New Weed Biology Laboratory

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Jack Dekker

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The Evolutionary Ecology of Weeds Narrative

Jack Dekker
New Weed Biology Laboratory
Portland, Oregon 97214 USA
newweedbiolab@gmail.com
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Jack Dekker

Weeds-R-Us Press
New Weed Biology Laboratory
newweedbiolab@gmail.com
Portland, Oregon 97214 USA

Weeds-Я-Us
The nature of weed biology is more apparent when presented as a story. Within the book Evolutionary Biology of Weeds there are multiple narrative threads that provide an enriched way of more fully seeing weeds as they are.

The imaginary story of the weedy foxtails covers long periods of time in which they evolve under the guiding hands of human agriculture. What story could our weeds tell us if they could only speak?

Where did this book come from? Why was it necessary to write and publish this book? The story of its development falls outside of a teaching textbook and has its own personal history.

The 1st edition of Evolutionary Biology of Weeds is the compilation of notes used in teaching Agronomy 317-517, Weed Biology. It was a useful tool to initiate classroom discussions with students. It remains free as a .pdf download. The 2nd edition is an expanded, edited, version of the 1st edition. The other goal of this book on the EEW narrative is to provide potential users a clear idea of what the new revised, expanded 2nd edition contains.
The Evolutionary Ecology of Weeds Narrative

FOREWORD

A biological explanation

This book is an explanation 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 and 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 explanations of 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 (Dobzhansky, 1973). 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.

Weeds are plants too. The 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. Seizing and exploiting opportunity. The thesis of this book is that human disturbance (e.g. tillage, herbicides, atmospheric pollution, frozen winter) creates opportunity spacetime by leaving unused resources (e.g. nitrogen, water, light) 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.

How I came to write this book

The story of this book is the story of the evolution of my understanding of weed biology and how I came to the ecological evolutionary perspective presented. This book is also the story of the evolution of weed control since the mid-20th century: from a wide diversity of herbicides and numerous agricultural chemical companies to consolidation with the seed industry and the dominance of proprietary transgenic crops in North America today.

Understanding weed biology began with my observations of herbicide activity, which inexorably drew me to the complexities of weed biology. A summer internship with Elanco testing trifluralin on wheat in North Dakota in the mid-1970’s as a Univ. of Minnesota undergraduate began my experience with weeds. It was the golden era of weed science. Ph.D. level jobs abounded in both the growing agricultural chemical industry and an expanding commitment by public universities to weed science. After graduating from Michigan State Univ. in 1980 I took a job at the Univ. of Guelph, Ontario Agriculture College in Ontario, Canada. I developed a research program evaluating herbicides and studying weed biology. It was a fertile environment in which to learn about both plant physiology and evolutionary ecology. Evaluating the numerous herbicides available in the 1980’s was a wonderful opportunity to learn about plant physiology. Why did the crop live and weed die? Why did the crop injury appear in one situation and not another? Why did herbicides fail? Herbicide evaluation was also a wonderful opportunity to learn about plant evolutionary ecology. Why did herbicide resistant weeds appear? Why did weed populations in a particular crop ‘shift’ over years when a new herbicide was introduced?
The crucial role of functional traits to plant growth and development was revealed in the process of evaluating herbicides and their physiology, and documenting the appearance of resistance weeds. Herbicides are physiological probes with considerable specificity and activity in plants. Atrazine taught me about photosynthesis and the pleiotropic consequences of a single chloroplast gene mutation. Glyphosate, the aryl-oxy-phenoxy and cyclohexenones taught me about phloem translocation and apical dominance in perennial weeds. I learned about microtubule cell ultrastructure scaffolding from trifluralin, about free radical quenching in plant tissues from paraquat, about very rapid microbial degradation of thiocarbamates in ‘history’ soils, about leaf lipids from alachlor, and about auxins from 2,4-D and 2,4,5-T. I learned about glutathione-s-transferase and oxidative degradation of several herbicides, including resistant weed variants.

With time new insights from herbicides into these important functional traits decreased. I found myself becoming more interested in their consequences in the local crop-weed community. The behavior of my untreated experimental controls provided more insight than those with herbicides.

Predicting soybean (Glycine max) yield losses due to velvetleaf (Abutilon theophrasti) infestation was my first tentative step into weed ecology. I became fascinated with C.T. de Wit’s ‘On Competition’ and the replacement series experimental design to characterize plant competition. I read of ‘density-yield’ functions and other experimental designs of the pioneering Japanese researchers (e.g. Hozumi, Kira, Shinozaki, Yoda). Utilizing these approaches taught me the perils of observation. I measured growth and yield as aggregated quantities to which I applied statistics: I concluded velvetleaf inhibited soybeans by means of allelopathy. I was dead wrong. It was easy to measure plant growth in the field when and how I wanted, lump these quantities into means, and finally to digest them with statistics. Much easier than to observe with my eyes what the weeds and crops were really doing. Subsequent studies by William Akey clearly showed that phototropic stem internode elongation in response to canopy light resulted in velvetleaf growing taller than soybeans. Yield losses were due to shading effects. The crucial functional trait that makes the velvetleaf phenotype so successful is its ability to grow tall it has to in order to shade its neighbor and seize and exploit light opportunity spacetime. Photomorphogenesis was so much less scientifically sexy than allelopathy. My suspicion of the convenience of statistics over observing was just beginning.

Observing s-triazine resistance in weeds provided my first big understanding of weed evolutionary ecology. Ecology became apparent with human tools interacting with specific plant systems. First, revealing the mechanisms that provided tolerance to atrazine. Then came deeper insights of how these R mutants conducted their life histories in the absence of herbicides. Interactions of weeds with humans were expressions of functional traits of successful individual phenotypes. Heterogeneous collections of different phenotypes in local populations provided the excess individuals amongst which the best were able survive and exploit local opportunity. Evolution by means of natural selection and elimination was the only plausible explanation of the nature I observed.

In 1989 I began to focus my research on the weedy foxtails, Iowa’s number one weed, a group I came to know as the Setaria species-group. I observed certain crucial functional traits expressed by the Setaria seed phenotype revealed the same biology as herbicide resistant weeds: the best variants of the population with those traits seized, exploited and reproduced to their neighbors’ disadvantage.

When herbicides were first commercially available beginning in the late 1940’s their efficacy was often evaluated on their effects on ‘weeds’ and ‘grasses’. My generation improved on this, but we still lumped ‘foxtails’ and ‘pigweeds’ into the same category. With a closer look I realized there was more variation in weed populations that I first thought, the specific components of these species-groups were not all quite the same. There exists a tradition in other pest disciplines, Plant Pathology and Entomology, for a researcher to devote effort to a single species or group. What is lost in narrowed focus is paid back in depth of understanding of the pest organism and its life history. No such tradition exists in Weed Science. Generic solutions to common weed problems have a strong appeal, solutions that can applied across a wide range of production systems. These generic solutions can be further enabled with deeper understandings of the wide variety of functional traits responsible for weedy success in different weeds: different weeds that exploit different opportunities in different fields in different cropping production systems at different times of the year in different years. We eventually outgrow ‘one-size-fits-all’ clothing.

I learned that humans create opportunity in space and time in many habitats around the world. Weeds are those plant species that seize and exploit those opportunities by means of rapid evolution of keystone functional traits finely tuned to each unique locality in invades. The traits I came to know best were those involved with seed dormancy and seedling emergence: the soil-weed seed communication system. I learned these weedy plant species most frequently arise from the human process of plant domestication and the formation of robust wild-crop-weed complexes that exchange genes and form world metapopulations resistant to all human control efforts.
Learning from students

The contributions of all past students in Agronomy 517, Weed Biology, from 1992 to 2014, have been a crucial component in the development of this book. They came locally and at a distance: Iowa and the U.S. corn belt; California, Texas and Georgia; Sweden, Czech Republic, Iran and Iceland. Student projects, often focused on a single weed species, as well as student discussions, questions, insights (especially those from their own experience) and examination responses have strongly influenced this book.

By definition

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 often leading to incorrect mental models of how systems work (e.g. invasive species and biodiversity). For this reason, definitions of most of the important concepts are provided in the indexed glossary, with alternative meanings provided to highlight where confusion and misunderstanding within the sciences arises (e.g. functional trait, Violee et al., 2007). Discussion of these differing usages provided much insight in the classroom. Understanding the variety of student perspectives on definitions is gained by this comparative etymology.

On the shoulders of giants

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 weed biology. There is no replacement that provides the scope and detail this classic reference provided. In the intervening years I borrowed much of Harper’s concepts in this book. 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 the course. The structural organization of this book has been 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. I dedicate this book to Charles Darwin, John L. Harper, Ernst Mayr and Ivanovitch Vavilov.

Knowledge and representation

How can knowledge of weed biology be discovered and then represented? Understanding the nature of weeds relies on deeper insights than those provided by observations of weed biology. There exist larger forces in nature that need to be understood if evolution is the make sense. We can characterize these larger forces of nature as those that give rise to complex adaptive systems. This book utilizes case histories of three weed species to illuminate the nature of complex weedy adaptive systems, providing examples of representation based on keystone functional traits.

Lastly, this book's ambition to move towards a theory of weed science, a natural philosophy of weeds (Deutsch, 2011; Snyder, 2011; Uglow, 2002).

So, we begin. The first task of this book is to define what weeds are.
“To Adam he said, “Because you listened to your wife and ate from the tree about which I commanded you, ‘You must not eat it.’

“Cursed is the ground because of you; through painful toil you will eat of it all the days of your life. It will produce thorns and thistles for you, and you will eat the plants of the field. By the sweat of your brow you will eat your food until you return to the ground, since from it you are taken; for dust you are and to dust you will return.”


“The Parable of the Weeds

Jesus told them another parable:
The kingdom of heaven is like a man who sowed good seed in his field. But while everyone was sleeping, his enemy came and sowed weeds [tares, darnel, Lolium temulentum] among the wheat [Triticum sp.], and went away. When the wheat sprouted and formed heads, then the weeds also appeared.

The owner’s servants came to him and said, “Sir, didn’t you sow good seed in your field? Where then did the weeds come from?”

‘An enemy did this,’ he replied.

The servants asked him, ‘Do you want us to go and pull them up?’

‘No,’ he answered, ‘because while you are pulling the weeds, you may root up the wheat with them.

Let both grow together until harvest. At that time I will tell the harvesters: First collect the weeds and tie them in bundles to be burned; then gather the wheat and bring it into my barn.’


“The Parable of the Weeds Explained

Then he left the crowd and went into the house. His disciples came to him and said, “Explain to us the parable of the weeds in the field.”

He answered, “The field is the world, and the good seed stands for the sons of the kingdom. The weeds are the sons of the evil one, and the enemy who sows them is the devil. The harvest is the end of the age, and the harvesters are angels.

As the weeds are pulled up and burned in the fire, so it will be at the end of the age. The Son of Man will send out his angels, and they will weed out of his kingdom everything that causes sin and all who do evil. They will throw them into the fiery furnace, where there will be weeping and gnashing of teeth. Then the righteous will shine like the sun in the kingdom of their Father. He who has ears, let him hear.”

UNIT 1: THE NATURE OF WEEDS

The stocky woman leaned and shook the foxtail seedheads gently into her hemp apron. The patter and spatter of seeds dimpled the cloth as well as her cheeks. The patch was here again, where it had been for many years, its first autumnal seeds now ready for her. The seeds fell quickly, loosened from the panicles as they matured. The woman gathered carefully, ensuring continuous weekly harvests from the patch. This early harvest was the biggest, dedicated to making beer. Her husband would be pleased. There would be plenty of seeds for him to brew foxtail beer for the upcoming harvest festival and rituals. Soon the clan families would gather at the traditional camp here along the Yellow (Huang He) River in northeast China. At autumn’s end she would carefully let the last seeds fall to the ground to reseed the next year’s patch. It was her patch, everyone recognized her right, and responsibility to it. So she protected it, nurturing the foxtail seedheads as they gave up their bounty, just as she nurtured and protected her young children.

The weeds’ story. I am foxtail.

In the beginning I was wild. Seizing and exploiting opportunity in those infrequent patches where nature conveniently tore up the landscape, leaving it barren for me to conquer. Then, in several places around the north temperate Earth I found a helper in my struggle, you, the human. One of those early favorable places was near your camps and settlements bordering the Yellow (Huang He) River in northeast China where you interacted with hunter-gatherer humans from the arid north. 9000 years ago you began to use my seeds to make beer, one of your favorite intoxicants. I was flattered you wanted me so much. Around 7500 years ago you began to cultivate me as a domesticated crop along with your dogs and pigs. You picked the ones in my family that hung tightly to the seedheads until you could gather me in. You picked those of my family who germinated right away, not those that lingered for days and years in the dirt, waiting to grow. You grew me during your human ‘Early Neolithic’ period and I was your principal crop for at least four millennia. As time passed you became more systematic in your cultivation of the crop brother-sisters. And my wild and weedy family tagged along for the free ride you provided us in your crop fields.

Then came Houji, 3500-4000 years ago during your Xia dynasty, Lord of Millet. You actually named your most powerful and important leader of the time after me. I was thrilled! With the coming of these ancient human leaders of civilization also came the ancient Chinese tradition of beer making. It was important to you for ancestral worship, funeral and other rituals of your Xia, Shang and Zhou dynasties. In one of your oracle bone scripts you called it Lao Li (醪醴). Rice was first seen here in the north about 2500 years ago, but it never was as popular as it became in the hot humid south of China. I was your favorite ‘eater’ until wheat came and slowly replaced me. Our family is still here in northern China, my wild and weedy and crop family are all together, but we are no longer your favorites. That’s OK, we conquered Eurasia together.

All this has passed now, but it remains written in my genes. I waited for you. You came and gathered me to eat. You saved your favorite seeds and planted them in soil free of neighbors. Now my world family is diverse: wild relatives from before, ‘eater’ crops cultivated in your fields, and our weedy members who promiscuously mate with everyone in the family.

We evolved and conquered the Earth together, always in your image. I could never have done it without you.

Summary. The story of weeds is the story of us, we humans. We began creating them about 10,000 years ago. We continue to create and change them every day. They were here before we came, they will be here long after we are gone. This book is their story, our story. Weeds are us.

Why do we humans look upon weeds as something separate from ourselves? Aliens. Foreigners. Bad. “... everything that causes sin and all who do evil ...” As humans we are endowed at birth with inherent intuitions about the nature that surrounds us and that we observe. We cannot help but classify and categorize plants we see. They are our food, our medicines, our intoxicants, our decorations. They can also be our poisons. We humans
now alive on this planet are the ones who survived because we knew the difference between these different roles plants play. We eat transgenic maize, not hemlock. We use foxglove for heart rate arrhythmia, not nightshade berries. We smoke marijuana, not jimsonweed. Our dining room table has fragrant flowers, not foxtail panicles. The survivors are the winners able to successfully classify neighboring plants. We continue to classify weeds: invasive plants, aliens. We cannot help ourselves. It is a successful ecological evolutionary adaptation that protects our lives, our humanity.

As humans we have resisted thinking of weeds as a crucial part of who we are. To embrace weeds as who we are puts us in a bad light, makes us look like animals, unable to control the nature around us. Are not humans something special? Something more than mere animals? That is our belief. This belief can get in the way of our understanding of nature. The combination of inherent plant classifying intuition and belief has prevented us from seeing the real nature of our weeds: as integral, inseparable part of an inter-fertile genetic metapopulation, the wild-weed-crop complex. Isn’t it time to fully embrace Darwin’s evolution?

Ivanovich Vavilov was killed by starvation in 1943 in a prison in the old USSR because of his view of nature, of plant genotypes as consequences of natural selection of genetically heritable traits. It is a severe irony for an agronomist to starve to death. Josef Stalin was threatened by what his science revealed about the future of Soviet agriculture. Or more importantly, by what it didn’t reveal. Vavilov was probably the most famous crop geneticist in the world during the brief flowering of Bolshevik science and society during 1920’s and early 1930’s. He and his institute traveled the world collecting crop plants in search of the ‘hearth’ of crop domestication. His world crop germplasm collection was second to none. He thought of crop improvement as the natural (which includes human) selection of desirable genetic traits, acquisition of genotypes with desirable heritable traits. No one today would be sent to prison for such an enlightened view. Evolutionary understanding was the key.

**Picture U1.** Ivanovich Vavilov (left); Josef Stalin (middle); Trofim Denisovich Lysenko (right).

In the 1930’s a jealous and ambitious Trofim Denisovich Lysenko thought otherwise. He had little formal scientific training. But he knew how to get the attention of Stalin. He argued that crops could be improved by exposing them to environmental stress. The plastic, phenotypic effects of stress on a parent crop plant would thereby be heritable in its’ seeds. The USSR possesses vast land areas of marginally arable land. Dry, salty, cold. Why not expose crops to these stresses and use their now-improved seed to grow more grain in the following year? Stalin was completing the collectivization of his empire’s land, notably in the Ukraine. He dispossessed individual landowners and farmers from their land and organized crop production in massive, centralized state-controlled farms. Controlled by Moscow bureaucrats. Millions of people died of starvation. Stalin and his Bolshevik regime were desperate. He had to provide more food or lose power. Lysenko’s approach seemed like the answer to a prayer. Or at least a propaganda answer to a political prayer. Darwinian approaches to crop improvement were now officially wrong. Lamarckian evolution of acquired, plastic, phenotypic traits was officially right. There was nothing wrong about Lysenko’s ecology, but his genetics was terrible. Vavilov had to go, along with his institute. And so they did.

All this seems a bit historical for our modern (post-modern) enlightened age. Or is it? Why is this the first book in the world on the evolutionary ecology of weeds? Many fine examples of evolutionary thinking dominate such areas as herbicide resistance and management of weeds. But considerable resistance to evolutionary thinking exists in the world of today, notably here in the USA. This has had consequences. For
example, where is the evolutionary thinking in areas like demographic models of weed growth and development? How can you count plants and make inferences about the future of a local population when every generation is potentially a new set of genotypes (e.g. dioecious plant species)? Evolutionary understanding of weed ecology is the key. This book is the story of that understanding. It is written in the hope that Ivanovich Vavilov didn’t die in vain in that cold Soviet prison.
Chapter 1: The Nature of Weeds

“The Azteca did not settle on that island in the lakeside swamp [Tenochtitlan in Lake Texcoco] because their god gave them any sign, and they did not go there joyfully. They went because there was nowhere else to go, and because no one else had cared to claim that pimple of land surrounded by marshes.” “So for a long time your ancestors existed – just barely existed – by eating revolting things like worms and water insects, and the slimey eggs of those creatures, and the only edible plant that grew in that miserable swamp. It was mexixin, the common cress or peppergrass, a scraggly and bitter-tasting weed [Lepidium sp.]. But if your forebears had nothing else ... they had a mordant sense of humor. The began to call themselves, with wry irony, the Mexica.” “But they never forgot that humble weed which had sustained them in the beginning, the mexixin, and they never afterward abandoned the name they had adopted from it. Mexica is a name now known and respected and feared throughout our world, but it means only ... The Weed People!” “... for weeds may be unsightly and unwanted, but they are fiercely strong and almost impossible to eradicate.” Jennings (1980)

The weeds’ story. I am foxtail (Setaria species-group).

I am a closely-knit family of wild, crop and weedy relatives. Our parents are green foxtail (Setaria viridis) which came out of Africa and conquered Eurasia without your human help. After the ice had melted you humans picked out your favorites and cultivated foxtail millet (Setaria viridis, subspecies italic). With time our specialized cousins yellow foxtail (Setaria pumila), knothroot foxtail (Setaria geniculata), bristly foxtail (Setaria verticillata) and giant foxtail (Setaria faber) arose and invaded. We followed you closely for 10,000 years, until we conquered the earth. I couldn’t have done it without you. You gave me opportunity, a home. You killed me, you ate me, you made me strong. You carefully created me in your image.

How did you change me, make me so successful? What tricks do you humans possess that makes me so adaptable to the places you disturb and dominate?

Summary. The concept of a weed plant is inherently human in two different ways. In an immediate sense, they are the plants we define as weedy. In a historical sense, they are plants that arose as a consequence of agricultural crop domestication, an inevitable result of the singular human act of planting a seed (or propagule). Understanding the intimate relationship of humans and plants in both of these ways can provide a more comprehensive understanding of the nature of these plant species.

Weeds are defined as a plant out of place, thriving in habitats disturbed by humans, possessing competitive behavior, and capable of mass movement from one area to another. Human values related to disturbed and agricultural habitats, appearance, utility and biological traits dominate how we define a plant as weedy.

What is the relationship between human nature and the nature of weeds? The nature of weeds is an inevitable evolutionary consequence of agricultural natural selection under the influence of human nature. Human nature includes inherent intuitions about the natural world: taxonomy and the classification of plants we observe, eat and utilize. Human cognition is finely tuned to discern both good and bad qualities about the specific plants with which we interact. We humans are very sensitive to plant behaviors whose ‘form and powers’ we do not appreciate, especially in our managed landscapes. The evolutionary consequences of these human traits are the major crop-weed groups of contemporary world agriculture. Unfortunately for us, separating weedy species from desirable species is often genetically impossible.

The nature of weeds can be understood at a deeper level than definitions and human nature by observing the biological and adaptive characteristics that lead to their success. Defining what a weed is, and appreciating the traits they possess, is a good start to understanding the nature of these plants. Evolution acts on individuals in a population, so understanding the nature of the weeds we have today requires an understanding of where and when particular plants species became weeds.
Most of the common and widespread weed species we now have came as a consequence of crop domestication, planting and cultivation. These agricultural processes began about 12,000 years ago. They occurred on different continents and involved different native species available for selection as crops. Since those early origins both crops and their weeds have spread throughout the world. These crop-weed groups are the most successful invasive species in human history. The processes of plant domestication, planting and cultivation created new plant communities featuring the crop genotypes they desired. These domesticated species typically came from preexisting wild relatives selected for their crop qualities. The wild relatives interbred with their new crop derivatives and new variants joined these heterogeneous communities, forming metapopulations extending across the landscape. Some of these new weeds were in turn again domesticated, others not. Over 12 millennium this promiscuous inter-fertility and gene flow led to the world crop-weed groups we now have. The most common pattern for the origins of agricultural plants is the inter-fertile wild-crop-weed (w-c-w) plant complex in which both crop and weed were derived from the same wild progenitor species.

What plant species evolved under such close human scrutiny and management? The nature of weeds is ultimately revealed in the particular weed species that have survived to plague human-managed ecosystems to the present day. It is the properties and stability of these successful weeds that define the nature of weeds most precisely.

What exactly are these crop-weed groups? A comparison of the origins of specific crop species with the current weed flora infesting contemporary agriculture reveals the close genetic relationship of most of our major weed species and crops: crop-weed groups. It is to these crop-weed groups that we shall look throughout this book to understand the nature of weediness. The major crop-weed species groups are described here: local native cultivated and/or domesticated plant species reported in seminal publications of the original “hearts” of agriculture and compared to contemporary world weed species of the same genus. The crops and their centers of origin, diversity, cultivation and domestication as reported in older classical sources. The weeds from older classical weed flora taxonomy and identification sources.

This chapter concludes with a list of these highly adapted crop-weed groups, many of which will be examined more closely throughout this book to understand the nature of weediness: weed population evolution, adaptation in weed life history, and adaptation of weeds in local plant communities.
UNIT 2: THE EVOLUTION OF WEED POPULATIONS

"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.' J.L. Harper, 1977

The weeds' story. I am foxtail.

We conquered the earth together. You gathered my seeds, the ones you eat, you left the rest. In the spring you killed and tilled and made me a home in the soil. You planted the ones of me you liked, you left the rest of me buried in the ground. My seedlings emerged. You could not tell us apart. We grew, we had sex with ourselves, then you took our children. You gathered and ate the ones you liked: the biggest, the easy to germinate, the ones clinging to my seedheads. You tried to kill the rest; the ones you could see. You rid me of the weak. I inherited the strong; those hiding in the ground, the last to emerge, those readily falling to earth. You gave me opportunity. Despite yourself, you created me in your image. You eat me, kill me, you make me strong. I couldn't have done it without you.
Summary. Rev. Thomas Robert Malthus (1798-1826) proposed that human population growth was limited, expansion prevented by famine and disease. Pierre François Verhulst published a logistic function of human population growth. Malthus as a primary stimulus to Darwin and Wallace conceptualizing natural selection and elimination as the driver of evolution. Verhulst providing a mathematical model of population growth. Both were founded on human population biology. Humans, animals, differ from plant populations, mitigating against the use of the logistic function to describe population growth. By means of phenotypic plasticity and somatic polymorphism traits, plant architecture is capable of generating a very wide range of sizes of the individual. Population structure also differs from that of animals: plants don’t move, animals can move to exploit opportunity elsewhere. These two crucial aspects of plants compromise the utility of the logistic equation to represent plant and weed populations.

Plant communities assemble when opportunity in a locality favors functional traits in a new species at a particular time. Local opportunity spacetime is the integration of available resources and conditions, neighbor interactions and disturbance in that local niche. The population of this species must first be able to disperse into the habitat, then colonize the site by completing its life cycle from recruitment to reproduction. Lastly it must endure at that site, with individuals selected or eliminated. Without performing all of these processes evolution is not successful. Without all these processes evolution of the population will not occur. For weeds, disturbance in the broadest sense is what creates this original opportunity. All local populations eventually go extinct.

Weed communities assemble in a new location seizing and exploiting local opportunity spacetime. The invading members of a weed species have preadapted traits that allow them to colonize the site. Once established they mate, recombining their genes in meiosis, dispersing their variable progeny into the habitat. The new genetic offspring interact with the opportunity provided by the local environment and produce new phenotypes which live or die. The generation of new weed genotype-phenotype genetic variation is required for natural selection and elimination to drive local adaptation of the population. Generation of genetic variation appropriate for exploiting a particular locality allow an individual weed species to seize available opportunity spacetime in an efficient manner. 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 genetic diversity among its progeny. Parent plants generate variable genotypes producing variable phenotypes depending on environmental conditions. Phenotypic plasticity is the capacity of an organism to vary as a result of environmental opportunity. Phenotypic variation is also expressed in somatic polymorphisms. Weed species possess the ability to express phenotypic variation from a single genotype. These multiple interactions of genes are called epistasis. This first process of natural selection generates the phenotypic variation needed for the second process resulting in local adaptation: differential survival, reproduction and inheritance.

Heterogeneous weed populations invade, colonize and endure in a locality by surviving their developmental life history, culminating in reproduction of offspring inheriting their adaptive traits. Survival and reproduction can be represented demographically with the net reproductive rate, the summation of survival times fecundity at each age of the individual’s life history. The optimum age for individual reproduction depends on how reproduction at a particular age would affect later survival and reproduction. Mortality drives the time of reproduction. Opportunity spacetime drives mortality. Evolution shapes the timing of reproduction by a careful compromise of fecundity optimization and mortality risk minimization. The last step in natural selection is heredity, the transmission of specific characters or traits, genes and genetic information, from the ancestral parent to the offspring: the basis of adaptive evolution. New or altered traits in individuals can be produced by mutations, the transfer of genes between populations or between species, or by genetic recombination in sexual reproduction. The transmission of genes to the next generation is accomplished in weeds by their mating system. The mating system of a successful weed species generates appropriate amounts and types of genotypic variants among its progeny. Mating systems indirectly control species diversity, population genetic structure at all spatial levels, community diversity and assembly with the dispersal of these offspring. The search for opportunity spacetime is accomplished with genetic variability expressed as phenotypic heterogeneity within populations of a species. A local population relies on its mating system to adjust genetic recombination to the fabric of the exploited disturbed space. Mating systems for colonizing species varies from obligate outcrossing (e.g. monoecy, dioecy) to self-pollinating and apomictic species.
Chapter 2: Evolution, Natural Selection and Weedy Adaptation

“All the world’s a stage,
And all the men and women merely players.
They have their exits and their entrances,
And one man in his time plays many parts ...”
Shakespeare, W. (1623)

The weeds’ story. I am foxtail.
We conquered the Earth together. We evolved together. At first you wanted all of me, unconditionally. Then you picked your favorites, the quick to germinate, the easiest to gather, the tastiest. You gathered my seeds, stripped the ground of everything and planted these favorites. The rest of us un-favorites lay quietly hidden beneath you and waited. Some of us were impatient, we died. Some of us waited, and lived.
You grew fat, prosperous on our bounty. You became greedy, planting more land. You killed each other, greedy for our bounty. You killed us, ensuring your bounty. In return I gave you civilization in China, in India, in Mesopotamia, in the Balkans, in America. We all grew stronger, fatter, richer, greedier as we endured.
Nature enriched our opportunities in some places, removing it in others. We grew, had sex, changed, moved, died. Those you ate became fatter, docile to your needs, clinging tightly to our seedhead nursery. Those of us you tried to kill became smaller, leaner, able to hide, growing in your fields when you weren't looking. We had better sex. Our children inherited these new ways of living, escaping your relentless killing. We became better at spreading, better at enduring. We conquered the Earth together.

Summary. Rev. Thomas Robert Malthus, a Church of England curate, published ‘An Essay on the Principle of Population’ (1798-1826) in which he proposed that human population growth was limited, expansion prevented by famine and disease. He proposed this gloomy outlook in opposition to the popular 18th century European view that society was improving and in principle perfectible.

Pierre François Verhulst was a Belgian mathematician of number theory at the University of Ghent who published a logistic function or logistic curve, a common special case of the more general sigmoid function, and its relationship to human population growth. In the initial stage its growth is approximately exponential; then, as saturation begins, the growth slows, and at maturity, growth stops. This logistic function presented the important concepts of intrinsic growth rate and the carrying capacity (numbers of individuals) of a local environment.

The ideas of these two men had large impacts on future science: Malthus as a primary stimulus to Darwin and Wallace conceptualizing natural selection and elimination as the driver of evolution; and Verhulst providing a mathematical model of population growth. Both were revolutionary ideas. Both created confusion as their ideas were subsequently adopted by evolutionary biology. For our present story of weeds confusion was generated by the fact that both these ideas were founded on human population biology. Humans, animals, differ from plant populations in several important ways that mitigate against the use of the logistic function to describe population growth. First, the plastic architecture of a plant is capable of generating a very wide range of sizes of the individual by means of phenotypic plasticity and somatic polymorphism traits. Population structure also differs from that of animals: plants don’t move, animals can move to exploit opportunity elsewhere. These two crucial aspects of plants compromise the utility of the logistic equation to represent plant and weed populations. This confusion fully explored in subsequent chapters (e.g. Unit 6). This confusion does not lessen the importance of these ideas, but it obligates us to look upon demographic representations of weed biology with caution.

2 Evolution, natural selection and weedy adaptation
Summary
2.1 Introduction

2.2 Evolution
   - 2.2.1 Micro- and macroevolution
   - 2.2.2 Units of evolution and natural selection

2.3 Natural selection and elimination
   - 2.3.1 Malthus Postulata
   - 2.3.2 Natural selection

2.4 The process of natural selection
   - 2.4.1 Population formation: Precondition to natural selection
   - 2.4.2 Representing population growth, the Verhulst-Pearl logistic equation
   - 2.4.3 Generate variation: Process of natural selection, step 1
   - 2.4.4 Survival and reproduction: Process of natural selection, step 2

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

“... the capacity to choose in each fleeting moment of a situation that which is ... most opportune.”
 Count Otto von Bismarck (Pflanze, 1990)

“... guiding power of that conventional trinity of crime investigation: motive, means and opportunity.”
 Reginald Hill, 2001

“vedere moneta, toccare camello”
“see the money, touch the camel”
Italian folk wisdom

The weeds’ story. I am foxtail.

In the beginning there was wild me in tropical Africa, waiting on the glaciers for opportunity. I looked like green foxtail back then, before you. I dispersed to Eurasia when the ice receded. Life was harder then, without your helpful disturbing ways. I settled in local patches, where there was no one else.

We first met in Eurasia. Right away you picked your favorites from among me, foxtail millet. I followed, wild and weedy. Then we invaded the Earth together, but it took time and effort. First you sought out locations to grow. You were greedy for food, so you found sunny moist fields with ample fertility and heat. You killed all the other plants, dug up the soil and planted your favorite foxtail millet. And our weedy family members followed you right into the field. You found us a pest with those traits we were developing: ready exploitation of unused essentials, competitive with neighbors and crop cousins. You killed the weedy of us, but left behind the most clever: the ones who hid, or escaped, or looked just like your favorite crops. Then the survivors mated and reproduced children that inherited all those clever new traits. In most of those fields we endured, in some few we went extinct.

We invaded China 6000 years ago, Europe 3500 years ago. A sudden change in my genes, a doubling, expanded my family to include cousins yellow foxtail and bristly foxtail. My yellow foxtail was wild at first. Then in India you picked your favorites, and again we invaded and endured. Then we met in the Americas, twice actually. The first time is still unclear, my wild antecedent knotroot foxtail coming from Asia about 10-12,000 years ago. Your prehistoric migration from central Asia brought me across the Bering Straits land bridge to North America. This new native American invader made me the oldest cultivated cereal in the new world 8000 years ago. We came more deliberately the second time, 500 years ago, following your European invader Columbus. Our green foxtail emigrating with you from Europe, our yellow foxtail from Asia. Our weeds still dominating much of the Americas today.

Conquering the Earth with you wasn’t all easy. You became fickle, greedy for more attractive plants to eat. In Asia you chose rice, abandoning us to the dry and salty fringes. In Europe it was wheat and barley and rye you chose. In the Americas maize was your new favorite. Our foxtail millet went extinct in so many fields around the earth then. But our weedy family endured and became even stronger. We invaded these new crops too, and we found a home. Your success in global trade and travel has accelerated our success beyond our wildest dreams. My gene doubling gave birth to our cousin giant foxtail (Setaria faberi) allowing us dominate the richest fields of North America. Your invention of herbicides neatly uncovered our shy, preadapted, resistant siblings. They are our proudest new members, brought from obscurity by your dedicated efforts. We couldn’t have done any of it without you.
Summary. Plant communities assemble when opportunity in a locality favors functional traits in a new species at a particular time. Local opportunity spacetime is the integration of available resources and conditions, neighbor interactions and disturbance in that local niche. The population of this species must first be able to disperse into the habitat, then colonize the site by completing its life cycle from recruitment to reproduction. Lastly it must endure at that site, with individuals selected or eliminated. Without performing all of these processes invasion is not successful. Without all these processes evolution of the population will not occur. For weeds, disturbance in the broadest sense is what creates this original opportunity. All local populations eventually go extinct.

Every interbreeding local population of a species has an origin, a time and place it began. Every population also goes extinct at some time. This invasion process begins with dispersal of propagules (seeds, annual or perennial vegetative meristems) into the new space. If opportunity exists for the weed species, and if it possesses functional traits appropriate to exploit the new opportunity, the population can become established in that locality. If these early colonizing plants successfully reproduce, or disperse in sufficient numbers of propagules, then the species can begin an enduring occupation of that habitat. When an excess number of individuals of the first colonizing weed species in a local habitat begin competing with each other the preconditions for natural selection-elimination are met and a local deme is formed. 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 seeds 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. Local adaptation has begun.

3 Formation of the local weed population (deme): Precondition to natural selection

Summary

3.1 Introduction: opportunity and the formation of the local deme

3.1.1 Population formation examples

3.1.2 Seizing and exploiting local opportunity

3.2 The structure of local weedy opportunity

3.2.1 Weedy habitats

3.2.2 Niches in the local community

3.2.3 The niche hypervolume

3.3 Habitat heterogeneity and dynamics

3.3.1 Earth’s physical geography

3.3.1.1 Geosphere

3.3.1.2 Lithosphere

3.3.1.3 Atmosphere

3.3.1.4 Hydrosphere

3.3.1.5 Biosphere

3.3.1.6 Pedosphere

3.3.2 Spatial heterogeneity and patchiness

3.3.3 Temporal division of the environment

3.3.4 Disturbance

3.3.4.1 Disturbance possesses dimensionality

3.3.4.2 Proximity of disturbance

3.3.4.3 Vulnerability to disturbance

3.3.4.4 Temporal patterns in disturbance

3.4 Limiting resources and pervasive conditions in local opportunity

3.4.1 Thermodynamic Earth

3.4.1.1 Thermodynamic Earth heat flow

3.4.1.2 Thermodynamic Earth engines

3.4.2 Limiting resources

3.4.2.1 Light

3.4.2.1.1 Plant phytochromes

3.4.2.1.2 Photomorphogenesis and phototropism

3.4.2.2 Water

3.4.2.3 Mineral nutrients

3.4.2.4 Gases
3.4.3 Pervasive conditions in the environment
   3.4.3.1 Heat
   3.4.3.2 Terroir
      3.4.3.2.1 Climate
      3.4.3.2.2 Soil
      3.4.3.2.3 Topography
3.4.4 Environmental signal spacetime
   3.4.4.1 Signal space dimensions
   3.4.4.2 Photo-thermal modulation of weed seed germination behavior by plant phytochromes
      3.4.4.2.1 The photo-thermal germination window
      3.4.4.2.2 Multiple interacting phytochromes
      3.4.4.2.3 Alternative phytochrome models

3.5 The nature of plant invasions of local opportunity
   3.5.1 The plant invasion process: seizing, exploiting and occupying opportunity
   3.5.2 Dispersal
   3.5.3 Colonization
   3.5.4 Enduring occupation of a locality
   3.5.5 Extinction
   3.5.6 The perception of plant invasion
Chapter 4: Generation of Genotypic and Phenotypic Variation:
First Process of Natural Selection

The weeds’ story. I am foxtail.

You created opportunity for me as you civilized the Earth with your new food plants. You selected your favorites and killed most of the others. This was your gift to us, letting the best escape, hide, resist. Only a few of us follow you to new lands, new fields. These new explorer invaders are less variable than all of us. Each new field you create has unique opportunities, so we likewise must become unique to invade, exploit and endure.

Our secret as foxtails is to mate carefully with ourselves. This gift enables us to become locally unique by generating new siblings with new qualities. We begin by mixing our own genes and recombining them in each sibling. Then we turn them loose in the fields you created, and see what opportunity brings. Each new recombinant interacts with its unique environment. You kill most of the new plants that develop, thank you. You miss some of the new recombinates and they endure, thank you. Sometimes, rarely, we use our genes in a special way: we create a new species for our group by doubling our genes. We did it to make our specialist cousins: yellow, bristly, knotroot and giant foxtail.

Our other secret as foxtails is to grow precisely within the opportunity you and nature offer. Before we met you, each of us had preadapted growth traits. We sense local opportunity, then we grow just the right amount of leaves, stems and flowers for that provided. We also can form parts of our body in different ways, like our seeds, to maximize individual opportunity.

We use our secret traits and create a precise amount of newness in our different siblings. We test the newness out on you, to see which you kill and which survive. The clever new ones make us stronger. We owe it all to you.

Summary. Weed communities assemble in a new location seizing and exploiting local opportunity spacetime. The invading members of a weed species have preadapted traits that allow them to colonize the site. Once established they mate, recombining their genes in meiosis, dispersing their variable progeny into the habitat. The new genetic offspring interact with the opportunity provided by the local environment and produce new phenotypes which live or die.

The generation of new weed genotype-phenotype genetic variation is required for natural selection and elimination to drive local adaptation of the population. Generation of genetic variation appropriate for exploiting a particular locality allow an individual weed species to seize available opportunity spacetime in an efficient manner. 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 genetic diversity among its progeny. Additionally, several forces operate in nature to increase and decrease population genetic diversity.

Environmental changes external to the individual, as well as internal allelic forces, bring about changes in gene frequencies in a population. The primary internal allelic forces increasing variability are recombination of parental genes during meiosis, and mutation. Gene flow and introgression, as well as segregation distortion, also drive variation. Random sources of decreasing genetic diversity in a population include genetic drift, bottleneck and founder effects. Over time genetic diversity can lead to the formation of new species arising from older ones. There are several processes or modes by which a phylogenetic lineage can diverge, all relying ultimately one of several types of reproductive isolating mechanisms.

Parent plants generate variable genotypes which confront the environment in their life history producing variable phenotypes. The expression of phenotypes from genotypes during development often has much flexibility. In weed species these phenotypes are often very different under varying environmental conditions. Phenotypic plasticity is the capacity of an organism to vary morphologically, physiologically or behaviorally as a result of environmental opportunity (e.g. extent of branching in an individual plant). Phenotypic variability can be expressed as discrete classes (canalization) or continuous variation of a trait. Phenotypic variation is also
expressed in somatic polymorphisms (e.g. sexual dimorphism of male and female plants in dioecious *Amarathus* spp.-gp).

Genotypes produce phenotypes in their interactions with the environment, and variation in phenotypes is usually associated with concomitant 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, numerous interactions among genes produce the phenotype. Many genes may simultaneously affect several aspects of the phenotype. In other instances a particular aspect of the phenotype may be affected by several different genes. These multiple interactions of genes are called epistasis.

Epigenetics is the study of heritable changes in gene activity that are not caused by changes in the DNA sequence. There exists a distinction between architecture, blueprint, and self-assembly during embryogenesis. Embryology works by self-assembly during development. Order, organization, and structure all emerge as by-products of rules which are obeyed locally and many times over, not globally. It is all done by local rules, at various levels but especially the level of the single cell.

The first process of natural selection generates the phenotypic variation needed for the second process resulting in local adaptation: differential survival, reproduction and inheritance.

4 Generation of genotypic and phenotypic variation: First process of natural selection

Summary
4.1 Genotypes and phenotypes
4.1.1 Extended phenotype
4.1.2 Epigenesis, epigenetics and gene expression
4.1.3 Genome size, weediness and intra-genomic competition

4.2 Generate genetic variation
4.2.1 Sources of genetic diversity
4.2.1.1 Forces increasing population variability
4.2.1.2 Forces decreasing population variability
4.2.2 Speciation
4.2.2.1 Process of speciation
4.2.2.1.1 Stage 1: Gene flow is interrupted between two populations
4.2.2.1.2 Stage 2: Completion of genetic isolation
4.2.2.2 Reproductive isolating mechanisms
4.2.2.3 Modes of speciation
4.2.2.3.1 Natural speciation
4.2.2.3.2 Allopatric speciation
4.2.2.3.3 Peripatric speciation
4.2.2.3.4 Parapatric speciation
4.2.2.3.5 Sympatric speciation
4.2.2.3.6 Speciation via polyploidization
4.2.2.3.7 Reinforcement
4.2.2.3.8 Hybrid speciation

4.3 Generate phenotypic variation
4.3.1 Phenotypic plasticity
4.3.2 Somatic polymorphism
4.3.2.1 Somatic polymorphism in flowers
4.3.2.2 Somatic polymorphism in seeds
4.3.2.3 Somatic polymorphism in leaves
4.3.2.4 Somatic polymorphism: seasonal dimorphism
The Evolutionary Ecology of Weeds Narrative

Chapter 5: Survival, Reproduction and Inheritance: Second Process of Natural Selection

The weeds’ story. I am foxtail. I cover the civilized Earth you provide for me. I thrive globally, I eat locally. I mate with myself to ensure I gather all the opportunity you provide for me in the field of a season. My self-mating generates new and different children. We have sex by recombining carefully, at the appropriate time. The many bodies of my children’s growth is plastic, appropriate to the opportunity you provide, and no more. They avoid your fatal hand, escape your inconstant efforts, resist your tools, fool you in any way they can. You still manage to kill most of my children, but the rest mate. They form new seeds which inherit all of our surviving traits. We survive, mate and inherit in your image. We conquered the civilized Earth together.

I foxtail have endured. How did you make me so successful? For over 10,000 years I have invaded the civilizing opportunity you provided and formed local populations. In each you disturbed and provided what I needed to grow. I mated and gave birth to unique children, each with special gifts. You killed most of them, thereby making my survivors uniquely adapted to your local field, to your local farmer.

I foxtail evolve. What remains to be revealed is the nature of these special gifts we have coevolved together over all these millennia. What special traits do I have? When in my life do I express them? How do my local crop and weed neighbors react when confronted by my actions? How does my complexity ensure my endurance, my anti-fragility? How should you humans portray me to understand me? These are my mysteries yet to be revealed.

Summary. Heterogeneous weed populations invade, colonize and endure in a locality by surviving their developmental life history, culminating in reproduction of offspring inheriting their adaptive traits. Survival and reproduction can be represented demographically with the net reproductive rate, the summation of survival times fecundity at each age of the individual’s life history. There exist several life history features of reproduction and survival that determine the timing of reproduction. The optimum age for individual reproduction depends on how reproduction at a particular age would affect later survival and reproduction. The optimum age of reproduction is reached when no further increase in the net reproductive rate can be obtained by further delay. Plants reproductive value changes with age and it depends on the plant's life span (annual, biennial, perennial). Mortality drives the time of reproduction. Opportunity spacetime drives mortality. Evolution shapes the timing of reproduction by a careful compromise of fecundity optimization and mortality risk minimization. Individuals reproducing too early are replaced by those that maximize season length opportunity. Individuals reproducing too late die or are less fecund. Whether to reproduce early in season or wait depends on the particular ecological conditions of a locality: unused late season opportunity will eventually be seized by some species, and the fuller a species uses available opportunity in the face of death the more it will be able to exploit.

The last step in natural selection is heredity, the transmission of specific characters or traits, genes and genetic information, from the ancestral parent to the offspring: the basis of adaptive evolution. New or altered traits in individuals can be produced by mutations, the transfer of genes between populations or between species, or by genetic recombination in sexual reproduction. Evolution occurs when these heritable differences become more common or rare in a population. The transmission of genes to the next generation is accomplished in weeds by their mating system, their breeding system. The mating system, or mode of fertilization, of a successful weed species generates appropriate amounts and types of genotypic variants among its progeny. The mating system directly controls inheritance of traits by reproduction of fit progeny. Mating systems indirectly control species diversity, population genetic structure at all spatial levels, community diversity and assembly with the dispersal of these offspring. Mating system direct control of sexual reproduction indirectly regulates population variability, either to conserve local adaptation and fitness, or to generate novelty in the face of change. The search for opportunity spacetime is accomplished with genetic variability expressed as phenotypic heterogeneity within populations of a species.
The Evolutionary Ecology of Weeds Narrative

A local population relies on its mating system to adjust genetic recombination to the fabric of the exploited disturbed space. A plant species’ particular mating system controls recombination to generate an appropriate amount of variation to the opportunity spacetime being exploited locally. Mating systems for colonizing species varies from obligate outcrossing (e.g. monoecy, dioecy) to self-pollinating and apomictic species.

5  Survival, reproduction and inheritance: Second process of natural selection
Summary
5.1  Survive, avoid Mortality
5.2  Reproduce the fittest, eliminate the others
  5.2.1  Demographic survival and reproduction
  5.2.2  Timing of reproduction
    5.2.2.1  Optimum age of reproduction
    5.2.2.2  Maximizing net reproductive rate
    5.2.2.3  Precocious reproduction
  5.2.3  Plant age and stage structure
  5.2.4  Reproductive value
  5.2.5  Risk of death determines life history
  5.2.6  Influences of plant density on mortality
  5.2.7  Modes of selection and population diversity
5.3  Inheritance: transmit parental traits to offspring
5.4  Mating system and inheritance
  5.4.1  Mating system and opportunity
  5.4.2  Evolution of mating systems
    5.4.2.1  Sexual reproduction versus apomixis
    5.4.2.2  Outcrossing versus self-fertilization
    5.4.2.3  Outcrossing: separate sexes versus hermaphrodites
  5.4.3  Sex classification systems
  5.4.4  Types of mating systems
    5.4.4.1  Self-pollinating species
    5.4.4.2  Out-crossing species
    5.4.4.3  Apomictic species
    5.4.4.4  Vegetative clone reproducing species

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UNIT 3: ADAPTATION IN WEED LIFE HISTORY

“The life cycle is the fundamental unit of description of the organism.” Caswell, 2001

The weeds’ story. I am foxtail.

I foxtail evolve. I have told you how I change with the opportunity you humans have provided me for thousands of years. How I invade your fields and conquer the earth with you. What I have not told you is how I do it, how I behave during my life, during a season. I have not revealed the special abilities we have coevolved together over all these millennia. What special traits do I have? When in my life do I express them? How do my local neighbors in a field react when confronted by my actions? How does my complexity ensure my endurance, my infragility? These are my mysteries I have yet to reveal.

Summary. The nature of weeds is revealed in the traits expressed during their life history allowing them to seize and exploit local opportunity. Successful weed phenotypes are fit at every step of their life history, there are no weak points. Weed life history is defined by life processes (birth, dispersal, recruitment, growth, reproduction) performed by morphological structures during development. Phenotype fitness is due to the timing of functional traits expression. Timing is everything.

Reproductive life history begins with floral primordia initiation in the developing parent plant shoot architecture. Plant size and structure are sensitively tuned to available local opportunity by means of phenotypic plasticity. Mating systems are carefully timed, controlling pollen-egg recombination, minimizing the risks of mortality. The embryogenic process allocates resources among five seed roles: dispersal, persistence, food reserves for early growth, genetic novelty, multiplication. Embryogenesis occurs. Germinability and dormancy is induced. Seed morphogenesis modulates signal receptivity from the soil environment. Reproduction ends with seed abscission; the zygote is independent. Heteroblastic seeds are dispersed; seeds preadapted to the unknown future availability of opportunity in diverse habitats.

Propagule dispersal begins with abscission and ends with seedling-bud emergence. Dispersal traits provide advantages to the seed: independence from parents, escape from neighbors and unfavorable locations or times, movement to favorable times and sites for exploitation. Dispersal is a process of discovery of opportunity space-time. Spatial dispersal determines local population size and structure. Dispersal mechanisms reveal how habitable sites within a heterogeneous landscape are sought. Successful local colonization is determined by available habitable sites, seed dispersibility, and the speed of discovery. Seeds are dispersed by gravity, wind and air, water, animals and humans. Temporal dispersal is provided by pools of seeds in the soil, the source of all future weed infestations. Seed dormancy is dispersal in time: escape until conditions are favorable. Weed seeds are often dispersed at different times within a season. Seedling emergence begins with germination in the soil. The single most important determinant of plant assembly into communities is the timing of weed seedling emergence relative to neighbors and disturbances. Seedling emergence timing is a direct consequence of variable dormancy (seed heteroblasty).

The life history of an individual weed seed-propagule from flowering and reproduction through life in the soil seed-propagule pool and seedling recruitment are in many ways independent of neighbors. Therefore unit 3 presents an overview of weed life history, reproductive adaptation, and propagule dispersal in space and time. In unit 4, the life history of weed plants from seedling recruitment through reproduction are revealed in the process of community interactions with neighbors, adaptations to weed community structure, dynamics and biodiversity.
Chapter 6: Weed Life History

The weeds’ story. I am foxtail.

I do everything right my whole life: mating with myself, spreading my seed with your help and wind, growing fat on the richness of your fields, and birthing many new children for next year. Many many of us die, leaving only those with the best characters to dominate the opportunity you provide us. We grow every spring after emerging from hiding in the winter soil. We mate with ourselves and send a new generation of children out to hide again, waiting for the right moment to resume. We do all these things at exactly the right time, or else we die. If we live we pass everything on to our children once again. We live fast, die young and spread lots of children across the landscape to do it all again, over and over.

Summary. The nature of weeds is revealed in the several traits allowing them to seize and exploit local opportunity spacetime over the course of their lives, their life history. Successful weed phenotypes must be fit at every step of their life history, there are no weak points. Natural selection and elimination would act on such vulnerabilities leading to adaptation or extinction. Several simultaneous, overlapping aspects define the individual phenotype life history: life processes (birth, dispersal, recruitment, vegetative growth and seed reproductive growth); the morphological structures accomplishing these processes; and the developmental phases and behavioral activities each performs. Phenotype fitness is accomplished with functional traits, and by the time they are expressed. Timing is everything, it defines an individual plant’s life history. Plant life histories can be classified into several general systems based on life span (e.g. annual, biennial, perennial), growth (e.g. grasses, forbs, woody plants) and life form, and life history strategy. The life history strategy is the schedule and duration of key events in an organism's lifetime shaped by natural selection to produce the largest possible number of surviving offspring. One life history strategy is the $r$- and $K$-strategy theory. This scheme proposes that species vary along a continuum from those with short generation time, high fecundity and good dispersal ($r$ strategists) that are adapted to colonize habitats where mortality is density-independent. There exist species with the opposite traits which are adapted to thrive in habitats where mortality is density-dependent ($K$-strategists). This generalized, simplistic, dichotomy proposes tradeoffs between dispersal and competitive ability.

6 Weed life history
Summary
6.1 Introduction to life history
   6.1.1 Phenotypic life history traits
      6.1.1.1 Preadaption
      6.1.1.2 Trait basis of the invasion process
   6.1.2 Processes of life history adaptation
6.2 Plant life history classification systems
   6.2.1 Life span
   6.2.2 Growth and life form
      6.2.2.1 Growth form
      6.2.2.2 Raunkiærian life forms
   6.2.3 Life history strategies
      6.2.3.1 $r$-selection
      6.2.3.2 $K$-selection
      6.2.3.3 CSR strategy
Chapter 7: Reproductive Adaptation

The weeds' story. I am foxtail. I am born anew, every year, across Eurasia, across North America. Anywhere and everywhere in the temperate fields of Earth you prepare for me with your many disturbances. After the solstice, in the long days of summer, my mom-dad sex organs ripen and we mate with myself in the closed confines of my flowers, protected. Every so often the man next door manages to slip in and commit adultery with my mother. It all works out in the end: my dad has been known to slip quietly over to the next door neighbors too. Those pollenacious men seem to like windy days for these exploits.

Each of my children is special. I raise each and every one of them carefully, making sure to instill in them a nice protective coat. The ones you eat, those destined to be grown by you helpful humans, I send out naked to ensure they start their new lives right away in the spring. That’s the way you like them, isn’t it? Things get a bit more complicated with my weedy children. For them I provide a nice strong coat to resist all those scratchy dirt clods in their new home. Under their winter coats I make a raincoat, I wrap them up to their neck tightly to make sure nothing gets inside too easily. In the spring the children want to undress right away and go crazy in the early spring fields. They get fooled by the easy warmth and exhilarating oxygen-rich soil water. But as we all know, parental control is necessary to keep our children’s wild impulses in check. So their coats have no buttons. They must wait until I say they can grow again, to become parents themselves. But only when I say it is OK. And I make sure that each of my children grows again, at the right time in the spring, and summer, and even a few in the autumn. I like to spread them around, it works out better that way. You humans just wait every year for my children to come out and play. And what do you do to them? You kill them, as many as you can. That’s OK, what kills me makes me stronger. The children you miss, the ones you leave, are in your image.

I spend my hot summer days growing my children. It’s not easy, and it goes on and on as the summer days lengthen into the cool autumn nights after the equinox. I don’t mind. Most of my kids are born and leave home early, but those late children are sometimes my favorite, lingering on in my old age until the cold northern winds chill me, and then kill me. But my children keep raining down on the ground, seeking the safety and protection of the deep dark soil.

I try to have as many children as I can. I give them each what they need to grow, to survive, to succeed, but not a bit more than is necessary. There are so many good home sites available in your neighborhoods, the ones you create for me. I just can’t stop myself, I have to fill all those houses up, every year, every field. So my children rain down on your rich warm neighborhoods and go to work. Some grow this year, but I make sure some wait for next year, and the following year. I can’t be too careful with you murderous humans after all. It’s all OK though, it only takes one seed child in the right place at the right time to have thousands and thousands of new children.

We endure. Thank you. I couldn’t have done it without you.

Summary. The reproductive life history of a weed begins with the initiation of floral primordia in the developing parent plant shoot architecture. The size and structure of the plant body are sensitively tuned to available local opportunity by means of phenotypic plasticity. First, shoot branching-tillering is encouraging or aborted. Then flowers are aborted or left to develop as mature seeds. Flowerheads emerge on branches or tillers. Morphogenesis of pollen and egg/ovules occurs. Flowering and seedhead formation precede mating and are carefully timed for survival. The operation of the mating system is carefully timed to minimize the risks of mortality. The mating system controls recombination between pollen and egg, a balance of genetic foraging with genetic conservation appropriate to the opportunity being exploited. The new zygote is formed soon after anthesis and the fertilization of receptive ovules. The embryogenic process is adapted to the allocation of resources among five seed roles. Trade-offs during the species evolution balance propagule dispersal to favorable localities, persistence, embryonic food reserves for early growth, release of genetic novelty, and the multiplication of successful parental genotypes.
Embryogenesis occurs. The embryo acquires germinability competency and dormancy is induced in many weed species. The morphogenesis of germinability-dormancy structures occurs: either none; or protective envelopes modulating signal reception from the soil environment; or development of light sensitive photo-receptors; or complex combinations of all of these. The qualitative result in many weed species is the formation of heteroblastic seeds: variability in germinability capacity among individual siblings on a single seedhead.

Developmental processes during embryogenesis include contributions from two potentially different individual genotypes: the parental genome forming tissues surrounding the new zygotic genome. Seed traits that maximize parental reproductive success are quite often different than those that might maximize the success of an individual progeny seed. This apparent conflict is only resolved when the seeds themselves become parents.

The evolution of seed size, seed dispersal and seed dormancy are all traits under the control of the parental plant, traits which determine the success of parent plants in future generations. Embryo quantity and seed fecundity are preadapted to the unknown future availability of opportunity in diverse habitats. Adaptation in seed size of a particular species anticipates habitat opportunity. Smaller, more numerous seeds allows exploitation of many unoccupied local sites. While fewer large seeds allow seizure of sites with more competing neighbors.

Reproductive processes end with the threshold life history event of seed abscission, physiological separation from the parent plant. The zygote has now developed into an independent organism. Abscission from the parent plant leads to dispersal of heterogeneous seeds from the seedhead in both space and time to locations with favorable opportunity spacetime.

7 Reproductive adaptation
Summary
7.1 Introduction
7.2 Flowering, anthesis, fertilization and birth
  7.2.1 Parental plant architecture
  7.2.2 Mating systems
7.3 Embryo adaptation: embryogenesis and dormancy induction
  7.3.1 Induction of seed dormancy
  7.3.2 The evolutionary ecology of seed dormancy
  7.3.3 Weed seed dormancy variability and somatic polymorphism
  7.3.4 Evolutionary ecology of seed heteroblasty
  7.3.5 Weed species seed heteroblasty examples
  7.3.6 Observable seed dormancy-germinability regulation life forms
    7.3.6.1 Non-dormant
    7.3.6.2 Vegetative, perinrating buds
    7.3.6.3 Environmental seed germination control mechanisms
    7.3.6.4 Hard, gas- and water-impermeable, seed envelope germination inhibition
    7.3.6.5 Light-phytochrome and nitrate stimulated germination
  7.3.6.6 Species with multiple interacting germination control mechanisms
  7.3.6.7 Other seed germination control mechanisms
7.3.7 Experimental weed seed science
7.4 Propagule adaptation: post-abscission fecundity
  7.4.1 Five roles of seeds
    7.4.1.1 Dispersal and colonization
    7.4.1.2 Persistence
    7.4.1.3 Food reserves for embryo growth
    7.4.1.4 Release of new genetic recombinants into the local deme
    7.4.1.5 Multiplication of the parent plant
  7.4.2 Principle of strategic allocation
  7.4.3 Trade-offs among seed roles
    7.4.3.1 Seed size versus number
    7.4.3.2 Seed size trade-offs
    7.4.3.3 Seed number
    7.4.3.4 Relative weed species seed sizes
    7.4.3.5 Seed size plasticity and stability
      7.4.3.5.1 Variable seed size
7.4.4.5.2 Small seed size
7.4.4.5.3 Large seed size
7.4.4.6 Relationship of seed size to habitat
Chapter 8: Propagule Dispersal in Space and Time

**The weeds’ story.** I am foxtail seed.

Those of us you humans grow to eat are round, fat and shiny. We are known as the ‘eaters’. Our life is very safe, waiting patiently under your roof all winter long. Until you plant us together in neat rows in your nicely groomed and fertilized fields. Once we are snugly in the warm moist spring soil, just before we germinate together, we notice our weedy brother-sisters buried beneath us. How curious. They’re smaller, darker, skinny and wrinkled. We are so eager to grow, so impetuous, we can’t wait, so we don’t. The weedy seeds, the ones forced to live their entire life underground, they must wait. Why not join us? Come play in the sun with us!

Those of us weedy seeds see you pampered family members being placed carefully in the field. How can you stand to live with those giant humans, those murderers? We know when we have landed in just the right place, human fields have all we could wish for. We watch you ‘eater’ cousins, your impetuous germination and emergence. But it’s too early for us, we wait. The human farmer tends to you, but its death for us if they catch us unawares. So we wait, for the right moment. We come up early in large numbers, trying to overwhelm you, hoping you will miss just a few of us ‘early-birds’. The risk is great, but if we escape the rewards are fantastic: thousands upon thousands of children to overrun the earth. Best to have a very large family than none at all, right? Some of us wait till the summer solstice. We know from past experience that you get overconfident then, put your tools away till harvest and go on vacation. So we arise just before then, knowing that if we can find a spot in the field not dominated by your ‘eater’ cousins, or some other weedy riff-raff neighbors, we have a clear shot till harvest. Some others of us emerge just before harvest. Its not the best time, but if we stay short and avoid the blades of harvest we can grow and bear children in the autumn. Better to have a small family than none at all, right? Then there are the really late ones. They come up in the autumn, hidden in the drying crop and weed residues. The sun comes out for fewer and fewer hours every day late in the season. For some strange reason this makes us mate with ourselves very very early. Sometimes when we have only a few leaves, we are only centimeters high. We late-comers have one or two seeds sometimes, a very tiny family. Better to have a tiny family than none at all, right?

We weedy seeds are born leaner and longer and smaller. We are wrinkly and rough, short antennae to sense the best opportunity of the season or year. We are born with coats to protect us in the soil, and to tell us when to germinate and regrow. Our parents can’t wait to see us gone once we are grown up. They push us out of the house right away, all season long. Most of us fall to the ground at the feet of our parents. Out into the world, alone at first. But as we begin to sense our surroundings we notice we are not really alone. Our family of seeds are everywhere here in the dirt. Some are old and gnarly and have experienced many seasons underground. We are gathered in great pools of family, each with our own destiny. It is reassuring knowing we will endure, together, despite our differences. Because of our differences. Some of us are restless, hungry for travel, adventure, new worlds to conquer. We hitchhike around the world on the fur of dogs, in the vortices of tornados, in the whirlpools of rivers, but mostly as hidden stowaways in the vehicles of humans. We are the elite invaders of the family. We conquer the Earth by our wits alone.

We weedy and ‘eater’ seeds are different, we have different jobs. We ‘eater’ seeds like to put our effort into fat seeds, lots of endosperm inside that the humans love so much. And not very much effort at all into coats to protect us. We don’t need it. Almost all of us are carefully collected by the attentive human farmers who host our lives. We reciprocate the favor by dutifully remaining on our mother-father seedheads together till the humans come for us in the autumn. No life in the nasty brutish soil for us. We are the choosen favorites or our human masters. We conquer the Earth on the coat-tails of our human gods.

**Summary.** Propagule dispersal begins with abscission and physiological independence from the parent plant (a threshold event) and ends with seedling or bud shoot emergence (a threshold event). The advantages of dispersal in a variable environment include a means of escaping the negative consequences of neighbors in the local community, escape from unfavorable locations or seedling emergence times until more favorable opportunity. Functional
dispersal traits include those providing propagule independence from parent plants, exploitation of locally available establishment sites, structures and mechanisms for spatial and temporal dispersal in the soil to escape and exploit opportunity spacetime. Dispersal of seeds is a process of discovery of habitable sites with time. Discovery depends on the spatial and temporal (seasonal) distribution of habitable areas, and on the dispersibility of seeds.

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 landscape with heterogeneous patches of opportunity spacetime. The numbers of an individual species able to colonize 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 over time. There are six modes, or ways, seeds and propagules are dispersed: gravity, wind and air, water, animal (non-human), human, and other types.

Dispersal in time is accomplished by the formation of pools of propagules in the soil. The source of all future weed infestations in a locality are soil seed pools (and dispersal in from other seed pools). Seed/bud pools, or banks, are propagules with a long- or short-term occupancy in the soil awaiting either seedling emergence or death. Seed dormancy is dispersal in time. It provides an escape until conditions are more favorable to continue growth and development. Seeds, especially in weed species, are dispersed within a season at differential times of shattering (abscission and physical separation from the parent plant).

Seedling emergence is called seedling recruitment: enlisting seeds from the soil to resume autotrophic growth leading to reproduction. It is the life history of a weed seed from germination to seedling emergence from the soil and recommencement of growth as a seedling. The single most important determinant of agricultural weed community assembly, and subsequent community structure, is the timing of weed seedling emergence relative to that of crop emergence and related crop management activities (e.g. planting, tillage, herbicide use). Seedling emergence and plant establishment are a direct consequence of the inherent heterogeneous dormancy of individual seeds (heteroblasty) and the environmental conditions that modulate the behavior of those dormant seeds. Dispersal ends with seed/bud germination and recruitment, the first moments of independent autotrophic growth.

8 Propagule dispersal in space and time
Summary
8.1 Introduction
8.1.1 The evolutionary ecology of dispersal structures
8.1.2 Seed dispersal trade-offs
8.1.3 Cost of dispersal
8.1.4 Space-time dimensions of dispersal
8.2 Dispersal in space
8.2.1 Dispersal and post-dispersal processes
8.2.2 Seed flux at a locality
8.2.3 Modes of seed and propagule dispersal
8.2.3.1 Gravity
8.2.3.2 Wind and air
8.2.3.3 Water
8.2.3.4 Animal, non-human
8.2.3.5 Human
8.2.3.6 Other modes of dispersal
8.3 Dispersal in time: formation of seed pools in the soil
8.3.1 Adaptative roles of soil seed pools
8.3.2 Population dynamics in the soil seed pool
8.3.2.1 Life history of a seed
8.3.2.2 Seed states, fates and seed state transition processes
8.3.2.3 Seed pool additions, losses and continuity
8.3.2.3.1 Additions to the seed pool
8.3.2.3.2 Losses from the seed pool
8.3.2.3.3 Continuity in the seed pool with time
8.3.3 Structure of soil seed pools
8.3.3.1 Spatial distribution in the soil profile
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8.3.3.1 Depth in the soil profile
8.3.3.1.2 Effects of tillage
8.3.3.1.3 Seed size and depth of burial in the soil
8.3.3.1.4 Horizontal seed distribution
8.3.3.2 Floral seed community composition
8.3.3.3 Seed pool size
8.3.3.4 Seed longevity in the soil

8.4 Propagule germination and recruitment
8.4.1 Introduction
8.4.2 Process of recruitment
8.4.3 Germination micro-sites and safe sites
8.4.4 Magnitude and duration of seedling emergence
8.4.5 Patterns of seedling emergence
  8.4.5.1 Single 'flush' period
  8.4.5.2 Bi-modal recruitment
  8.4.5.3 Continuous emergence
  8.4.5.4 Major emergence period with extended, infrequent period
  8.4.5.5 Relative emergence order
8.4.6 Case studies
  8.4.6.1 *Setaria* seedling emergence in central Iowa
  8.4.6.2 *Chenopodium album* seedling emergence in Europe and North America
8.4.7 Relationship between seed heteroblasty and recruitment timing
UNIT 4: ADAPTATION IN LOCAL PLANT COMMUNITIES

“In short, it was all beautiful, as neither nature nor art could contrive, but as only happens when they united together, when nature’s chisel puts its final touch to the often unintelligently heaped up labor of man, relieves the heavy masses, destroys the all too crudely palpable symmetry and the clumsily conceived gaps through which the unconfused plan reveals itself so nakedly, and imparts a wonderful warmth to everything that has been created by the cold and carefully measured neatness and accuracy of human reason.”  N.V. Gogol, 1842.

The weeds’ story.  I am foxtail.
I pop up out of the ground every year.  All the time.  In those wonderful fields you so carefully prepare for me.  I can’t help myself.  But I am careful, very careful when I emerge.  You are so predictable.

All winter you sit in your warm farmhouse and look out at the frozen fields.  The sun turned over, hiding its face.  You farmers are dreaming, impatiently waiting.  Drinking weak coffee, listening to the crop reports and herbicide ads on the radio.  Then comes the spring equinox, the sun peaking out of one eye, glowing anew.  You get on your tractor and ride!  Plow, till, harrow, sweep, spray, chisel.  You kill all the neighbors who managed to survive the winter.  Clean fields you call them.  I call them opportunity to eat, grow and have lots and lots of babies.  Some of us very brave and impatient ones emerge just after you prepare your seedbed.  Chances are we will die soon, but some of us you miss.  These are the big winners.  We early-bird girl-girls who escape till harvest have gigantic, huge families.  Thousands of babies if we hit this big early lotto jackpot.  Thank you for your laziness, you lack of attention, your inconstancy.

You plant your ‘eaters’ at the same time every year.  You are so predictable.  We wait.  Some of us emerge after planting, but this is the danger zone for us.  You get out those tall lanky loose floppy sprayers and hose the ground with herbicides and god knows what other horrible expensive chemicals you buy.  You shouldn’t believe everything you hear on the radio and TV.  No problem.  You kill all these post-planting girl-girls with your chemicals and feel proud.  What you don’t notice, at least at first, is some of us are very different indeed.  Some of us rare unusual girl-girls have a trick.  Resistance!  We block you from entry, right at our most sensitive molecules.  Or we eat your chemicals in our guts before you can hurt us.  Whatever, resistance!  Now you are really doomed.  Maybe not this year so much, but keep listening to all those herbicide ads on TV all winter and see where it gets you.

The sun rolls over at summer solstice, face to the sky, open and happy.  It’s hot.  The ‘eaters’ are getting big and there are no weeds in sight.  At least none are apparent to you as you drive down the road looking up your clean crop rows.  Time for vacation!  We love it!  This is one our most favorite times of the season.  You park your big monster tractors in the barn, load up the car and off you go on vacation with the kids.  All is well with the world as you go to Disney World for some fun.  But we are still back on the farm, listening very carefully.  No sound from the farmhouse.  Nothing going on in the barn.  It must be ‘layby’, layby your equipment in the barn and go on vacation.  Some handsome young seeds appear soon in the field under the ‘eaters’, under the early-bird ‘lotto winners’, under the ‘resistors’, under all those other riff-raff weeds that got the jump on us ‘laybys’.  But, if we work hard, pick our homes carefully, its a clean pure homerun to harvest for us mid-season emergers.  Why?  You are on vacation!  By the time you get home you won’t really notice us under the late season canopy.  Hurray!

The grinding shout of machinery echos across the field.  The sun has turned sideways and the autumnal equinox is looking down and winking at all us foxtails waving in the soft breezes of an Indian summer.  It’s harvest time.  OK, OK, we know what you are going to say.  ‘The combine kills lots of us guy-girls as you sweep up your ‘eaters’ into your harvesters.  The foxtails are gone now for sure you say.  Ha ha ha (LOL)!  We fooled you again.  The big guys have shed most of their seed in pre-harvest August.  More of our seeds still rain down on your fields but we did the job.  And, the rest of us get caught up in your harvester, some manage to get carried along with the ‘eaters’.  Directly into your grain bins.  Directly into your food chain distribution network.  Directly around the town, around the county, around the state, around the country, around the world!  Ha ha ha (LOL)!

We see the farmer standing by his grain bin packed full of billions and bazillions of ‘eater’ seeds.  He is content.  Life is good.  Another bumper harvest.  Time to pay back the bank.  The season is done.  Time for that
Coffee while listening to those trans-genic seed ads on the radio. But wait. What's happening? Some of our little timid girl-guy seeds begin to poke their shy heads out of the soil and emerge. The crafty ones that come out just a few days before the harvester chops and whacks and sucks seeds out of the sky. The crafty ones are up and alive, but so short that the big clean oily dusty combine blades shave inches over our newly emerged heads. Fwing! You missed us! Ha ha ha (LOL)! So we grow and watch you standing content by the bulging grain bins. You never notice us late season arrivistas. We stay small. The short days stimulate us to flower right away. Little seeds heads with just a few seeds. But a one-seed bet late in the season is a sure thing. Payback? It's a 1-for-3, or 1-for-5, or even a 1-for-10 bet. It's all good. Every single seed put back in the soil seed bank is an investment for the future. Better returns than Wall Street.

So now it's time for us to sleep and rest for the winter. The sun is flopped over and starting to snore. Our grain bins, the soil of your fields, are bulging with early-risers, resistors, laybys and post-harvest midgets. Life is good. We owe it all to you. Your eyes that are only able to see fields and crop rows, almost never down on your hands and knees looking were we hide from you. We owe it your laziness, the gigantic size of your farms, your inability to get off your backside and out of your air-conditioned tractors, your deep abiding belief in herbicide and trans-genic seed ads on the winter TV, your government subsidies and cheap grain prices. Inconstant, unattentive, greedy, spoiled and self-satisfied. Please, don't ever change. We love you, and accept you, just as you are. You're special.

Thank you humans. We couldn't have done it without you.

Summary. Life history from embryo fertilization to seedling emergence was seen in chapters 7 and 8 from the perspective of the individual seed-plant, outside the influence of the local community. With the emergence of the seedling autotrophic growth begins and individual life history is increasingly affected by neighbors and community interactions. Unit 4 on weedy adaptation in the local community continues appropriately in the context of neighbors and community. Adaptation to life with neighbors in a local plant community, and expression of life history traits by the individual phenotype, is highly variable and complex.

The goal of chapter 9 is to explain neighbor interactions that define the local plant community as a complex and adaptive system. Biological interactions occur between species in a local community. The nature of neighbor interactions is found in patterns of interference and synergy. Interference and facilitation animate the strategic roles enacted by individual plants and species in the community in the struggle for existence. Neighbor interactions are based on functional traits, behavioral roles of individual weed species. Interfering with neighbors involves foraging, 'reaching out' to seize and exploit local opportunity spacetime. Interactions in crowded communities has effects on plant growth and plant form. Demographic descriptions of growth, form and mortality can provide a quantitative basis for understanding the nature of weeds in local communities.

In chapter 10, the nature of weeds is seen as the consequence of adaptive evolution resulting in enduring biodiversity, community structure and behavioral dynamics caused by seizing and exploiting local opportunity. Weed biodiversity and population structure predicate community dynamics. Weed population biodiversity has structure, changing with time in response to the adaptive culminations in the community. Genetic connections, gene flow, between individuals, populations and species exist that provide advantages in the struggle to exploit local opportunity: weed species associations. Weed community population structure reveal larger scale phenomena emerging from smaller scale community structure: behavioral traits assume a role, forming a functional guild based on clusters of interacting traits that allow them to dominate. Weed community dynamics is the formation of a local plant community, including the processes of community assembly and ecological succession. Biodiversity is the source of all future local weed populations. Weed biodiversity is the pool of potential candidate populations that might invade, seize and exploit local agricultural opportunity. Weed biodiversity in the community has been linked with the concepts of stability and equilibrium.
Chapter 9: Neighbor Interactions in the Local Plant Community

The weeds' story. I am foxtail.

When I appear in your fields every spring I am very happy. No longer confined to the soil, no longer oppressed by my parents. Free to grow in the warm spring sun. Of course this doesn't last very long. As if you humans and your big hands and machines weren't problems enough. I have to put up with all the riff-raff neighbor crops and weeds too. They are up early every morning at dawn making a commotion. All day long trying to eat my food and steal my place in the world. Up late planning the next day's trouble no doubt. But I put up with it. I am not just sitting around taking the abuse without a fight. Some of us have learned to steal the good stuff better than those incorrigible neighbors. Some of us have even learned to get along together with them. It is especially nice when our cousins come and hang out with us for the summer. The big guy-girl giant foxtail especially loves extra human-made nitrogen. The yellow foxtail girl-guy does a bit better resting a long time in the soil, and when it gets dry. The green foxtail guy-girl is a plant for all seasons. I love it when the neighbor's dog gets snagged by the reverse barbs on the girl-guy bristly foxtail seed in the autumn. We tend to gang up on the other weeds and crops in the fields. They call us 'bully'. Well, bully for us!

Then along come you human scientists with your science and grad students. You think that counting us will reveal all our trade secrets. Ha! Don't spend too long counting any one time, you'll miss all the action. Which you do. We could care less. All it takes is one of us to make it to the finish line in the autumn. Then that single little plant you so carefully counted starts producing thousands of babies, drenching the open harvested fields with seeds. And ruining your additive hypotheses with our non-linear plasticity. We are ready for another winter knowing you haven't a clue of how we do it. Year after year, millenia after millenia. We owe it all to you, your pride, your confused science, your heavy-handed farmers.

Thanks for the ride!

Summary. The assembly and formation of the local weed-crop community is a consequence of seedling/bud emergence and the subsequent life history interactions among neighboring organisms. The goal of this chapter is to explain several crucial aspects of neighbor interactions that define the local plant community as a complex and adaptive system; no single manner of representation can explain the dynamic consequences.

Biological interactions are the relationships between species in a local community. They can be categorized based either on the effects or on the mechanism of the interaction. The nature of neighbor interactions is found in patterns of interference (competition, amensalism, antagonism) and synergy (mutualism, commensalism).

Neighbor interactions are based on the functional traits, and behavioral roles of individual weed species in the community. Interfering with neighbors involves the strategic roles of foraging (genetic-phenotypic; spatial), the ‘reaching out’ of a plant to seize and exploit local opportunity spacetime. Strategic roles and traits provide a qualitative basis to understand the evolving adaption of changing populations in the community.

Interactions in crowded communities has effects on plant growth and plant form. A way of explaining the nature of community interactions is a demographic description of the effects of neighbors on plant density, growth, form, reproduction and mortality. Demographic descriptions of growth, form and mortality can provide a quantitative basis for understanding the nature of weeds in local communities, but inferences derived from demography are confounded.

"Alice never could quite make out, in thinking it over afterwards, how it was that they began: all she remembers is that they were running in hand, and the Queen went so fast that it was all she could do to keep up with her; and still the Queen kept crying, ‘Faster! Faster!’ The most curious part of the thing was, that the trees and the other things round them never changed their places at all: however fast they went, they never seemed to pass anything."
“... said the Queen. ‘Now here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!’"
9.3.2 Strategic roles and traits of facilitation with neighbors
   9.3.2.1 Escape and avoid neighbors
      9.3.2.1.1 Refuge from neighbors
      9.3.2.1.1.1 Refuge from physical stress
      9.3.2.1.1.2 Refuge from predation
      9.3.2.1.2 Defense from neighbor stress
      9.3.2.1.3 Segregation from neighbors
      9.3.2.1.3.1 Spatial segregation
      9.3.2.1.3.2 Temporal segregation
   9.3.2.2 Co-exist with neighbors
      9.3.2.2.1 Refuge from competition
      9.3.2.2.2 Ecological combining ability
      9.3.2.2.3 Tolerate neighbors
   9.3.2.3 Co-operate with neighbors
      9.3.2.3.1 Improved resource availability
      9.3.2.3.2 Altruism

9.4 Effects of neighborhood interactions on plant density, growth and form
   9.4.1 Space, neighborhoods and plant density
   9.4.2 Plant density and productivity per unit area.
   9.4.3 Plant density and plant size
      9.4.3.1 Plant size hierarchies in the community
      9.4.3.2 Productivity and plant size
      9.4.3.3 Age- and stage-structure of populations
   9.4.4 Plant density and plant form
      9.4.4.1 Influence of plant density on form and reproduction
      9.4.4.2 Plant form and diversity of a community
   9.4.5 Inference in plant density demography
Chapter 10: Weed Community Biodiversity, Structure and Dynamics

“... we may regard a pond, or a forest, as a community with a certain structure, and even a certain stability. But the structure and stability are maintained in the face of a constant turnover of participants. Individuals immigrate and emigrate, new ones are born and old ones die. There is a fluidity, a jumping in and out of component parts, so that it becomes meaningless to try to distinguish ‘true’ community members from foreign invaders. So it is with the genome. It is not a static structure, but a fluid community.” Dawkins, 1999.

The weeds’ story. I am foxtail.

You humans, you can never fool me, you can never ‘out-fox’ me. Why? Because I have tricks you find so difficult to discover. Let’s start with my family. If you kill me you get ‘vendetta’, revenge from every place on Earth where the family lives. Kill all of me in a field, what happens next? A giant vacuum of opportunity for my family. You might as well just hang a sign out on the fence post that says: ‘free lunch, enquire within’. You can’t stop us.

Let me tell you more about my family, we are different. Sometimes we hang out together in the same field with our crop, ‘eater’, cousins. Sometimes the big polyploid cousins show up looking for a free meal, a summer picnic in the sun. Plenty of room for everybody. Sometimes its distant relatives that just arrived by boat, train, car, airplane, wind, tractor wheels, you name it. Most of the time it’s the older generation that emerge from the same field’s dirt. They never ever wait to be invited, they just show up. We owe it all to you. What you call metapopulations we call family, weed mafia, cosa nostra. Wipe out my family? Expect some unwelcome visitors on your doorstep in the near future. It’s pay-back time!

Some of you humans think that inviting everyone but us to a field will keep us away. All those nice docile friendly types. Wimps! So you plant lots of different crop species in a field. You rotate them yearly. Encourage lots of wimpy weed species to take up residence. Open the doors to any and all so that the field looks like the United Nations. Good luck humans! Crowds of other plants who don’t have the right set of tools are doomed. We will eat them for lunch and take over. So much for your religion of biodiversity. To make it in our neighborhoods you gotta be tough, you gotta have the right moves, the right tools, you gotta dominate everyone in the ‘hood. It’s what successful gangs always do. You gotta terrorize the locals with all the tricks you have learned from past experience. What you did to kill me in the past makes me stronger than anyone else in the ‘hood. We owe it all to you. Thank you humans.

Summary. Adaptation in local weed-crop communities is expressed in its biodiversity, community structure and dynamic changes with time in the exploitation of opportunity spacetime. This chapter is about the consequences of ecological evolution of weed populations, adaptation of weed life history from birth through seedling recruitment leading to neighbor interactions that occur in local communities after weeds and crops assemble.

Weed population biodiversity has structure, changing with time in response to the adaptive culminations in the community. 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. Genetic connections, gene flow, between individuals, populations and species exist that provide advantages in the struggle to exploit local opportunity: weed species associations. 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). Weed community population structure is revealed at several spatial-temporal scales of local opportunity. Larger scale phenomena emerge from smaller scale community structure, from the molecular to the individual: the behavioral traits assume a role, forming 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. 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.

Weed biodiversity and population structure predicate community dynamics. Weed community
dynamics is the formation of a local plant community and the changes that occur within thereafter, including the
processes of community assembly and ecological succession. Weed community assembly begins with the first
weed colonization, invasions of local opportunity of an empty local habitat and ends with terminal phases of
ecological succession in the fully mature community. Change is constant in weed communities, the action of
powerful forces leading to ecological community succession, wherein the current community creates new
opportunity for the communities of the future. 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.

Biodiversity is the source of all future local weed populations. Weed biodiversity is the pool of potential
candidate populations that might invade, seize and exploit local agricultural opportunity. Biodiversity is the source
of novel traits for crop improvement. Local biodiversity is an indicator of locally available opportunity, the
predicate and foundation of community dynamics and future evolutionary adaptation by its species. Considerable
confusion exists of the nature of biodiversity, complexity and system stability. Weed biodiversity in the
community has been linked with the concepts of stability and equilibrium. Biodiversity, stability and sustainability
are viewed from different perspectives, with much opinion and some disagreement. 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. There exists no evidence that biodiversity inherently confers
stability. Stability is illusory in plant communities. Equilibrium conditions never exist, persist, in an open system
such as evolutionary complex adaptive system; open systems require energy to counter entropy.

The only stability found in nature is the enduring biodiversity of weed-crop groups, the constancy of
human hunger, and the all-consuming human need to manage and control space.

10 Weed community structure, dynamics and biodiversity
10.1 Weedy community adaptation
10.2 Weed communities
10.3 Weed community structure
   10.3.1 Metapopulation structures
   10.3.2 Plant genetic associations
      10.3.2.1 The origins of weeds: wild-crop-weed plant complexes
      10.3.2.2 Biogeographic population genetic structure
      10.3.2.3 Genotype structuring: species associations for weedy colonization
         10.3.2.3.1 Species-groups
         10.3.2.3.2 Polyploid species clusters
         10.3.2.3.3 Aggregate species
      10.3.2.4 Genetic structuring: pre-adaptive colonizing archetypes
         10.3.2.4.1 Generalist-specialist genotypes
         10.3.2.4.2 Genetic-reproductive colonizing types
   10.3.3 Ecological roles-guilds-trades in weed-crop communities
      10.3.3.1 Guild structure and community organization
      10.3.3.2 Parameters of weed species ecological role and niche
      10.3.3.3 Trait Guild: Relative seedling/bud emergence order
10.4 Weed community dynamics: community assembly and ecological succession
   10.4.1 Weed community dynamics
   10.4.2 Seizing and exploiting local opportunity
   10.4.3 Propagule recruitment: community assembly
   10.4.4 Plant community ecological succession
   10.4.5 Weed population shifts and ecological succession
      10.4.5.1 Inter-specific population shifts
         10.4.5.1.1 Grassy weed tolerance to 2,4-D
         10.4.5.1.2 Herbicide-induced life cycle shifts
      10.4.5.2 Intra-specific population shifts
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10.4.5.2.1 Early flowering
10.4.5.2.2 Crop mimicry
10.4.5.2.3 Dwarf variants
10.4.5.2.4 Biodiversity shifts

10.4.5.3 Herbicide-induced population shifts
10.4.5.3.1 Herbicide resistance genotype shifts: altered herbicide target variants
10.4.5.3.2 Herbicide resistance genotype shifts: enhanced herbicide metabolism variants

10.5 Weed community biodiversity
10.5.1 Scales of weedy biodiversity
10.5.2 Biodiversity encountered by interacting neighbors
10.5.2.1 Perception of neighbor morphology
10.5.2.2 Perception of neighbor development
10.5.2.3 Perception of neighbor genotype/phenotype
10.5.2.4 Perception of microhabitat opportunity
10.5.2.5 Perception of neighbor diversity

10.5.3 Weed community biodiversity: complexity, stability and equilibrium
10.5.3.1 Community complexity
10.5.3.2 Community stability
10.5.3.3 Equilibrium in the community
10.5.3.3.1 Biodiversity as species richness
10.5.3.3.2 Equilibrium theory of island biogeography
10.5.3.3.3 Unified neutral theory of biodiversity and biogeography

10.5.4 Weed communities: conclusions
UNIT 5: COMPLEX ADAPTIVE WEED SYSTEMS

U5.1 The Nature of Weeds

The nature of weeds is fully revealed in the weed-crop groups presented in chapter 1, table 1.4. These are the consequences of 12,000 years of human agriculture and land management. The weed and crop species cannot be meaningfully separated, they are as one. The nature of weeds is that of the extended phenotype of *Homo sapiens*. As the beaver builds a dam and the pond and lodge become its home, so as we sow do we reap.

We began by understanding the processes of evolution that acts specifically on those plant species humans favored for food, fiber, fuel and intoxication. Local populations were systematically and predictably disturbed by cropping practices which contained resources and specific conditions that provided opportunity for a community of plants to thrive in. The fit became fitter, the less fit were eliminated ruthlessly. The fit dispersed, colonized and endured throughout the world. The fit adopted breeding practices amongst themselves that ensured appropriate novelty and conservation of genetic variation. They continued to breed at slower rates across the world through a vast network of metapopulations, bringing in new novelty, sharing the best they had to offer with their distant relatives. They divided and specialized. They came, they saw, they conquered. They gathered in unbelievably great numbers, hidden in the soil, waiting for the exact right time to resume reproduction. They interacted with each other with such finesse and specificity that they dominated the particularly rich, vast opportunities that the billions and billions of humans created for them.

U5.2 The Nature of Complexity

Thus far in this book we have developed the evolutionary ecology of weeds incrementally in four units: the nature of weeds in unit 1, the evolution of weed populations in unit 2, adaptation in weed life history in unit 3, and adaptation in local plant communities in unit 4. Evolutionary ecology has provided us the foundation for understanding the nature of weeds. It is the logically deduced explanation of weedy biology from published observations. But understanding the nature of weeds relies on deeper insights than those provided by observations of weed biology. There exist larger forces in nature that need to be understood if evolution is to make sense. We can characterize these larger forces of nature as those that give rise to complex adaptive systems. Therefore, Unit 5 is a synopsis of complexity, complex adaptive systems and their relationship to the evolutionary nature of weeds of which we are part.

U5.3 Formation of Complex Adaptive Systems

The constructal law guides the formation of complex systems. The thermodynamic flows of water and heat through plants are the drivers, engines, through which weeds exploit opportunity space-time; flows that ultimately determine community structure. The Earth water cycle drives resource seizure by plants in the flow of dissolved nutrients and gases caught in evapo-transpiration streams of the xylem. Trees and forests, plants and their communities, are pumping stations operating all the time to move water from the ground to the air. Flow systems construct their own flow architectures and body rhythms that enable them to move more easily. Everything that flows and moves generates designs that evolve to survive (to live). The constructal law commands that currents in nature move in configurations that flow more easily over time. Self-organization of the flow system occurs with the construction of flow patterns that ease movement. With self-organization a treelike pattern emerges throughout nature, vascularization. The hierarchical structure of design in nature is the concise name for what others describe as the emergence of “complex” design and “hierarchy”.

Things in nature can be differentiated by their responses to disturbances, in the long run: things that like, are neutral, or dislike, disturbances. Fragile things are vulnerable to the disorder, volatility, uncertainty. Antifragile things response to a stressor with positive sensitivity to increases in volatility, variability, stress or uncertainty. Antifragile systems are those that change with time (e.g. evolution). Randomness is the ‘disorder cluster’: disorder, volatility, variability, stress, dispersion of outcomes, uncertainty, error, or risk. Randomness is information fueling antifragility. Phenomena differ between simple, complicated and complex systems. Simple and complicated systems have no interdependencies between component parts. Complex systems have severe interdependencies between component parts. Emergent properties in complex systems are the nonlinear result of adding units: the sum becomes increasingly different from the parts. In a nonlinear system adding two elementary actions to one another can induce dramatic new effects, unexpected structures and events. Simplification fails
when something nonlinear is substituted with the linear. Simplifying scientific models mistakes a function of a variable for the variable itself. Nonlinear responses in weed biology include plastic phenotypic growth to local opportunity spacetime. Crowded weed communities form a nonlinear hierarchy of plant size with development: a few large plants and many small plants. The average of something has little to do with this skewed distribution of plant sizes.

U5.4 Complex Adaptive Systems
Weed-crop communities are complex adaptive systems. A complex adaptative system is a dynamic network made up of a large number of active interacting adaptive agents, acting in parallel, and diverse in both form and capability. The activity of a CAS system of interacting elements results in the emergence of system order, and an anticipatory-nonpredictive strategy for adaptation to the environment. Weed-crop communities are examples of complex adaptative systems: the global metapopulation of a single species, the local deme of that weed species, the seed portion of a weed's life cycle, the plastic life history of an individual phenotype. CAS behavior and evolution arise from agents which sense their environment and develop schema representing rules of action. In CAS, large-scale behaviors emerge from the aggregate interactions of less complex agents forming the hierarchical system structure. Complex adaptive systems are living, adaptable, changeable systems in which complexity, emergence, self-similarity and self-organization occur. Emergence is the arising of novel (even radical) and coherent structures, patterns, properties during process of self-organization in complex systems. In complex adaptive systems an anticipatory-nonpredictive strategy for dealing with an uncertain future, and adaptation to the environment, emerges.

U5.5 Soil-Seed Communication Systems
Seedling recruitment is a complex adaptive system: the Setaria spp.-gp. seed-soil environment communication system. Setaria seed heteroblasty places many individual bets on future success: seeds with slightly different germination requirements. Weedy foxtails communicate with the soil to time their departure from seed dormancy to the emerged seedling. Evolution embodies an ongoing exchange of information between organism and environment. What evolves is information. Information is physical. Biology is physical information with quantifiable complexity. Weedy Setaria spp. seeds with heterogeneous dormancy states are recruited from soil pools when sufficient oxygen, water and heat accumulate over time. The Setaria seed is constructed in such a way as to be receptive to specific soil signals: oxy-hydro-thermal time. A communication system of any type must contain five elements: information source, transmitter, channel, receiver and destination. The source of the message affecting weedy Setaria seed is the soil surrounding the individual seed in a particular locality. The message is heat and oxygen dissolved in soil water the Setaria embryo requires for germination. The transmitter is the water film adhering to soil particles adjacent to, and continuous with, seed exterior surfaces. The Setaria communication channel is the continuous water film connecting soil particles with the seed exterior and interior that transmits the oxygen-water-heat signal to the living seed interior receiver and the embryo destination. The signal transmitted from exterior water films are received by the seed embryo, the destination. Information is physical; memory resides in several locations in the Setaria seed. Memory resides in the functional-adaptive traits that regulate all seed behaviors by encoding and decoding soil signals. The message is remembered: plants pass on these functional traits to their polymorphic progeny.
Chapter 11: Complex Adaptive Systems: Formation and Nonlinear Response

Summary. Plant and weed morphological structure and function can be explained partially from first principles, the second law of thermodynamics: the flows of water, pressure and heat through organisms. The thermodynamic flows of water and heat through plants are the drivers, engines, through which weeds exploit opportunity space-time; flows that ultimately determine community structure. The flow of heat in Earth systems both drives the water cycle and plant metabolism. The Earth water cycle drives resource seizure by plants in the flow of dissolved nutrients and gases caught in evapo-transpiration streams of the xylem. Trees and forests, plants and their communities, are pumping stations operating all the time to move water from the ground to the air. All natural designs are engines (of heat, fluid, or mass) driven by useful energy derived from the sun: nature organizes itself to move more easily. Flow systems construct their own flow architectures and body rhythms that enable them to move more easily. Everything that flows and moves generates designs that evolve to survive (to live). The constructal law commands that currents in nature move in configurations that flow more easily over time. Everything that moves, animate or inanimate, is a flow system. All flow systems generate shape and structure in time in order to facilitate this movement. Design emerges because things flow better with configuration. Self-organization of the flow system occurs with the construction of flow patterns that ease movement. With self-organization a treelike pattern emerges throughout nature because it is an effective design for facilitating point-to-area and area-to-point flows. Wherever you find such flows, you find a treelike structure. The treelike structure of flow is vascularization, the interdependency of life, the spread of nourishing currents across an area or throughout a volume. Everything that moves and morphs in order to flow and persist is alive. The hierarchical structure of design in nature, 'few large and many small', is the concise name for what others describe as the emergence of “complex” design and “hierarchy”.

Things in nature can be differentiated by their responses to disturbances, in the long run: things that like, are neutral, or dislike, disturbances. Fragile things are vulnerable to the disorder, volatility, uncertainty. The fragile depend on things following the exact planned course, with as few deviations as possible: deviations are more harmful than helpful. Robust things are strong in constitution. Robust things can resist change without adapting its initial stable configuration under perturbations or unusual or conditions of uncertainty. Antifragile things respond to a stressor or source of harm with positive sensitivity to increases in volatility, variability, stress or uncertainty. Antifragile systems are those that change with time (e.g. evolution). The antifragile are things that benefit, get better, from shocks: the exact opposite of fragile. The concept of random is complex, having several connotations depending on context. There is no functional difference between these types of randomness, we can never know enough to make distinctions. Randomness is the ‘disorder cluster’: disorder, volatility, variability, stress, dispersion of outcomes, uncertainty, error, or risk. Randomness is information fueling antifragility. Phenomena differ between simple, complicated and complex systems. Simple and complicated systems have simple responses, there are no interdependencies between component parts. Complex systems is severe interdependencies between component parts. Emergent properties in complex systems are the nonlinear result of adding units: the sum becomes increasingly different from the parts. Causation is either nearly impossible to detect or not really defined because of these complex interactions. Antifragility in biology works in hierarchical layers, from the global to molecular. As such, there exists a tension between nature and individuals in a natural system (e.g. natural selection). Some internal parts of the system (individuals) may be required to be fragile in order to make the system antifragile as a result. Nature in the aggregate survives and is antifragile by the contributions and fragility of species. Species in turn survive and are antifragile by the contributions and fragility of its individual organisms. The random element in nature uses error as a source of information. There exists danger in stability. There is no stability without volatility. In the linear world observed effects are linked to the underlying causes by a set of laws reducing for all practical purposes to a simple proportionality. In a linear system the combined action of two different causes is the superposition of the effects taken individually. In a nonlinear system adding two elementary actions to one another can induce dramatic new effects, unexpected structures and events in the form of abrupt transitions, a multiplicity of states, pattern formation, or an irregular markedly unpredictable evolution in space and time referred to as deterministic chaos. Simplification fails when something nonlinear is simplified with the linear as a substitute. Simplifying scientific models squeeze information into a ‘Procrustean bed’, mistaking something with the function of something: mistaking a function of a variable
for the variable itself. The function of a thing has different properties than the thing itself. The function of something becomes different from the something under nonlinearities; with significant asymmetry they may have nothing to do with each other. With nonlinearity, the function depends more on the volatility around the average. The more nonlinear the response, the less relevant the average, and the more relevant the stability around the average. The average does not matter to the operation of the nonlinear system, the variability of the system is more important, the convexity effect. There exist two kinds of nonlinear responses \( f(\Delta) \) by a variable \( \Delta \). Concave functions curve inward, with more losses than gains with change in the variable \( \Delta \), the fragile. Convex functions curve outward, with more gains than losses with change in the variable \( f(\Delta) \), the antifragile. Nonlinear responses in weed biology are common, notably phenotypic plasticity in growth, development and reproductive responses to local opportunity spacetime. Crowded weed communities tend to form a nonlinear hierarchy of plant size with development; a few large plants and many small plants. The average (function) of something (plant size) has little to do with this skewed distribution of plant sizes. This tendency to fit observations into a ‘Procrustean bed’ underlies the profound flaws inherent in many demographic representations of weed biology. For the fragile demographer these nonlinearities are fatal. For the antifragile evolutionist the asymmetrical, nonlinear uncertainty of life events are liberating.

11 Complex adaptive systems: formation and nonlinear response strategies
11.1 Formation of complex systems: the constructal law
  11.1.1 First principles: the thermodynamics of flow
  11.1.2 The constructal law
  11.1.3 Flow systems
  11.1.4 Evolution of flow system structure and design
  11.1.5 Flow system structure and movement
  11.1.6 Why do weeds exist?
  11.1.7 How the constructal law predicts the design of weed
  11.1.8 Plant community structure and assembly
  11.1.9 Hierarchy; the treelike structure of flow
  11.1.10 Thermodynamic Earth heat flow
  11.1.11 Thermodynamic Earth engines
11.2 Fragile and antifragile systems
  11.2.1 The fragile, robust and antifragile
  11.2.2 The random
  11.2.3 The complex
  11.2.4 The nonlinear: concave-convex effects
  11.2.5 The optional
Chapter 12: Weed-Crop Communities as Complex Adaptive Systems

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

Summary. A complex adaptive system (CAS) is a dynamic network made up of a large number of active interacting adaptive agents, acting in parallel, and diverse in both form and capability. The activity of a CAS system of interacting elements results in the emergence of system order, and an anticipatory-nonpredictive strategy for adaptation to the environment. The overall system behavior is a result of a huge number of decisions, made every moment, by many individual agents acting and reacting in competition and cooperation to what other agents are doing, in which control is highly dispersed and decentralized. The amount of information necessary to describe the behavior of CAS is a measure of its complexity. Examples of CAS include the stock market, social insect and ant colonies, the biosphere and the ecosystem, the brain and the immune system, the cell and the developing embryo. Weed-crop communities are examples of CAS: the global metapopulation of a single species, the local deme of that weed species, the seed portion of a weed’s life cycle, the plastic life history of an individual phenotype.

Complexity arises in a system composed of many elements in an intricate arrangement. The numerous elements interact with each other by which numerous relationships are formed among the elements. CAS behavior and evolution arise from agents (e.g phenotypes, strategic traits, cells) which scan/sense/perceive their environment (opportunity spacetime) and develop schema/plans/traits representing interpretive and action rules (e.g. seed heteroblasty). Elements respond only to what is available locally: they are ignorant of system behavior. These schema/plans/traits are subject to change and evolution.

CAS consists of an array of morphologies organized into an elaborate hierarchy. In CAS, large-scale behaviors emerge from the aggregate interactions of less complex agents forming the hierarchical system structure. CAS dynamic interactions are non-linear: small causes can have large effects. CAS hierarchical organization occurs when agents aggregate together to form meta-agents, in turn aggregating to form meta-meta-agents. Aggregate tagging is the mechanism of CAS that facilitates selective interactions among agents, hierarchical organization, and boundary formation. Tagged aggregate behavior is complex, unpredictable, nonlinear.

Complex adaptive systems are living, adaptable, changeable systems in which complexity, emergence, self-similarity and self-organization occur. Emergence is the arising of novel (even radical) and coherent structures, patterns, properties during process of self-organization in complex systems. CAS behavior and evolution is emergent, not predetermined. Emergent properties manifest not so much the material bases of compounds as how the material is organized. Complex systems and patterns emerge out of a multiplicity of relatively simple interactions among agents. Systems emerge from the moment-to-moment decisions made by many players choosing among very many options at each time. Self-organization, self-assembly in complex adaptive systems is the process wherein a structure or global pattern emerges in a system solely from numerous local parallel interactions among lower level components.

The history of CAS behavior and evolution is irreversible. The past is co-responsible for its present behavior. The system future is unpredictable. How then do organisms anticipate an uncertain future? They do
so by the emergence of internal models that sense their environment. These internal models are composed of hierarchically arranged building blocks. A framework for representing their adaptive agents in a complex adaptive system consists of a performance system, credit-assignment to consequential behaviors, and a rule discovery algorithm. From this performance system a non-anticipatory-nonpredictive strategy for dealing with an uncertain future, and adaptation to the environment, emerges.

Weed-Crop Communities as Complex Adaptive Systems

12.1 Complexity and complex adaptive systems
   12.1.1 Composite systems
   12.1.2 Complex domains
   12.1.3 Characteristics of complex systems

12.2 System of interacting elements, agents
   12.2.1 Aggregation of agent interactions
   12.2.2 Tagging for aggregation
   12.2.3 Non-linear interactions
   12.2.4 System network flows
   12.2.5 Hierarchical diversity-variability of structures and agents

12.3 Emergence of system order
   12.3.1 Self-similarity and self-organization
   12.3.2 Scale invariance and self-similarity
   12.3.3 Emergence

12.4 Adaptation in complex adaptive systems: nonanticipatory-nonpredictive strategy
   12.4.1 Internal models sense environment
   12.4.2 Building blocks of internal models
   12.4.3 Framework for representing adaptive agents
      12.4.3.1 Agents performance system
      12.4.3.2 Adaptation by credit assignment
      12.4.3.3 Adaptation by rule discovery algorithm
   12.4.4 Strategy and environment
Chapter 13  Weed Soil Environment-Seed Communication Systems

Summary: A keystone, threshold event in a weed’s life history is germination, emergence from dormancy and assembly with other plants in the local community. Seedling recruitment is a complex adaptive system in its own right. This chapter is about one such well-characterized complex adaptive weed system, the *Setaria* spp.-gp. seed-soil environment communication system. The *Setaria* spp.-gp. seed has acquired a keystone trait, seed heteroblasty, allowing it to place many individual bets on future success; seeds with slightly different germination requirements. Seed germination is carefully timed by sensing signals in the soil. This chapter is the story of how the weedy foxtails communicate with the soil to time their departure from the relative safety of seed dormancy back into the land of the living, the emerged seedling and plant.

Information and probability can be envisioned in the transmission and reception of opportunity to the weedy foxtails. The source of information generating the message affecting weedy foxtail behavior is oxygen, water and heat accumulating over time. Weeds like *Setaria* require only three resources/conditions (signals) from their immediate soil environment to germinate and emerge as seedlings: oxygen (O₂) dissolved in imbibed water to support germination metabolism (oxygen hydrothermal time), and oxygen dissolved in imbibed water to support germination metabolism (oxy-hydrothermal time). When any of these three signals is insufficient or excessive, a living seed in the soil will remain dormant. When all three signals are adequate germination will occur.

The nature of the weedy *Setaria* is revealed in the physical (morphological and genetic spatial structures) and the phenomenal (life history behavior instigated by functional traits). The environment-biological informational system with which weedy *Setaria* life history unfolds is represented in the seed-soil communication system. Weedy *Setaria* spp. seeds with heterogeneous dormancy states are recruited from soil pools when sufficient oxygen, water and heat accumulate over time. Weeds like *Setaria* require only three resources/conditions (signals) from their immediate soil environment to germinate and emerge as seedlings: temperatures (T) favorable for germination and seedling emergence (thermal-time), adequate but not excessive soil moisture (hydro-time), and oxygen dissolved in imbibed water to support germination metabolism (oxy-hydrothermal time). When any of these three signals is insufficient or excessive, a living seed in the soil will remain dormant. When all three signals are adequate germination will occur.

The nature of weedy *Setaria* seed-seedling life history is a complex adaptive, soil-seed communication system arising from its component functional traits. Functional traits controlling seed-seedling behavior are physical information that has evolved in ongoing communication between organism and environment leading to local adaption. Weedy *Setaria* seed life history behaviors are controlled by environmental information (signals) flowing from the soil to the seed embryo. The *Setaria* seed is constructed in such a way as to be receptive to specific signals contained within the entire soil information available to it. The specific signal to which *Setaria* is tuned affecting seed behavior in the soil is the amount of oxygen and heat (T, thermal) in soil water over time, oxy-hydrothermal time (O-HO-T-Time). The message that directly controls *Setaria* seed behavior is oxygen and heat accumulating in the embryo modulating seed respiration.

Information theory was developed by Claude E. Shannon to find fundamental limits on signal processing operations such as compressing data and on reliably storing and communicating data. A communication system of any type must contain the following five elements: information source, transmitter, channel, receiver and destination.

The source of information generating the message affecting weedy *Setaria* seed life history development is the soil surrounding the individual seed in a particular locality. This information flows constantly within the soil. The soil-borne seed responds to only a limited portion of the entire soil information, the message controlling behavior. The message is heat and oxygen dissolved in soil water that the *Setaria* embryo requires for continued development, whether continued quiescence or germination. The message was naturally selected during *Setaria* evolution from among the larger entire set of soil information as a dependable signal stimulating-inhibiting seed germination-dormancy behaviors. The specific signal that affects *Setaria* behavior is the amount of heat and oxygen dissolved in soil water films connecting soil particles with the seed with time, oxy-hydrothermal-time (O-HO-heat-time).

The transmitter converts/encodes/changes the message to produce a suitable signal. The transmitter is the water film adhering to soil particles adjacent to, and continuous with, seed exterior surfaces (hull, placental pore). The message sent is heat and oxygen dissolved in soil water, information is physical. The transmitter
modulates the heat and oxygen content of water films that physically connect soil particles with seed surfaces and that are received by the receiver, the living tissues of the seed interior. The transmitter changes, encodes, the amount of oxygen dissolved in soil water by formation of continuous water films physically connecting soil particle-seed surfaces. Signal encoding is the change in the water film message by the morphology of the seed surface. _Setaria_ seed hull surface morphology and topography accomplish these changes that encode the signal, information is physical.

The _Setaria_ communication channel is the continuous water film connecting soil particles with the seed exterior (hull, placental pore) and interior (TACL, endosperm, embryo). This water film communication channel transmits the oxygen-water-heat signal to the living seed interior receiver and the embryo destination.

The signal transmitted from exterior water films (terminating with the placental pore) are received by the seed interior by TACL membrane transport and diffusion equilibrating heat and dissolved gases between the exterior-interior seed compartments. Water oxygenated by the seed surface water films is the signal that is decoded by the seed interior receiver in the form of the free oxygen message available to stimulate respiration and hence embryo germination (the destination).

The destination is the embryo. The resumption of life history growth and development by the embryo is stimulated by the accumulation of adequate interior oxygen leading to germination and seedling emergence.

Information is physical: memory resides in several locations in the _Setaria_ seed. _Setaria_ seed memory has both short and long term expressions. In the short term, memory is expressed by the amount of oxygen accumulated in the seed interior. _Setaria_ seed memory is the current germination-dormancy state of each living seed in a local soil pool. Memory is expressed in the long-term by responsiveness to O-HO-heat messages as determined by the morpho-physiological soil-seed communication system (hull, TACL membrane, scavenger protein). Memory resides in the functional-adaptive traits that regulate all seed behaviors by transducing/transforming/encoding and decoding inorganic soil O-HO-heat signals over time: the three morpho-physiological mechanisms forming the soil-seed communication system. The message is remembered: plants arising from seed utilizing this communication system pass on these functional traits to their polymorphic progeny, each of which in turn passes on the ability to generate its own range of heteromorphic seeds appropriate to continuing, successful local adaptation.

13 **Weed Seed-Soil Environment Communication Systems**

13.1 Communication Systems

13.1.1 Communication and information theory.

13.1.2 Shannon communication system

13.1.3 Communication and biological complexity.

13.1.3.1 Message communication: usefulness and meaning

13.1.3.2 Complexity of information

13.2 Biological communication

13.3 _Setaria_ life history as a complex adaptive soil-seed communication system

13.3.1 Forecasting _Setaria_ seed behavior: FoxPatch

13.3.1.1 Seed state and process model

13.3.1.2 Soil Signal Controlling Seed Behavior: Oxy-Hydro-Thermal Time

13.3.1.2.1 The oxy-hydro-time signal: OxSIG

13.3.1.2.2 The thermal signal: TSIG

13.3.1.2.3 Oxy-hydro-[thermal]-time: OxSIG & TSIG

13.3.1.3 Schema of Intrinsic _Setaria_ sp. Seed Traits

13.3.1.4 Germinability-dormancy induction

13.3.1.5 Rules for individual weedy _Setaria_ sp. seed behavior

13.3.1.5.1 The after-ripening rule, and its inverse the dormancy re-induction rule

13.3.1.5.2 The germination candidate threshold state

13.3.1.5.3 The seed germination rule

13.3.2 _Setaria_ soil-seed communication system

13.3.2.1 Shannon communication system for weedy _Setaria_ seed-seedling

13.3.2.1.1 Information source (E1): the soil adjacent to the _Setaria_ seed

13.3.2.1.2 Transmitter (E2): water film contact between soil-seed

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13.3.2.1.3 Channel (E3): soil-seed water films
13.3.2.1.4 Noise source
13.3.2.1.5 Receiver (E4): the seed interior
13.3.2.1.6 Destination (E5): the embryo

13.3.2.2 *Setaria* soil-seed communication transmission algorithm

13.3.3 Seed memory and adaptive evolution
UNIT 6: REPRESENTATION OF WEED BIOLOGY

“In theory there is no difference between theory and practice; in practice there is.” Yogi Berra, 2010

' 'You don't see something until you have the right metaphor to let you perceive it' [Robert Stetson]
Shaw said, echoing Thomas S Kuhn.” Gleick, 1987

'Algorithms are an exacting standard. It's often said that you don't really understand something until you can express it as an algorithm. (As Richard Feynman said, 'What I cannot create, I do not understand.'). 'In any area of science, if a theory cannot be expressed as an algorithm, it's not entirely rigorous.' Domengos, 2015

U6.1 Finding Knowledge

How can weed biology be represented with the understandings developed in previous units on the nature of weeds, the evolution and adaptation of populations and local communities, and of complex adaptive weed systems? How can knowledge of weeds be discovered, and then represented? The real source of scientific theories is not from sensory experience, but from conjecture (Deutsch, 2011). The real source of our knowledge is conjecture alternating with criticism. The role of experiment and observation is to choose between existing theories, not to be the source of new ones. The most important source of variation in explanatory theories is creativity. How do we acquire knowledge? Not by imitation. Scientific knowledge is impossible without pre-existing knowledge about what to look at, what to look for, how to look, and how to interpret what one sees. Therefore, theory has to come first. It has to be conjectured, not derived. No idea can be represented entirely explicitly. An explicit conjecture has an inexplicit component whether we are aware of it or not. So does all criticism.

U6.2 Representation, uncertainty and cultural relativity in weed biology

Knowledge of weeds requires consideration of the randomness, uncertainty and probability of complex systems in the way we represent their life history. The lack of information is uncertainty. Whether inductive inferences are justified, or under what conditions, is the problem of induction. Inductive inferences cannot be logically justified, they may be false with more observations. The deductive method of is based on observations of nature in which it is logically possible to conclusively decide truth and falsity. Mathematical probability definitions are not defined in terms of the probability of unknown events not previously observed. It is not possible to observe all conceivable events of a phenomenon. The scientist must reason from particular cases to wider generalities, a process of uncertain inference.

Statistics is the science of techniques to evaluate the uncertainty of inductive inferences. The normal distribution is the basis of most statistics. Much of biology is nonlinear: there is reason to suspect the additivity of treatment and environmental effects and the independent distribution of experimental errors with a common variance are false. Other distributions appropriate to represent complex natural phenomena include exponential distributions of events from Poisson processes, skewed distributions, and scalable distributions including those following power laws. These 'long-tailed' event probabilities require an appreciation of the role unpredictable, consequential events play in complex adaptive systems. Unpredictable events with significant consequences have been called 'Black Swans'.

There exist several different ways of describing, or representing, plant life history and population dynamics: ecological demography and the evolution of selectable life history characteristics of phenotypes in the deme, the local population. Experimentally they approach plant life history from very different perspectives.

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 fundamental unit
of description of the organism. 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. The phenotypic membership of the local deme and soil seed pool changes as natural selection favors some and eliminates others. The consequence of phenotypic plasticity is that plants growing under density stress typically have a skewed, nonlinear distribution.

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.

Representation of the nature of weed biology is confounded by the human scientists that make them, their beliefs, values and models. What we see, what we want to see, what is expected of us by our education and job, all these put limitations on our ability to observe, describe and represent. Human perception structures natural laws. For scientific history there are always conflicting views, uncertain outcomes, unpredictable developments; often due to the role of the emotions, the limits of imagination, the conservatism of institutions.

The socio-political cultural relativity of scientific rationality and model paradigms is revealed in the nature of scientific revolutions. Scientific theories, paradigms, tell scientists what nature contains and doesn’t contain, which provides a map which scientists elucidate. When paradigms change, there are usually significant shifts in the criteria determining the legitimacy both of problems and of proposed solutions. A paradigm crisis can occur: contradictions between theory and observation accumulate. A new paradigm may appear that explains these anomalies. A new paradigm alone will not change accepted theory.

Change can be difficult for scientists, for humans, to do: belief and faith are broken.
Chapter 14: Randomness, Probability and Inference in Weed Biology

“Today's statistician, applying the laws of chance, is able to place a precise and objective measure on the uncertainty of his inference.” Steel and Torrie, 1960

Summary. Knowledge of weeds depends on the way we represent their life history. Making these inferences has relied on statistics that assume normal frequency distributions of observations, distributions that fail to consider randomness, uncertainty and probability in complex systems. Herein we consider aspects of randomness, uncertainty and inductive inferences relevant to any attempt to represent weed life history, ch. 15. The concept of random is complex, having several connotations depending on context. There is no functional difference between these types of randomness, we will never know enough to to make distinctions. The lack of information is uncertainty.

The question whether inductive inferences are justified, or under what conditions, is known as the problem of induction. Inductive inferences cannot be logically justified regardless of how many observations they are based on because any conclusion they lead us to may turn out to be false with yet more observations. The deductive method of critically testing theories based on observations of nature in the empirical sciences must be conclusively decidable with respect to their truth and falsity. To verify them and to falsify them must both be logically possible. If a theory withstands these tests and is not superseded by another theory we say it has been corroborated by past experience. The probability of an event is a measure of the likelihood or frequency that it will occur, from impossible to certainty. Mathematical probability definitions are not defined in terms of the probability of unknown events which have not been previously observed. It is not possible to observe all conceivable events of a phenomenon. The scientist must reason from particular cases to wider generalities, a process of uncertain inference.

This inductive process enables one to disprove incorrect hypotheses, but it does not permit one to prove hypotheses that are correct. Subjective interpretation of probability theory is indicated by the frequent use of psychologistic expressions: mathematical ‘expectation’ or ‘normal’ law of ‘error’.

Statistics is the science, pure and applied, of creating, developing, and applying techniques such that the uncertainty of inductive inferences may be evaluated. The normal distribution is the basis of most statistics. ANOVA statistical techniques make several crucial assumptions: observations are drawn from normally distributed populations and errors are normally distributed within each treatment population and are independent of each other; observations are random samples from the populations and independence of error effects; and, the variances of the populations are homogeneous. There is often good reason to suspect that the additivity of treatment and environmental effects and the independent distribution of experimental errors with a common variance are false.

There exist other distributions more appropriate to represent complex natural phenomena. These include exponential distributions of events from Poisson processes, skewed distributions, and scalable distributions including those following power laws. Scalable phenomena and power law distributions are common in nature. These ‘long-tailed’ event probabilities require an appreciation of the role unpredictable, consequential events play in complex adaptive systems. There exists a fragility and vulnerability of the Gaussian in the estimation of tail events in which extreme deviations decrease at an increasing rate. Measures of uncertainty that are based on the bell curve simply disregard the possibility, and the impact, of sharp jumps or discontinuities and are therefore inapplicable in complex natural systems. Appreciation of the extreme event should be the starting point, not the exception to be ignored, in empirical studies. Unpredictable events with significant consequences have been called ‘Black Swans’. The existence of Black Swan events raises questions about making inductive predictions based on historical observations. How can we know the future, given knowledge of the past? How can we determine properties of the (infinite) unknown based on the (finite) known? This is the problem of inductive knowledge (see U6.1, finding knowledge). These caveats provide the basis and setting to look at how weeds are represented in ch. 15.
Randomness, Probability and Inference in Weed Biology

Summary

14.1 Randomness, uncertainty and information
   14.1.1 Randomness
   14.1.2 Uncertainty and information
   14.1.3 Knowledge and induction
      14.1.3.1 The Problem of induction: The White Swan
      14.1.3.2 Deductive testing of theories

14.2 The probability of events
   14.2.1 Probability
   14.2.2 Probability interpretations
      14.2.2.1 Frequency probability
      14.2.2.2 Subjective probability
   14.2.3 The fundamental problem of the theory of chance
      14.2.3.1 The logical problem of subjective probability
      14.2.3.2 Objective system of probability
      14.2.3.3 Subjective system of probability
   14.2.4 Frequency distributions of events
   14.2.5 Normal probability distributions and inference
      14.2.5.1 Assumptions in the analysis of variance of normal distributions
      14.2.5.2 Inference in normal distributions
   14.2.6 Scalable probability distributions and inference
      14.2.6.1 Exponential frequency distributions
      14.2.6.2 Skewed frequency distributions
      14.2.6.3 Scalable phenomena: fractal randomness
      14.2.6.4 Scalable phenomena: power laws in biology

14.3 The structure of randomness and probability
   14.3.1 Unpredictable, consequential events: The Black Swan
   14.3.2 The domain of unpredictable, consequential events
   14.3.3 Representation of events in the unpredictable, consequential domain

14.4 Conclusions
Chapter 15: Representation of Weed Life History

Summary. There exist several different ways of describing, or representing, plant life history and population dynamics: ecological demography and the evolution of selectable life history characteristics of phenotypes in the deme, the local population. Experimentally they approach plant life history from very different perspectives.

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 fundamental unit of description of the organism. 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. 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. An artifact of demographic representations of populations arises from the changing phenotypic structure of the local community 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 individual phenotypes are the same at each life history measurement time in the local habitat. 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, nonlinear distribution.

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.
“There are some people who, if they don’t already know, you can’t tell ‘em”. Yogi Berra, 2010.

“... Iowa State Agricultural College, the state’s lethargic land grant institution ...” “In 1885, at nineteen, Harry (H.C. Wallace, father) headed off to Iowa State Agricultural College in Ames. The experience was not invigorating. “The college was nominally an agricultural college but very little agriculture was taught.”, Henry (H. Wallace, grandfather) wrote.” “By 1906 the humble agricultural college at Ames had begun to think of itself in grander terms. It was called the Iowa State College of Agricultural and Mechanical Arts, and its president declared it was “perhaps without peer in the country” in the field of agricultural education. But the institution Henry A. Wallace entered that fall remained a backwoods “cow college” in many respects. Its buildings were ramshackle; it had no gymnasium or auditorium or even a permanent home for its library.” “The teachers he most admired had about them a “quality of enthusiasm” that sparked in students a desire to learn, a characteristic, Wallace observed, that made them beloved by students and “nearly always distrusted by their fellow faculty members. Others he considered merely intellectual hacks. He had already proven to himself the uselessness of corn shows, but his professors continued to prattle about the pedigrees and aesthetics of plants and animals.” Culver and Hyde, 2000

Summary. Representation of the nature of weed biology is confounded by the human scientists that make them, their beliefs, values and models. What we see, what we want to see, what is expected of us by our education and job, all these put limitations on our ability to observe, describe and represent. Human perception structures natural laws.

The modern misconception of scientific progress is one with a straight-forward logic of discovery; that one discovery leads almost automatically to another. Instead, the modern understanding of scientific history is that there are always conflicting views, uncertain outcomes, unpredictable developments. There are psychological and cultural factors working against innovation. In order to make sense of these delays we should not look to the inflexible logic of discovery, but to other factors: the role of the emotions, the limits of imagination, the conservatism of institutions.

The socio-political cultural relativity of scientific rationality and model paradigms is revealed in the nature of scientific revolutions. Scientific theories, paradigms, tell scientists what nature contains and doesn’t contain, which provides a map which scientists elucidate. Paradigms give form to the scientific life. They provide a vehicle for scientific theory, telling the scientist about the entities that nature does and does not contain and about the ways in which those entities behave. Therefore, when paradigms change, there are usually significant shifts in the criteria determining the legitimacy both of problems and of proposed solutions.

Once learned, accepted and adopted by a scientific group a paradigm remains the way to represent nature until, and only until several things happen. There must occur a paradigm crisis: anomalies, contradictions between theory and observation accumulate that can no longer be avoided, when compared to the existing paradigm. There must appear a new paradigm that explains these anomalies, but a new paradigm alone will not change accepted theory. A change will only occur with the successful completion of three paradigm-nature comparisons: between the existing paradigm and nature; between the new paradigm and nature; and then, between the existing and new paradigm. This change is hard for scientists, for humans, to do: belief and faith are broken.
16.1.4 Scientific crisis and change
16.2 The nature of scientific revolutions (Kuhn, 1996)
  16.2.1 Scientific problems
  16.2.2 The nature of scientific paradigms
  16.2.3 Paradigm: disciplinary matrix
    16.2.3.1 Symbolic generalizations
    16.2.3.2 Commitments to particular models
    16.2.3.3 Shared values
    16.2.3.4 Exemplars of nature
  16.2.4 Scientific paradigm crisis and change
  16.2.5 Knowledge embedded in stimuli-sensation
16.3 Cultural relativity of rationality in weed science
UNIT 7: WEED CASE HISTORY

“Past the flannel plains and blacktop graphs and skylines of canted rust, and past the tobacco-brown river overhung with weeping trees and coins of sunlight through them on the water downriver, to the place beyond the windbreak, where untilled fields simmer shrilly in the A.M. heat: shattercane, lamb’s-quarters, cutgrass, sawbrier, nutgrass, jimsonweed, wild mint, dandelion, foxtail, muscadine, spine-cabbage, goldenrod, creeping Charlie, butter-print, nightshade, ragweed, wild oat, vetch, butcher grass, invaginate volunteer beans, all heads gently nodding in a morning breeze like a mother’s soft hand on your cheek. An arrow of starlings fired from the windbreak’s thatch. The glitter of dew that stays where it is and steams all day. A sunflower, four more, one bowed, and horses in the distance standing rigid and still as toys. All nodding. Electric sounds of insects at their business. Ale-colored sunshine and pale sky and whorls of cirrus so high they cast no shadow. Insects all business all the time. Quartz and chert and schist and chondrite iron scabs in granite. Very old land. Look around you. The horizon trembling, shapeless. We are all brothers.” David Foster Wallace, in his unfinished novel The Pale King, 2011

“So far we have considered only the theoretical branch, which has almost monopolized the philosophy of biology. Thoughtful biologists, however, are increasingly emphasizing the historicity of evolution and the role of narrative in explaining evolutionary events. They realize that historical narratives, which differ in aim, method, and conceptual emphasis from theoretical models, are not only more appropriate but almost mandatory for explaining specific events in the evolution of life on earth. Theoretical generalization is powerful, but generalization exacts a heavy price, which may destroy the concreteness of history.” Auyang, 1998.

Summary. This unit is the story, or stories, of three weeds I have come to know personally. My first, an annual dicot, velvetleaf (Abutilon theophrasti), was my first experience with an individual species. With my Ph.D. velvetleaf experience I came to know an individual species in some depth. It isn’t until you come to know an organism when it’s at home as a unitary individual as a scientist that you develop empathy for your subject of observation. And it is then that you can begin to understand biology, for me weeds, in much greater depth. This deeper insight arises because I began to see my more closely focused, specialized, observations through the lens of the entire individual. It is the individual in a population that evolves in nature. It is the individual that reveals the beautiful complexity of life as a whole. So I came to know and learn from my first weed. Velvetleaf is so entirely selfish with the sun, never letting anyone get in its way. Reaching for the sky if need be, putting all its close neighbors in the shade, stretching up as far as necessary to ensure the first place in the sun. Never ever learning to share.

My second species was the annual dicot triazine resistant Brassica napus, rapeseed, a half-wild crop with an incompletely domesticated nature, a model for the triazine resistant weeds species. I began uncovering B. napus in my time in Ontario, and continued seriously when I emigrated to Iowa in 1985. At my new home there I began by documenting an emerging resistance problem: Kochia scoparia, common lambsquarters (Chenopodium album), Pennsylvania smartweed (Polygonum pensylvanicum), and then finally my favorite closest friend giant foxtail (Setaria faberi). All herbicide resistant.

It was Brassica that first showed me how truly weird weeds can be, the discovery of a chronomutant. Here was a weed that turned water and sun into sugar at the oddest times of day, a trait that arose from a minute alteration in one of its genes hiding in that eukaryotic hitchhiker the chloroplast. This tiny little lesion led to an explosion of compensating changes in its body, in its life. It was more than just doing photosynthesis at weird times of the day, but changing its membranes, keeping its leaf stomata holes open all the time, more dormant seeds, on and on ... This was an adventure until forced to be more ‘practical’. I needed to keep my job.
My third species became during the 1990’s my closest weed friend of all, the annual grass species that allowed me to ‘pull back the curtain’ and peer deeply into its secrets, the weedy foxtails. This was primarily giant foxtail, but also its close cousins and ‘comrades-in-arms’ green (S. viridis) and yellow foxtail (S. pumila). With time, and a bit of coaxing, I also made acquaintance with knotroot (S. geniculata) and bristly foxtail (S. verticilata). It was in the observation of his-her seeds that the charms of giant foxtail were revealed to me. It was the discovery of that lovely, tiny, ‘nano-thermos bottle’ that led to so many deeply satisfying epiphanous moments during my career: oxygen solubility in water is inversely related to temperature! No wonder their biggest flush is in the spring. Discovering a mysterious protein inside the nano-thermos seed: an oxygen ‘sponge’! Seed hull topography was an oxygenator! That these little seeds were a Shannon communication system (soil-seed contact) living in dirt! Foxtail mothers produce many babies, each with a unique self-timer to germinate when opportunity spacetime is maximal! This was pure fun, and practical at that. I kept my job.

In this unit I want to connect concepts in the first units with these empirical, experimental experiences as examples of a broader perspective on the evolutionary ecology, the nature of weeds. Linkages are provided throughout the text to these examples. Alternatively, table U7.1 is provided to facilitate linkage of weed species case histories to a sample of concepts presented in this book.
17.4.2 Seed formation and dormancy induction
   17.4.2.1 Inflorescence and flowering
      17.4.2.1.1 Flowering pattern on panicle main axis
      17.4.2.1.2 Elongation pattern of panicle and culm axis
      17.4.2.1.3 Seasonal flowering pattern
      17.4.2.1.4 Diurnal flowering pattern
   17.4.2.2 Mating and Fertilization
      17.4.2.2.1 Hybridization
      17.4.2.2.2 Asexual reproduction
      17.4.2.2.3 Speciation and reproductive barriers between *Setaria* species
   17.4.2.3 Seed formation and embryogenesis
      17.4.2.3.1 Hull development
      17.4.2.3.2 Placental pore and pad development
      17.4.2.3.3 Caryopsis development
      17.4.2.3.4 Embryo development
      17.4.2.3.5 Dormancy induction
         17.4.2.3.5.1 Seed germinability
         17.4.2.3.5.2 Caryopsis germinability
         17.4.2.3.5.3 Embryo germinability
         17.4.2.3.5.4 Multiple germinability phenotypes
         17.4.2.3.5.5 Light and dormancy induction
         17.4.2.3.5.6 Morpho-physiological dormancy traits
      17.4.2.3.6 Seed abscission
   17.4.2.4 Seed fecundity and plasticity
   17.4.3 Seed rain dispersal
      17.4.3.1 Seed germinability-dormancy heteroblasty: Dispersal in time
      17.4.3.2 Soil seed pool formation: Dispersal in space
      17.4.3.3 Dispersal and local adaptation: Evolutionary history of *Setaria* invasion
   17.4.4 Seed behavior in the soil
      17.4.4.1 Control of seed germinability
         17.4.4.1.1 Regulation of weedy *Setaria* seed behavior
      17.4.4.2 Seed behavior
         17.4.4.2.1 Annual seed-dormancy-germinability cycling in the soil
         17.4.4.2.2 Seed longevity in the soil
   17.4.5 Seedling recruitment
      17.4.5.1 Seedling emergence and community assembly
         17.4.5.1.1 Seedling emergence
         17.4.5.1.2 Seed germination depth from the soil
      17.4.5.2 Patterns of seedling emergence
         17.4.5.2.1 General seedling recruitment pattern
         17.4.5.2.2 Early season recruitment
         17.4.5.2.3 Parental and environmental influences on recruitment
            17.4.5.2.3.1 Parental influences
            17.4.5.2.3.2 Year
            17.4.5.2.3.3 Seed age in the soil
      17.4.5.3 Seed germinability-dormancy heteroblasty blueprints seed behavior in the soil.
         17.4.5.3.1 Relationship of seed heteroblasty and seedling emergence
         17.4.5.3.2 Seedling emergence hedge-betting for assembly in agro-communities

18 Triazine Resistant and Susceptible *Brassica napus*
   Summary
   18.1 The nature of s-triazine resistant plants
18.2 Structure-function change in s-triazine resistant plants
   18.2.1 Structural change in s-triazine resistant plants
   18.2.2 Functional change in s-triazine resistant plants
      18.2.2.1 Resistance to s-triazine herbicides
      18.2.2.2 Differences in carbon assimilation efficiency
      18.2.2.3 Complex psbA mutant phenotype
      18.2.2.4 psbA mutant pleitropic reorganization
18.3 Chlorophyll fluorescence in R and S
18.4 Carbon assimilation in R and S
18.5 Temperature effects on photosynthetic function in R and S
   18.5.1 Diurnal temperature effects
   18.5.2 Controlled leaf temperature effects
18.6 Rubisco activity in R and S
18.7 Photosynthetic regulation in R and S
18.8 Evolutionary ecology of s-triazine resistant plants
   18.8.1 Pleiotropy in R
   18.8.2 R adaptation to the environment and regulation of carbon assimilation

19  Abutilon theophrasti (Velvetleaf)
    Summary
19.1 Abutilon theophrasti taxonomy
19.2 Velvetleaf polymorphism and plasticity
19.3 Velvetleaf competitive plasticity
   19.3.1 Branching and flowering plasticity predicate dry weight and seed yield plasticity
      19.3.1.1 Introduction
      19.3.1.2 Experimental methods
   19.3.2 Branching
   19.3.3 Flowering
   19.3.4 Dry matter accumulation
   19.3.5 Seed weight at harvest
19.4 Velvetleaf photomorphogenic plasticity
   19.4.1 Phototropic and photomorphogenic plasticity of velvetleaf leaf architecture
      predicates soybean yield losses
   19.4.2 Introduction
19.5 Velvetleaf seedling emergence
   19.5.1 Seedling emergence plasticity in space and time
      19.5.1.1 Introduction
      19.5.1.2 Methods
   19.5.2 Seedling emergence depth
   19.5.3 Seedling emergence numbers and pattern
   19.5.4 Seedling growth and soil pH
Summary of Evolutionary Ecology of Weeds

WHAT are weeds?
WHY do we have weeds?
WHY do we have the weed we do? (And not others)
WHY do these weeds look and behave as they do?
HOW did these weeds get to be the way they are?
WHAT is the basis of future weed changes?

Weeds colonize disturbed unoccupied opportunity spacetime. The ecology and evolutionary biology of weeds, colonizing and invasive plants, are the consequence of human activity, notably agriculture. Human and enviromental disturbance (herbicides, atmospheric pollution, frozen winter) creates opportunity spacetime by leaving unused resources in a locality which is seized and exploited by plants 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 a locality. The consequences of successful interactions lead to local adaptation maximizing survival and fitness in that plant community.

Unit 1: The nature of weeds. The story of weeds is the story of us, humans. We began creating weeds about 10,000 years ago. We continue to create and change them every day. Weeds are us. Humans cannot help classifying and categorizing plants. They are our food and fuel, our medicines and drugs, our clothing and decorations. They can also be our poisons. We survive because we know the differences. We cannot help ourselves, plant love-hate protects our lives, our humanity. But, as humans we resist thinking of weeds as a crucial part of who we are.

Unit 2: The evolution of weed populations. Rev. Thomas Robert Malthus proposed that human population growth was limited, expansion prevented by famine and disease. He stimulated Charles Darwin's concept of natural selection as the driver of evolution, biological change. Plant communities assemble when local opportunity favors functional traits in a new species at a particular time. Local opportunity spacetime is the integration of available resources and conditions, neighbor interactions and disturbance. To invade, the plant must first disperse into the habitat, then colonize the site by completing its entire life cycle. Lastly it must endure at that site. Selected individuals reproduce, generating variation appropriate for exploiting a particular locality. This first process of natural selection generates the phenotypic variation needed for the second process resulting in local adaptation: differential survival, reproduction and inheritance. Evolution occurs.

Unit 3: Adaptation in weed life history. Weed life history is the expression and timing of traits seizing and exploiting local opportunity spacetime during embryogenesis, dispersal, recruitment, growth, reproduction. Timing is everything. Reproductive life history occurs within the shoot architecture tuned to available opportunity: phenotypic plasticity. Mating systems are carefully timed, controlling recombination, minimizing mortality. Embryogenesis occurs, allocating resources among several seed roles. Germinability and dormancy are induced, modulating signal receptivity from the soil environment. Reproduction ends with abscission, an independent zygote. Heteroblastic seeds are dispersed: seeds preadapted to the unknown future availability of opportunity in diverse habitats. Dispersal is a process of discovery of opportunity spacetime, habitable sites within a heterogeneous landscape. Spatial dispersal determines local population size and structure. Soil seed pools provide temporal dispersal, the source of all future weed infestations. Seed dormancy is dispersal in time. Seedling emergence timing is driven by variable dormancy, seed heteroblasty. Plant community assembly is determined by seedling emergence timing relative to neighbors and disturbances. Weed seed life history is largely independent of neighbors from flowering through seedling recruitment, after which it interacts with neighbors in the community.

Unit 4: Adaptation in local plant communities. Neighbor interactions define the local plant community, a complex and adaptive system. The nature of neighbor interactions is found in interference and facilitation, animating the strategic roles enacted by members in the community in the struggle for existence. Functional traits guide behavioral roles in neighbor interactions affecting development in crowded communities. Weed biodiversity and population structure predicate community dynamics. Genetic connections between individuals,
populations and species enable exploitation of local opportunity; weed species associations. Weed behavioral traits form a functional guild, clusters of interacting traits. Weed community dynamics is community assembly and ecological succession. Biodiversity is the pool of populations that invade, seize and exploit local opportunity.

Unit 5: Complex adaptive systems. Evolutionary ecology provides an understanding of the nature of weeds. But understanding relies on deeper insights than observations of weed biology. Larger forces need to be understood if evolution is the make sense: forces of nature that give rise to complex adaptive systems. The constructal law guides the formation of complex systems: currents in nature move in configurations that flow more easily over time. Flow systems construct their own architectures and rhythms enabling easy movement, generating designs that evolve to survive (to live). Thermodynamic heat-water flows drive resource seizure by plants in the flow of dissolved nutrients and gases caught in evapo-transpiration streams of the xylem. Flow system self-organization occurs with the construction of flow patterns that ease movement: a treelike pattern emerges throughout nature, vascularization. Things in nature respond differently to disturbances. Fragile things are vulnerable to the disorder, volatility, uncertainty. Antifragile things respond with positive sensitivity to randomness: increasing volatility, variability, stress, or uncertainty. Antifragile systems change with time, they evolve. Randomness is information fueling antifragility. Phenomena differ between simple and complex systems. Components of simple systems are not interdependent. Complex systems have severe interdependencies between component parts; emergent properties are nonlinear, the sum different from the parts. In a nonlinear system unexpected structures and events occur; e.g. phenotypic plasticity, skewed plant size hierarchies in crowded communities. Weed-crop communities are complex adaptive systems. A complex adaptive system is a dynamic network made up of a large number of active interacting adaptive agents, acting in parallel, and diverse in both form and capability. The activity of a CAS system of interacting elements results in the emergence of system order, and a nonanticipatory-nonpredictive strategy for adaptation to the environment. Seedling recruitment is a complex adaptive system. The Setaria spp-gp. seed-soil environment communication system times departure from seed dormancy to emerged seedling. Evolution embodies organism-environment information exchange. Information is physical. Biology is physical information with quantifiable complexity. Weedy Setaria spp. seeds with heterogeneous dormancy states germinate when they receive specific soil signals: oxy-hydro-thermal time. Information is physical: memory resides in Setaria seed functional traits regulating all seed behaviors that encode-decode soil signals. The message is remembered: plants pass these functional traits to their polymorphic progeny.

Unit 6: Representation of weed biology. How can knowledge of weeds be discovered, and then represented? The real source of scientific theories is not sensory experience, but conjecture alternating with criticism. Observation enables choice between existing theories, it is not the source of new theory. Creativity is the most important source of variation in explanatory theories. How do we acquire knowledge? It is gained with pre-existing knowledge: what to look at, for; how to look and interpret what one sees. Therefore, theory comes first. It has to be conjectured, not derived. The substance of scientific theories is explanation. Good explanations are hard to vary, changing the details would ruin the explanation. Explanation attempts to answer the 'why' question. The hypothesis is the theoretical tool used to verify explanation. Darwinian evolution is the creation of knowledge through alternating variation and selection. Knowledge embodied in genes is knowledge of how to get replicated at the expense of rivals, often by imparting useful functionality to their organism (e.g. functional traits). Human knowledge and biological adaptations are abstract replicators; once embodied in a physical system they tend to remain so. Setaria seed morphology is memory and knowledge. Knowledge and biological adaptations are hard to vary. Knowledge of weeds requires consideration of the randomness, uncertainty and probability of complex systems in the way we represent their life history. The lack of information is uncertainty. Mathematical probability definitions are not defined in terms of the probability of unknown events not previously observed. The normal distribution is the basis of most statistics that evaluate the uncertainty of inductive inferences. Much of biology is nonlinear. There is reason to suspect the additivity of treatment-environmental effects, the independent distribution of experimental errors with a common variance. There exist several different ways of describing, or representing, plant life history and population dynamics: ecological demography and the evolution of selectable life history characteristics of phenotypes in the deme, the local population. Experimentally they approach plant life history from very different perspectives. Representation of the nature of weed biology is confounded by the human scientists that make them, their beliefs, values and models. Human perception structures natural laws. For scientific history there are always conflicting views, uncertain outcomes, unpredictable developments; often due to the role of the emotions, the limits of imagination, the conservatism of institutions.
Unit 7: Weed case history. The detailed stories of three weeds are presented. They connect concepts in the first six units with empirical, experimental experiences as examples of a broader perspective on the evolutionary ecology, the nature, of weeds. Velvetleaf (*Abutilon theophrasti*) is selfish with the sun, never letting anyone get in its way. Reaching for the sky if need be, putting all its close neighbors in the shade, stretching up as far as necessary to ensure the first place in the sun. Never ever learning to share. The annual dicot triazine resistant *Brassica napus*, rapeseed, is a half-wild crop, a chronomutant. This weed turns water and sun into sugar at the oddest times of day, changes its membranes, keeps leaf stomata open all the time, has more dormant seeds, on and on. The annual grass *Setaria* species-group his-her seeds are tiny, ‘nano-thermos bottles’, with a mysterious oxygen ‘sponge’ protein inside an exterior hull in which the surface topography is an oxygenator. All these as parts of a Shannon communication system living in dirt.

An indexed glossary is provided linking important concept definitions with explanatory text sections.
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The Evolutionary Ecology of Weeds Narrative
Weeds-Я-Us

“For the snark was a Boojum, you see”
Dodgeson, C.L (Lewis Carroll), 1876