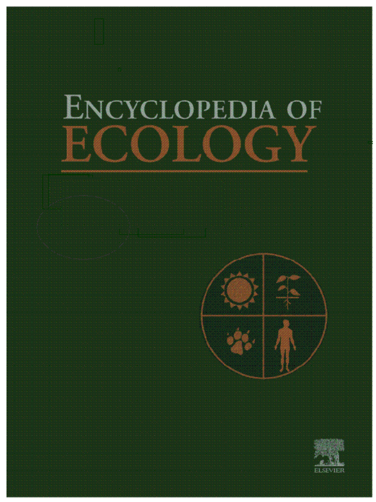

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Pioneer Species

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Introduction

In early ecological literature, the term pioneer was used to describe those plant species that initiate community development on bare substrate (primary succession). More recently, usage of the term has included microbial and invertebrate taxa, and describes the first colonists of sites affected by less extreme disturbance which undergo secondary succession. Pioneers of primary and secondary successions share some traits; in both cases colonization of new habitat depends on effective dispersal, which generally selects for high reproductive output and small propagule size. However, differences in resource availability between these habitat types result in different opportunities for growth and reproduction. Few species can be successful on both primary and secondary successions.

Pioneers in Primary Succession

Primary succession occurs when extreme disturbances, such as landslides and volcanic eruptions, create new habitats by removing or covering existing vegetation and soil. Pioneers that initiate primary succession must be able to establish and grow on substrates that are nutrient poor and that often have unfavorable moisture conditions. The most extreme sites are exposed unweathered rock surfaces. Here, colonization may be limited to cyanobacteria ('blue-green algae'), lichens, and bryophytes, with no further vegetation development. Somewhat more nutrient-rich conditions associated with weathered or fragmented bedrock surfaces, such as the scree slopes of landslides, are often dominated by tree species. Sites still richer in mineral nutrients, which may contain some residual organic soil, such as the depositional zones of glacial moraines, in turn are often colonized by herbaceous species and grasses with faster growth rates (Figure 1).

For pioneers in primary successions, nitrogen is often the most limiting resource. Unlike other mineral nutrients that can be released through weathering of underlying rock, nitrogen must either be transported to primary successions through leaching and deposition, or fixed *in situ*. Some of the most inconspicuous pioneers on exposed rock faces are nitrogen-fixing cyanobacteria. Rates of nitrogen fixation by cyanobacterial 'biofilms' on rock surfaces may be considerable; thus, nitrogen-rich leachate from these surfaces may affect community development at down-slope sites. Cyanobacteria may also form symbiotic associations with lichens (e.g., *Stereocaulon* spp.).

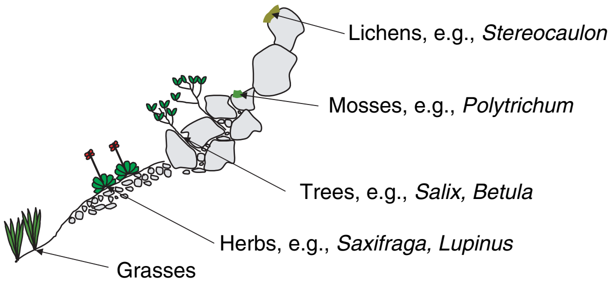

Figure 1 Pioneer species typical of substrate types exposed following deglaciation. More fertile (nitrogen-rich) substrates often support herbaceous species and grasses, whereas rock surfaces and glacial till support lichens, bryophytes, and woody species. Modified from Grubb PJ (1986) The ecology of establishment. In: Bradshaw AD, Goode DA, and Thorp E (eds.) *Symposium of the British Ecological Society, Vol. 24: Ecology and Design in Landscape*, pp. 83–97. Oxford: Blackwell.

These lichens are among the first colonists of landslides and lava flows (**Figure 2**). Nitrogen fixation by lichens on these sites (0.2–0.4 kg N ha^{-1} yr^{-1}) may be important in facilitating the later colonization of these sites by vascular plants.

Relatively few vascular plant pioneers are nitrogen fixing. An exception is the perrenial lupine (*Lupinus lepidus*). Lupine is a conspicuous pioneer of the extensive ash and pumice fields that were created by the eruption of Mt. St. Helens (Washington State, USA) in 1980. In the first decade after the eruption lupine patches spread rapidly, increasing available nitrogen in the soil tenfold, potentially facilitating the growth of other colonizing plant species. More recently, however, the spread of lupine patches has slowed as specialist insect herbivores have colonized the plants. The patchiness and unpredictability of vegetation colonization on Mt. St. Helens also highlights the importance of constraints other than nutrient availability that limit recruitment success. Dispersal limitation, described as the failure of seeds to arrive at suitable establishment sites, may limit the rate at which pioneers colonize available substrate, and may be important in shaping the trajectory of successional change. Similarly, requirements for safe sites that provide favorable conditions for seedling establishment may account for the nonrandom distribution of pioneers on substrates such as glacial till. Small seed size and wind dispersal are particularly common traits among vascular plant pioneers. Wind dispersal is favored when animal dispersal vectors are rare. Small seed size may increase the probability of seeds becoming trapped in cracks and small depressions where germination and seedling survival are likely to be enhanced. Conversely, it has been suggested that small seed size limits the initial nutrient resource supply available to the plant and may prevent seedlings from developing mutualisms with nitrogen-fixing bacteria.

Pioneers in Secondary Succession

Secondary succession occurs when the severity of disturbance is insufficient to remove all the existing vegetation and soil from a site. Many different kinds of disturbances, such as fire, flooding, windstorms, and human activities (e.g., logging of forests) can initiate secondary succession. Pioneers of secondary successions face quite different conditions from those that accompany primary succession. Secondary successions often start with resource-rich conditions associated with high light availability and reduced competition for nutrients and moisture. Disturbances may also be short-lived; for example, gaps created in forest canopies close as the crowns of surrounding trees expand and as seedlings and saplings in the understory grow up in response to increased light. Pioneers rely on recruitment from propagules present in the soil, or that disperse into the site after disturbance occurs. Pioneers are able to outcompete established vegetation that survived the disturbance by maintaining high juvenile growth rates. Some of the fastest growing trees are pioneers in tropical rain forests. Individuals of the balsa tree *Ochroma pyramidale*, for example, can grow from seedlings to adults with >30 cm trunk diameter in <10 years.

The difference between pioneer and nonpioneer species is difficult to delineate (**Table 1**). Attempts to define

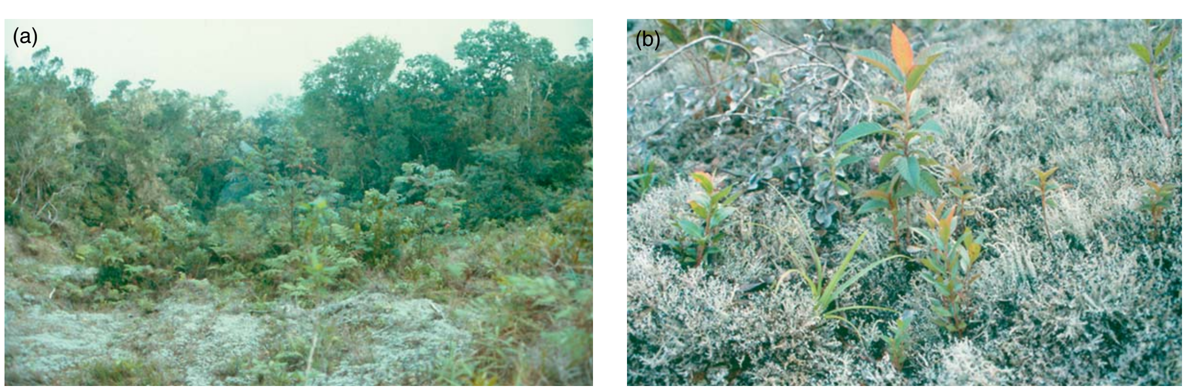

Figure 2 (a) A 15-year-old landslide scar at 1500 m in the Blue Mountains, Jamaica. (b) The whitish appearance of the landslide surface results from its coverage by a dense mat of *Stereocaulon* lichen (note recruitment of woody species).

Table 1 Characteristics of pioneer tree species in tropical forests that distinguish them from nonpioneer species

Pioneer species	*Nonpioneer species*
1. Juveniles recruit from seed following disturbance; seedlings are unable to survive beneath a forest canopy	Seedlings and saplings persist in the shade of a forest canopy
2. Seeds germinate in response to cues provided by changes in light, temperature, or soil nitrate concentrations indicating disturbance to canopy vegetation	Seeds germinate immediately after dispersal or seasonally during periods favorable for establishment
3. Seeds generally small; frequently dispersed by wind	Seeds may be large; frequently dispersed by vertebrates
4. Seeds often persist in the soil (weeks to decades after dispersal)	Seeds lack dormancy or remain in the soil for less than a year
5. High height growth rate and juvenile mortality rate	Lower height growth, crowns often show lateral spread in the shade
6. High maximal photosynthetic rate, light compensation point, and foliar nutrient concentrations	Low maximal photosynthetic rate, light compensation point, and foliar nutrient concentrations
7. Short-lived leaves with high leaf area per unit leaf mass	Leaves of juvenile plants may persist for several years with low leaf area per unit leaf mass
8. Open canopies with sparse branching	Closed canopies
9. Low wood density	Medium–high wood density
10. Low investment in chemical anti-herbivore defense	High investment in chemical and structural defenses
11. Often form defensive mutualisms with ants	Defensive mutualisms uncommon
12. Adult lifespan typically <100 years	Adult lifespan up to 500 years
13. Wide geographic and ecological range	Often restricted geographic range and habitat requirements

Adapted from Swaine MD and Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81–86.

distinct life-history strategies (implying coordinated evolution of life-history traits) are confounded because key traits such as propagule size and juvenile growth rate can vary over several orders of magnitude within a community and show broad overlap among species with contrasting habitat requirements. Nonetheless, interactions among traits can be used to describe some life-history tradeoffs that largely constrain the habitat requirements of pioneers. For vascular plants, paramount among these is a tradeoff between growth in the sun and survival in the shade (Figure 3). The high growth rates of pioneers are maintained by allocating a large fraction of the plant's resources to new leaf area production, and by investing in nutrient-rich leaf tissue that can attain high-maximum photosynthetic rates. A consequence of preferential allocation to leaf production is that few resources remain that can be used to defend the plant against herbivores and pathogens, or to recover from physical damage. This results in high mortality, particularly in the shade, where resources needed for tissue replacement are most limiting.

For pioneers growing in high light environments, abundant supplies of carbohydrate fixed through photosynthesis can be used to co-opt the services of predaceous insects that defend the plant against herbivores. Many pioneers have extra-floral nectaries that provide food for insect mutualists. Two of the dominant genera of pioneers in tropical forests – *Cecropia* (Urticaceae) in the neotropics and *Macaranga* (Euphorbiaceae) in the Asian tropics – have developed a more elaborate mutualism that provides a striking example of convergent evolution in morphological traits. In both genera the hollow stems of saplings are colonized by queen ants (*Crematogaster* in *Macaranga; Azteca* in *Cecropia*). The ant colonies are then provisioned

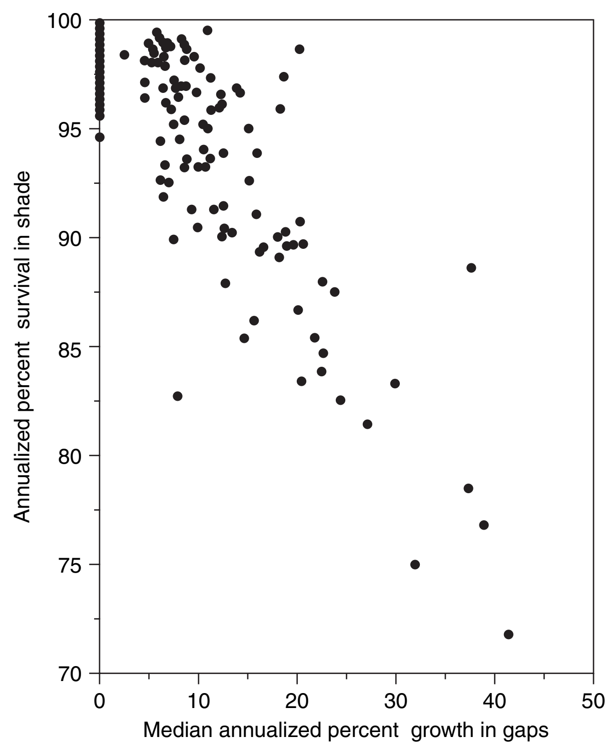

Figure 3 The negative correlation between annual survival of rate of saplings 1–4 cm diameter at breast height in understory shade versus the median annual growth in the sun in tree fall gaps. Data are for canopy and mid-story tree species growing in semi-deciduous tropical forest in the 50 ha forest dynamics plot on Barro Colorado Island, Panama. Each data point is an individual species. Pioneer species have high growth rates in gaps and low survival in shade. Note that there is a continuum of responses to sun and shade that prevents a clear delineation of the pioneer guild. Reproduced from Hubbell SP and Foster RB (1992) Short-term dynamics of a tropical forest: Why ecological research matters to tropical conservation and management. *Oikos* 63: 48–61, with permission from Blackwell Publishing.

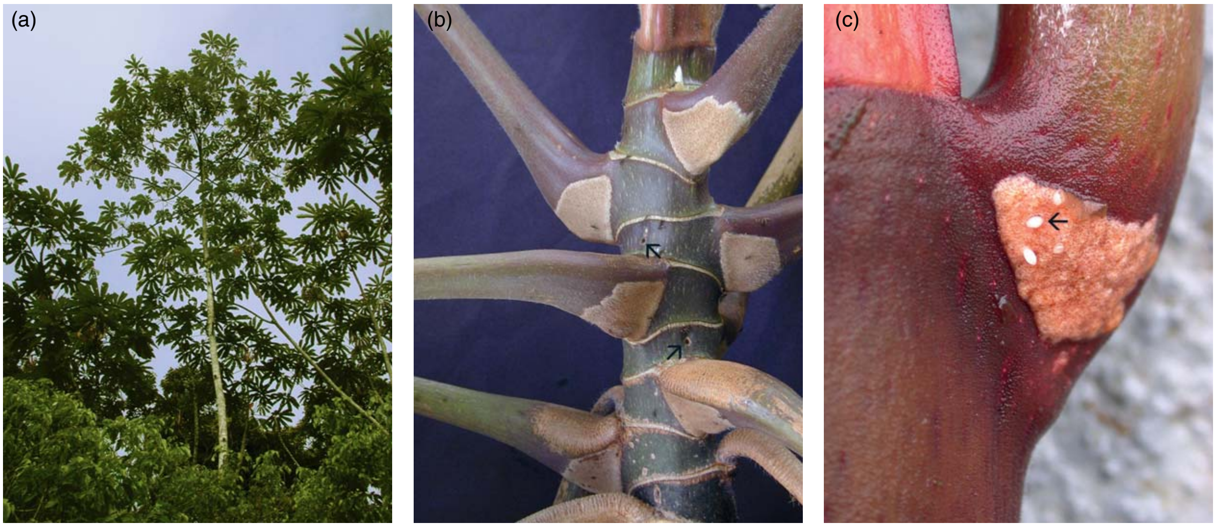

Figure 4 (a) *Cecropia engleriana*, growing along a roadside in Yasuní National Park, Ecuador. *Cecropia* spp. are the dominant pioneers of young secondary forests in the neotropics. (b) The hollow stems of most *Cecropia* species are inhabited by aggressive ants (*Azteca* spp.) that predate insect herbivores. Arrow shows nest entrance. (c) In return, the plant provides the ants with Mullerian food bodies (shown by arrow) produced on the trichilium, a structure at the base of the petiole.

with carbohydrate and lipid-rich food bodies produced on leaf surfaces, stipules, or petioles (Figure 4).

The transient and unpredictable occurrence of secondary successional habitats has selected for high dispersal ability among pioneers. Typically, pioneers are small-seeded reflecting selection for high reproductive output. Even so, seed mass may vary over four orders of magnitude among pioneers within a plant community, reflecting a second life-history tradeoff between colonization success (selecting for small seeds) and establishment success (selecting for larger seed reserves). For pioneers with limited dispersal, the probability of colonizing disturbances can be increased by maintaining populations of viable seeds in the soil. These soil seed banks may be transient, with seeds lasting a few weeks or months following dispersal, or may be persistent with seed surviving for decades. In temperate forests most seed bank-forming species are annual or perennial herbs. These are typically small-seeded species (<1 mg seed mass) that germinate in response to an increase in the intensity or red:far-red ratio of light associated with openings in the canopy or in the litter layer. In tropical forests both trees and herbs form seed banks with greater seed persistence common among the larger-seeded species (1–100 mg seed mass). Many of these species germinate in response to diurnal temperature fluctuations in the soil associated with large canopy gaps.

Changing land-use patterns have led to large increases in the abundance and distribution of many pioneer species. Many of the herbaceous pioneers that were originally restricted to forest gaps, or marginal habitats such as stream banks, have now become economically important weeds in agricultural systems. Similarly, in the tropics, clearance of old-growth forests, and abandonment of unproductive agricultural land has provided new habitats for pioneer tree species. Some of these pioneers can be quite long-lived and can produce valuable timber (e.g., teak, *Tectona grandis*; and laurel, *Cordia alliodora*).

See also: Succession.

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