A REVIEW ON THE POSSIBILITY OF FLOWERING AND SEED PRODUCTION OF CABBAGE IN THE TROPICS

G. Nyarko
University for Development Studies,
P. O. Box TL 1882, Tamale, Ghana, West Africa.

INTRODUCTION

Cabbage (*Brassica oleraceae* L. var. *capitata.*) is one of the most popular 'exotic' vegetables in tropical countries like Ghana. It is a high value crop because there is a demand from most expatriate staff, restaurants, hotels and a large section of the population, especially in the cities and urban areas. The crop is also popular because cabbages are easy to cultivate, durable in the market place, have high nutritive value (Dickson and Wallace, 1986; Norman, 1992) and there is increasing evidence that their consumption is associated with reduced incidence of some types of cancer (Chiang *et al.*, 1993; Rungapamestry *et al.*, 2006).

Almost all the seeds for cabbages grown in tropical countries are imported and the countries spend substantial amounts on importation of seeds of exotic vegetables. Seeds of cabbage are very expensive and this causes considerable constraint to its large scale production since few farmers can afford the high prices. The seeds are imported because cabbage requires low temperatures to induce flowering (Nieuwhof, 1969; Yamaguchi, 1983), a phenomenon known as vernalization, but the average annual temperature in Ghana, even at high altitudes, is about 24°C.

Despite these challenges, some scientists have advocated locally produced seeds in the tropics (George, 1984; Buttenschon, 1985) to overcome a shortage of foreign exchange, the dangers of importing poorly-adapted varieties, the fact that imported seed germination is often poor and to remove a potential route for the introduction of foreign seed-borne pathogens.

The need to investigate the possibility of producing cabbage seeds in tropical countries like Ghana has become very imperative. The objectives of this review are to highlight the concept of vernalization and some of the other factors that may enhance flowering and seed production of cabbage in the tropics and to sensitize interested scientists to research into this very important area.

VERNALIZATION AND FLOWERING

Vernalization has been defined as the exposure of a germinating seed or young plant to a prolonged low temperature to induce flowering in the adult plant (Sheldon *et al.*, 2000a). The term was originally applied to treatments given to imbibed seeds or seedling plants but later it was extended to include cold treatments, which have similar effects when applied to plants during later stages of development (Roberts and Summerfield, 1987). Some species will not flower without vernalization. In others, vernalization advances the time of flowering (Dennis *et al.*, 1996). The duration of the low temperature period within which vernalization can occur, and the range of effective temperatures, vary between species and even between lines of the same species (Bernier *et al.*, 1981). For most species, the optimum inductive range is 1° to 10°C and the low temperature must be maintained for 1-3 months.

It has also been reported that when long vernalization duration was applied to cabbage plants, high temperatures at the end of the cold period were not effective in causing devernalization (Heide, 1970 as cited in Wien and Wurr, 1997). Further, recent study in *Arabidopsis* revealed that plants that had been

cold-treated as seeds for less than 14 d did not bolt, whereas those that had been cold-treated for 28 d bolted easily 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 ensures that cold period of insufficient duration will not cause flowering. Thus, extending the vernalization period may facilitate flower induction of many cabbage lines.

Depending on the species, either the imbibed seed or growing plants can be vernalized (Dennis *et al.*, 1996). Vernalization of seed usually requires slow growth of the germinating seeds during low temperature treatment, obtained by soaking seeds and maintaining their water content above 50% of their dry weight (Chouard, 1960). Vernalization is regarded as a natural adaptation ensuring that flowering occurs only after winter, in order for flowers and seeds to develop under favourable conditions (Lin *et al.,* 2005; Sheldon *et al.*, 2006). Thus, some temperate species use this physiological phenomenon as a means of survival from the cold in winter.

It has been shown in a number of cases that it is the stem apex which is the sensitive region for the vernalization stimulus and that the apex has to reach required maturity before the cold treatment is effective (Ito *et al.,* 1966; Fernandez *et al.*, 1997; Bernier, 1988). Vernalization of excised shoot tips of cabbage and carrots (*Daucas carota* var. sativa) had been successfully used to demonstrate the perceptive role of the shoot apex (Lang, 1965), however, in peas (*Pisum sativum*) and a few other species, it is reported to be perceived by leaves (Bernier and Perilleux, 2005), and Wellensiek (1964) also observed that mitotically dividing cells in any part of the plant can respond to vernalization. This was confirmed when root and leaf cuttings of *Lunaria biennis,* which were mitotically active at the time of vernalization, regenerated into flowering shoots, whereas cuttings from fully grown leaves exposed to vernalization regenerated into vegetative shoots (Wellensiek, 1964). The observation that mitotically active imbibed seeds can respond to vernalization, whereas dry seeds cannot, further indicates that cell division is necessary for vernalization (Bernier *et al.*, 1981). It has also been reported that isolated cells (originating from different locations of the mother plants) and excised buds and embryo in tissue culture can also perceive vernalization especially when external supply of sugar is available (Metzger *et al.*, 1992; Dixon, 2006). The thermo-induced state is inherited through successive mitotic divisions but it is not passed through meiosis (Lang, 1965). This implies that the progeny from seed of vernalized plants require a vernalization treatment to induce flowering.

High temperature (25°-40°C) before or after the vernalization period may delay or even stop flower induction as well as flower development. These plant reactions are called anti-vernalization and devernalization respectively (Aditya and Fordham, 1995; Dennis *et al.*, 1996). This means that the vernalizing effect of low temperature is reversible in some species by exposure to such high temperatures. Although high temperature may lead to devernalization in the early stages of chilling, the vernalized condition is usually extremely stable once established (Vince-Prue, 1975). Devernalization temperatures are usually in the range of 20°-40°C. These effects are known for many vegetable crops (Lang, 1965; Wiebe and Liebig, 1989 ;) and have been well studied by Heide (1970) for cabbage as reported by Wiebe *et al.* (1992). Heide found that 15°C caused devernalization, whereas 12°C resulted in additional vernalization. Therefore it could be expected that, in the field, devernalization will occur when warm daytime temperatures alternate with low temperatures during the spring in temperate regions. This does not occur, probably because the fully vernalized condition reached after winter cold is stabilized (Heide, 1970). This assertion is confirmed in a recent finding (Corbesier and Coupland, 2006) that the vernalization pathway involves vernalization genes (*VRN*), which ensure the stabilization of the cold condition after return to the warm temperature.

Vernalization requirements in brassicas

Brassicas originated in temperate regions where they are grown as biennials. They require chilling

temperatures (4°-10°C) for 5-8 weeks for flower induction (Nieuwhof, 1969; Yamaguchi, 1983). The lower the temperature within this range, the shorter the time required. When green plants are vernalized, the older and larger the plants the shorter the period of exposure to low temperature required for effective vernalization (Heide, 1970) as reported by Friend (1985). Heide (1970) found out that temperature requirements for vernalization could not be separated from those of flower initiation. Vernalization may be needed both for inflorescence initiation in cabbage and for the full development of the inflorescence (Kagawa, 1956). Some lines of cabbages have obligate vernalization requirements and will stay vegetative for a number of years when grown continuously at high temperatures. For instance, Friend (1985) reported that cabbage plants which were kept in a warm greenhouse for 2 years did not flower but produced a branched growth habit with six heads and were more than 2m tall.

Friend (1985) also observed that some brassicas have a preferential vernalization requirement and will eventually flower at high temperatures although flowering is enhanced by low temperature treatments. For vernalization to take place, brassicas require a period of exposure to low temperature, either as germinating seeds (Nakamura and Hattori, 1961) or after a period of vegetative growth (Ito and Saito, 1961). It has also been reported that a head cabbage needs to reach a certain developmental stage (7 to 9 leaves or when the stem diameter reaches 5-6 mm) before it becomes sensitive to low temperature (Ito *et al.,* 1966; Friend, 1985; Lin *et al.*, 2005).

Physiological explanation of vernalization

There are several theories attempting to explain the mechanism of vernalization (Teroaka, 1992; Lee *et al.*, 1993; Dennis *et al.,* 1996). From work on *Arabidopsis thaliana* (hereafter called *Arabidopsis*), it has been suggested that there are two pathways for flowering. The first pathway (called vernalization-independent) is involved with the supply of carbohydrate to the apex while the other pathway (called vernalization-dependent) is concerned with gibberellic acid biosynthesis in the shoot apex (Bernier, 1988; Koornneef *et al.,* 1991). Dennis *et al.* (1996) supported this theory and also noted that non-vernalized plants are blocked in gibberellic acid synthesis in the apex and that this block is released by vernalization. They further reported that the *Arabidopsis* mutants *pgm, fca, fve, fpa, fy* and *ld* were said to undergo a vernalization independent pathway whereas *ga1-3* mutant undergoes a vernalization dependent pathway. In their hypothesised pathway of flowering (Figure 1.1), Dennis *et al.* (1996) were not certain whether irradiance, cytokinin and gibberellic acid (GA) influence the vernalization independent pathway or whether carbohydrate influenced the vernalization dependent pathway. However, they identified kaurenoic acid hydroxylase (KAH), an enzyme that catalyses an early step in GA biosynthesis, as the main enzyme responsible for flower promotion in the vernalization dependent pathway. Thus, vernalization results in expression of KAH in the

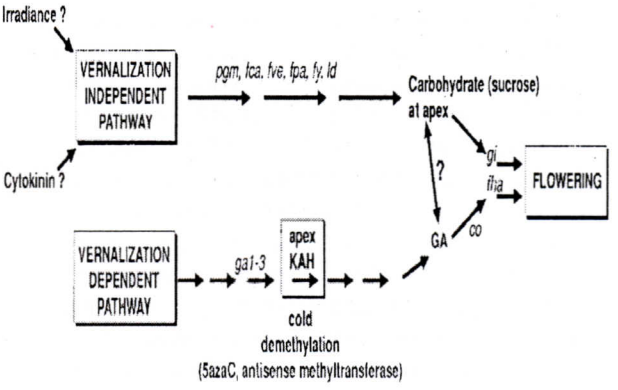

FIGURE 1.1: Pathways to flowering. Two pathways, a vernalization dependent and a vernalization independent pathway are shown. The step postulated to be blocked by methylation is indicated. The *Arabidopsis* mutants are in italics. (Source: Dennis *et al.,* 1996).

Recently, four main flowering promotive pathways have been proposed in *Arabidopsis*: the 'photoperiodic', 'autonomous', 'vernalization' and 'GA' pathways (Corbesier and Coupland, 2006) and each normally involves different gene(s). It appears

that these pathways interact in a complex manner and that all the genes involved are connected to special floral genes, usually referred to as floral integrators (*FLOWERING LOCUS T*, *FT*, and *SUPPRESSOR OF EXPRESSION OF CONSTANS 1, SOCI*), the activities of which promote expression of *APETALA 1* (*AP1*) and *LEAFY* (*LFY*) genes involve in floral initiation (Corbesier and Coupland, 2005). Apart from these four main pathways, light quality and changes in ambient temperature were also identified to strongly influence flowering time.

Sucrose has been identified as the carbohydrate most probably involved in vernalization. Changes in the carbohydrate content of shoot tips, leaves and roots of strawberry (*Fragaria ananassa* cv. Kordestan) have been investigated as a function of treatments inducing flowering and the most abundant soluble sugar, in all the organs tested, was sucrose (Eshghi and Tafazoli, 2006). Increased levels of soluble sugars in the apical bud of *Cheiranthus cheiri* L., a cold requiring plant, were detected in response to vernalization (Diomaiuto, 1988). Friend *et al.* (1984), in an experiment involving direct addition of sucrose to a medium in which seeds of *Brassica rapa* L. cv. Ceres were grown in sterile culture, concluded that sucrose may be an important controlling factor determining floral initiation in brassicas. Atherton *et al.* (1987) also confirmed that application of sucrose to the shoot tip of intact plants could partially replace the low temperature stimulus when sucrose solutions (50-100 mol l^{-1}) were supplied four times at intervals of five days to young leaves of cauliflower at the vicinity of the apical dome using a hypodermic syringe. Further, Roldan *et al.* (1999) reported that when the apex was in contact with sucrose, late flowering mutants of *Arabidopsis* were induced to flower early in the dark also suggesting that transport of photosynthate (sucrose) to the apex was important for flowering. Chilling during vernalization was found to suppress leaf initiation and leaf growth at the shoot apex, which consequently allowed increased availability of dry matter at the apical point (dome), thereby permitting its use for development to flower initiation. Sachs and Hackett (1969) suggested that reproductive development requires more energy than vegetative growth and postulated that flower initiation is as a result of increased assimilate supply to the apex. These results clearly showed that carbohydrates, especially sucrose, may be a very important factor for flowering in cabbage and the effect of sucrose supply on flowering will have to be investigated. Apart from sucrose, other substances such as nitrate, glutamine and cytokinins have recently been identified as floral signals in plants such as *Sinapis alba* (Bernier and Perilleux, 2005) and these should also be of interest to researchers.

Molecular studies of vernalization

Work on vernalization at the molecular level has been extensively reviewed (Sheldon *et al.*, 2000b; Nocker, 2001; Bernier and Perilleux, 2005; Corbesier and Coupland 2006). It has been reported that many genes have been identified to be involved in the vernalization requirements of different species (Napp-Zinn, 1987; Kinet, 1993; Boss *et al*, 2004). The fact that, in many species, a number of genes are involved suggests that several substances are implicated in the control of flowering. Genetic analysis of late and early flowering *Arabidopsis* ecotypes identified two major loci determining flowering time: *FRIGIDA* (*FRI*) on chromosome 4 and *FLOWERING LOCUS C (FLC)* on chromosome 5 (Lee *et al.*, 1993; Koorneef *et al.*, 1998; Sheldon *et al.*, 2000a). *FRI* and another gene, *PHOTOPERIOD INDEPENDENT EARLY FLOWERING 1 (PIE1)* (Michaels and Amasino, 2000; Michaels *et al.*, 2004) were subsequently identified as promoting the expression of *FLC*.

The duration of vernalization has been shown to be proportional to the degree of down-regulation of *FLC* (Sheldon *et al.*, 2000a) which suggests that *FLC* is main determining gene for vernalization. In fact, it has been identified as a major repressor of flowering in the vernalization pathway in *Arabidopsis* (Lin *et al.*, 2005; Finnegan *et al.*, 2005). It has been recently explained that vernalization pathway involves the function of a special vernalization gene, *VRN*, which is necessary for the stability of *FLC* repression after cold treatment to ensure flower initiation after plants return to warm temperature (Corbesier and Coupland, 2006).

FLC is expressed mainly in the shoot apical meristem and roots, but is absent from the inflorescence apex. It seems that the expression of *FLC mRNA* is not significantly decreased as the plant proceeds through the vegetative phase, suggesting that repression of flowering by *FLC* cannot be overcome by developmental progression (Sheldon *et al.*, 1999). The cloning of *FRI* has been reported; this gene encodes a protein that does not exhibit significant sequence identity to any other protein of known function (Johnson *et al.*, 2000). In addition to *FRI* and *FLC*, about 80 loci that influence flowering time have been identified by a mutational approach (Levy and Dean, 1998). It is not only known that cell division is a pre-requisite for vernalization to occur in plants and seeds but also that the stability of the vernalized state can be achieved through mitosis (Wellensiek, 1964). A possible reason given for this observation is the covalent modification of DNA cytosine methylation. Brock and Davidson (1994) and Burn *et al.* (1993) were among the first scientists to provide evidence for the involvement of DNA methylation in the vernalization response. They found that the promotion of flowering by extended cold (vernalization) in wheat and *Arabidopsis*, respectively, could be partially substituted by exposure of plants to the ribonucleotide analogue 5-azacytidine (5-azaC). Treatment with this compound was reported to result in demethylation of DNA. However, flowering was reportedly promoted only in lines that are known to respond strongly to vernalization (Burn *et al.*, 1993). Thus, the ability of 5-azaC to partly replace cold treatment for flower promotion seemed to suggest that it has an effect on the vernalization pathway. It was therefore hypothesised by Finnegan (1998) that vernalization results in the selective demethylation and the transcriptional activation of floral-promotive genes. Similarly, a combined effect of vernalization and 5-azaC treatment caused a substantial reduction in methylated cytosine (i.e. reduced the methylation of DNA) in winter wheat (*Triticum aestivum* L.) cultivar, Martonvasari 15 (Horvath *et al.*, 2003). Although the 5-azaC treatment reduced the methylation of the DNA in unvernalized plants, the treatment was not sufficient to induce flowering in wheat. Genger *et al.* (2003) confirmed that demethylation of DNA decreased *FLC* expression in the vernalized responsive mutants of *Arabidopsis*, but was not associated with a promotion of flowering. In some lines, it delayed flowering. This opposing effect of demethylation was attributed to another gene, *FWA*, which was activated in response to demethylation. However, Finnegan *et al.* (2005) observed later that DNA methylation is not part of the vernalization pathway of *Arabidopsis.*

As in *Arabidopsis,* other *Brassica* species such as cabbage rely on vernalization to promote flowering (Friend, 1985). Osborn *et al.* (1997) reported that vernalization-responsive flowering time loci of *Brassica* species segregate as two major quantitative trait loci that are co-linear with the regions of *FRI* and *FLC* in the *Arabidopsis* genome. Further work has also shown that several *FLC* homologues have been identified in *Brassica* species such as *B. napus* (Tadage *et al.*, 2001) and *B. oleraceae* (Scranz *et al.*, 2002). In addition, Tadage *et al.* (2001) were able to modify the flowering time in *B. napus* through genetic manipulation of *FLC*. These results revealed that *FRI* and *FLC* genes were very important in the control of flowering time through vernalization in other *Brassica* species.

OTHER FACTORS AFFECTING FLOWERING

Environmental factors

The vernalization and flowering responses may be influenced by environmental factors other than temperature. One of the most important factors is light, especially photoperiod and irradiance. Photoperiodism is the response of plants to the relative lengths of the daily light and dark periods. Photoperiod flowering responses are divided into five groups (Thomas and Vince-Prue, 1997): short day plants (SDP, flowering when length of the dark period exceeds a critical length); long day plants (LDP, flowering when length of the dark period is shorter than a critical length); day neutral plants (DNP, flower irrespective of day/night length); intermediate day plants (flower only when the day length is neither too long or short); and

amphiphotoperiodic day plants (dual-day length requiring plants, require SD and LD in a sequence). An earlier experiment by Garner and Allard (1931) with alternating light and dark periods of equal duration from 15 seconds to 12 hours indicated that, whereas LDP flowered rapidly under short light-dark cycles, SDP remained vegetative unless they received long uninterrupted dark periods. It has therefore been established that the dark period plays a central role in a plant's response to photoperiodism and that, whereas temperature during the photoperiod has little effect, the temperature during the dark period has a marked effect on the flowering response (Hamner and Bonner, 1938). However, it was shown that even SDP needed some light for flowering. Day length is usually believed to be effectively perceived by leaves but, in absence of leaves, there are indications that it can also be perceived by the stem (Havelange and Bernier, 1991; Bernier and Perilleux, 2005). In some species, however, very young leaves or excised apices grown *in vitro* are sensitive to photoperiodic treatments (Francis, 1987). These observations revealed that a direct response of the stems and shoot tips to photoperiod could occur, but do not challenge the fact that leaves are the main site of day length perception.

There is ample evidence that photoperiodism normally works with other factors to induce flowering. It has been shown, in some cases, that under long days, flowering is induced when the temperature, water availability or mineral nutrition are reduced (Kinet, 1993). There is also evidence that decreasing temperatures progressively nullify the day length requirement of absolute long day or short day plants (Bernier *et al.*, 1981), although the reverse has been reported for *Godetia quadrivulnera* which behaves as a day neutral plant at 20°-24°C and as an absolute long day plant at lower temperatures (Halevy and Weiss, 1991). Within species, the photoperiod requirements may vary between cultivars as was shown in ornamental *Helianthus annuus* L., sunflower (Yanez *et al.*, 2004), *Brassica rapa* L. var. *Rapifera*, turnip (Takahashi *et al.*, 1994) *and Brassica rapa* L. var. *Pekinensis*, chinese cabbage (Suge, 1984). Species of *Brassica* have either long day or day neutral photoperiod responses. The long day response may be either obligate, where the plants remain vegetative when maintained under constant short days (Friend, 1985), or preferential, as in Chinese cabbage where short days delay, but do not prevent, flowering. The day neutral response is found especially in rosette plants that require vernalization, such as head cabbage (Tindal, 1983). However some cabbages were reported to be LDP after vernalization (Kagawa, 1962).

It is also known that irradiance affects flower formation especially in autogamous flowering plants. Irradiance was found to affect earliness of flowering of many herbaceous ornamental plants (Warner and Erwin, 2001; Mattson and Erwin, 2005). For instance, Warner and Erwin (2001) showed that *Hibiscus surattensis* L. and *H. trionum* L. flowered developmentally earlier (fewer leaves below the first flower) as irradiance increased from ambient daylight to day light plus continuous 100 $\mu molm^{-2}s^{-1}$ high pressure sodium lighting. Low light conditions delay floral transition in tomato while, in tobacco, it may prevent flowering when the temperature is too high (Bernier *et al.*, 1981).

There is also much evidence that nitrogen nutrition plays an important role in flowering of many plants (Jeuffroy and Sebillotte, 1997; Xu *et al.*, 2001). Jeuffroy and Sebillotte (1997) found that early and prolonged nitrogen starvation prematurely stopped the progression of flowering in pea, while Xu *et al.* (2001) reported that gradually increasing the total N concentration with the progressing physiological stages from 3 to 9 mM increased the total set of flowers and fruits of sweet pepper (*Capsicum annuum* L). Similar findings have been reported earlier for some cold requiring plants. For example, Colder and Cooper (1961) reported that *Dactylis glomerata* lose their need for low temperature in the presence of high nitrogen levels. Shortage of nitrogen also delayed curd initiation and maturity in the cauliflower (Parkinson, 1952). It is probable that where nitrogen deficiency retards floral initiation it is due to a reduction of the level of metabolites at the stem apex. Recent evidence revealed that reduced N- compounds are among the floral signals

translocated from the leaves to stem apex to cause events that are specifically related to the induction of flowering (Bernier and Perilleux, 2005). Therefore nitrogen nutrition in relation to flowering of cabbage has to be investigated.

It has been found that vegetative propagation methods have promoted flowering in some crops, e.g. induction of cabbage flowers using ratoons (MnZava and Msikita, 1988).

Plant growth regulators

There are several reports that endogenous hormones, particularly 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 induction has been a controversial issue, mostly because experiments with different species have produced conflicting results (Bernier, 1988). The isolation by Went in 1928 of a plant hormone, which controlled extension growth and meristematic activity, as reported by Evans (1969), stimulated the search for a flowering hormone. Later, Chailakhyan (1936) proposed that the flowering process was under the control of a long distance factor called florigen. Bernier (1988) further suggested that the floral transition involves a multifactorial controlling system including different growth regulators and other substances acting either simultaneously or sequentially to trigger different steps. The recent identification of some hormones and some metabolites as long distance floral signals and the fact that all were not of equal importance in all the species studied (Bernier and Perilleux, 2005; Corbesier and Coupland, 2006) supported this 'mutifactorial control hypothesis'.

The role of gibberellins (GAs) in the control of flowering has been reviewed extensively (Metzger, 1990; Kinet, 1993). It has been found that GAs stimulate flower production in tulip, *Tulipa gesneriana* var. Cassini (Kurtar and Ayan, 2005), *Cordyline terminalis* (L) Kunth and various ornamental aroids, which are photoperiodically neutral and do not respond to the cold (Halevy, 1990). In contrast, GA inhibits flower initiation in several perennial angiosperms, particularly fruit trees and woody angiosperms (Davenport, 1990). Kinet (1993) also reported that one of the most consistent effects of GAs is hastening the floral transition in terms of time from sowing.

As for many plants, there are conflicting reports on effect of GA application on flowering of brassicas. Wittwer and Bukovac (1957) showed that GA treatments of brassicas stimulated flowering even under short days and also promoted earlier flowering in unvernalized cabbage lines (Brunswick and Sugar Loaf) at 100-200 ppm with 8 foliage sprays at intervals of one week. Kahangi and Waithaka (1981) also showed that GA_3 promoted earlier flowering of cabbage (kale cv Collards), but failed in cv Thousand Headed. Hamano *et al.* (2002) explained that although GA hastened flower bud development and increased stem elongation; it did not participate in inducing flowering in *B. oleraceae* var. capitata, at least in some cultivars. GA_3-treated rutabaga [*B. napus* subsp. *rapifera* (Metzeg.) Sinsk] failed to flower when it was not chilled (Ali and Machado, 1982). It seems that the biologically active GA_1 is the main growth-effective GA responsible for stem elongation and the subsequent flowering of brassicas. Both vernalization at 10°C and exogenous application of GA_3 increased the levels of endogenous GA_1 in cauliflower (Guo *et al.*, 2004) indicating that it is likely to be a causal factor in inflorescence stalk elongation and flowering.

Low doses of auxin are required for flower initiation to occur, but inhibition occurs at high levels (Bernier, 1988). The auxin indole acetic acid (IAA) inhibited and delayed flowering in *Pharbitis nil* and *Lens culinaris* respectively (Wijayanti *et al.,* 1997; Naeem *et al.,* 2004). *In vitro* studies also indicate that auxin included in the medium is essential, although an increased level inhibits flower formation in most experimental systems (Dickens and van Stadens, 1988). Therefore, the mode of action of auxin, either to promote or inhibit flowering, is still debatable, although the inhibitory effect of applied supraoptimal auxin concentrations has received much attention (Evans, 1969) and de Zeeuw (1955) confirmed that IAA inhibits flowering but hastens the end of the

juvenile phase to low temperature vernalization in Brussels sprout.

Reports indicating that cytokinins are involved in the control of floral transition differ with species. While they are reported to promote flowering in some species (Bernier *et al.*, 2002), in others there is no evidence that they affect flowering (Wang *et al.*, 1997; Bernier *et al.*, 1981). This discrepancy may be due to the fact that cytokinins' effects are highly dependent on the dosage. However, in most situations, exogenous cytokinins have a promotive effect (Bernier, 1988; Dennis *et al.*, 1996). Sotta *et al.* (1992) again showed that cytokinin levels in the shoot apex of *Sinapis sp.* usually increased during floral evocation thus giving evidence that the hormone was involved in flowering. Chailakyan *et al.* (1988) observed that, under non-inductive long days, cytokinin present in the culture medium induced flowering whereas it inhibited flowering under short days. The cytokinin, 6-benzyladenine (BA) has been reported to promote *in vitro* flowering in *Bambusa arundinacea (Retz)* (Joshi and Rajini, 1997) and *Kniphofia leucocephala* (Baijnath) (Taylor *et al.*, 2005). The latter authors also found that the effect of cytokinins was dose-dependent, with high BA inhibiting flower formation. The more recent evidence (Bernier *et al.*, 2002; Bernier and Perilleux, 2005) revealed that cytokinin of the isopentenyladenine type actually promoted flowering in *Sinapis alba.*

Like cytokinins, the effect of exogenous ethylene depends on the species (Bernier, 1988; Halevy, 1990). Treatment of bulbs with ethylene stimulates flowering in some species (Imanishi *et al.*, 1992; Botha *et al.*, 1998). Imanishi *et al.* (1992) found that when bulbs of tulip were stored at 20°C for 0-6 weeks ethylene increased the number that flowered but reduced the flowering period. In a range of geophytes and bromeliads, promotion usually occurs since flowering in these plants is stimulated by ethylene or ethephon application (Halevy, 1986). However, the use of ethylene to promote flowering should be handled with care because of the adverse effect it may have after flowering. The post harvest quality of many flowering plants is reduced by the ethylene treatment as it is known to cause premature wilting, colour fading and abscission of flower petals (Clark *et al.*, 1997; Jones *et al.*, 2001).

CONCLUSION

It is obvious from this review that vernalization, environmental factors (photoperiod, irradiance, ambient temperature and nutrition), growth regulators, and genotype may affect flowering and seed production of cabbage in the tropics. It is also clear that movement of the floral signals and the activities of floral genes are known to be triggered by environmental factors which were attributed mainly to winter cold, photoperiod or both. It therefore seems that flowering of cabbage in the tropics would be best handled from both physiological and genetic approaches, since the identification of floral control genes of a particular species and the knowledge of the right environmental factors to initiate the genes' actions require both disciplines. In the last couple of years, more complex pathways have been proposed for *Arabidopsis* because of the increasing interest of other secondary environmental factors, such as irradiance, ambient temperature, light quality, water availability and mineral availability, which may substitute for vernalization. Thus, easy induction of flowering in cabbage is likely to be achieved with a more comprehensive approach involving other environmental factors formerly considered as secondary, and understanding their relationships with floral genes and floral signals. The knowledge of these relationships is well advanced in *Arabidopsis* but it has not been applied in cabbage to determine whether there are similarities or *vice versa*. It will be of interest, in future research, to understand how these primary and secondary environmental factors affect floral genes and signals in cabbage.

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