

19 Plant strategies

19.1 Chapter summary

A plant uses the carbon gained during photosynthesis for maintenance and survival, to grow new materials such as foliage or roots, and for reproduction. Nitrogen and other nutrients are required to support these processes, and a plant must allocate its limited available resources among growth, maintenance, and reproduction in a manner such that the species persists over time. Different strategies for allocating resources, collectively known as life history patterns, have evolved through natural selection that allow plant species to persist in certain environments. A successful strategy might be to invest heavily in reproductive effort. The plant could be small, short lived, and have copious, widely dispersed seeds, such as a herbaceous annual. An equally successful strategy might be to be large, long lived, and have a small crop of large seeds, such as a tree. This life history favors maintenance over reproduction. There are multiple life history patterns that allow success in a given environment, but not all are successful in all environments. The environment selectively determines which strategy is successful. These life histories ensure the persistence of multiple species across the landscape in accordance with resource gradients and disturbance regimes. They give pattern to the arrangement of plant populations and communities in space and time. Three conceptualizations of plant strategies are the classifications of species into: *r*- and *K*-selected life histories; ruderal, competitor, and stress tolerator plants; and early and late successional species. More generally, plant functional types are broad classes of species that reduce the complexity of species diversity in ecological function to a few plant types defined by key physiological and life history characteristics.

19.2 Carbon balance of plants

The carbon balance of a plant is the difference between CO₂ uptake during photosynthesis and CO₂ loss during

respiration (Fig. 19.1). The photosynthetic uptake of an individual leaf (Chapter 17) must be summed over all foliage held by the plant (Chapter 18). Respiration loss must be summed over all tissues in the plant. Plant respiration is divided into growth respiration, which is independent of temperature, and maintenance respiration, which increases with higher temperatures (Ryan 1991). Growth respiration is the CO₂ released during the synthesis of new tissues. This synthesis involves the incorporation of carbon into organic compounds and the expenditure of metabolic energy to produce the compound. Growth respiration is typically about 25% of photosynthesis. Maintenance respiration is the CO₂ released during the carbohydrate breakdown that provides the energy needed to maintain living cells. Such processes include protein synthesis and replacement, membrane repair, and the maintenance of ionic gradients. Maintenance respiration is an exponential function of temperature, increasing with higher temperature until some maximum temperature beyond which physiological activity is inhibited. Respiration rates vary among plant structures. Foliage and roots have higher respiration rates for the same temperature than woody material (Fig. 19.1). The combined whole-plant respiration is typically about 50% of gross photosynthesis (Ryan 1991).

The carbon balance of a plant varies over the course of a year due to seasonal changes in photosynthesis and respiration. This is most obvious in woody plants growing in regions with a distinct growing season (Fig. 19.2). In winter, the daily carbon balance is usually negative; there is little or no photosynthetic uptake, but carbon is lost during maintenance respiration. Net carbon uptake, after accounting for respiration losses, occurs during the growing season when photosynthetic uptake exceeds respiration loss. The annual carbon balance (i.e., net production over the course of the year) is obtained by subtracting the wintertime loss from the growing season gain.

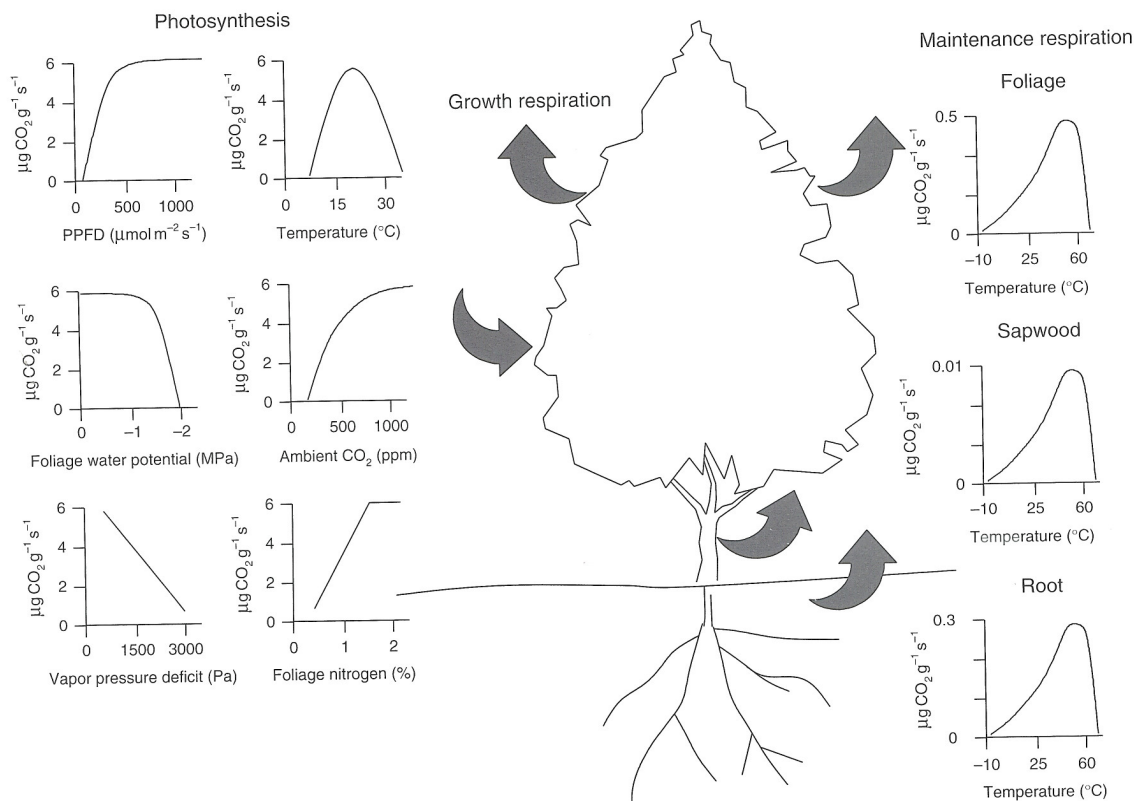


FIGURE 19.1. The carbon balance of a tree. Net carbon is the difference between carbon uptake during photosynthesis and carbon loss during maintenance and growth respiration.

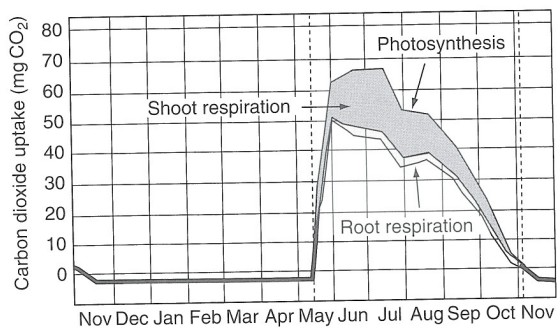


FIGURE 19.2. Carbon balance (net photosynthesis, shoot respiration, root respiration) of pine (*Pinus*) seedlings growing near treeline over the course of a year. Adapted from Larcher (1995, p. 133).

19.3 Seasonality of growth and development

Phenology is the study of the onset and duration of the different phases of a plant's development during the year. Temperature, moisture, and daylength control the timing

of these phases. Temperature is especially important. The rate of chemical reactions increases with higher temperatures, and nearly all physiological processes involved in plant growth are controlled by temperature. The opening of buds, the growth of leaves, shoots and roots, the onset of flowering, seed ripening, and seed germination are all initiated by specific temperature regimes. These temperature requirements are typically measured in terms of growing degree-days, which is the accumulated daily temperature above some threshold, typically about 5°C . Measures such as growing degree-days incorporate the accumulated effect of temperature on growth and development. Many developmental processes also have a chilling requirement in which temperatures have to be below some threshold value for a certain period of time before the process can be initiated. This is especially true for budbreak and seed germination, where exposure to low temperature over several weeks or months is needed to break dormancy. Chilling requirements are expressed as the accumulated daily temperature below some threshold.

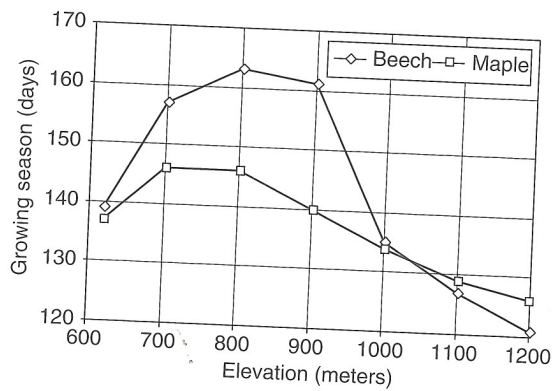


FIGURE 19.3. Length of growing season for beech and maple trees in relation to elevation in Austrian mountains. Data from Geiger (1965, p. 440).

The importance of temperature in determining the timing of developmental processes is demonstrated by comparing the phenology of plants growing on different slopes or elevations in mountains. For example, Fig. 6.21 shows a prominent mid-slope thermal belt in Austrian mountains. In these mountains, the growing season for beech (*Fagus*) and maple (*Acer*) trees is longest at 800 m elevation, where nighttime temperatures are warmest (Fig. 19.3). For beech, the growing season at the valley bottom is 25 days shorter than at mid-slope. The flowering of spring wildflowers illustrates the influence of hillslope on temperature and phenology (Fig. 19.4). On steep slopes of 100% (45°), the average flowering date is six days earlier on a south-facing slope than on the opposing north-facing slope despite being separated by a distance of only 46 m. This difference is related to microclimates. The south-facing slope receives

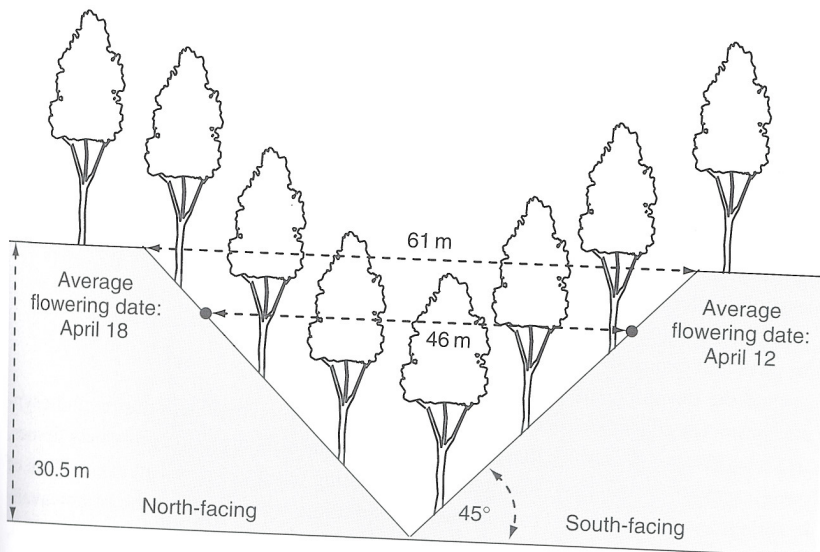
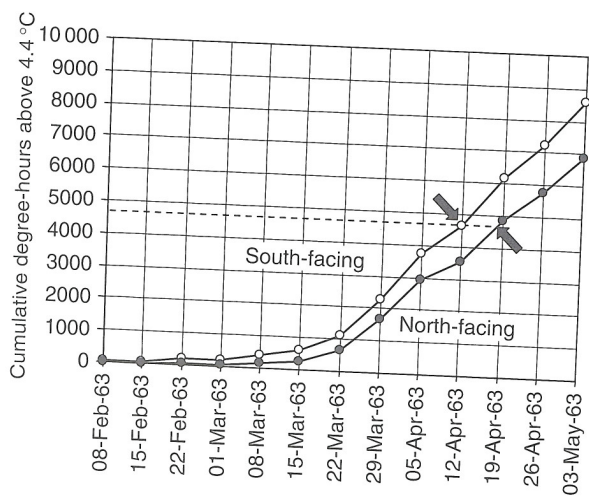


FIGURE 19.4. Average flowering for nine species of spring wildflowers in an Indiana woodland growing on north- and south-facing slopes separated by 46 m. Top: topographic setting. Bottom: cumulative degree-hours above 4.4 °C. Flowering occurs at about 4650 °C-hours, indicated by the large arrows. Data from Jackson (1966).



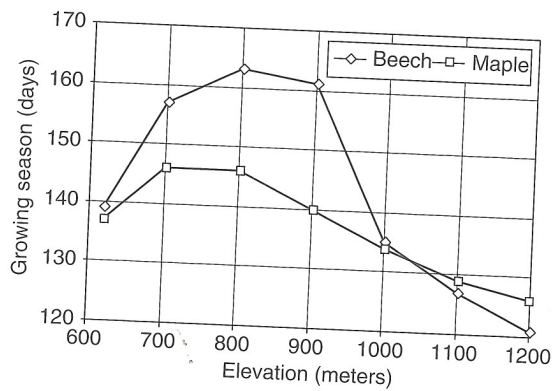


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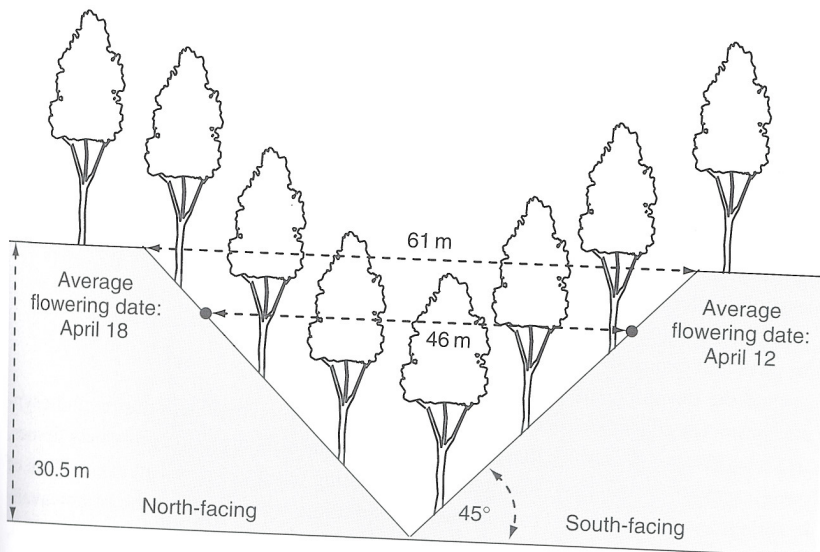
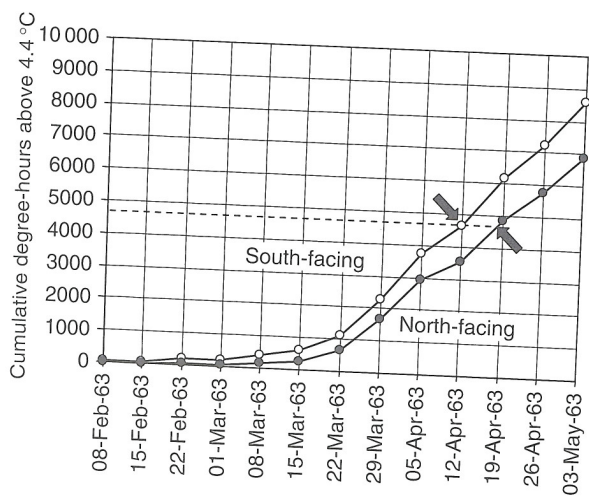


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more radiation and is warmer than the north slope. On both slopes, flowering is triggered when the accumulated degree-hours is about 4650 °C-hours, which occurs six days earlier on the south slope than on the north slope.

The length of the day is also critical to many developmental processes, triggering the onset of flowering, leaf fall, and winter dormancy in many herbaceous plants, shrubs, and trees. In middle to high latitudes, the length of day varies greatly over the course of a year (Fig. 4.7). At latitude 40°N, the minimum daylength is 9 hours in December; the maximum daylength is 15 hours in June. Further north, the seasonality of daylength is even more pronounced. Photoperiod, the relative duration of light and dark periods during the day, controls the timing of many physiological processes. For example, long-day plants flower in response to days longer than some maximum length; short-day plants flower when days are shorter than some maximum.

To grow in regions with seasonally freezing temperatures, plants must acclimate to the low temperatures or else be subjected to frost and chilling damage. Winter temperatures below -40 °C occur regularly in tundra, boreal forest, and alpine landscapes. In the cold of winter, when temperatures are well below freezing, water in a plant can freeze, destroying plant cells. Woody plants tolerate low temperature by becoming seasonally dormant. Frost hardy or dormant plants can successfully endure temperatures well below freezing that would severely damage them while actively growing. Short days and exposure to low temperatures initiate dormancy and the development of frost hardiness. Lack of water also promotes dormancy.

In temperate and boreal forests, the most obvious phenology is the seasonal greening and senescence of deciduous trees during the growing season. In spring, as temperatures increase and days become longer, buds break and new leaves emerge. In autumn, short days, long nights, and low temperatures trigger leaf senescence that prepares deciduous trees for winter dormancy. This seasonal pattern of growth produces alternating cycles of growth and inactivity and corresponding periods of carbon utilization and storage. In deciduous trees, the carbohydrates stored in the woody tissues and bark of branches, trunks, and roots are used in spring to provide the carbon for emerging leaves. These reserves are replenished during the growing season, and the surplus photosynthate is stored in branches, trunks, and roots at the end of the growing season. Needleleaf evergreen trees have less pronounced seasonal fluctuations in carbon reserves than deciduous trees. Foliage persists on these trees for several years. If weather is favorable, needleleaf evergreen trees photosynthesize throughout late autumn, winter, and early spring. The existing foliage can supply much of the carbon

needed to support new foliage and shoot growth when buds break in spring or early summer. Additional carbon requirements are supplied from reserves held in woody tissues.

The advent of satellite technology has allowed study of leaf phenology at large spatial scales. The normalized difference vegetation index (NDVI) is a satellite-derived index that is related to leaf biomass and plant productivity (equation 18.5). Figure 19.5 shows seasonal changes in the NDVI, illustrating the timing of leaf emergence, peak leaf area and production, and leaf senescence and dormancy. Low values indicate few leaves and low productivity; high values indicate a dense canopy and high productivity. Arid regions show little greening throughout the year. Tropical rainforests are productive year-round. Elsewhere, there are two distinct patterns to phenology represented by summergreen and raingreen plants. Winter deciduous plants in temperate and high latitudes drop leaves with the onset of cold temperature. In spring, as temperature increases and the days become longer, buds on these summergreen plants break open, new foliage emerges, and plants begin to photosynthesize. Peak production typically occurs in July and August, decreasing in autumn as plants again become dormant. In tropical and subtropical latitudes, drought-deciduous plants drop leaves seasonally in relation to low precipitation and drought stress. Leaves emerge on these raingreen plants in response to adequate precipitation.

19.4 Allocation

Plants use the carbon absorbed by leaves during photosynthesis to maintain cellular structures and grow new tissues. Maintenance of existing tissues requires an expenditure of carbon during respiration, which reduces the carbon available for new growth. The net carbon available to a plant, along with the nutrients required for new growth, is then allocated to the growth of leaves, roots, stems, flowers, seeds, and the production of chemicals for protection from insects and herbivores. Collectively, the partitioning of resources to plant parts and functions is known as allocation (Cannell and Dewar 1994; Bazzaz 1996; Barbour *et al.* 1999).

Allocation of available resources is a critical determinant of plant growth and success. For example, high allocation to foliage ensures more leaves to capture light and absorb CO₂ for new growth. However, allocation to foliage is inefficient if there is not enough water or nutrients to support the foliage. Moreover, there usually is a limited amount of resources to spend on growth, maintenance, and reproduction, and allocation to one function is typically at the expense of another function. Hence, plants must

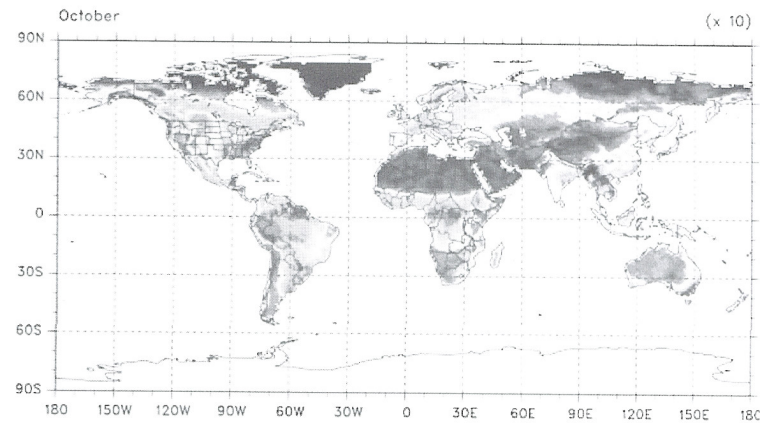
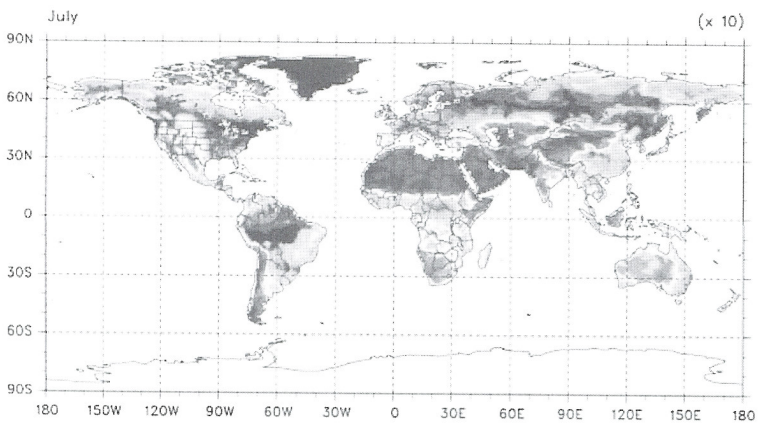
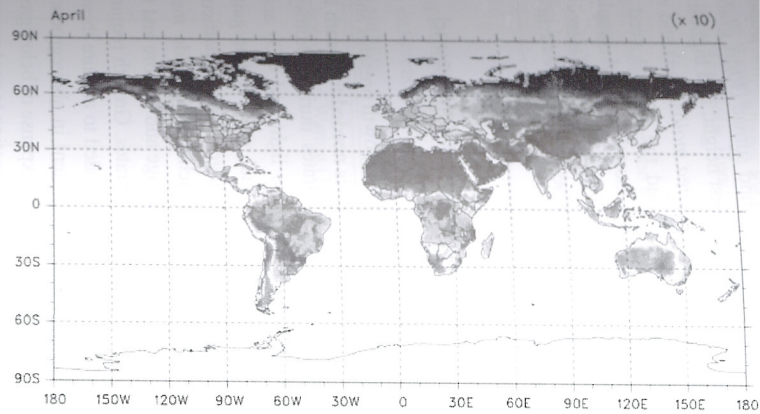
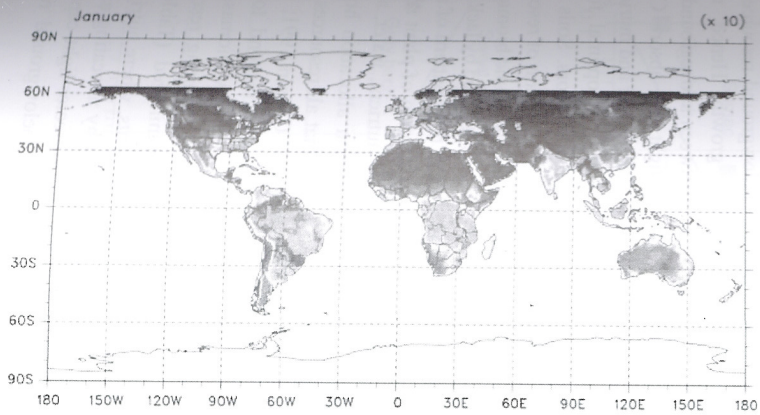


FIGURE 19.5. The normalized difference vegetation index averaged for January (top left), April (top right), July (bottom left), and October (bottom right) for 1982–1993. Low values indicate low production. High values indicate high production. Data from the NOAA/NASA Pathfinder data product archived at the NASA Goddard Space Flight Center Earth Sciences Distributed Active Archive Center (GSFC DAAC). See color plate section.

allocate resources in a way that balances conflicting needs. Variation among plants in growth rates is determined as much by differences in allocation and how plants balance resource limitations as by different photosynthetic rates.

19.4.1 Reproduction

Allocation of resources to reproduction illustrates compromises and tradeoffs (Harper 1977; Bazzaz 1996, 1997). Copious seed production increases the probability of descendants in future generations. Dispersal of a heavy blanket of seeds over a wide area ensures that at least some seeds are likely to fall on sites suitable for germination and establishment. However, high seed yield and high growth are not always compatible. Greater reproductive output diverts resources from vegetative growth and can lead to low stem or shoot growth during years of high seed production.

The number and size of seeds represent a compromise between dispersal and food reserves for germination (Grime and Jeffrey 1965; Leishman and Westoby 1994; Saverimuttu and Westoby 1996; Walters and Reich 2000; Westoby *et al.* 2002). The size of seeds varies from less than 10^{-6} g for the dust-like seeds of orchids to over 10^4 g for large coconuts (Harper 1977, p. 665). Tree seeds range in size from 10^{-4} g for light, wind-dispersed birch (*Betula*) seeds to 0.1–10 g for the large nuts of beech (*Fagus*), oak (*Quercus*), and chestnut (*Castanea*) trees. This wide range in seed size represents the outcome of reproductive tradeoffs. Seeds must contain sufficient carbohydrates and nutrients to give embryos support during germination but must be dispersed from the parent and produced in sufficient quantities to ensure a high probability of survival. Seed number and seed size are alternatives in reproductive strategy so that plants produce many small, light seeds or fewer, larger seeds. Small seeds carry few carbohydrates to support initial growth. The seedling must depend on its own photosynthate at an early stage. However, small seeds can be dispersed in large quantities and spread over large regions by wind, ensuring that some of the seeds fall on a favorable site for germination. In contrast, large, heavy seeds have enough initial reserves to continue growth for extended periods of time and survive in environments with low resource availability, but large seeds have a cost. They are produced in less quantity than small seeds, are not as widely dispersed, and are likely to be eaten by wildlife because they are highly nutritious.

A number of experimental studies have demonstrated the costs and advantages of seed size. For example, a study of seedling development in nine tree species growing in shade found that seedling height after 12 weeks increased

with seed weight while the number of seedlings that died decreased (Fig. 19.6). Gray birch (*Betula populifolia*), sweet birch (*Betula lenta*), and sumac (*Rhus glabra*) had the lowest seed weight, lowest height, and highest mortality. Chinese chestnut (*Castanea mollissima*) and northern red oak (*Quercus rubra*) had the highest seed weight, greatest height, and least mortality. Red maple (*Acer rubrum*), yellow poplar (*Liriodendron tulipifera*), white pine (*Pinus strobus*), and honey locust (*Gleditsia triacanthos*) were intermediate.

19.4.2 Aboveground and belowground growth

The acquisition of resources for growth presents another set of tradeoffs in plants. Foliage is needed to absorb light and CO_2 and construct carbohydrates during photosynthesis. More foliage allows for more light and CO_2 acquisition and, all other factors being equal, more carbon gain. Stems are needed to support this foliage. Trees in particular need large woody trunks and branches to provide mechanical support for their extensive foliage and to store and transport water, nutrients, and carbohydrates. Growth requires water and nutrients, and roots are needed to acquire these resources from soil. Greater investment in aboveground foliage and stem growth comes at the expense of belowground root growth. Conversely, greater allocation to root growth allows for increased acquisition of belowground resources but at the expense of aboveground growth. Hence, resource acquisition is a compromise between aboveground foliage and shoot growth to harvest light and absorb CO_2 and belowground root growth to obtain water and nutrients.

Natural environments are seldom optimal for plant growth. Tall plants shade short neighbors. Soils may be dry or deficient in nutrients. The allocation of resources to build and maintain above- and belowground biomass is not proportioned in fixed ratios. When stressed by lack of light, water, or nutrients, plants change their pattern of resource allocation. Allocation is an integration of plant responses to multiple stresses imposed by nutrient, water, and light availability. One theory of carbon allocation holds that plants adjust their allocation so that all resources equally limit growth (Bloom *et al.* 1985; Chapin 1991; Gleason and Tilman 1992). Plants typically respond to altered resource availability by allocating new biomass to the components that acquire the most limiting resource so that resource imbalances are minimized (Table 19.1). Plants in resource-rich environments, where nutrients and water are not limiting, grow best by allocating carbon to leaves. More foliage allows for greater light capture and photosynthesis. Deficiencies in belowground resources

such as water and nitrogen result in increased allocation to roots and reduced allocation to foliage. A nitrogen surplus or sufficient water allows for greater leaf production and reduced need for roots. Hence, irrigation and fertilization

can increase foliage growth where these are limiting. Cold temperatures favor increased root production because low temperatures reduce the ability of roots to absorb water and nutrients.

TABLE 19.1. Changes in carbon allocation in trees in relation to various stresses

Stress	Root growth	Foliage growth
Shade	Reduced	Increased
Drought	Increased	Reduced
Cold temperature	Increased	Reduced
Nitrogen deficiency	Increased	Reduced
Nitrogen surplus	Reduced	Increased

Source. Adapted from Waring (1991).

19.5 Life history patterns

The optimal allocation of limited resources to growth, maintenance, and reproduction is part of an overall inter-related suite of attributes that have evolved over time through natural selection. These functions and their necessary plant parts all interact to determine fitness, defined as the relative number of descendants in future generations. Natural selection selectively favors those individuals that contribute the most offspring to subsequent generations. However, allocation of carbon and nutrients among the various plant parts usually involves compromises.

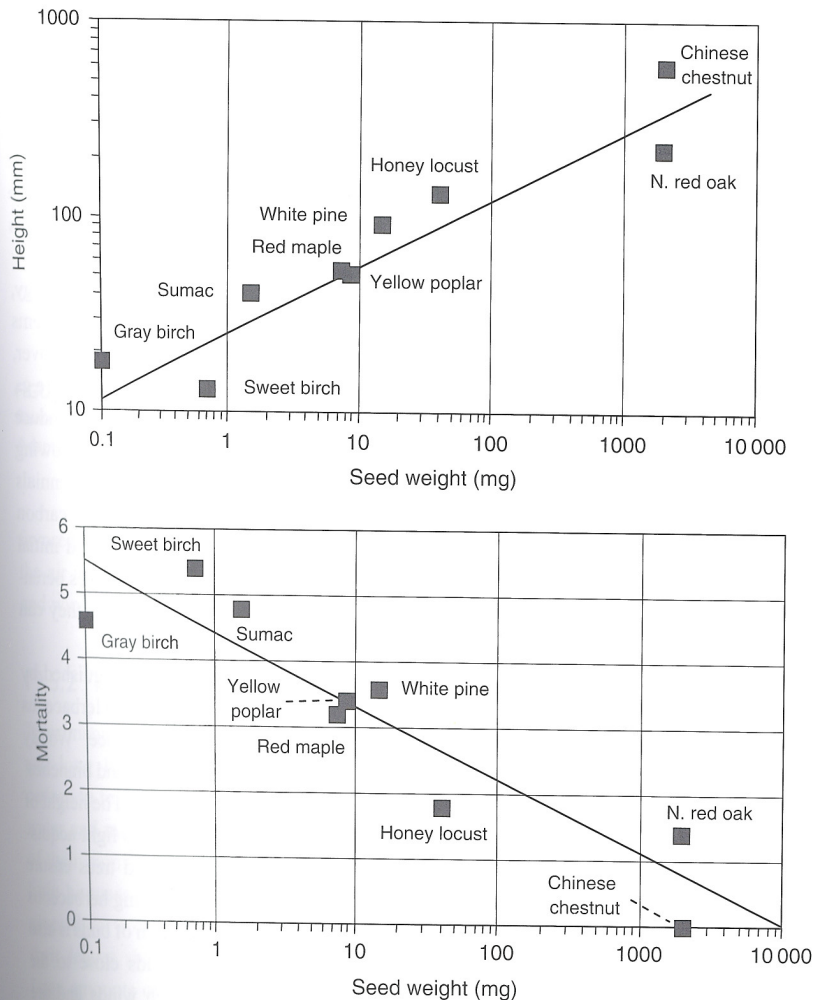


FIGURE 19.6. Relationship between seed weight and seedling growth and survival for nine species of trees grown in shade. Seeds were germinated and then transplanted to grow in shade. Top: height growth after 12 weeks. Bottom: number of seedlings that died over the 12 weeks. Adapted from Grime and Jeffrey (1965).

Different structures are alternatives, and gain in fitness from one may be offset by loss in another. For example, greater allocation to reproduction does not necessarily increase fitness. Less carbon is available for vegetative growth. The plant may not be able to successfully compete with neighbors. Conversely, a plant can increase its fitness by reducing its reproductive effort and investing more in increased growth. Light, water, and nutrients are usurped from neighbors, ensuring the plant survives and leaves descendants.

Natural selection acts to maximize individual fitness by optimizing the form of these compromises, creating a balanced system of resource allocation to plant parts (Bloom *et al.* 1985; Tilman 1988; Chapin 1991; Bazzaz 1996, 1997; Grace 1997). Resources are allocated in a way that maximizes fitness. Coordinated leaf traits (Chapter 17) and allocation of photosynthetic capacity in relation to light profiles (Chapter 18) are two examples of this balance of tradeoffs. More generally, the optimal allocation of resources is reflected in the morphology and life histories of plants, and the outcome of optimal resource allocation is not one specific pattern of allocation, morphology, and life strategy (Harper 1977; Grime 1979; Tilman 1988). Rather, light, water, and nutrients vary spatially and temporally. There are numerous alternative patterns of allocation that allow plants to successfully grow, survive, and reproduce in specific environments. Allocation must be flexible to allow for different patterns in different environments, but is constrained by the life history of a species.

A life history is an overall pattern of growth, reproduction, and longevity. A successful life history allows a species to persist through evolutionary time. A successful strategy may be to remain small and allocate resources to a single episode of copious seed dispersal. Plants that reproduce once and then die are called monocarpic or semelparous. They invest a large reproductive effort into a single flowering episode at the expense of future vegetative growth. An equally successful strategy may be to grow slowly, be long lived, and have repeated reproduction during a life cycle, which may extend from several years for herbaceous plants to hundreds of years for trees. Such plants are termed polycarpic or iteroparous.

Life histories are closely matched to environment; the environment determines which life histories are successful. Frequent, recurring disturbances that expose soil for revegetation favor plants that allocate resources to seed production and widespread dispersal. Monocarpic plants are favored in ephemeral environments with relatively low juvenile mortality and high adult mortality. However, this is a risky strategy when the environment is uncertain. A cold or dry year could destroy an entire cohort of plants,

removing their descendants from future generations. In contrast, polycarpic plants are favored where juvenile mortality is high, adult mortality is low, and in uncertain environments so that the risk of a bad year is spread out over several years of reproduction.

19.5.1 Annuals and perennials

The distinction between annual and perennial is one example of alternative morphologies and life histories based on longevity and age of first reproduction. Annual plants complete their life cycle in one year or less, germinating, growing, flowering, and setting seeds in a relatively short period of time. Initially, they allocate resources to foliage and stems. Roots are needed to supply the necessary water and nutrients for growth. Later, as the plant matures, resources are allocated to a single bout of copious seed production and dispersal before they die. *Senecio vulgaris* illustrates the ephemeral life strategy typical of herbaceous annuals (Fig. 19.7). A period of vegetative growth is followed by seed production culminating in death. Three distinct growth phases are evident. The first phase of growth is marked by development of roots and a leafy rosette. During the second phase, stems grow longer and flowers emerge. The end of this phase is marked by little vegetative growth, peak flower development, and the opening of the first seed heads. In the final stage, seeds mature, and leaves and roots begin to die.

Perennial plants take a longer-term allocation strategy, as illustrated by goldenrod (Fig. 19.8). Foliage and stems are maintained throughout the growing season. Moreover, perennials must allocate resources to perennial parts (e.g., buds) and storage (e.g., roots). Consequently, they produce fewer seeds than annuals, but in the subsequent growing season, while annuals start anew from seed, perennials begin growth with an established root system and carbon and nutrient stores. These stores allow more rapid initial growth than plants growing from seeds. This gives perennials an early-season height advantage, whereby they can capture light and shade neighbors.

There are several types of perennials distinguished by differences in position of buds on the plant. Herbaceous perennials have buds at or below the surface. Woody shrubs have buds above the ground on stems and branches. Buds on trees are even higher above ground. The height of buds above ground conveys an advantage to light acquisition. High buds on established shrubs and trees ensure leaves are likely to emerge above neighboring herbaceous plants, depriving them of light. The position of buds is also related to climate (Raunkiaer 1934). Buds close to the ground are sheltered from cold and high winds and are

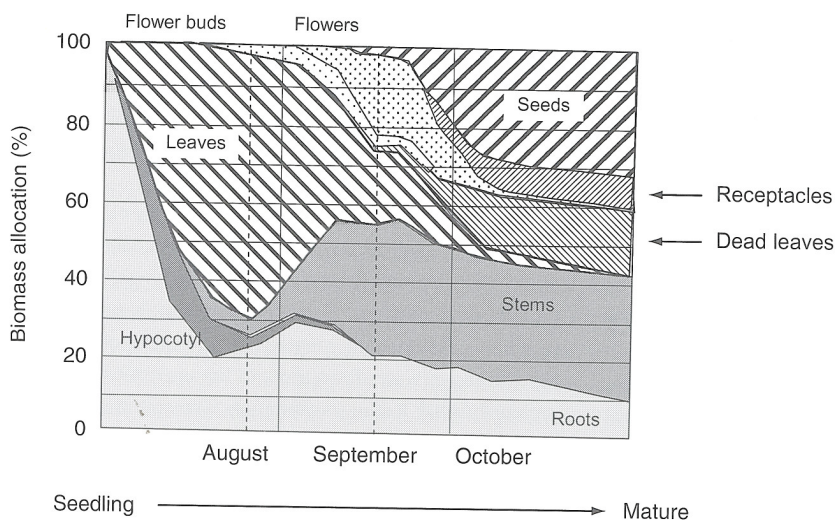


FIGURE 19.7. Whole plant allocation for *Senecio vulgaris*, an annual. Adapted from Harper and Ogden (1970).

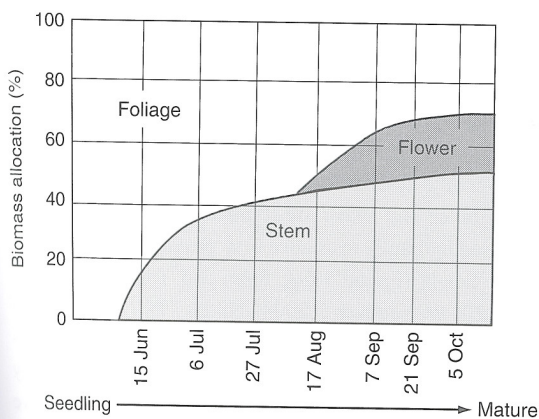


FIGURE 19.8. Aboveground allocation to foliage, stems, and flowers in a herbaceous perennial (goldenrod, *Solidago speciosa*). Adapted from Abrahamson and Gadgil (1973).

favored in harsh alpine and arctic climates. Buds high in the air are exposed to extremes in temperature, humidity, and wind.

19.5.2 Trees

Trees manage carbon in a way suited to their morphology and long lifespan. Young trees allocate much of their carbon to foliage to acquire carbon and to roots to acquire water and nutrients. As trees grow larger, however, much of their biomass is woody stems and branches; relatively little biomass is foliage (Fig. 19.9). The height of trees gives them a competitive advantage over smaller plants; their leaves shade the understory. However, the cost is large amounts of carbon expended in the production and

maintenance of trunks and branches for mechanical support and other tissues to transport water and nutrients.

Allocation in trees is modulated by allometric constraints that maintain certain dimensional relationships between diameter and foliage, branch, and stem biomass (Fig. 19.9). In particular, the structure and anatomy of trees is constrained by the need to transport water to leaves to replace that lost during transpiration and the need to provide mechanical support to foliage. Water flows through specialized structures within wood. However, not all of the woody material in trees conducts water. Large trees have an interior core of heartwood that provides structural support but which does not conduct water. Only the outer ring of sapwood provides the material to transport water. In angiosperms, vessels are stacked end-to-end in the xylem to form a continuous tube through wood. In gymnosperms, vertically stacked, overlapping tracheids form a pathway for water flow through xylem. Because of its role in water transport, the cross-sectional area of sapwood in a tree is closely related to the amount of foliage (Waring *et al.* 1982). Large leaf area requires a corresponding large area of sapwood to transport water to leaves. Hence, there is a functional interdependence between foliage, which fixes carbon and transpires water, and support structures that supply water and nutrients to leaves.

Species that grow in harsh environments support less leaf area for a given sapwood cross-sectional area compared with trees growing in more favorable climates (Table 19.2). For example, Sitka spruce (*Picea sitchensis*) and Douglas fir (*Pseudotsuga menziesii*), which grow in moderate or maritime climates along the Oregon coast, support two to six times as much leaf area for the same sapwood area as do mountain hemlock (*Tsuga mertensiana*),

ponderosa pine (*Pinus ponderosa*), and western juniper (*Juniperus occidentalis*), which grow in harsher inland climates. A study of leaf area and sapwood area in Scots pine (*Pinus sylvestris*) growing on a cool, wet site and a warm, dry site illustrates the effect of site conditions on allocation (Fig. 19.10). The trees on both sites were grown from the same seed source, minimizing genetic variation between sites, and the stands were of similar age, density, and fertility. The trees growing on the warm, dry site had less leaf area per unit sapwood area compared with the trees on the cool, wet site. Moisture limitation on the warm, dry site allowed for less leaf area per unit sapwood area.

The relationship between sapwood area and leaf area arises because foliage must be supported by a certain area of water-transporting sapwood. If sapwood area falls below the required amount, water transport is limited and foliage suffers water shortage. If there is too much sapwood, resources are allocated to non-essential tissue. This suggests a relationship between climate, soil water-holding capacity, and maximum leaf area index (Grier and Running 1977; Woodward 1987, 1993; Nemani and Running 1989).

TABLE 19.2. Ratio of leaf area to sapwood area for tree species growing along a west-to-east transect in Oregon from the coast to the mountains

Species	Climate	Ratio ($\text{m}^2 \text{cm}^{-2}$)
Sitka spruce	Maritime	0.44
Douglas fir	Moderate	0.32
Mountain hemlock	Subalpine	0.16
Ponderosa pine	Semi-arid	0.17
Western juniper	Arid	0.07

Source. Data from Waring (1991). See also Waring (1983) and Waring and Schlesinger (1985, p. 31).

Too much leaf area results in drought as evapotranspiration exceeds precipitation. Too little leaf area results in surplus soil water. Instead, there is an equilibrium between soil water, evapotranspiration, and leaf area whereby trees support a maximum leaf area for which evapotranspiration balances precipitation.

The hydraulics of water movement in trees also affects their height. Height conveys a competitive advantage to tall trees. With increased height relative to neighbors comes greater utilization of light for photosynthesis, but the resource advantage of greater height is tempered by the need to move water from roots to the uppermost leaves to replenish water lost in transpiration. Transpiration provides the force that pulls water from soil through roots up the trunk and out of the leaves. The water column from roots to leaves is connected and under tension. Cohesion between water molecules binds them together so that the pull on water exerted at the top of the tree by transpiration extends all the way down the trunk through the roots into the soil. The driving force is the gradient of decreasing (more negative) water potential from soil through the tree to the atmosphere. Leaf water potentials (-1 MPa) are typically 10–100 times that of roots (-0.1 MPa) or moist soil (-0.01 MPa).

Hydraulic resistance to water flow increases as a tree grows taller and water must travel a longer path. This increased hydraulic resistance may provide a physical limit to tree height (Friend 1993; Ryan and Yoder 1997; Koch *et al.* 2004; Woodward 2004; Niklas 2007). The rate of water transport from roots to leaves is related to the difference in water potential between leaves and roots divided by the hydraulic resistance. A higher tension (more negative water potential) is required to move the same amount of water through a tree with higher resistance. At high tension, air bubbles can form in the water column. These air bubbles interrupt the continuous column of water, hindering replenishment of water in the leaves and inducing stress. The increase in hydraulic resistance with greater height increases

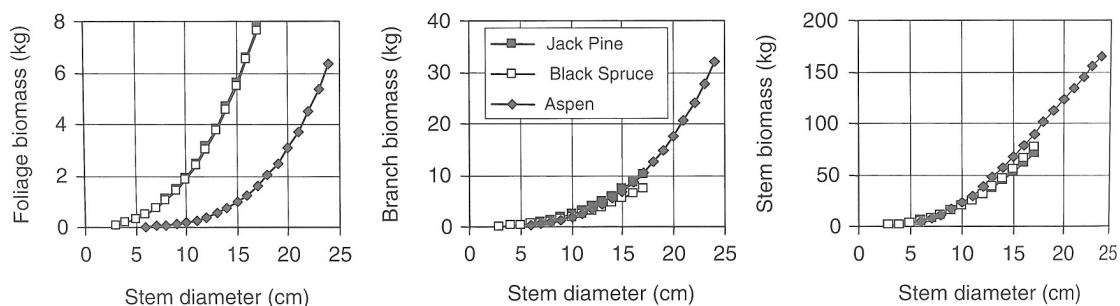


FIGURE 19.9. Relationship between stem diameter and foliage, branch, and stem biomass for jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and quaking aspen (*Populus tremuloides*) trees growing in Canada. Data from Gower *et al.* (1997).

water stress in the leaves, closing stomata and reducing carbon gain during photosynthesis.

The large investment in maintenance and support costs of trees requires compromises between growth, maintenance, and reproduction. Among broadleaf deciduous species, the typical age of maturity increases with longevity (Fig. 19.11). This suggests a high early investment in growth and support at the expense of reproduction. Growth rates also decline with increased longevity. Slow-growing broadleaf deciduous species are nearly three times as long lived as fast-growing species (190 years versus 68 years, on average). This suggests that long-lived trees invest more in maintenance than growth. Similar patterns have been found for needleleaf evergreen trees.

19.5.3 Disturbance and competition

The roles of recurring disturbances and competition for resources (light, water, nutrients) have dominated much

of the discussion of life histories among plants. Recurring disturbances such as fires or windthrows create an open environment where new plants are unlikely to be shaded by neighbors. Success favors those species whose seeds fall in such sites, germinate and become established in high light environments, and grow rapidly to dominate the canopy. At the other extreme, closed canopy forests, with little sunlight on the forest floor, favor species that can tolerate shade, grow slowly in the low light of the understory, and wait for a large tree to die and create a gap in the canopy.

This distinction between disturbance and competition is embodied in the classic notion of *r*- and *K*-selected life histories (MacArthur and Wilson 1967; Gadgil and Solbrig 1972). Species that are *r*-selected maintain their abundance in the landscape through high seed production and widespread dispersal. They are short lived, with relatively little allocation to growth and large allocation to reproduction. They have numerous small seeds dispersed over large areas. They are favored in temporally varying environments where recurring disturbance creates potential for rapid colonization of open sites. In contrast, *K*-selected species maintain their abundance at or near the maximum limit for an environment. They are typically long lived and slow growing, allocating a greater proportion of resources to growth and maintenance. This allows them to survive the intense competition for resources in high-density environments, but provides less energy for reproduction. Their seeds tend to be few and large to provide sufficient resources to germinate and become established in the low light environment of a dense canopy. While the concept of *r*- and *K*-selected species has dominated much of the study of life history patterns, these better represent the endpoints of a continuum of life histories rather than a stark dichotomy. Most plants fall in between these two extremes.

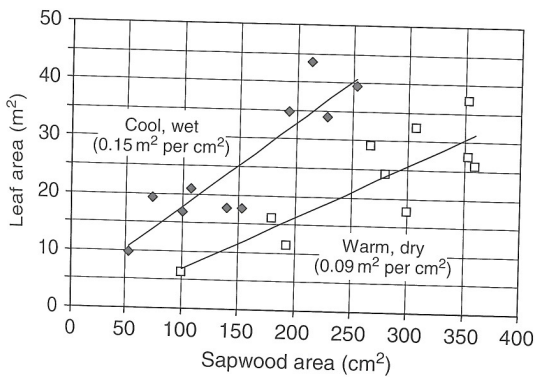


FIGURE 19.10. Relationship between leaf area and sapwood area for Scots pine trees growing on a cool, wet site and a warm, dry site. Adapted from Mencuccini and Grace (1994).

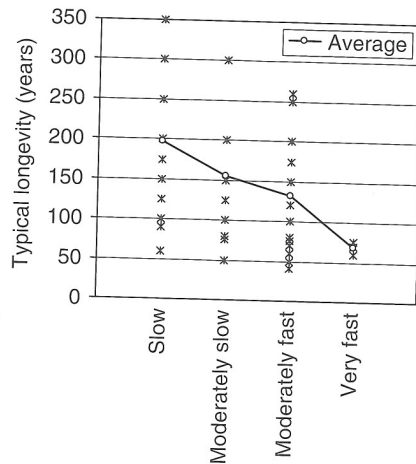
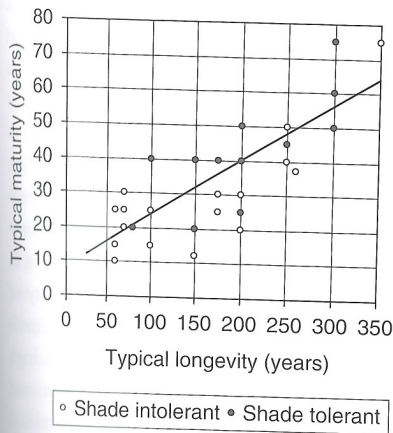


FIGURE 19.11. Relationships among growth, maturity, and longevity in 87 species of broadleaf deciduous trees. Left: typical age of reproduction in relation to typical longevity. Species are separated into shade intolerant and shade tolerant classes. Right: typical longevity in relation to growth rate. Data are shown for each species and as the average longevity for each growth class. Data from Loehle (1988).

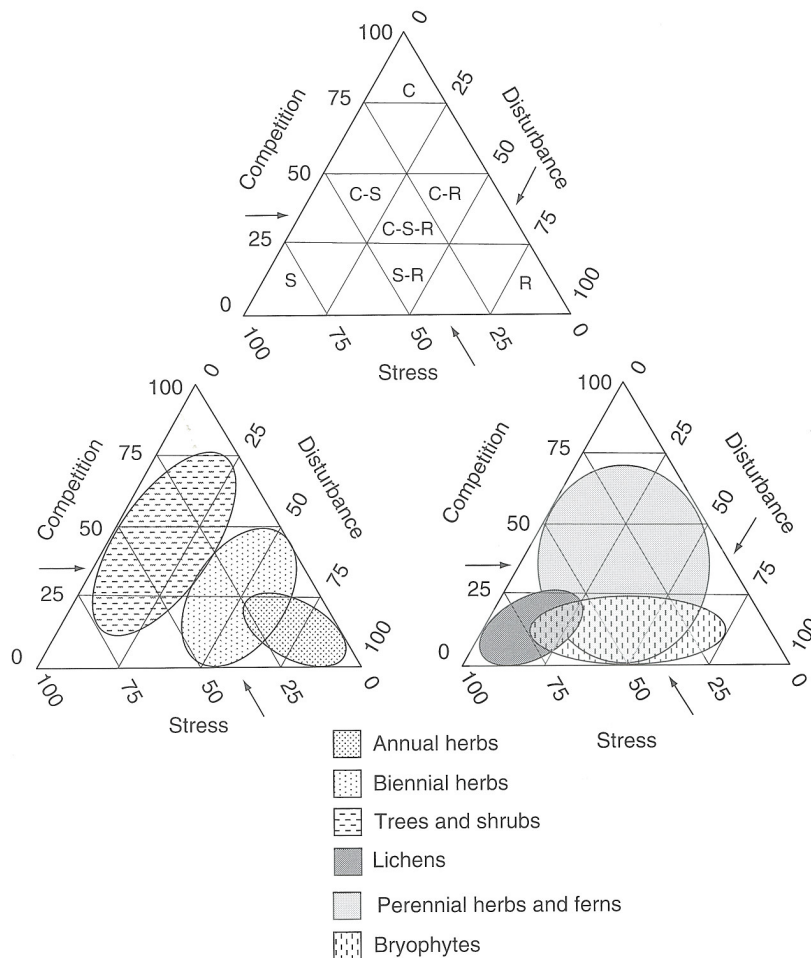


FIGURE 19.12. Classification of life history strategies based on relative importance of disturbance, competition, and stress. Top: The three axes of increasing relative competition, disturbance, and stress define seven life histories – competitor (C), ruderal (R), stress tolerator (S), competitive ruderal (C-R), stress tolerant competitor (C-S), stress tolerant ruderal (S-R), and C-S-R strategist. Bottom: Distribution of annual herbs, biennial herbs, and trees and shrubs (left) and lichens, perennial herbs and ferns, and bryophytes (right) with respect to competition, disturbance, and stress. Adapted from Grime (1979, p. 57, p. 73).

An alternative classification of life history strategies recognizes the importance of resource stressed environments in shaping life histories in addition to competition and disturbance (Grime 1979). Ruderal plants live in temporary or frequently disturbed environments. They are opportunistic species adapted to disturbance. They are short lived, grow rapidly, and have a large reproductive effort at an early age. Competitor plants live in crowded environments where disturbance is infrequent, stress is low, and competition for resources favors species that compete well with others for limited resources. These plants utilize resources more efficiently than others, allocate available resources to growth, and are typically long lived, mature later, and have a small reproductive effort. Stress tolerators live in environments with limited resources where plants are physiologically stressed due to lack of water, low temperatures, low nutrient availability, or low light. These plants persist under conditions of severe resource limitation by growing slowly and allocating resources to maintenance.

The responses of plants to disturbance, competition, and stress produce a variety of life histories intermediate to these three extremes (Fig. 19.12). Competitive ruderals are adapted to environments in which stress is low and competition is limited to moderate intensity by recurring disturbances. Stress tolerant competitors are adapted to relatively undisturbed environments with moderate stress. Stress tolerant ruderals are adapted to moderately disturbed, unproductive environments. A final type of plant, C-S-R strategists, is adapted to environments where the level of competition is restricted by moderate stress and recurring disturbances of moderate intensity. Major life forms segregate along these axes of disturbance, competition, and stress. Trees and shrubs are found in environments characterized by low to moderate intensity of disturbance and tolerate a wide range of stress and competition. Annual herbs are characterized by moderate to high intensity of disturbance, low intensity of competition, and low stress. Only perennial herbs and ferns are undifferentiated with respect to disturbance, competition, and stress.

TABLE 19.3. Physiological and life history characteristics of early and late successional plants

	Early succession	Late succession
<i>Seeds</i>		
Number	Many	Few
Size	Small	Large
Dispersal	Wind, birds	Gravity, mammals
Dormancy	Long	Short
Germination	Enhanced by light	Not enhanced by light
<i>Photosynthesis</i>		
Light saturation intensity	High	Low
Light compensation point	High	Low
Efficiency at low light	Low	High
Maximum rate	High	Low
Respiration rate	High	Low
Transpiration rate	High	Low
Stomatal resistance	Low	High
Resource acquisition	High	Low
<i>Morphology</i>		
Root-to-shoot ratio	Low	High
Size at maturity	Small	Large
Structural strength	Low	High
Lifespan	Short	Long

Source. Adapted from Bazzaz (1979, 1996) and Huston and Smith (1987).

Another useful distinction is between early and late successional species, which differ greatly in their physiology and photosynthetic response to light (Table 19.3). Early successional species are ones that colonize recently disturbed environments. They are exposed to full sunlight and to extremes in humidity, temperature, and wind. In contrast, seedlings of late successional species germinate under a forest canopy and are exposed to less sunlight and less variable microclimates. Seeds of early successional plants require light for germination and can lie dormant for many years in soil, waiting for a disturbance that opens the canopy. Seeds of late successional plants do not require full sunlight for germination and lose viability rapidly. Early successional plants are shade intolerant. They have high rates of photosynthesis at high light intensity and low rates at low light. Light saturation occurs at high light intensity. Late

successional plants are shade tolerant and are photosynthetically more efficient at low light intensities than early successional plants. Shade tolerance not only influences leaf physiology, but also is related to longevity. For example, the typical longevity of shade intolerant species of broadleaf deciduous trees averages 147 years while that of shade tolerant species averages 191 years (Fig. 19.11).

19.6 Plant functional types

The classification of species into *r*- and *K*-selected plants (MacArthur and Wilson 1967; Gadgil and Solbrig 1972), ruderal, competitor, and stress tolerator plants (Grime 1979), or early and late successional plants (Bazzaz 1979, 1996; Huston and Smith 1987) represents broad classes of plant functional types that reduce the complexity of species diversity in ecological function to a few plant types. Plant functional types are defined by key physiological and life history characteristics that determine vegetation dynamics and response to changing environment (Körner 1993; Smith *et al.* 1993, 1997; Woodward and Cramer 1996). The combination of physiological and morphological traits along with climatic preferences is one basis to define functional types. The distinction between annual or perennial, evergreen or deciduous, and broadleaf or needleleaf is particularly useful because these characteristics are observable from remote sensing and are key ecological properties determining stomatal conductance, photosynthesis, and carbon allocation. Such a classification results in six plant functional types (needleleaf and broadleaf evergreen perennial, needleleaf and broadleaf deciduous perennial, broadleaf annual, grass) based on permanence of above-ground biomass, leaf longevity, and leaf type (Running *et al.* 1995). Simple climate rules can then define thermal- and moisture-related varieties (Nemani and Running 1996; Bonan *et al.* 2002).

Figure 19.13 shows the geographic distribution by latitude of needleleaf, broadleaf, evergreen, and deciduous trees. Needleleaf evergreen trees are most abundant in the boreal forests of Canada, northern Europe, and Russia. They also occur in the montane forests of western United States and to a lesser extent in temperate forests of eastern United States, Europe, and China. Broadleaf evergreen trees dominate tropical forests along the equator. Needleleaf deciduous trees are mostly restricted to the boreal forests of east Siberia, where extreme winter temperatures and desiccation favor a deciduous habit (Gower and Richards 1990). Broadleaf deciduous trees are common throughout temperate forests, savannas, and tropical seasonal forests, where they lose their leaves in response to seasonal cold or drought. The distribution of needleleaf,

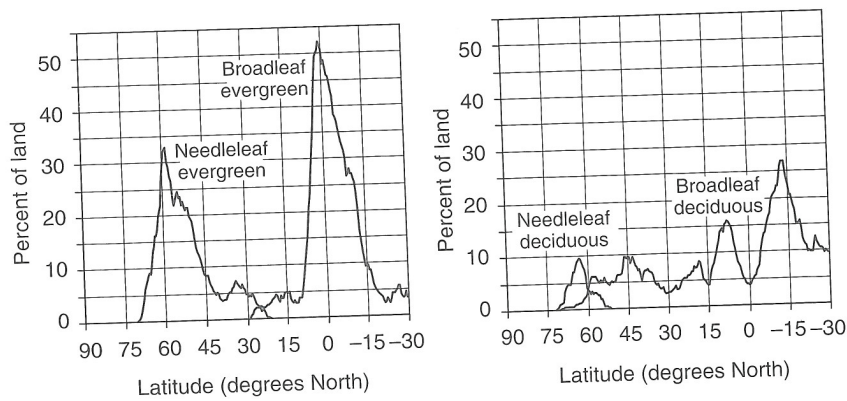


FIGURE 19.13. Geographic distribution of evergreen trees (left) and deciduous trees (right) showing the percentage of land area covered by trees in relation to latitude. Trees are distinguished by needleleaf and broadleaf types. Derived from DeFries *et al.* (1999, 2000a,b).

broadleaf, evergreen, and deciduous trees is related to climate. In particular, the ability of a species to survive cold winter temperatures greatly influences its biogeography (Woodward 1987). Chill-sensitive plants are killed by minimum temperatures of 0–10 °C. These are typically broadleaf evergreen. Other broadleaf evergreen trees can tolerate minimum temperatures of –15 °C. Below this threshold, the vegetation is typically broadleaf but winter deciduous. These species are able to tolerate temperatures as low as –40 °C. Needleleaf vegetation, both evergreen and deciduous, can tolerate even colder temperatures.

The distinction between evergreen and deciduous, and more generally the variation among trees in leaf longevity, represents an integrated plant response to environment (Chabot and Hicks 1982; Mooney and Gulmon 1982; Kikuzawa 1991; Reich *et al.* 1995; Westoby *et al.* 2002; Wright *et al.* 2004). Photosynthetic capacity, foliage nitrogen concentration, and specific leaf area decrease with increasing leaf longevity (Chapter 17). Evergreen trees have low photosynthetic capacity, low nitrogen concentration in foliage, and low leaf area per unit leaf mass. Their leaves have a high initial carbon cost to construct per unit photosynthesizing leaf area. However, evergreen trees, because they retain foliage throughout the year, can photosynthesize and gain carbon at all times of the year when weather is suitable. Because they retain foliage for several years, the high initial cost to construct foliage is spread out over a long period of time. Over the lifespan of their foliage, evergreen trees can, therefore, recoup the high initial investment to construct foliage despite low photosynthetic capacity. In contrast, deciduous trees shed their leaves annually. The benefit is that leaf shedding reduces transpiration and desiccation during times of the year when cold temperature or seasonal drought restrict photosynthesis. The costs are recurring annual investment of carbon to grow leaves and nutrient loss in litterfall. These costs are minimized by having a high specific leaf area so that the

carbon cost to construct photosynthesizing surface area is smaller than in evergreen trees. Moreover, these trees have a high photosynthetic capacity to compensate for the short leaf lifespan.

Deciduous and evergreen leaf habits are also related to defense mechanisms to protect against herbivory. Consumption by herbivores is generally high for leaves with high photosynthetic capacity because of their corresponding high nitrogen concentration. One successful strategy in the face of herbivory is to make foliage unpalatable through structure or chemical defenses. An alternative strategy is to have high photosynthetic rates in short-lived leaves. Evergreen leaves represent an allocation pattern to extend the payback period on the high initial carbon investment to form leaf area, maximize carbon gain despite low photosynthetic rates, conserve nutrients, and protect against herbivory. Deciduous leaves represent an alternative strategy whereby carbon gain is maximized by high photosynthetic rates in short-lived foliage that is either shed at the end of the growing season or consumed by herbivores.

These different life history patterns result in distinct geographic distributions to evergreen and deciduous trees (Fig. 19.13). Evergreen trees have a bimodal geographic distribution. They are abundant at tropical, subtropical, and warm temperate latitudes, less abundant at cold temperate latitudes, and abundant again in subarctic latitudes. Evergreen trees dominate in tropical rainforests where favorable conditions allow for photosynthesis and growth throughout the year. As climate becomes cooler and drier, deciduous trees gain in abundance. Evergreen trees become abundant again on dry, nutrient-poor soils, such as in Southeast United States. Here, efficient nutrient use and the compensating effect of increased leaf lifespan where carbon gain is low give evergreen trees a competitive advantage over deciduous trees (Monk 1966). Evergreen trees also dominate the forests of the North

American Pacific Northwest (Waring and Franklin 1979). In contrast to other temperate forest regions where summers are typically hot and humid and winters cold, the maritime climate of the Pacific Northwest is characterized by mild, wet winters and warm, dry summers. Mild temperatures permit substantial photosynthesis by evergreen trees during the relatively warm, wet autumn and winter months. In contrast, photosynthesis by deciduous trees is restricted to the summer months when leaves have emerged, but during which time soil water is likely to be limiting. The dominance of evergreen trees in subarctic climates is attributed to the cold temperatures, which restrict the growing season and limit mineralization of organically bound nutrients. Nutrient conservation is important. Moreover, the short, cool growing season and long cold winter limits carbon gain. An ability to quickly acquire carbon when conditions are favorable is important.

A physiological and morphological definition of plant functional types must be reconciled with an understanding of plant adaptations to disturbance, which is so critical to understanding vegetation responses to changing environments. Classifications such as *r*- and *K*-selection, ruderal, stress tolerant, and competitive, and early and late succession reflect the central role of disturbance in shaping community structure and composition. Other similar classifications include: exploitive and conservative species (Bormann and Likens 1979); gap and non-gap species (Shugart 1984, 1987, 1998); and vital attributes such as method of arrival following disturbance, method of persistence during and after disturbance, and ability to establish and grow to maturity (Noble and Slatyer 1980). In many cases, morphological and physiological considerations impose correlated life history traits. For example, early succession plants, in addition to their physiological traits of shade intolerance, high rates of photosynthesis, and high photosynthetic light compensation and saturation points, are also relatively short lived, fast growing, and have small seeds that are widely dispersed. Indeed, the consistent tradeoff between high investment in photosynthesis and growth versus preferential allocation to storage, defense, and reproduction imposes correlations among vegetative and regenerative traits.

19.7 Review questions

1. Describe the likely differences in leaf phenology and growing season length for three sites located at latitude 40° N: 10% south slope, 20% south slope, and 20% northeast slope.
2. A landscape architect in Boulder, Colorado (mean January temperature, 0 °C; mean July temperature, 23 °C; annual precipitation, 480 mm) designs a

suburban residential lawn using quaking aspen (*Populus tremuloides*) trees typically found in the mountains. Where would the trees likely grow better: on the north side of the house or on the west side?

3. Over the course of a year, a tree gains 1000 g C m⁻² yr⁻¹ in photosynthesis. Maintenance respiration is 250 g C m⁻² yr⁻¹ and growth respiration is 250 g C m⁻² yr⁻¹. Fractional allocation of carbon to foliage, sapwood, and root growth is 0.40, 0.35, and 0.25, respectively. The corresponding C:N ratio of these plant parts is 25 g C g N⁻¹, 250 g C g N⁻¹, and 200 g C g N⁻¹, respectively. How much nitrogen is needed to support this growth? How is the majority of this nitrogen used?
4. The following table gives aboveground (ANPP) and belowground (BNPP) net primary production from irrigation and fertilizer application experiments in Douglas fir (*Pseudotsuga menziesii*) stands growing in New Mexico. The treatments began in 1985. What do these experiments indicate about carbon allocation in trees?

	Control	Irrigated	Fertilized
ANPP (g m ⁻² yr ⁻¹)			
1984	1160	900	1008
1985	1296	1125	1348
1986	1306	1410	1716
BNPP/ANPP	0.46	0.31	0.23

5. Why is the ratio of root biomass to shoot biomass low in early successional species and high in late successional species?
6. Shade intolerant tree species cannot survive in the low light environment of a closed forest canopy. Explain how shade intolerant species can coexist in a forest landscape with shade tolerant species.
7. White spruce (*Picea glauca*) is a late successional tree species found in the boreal forests of Alaska and Canada. Describe its leaf economics spectrum. Characterize its general life history. Where is it typically found in relation to competition, disturbance, and stress?

19.8 References

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