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Critical photoperiod for short-day induction of flowering in black currant (*Ribes nigrum* L.)

By O. M. HEIDE[1] and A. SØNSTEBY[2]*
[1]Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P. O. Box 5003, NO-1432 Ås, Norway
[2]Arable Crops Division, Norwegian Institute for Agricultural and Environmental Research, NO-2849 Kapp, Norway
(e-mail: anita.sonsteby@bioforsk.no) *(Accepted 9 December 2010)*

SUMMARY
Actively growing, single-stemmed plants of three black currant cultivars, each with 15 – 16 nodes, were exposed to photoperiods of 10, 14, 15, 16, 17, 18, 20, and 24 h at 18°C for 8 weeks for determination of the critical photoperiods for growth cessation and floral initiation. In all three cultivars, growth cessation was induced by short day (SD) conditions, with a critical photoperiod of 16 h, and the response was advanced by decreasing the photoperiod. The critical photoperiod for 50% flowering was 16 h in the cultivars 'Öjebyn' and 'Ben Tron', and 17 h in 'Kristin'. Unexpectedly, however, 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 15 h in all cultivars. Apparently, this unexpected result was due to the fact that all plants had only 15 – 16 nodes at the start of the experiments, which is marginal for "ripeness to flower" in black currant. While growth cessation was almost immediate in a 10 h photoperiod, causing only a few additional leaves to be formed during the experiment, the slower response to longer photoperiods apparently enabled the plants to reach the critical size at an earlier stage of the treatment period. However, although plants with 15 – 16 nodes were only marginally responsive to SD induction, buds situated as far down the shoot as the fifth or sixth node were competent to flower. It is therefore suggested that the inability of small black currant plants to flower resides in limitations of the leaves to respond to SD and to produce a florigenic signal, while their buds are fully competent to respond to such a signal.

Black currant (*Ribes nigrum* L.) is a woody plant that is widely grown as a soft fruit crop in cold and temperate regions. It is reported to be a short-day (SD) plant that requires short photoperiods for the initiation of flower buds (Nasr and Wareing, 1958; 1961a, b; Tinklin *et al*., 1970). Under field conditions, floral primordia are initiated in late Summer, immediately after shoot extension growth has slowed down (Nasr and Wareing, 1961a; Tinklin *et al*., 1970). Sønsteby and Heide (2011) concluded that, under controlled environment conditions, growth cessation and floral initiation coincided as parallel responses to the SD signal.

Tinklin *et al*. (1970) subjected plants of the cultivar 'Wellington XXX' to photoperiods of 12, 14, or 16 h, combined with night/day temperatures of 12°/17°C and 22°/27°C, and found that, while photoperiod was of overriding importance, temperature was an important modifying factor. High temperatures delayed floral initiation in all day-lengths tested and, at a 14 h photoperiod where the temperature effect was greatest, a 10°C increase in temperature delayed floral initiation by 2 – 6 weeks. However, in a recent paper, Sønsteby and Heide (2011) reported that both growth cessation and flower formation were significantly promoted and advanced by increasing temperature, with an optimum in the 18° – 24°C range. Only in one cultivar out of five, was flowering reduced at 24°C compared with 18°C. This agrees with the results of Thomas and Wilkinson (1962) who reported that, under field conditions, 'Wellington XXX' initiated flowers > 3 weeks later in a cool and wet Summer than in the subsequent hot and dry Summer.

Nevertheless, the flowering behaviour of black currant cannot be explained entirely as responses to photoperiod and temperature alone. Thomas (1959) noted that rooted shoots with only eight nodes failed to initiate flowers, even after 11 months of exposure to 8 h SD. He therefore concluded that the black currant shoot must attain a stage of "ripeness to flower" before it can flower, and that this mechanism overrides the inductive effect of SD. This was later confirmed by Tinklin *et al*. (1970), who grew plants to varying sizes in a 18 h photoperiod, then exposed them to 8 h SD for 6 weeks. Dissections of the lateral buds revealed that only plants with 16 or more nodes had initiated flowers. Robinson and Wareing (1969) studied this juvenility phase-change in black currant plants raised from seed. Their results indicated that both the age and the size of the plant may be involved, but the underlying mechanisms are not understood.

The combined effects of shoot size, photoperiod, and temperature result in a large divergence of dates at which floral initiation takes place under field conditions at different latitudes. A review of such data by Tinklin *et al*. (1970) showed that the normal time of initiation varied from late-May to early-June in Italy, to mid-September in Finland at the Arctic Circle. In the south-

*Author for correspondence.

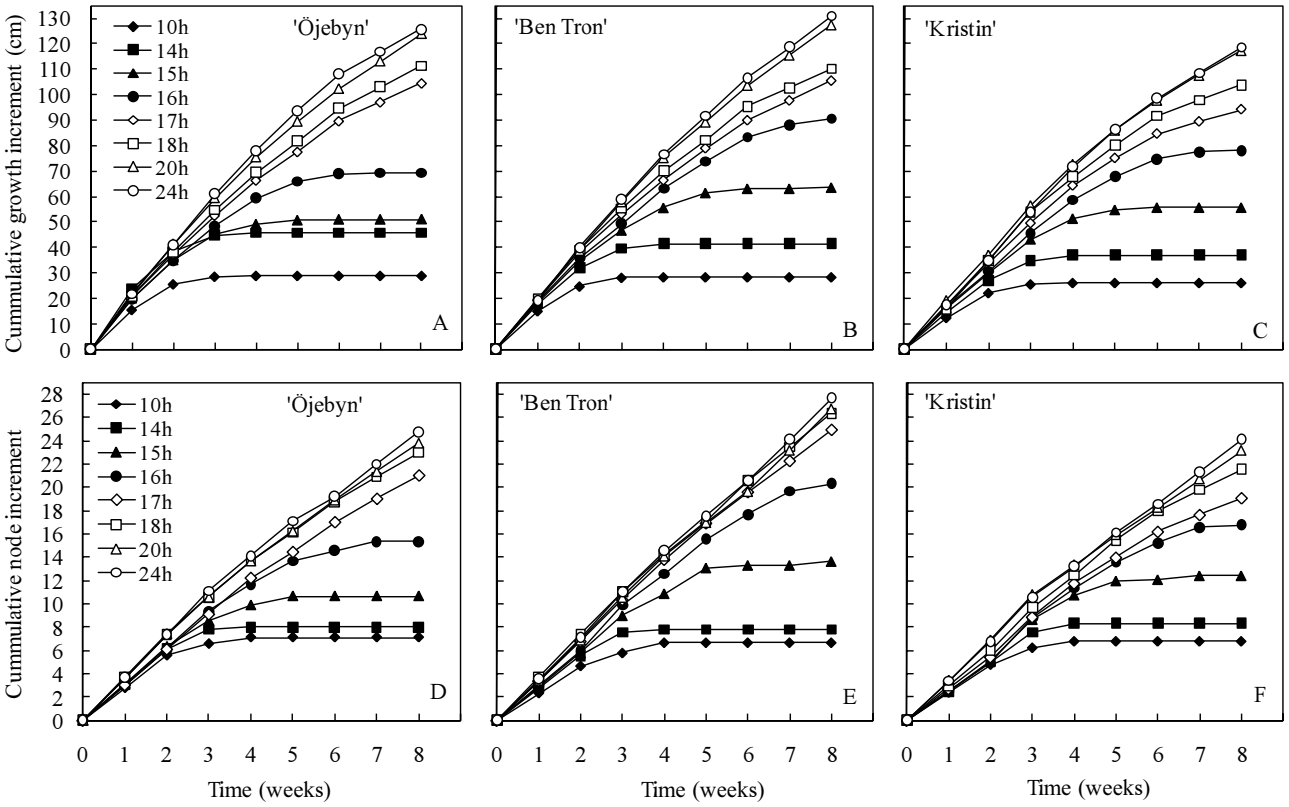

FIG. 1
Time-courses of cumulative shoot elongation (cm; Panels A – C) and the addition of new nodes (Panels D – F) in the black currant cultivars 'Öjebyn' (Panels A, D), 'Ben Tron' (Panels C, E), and 'Kristin' (Panels C, F) as affected by eight different photoperiods, as indicated, all at a temperature of 18°C. Each value is the mean of three replicates, each consisting of three plants of each cultivar. (n = 9).

east of England, floral initiation takes place in late-June/early-July when the natural day-length is at or near its maximum of 16.0 – 16.7 h (Tinklin *et al*., 1970). A critical day-length of approx. 16 h was also demonstrated for 'Wellington XXX' under controlled environment conditions (Tinklin *et al*., 1970). However, at this day-length, at least 10 weeks of exposure was required for floral initiation, while in 12 h and 14 h photoperiods flowers were initiated after 4 weeks of exposure. In contrast, 16 d of 8 h were sufficient for floral initiation in 'Baldwin', while 8 d were insufficient (Nasr and Wareing, 1961b).

In order to determine the critical day-length of modern black currant cultivars, we exposed three such cultivars with a northern pedigree to photoperiods ranging from 10 h to 24 h for 8 weeks, at a constant temperature of 18°C. The results are reported below.

MATERIALS AND METHODS

Plant material and cultivation

Single-stemmed plants of the black currant (*Ribes nigrum* L.) cultivars 'Ben Tron', 'Kristin', and 'Öjebyn' were propagated from semi-softwood cuttings as described by Sønsteby and Heide (2011), and raised in a greenhouse at 20°C with a 24 h photoperiod [natural winter daylight, supplemented with artificial light of approx. 150 µmol quanta m^{-2} s^{-1} from high pressure sodium (Philips Son-T 400 W) lamps]. When the plants had produced 15 – 16 leaves (nodes) and reached a mean height of 55 cm, they were moved into the Ås phytotron and exposed to eight different photoperiods ranging from 10 h to 24 h for 8 weeks. The experiment started on 23 February 2010. During the day-time (08.00 – 18.00 h) the plants were grown in a daylight compartment, while at night they were moved into a series of growth rooms for day-length extensions ranging from 0 h to 14 h with low intensity light provided by 70 W incandescent lamps at a photon flux density of 10 µmole quanta m^{-2} s^{-1}. Whenever the photon flux density in the daylight compartment 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. A temperature of 18° ± 1°C, which has been shown to be optimal for floral induction in these cultivars (Sønsteby and Heide, 2011), and a water vapour pressure deficit of 530 Pa were maintained throughout the experimental period.

After 8 weeks of treatment, all plants were stored in the dark at 2°C for 16 weeks, to break dormancy. On 1 August 2010, they were moved into a greenhouse with a minimum temperature of 20°C and natural long-day (LD) conditions to monitor bud break and flowering performance.

Experimental design, data observation, and analyses

The experiment was fully factorial, with a split-plot design, and replicated in three randomised blocks, each consisting of three plants of each cultivar at each day-length. During the 8 week photoperiodic treatment, plant growth was monitored by weekly measurements of plant heights and leaf (node) numbers. In the second (flowering) phase, the dates of bud burst and first anthesis were recorded for each plant by observation on every second day. Bud burst was defined as the stage

TABLE I

Final and incremental growth in shoot height and node number in three black currant cultivars after exposure to different photoperiods for 8 weeks at 18°C

Cultivar	Photoperiod (h)	Final shoot height (cm)	Growth increment (cm)‡	Final no. of nodes	Node increment‡
'Öjebyn'	10	82.6†	28.9	22.4	7.1
	14	93.6	45.8	22.8	8.0
	15	105.8	51.0	26.1	10.7
	16	125.0	69.3	30.6	15.3
	17	146.4	104.7	33.7	21.0
	18	156.8	111.2	35.6	23.0
	20	168.0	123.9	36.4	23.8
	24	173.4	125.7	37.4	24.8
	Mean	131.4 b*	82.6 b	30.6 c	16.7 b
'Ben Tron'	10	87.8	28.4	23.1	6.7
	14	99.9	41.4	23.9	7.8
	15	119.2	63.8	29.6	13.7
	16	147.9	90.7	36.2	20.3
	17	155.9	105.6	38.8	24.9
	18	160.1	110.1	39.6	26.3
	20	170.9	127.4	38.3	26.8
	24	174.2	131.0	39.8	27.7
	Mean	139.5 a	87.3 a	33.7 a	19.3 a
'Kristin'	10	80.7	26.1	23.1	6.8
	14	90.2	37.0	24.7	8.3
	15	108.3	55.7	28.2	12.4
	16	130.3	78.1	32.7	16.8
	17	141.8	94.1	34.2	19.1
	18	150.3	103.9	35.9	21.6
	20	160.0	117.4	35.8	23.1
	24	159.4	118.6	36.6	24.1
	Mean	132.9 c	78.9 c	31.9 b	16.5 b
Probability level of significance (ANOVA)					
Source of variation					
Photoperiod (A)		< 0.001	< 0.001	< 0.001	< 0.001
Cultivar (B)		< 0.001	< 0.001	< 0.001	< 0.001
A × B		0.004	0.001	< 0.001	< 0.001

†All data are the means of three replicates, each containing three plants of each cultivar.
‡Increments during the 8 week experimental period.
*Mean values within each column followed by a different lower-case letter are significantly different ($P \leq 0.05$).

when green foliage first appeared at the tip of the swelling bud. The number and position of the flowering nodes, together with the number of inflorescences and the total number of flowers, were also recorded for each plant at the end of the flowering period. All experimental data were subjected to analysis of variance (ANOVA) by standard procedures using a MiniTab® Statistical Software programme package (Release 15; Minitab Inc., State College, PA, USA). Percentage values were always subjected to arc sin transformation before ANOVA.

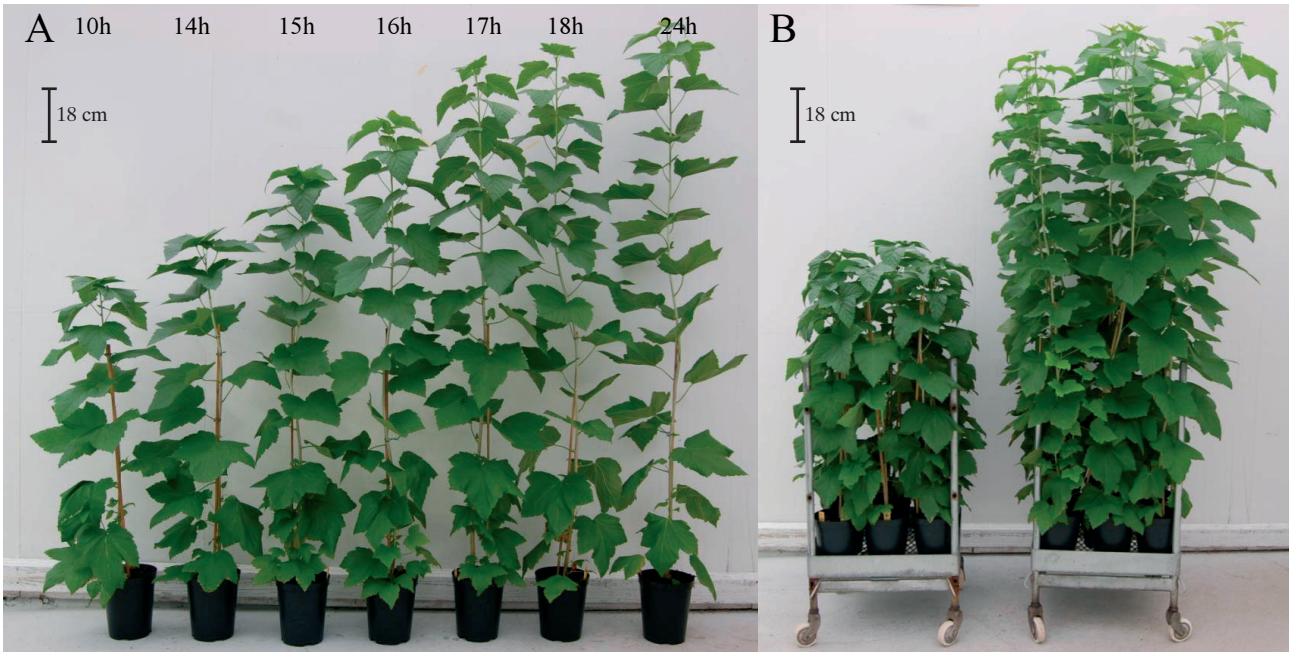

FIG. 2

Appearance of black currant plants after 6 weeks of exposure to different photoperiods, at 18°C. Panel A shows 'Ben Tron' plants exposed to seven different photoperiods as indicated. Panel B shows three plants of all three cultivars (i. e., one replicate) exposed to a 10 h (left) or a 24 h photoperiod (right), respectively. Scale bars = 18 cm.

TABLE II

Effect of photoperiod during floral initiation on the number of days to budburst and anthesis, and on the magnitude and distribution of flowering in three black currant cultivars

Cultivar	Photoperiod (h)	Days to bud burst	Days to anthesis	Flowering plants (%)	Flowers per plant	Flowers per inflorescence	Node with first flower‡	Nodes subtending first flower
'Öjebyn'	10	8.8†	28.0	77.8	31.1	8.8	17.0	9.6
	14	10.6	24.8	100.0	125.7	13.7	15.9	7.2
	15	11.0	24.3	100.0	146.6	14.8	18.6	10.4
	16	12.3	26.2	100.0	127.1	14.5	19.6	12.6
	17	12.3	36.0	22.2	11.4	10.4	16.0	12.7
	18	12.8	> 100	0.0	–	–	–	> 20
	20	12.0	> 100	0.0	–	–	–	> 20
	24	12.6	> 100	0.0	–	–	–	> 20
	Mean	11.5 a*	26.3 b	50.0 ab	55.2 c	12.9 b	17.7 b	14.7 a
'Ben Tron'	10	8.0	23.8	66.7	50.8	12.1	19.3	12.0
	14	9.1	25.0	100.0	208.2	17.9	16.6	6.1
	15	10.8	27.0	100.0	231.1	20.5	20.1	7.4
	16	11.7	33.9	100.0	195.3	18.9	23.9	9.9
	17	11.7	38.5	22.2	28.2	13.9	12.5	7.5
	18	11.0	> 100	0.0	–	–	–	> 20
	20	11.2	> 100	0.0	–	–	–	> 20
	24	11.2	> 100	0.0	–	–	–	> 20
	Mean	10.6 b	28.4 a	48.6 b	87.2 b	17.4 a	19.5 a	13.6 a
'Kristin'	10	7.3	23.8	88.9	79.7	11.9	18.2	6.0
	14	9.3	23.7	100.0	252.2	15.6	17.2	4.9
	15	9.1	23.8	100.0	331.4	19.1	19.6	5.6
	16	10.1	25.1	100.0	217.2	18.0	20.6	9.8
	17	11.4	34.1	77.8	98.4	14.7	14.0	6.7
	18	11.8	35.0	33.3	11.7	9.4	11.0	6.3
	20	11.4	> 100	0.0	–	–	–	> 20
	24	10.0	> 100	0.0	–	–	–	> 20
	Mean	10.8 b	26.4 b	53.7 a	123.8 a	15.6 a	17.6 b	11.0 b
Probability level of significance (ANOVA)								
Source of variation								
Photoperiod (A)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
Cultivar (B)	< 0.001	0.01	0.03	< 0.001	< 0.001	0.004	< 0.001	
A × B	ns	< 0.001	ns	< 0.001	0.002	0.02	0.008	

†All data are the means of three replicates, each containing three plants of each cultivar.
‡Counted from the base of the shoot. ns, not significant.
*Mean values within each column followed by a different lower-case letter are significantly different ($P \leq 0.05$).

RESULTS

The effects of photoperiod on shoot growth and the formation of new leaves (or nodes) are shown in Figure 1. In all cultivars, growth cessation was induced by short photoperiods with a critical photoperiod of approx. 16 h. The shorter the photoperiod, the more rapid was the cessation of growth. In a 10 h photoperiod, growth slowed down after only 1 week and, after 3 weeks of this treatment, it ceased completely; while, in a 16 h photoperiod, this happened after 5 – 7 weeks, depending on the cultivar. Leaf number increments continued for a further 1 week, due to the unfolding of already-initiated leaves. Incremental and final plant heights and node numbers are shown in Table I. The appearance of the plants after 6 weeks at the various treatments is shown in Figure 2. ANOVA revealed highly significant main effects ($P < 0.001$) of photoperiod and cultivar, as well as their interaction, on both shoot elongation and the increase in the number of nodes (Table I). Cultivar and interaction effects were mainly due to the more vigorous growth of 'Ben Tron' compared to the other two cultivars, and the delayed response of the former cultivar at intermediate day-lengths.

After chilling for 16 weeks, rapid bud burst took place when the plants were transferred to high temperature and LD conditions (Table II). In all cultivars, bud burst was earliest in plants from the 10 h photoperiod and was consistently delayed by a few days by increasing the photoperiod up to 16 h, then being more or less constant at longer photoperiods. Generally, the first anthesis was also delayed with increasing photoperiod during the floral induction period, but with some difference in the trend between cultivars. In 'Ben Tron', anthesis was successively delayed with increasing photoperiod during induction. In 'Kristin', only photoperiods longer than 15 h delayed anthesis; while in 'Öjebyn', earliness of flowering was optimal in the 14 h and 15 h treatments. In plants with normal flowering, anthesis first took place in plants induced with a 14 h photoperiod, and at the 16th and 17th nodes from the base.

While all plants flowered after exposure to a 14, 15, or 16 h photoperiod, only 67% ('Ben Tron') to 89% ('Kristin') of plants flowered in the 10 h treatment. The number of flowers per plant also increased several-fold in all cultivars as the photoperiod was increased from 10 h to 15 h, then decreased again at longer photoperiods. In parallel with this, the number of flowers per inflorescence also nearly doubled (Table II). Also, the percentage of flowering nodes was highest at a 14 h photoperiod, decreasing at both shorter and longer photoperiods, while the percentage of vegetative nodes varied in an inverse manner (Figure 3). In 'Öjebyn', some nodes at the base of the shoot had dormant buds that did not sprout, while this was not the case in the other two cultivars (data not shown). The proportion of such dormant buds was lowest at the 10 h and 14 h photoperiods, and highest in plants induced at a 15 h photoperiod. In all cultivars, the lowermost flowering node (node-5 to node-7 from the base) always occurred in plants induced in a 14 h photoperiod (Table II).

There were also highly significant differences in the abundance of flowering among cultivars, with 'Kristin' and 'Ben Tron' being superior to 'Öjebyn' in most

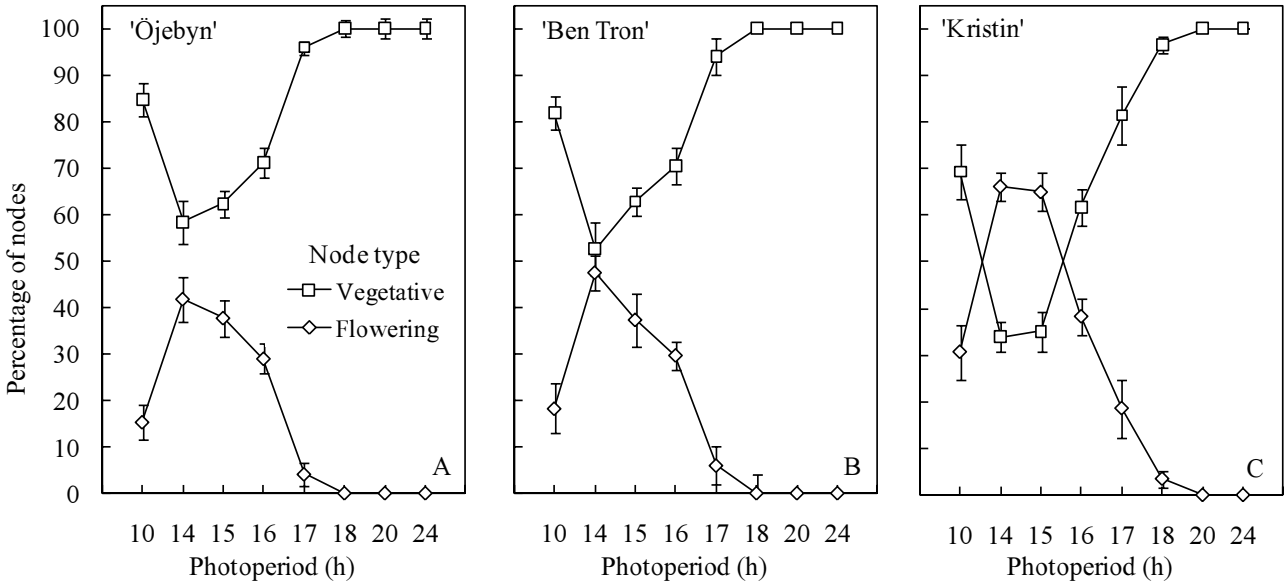

FIG. 3
Effects of photoperiod on the proportions of flowering and vegetative nodes in plants of three black currant cultivars. Values are the means ± SE of three replicates, each consisting of three plants of each cultivar.

quantitative flowering parameters. The critical photoperiod for > 50% flowering was 16 h in 'Öjebyn' and in 'Ben Tron', and 17 h in 'Kristin' (Table II). In the latter cultivar, however, most of the inflorescences initiated in a 17 h photoperiod were abnormal, with leaves interspaced between the florets (Figure 4). Such phyllody was also observed in the other two cultivars under marginal photoperiods for floral initiation.

FIG. 4
Typical phyllody of an inflorescence of the black currant cultivar, 'Kristin' induced to flowering in a 17 h photoperiod for 8 weeks at 18°C. Scale bar = 1.0 cm.

DISCUSSION

An unexpected result of this investigation was that SD induction of flowering did not increase with decreasing photoperiod. On the contrary, it increased with increasing photoperiods up to 15 h (Table II; Figure 3). This was unexpected as photoperiods of 8 h were highly effective in earlier investigations with other black currant cultivars (Nasr and Wareing, 1961b; Tinklin *et al.*, 1970). The latter authors also found that a 12 h photoperiod was more effective than 14 h or 16 h photoperiods. It is also a definition of SD plants, in general, that they flower earlier and more profusely with decreasing day-length (Thomas and Vince-Prue, 1997). The flowering result was even more surprising, as growth cessation was enhanced by decreasing photoperiod, and was optimal in a 10 h photoperiod (Figure 1; Figure 2). This differential effect suggests that, although the environmental signal for the induction of flowering and growth cessation is the same, the mediation of the response differed between the two processes.

However, this unexpected result was probably related to the juvenility of the black currant plants. Thus, Tinklin *et al.* (1970) found that plants with less than 16 nodes did not initiate flowers in respond to SD, and that the flowering response increased with increasing node number, up to at least 20 nodes. The present experiment was started with plants having 15 – 16 nodes, which is the critical size for "ripeness to flower" in black currant. Although growth ceased rapidly in the shortest photoperiods (Figure 1), a further seven nodes were added during the inductive experimental period in a 10 h photoperiod, bringing the mean final leaf number up to approx. 22 (Table II). However, at intermediate photoperiods, growth cessation was slower and hence the plants grew to a larger size during the treatment period. We suggest that this was the main reason for the unusual flowering response to a decreasing photoperiod in the present experiments. This is supported by significant correlations between plant size at the start and early stages of the photoperiodic treatments,

Table III
Pearson correlation coefficients for the total number of flowers vs. *shoot heights and node numbers at weeks 0, 1, and 2 of the photoperiodic treatments*[#]

Parameter	Flowers per plant
Shoot-height (week 0)	0.230*
Shoot-height (week 1)	0.383***
Shoot-height (week 2)	0.540***
No. of nodes (week 0)	0.240**
No. of nodes (week 1)	0.344***
No. of nodes (week 2)	0.405***

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.
[#]Data are for all cultivars exposed to a 10, 14, 15, or 16 h photoperiod (n = 108).

and the resulting number of flowers per plant, as shown in Table III. In addition, it is possible that intermediate photoperiods approaching the critical value might also have directly affected the quantitative parameters of flowering by causing a slower response and more long-lasting period of floral initiation and differentiation. Thus, inflorescence-size increased with increasing photoperiod, up to 15 h, producing remarkably large trusses with up to 20 flowers in a 15 h photoperiod in the cultivars 'Kristin' and 'Ben Tron'. The total number of flowers per plant was determined both by the number of flowering nodes and the number of flowers per inflorescence (Table II). Hence, the greater number of nodes on larger plants in the intermediate photoperiods also apparently contributed to the abundant flowering of these plants. However, it cannot be excluded that a gradual change of photoperiod, as occurs under natural Autumn conditions, is optimal for floral initiation in black currant, and that a sudden change from a 24 h to a 10 h photoperiod may somehow produce a shock effect that reduces flowering. This should be investigated in further experiments with fully-mature plants.

Juvenility in plants is a complex issue, the physiological basis of which is not well understood. In some herbaceous plants, it has been shown that the leaves of young plants are unable to, or have a limited ability to respond to inductive photoperiods. Moreover, the capacity to respond increases with plant age or the ontogenetic ranking of the leaves, while the meristems are perfectly able to respond to the flowering stimulus produced by older leaves (Bernier *et al*., 1981; Thomas and Vince-Prue, 1997). A prominent example is the long-short-day plant *Bryophyllum daigremontianum*, a perennial herb with a marked juvenile phase. While young plants of this species with four leaf pairs were unable to flower in response to inductive photoperiodic conditions, their meristems flowered rapidly and profusely when grafted onto flowering mature plants (Zeevaart, 1985). In such plants, it therefore seems that the flowering limitation of young plants resides in the leaves and not in the meristem. The present results suggest that this also applies to black currant. Even though a minimum of 16 or more leaves was required for "ripeness" of the black currant plant to respond to SD floral induction, buds situated at lower nodes were perfectly able to undergo floral initiation and differentiation. In the present experiment, flowering took place in buds situated as far down the shoot as the fifth node from the base in 'Kristin', and the sixth and seventh nodes, respectively, in 'Ben Tron' and 'Öjebyn' (Table II). This finding suggests that, although the leaves of young plants may be unable to respond to SD and produce the florigenic stimulus, the adjacent buds are able to respond to such a stimulus by floral evocation and initiation. This may explain, in part, the complex effects of plant age and size on "ripeness to flower" in black currant reported by Robinson and Wareing (1969).

Schwabe and Al-Doori (1973) demonstrated that the presence of roots produced by air-layering half-way up the stems of plants with more than 30 nodes inhibited flower initiation. They therefore concluded that the juvenile condition was related to the distance of the bud from the root. However, in the present experiment, flowers were formed as far down as the fifth or sixth node from the base, demonstrating that flowering under optimal conditions may occur in close proximity to the root, thus supporting the conclusion that the limitation to flowering does not reside in the buds, but in the leaves. In a recent paper, Sønsteby and Heide (2011) concluded that the position of the lowermost flowering node appeared to be a measure of the strength of floral induction in black currant. This is supported by the results of the present experiment (Table II) in which the lowermost flowering node was obtained in a 14 h or 15 h photoperiod. As in the previous experiment (Sønsteby and Heide, 2011), all buds above the lowermost flowering position, except the terminal bud, were usually floral.

As in earlier studies with 'Wellington XXX' (Tinklin *et al*., 1970), the critical photoperiod for floral initiation and growth cessation in black current was found to be relatively long for a SD plant (Table II; Figure 2). A critical photoperiod of 16 – 17 h agrees well with the timing of these processes under natural light conditions. (*cf*. Tinklin *et al*., 1970; Sønsteby and Heide, 2011). As discussed by Sønsteby and Heide (2011), the three cultivars used here belong to the same gene pool, while the cultivar 'Wellington XXX' used by Tinklin *et al*. (1970) apparently came from a different gene pool (Kronenberg and Hofman, 1965). Despite this, the critical photoperiods were quite similar. The longer critical photoperiod in 'Kristin' may render this cultivar particularly well-adapted to high latitude environments. On the other hand, the high latitude origin of 'Öjebyn' was not associated with a longer critical photoperiod. This supports the anecdotal notion that this cultivar was not native to the high latitude environment in which it was found (Hjalmarsson and Wallace, 2004), but rather that it originated at lower latitudes and was later naturalised to the high latitude environment.

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