

Elevated Autumn temperature promotes growth cessation and flower formation in black currant cultivars (*Ribes nigrum* L.)

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SUMMARY

Actively-growing, single-stemmed plants of five Scandinavian and British cultivars of black currant (*Ribes nigrum* L.) were exposed to autumn temperatures of 9°, 12°, 18°, and 24°C in daylight phytotron compartments with natural daylength conditions at Ås, Norway (59° 40' N) in order to evaluate the effects of elevated autumn temperature on growth cessation and floral initiation in this species. The treatments were started on 11 August and lasted until 13 October (9 weeks) when the plants were moved outdoors for cold-hardening for 7 weeks, then cold-stored at –2°C over the Winter. The following Spring, the plants were moved into a heated greenhouse at 15°C with natural daylength conditions and monitored for bud burst and flowering and fruiting performance. Unexpectedly, the cessation of growth in the Autumn was promoted by increasing temperature, and was earliest at 24°C. The high-latitude cultivar, 'Öjebyn', and the Norwegian-bred 'Kristin' were the most temperature-responsive cultivars, while the Norwegian cultivar, 'Narve Viking' was least influenced by Autumn temperature. Leaf senescence and abscission, which followed in due course, were also promoted by high Autumn temperature in 'Öjebyn', but by low Autumn temperature in all other cultivars. Bud burst in the following Spring was consistently delayed by a few days by high Autumn temperature, while flowering was earliest in plants from intermediate temperatures. Furthermore, the magnitude of flowering was increased several-fold by elevated Autumn temperature, usually reaching an optimum at 18°C. Again, this enhancement effect was least in 'Narve Viking', in which the extent of flowering was also significantly reduced when autumn temperatures increase from 18°C to 24°C. It is concluded that elevated Autumn temperature, as a consequence of global warming, does not represent a threat to the normal cessation of growth or floral initiation in black currant.

Black currant (*Ribes nigrum* L.) is an important soft fruit crop for cold and temperate regions. As first reported by Nasr and Wareing 1958; 1961 (a,b), and later confirmed by Tinklin *et al.* (1970), the initiation of floral primordia requires short-day (SD) conditions in this species. Under field conditions, floral initials are formed in late Summer, immediately after extension growth has slowed down (Nasr and Wareing, 1961a). These then develop to anthesis during the following Spring. Exposure to 16 short days was sufficient to induce flowering in the black currant cultivar 'Baldwin', while eight short days were insufficient (Nasr and Wareing, 1961b). The critical daylength for floral induction was found to be relatively long; for example, approx. 16 h in 'Wellington XXX' black currant (Tinklin *et al.*, 1970). At this daylength, however, at least 10 weeks of exposure was required for floral initiation. It was also found that young shoots with fewer than 12–15 nodes (leaves) did not attain "ripeness to flower" and were thus unable to respond to SD induction (Tinklin *et al.*, 1970).

Since photoperiod is a function of both season and latitude, the time of floral initiation will vary with latitude. Thus, collated data for a range of locations in Europe showed a general correlation between an increase in latitude and lateness of floral initiation (see

Tinklin *et al.*, 1970). The range varied from mid-May to early-June at Bologna, Italy (44° 30'N), to late-June to early-July in southern England (51°N), and from early-August in southern Scandinavia (60°N) to late-September in the Arctic Circle at Rovaniemi, Finland (*cf.* Hårdh and Wallden, 1965; Vestrheim, 1971). Although this trend may be interpreted as a straightforward latitudinal effect of photoperiod, it was interpreted by Tinklin *et al.* (1970) as a latitudinal effect of temperature on shoot growth, and hence, on the attainment of "ripeness to flower". The reasoning was that, at lower latitudes, where growth started earlier and the prevailing daylength conditions never exceeded the critical level required for flowering, floral initiation would take place as soon as the shoot had produced the minimum number of nodes. At higher latitudes, where growth started later and the growing temperature was lower, the critical shoot size was reached progressively later and, therefore, initiation would not take place until late in the season when both the critical number of leaves and the critical daylength were attained.

However, besides its effect on shoot growth, temperature is also an important controlling factor for flowering in many plants, either directly, or by interaction with the photoperiod (Thomas and Vince-Prue, 1997). This has not been studied extensively in black currant. Tinklin *et al.* (1970) subjected 'Wellington

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XXX' plants to photoperiods of 12, 14, and 16 h, combined with night/day temperatures of 12°/17°C and 22°/27°C. The results demonstrated that, while photoperiod was of overriding importance, temperature was an important modifying factor, especially under near-critical photoperiods. Under a 14 h photoperiod, where the effect was greatest, a rise in temperature of 10°C resulted in a delay in the formation of normal flowers of between 2–6 weeks. In contrast, Thomas and Wilkinson (1962) found that, under field conditions, the same cultivar initiated flowers more than 3 weeks later in the cool, wet Summer of 1958 than in the hot, dry Summer of 1959. It was not clear, however, whether this was a direct effect of temperature or a temperature-mediated effect of drought.

Temperature is also of fundamental importance for the regulation of dormancy in plants. In the majority of temperate-zone woody plants, the cessation of growth and bud dormancy are induced by short photoperiods in the Autumn, while release from dormancy requires exposure to low (chilling) temperatures for extended periods (for reviews, see Wareing, 1956; Vegis, 1964). With predicted and ongoing global warming (Sunley *et al.*, 2006), there is increasing concern in some parts of Europe that the performance of some soft fruit species, particularly black currant, may be adversely affected by mild Winters, with insufficient winter-chill, leading to uneven and poor bud development in the following Spring (Rose and Cameron, 2009; Jones and Brennan, 2009). The adverse effect of high temperature on floral initiation in black currant reported by Tinklin *et al.* (1970) also raises concern about the potential adverse effects of elevated Autumn temperatures on floral initiation in this species. This concern is accentuated by increasing interest in the production of black currants for fresh consumption, which would demand abundant flowering and large inflorescences that would facilitate hand-harvesting. Also, previous investigations by Nasr and Wareing (1961a,b) and Tinkling *et al.* (1970) revealed a coincidence between the decline in extension growth in the Autumn and floral initiation. Consistently, floral initiation was preceded by reduced extension growth, while the complete cessation of growth occurred later. However, any causal relationship between these two developmental processes was not clear.

Faced with these uncertainties, and incomplete knowledge on the physiological effects of photoperiod and temperature on growth and flowering in black currant, together with related concerns over the potential impact of global warming on commercial cropping of this species, we initiated a research programme to address some of these questions. Here, we present the results of an experiment in which five modern cultivars of black currant were exposed to a range of temperatures during the shortening days of late-Summer and Autumn, in order to assess the effects of Autumn temperature on the cessation of growth and on the subsequent flowering and cropping performance of the plants.

MATERIALS AND METHODS

Plant material and cultivation

Five commercially-grown Scandinavian and British black currant (*Ribes nigrum* L.) cultivars of relatively

recent origin were used for these experiments. The high-latitude cultivar 'Öjebyn' is of unknown origin as it was found by chance near the township of Öjebyn (65°20'N) in northern Sweden. 'Ben Tron' and 'Ben Hope' originate from the breeding programme at the Scottish Crop Research Institute, Invergowrie, Scotland. 'Kristin' and 'Narve Viking' were from the breeding programme at the Norwegian University of Life Sciences, Ås, Norway.

For these experiments, single-stemmed plants were produced from top cuttings collected in the field after bud burst in May. The basal part included a woody portion of the previous year's growth. The cuttings were rooted in plug trays filled with peat in a water-saturated atmosphere and maintained during the Summer in a greenhouse with a minimum temperature of 20°C and a 20 h photoperiod (natural daylength extended by low-intensity incandescent lights at approx. 10 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). Following rooting in plug trays, and establishment in 0.8 l pots, plants were transplanted into 3 l plastic pots at a plant height of approx. 35 cm. A coarse-textured sphagnum-peat growth medium, with a pH of 5.8 and fertilised with 300 g of Osmocote controlled-release fertiliser 80 l^{-1} (Scotts UK Ltd., Nottingham, UK) containing 14% (w/w) N, 4.2% (w/w) P, 11.6% (w/w) K plus micronutrients with a release rate of 3–4 months was used throughout.

On 11 August, when the plants had an average of 39 nodes and a height of 154 cm, they were moved into daylight compartments of the Ås phytotron and exposed to constant (24 h) temperatures of 9°, 12°, 18°, or 24°C with natural daylength (59°40'N) for 9 weeks. Temperatures in the phytotron were controlled within $\pm 1.0^\circ\text{C}$, and a water vapour pressure deficit of 530 Pa was maintained at all temperatures. Whenever the photosynthetic photon flux density (PPFD) fell below approx. 150 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$, as on cloudy days, an additional 125 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ were added automatically by Philips HPT-I 400 W lamps. On 13 October, the temperature treatments were terminated, and all plants were moved outdoors for 7 weeks for hardening (until 1 December). The plants were then cold-stored at -2°C over the Winter. In the following Spring (on 7 April), the plants were moved into a heated greenhouse maintained at a minimum of 15°C and monitored for their flowering and fruiting performance. During this period, the plants were fed by daily fertigation with the complete fertiliser solution described by Sønsteby *et al.* (2009). Fruit harvests were done at maturity for each cultivar. Total fruit yield and the number of berries were recorded for each plant.

Experimental design, observations, and data analysis

The experiment was fully factorial, with a split-plot design, and replicated in three randomised blocks, each containing three plants of each cultivar at each temperature. During the first year, extension growth was monitored by weekly measurements of plant heights, and the final number of nodes and the extent of leaf shedding were recorded for each plant at the end of the 9-week treatment period. In the second year, the dates of bud burst and anthesis (first open flower) were recorded by observations every second day. The number and positions of the flowering nodes, together with the total

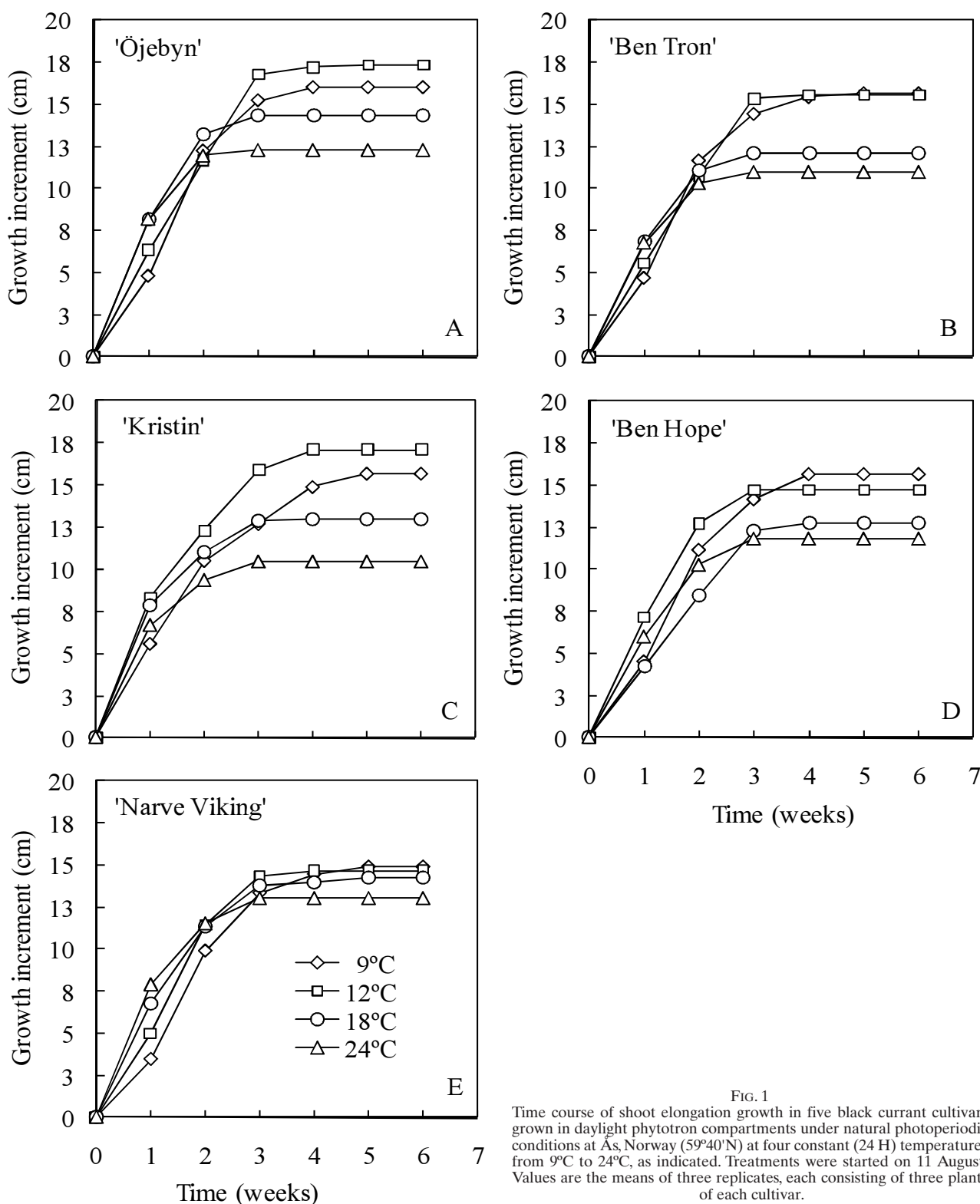


FIG. 1
Time course of shoot elongation growth in five black currant cultivars grown in daylight phytotron compartments under natural photoperiodic conditions at Ås, Norway (59°40'N) at four constant (24 h) temperatures from 9°C to 24°C, as indicated. Treatments were started on 11 August. Values are the means of three replicates, each consisting of three plants of each cultivar.

number of flowers at each node, were also recorded for each plant at the end of the flowering period.

The 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 the performance of ANOVA.

RESULTS

When exposed to a natural photoperiod from 11 August, extension growth began to level-off almost immediately in all cultivars, and usually ceased completely within 2–3 weeks (Figure 1). Unexpectedly, extension growth was promoted and advanced by increasing temperature, but to varying extents in the various cultivars. The temperature effect was most pronounced in



FIG. 2

The effect of Autumn temperature on leaf senescence and abscission in black currant 'Öjebyn' under natural photoperiodic conditions at Ås, Norway (59°40'N). From left-to-right: 24°C, 18°C, 12°C, and 9°C. The photograph was taken 9 weeks after the treatments started on 11 August. Scale bar = 18 cm.

'Kristin', followed by 'Öjebyn' and 'Ben Tron', while 'Narve Viking' was relatively insensitive to temperature. ANOVA of the growth increment data, after 6 weeks of treatment, revealed highly significant main effects of both temperature and cultivar ($P = 0.004$ and $P < 0.001$, respectively); while the temperature \times cultivar interaction was significant at $P = 0.02$. The cessation of growth was followed by leaf senescence and abscission, which started at the base and spread acropetally along the shoot axis (Figure 2). The process was earliest in the high-latitude 'Öjebyn' and, while abscission was promoted by increasing temperature in this cultivar, the reverse response was found in all other cultivars (Table I). Thus, after 9 weeks of treatment, the percentage of abscised leaves was highly significantly affected by both temperature and cultivar, as well as by their interaction.

In the following Spring, budburst was consistently delayed by a few days in plants exposed to high temperatures during the cessation of growth in the previous Autumn (Table II). Although this effect was not large, it was highly significant in buds at all positions along

TABLE I
Effects of Autumn temperature on the percentage of leaf abscission at the end of various temperature treatments in five black currant cultivars

Cultivar	Temperature (°C)				Mean
	9	12	18	24	
'Öjebyn'	49.2	48.1	64.5	69.4	57.5 a
'Ben Tron'	23.9	18.0	12.8	6.2	15.2 c
'Kristin'	45.7	40.1	19.6	17.6	31.1 b
'Ben Hope'	20.1	18.3	14.7	13.0	16.9 c
'Narve Viking'	22.8	20.0	9.2	6.4	15.0 c
Mean	32.3 a [†]	28.9 ab	24.3 bc	22.5 c	

[†]Mean values within the same column followed by different lower-case letters indicate a significant difference ($P < 0.05$) between treatments ($n = 9$).

Data are the means of three replicates, each with three plants of each cultivar in each temperature treatment.

the shoot axis, and the effect increased with increasing node position upward on the shoot. There was also a highly significant difference in the earliness of bud burst among cultivars, with 'Ben Hope' and 'Narve Viking' being later than the others. Also, time to anthesis was slightly, but significantly, affected by Autumn temperature. The earliest flowering took place in plants exposed to intermediate Autumn temperatures (Table II).

The number and percentage of flowering nodes increased highly significantly with increasing temperature in all cultivars, while the corresponding number and proportion of vegetative nodes decreased (Table III; Figure 3). Cultivars varied highly significantly in the magnitude of their response, the effect being particularly marked in 'Kristin' and 'Öjebyn' while, as with the promotion of growth cessation, 'Narve Viking' was less responsive, rendering the temperature \times cultivar interaction highly significant (Table III). Also, the total number of flowers per plant, and the number of flowers per inflorescence, increased highly significantly ($P < 0.001$) with increasing Autumn temperature, usually with an optimum at 18°C or 24°C (Figure 4). Again, the enhancing effect of temperature was least in 'Narve Viking', the only cultivar in which flowering decreased significantly when the temperature was increased from 18°C to 24°C, resulting in a highly significant ($P < 0.001$) temperature \times cultivar interaction. A small proportion (approx. 1.5 %) of nodes had two inflorescences (data not shown). In all cultivars, a small proportion of the buds did not grow-out in Spring. Most of these buds were dead, apparently due to mechanical injury or, in a few cases, to desiccation during cold storage. Although varying significantly among cultivars, the frequency of occurrence of such non-viable buds was not significantly affected by Autumn temperature (Table III).

Fruit yield was also significantly ($P < 0.001$) affected by both Autumn temperature and cultivar, although the full yield potential, as determined by the magnitude of flowering, was not realised (Table IV). In all cultivars, and at all Autumn temperatures, a significant proportion of flowers aborted at the immature fruit stage. In general, the percentage of aborted fruit was inversely related to the number of flowers, resulting in an optimum trade-off between flowering and fruit abortion at intermediate Autumn temperatures. There was also a marked trend towards reduced berry size in cultivars and under temperature conditions which produced high levels of flowering and large inflorescences with many flowers (Table IV).

TABLE II

Effects of Autumn temperature on the times to bud burst and anthesis in buds at varying shoot positions (Low, Middle, or Top) in five black currant cultivars

Cultivar	Temperature (°C)	Days to bud burst			Days to anthesis	
		Low	Mid	Top	Mid	Top
'Öjebyn'	9	9.9	9.1	11.8	> 50	31.7
	12	8.7	8.8	11.3	> 50	27.3
	18	10.2	11.1	15.0	25.4	29.3
	24	10.6	10.6	14.8	26.4	30.6
Mean	–	9.8 ab [†]	9.9 a	13.2 a	25.9	29.7 ab
'Ben Tron'	9	7.9	8.7	11.4	26.3	28.0
	12	8.4	8.7	11.1	24.7	27.4
	18	10.4	10.8	15.1	25.9	29.4
	24	9.8	10.2	18.3	27.4	31.8
Mean	–	9.1 a	9.6 a	14.0 a	26.0	29.2 a
'Kristin'	9	7.9	8.4	16.8	> 50	32.0
	12	8.3	8.6	17.1	25.3	30.9
	18	8.9	10.5	15.3	24.6	29.6
	24	10.1	10.2	17.1	26.2	31.4
Mean	–	8.8 a	9.4 a	16.6 b	25.4	31.0 bc
'Ben Hope'	9	11.0	12.2	15.6	> 50	33.4
	12	10.7	11.0	16.7	28.7	32.7
	18	11.0	12.4	17.0	28.5	31.3
	24	12.1	13.9	20.0	30.3	34.4
Mean	–	11.2 c	12.3 b	17.2 b	29.0	33.0 d
'Narve Viking'	9	9.9	11.1	16.1	28.0	31.6
	12	9.7	10.4	14.8	26.9	29.7
	18	11.6	10.9	18.0	26.3	31.4
	24	11.3	10.8	19.4	30.0	33.3
Mean	–	10.6 bc	10.8 c	17.0 b	28.2	31.4 c
Probability levels of significance by ANOVA						
Source of variation						
Temperature (A)		0.002	< 0.001	0.001	0.010	0.004
Cultivar (B)		< 0.001	< 0.001	< 0.001	0.010	< 0.001
A × B		n.s.	0.020	0.001	< 0.001	0.020

[†]Mean values within the same column followed by different lower-case letters indicate a significant difference ($P < 0.05$) between treatments ($n = 9$). Data are the means of three replicates, each with three plants of each cultivar in each temperature treatment.

TABLE III

Effects of Autumn temperature on the distribution of flowering along the shoot axis in five black currant cultivars

Cultivar	Temperature (°C)	Total number of nodes	Flowering nodes (%)	Vegetative nodes (%)	Non-growing nodes (%)
'Öjebyn'	9	42.4	18.5	73.1	8.4
	12	42.9	33.9	63.2	2.9
	18	43.8	53.9	43.6	2.5
	24	41.1	52.3	45.3	2.4
Mean	–	42.6 b [†]	39.7 b	56.3 a	4.1 bc
'Ben Tron'	9	46.1	42.3	55.7	2.0
	12	44.6	53.9	45.2	1.0
	18	44.0	62.0	35.3	2.8
	24	44.8	56.8	38.4	4.8
Mean	–	44.9 b	53.7 a	43.6 b	2.6 c
'Kristin'	9	40.8	25.3	61.5	13.2
	12	44.8	43.0	47.1	9.9
	18	43.1	65.0	29.6	5.5
	24	44.2	67.3	29.9	2.9
Mean	–	43.2 b	50.1 a	42.0 b	7.9 a
'Ben Hope'	9	42.4	29.0	64.4	6.7
	12	44.8	35.2	58.1	6.7
	18	42.4	50.3	45.7	4.0
	24	42.0	46.2	42.4	11.4
Mean	–	42.9 b	40.2 b	52.7 a	7.2 ab
'Narve Viking'	9	53.3	45.5	47.9	6.6
	12	52.2	55.1	41.4	3.5
	18	51.8	47.8	49.4	2.7
	24	50.9	55.5	38.2	6.3
Mean	–	52.1 a	50.9 a	44.3 b	4.8 abc
Probability levels of significance by ANOVA					
Source of variation					
Temperature (A)		n.s.	< 0.001	< 0.001	n.s.
Cultivar (B)		< 0.001	< 0.001	< 0.001	0.001
A × B		n.s.	< 0.001	0.020	0.010

[†]Mean values within the same column followed by different lower-case letters indicate a significant difference ($P < 0.05$) between treatments ($n = 9$). Data are the means of three replicates, each with three plants of each cultivar in each temperature treatment.

DISCUSSION

One unexpected result of these experiments was that floral initiation in black currant was highly significantly

promoted and enhanced by increasing temperature under natural daylength conditions in late-Summer and Autumn (Table II; Figure 3; Figure 4). This result is at

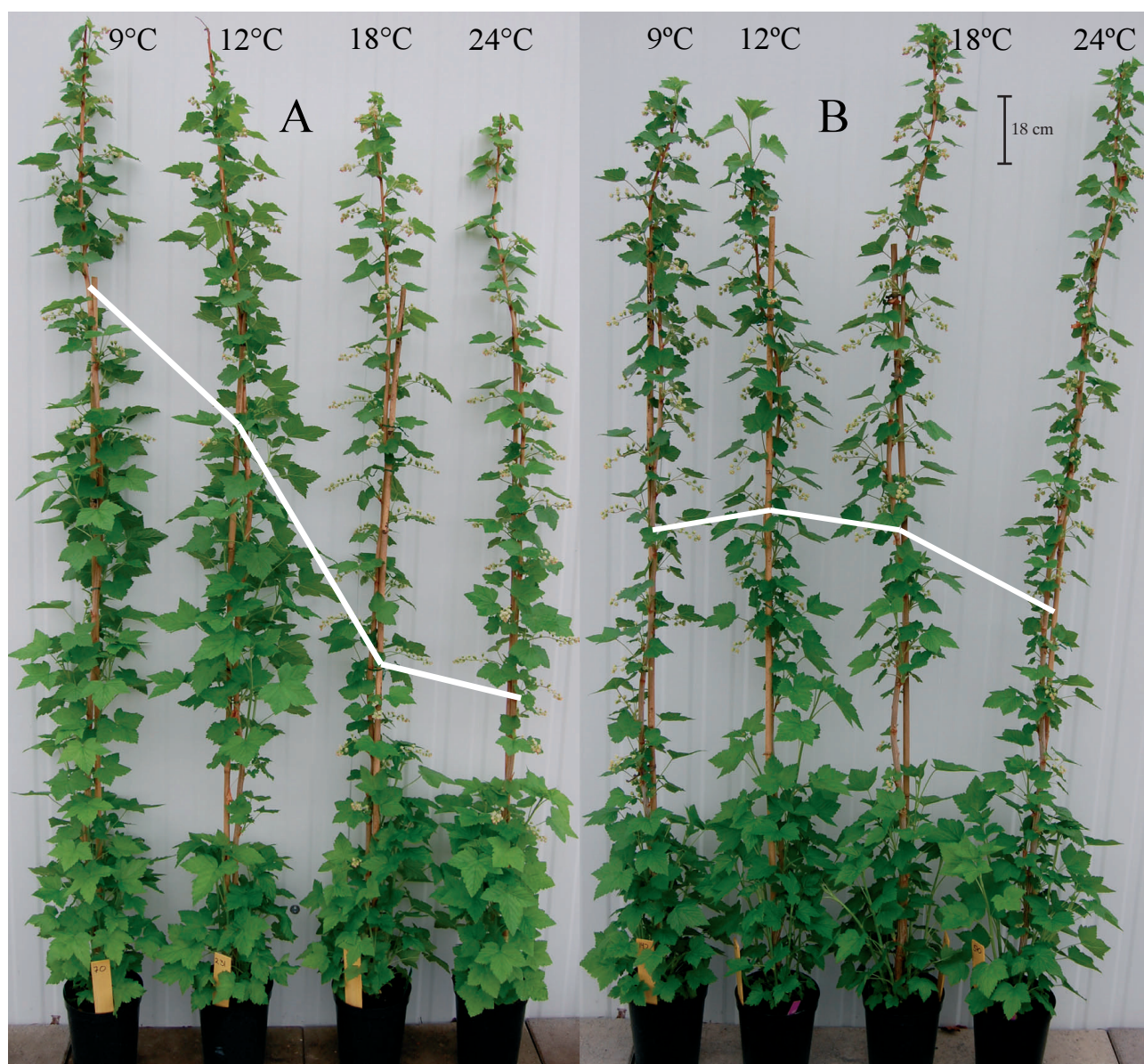


FIG. 3

The appearance of the black currant cultivars 'Kristin' (Panel A) and 'Narve Viking' (Panel B) during flowering in Spring, as affected by exposure to varying temperatures (as indicated) in the previous Autumn. The white lines of demarcation represent the position of the lowermost flowering node at each temperature in each cultivar. Scale bar = 18 cm.

variance with those of Tinklin *et al.* (1970), who found that, under a 14 h photoperiod, a 10°C rise in temperature delayed floral initiation in 'Wellington XXX' by 2–6 weeks. However, it has generally been reported that relatively high temperatures enhance the effect of SD on the induction of flowering in a range SD plants (Lang, 1965; Thomas and Vince-Prue, 1997). For example, similar effects of relatively high temperatures were reported on the SD induction of flowering in strawberry, another SD species (Sønsteby and Heide, 2008b).

The promotional effect of high temperature is not limited to the SD induction of flowering, but is also found in other SD-induced processes in plants, including SD induction of the cessation of growth and dormancy in boreal trees. Thus, an advance in the cessation of growth and prolonged dormancy after high-temperature SD induction have been reported in both conifers (Heide,

1974) and deciduous forest trees (Westergaard and Eriksen, 1997; Heide, 2003). The present results with black currant (Table II) are in full agreement with these findings, and suggest that this is an adaptive mechanism that has evolved in many woody plants that originate at high latitudes. It seems likely that such a mechanism may, to some extent, counter-balance the potential negative effects that milder Autumn conditions could have on the stability of Winter dormancy in such plants (Heide, 2003). Likewise, high temperatures enhanced the SD induction of flowering, resulting in a several-fold increase in flowering when the temperature was increased from 9°C to 18°C (Figure 4). These results also confirm the close connection between the cessation of growth and floral initiation previously reported by Nasr and Wareing (1961a,b) and Tinklin *et al.* (1970). Apparently, these two processes are parallel responses to the same environmental signal, as previously

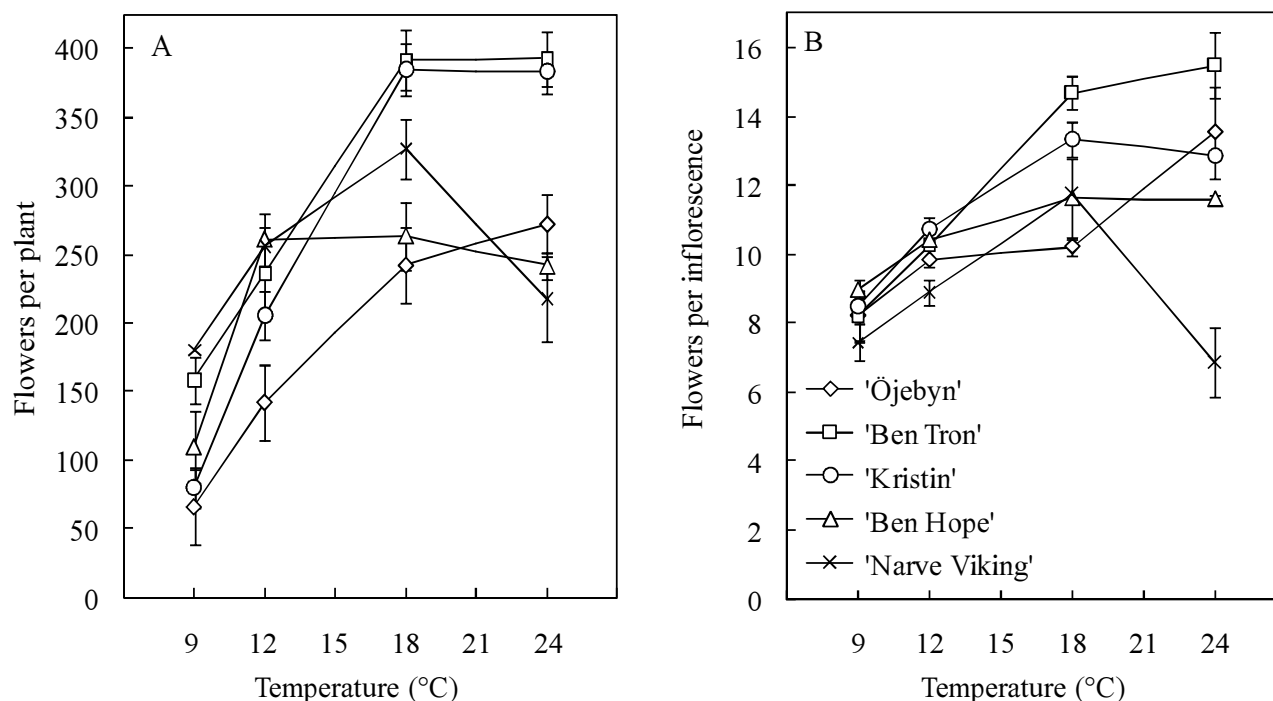


FIG. 4

The effects of Autumn temperature, under natural photoperiodic conditions at Ås, Norway (59°40'N), on the extent of flowering during the following Spring in five cultivars of black currant. Values are the means (\pm SE) of three replicates, each consisting of three plants of each cultivar.

demonstrated for biennial-fruiting red raspberry (Sønsteby and Heide, 2008a).

Variations in the extent of flowering among cultivars and temperature treatments were associated with marked differences in the extent and distribution of flowering nodes along the shoot axis (Figure 4; Table III). Invariably, those buds situated at the base of a shoot

were vegetative. This appears to be a trait that has evolved as a mechanism to ensure the regeneration of vegetative growth from the base. However, the number and the proportion of such basal vegetative buds were inversely related to the magnitude of flowering, and hence, to Autumn temperature. Although the response was less marked in 'Narve Viking' than in the other four

TABLE IV
Fruit yields in five black currant cultivars as affected Autumn temperature

Cultivar	Temperature (°C)	Fruit yield (g/plant)	Number of berries	Mean fruit weight (g)	Aborted flowers (%)
'Öjebryn'	9	39.4	31.3	1.6	52.7
	12	147.4	93.1	1.6	40.3
	18	195.0	125.0	1.6	50.7
	24	149.8	101.8	1.5	53.6
Mean	—	129.9 b [†]	85.8 c	1.6 a	49.1 c
'Ben Tron'	9	210.0	125.3	1.7	26.1
	12	291.7	163.7	1.8	30.3
	18	267.0	201.8	1.3	47.4
	24	255.5	195.5	1.3	48.0
Mean	—	256.0 a	171.6 b	1.5 a	38.4 b
'Kristin'	9	121.7	71.2	1.7	19.1
	12	309.3	197.3	1.6	12.9
	18	333.5	274.0	1.2	20.4
	24	322.2	287.5	1.1	46.6
Mean	—	271.7 a	207.5 a	1.4 a	26.4 a
'Ben Hope'	9	82.6	55.8	1.5	56.5
	12	251.6	177.6	1.4	42.3
	18	310.8	264.0	1.2	45.6
	24	269.4	218.2	1.2	45.0
Mean	—	228.6 a	178.9 ab	1.3 a	47.4 c
'Narve Viking'	9	101.7	76.3	1.3	39.6
	12	227.8	143.0	1.6	29.9
	18	180.0	110.0	1.6	55.3
	24	135.6	97.8	1.4	47.3
Mean	—	160.7 b	106.9 c	1.5 a	41.7 bc
Probability levels of significance by ANOVA					
Source of variation					
Temperature (A)		< 0.001	< 0.001	0.010	0.010
Cultivar (B)		< 0.001	< 0.001	n.s.	< 0.001
A \times B		0.040	< 0.001	n.s.	0.001

[†]Mean values within the same column followed by different lower-case letters indicate a significant difference ($P < 0.05$) between treatments ($n = 9$). Data are the means of three replicates, each with three plants of each cultivar in each temperature treatment.

cultivars, the number of basal vegetative nodes decreased significantly ($P < 0.001$) with increasing Autumn temperature in all cultivars (Table III). In other words, the higher the Autumn temperature, the lower the position of the lowermost flowering node. Above this node, and along the greater part of the shoot, there followed an uninterrupted range of flowering nodes (Figure 3), usually terminated by a vegetative terminal bud. Only occasionally did the terminal bud contain an inflorescence in a lateral position. This agrees with the results of Tinklin *et al.* (1970), who found that, at the end of the season, the terminal bud was always vegetative in a wide range of cultivars. However, the present finding that the position of the lowermost flowering node was related to the strength of flowering (Figure 3), questions the validity of the conclusion by Tinklin *et al.* (1970) that “initiation in the black currant shoot begins in the lower middle nodes and then spreads acropetally”. Actually, the present findings strongly suggest that floral initiation also spreads basipetally.

Although there was no obvious relationship between the origin of the cultivars and their Autumn temperature requirements, ‘Narve Viking’ varied significantly from the other cultivars by being relatively temperature insensitive. In this connection, it may be relevant that this cultivar has red currant (*Ribes rubrum*) in its pedigree (personal information from the breeder, Dr. J. Øydvin), a species which is known for its insensitivity to temperature. It should also be noted that both ‘Narve Viking’ and ‘Kristin’ have ‘Ben Tron’ as one of their parents and that ‘Ben Tron’ has ‘Öjebyn’ as a great grandparent, as a source of mildew resistance (Dr. J. Øydvin, personal information). Also,

while ‘Ben Tron’ originated from crosses made in Scotland, the cultivar was selected, in part, in Norway through a collaborative breeding programme. The similar Autumn temperature responses of these modern cultivars are, therefore, not surprising.

A significant proportion of the flowers did not develop to maturity, but aborted at an immature fruit stage (Table IV). The reason for this fruit drop is not clear, but a positive relationship between the magnitude of flowering and the proportion of fruit drop suggests a connection to a limitation in the fruit carrying capacity of the plants. Root restriction caused by the relatively small pots might have been a contributing factor. Another cause might have been sub-optimal pollination due to the scarcity of pollinating insects in the greenhouse during the flowering period.

In conclusion, the relatively high Autumn temperature optimum for floral initiation in black currant shows that, although there might be other concerns about possible adverse effects of global warming, there is little reason to worry about any adverse effects on flower formation in this crop. Indeed, in the cool Nordic environment where Autumn temperatures are obviously sub-optimal for SD floral induction (Figure 4), any increase in average Autumn temperature would actually be beneficial for floral initiation in black currant.

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REFERENCES

- HÄRDH, J. E. and WALLDEN, J. (1965). Mustaherukan kukankehitys ja marjanmodostus. *Maataloust Aikakausk*, **37**, 61–75.
- HEIDE, O. M. (1974). Growth and dormancy in Norway spruce ecotypes. I. Interaction of photoperiod and temperature. *Physiologia Plantarum*, **30**, 1–12.
- HEIDE, O. M. (2003). High autumn temperature delays bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology*, **23**, 931–936.
- JONES, H. G. and BRENNAN, R. M. (2009). Potential impacts of climate change on soft fruit production: the example of winter chill in *Ribes*. *Acta Horticulturae*, **838**, 27–32.
- LANG, A. (1965). Physiology of flower initiation. In: *Encyclopedia of Plant Physiology*. Volume XV/I. (Rhuland, W., Ed.). Springer-Verlag, Berlin, Germany. 1380–1536.
- NASR, T. A. A. and WAREING, P. F. (1958). Photoperiodic induction of flowering in black currant. *Nature*, **182**, 269.
- NASR, T. A. A. and WAREING, P. F. (1961a). Studies on flower initiation in black currant I. Some internal factors affecting flowering. *Journal of Horticultural Science*, **36**, 1–10.
- NASR, T. A. A. and WAREING, P. F. (1961b). Studies on flower initiation in black currant II. Photoperiodic induction of flowering. *Journal of Horticultural Science*, **36**, 11–17.
- ROSE, G. A. and CAMERON, R. W. (2009). Chill unit models for blackcurrant (*Ribes nigrum* L.) cultivars ‘Ben Gairn’, ‘Ben Hope’, and ‘Ben Tirran’. *Scientia Horticulturae*, **122**, 654–657.
- SØNSTEBY, A. and HEIDE, O. M. (2008a). Environmental control of growth and flowering of *Rubus idaeus* L. cv. Glen Ample. *Scientia Horticulturae*, **117**, 249–256.
- SØNSTEBY, A. and HEIDE, O. M. (2008b). Temperature responses, flowering and fruit yield of the June-bearing strawberry cultivars Florence, Frida and Korona. *Scientia Horticulturae*, **119**, 49–54.
- SØNSTEBY, A., MYRHEIM, U., HEIBERG, N. and HEIDE, O. M. (2009). Production of high yielding red raspberry long canes in a Northern climate. *Scientia Horticulturae*, **121**, 289–297.
- SUNLEY, R. J., ATKINSON, C. J. and JONES, H. G. (2006). Chill unit models and recent changes in the occurrence of winter chill and spring frost in the United Kingdom. *Journal of Horticultural Science & Biotechnology*, **81**, 949–958.
- THOMAS, G. G. and WILKINSON, E. H. (1962). Propagation of black currant from single bud cuttings. *Journal of Horticultural Science*, **37**, 115–123.
- THOMAS, B. and VINCE-PRUE, D. (1997). *Photoperiodism in Plants*. 2nd Edition. Academic Press, London, UK. 428 pp.
- TINKLIN, I. G., WILKINSON, E. H. and SCHWABE, W. W. (1970). Factors affecting flower initiation in the black currant *Ribes nigrum* (L.). *Journal of Horticultural Science*, **45**, 275–282.
- VEGIS, A. (1964). Dormancy in higher plants. *Annual Review of Plant Physiology*, **15**, 185–224.
- VESTRHEIM, S. (1971). Flower initiation in black currants in a Southern Norwegian location. *Scientific Reports of the Agricultural University of Norway*, **71**, 1–5.
- WAREING, P. F. (1956). Photoperiodism in woody plants. *Annual Review of Plant Physiology*, **7**, 191–214.
- WESTERGAARD, L. and ERIKSEN, E. N. (1997). Autumn temperature affects the induction of dormancy in first-year seedlings of *Acer platanoides*. *Scandinavian Journal of Forest Research*, **12**, 11–16.