Reproductive Ecology of Forest Trees

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Introduction

Plant reproductive processes encompass biotic interactions, such as pollination and seed predation and dispersal, and abiotic elements, notably disturbance that creates differential reproductive opportunities for plant groups and thereby maintains diverse forest formations.

There are several important stages in the regeneration of trees, the first of which is the allocation of resources to reproductive structures as opposed to vegetative growth. Among flowering plants, that comprise the majority of tree species, allocation to reproductive structures such as flowers, seeds, and fruit may vary enormously and may comprise a substantial portion of photosynthate. Even within plant families some trees (e.g., some dipterocarps of the genus *Shorea*) produce several million tiny flowers, while others (e.g., *Dipterocarpus*) produce only a few hundred relatively large flowers. Flower number and morphology reflect pollinator syndromes while the trade-off between seed size and number has also generated a huge variety of options for reproductive success. Beyond being a crucial step in seed production, pollination is the first of two stages by which gene flow is effected, by gamete dispersal within populations. Seed dispersal represents a second opportunity for gene flow as seeds are transported to new locations by a variety of dispersal vectors. Dispersed seed may enter a variable period of dormancy before germination and growth to seedling stages. Biotic agents of mortality acting at each of these life stages can reduce enormously the probability of ovule survival to maturity. Thus the diversity of reproductive strategies observed among trees reflects physical, competitive, and coevolutionary interactions among plants and their biotic and abiotic environments at each of these life history stages. This article describes the diversity of tree reproductive strategies in temperate and tropical forests, emphasizing flower and seed life stages.

General Reproductive Strategies

Vegetative Reproduction

Plants as sessile organisms reproduce by means of their modular architecture and their capacity for reiterative growth – indeed, all plants are potentially clonal in that each module contains both reproductive and somatic tissue. However, production of independent offspring by means of vegetative growth is rare among trees, although detached branches of willows and poplars can sprout if maintained in moist conditions. Most broadleaves can produce new stems from cut or burned stumps even when the rootstock is hundreds of years old. Trees cut specifically for this purpose are referred to as coppice and are an important management feature of many European woodlands. Some conifers can also coppice (e.g., redwoods), or sprout from burned trunks (e.g., pitch pine), but most regenerate from seed.

Fallen trees that retain some connection to the soil through roots may develop new stems from epicormic shoot production. Indeed, small-leaved lime in the UK has been referred to as practically immortal for both this reason and for its vigorous coppicing response. Similarly, broken crowns can regenerate through epicormic stem proliferation.

Some plants are able to produce seeds in the absence of fertilization by partial or total suppression of meiosis and fusion of gametes. Such a process is termed apomixis and may be widespread among tropical trees.

Sexual Reproduction

All trees, excepting tree ferns, are seed-bearing and reproduce sexually by wind or insect-mediated transfer of male gametophytes, as pollen, to ovules. The gametophytes of all seed plants are enclosed within sporophyte tissues and, unlike ferns or nonvascular plants, are no longer free-living at any stage of their life history. Fertilization occurs when male nuclei are transferred to an ovule by way of a pollen grain that has been received on a compatible and receptive stigmatic surface.

Seed plants are taxonomically separated into two primary lineages, the gymnosperms (about 770 species) and the angiosperms (some 235 000 species). The gymnosperms consist of four phyla that include conifers, cycads, gnetophytes, and Ginkgophyta (solely represented by the maidenhair tree *Ginkgo biloba*), of which only the conifers form forest trees. The angiosperms differ from the gymnosperms in that they have their reproductive structures contained within flowers. Pollen transfer in almost all gymnosperms is effected by wind (some gnetophytes and cycads may be beetle-pollinated) while the flowers of angiosperms evolved to attract insect and animal pollinators, although many angiosperms have secondarily evolved to be wind- or water-pollinated.

Coniferous gymnosperms Almost all trees within the gymnosperms are conifers and it is these that dominate the boreal forests of Eurasia and North America. Conifers have their reproductive parts aggregated in unisexual cones which may be borne on the same tree (monoecious) or on different trees (dioecious). Cones consist of numerous scales, each of which bears either two pollen sacs (males) or ovules (females). All conifers are wind-pollinated and, given the inefficiency of wind pollination, often produce huge amounts of pollen. Pollen grains consist of a reproductive sperm cell and a tube cell, and have two wings or air-filled bladders that aid transport by wind. Pollen grains landing near an ovule are drawn towards it by a drop of liquid that is absorbed into the female scale. Pollination occurs when the pollen grain penetrates the micropyle, a small opening in the integument of the ovule. Following pollination, the cone is sealed by a thickening of the scales. One of the two cells that comprise the pollen grain elongates into a pollen tube that, over a period of several months or more, eventually reaches the egg cell. Fertilization follows when the sperm cell migrates through the pollen tube to fuse with the egg. The embryo develops within a naked seed and, after a further year, the cones ripen, dry, and open to release the winged seeds. Most conifers differ only slightly from this general pattern of reproduction, although yew *Taxus* sp. is notable in that its ovules are solitary, its pollen grains lack the 'wings' of most other conifers, and its large seed develops in a fleshy red aril which ripens within a year.

Angiosperms Apart from the obvious presence of a flower, angiosperms differ morphologically from gymnosperms in that the female gametophytes are greatly reduced in size. Consequently, the process of development is much faster and more efficient. Unlike gymnosperms, the seed food store only develops after fertilization and is therefore not wasted if fertilization fails to occur. Increased reproductive efficiency is thought to have contributed substantially to the flexibility of reproductive strategies and to the current dominance and diversity of the angiosperms.

The ovules of angiosperms are completely enclosed within the carpel (hence angiosperm, meaning hidden seed), a development that may have arisen to protect the ovules and pollen from insects. A pollen grain landing on the stigmatic surface germinates and extends a pollen tube through the style to fertilize the ovule. The fertilized embryo develops within a seed that may be enclosed in a nut or fruit to attract animal dispersal agents, or may be formed so as to facilitate dispersal by wind, water, or passive animal transport. In many species seed germination is delayed as seeds enter a period of dormancy until such time as environmental conditions trigger release from dormancy. Some seeds can persist in a dormant stage for decades or even centuries and collectively form the soil seed bank. Other seeds (e.g., of the dipterocarps) are recalcitrant and germinate very soon after dispersal, though the seedlings may persist for many years in deep forest shade to form a seedling bank until a canopy gap forms, allowing renewed vigorous growth.

Pollination of Angiosperms

Pollination is effected by a variety of biotic and abiotic pollination vectors, with biotic pollinating agents predominating in tropical zones and wind being relatively more significant in temperate regions. About 98% of all flowering trees in tropical rain forests are animal-pollinated; bees are by far the most important pollinators (**Table 1**). Pollination by beetles, hummingbirds, and small bees is more common among subcanopy trees but even here medium to large bees form the dominant pollinator group. Wind pollination is rare and confined to very few canopy and understory trees.

Pollination by Vertebrates

Pollination by vertebrates in north temperate forests is virtually nonexistent, but it is relatively common in tropical forests, and is also important in south temperate zones in Australia and South Africa. Among vertebrates, bats and birds are the principal pollinators, although some trees may also be

Table 1 Frequencies of different pollination systems among canopy trees at La Selva, a lowland tropical rainforest in Costa Rica

Pollination vector	Percentage of tree species	
	Canopy (n = 52)	Subcanopy (n = 112)
Medium-large bees	44.2	19.6
Small diverse insects	23.1	12.5
Moths	13.5	16.9
Small bees	7.7	17.0
Bat	3.8	2.7
Wasp	3.8	4.5
Hummingbirds	1.9	5.4
Butterflies	1.9	6.2
Beetle	0	10.7
Wind	0	3.6

Data from Bawa KS, Bullook SH, Perry DR, Coville RE, and Grayum MH (1985) Reproductive biology of tropical lowland rainforest trees. II. Pollination systems. *American Journal of Botany* 72: 346–356 and Bawa KS (1990) Plant–pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21: 399–422.

pollinated by various nonflying mammals. Pollination by bats is particularly common among the Bombacaceae, and the genera *Parkia* (Mimosaceae) and *Bauhinia* (Caesalpiniaceae). Flowers of bat-pollinated trees open at dusk or soon after and are typically large, white or pale, have a musky odor, and produce copious amounts of nectar. While this is energetically costly, gene flow by bat-dispersed pollen is potentially very great.

In the neotropics hummingbirds are the main avian pollinators and feed exclusively on nectar, although they primarily visit understory shrubs rather than trees. Their Old World counterparts are sunbirds which visit a wide variety of trees but also feed on insects. Bird-pollinated flowers are typically red and contain plentiful but dilute nectar, so much so that showers of nectar are brought down when shaking the branches of the coral tree *Erythrina* spp.

Pollination by Invertebrates

Bees and wasps   Bee pollination is particularly important among canopy trees in tropical forests. Two groups of bees may be distinguished as pollinators: medium to large bees, including honeybees and a variety of solitary or semisocial bees; and small, mostly social bees of the Apidae family, notably the sweat bees. Large bees appear to predominate in forest canopies while small bees tend to visit understory trees (**Table 1**), though this pattern breaks down in more open dry forest formations. A diverse array of wasps and other hymenopteran insects visit generalized flowers on trees in taxa such as Anacardiaceae and Burseraceae, but their role is minor relative to other insect pollinator groups, the exception being agaonid wasps that are specialist pollinators of fig trees (*Ficus*, Moraceae).

Moths and butterflies   Moth pollination, particularly by sphinx moths, is prevalent across the tropics and includes trees within the genera *Dipterocarpus* (Dipterocarpaceae) and *Plumeria* (Apocynacea). Moth-pollinated flowers typically open at dusk and are usually pale with deep corolla tubes that emit strong sweet scents. Moths can carry substantial amounts of pollen and cover great distances between successively visited plants, making them good pollinators of widely spaced trees. Butterflies, by contrast, are rare pollinators of trees, although they do pollinate certain species-rich genera, e.g., *Eugenia* (Myrtaceae).

Beetles   Beetle pollination is common among Anonnaceae, Lauraceae, Myrtaceae, and Palmae. A range of beetles visit a wide variety of floral morphological forms, although most beetle-pollinated flowers open at dusk and emit strong odors.

Beetles generally consume pollen and flower parts rather than nectar. In Australian rainforests up to one-quarter of all plants may be pollinated by beetles, and such plants are found in all forest strata and include trees, shrubs, and epiphytes.

Flies   Flies certainly contribute to the pollination of understory forest shrubs but are probably of minor importance in the pollination of forest trees. Exceptions include cacao (*Theobroma cacao*), pollinated by midges.

Thrips   The synchronously flowering dipterocarps in Asian rainforests are thought to be primarily pollinated by thrips, tiny insects that can undergo massive population increases within a very short time in response to the sudden availability of floral resources generated by a mass flowering event. Dispersal of thrips is likely to be facilitated by winds above the forest canopy. Thrips also pollinate many species of Myristicaceae.

Wind Pollination

Other angiosperms have reverted to wind pollination and consequently have much reduced flowers, as visually attractive flowers are no longer necessary for pollinator attraction. While wind is ever-present, it is not a selective pollinator and is consequently inefficient over large distances. Wind pollination is therefore favored in species-poor forests where conspecifics are closely spaced. Wind-pollinated plants are associated with abundant pollen production and synchronous mass flowering events to ensure successful pollen transfer. To maximize the probability of catching randomly drifting airborne pollen, flowers are placed at the outermost edges of the crown or in pendant catkins to maximize exposure to wind, and stigmas are usually well exposed and have large surface areas.

Wind pollination is associated with temperate forests and dry, or seasonally dry, habitats where animal pollination vectors are comparatively rare and where rainfall rarely hinders pollen dispersal. The temperate forests of northern mid-high latitudes are dominated by species such as oak, beech, and birch, that rely on wind pollination. In the temperate rainforests of Chile, New Zealand, and the Pacific Northwest of America, wind pollination is again common, despite the wet climate. Open forests and savannas are particularly well represented by wind-pollinated trees. In the dense vegetation of a rainforest wind pollination is usually restricted to emergent coniferous trees (e.g., *Araucaria* and *Agathis*) and to trees occurring on ridge tops (*Balanops australiana*, *Nothofagus*). Wind pollination does, very rarely,

occur in the rainforest understory among more specialized angiosperm groups, including Euphorbiaceae, Pandanaceae, and Palmaceae.

Breeding Systems and Incompatibility

Individuals of most tree species bear both male and female reproductive organs, and often within the same flower. Consequently there is a high risk of self-fertilization that would restrict genetic mixing and seed viability through inbreeding. Breeding systems have therefore evolved to limit or prevent self-fertilization. Plant breeding systems range from obligate outcrossing to predominantly selfing. This range of systems is not distributed randomly among species, as woody plants are usually associated with outcrossing and annual herbs with selfing. Outcrossing can be achieved or enhanced by spatial separation of male and female flowers, either on different trees (dioecy) or within individual trees (monoecy), or by temporal separation of male and female reproductive organs by nonoverlapping maturation times (dichogamy). Where male and female reproductive parts are not separated, physiological self-incompatibility mechanisms that block pollen tube development may exist. Other strategies include selective abortion of selfed seed. There may be considerable variation in the reliability of self-incompatibility across and within species, and the proportion of selfed seed can be highly variable among individuals within a population.

Trees in both tropical and temperate systems are mostly outcrossed, although the mechanisms by which this is achieved vary between these regions. Temperate trees are mostly self-compatible, possibly an evolutionary response to unpredictable effectiveness of the pollination vector, and selfing is limited by the spatial separation of male and female flowers. Many conifers, for example, are monoecious and seed is mostly outcrossed. Tropical trees generally have hermaphroditic flowers but are mostly incapable of self-fertilization due to physiological self-incompatibility mechanisms. Spatial separation of flowers by dioecy is also common among tropical species. In tropical lowland forests of Guanacaste in Costa Rica, for example, 22% of trees are dioecious and a further 54% are physiologically self-incompatible.

Seed Morphology and Dispersal

Seed Size

Seed size varies among flowering plants from less than 10^{-6} g in orchids to more than 10^4 g in coco-de-mer. Small seeds can be produced in greater numbers but have less chance of establishing successfully, owing to fewer stored reserves, and size is largely a trade-off between these two selection pressures. This trade-off is subject to variation in response to physiological, ecological, and environmental conditions acting on seed and seedlings. Heavy predation of seeds, for example, near parent trees favors dispersal, which may increase or decrease seed size depending on the dispersal agent involved. The requirement for light for early seedling growth can also be mediated by seed size – large seed size confers an advantage to seedlings in low light owing to the greater reserves available to them, though this advantage is only apparent during the earliest stages of growth. Nevertheless, larger seeds are generally found among trees whose seedlings establish in shaded environments, as for tropical canopy trees.

Seeds that are mammal- or gravity-dispersed tend to be large while bird- and wind-dispersed seeds are relatively small. Thus in successional forest habitats there is increasing abundance of large-seeded species with age from the initial disturbance. This is associated with the increasing size and slower growth rates of the colonizing plants with time, and a shift from wind or bird dispersal, typical of many pioneer species, to mammal or gravity dispersal associated with canopy and emergent trees. Despite these generalizations, much variation in seed size remains unexplained and other variables, such as antiherbivore strategies, mycorrhizal associations, or soil type, might also affect seed size among forest tree species.

Seed Dispersal

Seeds are designed to be dispersed away from the parent plant to escape predation and seedling mortality near the parent, to colonize spatially and temporally ephemeral habitats, or to locate microsites suitable for establishment and growth. However, most seeds are not dispersed far from the parent. As such, seeds have evolved a variety of morphological forms to maximize dispersal efficiency by way of biotic dispersal vectors, including vertebrates (bats, rodents, and other mammals, birds, and fish), invertebrates (ants and beetles), and abiotic vectors such as wind and water.

Understory herbaceous plants in temperate and tropical forests often have barbed or sticky fruit that adhere to the coats of passing animals. Most animal-dispersed seed rely on active dispersal by offering animals a food reward in the form of a fleshy fruit. Such fruits have developed traits, such as color or odor, that increase their attractiveness to the appropriate dispersers. In tropical forest communities 50–75% or more of tree species produce fleshy fruits adapted for dispersal by birds or mammals. Many

temperate forest trees are also vertebrate-dispersed, although some, such as oak, lack obvious adaptations to attract dispersers. Plant–animal dispersal interactions, as for plant–pollinator interactions, tend to be generalized, with few being highly species-specific.

Abiotic dispersal mechanisms include gravity, wind, and water. Gravity-dispersed seeds simply fall beneath the parent tree, though the fruit may be adapted to drift laterally as it falls (as for dipterocarp trees). Wind-dispersed plants are relatively more common in dry, exposed, and open habitats. In tropical moist forests where wind dispersal is relatively rare, it is generally found among canopy trees or vines rather than understory plants. Dispersal by water is common among gallery forests and seasonally inundated floodplain habitats. Seeds of some coastal trees, notably coconut, are even dispersed on ocean currents.

Seed and Seedling Banks

The seeds of many plants undergo a period of dormancy which may be very short (on the order of a few days) or prolonged (several decades or more). The advantage of dormancy is that it allows a plant population to escape from certain environmental disturbances or temporally adverse conditions. Early successional and pioneer plants tend to have delayed seed germination until such time that light or water conditions become favorable for growth. The seeds remain in the soil, forming a soil seed bank, and only germinate when an appropriate environmental cue, such as increased light brought about by a tree fall, is received. Dormancy is also an effective strategy to avoid seedling desiccation during the dry season. Dormancy can be imposed by other traits, as in seeds carried by wind that are typically desiccated to facilitate dispersal and therefore need rehydration prior to germination. Similarly, dormancy of seeds dispersed by vertebrate consumption may be necessary to survive passage through animal digestive tracts.

In the deep shade environment of a tropical forest understory, intense competition for light favors seeds that germinate immediately, leading to the establishment of seedling banks. Although these seedlings have very slow growth, they are also best placed to take maximum advantage of light upon the formation of a canopy gap.

Natural Disturbance

Disturbance is a natural feature of all forest environments. Natural disturbances vary greatly in size and frequency, and they shape forest structure and composition. Disturbance creates new opportunities for propagules to establish and grow, from vertebrates turning over soil and leaves to expose a germinating seed to light, through tropical canopy gap formation following treefalls that release seedlings from light inhibition, to extensive windthrows of balsam fir forests that initiate regeneration waves of saplings. Regeneration of many forest trees is usually confined to gaps, and composition of the regenerating community is a function of gap size, shape, and location, and the coincidence between gap formation and a fruiting event. The establishment of some tropical trees, such as mahogany, is entirely dependent on large clearings created by high winds and subsequent fires, while seedlings of other species simply need canopy openings for further growth. Yet other species, such as beech and hemlock, are shade-tolerant and regenerate under closed canopies.

Natural fires occur in almost all forest systems, although coniferous and dry deciduous forests are more fire-prone. Conifers usually burn readily and, although some are well protected by thick bark, intolerant species survive by producing many widely dispersed seeds that germinate and grow rapidly following a fire. Some species, such as lodgepole pine, even need fire to stimulate the release of seeds, which then fall on to soil fertilized by ash and which is free from other competing species. Fire is an important ecological factor in many north temperate forests and serves to maintain forests in a non-equilibrium state. Fire-prone coniferous woodland, for example, develops a broad-leaved understory which, in the absence of fire, will eventually replace the conifers.

Recruitment to seedling cohorts is frequently episodic as seed production, dispersal, and the breaking of dormancy are often facilitated by unusual or periodic climatic and disturbance events. Mast seed production is widespread among tropical and temperate trees and may be initiated by El Niño climatic events (e.g., dipterocarps in Southeast Asia) or fire (e.g., ponderosa pine in the Rocky Mountains of North America). Irregular heavy seed production may satiate seed predators, allowing for at least some seed survival, or may simply be a response to conditions that are optimal for germination. Alternatively, an episodic pattern of regeneration may be imposed at a later regeneration stage should, for example, a pest or disease outbreak cause the mortality of all young saplings.

Conclusion

Successful reproduction of trees is a function of several sequential ecological processes, pollination

and fertilization, seed development and maturation, seed predation, dispersal and germination, and seedling growth, many of which are mediated by mutualistic and antagonistic interactions with animals acting as pollinators, dispersers, seed predators, and leaf herbivores. These processes unfold in the context of the disturbance regime, which creates differential opportunities for propagules and seedlings. Quite different reproductive strategies exist among forest trees within and among communities. The most obvious is the overwhelming dependence of tropical trees on animal interactors for pollination and seed dispersal, compared to temperate species, for which abiotic agents are comparatively more important. Such differences in pollination and seed dispersal vectors are reflected in the efficiency of gene transfer and patterns of gene flow, and information about seed production and gene flow is critical for the design of forest management plans and strategies for the conservation of plant genetic resources.

Currently, there is little information about the pollinators and seed dispersers of many forest trees, or indeed about the importance of flower and fruit resources to animal communities. Even basic knowledge about factors that regulate seed production, viability, dormancy, and germination for many tree species remains to be discovered, and only recently have we begun to understand the importance of natural disturbance in shaping plant communities through differential reproductive success. Our ability to rehabilitate, conserve, and manage existing forests will continue to be improved by continued research on tree reproductive ecology within the context of the natural disturbance regime.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation; Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Tree Physiology**: Physiology of Sexual Reproduction in Trees.

Further Reading

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Forest Canopies

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Importance

The word canopy is derived from the Latin *conopeum*, describing a mosquito net over a bed. For canopy researchers in many tropical and temperate forests, this derivation is all too fitting. Forest canopies are home to perhaps 50% of all living organisms, many of which are uniquely specialized for life in the treetops and seldom, if ever, venture to the ground below. The canopy is the photosynthetic powerhouse of forest productivity which fuels this spectacular diversity of species. Over 90% of photosynthesis occurs in just the upper 20% of tree crowns. Here, over 60% of the total organic carbon in forests is fixed and stored, forming an important buffer in the global carbon cycle. Other ecophysiological processes within tree crowns mediate the flow of nutrients through soil, regulate nutrient cycling processes that affect site productivity and the biomass distributions of plants and animals, as well as moderate the rates of transpiration and CO_2 exchange to the atmosphere that are crucial components of regional climatic circulation. In a very real sense, forest canopies form the substrate, the buffer, and the catalyst for interactions between the soil and the atmosphere. In this article, we highlight many aspects of forest ecosystem dynamics that are controlled directly by canopy processes. More importantly, however, detailed understanding of the structural and functional complexities of forest canopies has advantages beyond the scale of ecosystem functioning of local forest stands. Forest canopy dynamics are now incorporated as vital variables when modeling forest responses to the three most pressing issues in global change biology: the maintenance of biodiversity, the sustainability of forest production, and the stability of global climate.

Definition

For much of the early development of canopy biology, the nature and limits of forest canopies have been poorly defined. In a functional sense, the forest canopy includes all aboveground plant structures and the interstitial spaces between them, which collectively form the interface between the soil and the atmosphere. Historically, there was a tendency to use