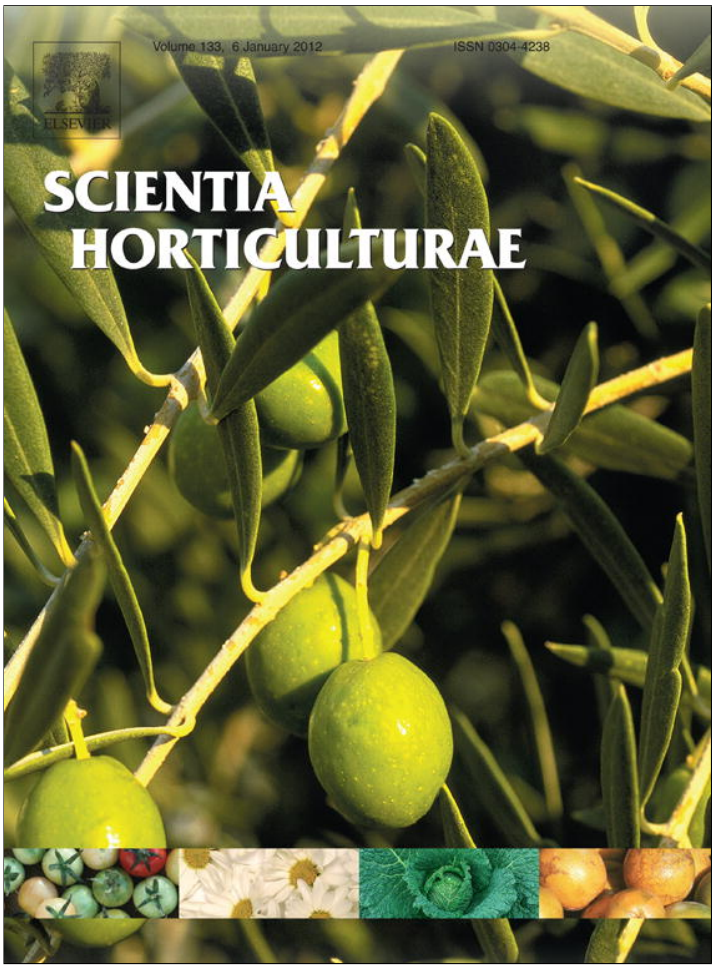

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Floral initiation in black currant cultivars (*Ribes nigrum* L.): Effects of plant size, photoperiod, temperature, and duration of short day exposure

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ABSTRACT

Effects of plant size, photoperiod, temperature and duration of short day (SD) exposure on flowering and dormancy induction in black currant cultivars (*Ribes nigrum* L.) were studied under controlled environment conditions. In concurrence with our earlier findings (Heide and Sønsteby, 2011), it was confirmed that flowering increased several-fold when plants were exposed to the near-critical photoperiod of 15 h compared with the presumed optimal photoperiod of 10 h. It is suggested that this unusual response of a SD plant in some way may be associated with the strong dormancy inducing effect of the shorter photoperiod, resulting in termination of the floral initiation process at an early stage. Clearly, a gradual change to shorter photoperiods, as takes place under natural seasonal changes, is optimal for the sustained floral initiation that is required for abundant flowering in the black currant. In agreement with earlier studies with other cultivars, approx. 14 d of SD exposure (10 h) were needed for 100% floral initiation in the cultivars 'Ben Tron' and 'Narve Viking' at temperatures of 15–21 °C, while 21 SDs were required for flowering of cv. Ben Hope at the same temperatures. In this cultivar the induction requirement exceeded 21 SDs at 9 °C. However, in the high latitude cultivar 'Imandra' full flowering was triggered by as little as 7 SDs even at 9 °C. High temperature during SD dormancy induction resulted in a deep dormancy state that was manifest by delayed bud-burst after chilling.

1. Introduction

While flowering in most temperate horticultural tree crops is considered to be controlled by internal developmental cues, so-called autonomous flowering control (Wilkie et al., 2008), flowering in the black currant is induced by external environmental factors such as photoperiod and temperature (Wright, 1985). However, like many other tree crops, black currant plants have a distinct juvenile-like phase and must develop a certain number of leaves (nodes) before they can be induced to flower (Nasr and Wareing, 1961; Tinklin et al., 1970; Schwabe and Al-Doori, 1973). Tinklin et al. (1970) found that plants with less than 16 leaves did not initiate flower buds in response to short day (SD) conditions, and that the responsiveness to SD increased with further increase in plant size up to 20 leaves. Thus, it is clear that both internal developmental cues and external signals are involved in the control of flowering in this plant.

The main external factors controlling floral initiation in black currant are photoperiod and temperature (Wright, 1985). Short day induction of flowering was first reported by Nasr and Wareing (1958, 1961) and confirmed by Tinklin et al. (1970) and lately by Sønsteby and Heide (2011) and Heide and Sønsteby (2011) in a range of cultivars. While the early investigations by Tinklin et al. (1970) indicated an enhancement of the SD induction process by low temperature (17/12 °C vs. 27/22 °C day/night), recent investigations under well controlled temperature conditions showed that SD floral initiation was highly significantly enhanced by increasing temperature over the 9–24 °C range (Sønsteby and Heide, 2011). Because growth and production of new leaves are promoted by high temperature under long day (LD) conditions (Sønsteby and Heide, 2011), flowering is also indirectly promoted by high temperature during the growing season by advancement of the transition from the juvenile-like condition (Sønsteby et al., 2012).

Floral initiation in black currant is associated with growth cessation and dormancy induction which are likewise induced by SD and enhanced by high temperature (Sønsteby and Heide, 2011). Under both natural conditions in the field (Nasr and Wareing, 1961; Tinklin et al., 1970) and in controlled environment (Sønsteby et al., 2012), floral initiation follows immediately after growth has started to slow down. Apparently, the two developmental events are sequential responses to the same external signals (Sønsteby et al., 2012). Exposure to 16 SD of 8 h was sufficient to induce flowering in cv. Baldwin under out-door conditions, while 8 SD were insufficient (Nasr and Wareing, 1961). In cv. Wellington XXX,

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Tinklin et al. (1970) found that 14 SD of 12 or 14 h were sufficient to induce marginal flowering at a day/night temperature of 17/12 °C, while 28 SD were required at 27/22 °C. Under all conditions flowering increased quantitatively when SD exposure was extended for up to 10 w.

The critical photoperiod for SD induction of flowering is approx. 16 h in most cultivars (Tinklin et al., 1970; Heide and Sønsteby, 2011), while that for growth cessation is approx. 1 h longer (Heide and Sønsteby, 2011; Sønsteby et al., 2012). However, although flower initiation in a range of cultivars only took place at photoperiods shorter than a critical length, not all plants flowered after exposure to a 10-h photoperiod, and the number of flowers per plant increased several-fold as the photoperiod was increased from 10 h to the near-critical photoperiod of 15 h (Heide and Sønsteby, 2011). It was suspected that this puzzling result was due to the fact that the plants had only 15–16 nodes at the start of the experiment, which is marginal for "ripeness-to-flower" in black currant (Tinklin et al., 1970). It was observed that while growth cessation was almost immediate in a 10 h photoperiod, permitting only a few additional leaves to be formed during the experimental period, the slower response to longer photoperiods apparently enabled the plants to reach the critical size at an early stage of the treatment period. Highly significant correlations ($P \leq 0.001$) between flower number and plant size at early stages of the SD period supported this assumption. However, as discussed by Heide and Sønsteby (2011), it cannot be excluded that a gradual change in photoperiod, as occurs under natural late summer conditions, might produce a more lasting, albeit less intensive, flower-inducing signal and thus enhance the quantitative flowering response compared with a sudden change to a shorter photoperiod. Possibly, the early dormancy induction that took place in 10 h photoperiod might have terminated the initiation process at an early stage.

The aim of the present investigation was to study this puzzling response in some greater detail by exposing plants of various sizes to short and near-critical photoperiods. In addition, the critical duration of SD exposure at varying temperatures has been studied in four contrasting black currant cultivars.

2. Materials and methods

2.1. Plant material and cultivation

Single-stemmed plants were propagated from semi-softwood cuttings and raised in a greenhouse at 20 °C in 20 h photoperiod as described by Sønsteby and Heide (2011). When reaching a height of approx. 30 cm, the plants were transplanted into 3 L plastic pots in which they remained for the entire experiments. A coarse-textured sphagnum peat medium with pH 5.8 and fertilized with Osmocote controlled-release fertilizer as described by Sønsteby and Heide (2011) was used throughout. After production of a certain number of nodes, as indicated for each experiment, the plants were moved into the Ås phytotron and exposed to different temperature and day-length conditions as specified for each experiment. During the daytime (08.00–18.00 h) the plants were grown in natural daylight compartments, while at night they were moved into adjacent growth rooms with darkness or low intensity light from 70 W incandescent lamps (10 μmol quanta m^{-2} s^{-1}) for photoperiodic manipulation. Whenever the photon flux density in the daylight compartments fell below approx. 150 μmol quanta m^{-2} s^{-1}, an additional 125 μmol quanta m^{-2} s^{-1} was automatically added using Philips HPI-T 400 W lamps. Temperatures were controlled to ±1 °C and a water vapour pressure deficit of 530 Pa was maintained at all temperatures.

Three experiments were performed. In Experiment I, 'Ben Tron' plants of four different sizes (10, 15, 20 or 25 leaves) were exposed to photoperiods of 10 or 15 h at 18 °C for 8 w. In addition, control plants with 25 leaves were exposed to 24-h LD at the same conditions. Propagation of the plants was started in succession in such a way that plants of the various sizes were all available when the experiment was started on 15 February. In Experiment II, 'Ben Tron' plants with 25 leaves were exposed to 10 h photoperiod for 7, 14 or 21 d at temperatures of 12 and 18 °C, followed by 7 LD (20 h) at the same temperatures. This experiment was started on 1 March. In Experiment III, which started on 26 April, plants of the cultivars 'Ben Hope', 'Narve Viking' and 'Imandra' with 20–25 leaves were exposed to 10 h photoperiod for 7, 14 or 21 d at temperatures of 9, 15 and 21 °C, followed by 7 LD at the same temperatures. In all experiments, the plants were moved directly into a cold store after completion of the treatments and chilled at 2 °C in darkness for breaking of dormancy. After 10–12 w of chilling, the plants were forced in a heated greenhouse with minimum 15 °C and 20-h LD for recording of bud-burst and flowering performance.

2.2. Experimental design, data observation and analysis

The experiments were fully factorial, with a split-plot design, and replicated in three blocks, each containing three plants of each cultivar in each treatment. During the experimental period in the phytotron, plant growth was monitored by weekly measurements of plant heights and counting of leaf (node) numbers of each plant. During the subsequent forcing period, the time of the earliest bud-burst and anthesis were recorded in each plant by second-daily observations. Furthermore, the number and position of flowering nodes and the total number of flowers in each plant were also recorded at the end of the flowering period.

Experimental data were subjected to analysis of variance (ANOVA) by standard procedures using a MiniTab® Statistical Software program package (Release 15; Minitab Inc., State College, PA, USA). Percentage values were always subjected to an arc sin transformation before ANOVA.

3. Results

3.1. Interactions of plant size and photoperiod (Experiment I)

The results in Fig. 1 demonstrate that plants of all sizes had an earlier growth cessation in 10 h than in 15 h photoperiod, resulting in smaller final plant size in the shorter photoperiod. In 10 h photoperiod, all plants with 25 and 20 leaves came to a complete growth cessation after 2 w, while in plants with 15 and 10 leaves; this was delayed to week 3. In 15 h photoperiod, however, complete growth cessation did not take place until week 3 even in the largest plants with 25 leaves, the process being gradually delayed by one additional week in plants of successively smaller size, to week 6 in the smallest plants with 10 leaves. The same trends were seen on the accumulation of new leaves, the effects of both plant size and photoperiod and their interaction all being highly significant ($P \leq 0.001$) on both these parameters (Table 1). As a result, the small plants with 10 leaves, added only 22 cm to their height and accumulated 6 new leaves during 8 w in the 10 h photoperiod, compared with 60 cm and 14 leaves in the 15 h photoperiod. For comparison, the control plants (with 25 leaves) in 24-h photoperiod grew continuously, adding 80 cm and 25 leaves to their size during the 8-w experimental period (Fig. 1).

After chilling for 10 w, rapid bud-burst took place after transfer to 15 °C and LD (Table 1). In plants of all sizes, bud-burst was earlier in plants from the 10 h photoperiod and, at this photoperiod, bud-burst was successively delayed by approx. 2 d in plants of the increasing size groups, while in 15 h photoperiod the effect of plant size was less clear. However, the main effects of both plant

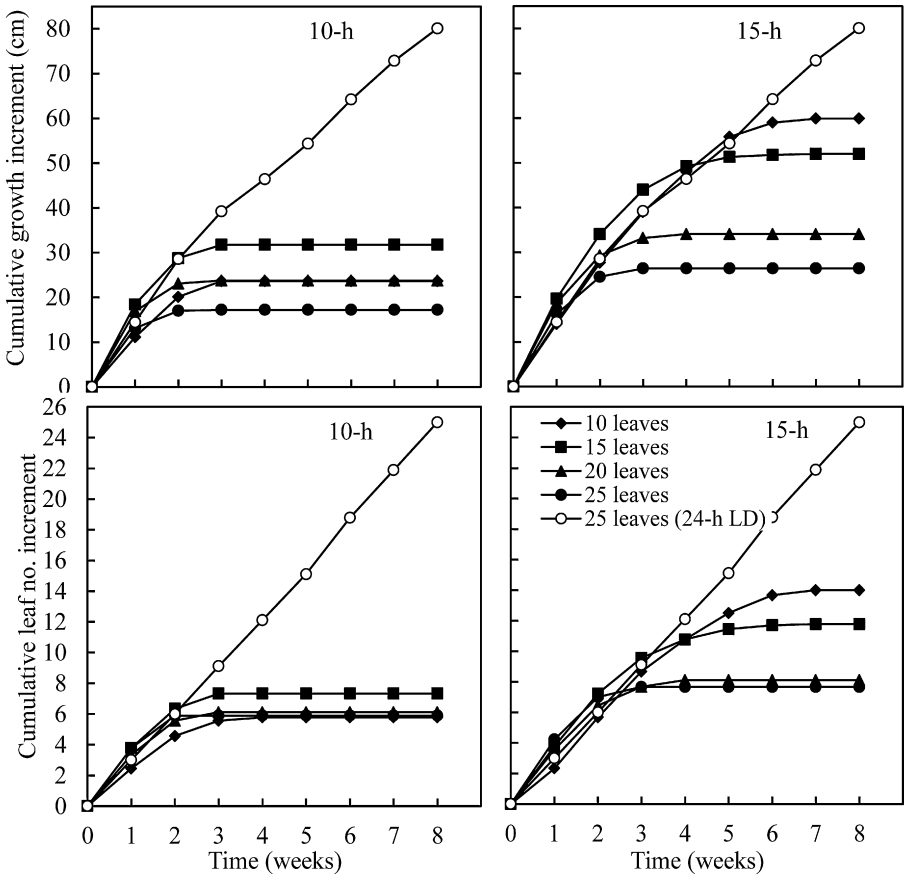

Fig. 1. Time courses of height growth and accumulation of new leaves in 'Ben Tron' black currant plants of varying sizes during exposure to 10, 15 or 24 h photoperiods at 18 °C. Data points are the means of weekly measurements of 9 plants from three replications.

size and photoperiod and their interaction were all highly significant ($P \leq 0.002$) in the ANOVA. On the other hand, the time to the first anthesis was not significantly affected by plant size, although with a significant advancement effect of 10 h photoperiod (Table 1).

The flowering response of plants of varying sizes varied highly significantly with the photoperiodic conditions during floral initiation (Figs. 2 and 3). After exposure to 10-h photoperiod, only 33 and 89% of the plants with 10 or 15 leaves, respectively, were able to flower, while all plants of all sizes flowered after exposure to 15 h photoperiod. The number of flowers per plant was also several-fold higher in the 15-h than in the 10-h treatment, the number of flowers increasing nearly linearly with increasing plant size in both photoperiods (Fig. 2). The proportion of flowering nodes, although increasing significantly ($P = 0.008$) with increasing plant size, was also significantly ($P = 0.01$) higher in plants exposed to 15 h photoperiod (Fig. 3). Also, the mean number of flowers per inflorescence was significantly higher in the 15-h plants and tended to decrease with increasing plant size in both photoperiods (Table 1). However, due to a highly significant interaction ($P = 0.007$) of photoperiod and plants size, the main effect of photoperiod was not

Table 1
Growth and flowering responses of 'Ben Tron' black currant plants of varying sizes after exposure to 10 h or 15 h photoperiods for 8 w at 18 °C.

Photo-period (h)	Plant size (no. of leaves)	Final no. of leaves	Leaf no. increment	Days to bud burst	Days to first anthesis	Flowers per inflorescence
10	10	14.9 d[a]	5.8 c	4.0 f	20.0 a	10.3 a
	15	22.1 c	7.0 c	6.2 e	21.3 a	12.5 a
	20	25.2 bc	6.1 c	6.4 de	20.4 a	10.5 a
	25	31.3 a	5.9 c	7.2 cd	21.1 a	8.7 a
	Mean	23.4	6.2	6.0	20.8	10.5
15	10	23.2 c	14.0 a	7.8 bc	22.8 a	17.1 a
	15	26.9 b	11.8 b	8.4 ab	22.8 a	13.0 a
	20	26.7 b	8.1 c	8.9 a	22.3 a	13.9 a
	25	32.7 a	7.7 c	7.9 bc	22.8 a	13.4 a
	Mean	27.4	10.4	8.3	22.7	14.2
Probability level of significance (ANOVA)						
Source of variation						
Photoperiod (A)		0.003	0.02	0.002	0.03	n.s.
Plant size (B)		<0.001	<0.001	<0.001	n.s.	n.s.
A × B		<0.001	<0.001	<0.001	n.s.	0.007

The data are means of three replicates, each comprising three plants.
n.s., not significant.
[a] Mean values within each column followed by a different lower-case letter are significantly different at $P \leq 0.05$ for variable plant size.

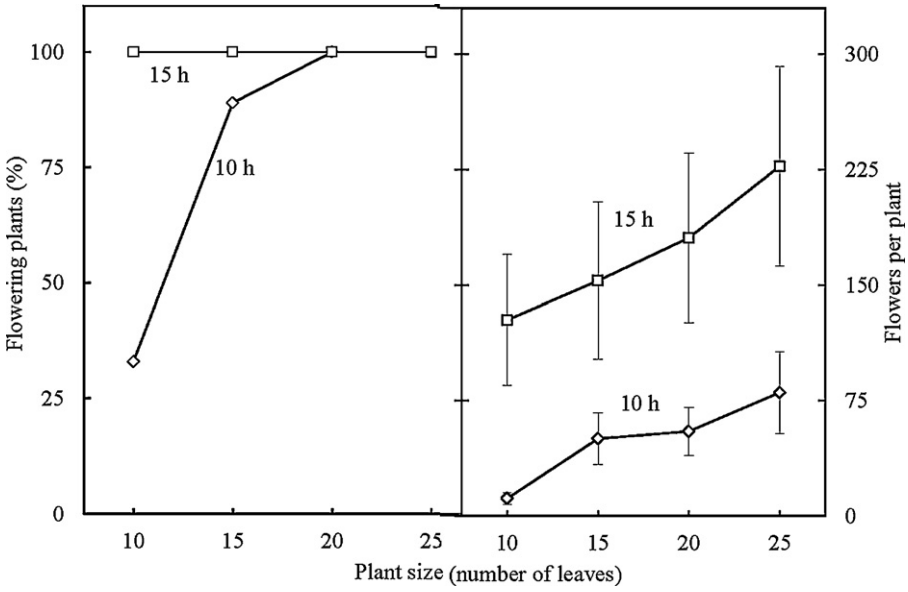

Fig. 2. Flowering responses of 'Ben Tron' black currant plants of varying sizes after exposure to photoperiods of 10 h and 15 h at 18 °C for 8 w. Data are the means of three replicates, each consisting of three plants per treatment.

significant for this parameter. None of the control plants in LD did flower, and these plants were therefore, excluded in all the ANOVA analyses.

3.2. Temperature modification of the critical duration of SD exposure (Experiments II and III)

When 'Ben Tron' plants with 25 leaves were exposed to an increasing number of 10-h SD cycles at 12 and 18 °C, their growth gradually levelled off, and after 3 w of SD it came to a complete stop (Fig. 4). When returned to 24-h LD after 1 w of SD exposure, the plants continued growth at almost the same rate as before, while after 2 w of SD, growth was strongly restrained, and after 3 w of SD, the plants were no longer able to resume growth in LD. Although growth during the first week was faster at 18 °C than at 12 °C, it also started to level off slightly earlier at the higher temperature (Fig. 4). Similar, but less marked effects were observed on leaf number increment (Table 2).

When forced at 15 °C after 12 w of chilling, rapid bud-burst took place in all plants with no significant effects of the previous induction treatments, while the time to the first anthesis decreased significantly with increasing number of SD cycles and increasing temperature (Table 2).

No flowering took place in 'Ben Tron' plants exposed to 7 SD cycles at either temperature condition, while all plants flowered after exposure to 14 SD cycles at 18 °C. At 12 °C on the other hand, 21 SDs were required to bring about flowering in all plants, while only 44% flowered after 14 d of SD exposure (Fig. 5A). Also, the number of flowers per plant (Fig. 5B) and the percentage of flowering nodes (Fig. 5C) increased highly significantly with increasing exposure to SD at both temperatures, the increase being much larger at 18 °C than at 12 °C, resulting in a highly significant ($P = 0.002$)

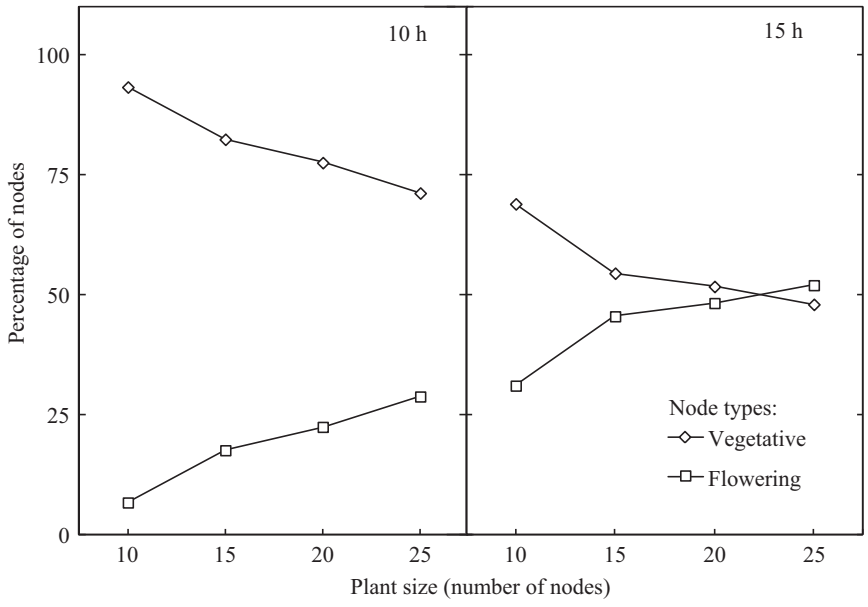

Fig. 3. Effects of exposure to 10 h and 15 h photoperiods for 8 w at 18 °C on the proportion of flowering and vegetative nodes in 'Ben Tron' black currant plants of varying sizes. Values are the means ± SE of three replicates, each consisting of three plants per treatment.

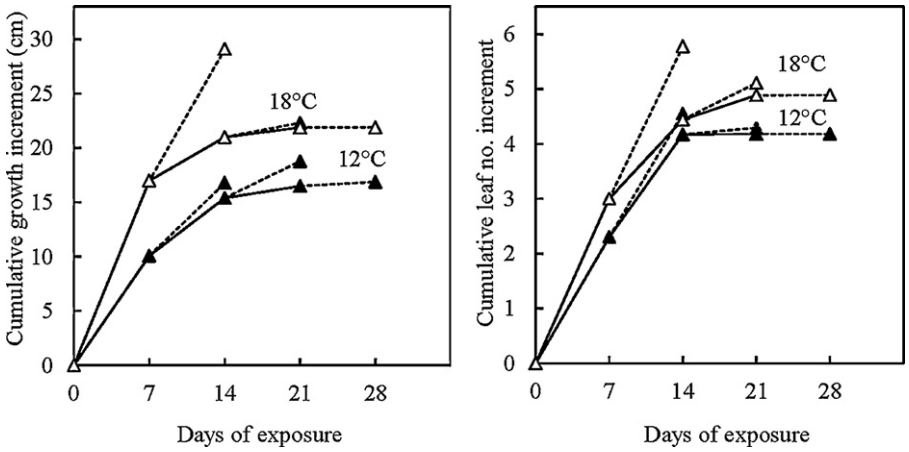

Fig. 4. Time courses of height growth and accumulation of new leaves in 'Ben Tron' black currant plants as influenced by an increasing number of 10-h SD cycles at 12 and 18 °C. The stippled lines denote growth in LD (20 h) at the same temperatures during the first week after termination of SD. Data are the means of three replicates, each consisting of three plants per treatment.

interaction of SD and temperature. Likewise, the number of flowers per inflorescence (Table 2) also increased highly significantly with increasing SD exposure ($P < 0.001$), the effect being significantly enhanced at the higher temperature (main effect of temperature and the interaction both significant at $P = 0.03$).

Similar modifications of the SD response were obtained when the cultivars 'Ben Hope', 'Narve Viking' and 'Imandra' were exposed to an increasing number of SD cycles at temperatures of 9, 15 and 21 °C (Experiment III). As in the previous experiment, the initial growth rate increased with increasing temperature in all cultivars, while the SD induced decline and cessation of growth were advanced and strengthened by increasing temperature (Fig. 6). When the plants were returned to LD after 7 d of SD exposure at 9 °C, growth continued at nearly the initial rate, whereas after 14 and 21 d of SD exposure, continuation of growth was increasingly inhibited. This effect was accentuated with increasing temperature, and it was most marked in 'Imandra' which exhibited a particularly early growth cessation even at low temperature. Very similar responses were observed on the accumulation of new leaves which was also highly significantly affected by cultivar, temperature and duration of SD exposure (data not shown). Details of the additional growth during the terminal week in LD are shown in Table 3.

When the plants were moved into a heated greenhouse after 10 w of cold storage, bud burst was earliest in plants from the lowest temperature and shortest exposure time, both effects being highly significant (Table 4). There were also highly significant differences in earliness of budburst among the cultivars, 'Imandra' being the earliest cultivar. Also, while bud-burst was consistently delayed by a few days with increasing time of SD exposure at all temperatures in 'Narve Viking', the effect varied in the other cultivars. This resulted in significant two-factor interaction of short-day exposure × cultivar on this parameter (Table 4). Time to the first anthesis also generally decreased with increasing temperature and extended SD exposure, although the responses varied among the cultivars because of the many non-flowering plants of 'Ben Hope' and 'Narve Viking'. As a result, the ANOVA revealed significant two- and three-factor interactions of temperature, SD exposure time and cultivar on earliness of flowering (Table 4).

No flowering took place in the 'Ben Hope' plants exposed to SD at 9 °C, even with 21 d of SD exposure, nor did any plants of this cultivar flower after 7 or 14 SDs at 15 °C, or after 7 SDs at 21 °C (Table 4). 'Narve Viking', which was slightly more sensitive to SD exposure, needed 21 SDs for floral initiation at 9 °C, or 14 or more SDs at 15 and 21 °C. In 'Imandra', however, all plants flowered under all inductive conditions, even after 7 d of SD exposure at 9 °C (Table 4). The magnitude of flowering expressed as flowers per plant or the percentage of flowering nodes also increased in a similar way with increasing temperature and extension of SD exposure. Also on these parameters the different sensitivity of the cultivars to SD exposure was clearly expressed, 'Imandra' being the most sensitive, and 'Ben Hope' the least SD sensitive cultivar. A puzzling response on these flowering variables was, however, observed in 'Imandra' at 9 °C,

Table 2
Growth and flowering responses of 'Ben Tron' black currant plants to varying number of 10-h SD cycles at 12 °C and 18 °C.

Temperature (°C)	Number of SD cycles (10 h)	Final no. of nodes	Leaf no. increment	Days to bud burst	Days to first anthesis	Flowers per inflorescence
12	7	30.2 a[a]	4.6 ab	6.2 a	>60 a	–
	14	30.7 a	4.2 b	5.8 a	48.9 b	9.6 ab
	21	31.2 a	4.4 b	5.2 a	21.7 d	6.9 b
	Mean	30.7	4.4	5.7	43.5	7.8
18	7	30.7 a	5.8 a	5.9 a	>60 a	–
	14	30.0 a	5.1 ab	6.4 a	23.7 c	14.6 a
	21	29.4 a	4.9 ab	6.8 a	22.1 d	13.7 a
	Mean	29.9	5.3	6.4	39.4	14.2
Probability level of significance (ANOVA)						
Source of variation						
Temperature (A)		n.s.	0.02	n.s.	0.03	0.03
No. of SD cycles (B)		n.s.	0.05	n.s.	<0.001	<0.001
A × B		n.s.	n.s.	n.s.	<0.001	0.03

The data are means of three replicates, each comprising three plants of each cultivar.
n.s., not significant.
[a] Mean values within each column followed by a different lower-case letter are significantly different at $P \leq 0.05$ for variable number of SD cycles.

Table 3
Effects of temperature during SD and number of SD cycles (10 h) on the amount of additional growth during a subsequent final week in LD at the same temperatures.

Cultivar	Temperature (°C)	Number of SD cycles	Height growth increment (cm)	Node number increment
'Ben Hope'	9	7	9.0	1.4
		14	6.0	1.0
		21	2.7	0.4
		Mean	5.9	1.0
	15	7	9.9	1.9
		14	3.8	0.4
		21	0.4	0.7
		Mean	4.7	1.0
	21	7	9.6	2.1
		14	1.4	1.3
		21	0.0	0.0
		Mean	3.7	1.1
'Narve Viking'	9	7	7.8	2.1
		14	4.7	1.0
		21	2.7	0.3
		Mean	5.0	1.1
	15	7	9.4	2.4
		14	2.2	0.6
		21	0.2	0.4
		Mean	4.0	1.1
	21	7	6.9	2.3
		14	1.7	1.0
		21	0.0	0.1
		Mean	2.9	1.1
'Imandra'	9	7	8.2	2.0
		14	3.6	0.6
		21	0.0	0.0
		Mean	3.9	0.9
	15	7	6.6	1.3
		14	0.3	0.3
		21	0.0	0.1
		Mean	2.3	0.6
	21	7	3.2	1.4
		14	0.2	0.6
		21	0.0	0.3
		Mean	1.1	0.8
Probability levels of significance (ANOVA)				
Source of variation				
Temperature (A)			<0.001	n.s.
Number of SD cycles (B)			<0.001	<0.001
Cultivar (C)			<0.001	<0.001
A × B			<0.001	0.01
A × C			n.s.	n.s.
B × C			0.002	0.03
A × B × C			<0.001	0.01

The data are means of three replicates, each comprising three plants of each cultivar.
n.s., not significant.

where flowering successively decreased with increasing duration of SD exposure (Table 4). The number of flowers per inflorescence also increased with increasing temperature and extension of SD exposure in all cultivars, although in this respect, with a different ranking among the cultivars. Thus, with saturated flowering at the optimal floral induction conditions, 'Ben Hope' had the largest inflorescences and 'Imandra' the smallest ones (Table 4), indicating genetic differences. As shown in Table 4, the main effects of the experimental variables and their interactions were all highly significant on these flowering parameters.

4. Discussion

The results of Experiment I confirm the finding by Heide and Sønsteby (2011) that the flowering response of the SD plant black currant increased several-fold when photoperiod was increased from the presumed optimum of 10 h to the near-critical photoperiod of 15 h. In view of the flowering response of SD plants in general, which is characterized by increased flowering intensity in photoperiods shorter than the critical length and usually, with an optimum in the 8–10 h range (Thomas and Vince-Prue, 1997), this is a puzzling and highly unexpected result. The effect was particularly marked in small plants with only 10 or 15 leaves, which had not reached the stage of "ripeness-to-flower" (Tinklin et al., 1970) at start of the experiment, but it was also highly significant even in mature plants with 25 leaves (Figs. 2 and 3). The larger effect in the small plants can be explained by the differential growth effects of the two photoperiods in plants of varying size. In 15 h photoperiod, the smallest plants were able to continue growth for several weeks and added 14 new leaves during the treatment period, while in 10 h photoperiod, where growth cessation was nearly instantaneous, only 6 new leaves were added, bringing the final leaf number up to 15 only (Table 1). In the larger plants on the other hand, the differential growth effect of the two photoperiods was much less, so that nearly the same number of additional leaves were formed in the two photoperiods. Thus, due to the delayed growth cessation of the small plants in 15-h photoperiod, even the smallest plants reached the critical size before the induction treatments were

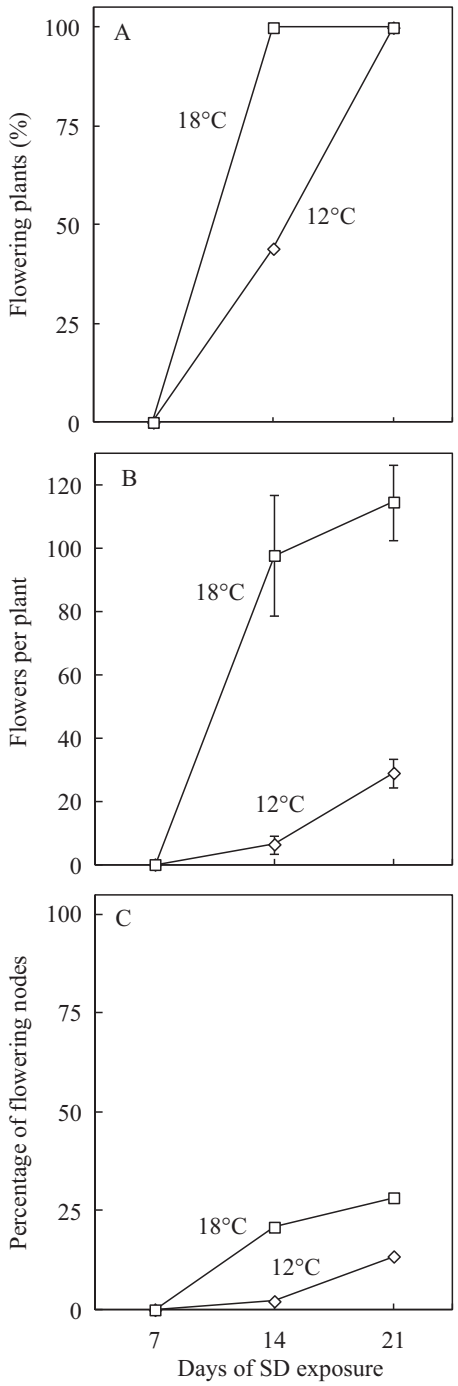

Fig. 5. Flowering responses of 'Ben Tron' black currant plants to an increasing number of 10-h SD cycles at 12 and 18 °C. Data are the means of three replicates, each consisting of three plants per treatment.

terminated, and this explains why some marginal flowering took place in some of these plants, although the time under inductive conditions obviously became sub-optimal for a saturated flowering response. This concurs with the results and interpretations of Heide and Sønsteby (2011). However, the stronger flowering response to 15 h compared with 10 h photoperiod also in the larger plants with 25 leaves; clearly demonstrate an additional and apparently, direct effect of the longer and near-critical photoperiod of 15 h. As discussed by Heide and Sønsteby (2011), it is possible that the sudden growth cessation occurring upon transfer from 20-h to 10-h photoperiods (Fig. 1), also might terminate the floral initiation process at an early stage. This suspicion was strengthened by the responses of 'Imandra' to an increasing number of SDs at 9 °C, as shown in Table 3. In this cultivar and the similar cultivar 'Murmanschanka' originating from the same region, the combination of SD and low temperature has a very strong dormancy inducing effect that in fact suppresses floral initiation (Sønsteby et al., 2012). It is also evident from the present and earlier experiments (Sønsteby and Heide, 2011; Heide and Sønsteby, 2011; Sønsteby et al., 2012), that a gradual change to shorter photoperiods, as occurs under natural autumn conditions, is optimal for the sustained floral initiation that is required for abundant flowering in the black currant. The results of Experiment I also confirm our previous finding (Sønsteby et al., 2012) that SD induction of growth cessation can take place even in small plants with only 10 leaves, despite that those small plants are unresponsive to SD induction of flowering.

While the flowering responses expressed as percent flowering plants, percent flowering nodes, and number of flowers per plant all increased highly significantly with increasing photoperiod and plant size at start of treatment (Figs. 2 and 3), number of flowers per inflorescence showed the opposite trend (Table 1). This effect of photoperiod concurs with our previous findings (Heide and Sønsteby, 2011) in which inflorescence size of 'Ben Tron' and two other cultivars consistently increased with increasing photoperiod from 10 h to 15 h, whereupon it decreased again at still longer photoperiods. Such results may be explained by source limitations in plants with many inflorescences, and they support the suggestion of a slower but yet, more long-lasting and sustained floral initiation response under near-critical photoperiodic conditions.

A critical number of 14 SD cycles for floral initiation as found in Experiment II for 'Ben Tron' also compares well with requirements of 16 SDs as previously reported for the cultivars 'Baldwin' (Nasr and Wareing, 1961) and 14 SDs for 'Wellington XXX' (Tinklin et al., 1970), with 8 SDs and 7 SDs, respectively, being insufficient. However, in the slower responding cultivar 'Ben Hope', a minimum of 21 SDs were required for 100% flowering even at optimal temperatures of 15 and 21 °C (cf. Sønsteby and Heide, 2011; Sønsteby et al., 2012). On the other hand, the Russian cultivar 'Imandra' with origin in the Kola Peninsula produced 100% flowering with as little as 7 SDs even at the marginal temperature of 9 °C (Table 4). Like the cultivar' Murmanschanka' originating from the same high latitude region (Sønsteby et al., 2012), it was very sensitive to SD for induction of flowering as well as growth cessation. As discussed by Sønsteby et al. (2012), these high-latitude cultivars seem to be genetically distinct from most West European cultivars which vary little in their environmental responses (Sønsteby and Heide, 2011) and seem to represent a common gene pool. Beside the cultivar differences, the sensitivity to SD for floral initiation (and growth cessation) also varied markedly with the prevailing temperature. The general conclusion from the present and earlier experiments (Tinklin et al., 1970; Sønsteby and Heide, 2011; Sønsteby et al., 2012) is that the sensitivity to SD increases with increasing temperature from 9 °C to an optimum at 18–21 °C, while it decreases again at still higher temperatures. This decline was especially marked in 'Narve Viking' (Table 4) which has been shown to have a relatively low temperature optimum for SD induction of flowering (Sønsteby and Heide, 2011).

The present results also confirm the finding by Måge (1976), Sønsteby and Heide (2011), and Sønsteby et al. (2012) that warm temperatures during the period of SD induction result in a deep state of dormancy in black currant buds that is manifest in prolonged rest and delayed bud-burst after chilling (Table 4). This is a phenomenon that has been demonstrated in a range of temperate trees and shrubs (Heide, 2003) and appears to be ubiquitous in such plants. The mechanism may have important adaptive implications under a scenario of climatic warming, as it may counterbalance the tendency to premature bud burst in mild winters and hence, reduce the risk of late frost damage. The enhanced dormancy effect of high

Table 4
Effects of temperature during SD and number of SD cycles (10 h) on timing of bud burst and flowering performance in three black currant cultivars.

Cultivar	Temperature (°C)	Number of SD cycles	Days to bud burst	Days to anthesis	Flowering plants (%)	Flowers per plant	Flowering nodes (%)	Flowers per inflorescence
'Ben Hope'	9	7	2.9	>90	0	0	0	–
		14	4.2	>90	0	0	0	–
		21	6.2	>90	0	0	0	–
		Mean	4.4	>90	0	0	0	–
	15	7	3.6	>90	0	0	0	–
		14	6.2	>90	0	0	0	–
		21	6.6	39.3	100	91.1	24.7	14.2
		Mean	5.4	73.1	33	30.4	8.2	14.2
	21	7	5.8	>90	0	0	0	–
		14	6.8	33.8	44	2.7	2.5	4.0
		21	7.9	35.8	100	167.3	36.0	17.2
		Mean	6.8	53.2	48	56.7	12.8	14.8
'Narve Viking'	9	7	2.0	>90	0	0	0	–
		14	5.0	>90	0	0	0	–
		21	6.7	25.1	100	57.0	26.4	7.8
		Mean	4.6	68.4	33	19.0	8.8	7.8
	15	7	4.0	>90	0	0	0	–
		14	6.4	32.2	100	71.3	23.3	11.7
		21	6.6	25.8	100	88.6	29.5	10.6
		Mean	5.7	49.3	67	53.3	17.6	11.1
	21	7	5.8	>90	0	0	0	–
		14	6.9	26.1	100	70.2	24.0	9.9
		21	8.3	22.4	100	153.7	38.4	13.7
		Mean	7.0	46.2	67	74.6	20.8	11.8
'Imandra'	9	7	2.2	20.1	100	74.3	29.8	8.1
		14	2.4	21.7	100	63.0	24.7	8.2
		21	3.7	23.1	100	32.3	13.5	8.2
		Mean	2.8	21.6	100	56.6	22.7	8.2
	15	7	5.3	19.0	100	140.8	52.3	8.9
		14	4.2	19.9	100	145.6	53.1	8.9
		21	4.3	18.6	100	155.8	56.6	9.1
		Mean	4.6	19.1	100	147.4	54.0	9.0
	21	7	5.7	20.4	100	205.4	58.6	11.9
		14	6.0	18.7	100	234.2	63.6	11.7
		21	6.3	18.0	100	215.7	60.8	12.1
		Mean	6.0	19.0	100	218.4	61.0	11.9
Probability levels of significance (ANOVA)								
Source of variation								
Temperature (A)			<0.001	0.002	<0.001	<0.001	0.001	–
Cultivar (B)			<0.001	<0.001	<0.001	<0.001	<0.001	–
Days of SD exposure (C)			<0.001	<0.001	<0.001	<0.001	<0.001	–
A × B			0.001	<0.001	<0.001	<0.001	<0.001	–
A × C			n.s.	<0.001	<0.001	<0.001	<0.001	–
B × C			<0.001	<0.001	<0.001	<0.001	<0.001	–
A × B × C			n.s.	<0.001	<0.001	<0.001	<0.001	–

The data are means of three replicates, each comprising three plants of each cultivar.
n.s., not significant.

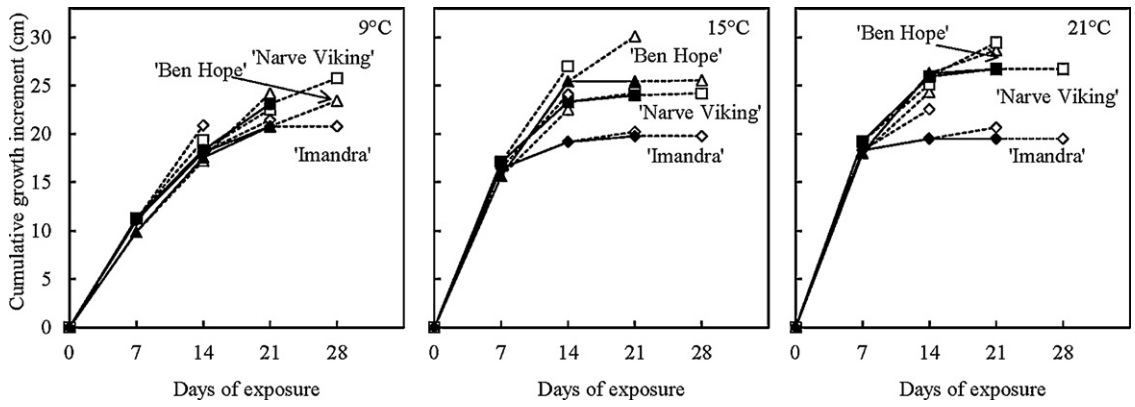

Fig. 6. Time courses of height growth of three black currant cultivars as influenced by an increasing number of 10-h SD cycles at temperatures of 9, 15 or 21 °C as indicated. The stippled lines denote growth in LD (20 h) at the same temperatures during the first week after termination of SD. Data are means of three replicates, each consisting of three plants per treatment.

temperature was further strengthened by prolonged SD exposure (Table 4). Also, as judged by the earliness of bud-burst, mature plants with 20–25 leaves, which responded rapidly to SD exposure, entered a deeper state of dormancy than the slow-responding smaller plants (Table 1). This may in part explain the commonly experienced vulnerability of small plants to winter damage. In conclusion, the reported effects of plant size, photoperiod, and temperature on growth and flowering in black currant concur with earlier findings (Tinklin et al., 1970), and explain the large latitudinal variation in flowering time of this species under natural environmental conditions.

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References

Heide, O.M., 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climate warming. Tree Physiol. 23, 931–936.

Heide, O.M., Sønsteby, A., 2011. Critical photoperiod for short-day induction of flowering in black currant (*Ribes nigrum* L.). J. Hort. Sci. Biotechnol. 86, 128–134.

Måge, F., 1976. Bud dormancy and root formation in cuttings of currants. Meld. Nor. Landbrukshøgsk. 55 (26), 10 pp.

Nasr, T.A.A., Wareing, P.F., 1958. Photoperiodic induction of flowering in black currant. Nature 182, 269.

Nasr, T.A.A., Wareing, P.F., 1961. Studies on flower initiation in black currant II. Photoperiodic induction of flowering. J. Hort. Sci. Biotechnol. 36, 11–17.

Schwabe, W.W., Al-Doori, A.H., 1973. Analysis of a juvenile-like condition affecting flower initiation in the black currant (*Ribes nigrum*). J. Exp. Bot. 24, 969–981.

Sønsteby, A., Heide, O.M., 2011. Elevated autumn temperature promotes growth cessation and flower formation in black currant cultivars (*Ribes nigrum* L.). J. Hort. Sci. Biotechnol. 86, 120–127.

Sønsteby, A., Opstad, N., Heide, O.M., 2012. Effects of summer temperature on growth and flowering in black currant cultivars (*Ribes nigrum* L.). J. Hort. Sci. Biotechnol. 87, 157–164.

Thomas, B., Vince-Prue, D., 1997. Photoperiodism in Plants, 2nd ed. Academic Press, London, UK, 428 pp.

Tinklin, I.G., Wilkinson, E.H., Schwabe, W.W., 1970. Factors affecting flower initiation in the black currant *Ribes nigrum* (L.). J. Hort. Sci. 45, 275–282.

Wilkie, J.D., Sedgley, M., Olesen, T., 2008. Regulation of floral initiation in horticultural trees. J. Exp. Bot. 59, 3215–3228.

Wright, C.J., 1985. Ribes. In: Halevy, A.H. (Ed.), Handbook of Flowering, vol. IV. CRC Press, Boca Raton, FL, pp. 198–201.