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Growth and Development of Blackberry Cultivars

Mirjana Sadojevic
MSc Biology

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Supervised by Siv Fagertun Remberg

Norwegian University of Life Sciences (NMBU)

Co-supervised by Anita Sønsteby

Norwegian Institute of Bioeconomy Research (NIBIO)

Foreword

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Abstract

Environmental control of growth and flowering is generally well understood in raspberries, but a complete understanding of the processes is missing in blackberries. To get a better understanding of growth and flowering in blackberries, five cultivars, ‘Loch Ness’, ‘Loch Tay’, ‘Natchez’, ‘Ouachita’, and ‘Sweet Royalla’, were studied in the phytotron at 16°C and 12, 13, 14 and 15h photoperiod, and under natural temperature and daylength conditions at Apelsvoll, Norway (60.7° N). The results demonstrate that origin and genetic background of cultivars play a crucial role in how they respond to environmental signals. ‘Natchez’ had a critical photoperiod of 14h for cessation of growth at 16°C, while ‘Loch Ness’ continued to grow independently of photoperiod treatment. Photoperiod in the 12-15h range was not critical for flower bud initiation in ‘Natchez’ and ‘Loch Ness’. All five cultivars initiated flower buds before cessation of growth under out-door conditions. In both experiments, the cultivars that reached growth cessation first, also had the most advanced flower buds, except for ‘Ouachita’. Flower bud initiation in ‘Loch Ness’ and ‘Natchez’ began in the mid-section of the cane and continued in both basipetal and acropetal directions. Three ‘Loch Ness’ plants from each photoperiod treatment were forced in the greenhouse after sufficient chilling to examine the flowering performance of the buds that were initiated before growth cessation. Plants at 15h photoperiod, had the highest percentage of flowering nodes, most flowers per plant and fewest days to anthesis at forcing, but all plants from all treatments developed flowers. The position of the flowering nodes along the cane corresponded to the position of the initiated flower buds dissected in ‘Loch Ness’ prior to chilling. The results suggest that temperature, rather than photoperiod, may be the main factor affecting both growth cessation and flower bud initiation in blackberries.

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1 Introduction

Blackberry (*Rubus* subgenus *Rubus* Watson.) production for the fresh market has expanded rapidly in the last two decades due to increased consumer demand, advanced production methods, year-round product availability, and new cultivars (Worthington et al., 2020). The biggest producer of fresh market blackberries is Mexico, where production occurs continuously from October to June and provides a reliable fruit supply to the US and Europe (Clark and Finn, 2014). At the same time the interest in locally produced fresh berries has also increased in Norway, where field production of blackberries is limited because of low winter temperatures and a short season. The interest in so-called ‘long-cane’ production of raspberries and blackberries in growing media in plastic tunnels had increased in Europe in the past decade, originating in the Netherlands, the UK and Belgium (Dickson et al., 2023). Long-cane blackberry plants are ‘ready to flower’ single-cane plants grown in protected environments, such as tunnels and greenhouses, and are used for one production season, thus expanding the production season, and eliminating the need for overwintering of plants after harvest.

Long-cane production of blackberries is an expensive and time-consuming process that takes place over two years. It includes growing vegetative canes to suitable length during the summer, flower bud initiation in the autumn, satisfying chilling requirements for breaking of bud dormancy in cold storage during winter, and finally forcing the plants to flower and develop fruits in tunnels or greenhouses the second year (Dickson et al., 2023). All these processes must happen in sequence and under optimal environmental conditions (temperature and daylength) to produce long canes with an optimal yield potential. A better understanding of how and to what extent temperature and daylength affect the mechanisms behind cessation of growth and flower bud initiation and development is needed to secure a dependable high quality long-cane production. In addition, the long-cane production system may also enable growers to schedule the production to high market demand as well as enable out-of-season production.

Generally, in *Rubus* species, cessation of growth and flower bud initiation occur under short days and low temperatures. Sønsteby and Heide (2008) found that flowering and dormancy induction in biennial fruiting red raspberry take place simultaneously and are controlled by the interaction of low temperature and short photoperiods. Low temperature being a crucial factor, since neither process takes place at temperatures above approximately 15°C, regardless of photoperiod.

However, a complete understanding of the physiological relationship between growth cessation and flower bud development is missing in blackberries. The initiation of flower buds may occur prior to the onset of dormancy, and floral differentiation may continue throughout the dormant period within the buds of some cultivars (Takeda and Wisniewski, 1989). While flower bud initiation can occur before the onset of dormancy in some cultivars grown in the field, most of the buds remain vegetative until dormancy release, after which the development proceeds rapidly and uniformly (Takeda et al., 2002). Sønsteby and Heide (2023) have shown that under controlled temperature conditions, flower bud initiation can take place one or two months earlier in the season than previously reported for other cultivars under field conditions.

There is an agreement that temperature plays a major role in both flower bud initiation and in the extent of bud differentiation (Sønsteby and Heide, 2023; Takeda et al., 2002; Takeda and Wisniewski, 1989). What role, if any, photoperiod plays in flower bud initiation and dormancy induction in biennial fruiting blackberries is unclear.

The aim of this study was therefore to examine the effects of photoperiod and temperature on growth, flower initiation and development of five blackberry cultivars under natural and controlled daylength conditions.

2 Literature Review

2.1 The Blackberry Plant, Origins and Classification

The first attempt to classify blackberries was made by Linnaeus in 1753. In his book “Species Plantarum” he distinguished two European forms of blackberry, *Rubus fruticosus* and *Rubus caesius*. The number of forms described has expanded to include many thousands of species and there have been several comprehensive attempts to classify them (Jennings, 1988). Today the blackberry plant is designated as *Rubus* subgenus *Rubus* Watson. as there are several species in the ancestry of all cultivars (Clark and Finn, 2014; Foster et al., 2019).

All blackberry cultivars are derived from domesticated wild blackberries. One of the most important domesticated European blackberries is *R. laciniatus*. In Britain it occurs naturally in the wild and was imported to America from France in 1860 (Jennings, 1988). There are several different variants of *R. laciniatus*, but the most commercially important today is the thorn-free variant discovered in the wild around 1930 and named ‘Thornless Evergreen’ (Darrow, 1931). *R. procerus* has spread across southern Europe to France from northern Iran and was introduced to America under the name ‘Himalaya Giant’ in 1895 (Jennings, 1988). *R. nitidoides* was one of the species chosen by the John Innes Institute in 1920 for improvement by breeding. A selection of *R. nitidoides* was named ‘Merton Early’ in 1936. The recessive gene for thornlessness from *R. rusticanus* var. *inermis* is still important as the genetic source of thornlessness used by breeding programmes. One of the first thornless cultivars developed using this source was ‘Merton Thornless’ in 1938 (Jennings, 1988).

R. allegheniensis, *R. argatus* and *R. frondosus* are wild blackberries of eastern North America with erect growing habit. *R. allegheniensis* and *R. argatus* are thought to be the parents of ‘Eldorado’. ‘Lawton’, one of the first American cultivars to be named is a hybrid of *R. allegheniensis* and *R. frondosus* (Darrow, 1937). *R. baileyanus* is a wild trailing blackberry of eastern America and ‘Austin Mayes’ that was discovered in 1880 is thought to be a hybrid of *R. baileyanus* and *R. argatus* (Darrow, 1937). A thorn-free variant known as ‘Austin Thornless’ was discovered later (Jennings, 1988).

Further breeding efforts involving ‘Eldorado’ resulted in the erect and early flowering ‘Darrow’ released in the 1950s. In 1966 ‘Thornfree’ was developed by transferring the recessive gene for thornlessness from ‘Merton Thornless’ (Scott and Ink, 1966). In 1966 the Scottish Crop Institute started using these cultivars to improve blackberries for northern Britain, and after

several generations of breeding ‘Loch Ness’ was the first cultivar to be produced by the institute in 1989 (Jennings, 1988).

Blackberries, as other plants in the genus *Rubus* have a perennial root system with biennial canes. The two cane types are primocanes, vegetative first-year (annual) canes, and floricanes, which are the overwintered primocanes that produce fruit the following year (biennial) (Clark and Finn, 2014).

Blackberries can be grouped by three plant characteristics:

- Growth habit (trailing, semi-erect and erect)
- Fruiting habit (biennial (floricane-fruiting) and annual (primocane-fruiting))
- Presence or absence of thorns (thorny and thornless)

Erect and semi-erect blackberries produce primocanes that grow upright, while the primocanes of trailing blackberries are not self-supporting and will grow along the ground (Figure 1). Canes will continue to grow in length until cold weather in the autumn limits their development or dormancy occurs (Strik and Finn, 2012).

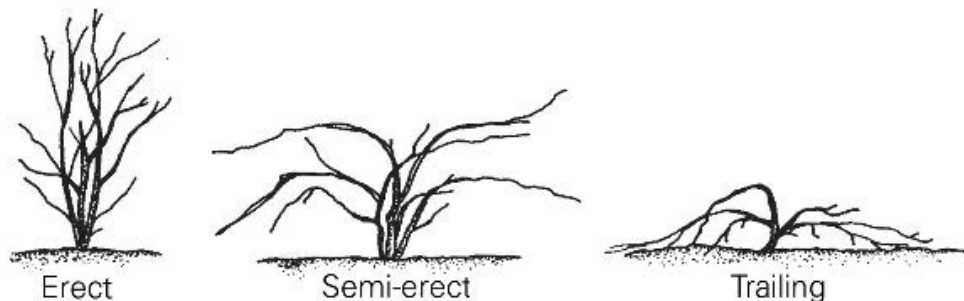


Figure 1 Blackberry growing habit (Fernandez et al., 2023).

In biennial-fruiting blackberries vegetative primocanes grow vigorously and often produce lateral shoots that remain vegetative in the first year. Primocanes enter dormancy as a result of shortened photoperiod and low and moderate temperatures in autumn, and exit after sufficient winter chilling (Takeda et al., 2002). Fruiting laterals grow from buds along the main cane or lateral branches (Figure 2). The floricanes die after having produced a crop and are removed after harvest to make space for the primocanes that have emerged from the crown. Primocanes and floricanes differ in the number of leaflets on their leaves. Primocane leaves have five leaflets, while floricane leaves have three. Floricane leaves are also smaller and usually darker than primocane leaves (Fernandez et al., 2023).

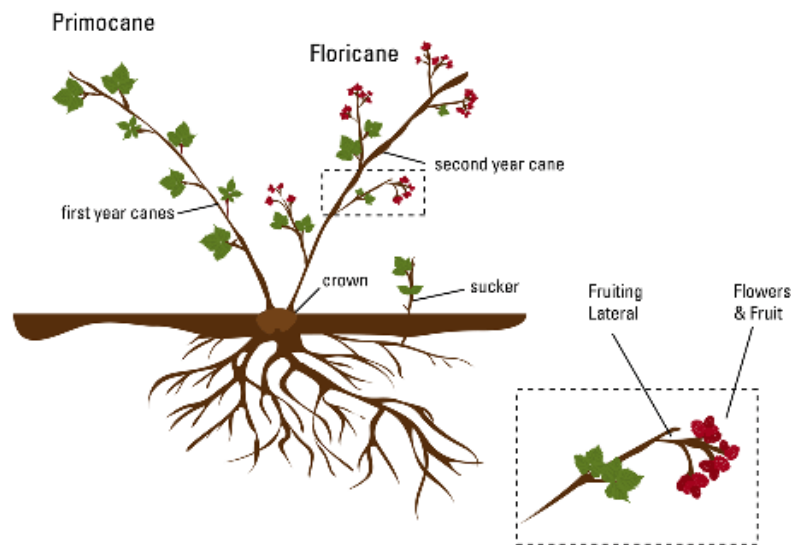


Figure 2 Blackberry plant growth cycle for biennial-fruiting plants with primocanes and floricanes (Fernandez et al., 2023).

Annual-fruiting blackberries produce flowers and fruit on the first-year cane, the primocane, in addition to the second-year cane, the floricane. In the late summer and autumn tips of the first year's cane flower and produce fruit, the fruiting portion of the cane then dies. When grown only for the annual crop, canes are removed from the field, but if they are allowed to grow into the second year, the canes become floricanes and flower and produce fruit next spring below the area that fruited during the first year. The practice of fruiting the primocane in the late summer and autumn and again in the spring is called 'double cropping (Figure 3) (Fernandez et al., 2023).

Thornlessness in blackberries is a desired trait. Thorns can be a serious contaminant in cultivars that are machine harvested and is of great concern for the pick-your-own market. Advances in thornless breeding have been made using the thornless genes. It is expected that with the resulting increase in thornless parents a higher proportion of new cultivars will be thornless in the future (Clark and Finn, 2008).

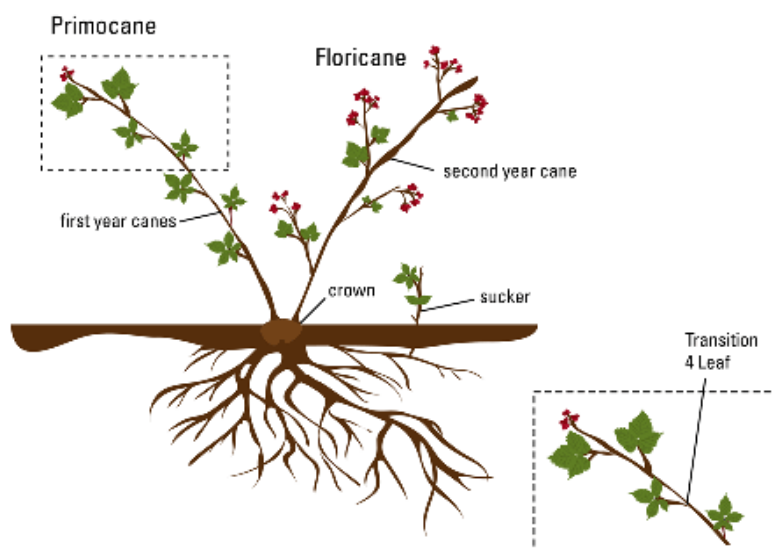


Figure 3 Blackberry plant growth cycle for annual-fruiting plants with primocanes and floricanes. The transition of the primocane from vegetative to reproductive growth occurs when the leaves on the canes change from five leaflets (vegetative) to three leaflets (reproductive) (Fernandez et al., 2023).

2.2 Breeding and Cultivation

Formal breeding of blackberries has its 115th anniversary in 2024. The first public breeding program was started at Texas A&M University in 1909 (Darrow, 1937). Since then, breeding has been conducted by various public, and more recently, private organizations in the world. In the past twenty years, interest in cultivar improvement has been increasing. Possible reasons for this include: 1) blackberries are a new crop to many areas in the world; 2) they share many similarities with raspberries and as raspberry production expands, blackberries often follow; 3) blackberries are less expensive to produce due to less frequent replanting and have fewer pest control issues; 4) improved cultivars have been developed that ship better, ripen earlier and/or later, taste better, are thornless, etc.; and 5) the growing awareness of nutritional value of blackberries and their high anthocyanin levels (Clark and Finn, 2008).

Today, there are 11 breeding programs in six countries, primarily in Europe and North American (Table 1). There are also additional private blackberry breeding efforts underway at various locations in the world, though the details of all these activities are not publicly available (Clark and Finn, 2008; Finn and Knight, 2002).

Table 1 Blackberry breeding programs worldwide (Clark and Finn, 2008; Finn and Knight, 2002).

Country	Location
Brazil	Brazilian Agricultural Research Corporation (EMBRAPA)
New Zealand	New Zealand Institute for Plant and Food Research Ltd.
Poland	Brzezna
Serbia	Čačak
Scotland	James Hutton Ltd
Arkansas, USA	University of Arkansas, Fayetteville
California, USA	Driscoll's Assoc., Watsonville
Maryland-New Jersey, USA	Univ. of Maryland, Rutgers Univ., Virginia Tech
Mississippi, USA	USDA-ARS, Poplarville
North Carolina, USA	N.C. State University, Raleigh
Oregon, USA	USDA-ARS, Corvallis

Traits that are the focus of these breeding programmes include: 1) fruit quality; 2) fruit size; 3) thornlessness; 4) plant adaptation and habit; 5) annual fruiting; and 6) pest resistance. Flavour enhancement has priority in most breeding programs today. Enhancing the sweetness of berries along with reduced acidity is most important for improving consumption of blackberries (Clark, 2005). Postharvest quality is important for fresh markets and the breeding efforts include improvements in postharvest appearance, firmness, and flavour. Limitations such as presence of decay, leakage of juice, obvious mushiness of fruit, presence of substantial red drupelet colour limit consumer appeal, while shiny, fully black berries are desired (Perkins-Veazie and Clark, 2005). On the other hand, the processing industry demands blackberries that have intense colour and flavour, high soluble solids and titratable acidity levels, low pH, and perception of low “seediness” (Hall et al., 2002).

In the past, blackberry breeding has largely focused on winter hardiness, with lesser emphasis on reduced chilling requirement. However, with the expansion of production to areas with low winter temperatures, and generally a warmer climate, these efforts have increased (Clark and Finn, 2008).

Blackberry production using annual-fruiting cultivars has several advantages including: 1) later-season (autumn) fruiting period; 2) potential to schedule production based on primocane management; 3) potential of the two crops on the same plant in the same year (floricane fruiting followed by primocane fruiting); 4) reduction in pruning costs by mowing of canes (primocane crop only); 5) avoidance of winter injury; and 6) production of fruit in an extended geographic area (such as low- or non-chill environments) (Clark, 2008).

Annual-fruited red raspberries have served a critical role in the expansion of the raspberry industry. It allowed growers to grow the crop in areas of low or no chill and better control cropping time. This has resulted in red raspberries being grown in a short-term perennial production system where yield, fruit size, and fruit quality are maximized. As improved cultivars of annual-fruited blackberries are developed, it is expected that they will have the same kind of impact on fresh production (Clark et al., 2012).

Advances in thornless breeding have been made possible by using either the recessive ‘Merton Thornless’ source, the dominant thornless in ‘Austin Thornless’ or non-chimeral, dominant-thornless Loganberry type. It is expected that with the resulting increase in thornless parents a higher proportion of new cultivars will be thornless in the future (Clark and Finn, 2008).

A survey of global blackberry production in 2005 estimated that cultivated blackberries are grown on more than 25 000 ha worldwide and that worldwide production is estimated to be 140 292 metric tonnes (Foster et al., 2019; Strik et al., 2008). The fresh blackberry industry expanded greatly in Mexico in the 2000s due to cultural manipulations that allowed biennial-fruited blackberries to be forced into fruiting without a dormancy period. The primocanes are defoliated and treated with growth regulators to induce flowering, this is combined with the pruning of laterals after the harvest to induce second flower bud break. This production system is cultivar dependent and was first developed with the thorny cultivar ‘Brazos’ that had an estimated chilling requirement of approximately 300 h. As a result, blackberry production in Mexico occurs continuously from October to June providing dependable supply of blackberries during the “off” season in both Europe and the US. It is estimated that blackberries are produced on 6 500 – 8 000 ha in Central Mexico. Fresh market blackberries are also grown in the US, UK, Spain and Italy, but these productions are small compared to that of Mexico (Clark and Finn, 2014)

In Europe, Serbia is the main producer of blackberries for the processing market with over 5 000 ha, followed by the Pacific Northwest in the US with more than 3 500 ha. While the fresh blackberry industry has rapidly expanded, the processing industry has remained relatively stagnant (Clark and Finn, 2014).

2.3 Growth and Development

2.3.1 First Year's Growth

The biennial growth cycle of raspberries starts when an adventitious bud below soil begins to develop. Depending on the position of the bud it can develop into a root or a stem sucker. Root suckers arise laterally from buds on uninjured roots, while stem suckers arise from basal axillary buds of fruiting canes (Jennings, 1988).

Further elongation of the suckers into primocanes starts in the spring and continues until autumn, and the canes may grow to a height of more than 2 - 3 m. Sønsteby and Heide (2023) showed that both cane elongation and initiation of new leaves increased significantly with increasing temperature in 'Loch Ness', 'Ouachita' and 'Sweet Royalla' primocanes when grown under controlled temperature conditions. The rate of growth varied between the cultivars, being lower in 'Ouachita' than in the other cultivars. Early cessation of growth occurred in 'Ouachita' at both 12°C and 16°C, while for other cultivars only at 12°C and later in the experimental period. Apart from 'Ouachita', growth rate of the cultivars was generally markedly higher than that observed in red raspberry under similar conditions.

Canes of annual-fruiting blackberries can be shorter than those of biennial-fruiting cultivars because early cane growth, with a parallel apical flower initiation will stop the cane elongation. Buds in the leaf axils immediately below the soil become specialized and larger than those upward on the cane. These buds are often called "replacement buds" as they may develop into replacement shoots a year later (Figure 4). These shoots can sometimes initiate flower and produce fruit late in the season, but should be distinguished from canes of annual-fruiting cultivars, which initiate flowers independent of their origin (Jennings, 1988).

The roots also show a seasonal pattern of growth. Shoot and root growth begins at about the same time, but root growth continues until much later in the year and is influenced by soil temperature (Atkinson, 1973).



Figure 4 “Replacement” buds just below soil level on a fruiting cane (Jennings, 1988)

2.3.2 Onset of Dormancy

Biennial-fruiting species in the genus *Rubus* have a clearly defined seasonal pattern of dormancy, when grown under temperate-zone growing conditions. They enter the dormant phase because of decreasing photoperiod and low and moderate temperatures in autumn and exit after sufficient winter chilling (Moore and Caldwell, 1985). In biennial-fruiting red raspberry, decreasing photoperiod and falling temperatures in autumn cause growth cessation. The leaves continue to expand, but in the absence of elongation they form a rosette at the shoot tip (Jennings, 1988). Williams (1960) found that ‘Malling Promise’ plants grew continuously and remained vegetative at 21°C in both 9h and 16h photoperiods, while at 10°C they ceased growing in both daylengths. The results were later confirmed by Sønsteby and Heide (2008) with ‘Glen Ample’, where the canes grew continuously at 18°C, even under short day conditions. At intermediate temperature (15°C), short photoperiods are necessary for growth cessation (Williams, 1959). Critical photoperiod for growth cessation in ‘Glen Ample’ raspberry was found to be 15h (Sønsteby and Heide, 2008). The onset of dormancy is a gradual process that can extend over several weeks. In ‘Malling Promise’ exposure to 10°C and 9h photoperiod for 10 weeks was required to establish dormancy (Williams, 1959), while exposure to the same conditions for 5 or 6 weeks resulted in complete growth cessation and induction of dormancy in ‘Glen Ample’ (Sønsteby and Heide, 2008). Before a deep dormancy is reached, it

can be experimentally reversed if the plants are returned to long days and high temperatures. Plants exposed to 10h photoperiod at 9°C for 2-4 weeks showed a temporary suppression of growth, followed by resumed growth when they were returned to high temperature and long day conditions (Sønsteby and Heide, 2008). A stage of deep dormancy is eventually reached and cannot be reversed without chilling.

Blackberries are different from red raspberries both in time of dormancy initiation and in the depth of dormancy attained. In blackberries, growth continues well into the autumn and the canes do not form a terminal rosette of leaves. Growth is rather stopped by rooting of the tips and by low temperatures, than by the onset of dormancy (Jennings, 1988). A complete understanding of environmental controls of dormancy initiation in blackberry is currently missing. Furthermore, the physiological relationship between dormancy and reproductive bud development in blackberries is not well understood. The initiation of flower buds can occur prior to the dormant phase and bud differentiation may continue within a dormant bud of some cultivars but not in others (Takeda and Wisniewski, 1989).

2.3.3 Initiation and Development of Flower Buds

Generally, short days and low temperatures cause flower bud initiation in raspberries (Williams, 1959). The initiation of flower buds usually starts in parallel with dormancy initiation, but the two processes can also occur independently. For example, flower bud initiation occurs before the onset of dormancy in annual-fruiting cultivars, and in most blackberries, and dormancy occurs without flower bud initiation in juvenile canes (Jennings, 1988). The onset, progression and completion of reproductive development appear to be highly variable among blackberry cultivars and are seemingly influenced, in part, by environmental and some internal factors (Takeda et al., 2003)

Takeda and Wisniewski (1989) examined the patterns of flower bud initiation in two eastern thornless blackberry cultivars in West Virginia, USA and reported that the time for flower bud initiation was in the autumn for ‘Black Satin’ but in spring for ‘Hull Thornless’. Similarly, Takeda et al. (2002) reported that flower bud initiation in the erect ‘Cherokee’ occurred in early October in both Oregon and Arkansas, USA but the rate of flower bud development during the winter was higher in Oregon where temperatures remained above 0°C, while little or no bud development occurred in Arkansas when the daily mean temperatures were near or below 0°C. For the semi-erect ‘Chester Thornless’ flower bud initiation took place in January in Oregon, but not until April in Arkansas and West Virginia. The results of these studies suggest that

temperature has a profound effect on the rate of flower bud development. In environments such as in Oregon with moderate winter temperatures, the rate of flower bud development that occurs during winter is likely related to the number of chilling hours required to remove dormancy. Cultivars with low chilling requirements and capacity to develop flower buds continuously in mild winter conditions, may be better suited for greenhouse production, or in climates such as in Oregon or New Zealand (Takeda et al., 2002). On the other hand, once the flower buds are initiated in the spring, subsequent bud differentiation is rapid and uniform (Takeda and Wisniewski, 1989). Robertson (1957) also reported that flower bud development in spring in ‘Himalayan Giant’ blackberry occurred at a much higher rate than in ‘Lloyd George’ raspberry. The rate and degree of floral development in spring is probably associated with the accumulation of growing degree hours (Takeda et al., 2002).

Takeda and Wisniewski (1989) examined the pattern of floral bud differentiation in an inflorescence and reported that after the terminal flower in an inflorescence is fully differentiated, the subsequent differentiation of floral buds within an inflorescence occurred acropetally (Figure 5).

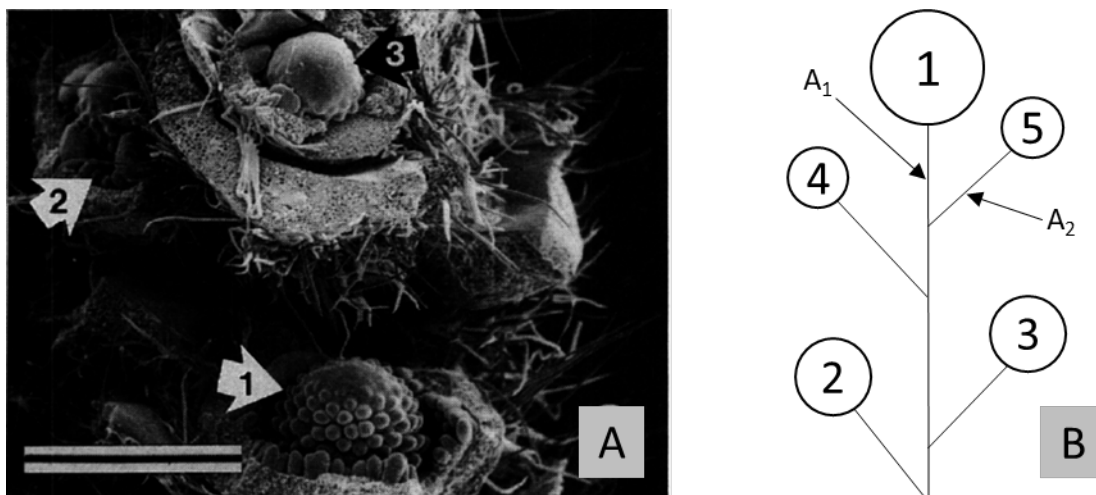


Figure 5 Patterns of floral bud differentiation within an inflorescence. **A:** primary inflorescence axis with terminal flower removed. Acropetal differentiation of flowers (arrows) is evident. Numbers indicate order of maturation (Takeda and Wisniewski, 1989). **B:** Structure of floral bud differentiation pattern. Numbers indicate order of maturation. A_1 : primary inflorescence axis; A_2 : secondary inflorescence axis (modified from Thompson et al. (2007))

Takeda et al. (2003) studied the pattern of flower bud differentiation along the main cane in trailing ‘Boysen’ and ‘Marion’ blackberries grown in Oregon, USA and erect ‘Cherokee’ cultivar grown in Arkansas and Oregon, USA. While they were unable to determine precisely

at which node flower bud initiation started, they were able to determine that the buds located in the mid-section or lower section of canes were more advanced than the buds located at the terminal one-third section. They also established, for all cultivars, that the development was more advanced in the region of the cane where floral initiation had started. They concluded, therefore, that flower bud initiation begins in the mid-section of canes and proceeds toward the basal and terminal nodes. The reason for this delay in development in the upper section of the canes, may be due to the late growth cessation in blackberries. Blackberry canes do not develop a distinct terminal bud and the stem tissue and terminal portion is less mature than the middle or basal portions (Figure 6). As a result, buds in the terminal portions of these canes is less advanced in flower bud development than the buds in the middle or basal portion of the canes (Takeda et al., 2003).

Robertson (1957) investigated flower bud initiation in Loganberries and blackberries and similarly reported that differences between basal, central and tip zones in blackberry canes indicated that the central zone buds were earliest to begin flower initiation and formed slightly larger inflorescences than buds in other zones. Robertson (1957) also reported that while a large number of flowers on blackberry laterals emerged by mid-May and were located on the terminal cluster and several branches immediately below it; most of the lower leaves of the laterals subtended small clusters of flowers which opened from August to October. Indicating that flower initiation continues basipetally along the lateral from the end of March until about mid-June.

Sønsteby and Heide (2023) confirmed that in blackberry canes grown under controlled temperature conditions floral initiation starts in lateral buds located several nodes below the apex and then proceeds in both basipetal and acropetal directions. Furthermore, they showed that under controlled temperature conditions, flower bud initiation of blackberries took place one to two months earlier than previously reported by Robertson (1957), Takeda and Wisniewski (1989), and Takeda et al. (2002, 2003) under field conditions.



Figure 6 Underdeveloped terminal one-third section of ‘Loch Ness’ long-cane plants after 6 weeks of cultivation at 16°C and 12h photoperiod (left) and 15 weeks of cultivation under ambient temperature and natural daylength (June-October) (right)

Young shoots of red raspberry have a juvenile phase in which floral induction cannot take place (Sønsteby and Heide, 2008; Williams, 1960). Williams (1960) found that the biennial-fruiting ‘Malling Promise’ needed to form 15 or more leaves before it could be induced to flower. This was confirmed by Sønsteby and Heide (2008) with the cultivar ‘Glen Ample’. The juvenile shoots do anyway respond to low temperatures and short-day conditions with cessation of growth and onset of dormancy, without floral initiation. Whether young blackberry shoots also exhibit a juvenile phase, has not been fully researched yet.

2.3.4 Acclimation of Canes

Acclimation of canes is influenced by the same environmental factors as cessation of growth and the onset of dormancy and involves a reduction in water content of the canes. Cultivars that are prone to winter injury, typically reach growth cessation late in autumn, and the acclimation process is delayed and short. Consequently, water content in the canes remain high longer in the autumn. The cultivars with low chilling requirements for dormancy breaking may show a

very early rise in water content because they are able to respond to weather fluctuations during most of the winter (Jennings, 1988).

The changes in water content are accompanied by movement of food reserves between canes and roots. Under temperate zone conditions the starch content of the canes reaches its minimum level in late November and remains relatively low until February, while their sugar content is higher than that of the roots during winter. The starch content of roots reaches its maximum in November. These changes, however, may be induced by the onset of frost and not by the onset of dormancy (Jennings and Carmichael, 1975)

The canes of raspberries normally shed their leaves during the period of acclimation. However, because blackberries can continue to grow into late autumn, natural defoliation may not occur by late winter, and in some years, defoliation does not take place at all (Takeda et al., 2002; Warmund and Krumme, 2005).

2.3.5 Chilling Requirements and Breaking of Dormancy

Blackberries require a certain amount of chilling to break dormancy for a successful budbreak and normal cane and flower development in the next season. The depth of dormancy is defined as the time required to force buds through dormancy (Miles, 1965; Warmund and Byers, 2002), while chilling requirement is the amount of cold needed to break dormancy and is often cultivar specific (Fear and Meyer, 1993). Failure to meet this requirement results in reduced or sporadic budbreak and a reduced number of fruiting laterals (Jennings, 1988). Temperatures in the range +5°C to -5°C were found to be optimal in satisfying chilling requirements in raspberries (Sønsteby and Heide, 2014), and a requirement of approximately 1500h was reported for single buds (on isolated nodes) of raspberries, while buds on intact plants required additional 1000h chilling (Mazzitelli et al., 2007).

Dormancy in blackberries is less deep than that of raspberries and blackberries have a lower chilling requirement for bud break (Jennings, 1988; Westwood, 1993) When Carter et al. (2006) examined chilling requirements of Arkansas blackberry cultivars they found that they could be grouped into cultivars with low- (100-300h), medium- (300-600h) and high chilling requirement (700h and more). They also showed that the response to chilling in intact canes was consistent with stem cuttings in both high- and low- chill cultivars, indicating that stem cuttings may be used to determine chilling requirement. This is in contrast to raspberries, where the use of stem cuttings was found to underestimate the chilling requirement (Mazzitelli et al., 2007; Sønsteby and Heide, 2014). Buds that were separated from the cane were released from

the apical dominance and correlative inhibition, thus their chilling requirement for bud burst was reduced (Sønsteby and Heide, 2014).

In raspberries, and to a lesser extent in the other *Rubus* species, the time when dormancy begins and its depth are influenced by the prevailing conditions (environmental factors, fertilization etc.) during the growing season, by the age of the plant and by genetic cultivar differences. Hence, the amount of chilling required to break dormancy cannot be regarded as a constant characteristic of a cultivar (Jennings, 1988). Jennings et al. (1972) showed that dormancy was less deep in canes of two-year old plants compared to canes of a seven-year old plant in a range of raspberry cultivars. Måge (1975) showed that the dormancy of raspberry canes in southern Norway was more intense than that of canes in northern Norway. The difference was due to higher summer temperatures and shorter daylength in the south. In regions with low winter chilling, such as Australia and New Zealand, poor bud break and the consequential reduction in yield may be a combined effect of mild winters and high summer temperatures (Atkinson et al., 2013).

Warmund and Byers (2002) examined the time of dormancy completion of seven blackberry cultivars grown in Missouri, USA. They found that only one cultivar had completed dormancy by December, 19-29 days after exposure to warm temperatures in the greenhouse. In January cultivars broke bud at an average of 18-24 days (8-58% bud break). In February, average bud break for all cultivars occurred within 5-12 days (20-84% bud break) after placement in the greenhouse. By March, all buds broke within 2-6 days (78-95 % bud break). Buds at maximum dormancy depth cannot be forced to grow, while those that can be forced in less than two weeks are at low dormancy depth. The results of Warmund and Byers (2002) indicate that all 7 blackberry cultivars were at maximum dormancy depth in December, and by February all cultivars were at low dormancy depth.

2.3.6 Second Year's Growth and Flowering

In the spring of the second year the previous year's primocanes become fruiting canes. Axillary buds along the cane develop into fruiting laterals. The number of fruiting laterals depends on the total number of nodes on the cane and on the proportion of nodes that develop into laterals. These components are influenced by both cultivar and environmental factors. On average, about two-thirds of the nodes develop fruiting laterals because the apical dominance of the upper buds limits the development of the lower ones, but other factors can also interact with the apical effects. Canes with buds that have not received adequate chilling, may only develop a few

terminal laterals, no laterals in the middle portion and bear most of their laterals towards the base (Jennings, 1988).

Typically, only one fruiting lateral, from a primary bud, develops at each node. Secondary buds usually remain dormant unless the primary bud or lateral is injured. Robertson (1957) found that in some years many secondary buds in blackberries developed slowly during the summer and flowered in August, while in other years secondary laterals were formed only when the primary buds had died or been damaged. The laterals developing from secondary buds were as strong and carried as many flowers as most of the primary laterals. Tertiary buds were either vegetative or contained small inflorescence primordia that developed very late. The fruiting laterals of blackberries form a characteristic terminal cluster of fruits. Robertson (1957) reported that about half of the flowers on a blackberry lateral develop in the terminal cluster and the rest on three to seven branches immediately below it.

Long-cane blackberry plants are grown in substrates and are forced in protected environments, such as plastic tunnels or greenhouses. Varying the length of cold storage and the environmental conditions during forcing, particularly the air temperature, can be a strategy for scheduling crops so that the harvest coincides with important and off-season market weeks (Sønsteby et al., 2013). Dickson et al. (2023, 2024) examined forcing temperature effects of long-cane blackberry cultivars grown in soilless substrate. The difference in time to flowering and fruiting between cultivars was greater when the plants were grown at lower temperatures in a high tunnel, whereas the cropping dates between the cultivars were more similar when grown at higher temperatures in the greenhouse. Overall, flowering and fruiting in a high tunnel required nearly double the amount of time as compared to green house, because of lower average daily temperatures in the high tunnel. This suggests that temperature has a dominant influence on harvest time, but other factors such as photosynthetic light, available pollinators and factors linked with source-sink relations between leaves and developing fruits need to be further examined.

3 Materials and Methods

3.1 Plant Material and Cultivation

A total of five blackberry cultivars were studied in two experiments. ‘Loch Ness’ and ‘Loch Tay’ are cultivars developed in Scotland; ‘Loch Ness’ is the main commercial cultivar in Norway, and ‘Loch Tay’ has been tested recently by Norwegian producers in an attempt to replace ‘Loch Ness’ with a better tasting variety. ‘Natchez’ and ‘Ouachita’ were developed in Arkansas and have therefore been bred for a different climate than the other cultivars used in this experiment. ‘Sweet Royalla’ is a new promising cultivar developed in Belgium, that has recently been made commercially available in Norway. An overview of all the cultivars used in the experiments is shown in Table 2. All the cultivars were used in an open tunnel experiment, while only ‘Loch Ness’ and ‘Natchez’ were used in a phytotron experiment.

Table 2 Overview of the five blackberry cultivars used in the experiments, their origins, year of release, and growth habit.

Cultivar	Breeder	Pedigree	Country of origin	Year	Growth habit
‘Loch Ness’	The James Hutton Institute	Complex	Scotland	1989	Semi-erect
‘Loch Tay’	The James Hutton Institute	‘Loch Ness’ x SCRI 82417D	Scotland	2002	Semi-erect
‘Natchez’	University of Arkansas	Ark.2005 x Ark. 1857	USA	2008	Erect
‘Ouachita’	University of Arkansas	‘Navaho’ x Ark.1506	USA	2005	Erect
‘Sweet Royalla’	Royakkers	Unknown	Belgium	2022	Erect to semi-erect

Roots of all cultivars were stored at -1.5°C during winter. In early spring 2023, root pieces were divided in trays (60 x 30 x 0.7 cm) filled with peat and placed in a greenhouse at 20°C and continuous light (24h photoperiod) for sprouting. After reaching 2-3 fully developed leaves, the plantlets were transplanted into pots (0.33L) filled with peat substrate and placed under plastic cover to maintain high air humidity (> 95% RH) until rooted (Figure 7A). Fully rooted plants were re-potted into 3.5L pots with peat (Figure 7B) and placed either in the greenhouse at 20°C and continuous light (‘phytotron experiment’) (Figure 7C) or in an open polytunnel under ambient temperature and natural light conditions (‘open tunnel experiment’).

3.1.1 Phytotron Experiment

When the plants had developed about 17 leaves, on 1 June, 36 plants of the cultivars ‘Loch Ness’ and ‘Natchez’ were placed on trolleys in the phytotron at the Norwegian University of Life Sciences at Ås, Norway (59°40' N, 10°45' E) (Figure 7C). The plants were exposed to constant temperature of 16°C, and photoperiods of 12h, 13h, 14h and 15h. The plants were grown in daylight rooms at natural daylight from 08.00 – 18.00 h (Figure 7C) and were moved to growth rooms where they received low intensity light ($6 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ given by 75 W incandescent lamps) for 2, 3, 4 and 5h, depending on the photoperiodic treatment. Whenever the quantum flux in the daylight rooms fell below $150 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ as on cloudy days, an additional $125 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ was automatically added using Philips HPT-I 400W lamps.

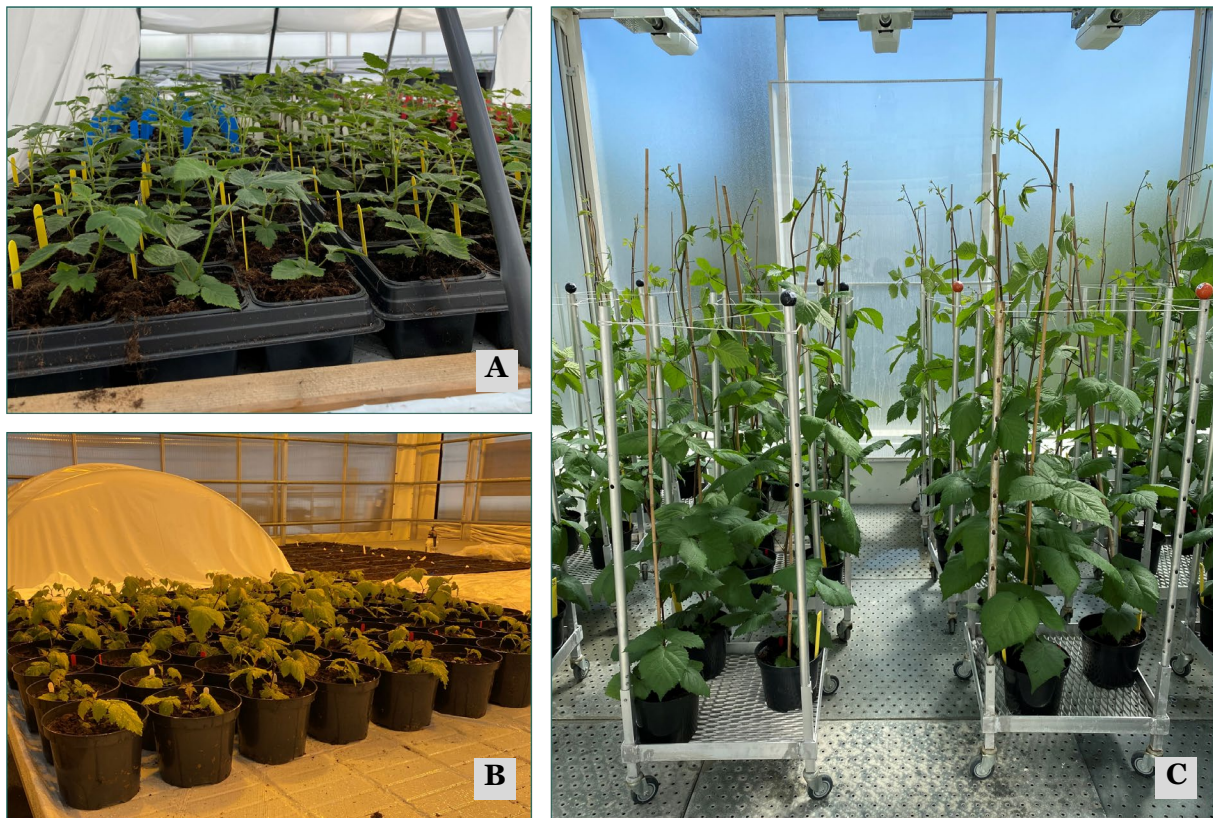


Figure 7 Propagation of plants for the experiments. **A:** Blackberry sprouts placed under a plastic cover until rooted. **B:** Fully rooted plants re-potted into 3.5L pots. **C:** Plants placed on trolleys in the daylight phytotron after developing approx. 17 leaves (photo taken on 1 June 2023).

The temperature in the phytotron was maintained at $\pm 1 \text{ }^\circ\text{C}$ and the water vapour pressure deficit was set at 530 Pa. The plants were fertigated one to two times per day with a fertilizer solution consisting of a 1:1 mixture of Kristalon Indigo (9-11-30% NPK) and Calcinit (15.5% N and 19% Ca), from Yara International (Oslo, Norway) with electric conductivity (EC) of 1.0 mS cm^{-1} to maintain soil humidity above 45%. After 6 weeks of cultivation, buds from all 36 plants

of ‘Natchez’ and 24 plants of ‘Loch Ness’ were dissected under a microscope to determine the stage of floral bud development. The 12 remaining ‘Loch Ness’ plants were moved into a cold store at 0.5°C. After 13 weeks of chilling, on 16 October, plants were forced in a greenhouse at 20°C and a photoperiod of 18h. Plants were fertigated daily (3 x 5 min) with a standard fertilizer solution (EC=1.0 mS cm⁻¹). After 11 weeks of cultivation the flowering performance of all plants was determined.

3.1.2 Open Tunnel Experiment

On 29 June, 9 plants each of the cultivars ‘Loch Ness’, ‘Loch Tay’, ‘Natchez’, ‘Ouachita’ and ‘Sweet Royalla’ were placed in an open polytunnel at Apelsvoll research station of Norwegian Institute of Bioeconomy (60.7° N, 10.9° E). Plants were grown at natural daylight and ambient temperature and were fertigated daily with a standard fertilizer solution (EC=1.0 mS cm⁻¹), the plants were fertigated 5 minutes per watering, and the number of waterings was adjusted according to the weather. After 15 weeks of cultivation, the plants were moved to cold storage (0-1°C). Temperature and photoperiod during the experimental period are shown in Figure 8.

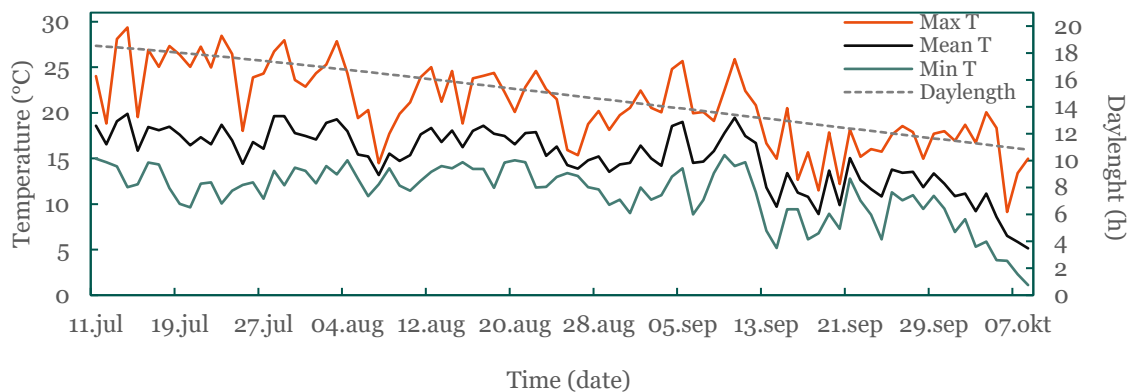


Figure 8 Daily maximum, mean and minimum temperature (T) (°C) and ambient daylength (h) during plant cultivation, growth measurements and axillary bud sampling in the open tunnel experiment in 2023. Daylength is defined as hours between sunrise and sunset.

3.2 Study Design

3.2.1 Phytotron Experiment

The experiment was set up as a factorial split-plot design with photoperiod as main plot and cultivar as sub-plot. Each treatment consisted of 3 replicates with 3 plants each, with a total of 9 plants per treatment. Randomization was achieved by placing one plant from each replicate on a separate trolley (Figure 7C), with 24 trolleys in total (4 treatments x 3 trolleys x 2 cultivars).

The trolleys were then divided into two daylight phytotron rooms, so that each room contained 6 trolleys per cultivar (Figure 9). Every day at 18.00 h, 2 trolleys per cultivar from each daylight room were moved to a corresponding dark-room for photoperiod manipulation and then returned to the daylight room the next morning at 08.00h.

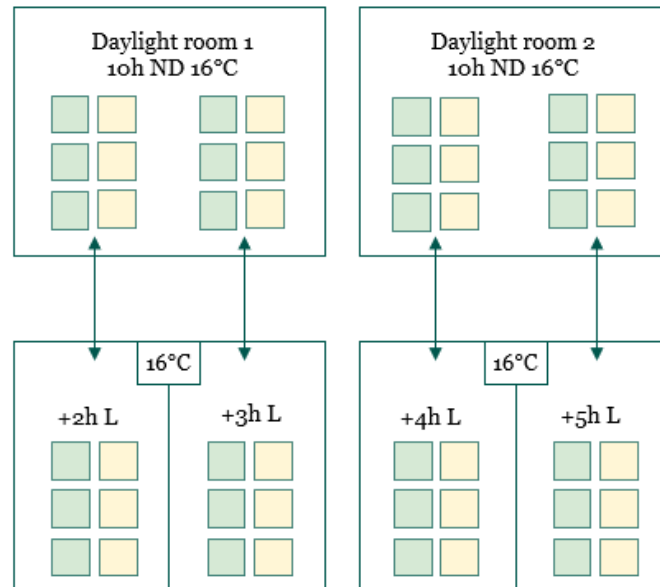


Figure 9 Illustration of the organization of the plants in the phytotron experiment with two daylight rooms and the adjacent dark rooms used for daylight extension. Each square in the individual panels represents one trolley with three plants; colours represent the two cultivars (ND: natural daylight; L: low intensity light).

3.2.2 Open Tunnel Experiment

The experiment was set up as a randomized complete block design with 5 cultivars x 9 plants, a total of 45 plants. 6 plants of each cultivar were used for monitoring of plant growth, and the remaining 3 plants were used for axillary bud collection and later dissection for determination of time of floral initiation and the development stage.

3.3 Data Sampling

3.3.1 Plant Growth Monitoring

Measurement of shoot height (cm) and leaf node count was performed weekly and was done from the base of the shoot to the apical bud. In the phytotron, plant growth was monitored weekly for the 6 weeks duration of the experiment. In the open tunnel, plants were monitored weekly from 11 July, when the plants had developed approximately 10 leaves, to 10 October, when growth cessation of all cultivars was reached. The measurements were then used to

calculate weekly incremental shoot growth and leaf number to determine the date of growth cessation.

3.3.2 Dissection of Buds

At the end of the phytotron experiment fresh axillary buds along the whole cane length were dissected and their flower development stage and position on the cane was recorded. Dissection of buds was done under a stereo microscope starting from the apical bud and working towards the base of the cane.

From 1 August to 17 October, axillary buds were collected weekly in the open tunnel experiment. Buds were removed with a shallow longitudinal slit and stored in 70% ethanol for later dissection under a stereo microscope. Collection of buds started from bud no. 10 from the base moving upwards each week. Three plants from each cultivar were used for the bud dissection. The flower development stage was scored according to the scale developed by Takeda and Wisniewski (1989). Fully vegetative buds were scored as Stage 1, buds with a few visible leaf-, phyllome- and bract primordia was scored as Stage 2, and a fully developed flower with visible gynoecial structures was scored as Stage 7. Stages with descriptions are presented in Figure 10.

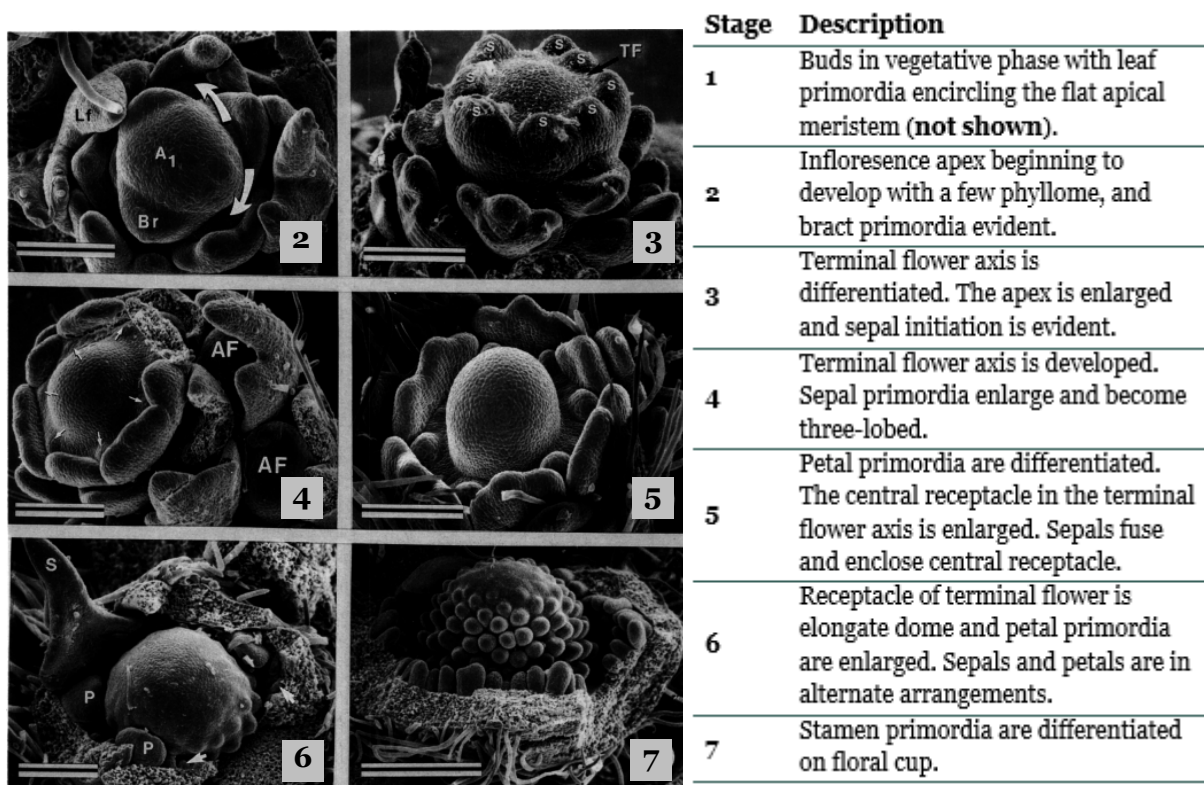


Figure 10 Flower bud initiation and differentiation in blackberries with description of stages of bud development. Modified from Takeda and Wisniewski (1989). (A₁: primary flower; Lf: leaf; Br: bract; S: sepal primordia; AF: subtending flowers; P: petal primordia.

3.3.3 Phenological Observations and Flowering Performance

Date for anthesis (first open flower) for all 12 ‘Loch Ness’ plants forced in the greenhouse was recorded to determine the number of days to flowering for all treatments. After 11 weeks of cultivation all plants were harvested, and the number of flowering plants was recorded. All nodes on each plant were scored on a scale from 1-3, where 1 = a non-breaking node, 2 = a vegetative node and 3 = a flowering node. Number of open flowers and visible flower buds per plant were recorded. Flowering performance for each treatment was determined by calculation of the percentage of flowering plants, the number of flowering nodes, as well as the total number of flowers per plant.

3.4 Statistical Analysis

Experimental data were subjected to analysis of variance (ANOVA) by standard procedures and means between treatments were compared by Tukey’s multiple comparison test. The Minitab Statistical Software program package (Release 20.2 Minitab Inc., PA, USA) was used for the calculations.

4 Results

4.1 Phytotron Experiment

4.1.1 Plant Growth

The two cultivars showed differing effect of photoperiod on shoot growth and leaf number increment (Figure 11, Table 3). There was no effect of photoperiod on either shoot growth or leaf number in ‘Loch Ness’. The rate of shoot growth started to slow down after 4 weeks of treatment in ‘Loch Ness’, while leaf no. increment did not stop during the 6-week experiment.

There was, however, a significant difference ($p=0.004$) between shoot growth at 15h photoperiod (196 cm) and 12 and 13h photoperiods (164 and 163cm, respectively) in ‘Natchez’ (Table 3). Similarly, a significant difference ($p=0.002$) was observed for leaf no. at 15h photoperiod (19 leaves) and 12 and 13h photoperiods (16 leaves), as well as between 14h (18 leaves) and 13h photoperiod (16 leaves).

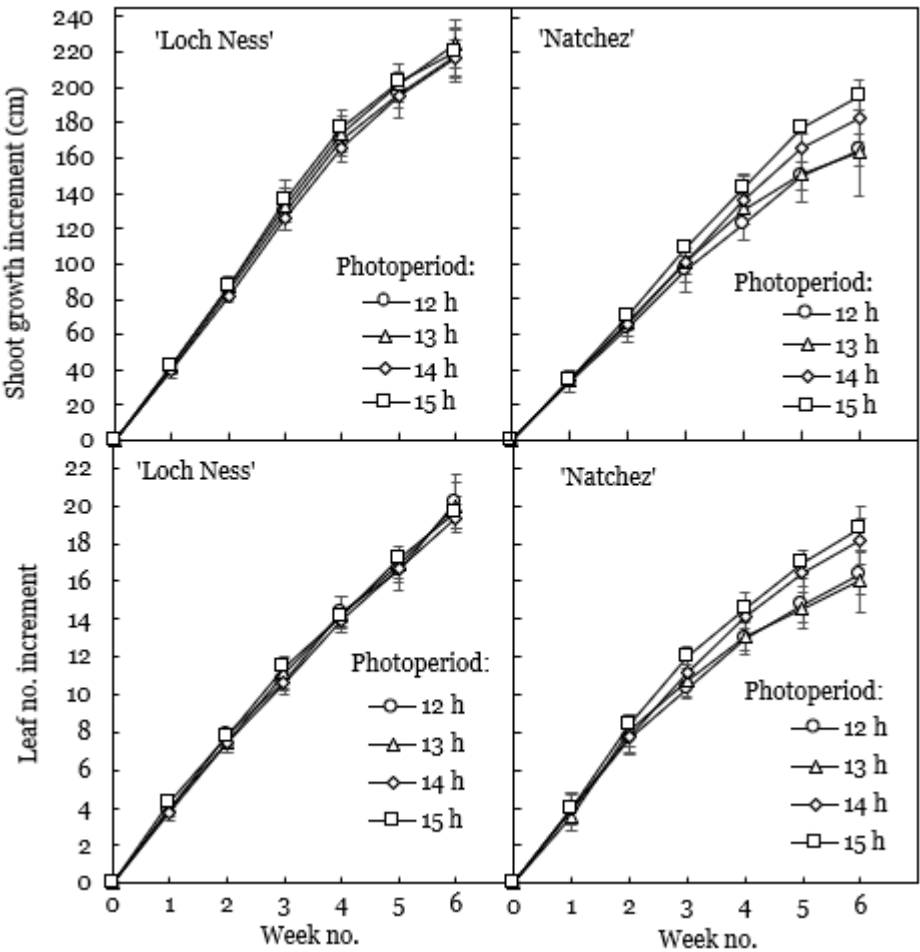


Figure 11 Incremental shoot growth (cm) and leaf no. increment in two blackberry cultivars during 6 weeks of cultivation at 16°C and photoperiods of 12, 13, 14 and 15h. Data are the means \pm SE of 9 replicate plants for each treatment and cultivar.

Table 3 Incremental shoot growth and leaf no. in two blackberry cultivars after 6 weeks of cultivation at 16°C and photoperiods of 12, 13, 14h; and percent generative and vegetative buds and mean development stage of flower buds determined by dissection of the buds at the end of the experiment.

Cultivar	Photo-period (h)	Incremental shoot growth (cm)	Incremental leaf no. growth	Vegetative buds (%)	Generative buds (%)	Mean floral dev. stage
'Loch Ness'	12	218.1 ab	20.2 a	68 a	32 b	3.0 bc
	13	225.0 a	20.0 a	64 ab	36 ab	2.5 c
	14	216.3 ab	19.3 ab	63 ab	37 ab	2.8 c
	15	220.2 a	19.7 ab	63 ab	37 ab	2.9 c
<i>Mean</i>		219.9	19.8	65	35	2.8
'Natchez'	12	164.2 d	16.4 cd	64 ab	36 ab	3.6 ab
	13	163.0 d	16.0 d	53 b	47 a	3.8 a
	14	182.6 cd	18.1 bc	59 ab	41 ab	3.5 ab
	15	195.8 bc	18.8 ab	59 ab	41 ab	3.5 ab
<i>Mean</i>		176.8	17.4	58	42	3.6

Probability level of significance by ANOVA

Source of variation

Photoperiod (A)	0.016	0.04	n.s.	n.s.	n.s.
Cultivar (B)	<0.001	<0.001	0.007	0.007	<0.001
A x B	0.002	<0.001	n.s.	n.s.	0.049

Values within the column followed by different letters are significantly different at $p \leq 0.05$ by Tukey's test for the different photoperiods and cultivars. Data are the means of 9 replicate plants in 'Natchez' for all recordings, and 9 in 'Loch Ness' for plant growth and 6 plants for percentage of vegetative vs. generative buds and mean development stage.

Both shoot growth and leaf no. increased with increasing photoperiod in 'Natchez'. This response started after 2 weeks of treatment and increased throughout the experiment.

There was a significant difference between the cultivars ($p < 0.001$) for the measured responses, with 'Loch Ness' having higher values for both shoot growth and leaf no. There was a significant photoperiod x cultivar interaction for both shoot growth ($p = 0.002$) and leaf no. ($p < 0.001$) (Table 3). 'Natchez' had the lowest values for both shoot growth and leaf no. at 13h photoperiod, while 'Loch Ness' had the highest values for the same photoperiod. There was a similar effect for leaf no. at 12h photoperiod treatment, where 'Natchez' had lowest leaf no., and 'Loch Ness' the highest (Figure 12).

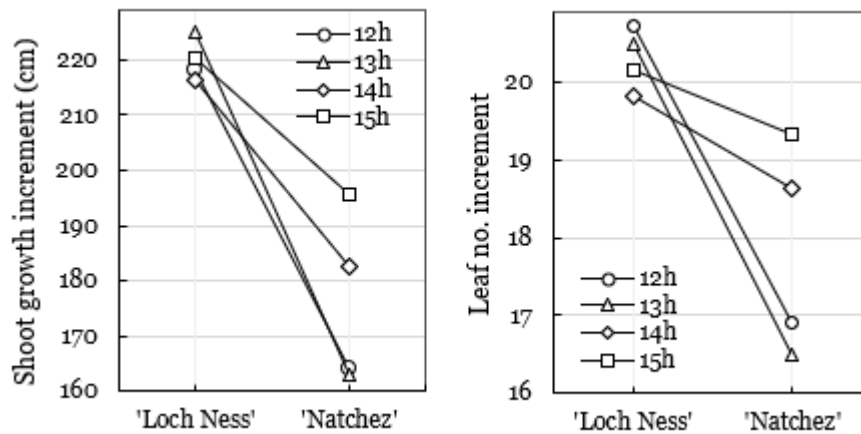


Figure 12 Interaction plots for photoperiod x cultivar for incremental cane growth and leaf no. in two blackberry cultivars grown at 16°C and photoperiods of 12, 13, 14 and 15h for 6 weeks. Data are the means of 9 replicate plants for each treatment and cultivar.

4.1.2 Dissection of Buds

The percentage distribution of vegetative and generative buds and their mean development stage (MDS) are presented in Table 3. 'Natchez' had, on average, a higher percentage of generative buds with higher MDS than 'Loch Ness'. The photoperiod x cultivar interaction was statistically significant for MDS, as 'Loch Ness' at 13h photoperiod had the lowest MDS of 2.5, while 'Natchez' had the highest of 3.8 (Figure 13). However, there was no significant effect of photoperiod within or between cultivars for the number of vegetative vs. generative buds along the shoot, or on the development stage of generative buds (Figure 14, Table 3).

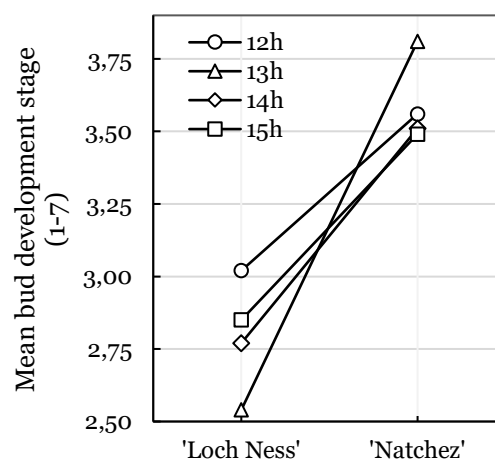


Figure 13 Interaction plot for photoperiod x cultivar for mean bud development stage in two blackberry cultivars grown at 16°C and photoperiods of 12, 13, 14 and 15h for 6 weeks. Data are the means of 9 plants for 'Natchez' and 6 for 'Loch Ness'.

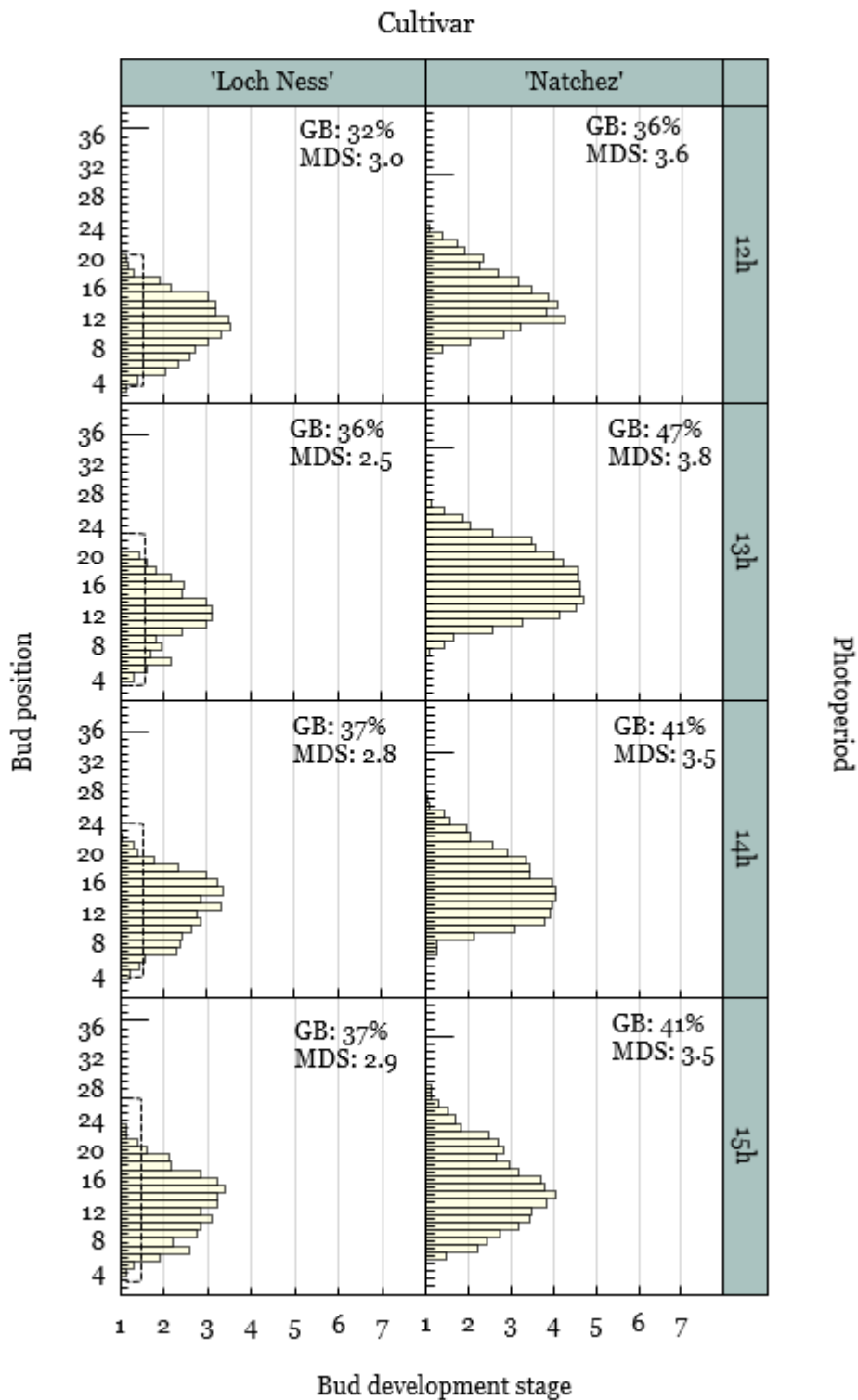


Figure 14 Profiles of flower development stages of lateral buds along the entire length of the cane of two blackberry cultivars after 6 weeks of cultivation at 16°C and photoperiods of 12, 13, 14 and 15h. Data are the means of 9 plants for 'Natchez' and 6 for 'Loch Ness'. Long ticks mark the mean position of the apical bud. GB: % generative buds, MDS: mean bud development stage. Dashed lines indicate the position of flowering nodes after 11 weeks of forcing of the remaining (not dissected) three 'Loch Ness' plants.

4.1.3 Flowering Performance

Flowering performance and shoot architecture of the 12 ‘Loch Ness’ plants are shown in Table 4. All plants from all four treatments (photoperiods) developed flowers. However, days to anthesis decreased with increasing photoperiod and there was a significant difference ($p=0.01$) between plants exposed to 15h and 12h photoperiod, with 39 and 45 days to anthesis, respectively. The plants exposed to 15h photoperiod had on average 193 flowers per plant compared to 73 flowers in plants exposed to 12h photoperiod.

Table 4 Flowering performance and plant architecture of ‘Loch Ness’ blackberry after exposure to photoperiods of 12, 13, 14 and 15h for 6 weeks at 16°C, 13 weeks of chilling at 0-1°C and 11 weeks of forcing at 20°C and 18h photoperiod.

Cultivar	Photo-period	Flowering plants (%)	Days to anthesis	Flowers per plant	Flowering nodes (%)	Non-breaking nodes (%)	Flowers per lateral
‘Loch Ness’	12h	100	45 a	72.7 b	21 b	60 a	8.7 a
	13h	100	42 ab	140.3 ab	33 ab	44 bc	11.0 a
	14h	100	41 ab	113.3 ab	29 ab	49 ab	11.1 a
	15h	100	39 b	192.7 a	45 a	34 c	11.7 a
Mean		100	42	129.8	32	47	10.6
p-value			0.01	0.03	0.02	0.003	n.s.

Values within the column followed by different letters are significantly different at $p \leq 0.05$ by Tukey’s test for the different photoperiods and cultivars. The data are the means of 3 replicate plants for each treatment.

The distribution of flowering and non-breaking nodes was also affected by photoperiod. Plants exposed to 15h photoperiod in the phytotron had on average 45% flowering nodes compared to 21% for plants exposed to 12h photoperiod. The position of flowering nodes along the cane of ‘Loch Ness’ is shown in Figure 14 as a dashed line. Photoperiod had no significant effect on number of flowers per lateral, but a positive trend was observed for number of flowers per lateral with increasing photoperiod.

4.2 Open Tunnel Experiment

4.2.1 Plant Growth

‘Loch Ness’ and ‘Loch Tay’ had the tallest plants with an average shoot height of 237 and 288 cm, respectively. ‘Natchez’ and ‘Sweet Royalla’ had an average plant height of 93 and 122 cm, respectively, while ‘Ouachita’ had the shortest plants with an average shoot height of 51 cm (Table 5). The ‘Sweet Royalla’ plants exhibited large variation in shoot growth rate, with shoot length ranging from 67 to 173 cm among plants. Node and leaf number growth followed the same pattern as shoot growth. ‘Loch Tay’ had on average 41 nodes per shoot, followed by ‘Loch Ness’ with 34 and ‘Sweet Royalla’ with 30 nodes. Average number of nodes in ‘Natchez’ and ‘Ouachita’ was 21 and 19, respectively. Internode length also varied highly among the

cultivars; being highest in ‘Loch Ness’ and lowest in ‘Ouachita’, with 8.2 cm and 3.2 cm, respectively. It is interesting to note, however, that even though plants of ‘Natchez’ were twice as tall as the ‘Ouachita’ plants, they had almost the same number of nodes along the shoot.

Table 5 Total shoot height and leaf numbers of five blackberry cultivars after 14 weeks of cultivation in an open polytunnel at ambient temperature and natural daylight conditions at NIBIO Apelsvoll.

Cultivar	Shoot height (cm)	Total no. of nodes	Internode length (cm)
‘Loch Ness’	237.2 a	34.0 b	8.2 a
‘Loch Tay’	287.5 a	40.5 a	8.1 ab
‘Natchez’	93.3 bc	21.0 d	6.0 bc
‘Ouachita’	50.7 c	19.0 d	3.2 d
‘Sweet Royalla’	121.6 b	30.0 c	5.0 c
<i>Mean</i>	134.7	26.8	5.8
<i>p-value</i>	<0.001	<0.001	<0.001

Values within the column followed by different letters are significantly different at $p \leq 0.05$ by Tukey’s test for the different photoperiods and cultivars. The data are the means of 6 replicate plants per cultivar.

Growth cessation was earliest in ‘Natchez’ and ‘Ouachita’, by 1 September followed by ‘Sweet Royalla’ 4 weeks later, by 25 September, while ‘Loch Ness’ and ‘Loch Tay’ did not stop vegetative growth before 1 October (Figure 15). In ‘Loch Ness’ and ‘Loch Tay’ the number of leaf development stopped simultaneously with vegetative growth, in ‘Sweet Royalla’ leaf development ceased one week after growth cessation, while in ‘Ouachita’ and ‘Natchez’ leaf development continued for 2-3 weeks after growth cessation.

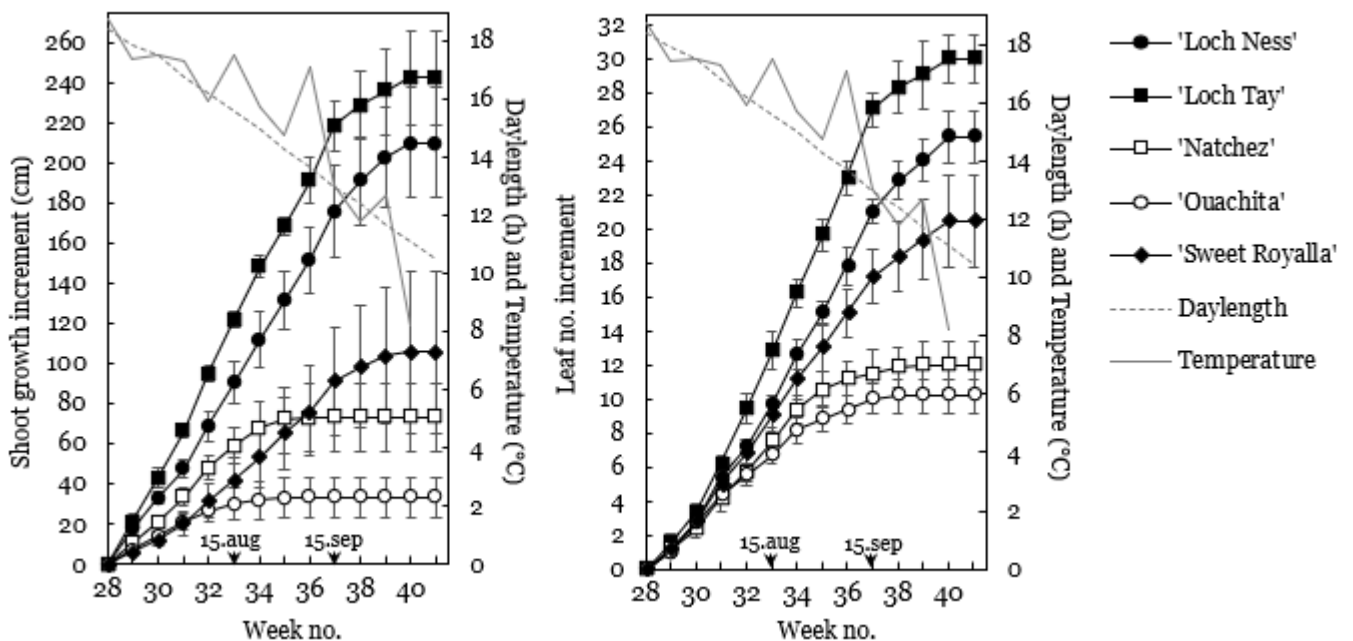


Figure 15 Incremental shoot growth and leaf no. increment in 5 blackberry cultivars during 15 weeks of cultivation in an open polytunnel at ambient temperature and natural daylight conditions at NIBIO Apelsvoll. Data are the means \pm SE of 6 replicate plants per cultivar.

4.2.2 Dissection of Buds

‘Natchez’ was the first to reach a generative stage of flower bud development by 1 September, followed by ‘Loch Ness’ and ‘Sweet Royalla’ one week later (Figure 16). ‘Natchez’ was also the cultivar that reached the highest floral bud development stage of 5.5, while ‘Sweet Royalla’ and ‘Loch Ness’ reached bud development stages of 4.0 and 4.5, respectively. ‘Loch Tay’ and ‘Ouachita’ did not develop any generative flower buds by the end of the sampling period mid-October.

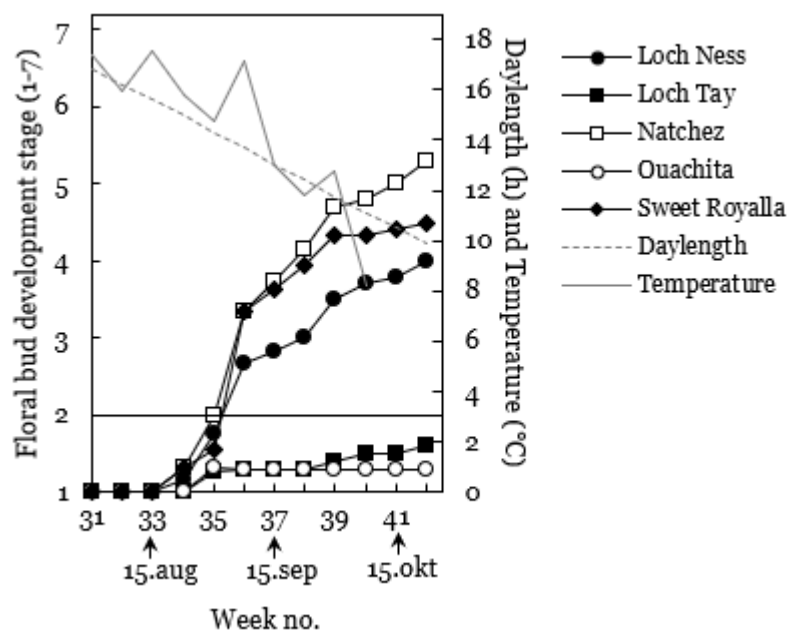


Figure 16 Floral bud development stages of 5 blackberry cultivars during 15 weeks of cultivation in an open polytunnel at ambient temperature and natural daylight conditions at NIBIO Apelsvoll. Data are the means of 3 replicate buds per cultivar per week.

5 Discussion

The aim of this study was to examine environmental control, specifically photoperiod and temperature, of growth, flower initiation and development of five blackberry cultivars under natural environment and controlled daylength and temperature conditions.

The observed shoot growth and leaf number presented in Figure 11 indicates that daylength below 14h is critical for growth cessation at 16°C in ‘Natchez’, while the same daylength has no such effect on ‘Loch Ness’. Furthermore, when grown under natural daylength and temperatures conditions in an open plastic tunnel, ‘Natchez’ and ‘Ouachita’ reached growth cessation a whole month before ‘Loch Ness’ and ‘Loch Tay’. At the time of growth cessation of ‘Natchez’ and ‘Ouachita’, the mean temperature and daylength in the open tunnel were below 15°C and 15h, whereas at the time of growth cessation of ‘Loch Ness’ and ‘Loch Tay’, the mean temperature and daylength were below 12°C and 12h. The response time from when the plants receive the environmental signals to cessation of growth can differ between cultivars, still the results indicate that ‘Loch Ness’ and ‘Loch Tay’ need shorter days and/or lower temperatures than ‘Natchez’ and ‘Ouachita’ to stop growth in the autumn. This difference between the Scottish and Arkansas cultivars can be explained by their differing origin and genetic background. ‘Natchez’ and ‘Ouachita’ were bred and selected in Arkansas, USA where temperatures in autumn never fall below 20°C until October, and daylength is below 14h from the end of July. ‘Loch Ness’ and ‘Loch Tay’ on the other hand, were bred and selected in Scotland, where climate is more like that of East-Norway where the average temperature often falls below 15°C already in August, and with daylength longer than 14h until September. Sønsteby and Heide (2023) reported similar results for ‘Ouachita’ and ‘Loch Ness’ when plants were grown under controlled temperature conditions. Early cessation of growth occurred in ‘Ouachita’ at both 12°C and 16°C in mid-August, when daylength was above 16h, while at 20°C ‘Ouachita’ plants continued to grow until the end of the experiment in mid-October, when daylength was about 10h. ‘Loch Ness’ plants continued to grow at all three temperatures, but the rate of growth increased with increasing temperature, and cessation of growth occurred at 12°C by the end of September. These results indicate that for Arkansas cultivars grown in Norway, temperature is the main limiting factor for growth in autumn.

All plants of both ‘Loch Ness’ and ‘Natchez’ had initiated flower buds at the end of the phytotron experiment even though none of the plants reached growth cessation. This confirms the findings of Jennings (1988) and Takeda and Wisniewski (1989) that initiation of flowers in

blackberries can occur before growth cessation and the onset of dormancy. Furthermore, all plants had initiated flowers by mid-July in the phytotron experiment, which is two to three months earlier than previously reported for other cultivars under field conditions (Robertson, 1957; Takeda et al., 2002; Takeda and Wisniewski, 1989), and controlled temperature conditions in ‘Loch Ness’, ‘Ouachita’, and ‘Sweet Royalla’ (Sønsteby and Heide, 2023). Since there was no significant photoperiod effect on flower bud development in the phytotron, the advanced flower bud initiation seems to be mainly caused by temperature. The temperature in the phytotron was constant at 16°C, which is lower than the summer temperatures under natural conditions in Norway. This suggests that low temperature, rather than shortened daylength, is the main factor affecting growth cessation and flower bud initiation in blackberries.

Plants of ‘Loch Ness’ initiated flower buds only in the lower half of the cane, while the upper half remained vegetative. ‘Natchez’ initiated and had the most advanced flower buds in the midsection of the canes. This is in agreement with previous findings by Takeda et al. (2003) and Sønsteby and Heide (2023) that flower bud initiation begins in the mid-section of the blackberry cane and proceeds in both acropetal and basipetal directions. It also demonstrates that in vigorous growing blackberry plants the terminal part of the cane is under-developed and less mature than the mid- and basal parts as previously discussed by Takeda et al. (2003).

Three ‘Loch Ness’ plants from each photoperiod treatment were forced in the greenhouse after sufficient chilling to examine the flowering performance of the buds that were initiated before growth cessation and onset of dormancy. All plants from all treatments developed flowers and the position of the flowering nodes along the cane corresponded to the position of the initiated flower buds dissected in ‘Loch Ness’ prior to chilling (Figure 14). The terminal part of the ‘Loch Ness’ canes remained vegetative even after sufficient chilling and forcing. This further demonstrates that the terminal buds were less developed, and unable to initiate flowers, compared to buds in the middle and basal parts. From the point of view of long cane production of blackberries this would not affect yield potential since the canes are usually tipped at 1.6 to 1.8 m height. The ‘Loch Ness’ canes in the phytotron experiment were not tipped or decapitated, and therefore reached the height of up to 3.5 m. Tipping the canes would remove the vegetative terminal portion and the percentage of flowering nodes would increase significantly. Also, tipping of the canes would remove the apical dominance of the terminal bud and advance the development of sub-apical lateral buds (White et al., 1998).

The results of the phytotron experiment indicate that photoperiod, in the range of 12 to 15h, is not a limiting factor for flower bud initiation in ‘Natchez’ and ‘Loch Ness’ grown at 16°C.

Nevertheless, there was a significant photoperiod x cultivar interaction for mean development stage of flower buds, suggesting that the length of the photoperiod did influence the time of the initiation of flower bud development. ‘Natchez’ plants grown at 12h and 13h photoperiods that exhibited early signs of growth cessation had the most developed flower buds. Furthermore, at 13h photoperiod ‘Loch Ness’ had the highest shoot growth rate, but the least developed flower buds, while ‘Natchez’ had lowest shoot growth rate and the most developed flower buds. Hence, even though these blackberry cultivars can initiate flowers before growth cessation and the onset of dormancy, there may be an underlying physiological relationship between growth cessation and the time of flower bud initiation. Interestingly, this trend did not continue after the plants received sufficient chilling. ‘Loch Ness’ at 12h photoperiod had the most developed flower buds before chilling, but required more days to anthesis, had lower percentage of flowering nodes and fewer flowers per plant after forcing than plants grown at the other photoperiods. In fact, ‘Loch Ness’ at 15h photoperiod, had the highest percentage of flowering nodes, most flowers per plant and fewest days to anthesis at forcing. These results indicate that while shorter photoperiods before chilling can advance the time of flower bud initiation, the longer photoperiods can have a positive effect on the number of flowering nodes on the cane, possibly increasing the yield potential of the plants. A possible explanation is that longer photoperiods before chilling lead to a lower proportion of underdeveloped buds in the terminal portion of the cane, thus increasing the number of flowering laterals.

Under natural temperature and daylight conditions in the open tunnel, ‘Natchez’ reached growth cessation first and had buds with the most advanced flowers by the end of the experiment. ‘Sweet Royalla’ that reached growth cessation three weeks later, had less developed flower buds than ‘Natchez’, but more developed than ‘Loch Ness’ that reached growth cessation four weeks later than ‘Natchez’. Takeda et al. (2002) similarly found that under field conditions in Oregon and Arkansas, USA erect-growing blackberry cultivars initiated flowers two to three months earlier than semi-erect cultivars. Plants of ‘Natchez’, ‘Sweet Royalla’ and ‘Loch Ness’, produced with the same method and at the same time as in this experiment, were used in a dormancy breaking experiment during the winter of 2024. When these plants were forced in the greenhouse after sufficient chilling ‘Natchez’ was the first to reach anthesis, ‘Sweet Royalla’ three to four days later, and ‘Loch Ness’ over a week later than ‘Natchez’ (unpublished data). This suggests that under natural daylength and temperature, more advanced flower buds prior to chilling lead to earlier flowering and fruiting post-chilling.

‘Ouachita’ and ‘Loch Tay’ did not develop any flower buds before they reached growth cessation in the open tunnel experiment. When ‘Ouachita’ plants were forced in the dormancy experiment, they did develop flowers, but more than two weeks later than ‘Natchez’, and only at one or two nodes in a few plants (unpublished data). At the time of growth cessation, the ‘Ouachita’ plants were only 50 cm tall, yet they had developed 19 nodes in average along the cane, which is roughly the same number of nodes as ‘Natchez’. Thus, it is unlikely that the ‘Ouachita’ plants were still in a juvenile phase at the time of growth cessation. Another possible explanation for the poor flowering performance in ‘Ouachita’ is that in such short plants, or generally in ‘Ouachita’, apical dominance might be so strong that it prevents the development of lateral buds. This is further supported by poor budbreak in forced ‘Ouachita’ plants, where the plants only had a couple of vegetative laterals and the fruiting lateral usually developed from the terminal bud (unpublished data).

‘Loch Tay’ was not used in the dormancy experiment, so it is not possible to compare dissection results with the flowering performance in ‘Loch Tay’. However, Sønsteby and Heide (2023) reported that all forced ‘Loch Tay’ plants grown in controlled temperature conditions developed flowers after chilling. In the open tunnel experiment here, ‘Loch Tay’ had the highest growth rate of all the cultivars and the collection of axillary buds for dissection started at bud no. 10 upward from the base. The first sign of flower bud initiation in ‘Loch Tay’ was observed around 1 September but the flower buds did not reach the generative stage. There is a possibility that further development of flower buds was missed in ‘Loch Tay’ because axillary buds collected in later weeks might have been in an underdeveloped terminal portion of the cane, and that the sampling of buds in vigorous growing cultivars should start closer to the base to avoid this. Another possibility is that ‘Loch Tay’ plants may initiate flower buds early in the autumn, but do not reach a generative stage before winter or spring. Takeda et al. (2002) reported that semi-erect cultivars started to initiate flowers in October yet did not reach a generative stage before January in Oregon, USA, and April in Arkansas and West Virginia, USA.

6 Conclusions

The aim of this study was to get a deeper understanding of the physiological relationship between growth cessation and flower bud development in blackberries and give a greater insight of the role of photoperiod and temperature on these processes.

The results demonstrate that origin and genetic background of cultivars plays a crucial role in their response to environmental signals. ‘Natchez’ had a critical photoperiod of 14h for cessation of growth at 16°C, while ‘Loch Ness’ continued to grow independently of photoperiod treatment at this temperature.

Photoperiod in the 12-15h range was not critical for flower bud initiation in ‘Natchez’ and ‘Loch Ness’ grown at 16°C, and all cultivars initiated flower buds before cessation of growth. However, in both experiments, the plants that reached growth cessation first, also had the most developed flower buds, except for ‘Ouachita’, indicating an underlying physiological relationship linking growth cessation and flower bud development.

Furthermore, early flower bud initiation in the phytotron compared to natural environmental conditions suggests that temperature, rather than photoperiod, may be the main factor affecting both growth cessation and flower bud initiation.

‘Loch Ness’ at 15h photoperiod, had the highest percentage of flowering nodes, most flowers per plant and fewest days to anthesis at forcing. The results indicate that the longer photoperiods can have a positive effect on the number of flowering nodes on the cane, increasing yield potential of the plants.

The results also suggest that blackberries may be day-neutral and not dependent on photoperiod for growth cessation and flower initiation. However, due to the high genetic variation in blackberry cultivars, further experiments with more, genetically diverse, cultivars are required to fully understand the role of photoperiod in flower bud development of blackberries.

Experiments that further examine the effects of temperature and photoperiod, and more importantly, the interaction between the two, on growth cessation and flower bud initiation would give a better understanding of the environmental control of growth and flowering in blackberries.

7 References

- Atkinson, C. J., Brennan, R. M., & Jones, H. G. (2013). Declining chilling and its impact on temperate perennial crops. *Environmental and Experimental Botany*, 91, 48-62.
<https://doi.org/https://doi.org/10.1016/j.envexpbot.2013.02.004>
- Atkinson, D. (1973). Seasonal changes in the length of white unsuberized root on raspberry plants grown under irrigated conditions. *Journal of Horticultural Science*, 48(4), 413-419.
- Carter, P. M., Clark, J., Particka, C., & Crowne, D. (2006). Chilling response of Arkansas blackberry cultivars. *Journal of the American Pomological Society*, 60, 187-197.
- Clark, J. R. (2005). Changing times for eastern United States blackberries. *HortTechnology*, 15(3), 491-494.
- Clark, J. R. (2008). Primocane-fruited blackberry breeding. *Hortscience*, 43(6), 1637-1639.
- Clark, J. R., & Finn, C. E. (2008). New Trends In Blackberry Breeding. *Acta Hort.*, 777, 41-48.
<https://doi.org/10.17660/ActaHortic.2008.777.2>
- Clark, J. R., & Finn, C. E. (2014). Blackberry Cultivation in the World. *Revista Brasileira De Fruticultura*, 36(1), 46-57. <https://doi.org/10.1590/0100-2945-445/13>
- Clark, J. R., Strik, B. C., Thompson, E., & Finn, C. E. (2012). Progress and Challenges in Primocane-Fruited Blackberry Breeding and Cultural management. *Acta Hort.*, 926, 387-392.
<https://doi.org/10.17660/ActaHortic.2012.926.54>
- Darrow, G. M. (1931). European blackberry seedlings and hybrids in the Pacific North-west. *J. Hered.*, 22, 143-146.
- Darrow, G. M. (1937). Blackberry and raspberry improvement. *Yearbook of the United States Department of Agriculture*, 496-533.
- Dickson, R. W., Machesney, L. M., & Henderson, E. O. (2023). Forcing Temperature Effects on Plant Development for Containerized Blackberry Grown Using Long-Cane Techniques. *Horticulturae*, 9(10), 1090. <https://www.mdpi.com/2311-7524/9/10/1090>
- Fear, C. D., & Meyer, M.-D. L. (1993). Breeding and variation in *Rubus* germplasm for low winter chill requirement. VI International Symposium on *Rubus* and *Ribes* 352,
- Fernandez, G., McWhirt, A., & Bradish, C. (2023). *Southeast Regional Caneberry Production Guide*. NC State Extension Publications. Retrieved 10.02.2024 from
<https://content.ces.ncsu.edu/southeast-regional-caneberry-production-guide>
- Finn, C., & Knight, V. H. (2002). What's Going On in the World of *Rubus* Breeding? *Acta Hort.*, 31-38. <https://doi.org/10.17660/ActaHortic.2002.585.1>
- Foster, T. M., Bassil, N. V., Dossett, M., Leigh Worthington, M., & Graham, J. (2019). Genetic and genomic resources for *Rubus* breeding: a roadmap for the future. *Horticulture research*, 6(1), 116. <https://doi.org/10.1038/s41438-019-0199-2>
- Hall, H. K., Stephens, M. J., Stanley, C. J., Finn, C., & Yorgey, B. (2002). Breeding New 'Boysen' and 'Marion' Cultivars. *Acta Hort.*, 91-95. <https://doi.org/10.17660/ActaHortic.2002.585.11>
- Jennings, D., & Carmichael, E. (1975). Some physiological changes occurring in overwintering raspberry plants in Scotland.
- Jennings, D., Carmichael, E., & Costin, J. (1972). Variation in the time of acclimation of raspberry canes in Scotland and Ireland and its significance for hardiness. *Hort. Res.*, 12, 187-200.
- Jennings, D. L. (1988). *Raspberries and blackberries: their breeding, diseases and growth*. Academic press.
- Mazzitelli, L., Hancock, R. D., Haupt, S., Walker, P. G., Pont, S. D., McNicol, J., Cardle, L., Morris, J., Viola, R., & Brennan, R. (2007). Co-ordinated gene expression during phases of dormancy release in raspberry (*Rubus idaeus* L.) buds. *Journal of experimental botany*, 58(5), 1035-1045.
- Miles, N. W. (1965). A study of rest period in Latham raspberry: environmental conditions which affect the rest period and relationships of rest to winter hardiness. *Diss. Abstr.*, 15, 314-315.
- Moore, J. N., & Caldwell, J. D. (1985). *Rubus*. In A. H. Halevy (Ed.), *CRC Book of flowering* (Vol. 4, pp. 226-238). CRC Press.
- Måge, F. (1975). Dormancy in buds of red raspberries. *Meld. Norges landbrukshøgsk.*, 54, No. 21.
- Perkins-Veazie, P., & Clark, J. (2005). Blackberry research in Arkansas and Oklahoma. Proceedings of the North American Bramble Growers Association Annual Meeting,
- Robertson, M. (1957). Further Investigations of Flower-Bud Development in the Genus *Rubus*. *Journal of Horticultural Science*, 32(4), 265-273.
<https://doi.org/10.1080/00221589.1957.11513907>
- Scott, D., & Ink, D. (1966). Origination of "Smoothstem" and "Thornfree" blackberry varieties. *Fruit Var. Horticult. Dig*, 20, 31-33.

- Strik, B. C., & Finn, C. E. (2012). Blackberry Production Systems - a Worldwide Perspective. *ActaHortic.*, 946, 341-347. <https://doi.org/10.17660/ActaHortic.2012.946.56>
- Strik, B. C., Finn, C. E., Clark, J. R., & Pilar Banados, M. (2008). Worldwide Production of Blackberries. *ActaHortic.*, 777, 209-218. <https://doi.org/10.17660/ActaHortic.2008.777.31>
- Sønsteby, A., & Heide, O. (2008). Environmental control of growth and flowering of *Rubus idaeus* L. cv. Glen Ample. *Scientia horticultrae*, 117, 249-256. <https://doi.org/10.1016/j.scienta.2008.05.003>
- Sønsteby, A., & Heide, O. M. (2014). Cold tolerance and chilling requirements for breaking of bud dormancy in plants and severed shoots of raspberry (*Rubus idaeus* L.). *The Journal of Horticultural Science and Biotechnology*, 89(6), 631-638. <https://doi.org/10.1080/14620316.2014.11513131>
- Sønsteby, A., & Heide, O. M. (2023). Temperature and Daylength Effects on Growth and Floral Initiation in Biennial-Fruiting Blackberry. *Horticultrae*, 9(12), 1285. <https://www.mdpi.com/2311-7524/9/12/1285>
- Sønsteby, A., Stavang, J. A., & Heide, O. M. (2013). Production of high-yielding raspberry long canes: The way to 3 kg of fruit per cane. *The Journal of Horticultural Science and Biotechnology*, 88(5), 591-599. <https://doi.org/10.1080/14620316.2013.11513011>
- Takeda, F., Strik, B. C., Peacock, D., & Clark, J. R. (2002). Cultivar Differences and the Effect of Winter Temperature on Flower Bud Development in Blackberry. *Journal of the American Society for Horticultural Science jashs*, 127(4), 495-501. <https://doi.org/10.21273/jashs.127.4.495>
- Takeda, F., Strik, B. C., Peacock, D., & Clark, J. R. (2003). Patterns of Floral Bud Development in Canes of Erect and Trailing Blackberries. *Journal of the American Society for Horticultural Science jashs*, 128(1), 3-7. <https://doi.org/10.21273/jashs.128.1.0003>
- Takeda, F., & Wisniewski, M. (1989). Organogenesis and Patterns of Floral Bud Development in Two Eastern Thornless Blackberry Cultivars. *Journal of the American Society for Horticultural Science*, 114(4), 528-531. <https://doi.org/10.21273/jashs.114.4.528>
- Thompson, E., Strik, B. C., Clark, J. R., & Finn, C. E. (2007). Flowering and Fruiting Patterns of Primocane-fruited Blackberries. *Hortscience*, 42(5), 1174-1176. <https://doi.org/10.21273/hortsci.42.5.1174>
- Warmund, M. R., & Byers, P. L. (2002). Rest Completion in Seven blackberry (*Rubus* sp) Cultivars. *ActaHortic.*, 585, 693-696. <https://doi.org/10.17660/ActaHortic.2002.585.115>
- Warmund, M. R., & Krumme, J. (2005). A Chilling Model to Estimate Rest Completion of Erect Blackberries. *HortScience* 40(5), 1259-1262. <https://doi.org/10.21273/hortsci.40.5.1259>
- Westwood, M. N. (1993). *Temperate-zone Pomology: Physiology and Culture*. Timber Press. <https://books.google.no/books?id=J9CvzwEACAAJ>
- White, J., Wainwright, H., & Ireland, C. (1998). Endodormancy and paradormancy in the raspberry cultivar 'Glen Clova'. VII International Symposium on *Rubus* and *Ribes* 505,
- Williams, I. (1959). Effects of environment on *Rubus idaeus* L.: IV. Flower initiation and development of the inflorescence. *Journal of Horticultural Science*, 34(4), 219-228.
- Williams, I. (1960). Effects of environment on *Rubus idaeus* LV Dormancy and flowering of the mature shoot. *Journal of Horticultural Science*, 35(3), 214-220.
- Worthington, M. L., Aryal, R., Bassil, N. V., Mead, D., Fernandez, G. E., Clark, J. R., Fernandez-Fernandez, F., Finn, C. E., Hummer, K. E., & Ashrafi, H. (2020). Development of new genomic resources and tools for molecular breeding in blackberry. *ActaHortic.*, 1277, 39-46. <https://doi.org/10.17660/ActaHortic.2020.1277.6>



Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway