

IMPORTANCE OF CABBAGE (*Brassica oleracea*) VERNALIZATION ON SEED PRODUCTION: A REVIEW

IMPORTANȚA VERNALIZĂRII LA VARZĂ (*Brassica oleracea*) ASUPRA PRODUCȚIEI DE SEMINȚE: RECENZIE

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Abstract. *The seed-to-seed method is the most often used process in cabbage seed production. The transition from vegetative phase to generative one requires vernalization in terms of bolting and flowering.*

Vernalization is a physiological process that converts vegetative meristem tissue to reproductive tissue. It is a natural adaptation that ensures flowering happens only after the exposure to low positive temperatures for an extended period of time, allowing flowers and seeds to mature under normal conditions. The purpose of this research was to present the vernalization demands of Brassicas, the mechanism of vernalization, molecular changes of vernalization, and the factors influencing flowering, such as environmental factors and plant growth regulators, in cabbage seed production.

Key words: generative, reproduction, flowering, temperature

Rezumat. *Procesul de la sămânță la sămânță este metoda cea mai des folosită în producerea de semințe de varză. Trecerea de la faza vegetativă la cea generativă necesită procesul de vernalizare pentru formarea lăstarilor floriferi și înflorirea. Vernalizarea este un proces fiziologic care transformă țesutul meristematic vegetativ în țesut reproducător. Este o adaptare naturală care asigură că înflorirea are loc numai după expunerea la temperaturi pozitive scăzute pentru o perioadă lungă de timp, permițând florilor și semințelor să se maturizeze în condiții normale. Scopul acestei cercetări a fost de a prezenta cerințele de vernalizare ale Brassicaceelor, mecanismul de vernalizare, schimbările moleculare ale vernalizării și factorii care influențează înflorirea, cum ar fi factorii de mediu și regulatorii de creștere a plantelor, în producția de semințe de varză.*

Cuvinte cheie: generativ, reproducere, înflorire, temperatură

INTRODUCTION

One of the most commercially significant plant groups in the world is made up of the plants belonging to the family *Brassicaceae*. They include noxious weeds, leaf and root vegetables, oilseed, condiment crops and more. The cole vegetables are arguably the most well-known category. *Brassica oleracea* is a commercially

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important cruciferous plant, producing around 100 million tons globally in 2018. *B. oleracea* has significant morphological variability, with agricultural crops including cabbage, broccoli, cauliflower, kale, and Brussels sprouts, which are cultivated for their leaves, flowers and stems (Wang *et al.*, 2022).

The cole crops are also well-known considering that they are easy to cultivate, sustainable in the marketplace, rich in nutrients (Dickson and Wallace, 1986; Norman, 1992), and there is increasing proof that consuming cole vegetables may reduce the risk of developing some forms of cancer (Chiang *et al.*, 1993; Rungapamestry *et al.*, 2006). Some of its cultivars, particularly in broccoli, cabbage, and kale, are great source of vitamins, fiber, and secondary metabolites such as carotenoids, phenols and glucosinolates, which are well known for their antioxidant activity and for their anti-carcinogenic attributes (Munteanu, 2019).

Understanding *Brassica* vegetables includes taking a fascinating biological journey through evolutionary time and observing stable hybrids being created as wild cross-pollinated plant populations. The genus *Brassica*, one of 51 genera in the *Brassicaceae* family, is the most significant economic genus since it contains 37 unique species (Gomez-Campo, 1980).

All the many varieties of *Brassica oleracea* represent the most conspicuous examples of polymorphism among the plants classified as vegetables. Helm (1963) defined the ancestor of this diversified group of plants as a polymorphic perennial herb with a stem that was moderately branched and typically reached 60–100 cm in height. It is believed to have originated 3 million years ago on the Mediterranean coast and islands, then spread from there to all of Europe and, subsequently, to East Asia (Hammer *et al.*, 2013; Arias *et al.*, 2014).

The first selections were presumably done to decrease the amount of bitter glucosinolates, which were present in high concentrations in the wild varieties. People of the Mediterranean region presumably initially ended up eating the single-stemmed kales, which had either smooth or ruffled leaf shapes, as early as 600 BC (Thompson, 1976).

Plants from the ancient *Brassica* family were utilized in a variety of ways. According to a review of classical literature and archeological data, 30 species were utilized as medicines, food or for magical or decorative reasons (Toscano *et al.*, 2013). A roughly equivalent range of species and their purposes may still be found in regions of Italy today, such as Sicily (Romano *et al.*, 2013).

The exact path of selection for today's popular cabbage family vegetables is uncertain. Thompson (1976) hypothesized that when *B. oleracea* moved northward, varieties with a biannual flowering habit became prevalent, necessitating a two to three-month cool interval to initiate flowering. Among them, varieties with a much-shortened stem and a large apical bud surrounded by numerous leaves were chosen. Cabbage first appeared in Germany in the 12th century (Helm, 1963). Selection of plants with small, swollen fleshy stems resulted in our contemporary day kohlrabi, which was originally reported in the 1500s in the same region. The eastern Mediterranean region appears to have been the site of selection for types with short,

densely branching fleshy inflorescences. Cauliflower was identified in the 16th century, but broccoli did not exist for another 100 years (Thompson, 1976). Brussels sprouts are the most recent addition to the common cole crops, having been selected in Belgium in the 18th century, as the name suggests.

The comprehensive work on *Arabidopsis thaliana*, a weed in the *Brassicaceae* family, has contributed in the study of the *Brassica* family of vegetables. Although *Arabidopsis* and the *Brassica* crops diverged 17 million years ago (Golicz *et al.*, 2013), they share numerous gene systems and physiological functions.

Schiessl *et al.* (2017), for instance, investigated the 35 gene systems that drive flowering in *Arabidopsis* for shared characteristics in *Brassica* processes such like vernalization, photoperiod pathways, and flowering temperature regulation. Ajisaka *et al.* (2001), discovered a quantitative trait loc for very late bolting in Chinese cabbage.

Before vegetables are harvested, before they grow and develop, even before the seedling becomes photosynthetically competent, the source of the vegetable, the seed, holds crucial keys to end product yield. To thoroughly understand the complexity of vegetable crop growth and development, we must first understand seed physiology as it relates to storage, germination, quality, and improvements. Seed quality is a comprehensive word that incorporates numerous seed characteristics such as germination and seedling performance.

As for *Brassicacae*, when seed reaches maximal viability and vigour, it is physiologically mature, and deterioration occurs (Powell and Matthews, 1984). Ideally, seed should be picked when it has reached physiological maturity and has not begun to degrade for maximum seed quality.

The "seed vigour" refers to the totality of the qualities of seed that influence its potential activity and performance during germination and seedling emergence (Perry, 1978). Throughout seed production, seeds are subjected to varied degrees of water and temperature stress, maturity, harvest, and storage, and then again during rehydration and germination after sowing. High vigour seeds may germinate quickly and establish robust seedlings, resulting in effective crop output.

Seedling quality supports the development of modern seed production technology and facilitates the development of criteria for easy evaluation and identification of competitive planting material (Bute *et al.*, 2022)

The transition of plants from the vegetative phase to the reproductive one is a particularly critical problem, with seed production being the final phase in vegetable breeding. For this purpose, cold treatment is used to induce vernalization or winterization, a complex physiological process required for floral induction (Munteanu, 2019). Sensibility to vernalization is determined by the variety as well as the environmental conditions in which the seed was produced (Indrea and Apahidean, 1995).

MATERIAL AND METHOD

This review is based on a thorough examination of resources accessible in the worldwide literature. The data for this analysis were acquired from open access online sources such as Google School, Google Academic, Free Full PDF, Research Gate, and Science Direct. We used keywords and phrases like "vernalization", "*Brassica*", "*Arabidopsis*", "cabbage," "flowering," and "seed production" to discover work material. This study included research on *Brassica oleracea* (cole crops) that was linked to mechanisms of vernalization, molecular analyses of vernalization, and factors influencing flowering and were available as free complete publications in English. According to the analysis of the selected documents, the results show that *Brassica oleracea* vernalization, photoperiod pathways, and flowering temperature regulation are extremely broad and extensive internationally. Two inclusion criteria were considered: thematic focus (referring to mechanism of vernalization, molecular analyses of vernalization, and the factors influencing flowering) and document type (journal and books chapters). Following these guidelines, 90 studies and experiments were chosen that have both positive and negative features. The purposes of this review are to highlight the notion of vernalization and some of the other variables that may improve cabbage flowering and seed production, as well as to encourage interested scientists to do research in this critical area.

RESULTS AND DISCUSSIONS

The division of the life cycle into vegetative and generative stages is valid, but the transition from one to the other is a particularly complicated process, susceptible to the impact of environmental factors whose control is dependent on the effectiveness of breeding works. Detailed studies of morphology, anatomy, and physiology have highlighted several stages of development, depending on the constant changes, as for breeding purposes it is considered sufficient to divide the vegetation period into four phases: the juvenile phase, the floral induction phase, the edible parts formation phase, and the flowering phase (Munteanu, 2019).

JUVENILE PERIOD

The induction of flowering in *Brassica oleracea* is caused by relatively low temperatures, a process known as vernalization, however the temperatures are only effective if the plants have passed what is known as the juvenile stage.

The juvenile phase is the initial stage of the life cycle, during which only leaves are being developed from the terminal bud. This stage is just for quantitative accumulation and lasts a certain amount of time depending on the variety, as well as the temperature (Munteanu, 2019).

This phase lasts 6 – 12 weeks in cabbage and corresponds to a habitus of 5 – 12 leaves. The period lasts 5 – 8 weeks (5 – 7 leaves) for cauliflower and up to 10 – 15 weeks for broccoli (20 – 30 leaves) (Rahn and Herve, 1979).

Exposing plants of various ages to low temperatures and counting how many leaves grow on the main stem before the apex converts to a reproductive structure provides evidence for the existence of a juvenile stage. If the plant is still young when the cold treatment is applied, the eventual leaf number will be similar to that

of non-cold-treated plants. After the plants reach the adult vegetative stage, cold treatment reduces not just the quantity of leaves generated, but also the rate at which the plants develop. It is therefore more physiologically appropriate to measure the efficiency of vernalization by leaf number developed rather than temporal time to specific reproductive processes (Sadik, 1967; Wiebe, 1972; Hand and Atherton, 1987).

Stokes and Verkerk (1951), Wiebe (1972), and Thomas (1980) demonstrated the presence of the juvenile stage by revealing that germinating seeds could not be vernalized. However, the existence of a juvenile phase has been put into question in several instances. There was a modest drop in final leaf number with vernalization of imbibed seeds in cabbage (Nakamura and Hattori, 1961) and cauliflower (Fujime and Hirose, 1979), indicating that there was no juvenile stage.

It appears that there are significant changes in juvenility between cultivars and species, and it is possible that sensitivity to induction reduces and then rises as plants age.

In practice, the presence of a juvenile period allows the plant to develop to an acceptable size before being induced to flower. In climatic conditions where a moderate cold phase would enable the crop to live but not actively grow, a cole crop such as cabbage can be planted at the start of the cold period and survive until the next warm season without being induced to flower. Indeed, cabbage overwintering was formerly a prevalent technique used (Boswell, 1929).

VERNALIZATION AND FLOWERING

Vernalization is described as the extended exposure of a germinating seed or young plant to a low temperature in order to trigger flowering in the adult plant (Sheldon *et al.*, 2000). The phrase was initially referred to treatments administered to imbibed seeds or seedling plants, but it was later expanded to include cold treatments, which have comparable effects when administered to plants at later stages of development (Roberts and Summerfield, 1987).

Some species will not flower until vernalization occurs. In others, vernalization extends flowering time (Dennis *et al.*, 1996). The duration of the low temperature period during which vernalization can occur, as well as the temperature range at which it can occur, differ amongst varieties and even within lines of the same variety (Bernier *et al.*, 1981). The optimal inductive range for most species is 1° to 10°C, and the low temperature must be maintained for 1 – 3 months.

It has also been observed that when cabbage plants were subjected to a prolonged vernalization period, high temperatures at the end of the cold period were ineffective in inducing devernalization (Heide, 1970 as referenced in Wien and Wurr, 1997). Furthermore, a *Arabidopsis* research found that plants that were cold-treated as seeds for fewer than 14 days did not bolt, but those that were cold-treated for 28 days bolted effortlessly at 23°C (Sung and Amasino, 2004; Sheldon *et al.*, 2006). It is also known (Ratcliffe *et al.*, 2003) that the vernalization pathway involves two genes, *VERNALIZATION-INSENSITIVE 3 (VIN3)* and *MAD AFFECTING FLOWERING 2 (MAF2)*, which guarantees that a short cold phase does not result in flowering.

By prolonging the vernalization period, several cabbage varieties may be able to flower earlier.

Vernalization can occur in either the imbibed seed or the developing plants, depending on the species (Dennis *et al.*, 1996). Vernalization of seeds often necessitates slow development of germinating seeds under low temperature treatment, which may be accomplished by soaking seeds and keeping their water content above 50% of their dry weight (Chouard, 1960).

Vernalization is considered to be a natural adaptation that ensures flowering happens just after winter, allowing flowers and seeds to mature under favorable circumstances (Lin *et al.*, 2005; Sheldon *et al.*, 2006). As a result, certain temperate species utilize this physiological process to protect themselves from the cold in the winter.

High temperatures (25° – 40°C) before to or after the vernalization phase may delay or even interrupt flower induction and development. These plant responses are referred to as anti-vernalization and devernalization (Aditya and Fordham, 1995; Dennis *et al.*, 1996). This suggests that exposure to such high temperatures can reverse the vernalizing impact of low temperatures in some species. Although high temperatures might cause devernalization in the early phases of cooling, once established, the vernalized form is typically highly stable (Vince-Prue, 1975). Devernalization temperatures are typically in the 20°-40°C range.

Devernalization temperatures typically vary from 20° to 40° C. These effects are widely recognized for numerous vegetable crops (Lang, 1965; Wiebe and Liebig, 1989) and have been thoroughly examined by Heide (1970) for cabbage, as reported by Wiebe *et al.* (1992). Heide discovered that 15°C produced devernalization whereas 12°C caused further vernalization. As a result, devernalization might be predicted in the field when high daytime temperatures alternate with cold temperatures during the spring in temperate zones. This does not happen, most likely because the completely vernalized state achieved after the winter cold is maintained (Heide, 1970). This assumption is supported by the discovery of (Corbesier and Coupland, 2006) that the vernalization pathway includes vernalization genes (VRN), which ensure cold condition stability following return to warm temperature.

Vernalization explained physiologically

Several hypotheses have been proposed to explain the process of vernalization (Teroaka, 1992; Lee *et al.*, 1993; Dennis *et al.*, 1996). It has been proposed that there are two flowering pathways in *Arabidopsis thaliana* (hereinafter referred to as *Arabidopsis*). The first (vernalization-independent) pathway is associated with carbohydrates delivery to the apex, whereas the second (vernalization-dependent) system is concerned with gibberellic acid biosynthesis in the apical meristems (Bernier, 1988; Koornneef *et al.*, 1991).

This theory was reinforced by Dennis *et al.* (1996), who also noticed that non-vernalized plants are inhibited in gibberellic acid synthesis in the apex, and that this inhibition is reversed by vernalization. They also stated that the *Arabidopsis* mutants *pgm*, *lea*, *fve*, *fpa*, *fy*, and *ld* go via a vernalization independent route, but the *gal-3* mutant goes through a vernalization dependent pathway. Dennis *et al.* (1996) were unsure if irradiance, cytokinin, and gibberellic acid (GA) impacted the vernalization independent pathway or the carbohydrate influenced the vernalization dependent pathway in their proposed flowering mechanism (fig. 1). The major enzyme responsible for flower stimulation in the vernalization dependent pathway, however, was identified as kaurenoic acid hydroxylase (KAH), an enzyme that catalyzes an early step in GA production.

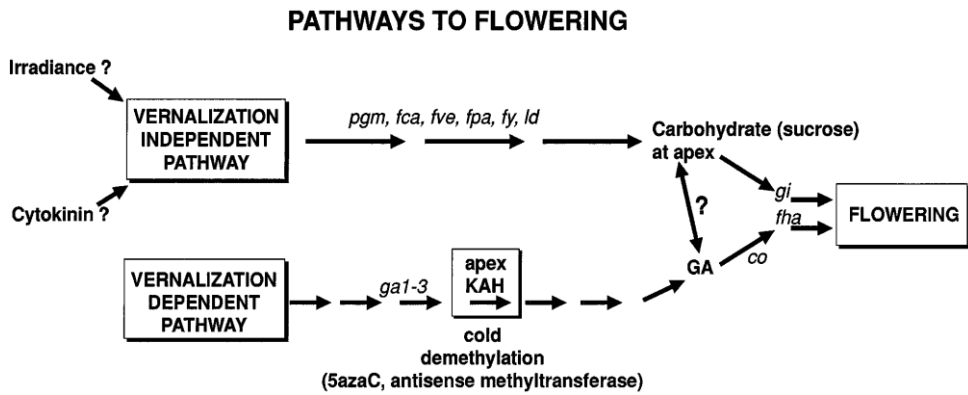


Fig 1: Pathways to flowering. Two pathways, a vernalization dependent and a vernalization independent pathway are shown. The step postulated to be blocked by methylation is indicated. The *Arabidopsis* mutants are in italics. (Source: Dennis *et al.*, 1996).

In *Arabidopsis*, four primary flowering constructive pathways have been proposed: the “photoperiodic”, “autonomous”, “vernalization”, and “GA” pathways (Corbesier and Coupland, 2006), and each generally requires a separate gene. It appears that these pathways interact in a complex way, and that all of the genes involved are linked to floral integrators (*FLOWERING LOCUS T*, *FT* and *SUPPRESSOR OF EXPRESSION OF CONSTANS 1*, *SOC 1*), the activities of which promote expression of *APETALA J* (*AP J*) and *LEAFY* (*LFY*) genes involved in floral induction (Corbesier and Coupland, 2005). Aside from these four major channels, light quality and variations in temperature were shown to have a significant impact on flowering time.

Molecular genetics of vernalization

The work on molecular level vernalization has been thoroughly reviewed (Sheldon *et al.*, 2000b; Nocker, 2001; Bernier and Perilleux, 2005; Corbesier and Coupland 2006). Many genes have been discovered as being involved in the vernalization

needs of various species (Napp-Zinn, 1987; Kinet, 1993; Boss *et al.*, 2004). The presence of many genes in various species shows that different chemicals are involved in flowering regulation. *FRIGIDA (FRI)* on chromosome 4 and *FLOWERING LOCUS C (FLC)* on chromosome 5 were discovered as key loci controlling flowering time in late and early flowering *Arabidopsis* ecotypes (Lee *et al.*, 1993; Koorneef *et al.*, 1998; Sheldon *et al.*, 2000a). *FRI* and another gene, *PHOTOPERIOD INDEPENDENT EARLY FLOWERING 1 (PIE 1)* (Michaels and Amasino, 2000; Michaels *et al.*, 2004), were later found to be able promote *FLC* expression.

The duration of vernalization has been found to be related to the degree of *FLC* down-regulation (Sheldon *et al.*, 2000a), implying that *FLC* is the predominant gene of vernalization. It has been discovered as a key regulator of flowering in the *Arabidopsis* vernalization pathway (Lin *et al.*, 2005; Finnegan *et al.*, 2005). According to Corbesier and Coupland (2006), the vernalization pathway involves the action of an unique vernalization gene, *VRN*, which is required for the stability of *FLC* repression following cold treatment to enable flower induction once plants return to warm temperatures.

Other *Brassica* species, such as cabbage, rely on vernalization to promote flowering, as does *Arabidopsis* (Friend, 1985). Osborn *et al.* (1997) found that vernalization-responsive flowering time loci in *Brassica* species segregate as two main quantitative trait loci that are co-linear with the *Arabidopsis* genome's *FRI* and *FLC* regions. Several *FLC* homologues have also been found in *Brassica* species such as *B. napus* (Tadage *et al.*, 2001) and *B. oleraceae* (Scranz *et al.*, 2002). Furthermore, Tadage *et al.* (2001) used genetic modification of *FLC* to change the flowering period in *B. napus*. These findings demonstrated that the *FRI* and *FLC* genes were crucial in controlling flowering time in several *Brassica* species through vernalization.

***Brassica* vernalization requirements**

Brassicacae are biennial plants that originate from temperate climates. During flower induction, they require cold temperatures (4 – 10°C) for 5 – 8 weeks (Nieuwhof, 1969; Yamaguchi, 1983). The shorter the time necessary, the lower the temperature within this range. When green plants are vernalized, the older and larger the plants are, the shorter the length of exposure to low temperature necessary for successful vernalization (Heide, 1970), according to Friend (1985). Heide (1970) discovered that the temperature requirements for vernalization and flower initiation could not be separated. Vernalization may be required for both flower initiation and for complete inflorescence development in cabbage (Kagawa, 1956).

Temperatures that induce vernalization varies depending on the species and range from -8°C to $+9^{\circ}\text{C}$. Since vernalization is an active biological process, it cannot occur at temperatures lower than the plant's biological threshold, the process might take anywhere from a few days to 6 – 8 weeks. During the period with low temperatures, vernalization, in the first part, is a reversible process, after which it becomes irreversible. This suggests that if a time of optimal vernalization temperatures is followed by a brief period of high temperatures, the vernalization effect is decreased or even cancelled (Munteanu and Fălticeanu, 2008).

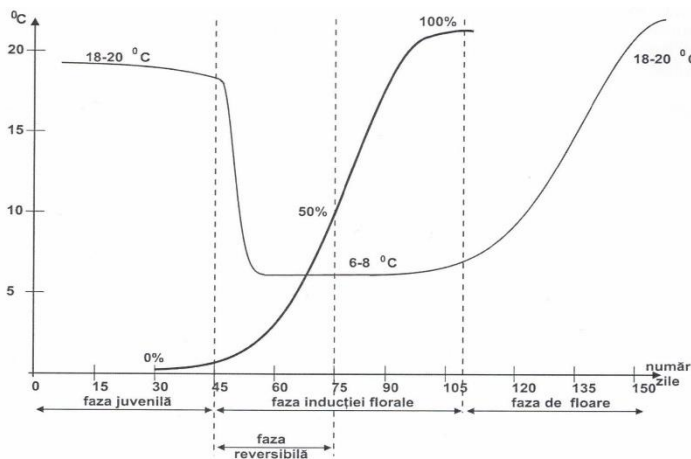


Fig 2: Theoretical diagram of vernalization (Source: Munteanu and Fălticeanu, 2008).

Some cabbage lines have mandatory vernalization needs and will remain vegetative for several years if cultivated constantly at high temperatures. For example, Friend (1985) reported that cabbage plants grown in a heated greenhouse for two years established a branching growth pattern with six heads and grew to be more than 2 meters tall. Friend (1985) also discovered that some *Brassicas* have a preferred vernalization requirement and will eventually flower at high temperatures, despite the fact that low temperature treatments enhance flowering.

Brassicas require a time of cold exposure to vernalize, either as germinating seeds (Nakamura and Hattori, 1961) or after a period of vegetative development (Ito and Saito, 1961). It has also been claimed that before a head cabbage becomes susceptible to low temperatures, it must reach a specific developmental stage (7 to 9 leaves or when the stem diameter reaches 5 – 6 mm) (Ito et al., 1966; Friend, 1985; Lin et al., 2005).

OTHER FACTORS AFFECTING VERNALIZATION

Environmental factors

Other environmental factors besides temperature may impact vernalization and flowering responses. Light, particularly photoperiod and irradiance, is one of

the most significant variables. Photoperiodism is the plant's reaction to the durations of the daily light and dark phases.

Thomas and Vince-Prue (1997) divides photoperiod flowering responses into five groups: short day plants (SDP, flowering when the length of the dark period exceeds a critical length); long day plants (LDP, flowering when the length of the dark period is shorter than a critical length); day neutral plants (DNP, flower regardless of day / night length); intermediate day plants (flower only when the day length is neither too long nor too short); and amphiphotoperiodic (dual-day length requiring plants, require SD and LD in a sequence).

Garner and Allard (1931) found that, although LDP flowered fast under short light-dark cycles, SDP remained vegetative unless they experienced extended uninterrupted dark periods. As a result, it has been proven that the dark period is critical in a plant's response to photoperiodism and that, although temperature during the photoperiod has minimal influence, temperature during the dark period has a significant effect on flowering response (Hamner and Bonner, 1938). However, it was discovered that even SDP need some light to flower. Day length is typically thought to be successfully detected by leaves, although there are evidence that it can also be perceived by the stem in the absence of leaves (Havelange and Bernier, 1991; Bernier and Perilleux, 2005). However, photoperiodic treatments are sensitive to very immature leaves or removed apices generated in vitro in several species (Francis, 1987). These findings suggest that stems and shoot tips can respond directly to photoperiod, but they do not call into question the fact that leaves are the primary location of day length perception.

Plant growth regulators

There have been several reports that endogenous hormones, especially gibberellins, are involved in cold-induced stem elongation and flowering in plants (Mander *et al.*, 1991; Chen *et al.*, 2003); however, the role of plant growth regulators in floral initiation has been a contentious issue, owing to conflicting results from experiments with different species (Bernier, 1988). According to Evans (1969), Went's 1928 identification of a plant hormone that regulated extension growth and meristematic activity sparked the quest for a flowering hormone. Later, Chailakhyan (1936) hypothesized that the flowering process was controlled by a long distance factor known as florigen.

Bernier (1988) also proposed that the floral transition is controlled by a multivariate system that includes several growth regulators and other compounds that interact either simultaneously or sequentially to activate distinct phases. The discovery of several hormones and metabolites as long – distance floral signals, as well as the fact that they were not all equally important in all of the species tested (Bernier and Perilleux, 2005; Corbesier and Coupland, 2006), strengthened this “multifactorial control hypothesis”.

The significance of gibberellins (GAs) in flowering regulation has been widely examined (Metzger, 1990; Kinet, 1993). As with many plants, there are

contradictory reports on the effect of GA treatment on *Brassica* flowering. Wittwer and Bukovac (1957) demonstrated that GA treatments of *Brassicaceae* accelerated flowering even on short days and promoted earlier flowering in unvernallized cabbage lines (Brunswick and Sugar Loaf) at 100-200 ppm with 8 foliar sprays spaced one week apart. Kahangi and Waithaka (1981) also shown that GAs induced early flowering in cabbage (kale cv. Collards), but not in cv. Thousand Headed. According to Hamano *et al.* (2002), while GA accelerated flower bud development and enhanced stem elongation, it did not participate in initiating flowering in *B. oleraceae* var. *capitata*, at least in certain cultivars.

The method of action of auxin indole acetic acid (IAA), whether it promotes or inhibits flowering, remains unclear. Despite the fact that the inhibitory impact of applied supraoptimal auxin concentrations has attracted significant attention (Evans, 1969), de Zeeuw (1955) proved that IAA reduces flowering but accelerates the end of the juvenile period to low temperature vernalization in Brussels sprout.

The discovery that bracting can be generated by ethephon foliar sprays (Booij, 1990) and gibberellin treatment (Duclos and Bjorkman, 2015) may illustrate how such selection may be made. The quest for broccoli lines that can be produced effectively in warmer regions has proved increasingly fruitful, and this crop may soon be able to be cultivated in locations with greater summer temperatures.

CONCLUSIONS

1. The diverse range of cultivated plant varieties developed for human use within *Brassica oleracea* brings with it a confusing diversity of optimum growth habitats and hence cultural practice needs. Selection within each type has resulted in the production of cultivars that are suited to environments ranging from tropical to cold temperate, as well as seasons varying from summer to winter.

2. This review clearly shows that vernalization, environmental conditions (photoperiod, irradiance, temperature and nutrition), growth regulators and genotype may all influence cabbage flowering and seed production.

3. Environmental conditions such as winter cold, photoperiod, or both are known to activate the movement of floral signals and the activity of floral genes.

4. More complicated pathways for *Arabidopsis* have been proposed because of the increasing interest in various secondary environmental parameters, including as irradiance, ambient temperature, light quality, water availability, and mineral availability, which may substitute for vernalization, more complicated pathways for *Arabidopsis* have been proposed.

5. A more thorough strategy integrating additional environmental parameters previously considered secondary, as well as understanding their interactions with floral genes and floral signals, is anticipated to result in straightforward induction of flowering in cabbage.

6. Although knowledge of these linkages is advanced in *Arabidopsis*, it has not yet been used in cabbage to establish whether there are similarities or conversely. It will be interesting to see how these primary and secondary

environmental influences influence floral genes and signals in cabbage in the future.

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