and Hargrove, 2002). The light environment (photoperiod) of the flowering *Setaria* synflorence is the effective environmental signal modulating the development of these three morpho-physiological traits controlling seed heteroblasty (Atchison, 2001; Dekker, 2003). The traits affecting light interception include plant shoot-tiller architecture and individual seed position on the flowering synflorescence. Experimentally seed heteroblasty is determined by seed germination assays at abscission (figure 2; Atchison, 2001; Jovaag, 2006): after-ripening (AR; 4°C, moist, dark) followed by germination assay (e.g. 15-35°C, moist, light). Induction of heterogeneous seed dormancy occurs at several observable time scales: during the ca. 12d embryogenic period of individual seeds on a parent plant (figure 2, left; Dekker et al., 1996); and within and among populations with seasonal time (figure 2, right; table II). The declining diurnal light period induces increasing germinability (decreasing dormancy) capacity in *S. faberi* seeds as time and photoperiod change (July to November).

Figure 2. *S. faberii* seed germination heterogeneity among individual seeds of a single Ames, Iowa, USA population collected in Julian weeks (JW) 32, 36, and 40, 1998; left: JW 32, frequency/cumulative distributions; right: JW 32, 36, 38, frequency distribution.

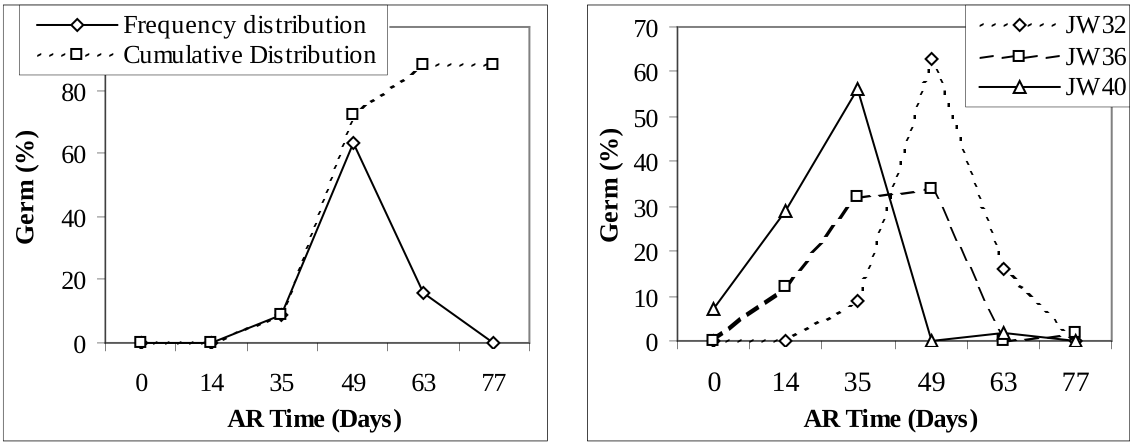


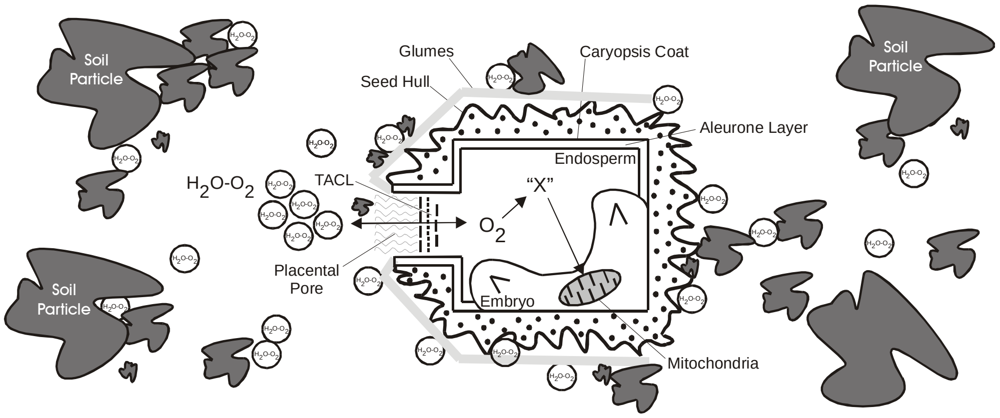
Table II. Difference in *S. faberi* germination (% germ; least square mean) of four 1998 and 1999 populations collected during early (Julian week (JW) 32), middle (JW36) and late (JW40) seasonal periods. [1]ANOVA contrast, probability (p)>.05, ***=p<.001.

CONTRAST [1]	% GERM DIFFERENCE	
	1998	1999
Early - Middle	-37.8***	-23.8***
Early - Late	-58.6***	-48.3***
Middle - Late	-20.9***	-24.4***

Phenotypic variation in a locality is also supplied by seed and pollen dispersal in space (gene flow) at metapopulation scales from landscape to global (population genetic structure; Wang et al., 1995a, b).

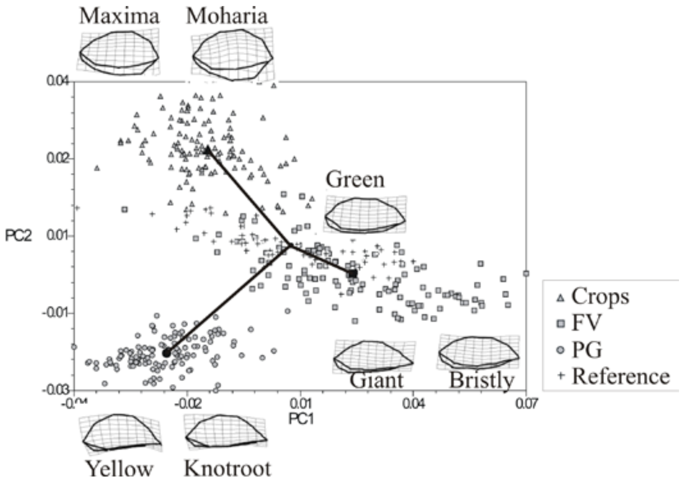
Process of Natural Selection 2: Survival and Reproduction of the Fittest Phenotypes. The second process of natural selection is the survival and reproduction of the variable phenotypes generated by the parent plant. FoxPatch represents this evolutionary process during the *Setaria* seed-seedling life history as the consequence environmental modulation of functional traits stimulating developmental change of seeds in the soil. Heteroblastic seeds begin their life with dispersal in both space and time. Dispersal in time is the formation of persistent soil seed pools in a locality. Seed states and processes of the local population in the soil are regulated by the interaction of three inherent morpho-physiological mechanisms with oxy-hydro-thermal-time (Dekker et al., 2003; Dekker and Hargrove, 2002). These trait-process interactions with soil signals are schematically presented in figure 3 (Dekker et al., 2003).

Figure 3. Schematic diagram of the *Setaria* sp. seed, surrounding soil particles and oxygen dissolved in water (H_2O-O_2). The seed interior (aleurone, TACL, endosperm, O_2-scavenging protein (X), embryo) is surrounded by the non-living glumes, hull, placental pore and the gas- and water-impermeable caryopsis coat.



The seed exterior hull acts as an environmental ‘antenna’ transducting soil signals (oxy-hydro-thermal-time) to the interior embryo. Soil-seed contact allows the accumulation and oxygenation of water on the rugose surface of weedy *Setaria* hull. Oxygenated water is channeled to the placental pore (hence into the interior embryo) by hull morphology. The role of seed hull morphology is apparent in the changes in shape and surface-to-volume ratios in weedy and domesticated *Setaria* species (figure 4; Donnelly et al., 2009). Soil contact, and the formation of oxygenated water films on the hull, play a crucial role in seed germination (Dekker & Luschei, 2009).

Figure 4. A principal components plot of the trajectory analysis for the lateral seed view. All vector magnitudes from the reference (*Setaria viridis* subsp. *viridis*) are significantly different. FV direction (*S. faberi*, *S. verticillata*) is significantly different from crops (*S. viridis* subsp. *italica* races maxima and moharia) and PG (*S. pumila*, *S. geniculata*). FV and PG are not significantly different.



The *Setaria* seed is surrounded by the caryopsis coat composed of several crushed cell layers (Rost, 1971). It is water- and gastight, and continuous except at the placental pore opening on the basal end of the seed. The mature seed is capable of freely imbibing water and dissolved gases, but entry is restricted and regulated by the placental pore and membrane control by the TACL (Rost & Lersten, 1970). Gases entering the moist seed interior must be dissolved in the imbibed water. This seed morphology strongly suggests that seed germination is restricted by water availability in the soil and by the amount of oxygen dissolved in water reaching the inside of the seed symplast to fuel metabolism (Dekker and Hargrove, 2002).

Carbon monoxide (CO) stimulated germination in *S. faberi* has provided evidence of O_2-scavenging in the seed that delays or buffers the germination process: CO was found to poison this O_2 scavenging system (X) and thus speed the time until the critical, germination-threshold amount of O_2 is present in the symplast (Dekker and Hargrove, 2002; Sareini, 2002).

<u>FoxPatch representation of soil environmental signal modulation of seed germinability-dormancy behavior</u>. FoxPatch represents each *Setaria* seed process by a behavior rule, and an algorithmic prediction rule (Dekker et al., 2003). Rules for each life history process (C-E) are a specification of these more general rules:

general seed behavior rule: the behavior of an individual weedy *Setaria* seed in the soil is regulated by the amount of oxygen dissolved in water (the O_2-H_2O signal) that accumulates in the seed symplast, and temperatures favorable (or not) to germination growth (the germination temperature signal), over some time period (cumulatively O_2-H_2O -thermal time).

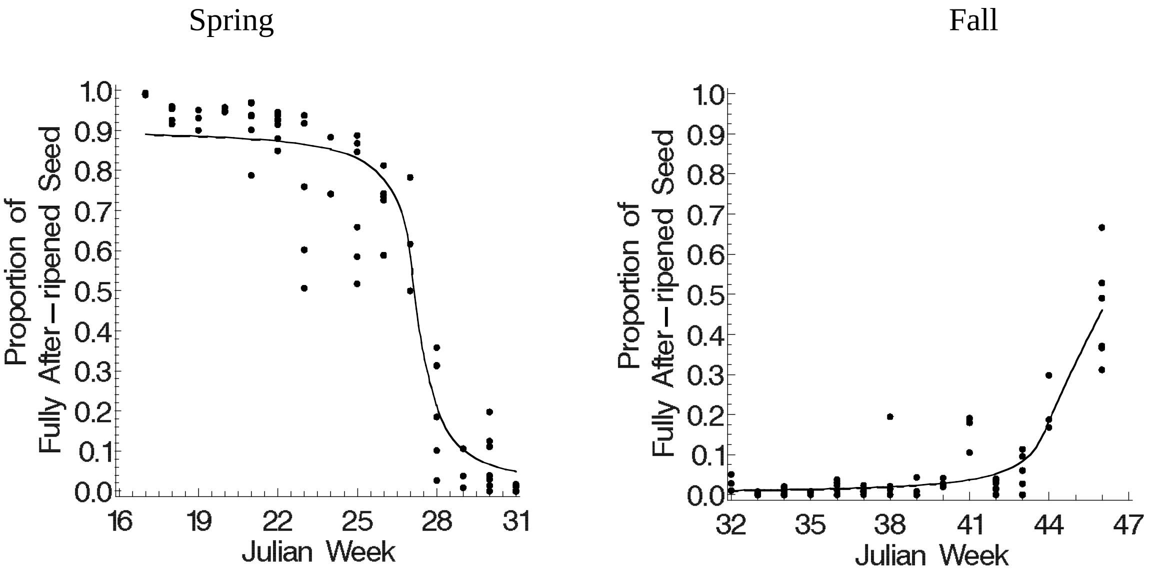
general prediction algorithm: an individual weedy foxtail seed will change state when the minimum inherently-required O_2-H_2O-thermal-time signal is received from its realized environment (plus signals not causing an effect due to inefficient transduction or insensitivity).

The inherent germinability-dormancy capacity induced in an individual seed by the time of abscission (seed starting condition) can be experimentally determined in optimal conditions:

initial individual seed germinability-dormancy capacity: the minimum O_2-H_2O-thermal-time signal required to stimulate germination at abscission

Each seed state change process can be experimentally determined in the field by frequent (e.g. hourly) measurement of soil temperature (thermal time; calculated O_2 solubility at temperature) and H_2O content in the soil-seed profile.
Survive in the soil environment (dispersal in time). Seed in the soil cycle between two reversible states (dormant, germination candidate) until effective signals permit irreversible germination growth leading to seed germination. Seeds dispersed in the local soil seed pool remain alive until they emerge and begin autotrophic vegetative growth to exploit locally available opportunity spacetime. Typically *Setaria* seed germinability-dormancy cycles during the year: relatively greater O_2-H_2O-thermal-time signals increase germinability (e.g. cool moist spring), while relatively lesser signals reinduce secondary dormancy (e.g. hot dry summer) (Figure 5, Jovaag, 2006).

Figure 5. Proportion of highly germinable seed (fully after-ripened) versus Julian week (JW) for spring (JW 16-31, left) and fall (JW 32-47, right), first year after burial of four *S. faberi* Iowa, USA, populations. Dots: individual replicate observations. Solid lines: fitted model (3 parameter Lorentzian functions with a power of the mean variance model.



Emerge as a seedling at opportune seasonal times. Seedling recruitment timing is the single most important determinant of the subsequent interactions between an individual phenotype and its neighbors in a local community that directly determine survival and reproduction. Seed in the soil reversibly cycle between dormant and germination candidate states until conditions permit irreversible germination growth leading to germinated seed. As with all living seed processes in the soil, the effective signal stimulating germinative growth in heterogeneous seed is O_2-H_2O-thermal-time.

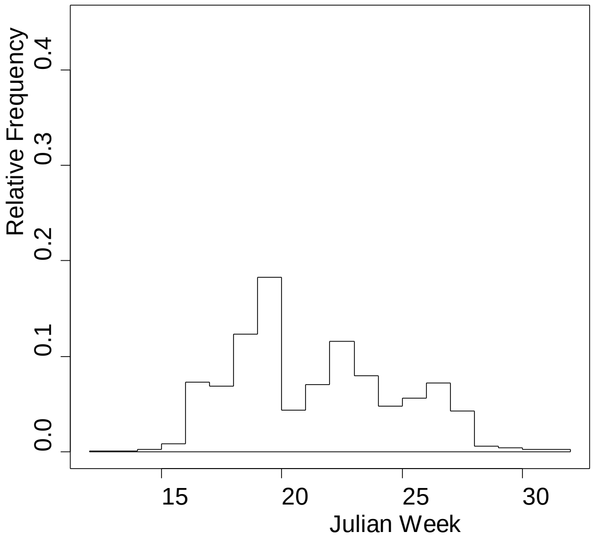

Relative Frequency
0.0
0.1
0.2
0.3
0.4
15
20
25
30
Julian Week

Table III. Calendar of historical, seasonal times (Julian week, month) of agricultural field disturbances (seedbed preparation; planting; weed control, including tillage and herbicides; time after which all cropping operations cease, layby; harvest and autumn tillage), and seedling emergence timing for central and southeastern Iowa, US, *Setaria faberi* population cohorts (all *S. faberi* combined: time, +/- S.E.; mean proportion; see table 3) (Jovaag thesis)

	Month	APRIL			MAY				JUNE					JULY					AUGUST				SEPTEMBER				OCTOBER					NOVEMBER				DEC	
	Julian Week	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Maize	Seedbed Prep		■	■	■																																
	Planting				■	■	■																														
	Weed Control				■	■	■	■	■	■	■																										
	Layby				░	░	░	░	░	■	■																										
	Harvest																										■	■	■	■	■						
	Autumn Tillage																										░	░	■	■	■	■	■				
S. faberi Recruitment Cohorts	Early Spring		■	12	■																																
	Mid-Spring				■	38	■																														
	Late Spring								■	30	■																										
	Early Summer												■	20	■																						
	Summer																		■	0.2	■	■															
	Autumn																															■	0.1	■	■	■	
Soybeans	Seedbed Prep				■	■																															

Planting					░	■	■	░	░	░																										
Weed Control						■	■	■	■	■																										
Layby								■	■	■																										
Harvest																							■	■	■	■	■	■								
Autumn Tillage																												■	■	■						

There exist predictable sources of mortality and recruitment opportunities for these *S. faberi* populations in Iowa, USA, agroecosystems over the course of their annual life histories (table III). The majority of seedlings were recruited in the spring when the risk of mortality is very high from crop establishment practices (seedbed preparation, planting, weed control) and the fecundity potential is the greatest. Weed seedlings emerging early have the greatest time available for biomass accumulation and competitive exclusion of later emerging neighbors. Subsequent fitness devolves on those individual *S. faberi* plants that escape these disturbances (Jovaag, 2006). As seasonal seedling recruitment proceeds potential fecundity and risk change. These factors result in differential seedling recruitment investment and strategy among the remaining emergence cohorts in response to changing opportunity spacetime (tables III, IV).

Table IV. *S. faberi* seedling recruitment cohort (time, Julian week (JW)) exploitation of changing opportunity spacetime in Iowa, USA, maize-soybean cropping fields.

COHORT	1	2	3	4	5	6
SEASON	EARLY				LATE	
	Early Spring	Mid-Spring	Late Spring	Early Summer	Summer	Autumn
TIME (JW)	16-18	18-20	22-24	26-28	32-35	45-49
Fecundity Potential	very high	very high	high	medium	low	very low
Mortality Risk	very high	very high	high	low	low	low
Source(s) of Risk	crop disturbance	crop disturbance	crop disturbance	neighbors	neighbors	crop disturbance; climate
Weed Strategy	escape cropping	escape cropping	escape; post-layby opportunity	post-layby opportunity	post-layby opportunity	post-harvest opportunity
Seedling Investment	12%	38%	30%	20%	0.2%	0.1%

CONCLUSION

There exists a relationship between seed heteroblasty at abscission and its subsequent behavior in the soil that can be exploited to predict recruitment pattern: seed heteroblasty ‘blueprints’ seedling recruitment. Seedling numbers and temporal emergence patterns exploit local opportunity spacetime (Jovaag, 2006). Evidence of this relationship between heteroblasty and emergence numbers was provided by the positive Spearman correlation between dormancy capacity at abscission and the cumulative number of seeds emerged during the first year after burial for both the 1998 and 1999 *S. faberi* populations. Additionally, more dormant populations had lower emergence numbers during the first year after burial than less dormant populations. Early maturing seed was the most dormant and had the least number of seeds emerging. Seed maturing late in the season was the least dormant and had the greatest number of seeds emerging.

Appendix 4

The population genetic structure of the weedy *Setaria* species-group.

[summary statement to start]

Genetic diversity in local populations of several weedy *Setaria* species (*S. faberi*, *S. geniculata*, *S. pumila*, *S. viridis*) from locations around the north temperate regions of the world was evaluated using many allozyme molecular markers to identify specific genotypes (Wang et al., 1995a, 199b).

The pattern of genetic diversity within an individual foxtail species was characterized by unusually low intra-population genetic diversity, and unusually high genetic diversity between populations at a locality, compared to an "average" plant (Dekker, 2003, 2004a; Hamrick and Godt, 1990; Wang et al., 1995a, 199b). These two patterns of population genetic structure appear to typify introduced, self-pollinated weeds that are able to rapidly adapt to local conditions after invasion and colonization (e.g. Brown and Marshall, 1981; Rice and Jain, 1985; Barrett and Richardson, 1986; Barrett, 1988; Barrett and Shore, 1989).

Hamrick and Godt (1990) developed a framework for interpretation of genetic diversity in plants in which diversity estimates for 449 species were summarized and an attempt was made to find correlations between the amount and distribution of allozyme diversity and various life history features. In comparison to an "average" plant species, all four weedy foxtail species contain low to exceedingly low amounts of total genetic variation. Among the four species studied, *S. geniculata* exhibits the highest diversity levels, followed by *S. viridis*, *S. pumila*, and finally *S. faberi*, which is nearly monomorphic as a species. These low diversity estimates are especially noteworthy given the geographic breadth of sampling of each of the four species studied, which in all cases included accessions from at least three different continents (Wang et al., 1995a, 199b).

Although relative genetic diversity within each of the several foxtail species is very low, differences between homogeneous populations at a locality is high, indicating a strong tendency for local adaptation by a single genotype. The limited diversity contained within weedy foxtails is partitioned across the landscape, continent and world among populations as alternative homozygous genotypes. Heterozygosity was rarely detected, suggesting strong inbreeding in nearly all populations of the four species, either in the generalized sense or as a specific consequence of self-pollination. Apomixis in the foxtails cannot be ruled out (Emery, 1957).

Nearly all populations were found to consist of a single multilocus genotype. Foxtail populations are homogeneous but are differentiated from one another by fixation of different alleles at one or more loci. Best expressed as the coefficient of population differentiation (GST), which is much higher in the weedy foxtails (*S. pumila*, 0.73; *S. geniculata*, 0.91; *S. viridis*, 0.65) than in the "average" plant species (0.22; Hamrick and Godt, 1990) (Wang et al, 1995b). In contrast to this indication of population divergence (specialized adaptation), a common multilocus genotype of both *S. viridis* and *S. pumila* occurred in many accessions from widely separated geographic areas (general adaptation).

In addition to the potential selective forces responsible for low genetic diversity and high population differentiation, stochastic forces have played a major role in shaping foxtail population genetic structure. Perhaps the most important phenomenon, in this respect, has been a history of genetic bottlenecks associated with founder events, genetic drift, and natural selection. The effects of these stochastic and selective forces are evident in the allozyme data (Wang et al., 1995a, 1995b).

Green foxtail. The founder effect was observed in *S. viridis* to a certain degree. *S. viridis* accessions from North America had reduced allelic richness compared to those of Eurasia: fewer unique alleles, lower percentage of polymorphic loci, and fewer alleles per locus. Genetic drift probably has occurred in *S. viridis*, as indicated by the many fixed alleles in North American accessions. On the other hand, heterozygosity was equal between Eurasian and North American accessions, and Nei's genetic identity between them was 1.0.

Multiple introductions of *S. viridis*, in the absence of local adaptation, should have produced a random, mosaic pattern of geographic distribution among North American accessions. Instead, a strong intra-continental differentiation was observed in *S. viridis* populations, both in Eurasia and North America (Jusef and Pernes, 1985; Wang et al., 1995a). *S. viridis* populations in North America were genetically differentiated into northern and southern groups separated on either side of a line at 43.5° N latitude. The northern type was less variable than southern type. This regional divergence suggests that natural selection has partitioned *S. viridis* along a north-south gradient. Populations with genotypes more suitable to northern conditions probably flourished there, while those more suited to southern conditions had a fitness advantage in the south.

These results were interpreted to imply that the present patterning among *S. viridis* populations in North America is the consequence of multiple introductions into the New World followed by local adaptation and regional differentiation.

The geographic distance (from global to local) separating foxtail populations does not indicate the genetic distance separating them. The size of the geographic range from which populations were sampled was not an accurate indicator of the extent of genetic diversity found among populations from that region. The degree of genetic differentiation of *S. viridis* local populations at the state, county and farm level showed little hierarchical patterning (Wang et al., 1995a). The genetic diversity of *S. viridis* populations from a particular local geographic area was probably largely determined by both the number of independent introductions to that area, and the intensity and duration of natural selection pressures at those sites.

Yellow foxtail. *S. pumila* local populations are genetically clustered into overlapping Asian, European, and North American groups (Wang et al., 1995b). *S. pumila* populations from the native range (Eurasia) contained greater genetic diversity and a higher number of unique alleles than those from the introduced range (North America). Within Eurasia, Asian populations have greater genetic diversity than those from Europe; more unique alleles were found in Asian populations. These results were interpreted as indicating the there have been numerous introductions of *S. pumila* from Eurasia to North America. The Asian cluster was most diverse, although it represented the smallest numbers of samples, indicating *S. pumila* originated in Asia, not Europe. The majority of introductions of *S. pumila* to North America are from Asia.

The pattern of *S. pumila* genetic variability in North American was unexpected (Wang et al., 1995b). Within the distinct cluster from North America, nearly the entire diversity of *S. pumila* appears to be encompassed by accessions from local Iowa populations, whereas those collected from the other North American locations were nearly monomorphic for the same multilocus genotype. In this respect, it is significant or coincidental that this pattern was repeated in the diversity data for *S. viridis*, also a native of Eurasia (Wang et al., 1995a). Iowa possesses a surprising genetic diversity in the foxtails. All five weedy foxtail species are present: *S. verticillata*, *S. faberi*, *S. viridis*, *S. geniculata* and *S. pumila*. Typically two or more *Setaria* species occur in same field at the same time. It was also noted that Iowa is the center of the north-south agro-ecological gradient in North America, perhaps leading to greater environmental heterogeneity and opportunity for the several species to coexist.

Knotroot foxtail. Despite originating on different continents, the genetic diversity patterns for *S. geniculata* reflect those for *S. pumila* and *S. viridis*: greater genetic diversity was observed in accessions from the New World than in those from the introduced range (Eurasia) (Wang et al., 1995b). These data most likely reflect genetic bottlenecks associated with sampling a limited number of founding propagules and the history of multiple introductions from the Americas to Eurasia. The population genetic structure of *S. geniculata* consists of three nearly distinct clusters, groups from Eurasia, northern United States, southern United States. Accessions from Eurasia and North America are approximately equally diverse genetically. Within North America, *S. geniculata* accessions were strongly differentiated into southern and northern groups at about the Kansas-Oklahoma border (37° N latitude); indicating greater genetic differentiation within North American populations than between North American and Eurasian populations.

Giant foxtail. *S. faberi* contains virtually no allozyme variation. A native of southern China, fifty of the 51 local accessions of *S. faberi* surveyed were fixed for the same multilocus genotype (Wang et al., 1995b).

GLOSSARY

adaptation:
1: the process of adjustment of an individual organism to environmental stress; adaptability;
2: process of evolutionary modification which results in improved survival and reproductive efficiency;
3: any morphological, physiological, developmental or behavioral character that enhances survival and reproductive success of an organism
4: a positive characteristic of an organism that has been favored by natural selection and increases the fitness of its possessor (Wikipedia, 5.08)

age structure: the number or percentage of individuals in each age class of a population; age distribution; age composition

agroecosystem: an agricultural ecosystem: row crop (i.e. corn), solid planted crop (i.e. wheat), perennial forage, managed forest, rangeland, etc.; crop rotation

agroecotype: an edaphic ecotype adapted to cultivated soils

agrestals: growing on arable land

allele: any of the different forms of a gene occupying the same locus (q.v. on homologous chromosomes), and which undergo meiotic pairing (q.v. and can mutate one to another)

amensalism: an interspecific interaction in which one organism, population or species is inhibited, typically by toxin produced by another (amensal), which is unaffected

androdioecious: used of plant species having male and hermaphrodite flowers on separate plants

apomixis: in botany, apomixis (also called apogamy) is asexual reproduction, without fertilization. In plants with independent gametophytes (notably ferns), apomixis refers to the formation of sporophytes by parthenogenesis of gametophyte cells. Apomixis also occurs in flowering plants, where it is also called agamospermy. Apomixis in flowering plants mainly occurs in two forms:

> **agamogenesis**: (also called gametophytic apomixis), the embryo arises from an unfertilized egg that was produced without meiosis.
>
> **adventitious embryony**, a nucellar embryo is formed from the surrounding nucellus tissue.

archetype: 1. a perfect or typical specimen; 2. an original model or pattern; prototype

biodiversity
1: the variety of organisms considered at all levels, from genetic variants of a single species

through arrays of species to arrays of genera, families and still higher taxonomic levels;
2: includes the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live;
3: the totality of biological diversity

bottleneck (genetic): a sudden decrease in the size of a population with corresponding reduction of total genetic variability

bottleneck effect: a conceptual □occurence of genetic drift in populations reduced in size through fluctuations in abundance.

catastrophes:
1: an event subverting the order or system of things; significant population decrease, possible local extinction
2: disaster, a horrible event (Wikipedia, 5.08)

> **catastrophe theory**: a field of mathematics that studies how the behaviour of dynamic systems can change drastically with small variations in specific parameters (Wikipedia, 5.08)

colonization:
1: the successful invasion of a new habitat by a species (Lincoln et al., 1998)
2: the occupation of bare soil by seedlings or sporelings (Lincoln et al., 1998)
3: (of plants and animals) to become established in (a new environment) (Anonymous, 1979)

colonizing species: a plant, typically r-selected, which invades and colonizes a new habitat or territory

□**commensalism**: symbiosis in which one species derives benefit from a common food supply whilst the other species is not adversely affected

community
1: any group of organisms belonging to a number of different species that co-occur in the same habitat or area and interact through trophic and spatial relationships; typically characterized by reference to one or more dominant species (Lincoln)
2: in ecology, an assemblage of populations of different species, interacting with one another; sometimes limited to specific places, times, or subsets of organisms; at other times based on evolutionary taxonomy and biogeography; other times based on function and behavior regardless of genetic relationships (Wikipedia, 6.08)

> **biological community**
> 1: biocoenosis, biocoenose, biocenose
> 2: all the interacting organisms living together in a specific habitat (or biotope); biotic community, ecological community; the extent or geographical area of a biocenose is limited only by the requirement of a more or less uniform species composition. (Wikipedia, 6.08)

competition:
1: the simultaneous demand by two or more organisms or species for an essential common resource that is actually or potentially in limited supply (exploitation competition)
2: the detrimental interaction between two or more organisms or species seeking a common resource that is not limiting (interference competition)
3: the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space (mechanistic; Grime, 1979)
4: an interaction between species in a mixture in which each lowers the net reproductive rate of the other (demographic outcome)

competitive exclusion: the exclusion of one species by another when they compete for a common resource that is in limited supply

competitive exclusion principle: a theory which states that two species competing for the same resources cannot stably coexist, if the ecological factors are constant; complete competitors cannot coexist. Either of the two competitors will always take over the other which leads to either the extinction of one of the competitors or its evolutionary or behavioural shift towards a different ecological niche (Wikipedia, 5.08).

cycle:
1: happening at regular intervals
2: an interval of space or time in which one set of events or phenomena is completed
3: a complete rotation of anything
4: a process that returns to its beginning and then repeats itself in the same sequence (Wikipedia, 5.08)

demography: the study of populations, especially of growth rates and age structure

dioecious: having unisexual reproductive units with male and female plants (flowers, conifer cones, or functionally equivalent structures) occurring on different individuals; from Greek for "two households". Individual plants are not called dioecious: they are either gynoecious (female plants) or androecious (male plants).

> **androecious**: plants producing male flowers only, produce pollen but no seeds, the male plants of a dioecious species.
>
> **gynoecious**: plants producing female flowers only, produces seeds but no pollen, the female of a dioecious species. In some plant species or populations all individuals are gynoecious with non sexual reproduction used to produce the next generation.

dispersal
1: the act of scattering, spreading, separating in different directions (Anonymous, 2001)
2: the spread of animals, plants, or seeds to new areas (Anonymous, 1979)
3: outward spreading of organisms or propagules from their point of origin or release

(Lincoln et al., 1998)
4: the outward extension of a species' range, typically by a chance event (Lincoln et al., 1998)
5: the search by plant propagules (e.g. seeds, buds) for opportunity space

disturbance
1: the act of disturbing or the state of being disturbed (Anonymous, 1979, 2001)
2: an interruption or intrusion (Anonymous, 1979, 2001)
3: destruction of biomass by any natural or human agency (Silvertown and Charlesworth, 2001)
4: an interruption or intrusion with direct and indirect spatial, temporal, biological or abiological effects that alters or destroys a biological individual or community

ecological guild:
1: a group of species having similar ecological resource requirements and foraging strategies, and therefore similar roles (niches) in the community
2: groups of species that exploit resources in a particular way (Silvertown, 2001)

ecology: the study of the interrelationships between living organisms and their environment

ecosystem
1: a community of organisms and their physical environment interacting as an ecological unit; the entire biological and physical content of a biotope
2: an ecosystem is a natural unit consisting of all plants, animals and micro-organisms (biotic factors) in an area functioning together with all of the non-living physical (abiotic) factors of the environment (Wikipedia, 6.08)
3: a biotic community along with its physical environment (Tansley, 1935)

ecotype:
1: a locally adapted population; a race or infraspecific group having distinctive characters which result from the selective pressures of the local environment; ecological race;
2: a subunit capable of interbreeding with members of that and other ecotypes q.v. comprising individuals capable of interbreeding with members of that and other ecotypes within the ecospecies but remaining distict through selection and isolation;
3: biotype

epistasis
1: a class of interactions between pairs of genes in their phenotypic effects; technically the interactions are non-additive which means, roughly, that the combined effect of the two genes is not the same as the sum of their separate effects; for instance, one gene might mask the effects of the other. The word is mostly used of genes at different loci, but some authors use it to include interactions between genes at the same locus, in which case dominance/recessiveness is a special case (Dawkins,1999)
2: the interaction of non-allelic genes in which one gene (epistatic gene) masks the expression of another at a different locus (Lincoln, et al.)

3: the nonreciprocal interaction of nonallelic genes; the situation in which one gene masks the expression of another.

epigenesis:
1: 'in addition to' genetic information encoded in DNA sequence
2: heritable changes in gene function without DNA change

epigenetics
1: the study of the <u>mechanism that produces phenotypic effects from gene activity</u>, processes involved in the unfolding development of an organism, during differentiation and development, or heritable changes in gene expression that do not involve changes in gene sequence.
2: the study of how environmental factors affecting a parent can result in changes in the way genes are expressed in the offspring, heritable changes in gene function without DNA change.
3: the study of reversible heritable changes in gene function that occur without a change in the sequence of nuclear DNA: how gene-regulatory information that is not expressed in DNA sequences is transmitted from one generation (of cells or organisms) to the next,.

establishment
1: growing and reproducing successfully in a given area (Lincoln et al., 1998)

evolution
1: Any gradual directional change, unfolding;
2: Any cumulative change in the characteristics of organisms or populations from generation to generation; descent or development with modification;
3: change in the frequency of genes in a population

> **microevolution**:
> 1: minor evolutionary events usually viewed over a short period of time, consisting of changes in gene frequencies, chromosome structure or number within a population over a few generations (Lincoln)
> 2: the occurrence of small-scale changes in allele frequencies in a population, over a few generations, also known as change at or below the species level (Wikipedia, 5.08)
>
> **macroevolution**:
> 1: major evolutionary events or trends usually viewed through the perspective of geological time; the origin of higher taxonomic categories; transspecific evolution; macrophylogenesis; megaevolution (Lincoln)
> 2: a scale of analysis of evolution in separated gene pools; change that occurs at or above the level of species (Wikipedia, 5.08)

extinction
1: the process of elimination, as of less fit genotypes
2: the disappearance of a species or taxon from a given habitat or biota, not precluding later recolonization from elsewhere

fecundity
1: the potential reproductive capacity of an organism or population, measured by the number of gametes or asexual propagules (Lincoln et al., 1998)
2: potential fertility or the capability of repeated fertilization. Specifically the term refers to the quantity of gametes, generally eggs, produced per individual over a defined period of time

feral plants: a plant that has reverted to the wild from a state of cultivation or domestication; wild, not cultivated or domesticated

fitness:
1: the average number of offspring produced by individuals with a certain genotype, relative to the numbers produced by individuals with other genotypes.
2: the relative competitive ability of a given genotype conferred by adaptive morphological, physiological or behavioral characters, expressed and usually quantified as the average number of surviving progeny of one genotype compared with the average number of surviving progeny of competing genotypes; a measure of the contribution of a given genotype to the subsequent generation relative to that of other genotypes (Lincoln, et al., 1998)
3: the relative ability of an organism to survive and transmit its genes to the next generation

founder effect: that only a small fraction of the genetic variation of a parent population or species is present in the small number of founder members of a new colony or population

frequency-dependent selection: selection occurring in the situation in which the relative fitness of alternative genotypes is related to their frequency of occurrence within a population

gene flow:
1: the exchange of genetic factors within and between populations by interbreeding or migration; incorporation of characteristics into a population from another population
2: in population genetics, gene flow (also known as gene migration) is the transfer of alleles of genes from one population to another (Wikipedia, 5.08).

genet:
1: unit or group derived asexually from a single zygote: seedling, clone.
2: a clonal colony, a group of genetically identical individuals that have grown in a given location, all originating vegetatively (not sexually) from a single ancestor.

ramet: an individual in a plant genet

genetic drift:
1: the occurrence of random changes in the gene frequencies of small isolated populations, not due to selection, mutation or immigration; drift; Sewall Wright effect; equivalent to static noise in system; adaptive alleles can be lost in process, especially in small populations

2: in population genetics, genetic drift (or more precisely allelic drift) is the evolutionary process of change in the allele frequencies (or gene frequencies) of a population from one generation to the next due to the phenomena of probability in which purely chance events determine which alleles (variants of a gene) within a reproductive population will be carried forward while others disappear (Wikipedia, 5.08).

genotype:
1: The hereditary or genetic constitution of an individual; all the genetic material of a cell, usually referring only to the nuclear material;
2: All individuals sharing the same genetic constitution; biotype;
3: The specimen on which a genus-group taxon is based; the primary type of the type species

guild:
1: a group of species having similar ecological resource requirements and foraging strategies, and therefore similar roles (niches) in the community
2: groups of species that exploit resources in a particular way (Silvertown, 2001)

gynodioecious: used of plants or plant species having female (pistillate) and hermaphrodite (perfect) flowers on separate plants in a population or species

habitat:
1: the locality, site and particular type of local environment occupied by an organism
2: local environment
3: the physical conditions that surround a species, or species population, or assemblage of species, or community (Clements and Shelford, 1939).4: an ecological or environmental area that is inhabited by a particular species; the natural environment in which an organism lives, or the physical environment that surrounds (influences and is utilized by) a population (Wikipedia, 5.08).

> **microhabitat**: a physical location that is home to very small organisms (e.g. a seed in the soil); microenvironment is the immediate surroundings and other physical factors of an individual plant or animal within its habitat.

Hardy-Weinberg equilibrium: the maintenance of more or less constant allele frequencies in a population through successive generations; genetic equilibrium

Hardy-Weinberg law: that allele frequencies will tend to remain constant from generation to generation and that genotypes will reach an equilibrium frequency in one generation of random mating and will remain at that frequency thereafter; demonstrating that meiosis and recombination do not alter gene frequencies

hedge-betting: strategy of spreading risks to reduce the variance in fitness, even though this reduces intrinsic mean fitness; favored in unpredictable environments where the risk of death is high because it allows a species to survive despite recurring, fatal, disturbances; risks can be spread in time or space by either behavior or physiology; risk spreading can be conservative (risk avoidance by a single phenotype) or diversified (phenotypic variation within a single genotype) (Jovaag et al., 2008C)

heredity: the mechanism of transmission of specific characters or traits from parent to offspring.

hybridization: any crossing of individuals of different genetic compostion, typically belonging to separate species, resulting in hybrid offspring

inheritance: the transmission of genetic information from ancestors or parents to descendants or offspring.

introgression: the spread of genes of one species into the gene pool of another by hybridization and backcrossing; introgressive hybridization

invasive species:
1: organism undergoing a mass movement or encroachment from one area to another (Lincoln et al., 1998)
2: an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health (Anonymous, 1999 in dekker 05)
3: a species that is non-native (or alien) to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm human health (Anonymous, 2004 in dekker 05)

life history:
1: the significant features of the life cycle through which an organism passes, with particular reference to strategies influencing survival and reproduction
2: how long it typically lives, how long it usually takes to reach reproductive size, how often it reproduces and a number of other attributes that have demographic and fitness consequences (Silvertown & Charlesworth, 2001)

locality: the geographic position of an individual population or collection

microhabitat:
1: a physical location that is home to very small organisms (e.g. a seed in the soil); microenvironment is the immediate surroundings and other physical factors of an individual plant or animal within its habitat
2: a very localized habitat (e.g. on the size scale of an individual seed in the soil seed bank)

microsite: analogous to a microhabitat; e.g. the site perceived by a seed in the seed bank, or a seedling in a field.

mortality: death rate as a proportion of the population expressed as a percentage or as a fraction; mortality rate; often used in a general sense as equivalent to death; often divided into these partially overlapping concepts:

density-dependent mortality: mortality and a decrease in population density (numbers per unit area) due to the effects of population density (self-thinning)

density-independent mortality: mortality and a decrease in population density due to any factor which is independent of population density

mutation
1: a sudden heritable change in the genetic material, most often an alteration of a single gene by duplication, replacement or deletion of a number of DNA base pairs;
2: an individual that has undergone such a mutational change; mutant

mutualism: a symbiosis in which both organisms benefit, frequently a relationship of complete dependence

natural selection:
1: the non-random and differential reproduction of different genotypes acting to preserve favorable variants and to eliminate less favorable variants;
2: viewed as the creative force that directs the course of evolution by preserving those variants or traits best adapted in the face of natural competition
3: essence of theory of evolution by natural selection is that genotypes with higher fitness leave a proportionately greater number of offspring, and consequently their genes will be present in a higher frequency in the next generation

niche:
1: the ecological role of a species in a community; conceptualized as the multidimensional space, of which the coordinates are the various parameters representing the condition of existence of the species, to which it is restricted by the presence of competitor species;
2: loosely as an equivalent of microhabitat
3: the relational position of a species or population in its ecosystem; how an organism makes a living; how an organism or population responds to the distribution of resources and neighbors and how it in turn alters those same factors (Wikipedia, 5.08)

fundamental niche: the entire multidimensional space that represents the total range of conditions within which an organism can function and which it could occupy in the absence of competitors or other interacting (neighbor) species

realized niche: that part of the fundamental niche q.v. actually occupied by a species in the presence of competitive or interactive (neighbor) species

n-dimensional niche hypervolume:
1: the multi-dimensional space of resources and conditions available to, and specifically used by, organisms in a locality
2: the phenotype is described by the niche hypervolume; phenotype = G x E = realized niche; the selection pressure consequence of the G x E interaction
3: the limits or borders within which which a species has adapted,

4: experimentally defined by the testable parameters (dimensions) one can evaluate; the parameters determining the form of existence of a plant

parasitism: an obligatory symbiosis between individuals of two different species, in which the parasite is metabolically dependent on the host, and in which the host is typically adversely affected by rarely killed

phenotype:
1: the sum total of observable structural and functional properties of an organism; the product of the interaction between the genotype and the environment; reaction type; phenome
2: the characters of an organism, whether due to the genotype or environment.
3: "The manifested attributes of an organism, the joint product of its genes and their environment during ontogeny. A gene may be said to have phenotypic expression in, say, eye colour. In this book the concept of phenotype is extended to include functionally important consequences of gene differences, outside the bodies in which the genes sit." (Dawkins,1999), p.299)

extended phenotype: "All effects of a gene upon the world. As always, 'effect' of a gene is understood as meaning in comparison with its alleles. The conventional phenotype is the special case in which the effects are regarded as being confined to the individual body in which the gene sits. In practice it is convenient to limit 'extended phenotype' to cases where the effects influence the survival chances of the gene, positively or negatively." (Dawkins, 1999, p.293).

phenotypic plasticity:
1: The capacity of an organism to vary morphologically, physiologically or behaviorally as a result of environmental flucuations; reaction type
2: the capacity for marked variation in the phenotype as a result of environmental influences on the genotype during development [during the plants life history]

ploidy: the number of sets of chromosomes present (e.g. haploid, diploid, □orphologi)

polyploidy: multiple sets of homologous chromosomes in an organism (e.g. tetraploid, octaploid)

population:
1: all individuals of one or more species within a prescribed area;
2: a group of organisms of one species, occupying a defined area and usually isolated to some degree from other similar groups

population biology: Study of the spatial and temporal distributions of organisms

population genetics: Study of gene frequencies and selection pressures in populations

population genetic structure: the genetic composition and gene frequencies of individuals in a population

population dynamics: the study of changes within populations and of the factors that cause or influence those changes; the study of populations as functioning systems.

productivity
1: the potential rate of incorporation or generation of energy or organic matter by an individual, population or trophic unit per unit time per unit area or volume; rate of carbon fixation
2: fertility

reaction norm:
1: set of phenotypes expressed by a singe genotype, when a trait changes continuously under different environmental and developmental conditions
2: phenotype space; opportunity space; hedge-bet structure
3: a norm of reaction describes the pattern of phenotypic expression of a single genotype across a range of environments (Wikipedia, 5.08)

recombination
1: any process that gives rise to a new combination of hereditary determinants, such as the reassortment of parental genes during meiosis through crossing over; mixing in the offspring of the genes and chromosomes of their parents.
2: event, occurring by crossing over of chromosomes during meiosis, in which DNA is exchanged between a pair of chromosomes of a pair. Thus, two genes that were previously unlinked, being on different chromosomes, can become linked because of recombination, and linked genes may become unlinked.

recruitment
1: seedling and bud shoot emergence
2: the influx of new members into a population by reproduction or immigration (Lincoln et al., 1998)

reproduction: the act or process of producing offspring

reproductive isolating mechanism: a cytological, anatomical, physiological, behavioral, or ecological difference,or a geographic barrier which prevents successful mating between two or more related groups of organisms.

reproductive isolation
1: the absence of interbreeding between members of different species
2: the condition in which interbreeding between two or more populations is prevented by intrinsic factors

ruderals: a plant inhabiting a disturbed site

segregation distortion: the unequal segregation of □genes in a heterozygote due to:

1: an aberrant meiotic mechanism; e.g. meiotic drive: any mechanism operating differentially during meiosis in a heterozygote to produce the two kinds of gametes with unequal frequencies;
2: other phenomena that result in altered gametic transmission ratios; e.g. in pollen competition where one allele results in a more slowly growing pollen tube than an alternate allele. Gametes bearing this allele will therefore show up in zygotes at a frequency less than 50%, as will all genes linked to the slow growing pollen tube allele (Wendel, pers. comm., 1998).

selection:
1: gametic and zygotic differential mortality; non-random differential reproduction of different genotypes in a population
2: certain traits or alleles of a species may be subject to selection in the context of evolution. Under selection, individuals with advantageous or "adaptive" traits tend to be more successful than their peers reproductively: they contribute more offspring to the succeeding generation than others do. When these traits have a genetic basis, selection can increase the prevalence of those traits, because offspring will inherit those traits from their parents. When selection is intense and persistent, adaptive traits become universal to the population or species, which may then be said to have evolved (Wikipedia, 5.08).

natural selection: the non-random and differential reproduction of different genotypes acting to preserve favorable variants and to eliminate less favorable variants; viewed as the creative force that directs the course of evolution by preserving those variants or traits best adapted in the face of natural competition

artificial selection: selection by humans; domestication; selective breeding.

directional selection: selection for an optimum phenotype resulting in a directional shift in gene frequencies of the character concerned and leading to a state of adaptation in a progressively changing environment; dynamic selection; progressive selection

disruptive selection: selection for phenotypic extremes in a polymorphic population, which preserves and accentuates discontinuity; centrifugal selection; diversifying selection.

stabilizing selection: selecting for the mean, mode or intermediate phenotype with the consequent elimination of peripheral variants, maintaining an existing state of adaptation in a stable environment; centripetal selection; normalizing selection.

somatic polymorphism
1: production of different plant parts, or different plant behaviors, within the same individual plant; the expression of somatic polymorphism traits is not much altered by the environmental conditions it encounters (as opposed to phenotypic plasticity)
2: the occurrence of several different forms of a structure-organ of a plant body; distinctively different forms adapted to different conditions

speciation
1: The formation of new species;
2: the splitting of a phylogenetic lineage;
3: acquistion of reproductive isolating mechanisms producing discontinuities between populations;
4: process by which a species splits into 2 or more species
5: the evolutionary process by which new biological species arise (Wikipedia, 5.08)

species
1: a group of organisms, minerals or other entities formally recognized as distinct from other groups;
2: a taxon of the rank of species; in the hieracrchy of biological classification the category below genus; the basic unit of biological classification; the lowest principal category of zoological classification
3: a group of morphologically similar organisms of common ancestry that under natural conditions are potentially capable of interbreeding
4: a species is a group of interbreeding natural populations that are reproductively isolated from other such groups (Lincoln)
5: the basic units of biological classification and a taxonomic rank; a group of organisms capable of interbreeding and producing fertile offspring (Wikipedia, 5.08)

species-group: A group of closely related species, usually with partially overlapping ranges; sometimes used as an equivalent of superspecies. [NOTE: the idea here is that the related species occupy overlapping niches]

stability: [dictionary, lincoln[

> **ecological stability**:
> 1: connoting a continuum, ranging from resilience (returning quickly to a previous state) to constancy (lack of change) to persistence (simply not going extinct); the precise definition depends on the ecosystem in question, the variable or variables of interest, and the overall context
> 2: in conservation ecology, populations that do not go extinct; in mathematical models of systems, Lyapunov stability (dynamical system that start out near an equilibrium point stay there forever) (Wikipedia, 6.08)
>
>> **ecological stability, constancy and persistence**: living systems that can remain unchanged in observational studies of ecosystems (Wikipedia, 6.08)
>>
>> **ecological stability, resistance and inertia (or persistence)**:
>> 1: a system's response to some perturbation (disturbance; any externally imposed change in conditions, usually happening in a short time period)
>> 2: resistance is a measure of how little the parameter of interest changes in response to external pressures

3: inertia (or persistence) implies that the living system is is able to resist external fluctuations (Wikipedia, 6.08)

ecological stability, resilience, elasticity and amplitude:
1: resilience is the tendency of a system to return to a previous state after a perturbation
2: elasticity and amplitude are measures of resilience; elasticity is the speed with which a system returns; amplitude is a measure of how far a system can be moved from the previous state and still return (Wikipedia, 6.08)

sustainability:
1: humanity's investment in a system of living, projected to be viable on an ongoing basis that provides quality of life for all individuals of sentient species and preserves natural ecosystems
2: a characteristic of a process or state that can be maintained at a certain level indefinitely.
3: environmental, the potential longevity of vital human ecological support systems, such as the planet's climatic system, systems of agriculture, industry, forestry, fisheries, and the systems on which they depend
4: how long human ecological systems can be expected to be usefully productive; emphasis on human systems and anthropogenic problems (Wikipedia, 6.08)

trait:
1: a character: any detectable phenotypic property of an organism
2: any character or property of an organism
3: a characteristic feature or quality distinguishing a particular person or thing

weed: [see chapter 1]

Bailey weed: useless, unwanted, undesirable

Baker weed: a plant is a weed if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed my man (without, of course, being deliberately cultivated plants)

Brenchley weed:
1: competitive and aggressive behavior
2: appearing without being sown or cultivated

Dekker weed: plant not desired by humans persistant in a disturbed location

Emerson weed: a plant whose virtues have not yet been discovered

Gray weed: persistance and resistance to control (1879)

Harper weed: a plant that grows spontaneously in a habitat greatly modified by human action

Thomas weed: unsightly

WSSA weed: a plant out of place (as determined by humans)

INDEX