

# THE EFFECT OF TEMPERATURE ON FLOWERING

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## ABSTRACT

The effects of temperature on flower initiation are described and explained in terms of their influence on the balance between flowering promoters and inhibitors. It is suggested that inductive photoperiods act by increasing promoter relative to inhibitor. The hypothesis is proposed that the indirect response to low temperature (vernalization) is a stage on the way to the direct response (low temperature initiation).

## INTRODUCTION

Information on the physiology of flowering in general is available in excellent reviews by Chouard (1960), Lang (1965), Evans (1971) and Zeevaart (1976). Up to now research has been directed towards the elucidation of the details of two major mechanisms of environmental control, namely photoperiodism and vernalization; and considerably more emphasis has been placed on the former than the latter. The effects of variations in temperature over the range from low to high have been relatively little studied and the few plants in which they have are mostly photoperiodically sensitive. Information on effects of temperature thus relates mostly to the processes of photoperiodism and of vernalization as strictly defined (see later), little being available for plants in which the time of onset of flowering is less dependent on these processes. One exception is the tomato (*Lycopersicon*), a daylength neutral plant for which considerable information is available on the effects of both high and low temperatures. The lack of experimental endeavour in this area, however, should not be taken as an indication of the lack of effect of temperature. In New Zealand's natural environment temperature is at least as important a controlling factor as daylength.

As temperature affects the rate of every chemical reaction in a plant, an understanding of its influence on flowering must of necessity be based on a clear understanding of all the processes that regulate flowering. In this paper only the first step in the flowering process, viz. inflorescence and flower initiation, is discussed; post-initiation development and those cases (which are, unfortunately, numerous) in which it is not clear from published results which stage was being studied have been omitted.

### The effects of temperature on the internal control of flower initiation.

The basic mechanism regulating the onset of floral initiation is internal, and environmental influences such as photoperiod, mineral nutrient availability, water stress and temperature must act via this internal control system. To understand the effects of temperature, then, it is essential first to understand the internal mechanisms of control. This is best done by considering the development of an annual plant the flowering of which is insensitive to daylength (viz.

a daylength neutral plant).

The first phase of growth of a seedling is normally completely vegetative. Its failure to initiate flower primordia during this stage is commonly taken to indicate that the plant is not 'competent' or 'ripe-to-flower'; that is, the plant is incapable of initiating flower primordia. The cause of failure to initiate flowers during this phase, often described as the juvenile phase, is unknown. To what extent the development of the stem apex (the site of initiation of flower primordia) is under autonomous control and to what extent it is regulated from the rest of the plant is unclear. Evidence relating to the phenomenon of juvenility in woody plants suggests that the development of a stem apex is influenced by 'meristematic ageing' (Robinson and Wareing, 1969), but the results of experiments designed to test for this in herbaceous plants indicate that the apices of young, juvenile, plants are fully capable of initiating flowers and suggest that the transition to flowering is largely determined by factors originating in the rest of the plant (Holdsworth, 1956; Zeevaart, 1976).

Failure to initiate flowers could result from either the lack of an adequate level of a necessary flower promoter or the excessive concentration of an inhibitory compound at the stem apex, and available evidence suggests strongly that both are involved (Lang, *et al.*, 1977).

To date, most attention has been paid to the effects of environment, particularly photoperiod, on flower initiation, at the expense of studying internal, correlative, control in daylength neutral plants. From the few studies that have been made, however, it is becoming clear that the development of the stem apex to the flowering state is strongly under the control of the rest of the plant. In *Scrofularia arguta* and *Chenopodium polyspermum*, for example (Miginiac, 1974; Sotta and Miginiac, 1975), flower initiation is stimulated by the removal of roots. In this case the inhibitory effect of roots can be simulated by the application of cytokinins to plants from which roots have been removed. In plants as diverse as apple trees and *Chenopodium rubrum* there is evidence to suggest that rapidly enlarging leaf primordia at the stem apex prevent the initiation of flower primordia thereon and that flower initiation occurs most readily when growth of leaf primordia at

the apex is reduced (Fulford, 1965, 1970; Seidlova and Opatrna 1978).

Considering the plant as a whole, it is likely that the development of stem apices is under correlative control both by relatively long distance influences from roots, stems and mature leaves, and by shorter distance influences from the leaf and axillary bud primordia immediately adjacent to the apical meristem. Any factor in the environment that affects these parts must influence the development of the stem apex. Temperature would be expected to have little or no effect on pattern of development if all reactions within a plant were affected by it to the same degree. When different parts of a plant and processes within them show different responses to temperature, however, the internal balance must be influenced and changes in the pattern of growth and development are to be expected.

With regard to flower initiation, experiments with broad beans (Evans, 1957) and the tomato cultivar San Jose Canner (Went, 1957) showed that the position of the first inflorescence to form in seedlings was uninfluenced by temperature over the range 10 to 30°C. In other cultivars of tomato, however, it has been found that the lowest node at which inflorescence initiation occurs can be altered from node 10.75 to node 8 in cv. Potentate and from node 14.2 to 8.2 in cv. Ailsa Craig by lowering temperatures from 27/27°C day/night to 15/10°C (Calvert, 1957). The site of action of the lower temperature in this case is unclear but experiments by Phatak *et al.* (1966) show it to be located in the shoot rather than the roots.

There are several ways in which temperature might act to affect development at the stem apex. These include: increasing or decreasing the rates of translocation from basal tissues to the apex (Geiger and Sovonick, 1975); differentially affecting the rates of production of inhibitors and promoters of flower initiation both within the apex itself and in the rest of the plant; and influencing the size relationships between the apical dome and the youngest leaf primordia produced by it. In cases where the time of flower initiation is controlled by the supply of an inhibitor from the root system (e.g. Miginiac, 1974), decreasing translocation rates from roots to stem apices would be expected to favour flower initiation. Where inhibitor synthesis in roots, leaves or stem apices is more sensitive to temperature than is promoter synthesis, lowering the temperature should again favour flower initiation. The rate of leaf initiation at a stem apex is strongly influenced by temperature (e.g. Thomas, 1979) with the result that the ratio of the volume of the apical dome to that of the subtending leaf primordia tends to change. Lyndon (1977) has suggested on the basis of experiments with *Silene* that the transition of an apex from a vegetative to a reproductive state might be controlled in some way by the ratio of meristematic dome volume to leaf primordium volume, optimum temperatures for flower initiation being those that lead to the development of relatively larger domes. This hypothesis is supported by the findings of Seidlova and Opatrna (1978).

#### Temperature effects in relation to photoperiodism

It has frequently been stated that the

photoperiodic timing mechanism is insensitive to temperature and that this enables the internal 'biological clock' or basic oscillator to keep time accurately. This is only so over a limited temperature range, however. Between ca. 12 and 28°C the frequency of free running endogenous rhythms is found to vary little, but at lower and higher temperatures it is strongly affected. If, as evidence suggests (Hillman, 1976), the measurement of daylength by a plant is mediated by a basic oscillator, we would expect the critical daylength over the range of ca. 12 to 28°C to be little affected by temperature. Outside this range, however, critical daylength might well be lengthened or shortened by changes in temperature and there is, indeed, considerable evidence that critical daylength can be influenced this way.

The photoperiod in which a plant is growing affects the production both of flowering promoters and inhibitors (e.g. Guttridge 1969, Lang *et al.*, 1977). After the synthesis of one or the other is triggered by the time-measuring mechanism, it is to be expected that the rate of synthesis will be greatly affected by temperature. The results of investigations into the effects of temperature are in good agreement with these expectations. Thus in both long- and short-day plants higher temperatures during the favourable phase of an inductive photoperiodic treatment (*viz.* the dark period in short-day plants, SDP, and the light period in long-day plants, LDP) usually promote flower initiation whereas lower temperatures have the opposite effect. In *Pharbitis*, *Perilla*, *Fragaria*, and soybean, all SDPs, low dark temperatures decrease flower initiation in short days, SD, and warm dark conditions promote. The reverse holds for the LDPs *Silene*, *Anagallis*, *Trifolium repens*, *Sinapis* and *Lolium temulentum* in which high temperatures during the light period enhance flower initiation (see Evans, 1969). This type of observation is readily and simply understood on the basis that promoters of flower initiation are produced under favourable photoperiodic conditions and their synthesis enhanced by higher and decreased by lower temperatures.

Conversely, both in LDPs and SDPs growing in non-inductive photoperiodic conditions (*viz.* SD and LD respectively), flower initiation is often promoted by low temperatures, supporting the hypothesis that flower initiation under such conditions is prevented by excessive production of inhibitors, the amount of which is decreased by low temperatures. An outstanding example of this is the flowering of the SDP *Pharbitis* at low temperature (optimally 15°C) in continuous light (Kimura and Takimoto, 1963), and similar, albeit less extreme, effects occur in the SDPs soybean, *Perilla* and *Fragaria* (see Evans, 1969). Promotion of flower initiation by low temperatures in LDPs growing in SD has been frequently reported (see below).

One consequence of these effects of temperature is the modification of critical daylengths. Thus in the SDPs *Xanthium* (Salisbury, 1963) and *Pharbitis* (Takimoto and Hamner, 1964) the critical duration of a single inductive dark period is increased from ca. 9 hr at between 15 and 30°C to ca 10½ hr at 10°C in the former and from ca. 8 hr at 25°C to 17 hr at 18°C and 24 hr at 17° in the latter. Equivalent data

on the effect of temperature during a single inductive light period on the critical duration of that period in LDPs are not available. In LDPs the most frequently observed effect of temperature is a decrease in critical daylength with decreased dark temperatures and this is frequently interpreted as indicating a decrease in the synthesis of inhibitors in the dark period. This is the case for example in *Hyoscyamus* (see Lang, 1965) in which the critical daylength was reduced from 11½ to 8½ hours by a reduction in temperature from 28° to 16° C, and *Phalaris* (Ketellapper, 1969) in which it was reduced from 13½ and 14¼ hours at 29° C in two distinct geographic strains to 12½ and 13¼ hours, respectively, at 15° C. The effect of low temperature on the critical daylength in LDPs is far more widespread than commonly acknowledged, however. In very many such plants, flower initiation occurs with photoperiods as short as 8 to 10 hours when growth takes place at temperatures between 0 and 12° C (see next section).

Available evidence thus supports strongly the hypothesis that temperature affects the rates of synthesis of inhibitors and promoters of flower initiation in both long- and short-day plants. The site of its action, however, is not certain although it has been assumed, on the basis of rather scant evidence, to be the leaves (which are the sites of photoperiodic perception). This does indeed appear to be true in the SDP Biloxi soybean (Borthwick *et al.*, 1941; Parker and Borthwick, 1943) where low temperatures certainly reduce the stimulatory response of leaves to SD. In experiments with the LDP white clover, however, high temperatures apparently act on the stem apices rather than the leaves to enhance flower initiation in LD (Ridley and Laude, 1968).

Finally, it should be made clear that not all effects of temperature can be so simply explained. In the LDPs *Bouvardia humboldtii*, *Rudbeckia bicolor* and *Silene armeria*, for example, temperatures above 30° C can cause flower initiation in SD (see Evans, 1969) and in *Trifolium repens* initiation occurs in SD at day/night temperatures of 14/28° C (Thomas, unpublished). The mode of action in these cases is far from understood. Such high temperatures do affect endogenous rhythms, however, and they might thus act via the time-measuring system, although in *Silene* evidence indicates that high temperatures might act via the root system.

### Low Temperature Responses

An aspect of flower initiation to which little attention has been paid is its cessation under apparently favourable conditions. The LDP white clover stops flowering in summer, for instance, and the lateral shoots of long-day grasses and herbaceous perennials frequently fail to initiate flowers in their first growing season. This can be considered to be a mechanism that ensures maximum vegetative growth during the autumn and prevents the formation of flowers so late in the growing season that insufficient time is left for seed ripening before winter sets in (Thomas, 1980). In all these cases flower initiation becomes possible again after exposure to the low temperatures that occur naturally during winter. The responses to low temperature are usually considered to be of two types: vernalization and low temperature initiation.

#### (a) Vernalization

Classical investigations into low temperature responses (e.g. Purvis, 1961) were directed towards an understanding of the physiological processes involved in cereals. Spring varieties of cereals are capable of initiating inflorescences without exposure to cold; winter varieties require a period of low temperature pretreatment (commonly for from one to three months at a temperature between 0 and 10° C with an optimum at ca. 5° C) before they are capable of initiating inflorescences in subsequent warm conditions. Exposure to such low temperature treatment is termed vernalization, and plants that have been rendered capable of initiating flowers by such treatment are said to be 'competent' or 'ripe-to-flower'. In cereals, vernalization of grain is very effective; in other plants, of which a thoroughly studied example is *Hyoscyamus* (see Lang, 1965), seedlings and older plants are often more responsive than seeds to vernalization.

Vernalization does not directly cause initiation of flowers or inflorescences; it only leads to 'competence' which in turn enables the plant to enter the reproductive phase of development under subsequent warm conditions. It has been distinguished, therefore, by Lang (1965) as an indirect response.

#### (b) Low temperature initiation

A second response to low temperatures, which is usually looked upon as quite distinct from vernalization, can be termed low temperature initiation. This is, in Lang's (1965) terminology, a direct response, in that low temperatures lead directly to the initiation of flower primordia while plants are growing in cool conditions. It has been described as occurring in a wide range of plants including Brussels sprouts (Verkerk, 1954), white clover (Britten, 1960; Thomas, 1979), subterranean clover (Evans, 1959), *Dactylis* (Wilson and Thomas, 1971), S.24 perennial ryegrass (McWilliam & Jewiss, 1973) and sainfoin (Sheely, 1977).

#### (c) Variation in response of ecotypes to low temperature in relation to geographic origin.

Plants adapted to climates with warm winters show no low temperature requirements, but a high proportion of those from climates with cold winters do exhibit such a requirement for flower initiation, and it is usually found that plants from higher latitudes or altitudes where the winters are more severe require a longer exposure to cold than those from lower latitudes and altitudes with less severe winters. This has been demonstrated convincingly for grass plants originating at different points along a cline of increasing winter harshness from the south to north of Europe (Cooper, 1963). In many cases, e.g. in *Lolium* (Cooper, 1960), plants adapted to the colder winters of northern Europe require vernalization whereas those from the warmer Mediterranean climes do not. Low temperature initiation commonly occurs in plants of Mediterranean origin in which growth and flowering are most vigorous during winter and decline during the hot dry summer. Sheely (1977) found that an Italian ecotype of sainfoin (*Onobrychis*) has no

vernalization requirement but does undergo low temperature initiation; a Russian cultivar, 'Krasnodar', however, did not flower in warm LD without previous exposure to low temperature. Very little true vernalization requirement has been found in *Trifolium repens* but all cultivars studied initiate inflorescences at low temperatures. Those from ca. 30°N, such as 'Tamar' and 'Louisiana', initiate inflorescences in early autumn (March/April) in Palmerston North after minimal exposure to cool conditions. In populations originating at successive points along the temperature cline from south to north in Europe, inflorescence initiation in winter is increasingly delayed. Thus Spanish ecotypes initiate in May, cv. 'Huia' (considered to be a selection from plants of southern French origin) in June/July, cv. 'Kent Wild White' in late July/early August and Russian cultivars from ca. latitude 60°N in mid August (Thomas, unpublished).

(d) *The relationship between vernalization and low temperature initiation.*

The physiological nature of low temperature initiation and its relationship to vernalization in the strict sense are unclear. Amongst the few plants for which data are available, some exhibit both vernalization and low temperature initiation. Thus the results obtained by Evans (1959) for *Trifolium subterraneum* indicate clearly that three of the seven cultivars he studied initiated inflorescences sooner in continuous light after vernalization for from one to four weeks than without low temperature pretreatment; these three also initiated inflorescences after about five weeks' growth at 7°C in 8-hour photoperiods, as did the other cultivars in which the time of inflorescence initiation in continuous light was uninfluenced by vernalization. Likewise, data obtained for S.24 ryegrass by McWilliam & Jewiss (1973) showed that plants of this cultivar can be vernalized by exposure to temperatures between 0 and 3°C for 12 weeks, while low temperature initiation occurs in plants grown for 16 weeks or more in 8-hour photoperiods at day/night temperatures of 9/4°C. Sheely's (1977) data for sainfoin indicate that some cultivars of this plant also exhibit both low temperature initiation and a vernalization response.

There is a strong positive correlation between a plant's capacity to grow during the cold conditions of winter and its ability to initiate flowers at low temperatures, low temperature initiation being associated with better winter growth. The indirect, vernalization, response is most strongly developed in those plants in which growth almost stops in winter. If vernalization and low temperature initiation are two distinct processes, plants intermediate in their capacity for winter growth could be expected to show both a poor vernalization response and a weak initiation response to low temperature. It is not known whether this is so. Alternatively, however, evidence suggests that there is no clear distinction between vernalization, as originally defined, and low temperature initiation. In at least some species, and possibly in very many others, short term exposure to low temperatures leads to vernalization while longer exposure results in initiation. In other words

vernalization can be considered to be a step on the way to low temperature initiation. In species or their ecotypes adapted to colder winters, low temperature initiation occurs only after long cold treatment; in plants adapted to milder winters a much shorter exposure is required. If this hypothesis is correct, it should be possible to vernalize plants in which low temperature initiation occurs by exposing them to periods of low temperature that are of too short a duration for initiation to take place. Such tests have yet to be made.

(e) *The relationship between photoperiod and low temperature responses – an hypothesis.*

Low temperature initiation, which has apparently been reported only for LDPs, is possibly closely related to the effect of low temperature on the critical daylength in LDPs mentioned earlier. The response to low temperature might be no more than an extreme shortening of the critical daylength.

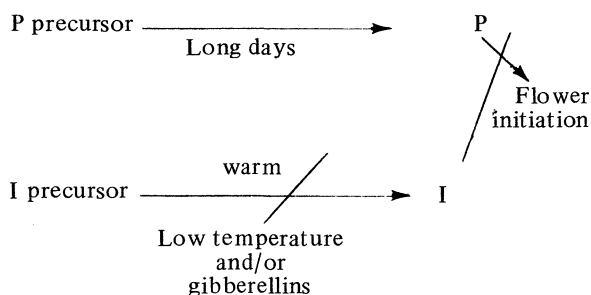
A further relationship with photoperiod is frequently apparent, also; namely, a period in warm SDs can often substitute for low temperature as a means of inducing ripeness-to-flower. In these cases SDs have the same effect as vernalization. Warm SDs never lead to floral initiation in LDPs, however, whereas low temperatures frequently do.

In recent years there has been an increasing feeling, expressed by several writers (e.g. Miginiac, 1974), that the earlier concept of a single flowering hormone ('florigen') or a single product of vernalization ('vernalinal') is incorrect, and that, because of the diversity of responses to environment shown by plants, it is more likely that there are many different response mechanisms. While concurring with this sentiment, it is nevertheless intriguing that so many response mechanisms in such diverse genera and plant forms as grasses, cereals, forage legumes, ephemeral herbs and biennial rosette plants should be so strategically similar. The current relative lack of research into the physiology of flowering is possibly in part a result of the present views. The earlier unity of purpose in striving to elucidate the nature of a common 'florigen' has been weakened by the suggestion that the control mechanism within each plant might be different. There is much to be gained by reintroducing a simple common model to explain the diversity of responses to low temperature and photoperiod, and recent ideas developed from data collected over the past few years are of possible assistance in this respect.

The outstanding studies by Reid and Murfet (1975) on the physiology of flowering in the pea have led to the notion that, in that plant, flower initiation is controlled by a balance between promoters and inhibitors. Investigations into flowering in white clover have led, quite independently, to the development of a similar hypothesis (Thomas, 1979). In neither case has the concept of a fundamental common flower promoter been abandoned altogether.

The classical hypotheses of the relationships between the products of low temperature ('vernalinal') and photoperiod ('florigen') propose that their actions are sequential, 'vernalinal' being a promoter the presence of which is necessary to induce ripeness-to-flower before 'florigen' can act (Lang,

1965). An hypothesis developed for white clover, which is similar in many respects to that proposed for the pea system and which both accounts for the relationship between low temperature and photoperiod and seems applicable to a wide range of plants, proposes that the ultimate synthesis of a flower promoting factor is dependent on the ratio between inhibitors and promoters rather than on a sequence of events. Such an hypothesis has the very great advantage over earlier ones that we do not have to suggest that low temperatures and continuous light lead to flowering in LDPs as a means of explaining how it is that non-vernalized plants that require vernalization for flowering in 16-hour photoperiods are often promoted to initiate flowers by continuous light. On the basis of an hypothesis involving a balance between a promoter (P) and an inhibitor (I), an excess of P over I can be achieved both by increasing P (e.g. in continuous light in LDPs) and by decreasing I (e.g., perhaps, at low temperatures). Such a model, presented below in its simplest form, has a similar basis to that proposed by Lang (1965) to explain the mechanism of low temperature response, but extends his suggestion to incorporate the effects of photoperiod.



The hypothesis that low temperature acts by removing an inhibitor (both during vernalization and during low temperature initiation) closely parallels our current understanding of the role of low temperature in the breakage of dormancy by removal of inhibitors (Wareing and Saunders, 1971). Indeed, Chouard (1960) has suggested that the unvernallized state of plants can be regarded as a form of partial dormancy.

(f) *Growth substances and low temperature responses.*

Of the four major classes of plant growth substances only the gibberellins have so far been shown to be significantly involved in low temperature responses. Auxins appear to play no direct part (Lang, 1961); but studies of cytokinins and abscisic acid suggest that their involvement cannot be ruled out. Thus Reda (1976) has shown that vernalization of winter wheat grain leads to increases in cytokinin content and other studies indicate that cytokinins and gibberellins increase and abscisic acid content perhaps decreases during cold treatment of dormant buds (Saunders & Wareing, 1971).

Gibberellins have been reported by several workers to substitute for vernalization in cold-requiring plants and for LDs in many non-cold-requiring LDPs, and even although there are many other recorded cases in

which gibberellins have failed to substitute for low temperatures it is uncertain whether these were caused by use of ineffective gibberellins and/or inadequate duration of treatment or whether in these instances gibberellins are totally ineffective. It is nevertheless true that in some plants (e.g. hollyhock; Harada, 1962) gibberellin content has been recorded to increase during cold treatment.

The dual nature of the responses to gibberellins which is reflected in their ability to substitute for LDs in plants not requiring vernalization but only to substitute for vernalization when applied in LDs has led in the past to the suggestion that gibberellins must be acting in at least two different ways. Referring back to the hypothesis proposed in section (e), however, it will be seen that these two different effects would be simply explained if gibberellins prevent in some way the action of the postulated inhibitor either by causing its breakdown or blocking its synthesis. In a non-cold-requiring plant, a low level of promoter in SDs might be adequate to lead to flowering in the absence of inhibitor. In this case, gibberellins would stimulate initiation in SDs, whereas in an unvernallized cold-requiring plant, with an initially much higher inhibitor content, gibberellin treatment might well not reduce the inhibitor level sufficiently to allow the lower level of promoter present in SDs to be effective. Thus, LDs would be required to raise the level of promoter enough to allow flower initiation.

### CONCLUSIONS

From the foregoing account it is clear that temperature has a strong influence on flower initiation probably by influencing the synthesis of both promoters and inhibitors. In the field situation in New Zealand the time of initiation is strongly affected in many LDPs, being promoted both by high temperatures in summer and by low temperatures in autumn, winter and spring. The time and vigour of initiation in SDPs are less affected by temperature in the field, however, as those temperatures known to affect the critical daylength in such plants (viz. cold light periods in LDs and warm dark periods in SDs) do not occur naturally.

The most significant effect of temperature in the New Zealand environment is almost certainly the initiation of flowering in LDPs during the SDs of autumn, winter and early spring. Studies made under the cool temperate conditions of Europe, where winters are cooler and plants pass rather rapidly through a short spring into the warm LD conditions of summer, often fail to reveal patterns of flowering behaviour that are more apparent in plants grown in the milder winters of New Zealand and California. During a rapid transition from a cold winter to a warm summer it is difficult to distinguish between low temperature initiation and initiation in LD following vernalization because both will tend to occur at roughly the same time when temperatures, and growth, increase in the spring. In New Zealand, where the transition from winter to summer is much more protracted, the difference between plants of Mediterranean origin and those originating at higher latitudes is very much clearer, the former showing vigorous flower initiation during winter while the latter tend not to initiate until early spring. Flowers

on 'Mediterranean' cultivars thus emerge very much earlier than those on plants from higher latitudes.

Greater advantage should be taken of the opportunities the natural New Zealand environment provides for increasing our understanding of the effect of temperature on flower initiation.

## REFERENCES

- Borthwick, H.A., Parker, M.W., Heinze, P.H. 1941. Influence of localized low temperature on Biloxi soybean during photoperiodic induction. *Botanical Gazette* 102: 792-800.
- Britten, E.J. 1960. Genetic and environmental control of flowering in *Trifolium repens* in the tropics. *Science N.Y.* 131: 100-1.
- Calvert, A. 1957. Effect of the early environment on development of flowering in the tomato. I. Temperature. *Journal of Horticultural Science* 32: 9-17.
- Chouard, P. 1960. Vernalization and its relations to dormancy. *Annual Review of Plant Physiology* 11: 191-238.
- Cooper, J.P. 1960. Short-day and low temperature induction in *Lolium*. *Annals of Botany* 24: 232-46.
- 1963. Species and population differences in climatic response. In "The Environmental Control of Plant Growth" Ed. L. T. Evans, Academic Press.
- Evans, L. T. 1957. The broad bean In "Experimental Control of Plant Growth" pp. 124-8, Ed. F.W. Went, Chronica Botanica.
- 1959. Flower initiation in *Trifolium subterraneum* L. I. Analysis of the partial processes involved. *Australian Journal of Agricultural Research* 10: 1-16.
- (Ed.) 1969. "The Induction of Flowering". Macmillan.
- 1971. Flower induction and the florigen concept. *Annual Review of Plant Physiology* 22: 365-94.
- Fulford, R.M. 1965. The morphogenesis of apple buds. I. The activity of the apical meristem. *Annals of Botany* 29: 167-80.
- 1970. The effect of chemical defoliation on the development of apple spurs. *Ibid.* 34: 1078-88.
- Geiger, D.R., Sovonick, S.A. 1975. Effects of temperature, anoxia and other metabolic inhibitors on translocation. *Encyclopedia of Plant Physiology, New Series. 1:* 256-86.
- Guttridge, C.G. 1969. *Fragaria*. In "The Induction of Flowering". pp. 247-67. Ed. L.T. Evans, Macmillan.
- Harada, H. 1962. Etudes des substances naturelles de croissance en relation avec la floraison. Isolement d'une substance de montaison. *Revue générale de botanique* 69: 201-97.
- Hillman, W.S. 1976. Biological rhythms and physiological timing. *Annual Review of Plant Physiology* 27: 159-79.
- Holdsworth, M. 1956. The concept of minimum leaf number. *Journal of Experimental Botany* 7: 395-409.
- Ketellapper, H.J. 1969. Growth and development in *Phalaris* III. Effect of temperature on critical daylength in geographic strains of *P. tuberosa* L. *Plant and Cell Physiology* 10: 461-3.
- Kimura, K., Takimoto, A. 1963. Floral initiation in *Pharbitis nil* subjected to continuous illumination at relatively low temperatures. I. Effect of various temperatures. *Botanical Magazine Tokyo* 76: 67-73.
- Lang, A. 1961. Auxins in flowering. *Encyclopedia of Plant Physiology* 14: 909-50.
- 1965. Physiology of flower initiation. *Encyclopedia of Plant Physiology* 15/1: 1380-1536.
- Chailakhian, M.K., Frolova, I.A. 1977. Promotion and inhibition of flower formation in dayneutral plant in grafts with a short-day plant and long-day plant. *Proceedings National Academy of Science U.S.A.* 74: 2412-16.
- Lyndon, R.F. 1977. Interacting processes in vegetative development and in the transition to flowering at the shoot apex. *Symposium Society of Experimental Biology* 31: 221-50.
- McWilliam, J. R., Jewiss, O. R. 1975. Flowering of S24 perennial ryegrass (*Lolium perenne* L.) in short days at low temperature. *Annals of Botany* 37: 263-65.
- Migniac, E. 1974. Flowering and correlations between organs in *Scrofularia arguta* Sol. In "Mechanisms of Regulation of Plant Growth". Eds. Bielecki, R.L., Ferguson, A.R., Cresswell, M.M. Bull. 12 Royal Society of New Zealand, Wellington: 539-45.
- Parker, M.W., Borthwick, H.A. 1943. Influence of temperature on photoperiodic reactions in leaf blades of Biloxi soybean. *Botanical Gazette* 104: 612-19.
- Phatak, S.C., Wittwer, S.H., Teubner, F.G. 1966. Top and root temperature effects on tomato flowering. *Proceedings American Society of Horticultural Science* 88: 527-31.
- Purvis, O.N. 1961. The physiological analysis of vernalisation. *Encyclopedia of Plant Physiology* 16: 76-122.
- Reda, F. 1976. Endogenous cytokinins in vernalized winter wheat grains. *Planta* 130: 265-8.
- Reid, J.B., Murfet, M. 1975. Flowering in *Pisum*: the sites and possible mechanisms of the vernalization response. *Journal of Experimental Botany* 26: 860-67.
- Ridley, J.R., Laude, H.M. 1968. Temperature and the flowering intensity of Ladino clover stolons. *Crop Science* 8: 519-21.
- Robinson, L.W., Wareing, P.F. 1969. Experiments on the juvenile-adult phase change in some woody species. *New Phytologist* 68: 67-78.
- Seidlová, F., Opatrna, J. 1978. Change of growth correlations in the shoot meristem as the cause of age dependence of flowering in *Chenopodium rubrum*. *Z. Pflanzenphysiologie* 89: 377-92.
- Sheely, P.J. 1977. The influence of environment on growth and development in the forage legume sainfoin (*Onobrychis viciifolia* Scop.) Unpublished M.Sc. thesis, Massey University, 152p.
- Sotta, B., Migniac, E. 1975. Influence des racines et d'une cytokinine sur le développement floral d'une plante de jours courts, le *Chenopodium polyspermum* L. C.R. *Académie des sciences, Paris* 281: 37-40.
- Takimoto, A., Hamner, K.C. 1964. Effect of temperature and preconditioning on photoperiodic response of *Pharbitis nil*. *Plant Physiology* 39: 1024-30.
- Salisbury, F.B. 1963. Biological timing and hormone synthesis in flowering of *Xanthium*. *Planta* 59: 518-34.
- Thomas, R.G. 1979. Inflorescence initiation in *Trifolium repens* L.: influence of natural photoperiods and temperatures. *N.Z. Journal of Botany* 17: 287-99.
- 1980. Flowering responses of white clover (*Trifolium repens* L.) growing in arctic Norway. *Acta agriculturæ scandinavica* 30 (in press).
- Verkerk, K. 1954. The influence of low temperature on flower initiation and stem elongation in Brussels sprouts. *Proc. Kon. Nederlandse Akademie van Wetenschappen C* 57: 339-46.
- Wareing, P.F., Saunders, P.F. 1971. Hormones and dormancy. *Annual Review of Plant Physiology* 22: 261-88.
- Went, F.W. 1957. The tomato and other Solanaceae In "Experimental Control of Plant Growth". pp. 99-144. Ed. F.W. Went, Chronica Botanica.
- Wilson, D., Thomas, R.G. 1971. Flowering responses to daylength and temperature in *Dactylis glomerata* L. *N.Z. Journal of Botany* 9: 307-21.
- Zeevaart, J.A.D. 1976. Physiology of flower formation. *Annual Review of Plant Physiology* 27: 321-48.