Temperature rather than photoperiod controls growth cessation and dormancy in Sorbus species

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Abstract

Environmental regulation of growth and dormancy of four Sorbus genotypes was studied in controlled environments. Emphasis was placed on assessment of the presence and nature of the deficient photoperiodic dormancy regulation system that has previously been reported for some woody Rosaceae species. Two genotypes of Sorbus aucuparia L. maintained indeterminate growth for 8 weeks and 9 weeks at temperatures of 15 °C and 21 °C in both 20 h and 10 h photoperiods, while at 9 °C, in the same photoperiodic conditions, they immediately ceased growing. At the higher temperatures, initiation of new leaves (nodes) was unaffected by photoperiod, while internode elongation was significantly enhanced by long days (LD). However, even after prolonged exposure to 9 °C, most plants resumed growth when moved to high temperature and LD, indicating a shallow state of dormancy. Seedlings of Sorbus intermedia (J. F. Ehrh.) Pers. and micro-propagated plantlets of S. commixta Hedl. ‘Dodong’ were also unaffected by photoperiod during primary growth, but failed to elongate and gradually became dormant regardless of temperature and day-length conditions. However, after chilling and breaking of dormancy, the plants elongated vigorously but changed to a determinate mode of growth. Furthermore, a temperature of 9 °C was found to be fully effective for breaking dormancy in S. intermedia plants. It is concluded that deficient photoperiodic dormancy control seems widespread in the Rosaceae and that, in such plants, both dormancy induction and release is brought about by low temperature. The potential impacts of climate change on such trees are discussed.

Key words: Climate, dormancy, growth cessation, photoperiod, Rosaceae, Sorbus, temperature.

Introduction

The seasonal regulation of growth and dormancy is crucial for winter survival and regulation of timely growth activity of perennial plants in temperate and cold climates. This requires the mediation of a reliable seasonally controlled environmental signal. Since the pioneering discovery by Garner and Allard (1923), the important role of short photoperiods in the autumn as the dormancy-inducing signal has been amply demonstrated and documented in a wide range of woody plants (Kramer, 1936; Downs and Borthwick, 1956; Wareing, 1956; Nitsch, 1957; Heide, 1974a; Junttila, 1976; Håbjørg, 1978; Böhlenius et al., 2006). An important exception to the short-day (SD) control of growth cessation and dormancy induction in woody plants had already been noted by Garner and Allard (1923) for apple (Malus pumila Mill.), which was not affected by photoperiod. This was confirmed and extended to several other genera of the Rosaceae by Nitsch (1956) and Heide and Prestrud (2005). As no other environmental signal was known to control dormancy induction in these plants, their dormancy was considered to be entirely under endogenous control (Wareing, 1956; Battey, 2000). However, Heide and Prestrud (2005) demonstrated that temperatures below 12 °C consistently induced growth cessation and bud dormancy in apple and pear rootstocks under both SD and long-day (LD) conditions, while at 15 °C and 21 °C they maintained active growth regardless of photoperiodic conditions. Chilling at 6–9 °C for about 1000 h was required for dormancy release and growth resumption of the dormant plants. Similar responses were demonstrated in several species of the genus Prunus (Heide, 2008).
Modern phylogenetic analyses have divided the Rosaceae into three subfamilies, Dryadoideae, Rosoideae, and Spiraeoideae (Potter et al., 2006). All the above-mentioned genera are included in the Spiraeoideae subfamily which also comprises a range of other important fruit and landscape trees and shrubs of great horticultural importance. An important example is the genus Sorbus which comprises a number of widely cultivated landscaping species and cultivars from the temperate and cold regions of the Northern hemisphere. It was therefore considered of both general biological interest and horticultural interest to explore the environmental control of growth and dormancy in such species. Of special interest would be to find out how widespread the deficient photoperiodic control mechanism is within the Rosaceae. The responses to photoperiod and temperature of four contrasting Sorbus species and cultivars have therefore been studied under controlled environment conditions, and the results are presented below.

Materials and methods

Plant material and cultivation

The experiments were carried out during spring and summer of 2009 and 2010 in the Ås phytotron in daylight compartments combined with adjacent growth rooms for photoperiodic manipulation as described by Heide (2008). The complete scientific names of the Sorbus species and cultivars included in the experiments are listed in Table 1. In vitro micro-propagated plantlets of S. aucuparia ‘Sunshine’ (a cultivar with yellow berries) and S. commixta ‘Dodong’ were obtained from a commercial nursery in mid-April 2009 and subjected to experimental treatments for 9 weeks from 24 April 2009. The wild-type S. aucuparia, and S. intermedia plants were propagated from seed. Fruits were collected in early October 2009 from a single tree of each species located in the park of the University campus at Ås (59°40’ N, 10°40’ E). The berries were gently crushed and the resulting slurry thoroughly washed with water and the remains, including the seeds, were mixed with moist vermiculite and exposed to chilling at 5 °C for 21 weeks (~3500 h) for breaking of seed dormancy. On 3 March 2010 the seeds were sown in a peat-based soil mixture (see below), and germinated and raised at 21 °C in continuous light until the plants had reached a height of 5-6 cm, and the experimental treatments were started on 20 April 2010. Both years, the plants were grown in 12 cm plastic pots filled with a peat-based potting compost (84%peat, 10% fine sand, and 6% clay) with the addition of 300 g per 80 l of Osmocote controlled-release fertilizer (14% N, 4.2% P, 11.6% K plus micronutrients; release rate 3-4 months) from Scotts UK Ltd, Nottingham, UK. The plants were watered daily with tap water as required.

In the phytotron, all plants received natural spring and summer daylight for 10 h per day (08.00–18.00 h). Whenever the photosynthetic photon flux (PPF) in the daylight compartments fell below approximately 150 μmol m⁻² s⁻¹, as on cloudy days, an additional 125 μmol m⁻² s⁻¹ quanta were automatically added by high-pressure metal halide lamps (400 W; Philips HPI-T). Day-length extension to 20 h was provided by low-intensity light from 75 W incandescent lamps (~7 μmol m⁻² s⁻¹ PPF) in such a way that the plants were in darkness from 22.00 h to 02.00 h. Plants receiving SD treatment were in the dark from 18.00 h to 08.00 h. The day-length extension light amounted to less than 2% of the total daily radiation, the plants thus receiving nearly the same daily light integral in both photoperiods. Temperatures were controlled to ±1.0 °C and a water vapour pressure deficit of 530 Pa was maintained at all temperatures.

Experimental design, data observation, and analysis

Two main growth experiments were carried out in 2009 (Experiment 1, with S. aucuparia ‘Sunshine’ and S. commixta ‘Dodong’) and in 2010 (Experiment 2, with wild-type S. aucuparia and S. intermedia plants). In both experiments, the plants were exposed to three constant temperatures (9, 15 or 21 °C) combined with photoperiods of 10 h and 20 h. A third experiment examined the responses to the same temperature and day lengths of ‘second year’ S. intermedia plants which had experienced a full growth/dormancy/chilling cycle (Experiment 3). The dormancy state of S. aucuparia plants which had ceased growing in LD at 9 °C was assessed by transferring batches of plants back to 21 °C and 20 h photoperiod after varying lengths of exposure to the low-temperature condition (Experiment 4). Finally, the dormancy-breaking effect of 9 °C temperature was examined in dormant S. intermedia plants by exposing them to 9 °C in the dark for 3–12 weeks followed by forcing at 21 °C in 24 h photoperiod (Experiment 5).

All experiments were factorial with a split-plot design with temperatures as main plots and photoperiods and species/cultivars as sub-plots. Each treatment had three replications comprising five plants of each genotype on a separate trolley (15 plants of each species per treatment). Elongation growth and production of new leaves and new suckers were measured as growth responses with marked effects of temperature condition (Experiment 1), with 9 °C and 15 °C they

Table 1. Identity and propagation methods of the plants used in the experiments

| Scientific name      | Type   | Origin       | Propagation method     |
|----------------------|--------|--------------|------------------------|
| S. aucuparia L.      | Wild species | Europe       | Seedlings              |
| S. intermedia (J. F. Ehrh.) Pers. | Wild species | Europe       | Seedlings              |
| S. aucuparia L. ‘Sunshine’ | Cultivar | Asia (Korea) | In vitro propagated    |
| S. commixta Hedl. ‘Dodong’ | Cultivar | Asia (Korea) | In vitro propagated    |

Results

Experiment 1 (2009)

The two Sorbus cultivars differed greatly in their treatment responses. While the ‘Dodong’ plants elongated very little and gradually became dormant under all temperature and day-length conditions (Fig. 1A), the ‘Sunshine’ plants exhibited diverse growth responses with marked effects of temperature and daylength (Figs 1B, 2). Thus, at low temperature (9 °C), the ‘Sunshine’ plants never started growing in either SD or LD, while at 15 °C and 21 °C they...
resumed vigorous and indeterminate growth after a lag period in both photoperiods, although with a significant growth enhancement by LD. Although the lag phase was about two weeks longer at 15 °C than at 21 °C, the growth rates were nearly identical when first started. At both temperatures, and in both SD and LD, a few plants produced intermittent growth with short periods of halted growth followed by renewed elongation. Because of this, the average growth rates declined somewhat with time (Fig. 1B). A separate ANOVA for growth increment of the ‘Sunshine’ plants after 9 weeks of cultivation revealed significant effects of both temperature (P < 0.001) and photoperiod (P=0.03), with no significant interaction of the two variables. However, while the production of new leaves was also significantly (P=0.001) enhanced by increasing temperature, photoperiod had no significant effect on leaf production (Table 2), the LD growth enhancement effect thus being due to enhanced internode elongation only.

Although the ‘Dodong’ plants elongated only a few cm even under high temperature and LD conditions, they all produced some new leaves, the number increasing significantly with increasing temperature, but with no significant effect of photoperiod (Table 2). After some time, the plants developed typical winter buds in both daylengths, the process being advanced by high temperature. While stem elongation was not significantly affected by temperature, leaf length of the ‘Dodong’ plants increased highly significantly (P < 0.001) with increasing temperature, while photoperiod had no significant effect on leaf length (Table 3).

After 9 weeks of treatment all plants of both cultivars were moved into a greenhouse with a minimum temperature of 20 °C and a 24 h photoperiod where they remained for 8 weeks. All the ‘Dodong’ plants remained non-growing throughout this period and developed large winter buds. However, after chilling at 5 °C in darkness for another 8 weeks, they immediately resumed growth when returned to high temperature and LD with a mean elongation of 31 ± 2 cm and the formation of 13 ± 0.5 leaves within 4 weeks. Regrettably, the effect of photoperiod on the growth performance of these plants was not studied.

On the other hand, most of the ‘Sunshine’ plants from 15 °C and 21 °C continued growing when moved to LD at 20 °C, some reaching a height of 1.5 m within 8 weeks (plants from both day lengths). As before, a few plants had intermittent growth, while a couple of plants ceased growing permanently and developed large resting buds. Also, most of the ‘Sunshine’ plants from 9 °C in both LD and SD resumed growth at high temperature after a lag period of 2–3 weeks. However, in some of these plants, only lateral buds at the base of the shoot initiated new growth while the terminal bud remained dormant, demonstrating a deeper state of dormancy in terminal than in lateral buds (data not shown).

### Table 2. Effects of temperature and photoperiod on the production of new leaves (nodes) in two Sorbus cultivars after 9 weeks of cultivation

| Cultivar     | Temperature (°C) | Photoperiod (h) | 10   | 20   |
|--------------|-----------------|-----------------|------|------|
| ‘Dodong’     | 9               | 3.5±0.1         | 4.1±0.1 |
|              | 15              | 7.8±0.2         | 8.7±0.2 |
|              | 21              | 9.7±0.3         | 10.4±0.2 |
| ‘Sunshine’   | 9               | 3.2±0.1         | 3.3±0.2 |
|              | 15              | 14.2±0.3        | 15.8±0.2 |
|              | 21              | 18.8±0.9        | 17.7±0.8 |

### Table 3. Effects of temperature and photoperiod on leaf length of Sorbus ‘Dodong’ plants after 9 weeks of cultivation

| Temperature (°C) | Photoperiod (h) | 10   | 20   |
|-----------------|-----------------|------|------|
| 9               | 6.4±0.2         |      |      |
| 15              | 21.6±0.7        | 25.4±0.8 |
| 21              | 32.3±0.4        | 33.3±0.5 |
Experiment 2 (2010)

This experiment was done with seedlings of wild-type *S. aucuparia* and *S. intermedia*. The *S. aucuparia* plants maintained a nearly constant rate of elongation for 8 weeks in both LD and SD at 15 °C and 21 °C, while at 9 °C they ceased growing in both day lengths after about 2–3 weeks. At the highest temperature the plants elongated more than 1 m in LD during the 8-week experimental period, while at 9 °C they grew only 5–6 cm before they ceased growing (Fig. 3A). Growth was highly significantly ($P = 0.001$) increased by increasing temperature and photoperiod and, since photoperiod had no significant growth effect at 9 °C, there was also a highly significant interaction of photoperiod and temperature ($P < 0.001$). The initiation of new leaves also increased highly significantly ($P < 0.001$) with increasing temperature, while the main effect of photoperiod was barely significant ($P = 0.056$). While leaf formation continued at a nearly constant rate at the higher temperatures in both LD and SD, it ceased after about 5 weeks at 9 °C in both day lengths (Fig. 3B).

On the other hand, the *S. intermedia* plants elongated very little and, after 4–5 weeks, they all ceased growing and formed rosettes regardless of temperature and day-length conditions (Fig. 3C). Only in LD at 21 °C was there a measurable amount (11 cm) of growth, resulting in highly significant ($P < 0.001$) effects of both temperature and day length as well as their interaction. Despite the small amount of elongation growth, the plants continued to form new leaves for 5–6 weeks whereupon leaf formation also levelled off. The rate of leaf formation also increased significantly ($P = 0.001$), with increasing temperature and day length (Fig. 3D). Under all conditions the *S. intermedia* plants entered dormancy and after 10 weeks they needed several weeks of chilling for growth resumption (see Experiment 5).

Experiment 3 (2010)

A separate batch of 100 *S. intermedia* plants were grown at 15 °C and natural long summer day length (17–19 h) for 10 weeks in parallel with the preceding experiment. The plants then had pencil-thick stems with a mean height of 5.8 ± 0.2 cm and had not been growing for the last 6 weeks. After chilling at 5 °C in darkness for 10 weeks in order to break dormancy, the plants were randomly allotted into six groups of 15 plants each and exposed to temperatures of 9, 15 or 21 °C and 10 h or 20 h photoperiods as in the previous experiment. Unlike the seedlings of the previous experiment, these ‘second year’ plants grew vigorously at all

| Weeks at 9 °C | Per cent bud burst | Days to bud burst | Terminal shoot length |
|---------------|--------------------|-------------------|----------------------|
|               | Lateral | Terminal | Lateral | Terminal | Terminal (cm) |
| 3             | 0       | 0        | >120     | >120      | 0             |
| 6             | 80      | 0        | 89.5     | >100      | 0             |
| 9             | 100     | 90       | 29.5     | 39.2      | 15.2          |
| 12            | 100     | 100      | 15.2     | 20.5      | 25.5          |
temperatures, even at 9 °C (Fig. 4). However, regardless of temperature and day-length conditions, the plants ceased growing after the development of about 12 leaves. Growth rate increased with increasing temperature in the usual way and, due to increased internode length, final plant heights at the end of the elongation period were also significantly enhanced by increasing temperature ($P=0.004$) and photoperiod ($P <0.001$). After completion of this growth cycle, the plants formed new winter buds and entered dormancy again.

**Experiment 4 (2010)**

On 20 April 2010, 45 plants of *S. aucuparia* were placed in a phytotron daylight compartment maintained at 9 °C and exposed to 20 h photoperiod. After 6, 9 or 12 weeks of exposure to these conditions, groups of 15 plants were returned to high temperature (21 °C) and 20 h photoperiod for assessment of their state of dormancy. As shown in Fig. 5, the plants ceased growing at 9 °C after a few centimetres of elongation and the production of approximately one new leaf. With increasing time of exposure to the low-temperature condition, the plants developed a typical dormant appearance with red, senescent leaves that started to abscise from the base, while formation of winter buds progressed only slowly. However, when returned to high temperature and LD after 6 weeks at 9 °C, most plants (88%) resumed growth after a short lag period (Fig. 5). However, when the low temperature exposure was extended to 9 or 12 weeks, an increasing proportion of the plants remained dormant so that after 12 weeks only 63% of the plants resumed growth from the terminal bud. Elongation growth and production of new leaves declined in parallel (Fig. 5). As with the ‘Sunshine’ plants in Experiment 1, many of the plants with dormant terminal buds, initiated new growth from basal lateral buds when returned to high temperature conditions (data not shown).

**Experiment 5 (2010)**

Forty seedlings of *S. intermedia* grown in LD at 21 °C as described in Experiment 2 were used for the experiment. After 12 weeks under these conditions, the plants had a mean height of 8.0±0.2 cm and had developed typical winter buds. The plants were then moved into darkness in a growth room maintained at 9 °C for the breaking of dormancy. After 3, 6, 9 or 12 weeks under these conditions, batches of 10 plants were returned to 21 °C and 20 h LD and forced under these conditions in order to examine whether dormancy had been released by the 9 °C treatment.

As shown by Table 4 and Fig. 6, chilling at 9 °C was highly effective in breaking bud dormancy, although a minimum of 9 weeks was necessary for bud burst of terminal buds which had a markedly larger chilling requirement than had lateral buds. Time to bud burst also decreased with increasing length of chilling while elongation of the developing shoots increased in parallel (Table 4).
Discussion

The results of these experiments revealed some puzzling variation in the environmental growth responses of the Sorbus species and cultivars studied. On the one hand, two genotypes of S. aucuparia maintained indeterminate growth at temperatures of 21 °C and 15 °C in both 10 h SD and 20 h LD conditions, whereas at 9 °C they consistently ceased growing in both SD and LD (Figs 1–3). In other words, growth cessation was controlled by low temperature and not by SD as established for most other woody species (Wareing, 1956). This deficient photoperiodic control is consistent with previous findings for apple and pear and some other species of the Rosaceae (Garner and Allard, 1923; Nitsch, 1957; Heide and Prestrud, 2005), while the dormancy-inducing effect of low temperature confirms and extends previous findings for apple, pear, and Prunus species (Heide and Prestrud, 2005; Heide 2008).

On the other hand, micro-propagated plants of S. commixta ‘Dodong’ and seedlings of S. intermedia attained a rosette growth habit with little internode elongation and gradually became dormant, regardless of temperature and day-length conditions (Figs 1–3). However, after chilling at 5 °C for breaking of dormancy, both species produced vigorous growth with normal internode elongation regardless of temperature and day-length conditions, although now with a determinate mode of growth. Thus, the S. intermedia plants, which were examined in some detail, ceased growing after the production of about 12 leaves (nodes), regardless of temperature and day-length conditions. However, while final leaf numbers were unaffected by temperature and day length, the final plant heights were significantly enhanced by both increasing temperature and photoperiod (P=0.005 and P <0.001, respectively), due to the enhancement of internode length (Fig. 4). It should be noted that, when in this growth modus, the plants also grew vigorously at 9 °C, producing the same number of leaves as at higher temperatures. Although the situation was not examined in detail in S. commixta ‘Dodong’, the responses seem to have been the same. This demonstrates that, after passing through the first dormancy period, these genotypes changed to a determinate or fixed growth pattern and, accordingly, stopped growing after developing the leaves and internodes that were initiated and present in the bud at the end of the previous growth period (Fig. 4). While such a shift from indeterminate or free growth to determinate (fixed) growth after passing through the first dormancy period is the general rule for coniferous species (for references, see Heide,
The restricted growth habit of *S. intermedia* seedlings and *in vitro*-propagated *S. commixta* ‘Dodong’ plantlets is rather puzzling. Although it cannot be excluded that the ‘Dodong’ plants might have experienced short periods of dormancy-inducing low temperature at an early stage, this possibility can be ruled out for the *S. intermedia* seedlings which were carefully controlled at 21 °C throughout germination and early growth. Dwarfing, as a result of inadequate seed chilling as demonstrated for embryo-cultured seedlings of peach, apple, and hawthorn by Flemion (1934), can also be ruled out since the *S. intermedia* seeds were chilled at 5 °C for 21 weeks, a treatment which produced optimal and rapid germination. The physiological basis for this dwarf growth habit is therefore an enigma. Possibly, it may be a characteristic that has evolved as a mechanism to ensure early growth cessation in the otherwise vulnerable first-year seedlings of photoperiod-insensitive species. Also, the early dormancy release of basal lateral buds of the studied species may explain the common occurrence of multistem trees in rowan and other *Sorbus* species.

Dormancy is not an all or none situation, but a quantitative condition that is gradually established and lost (Thomas and Vince-Prue, 1997; Juntila, 2007). The results with *S. aucuparia* shown in Fig. 5, demonstrate that the plants did not enter a deep state of dormancy, even after extended exposure to low temperature. However, realizing that a temperature of 9 °C was also fully effective in breaking dormancy in *Sorbus* plants (Fig. 6; Table 4), this is actually what would be expected. Paradoxically, low growth temperature seems to have dual and opposing effects, not only inducing dormancy, but also continuously negating the dormancy-inducing effect. That the depth of dormancy is affected by the temperature conditions during dormancy induction, is not specific for photoperiod-insensitive species such as *Malus* and *Sorbus*, but is reported for a range of boreal trees with the normal photoperiod-induced dormancy, such as *Betula*, *Alnus*, *Acer*, *Picea*, and others (Heide, 2003, and references therein). In all these trees, the depth and duration of dormancy increased with increasing temperature during SD dormancy induction. Parallel responses were even found in both cultivated and wild strawberries (Sonstebey and Heide, 2006, 2011), in which relatively high temperatures are required for SD induction of dormancy. In all these cases it seems that the dormancy-inducing effect of SD is continuously negated by low temperature, thereby establishing a relatively shallow state of dormancy (Sonstebey and Heide, 2011).

The results are of special interest in the context of the potential impacts of the predicted and ongoing climatic warming (Serreze et al., 2000). In a scenario of changing temperature, photoperiodic regulation of dormancy is an obvious advantage for the timely synchronization of plant development with seasonal changes in the environment. Therefore, the deficient photoperiodic regulation of many Rosaceae woody species (Nitsch, 1957; Heide and Prestrud, 2005; Heide, 2008) is likely to render these plants especially vulnerable to global warming, as the alternative regulation by low temperature may provide a less reliable signal. However, the demonstrated restrictive growth strategy of first year plants of *S. intermedia* and *S. commixta*, and their shift to a determinate mode of growth in older plants, are modifying mechanisms that, to some extent, may compensate for the deficient photoperiodic regulation.

Despite the lack of photoperiodic sensitivity for dormancy regulation in *Sorbus* and other studied Rosaceae trees, their enhanced internode elongation under LD conditions (Fig. 3A) indicates that the phytochrome system is still operative in these plants. Thus, day-length extension by incandescent lamps as performed in these and earlier experiments (Heide and Prestrud, 2005, Heide, 2008), which is highly efficient in this type of photoperiodic response (Vince-Prue, 1981), is also well known to be mediated by the phytochrome pigment (Thomas and Vince-Prue, 1997). Accordingly, the deficient photoperiodic sensitivity of Rosaceae trees appears not to reside in deficient light-sensing mechanisms, but rather in some deficient transduction mechanism(s). While little is still known about the genetic and molecular mechanisms underlying temperature sensing for dormancy regulation (Mazzitelli et al., 2007), the
Rosaceae trees lend themselves as useful experimental materials for such studies by providing a system for the separation of photoperiodic and temperature responses.

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