Effects of summer temperature on growth and flowering in six black currant cultivars (*Ribes nigrum* L.)

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SUMMARY

Growth and flowering were studied in six black currant cultivars grown under natural photoperiodic conditions at Ås, Norway (59°40'N) at constant temperatures of 9°C, 15°C, or 21°C during an entire growing season (May to late-September). Growth cessation and floral initiation were advanced and promoted by increasing temperature in the cultivars 'Öjebyn', 'Ben Tron', 'Kristin', 'Ben Hope', and 'Narve Viking', while early cessation of growth was advanced by low temperatures in 'Murmanschanka', a cultivar originating from the Kola Peninsula. In all cultivars, flowering was significantly increased by warm temperatures during the preceding growing season. A decline in growth preceded floral initiation by 2 – 3 weeks, indicating critical photoperiods of approx. 17 h and 16 h at 21°C for the two processes, respectively, for all cultivars except 'Murmanschanka', which initiated floral primordia shortly after mid-Summer. Warm summer temperatures also affected flowering indirectly by the promotion of growth and advancement of the transition from the juvenile stage. Although the cessation of growth was normally associated with floral initiation, small plants with less than 20 nodes ceased growing under natural short-day conditions, but were unable to undergo floral initiation. It is concluded that summer temperatures influence flowering both directly, by enhancing short-day floral induction, and indirectly, by the enhancement of growth and, thereby, advancement of the transition from the juvenile stage.

Black currant (*Ribes nigrum* L.) is a soft fruit species that is widely grown in temperate and cold regions. It is a woody plant in which growth and development are intimately controlled by, and synchronised with, seasonal changes in photoperiod and temperature (Wright, 1985). Floral initiation requires short photoperiods (Nasr and Wareing, 1958; 1961; Tinklin *et al*., 1970), and is causally and temporally associated with the cessation of growth and the induction of dormancy (Sønsteby and Heide, 2011; Heide and Sønsteby, 2011). The critical day-length for floral initiation in a wide range of black currant cultivars has been shown to vary between 16 h and 17 h (Tinklin *et al*., 1970; Heide and Sønsteby, 2011). However, while early investigations indicated an enhancement effect of low temperatures on the short-day (SD) induction process, recent investigations under well-controlled temperature conditions revealed the opposite (Sønsteby and Heide, 2011). Thus, both growth cessation and floral initiation were highly significantly promoted and advanced by increasing temperature, with an optimum in the 18° – 24°C range.

Because of this interaction of photoperiod and temperature, and since seasonal changes in photoperiod and temperature are functions of both latitude and season, floral initiation in black currant is successively more delayed at locations of increasing latitude (Tinklin *et al*., 1970). The situation is further amplified by the fact that young shoots of black currant exhibit a form of

juvenile phase and must attain a minimum size before they are able to respond to SD by floral initiation (Tinklin *et al*., 1970; Schwabe and Al-Doori, 1973). Declining temperatures and growth rates at higher latitudes will, therefore, further delay floral initiation at such locations. Consequently, the timing of floral initiation of black currant cultivars varies clinally by several months among different latitudinal locations across Europe (see Tinklin *et al*., 1970). The range extends from late-May at Bologna, Italy (44° 30'N) to late-June – early-July in southern England (51°N), and from early-August in southern Scandinavia (60°N) to mid-September in the Arctic circle at Rovaniemi, Finland (Hårdh and Wallden, 1965; Vestrheim, 1972).

While the latitudinal effects of photoperiod are quite well understood in this connection (Tinklin *et al*., 1970; Heide and Sønsteby, 2011), the roles of summer temperature for shoot growth and the attainment of a critical shoot size are not so clear. Therefore, we grew six black currant cultivars of contrasting origin at constant temperatures of 9°C, 15°C, or 21°C under natural day-length conditions at 60°N over an entire growth season (May-September), and studied the effects of temperature on shoot growth and flower formation. The results are presented and discussed below.

MATERIALS AND METHODS
Plant material and cultivation

Single-stemmed plants of the black currant (*Ribes*

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nigrum L.) cultivars 'Öjebyn', 'Ben Tron', 'Kristin', 'Ben Hope', 'Narve Viking' (see Sønsteby and Heide, 2011), and the Russian high-latitude cultivar 'Murmanschanka' (Samuelsen and Nilsen, 2008), were propagated from semi-softwood cuttings, as described by Sønsteby and Heide (2011). On 18 May 2010, when the plants were 5 – 6 cm tall and had produced three-to-four leaves, they were moved into daylight compartments of the Ås phytotron (59°40'N) where they were exposed to natural day-length conditions and temperatures of 9°C, 15°C, or 21°C throughout the Summer. Temperatures were controlled within ± 1.0°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 µmol quanta m^{-2} s^{-1}, as on cloudy days, an additional 125 µmol quanta m^{-2} s^{-1} were added automatically using Philips HPT-I 400 W lamps. When reaching a height of approx. 30 cm, the plants were transplanted into 3 l plastic pots in which they remained for the entire experiment. A coarse-textured sphagnum peat growth medium with a pH of 5.8 and fertilised with Osmocote™ controlled-release fertiliser, was used throughout, as described by Sønsteby and Heide (2011).

Experimental design, data collection, and analysis

The experiment was fully factorial, with a split-plot design, and replicated in three blocks, each containing three plants of each cultivar at each temperature. During the experimental period, plant growth was monitored by weekly measurements of plant heights and the counting of leaf (node) numbers on all plants. Starting on 20 July, buds were collected by weekly sampling from all plants for determinations of floral initiation and their differentiation status. For this purpose, on each sampling date, the bud at node-12 (numbered from the top) was removed by a shallow longitudinal slit and the bud was stored in 70% (v/v) ethanol until it was dissected and examined under a stereo-microscope.

Floral development was scored on a six-stage scale, in which vegetative buds were assigned stage 0, while buds with the first sign of floral initiation (i.e., visible sepal primordia in the primary flower) were assigned stage 1. Buds in which all floral organs were initiated in the primary flower were assigned stage 5. In addition, on 17 August, three plants in each treatment were terminated and all buds were dissected and examined for their stage of floral development. The remaining six plants in each treatment continued growth under their respective conditions until 21 September, when all treatments were terminated and the plants were moved into a cold-store maintained in the dark at –2°C. The extent of leaf abscission was recorded in each plant at this stage.
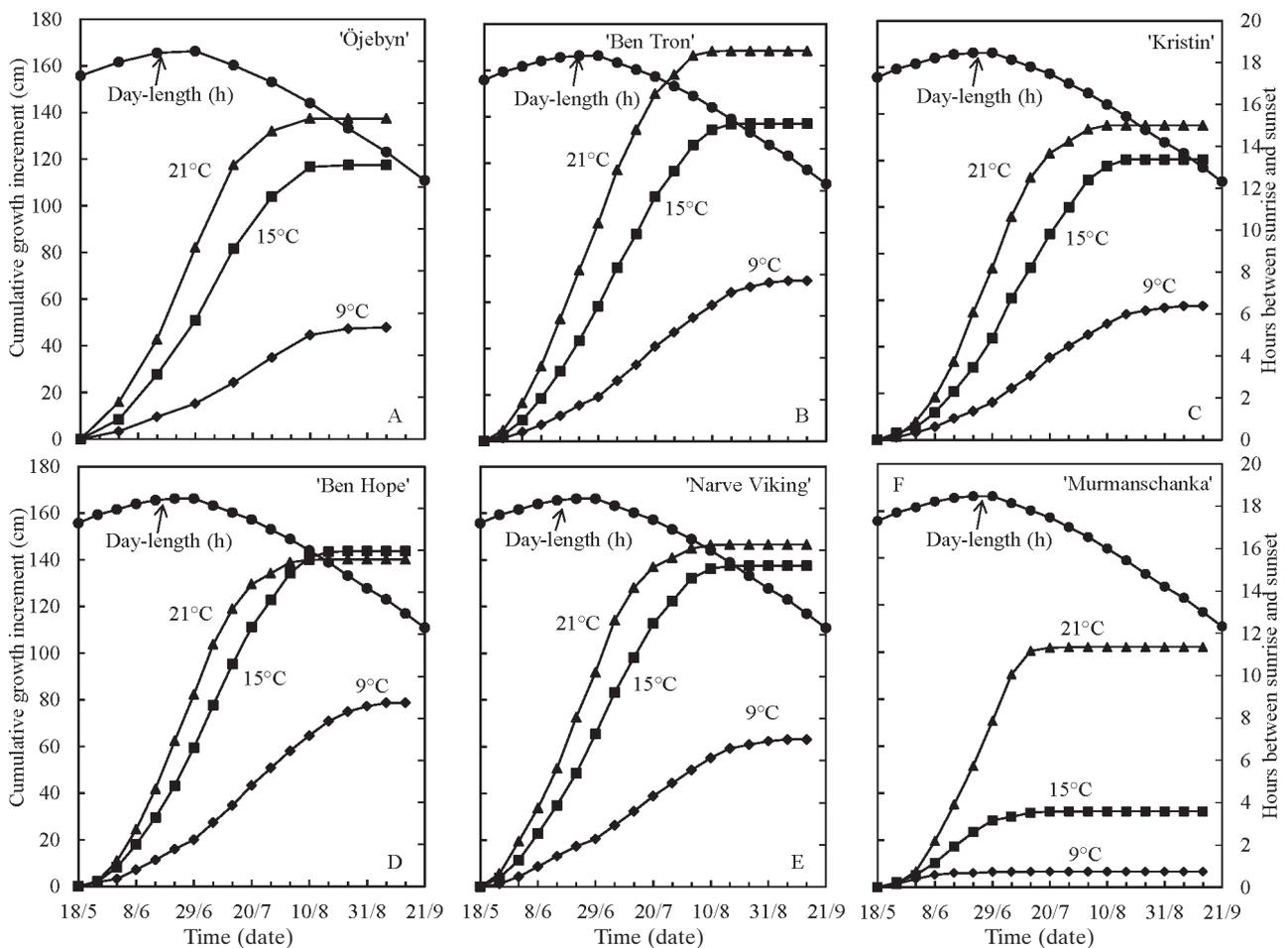

FIG. 1

Time-courses of cumulative shoot elongation (growth increments in cm) in six black currant cultivars grown in phytotron daylight compartments under natural photoperiodic conditions at Ås, Norway (59°40'N) and constant temperatures of 9°C, 15°C, or 21°C, as indicated. All values are the means of three replicates, each consisting of three plants of each cultivar.

After 24 weeks of cold storage (i.e., on 11 March 2011), the plants were moved into a heated greenhouse maintained at a minimum of 15°C and monitored for bud burst and flowering performance. During this phase, all plants were fed by daily fertigation with a complete fertiliser solution, as described by Sønsteby *et al.* (2009). The times of the earliest bud burst and of anthesis were recorded for each plant by observation every 2 d. The numbers and positions of flowering nodes, together with the total numbers 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 16; Minitab Inc., State College, PA, USA). Percentage values were always subjected to an arc sin transformation before the performance of ANOVA.

RESULTS

Rates of elongation growth and the addition of new leaves increased with increasing temperature in all cultivars, as expected (Figure 1; Figure 2). However, under the present natural day-length conditions, the decline and cessation of growth were also advanced by increasing temperature in all cultivars except 'Murmanschanka'. In 'Öjebyn', 'Kristin', 'Ben Tron', 'Ben Hope', and 'Narve Viking', growth started to level-off at 21°C by 20 July, followed by a complete cessation of growth 2 weeks later. Both these stages were delayed by approx. 2 and 4 weeks at 15°C and 9°C, respectively. On the other hand, the opposite trend was observed in 'Murmanschanka'. In this cultivar, growth started to slow down almost immediately at 9°C, with a complete cessation of growth by 15 June, when the plants had reached a height of only 10 cm. At higher temperatures, growth continued for a further 2 or 4 weeks approximately, at 15°C and 21°C, respectively. However, even at 21°C, which supported the longest period of growth, 'Murmanschanka' had completely ceased growing by 20 July, at which time growth of the other five cultivars had only started to level-off (Figure 1). Because of this early cessation of growth, 'Murmanschanka' also developed large, swollen buds at an early stage.

Serial dissections of buds confirmed the distinct response of 'Murmanschanka' compared with the other five cultivars. In the former cultivar, fully differentiated flower buds (stage 5) were already present on the first sampling date (20 July) at 15°C. At this time, floral buds were also visible in plants kept at 21°C, but at a mean floral development stage of only 2.5, while no floral buds
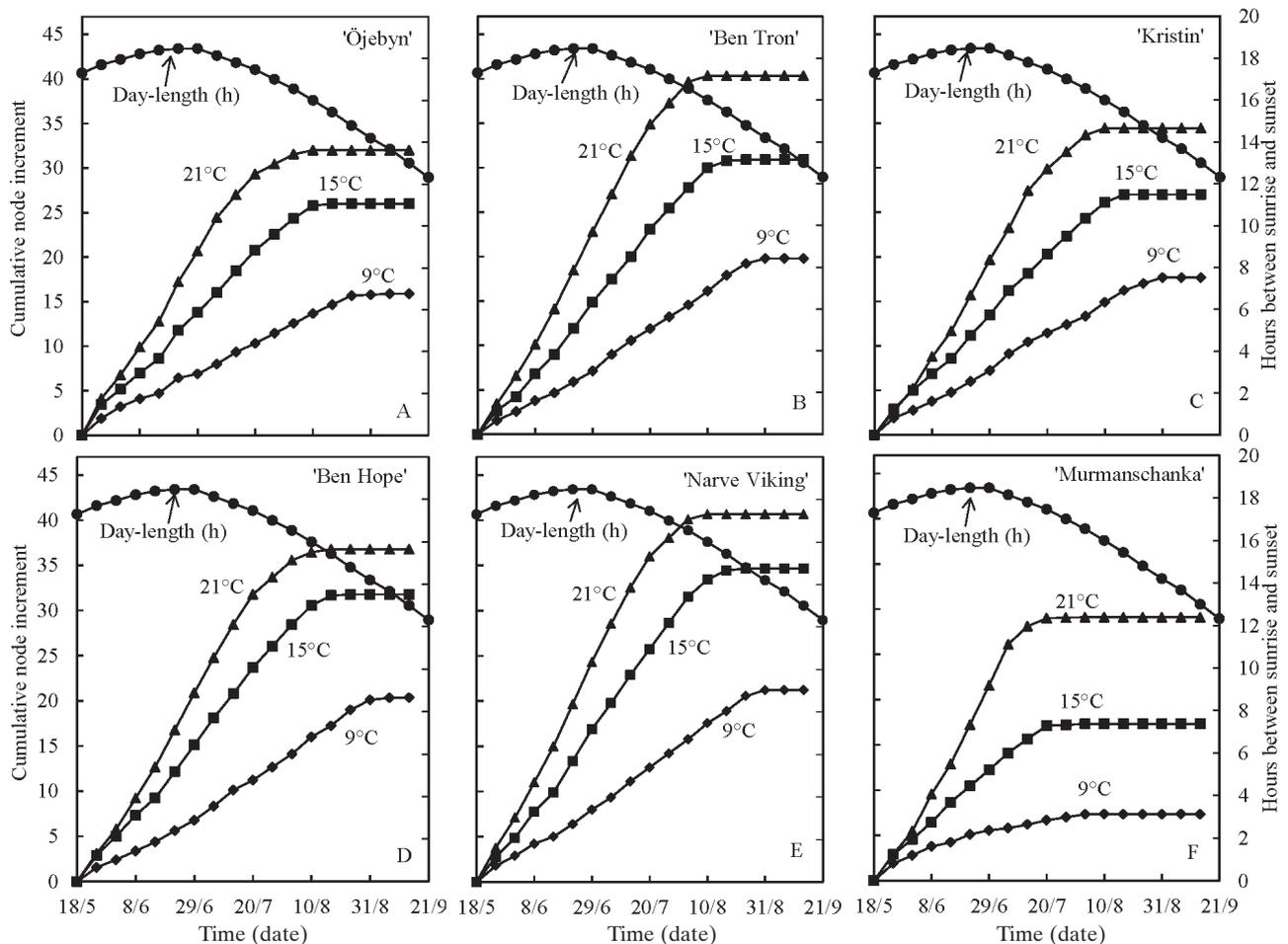

FIG. 2
Time-courses of the cumulative addition of new leaves (node increments) in six black currant cultivars grown in phytotron daylight compartments under natural photoperiodic conditions at Ås, Norway (59°40'N) and constant temperatures of 9°C, 15°C, or 21°C, as indicated. All values are the means of three replicates, each consisting of three plants of each cultivar.

could be detected on the small plants at 9°C (Figure 3). However, floral initiation was advanced by increasing the temperature in all other cultivars, although floral stages above 4 did not occur until 31 August in the earliest of these cultivars. At 21°C, the first sign of floral initiation was detected in 'Kristin' by 4 August, in 'Öjebyn' and 'Ben Tron' by 10 August, and in 'Ben Hope' and 'Narve Viking' by 17 August. At 15°C, floral initiation occurred 1 – 2 weeks later in these cultivars, while, at 9°C, initiation was even later and could not be observed before the first week of September. In 'Öjebyn', no floral initiation could be observed at 9°C before bud sampling was discontinued on 21 September (Figure 3).

These trends in the timing of floral initiation were confirmed by dissections of all buds along the entire shoot length of three plants of each cultivar in the 21°C treatment on 17 August (Figure 4). Again, 'Murmanschanka' plants were found to be far ahead of the other cultivars by having fully-differentiated floral buds at stage 5 at all nodes from node-6 and upwards, including the terminal bud. Among the five other cultivars, 'Kristin' was again found to be the most advanced, followed by 'Öjebyn' and 'Ben Tron', and
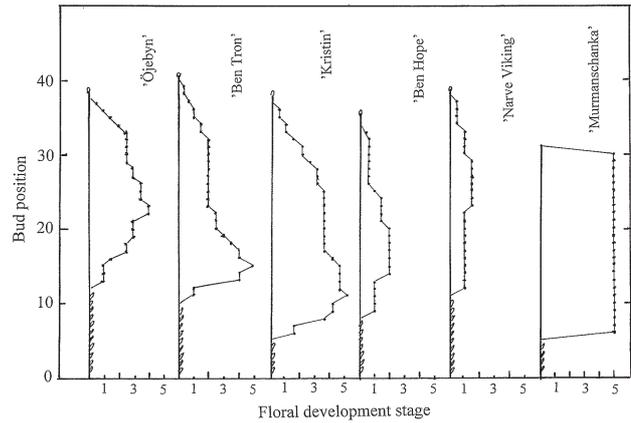

FIG. 4
Profiles of the stages of flower development of buds at each node along the entire shoot length in six black currant cultivars grown at a constant 21°C under natural photoperiodic conditions at Ås, Norway (59°40'N). All buds were sampled on 17 August. Bud positions were counted from the base of the shoot. All values are the means of three plants of each cultivar in each treatment.

finally 'Ben Hope' and 'Narve Viking', which were relatively slow to respond (Figure 4). The bud profiles also demonstrated consistent cultivar differences in the
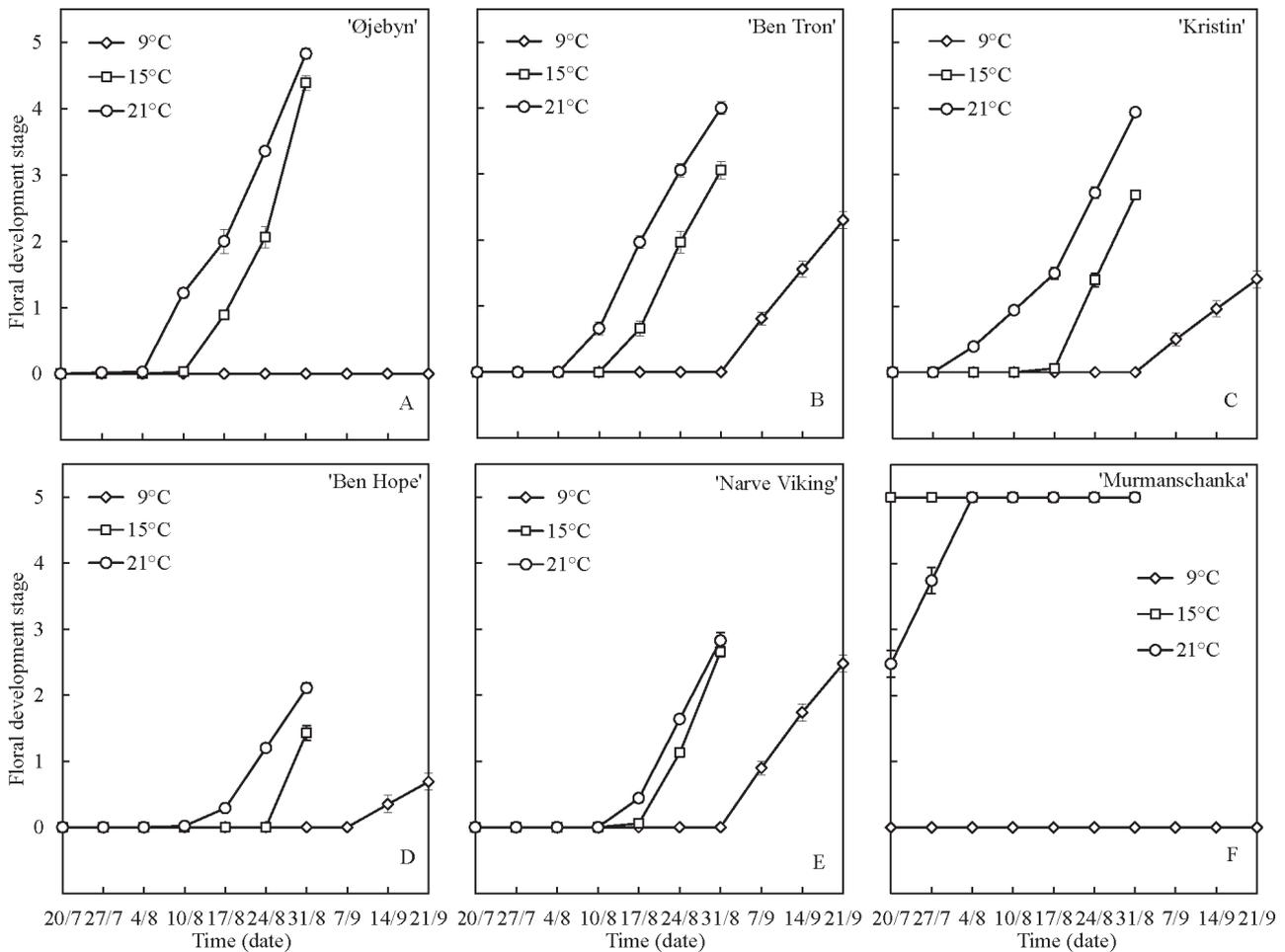

FIG. 3
Progression of the stages of floral development in six black currant cultivars grown in phytotron daylight compartments under natural photoperiodic conditions at Ås, Norway (59°40'N) and constant temperatures of 9°C, 15°C, or 21°C, as indicated. Floral stages were scored on a six-stage scale, in which stage 0 represented vegetative buds, stage 1 represented the first visible sign of floral initiation (sepal primordia visible in the primary flower) and stage 5 represented fully-differentiated floral primordia in the primary flower. Values are the means ± SE of three replicates, each consisting of three plants of each cultivar.

TABLE I

Effects of growth temperature on the percentage of abscised leaves in six black currant cultivars after 18 weeks of cultivation under natural photoperiodic conditions at 59°40'N

Cultivar	Temperature (°C)			
	9	15	21	Mean
'Öjebyn'	6.5[†]	27.2	48.0	27.2 b
'Ben Tron'	6.1	9.9	9.0	8.3 e
'Kristin'	5.4	28.4	20.1	18.0 c
'Ben Hope'	4.7	10.4	17.9	11.0 d
'Narve Viking'	4.5	7.8	5.3	5.9 e
'Murmanschanka'	87.9	39.5	27.5	51.6 a
Mean	19.2 a*	20.6 a	21.3 a	

[†]Data are the means of three replicates, each containing three plants of each cultivar at 9°C and 15°C, and two plants of each cultivar at 21°C.
*Mean values within each column followed by a different lower-case letter are significantly different ($P \leq 0.05$).

nodal positions of the lower-most, and most advanced floral buds. Apart from 'Murmanschanka', 'Kristin' was the only cultivar with floral primordia observed as far down as node-6, followed by 'Ben Hope', 'Ben Tron', 'Narve Viking', and finally 'Öjebyn', the latter having the lower-most floral bud at node-13. This sequence was paralleled by a similar trend in the nodal position of the most advanced bud, 'Kristin' peaking at node-11, and 'Öjebyn' and 'Narve Viking' peaking at around node-24 (Figure 4).

The extent of leaf abscission, recorded at the time of termination of the temperature treatments on 21 September, varied significantly ($P < 0.001$) among cultivars, which also exhibited contrasting responses to temperature (interaction was significant at $P < 0.001$). The early cessation in growth in 'Murmanschanka' at low

temperatures was associated with the advancement of leaf senescence and abscission, while, in all other cultivars in which growth cessation was advanced by high temperatures, leaf abscission was also advanced by increasing temperature (Table I). Among the latter five cultivars, leaf abscission was earliest in 'Öjebyn' and 'Kristin', and latest in 'Ben Tron' and 'Narve Viking'. Again, these differences tended to be associated with the earliness of the cessation of growth (Figure 1).

When plants were "forced" after cold storage, bud burst was consistently advanced, while flowering (anthesis) was delayed by decreasing temperature during the previous season (Table II). Both effects were highly significant ($P = 0.001$) and, due to the early development of 'Murmanschanka', the cultivar effect and the interaction of temperature and cultivar were also highly significant for both parameters. Bud burst was particularly early in 'Murmanschanka', while it was late in 'Ben Hope' and 'Narve Viking' (Table II).

The abundance of flowering was also highly significantly ($P < 0.001$) affected by temperature, cultivar, and their interaction. The number and proportion of flowering nodes increased with increasing growth temperature, usually with an optimum at 15°C (Figure 5), whereas the total number of flowers per plant increased continuously up to 21°C in all cultivars (Table III). The largest number of flowers per plant was recorded in 'Kristin' at 21°C, followed by 'Ben Tron' at the same temperature. The proportion of flowering nodes was highest in 'Kristin' at 15°C and 21°C, together with 'Murmanschanka' at 21°C. Overall, 'Öjebyn' had

TABLE II

Effects of growth temperature during the preceding Summer on time to bud-burst and anthesis in six black currant cultivars

Cultivar	Temperature (°C)	Days to bud burst	Days to anthesis
'Öjebyn'	9	5.0[†]	> 50
	15	7.0	20.0
	21	7.2	18.8
Mean		6.2 b*	46.3 d
'Ben Tron'	9	5.1	20.7
	15	7.0	19.8
	21	8.0	18.8
Mean		6.5 b	19.9 b
'Kristin'	9	5.1	22.9
	15	6.7	19.3
	21	8.0	19.8
Mean		6.4 b	21.0 b
'Ben Hope'	9	6.8	24.8
	15	7.8	21.0
	21	8.7	23.7
Mean		7.6 a	23.4 c
'Narve Viking'	9	7.0	21.9
	15	7.7	20.2
	21	8.2	21.7
Mean		7.5 a	21.3 bc
'Murmanschanka'	9	1.8	21.5
	15	3.0	14.0
	21	5.0	14.5
Mean		3.0 c	15.1 a
Probability levels of significance by ANOVA			
Source of variation			
Temperature (A)	0.001	< 0.001	
Cultivar (B)	< 0.001	< 0.001	
A × B	0.001	< 0.001	

[†]Data are the means of three replicates, each containing three plants of each cultivar at 9°C and 15°C, and two plants of each cultivar at 21°C.
*Mean values within each column followed by a different lower-case letter are significantly different ($P \leq 0.05$).

TABLE III

Effects of growth temperature during the preceding Summer on flowering in six black currant cultivars

Cultivar	Temperature (°C)	Total number of flowers	Flowers per inflorescences
'Öjebyn'	9	0.0[†]	0.0
	15	167.9	11.2
	21	186.2	11.6
Mean		109.5 d*	7.1 b
'Ben Tron'	9	78.0	9.7
	15	245.4	13.1
	21	323.5	13.6
Mean		202.2 ab	12.0 a
'Kristin'	9	48.2	9.9
	15	266.4	12.8
	21	381.0	14.1
Mean		213.3 a	12.0 a
'Ben Hope'	9	67.6	9.4
	15	230.0	11.6
	21	253.3	12.6
Mean		174.9 bc	11.1 a
'Narve Viking'	9	42.4	7.4
	15	196.1	9.7
	21	224.8	9.9
Mean		145.7 cd	8.9 b
'Murmanschanka'	9	0.3[‡]	0.3[‡]
	15	69.9	6.9
	21	264.7	14.5
Mean		92.5 d	6.3 b
Probability levels of significance by ANOVA			
Source of variation			
Temperature (A)	< 0.001	< 0.001	
Cultivar (B)	< 0.001	< 0.001	
A × B	< 0.001	< 0.001	

[†]Data are the means of three replicates, each containing three plants of each cultivar at 9°C and 15°C, and two plants of each cultivar at 21°C.
*Mean values within each column followed by a different lower-case letter are significantly different ($P \leq 0.05$).
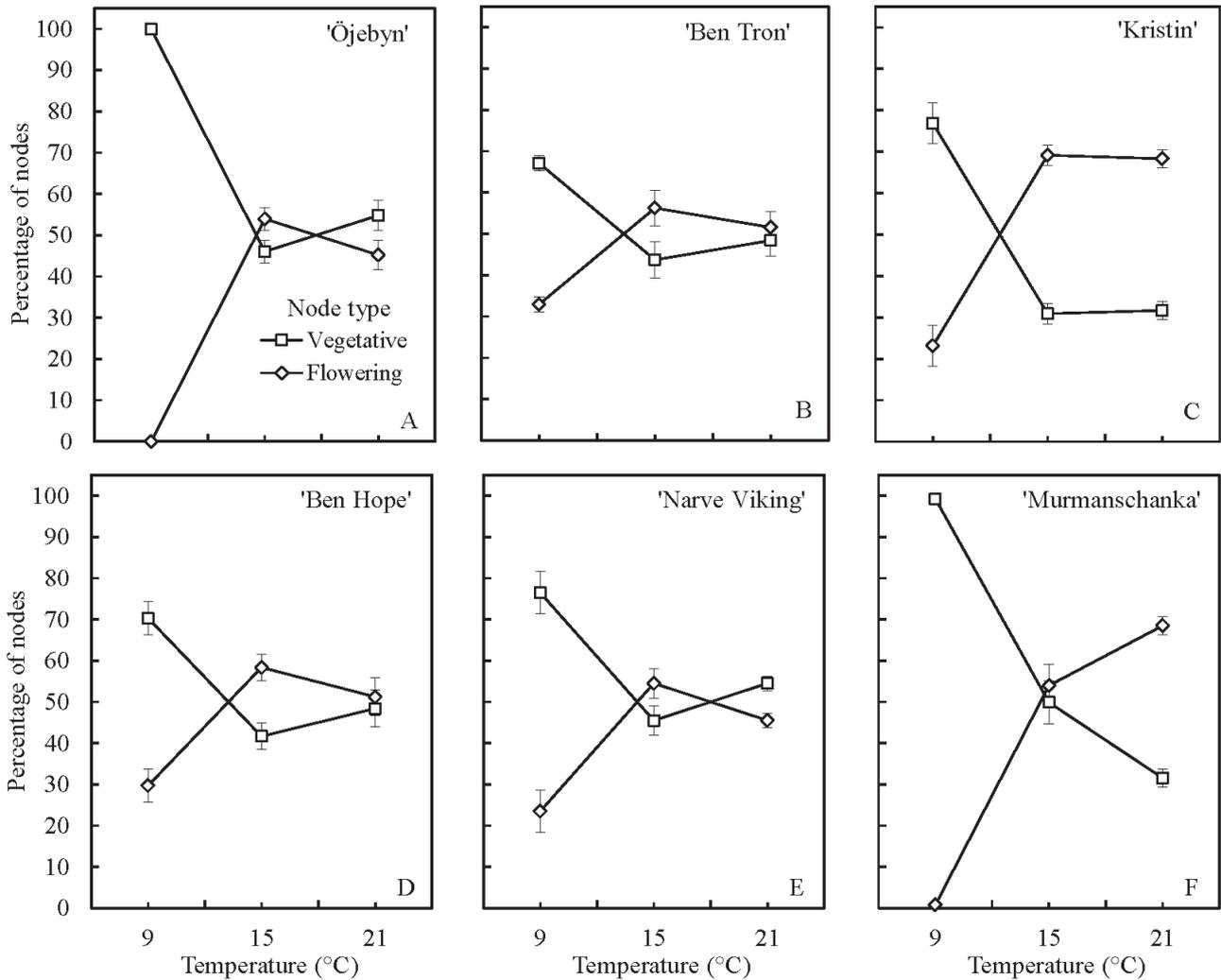[‡]Means of four flowering plants.

FIG. 5

The proportion of flowering nodes *vs*. vegetative nodes in six black currant cultivars grown during the previous season in phytotron compartments under natural photoperiodic conditions at Ås, Norway (59°40'N) and constant temperatures of 9°C, 15°C, or 21°C, as indicated. Values are the means ± SE of three replicates, each consisting of three plants of each cultivar at 9°C and 15°C, and of two plants at 21°C.

the lowest flowering, followed by 'Murmanschanka'. In these cultivars, no (or almost no) flowering took place in plants grown at 9°C (Table III). Also the number of flowers per inflorescence increased with increasing growth temperature during the preceding Summer; but,
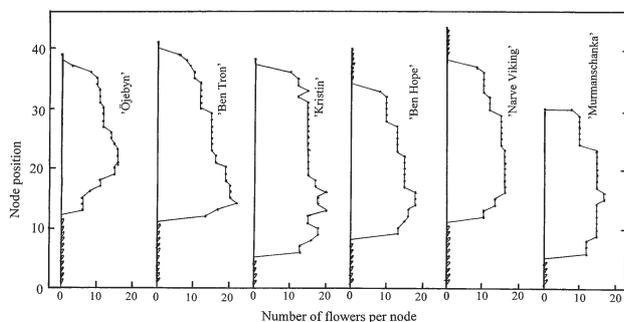

FIG. 6
Profiles of flower numbers at each node along the entire shoot length in six black currant cultivars grown during the previous season at a constant 21°C under natural photoperiodic conditions at Ås, Norway (59°40'N). All values are the means of three replicates, each with two plants of each cultivar in each treatment.

with the exception of 'Murmanschanka', the increase levelled-off markedly at 21°C (Table III).

The six cultivars also varied significantly in the extent and distribution of flowers at each node along the entire length of the shoot (Figure 6). In most cultivars, the highest number of flowers per node occurred in buds positioned approx. one-third up from the ground. From there upwards, the number of flowers decreased, first gradually, then abruptly, towards the apex. The exception was 'Murmanschanka' in which the number of flowers varied relatively little with bud position. Another unique characteristic of this cultivar was that even the terminal bud flowered, while the terminal bud was always vegetative in the other five cultivars. In 'Ben Hope' and 'Narve Viking', several buds at the top of the shoot were dead after cold storage. As with bud dissections performed in August, the cultivars varied significantly in how far down the shoot they flowered. While only the lower-most five buds near the ground were vegetative in 'Kristin' and 'Murmanschanka', the numbers of vegetative buds at the base were more than twice as high in 'Öjebyn', 'Narve Viking', and 'Ben Tron', giving these cultivars a somewhat "leggy" appearance (Figure 6).

DISCUSSION

The present results concur with our earlier finding (Sønsteby and Heide, 2011) that high temperatures promote and advance SD-induced floral initiation in black currant. Thus, under natural day-length conditions during late-Summer and early-Autumn at 60°N, floral initiation in all cultivars, except 'Murmanschanka', was progressively delayed by decreasing temperature (Figure 3). This was accompanied by parallel reductions in flowering in the following season (Table III). However, in the present experiments in which the temperature treatments were applied throughout the growing season, the negative effect of low temperature was further enhanced due to retarded shoot growth at low temperature. Because of the juvenile condition of black currant plants with less than approx. 20 leaves (Tinklin et al., 1970), the growth-retarding effect of low temperature delayed, or in some cases even prevented, plants from reaching the "ripeness-to-flower" stage before the treatments were terminated on 21 September. Thus, the cultivars 'Öjebyn' and 'Murmanschanka', which grew poorly at 9°C, did not flower at all, or flowered only marginally at this temperature (Figure 3; Table III).

These results also demonstrate that 'Murmanschanka' differed fundamentally from the other five cultivars in its environmental responses. While the slowing down and cessation of growth were advanced by high temperatures, in parallel with floral initiation, in all other cultivars (cf. Sønsteby and Heide, 2011), the opposite trend was found in 'Murmanschanka' (Figure 1). While the cessation of growth in the latter cultivar took place in early June at 9°C, when day-length was still increasing, the cessation of growth was gradually delayed at higher temperatures up to 13 July at 21°C. Likewise, although no floral initiation was detected in the small 'Murmanschanka' plants at 9°C, floral initiation was earlier at 15°C than at 21°C (Figure 3), despite the larger plant size at the higher temperature (Figure 1). Nevertheless, the total numbers of flowers were much higher in plants at 21°C than in plants at 15°C (Table III) due to the presence of much larger plants at the higher temperature. Moreover, the presence of advanced floral primordia in 'Murmanschanka' by 20 July, when the natural day-length at Ås (60°N) was still approx. 18 h, indicated a critical photoperiod which was at least 2 h longer than the critical photoperiod for floral initiation in a range of other black currant cultivars (Tinklin et al., 1970; Heide and Sønsteby, 2011). Originating on the Kola Peninsula, it appears that 'Murmanschanka', like many other high-latitude woody plants (Heide, 1974; Håbjørg, 1978), requires almost continuous daylight for the maintenance of growth.

While most modern black currant cultivars grown commercially in Western Europe vary little in their environmental responses, and seem to represent a common gene-pool (see discussions by Sønsteby and Heide, 2011; Heide and Sønsteby, 2011), the present results with 'Murmanschanka' suggest a distinct origin and genetic constitution of this cultivar. The unique growth and flowering responses of this cultivar make it especially interesting for high-latitude environments, and preliminary trials have shown promising results under such conditions (Samuelsen and Nilsen, 2008). However, the habit of this cultivar to terminate growth early in the season at low temperatures may limit its potential for high-latitude environments (Figure 1; Figure 2). While this may be a useful survival response that has evolved in a cool and changing natural environment, the resulting growth restriction may represent a problem for commercial cultivation.

The results shown in Table II confirm our earlier finding (Sønsteby and Heide, 2011) that high temperatures during late-Summer and Autumn delay bud-burst in the following Spring. This was also demonstrated by Måge (1976), who found a highly significant negative correlation between October temperature and the capacity of red and black currant buds to burst during December and January, and a weaker correlation with temperatures during the summer months. Such a relationship between warm autumn temperatures and delayed bud-burst in the Spring has been demonstrated in a range of temperate trees and shrubs (Heide, 2003), including red raspberry (Måge, 1975), and appears to be a common feature of woody plants adapted to high-latitude environments. This phenomenon may have important implications for the ability of these plants to adapt to global warming. However, the contrasting effect on days-to-anthesis (i.e., delayed anthesis in low-temperature plants), was apparently an effect of late floral initiation in the cool environment (Table II).

The profiles of the stages of floral differentiation at each node along the entire length of the shoot in the various cultivars, recorded in August (Figure 4), closely resembled the corresponding profiles of flowering during the following season (Figure 6). Both profiles demonstrated large cultivar variations in the extension of flowering towards the base of the shoot, with the most extensive flowering towards the base in 'Kristin' and 'Murmanschanka'. The early and spatially extensive floral initiation in 'Kristin' was associated with abundant flowering along the entire length of the shoot, while the late and restricted floral initiation in 'Öjebyn', 'Ben Hope', and 'Narve Viking' was associated with lower total numbers of flowers. The early floral initiation in 'Murmanschanka' and 'Kristin' at 21°C was also associated with large inflorescences, each having many flowers (Table III).

The most advanced floral buds (Figure 4) and the highest numbers of flowers (Figure 6) were present on the lower-most one-third of the shoots, usually well below node-20, which represents the critical leaf number for "ripeness-to-flower" in black currant (Tinklin et al., 1970; Heide and Sønsteby, 2011). This indicates that floral initiation had started approx. 5 – 8 nodes below the apex when the plants had reached the critical size of 20 leaves, and that the floral initiation process then progressed both basipetally and acropetally, as suggested by Sønsteby and Heide (2011). The results in Figure 4 demonstrate marked variations in the lower-most and peak positions of floral initiation, with the highest positions in the late (slow-responding) cultivars, 'Narve Viking' and 'Ben Hope'.

Comparisons of the time-courses for elongation growth and floral initiation (Figure 1; Figure 3, respectively) demonstrated that, in all cultivars except 'Murmanschanka', growth started to level-off approx. 2 weeks before floral initiation was observed. It can also be

seen from Figure 1 that growth started to slow-down 2 – 3 weeks before the photoperiod had decreased to 16 h, which is the critical photoperiod for floral initiation in most black currant cultivars (Tinklin *et al.*, 1970; Heide and Sønsteby, 2011). An exception was 'Murmanschanka', which ceased growing by 13 July at 21°C, and had fully-differentiated floral primordia by 20 July, when the day-length was still approx. 18 h. These results concur with early observations by Nasr and Wareing (1961) and Tinklin *et al.* (1970), who reported that, under field conditions, floral primordia were initiated in late-Summer, immediately after growth had started to slow down. This indicates that, although the cessation of growth and floral initiation are both induced by SD conditions, the critical photoperiod for floral initiation is approx. 1 h shorter than that for growth cessation. This means that growth cessation and floral initiation are sequential responses, and not parallel responses to the same environmental signal, as suggested by Sønsteby and Heide (2011).

The results for 'Öjebyn' and 'Murmanschanka' (Figure 1; Table III) also demonstrated that sequential growth cessation and floral initiation may, under certain conditions, not apply. Thus, at 9°C, all 'Öjebyn' plants, and more than 50% of 'Murmanschanka' plants, remained vegetative despite their early cessation of growth. This was apparently related to the juvenile state of the small black currant plants. The results demonstrated that plants of these two cultivars with less than 20 nodes did respond to SD by cessation of growth, while they were unable to undergo floral initiation. A similar separation of growth cessation and floral initiation was reported for juvenile plants of red raspberry (Sønsteby and Heide, 2008).

In conclusion, the present results show that summer temperature affects flowering in black currant, both directly and indirectly. As previously reported by Sønsteby and Heide (2011), warm summer temperatures affect flowering directly by promoting and enhancing SD-induced floral initiation during late-Summer and Autumn. In addition, warm summer temperatures also affect flowering indirectly by the enhancement of growth, resulting in an advancement of the transition from the juvenile state, and in the production of longer shoots with many nodes as potential sites for flowering in black currant.

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