

Physiology of flowering and dormancy regulation in annual- and biennial-fruited red raspberry (*Rubus idaeus* L.) – a review

By O. M. HEIDE¹ and A. SØNSTEBY^{2*}

¹Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P. O. Box 5003, NO-1432 Ås, Norway

²Arable Crops Division, Norwegian Institute for Agricultural and Environmental Research, NO-2849 Kapp, Norway

(e-mail: anita.sonsteb@bioforsk.no)

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SUMMARY

Recent research on how the structure and physiological development of red raspberry (*Rubus idaeus* L.) plants are controlled by genotype and the climatic environment is reviewed. Some older work, especially on plant structure relations, is also included. Physiological differences between annual- and biennial-fruited plant types are highlighted. One major difference is the different requirements for flower formation. While biennial-fruited cultivars have an absolute low temperature (\leq approx. 15°C) requirement for floral initiation, annual-fruited cultivars readily initiate floral primordia at temperatures as high as a constant 30°C. Also, while biennial-fruited cultivars are facultative short-day plants with a critical photoperiod of 15 h at intermediate temperatures, flowering is promoted by long photoperiods in at least some annual-fruited cultivars. However, the essential difference that determines whether the shoot life-cycle becomes annual or biennial is that, in biennial-fruited genotypes, floral initiation is linked to the induction of bud dormancy; whereas, in annual-fruited cultivars, floral initiation is followed by direct flower development. Although this is genetically determined, it is a plastic trait that is subject to modification by the environment. Thus, at low temperatures and under short photoperiods, the majority of initiated buds also enter dormancy in annual-fruited cultivars, with tip-flowering as a result. Practical applications are discussed, and it is concluded that our present physiological knowledge-base provides excellent opportunities for the manipulation of raspberry crops for out-of-season production and high yields. It also provides a firm platform for further exploration of the underlying molecular genetics of plant structures and response mechanisms.

The red raspberry (*Rubus idaeus* L.) is a temperate shrub with short-lived, woody shoots borne on a long-lived perennial root system. It is an important soft fruit species that is widely grown across all temperate and cold regions of the World. Two groups of cultivars with different life-cycles are commonly recognised. In the more common, biennial-fruited cultivars the shoots (canes) have a 2-year life-cycle during which they pass through a sequence of seasonal phases involving vegetative growth, flower formation and fruiting, as well as induction and breaking of winter bud dormancy (Hudson, 1959; Williams, 1959b; c; Sønsteb and Heide, 2008). In the annual-fruited cultivars, on the other hand, the entire cycle of vegetative growth, flowering and fruiting is normally completed in a single growing season (Keep, 1988; Carew *et al.*, 2000). A third, so-called tip-flowering type, is also sometimes considered (Ourecky, 1976; Carew *et al.*, 2000; Dale, 2008). In such cultivars, a few flowers and fruits are produced at the tip of the shoot at the end of the first growing season, while the rest of the buds will flower and fruit in the second year. However, this type of behaviour can also be found in both biennial- and annual-fruited cultivars (Williams, 1960; Carew *et al.*, 2000) and, as demonstrated by Sønsteb and Heide (2008; 2009), it is a plastic trait

which, to a large extent, is under environmental control (*cf.* Slate, 1940; Ourecky, 1976).

In the literature, annual-fruited cultivars are commonly referred to as primocane-fruited cultivars, and terms such as autumn-fruited, autumn-cropping, everbearing, and tip-fruited are also variously used (Keep, 1988), whereas biennial-fruited cultivars, sometimes referred to as summer-cropping cultivars, are now often referred to as floricanes-fruited cultivars (e.g., Carew *et al.*, 2000; Oliveira *et al.*, 2001; Dale *et al.*, 2005). Since none of these terms are self-explanatory, and since annual- and biennial-fruited are the terms that best and adequately explain the essential difference, namely a 1-year or 2-year life-cycle, we have suggested that these terms should be generally adopted (Sønsteb and Heide, 2009).

Because of the commercial importance of raspberry, the environmental control of growth and flowering has been extensively studied in this species. The literature in this field was reviewed by Moore and Caldwell (1985), and later by Carew *et al.* (2000). A substantial body of new research has, however, been produced during the last decade. Increasing interest in out-of-season production of raspberry, and production in warmer climates, has stimulated new research to improve our understanding of the underlying control mechanisms for the manipulation of raspberry plants. The present review

*Author for correspondence.

emphasises the results of these more recent investigations and focuses on the contrasting physiological responses of annual- and biennial-fruiting cultivars that have emerged from these studies.

PLANT STRUCTURE RELATIONS

A detailed account of the morphological structure of the raspberry plant and its seasonal phases of development was presented by Hudson (1959), who also defined a number of terms for referring to the various plant parts and structures. Raspberry shoots can arise in three different ways: (a) as root suckers from adventitious buds formed on the roots; (b) as stem suckers from axillary buds situated on the annual shoot at ground level [the “replacement shoots” of Hudson (1959)]; or, more rarely, (c) as lateral branches from axillary buds higher up on the shoot. Each type of shoot behaves in a different way in response to its environment (Hudson, 1959). In this review, emphasis is placed on the fate of shoots arising as root suckers. The morphology of the shoot depends primarily on (a) whether the apical and lateral buds initiate leaf or flower primordia, and (b) whether these primordia expand or become dormant. Shoot morphology is further modified by the rate and extent of elongation of the main shoot internodes, and the length and distribution of lateral fruiting branches (Sønsteby and Heide, 2008; 2009). While the initiation of flower primordia starts at the terminal (apical) bud and spreads basipetally in annual-fruiting cultivars (Sønsteby and Heide, 2009), in biennial-fruiting cultivars the first floral primordia are formed laterally in buds situated five-to-ten nodes below the shoot tip, and the process then progresses both basipetally and acropetally (Mathers, 1952; Williams, 1959c; Sønsteby and Heide, 2008). Details of the progress of floral initiation and differentiation of flower buds have been described by Williams (1959c).

The inflorescence of red raspberries is a cyme, in which the terminal flower develops first, followed by the sequential development of flowers further down the inflorescence axis. While the uppermost lateral buds produce only one-to-three inflorescences, the complexity of the flowering laterals increases gradually in buds at lower positions (Sønsteby and Heide, 2008; 2009). The number of flowers in each inflorescence varies widely, and the number of inflorescences on each fruiting lateral increases steadily from the top to the base of the main shoot (Sønsteby and Heide, 2008). Also, raspberry canes typically bear two or more axillary buds at each node (Jennings, 1979), and these accessory buds can give rise to double or multiple laterals (Robertson, 1957; Williams, 1959c). Jennings (1979) noted that large-diameter canes are more likely to produce such multiple laterals. Although the accessory buds frequently do not develop into fruiting laterals, they are important for the production of replacement laterals if the primary bud is injured by frost or mechanical damage (Jennings, 1979).

PROPAGATION AND JUVENILITY

In nature, raspberry spreads both sexually, by seed, and vegetatively by root suckers. Typically, clumps of genetically-identical plants (clones) are established and

spread vigorously (Hudson, 1959; Williams, 1959a). With time, such clones can cover quite substantial areas. For commercial production, raspberry is propagated from adventitious buds that arise laterally on the roots (Hudson, 1954). Such adventitious buds are present in large numbers on intact roots at all times of the year, but are most conspicuous from Autumn to Spring (Hudson, 1954). However, their capacity to grow into shoots (suckers) varies greatly during the year, with an “on season” during Autumn and Winter, and an “off season” during Spring and Summer. For isolated root cuttings (Hudson, 1954), the “on season” lasted from August-to-April, with a marked optimum in January and February. Similar patterns were also found in intact plants in the field, except for the suspension of growth during the coldest Winter months (Williams, 1959a). Also, while cuttings from roots lifted in Autumn and early Winter produced the highest number of shoots when planted in a cool environment, those lifted in the late Winter months performed best when planted in a warm environment (Hudson, 1954). This suggests the need for a certain amount of chilling to achieve the optimum performance of root buds, an assumption that was confirmed by the results of Carew *et al.* (2001). Using the annual-fruiting cultivar ‘Autumn Bliss’, these authors found that the shoots on roots lifted in early October grew poorly and only developed into short rosettes if not chilled. As chilling was increased, or lifting was delayed, vegetative growth increased. Therefore, for commercial production and experimental purposes, roots should be lifted in Autumn and cold-stored (chilled) for several weeks before they are used for propagation purposes (Carew *et al.*, 2001; Sønsteby and Heide, 2008; 2009).

As discussed later, raspberry plants, even when propagated vegetatively from adventitious buds, have a juvenile phase during which they cannot be induced to flower. Bearing in mind that these plants originated from mature plants, this means that a rejuvenation process must have taken place during adventitious bud formation. This is analogous to the situation in apple rootstocks regenerated from callus tissue by micropropagation techniques, which are also juvenile (Heide and Prestrud, 2005). This interesting phenomenon was likewise observed during adventitious bud formation in *Begonia* leaf cuttings (Heide, 1964), showing that, in this respect, adventitious bud formation resembles somatic embryogenesis.

ANNUAL GROWTH CYCLE AND LIFE HISTORY

In their temperate natural environment, both annual- and biennial-fruiting raspberry cultivars form new shoots as root suckers as the temperature rises in Spring. During Spring and Summer, the shoots then go through a phase of continuous vegetative growth with a typical sigmoid time-course. From then on, the developmental paths differ in the two types (Figure 1). While the growth of annual-fruiting cultivars is stopped relatively early in Summer by the formation of terminal flowers which develop directly and set fruit (Williams, 1959c; Keep, 1988; Carew *et al.*, 2000; Sønsteby and Heide, 2009), biennial-fruiting cultivars continue to grow towards the end of the season, when growth slows down and eventually comes to a complete stop. Simultaneously, the

terminal and uppermost lateral buds initiate floral primordia and enter a state of dormancy (Williams, 1959b; Sønsteby and Heide, 2008). The process progresses basipetally and, by end of the season, all lateral buds except those at ground level are floral and all buds are dormant (Williams, 1959c). The dormant state is broken by the action of low temperature (chilling) during Winter and, with the rise in temperature, the lateral buds will sprout in Spring to produce flowering and fruiting laterals. While the terminal bud and a varying number of the uppermost lateral buds in annual-fruiting cultivars will flower during the first season, buds further down the shoot will become dormant and, like those on biennial-fruiting cultivars, will flower and fruit in the second year. After flowering and fruiting, the shoots die and their life-cycle is then complete, while new shoots are formed from root suckers and axillary buds at the base of the old shoot to sustain the perennial performance of the plant as a whole.

In their review article, Carew *et al.* (2000) concluded that, apart from the timing of floral initiation, the growth cycles and their environmental control appeared to be very similar in annual- and biennial-fruiting cultivars and, in their opinion, the two groups had been distinguished largely for reasons of convenience. However, it has become clear from later investigations that annual- and biennial-fruiting raspberry cultivars do differ fundamentally in their developmental physiology and in the environmental control of their annual growth cycles. For this reason, the two cultivar groups are dealt with separately in the following presentation.

ENVIRONMENTAL CONTROL OF GROWTH AND DEVELOPMENT

Biennial-fruiting cultivars

In biennial-fruiting raspberry, growth cessation and floral initiation are jointly controlled by the interaction of low temperature and short-day (SD) conditions, and the processes coincide in time in both natural and controlled environments (Williams, 1959c; 1960; Sønsteby and Heide, 2008; Sønsteby *et al.*, 2009). Apparently, growth cessation and floral initiation are parallel outputs from the same internal induction mechanism (Sønsteby and Heide, 2008). Continued shoot growth requires high temperatures and is enhanced by long photoperiods. Williams (1960) found that 'Malling Promise' plants grew continuously and remained vegetative at 21°C in both 9 h and 16 h photoperiods, while at 10°C they ceased growing and initiated floral primordia in both day-lengths. Williams (1960) further demonstrated that 'Malling Promise' plants remained vegetative for 18 months and grew to a height of almost 7 m in a heated greenhouse with a 16 h photoperiod. These results were confirmed by Sønsteby and Heide (2008) with the cultivar 'Glen Ample', which produced continuous growth with no floral initiation at 18°C, even under SD conditions. At an intermediate temperature of 15°C, at which short photoperiods are necessary for growth cessation and floral initiation (Williams, 1959c), the critical photoperiod for these processes was found to be approx. 15 h (Sønsteby and Heide, 2008).

Nestby (1986) found that even under natural continuous light conditions at high latitudes, a range of biennial-fruiting raspberry cultivars and selections ceased growing and became dormant at Summer temperatures below approx. 10°C. The same response was found in 'Glen Ample' plants grown in greenhouses for the production of high-yielding long canes (Heiberg *et al.*, 2008; Sønsteby *et al.*, 2009). When such plants were moved outside in Spring, before the temperature had risen above approx. 10°C, temporary or permanent cessation of growth was frequently observed. The absence of photoperiodic control of growth cessation, and its replacement by low temperature control, has also been reported in a range of other woody species of the *Rosaceae* family (Nitsch, 1957; Heide and Prestrud, 2005; Heide, 2008). For a discussion of this phenomenon, see Heide (2008).

When 'Glen Ample' plants were exposed to controlled temperatures and natural light conditions at 60°N at Ås, Norway, from 10 August, they exhibited an immediate suppression of growth at 9°C and 12°C, with complete growth cessation after 4 weeks (by 7 September). This coincided with the first appearance of floral primordia in dissected buds (Sønsteby and Heide, 2008). Plants exposed to a 10 h photoperiod at 9°C for 2–4 weeks showed a transient suppression of growth, followed by resumed growth when they were returned to high temperature and long-day (LD) conditions. While Williams (1959c) found that exposure to 10°C and 9 h SD for 10 weeks was required to establish dormancy in 'Malling Promise', exposure to the same conditions for 5 or 6 weeks, resulted in complete growth cessation and the induction of dormancy in 'Glen Ample' (Sønsteby and Heide, 2008). The critical induction period for floral initiation was 3 weeks, although no visible changes were observed in buds before week-4. When exposed to inductive conditions for marginal periods of 3 or 4 weeks, a large proportion of the 'Glen Ample' plants behaved like annual-fruiting cultivars and produced a few terminal flowers (Sønsteby and Heide, 2008).

Vegetative growth rates and final shoot heights vary between cultivars (e.g., Jennings and Dale, 1982), and are strongly enhanced by high temperature (Sønsteby and Heide, 2008; Sønsteby *et al.*, 2009). In their natural environment, raspberry canes continue to grow until late Summer, when growth gradually decreases (Sønsteby and Heide, 2008), and a small rosette of leaves is formed at the top of the shoot because of constrained internode elongation. Similarly, root suckers that emerge late in the season do not elongate beyond the stage of a rosette of leaves which are formed at emergence (Hudson, 1959). A critical photoperiod of 15 h for growth cessation and floral initiation at 15°C, as found under artificial light conditions (Sønsteby and Heide, 2008), agrees with the results from natural light conditions. Thus, Mathers (1952) and Robertson (1957) found that, in Scotland, the cultivars 'Malling Promise', 'Malling Landmark', and 'Lloyd George' were vegetative in July, but all had initiated floral primordia by the middle of September. Likewise, Williams (1959c) found that, in Southeast England, floral primordia in the apical and uppermost ten-to-15 lateral buds of 'Malling Promise' appeared in the second week of September. Thereafter, initiation took place in buds progressively further down the shoot.

By early December, floral primordia were visible in all axillary buds except the lowermost ten-to-12 and, by the end of January, in all buds above soil level. Under natural day-length conditions at Ås, Norway (60°N) and a constant temperature of 15°C, floral primordia first appeared by 21 September, when the natural photoperiod is approx. 12 h (Sønsteby and Heide, 2008). However, since it took 4 weeks from the commencement of the inductive conditions to the appearance of primordia, the actual critical photoperiod would have been reached by the last week of August, when the day-length at 60°N is approx. 15 h. At 9°C and 12°C, on the other hand, where SD conditions are not required for growth cessation and floral initiation, induction was effective from 10 August, when the photoperiod at 60°N is over 16 h (Sønsteby and Heide, 2008). This agrees well with the results of Måge *et al.* (1989), who found that a range of raspberry cultivars formed floral primordia under field conditions at Ås from late August to early September. These results show that, while the cessation of raspberry growth and floral initiation in Southeast England must await reductions in day-length and temperature to about 15 h and 15°C, respectively, these processes can take place 2–3 weeks earlier in Norway under much longer photoperiods because of the lower temperatures prevailing at the higher latitude.

Raspberry plants also have a juvenile phase during which they cannot be induced to flower. Williams (1960) found that the biennial-fruiting 'Malling Promise' needed to form 15 or more leaves before it could be induced to flower, and this was confirmed by Sønsteby and Heide (2008) with the cultivar 'Glen Ample'. While the transition from juvenility was abrupt in 'Glen Ample', it was more gradual in 'Malling Promise' in which only some plants initiated flowers at the 15-leaf stage. No flowering took place in plants with five or ten leaves, even after extended exposure to inductive

conditions. Nevertheless, such small plants did respond to low temperatures and SD conditions with cessation of growth, although, with marginal inductive periods of up to 6 or 7 weeks, the buds did not enter full dormancy but resumed growth after 6 weeks of exposure (Williams, 1960; Sønsteby and Heide, 2008). Likewise, root suckers that emerged late in the season ceased growing and entered a stable state of dormancy under the prevailing low temperature and SD conditions of Autumn, without the initiation of flowers (Hudson, 1959; Williams, 1959a). Therefore, even though growth cessation and floral initiation are interrelated by both cause and time (*cf.* Figure 1), they may, under certain circumstances, be separated.

Release from the state of endodormancy (Lang *et al.*, 1987) attained by the end of the season, requires exposure of the dormant buds to low temperatures (chilling) during Winter. Under field conditions in Southeast England, 'Malling Promise' plants attained the deepest state of dormancy in October and November, after which time, dormancy was gradually reduced (Williams, 1959c). In an extensive study over 6 years, with a total of 12 biennial-fruiting cultivars grown at eight locations in Norway and Sweden, Måge (1975) found that buds entered dormancy in late August and reached the deepest state of dormancy in October. The release from dormancy, as determined by forcing of single-node cuttings at 18°C, then progressed quickly during November and December and, by early January, all healthy buds were able to burst within 17 d, whereupon the time to bud-burst continued to decrease slightly until the beginning of April. Under conditions of artificial chilling, a requirement for 800–1,500 h below approx. 7°C has been reported for buds on intact raspberry plants (Lamb, 1948; White *et al.*, 1999). Temperatures in the range 0°–7°C were found to be more effective than sub-freezing temperatures (Lamb, 1948). In fully

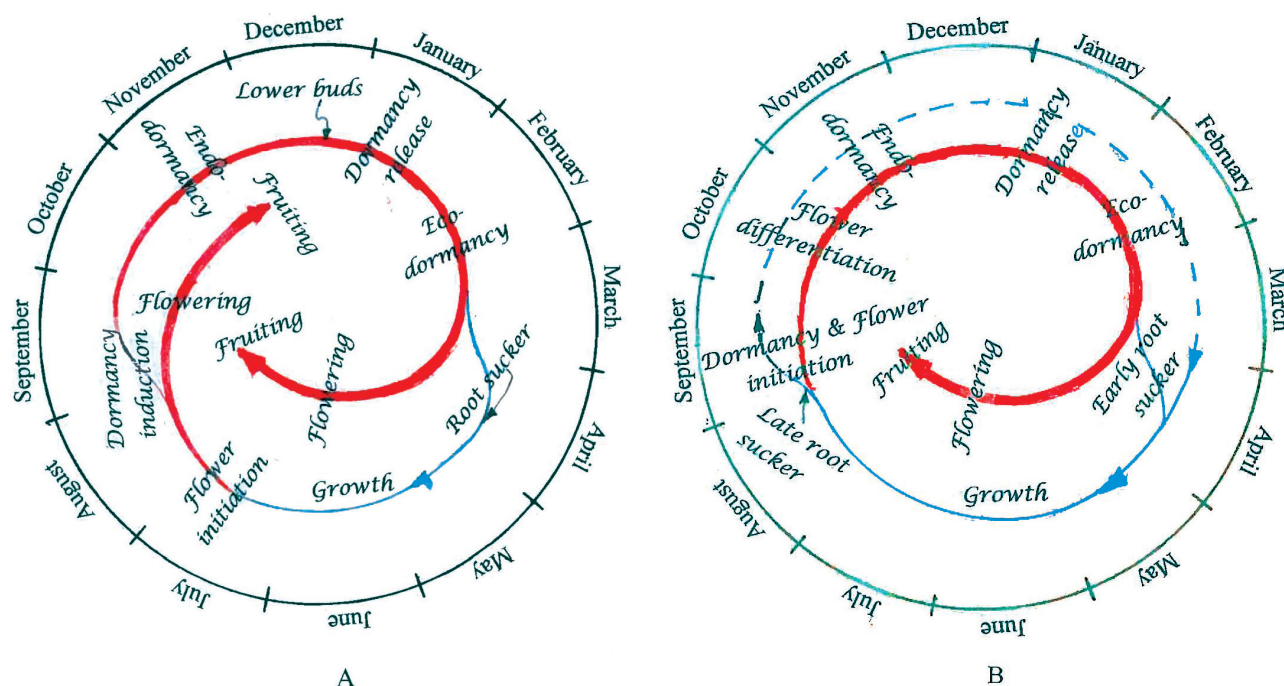


FIG. 1

Illustrations of the annual growth cycles of annual-fruiting (A) and biennial-fruiting (B) raspberries. The blue colour denotes the vegetative phases and the red colour the reproductive phases of plant development.

dormant plants which had been exposed to 10°C and SD for 16 weeks, 6–8 weeks (i.e., approx. 1,000–1,500 h) of chilling at 3°–4°C were sufficient for breaking of dormancy and the resumption of growth in intact plants of 'Malling Promise' (Williams, 1959c). However, as demonstrated by Måge (1975) and White *et al.* (1999), bud-burst responses are different in isolated buds and on intact canes, because of interference by the inhibitory action of adjacent buds on intact plants or canes [so-called correlative inhibition or paradormancy; Lang *et al.* (1987)]. While approx. 1,500 h of chilling at 4°C was adequate for almost 100% bud-burst on isolated nodes, regardless of the positional origin of the bud, only about 60% of buds from the uppermost part of the cane were able to burst on intact canes after the same amount of chilling, with the proportion progressively decreasing in buds from lower positions on the shoot (White *et al.*, 1999). These findings were confirmed by Mazzitelli *et al.* (2007), who found that nearly 2,500 h of chilling at 4°C were required to burst all buds on the upper part of intact plants. They further demonstrated that the phases of dormancy release were associated with co-ordinated changes in the expression of several dormancy-related genes.

However, the depth and duration of dormancy are also affected by temperatures during shoot growth and dormancy induction, a phenomenon that has been demonstrated in a number of woody plants, including raspberry (for references, see Heide, 2003). Thus, Måge (1975) found that raspberry plants produced in years, or at locations with high summer temperatures consistently had particularly deep and lasting dormant periods. Highly significant correlations were found between the percentage of bud-burst (or the forcing requirements of buds sampled in December), and the mean temperature during each of the preceding summer months. The highest coefficient of correlation was that for August ($r = 0.674$; $P \leq 0.05$), while that for July was almost as high. By using the mean temperature for these 2 months, higher coefficients of correlation were obtained than for any single month (Måge, 1975). Such effects provide scope for substantial variations in the chilling requirements reported in different investigations. It should be noted that the plants used by Mazzitelli *et al.* (2007) were grown in an unheated greenhouse throughout the Summer (May–September), and would thus have experienced elevated temperatures compared with plants in the field. The large chilling requirement reported for these plants should therefore be viewed in the context of their high temperature background.

Nevertheless, complete dormancy release in all buds along the cane is essential for the production of fruiting laterals along the entire length of the shoot, and hence for high yields in protected raspberry crops. As an example, the long single-cane 'Glen Ample' plants used by Sønsteby *et al.* (2009), which yielded almost 4 kg of fruit per plant, were cold-stored at -1°C for more than 6 months before they were moved to forcing conditions (Figure 2). Also, Williams (1960) noticed that rarely more than six fruiting laterals developed in plants chilled for 6 weeks, although the plants had a total of twenty nodes. He interpreted this to suggest "that factors other than the environment regulate the number of laterals which a plant of specific size will develop". However, today we

may conclude that inadequate chilling was the main reason for these observations. Although 6–8 weeks of chilling are sufficient to break dormancy in the uppermost buds (Williams, 1960; Sønsteby and Heide, 2008), considerably longer chilling periods are apparently needed to release all buds along the cane (*cf.* White *et al.*, 1999; Mazzitelli *et al.*, 2007).

As illustrated in Figure 2, it is particularly important that buds situated on the lower part of the shoot are able to grow, as these have the highest potential for producing long fruiting laterals with many flowers and fruits. A stepwise regression analysis of the relationship between yield and plant architecture traits identified five components that accounted for 92% of the yield variation. Most important among these traits was lateral shoot length, which alone accounted for 82% of the variation (Sønsteby and Heide, 2009). It was concluded that the optimum fruiting plant architecture was determined mainly by an adequate summer temperature for vigorous shoot growth, followed by exposure to low temperatures for timely floral initiation and dormancy induction, as well as adequate chilling for saturated bud dormancy release.

Spraying of raspberry canes with gibberellic acid (GA₃) in August or September delayed the cessation of growth, the induction of dormancy, and leaf abscission under field conditions in Norway, with a corresponding delay in the release from dormancy in buds forced during Winter (Måge, 1976). GA sprays also delayed the initiation of floral primordia by almost 1 month, and increased winter injury of plants in the field and in the buds of canes exposed to artificial freezing. Thus, GA imitated the effects of high temperature and LD conditions, suggesting an involvement of GA in the mediation of the environmental effects.

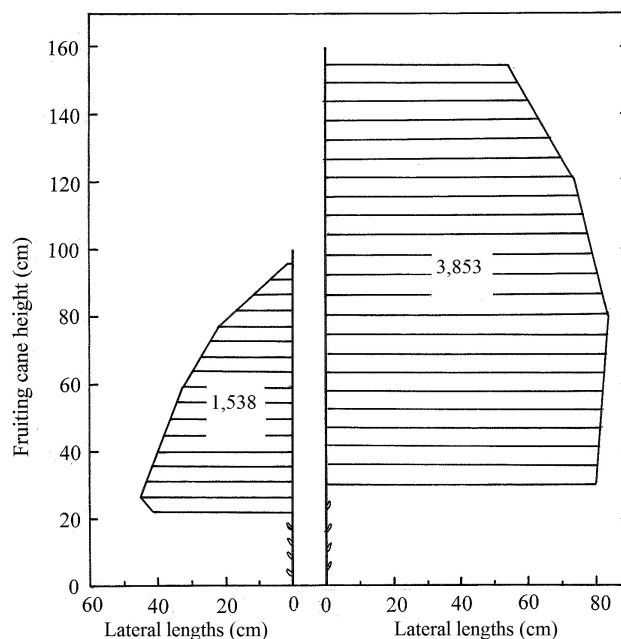


FIG. 2

Illustration of fruiting cane architecture of high-yielding (right) and lower yielding (left) canes in 'Glen Ample' raspberry. For simplification, all laterals are drawn on only one side of each stem. Numbers denote fruit yields (in g/cane) of the respective type of cane. Note the long fruiting laterals at the upper part of the high-yielding canes after tipping at 160 cm height. From Sønsteby *et al.* (2009).

Annual-fruiting cultivars

As in biennial-fruiting cultivars, height growth and the rate of leaf formation in annual-fruiting raspberry cultivars increased with increasing temperature, up to a broad optimum in the mid-20°C range (Carew *et al.*, 2001; Sønsteby and Heide, 2009). However, while the former authors found no consistent effect of photoperiod (8, 11, 14, or 17 h) on growth rate in the cultivar 'Autumn Bliss', long photoperiods (24 h) consistently enhanced the rate of shoot growth compared with 10 h SD in the cultivar 'Polka' (Sønsteby and Heide, 2009). On the other hand, photoperiod had no effect on the rate of leaf (node) initiation in 'Polka', thus the LD stimulation of shoot growth was due to an increase in internode length only (*cf.* Figure 3).

Another growth effect of photoperiod was that plants attained an arching or para-geotropic growth habit under SD conditions (Sønsteby and Heide, 2009). However, unlike biennial-fruiting cultivars, the annual-fruiting cultivars did not become dormant in SD at low temperatures, but progressed directly to anthesis under both SD and LD conditions across a range of temperatures from 9° - 30°C (Carew *et al.*, 2003; Sønsteby and Heide, 2009).

Since shoot growth is terminated by the formation of a terminal flower in annual-fruiting cultivars (Figure 3), the number of leaves subtending the flower (*i.e.*, the final leaf number) is a useful physiological index of earliness of flowering that is independent of the vegetative growth rate. Using this technique, Sønsteby and Heide (2009) found that flowering in 'Polka' consistently took place at lower nodes and in shorter real-time in LD than in SD at temperatures ranging from 12° - 30°C. Since a 3 h night interruption in the middle of a 14 h dark period also significantly advanced flowering and reduced the number of leaves subtending the flower in the same way as day-length extension, it was concluded that this was a specific photoperiodic effect and not merely an effect of a 2% increase in the daily light integral in the 24 h, compared to the 10 h, photoperiod (Sønsteby and Heide, 2009). Similarly, Lockshin and Elfving (1981) observed that early flower initiation took place in the annual-fruiting cultivar 'Heritage' in a 16 h photoperiod under two temperature regimes. On the other hand, as with growth rate, Carew *et al.* (2003) found no consistent effect of photoperiod on flowering in the cultivar 'Autumn Bliss'. Further experiments with more cultivars would, however, be desirable to establish whether the LD promotion of flowering is a general feature of annual-fruiting raspberries.

The effect of temperature on flower formation in annual-fruiting raspberry has been a matter of some debate. As with biennial-fruiting cultivars, these cultivars require several weeks of chilling of the root system to break dormancy of the adventitious buds (*see above*). However, as proposed by Carew *et al.* (2001), there appears to be an additional and distinct low temperature effect on flowering. Nevertheless, Dale *et al.* (2005) reported that annual-fruiting cultivars flowered and fruited on their primocanes for three consecutive years in the absence of chilling (*i.e.*, at temperatures > 16°C). Also, Vasilakakis *et al.* (1980) and Takeda (1993) found that low temperature was not an absolute requirement for flowering in the annual-fruiting cultivar 'Heritage'.

However, flowering of non-chilled plants was erratic and took place only after 240 d and the production of 80 - 90 nodes; while, after some weeks of chilling, flowering was greatly advanced and the number of nodes reduced to approx. 30. Therefore, although chilling is not an absolute requirement, flowering in annual-fruiting raspberry is strongly promoted by such treatment. Unfortunately, the effect of chilling on dormancy release and its separate effect on flowering were not separated in these experiments.

On the other hand, by exposing young 'Autumn Bliss' plants which had been produced from adequately-chilled roots, to additional chilling at 7°C for up to 10 weeks, Carew *et al.* (2001) found that the number of nodes produced before flowering decreased from 36 in non-chilled plants to 22 in plants chilled for 10 weeks. Although the time to anthesis did not decrease, but tended to increase with extended chilling, they therefore concluded that there was an additional vernalisation-like effect of low temperature on flowering in annual-fruiting raspberries, which was distinct from its effect on dormancy release. This was confirmed by Sønsteby and Heide (2009) using the cultivar 'Polka'. When actively growing plants with five leaves (produced from adequately-chilled roots) were exposed to 6°C for 7 weeks, then transferred to 24°C, both plant height and the number of leaves at flowering decreased significantly compared with plants grown continuously at 24°C. Although the plants grew little at 6°C, after transfer to 24°C they immediately resumed the same rate of growth as plants grown continuously at 24°C, indicating a non-dormant state. Moreover, while plants grown continuously at 12°C had a high proportion of dormant buds (Figure 4), plants exposed at an early stage to 6°C for 7 weeks had the same proportion of dormant and flowering nodes as those grown continuously at 24°C (Sønsteby and Heide, 2009). All these results are consistent with the hypothesis of a distinct vernalization-like advancement effect on flowering in annual-fruiting raspberries.

The responsiveness of small plants to chilling treatments raises the question of juvenility in annual-fruiting raspberry, which, to our knowledge, has not yet been examined satisfactorily. Since plants with only five leaves were able to respond to chilling, Sønsteby and Heide (2009) concluded that these plants had no unresponsive juvenile stage, as demonstrated for biennial-fruiting cultivars (Williams, 1960; Sønsteby and Heide, 2008). However, the process of vernalization does not bring about flowering directly, but is an inductive process that creates the capacity for subsequent flowering under the right environmental conditions (Chouard, 1960; Thomas and Vince-Prue, 1997). Therefore, the apparent non-juvenile state of the plants should be judged with caution.

Temperature during the following main growth phase is also important for earliness and the extent of flowering in annual-fruiting raspberry. Lockshin and Elfving (1981) found that 'Heritage' plants produced earlier and more profuse flowering at high (29°/24°C day/night) than at lower (25°/20°C) temperatures, and this effect was enhanced by a high nitrogen supply. This promotive effect of a high growth temperature was confirmed in other cultivars by Carew *et al.* (2003) and by Sønsteby

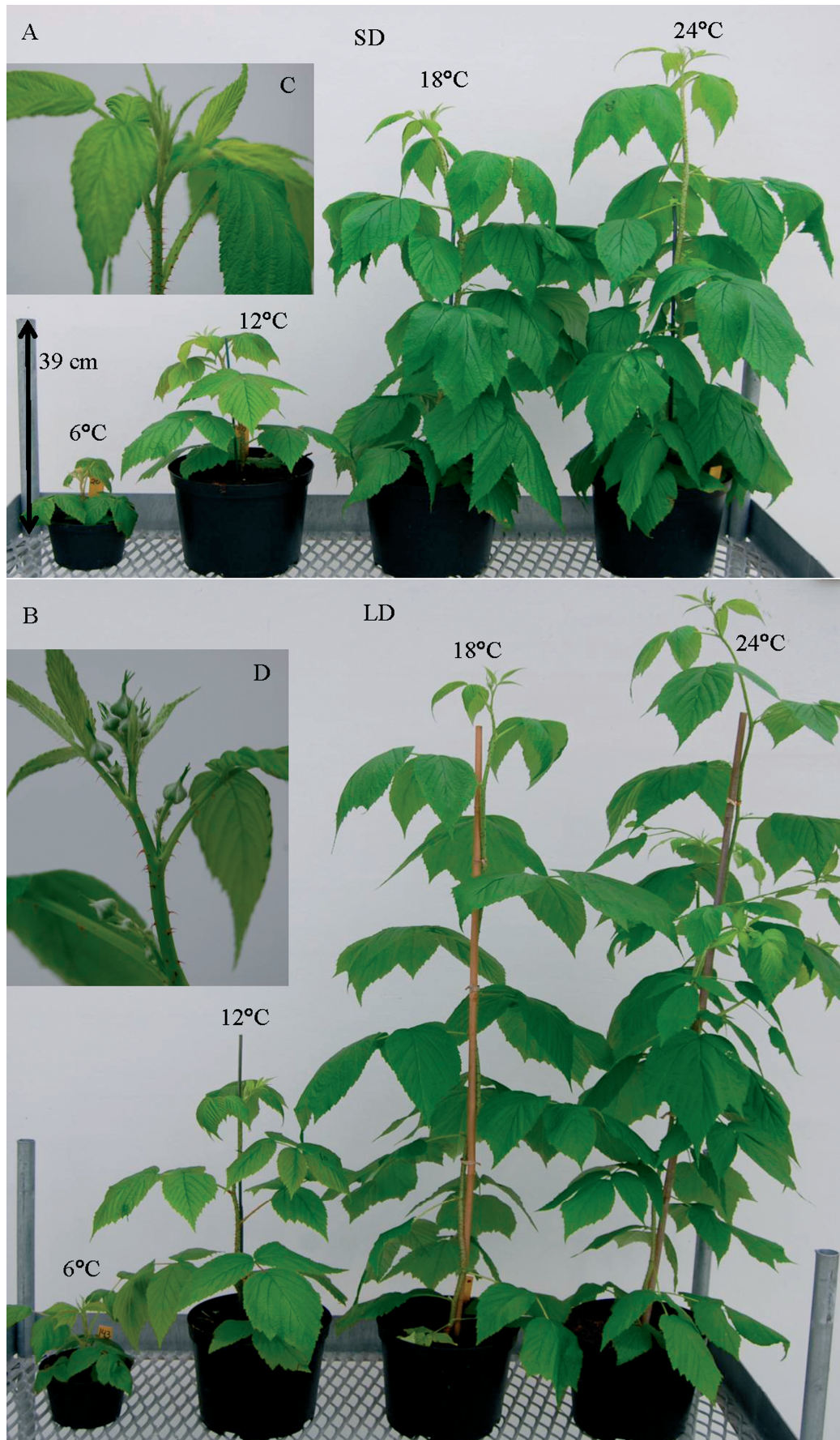


FIG. 3

Appearance of annual-fruited 'Polka' raspberry plants after 7 weeks of cultivation under SD (Panel A) or LD conditions (Panel B) and a range of temperatures, as indicated. Inserted are close-ups of the shoot tips of plants grown at 24°C under SD (Panel C) or LD (Panel D) conditions. Note the termination of growth by a terminal flower in Panel D. From Sønsteby and Heide (2009).

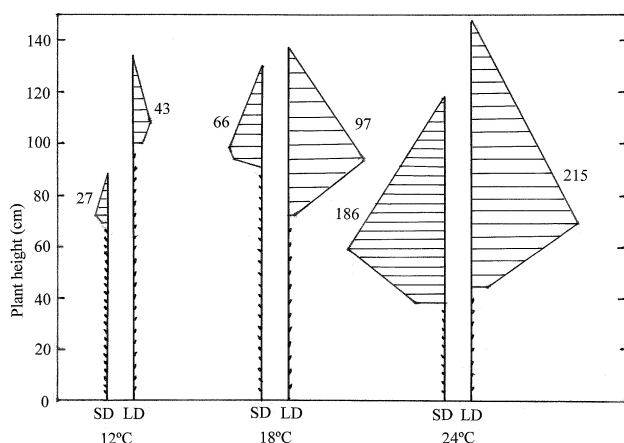


FIG. 4

Illustration of fruiting plant architecture (plant height, total number of nodes, number and length of laterals, and number of dormant buds) in annual-fruited 'Polka' raspberry plants grown under different temperature and day-length conditions, as indicated. For simplification, all laterals are drawn on only one side of each stem. Numbers denote the total number of flowers per plant in the respective treatments. From Sønsteby and Heide (2009).

and Heide (2009). However, although time-to-anthesis decreased with increasing growth temperature, up to approx. 24°C (Carew *et al.*, 2003; Sønsteby and Heide, 2009), the number of leaves formed before the first flower appeared increased with increasing temperature across the entire range of temperatures tested (Sønsteby and Heide, 2009). This demonstrates the dual effect of growth temperature on flowering in annual-fruited cultivars; namely, the advancement of flowering and fruiting by increasing temperature due to an enhancement of growth, and the specific delay of floral initiation to nodes higher up the plant. More importantly, however, temperature also dramatically changes the architecture of flowering shoots by altering the proportion of dormant vs. growing and flowering buds (Sønsteby and Heide, 2009). As demonstrated in Figure 4, 'Polka' plants grown at 12°C typically became tip-flowering, producing only a few, short flowering laterals at the top of the cane, with the majority of the remaining buds becoming dormant. Dissections of such non-growing buds revealed floral primordia at an advanced stage; but, as in biennial-fruited cultivars, the buds were dormant and required several weeks of chilling to break dormancy. This explains why, under certain conditions, annual-fruited cultivars produce a negligible first year crop and essentially become biennial-fruited (e.g., Oliveira *et al.*, 1998; 2001). Because of the contrasting behaviour of buds at different positions on the cane, Oliveira and Dale (2007) and Dale (2008) speculated that their initiation was controlled by different conditions, but Sønsteby and Heide (2009) could show that both types of buds were initiated simultaneously under both SD and LD conditions at both high and low temperatures. With increasing growth temperature, an increasing proportion of buds further down the shoot grew out and produced long and fruitful laterals. There were also basipetal increases in the final length of, and the number of flowers on the laterals, and a concomitant gradual delay in the time of flowering and fruit maturation (Sønsteby and Heide, 2009).

These plant responses have important practical implications and show that, in order to produce plants with many laterals and large numbers of flowers and fruit, annual-fruited cultivars should be grown at relatively high temperatures (around 20° – 25°C) throughout the growing season. This would also produce the earliest fruit maturation in most cultivars. A notable exception was the cultivar 'Autumn Treasure', in which flowering was significantly reduced and increasingly delayed by temperatures above 20°C (Sønsteby and Heide, 2010).

Flowering and fruit maturation were also advanced by increasing photosynthetic photon flux density (PPFD) in biennial-fruited cultivars (Carew *et al.*, 2003; Sønsteby *et al.*, 2009). This is consistent with the source-limited characteristics of raspberry in general (Fernandez and Pritts, 1994), and the intense competition for assimilates between the fruiting cane, the vegetative canes, and the root system (Braun *et al.*, 1989; Palmer *et al.*, 1987; Fernandez and Pritts, 1994). As a consequence, large positive yield effects were obtained by removal of rapidly growing, new vegetative shoots (Waister *et al.*, 1977; Crandall *et al.*, 1980; Sønsteby *et al.*, 2009).

In a recent publication, Palonen *et al.* (2011) reported that the growth and cropping performance of annual-fruited raspberries were significantly modified when plants were grown under a far-red (FR)-absorbing greenhouse film. In the cultivars 'Autumn Bliss' and 'Polka', the number of flowers per plant increased by approx. 15% in the modified light spectrum, while the opposite effect was observed in the biennial-fruited cultivars 'Glen Ample' and 'Tulameen' when the treatment was applied during the first year. In 'Polka', the number of berries and their ellagic acid content were also significantly increased, while the contents of other chemical components were unaffected. The FR-absorbing film also reduced slightly the number of internodes formed before flowering, and hence the final cane height.

GENETIC BACKGROUND

The genetic basis for the differences between annual- and biennial-fruited raspberries is not well known (Keep, 1988). Lewis (1941) reported that annual fruiting was controlled by a single recessive gene, and Haskell (1960) assigned the gene designation, *af*, for the autumn fruiting character. However, wide variations in segregation for this character have been reported (Slate, 1940; Waldo and Darrow, 1941; Oberle and Moore, 1952), and there is ample evidence that several minor genes are probably acting additively to control expression of this character (Slate, 1940; Ourecky, 1976; Fejer, 1977; Keep, 1988). Several workers (Slate, 1940; Waldo and Darrow, 1941; Ourecky, 1976) have also emphasised the effect of environment on expression of the annual-fruited character. It should also be kept in mind that a number of *Rubus* species such as *R. arcticus*, *R. odoratus*, *R. spectabilis*, and others have contributed to the gene-pool of annual-fruited raspberries (Keep, 1988), thus providing the diverse and complex genetic constitution of present-day cultivars.

Research on the molecular genetics of raspberry is progressing rapidly (Woodhead *et al.*, 2010), although

such information related to life-cycle characteristics is still scarce. However, Mazzitelli *et al.* (2007) monitored the expression of a large number of genes during release from dormancy in 'Glen Ample' raspberries and identified a number of genes that were differentially expressed. Bearing in mind the contrasting relationships between the induction of dormancy and floral initiation in annual- and biennial-fruiting raspberry cultivars (Sønsteby and Heide, 2008), further molecular studies on dormancy-related genes, and especially genes involved in the induction of dormancy, would be of significant interest. Certainly, our present physiological knowledge-base would provide a solid platform for such an endeavour.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Recent research in the field has demonstrated the remarkably different, in fact contrasting, regulation of flowering and dormancy in annual- and biennial-fruiting raspberries. While biennial-fruiting cultivars have an obligatory low temperature requirement (\leq approx. 15°C) for the cessation of growth and floral initiation, annual-fruiting cultivars have no such requirement for low temperature (Lockshin and Elfving, 1981; Carew *et al.*, 2003; Sønsteby and Heide, 2009; 2010), and flower freely at temperatures as high as a constant 30°C (Sønsteby and Heide, 2009). Furthermore, while floral initiation is associated with growth cessation and bud dormancy in biennial-fruiting cultivars, floral initiation is followed by continued growth and direct flowering in annual-fruiting cultivars (Sønsteby and Heide, 2009). Carew *et al.* (2000; 2003) concluded that since annual-fruiting cultivars initiate floral primordia relatively early in the Summer, when the day-length is still long and temperatures are relatively high, it is the time of

initiation that determines whether a cultivar is annual- or biennial-fruiting. However, both their own experiments (Carew *et al.*, 2003) and those of Sønsteby and Heide (2009) clearly demonstrated that annual-fruiting cultivars developed directly to anthesis, even in photoperiods as short as 8 h or 10 h, and at both low and high temperatures. It is therefore, evident that the different life cycles of the two types of plant have a more fundamental basis than simply the seasonal timing of floral initiation. As pointed out by Sønsteby and Heide (2009), the essential difference resides in whether the newly-initiated floral buds enter dormancy or progress directly to anthesis, a feature that governs whether the shoot life-cycle becomes annual or biennial.

Present knowledge of raspberry plant structure and function, and their developmental regulation by genotype and the environment, provides excellent opportunities for the construction of commercial programmes for all-year-round production and high yields. This can be achieved by the manipulation and optimisation of the photo-thermal environment of protected crops and the use of cold-stored canes with ready-to-flower floral primordia (*cf.* Sønsteby *et al.*, 2009). Furthermore, with this knowledge, it is also possible to select geographic locations with the most suitable climates for outdoor production. In the context of present scenarios for future climatic conditions, it may also be concluded that biennial-fruiting raspberry cultivars, with their obligatory low-temperature requirement for flowering (Williams, 1959c; 1960; Sønsteby and Heide, 2008), would be vulnerable to elevated autumn temperatures as a result of climatic warming. Likewise, if winter temperatures continue to rise, as observed during the last 50 years (Sunley *et al.*, 2006), it is also likely that inadequate winter chill may become a limiting factor for successful raspberry production in geographic regions with mild winter climates.

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