REVIEW ARTICLE

Aspects of seasonality

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Abstract

The seasons are astronomical, astrological, meteorological, biological, and agricultural. From a perspective outside the biological sciences, the questions of interest about plant seasonality are linked to this wider context. In this review I try to see flowering time, as one important aspect of seasonality, from an outsider’s point of view, and describe what is known about it in different types of plants. What is known about it is conditioned by what particular scientists have asked about it, so the variety of approaches to seasonality is another point of emphasis. Detailed consideration is given to flowering seasonality in perennials compared with annuals, and both molecular and whole plant perspectives are presented.

Key words: Seasonality, flowering time, annuals, perennials.

Now all the knowledge of the heavens pertinent to Agriculture, standeth principally upon three sorts of observations, to wit, the rising of the fixed stars; the setting of the same; and the four cardinal points, to wit, of the two Tropickes or Sunsteads, and the double Aquinox, which divide the whole year into four quarters and notable seasons.

Pliny

Introduction

Seasonality refers to both a regularly changing environment and the biological responses conditioned by that environment. Agricultural practices are strongly related to the changing seasons, as are cultural events: for example, great efforts have been made historically to keep religious calendars synchronized with the seasonal cycle. Seasonality is, therefore, an interesting topic because it converges a variety of ways of viewing the world.

Plant growth and development is entrained by the seasonal cycle, and so the seasons act as a natural integrator. Research aimed at understanding the mechanisms behind this entrainment has tended to partition the plant response cycle, subdividing it into dormancy, flowering, fruiting and so on. More recently, as molecular information has become increasingly detailed, each division has been further subdivided. However, flowering time genes can also control flower development (Simpson et al., 1999), and genes from families associated with flower development regulate aspects of fruit development (Liljegren et al., 2000). Molecular biology and genomics research therefore emphasizes the need for more integrated understanding. This was the objective of a previous generation of seasonality/phenology researchers: to provide a complete description of the response of plants and animals to their environment (see, for example, Lieth, 1974). Here a perspective on whole plant responses to seasonal change is proposed and the integrative approach is given some substance by linking it to advances in molecular understanding in Arabidopsis. The focus is on the flowering aspect of seasonality, particularly on the links between flowering time strategies in annuals and perennials.

Seasons and time: methods of time measurement are closely related to seasonality

The Northumbrian monk the Venerable Bede (AD 673–735) provided, in The Reckoning of Time, an account of the intricacies of time measurement (Bede in Wallis, 1999). The book is full of reference to the seasons, showing how they have been crucial for time reckoning throughout history. The Giuli months of the Anglo-Saxon English (now known as December and January), take their name from the day when the sun turns back from its passage towards the southern horizon and starts to increase in height again; several of the other old English month names relate to seasonal activities: Thrimilchi (May) records the fact that in that month the cattle could be milked three times a day; Weodo monath (August) means ‘month of tares’, which were abundant at that time of year. To keep the lunar calendar

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synchronized with the solar year, an extra month was intercalated in summer as necessary, in so-called 'embolismic' years.

Later, further trouble arose from the need to reconcile the seasons with time. When September 2 was followed by September 14 in 1752 there was rioting on the streets of Britain ('Give us back our 11 days!'); the country had belatedly accepted the change from the Julian calendar, in which leap years occurred every fourth year, to that of Pope Gregory XIII, who in 1582 had limited the century years that could be leap years to those that were divisible without remainder by 400. Hence 2000 is a leap year; 1900 was not (O'Neil, 1975). This adjustment was necessary because the time it takes for the Earth to travel once around the Sun is not a whole number (it is 365.2422 d); calendars without leap year adjustments lose track of the seasons. On a more local scale, the movement of the sun provided the earliest methods for time reckoning: first simply as day/night, later using a sundial to divide the daylight period. Up until the middle ages 'seasonal hours' were still in use, in which the day (and night) was divided into 12 parts throughout the year, so that in summer the daylight 'hour' was longer than in winter. The calculation of seasonal hours was made precise by the use of the astrolabe, described in detail by Chaucer (North, 1988), but the ancient Egyptians also used a similar convention: daylight 'hours' were 75 min in summer, but only 55.5 min in winter; night-time 'hours' were 45 min in summer and 69.5 min in winter (O'Neil, 1975). The seasons have, therefore, been closely bound up with the measurement of time, but their precise definition is not straightforward.

Defining the seasons: by constellations, weather, and plant and animal activities

There are many ways to measure the seasons. In old England there used to be only two seasons: summer, the six months in which the days are longer than the nights; and winter (Bede in Wallis, 1999). Now, most people would think of four seasons, spring, summer, autumn, and winter. In the northern hemisphere the astronomical first day of spring is the vernal equinox on March 21, when the day and night lengths are equal and the sun rises due east and sets due west: an important day indeed, which until relatively recently marked the beginning of the year in England and was contained in the first month in the original Roman year. The summer solstice on June 21 marks the first day of astronomical summer in the northern hemisphere, and is the time when the sun rises and sets furthest north and casts the shortest shadow at midday. Similarly, the autumnal equinox and winter solstice represent the astronomical beginnings of autumn and winter. On the other hand, meteorologically speaking, over much of the northern hemisphere December to February is winter; March to May, spring; the three warmest months, June, July and August are summer, and autumn falls from September to November. These meteorological seasons are, in a sense, most important for those societies in which the seasons relate to the yearly cycle of food production from the land; and also to biological seasonality, one of the main concerns of this review. The Chinese half-month phenological calendar, with sections with names such as ‘Awakening insects’ (6/3), or ‘Clear and bright’ (5/4), illustrates the way biological changes synchronized to seasonal weather have been employed as time markers (Lamb, 1964). Similar records have been widely documented in many different countries over the centuries (Table 1). However, the biological seasons do not just track the meteorological seasons: there is a detectable periodicity in atmospheric CO₂ which is attributed to seasonality of photosynthesis (Keeling et al., 1996).

Probably the most ancient systems that track the seasons are astrological, in which the movement of the sun is followed through the zodiacal constellations. The moon and planets are always close to this 'ecliptic' path, and it is natural to notice the constellations through which the ecliptic passes during the year (Fig. 1). The vernal and autumnal equinoxes occur when the ecliptic crosses the celestial equator, so linking stars, sun and earth through the passage of time. The names of our weekdays, and the fact that there are seven of them, probably reflect astrological assumptions concerning the significance of the sidereal periods of the planets (Table 2; Neugebauer, 1952).

Hesiod, in about 750 BC records how some stars, and their conjunction with the sun, were used as a marker for the seasons:

Pleiades rising in the dawning sky,
Harvest is nigh.
Pleiades setting in the waning night,
Ploughing is right.
Forty days and nights in the turning year
They disappear.
When they shine again in the morning shade,
Sharpen your blade.

Table 1. Flowering dates

The following list of the average first dates for the flowering of common plants and trees in south-east England is taken from the Royal Meteorological Society’s Phenological Report (1949–50), prepared by Major HC Gunton, MBE.

<table>
<thead>
<tr>
<th>Plant</th>
<th>Date</th>
<th>Native Plant</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hazel</td>
<td>Jan 9</td>
<td>White ox-eye</td>
<td>May 5</td>
</tr>
<tr>
<td>Coltsfoot</td>
<td>Jan 31</td>
<td>Elder</td>
<td>May 10</td>
</tr>
<tr>
<td>Wood anemone</td>
<td>Mar 2</td>
<td>Dog rose</td>
<td>May 23</td>
</tr>
<tr>
<td>Garlic hedge mustard</td>
<td>Mar 31</td>
<td>Greater bindweed</td>
<td>June 13</td>
</tr>
<tr>
<td>Horse chestnut</td>
<td>April 20</td>
<td>Harebell</td>
<td>June 21</td>
</tr>
<tr>
<td>Purple lilac</td>
<td>April 22</td>
<td>Madonna lily</td>
<td>June 21</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>April 25</td>
<td>Autumn crocus</td>
<td>Aug. 14</td>
</tr>
<tr>
<td>Laburnum</td>
<td>April 27</td>
<td>Ivy</td>
<td>Sept. 1</td>
</tr>
</tbody>
</table>

*after Inwards, 1950.
Fig. 1. Passage of the ecliptic through the zodiacal constellations (based on Klepestr a and Rükl, 1969). ♈—Aries; ♉—Taurus; ♊—Gemini.

Table 2. The stewardship of the days

Explanation of the order of the planetary names for the weekdays. Each hour is supposed to be controlled successively by the planets in order of their sidereal periods (time taken to return to a specified position in the fixed stars—Saturn longest, The Moon shortest). Each planet has stewardship over the day whose first hour it controls.

<table>
<thead>
<tr>
<th>Planet</th>
<th>Hours in the day</th>
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<tbody>
<tr>
<td>Saturn</td>
<td></td>
</tr>
<tr>
<td>Jupiter</td>
<td></td>
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<tr>
<td>Mars</td>
<td></td>
</tr>
<tr>
<td>The Sun</td>
<td></td>
</tr>
<tr>
<td>Venus</td>
<td></td>
</tr>
<tr>
<td>Mercury</td>
<td></td>
</tr>
<tr>
<td>Moon</td>
<td></td>
</tr>
</tbody>
</table>

Equivalent gods in Teutonic/Roman mythologies are Twia/Mars; Woden/Mercury; Thor/Jupiter; Frigga/Venus. Hence Tuesday, Wednesday, Thursday, Friday in English.
Although the fanciful linkage of zodiacal constellations to ‘starsigns’ has exposed astrology to ridicule, prediction based on the stars can be useful in agriculture; Andean farmers in the sixteenth century used the apparent brightness of the Pleiades to forecast drought associated with El Niño years (Orlove et al., 2000). Star monitoring tries to connect the heavenly and earthly worlds, also an ambition of science (Lindsay, 1972). But Hesiod illustrates, by the range of examples he derives from agricultural practice, how a combination of characters—stars, climate, time, and phenological events themselves—really define the seasons. Knowing how plants respond to the sequence of environmental changes through the year is therefore an important topic, not just for the plant sciences, but also because of the role of plants in daily life: this aspect of seasonality forms a bridge for public understanding (Fig. 2).

**Bud-burst and spring flower emergence: dormancy plays a key role in flowering time**

The sense of seasons changing is probably strongest in early spring, when the sudden acceleration of biological activity matches the rapid change in daylength around the equinox (Fig. 3). And the clear impression is that flowering time is bud-burst time. In some cases, for example, hawthorn and rowan, leaves appear before flowers; in others, like blackthorn, pear and willow, the flowers are first visible. But the timing difference is relatively small. So for a big group of perennials, and those most strongly associated with spring seasonal change, the mechanisms that control flowering time are those that control bud-burst. The young leaves and flower initials have overwintered in the buds and are ready to form the new shoots and flowers when warm temperatures return. What are the mechanisms that schedule when these buds go dormant in winter? And why do species differ in the timing of renewed growth? These questions have exercised the minds of generations of physiologists, but although the environmental responses could be described as broadly being understood, the understanding of mechanisms controlling these has remained rudimentary.

The onset of bud dormancy in many temperate trees follows flower initiation and is typically accelerated by decreasing photoperiod (Wareing, 1956; Vaartaja, 1959; Thomas and Vince Prue, 1997), although other environmental factors, including nutrient stress and low light intensity can also play a role (Noodén and Weber, 1978). Interestingly, although temperature can affect the onset of bud dormancy, this is often because of an interaction with photoperiod (Heide, 1974). Apparent exceptions to the rule that dormancy is promoted by short photoperiods are fruit trees like apple, pear and cherry, in which it seems to be entirely controlled by endogenous factors (Wareing, 1969; Thomas and Vince Prue, 1997). In bulbs like narcissus and tulip photoperiod effects on dormancy are also absent, and it is initially a consequence of meristem position due to apical dominance (i.e. correlative effects). It is also worth noting that in many trees environmental effects may best be considered as moderating the rate of onset of the dormant phase of an endogenous cycle, rather than triggering dormancy. Thus, Noodén and Weber comment that ‘mature trees in the North Temperate zone cease elongation and develop dormant-type buds long before unfavourable weather occurs or the critical daylength for the induction of dormancy is reached’ (Noodén and Weber, 1978). A similar interpretation can be made for herbaceous perennials like *Chrysanthemum*, in which some buds are saved from flowering, apparently by entering a dormant condition (see below and Vince Prue, 1975).

Rees provides an illuminating approach to the origins and regulation of the dormant phase, illustrated by bulbs (Rees, 1981, 1989). Such herbaceous monocots are envisaged as evolving in the relatively uniform environment of the moist tropics. Here continuous growth is possible; dormancy would be imposed upon meristems not by the environment but by endogenous factors, for instance apical dominance. When the plant encountered a more seasonal climate, this correlative dormancy would provide a basis for survival under unfavourable conditions. More complex, environmentally regulated ‘innate’ dormancy might then be superimposed, accompanied by the development of storage tissues and other morphological adaptations associated with the resting condition. On release from this dormancy by appropriate environmental conditions (such as low temperature), the meristem would remain in a state of ‘imposed’ dormancy, in which growth awaits only the arrival of favourable conditions (Rees, 1981, 1989). This view of the origins of different phases or types of dormancy finds an echo in the categories proposed by Lang and co-workers (Lang et al., 1987): ‘paradormancy’ is approximately equivalent to correlative dormancy, ‘endodormancy’ to innate dormancy, and ‘ecdormancy’ to the final phase of imposed dormancy. It is also consistent with the idea that environmental control is superimposed upon an endogenous cycle of growth that includes a resting or dormant phase. Even plants that grow in relatively uniform climates, like oil palm and banana, and apparently have no seasonality and no dormancy, have apical dominance and correlative inhibition of meristem growth.

In conceiving of mechanisms of bud dormancy, ideas that stressed the metabolic restraint (O₂ reduction) on buds during dormancy (Vegis, 1964) were eclipsed by those favouring hormonal control—either the absence of growth factors, or the presence of inhibitors like abscisic acid (summarized in Wareing and Saunders,
Fig. 2. Illustration for the month of June from the Rohan Master Book of Hours, a prayer book based on the calendar of religious events through the year. The illustrations in such medieval prayer books represented the work of the season: here a peasant mows a meadow. The crayfish in the sky represents the zodiacal sign of Cancer. The marginal painting depicts the tree of life in the Garden of Eden, in this case bearing human heads instead of fruit. (Reproduced from the Rohan Master Book of Hours.)
1971). However, from the current perspective, it is the emphasis that Vegis laid on the changing response of buds to temperature that seems most useful: dormancy places a restriction on the temperature range over which buds will grow; dormancy release widens this temperature range (Vegis, 1973). This provides a foundation for an analysis of the way in which the environment allows bud growth in the spring.

The review by Cannell provides an excellent summary of the approaches that have been used to disentangle the two principal responses that determine bud-burst and flowering time in spring: the breaking of dormancy by chilling; and the effects of temperature on subsequent growth during early spring (Cannell, 1989). Chilling is a rather ill-defined, but much used word, typically referring to temperatures below about 10 °C that act to release perennial plants from dormancy. The optimum chilling temperature is usually around 2–4 °C. After chilling has broken dormancy, buds will start to grow provided temperatures are warm enough. In both dormancy breaking and spring growth, temperature therefore has a key role; photoperiod can also be important, but it is usually critical only when chilling requirements are not satisfied (Wareing, 1956). In general, it seems that long photoperiods can at least partly compensate for lack of chilling (Campbell and Sugano, 1975; Campbell, 1978; Cannell and Smith, 1983; Nizinski and Saugier, 1988).

Cannell focuses on the response to temperature, and places the research approaches to explain the flowering time (bud-burst) of trees, into three main groups, as follows. Some methods simply use thermal time accumulation (above a base temperature). A second group of methods considers that there are distinct physiological phases (for example, pre-dormancy, dormancy and post-dormancy—see also Lang et al., 1987, as discussed above); the temperature response of each then needs to be defined. The chilling requirement becomes the key parameter, and the plant is envisaged as passing through the dormant phase as a result of chilling, and then entering a new phase of spring growth which has its own, separate temperature response that in the end leads to bud-burst and flowering (Richardson et al., 1974; Kobayashi et al., 1982; Kobayashi and Fuchigami, 1983). This kind of thinking, to derive so-called ‘chill unit’ models, has been applied to numerous species, particularly perennial fruit crops like strawberry and cherry (Battey et al., 1998; Mahmood et al., 2000a, b). Its problem is that developmental phases (or physiological states) like dormancy and post-dormancy are clearly part of a continuum and it is very hard to define the beginning or end of each (Seeley, 1996). This is where Cannell’s third group of methods is attractive: they assume a continuous, changing response to temperature from autumn, through to spring flowering, so that the need for chilling temperatures is related to the thermal time requirement for flowering. As chilling proceeds, this thermal time decreases progressively. Methodologically, a similar approach to that adopted to derive ‘chill unit’ models can be used, so that after varying chilling periods thermal time to flowering is recorded. But the analysis hinges on the relationship

Fig. 3. Change of daylength during the year at latitudes 0°–60° (after Withrow, 1959).
between chilling and time to flowering; chilling progressively increases subsequent bud growth rate (Fig. 4a). Characterizing the response of chilled buds to a range of temperatures shows this clearly (Fig. 4b).

Cannell adopted this third approach, and designed experiments to predict bud-burst time and the effects of climatic warming on bud-burst in trees. This built on earlier analysis of the responses of Douglas fir to climate (Campbell, 1978). As could be anticipated from the foregoing discussion, the effects are complex, depending on the thermal time and chilling requirements of each species (Murray et al., 1989). Species like *Fagus sylvatica* (beech) have a large chilling requirement and thermal time for bud-burst (they burst buds in late spring). Climatic warming, by reducing the chilling accumulation, would increase the thermal time required for bud-burst (making the buds burst even later). Species like *Crataegus monogyna* (hawthorn), on the other hand, have a small chilling requirement easily met by the British climate; climate warming would in these cases cause earlier bud-burst. Actual data from the European phenological gardens reveal a general tendency for earlier bud-burst in spring and later leaf fall in autumn over the last 20 years (Menzel and Fabian, 1999). Most of the seasonal lengthening can be attributed to warmer temperatures.

**Fig. 4.** (A) Relationship between the rate of growth to budburst and previous chilling history (data for *Pseudotsuga menziesii* from Campbell and Sugano, 1975, 1979; presentation as by Cannell, 1989). (B) Chilling increases the rate of bud growth as a function of temperature in *Pseudotsuga menziesii* (after Campbell, 1978; Cannell, 1989).

**Patterns of flower initiation in annuals and perennials: their significance and relation to the yearly cycle**

In most annual species flower initiation (the morphological changes at the meristem which change it into a flower) is followed without arrest by flower emergence. There are examples of different environmental cues for flower initiation and emergence but in many cases, in particular *Arabidopsis thaliana*, in a constant environment flower emergence is taken to reflect flower initiation time. The control of flower initiation by daylength, temperature or other factors can therefore be considered to be directly adaptive, acted on by selection to ensure flowering and fruiting at an optimum time, and within one growing season. Classic examples include the cereals, in which species of tropical origin (rice, sorghum, maize) are short-day plants, and specific landraces, for instance of sorghum, respond to short days so that heading occurs at the end of the rainy season (Curtis, 1968; Bunting and Pickersgill, 1996). Cereals of temperate origin (e.g. wheat, barley, rye) are typically long-day plants, and this causes heading during spring and early summer, so that the crop ripens towards the end of the growing season (Roberts, 1991; Roberts et al., 1997). A vernalization requirement, in which a period of cold temperature is needed for flowering in subsequent inductive conditions, allows the plant to establish in the autumn without flowering and to adopt the winter annual strategy.

In woody perennials, particularly those of temperate origin, there is a noticeable tendency for a delay between flower initiation and emergence. This is true for conifers and most tree fruit crops (Sedgley and Griffin, 1989) and also of herbaceous perennials like *Fragaria vesca* (see below), as well as many bulbous plants. There are exceptions, for instance pecan and kiwifruit, which initiate flowers immediately before emergence (Sedgley, 1990), but if not a rule it is certainly a common feature. Further, the process of flower initiation is less obviously under the control of the environment than in the annuals described above. This may be because the timing of flower initiation bears less relation to flowering and fruiting time and is, therefore, not under such direct selective pressure. The processes leading to spring bud-burst, described in the preceding section, are probably where the focus of selective pressures regulating flowering times has acted in these perennials. Of potential value in understanding the molecular basis for dormancy and time to bud-burst are the non-dormant hazel mutants, in which a single gene controls the dormancy character (Thompson et al., 1985).

The annual habit is considered by some to have evolved from the perennial (Corner, 1964). It has been suggested that *Lolium temulentum*, the ‘tares’ of the bible and Weodmonath, evolved from a perennial progenitor
(requiring vernalization) into an annual, under the intense selection pressure associated with being a weed of cereal fields (Gay and Thomas, 1995). The accompanying review nicely shows how closely and quantitatively related the two habits can be, indicating that switching between the two may have occurred many times during evolution (Thomas et al., 2000). This is also suggested by those plants with something of both habits in their flowering behaviour. Biennials like beet, foxglove and carrot represent a halfway-house between annual and perennial: they can often be converted to a perennial habit if prevented from flowering (Harper, 1977). They are interesting because overwintering achieves vernalization, as in winter annuals, but the biennial habit is typically monocarpic, so there is no mechanism to conserve meristems for future years, something central to the habit of most true perennials. There are also herbaceous perennials like *Chrysanthemum*, which have a vernalization/devernalization cycle and initiate flowers in response to short days in the same year as flower emergence (Cockshull, 1985; Yahal et al., 1985). In this case devernalization may result from inhibited growth and may be similar to endogenous bud dormancy, characteristic of apple (Vince Prue, 1975).

In perennial forage grasses and clovers, flowering patterns are governed by a combination of photoperiod and cold requirements differently developed in different genotypes. For example, in *Lolium perenne* the cold requirement differs between varieties and this influences the seasonal pattern of flowering; varieties with a high cold requirement do not initiate flowers until early spring, whereas a low requirement allows flower initiation in winter (Aitken, 1985). On the other hand, in *Trifolium pratense* (perennial red clover) varietal differences in photoperiod response cause flower initiation either in late winter or late spring.

A herbaceous perennial which has a number of attractive features for the study of seasonal flowering is the strawberry, *Fragaria*. There is a well-defined cycle of flower initiation, under clear environmental control (making it similar, in this respect, to annuals); but there is also a defined period of winter dormancy, chilling that promotes vegetative growth, and a flower emergence and fruiting phase. The environmental control of the yearly cycle has been intensively studied in the octoploid, commercially important ‘Junebearing’ cultivars of strawberry (*Fragaria × ananassa*) and provides useful background for an analysis of the molecular mechanisms that underlie seasonality of flowering. Figure 5 shows the main events in this seasonal calendar. Flower initiation in late August/early September is induced by cool temperatures and shortening photoperiods. Initiation continues until autumn temperatures become too cool to sustain growth. From September the plants start to enter dormancy so that by late October it is at a maximum. Winter chilling has two principal effects: it removes dormancy, so that when warm conditions return in the spring the plants have renewed vegetative vigour. Second, it switches off flower initiation. Chilled plants appear to be insensitive to inductive conditions after chilling, offering an explanation for the failure of plants to initiate flowers during the spring. The autumn-initiated flowers emerge in the spring, and after anthesis in May, the fruiting period is accompanied and followed by runner production, a response to long days. During August as daylength shortens, branch crown formation takes over from runner production; branch crowns form new growth axes within the parent plant, and represent an alternative strategy of vegetative reproduction. Branch crown production is a photoperiod-induced response, and has the effect of maximizing the sites for flower initiation when this begins again in September. (This summary is based on data in Guttridge, 1985; Le Miére et al., 1996, 1998; Tehranifar et al., 1998; Battey et al., 1998.)

**The molecular basis for seasonal flowering**

*Fragaria vesca* has some advantages for the molecular analysis of flowering seasonality (Battey et al., 1998; Table 3), and a similar yearly cycle to the octoploid strawberry can be inferred (Brown and Wareing, 1965; Battey et al., 1998). Seasonal flowering is characteristic.

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**Fig. 5.** The seasonal calendar of *Fragaria*. 
of *F. vesca* and is conferred by the dominant allele of a single gene. The alpine type, *F. v. semperflorens*, has the recessive allele and is overflowering (Brown and Wareing, 1965; Battey *et al.*, 1998): in this situation the annual cycle shown in Fig. 5 is modified; flowers are initiated during the growing season as well as in the autumn. Runner production is very infrequent and instead branch crowns are produced freely. The exact roles of dormancy and chilling are not clear: it seems that flower initiation is not prevented by winter chilling as it is in seasonal flowering *F. vesca*. In primocane fruiting varieties of raspberry, which can be considered similar to overflowering strawberries (Carew *et al.*, 2000a), chilling not only breaks dormancy, but can also be separated from a vernalization effect on flower initiation (Carew *et al.*, 2000b).

In considering how the seasonal cycle of flowering is controlled in *F. vesca* and other perennials like it, it is useful to look for clues from the genetics of flowering time in the model annual, *Arabidopsis thaliana*. Progress in this field has been reviewed frequently (Levy and Dean, 1998; Simpson *et al.*, 1999; Reeves and Coupland, 2000); just two features of particular interest will be highlighted here. First, late flowering *Arabidopsis* ecotypes have dominant alleles at the *FRIGIDA (FRI)* locus (Fig. 6a). These alleles delay flowering, but their effects can be overcome by vernalization. Variation at the FRI locus is a major determinant of flowering time and the winter annual habit could be said to be a consequence of this gene. A second locus *FLOWERING LOCUS C (FLC)* also delays flowering and alleles at the FRI and FLC loci interact synergistically. FRI acts through FLC, as does VRN2, one of the VRN genes that mediate the vernalization response (Reeves and Coupland, 2000). FLC has, therefore, emerged as a central repressor of flowering, whose synthesis is promoted by FRI and inhibited by VRN (Sheldon *et al.*, 1999; Michaels and Amasino, 1999). Methylation may play a part in the regulation of FLC expression (Sheldon *et al.*, 1999), but it is not clear that methylation can account for all the effects of vernalization (Finnegan *et al.*, 1998; Simpson *et al.*, 1999). Evidence that genes similar to FRI and FLC are also important in vernalization in other species (and therefore in winter annual phenotypes) comes from *Brassica*, where the *VFN* and *VFR* loci cosegregate with markers linked to FRI and FLC (Osborn *et al.*, 1997).

The second point of particular interest for perennial flowering is that, in the absence of a dominant FRI allele, as in the rapid-cycling laboratory ecotype Landsberg erecta, crosses with an ecotype from the Cape Verde Islands reveal that there are four main loci that regulate flowering time (Alonso-Blanco *et al.*, 1998). In spring, the combined action of these genes, featuring an increased input from the photoperiod-sensitive pathway, determine flowering time. These two points suggest that in annuals a succession of pathways regulates flowering time in response to different seasonal environments. If the annual habit evolved from the perennial, then related mechanisms controlling flower initiation time would be found in perennials. It would be very interesting to examine the roles of VRN, FRI and FLC in perennial *Arabidopsis novae-angliae* (Chaffey, 1999). In perennial barley (*Hordeum bulbosum*) dormancy release followed just the pattern highlighted by Vegis and emphasized by Cannell (see earlier), and corresponded to a widening of the temperature range for growth (Ofir *et al.*, 1967; Noodén and Weber, 1978). Dormancy appears to be a key feature in arresting the growth of some buds and so ensuring survival of the plant until the next growing season.

<table>
<thead>
<tr>
<th>Table 3. <em>Fragaria vesca</em>: useful features of a model perennial plant</th>
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</thead>
<tbody>
<tr>
<td>Diploid: 2n=14</td>
</tr>
<tr>
<td>Small genome size: 1C=0.17 pg</td>
</tr>
<tr>
<td>Transformation system described (El Mansouri <em>et al.</em>, 1996)</td>
</tr>
<tr>
<td>Short generation time (4 months, seed to seed)</td>
</tr>
<tr>
<td>Small plant size for controlled environment work</td>
</tr>
<tr>
<td>Clear vegetative-reproductive cycle, under single gene control</td>
</tr>
</tbody>
</table>

Fig. 6. (A) Scheme showing control of flowering time in *Arabidopsis* ecotypes with a dominant FRI allele (redrawn from Reeves and Coupland, 2000). (B) Scheme showing potential pathways of cold perception and action in perennials.
In *Fragaria* there is long-standing evidence that flower initiation follows from a lifting of floral repression (Gutteridge, 1985; Battey *et al.*, 1998, for reviews). This suggests that a homologue of *FLC* may be central to the control of flowering, and that its activity is suppressed by homologues of the photoperiod promotive pathway in *Arabidopsis*. But the role of winter cold is less clear. Chilling prevents flower initiation in *Fragaria*, rather than accelerating it as vernalization does in winter annuals. Yet the physiological characteristics of chilling and vernalization are very similar (Metzger, 1996). Perhaps the simplest hypothesis is that an *FRI/FLC* regulated pathway can be linked to inhibition of flowering, whilst the *VRN* pathway widens the range at which bud growth can occur (causing dormancy release). The consequence of this would be bud burst and flower emergence (as modelled by Cannell, 1989). This would allow that cold need not always oppose the action of *FRI* by repressing *FLC* (Fig. 6b).

**Conclusions**

Flowering is a seasonal phenomenon but there is a need to distinguish flower emergence from flower initiation, particularly in perennials. The environment controls both processes, and the work discussed here illustrates how research at both whole plant and molecular levels contributes to an understanding of the seasonal cycle. The importance of dormancy for seasonality of flowering is apparent from this review, and arises from the consideration of annuals and perennials together. Seed dormancy and bud dormancy represent alternative strategies for annuals and perennials, and this may explain why seed vernalization and bud chilling/vernalization are so similar.

Consideration of seasonal changes emphasizes how plants do not just respond to their environment, but predict or anticipate it. This is most clear in rosaceous fruit trees that go dormant in preparation for winter, and not in response to environmental cues. It can also be seen in the repression of flowering by *FRI* in winter annual *Arabidopsis* ecotypes: this leads to a requirement for cold to promote flowering. The ability to predict the responses of plants to the seasons has in turn been the aim of the models of bud-burst in perennials (Cannell, 1989) and of flowering time in annuals (Roberts *et al.*, 1997). The Assyrians believed the god Shamash the Sun sent messages to inform the haruspex (reader of entrails) of the structure of the universe at the moment the sacrificial knife struck the victim (Lindsay, 1972). Thus, from at least 1000 BC to the present, anticipating the future has been a central need. Eliot does not distinguish science from superstition when he identifies the time-bound nature of this spirit of enquiry (Eliot, 1944); he only identifies what may lie outside it:

> To communicate with Mars, converse with spirits,  
> To report the behaviour of the sea monster,  
> Describe the horoscope, haruspice or sery,  
> Observe disease in signatures, evoke  
> Biography from the wrinkles of the palm  
> And tragedy from fingers; release omens  
> By sortilege, or tea leaves, riddle the inevitable  
> With playing cards, fiddle with pentagrams  
> Or barburtic acids, or dissect  
> The recurrent image into pre-conscious terrors –  
> To explore the womb, or tomb, or dreams; all these  
> are usual  
> Pastimes and drugs, and features of the press:  
> And always will be, some of them especially  
> When there is distress of nations and perplexity  
> Whether on the shores of Asia, or in the Edgware Road.  
> Men’s curiosity searches past and future  
> And clings to that dimension. But to apprehend  
> The point of intersection of the timeless  
> With time, is an occupation for the saint –  
> No occupation either, but something given  
> And taken, in a lifetime’s death in love,  
> Ardour and selflessness and self-surrender.

From ‘The Dry Salvages’

**The future of the seasons**

When we think of plants and the changing seasons, we think of something independent which we can use as a reference point. As we live in an increasingly manufactured world, where plant responses are modified to suit urban needs, it may be useful to become more sensitive to the weather. As Camus puts it: ‘How conjure up a picture, for instance, of a town without pigeons, without any trees or gardens, where you never hear the beat of wings or the rustle of leaves—a thoroughly negative place, in short? The seasons are discriminated only in the sky. All that tells you of spring’s coming is the feel of the air, or the baskets of flowers brought in from the suburbs by hawkers; it’s a spring cried in the market-places.’ (Camus, 1960).

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