L1 ECOLOGY OF FLOWERING AND POLLINATION

Key Notes

The dual function of flowers

Cross-pollinating hermaphrodite flowers must disseminate pollen and receive pollen from other flowers, these two functions involving different adaptations. The functions are separated in unisexual flowers.

Seed and fruit set

There is great variation in size and resource input into fruits and seeds by different plants. In some the resources of the parent plant limit seed or fruit set whereas in others the amount of pollination is limited. Many plants are limited by a combination of factors.

The dissemination of pollen

Wind-pollinated plants produce large quantities of pollen. Pollinating animals have different abilities to carry pollen with some more effective than others. Some plants have precise adaptations for particular pollinators. Pollen is deposited in decreasing quantity on the stigmas of up to the next thirty flowers visited.

Effective fertilization

Once pollen has reached a stigma there may be competition between pollen grains with some pollen tubes growing faster than others and potentially complex interaction with the styles. There may be selective abortion, particularly of selfed seeds.

Self and cross fertilization

Hermaphrodite flowers always have the potential for self-pollination and some plants are habitually self-fertilized. Advantages of self-fertilization are assured seed set, less resources needed for flowers and, after some generations with high mortality, identical seedlings with no new unfavorable combinations. Disadvantages are lack of variation allowing no adaptation to changing environments or pathogen attack and inbreeding depression. Inbreeding depression from self-fertilization is manifest in nearly all plants studied at some stage in the life cycle.

Related topics

The flower (D1)
Breeding systems (H2)

Polymorphisms and population genetics (L4)

The dual function of flowers

Most flowers are hermaphrodite and perform two functions: disseminating pollen to other flowers, and receiving pollen to fertilize their own ovules. These functions involve slightly different adaptations. Here we consider a cross-pollinating hermaphrodite plant; self-fertilizing plants are considered later and unisexual flowers (Topic H2) have separated the functions. There is a selective advantage for a flower to disperse its pollen as widely as possible to give it the maximum chance of siring seeds. In its capacity as a female parent the flower must receive enough pollen for maximal fertilization, but the plant must also provide enough energy and nutrients for the formation of seeds and fruits.

If nectar is the food reward for insect visitors this must be produced in sufficient quantities and of suitable concentration to attract insect pollinators, and one plant species may have to compete with coexisting species for the attention of visiting insects. More insect visits will generally lead to greater pollen dispersal but not necessarily greater seed set (see below).

Seed and fruit set

The success of a plant as a female parent is easier to measure than its success as a pollen donor, since the plant forms its seeds on the plant. Plants differ greatly in the size and number of seeds and fruits produced and how many pollinations they require for maximal seed formation. Plants with many seeds per fruit may require few insect visits for full seed set if they are effective pollinators. The most extreme example is the orchids which produce pollen in sticky pollinia (Topic D1) and have thousands of microscopic seeds per fruit. They require just one successful insect visit per fruit so need attract much smaller numbers of pollinators than other plants. In contrast, members of several families, such as the daisy family and grasses, have one-seeded fruits, so each flower or floret must be pollinated separately. The amount of resources required from the parent plant is highly variable. Small fruited species such as grasses and orchids require few resources compared with those with large fruits such as coconuts (here mainly the seed) or water melons that set only a few fruits, each with a large amount of resources. On some plants with large fruits, such as many fleshy-fruited trees, only a small proportion of flowers can mature into fruits because of shortage of space.

In most flowers, seed set is limited by a combination of the amount of pollination and resources available for the developing seeds. In large-fruited plants, the resources from the plant limit fruit set and it is well known that many plants have a poor fruiting year after a good one, suggesting that there are insufficient resources for two consecutive years of high yield. Pollination may also limit fruit set, and in many studies in which the amount of pollination has been increased experimentally, more fruit has been set. This has often led to poorer growth or less fruit set the following year even in quite small-fruited plants, so clearly these two factors interact.

In dioecious plants (Topic H2) female flowers are frequently produced in smaller numbers than male flowers and there is also a smaller floral display suggesting that limitation of resources is important.

The dissemination of pollen

For pollen to spread to its maximum, many pollinator visits or effective spread of the pollen by wind is required. Few resources are needed for the pollen grains compared with fruit and seed set, and attraction of numerous insects to a flower will mainly enhance pollen dissemination. This suggests that, in many animal-pollinated species, much of the floral display is in relation to a flower's male function. In wind-pollinated flowers, wide dissemination of pollen is assured by the plants producing an enormous quantity on fine days, as hay-fever sufferers know only too well.

In animal-pollinated flowers the quantity and nature of the pollen depends on the animal. The furry bodies of many bees, moths and bats, as well as the feathers of birds can carry much more pollen than the smooth bodies of flies, some bees or the thin proboscis of a butterfly. They are likely to be more efficient as pollinators as a result, but their efficiency will also depend on their behavior. For instance, bees forage systematically, visiting adjacent flowers, often on the same plant and sometimes crawling, with occasional long flights.

They frequently groom themselves to remove the pollen on their bodies. Butterflies take mainly longer flights between flower visits so potentially take pollen further, and vertebrates are active fliers but require more nectar resources. Different species within each pollinator group behave differently with, e.g. some birds and some bees being territorial and some pollinators making a hole in the flower by the nectar, potentially avoiding the anthers. Different flowers are adapted to particular pollinators in the way their flowers are presented and the quantity and position of the pollen and nectar.

Once pollen has been picked up from a flower it may be deposited on many subsequent flowers in diminishing quantity, depending on the pollinator, with pollen being recorded travelling to 30 or more flowers visited (*Fig. 1*). In a self-incompatible plant the first flowers visited may be on the same plant or an adjacent sibling or offspring which will be incompatible with it, so pollen flow further than that may be essential for effective fertilization.

Effective fertilization

Once pollen has reached a compatible stigma it may be in competition with other pollen grains for fertilization. Pollen grains vary in their effectiveness in growing pollen tubes through genetic differences or because of where they land on the stigma and through interaction with other pollen tubes growing down the style. There may be different interactions between certain pollen grains and the stylar tissue affecting which pollen fertilizes the ovules. Vigorous pollen tube growth may lead to vigorous seedlings. Once the ovule is fertilized, if resources are limiting seed set, there may be selective abortion of the ovules. Some plants abort self-fertilized seeds selectively and may abort weaker cross-fertilized seeds, though evidence of this is limited.
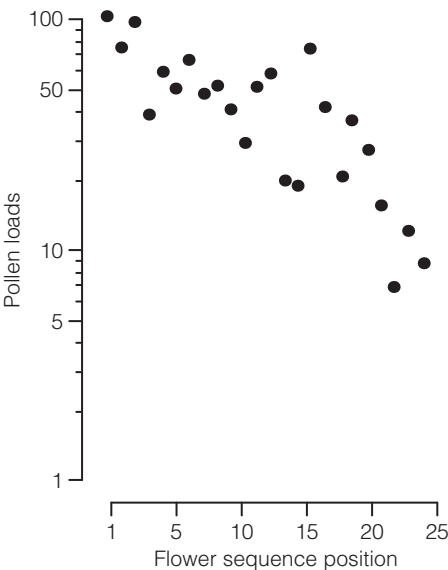

Fig. 1. The number of pollen grains deposited by bee pollinators on stigmas of successive flowers visited on the larkspur Delphinium nelsonii. *(Redrawn from Waser NM,* Functional Ecology *1988; **2**, 41–48).*

Self and cross fertilization

Flowers originally evolved for cross-pollination, but there is always the potential for self-pollination in a hermaphrodite flower and some species can produce full seed set from self-fertilization (Topic H2). They do not require any of the adaptations for pollen dissemination or receipt and many have small flowers with a limited amount of pollen. A much larger number of plants are self-compatible and can self-fertilize, although they normally cross-fertilize. In these, self-fertilization frequently occurs only if cross-fertilization has failed, often with the pollen tubes of a plant's own grains growing slower than those from another plant, or the pollen only reaching receptive stigmas as the flower ages.

The advantages of self-fertilization are that no external pollinating agent is needed so flowers can be small, providing no attractive parts and producing only enough pollen to fertilize their own ovules. Seed set is assured, and with fewer resources being used in flowers, it may be able to flower at an earlier developmental stage (Topic H2). This has particular advantages in colonizing situations and in ephemeral habitats.

Constant selfing will mean that the plant loses much of its genetic variation and, after a few generations, will be **homozygous** at almost all its genes, i.e. each gene copy will be identical. This can lead to deleterious genes being manifest and much mortality in the early generations, but once any deleterious genes have disappeared the plants will be all identical. This means that only proven successful plants will be produced and no seeds are 'wasted' on poor gene combinations. Many habitual selfers are polyploid so have several copies of each gene anyway, avoiding some of the problems of homozygosity.

The disadvantages of self-fertilization are the lack of new gene combinations leading to much reduced variation, dependent only on new mutations. This means that they may not be able to adapt to a changing environment, particularly important in developing resistance to herbivores or pathogens or in colonizing new sites. It also means that they never have the advantages of hybrid vigor which probably arise from a plant having two different forms of certain genes in each cell (Topic M5).

In plants that may cross or self-fertilize there is nearly always a disadvantage to selfing. This may be manifest in lower seed set, smaller or less resistant seeds, difficulties in germination, ability of the seedling to establish, vigor and survival of the offspring or their ability to reproduce or any combination of these features. This is known as **inbreeding depression**. Even in most habitual self-fertilizing plants studied, experimental cross-pollination has led to more vigorous plants than selfing and almost all plants do occasionally cross-fertilize.

L2 SEED ECOLOGY

Key Notes

Dispersal by the elements

Seed size is a compromise between small size for dispersal and large size for germination and establishment. Wind-dispersed seeds may be tiny, often with specialized germination requirements, or have an attached sail. Some other plants have a flexible stalk but no adaptations in the seed. Many fresh water and coastal plants have seeds dispersed by water.

Fruit and seed eating

Seeds of fleshy fruited plants are dispersed internally by vertebrates and many have a resistant seed coat. Fruits relying on specialist frugivores often have nutrient-rich hard fruits, whereas smaller sugar-rich fruits are typical for opportunist frugivores. Some nutrient-rich seeds, particularly of trees, are hoarded by rodents and birds which leave some to germinate. Ants disperse some seeds a short distance mainly into safe germination sites.

Other modes of dispersal

Seeds with burs or hooks are effectively dispersed externally on mammals or birds. Some plants have explosive fruits that scatter the seeds. Many plants have no obvious adaptation for dispersal but high winds, floods and transport in mud on animals' feet must be very important for long-distance dispersal. Some rainforest trees have almost no dispersal powers.

The measurement of dispersal

Effective dispersal is hard to measure. Initial dispersal is mainly close to the parent with rapid tailing off, but effective dispersal requires the seed to land at a safe germination site. The floras of oceanic islands have many bird-dispersed seeds, with fleshy fruits on wet islands, mainly burs on dry islands, and few wind-dispersed seeds, suggesting that bird dispersal is the most effective for long distances.

Dormancy

Seeds vary in their dormancy from days to centuries. Many plants of mature communities in predictable climates have no or little dormancy, whereas pioneer plants and those in unpredictable climates may have long dormancy. Dormancy may be (i) innate with all seeds requiring some treatment before germinating; (ii) enforced in unfavorable conditions; or (iii) induced by initial unfavorable conditions and then requiring particular conditions to germinate. Dormancy is caused by a thick seed coat or chemical constitution and is broken by abrasion or heavy rain or temperature extremes.

Variation in seeds

Some species produce seeds of constant weight but in others it varies considerably. Larger seeds are associated with dry conditions and small seeds with increased dormancy. Some plants produce more than one type of seed which differ in dispersal and dormancy characteristics.

Seed banks	Normal soils contain 100–100 000 seeds m^{-2}. In a frequently disturbed community these will overlap with species present, but in a mature community they may overlap infrequently or not at all, consisting mainly of pioneer species. The seed bank will vary seasonally with fruiting seasons and degree of dormancy. In seeds with long dormancy, generations will overlap. A few plants in fire-prone areas can retain dormant seeds on the plants for decades.

Related topics

The seed (D3)
Fruits (D4)

Seed development, dormancy and
  germination (H4)
Regeneration and establishment (L3)

Dispersal by the elements

The large differences in seed size between species (Topic D3) reflect differences in their modes of dispersal and germination. Seeds may be dispersed by **wind**, **water** or **animals**. Small seeds are likely to travel further than large ones and can be produced in larger numbers at a similar cost to the plant, but larger seeds contain more nutrient stores for germination and rapid establishment. Seeds are a compromise between these opposing selection pressures.

Some seeds that are mainly wind dispersed are tiny, such as those of orchids, heathers and some parasitic plants, and rely solely on their size for effective dispersal. These plants often produce enormous numbers of seeds but many have specialized **germination requirements** involving mycorrhizal fungi (Topic M1) or, for the parasites, a host plant, and the seed has few stored nutrients. Other wind-dispersed seeds or small fruits (Topic D4) have a cottony **sail**, such as many members of the daisy family, willows, Malvaceae such as cotton and others. Other seeds are attached to a papery winged fruit (known as a **samara**) which can be caught by the wind. Many trees such as the maples and birches with larger seeds than those with cottony sails, have these. Many others have no particular organs to aid wind dispersal but the seeds may be transported at least a short way by the wind, particularly if the fruiting stalk is long and flexible. Some have dry fruits opening at or near the tip so seeds will mainly be shed when there is a powerful wind.

Many freshwater plants have seeds dispersed by **water**, in contrast to pollen which is rarely water-dispersed, and many coastal plants have seeds that are partially resistant to salt water so they can drift with **ocean currents**. Many species that occur by coasts are widespread in distribution and colonize islands easily.

Fruit and seed eating

Animals disperse seeds in several different ways. In those plants with **fleshy fruits** (Topic D4) vertebrates, usually birds or mammals, ingest the seeds and they may pass through the digestive tract. Many of these seeds have a thick resistant seed coat and may germinate more freely after passage through a vertebrate gut. Passage through a gut can take from a few hours to days or even weeks and dispersal may be most effective, as shown by the fact that there are many fleshy-fruited plants on oceanic islands. Some fleshy-fruited plants have a seed that is discarded or regurgitated rather than ingested. Fruits dispersed by specialist **frugivorous birds** frequently have a different chemical composition from those attractive to opportunists, with much more protein and fat and often a larger seed. Opportunist frugivores take softer sugar-rich fruit and some

damage the seeds. This is compensated for by large numbers of fruit produced with much lower nutrient investment in each.

Some **nutritious seeds**, particularly those of trees, are themselves a food source for vertebrates, particularly rodents and some birds such as jays and other members of the crow family. Some of these animals store the seeds, often burying them as a long-term food supply, after which they may not need them or they may forget where they have put them or may even be killed before they return.

Ants can be important seed dispersers and seeds dispersed by ants often have a nutrient-rich body attached to them which the ants remove once the seed is in the nest, before discarding the seed to a refuse pile or leaving it outside. The distances of dispersal are short and the main advantage is thought to be that the seeds cease to be so vulnerable to predation and are taken to a good germination site.

Other modes of dispersal

Seeds may be transported **externally** by vertebrates. Some plants have seeds with spikes or hooks formed by the fruit or other floral organs which attach themselves to fur (or clothing), such as those forming **burs** or awned grass fruits (Topic D4). Some of these may be dispersed mainly by one particular species of mammal, and may be adapted in some way to it. This can be most effective as a dispersal mechanism with long distances being covered and some colonizing oceanic islands.

Some plants have an **explosive** fruit which throws the seeds out, such as some legumes and balsams, although the distances covered are likely to be short and the seeds may have other mechanisms of dispersal as well, e.g. by ants.

For many seeds with no obvious form of dispersal, a chance strong wind or **flood** may transport them for some distance and many are transported in **mud** adhering to the feet of mammals or birds. Many of these seeds can remain dormant for months or years increasing their chances of dispersal. Frequently, dispersal by these methods will be distant and may be the most important for the future of the species, but is the least easily studied.

Some plants, particularly rain forest trees, have large seeds with no clear dispersal mechanism and almost no dormancy. In these, dispersal is extremely limited and they often have a restricted natural distribution and do not colonize islands.

The measurement of dispersal

True effective seed dispersal is notoriously hard to measure since, if a seed can lie dormant, chance dispersal may happen at any time over a long period. Initial dispersal is easier to measure. Studies on plants that are not dispersed by animals suggest that the great majority of seeds land close to the parent with a rapid falling off of numbers with distance (*Fig. 1*), but this is unlikely to reflect the **effective dispersal** unless the plant is in a new area and can colonize densely. A seed must be dispersed to a **safe site** for germination to be effective and, for many, this will not be immediately beside the adult. Safe sites may be common or infrequent and, if infrequent, at least a few seeds must disperse a long way. Colonizing species in particular must have effective long-distance dispersal.

We can infer the effectiveness of different dispersal types by examining the floras of remote islands. One remarkable fact is that, although some island plants are wind-dispersed and probably arrived by wind, the number is quite small and wind dispersal is rarer than on continents. This is underlined by the
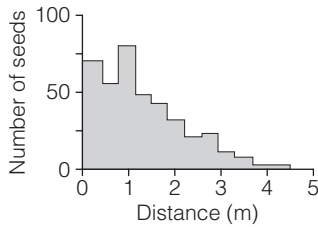
Fig. 1.   Initial seed dispersal from the herb Phlox pilosa. *(Redrawn from D.A. Levin and H.W. Kerster, Local gene dispersal in* Phlox. Evolution *1968;* **22***, 130–139.)*

fact that the most remote islands have the fewest wind-dispersed species. The commonest means of seed dispersal on oceanic islands is by birds and they appear to be the most effective long-distance seed vectors. Many plants on wetter islands have small fleshy fruits. On dry islands there are many burred plants, perhaps through shortage of water for fleshy fruits, and colonization appears to have come through external transport by birds. Sea drift is important for coastal plants. Chance events such as storms probably play an important part in driving the birds there since successful colonization needs to have happened only once in every few thousand years on average to account for the present floras, though much of it is likely to have happened in the early years.

Dormancy   Seeds vary considerably in their ability to go dormant. Dormancy in some can last only a few weeks or even days whereas in others it can last centuries. There are some relationships with climate and biome. Dormancy may be caused by the presence of a thick seed coat or by inhibitory compounds that can be broken by appropriate conditions (Topic H4). Trees of the tropical rainforest characteristically do not have dormant seeds and these will die after a few weeks, though there are exceptions. Some mangrove trees show no dormancy whatever and have seeds that germinate before they disperse from the trees; these possess a radicle that plants itself in the mud on release from the parent. In temperate zones many seeds go dormant for a few months but no longer. In contrast, ephemeral plants in deserts, many agricultural weeds and many pioneer species everywhere have seeds that can remain dormant for many years. In general, plants from a predictable climate and environment have less dormancy than those in unpredictable climates and the dominant plants in a mature community have less dormancy than colonizers.

Dormancy may be **innate**, in which case the seed requires a period of dormancy even in good conditions for germination (Topic H4). This is most clearly seen in many temperate plants that have a requirement for chilling before they will germinate, known as **vernalization**, and for seeds of fleshy fruits which require passage through a gut. Since many mammals and some birds across the world have become extinct, this latter requirement has proved to be a most unfortunate adaptation for some plants: one near-extinct plant from Mauritius has seeds that require passage through the gut of a dodo; some tropical American plants have seeds adapted to the extinct giant ground sloths. Other animals can sometimes provide a substitute but often germination is less and dispersal patterns will be different.

Dormancy can be **enforced** on seeds in unsuitable conditions such as waterlogging or lack of light and many seeds can be kept dormant in a cold dry

atmosphere for much longer than in other conditions, a most useful fact for plant nurseries. Dormancy can be **induced** following an initial unfavorable period. These seeds will germinate immediately on release from the parent, e.g. in light or dark, given good conditions, but following a period in unfavorable conditions, they will germinate only in the light. There may also be **annual cycles** in the degree of dormancy of particular species, often giving maximal germination in particular seasons.

Variation in seeds

Seed size and weight can be remarkably constant in some species despite different sizes of adults growing in different conditions; the 'carat' measure in jewellery is named after the seeds of the carob tree, *Ceratonia*, because they were used as jewellers' weights. Other species vary more depending on conditions experienced by the adult, with the weight frequently declining through a flowering season or varying depending on daylength or growth conditions. Smaller seeds frequently show greater dormancy than larger ones and plants growing in dry places often have larger seeds than those in wet places, perhaps because rapid growth is important to avoid drought. In some species there may be up to a 100-fold difference in weight between seeds on one plant. In grasses and composites, and perhaps others, the position of the seed within the inflorescence determines its size, shape and dormancy, and some species have two totally different types of seed (*Fig. 2*). In these, the seeds with the greater dispersal powers have less dormancy and it seems that these species can disperse in time and space using the different types of seeds.

Seed banks

Seeds that remain dormant in a soil build up a seed bank. Normal soils contain 100–100 000 seeds m^{-2} of surface, the higher numbers present in soil that is frequently disturbed. Usually, a seed bank consists largely of **pioneer** species and in disturbed conditions most species will be the same as in the standing vegetation. In mature communities, the seed bank is quite different in species composition from the existing vegetation and there may be almost no overlap in the species present since many species typical of mature plant communities have no or little dormancy. A full description of a plant community should include the seed bank. A seed bank will be constantly shifting and be different in constitution at different times of year, depending on short-term dormancy differences and timing of seed production. In most soils the viable seeds are nearly all near the surface although ploughing will bury some deeper.
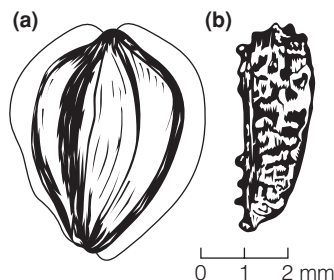

(a)   **(b)**

0   1   2 mm

Fig. 2.   Two different types of seeds of the composite Dimorphotheca pluvialis. *(a) from ray florets; (b) from disc florets. (Redrawn from Fenner M.* Seed Ecology. *1985. Kluwer Academic Publishers.)*

Dormancy creating such a seed bank allows **dispersal of seeds in time** as well as in space. The seed bank of a species with potentially long-lived seeds can consist of the seeds from many different generations of the plant and, when favorable germination conditions arise, these generations will mix. This mixing will prevent any short-term genetic change from occurring.

A seed bank can be retained on the plant itself in a few places, particularly where fire is a regular feature of the community. Some conifers and plants of Australian savannahs, such as some *Eucalyptus* trees and other genera, retain dormant seeds in dry cones or fruits on the plant. They can remain there for decades until a fire breaks the dormancy and they germinate.

L3 REGENERATION AND ESTABLISHMENT

Key Notes

Seed germination	Seeds need gaps in vegetation to germinate. Seeds may be sensitive to quality of light, temperature fluctuations, water regime in the soil, soil consistency and other factors. Different species germinate under different sets of conditions.
Initial growth	Initial growth is dependent on seed size. Larger seeds will grow more quickly than small seeds and there will be selection for the larger seeds. Seedlings from species with small seeds are often light-demanding and epigeal; those from large seeds are shade-tolerant and hypogeal.
Establishment	This stage is probably the most critical in a plant's life cycle. Gaps vary enormously in size, shape and how they are formed, and different plant species are favored in particular conditions. The timing of gap formation within a year and between years can influence which species establish. Conditions in small gaps are buffered and many seedlings are likely to appear, resulting in intense competition. In large gaps conditions will be harsher and there will be fewer seedlings. Early germination and seedling growth have great advantages.
Related topics	Plant communities (K2) Seed ecology (L2)

Seed germination

Seeds will only germinate if they reach a suitable place. Germination conditions differ greatly between different species. For a seed to germinate and begin to grow there needs to be a gap in the vegetation and in dense plant cover there is almost no regeneration by seed. But gaps are constantly present, caused by the death of established plants, by climatic factors such as frost, wind or flood and by animals through herbivory, trampling or burrowing, defecating, etc. Even in a tropical rainforest gaps are frequent (*Fig. 1*), one published figure being approximately one per hectare with a mean size of 89 m^2. Gap size and the environmental conditions within the gap will vary.

Environmental conditions in a gap are different from conditions under a vegetation canopy and these can be detected by seeds. In a gap, light reaching the soil will not be filtered through leaves to the same extent as under a canopy, giving more light with a different quality. Leaves filter out red light and many seeds respond to the ratio between red and 'far-red' light, which is filtered much less, using phytochrome (Topic G1). They germinate when the proportion of red light increases, i.e. when not under a leaf canopy, with different species responding to different levels. Shade-tolerant species do not respond like this. Some seeds respond to daily fluctuations in temperature, which will be greater by 5ºC or more within a gap with less surrounding vegetation as buffer,
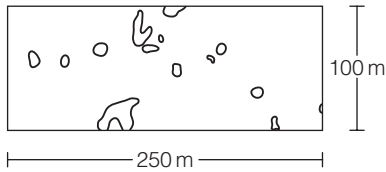
*Fig. 1.   Gaps in a primary lowland tropical rainforest in Sumatra (redrawn from E.F. Torquebiau.
J Trop Ecol 1986; 2: 301–325. Cambridge University Press).*

although certain species will only respond to temperature under particular light regimes. The parameters will also be affected by whether the seed is buried, since soil will buffer fluctuations; there will be more germination near the surface.

Conditions in the soil vary greatly. The water regime and humidity and nutrient conditions must be favorable for each species, many seeds being particularly sensitive to nitrate concentration, only germinating where it is high enough. The type of soil and nature of the disturbance will affect how a seed lies on the soil, e.g. to allow it imbibe water for germination. If a seed is buried, there is likely to be a higher CO_2 concentration than in the atmosphere and this can inhibit germination. All the factors mentioned continuously vary. Plant species vary enormously in their sensitivity to the different factors and the interaction between them, leading to great differences in germination conditions for different species.

Initial growth

The speed of initial growth of a seedling will depend on seed size. Larger seeds have more stored nutrients and often a greater proportion of carbohydrate in the seeds, and the seedlings will be able to grow more quickly than seedlings from small seeds. Quicker growth at this early stage can be critical for the seedling to get established ahead of others, so it is likely that there will be selection pressure for increase in seed size within any one species. Between species, seedlings from larger seeds are more shade tolerant and drought tolerant than small ones in the early stages of growth when dependent on the stored nutrients in the seed. Most small seeds are epigeal (Topic D3) and the cotyledons are needed as the plant's first leaves. Many of these species are light demanding pioneers. By contrast, many large seeds are hypogeal, more reliant on the seed's food stores.

There are exceptions to the generalities outlined here and there is much still to be learned about germination and early seedling growth and the relative advantages of the differences between seeds.

Establishment

The stage between initial seedling growth and establishment as an adult is the most critical stage in a plant's life cycle. It is in this stage that it will face the greatest competition from other plants and be most vulnerable to attack by herbivores and pathogens of all kinds. It is key to understanding diversity in plant communities. Many of the dominant plants in a community such as the trees or the grasses that form the sward in a grassland are long-lived, some living for centuries once established, so study of these plants in their critical stage is often impossible.

Gaps in vegetation are diverse (*Fig. 1*) and which species will establish in a gap will depend on numerous properties of the gap. Most obviously, gaps differ in size. Small gaps, perhaps created by the death of a single large plant, will remain mainly surrounded by vegetation and heavily influenced by shade and by root growth of the surrounding plants. Very large gaps, normally created by human clearance or a natural disaster, may have in their centers in which there is no influence of any surrounding vegetation, grading to their edges in partial shade and with roots from neighboring plants. The different gap conditions may be colonized by a whole range of different species. As the gap ages, conditions will change and there will be succession (Topic K2) with the new conditions favoring different species.

The timing of the creation of the gap will be critical. In nearly all communities the plants flower and set seed at particular seasons and the degree of dormancy of the seeds is variable. This indicates that a gap created at one time of year may be colonized by a different suite of species from a similar gap formed at another time. In addition, many of the long-lived plants of a community do not set fruit every year, or the fruits vary greatly in their abundance, so different years will differ.

For successful establishment it is vital for a plant to have seeds there at the beginning and for these to germinate and grow quickly. Small gaps are usually colonized by many different individuals and species. The conditions for growth are often favorable, without extremes of temperature or other weather conditions since they are buffered by the surrounding vegetation. There will be a period of intense competition. In a large gap, depending on its nature and formation, fewer seeds may be present and these are more susceptible to weather extremes, particularly drought, so if the seedling can survive its initial growth, competition will be less intense and the resulting survivors more dependent on which seeds were present at the start. Early growth may be critical for survival since the first to grow will overtop later seedlings and differences are likely to increase. There is evidence that the smaller seedlings are more susceptible to herbivore attack, e.g. from molluscs, and less resistant to pathogens too. Differences of one or a few days in germination time can be critical for survival over the subsequent years.

L4 POLYMORPHISMS AND POPULATION GENETICS

Key Notes

Visible variation	Species may vary geographically or in response to ecological conditions. Some variation is continuous, some discontinuous. When there is discontinuous variation within a population it is known as a polymorphism.
Biochemical variation	Polymorphisms in enzymes can be detected by electrophoresis and many hundreds of plants have been studied. A further range of variation is known through analysis of DNA using restriction fragment length polymorphism (RFLP) and random amplified polymorphic DNA (RAPD) techniques. Some enzymes and DNA fragments do not vary across a wide taxonomic range, but some are highly variable between individuals.
Gene flow	There are two components: pollen flow and seed dispersal, both of which are restricted in all plants. Self-incompatible wind-pollinated plants with good seed dispersal have potentially long-distance gene flow compared with self-fertile plants with poor seed dispersal.
Natural selection	The importance of natural selection in the maintenance of genetic variation is much disputed. Very little of the biochemical variation detected has a known selective basis but it may be hard to detect. Heterozygous plants appear to be at an advantage in many species, indicating that cross-fertilization will be selected for.
Population genetic structure	The total amount of genetic variation differs greatly between plants and how it is distributed between individuals within each population or between populations. This depends on the breeding system and seed dispersal and if these are restricted then restricted gene flow is the dominating influence. If the plant is self-incompatible with good seed dispersal, frequently the dominant plants, natural selection appears to be more important. Isolated small populations are frequently limited by a small number of founders or random extinction of some morphs.
Related topics	Breeding systems (H2) Populations (K4) Ecology of flowering and pollination (L1) Seed ecology (L2)

Visible variation   Individual plants in any one species vary. Marked differences between individuals are most commonly seen as geographical variations or variations in response to ecological conditions. These are known as **subspecies** if the variation appears to have no obvious ecological basis, or **ecotypes** if it is a

response to ecological conditions. Plants are only considered to be ecotypically distinct if the differences have a genetic basis. Plants can respond directly to environmental conditions by longer stems and smaller leaves in dark places for example, but if any differences remain when the plants are grown in uniform conditions it indicates a genetic basis. Many ecotypes are morphological, such as short-growing ecotypes from exposed or heavily grazed places, and some may be physiological, such as salt-tolerant ecotypes near coasts.

Variation may occur within populations too, and some plants show a range of morphological variation. This may be continuous, e.g. in leaf shape, or discontinuous such as variation in flower color or the presence of hairs on the seeds. Some of the variants, or **morphs**, occur at a low frequency of less than 1 in 20 plants, and are maintained only by the occasional recurrent appearance from mutation or rare gene combination. Many blue or purple-colored flowers have occasional white morphs at low frequency. When morphs occur at greater frequency than 1 in 20, the feature is **polymorphic** and the plant shows a polymorphism.

Biochemical variation

A great range of polymorphic variation occurs in proteins, most easily detected in enzymes using a technique known as **electrophoresis** developed in the 1970s (*Fig. 1*).

Isozymes

Isozymes are genetic variants of enzymes that have differing electrophoretic mobilities, due to changes in overall charge following amino acid substitution or changes in size of the molecule. Measurement is usually made using enzyme-specific colorimetric stains. Reliance on measurable changes in mobility means that much variation will go undetected, but the method is robust and fairly cheap. Many hundreds of plant species have been screened in this way and at least a little variation has been detected in almost all sexually reproducing plants. In a variation of this technique, **iso-electric focussing**, isozymes are focussed to a point of equal charge and migrate according to size.

Fig. 1. A diagramatic representation of a gel showing isozyme variation detected by electrophoresis. Each column derives from leaf extract of a different plant and the isozymes have migrated across the gel (upwards in this picture) in an electric current. The gel is stained to detect their presence.

Restriction fragment length polymorphism (RFLP)
Since the 1990s, DNA content has been analyzed directly. The RFLP method relies on the detection of sequence changes in DNA through the use of sequence-specific **restriction enzymes** isolated from certain bacteria. These cleave DNA at a target site; mutations at this site will prevent cleavage leading to changes in the length of the target DNA. The sites are examined by a DNA hybridization technique known as **Southern blotting** or by using a **polymerase chain reaction (PCR)** to amplify the DNA fragments which are then separated by electrophoresis and detected using probes of luminescent or radioactively marked DNA or RNA sequences that bind to the DNA.

Random amplified polymorphic DNA (RAPD)
In techniques involving RAPD, copies of DNA are generated by synthesizing fragments of DNA between two identical short sequences known as **primers** (usually 10 bp) using PCR. It is possible to sample many sites in the genome at once using this technique. Two sites for a single primer may exist in close proximity on a genome and the intervening fragment will be amplified, but for each primer a variable number of such sites will exist so a variable number of different-sized fragments will be produced. These can be analyzed using electrophoresis and the multiplicity of the sites means that different individuals may differ in the fragments amplified. The problems with this technique are that small changes in primer concentration or precise conditions in the experimental set-up can lead to different results and that certain DNA fragments may migrate at the same speed as other unrelated fragments so analysis of the bands can be problematic.

A combination of RFLP and RAPD techniques may be used to give a **DNA 'fingerprint'**, used in forensic testing and taxonomic studies as well as in the study of variation. Certain stretches of DNA do not vary at all within species or between species and sometimes across orders or even kingdoms, whereas others show so much variation that every individual is different. The most useful differences for studying variation in plants and their populations are those between these two extremes.

Gene flow
Study of plant polymorphisms has given much insight into gene flow in plants, since the distribution of individual genes can be mapped between individuals within a population and between populations. There are two phases of gene dispersal in a plant's life cycle: pollination in which only the pollen moves and which determines how the genes will mix to form the next generation; and seed dispersal in which the new generation moves.

Gene flow is restricted in all plants, with the great majority of pollen and seeds dispersing only a short distance. This potentially divides many populations into part-separated **neighborhoods**, defined initially as 'an area from which about 86% of the parents of some central individual may be treated as if drawn at random'. The most extreme restriction in pollen flow is self-fertilization where there is no genetic mixing, and after a few generations all the offspring will be genetically identical. If this is coupled with poor seed dispersal then gene flow is minimal. The opposite extreme is found in self-incompatible plants (Topic H3) with pollen dispersed by wind; in these plants pollen can travel a long way and connect populations genetically. If these plants have an effective seed dispersal mechanism too there may be effective long distance gene flow and neighborhood size will be large. Plants pollinated by insects and

vertebrates have an intermediate level of pollen dispersal, with birds, butterflies and moths dispersing pollen further than bees or flies, although these are general trends and individual species of pollinator differ in their effectiveness. At the seed dispersal stage, vertebrate-dispersed seeds travel furthest followed by wind-dispersed seeds, although many seeds have no clear dispersal mechanism beyond random events such as high winds or floods (Topic L2).

Natural selection

There is much debate on the relative importance of natural selection and **restricted gene flow** in determining how plant populations are organized genetically. Some isozymes are known to respond differently to particular environmental conditions, e.g. isozymes with different sensitivities to temperature, but in most no such differences are known and the variation has no known basis in natural selection. No selection is known that favors particular DNA sequences. This does not necessarily mean that natural selection is not important, just that we have not detected the mechanism. For all conclusions on the genetic organization of plant populations, the variation is assumed to be neutral in operation. If selection is operating, favoring one or another of the isozymes in different conditions, such as a wet or dry microhabitat in any one area, then any conclusions about gene flow must take this into account. It seems likely that many of the observed polymorphisms in plant populations are maintained in part by natural selection, since their distributions are not as predicted considering only gene flow and a relationship between certain enzyme forms and micro-environmental conditions have been found in some plants. Usually no mechanism is known involving the detected enzyme morphs but it may be a response of other linked genes or the workings of the gene in question in a particular context within the plant.

There is evidence, from some species, that **heterozygous** plants with two different versions of a gene are at an advantage over **homozygous** plants with two genes the same. Heterozygosity normally results from a cross between two parents that are genetically distinct and frequently a self-incompatible plant will be heterozygous at many loci. In self-fertilizing plants each generation will lose, on average, half the heterozygous genes so it will rapidly become homozygous at most genetic loci. The advantage of cross-fertilization has been well known to plant breeders for centuries (Topic O1), known as **hybrid vigor** and is mainly because of increased heterozygosity. Many deleterious mutations will be masked by an alternative form and, if an enzyme occurs in two different forms, it may be able to work across a wider range of conditions. Although there is evidence from some species that heterozygotes are at an advantage, it does not appear to be universally true. Many polyploid plants, particularly those deriving initially from hybridization, can retain some heterozygosity despite self-fertilization through having two different genes from different parent species on their **homeologous** genes, i.e. the equivalent genes from the two parents. Many polyploids do self-fertilize.

Population genetic structure

The total amount of genetic variation within a species is highly variable, with species that are restricted to a small area usually much less variable than widespread species, although there are many exceptions. It is likely that the distribution of genes within a population results from a balance between natural selection and restricted gene flow. The variation that occurs can be divided into that which exists within each population and that which occurs between populations.

In some plants, the populations differ but individuals within each population vary little or not at all, a situation characteristic of self-fertilizing plants and others with restricted gene flow. In these plants restricted gene flow has the predominant effect. In others, individuals within each population vary widely but each population has a similar range of variation. This is true of plants with the potential for long-distance gene flow (see above) and particularly of many plants that dominate plant communities. In these, natural selection is likely to be much more important, and studies that have looked at gene flow directly by examining pollen and seed dispersal have consistently underestimated the extent of genetic mixing and the effective gene flow within these species. If there is strong natural selection on plants it is likely that there will be mechanisms to avoid self-fertilization since it is nearly always disadvantageous (Topic L1).

Those plants that spread clonally may have a 'population' without any variation, i.e. consisting of a single genetic individual. In most clonal species, though, there is sexual reproduction, often with a mechanism favoring cross-fertilization and, taken overall, their genetic structure may be similar to that of non-clonal species but with fewer individuals, each covering a large area.

Small populations of many plants that are isolated from any other population often have little genetic variation. This may be because of the **founder effect**, each being founded by one or a small number of plants at one time so have always been restricted genetically, or it may be because of **genetic drift**: some variants becoming extinct at random because they cannot be maintained in small populations.