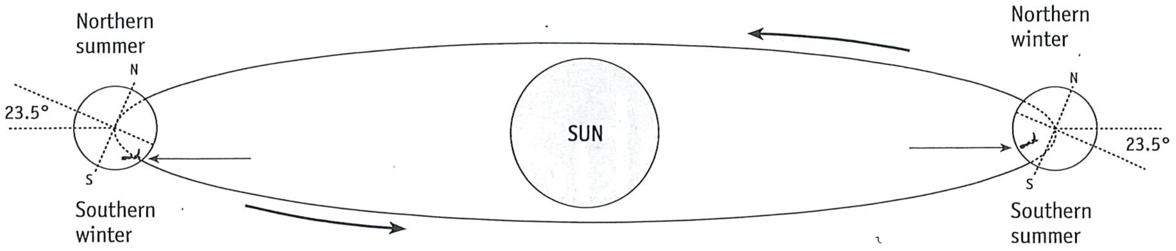

Fig. 3.1 On the right, the southern hemisphere is tilted towards the sun and on the left it is tilted away.

Preparation for reproduction begins long before the young are produced. In many birds and mammals the gonads (ovaries and testes) increase in size 50–100 times prior to reproduction, a process that takes between one and two months. On top of all this, many male birds have to compete for territories and mates well before mating. Plants, too, must begin their reproductive effort long before the offspring are produced; a young shoot switches from leaf to flower production long before the flower buds become visible.

For many animals, winter is a time to avoid, by *migration* or *hibernation*. Migration (Ch. 4) begins long before the winter sets in, and hibernation is preceded by the laying down of food reserves. In perennial plants, energy storage begins in late summer.

What all this means is that organisms must *anticipate* seasonal changes in order to take advantage of them. This requires advance information about the future; producing young at the wrong time could be disastrous. Of all the various physical factors, by far the most reliable cue is daylength, or **photoperiod**. The sensitivity of organisms to changes in day length is called **photoperiodism**.

Photoperiodism in plants

Plants show a number of seasonal changes in their growth, for example:

- Production of flowers.
- Formation of bulbs and tubers (induced by long days).
- Autumn leaf-fall in deciduous trees.
- Formation of winter buds during late summer in deciduous trees.
- Formation of runners in strawberry plants (induced by long days).

The fact that plants use photoperiod to tell the time of year was discovered early last century by two plant breeders, Wightman Garner and Harry Allard. They were working with a new tobacco variety called 'Maryland Mammoth', so-called because it grew up to five metres high. They were puzzled because under normal conditions (outside) it wouldn't flower. When they put the plants in a glasshouse, however, even small plants flowered. After experimenting with temperature, light intensity and other factors, they found that *photoperiod* was the stimulus for flowering. It became clear that short days were necessary to induce flowering, but outside the frosts of killed them before they could flower.

Garner and Allard investigated the flowering requirements for many other plants, and concluded that they could be divided into three types:

- **Short-day plants** (**SDP**) flower when the photoperiod is *less* than a certain **critical daylength** (**CDL**).
- **Long-day plants** (**LDP**) flower when the photoperiod *exceeds* the CDL.
- **Day-neutral plants** are insensitive to photoperiod, for example dandelion, garden pea, tomato. In these plants, flowering is under internal control. Many plants living in deserts are day-neutral. These habitats tend to experience short, irregular periods of heavy rain, so plants must grow and flower as quickly as possible.

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The CDL of an SDP may be more than 12 hours, and that of an LDP may be less than 12 hours. The CDLs of SDP and LDP may therefore overlap. For example henbane, an LDP, has a CDL of 11 hours and most varieties of *Chrysanthemum*, an SDP, have a CDL of about 13 hours. Since the CDLs of SDPs and LDPs overlap, could SDPs and LDPs flower at the same time? Actually no, because SDPs flower when days are *shortening* (autumn) and LDPs flower when days are *lengthening* (late spring or summer). Note that early spring-flowering perennials such as daffodil, tulip and other 'bulbs', and corms such as crocus, form their flower buds the previous autumn.

Conditions for flowering are actually more complicated, as photoperiodic requirements can be influenced by age of the plant, temperature, and other factors.

Most plants require a succession of several of the appropriate photoperiods to induce flowering. The process in which photoperiod stimulates the apical meristem to switch from vegetative to reproductive growth is called **photoperiodic induction**. This switch occurs long before the flower buds become visible; in daffodil and other spring-flowering bulbs, it occurs the previous autumn.

Plants actually measure night length

Garner and Allard's categorisation of plants as 'short-day' or 'long-day' turned out to be not quite right, as the following experiments showed.

Night interruptions

Fig. 3.2 shows the results of an experiment to distinguish between the effects of varying day length and night length. In A, SDP and LD are both given short days and long nights, and in B, plants are given long days. In C the treatment is the same as in A but the night is interrupted with a pulse of several minutes light. In D, long days are interrupted with a short period of darkness.

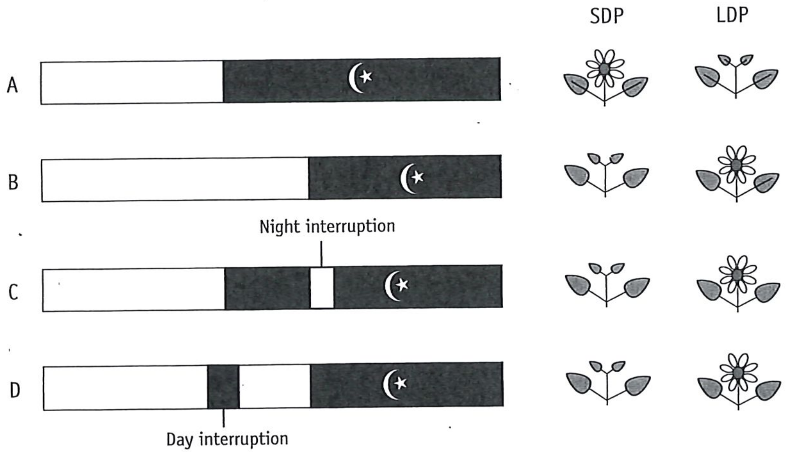


Fig. 3.2 Effect of a night interruption on flowering

Non-24-hour cycles

Cocklebur is an SDP with a CDL of 15.5 hours. When cocklebur plants were given cycles of 4 hours light and 8 hours dark, they did not flower, even though the 'day' was only a quarter of their CDL. With cycles of 16 hours light and 32 hours dark, they did flower, even though the 'day' was far longer than the CDL (Fig. 3.3).

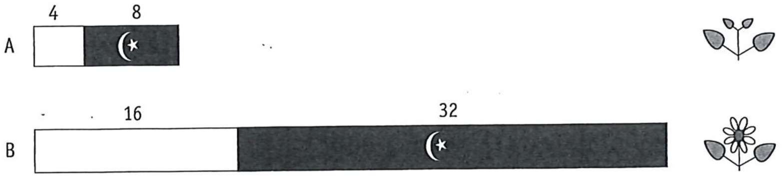


Fig. 3.3 Effect of non-24 hour cycles on flowering

The results of these experiments show that night length rather than day length is the important factor. *Short-day plants are thus really long-night plants*, and vice-versa for long day plants (Fig. 3.4). The trouble is that the terms 'short-day' and 'long-day' had become too well established to be changed.

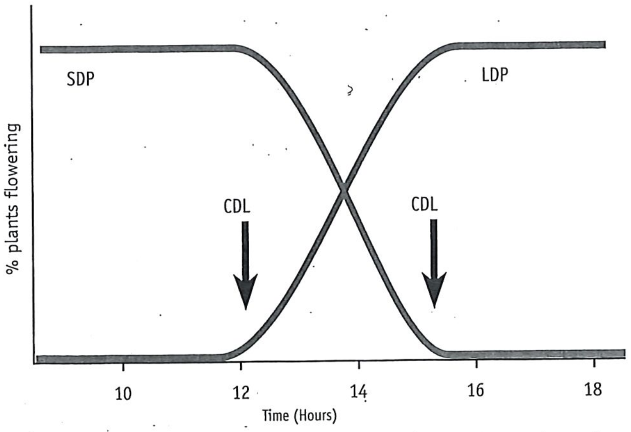


Fig 3.4 Critical day length in short-day and long-day plants

Sensitivity to a night break shows a circadian rhythm

Over 70 years ago, Erwin Bünning suggested that plants measure night length using a circadian clock. This far-sighted hypothesis

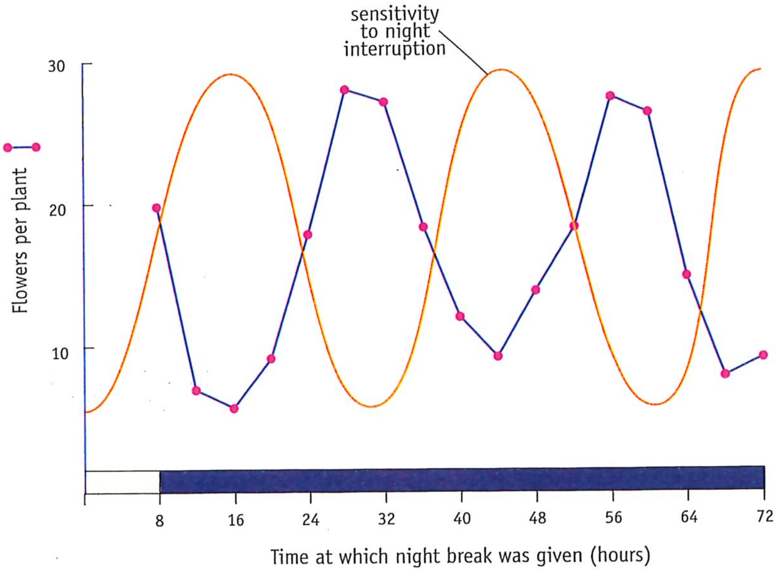


Fig. 3.5 Evidence that a circadian rhythm is involved in photoperiodic induction of flowering

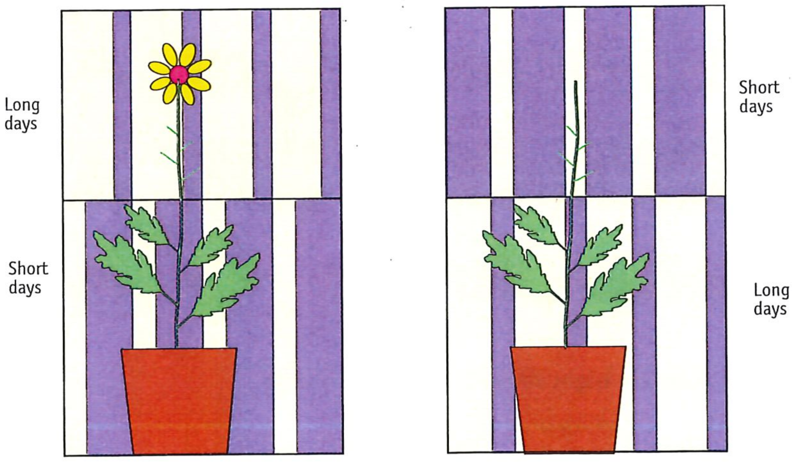
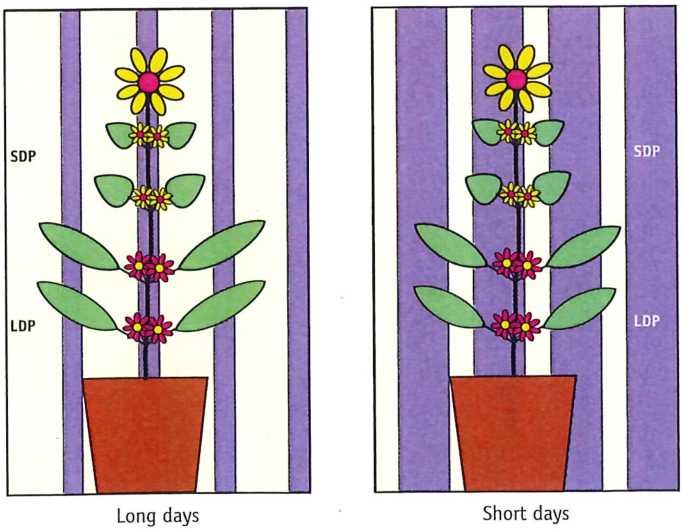


Fig. 3.6 Evidence that photoperiod is perceived by the leaves.



FFig. 3.7 Evidence from grafting experiments that the internal flowering signal is the same in SDPs and LDPs

has gained support from experiments in which light interruptions were given in very long nights.

Fig. 3.5 shows the results of an experiment in which soybean plants, which are SDP, were subjected to an 8-hour light period followed by 64 hours of darkness. The plants were divided into 17 groups, and each group was given one 30-minute light break at a particular time during the 'night'. The mean number of flowers produced was then plotted against the times at which the light breaks had been given. The number of flowers produced showed rhythmic rise and fall, the time between successive peaks being approximately 24 hours.

Bearing in mind that a light break inhibits flowering in an SDP, the inhibition of flowering in Fig. 3.5 is maximal when flowering is minimal. Thus the sensitivity to a light interruption is maximal when flowering is minimal (smooth line in Fig. 3.5). In an LDP the reverse is true; a night interruption promotes flowering, so the peaks of the curves for flowering and sensitivity to night interruption coincide.

Leaves detect photoperiod

By exposing different parts of a chrysanthemum (an SDP) plant to differing photoperiods it was found that the leaves are the receptive parts. The young shoots that are potentially capable of producing flowers are insensitive (Fig. 3.6).

In other experiments, closely related SDPs and LDPs were grafted together. Regardless of photoperiod, both parts were induced to flower, showing that the flowering signal transmitted from the leaves to the meristems must be the same for both SDP and LDP (Fig. 3.7).

The flowering 'signal' was named *florigen* in 1930, but it defeated attempts to identify it. All that was known was that it was transmitted at about the same rate as the sap in the phloem. Very recently, evidence has been obtained suggesting that the flowering hormone is a small globular protein called FT, which interacts with genes in the apical meristem, activating the flowering process.

The role of phytochrome

The sensitivity of photoperiodic responses to night interruption suggested a follow-up experiment. By comparing the effectiveness of different wavelengths (but equal intensities), some idea of the nature of the photosensitive pigment can be obtained. Fig. 3.8 shows the results of such an experiment. The graph is called an action spectrum. The fact that *red* light of wavelength 660 nm was the most effective night interruption showed that a *blue* pigment must be involved.

The peak effectiveness of 660 nm light was known to be characteristic of processes involving a pigment called **phytochrome**. This pigment was already known to be involved in a number of plant growth processes such as the germination of some kinds of seeds (see below).

A unique property of phytochrome is that it exists in two inter-convertible states, one absorbing red and the other far-red, at the extreme end of the visible spectrum. If night interruption does involve phytochrome, it should be cancelled out if it is immediately followed by far-red. This turned out to be the case (Fig. 3.9).

The form of phytochrome that absorbs maximally at 660 nm is called P_r because it absorbs mainly red light. The other is called P_{fr} because it absorbs maximally in the far-red region (730 nm). This can be shown graphically as an **absorption spectrum**. Light of different wavelengths is beamed through a dilute solution of the pigment, and the proportion of the light absorbed is measured (Fig. 3.10). Notice that the spectra overlap, so there can never be complete conversion of either form into the other.

When P_r absorbs red light it is converted to P_{fr}, and when P_{fr} absorbs far-red light it is converted to P_r. In the dark, P_{fr} is slowly converted back to P_r (Fig. 3.11).

Phytochrome is a soluble protein and has been extracted and purified. The P_r form is blue and the P_{fr} form is blue-green. It is a *dimer*, consisting of two polypeptide chains, one of which is synthesised in the chloroplasts.

Although sunlight contains both red and far-red light, it contains more red than far-red, so in sunlight most of the phytochrome will be in the P_{fr} form. Experiments have shown that the physiologically active form is P_{fr}.

How do plants measure photoperiod?

One early hypothesis was that the slow conversion of P_{fr} back to P_r acted as a kind of hourglass. According to this view, red light acted to re-invert the hourglass to start it going again. This hypothesis had to be abandoned, for two reasons:

- The reversion of P_{fr} back to P_r occurs within 2-3 hours. This is far too rapid to measure nights 6–16 hours long.

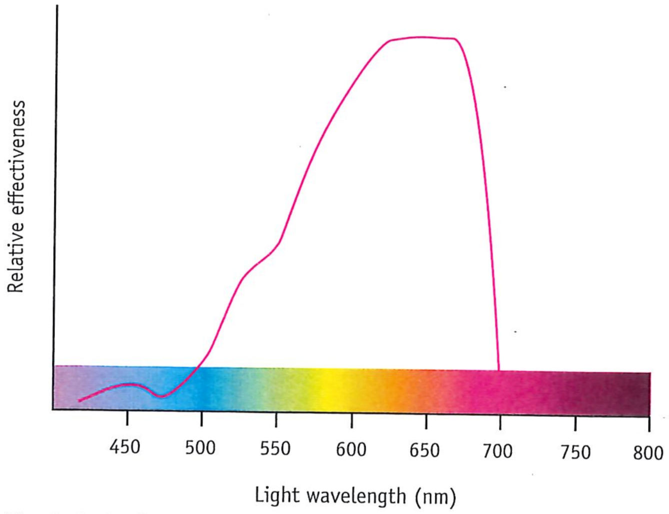


Fig. 3.8 Action spectrum for effectiveness of night interruption in inhibiting flowering in SDP and promoting flowering in LDPs

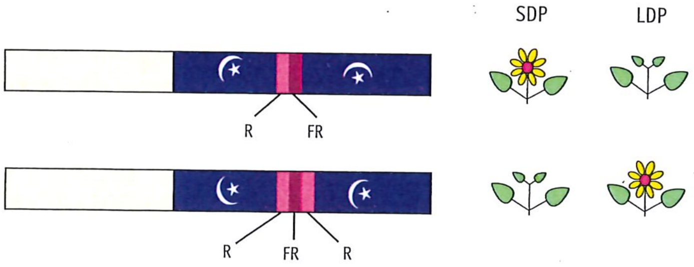


Fig. 3.9 When the night is interrupted by red light followed by far red, the effect is as if the red light has not been given: the far red light has nullified the effect of the red light

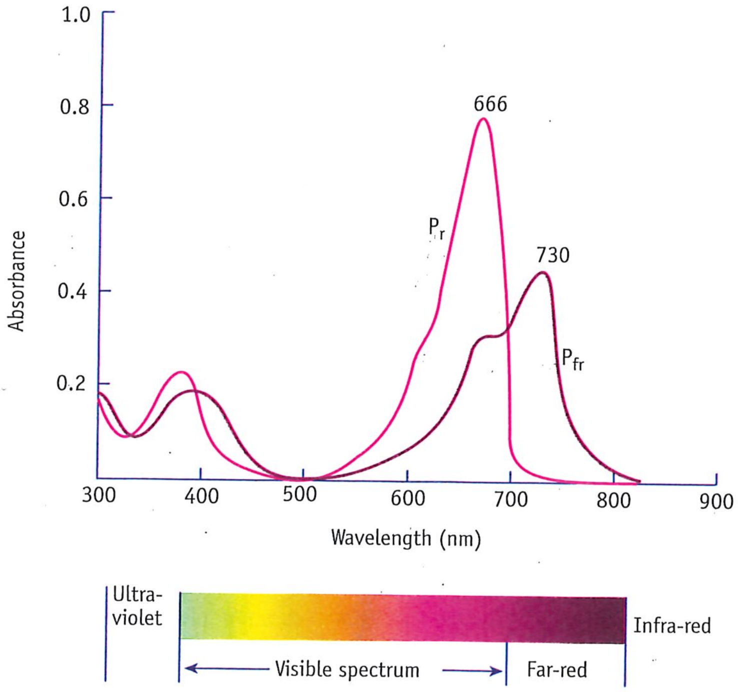


Fig. 3.10 Absorption spectra for P_r and P_{fr}

- The reversion is sensitive to temperature-sensitive, whereas critical daylength is not.

So, how does it work? As explained earlier, the induction of flowering involves rhythmic changes in sensitivity to light. Phytochrome is responsible for detecting the light, and P_{fr} is the active form of phytochrome. The key question is therefore: how does P_{fr} interact with the oscillator and trigger flowering? The details are not yet fully worked out, and what is known is too complicated for Year 13 (and me).

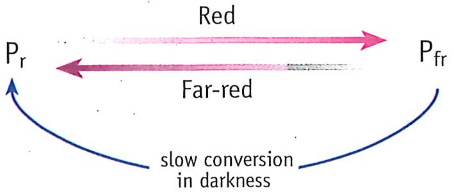


Fig. 3.11 Interconversion of P_r and P_{fr}

Ecological significance of flowering season

Most plants flower in spring, summer or autumn; only a few flower in winter. There are obvious advantages in this:

- Insect pollinators and animal dispersal agents are more active in warmer weather.
- The production of seeds (which are rich in energy, as are many fruits) requires a heavy input of energy from photosynthesis, which is favoured by warmer conditions.

Many wind-pollinated trees (e.g. oak) flower early in the year, before the leaves expand and when the air flows more freely. In these plants the extra organic material needed for reproduction has been produced the previous summer.

Phytochrome and germination

Although most seeds do not need light to germinate, some small *photoblastic* seeds do, for example foxglove and some varieties of lettuce. Once the seeds have absorbed water, a few minutes illumination with red light promotes germination. If the red light is followed by far-red, germination is inhibited, and if the far-red is followed by red light, germination is stimulated. In fact in an alternating succession of red and far-red, the last to be given determines whether germination is promoted or inhibited:

R	promoted
R — FR	inhibited
R — FR — R	promoted
R — FR — R — FR	inhibited
R — FR — R — FR — R	promoted

Why should the germination of some small seeds require red light and be inhibited by far-red? Small seeds only have enough stored energy to grow for a short period without photosynthesis, and so must germinate close to the surface. Far-red light is not useful in photosynthesis, but red light is. Light under a leafy canopy contains relatively more far-red than red light. It would thus be disadvantageous for a small seed to germinate with a leafy canopy above. When the plant creating the shade dies, much more red light reaches the seeds, triggering germination.

The phytochrome involved in flowering is actually one of a family of phytochromes, which are involved in various light-mediated processes.

Vernalisation

Besides photoperiod, some plants have another source of information about time of year. In carrots, swedes and other biennials, the first year's growth is vegetative, in which they store energy reserves. Flowering occurs in the second year, but only if the plant is first subjected to several weeks of cold (1–7° C), and some biennials fail to flower in the second year if the winter is too mild.

Promotion of flowering by chilling is called **vernalisation**. Many herbaceous perennials such as

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Michaelmas daisy and wallflower have a vernalisation requirement. Some plants require chilling followed by appropriate photoperiods to flower. Henbane, an introduced weed, requires long days to flower, but only if these are preceded by chilling (Fig. 3.12).

A vernalisation requirement is not limited to mature plants. Seeds of winter annuals such as some cereal varieties, are sown in the autumn and flower the following spring. If previously soaked seeds are chilled, they can be planted in the spring and flower the same year.

Unlike photoperiod, chilling acts directly on the apical meristem. Vernalisation is not to be confused with the chilling requirement that some seeds (such as sycamore), and winter buds, have to break dormancy. The breaking of dormancy by cold involves an increase in the *rate* of growth (i.e. a *quantitative* change), whereas vernalisation results in a change in the *kind* of growth (i.e. a *qualitative* change).

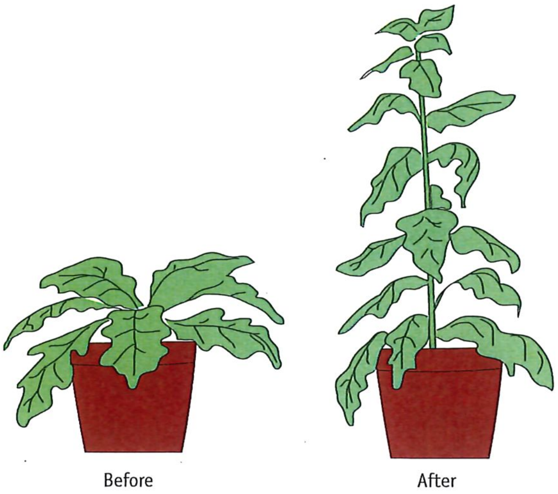

Fig. 3.12 Vernalisation in henbane

Bud dormancy in deciduous trees

Towards the end of the summer, the apical meristem of deciduous trees and shrubs begins to produce the buds that will open the following spring. The first leaves are on the outside of the buds and are the protective bud scales, and the inner leaves are the foliage leaves. These remain minute until they expand the following spring. During the winter, the buds remain in a dormant state, in which growth is inhibited by the hormone abscisic acid (ABA). Bud dormancy is broken by exposure to several weeks cold.

Photoperiodism in animals

Seasons exert a profound effect on animals, for several reasons:

- Directly or indirectly, animals depend on plant growth for food, and the rate of photosynthesis varies with seasonal changes in temperature and rainfall. Not surprisingly, seasonal changes in food supply are closely linked to the timing of reproduction.
- Animals are also directly affected by changes in physical conditions such as temperature and rainfall. Ectothermic ('cold blooded') animals become less active in cooler weather, and endothermic ('warm-blooded') animals need more energy in winter — yet their food supply decreases.
- Many Arctic mammals and birds undergo a change of coat to white, helping to blend against a background of snow.

Although some animals are adapted to endure such adverse conditions, many avoid them by taking evasive action, of two kinds:

- They may stay put, 'shutting down' almost all activity.
    - In winter this is called **hibernation** (e.g. bears, hedgehogs).
    - In summer drought it is called **aestivation** (e.g. land snails).
    - In many insects and other arthropods the suspension of activity is called **diapause**. Here the suspension of activity occurs at a particular stage of the life history.
- They may move out of the area altogether, by **migration**.

In all the above cases the animal begins to take evasive action well before times get hard. The environmental cue that tells them it's time to prepare is usually changing *photoperiod*.

Photoperiodism and reproduction

In most animals, as with most plants, young enter the world at the most favourable time of the year, when food is most abundant. The eggs of many marine animals hatch at about the same time as the 'bloom' of the phytoplankton (single-celled, photosynthetic organisms). Birds time their reproduction so as to synchronise the greatest demands of the young with the greatest availability of food. To achieve this timing, animals must begin their reproductive 'effort' long before the young arrive.

Annual rhythms can involve two quite different endogenous oscillators:

- Using a *circadian clock* to measure seasonal changes in daylength. This is the kind of mechanism occurs in many animals and in the photoperiodic control of flowering, and is called a **Type I** seasonal rhythm.
- Using a *circannual calendar* that under constant conditions has a period of about a year and gives rise to a **circannual** rhythm. This kind of cycle is called a **Type II** seasonal rhythm.

Most seasonal rhythms in animals are of Type I and are based on the effect of changes in daylength on a circadian clock. Fig. 3.13 shows the results of an experiment on Japanese quail, in which the birds were divided into nine groups. Each group was given 24-hour cycles of 6 hours daylight beginning at dawn, followed by 18 hours of darkness, interrupted by a 15 minute light break. The time of the light break varied in different groups, and for each group the increase in testicular size was measured over the next few weeks.

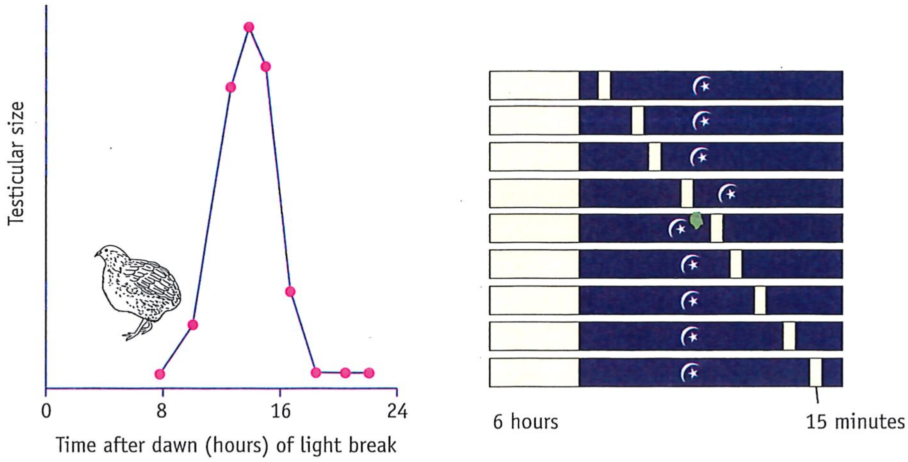

Fig. 3.13 The effect of 15-minute light breaks on the rate of testicular growth in Japanese quail kept under a six-hour photoperiod (After Follett and Sharp)

The results showed that the birds were only stimulated to come into breeding condition when the light break was between 12 and 16 hours after dawn, with peak sensitivity at 14 hours after dawn. Thus in the short days of winter, the photo-inducible phase would fall after dusk, but as the days lengthen it begins to occur in daylight.

How is photoperiod detected in birds? The photoreceptors are deep in the brain, and receive light directly through the skull — neither the retina nor the pineal is receptive to photoperiod. The photoperiodic signal is then transmitted via the SCN to the pituitary gland, which controls the ovaries and testes by hormones.

In mammals, photoperiod is detected by the retina and the information is transmitted to the SCN and then to the pineal gland. This produces the hormone *melatonin*, whose output rises at night and falls to zero in the daytime (Fig. 3.14). As daylength increases, the period in which melatonin is present in the blood gets progressively shorter, and vice versa as the days get shorter.

In sheep, ovulation occurs in short days (long nights), when melatonin is present for a higher proportion of each daily cycle. In hamsters the reverse is the case.

Melatonin does not act directly on the gonads; it first acts on the SCN, which then stimulates the pituitary to release hormones that stimulate the gonads.

Diapause

In their life cycles, many insects native to climates with a cold season pass through a period of arrested development called *diapause*. For example, in the black field cricket the eggs are laid in autumn but, even if the temperature is favourable, they will not hatch until they have been through a period of cold (Fig. 3.15).

In the cricket, external conditions are needed to break diapause; the eggs are already in that state when they are laid. In most insects diapause is initiated by an external signal, which is usually shortening photoperiod. In the cabbage butterfly, spring and summer generations do not enter diapause, but the pupae of the autumn generation do. The stimulus is shortening days in the last larval stage.

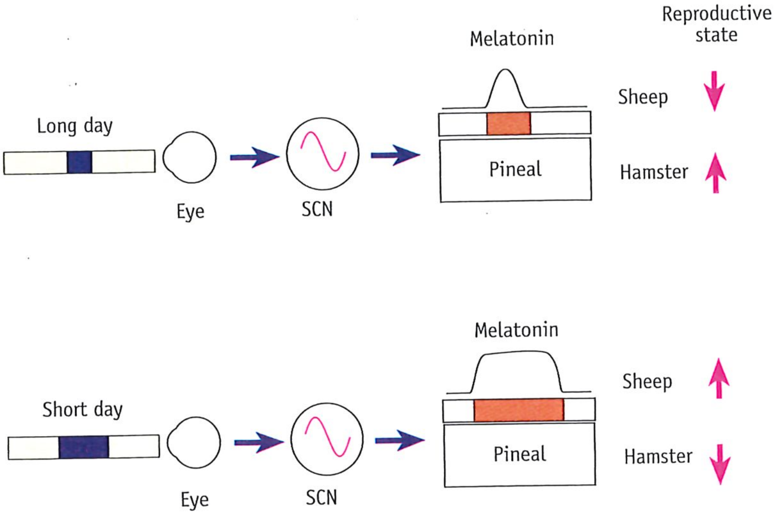

Fig. 3.14 Melatonin is the internal signal that controls reproductive activity in mammals

Circannual rhythms

Circannual rhythms are difficult to demonstrate, since the animals must be kept under constant conditions for several years. Usually they are kept under 12 hours light : 12 hours dark (12L : 12D). Despite these practical difficulties, a considerable number of mammals (e.g. sheep) and birds (e.g. starlings) have been shown to have circannual clocks, as have some seaweeds. Like circadian clocks, circannual oscillators must be entrained by external rhythms. It is believed that the annual *zeitgeber* is the rhythmic variation in photoperiod.

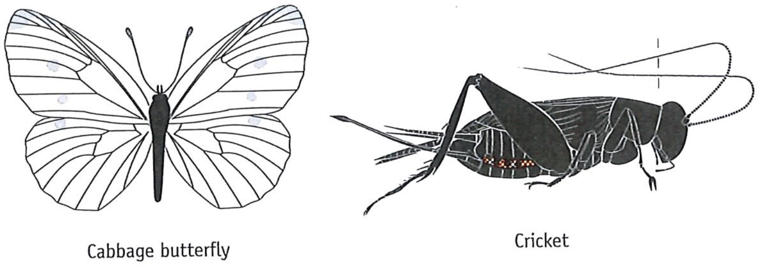

Fig. 3.15 Some insects showing diapause

Summary of key ideas in this chapter

- ○ Many seasonal activities, such as flowering, are controlled by daylength.
- ○ The terms 'short-day plant' and 'long-day plant' were coined before it was discovered that plants actually measure the length of the night.
- ○ Measurement of night length by plants involves a circadian clock.
- ○ Photoperiod is perceived by the leaves and the stimulus transmitted to the meristems via the phloem.
- ○ The signal transmitted from leaves to meristems is the same in short-day and long-day plants.
- ○ The pigment responsible for absorbing the photoperiodic stimulus in plants is *phytochrome*.
- ○ Phytochrome exists in two photo-reversible states, P_r and P_{fr}. P_r is converted to P_{fr} by red light and the reverse reaction is brought about by far-red light.
- ○ Phytochrome is involved in many other plant processes besides flowering.
- ○ Some plants require a period of cold before they will flower.
- ○ Many seasonal activities in animals, such as hibernation and migration, are controlled by photoperiod.
- ○ Most seasonal rhythms in animals are under control of a *circadian* clock, but some are regulated by a *circannual* rhythm or internal 'calendar'.

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Test your basics

Copy the following, filling in the missing words.

1. The seasons are the result of the ___*___ of the earth's ___*___ with respect to the ___*___ of its ___*___ round the sun.
2. One of the most important aspects of the seasons is the regular rhythm of daylength or ___*___.
3. In short-day plants, flowering is induced when the photoperiod is ___*___ than a certain critical value. In long-day plants the critical photoperiod must ___*___ a certain value. In ___*___ ___*___ plants, flowering is insensitive to photoperiod.
4. Long-day plants normally flower in ___*___ or late ___*___. Short-day plants produce flowers in the ___*___, when photoperiod is ___*___.
5. The critical factor in inducing flowering is actually the length of the night, so in short-day plants the night must ___*___ a certain length.

In plants, photoperiod is detected by the ___*___, and the signal is then communicated to the ___*___ ___*___ by a substance that was called ___*___, and has since been identified as a small globular ___*___.

An important component of the photoperiod-detecting mechanism is a blue protein called ___*___. This can exist in either of two inter-convertible states. One absorbs maximally in the ___*___ region of the spectrum and is called P_r, and the other absorbs maximally in the ___*___ ___*___ region and is called P_{fr}

6. Some plants require exposure to a period of cold to flower; this process is called ___*___.
7. In animals, photoperiodism plays a key part in seasonal behaviour such as m___*___, h___*___, and changes in coat c___*___ and t___*___.
8. When animals cease activity during a period of cold, this is called ___*___. Surviving a period of dryness by ceasing activity is called ___*___. Many insects survive the cold season by ceasing activity during a particular stage of the life cycle; this is called ___*___.