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**Joseph M. Craine: Resource Strategies of Wild Plants**

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## The Basis for Plant Strategies

BY BEST ESTIMATES, the past 325 million years of evolution have left us with approximately 250,000 species of seed-producing plants in the world today (Thorne 1992). The number of extant seed plants can be considered either large or small, depending on the context and one's perspective. The question of concern in this book, however, is not the overall number per se but the patterns of one of the most important evolutionary radiations in the history of Earth, and the forces that drove the radiation in those patterns.

The quarter million plant species on Earth today occupy an immensely diverse set of environmental conditions. Some plants have evolved to endure air temperatures as low as  $-80^{\circ}\text{C}$  and others to exist in soil temperatures as high as  $70^{\circ}\text{C}$ . Plants may grow to 100 m for light and send their roots as deep as 60 m for water (Schulze et al. 1998). Plants grow in soils devoid of oxygen and in soils with levels of heavy metals that cause most plants to curl up and die. Somehow, the quarter million plant species are able to grow and reproduce even as they fend off attacks from everything from viruses to weevils to rhinoceroses.

Although processes such as vicariance and drift are responsible for some of the differences among plant species, it is natural selection that has shaped much of the modern flora. With natural selection, differences in the characteristics of the individuals lead to differential reproductive success in the face of environmental factors that can restrict growth. For example, a plant with the potential to develop deep roots would have had an advantage over a plant with shallow roots in a dry environment where water was present at depth. Deep roots allow greater water acquisition, which in turn leads to greater acquisition of other resources and eventually greater production of seeds. In a Malthusian world, not all individuals survive. Over long time scales, it is the characteristics of individuals that separate the survival of the fit from the death of the rest.

### ASSESSING NATURAL SELECTION

The continued generation of novel characteristics and differential reproduction mediated by a plant's traits and the environment progressively shape lineages. A trait is a heritable characteristic of a plant. Some traits

are directly important in the reproduction of plants (reproductive trait), such as flower color or seed size. Other traits are important for the vegetative growth of plants (functional or resource traits), such as types of light-acquiring pigments in a leaf or the depth to which plants can produce roots. Violle et al. (2007, p. 882) define functional traits as “morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction, and survival.” This definition seems to cover what aspects of plants are considered traits and what makes them functional. Other traits can be heritable but have no known importance in the vegetative growth or reproduction of plants. These are considered nonfunctional traits, and although they are often useful for understanding past environments or reconstructing phylogenetic relationships, they are not of interest here. Both reproductive and vegetative traits can be *quantitative* if variation in the trait among plants is discrete. For example, flowers can be yellow or red, stems can have thorns or not. Traits can also be *qualitative* if they vary continuously among plants, such as the intensity of a given color in a flower or the length of thorns on plants’ stems.

Natural selection operates to change the frequency of genes in a population and, over long time scales, works in concert with processes such as mutation that generate new genes. Any given plant today might have on the order of 50,000 coding genes (Tuskan et al. 2006). Many of these genes are common to all life, while a smaller subset is common to the quarter million seed plants. It is this subset of genes that separates plants from other organisms. How many of these genes are unique to all plants and how many are responsible for the floral diversity of the world are questions without good answers. The genomes of different plant species are only just beginning to be compared. For example, a comparison of the genomes of *Arabidopsis thaliana* and *Populus nigra* revealed approximately 2,300 genes that were unique to *Arabidopsis* and approximately 5,200 that were unique to *Populus* (Tuskan et al. 2006). From analyzing the genomes of just these two species, a comparison of the effects of natural selection on different species could involve the products of tens of thousands of genes. Although how many traits and which traits are analyzed are both important, whether those traits are the product of ten genes or 10,000 genes has little bearing on the approach to understanding plant traits.

### *Uniformitarian Principles for Natural Selection*

Characterizing the natural selection that produced the modern flora relies on uniformitarian principles. The processes that shaped the modern world are assumed to have shaped past worlds. Although the relative importance of different factors is not assumed to have remained constant,

physical laws, whether those governing the diffusion of nutrients in soil solutions or those behind the tension that arises in a water column as leaves are placed farther from the ground, have been constant throughout the evolutionary history of any species. It is also assumed that plants' struggle for existence has been shaped by a small number of major selective agents throughout their evolutionary history. Put simply, there are only so many basic reasons why plants die before reproducing.

Although it would seem straightforward to assess the contemporary manifestations of natural selection, understanding the growth and reproduction of plants in the modern world remains a challenge. Growth is the process by which plants accumulate resources from the environment and then use those resources to generate structures. Vegetative growth is defined as the construction of novel structures associated with the acquisition of resources. Reproduction is the production of structures that are associated not with the acquisition of resources but with the production of new individuals. Vegetative reproduction would seem to sit squarely between the two, but it is more akin to vegetative growth than to sexual reproduction. Along these lines, some traits directly affect both growth and reproduction, such as the production of stems that hold up flowers and leaves.

Much of this book focuses on forging a better understanding of natural selection by characterizing the growth of plants in environments of limited resource availability. At the outset, it should be noted that the details of how plants acquire and allocate scarce resources such as nutrients and reduced carbon are still being learned. For example, when Charles Darwin planted seedlings in his Down House lawn, he observed that many soon perished. Yet Darwin was unable to discern whether seedlings died as a result of acquiring too little water or because neighboring plants reduced nutrient availability below some minimum threshold required to persist. Even the observation that some of the seedlings' leaves were consumed by garden snails does not answer whether this would have happened had more resources been available to the plants. Would a better defended plant have been able to resist herbivory and survive to produce the next generation of weeds in Darwin's lawn? Did competition among the seedlings for scarce resources cause the seedling to be more susceptible to the herbivore?

Observing death is far removed from understanding the proximal and distal reasons why plants die. Even if the modern relationships between the characteristics of plants and the probability that agents kill some plants could be quantified perfectly, this perfect knowledge would be insufficient to characterize the mechanisms that produced the modern flora, for two main reasons. First, modern selective agents act on the product of past selection. The factors that mold plants today might not be the

same as the factors that molded them in the past. Two plant species may exist side by side in a given habitat with minimum effect on each other, but their minimal interaction comes as a result of competition between their ancestors (Connell 1980). Second, some selective agents no longer exist today, and the relative importance of the ones that remain is different from what it was in the past. An observer of the modern world standing beneath an osage orange tree (*Maclura pomifera*) might have difficulty deducing the benefit of producing the cannonball-size fruits that litter the ground. Unlike 12,000 years ago, mastodons no longer pass under these trees to collect the fallen fruit. Although uniformitarianism is an important component of understanding the processes that produced the modern flora, it has its limits.

### *Characterizing Natural Selection from the Patterns Left Behind*

If the forces of natural selection that shaped the modern flora cannot be characterized solely from an analysis of modern species and environments, what hope is there to better characterize past natural selection? For an analogy, imagine attempting to deduce that continental-scale glaciers thousands of meters thick once covered much of North America by watching snow fall on a winter's day. One could inquire into the consequences of more snow falling than melting for a few thousand years. Yet it would be hard to start from first principles while staring out a window and arrive at an ice sheet like the one that covers Greenland. Could one eventually imagine enough ice covering North America to depress the continental crust into the mantle? Would one arrive at the idea that the mass of the ice caused it to flow like molasses, carving out valleys and depositing ridges of ground-up rock hundreds of meters high at its terminus?

As the example of the Ice Age glaciers suggests, characterizing natural selection requires constraining uniformitarian principles with the patterns the processes left behind. For the continental glaciers, the processes involved in snow accumulation and the observed movement of smaller glaciers are used to interpret the moraines, drumlin fields, and kettle lakes that the glaciers left behind during previous glacial cycles. For natural selection, the modern ecology of plants must be observed, but also the analogs of glacial features.

Just as glaciers pushed boulders well beyond the source bedrock, natural selection has pushed the traits of species outward. The patterns that natural selection left behind are the traits encoded in the genomes of different species. As such, the 100-m trunks of redwood and eucalyptus should be as informative of past processes as a 100-m ridge of till lying across the landscape. Although individual traits are compared among species at a time, natural selection operates on hundreds of traits over time,

as evidenced by the analysis of the genomes of *Arabidopsis* and *Populus*. Even though the focus broadens to include a diverse number of traits, it is instructive to consider how to compare individual traits among species before moving on to more complicated analyses of multiple traits.

#### FROM SINGLE TRAITS TO MULTITRAIT STRATEGIES

In 1837, Darwin presented John Gould with birds he had collected from the Galápagos Islands (Quammen 2006). On first examination, these birds were as different as the blackbirds, “gross-beaks,” and finches of England, but Gould soon informed Darwin that they were all finches. The large ground finch (*Geospiza magnirostris*) had a large beak and the warbler finch (*Certhidea olivacea*) had a small beak. Likely all the finches were derived from a common ancestor and had radiated to fill different niches on the islands. Although Darwin never mentions the finches in the *Origin of Species*, the diversity of beak morphology among the finch species became a fundamental lesson for Darwin in his theory of evolution by natural selection. Even though the finch beaks represent a set of tightly connected traits (shape, depth, length, attached muscles), Darwin’s finches are an excellent example of the radiation of what can be considered an individual trait.

In contrast to the focus on changes in individual traits, the overwhelming pattern left behind by natural selection is one of coordinated changes in multiple traits. Although the beaks of the finches are foundational examples of adaptive radiation of individual traits, the finches have evolved strategies that exceed a single trait. A key principle to remember in examining the traits of plants is that natural selection does not operate on individual traits. Natural selection is a result of the differential reproductive success of individuals. Natural selection by and large operates on whole organisms, and reproductive success depends on more than a single trait. These unique sets of traits, shaped by natural selection, are considered to represent strategies for successfully growing and reproducing in a given environment. Or, to frame the situation in the negative, trait sets are strategies for not dying before reproducing.

Philip Grime has defined strategies as “groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology” (Grime 2001, p. xix). This definition is not a bad start, but there are important questions to address regarding whether the trait sets need to have evolved multiple times to be considered a strategy. Moreover, the phrase “similarities in ecology” is vague. For example, most tropical plants die in a similar manner when exposed to freezing temperatures, but disruption of cell mem-

branes and xylem cavitation are not part of a strategy. The definition of strategy must reflect (1) the importance of multiple traits over single traits, (2) the patterns of traits emerging as a result of natural selection, and (3) the identification of trait sets with successful growth in a given environment or set of environmental conditions. Therefore, a better definition of a plant strategy is *a set of interlinked adaptations that arose as a consequence of natural selection and that promotes growth and successful reproduction in a given environment.*

To illustrate the transition from assessing traits to strategies, it is informative to revisit Darwin's finches. In the 170 years since Darwin first collected them, more has been learned about other aspects of finches that allows beaks to be examined in a broader array of traits of the whole organism as shaped by natural selection. For example, for some finches, changes in beak morphology have been linked to changes in foot morphology (Grant and Weiner 1999). There is no necessary genetic linkage among these traits; rather, the linkages are likely a result of natural selection at the whole-organism level selecting for both altered beak and foot morphology. Ground finches scratch the soil in search of seeds. To go with their large beaks, which are used to crush large seeds, they have a longer hallux (hind toe and claw) than other finches.

Differences in beaks have also been linked to changes in internal organs, a logical conjunction when we consider the ecology of the species. For example, vegetarian finches eat low-quality leaves and buds. To access these foods, they have a large beak that operates like gripping pliers. These food types are low in available energy, and the internal organs of vegetarian finches have also changed to reflect the low-energy diet. To go with the large beak, the finches have also undergone selection for larger gizzards that grind the material better, allowing more energy to be extracted. And they have smaller hearts, most likely associated with the lower metabolic rate common in animals that feed on low-energy foods, such as sloths and koala.

The goal in understanding plants is similar to the analysis for the finches: to understand the patterns of differences in multiple, ecologically significant traits among plant species. Natural selection is not limited to a single level of organization but acts on plant biochemistry, the structure of tissues, the organization of tissues into organs, and the effects of plants on their environment.

Natural selection has shaped a broad array of plant traits, and a multi-level approach has a history as long as ecology. For example, Eugenius Warming in his 1909 book, *The Oecology of Plants*, described the adaptations of plants to dry conditions. Even a hundred years ago, his analysis covered chemical compounds such as the group of pigments known as anthocyanins, specialized cells such as epidermal hairs, tissues such as the

leaf palisade, the morphology of entire leaves, and the arrangement of leaves in a canopy. As evidenced by Warming's analysis, mere survival and reproduction in a given environment are complicated endeavors. Plants must acquire a multitude of resources while resisting or responding to a variety of agents of disturbance and stress. If plant species have been selected to differentially succeed under different environmental conditions, then natural selection likely has coordinated the adaptations of roots, leaves, and support structures so that individual plants can successfully acquire and allocate limiting resources to successfully grow and reproduce in that environment, given the typical patterns of resource availability in that environment and other factors that reduce growth.

Broadly, traits can be divided into those that are important for the vegetative growth of plants and those that are associated with reproduction. It is true that resources must be allocated for an individual to reproduce, and understanding the resource strategies of plants cannot be divorced from understanding reproduction. For example, approximately 10% of the nitrogen that pine trees acquire during a year can be allocated to pollen production alone (Lee and Booth 2003). The reproductive traits of plants can determine patterns of resource acquisition. For example, the resources stored in a large seed are important because they allow some plants to project their leaves through litter and past other plants to access sunlight.

Although the growth and reproductive traits go hand in hand when one considers individual survival and evolution of the species, in 1909 Warming drew a distinction between reproductive and resource strategies:

The vegetative shoot adapts itself to the conditions prevailing in regard to its nutrition; but the flower follows other laws, other aims, and particularly adopts very diverse methods of pollination. In the morphology and anatomy of the vegetative shoot are reflected the climatic and assimilating conditions; whereas floral structure is scarcely or not at all influenced by climate, but preserves the impress of phyletic origin under very different conditions of life. (Warming 1909, p. 4)

Reproduction is assuredly a critical phase in the life cycle of plants and under strong natural selection. In this book, however, I shall contribute to the long history of separation by focusing on vegetative traits. Trait sets and associated strategies for using resources are a complex enough subject to warrant an exclusive treatment. Eventually, vegetative strategies and regeneration strategies should be examined together (Grime 1979, 2001), as there is evidence they are not completely orthogonal (Lambrecht and Dawson 2007).

## QUANTIFYING PLANT TRAITS AND STRATEGIES

In beginning to assess plant strategies, it is important to consider why different strategies exist at all. Why isn't there just one set of traits that allows one plant to dominate the entire world? This is a well-worn line of questioning (MacArthur and Wilson 1967; Tilman 1988). The simple answer is that traits that lead to success in one environment do not lead to success in another environment. There are trade-offs among traits such that the presence of a trait favorable in one environment precludes having a different trait that might be favorable in a different environment. The traits that allow a tree to grow tall might preclude it from growing well in other environments, such as a closely grazed grassland. If this is so, why are there not plants with the ability to be short or tall, depending on the environment? Even if a given plant had the potential to generate any combination of traits, it is a stochastic world. Perfect adjustment requires perfect knowledge of the future, and death can come swiftly, with little opportunity to adjust. There are also likely costs to certain degrees or types of plasticity that favor less plastic species. Although plasticity of traits is important to plant strategies, one should look elsewhere for worldviews centered on the plasticity of traits (e.g., Grubb 1998).

*Quantifying Plant Traits*

To identify the strategies of plants, the traits of different species must be compared. Much as with Darwin's finches, traits are measured for a set of species and then compared across species. It is not easy to quantify many of the traits of species. The genetic basis of traits is independent of the environment in which the traits are assessed, but many traits vary with environmental conditions. The maximum height of a tree is likely to be greater when it is well watered than when it is insufficiently watered. Insofar as environmental conditions can affect the expression of traits, it is not straightforward to ascertain under what conditions the height of different trees can be meaningfully measured. To understand the role of tree height in strategies for ecosystems where water is plentiful, it might be appropriate to measure the height of well-watered trees. Alternatively, measuring the height of poorly watered trees might better advance an understanding of strategies in ecosystems where water is scarce. Plants also alter their environments in ways that preclude a clean separation of the influence of genes and environment when comparing species. Species that differ in water usage, for example, make it difficult to determine whether there are inherent interspecies trait differences or whether one species dries out the soil more than another, causing it to respond to water stress.

### *Quantifying Plant Strategies*

If we put to one side the question of what set of environmental conditions plants should be grown in to assess their traits, the process of quantifying plant strategies is more than compiling lists of traits. As Grime (1993) detailed, quantifying plant strategies is an iterative process that bounces back and forth between assessment of traits and assessment of performance in different environments. Differences in environments can occur as a result of natural contrasts or through manipulation, while the traits that are assessed come from theoretical or conceptual models of the relationship between traits and performance in an environment.

A typical progression of research might be to first identify differences in the relative abundance of species along a natural environmental contrast, followed by the generation of competing hypotheses about the mechanisms that lead to differences in performance. Key traits are then assessed for the target plant species and their ability to predict abundance along the environmental contrast is tested, the researcher working within the initial model of plant function in the environment. This approach often leaves us with competing hypotheses, for reasons detailed in this book. As examples, traits are not easy to measure, and genes and environment cannot always be separated completely. There are also competing hypotheses about what factors structure assemblages in different environments, and it is not always clear what traits should be tested in determining a plant's strategy.

### RANKING STRATEGIES

Let us assume for now that it is simple to compile a number of traits for a number of species. Each species has its own unique set of traits, but does that mean that each species has its own strategy? How are general strategies identified? When faced with as many unique combinations of traits as there are species, how does one progress from individual examples to broad patterns? In part, this is a statistical question, but statistical approaches rely on concepts of how to compare and aggregate sets of traits. If we assume for now that strategies can be generalized, a more pressing question arises. How are strategies ranked in importance, and how can minor and major strategies be separated?

### *Considering Phylogeny When Ranking Strategies*

In beginning to examine plant strategies, unless one considers all strategies to be equally important, some separation of the importance of differ-

ent strategies is essential. One approach to ranking strategies is to base the importance of a strategy on the phylogenetic relationships of species. For example, the most basic separations of strategies might have arisen first, with later divergences representing a progressive refinement of the basic strategies. In this case, the most basal divergences of taxa might relate to basal divergences in strategies. For example, angiosperms diverged from gymnosperms approximately 140 million years ago. Might not the differences between angiosperms and gymnosperms represent two basic strategies?

Unfortunately, the phylogenetic tree of plants does not necessarily reconstruct divergence of resource strategies. Processes that are associated with divergence can be independent of resource strategies. For example, lineages can become reproductively isolated from one another without any change in the fundamental resource strategy. Much of radiation could be due to novel reproductive strategies, and not directly related to resource strategies. For example, although angiosperms and gymnosperms differ in how xylem tracheids are connected, angiosperms can also be separated from gymnosperms by the process of double fertilization in producing seeds. As opposed to more ancient lineages of dicotyledonous plants, eudicots—roses and asters—are characterized by triaperturate pollen (Soltis and Soltis 2003), which likely has little effect on resource strategies but is also likely to be strongly conserved. Lineages can also differ in certain traits, but the trait divergence does not necessarily have to represent a fundamentally new strategy. For example, the sister taxon of all angiosperms, *Illicium*, the star anise tree, does not appear to exhibit a clearly recognizable difference in basic resource strategies relative to those of all other angiosperms. Although species of the genus have some unique organic compounds in their leaves and fruits, any differences in other traits are not obvious, and there is no evidence that the unique compounds form part of a major strategy, at least in the modern world.

Alternatively, the relative importance of strategies might best be assessed not by examining the oldest divergences but by counting the number of times that a given strategy has arisen or the number of species that possess the strategy. A strategy that evolved once might be important, but one that evolved multiple times is likely to be more important. A strategy held by just one species is probably less important than one held by thousands. For example, the C<sub>4</sub> photosynthetic pathway has arisen more than 45 times, and more than 7,000 species are known to have the C<sub>4</sub> photosynthetic pathway (Sage 2004). However, ranking strategies in this manner has its own problems. Although a given trait set evolving multiple times seems like good circumstantial evidence of the importance of a strategy, it is not a perfect quantitative metric of importance. A given strategy might entail changes in multiple genes, with odds being low that the

changes happened twice, and the strategy probably evolved just once. That a strategy evolved just once is a poor reason to consider it less important. Similarly, a given trait held by a large number of species might reflect the presence of another factor that has affected the speciation rate, and its appearance in multiple species does not mean that the strategy is more important than one associated with fewer species.

### *Considering Modern Ecology When Ranking Strategies*

It is useful to understand when a strategy first arose, how many times it arose, and how many species hold the strategy currently. Phylogeny alone is insufficient to assess the relative importance of strategies. Strategies are by definition approaches to successful growth and reproduction in the face of ecological forces that render other approaches less successful. Assessing that a given trait set forms part of a strategy requires understanding the contribution of the trait set to ecological performance. Similarly, assessing the relative importance of different strategies requires assessing ecological performance. Unfortunately, assessing the relative importance of strategies cannot be separated from making arbitrary choices about the importance of different environments.

Assessing the relative importance of strategies would entail determining the relative importance of different environmental factors in natural selection. The unfit have many reasons for failing to survive. Some individuals might have been unable to acquire resources that were in short supply and ended up with too little light, water, nutrients, or carbon to reproduce. Others might not have been able to withstand the presence of herbivores or disease agents. Some plants perish as a result of extreme heat or cold, soil flooding or drought, fire or wind. Can the relative importance of these environmental factors in determining the abundance and distribution of species be ranked in advance as a way of erecting parallel strategies?

To some degree, ecological factors *can* be ranked. For example, a few species have adapted to a high soil availability of heavy metals, such as zinc or magnesium. These habitats are relatively rare but common enough that some species are adapted to grow on them. Yet it is not hard to argue that strategies for dealing with a high availability of heavy metals are less important than strategies for dealing with low water availability, which occurs more frequently in space and time. This raises a further question: should the relative importance of a strategy be scaled by the surface area over which it is important?

Even if the relative importance of different environmental factors on the modern planet could be ranked, this ranking would not necessarily correspond to the evolutionary history of plants, for it would identify

modern strategies but might miss evolutionarily important ones. For example, ancient environments were generally warmer and wetter than today's environments, with higher CO<sub>2</sub> availability and lower nitrogen availability. Atmospheric CO<sub>2</sub> was generally two to five times higher for most of the past 300 million years than during the Pleistocene era (the past 1.8 million years) (see chapter 10). Likewise, the N<sub>2</sub>-fixing symbiosis of legumes evolved only relatively recently (about 60 MYA) (Sprent 2007). With high CO<sub>2</sub> concentrations and the lack of N<sub>2</sub> fixation from legumes, ancient environments might have had lower nitrogen availability than modern environments. Deserts and extensive dry habitats were largely absent for most of the evolutionary history of plants and did not arise until continental uplift of mountain regions such as the Himalayas and American cordillera cut off moisture to vast areas, and decreased global temperatures reduced evaporation from oceans. Our cold, dry world of relatively low CO<sub>2</sub> levels and high nitrogen availability is likely much different from the worlds in which most of the modern flora evolved.

### *The Need for Arbitrary Elevation of Strategies*

At this point, there seems to be no pure path to assessing the relative importance of strategies. Relying on phylogeny alone does not allow assessment of whether a particular set of traits is or was ecologically important. Furthermore, this approach is subject to the limited resolution of phylogenetic relationships among plant species. Relying on ecological gradients to guide rankings forces arbitrary assessments of the relative importance of different ecological gradients, including environments for which no modern analog might exist. Putting phylogeny and ecology together might improve the situation, but this approach does not eliminate their individual deficiencies.

At this point, arbitrary decisions on the rankings of factors are necessary. For resources, it is important to develop the strategies associated with growing successfully in environments where there is low availability of each of the major plant resources: nutrients (mainly nitrogen and phosphorus), light, water, and CO<sub>2</sub>. Most of the discussion on strategies for low resource availability is concerned with nutrients and light. Less is known about strategies that have arisen as a consequence of low water availability or low CO<sub>2</sub>, making it difficult to delineate the strategies associated with these environments. In addition to the strategies associated with low availability of specific resources, strategies associated with environments with high water, nutrient, and light availability are also important to include, and these environments occur only when plants have recently been damaged severely. For the reasons stated above, it is unhelp-

ful to rank strategies associated with each resource, even though they may be important strategies. This book pays more attention to nutrients and light than to water or CO<sub>2</sub> for the simple reason that strategies associated with low availability of light and nutrients are better understood than strategies associated with low availability of water and CO<sub>2</sub>.

With the resources of interest for analyzing strategies selected and the basic comparative approach outlined in this chapter, the next chapter reviews the foundations of plant strategy theory and the approaches that have been taken to understanding resource strategies, before moving on to the specific components of strategies. Some of the history of research on plant strategies is reviewed first, including the work of three modern ecologists that have contributed the most to understanding plant strategies. Some of the key components that form the foundation of the strategies are identified, and the competing hypotheses that need to be addressed as part of this process are introduced and evaluated.

## SYNTHESIS

A first step in characterizing the major patterns of natural selection that generated the current flora of a quarter million species of seed plants entails comparing the traits of species and the characteristics of different habitats, and assessing how plants grow in different environments. Traits are defined as heritable characteristics of plants. Most of the analyses of natural selection have focused on individual traits, such as the beaks of Darwin's finches. Natural selection, however, operates at the level of the organism and coordinates multiple traits at many levels of organization. Darwin's finches differed in more than just their beaks.

Plant strategies are sets of traits that lead to successful growth and reproduction in a particular environment. More formally, strategies may be defined as a set of interlinked adaptations that arose as a consequence of natural selection and that promote growth and successful reproduction in a given environment. Strategies are assessed by examining the patterns of traits among species and assessing the relationship between sets of traits and plant performance in different environments. The traits associated with plant resource strategies are important for the vegetative growth of individual plants and determine the acquisition, allocation, and loss of resources that support successful growth under a particular set of environmental conditions. These traits range from the biochemistry of cells to tissue construction to plant effects on the abiotic environment. Reproductive strategies are not necessarily independent of resource strategies, but are not covered here.

Although phylogenetic issues should be considered when assessing the relative importance of plant strategies, phylogenetic reconstructions are not sufficient to assess the relative importance of strategies. The age of a particular divergence of two lineages does not necessarily correlate with the relative importance of any differences in their strategies. Likewise, the number of times a particular set of traits has arisen or the number of species that hold it is not sufficient for ranking different strategies. Neither is an analysis of the modern ecology of species, such as species' performances in modern environments, sufficient to rank strategies. The importance of factors in the selection of plants might not scale with their importance weighted by land area. The relative importance of factors in any one habitat is influenced by past selection and cannot be used alone to rank strategies.

If a given strategy is to be elevated over another, one should be clear about the criteria used to rank the strategies. At this time, there is no recourse but to arbitrarily elevate some factors over others, and therefore to elevate some strategies, too. In later chapters the strategies for success in environments with low availability of nutrients, light, water, and CO<sub>2</sub> are examined, as well as strategies for success in disturbed environments with high availability of nutrients, light, and water.