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THE PHYSIOLOGICAL ECOLOGY OF PLANT SUCCESSION

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INTRODUCTION

Succession is a process of continuous colonization of and extinction on a site by species populations. The process has long been central in ecological thinking; much theory and many data about succession have accumulated over the years.

Since nearly all species in all communities participate in successional interactions, and because physiological ecology encompasses everything that a plant does during its life cycle, a complete review of physiological ecology of all species in all successions is not possible. Thus in this review I discuss the physiological adaptations of species of one successional gradient—from open field to broad-leaved deciduous forest. I concentrate on the physiological adaptations of early successional plants to environmental variability and collate the literature on tree physiology to make comparisons with early successional plants. My discussion may not be applicable to seres where there is little difference in physiognomy between early and late successional plants or where the designation of species as early or late successional is unjustified (e.g. for certain desert and tundra habitats). I discuss the nature of successional environments, seed germination, seedling and mature plant development, plant growth, photosynthesis, water use, and the physiological ecology of competition and interference.

THE NATURE OF SUCCESSIONAL ENVIRONMENTS

The environment of a plant may vary daily, seasonally, vertically, and horizontally. The level of variability is determined by many factors including climate, geographical location, geomorphological features, the nature of site disturbances, and the number and kind of species present. The influence of the environment on the plant depends not only upon the level of environmental variability and the predictability of that variation, but also on the

change in plant size and physiology through time. It is generally thought that environmental variability in open, early successional habitats is higher than in closed, late successional ones. The variability of the physical environment is related mainly to the amount of energy that reaches the soil surface and the way in which it is dispersed from the surface. In an open field, energy exchange occurs at or near the soil surface, light energy reaches the surface unaltered and maximum temperature fluctuations occur there. In a later successional forest the surface of energy exchange is the upper layers of the canopy. Temperature fluctuations below the canopy are buffered by the vegetation itself, and progressively less energy penetrates toward the forest floor; light at the floor is markedly depleted of photosynthetically active wavelengths and is high in far-red wavelengths. Thus seedlings of the late successional species, except in large light gaps, experience a less variable and less extreme environment in the forest with respect to temperature, humidity, and wind. However, sunflecks under a canopy result in extremely variable light intensity and perhaps rapid fluctuation of leaf temperature. The extent, frequency, and magnitude of these events, and the physiological response of plants to them, have not been investigated.

Maximum fluctuation in temperature and soil moisture occurs at or near the soil surface in open early successional habitats (70, 73). Thus germinating seeds and young seedlings may experience a wider range of fluctuations in these two variables than do mature plants. In open early successional habitats CO₂ concentrations are higher than ambient just above the soil surface, increase with soil depth, and reach maximum values just above the water table (80). In forests CO₂ concentrations may rise above ambient levels within the forest canopy, especially early in the day and late at night (29, 100).

Although there is general agreement about the relative levels of environmental variability in early and late successional habitats, quantification and interpretation of this variability are still rather difficult and may be frustrated by phenomena such as sunflecks. A more serious problem, however, is the fact that the plant itself and not variation in the physical factors per se determines the effect of variability. It is likely that similar levels of variation of an environmental parameter cause quite different responses in different species: For some a certain level may be of no consequence to their function; for others it may be detrimental or stimulatory.

ECOPHYSIOLOGICAL CHARACTERISTICS OF SUCCESSIONAL PLANTS

Seed Germination

Seeds of many early successional plants live for years in the soil (45, 87). Seeds of early successional trees long dormant in the soil may germinate in

large numbers when the canopy opens (54). In contrast, seeds of late successional trees lose viability quickly (e.g. 2, 83).

The relationship between seed germination and various parameters of the physical environment has been reviewed, with emphasis on its adaptive significance (e.g. 46, 90). Early and late successional environments differ primarily with respect to light intensity and spectral quality. Seeds of early successional plants are sensitive to light (37, 38, 79, 94) and their germination is strongly inhibited by vegetation-filtered (high far-red/red) light (30, 44, 81, 85). In contrast, seeds of later successional plants, especially those found in climax forests, do not require light for germination—e.g. *Fagus grandifolia* (77) and *Acer saccharum* (59). Furthermore, seeds of species from open habitats require more light for germination than do those of woodland species (34). Fluctuating temperatures also enhance the germination of many species and may be the most important factor in seed germination of annuals (22, 86, 91).

Seeds of early successional plants germinate at or near the soil surface. Here the seeds experience unfiltered light, high daytime temperatures early in the growing season, much variation in daily temperature, and low CO₂ concentrations. Thus seed germination of early successional plants is related to disturbance that brings some seeds from deep in the soil closer to the soil surface. Furthermore, both unfiltered high light (rich in red wavelengths) and fluctuating temperatures are associated with disturbance in forests, and the germination of some successional trees is also keyed to this disturbance (e.g. *Prunus pensylvanica* (54) and *Betula alleghaniensis* (25)). Seed germination of early successional plants may be linked to disturbance in other ways. For example, KNO₃ and other nitrate salts enhance seed germination of several species, including some early successional herbs (36, 46, 66). In devegetated areas a flush of nitrates may occur early in the spring (88) and act as a cue for germination as well as a resource for the young seedlings.

Another aspect of germination in early successional plants is the development of induced (secondary) dormancy—e.g. in *Ambrosia trifida* (22), *A. artemisiifolia* (5), and *Amaranthus* sp. (26). This strategy should protect the seed bank in the event that the site is disturbed again when environmental conditions may be unsuitable for seedling growth.

Ambrosia artemisiifolia, perhaps the most common annual of oldfield succession, possesses a complex germination strategy combining several of the features common to colonists. Germination of the species is closely linked to disturbance, which ensures the availability of resources and reduces the probability of competition with later-successional species (Figure 1). The seeds are dormant when shed. After winter stratification a shift in germinator/inhibitor ratio takes place (97) and the seeds become ready to germinate. If the seeds are brought up to or near the surface by disturbance

they experience unfiltered light, fluctuating temperatures, and reduced CO₂ concentrations, all factors that have been shown to increase seed germination in this species (4, 5, 67). If there is no disturbance some seeds germinate; most do not, and after some time these develop an induced dormancy. Later disturbance causes little germination; the remainder of the seeds require another stratification before they germinate. Seed germination of this species and of several other early successional plants is not an all-or-none phenomenon. Some germination occurs regardless of environmental conditions; additional germination occurs after restratification. This suggests polymorphisms for germination in this and several other species (3, 62, 98).

Germination in early successional plants is epigeal. The cotyledons green up quickly, are photosynthetic (7, 66, 78), and enlarge their surface quickly. Forest trees with large seeds—e.g. *Aesculus* and *Quercus*—have hypogeal germination, while those with small seeds—e.g. *Fagus* and *Acer*—have epigeal germination. The photosynthetic advantages of epigeal germination have associated costs: expenditures for mechanical support and the apparancy of cotyledons to above-ground predators.

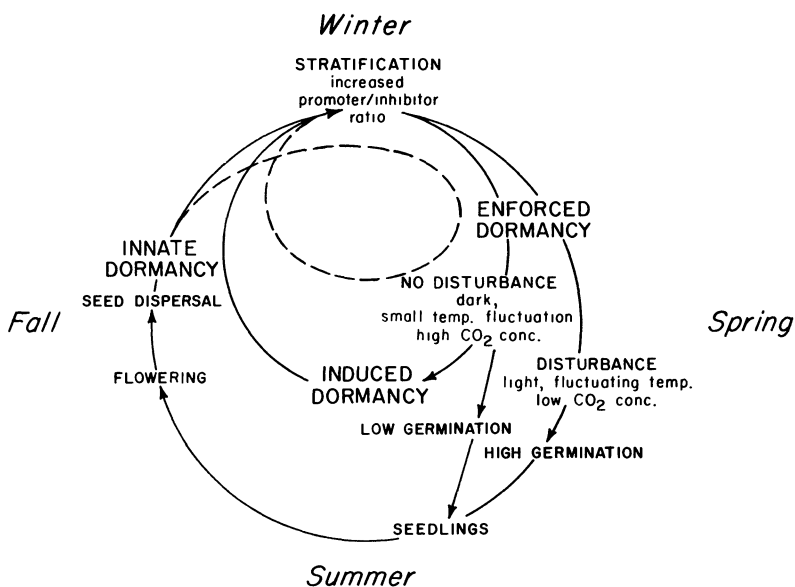


Figure 1 Schematic representation of seed germination in *Ambrosia artemisiifolia* L., a common colonizer in oldfield succession. Dashed line represents seed morphs that require more than one stratification cycle to germinate.

Emergence and Physiology of Seedlings of Herbaceous Colonizers

Winter annuals (mostly composites) have small seeds adapted for long-distance dispersal. They have little or no innate dormancy (37, 43) and are ready to germinate as soon as they land in a suitable site. They germinate under a wide range of temperatures in the field in late summer and fall. Their emergence may be spread over weeks or months, however, and flushes of germination seem to follow periods of rain (73). The seedlings develop into rosettes that overwinter. Most rosettes die in winter owing to frost heaving; the probability of survival is higher for larger ones (73). However, these rosettes are capable of photosynthesizing at relatively high rates and accumulate reserves during winter. They photosynthesize over a wide range of temperatures, utilize a wide range of light intensities, lower their light compensation points at low leaf temperatures in winter, and begin photosynthesis within minutes after exposure to light. In summer their photosynthetic optima shift to higher temperatures (72). Summer annuals produce relatively large seeds that are well protected by heavy seed coats. They are dormant when shed, have complex dormancy mechanisms (Figure 1), and remain inactive for extended periods until the environment becomes conducive to their germination. They then germinate quickly. In the presence of winter annuals, the summer annuals are much suppressed and contribute little to community production. The dominance of the winter annuals is achieved by the preemption of environmental resources—e.g. light, water, space, and especially nutrients (71).

Time of seed maturation, dormancy characteristics, and response to temperature interact to determine the time of seedling emergence and therefore the period of growth of the winter annuals and their time of prominence in the field. Such differences in phenology may contribute to coexistence of these species. Seedlings of the summer annuals emerge in the spring somewhat according to their temperature requirements for germination. Recruitment of new seedlings into the population usually stops in early summer.

In open habitats moisture fluctuates widely near the soil surface but much less below (73), and maximum daily temperature fluctuations occur at the soil surface (10, 70). The growing seedlings should be selected for ecophysiological adaptations to these variable environmental factors: They must be broad-niched. They must be able to grow rapidly, both above and below ground, to escape this zone of maximum variability. Evidence for broad response may be deduced from germination and emergence of some early successional plants over a wide range of temperature (e.g. 37, 67, 89) and moisture (68, 70). Although the physiological ecology of seedlings has not

been studied in many species, our data (7, 66) suggest that early successional plants have high rates of photosynthesis and respiration over a wide range of temperatures and soil moisture. Comparative studies of seedling physiology of early and late successional plants are required for a better understanding of the modes of adaptation to the contrasting physical and biological environments of these plants. Young seedlings of *A. artemisiifolia* exhibit another adaptation to the variable conditions near the surface. They may become desiccated in the field, but upon wetting they develop new roots and the seedlings resume growth. Since soil disturbance could occur at any time during the germination period, and because plowing may expose already established seedlings to the drying conditions at the soil surface, this behavior may be adaptive. Whether this is common in early successional plants is unknown.

Growth and Development

PHOTOSYNTHESIS Light has been recognized as a major factor in species replacement, especially in forest succession (14, 47, 48, 52, 53). The degree of shade tolerance and the arrangement of the foliage and branching patterns are important in determining successional sequences in deciduous forest (40, 95). Most ecophysiological research has emphasized photosynthesis because of its direct relationship to plant survival and growth (56). The light saturation curve (Figure 2), has proven useful in comparing plants from contrasting habitats. It shows several physiological properties of the plants—i.e. rate of dark respiration, the initial slope of photosynthesis (an index of quantum efficiency), the light compensation point, the light saturation point, and the maximum rate of photosynthesis. If the environment around the leaf is closely monitored and transpiration is simultaneously measured with photosynthesis, a variety of other parameters of ecological interest (e.g. leaf resistance and water use efficiency) can be obtained.

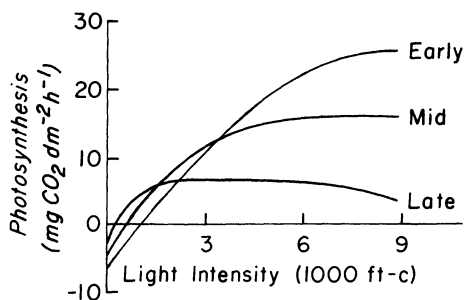


Figure 2 Idealized light saturation curves for early-, mid-, and late-successional plants.

Rates of photosynthesis are often higher in sun-adapted than in shade-adapted species (13). Herbaceous species have higher photosynthetic rates than woody species (49, 50, 56). Data from our work and various other sources (Table 1) show that the rate of photosynthesis per unit of leaf area generally declines with succession (Figure 3). Under optimal conditions the rate of photosynthesis of early successional plants may be as high as 50 mg CO₂ dm⁻² h⁻¹. This is not merely a reflection of their herbaceous growth habit, since late successional herbs of deciduous forest have lower rates. Early successional trees have intermediate rates and late successional plants have low rates. Furthermore, the rate of photosynthesis in the late successional group tends to decline with increased shade tolerance (Table 1).

The light saturation curves of photosynthesis of early and late successional plants show how they differ in a number of ways (Figure 2). First, light saturation occurs at higher light intensities in early successional plants (7, 66, 73, 96). Early successional trees also saturate at high light intensity (1, 11, 47, 48, 61, 74). Light saturation in late successional plants occurs at much lower light intensities (~10–15% of full sunlight). This has been shown for several important, late successional trees—e.g. *Fagus grandifolia*, *Quercus rubra* (51), *Acer saccharum*, and *Quercus coccinea* (101). In early

Table 1 Some representative photosynthetic rates (mg CO₂ dm⁻² h⁻¹) of plants in a successional sequence^a

Plant	Rate	Plant	Rate
<u>Summer annuals</u>		<u>Early successional trees</u>	
<i>Abutilon theophrasti</i>	24	<i>Diospyros virginiana</i>	17
<i>Amaranthus retroflexus</i>	26	<i>Juniperus virginiana</i>	10
<i>Ambrosia artemisiifolia</i>	35	<i>Populus deltoides</i>	26
<i>Ambrosia trifida</i>	28	<i>Sassafras albidum</i>	11
<i>Chenopodium album</i>	18	<i>Ulmus alata</i>	15
<i>Polygonum pensylvanicum</i>	18		
<i>Setaria faberii</i>	38	<u>Late successional trees</u>	
		<i>Liriodendron tulipifera</i>	18
<u>Winter annuals</u>		<i>Quercus velutina</i>	12
<i>Capsella bursa-pastoris</i>	22	<i>Fraxinus americana</i>	9
<i>Erigeron annuus</i>	22	<i>Quercus alba</i>	4
<i>Erigeron canadensis</i>	20	<i>Quercus rubra</i>	7
<i>Lactuca scariola</i>	20	<i>Aesculus glabra</i>	8
		<i>Fagus grandifolia</i>	7
<u>Herbaceous perennials</u>		<i>Acer saccharum</i>	6
<i>Aster pilosus</i>	20		

^aLate successional trees are arranged according to their relative successional position. Data from sources cited in text.

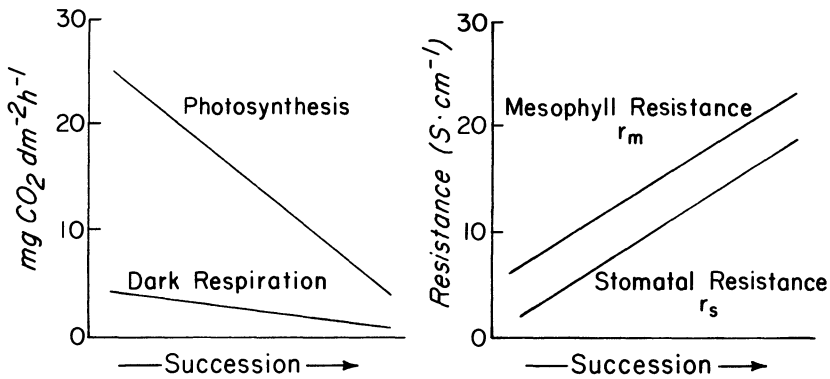


Figure 3 General trends of photosynthesis, dark respiration, mesophyll, and stomatal resistances in relation to successional position.

successional herbs and trees (the sun-adapted plants) the rate of photosynthesis remains unchanged if the leaves are exposed to intensities above saturation. However in late successional plants the photosynthetic rates may decline under similar conditions (solarization) (e.g. 14, 19, 47). Furthermore, solarization occurs faster in the more shade-adapted tree species.

The initial slope of the light response curve has been analyzed for a number of species and has been shown to be steeper for shade-adapted than for sun-adapted species (15, 51) and for climax than for successional trees (48). Thus late successional trees are photosynthetically more efficient at low light intensities than early successional herbs. Early successional trees have values between those of early successional herbs and those of late successional trees (1).

RESPIRATION The rate of dark respiration is high in early successional plants and generally decreases with succession. It ranges from ~ 5 mg CO₂ dm⁻² h⁻¹ for *Ambrosia artemisiifolia* (7) to less than 1 mg CO₂ dm⁻² h⁻¹ in *Fagus grandifolia* and several other late successional trees (51). These trends are consistent with the fact that sun-adapted species have higher respiration rates and generally faster metabolism than do shade-adapted species (31, 49, 50, 92). Early successional trees have intermediate dark respiration rates (1, 11, 61, 74). The rate of decline of dark respiration with succession seems to be less than that of photosynthesis (Figure 3). Thus the photosynthesis/respiration ratio decreases with succession. The rate of dark respiration and the initial slope of photosynthetic response to light determine the light compensation point, the intensity at which photosynthesis balances light respiration. The light compensation point is predictably lower for shade-adapted, late successional plants than for sun-adapted,

early successional ones (Figure 2). Supportive evidence for this is found in many of the studies on photosynthesis and respiration discussed above.

In climax forests photosynthetic production in the understory is limited by light intensity. Most species of the mature forest are capable of photosynthesizing at rates higher than those usually achieved under the canopy. Whereas dark respiration rates are similar for *Acer saccharum*, *Quercus rubra*, and *Q. alba* whether in a gap or under the shade of a closed canopy, their photosynthetic rates are significantly lower in the shade (29). But respiration rates of *Fagus grandifolia* and *Liriodendron tulipifera* increase significantly when grown under low light (51). Whether dark respiration rates are the same in a gap and under closed canopy or significantly decline in the shade, the decline of photosynthesis in the shade results in a less favorable carbon balance. The photosynthesis to respiration ratios (P/R) of a species in the shade and in a gap reflect the level of its shade adaptation and successional position. The P/R of *A. saccharum* is highest under shade and lowest in the gap. The reverse is true for *Q. alba*, while *Q. rubra* is intermediate under both light conditions. Thus the climax *A. saccharum* has a more favorable carbon balance in the shade, while the successional *Q. alba* has a more favorable carbon balance in the gap.

When the CO₂ fluxes into and out of the leaf in a closed illuminated container become equal, CO₂ concentration in the surrounding air ceases to change and the CO₂ compensation point is reached. This point varies among plants and is an indicator of photorespiration (42). Since photorespiration is known to increase with light intensity, the sun-adapted, early successional plants may have higher rates than shade-adapted late successional plants. Measurements of CO₂ compensation points for 5 early successional herbs and 5 early successional trees revealed no differences between the two groups ($\bar{x} = 48.1 \pm 3.7$ and 50.5 ± 2.2 ppm CO₂, respectively). Since no data are available for late successional species comparisons are not possible.

TRANSPIRATION, PLANT RESISTANCE, AND WATER USE Data from numerous sources indicate that transpiration rates are generally high in early successional plants. In this respect early successional plants behave much like other herbaceous sun-adapted plants as reported by Larcher (50). Late successional plants generally have low rates of transpiration (about one quarter that of early successional plants). The differences in rates of transpiration and photosynthesis between early and late successional plants reflect differences in stomatal and mesophyll resistances, both of which generally increase with succession [Figure 3, based on data from (9, 24, 39, 101–103)]. Energy balance considerations of open and shaded environments indicate that low leaf resistances in early successional species may be effective in

preventing harmfully high leaf temperatures. In contrast, the high leaf resistances of shaded, late successional species may be necessary to prevent excessive cooling. In shade-adapted herbs, transpiration rates seem to be higher than those of the trees.

Water use efficiency (WUE) is a measure of the amount of water expended in transpiration to obtain a unit of carbon dioxide from the surrounding air. It is influenced by the magnitudes of the leaf resistances (boundary layer, stomatal, and mesophyll) to gas exchange. Generally mesophyll resistance is highest, stomatal resistance is intermediate, and boundary layer resistances are lowest (39). The general water status of the plant is further influenced by the total plant resistance to water transport from the soil to the leaf. There are few measurements of resistance to water flow in plants. However, herbaceous plants have lower resistance to water transport than do deciduous trees (50) because herbs have a more efficient water transport system than do woody species (18). In 4 early successional annuals [(9) and F. A. Bazzaz, unpublished data] we found very low plant water resistance values ranging from 0.5×10^6 to 1.6×10^6 s cm⁻¹. In contrast the value for *Acer saccharum* was 2.3×10^6 s cm⁻¹. The measurement of this and the other three resistances requires accurate control and measurement of the plant's environment and are not common in ecological literature.

The ratio rate-of-photosynthesis/rate-of-transpiration per unit area per unit time for several early successional plants [(69), F. A. Bazzaz, R. W. Carlson, unpublished] suggests that, under optimal conditions, WUE is high (~ 7.2 mg g⁻¹). Using a different method of calculation [resistance to water vapor diffusion (R_{H_2O})/resistance to CO₂ assimilation (R_{CO_2}) (39)] Wuenschel & Kozlowski (101, 102) concluded that WUE was higher for the xeric, early successional *Quercus velutina* than for the climax *Acer saccharum*. Generally, however, resistance to H₂O and CO₂ diffusion and water use efficiencies found in the literature are difficult to compare and relate confidently to successional position because of (a) the different ways they are measured and expressed and (b) their dependence on leaf age (23, 24) and soil moisture levels during growth (69).

The speed and the degree of change of stomatal resistance to changes in light intensities may be adaptive and may be related to the successional position of the species. Stomatal opening in response to increased light is consistently faster in shade-tolerant than shade-intolerant trees (99). *Acer saccharum* seedlings respond faster than do *Fraxinus americana* seedlings. Transpiration declines faster in *Acer* and at less negative water potentials than in *Fraxinus* (21). Thus in the shade *Acer* can function better than *Fraxinus* because of its ability to use sunflecks but is less capable of surviving if subjected to water limitation.

RESPONSE TO WATER LIMITATION When water potential of the leaves declines, stomata begin to close; CO₂ and water vapor exchange also decline. Stomatal sensitivity to changes in leaf water potential differs widely among plants, especially with regard to the water potentials at which reduction in photosynthesis and respiration begin, the steepness of their decline, and the potential at which they become negligible (16). In contrast to plants with low photosynthetic rates, plants with high photosynthetic rates do not extract water from dry soil. Their photosynthetic rates decline quickly with decreased potential of the soil (60). This may suggest that photosynthesis declines at less negative water potentials in early successional plants (high photosynthetic rates) than in late successional plants (low photosynthetic rates). There are a few data on the relationship between photosynthetic rates and water potential in successional species, but generalizations may be difficult to draw without a thorough study of this relationship for plants in a sere. It appears, however, that late successional plants are perhaps more sensitive to declining moisture levels (Figure 4). For example, photosynthesis in *Acer* begins to decline at about -200 kPa and becomes quite low at -1000 kPa. In *Ambrosia* it begins to decline at about -800 kPa and continues at 20% of maximum at -2200 kPa (7). In some early successional trees

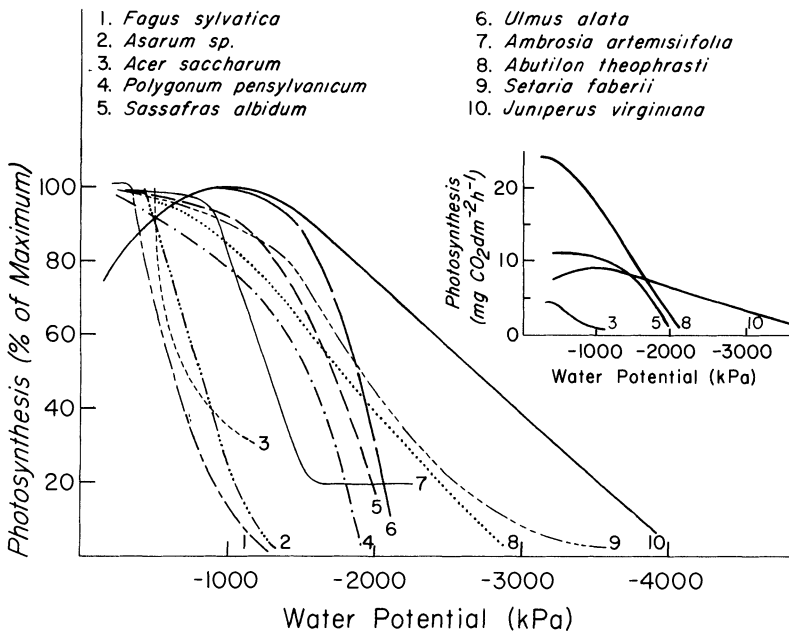


Figure 4 Relationship between photosynthetic rate and water potential in species from early- (4, 7, 8, 9), mid- (5, 6, 10), and late- (1, 2, 3) successional habitats.

photosynthetic rates may not decline until water potentials are as low as -1500 kPa (Figure 4). In *Ulmus alata* and *Juniperus virginiana* photosynthesis even rises initially with decrease in leaf moisture level, and maximum photosynthetic rates are reached at moisture levels that these plants experience in the field (1, 61).

Differences in photosynthetic responses to water potential may be found within successional groups. *Setaria faberii* and *Polygonum pensylvanicum* are early successional annuals that exhibit quite different daytime patterns in leaf water potential. Whereas *Polygonum* maintains its potential at about -400 kPa, *Setaria* potentials vary from -200 to -2200 kPa. The differences are related to their root locations in the soil (63, 96). However *Setaria* maintains near-maximum photosynthesis to as low as -1200 kPa and photosynthesizes at 30% of maximum at -2400 kPa. Photosynthesis in *Polygonum* begins to decline at ~ -400 kPa and becomes negligible at -1800 kPa. Both species maintain active photosynthesis in the field environment by using compensatory strategies and therefore coexist.

In early successional plants the recovery of leaf water potential, transpiration, and photosynthesis after watering moisture-stressed plants is rapid but not uniform among species. Maximum rates are restored within several hours after watering several annuals (1, 7, 17, 61, 96). Recovery in late successional plants has not been examined except in *Acer saccharum*. Seedlings were found to recover fully 4 days after rewatering (J. W. Geis, R. L. Tortorelli, unpublished).

Since early successional plants generally key in on disturbance they stand astride pulses of available resources. Rapidly obtaining and using them before they subside and preventing competitors from obtaining them may be adaptive. The rapid increase in the growth rate of early successional trees and herbs when the canopy above them is removed (54, 65) is an example of this strategy.

GROWTH RATES No systematic study has yet used formal growth analysis techniques to compare the growth, under uniform conditions, of species of a sere. However, Grime (31) found that the shade-adapted climax species *Acer saccharum* and *Quercus rubra* had lower rates than the sun-adapted successional trees *Ailanthus altissima*, *Rhus glabra*, and *Fraxinus americana*. He also found that relative growth rates were highest for several arable weeds (including some early successional herbs). Additional supportive data are found in (35). In another study Grime & Hunt (34) investigated the relative growth rates under optimal conditions, (R_{\max}), of 132 species from a wide range of habitats in Britain. They found that woody species generally exhibited a bias toward low R_{\max} , that annual plants were most frequent in the high R_{\max} category, and that in disturbed habitats fast-growing species were predominant.

Early successional plants are fugitives. Their continued survival depends on their dispersal to open sites. Being competitively inferior they must grow and consume available resources rapidly. High relative growth rate is therefore an integral component of their fugitive strategy.

Compression of Environmental Extremes

In addition to their broad physiological response to environmental gradients, early successional species may be capable of compressing environmental variability around them. In the field on a clear day in July we found that leaf temperature of *Polygonum* and *Abutilon* remained rather constant between 25–28°C, near optimum for photosynthesis (96), from 900–1600 hr while air temperature was 33–35°C. The reduction of leaf temperature variation relative to air temperature in *Abutilon* has been attributed to a more or less passive energy balance phenomenon (103) and is related to the air-temperature–leaf-temperature crossover described by Gates (28). More active control, however, may be possible through alteration of the angle of the leaf relative to the sun. *Abutilon* normally displays variation in leaf angle from 0°–60° off horizontal. Such shifts of leaf angle can result in differences in leaf temperatures as high as 8°C when the sun is directly overhead. The generality of compression of environmental variability in early successional plants and the difference from late successional plants in ability to ameliorate environmental stress should be investigated.

Acclimation

Another aspect of the physiological ecology of early successional plants that has adaptive value in their variable environments is their ability to acclimate rapidly. The rapid and efficient acclimation of several winter annuals—e.g. *Erigeron canadensis*, *E. annuus*, and *Lactuca scariola*—to seasonally changing temperature (72) is an example of this adaptation (Figure 5). Acclimation to the light environment that the plants experience during their growth seems to be more pronounced in the early (6, 12, 20, 64) than in the several late successional plants we examined (Figure 6). The seeds of *Aster pilosus* usually germinate under the shade of other plants. However the rosettes develop under less shade and the plants bolt and flower in full sun after the opening of the canopy by the demise of annuals above them. The different photosynthetic response to light intensity of the three stages reflects their respective light environments (66). The curves are respectively similar to those of shade-adapted late successional, mid-successional, and sun-adapted early successional plants.

Forest Herbs

Herbaceous plants of temperate deciduous forests may experience an environment that has features of early and late succession. Growth in several

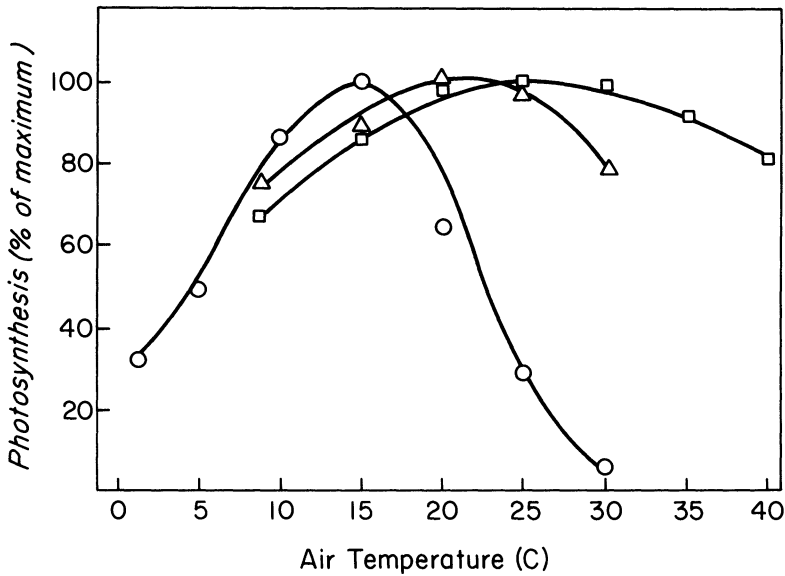


Figure 5 Shifts in photosynthetic response to temperature in *Erigeron canadensis*. Measurements made in February (○), July (□), and October (△). Data from (72).

of these species begins soon after temperatures rise above freezing and continues after canopy closure. The development of the canopy results in reductions in light intensity, temperature fluctuation, vapor pressure deficit, and windspeed (57). Sparling (82) studied dark respiration rates, light compensation points, light saturation, and maximum photosynthetic rates before, during, and after canopy closure in 25 species of woodland herbs. Based on their responses he divided the plants into 3 groups. First are those that are light saturated at 1000–3000 fc and have a compensation point above 40 fc. They behave as sun species and usually become dormant after canopy closure. Second are those that are light saturated between 250 and 1000 fc and have lower compensation points than plants of the first group. Their metabolic activities decline with canopy closure (84). Finally, a number of species are shade-tolerant. They light-saturate at <250 fc and have compensation points <25 fc. They also have a steeper initial slope of photosynthesis, indicating that they are more efficient at low light intensities than the sun-adapted group. Photosynthetic efficiency at low light intensity is aided by the general increase in chlorophyll content of leaves after canopy closure (8). Further examination of Sparling's data reveals that members of the sun-adapted group have, on the average, the highest mean photosynthetic rates ($8.8 \text{ mg CO}_2 \text{ g h}^{-1}$), members of the second group have interme-

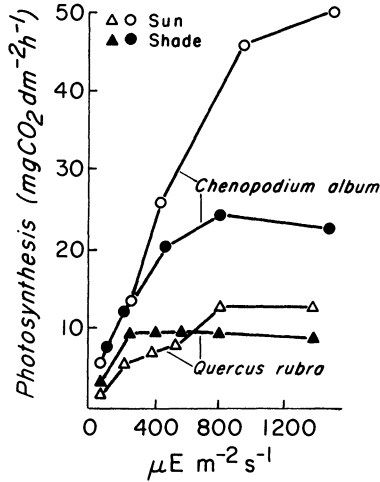


Figure 6 Light saturation curves for *Chenopodium album*, an early successional annual, and *Quercus rubra*, a late successional tree, grown in sun and in shade (F. A. Bazzaz, R. W. Carlson, unpublished data).

diate rates ($6.1 \text{ mg CO}_2 \text{ g h}^{-1}$) and the shade-adapted plants have the lowest rates ($3.5 \text{ mg CO}_2 \text{ g h}^{-1}$).

A remarkable adaptation to the changing light environment of a deciduous climax forest is that found in *Hydrophyllum appendiculatum* (57). The species produces two types of leaves with two different morphologies. The first, produced under open canopy (sun leaves), light-saturate at 2500 fc., light-compensate at 100 fc, photosynthesize at $8.5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$, and respire at $1.8 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$. The second, produced under closed canopy (shade leaves), have corresponding values of 700 fc, 60 fc, 2.4, and $0.5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$. The initial rise in photosynthetic rate with increased light is steeper in the shade than in the sun leaves. These leaf types behave like early successional and late successional leaves, respectively.

Members of the sun-adapted group, like early successional plants, are expected to respond quickly to changes in the environment, including rapid uptake of nutrient flushes. This behavior has been observed in *Erythronium americanum*, which begins its growth with a quick increase in plant weight and fast uptake of spring nutrient flushes (58).

Competition and Interference

Competition may be absent only early in the initial stages of colonization; as the young seedlings grow, competition between them begins. Later in succession the situation becomes more complex, and seedlings may compete

with individuals of different ages and sizes belonging to many species. Competition between early successional plants is preemptive (93). Individuals and species that arrive first use up resources and starve later arrivals. Competitive losers become winners later if their life history characteristics allow them to grow when their competitors become inactive (66, 72). Competitive interactions as causal factors in succession have been discussed recently (32). The replacement of the pioneer *Erigeron* by *Aster*, and that in turn by *Andropogon*, involves increased competitive ability (43). Suppression of summer annuals is caused by preemption of resources by the already established winter annuals (71, 73). In the Piedmont the failure of pine seedlings to compete with the established trees leads to their replacement by the climax oaks, which compete for water better than pines (47). In late succession individuals and species that have survived at a low level of activity (having been suppressed by preemption and contest competition from neighbors) may replace their competitors when these weaken or die. Thus species replacement involves the interaction of competition with stress tolerance.

Detailed studies of the role of allelopathy in succession in Oklahoma (76) have shown that several members of the first "stage" of succession produce toxins, mostly phenolic compounds, that are inhibitory to several other species from that stage and sometimes to themselves. For example, the rapid disappearance of certain pioneer weeds and their replacement by *Aristida oligantha* are caused by allelopathic interference. Most of the pioneer plants do not inhibit *A. oligantha*; but extracts from several of the species and from *A. oligantha* inhibit nitrogen-fixation by soil algae and bacteria. *Aristida oligantha* stands are maintained for a long time because they occupy nutrient-poor habitats that are kept poor by allelopathy and are not suitable for the "climax" *Andropogon scoparius*. Thus, allelopathy speeds succession to *A. oligantha* and slows its replacement by the climax grasses. Chemicals released from several plants at various positions along this successional gradient control nutrient availability by differentially inhibiting nitrifying organisms (76), thereby influencing species replacement and community composition.

Allelochemicals are also produced by some midsuccessional herbs and early successional trees. The perennial *Andropogon virginicus* produces chemicals that inhibit invasion by shrubs and therefore maintains itself in large populations (75). Allelopathic effects of *Solidago*, *Aster*, and grasses, prevent tree regeneration in glades (41). The presence of patches of early successional trees with little understory may be caused by their allelopathic action—e.g. in *Ailanthus altissima* (55) and *Rhus copallina* (76). *Sassafras albidum* maintains itself in pure patches by producing inhibitory chemicals (27), but there may be alternate explanations for this clumping (4).

The role of allelopathy in community composition is controversial. Several contradicting reports exist on whether a species is strongly, mildly, or nonallelopathic. Furthermore, the relative contributions of allelopathy and competition for environmental resources in determining both community composition and the rate of species replacement are still unknown.

CONCLUSIONS

Early and late successional plants in seres from open field to forest have many contrasting physiological attributes (Table 2). Evidence for some of these characterizations is strong; for others, additional research is required. Research on the physiological ecology of successional plants in tropical habitats is needed for a more accurate comparison with temperate succession. Studies should be conducted on the physiological ecology of plants in seres in which there is little change in growth form with succession—e.g. in grasslands. Finally, because of the increasing interest in species turnover

Table 2 Physiological characteristics of early and late successional plants

Attribute	Early successional plants	Late successional plants
Seeds		
dispersal in time	long	short
secondary (induced) dormancy	common	uncommon ?
Seed germination enhanced by		
light	yes	no
fluctuating temperatures	yes	no
high NO ₃ ⁻ concentrations	yes	no ?
inhibited by		
far-red light	yes	no
high CO ₂ concentrations	yes	no ?
Light saturation intensity	high	low
Light compensation point	high	low
Efficiency at low light	low	high
Photosynthetic rates	high	low
Respiration rates	high	low
Transpiration rates	high	low
Stomatal and mesophyll resistances	low	high
Resistance to water transport	low	high
Acclimation potential	high	low
Recovery from resource limitation	fast	slow
Ability to compress environmental extremes	high	low ?
Physiological response breadth	broad	narrow
Resource acquisition rates	fast	slow ?
Material allocation flexibility	high	low ?

in forest gaps and their role in regulating species diversity and coexistence, research on the physiological ecology of gap species in temperate and tropical forests would increase our understanding of species replacement in nature.

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