

Introduction to
Plant Population Biology

For Rissa, Eva, Alfred, Brian and Jane

Introduction to Plant Population Biology

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Introduction

1.1 Plants

Plants and their products are all around and inside us. This book you are holding was once a plant. The oxygen you are breathing was freed to the air by photosynthesis. The clothes you are wearing may be made from plant fibres; if they are not, the chances are that they are spun from polymers derived from oil, which was once ancient chlorophyll. Perhaps you have a cup of coffee or tea by your side? If so, the secondary compounds which defend the seeds of *Coffea arabica* or the leaves of *Camellia sinensis* from their natural enemies will help you stay awake while you read this book! There is nothing dull about plants, but it does require some subtlety to appreciate their peculiar ways. There is enough promiscuous sex and sudden death in the plant kingdom to furnish a hundred cable TV channels, but it all happens with the sound turned off.

This book is an *introduction* to the population biology of plants. In it we seek to understand how plant populations are structured and how they change from an ecological and evolutionary perspective. The fundamental ecological and evolutionary principles of the subject are not exclusive to plants; indeed plants are ideal model organisms in which to study those fundamentals. However, being sessile autotrophs means that plants experience and respond to their environments in ways that are sometimes difficult for mobile heterotrophs, such as ourselves, to fathom intuitively. Therein lies the fascination of the plant world.

1.2 Population biology

A **population** is a collection of individuals belonging to the same species, living in the same area—the water hyacinth *Eichhornia crassipes* in a ditch, the grass *Lolium perenne* in a lawn, or Norway spruce *Picea abies* in a forest are examples. This definition has two components, a genetic one (individuals belong to the same species) and a spatial one (individuals live in the same area), but populations are neither genetically nor spatially homogeneous. Populations have several kinds of structure. The **genetic structure** describes the patchiness of gene frequency and genotypes, and the **spatial structure** describes the variation in density within a population. Populations also have an **age structure** that describes the relative

numbers of young and old individuals, and a size **structure** describing the relative numbers of large and small individuals. Population biology attempts to explain the origin of these different kinds of structure, to understand how they influence each other, and how and why they change with time. Changes over time in the genetic make-up of a population are the subject of **evolution**; change in numbers with time is the subject of **population dynamics**. These are the two principal organizing themes of this book. We deal with the special characteristics of plants that affect their population biology in the second half of this chapter.

1.2.1 Demography

The essence of population biology is captured by a simple equation that relates the numbers per unit area of an organism N_t at some time t to the numbers N_{t+1} one time unit (e.g. year) later:

$$N_{t+1} = N_t + B - D + I - E, \quad (1.1)$$

where B is the number of births, D the number of deaths, and I and E are, respectively, immigrants into the population and emigrants from it. B, D, I and E are known as **demographic parameters** and are central to both population dynamics and evolution. The dynamics of a population may be summarized by the ratio N_{t+1}/N_t , which is called the **annual** or the **finite rate of increase**, and is given the Greek symbol λ (lambda). The balance between the two demographic parameters which increase N_t (B & I) and those which decrease it (D & E) determines whether the population remains stable ($N_{t+1} = N_t$ and $\lambda = 1$), increases ($N_{t+1} > N_t$ and $\lambda > 1$) or decreases ($N_{t+1} < N_t$ and $\lambda < 1$). Among other things, the values of B, D, I and E in natural plant populations are variously influenced by pollinators, herbivores, diseases, animals that disperse seeds, soil, climate, by the density of the population itself and by that of other plant species.

Furthermore, the influence of these factors on the demographic parameters often has a genetic component, because there is often genetic variation in natural populations: some individuals are more susceptible to disease than others, for instance, and some are more distasteful to herbivores, and some more tolerant of climatic extremes. A consequence is that one genotype may be favoured in one locality, and another somewhere else, and this may produce local differences in allele frequency that correlate with environmental conditions. For example, allele frequencies at an acid phosphatase (APH) locus in *Picea abies* correlate with altitude in the Seetaler Alps of Austria (Fig. 1.1e), and on a larger scale with latitude in northern Europe (Fig. 1.1d). Polymorphism at this locus appears to be an indication of a more general correlation between the genetic composition and geographical location of *P. abies* populations in Europe. Using 22 enzyme loci to characterize genotypes, Lagercrantz and Ryman (1990) found a similar geographical correlation stretching across populations sampled from most of the species' natural range. Note that *correlations* between allele frequencies and environment do not mean that the particular loci studied are necessarily the direct *cause* of

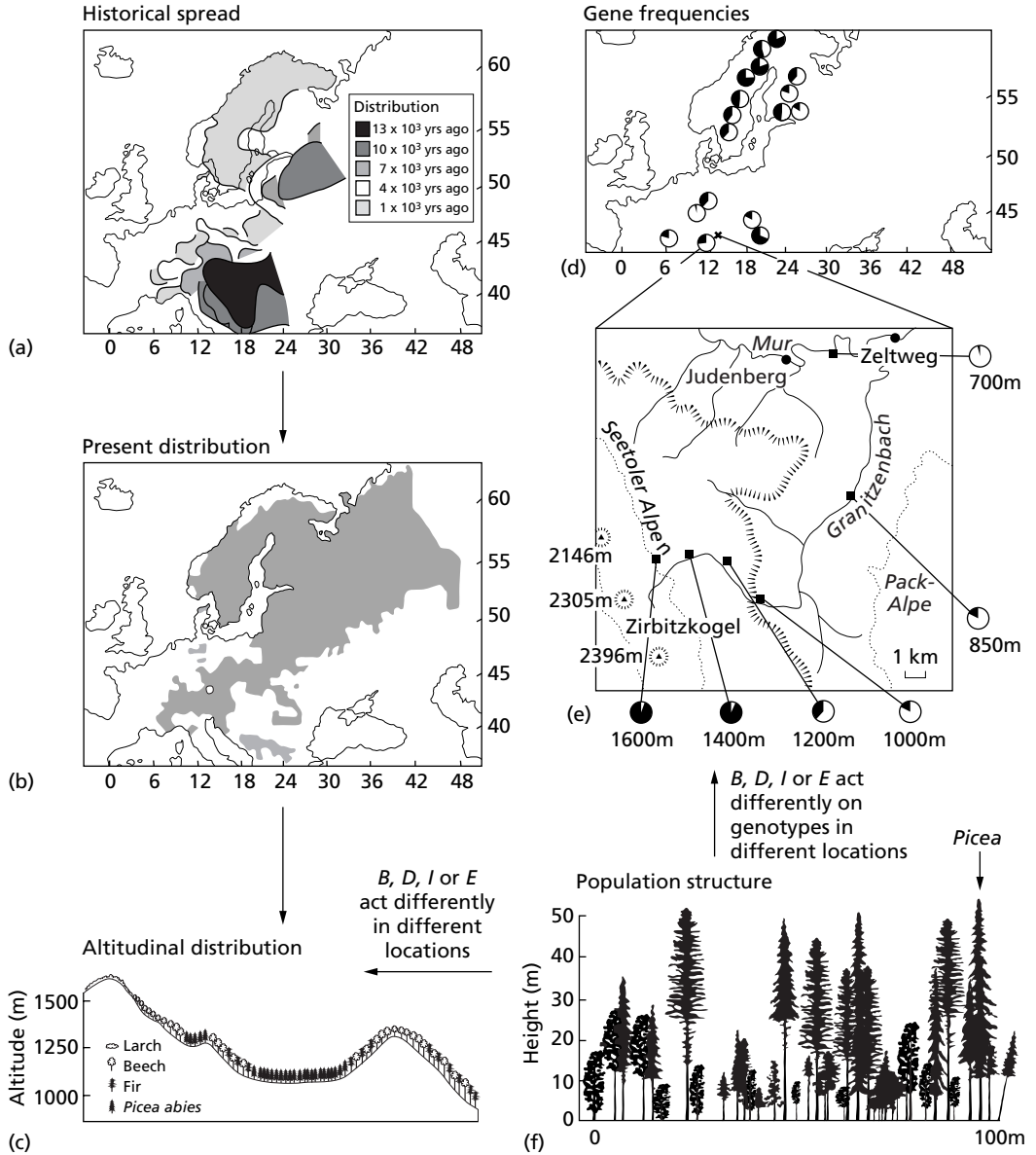


Fig. 1.1 How demographic parameters in populations of Norway spruce (*Picea abies*) in Europe underlie its (a) historical spread, (b) present geographical distribution, (c) local, altitudinal distribution, (d & e) APH allele frequencies, and (f) population structure (from Silvertown 1987a).

ecological differences between genotypes. Because the causative relationship between loci such as APH and the genes responsible for ecological differences is unknown, such loci are referred to as genetic markers (see next paragraph and Chapter 2).

Demographic processes underlie the distribution of species as well as the distribution of genotypes within species. At a local scale, differences in B, D, I and E must explain why *Picea abies* forms a distinct altitudinal belt in the Alps (Fig. 1.1c). Distributions can be investigated experimentally by sowing or planting the species along transects that cross the boundary of its natural range, to assess why boundaries lie where they do (Chapter 7). Climate changes and, in response, species' boundaries are, to varying degrees, dynamic. On a continental scale this is easily seen by comparing the historical spread of *P. abies* since the last glaciation (Fig. 1.1a) with its present geographical distribution (Fig. 1.1b). If rates of migration are slower than climatic change, boundaries may reflect historical limits rather than demographic ones. This is true of the distribution and genetic structure of Norway spruce in Europe today. The pollen record shows that the postglacial recolonization of western Europe by *P. abies* occurred from two refugia: one south of the Alps, in a region including northern Italy, and another on the eastern side of the Baltic Sea (Fig. 1.1a). Norway spruce populations found in these two areas today have distinctive genetic markers in their chloroplast DNA that reflect their different historical origins (Vendramin *et al.* 2000). The migratory history of a population can often be read in the present-day distribution of selectively neutral genetic markers. This is the science of **phylogeography**, which is discussed in Chapter 7.

1.2.2 Fitness and natural selection

The genetic structure of a population is subject to a number of forces that may bring about evolutionary change. The two principal forces are **gene flow** and **natural selection**. Gene flow simply describes the changes in gene frequency brought about by the migration of individuals, their seeds and their pollen. Special attention is given to natural selection because this is the only known process that can produce **adaptive** evolutionary change. This was the great, enduring insight in Charles Darwin's book *The Origin of Species*, first published in 1859. Three conditions are necessary for natural selection to operate:

- Variation between individuals;
- Inheritance of the variation;
- Differences in fitness between variants.

Fitness (usually denoted by the symbol w or W) is defined in population genetics terms in Section 3.5.2.1. For our purposes, it is usually accurate to define the fitnesses of different genotypes as the relative success with which they transmit their genes to the next generation. This definition also makes it possible to define fitnesses of phenotypes, as we shall see when we discuss evolution of plant breeding systems in Chapter 9. However, we do not always need to be so formal in our use of the word fitness, particularly as the strict definition of fitness is rarely something we can measure in the real world. The term is also used more generally, for instance in the term 'components of fitness' to refer to characteristics that we

expect to correlate with increased fitness (although it may often be better to be explicit, and speak directly of survival or fertility).

Ecologists sometimes use the term fitness in an even more general way, and ignore the fact that, in sexually reproducing populations, individuals with different genotypes breed with one another. The concept of phenotypic fitnesses can sometimes justify use of the simplifying assumption that different genotypes do not interbreed. This assumption can, for instance, lead to approximately correct inferences when a new phenotype enters a population (e.g. by a new mutation), and we are interested in asking whether it will increase in frequency. In that case, we may use λ to estimate fitnesses by applying Eqn 1.1 separately to different phenotypes. For example, in *Picea abies* we could compare λ_H for the high altitude phenotype with λ_L for trees with the low altitude phenotype in different parts of the Seetaler Alps. At low altitudes we might expect $\lambda_L > \lambda_H$, and at high altitudes we might expect $\lambda_H > \lambda_L$. By convention, the phenotype with the highest fitness has a value $W = 1$, and the fitness of other phenotypes is given as a proportion of this. Fitnesses usually change with environmental conditions. So, *if* the APH phenotypes are adapted to the respective environments in which they are most frequent (and this has *not* yet been tested experimentally), at low altitudes the fitness of the low phenotype W_L would be 1, and the fitness of the high phenotype $W_H < 1$, while at high altitudes $W_H = 1$ and $W_L < 1$.

Given heritable variation and fitness differences between variants (i.e. certain genotypes have phenotypes that cause their genes to multiply faster than those in others), there is the potential for adaptive evolutionary change to take place. Whether change actually occurs, and what direction of changes occur, may depend upon the fitnesses in other populations of a species, and on the rate of migration of seeds and pollen from neighbouring areas, where selection may have a different direction. Field observations have shown that natural selection may be strong enough to produce marked genetic differences between adjacent populations of the same species and to produce adaptation to local conditions. For example, the annual *Veronica peregrina* grows in and around temporary pools, called vernal pools, that form in early springtime in the Central Valley of California, USA. Although pools are only a few metres wide, plants in the centre are genetically different from those around the periphery (Keeler 1978). Phenotypically, they are more tolerant of flooding (Linhart & Baker 1973), and differ in a number of other ways that adapt them better to the conditions of intense intraspecific competition that occur in the centre than to competition with grasses that affects those genotypes growing at the pool edge (Fig. 1.2) (Linhart 1988). We shall explore natural selection and other evolutionary forces in more detail in Chapter 3.

1.2.3 Life tables and age dependence

The probability that an individual dies or reproduces is often related to its age; thus, the age structure of a population is likely to affect its future. The proportion

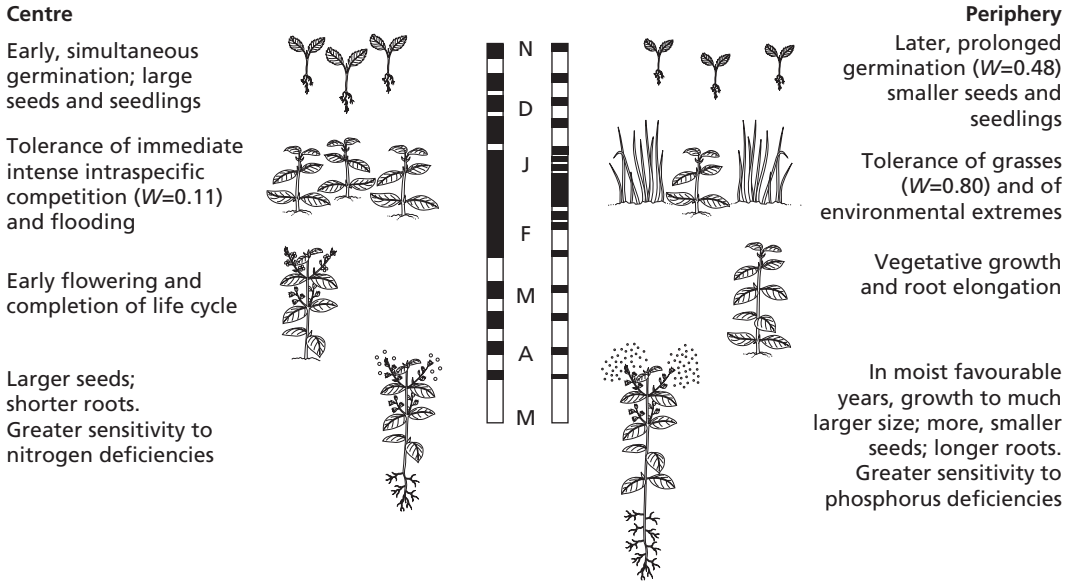


Fig. 1.2 Genetically determined differences between plants of *Veronica peregrina* sampled from the centre and periphery of a vernal pool. Bars show the periods between November and May of adequate soil moisture in the two microhabitats. 'W' indicates the relative fitness, based upon seed production, of plants from the other microhabitat when grown experimentally in the conditions indicated (after Linhart 1988).

of youngsters is an indication of the likely future, but this does depend upon the chances of surviving to adulthood. This information is conventionally summarized in a life table (Table 1.1).

Acacia suaveolens is a small shrub that grows in fire-prone arid habitats of SW Australia. Figure 1.3 shows a survivorship curve for *A. suaveolens*, based upon the data in the life table. The life table and survivorship curve for *A. suaveolens* indicate that substantial mortality occurs throughout the lifespan of the population. In fact, the mortality rates affecting this population of *A. suaveolens* are quite modest by comparison with many plant populations that have been studied, for which 90% mortality in the first year of life is not unusual. Such mortality may alter the genetic structure of a population if some genotypes are more susceptible than others.

Life tables were originally devised as a means of studying the human population, and are used by actuaries to calculate the risk of insuring the life of their clients (Hutchinson 1978). A person's age is, of course, not the only factor that influences their longevity; nor is this so in plants. Although life tables are used for plant populations, in many ways they are inappropriate to the peculiarities of plants. The rate of growth in plants is highly dependent upon the local environment and consequently is very variable, so that two genetically identical plants of the same age may be quite different in size. This is an example of phenotypic

Table 1.1 Life table and fecundity schedule for a population of the shrub *Acacia suaveolens*, in Australia (data from T. Auld & D. Morrison pers. comm.).

Age (yr) x	Number N_x	Survival l_x	Mortality d_x	Mortality rate, d_x/l_x q_x	Survival rate, $1 - (d_x/l_x)$ p_x	Seeds / plant m_x
0	1000	1	0.174	0.174	0.826	0
1	826	0.826	0.145	0.176	0.824	41
2	681	0.681	0.159	0.233	0.767	33
3	522	0.522	0.122	0.234	0.766	31
4	400	0.4	0.093	0.233	0.768	31
5	307	0.307	0.076	0.248	0.752	18
6	231	0.231	0.057	0.247	0.753	9
7	174	0.174	0.043	0.247	0.753	9
8	131	0.131	0.015	0.115	0.885	9
9	116	0.116	0.013	0.112	0.888	7
10	103	0.103	0.012	0.117	0.883	5
11	91	0.091	0.011	0.121	0.879	3
12	80	0.08	0.009	0.113	0.888	6
13	71	0.071	0.009	0.127	0.873	-
14	62	0.062	0.007	0.113	0.887	-
15	55	0.055	0.007	0.127	0.873	2
16	48	0.048	0.005	0.104	0.896	4
17	43	0.043	-	-	-	3

- indicates missing values

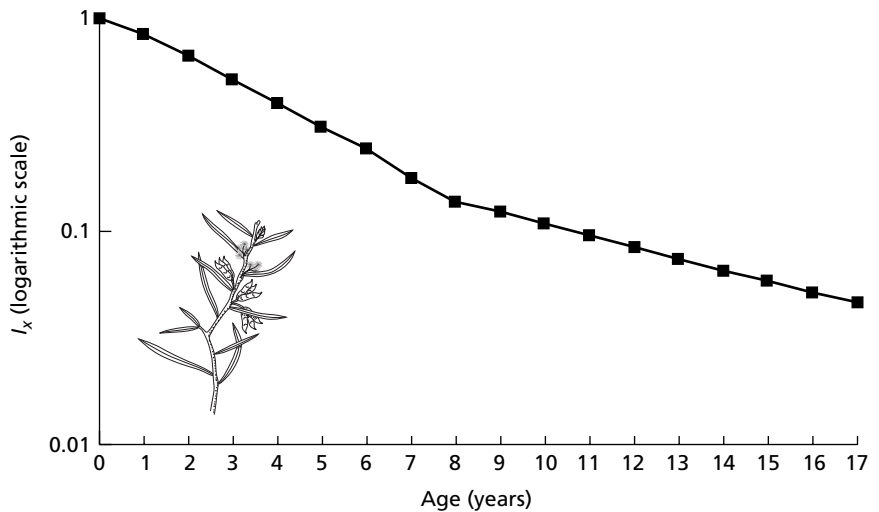


Fig. 1.3 A survivorship curve for *A. suaveolens* (pictured), based upon the data in Table 1.1.

plasticity, a feature in which plants excel (Chapter 2). Genetically identical plants may have quite different phenotypes if they have been exposed to different environments.

1.2.4 Life cycle graphs and stage dependence

Size is a major influence on the fate of individual plants and on their fecundity (Fig. 1.4). Because of phenotypic plasticity, size and age tend to be only loosely correlated. The dependence of plant fate on age is further weakened by the existence of dormant stages – notably seeds, but also tubers and stunted seedlings – that may persist for many years before entering a phase of active growth. Thus, while it is clearly possible to draw up plant life tables, and for some purposes it is useful to do so, this approach leaves much demographic variation in plant populations unaccounted for.

A simple alternative to the life table that uses age or plant stage to classify individuals in the population is the **life cycle graph** (Hubbell & Werner 1979). Each age-class or stage in the life cycle is represented by a node, and transitions between nodes are shown by arrows joining them (Fig. 1.5a,b). Appropriate rates of transition between stages and seed production are obtained from field studies. For example, Werner (1975) studied a population of the herb *Dipsacus sylvestris* in an abandoned field in Michigan, and classified plants into several stages: (1) first-year dormant seeds, (2) second-year dormant seeds, (3) small rosettes, (4) medium rosettes, (5) large rosettes and (6) flowering plants. A life cycle graph based on the annual rates of transition between these stages is shown in Fig. 1.5(c). *D. sylvestris* dies after flowering, so the arrows from (6) to the other stages all represent numbers of individuals in those stages that were produced from seed that were produced that year.

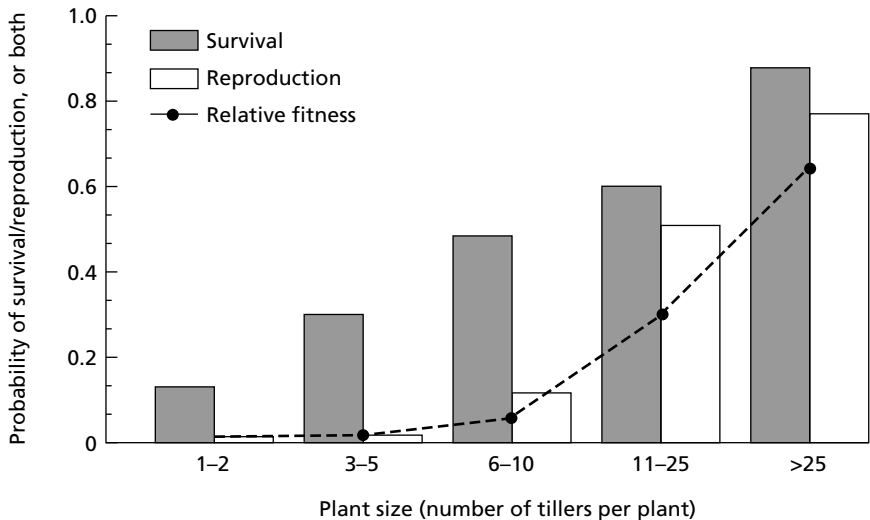


Fig. 1.4 Relationships between size and survival, reproduction and relative fitness (survival \times reproduction) of the grass *Bouteloua rigidisetata* (data from Fowler 1986).

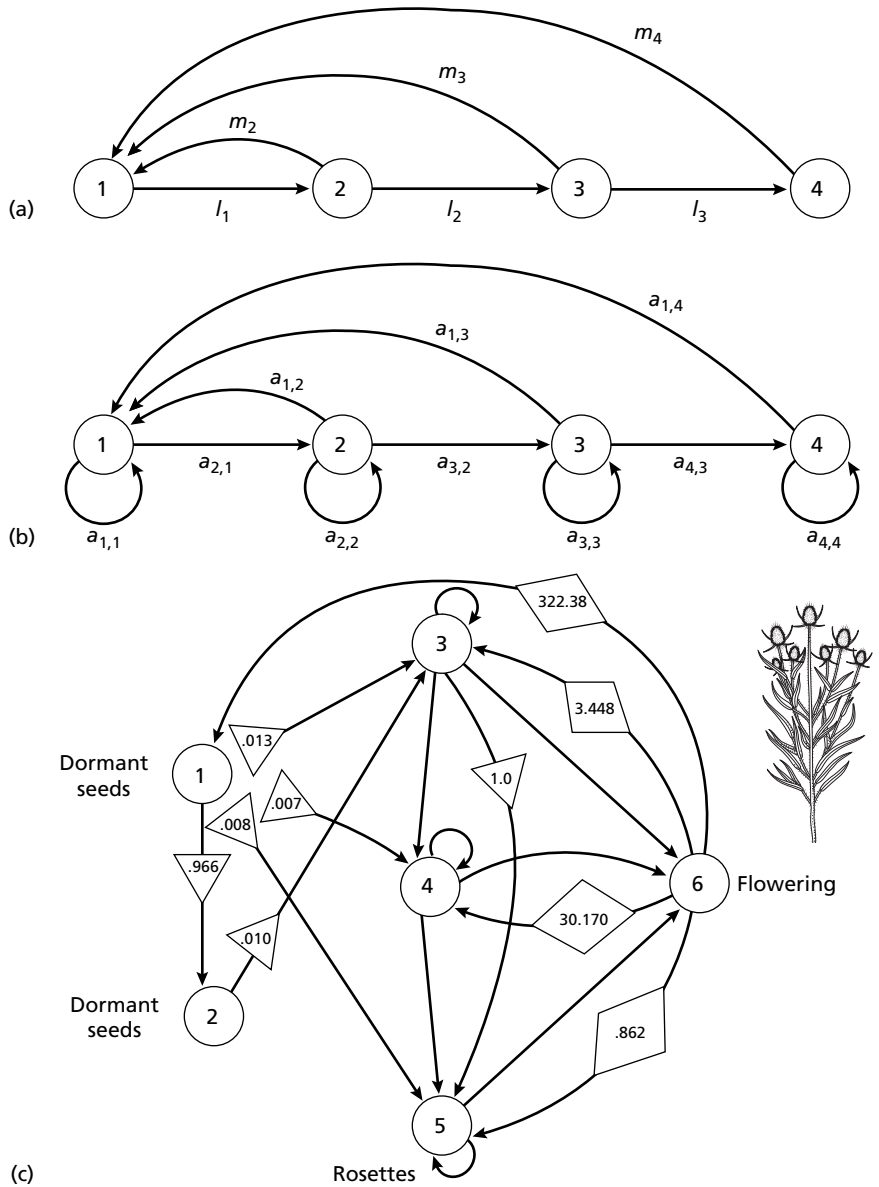


Fig. 1.5 Examples of life cycle graphs. Diamonds represent numbers (of seeds) making a transition, and triangles show rates of transition between nodes. Graphs for: (a) an age-classified life cycle, (b) a stage-classified life cycle, and (c) the life cycle graph for a population of the herb *Dipsacus sylvestris* (pictured; Caswell 1989).

1.3 Some consequences of being a plant

Two features shared by all plants deserve special mention because of their fundamental consequences for the population biology of these organisms: plants' growth and development from meristems, and the fact that they are sessile.

1.3.1 Meristems

Not all cells in a plant are capable of dividing. Dividing cells occur in discrete regions called **meristems**, predominantly found in the apices of shoots, in the buds in the axils of leaves, near the tips of roots, and in the cambial layer beneath the surface of the stem in dicotyledonous plants and gymnosperms.

1.3.1.1 *Structure and life history*

The number and distribution of meristems on a plant, which of them develop and when, determine how a plant grows and its overall structure (Fig. 1.6). A bud that develops into a shoot usually multiplies the number of meristems on a plant, because each shoot has its own meristems. This produces the **modular construction** typical of plants. A bud that develops into a flower or inflorescence consumes the meristem and ends its career, so the plant must use other meristems for vegetative development if it is to continue to grow and survive. For example, when the shoot of a grass, called a **tiller**, flowers its apical meristem differentiates, causing the death of the tiller after reproduction. If all the individual tillers on a grass plant flower simultaneously, the whole plant will die.

The **life history** of a plant describes how long it typically lives, how long it usually takes to reach reproductive size, how often it reproduces and a number of other attributes that have consequences for demography and fitness. Because of the manner in which plants develop from meristems, there is a close relationship between the structure of a plant and its life history. Torstensson and Telenius (1986) found that the major difference in life history between the annual herb *Spergularia marina* and the related perennial *Spergularia media* was the result of a difference in how their axillary meristems behaved. Axillary meristems were committed to flowering at the 6th or 7th node in the annual, but in the perennial these meristems produced shoots instead and flowering began much later in development.

As well as allowing plants to grow and branch vertically, meristems allow plants to proliferate and spread horizontally. This is **clonal growth** (Fig. 1.6d). The whole plant comprises the **genet**, which is defined as an individual arising from seed, which (barring mutation) will be a single genotype, however large and fragmented it may later become through clonal growth. A clonally produced part of a plant, with its own roots and a potentially independent existence, is known as a **ramet**. The tillers produced from lateral meristems in grasses are an example. The branching pattern of growth produced by meristem activity results in a hierarchical structure: a genet is composed of ramets, ramets are composed of one or more

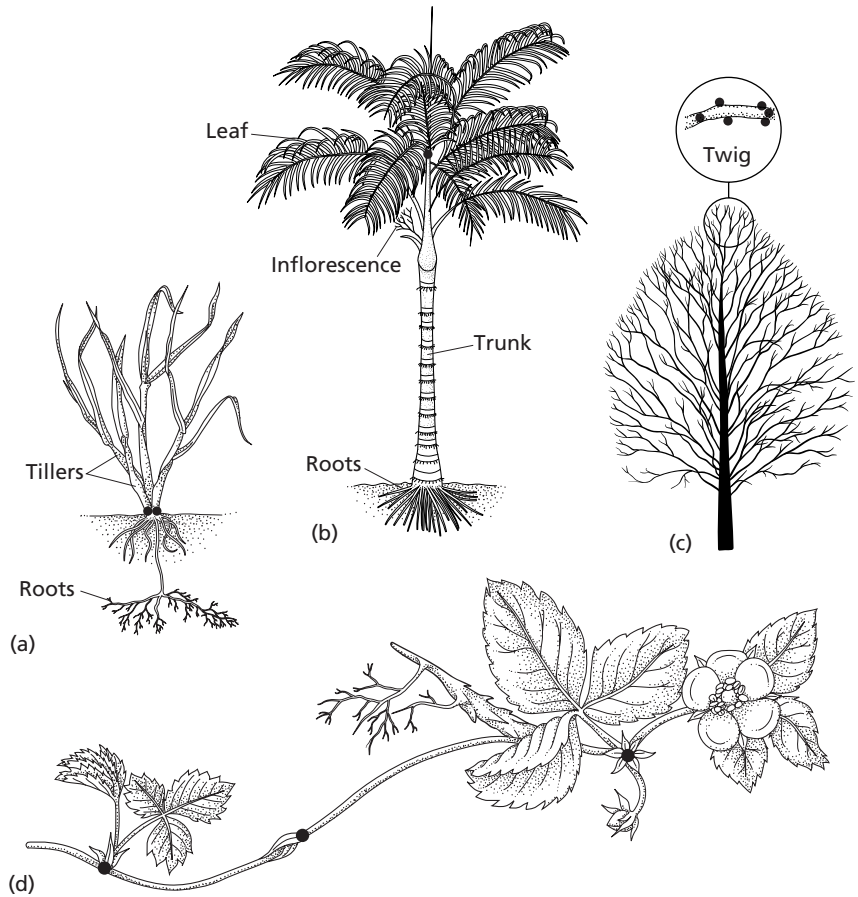


Fig. 1.6 Schematic diagrams showing plant construction and the distribution of shoot meristems, indicated by dots, in (a) a grass, (b) a palm, (c) a dicot tree, and (d) a dicot clonal herb.

branches, these bear inflorescences, inflorescences bear flowers, and flowers contain ovules and pollen. This hierarchical structure affects life history because the survival and reproduction of the genet depends upon the behaviour of ramets, and ramets depend upon the behaviour of their parts (Silvertown 1989). Flowering terminates the life of a meristem, so if all meristems on a branch produce flowers the branch will die, if all branches flower the ramet dies, and if all ramets flower the genet dies. Plants in which the genet dies after flowering are termed **semelparous** (or monocarpic), and those which can flower more than once are **iteroparous** (or polycarpic). An extreme example of semelparity occurs in some bamboos. The plant is clonal, forming many, perennial ramets, but all of them flower at the same time and then the whole genet dies. In the giant semelparous bamboo *Phyllostachys bambusoides* the prereproductive period is 120 years! (Janzen 1976).

There is a continuum of types of plant structure between trees, whose branches all depend upon a common trunk, and clonal plants, in which the 'trunk' is

reduced to no more than the crown of a rootstock and the 'branches' develop roots of their own. Both extremes can be seen by comparing *Salix pentandra*, which is a small tree, with *Salix herbacea*, which is a dwarf, creeping shrub (Fig. 1.7a). There are similar contrasting examples among birches (*Betula* spp.) and dogwoods (*Cornus* spp.). Among clonal plants there is also great diversity in the method of spread, including stolons (above-ground creeping stems), rhizomes (below-ground creeping stems), tubers like the potato, bulbs such as the onion, or corms as in crocus.

Once a ramet has its own roots, it is usually self-sufficient in carbon, although water and minerals may still be imported from other parts of the clone if the connections between ramets persist (see Section 10.5). Plant species vary a good deal in how long the connections between ramets last. In white clover the stolons that connect ramets together are short-lived and the parts of a genet can wander far from each other, so that a single successful genet may be represented in many parts of a field. At the other extreme is what is probably the biggest tree on earth: a banyan *Ficus benghalensis* growing in Calcutta, India. It is a clone over 200 years in age, with a thousand connected tree trunks covering more than 1.5 ha.

1.3.1.2 Genetics and evolution

Meristematic growth and modular construction have a number of genetic and evolutionary consequences for plants. First, the number of flowers a plant is

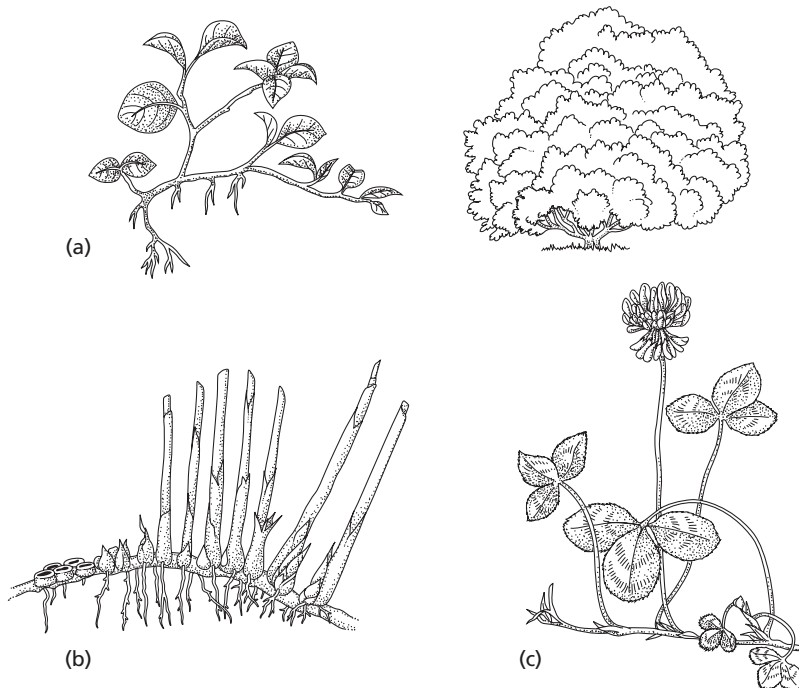


Fig. 1.7 (a) The growth form of *Salix herbacea* (left) and *S. pentandra*; (b) rhizome of *Cyperus alternifolius*, and (c) *Trifolium repens*.

capable of producing is limited by the number of meristems, so its size is likely to be a major determinant of its total reproductive success and fitness. Secondly, meristems are like perpetually embryonic tissue—they are ‘forever young’, so it is possible for a very old and large genet to be entirely composed of much younger ramets that perpetually replace themselves by clonal growth. Huge clones in which the genet is inferred to be thousands of years old are known in many species. Probably the record is held by creosote bush *Larrea tridentata*, which has some clones in SW USA that, judged by their size and rate of growth, may be 11 000 years old (Vasek 1980). This is as ancient as the deserts in which they live.

1.3.1.3 Behaviour

Textbooks of ethology are strangely reluctant to define ‘behaviour’; although ethologists clearly know what they mean by the word, some mistakenly believe plants to be incapable of any activities that deserve the term. To encompass all the *animal* activities that ethologists study, behaviour must be defined broadly, for example as a response to some event or change in the organism’s environment (Silvertown & Gordon 1989). Most plants are capable of some kind of movement, for example in the orientation of leaves, and *Mimosa pudica*, the ‘sensitive plant’, is able immediately to fold up its leaves, exposing a spiny stem, when touched by a herbivore. However, rapid movement is rare and the chief method of behavioural response in plants depends upon their modular pattern of growth and the ability to alter the size, type and location of new organs to match an environmental change. Thus, for example the tropical rainforest liana *Ipomoea phillomega* produces several types of shoot, depending upon the nature of the light environment. In shaded conditions, stolons with long internodes and rudimentary leaves extend rapidly over the ground (Fig. 1.8). When a gap is reached, twining shoots with large leaves are produced and these ascend to the tree canopy where the liana forms a crown of its own (Peñalosa 1983).

The parallel between the behaviour of *Ipomoea phillomega* and animal foraging is difficult to resist. Such behaviour is especially common in climbers which, because of their extensive shoot systems, traverse several types of microenvironment during

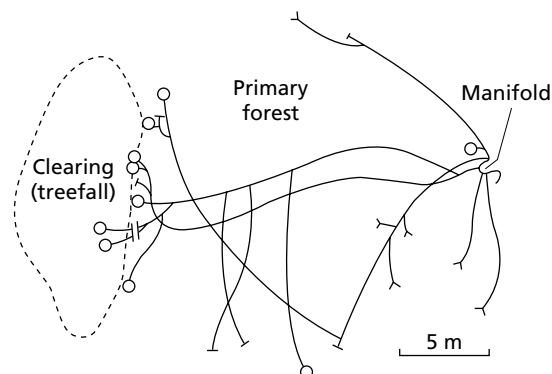


Fig. 1.8 A map of the shoot system of *Ipomoea phillomega* on the floor of a tropical rainforest in Veracruz, Mexico. This plant originated at the ‘manifold’, which has an ascending shoot and a crown in the canopy. Circles represent ascending shoots with crowns. Stolons that have lost their tips end in a ‘T’, and those that are still growing are shown with a ‘Y’ (Peñalosa 1983).

growth and often have different types of leaf or shoot to match. Perhaps the simplest behaviour of which virtually all plants are capable is etiolation in response to shade. Most plant responses to shade from other plants are mediated by the substance **phytochrome**, which has two forms that interconvert with each other. The Pr form absorbs red light and is then converted to the Pfr form, which absorbs far-red light. The equilibrium between the two forms is determined by the *ratio* of red to far-red light. Leaves absorb red and blue light (this is why they are green), but are relatively transparent to far-red light, so a plant can detect the presence of leaf shade by the effect this has on the Pr : Pfr ratio. In fact, the system is so sensitive that plants can detect the quality of reflected light and respond to the presence of neighbours that do not shade them directly (Ballaré *et al.* 1990; Novoplansky *et al.* 1990). Using the phytochrome system, seeds of many species can discriminate between shade caused by other plants and darkness caused by burial. They will germinate in the dark but not when shaded by leaves (Silvertown 1980a).

In *Arabidopsis thaliana* and many other broad-leaved flowering plants there are five phytochrome genes (*PHYA-PHYE*) with partly complementary but often overlapping functions (Mathews & Sharrock 1997; Smith 2000). Genotypes with mutations that disable one or more of these genes can be used to test the adaptive significance of plant behavioural responses to shading by neighbours (Schmitt *et al.* 1999). Cucumbers with a mutation in the *PHYB* gene, which in the wild type modulates response to shade, were unable to find light gaps in a canopy of maize, while normal cucumbers could do so (Ballaré *et al.* 1995).

1.3.2 Sessileness

1.3.2.1 *Defence, dormancy and dispersal*

The fact that plants are rooted to the spot has a number of important consequences. Plants are unable to escape their herbivorous enemies by flight, but they are often packed with toxins that make them unpalatable. Others resist grazing with spines or, as grasses and sedges do, by hiding their meristems in the very base of the plant. Plants cannot migrate in unfavourable seasons of the year, but they have a range of protective strategies that include leaf deciduousness, seed dormancy and retreating to underground storage organs from which they may regrow in the next season. Some movement is of course possible, but creeping stems and roots grow too slowly to form any effective means of escape from most hazards. However, by forming an extensive network, stolons and roots can reduce the risk that local damage will kill the entire plant, and it has been suggested that this is a major advantage of the clonal growth habit (Eriksson & Jerling 1990).

Although plants are sessile, their genes are mobile and are transported in seeds and pollen, both equipped with a variety of dispersal aids. Pollen grains are produced in vast numbers, and wind-dispersed grains are light and sometimes, as in pines, have buoyancy aids attached to them. Animal-pollinated plants have colourful, fragrant flowers that attract insects, bats and birds as pollinators that are

often rewarded with nectar (Chapter 2). It is worth remembering that the fruit and flowers so enjoyed by humans originate from organs evolved by sessile organisms that rely on animals for transport.

Virtually all plants disperse most of their seeds. Seed dispersal is often a two-stage process involving a primary stage in which seeds leave the mother and reach the ground and a secondary stage when seeds that reach the ground are moved again by animals or water. A wide range of mechanisms is involved in primary seed dispersal: ballistic expulsion of seeds by exploding fruits such as in the cucumber *Echballium elaterium*; wind transport aided by a wing or pappus such as in the dandelion *Taraxacum officinale*; transport of seeds in hooked structures that become trapped in animal fur; and carriage in the guts of animals that have eaten berries and which defecate viable seeds (Fig. 1.9). Each mechanism produces a characteristic distribution of seeds around the mother, or seed shadow. Wind dispersal mostly carries seeds further than primary dispersal by animals (Willson 1993; Clark *et al.* 1999), but in all cases dispersed seeds are most concentrated near the parent (Fig. 1.10).

Harvester ants in deserts and various vertebrate seed predators (particularly rodents) in forests are important agents of secondary seed dispersal. Both cache their food but fail to consume all of it before some seeds germinate (Brown *et al.* 1979; Forget 1996). In several species of woodland violet *Viola* spp., seeds are expelled from dehiscent fruit and then they are collected from the ground by ants that carry them to their nests (Beattie 1985). There, ants remove a fatty appendage from the seed, called the elaiosome, and deposit the seed, still viable, on their refuse heap. In a study of the ant-transported herb *Corydalis aurea* growing in the Rocky Mountains, USA, Hanzawa *et al.* (1988) compared the fitness of seeds transported by ants with that of seeds not carried away, and found that ant transport increased λ by 38%.

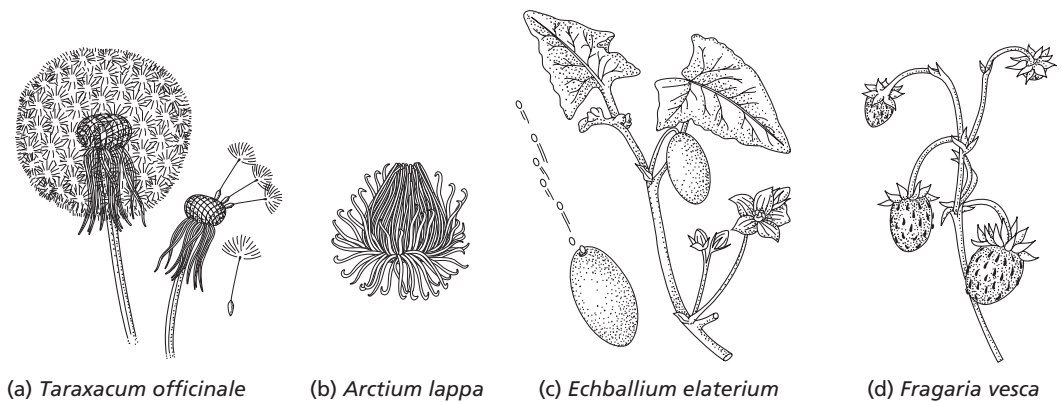


Fig. 1.9 Examples of modes of seed dispersal (a) Wind dispersed seeds of *Taraxacum officinale*, (b) hooked, animal dispersed seed head of *Arctium lappa*, (c) seeds explosively expelled from the fruits of *Echballium elaterium*, and (d) fleshy, animal-dispersed 'berry' of *Fragaria vesca*.

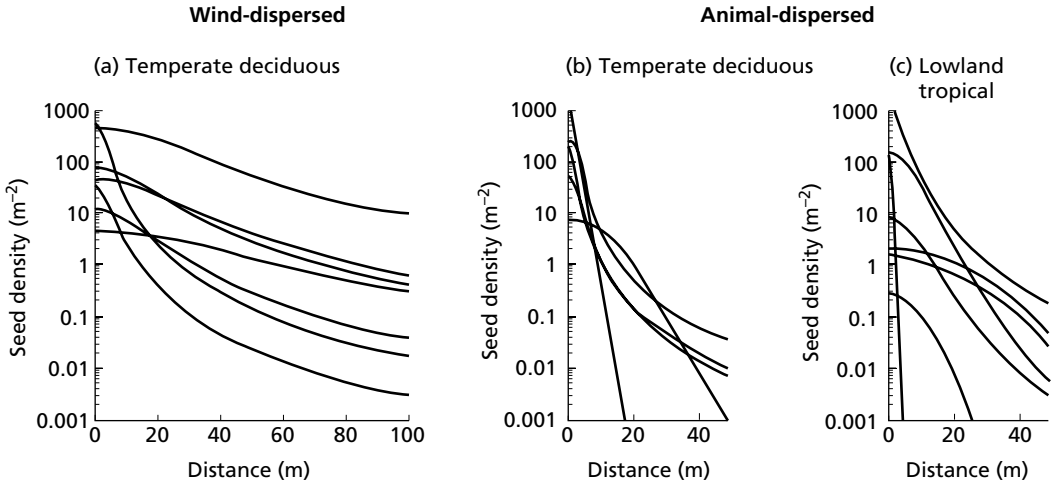


Fig. 1.10 Primary seed dispersal curves estimated by inverse modelling for (a) seven wind-dispersed deciduous tree species and (b) five animal-dispersed deciduous tree species of temperate North American forest; (c) seven animal-dispersed species of lowland tropical forest (from Clark *et al.* 1999).

The shape and length of the tail of seed dispersal curves is hard to quantify because it is difficult to identify the source of a seed when it has travelled a long way. However, two techniques offer a solution to this problem. One is the use of genetic markers such as microsatellites to identify the parents of seedlings (Chapter 3.3.2). The other employs a statistical method known as inverse modelling to estimate the entire seed shadows of individual forest trees from the distribution of dispersed seeds around the mapped locations of adults. This method predicts long, 'fat' tails for many tree species (Fig. 1.10; see Clark *et al.* 1999). Such distributions account for observed rates of spread of trees into the northern temperate zone in postglacial times (e.g. Fig. 1.1a) much better than earlier methods of estimation have (Clark 1998), suggesting that the dispersal curves produced by inverse modelling are biologically realistic.

1.3.2.2 *Mates and neighbours*

Because they are sessile, most of the ecological and genetic interactions between plants are with their immediate neighbours. Despite the agency of wind and animals in moving pollen, most plants mate with their neighbours and are frequently surrounded by relatives, creating genetic patchiness, even within continuous populations (Chapter 3). The genetic and spatial structures of populations interact with one another. Spatial patchiness in the density of populations reinforces the genetic isolation of patches, and this can lead to genetic divergence.

If below-ground resources such as water or nutrients limit plant growth, competing neighbours will interact chiefly by the depletion of resources in the common pool. However, when plants grow in a closed stand and light limits growth, a plant that is taller than its neighbours will not only receive a disproportionate share, but is

also likely to *suppress* the neighbours in its shade. As a result of this inherent asymmetry among plants competing for light, even a slight difference in height or canopy area can be decisive in determining which plant wins (Chapter 4). This introduces a further complication, because the plant that is initially the largest among its neighbours is often merely the one that germinated first. The early plant catches the light. So, because plants are sessile, not only *where* a plant is but also precisely *when* it appeared there may be a matter of life and death.

1.4 Summary

A **population** is a collection of individuals belonging to the same species, living in the same area. Population biology aims to explain **spatial structure**, **age structure** and **size structure** in terms of the four basic **demographic parameters** which measure birth, death, immigration and emigration rates. Changes in numbers of individuals over time are the subject of **population dynamics**. When rates affect genotypes differently they may produce **evolutionary change** in the frequencies of alleles at genetic loci. Fitness differences can often be quantified in models of evolutionary change in terms of differences in numbers of genes transmitted from parental to progeny generations. The principal force leading to **adaptive** evolutionary change is **natural selection**. Natural selection can operate only when there is variation between individuals in heritable characters that affect fitness. The dynamics of a population may be summarized by the ratio N_{t+1}/N_t , which is called the **annual** or the **finite rate of increase** (λ). The finite rate of increase for a genotype can sometimes be used as a measure of its Darwinian **fitness**.

Birth and death rates are influenced by the age and size of individuals. Plant size is particularly sensitive to local environmental conditions and shows great **phenotypic plasticity**. A **life table** may be used to describe the age-dependence of demographic parameters and a **life cycle graph** to describe a stage- (or size-) classified population. The **life history** of plants tends to be tied up closely with their **modular construction**, which arises from **meristematic** development. **Clonal growth** is common in plants. The individually rooted parts of a clone are called **ramets**, and the whole clone is called a **genet**. Unlike in unitary animals where gametes and somatic tissues derive from separate cell lines, in plants both cell types derive from meristems. This has the important consequence that clonal plants may be potentially immortal.

Modular growth and the ability to produce structures that match a change in the environment give plants a **behavioural repertoire** that enables them to forage for light and avoid competitors. Because plants are unable to escape their animal enemies, they often rely on **chemical defences**. Seeds and pollen transport plants' genes, but plants still usually end up mating with their **neighbours**.

1.5 Further reading

Bell, A. D. (1991) *Plant Form*. Oxford University Press, Oxford.

CHAPTER 1

Harper, J. L. (1977) *Population Biology of Plants*. Academic Press, London.

Hutchinson, G. E. (1978) *An Introduction to Population Ecology*. Yale University Press, New Haven, CT.

Raven, P. H., Evert, R. F. & Eichorn, S. E. (1998) *Biology of Plants*. Worth, New York.

1.6 Questions

- 1 Program a spreadsheet to calculate all the terms of the life table shown in Table 1.1 from the values of N_x given.
- 2 What is meant by *fitness* and why is the concept so important in population biology?
- 3 Why is age usually a less useful predictor of a plants' fitness than its size?
- 4 How do modularity, sessileness, phenotypic plasticity and behaviour relate to one another in plants?
- 5 Explain why neighbours are so important in plant population biology.

Variation and its inheritance in plant populations

2.1 Introduction

The two foundation stones of modern biology are Darwinian evolution and Mendelian genetics. Both are based on an understanding of variation within populations, the subject of this and the next chapter. Darwin's theory of evolution by natural selection is central to all biology (Maynard Smith 1993). It is founded on the realization that heritable variation among individuals in a population could be the raw material for evolutionary change. Darwin's work on inheritance in plants and animals is, however, little known today because he failed to understand how inheritance worked. Darwin did several experiments with cabbages and antirrhinums. With hindsight, we can now make sense of his results in terms of Mendelian genetics. He crossed a peloric snapdragon (*Antirrhinum majus*), which has narrow tubular flowers, with pollen of plants with the normal asymmetrical snapdragon flowers, and the latter reciprocally with pollen of peloric plants (see Fig. 2.1a). Among the many seedlings produced, none was peloric. When these progeny plants were allowed to self-fertilize, 88 seedlings out of 127 had normal snapdragon flowers, two had flowers of an intermediate condition, and 37 were perfectly peloric (Darwin 1868). He also reported that, when seeds are obtained from the short-styled floral form of *Primula auricula* (a heterostyled species, see Fig. 2.8b, in which this flower morph is a heterozygote) 'about one-fourth of the seedlings appear long-styled' (Darwin 1877, p. 223) but, lacking a satisfactory theory of inheritance, he failed to appreciate the significance of this 3:1 ratio.

Mendel realized that a 3:1 ratio in the second generation of such a cross implies that the traits are inherited as particles, which we now call genes. If each plant has two variants of a gene (in modern terminology, two 'alleles', say A and a), and one allele (A) is dominant to the other, then the initial cross can be symbolized by $AA \times aa$, and the first generation (F_1) progeny will be Aa . If the F_1 plants are self-fertilized, half of the ovules or pollen will receive the A allele, and the other half will receive a . The combinations of progeny genotypes in the progeny, or F_2 , generation, will therefore be the familiar 'Mendelian single factor ratio' 1 AA : 2 Aa : 1 aa , or one quarter of recessive homozygotes (3 of the dominant to 1 of the recessive phenotype). The particulate basis of inheritance could be

discerned by Mendel because he chose (perhaps deliberately) to study character differences which were each determined by a single gene.

By the 1930s, Darwin's theory of evolution had been combined with Mendelian genetics (Maynard Smith 1993). This is called the Neo-Darwinian synthesis, or the 'Modern Synthesis' (Huxley 1942). In this chapter, we review heritable variation, and also describe the diversity of breeding systems of plant populations, which affect how genes are transmitted from generation to generation. The following chapter outlines some simple population genetics concepts that will be used throughout the rest of the book, particularly in Chapters 7, 9 and 10. We will see how genetic variability is measured and how the genetic structure of plant populations can be described, based on frequencies of alleles and genotypes in populations. We will also show how various factors, including breeding systems and natural selection, affect these frequencies.

2.2 Types of trait

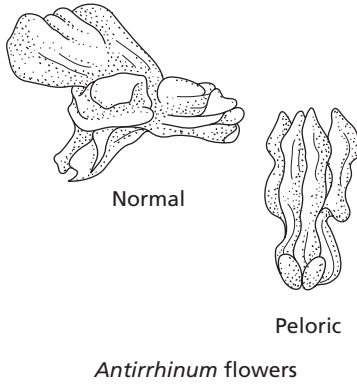
Individuals of a plant species or population are often as different from one another as individuals in human populations. Morphological and physiological variants range from discontinuous differences to continuous variability (Fig. 2.1). **Discontinuous variation** between plants, such as the difference between peloric and normal *Antirrhinum* flowers (Fig. 2.1a) or the phenotypic differences studied by Mendel, is variation that falls into 'discrete' phenotypic classes. These often correspond to different genotypes with a simple underlying genetic basis, such as single gene inheritance. This is often called **major gene inheritance**. Such traits show less variability within genotypes (caused by environmental influences) than between different genotypes. Flower colour is an example of a phenotype that is often controlled by major genes, and is variable in some natural plant populations (e.g. *Ipomoea purpurea*; Section 3.5.6). Another well-known example of polymorphism occurs in populations of white clover *Trifolium repens*, in which some individuals have the ability to produce cyanogenic glucosides and to release cyanide from them when leaves are damaged (an antipredator defence), while others (acyanogenic) do not (Ennos 1981). The ability to produce cyanogenic glucoside is controlled by the presence of an allele, *Ac*, at a single locus and cyanide release requires an active enzyme, linamarase. Plants of the genotype *li/li* at a second locus have no active linamarase, and only plants with the *Li* allele can release cyanide. The variability in phenotypes is thus caused by variability at two loci. A special category of genes with clear-cut, discrete inheritance patterns are molecular genetic variants, including **marker genes**. These will be described in more detail in Section 2.5.1.

Quantitative variability, on the other hand, is the situation when variability is more or less **continuous**, without distinctly demarcated phenotypic classes (e.g. Figure 2.1b). Such characters are often subject to strong environmental effects. Plant size, and size of plant parts, for example, are often heritable, but because many genes, as well as many environmental influences, can affect size, its genetic basis is difficult to discern. The genes underlying such **quantitative characters** are

Trait variation

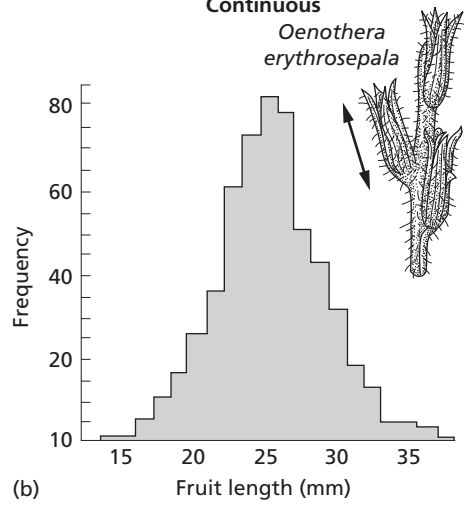
Between genotypes

Discontinuous



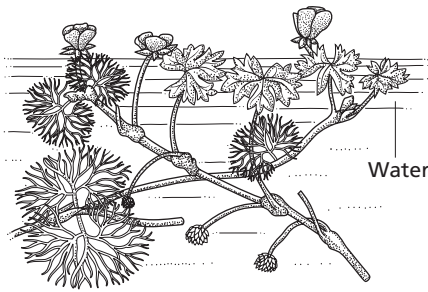
(a)

Continuous

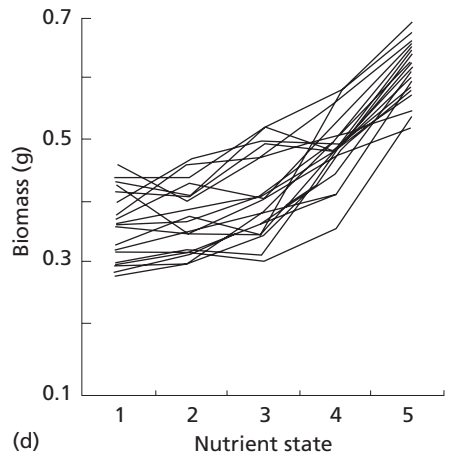


(b)

Within genotypes



(c)



(d)

Fig. 2.1 Types of plant trait. (a) Segregation of peloric snapdragon (*Antirrhinum majus*), a trait controlled by major gene variants. In this case the normal corolla is dominant to peloric. (b) Quantitative variation in length of fruit of the evening primrose *Oenothera erythrosepala*. (c) Heteromorphism in leaves of *Ranunculus heterophyllus*. (d) The reaction norm of plant size in response to a nutrient gradient for the progeny of 20 maternal families of *Abutilon theophrasti*. Each line represents the mean sizes for a family grown at different points along the gradient.

sometimes called QTLs (Quantitative Trait Loci). They have also been called polygenes, but this has misled people into thinking that there is a special kind of gene involved in the control of such characters. There is a large body of evidence suggesting that QTLs are normal Mendelian genes, that are carried on the chromosomes and segregate just like other genes, which can be mapped with respect to other loci in the plants' chromosomes (see, e.g., Falconer & Mackay 1996). Individual gene differences at QTLs do not affect the phenotype enough to stand

out above the environmental 'noise' in the character, and can be detected only by statistical approaches.

2.3 Genotype and phenotype

The phenotype expressed by a given genotype depends, to some degree, on its environment. A change in phenotype in response to the environment is called **phenotypic plasticity**. Most plant characters are phenotypically plastic to a greater or lesser extent. Discontinuous variation in a trait, for example between the floating and submerged leaves of aquatic plants (Fig. 2.1c) or the two kinds of flowers of cleistogamous species (Section 2.7.2.4) is known as **heteromorphism**, whereas a more or less continuous set of phenotypes expressed by a single genotype across an environmental range is called a **reaction norm** (Fig. 2.1d). MacDonald and Chinnappa (1989) investigated plasticity in five populations of *Stellaria longipes*. Means for 11 traits were generally different between populations, most of which proved to be the result of phenotypic plasticity. The phenotypic plasticity of a trait may itself have a heritable component and can be selected independently of the trait itself (Bradshaw 1965; Schlichting & Levin 1986; Sultan 1987). For example, the phenotypic response of plants to changes in light quality caused by shading from competitors is controlled by a family of phytochrome genes whose function and evolution is now well understood at the molecular level (Pigliucci *et al.* 1999; Mathews *et al.* 1995).

When phenotypic differences between genotypes vary between environments, this is called a **genotype \times environment interaction**. For example, in *Arabidopsis thaliana*, cold treatment of seeds or rosettes for about 4 weeks dramatically reduces the interval between germination and flowering (under a given light regime), for plants from some parents, but not others (Figure 2.2a, Nordborg & Bergelson 1999). Figure 2.2b illustrates one way to investigate genotype \times environment interactions. Twenty inbred lines of the poppy *Papaver dubium* were studied in 16 soils with different nutrient status (Zuberi & Gale 1976). For each trait, some environments yielded low means over all inbred lines, while others gave high overall means. The regression was calculated for each genotype's mean in the different environments against the means for all genotypes. When regression slopes differ significantly from one another, as in this example, this tells us that genotypes respond in different ways to environmental variation, i.e. genotype \times environment interaction occurs. When the regression lines cross each other, the 'best' genotype depends upon the environmental conditions. For one character, leaf number at 10 weeks, the genotype that produced the largest plants in the treatment with the best soil, produced almost the smallest plants on the poorest soil. All 11 quantitative traits studied showed significant genotype \times environment interactions.

Phenotypic variation can be separated into environmental and genetic variability by growing plants in a uniform environment such as a 'common garden'. Phenotypic differences between the plants should then be largely genetic, provided that precautions are taken to prevent the carry-over of environmental effects from the