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Variation in seasonal timing of flower bud initiation in black currant (*Ribes nigrum* L.) cultivars of contrasting geographic origin

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SUMMARY
Seasonal time-courses of flower bud initiation and differentiation were monitored during two growing seasons (2011 and 2012) in 19 black currant cultivars of distant geographic origin, grown in the field at a South Norwegian locality (60°40'N, 10°52'E; 250 m asl). For comparison, the time-courses of shoot elongation growth in 15 of the same cultivars were also monitored during the 2012 growing season. The results revealed widely different seasonal timings of growth cessation and floral initiation in cultivars of different latitudinal origin. High latitude cultivars originating from crosses and selections of local, wild black currant populations from the Kola peninsula and Swedish Lapland were particularly early and had ceased growing and had initiated floral primordia by mid-June. This was approx. 5 – 6 weeks earlier than any of the other cultivars from lower latitudes. However, these also varied in their earliness of growth cessation and flower initiation in relation to their latitudinal origin. Many cultivars bred and selected in Southern Scandinavia, Scotland, and Poland did not cease growing and initiate floral primordia until late August, 9 weeks after the early, high-latitude cultivars. Overall, the 19 cultivars constituted a typical latitudinal cline in their photoperiodically controlled timing of growth and flowering responses. The high-latitude Russian cultivars 'Imandra' and 'Murmanschanka' represent valuable additions to the limited diversity of the available black currant gene-pool, and may be of particular use for breeding cultivars adapted to the sub-Arctic environment.

Flower bud initiation in black currant (*Ribes nigrum* L.) takes place in late-Summer in response to declining photoperiods (Nasr and Wareing, 1958; 1961a, b; Tinklin *et al*., 1970; Sønsteby and Heide, 2011). The critical photoperiod for this short day (SD) response was found to be relatively long (approx. 16 h) in a range of West European cultivars (Tinklin *et al.,* 1970; Heide and Sønsteby, 2011). Under natural day-length conditions, floral initiation was consistently preceded, by approx. 2 weeks, by a decline in shoot elongation growth, which was then followed by a complete cessation of growth (Nasr and Wareing, 1961a, b; Tinklin *et al.,* 1970; Sønsteby and Heide, 2011; Sønsteby *et al.,* 2012). Thus, although both growth cessation and floral initiation were induced by SD conditions, the successional responses showed that the critical photoperiods for the two responses differed by approx. 1 h (Sønsteby *et al.,* 2012). While early investigations indicated that low temperatures enhanced the SD induction process (Tinklin *et al.,* 1970), recent investigations under well-controlled temperature conditions revealed that both growth cessation and floral initiation were significantly enhanced and promoted by increasing temperatures in the 9º – 24ºC range (Sønsteby and Heide, 2011; Sønsteby *et al.,* 2012).

However, while these responses applied to a wide range of commercially cultivated black currant cultivars, which varied little in their environmental responses and seemed to represent a common gene pool (Kronenberg and Hofman, 1965; Sønsteby and Heide, 2011), the high-latitude Russian cultivars 'Imandra' and 'Murmanschanka', originating from the Kola peninsula, were found to deviate markedly from other cultivars in their temperature responses, seasonal timing of growth cessation, and flower bud initiation (Sønsteby *et al.,* 2012; Heide and Sønsteby, 2012). Thus, under natural day-length conditions at Ås, Norway (59º40'N), cessation of growth in 'Murmanschanka' plants occurred in mid-June, at 9ºC, when the day-length was still increasing; while, at higher temperatures, it was gradually delayed, up to 13 July at 21ºC (Sønsteby *et al.,* 2012). At this temperature, cessation of growth did not occur until the first week of August in five other cultivars. Similarly, 'Murmanschanka' had formed fully differentiated floral primordia by 20 July (the earliest sampling date), when the natural day-length at Ås was still approx. 18 h. This was more than 6 weeks ahead of any of the other five cultivars, which varied internally by ± 2 weeks in their timing of floral initiation. Earliest among these was 'Öjebyn', while 'Narve Viking' and 'Ben Hope' were particularly late (Sønsteby *et al.,* 2012). It has also been found that the cultivar 'Imandra', which is one of the parents of 'Murmanschanka', differed from the common commercial cultivars in its sensitivity to SD. While 7 d of SD exposure (10 h) were enough to trigger flowering in all 'Imandra' plants at temperatures ranging from 9º – 21ºC, 14 d of SD exposure were required for 'Ben Tron' and 'Narve Viking' at temperatures of 15º – 21ºC, while 21 SDs were needed for the same response in 'Ben Hope'

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at the same temperatures (Heide and Sønsteby, 2012). In the latter cultivar, the induction requirement exceeded 21 SDs at 9ºC.

On the basis of these findings, we have studied the seasonal timing of growth cessation and floral bud initiation in a total of 19 black currant cultivars of varying geographic origin under field conditions over 2 years at a South Norwegian location. The progress of floral bud initiation and differentiation were determined by repeated weekly sampling of buds and examination of the dissected buds under a stereo-microscope. The results are reported and discussed below.

MATERIALS AND METHODS

Field-grown bushes of 19 black currant (*Ribes nigrum* L.) cultivars from a cultivar field repository were used for these investigations. The repository was established in 2009 at the Bioforsk Experimental Centre Apelsvoll, in the central part of South Norway (60º40'N; 10º52'E; 250 m asl). Bushes were planted at a spacing of 1.5 m x 4 m, and pruned and fertilised according to standard commercial recommendations. During the 2011 and 2012 growing seasons, the initiation and differentiation of flower buds were monitored on a selected shoot in each of five bushes of each of the 19 cultivars. In the 2012 season, shoot growth was also monitored in nine bushes of 15 of the same cultivars. Separate shoots were used for growth and flowering observations. The names and geographic origins of the 19 cultivars used in the investigation are listed in Table I.

Vigorously growing, 1-year-old shoots were selected and labelled, different shoots being used each year. Incremental growth of the terminal shoot on each selected shoot was monitored by weekly measurements of the new growth. Starting in the second week of June, lateral buds on the selected shoots were sampled every week to determine their flowering stage. Buds from the middle part of each shoot were removed by a shallow slit with a sharp scalpel, and the flowering stages were determined by dissection and examination of the fresh buds under a stereo-microscope. The flowering stage of the primary flower was scored according to the examples shown in Figure 1. Bud sampling was terminated when

TABLE I
Geographic location and latitude of origin of the 19 black currant cultivars used in this investigation

Cultivar name	Geographic location of origin	Latitude of origin
'Imandra'	Apatity, Kola, Russia	67º30' N
'Murmanschanka'	Apatity, Kola, Russia	67º30' N
'Surprise of Jelsakova'	Apatity, Kola, Russia	67º30' N
'Kola Souvernir'	Apatity, Kola, Russia	67º30' N
'Nordlys'	Apatity, Kola, Russia	67º30' N
'Sunderbyn II'	Sunderbyn, near Luleå, Sweden	65º40' N
'Öjebyn'	Öjebyn, near Piteå, Sweden	65º20' N
'Sunniva'	Ås, Norway	59º40' N
'Hedda'	Ås, Norway	59º40' N
'Kristin'	Ås, Norway	59º40' N
'Narve Viking'	Ås, Norway	59º40' N
'Ben Alder'	Invergowrie, Dundee, Scotland	56º30' N
'Ben Tron'	Invergowrie, Dundee, Scotland	56º30' N
'Ben Tirran'	Invergowrie, Dundee, Scotland	56º30' N
'Ben Avon'	Invergowrie, Dundee, Scotland	56º30' N
'Ben Dorain'	Invergowrie, Dundee, Scotland	56º30' N
'Ben Hope'	Invergowrie, Dundee, Scotland	56º30' N
'Intercontinental'	Balsgård, Kristianstad, Sweden	56º10' N
'Tiben'	Skierniewice, Poland	51º58' N

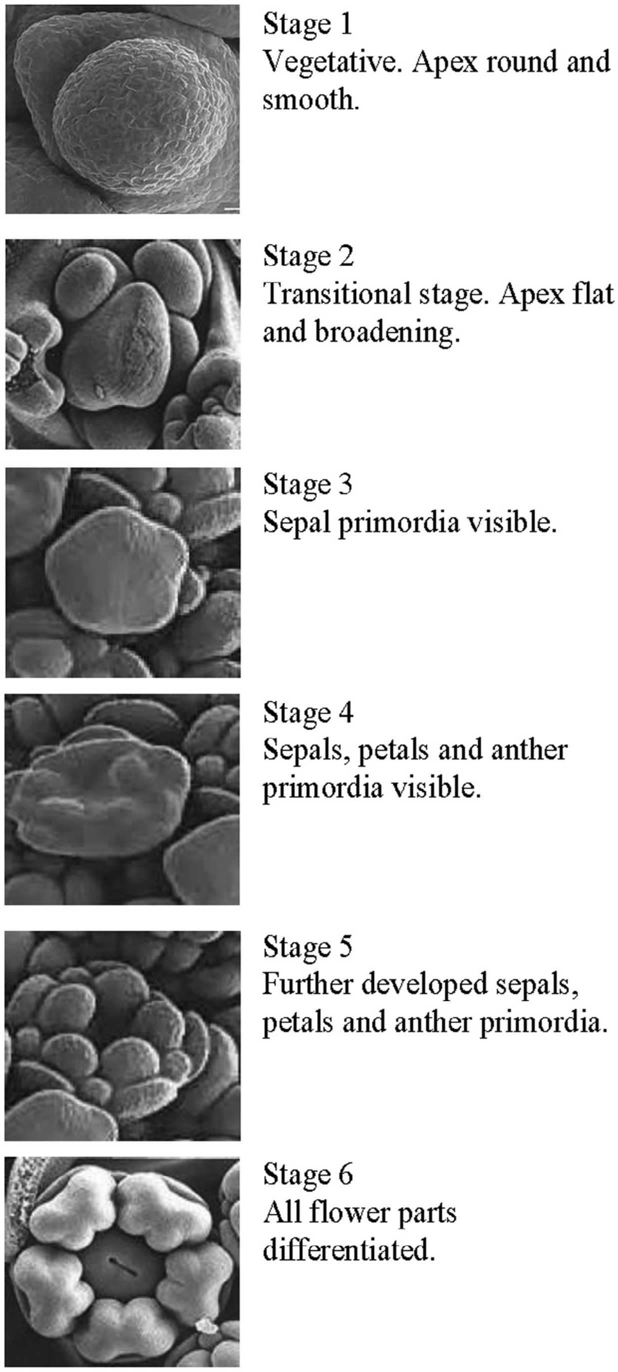

FIG. 1
Scanning electron microscopy images of black currant flower bud primordia at different stages of differentiation. Buds at Stages 1, 2, 3, 4, 5, and 6 are indicated. Reproduced from Kvam (1986) by courtesy of the Department of Plant and Environmental Sciences, Norwegian University of Life Sciences, Ås, Norway.

the primary flower of all buds had formed carpel primordia (Stage 6). The daily average monthly mean temperatures at Apelsvoll for June, July, and August in 2011 and 2012, and the 30-year (1961 – 1990) normal temperatures for the same months, are shown in Table II.

The results are presented as the means of five plants for each weekly observation of flowering stage, and of nine plants for the shoot growth measurements. No further statistical treatments of the results were performed.

TABLE II
Monthly mean temperatures for June, July and August 2011 and 2012, and the corresponding 30-year normal temperatures for the period 1961-1990 at the Bioforsk Experimental Centre Apelsvoll, Norway (60º40'N; 10º52'E; 250 m asl)

Month	Mean temperature (ºC) 2011	Mean temperature (ºC) 2012	Normal temperature (1961-1990)
June	14.6	12.1	13.7
July	15.8	14.5	14.8
August	14.2	14.1	13.5
Mean of means	14.9	13.6	14.0

Data are from the Norwegian Meteorological Institute, Oslo.

RESULTS

In both years, flower bud initiation was earliest and occurred simultaneously in the high-latitude, Russian cultivars 'Imandra', 'Murmanschanka', 'Kola Souvernir', 'Nordlys', and 'Surprise of Jelsakova', all of which originating from the Kola peninsula (Figure 2A, B). In these cultivars, the first visible changes at the apical meristem were observed in mid-June. One week later, just after the Summer solstice, the same changes were observed in the cultivar 'Sunderbyn II', originating from the township of Sunderbyn in Northern Sweden. In these six cultivars, the differentiation of floral primordia progressed rapidly such that, by the first week of July, primordia of all flower parts were visible in the primary flower of all plants (Stage 6).

The first visible signs of flower initiation were observed in the Norwegian cultivars 'Sunniva' and 'Hedda', and in the Swedish cultivar 'Öjebyn', approx. 5 – 6 weeks after the Russian cultivars. In 2011, these three Scandinavian cultivars were almost synchronous; while, in 2012, 'Sunniva' was slightly earlier than the other two. In this group of cultivars, and in particular in the cooler 2012 season (Table I), differentiation of floral primordia progressed a little more slowly than in the early Russian group, resulting in a further delay of 1 week at Stage 6. Another group consisting of the Scottish cultivars 'Ben Alder', 'Ben Tron', and 'Ben Tirran', the Norwegian cultivar 'Kristin', and the Polish 'Tiben' then followed, with some variation between years. The latter initiated floral primordia approx. 2 – 3 weeks after the three Scandinavian cultivars. Finally, the late cultivars 'Narve Viking', 'Ben Avon', 'Ben Dorain', 'Ben Hope', and 'Intercontinental' underwent floral initiation and differentiation. These cultivars started floral initiation in late-August, 9 weeks after the high-latitude Russian cultivars, and completed differentiation of all parts of the primary flowers 11 weeks after the latter (Figure 2).

Shoot elongation growth was monitored in the 2012 season in 15 cultivars, representing all major response types. The results in Figure 3 show that the cultivars also varied widely in their earliness of growth cessation, and that the timing of the process was closely related to the timing of floral initiation. In general, shoot growth started to slow-down approx. 2 weeks before floral primordia became visible in the dissected buds, while the complete cessation of shoot growth usually followed 1 week later. Particularly early were the high-latitude Russian cultivars 'Imandra' and 'Murmanschanka', which ceased growth by 11 June, followed 1 week later by 'Sunderbyn II'. These were followed, in due course, by an intermediate group consisting of 'Sunniva', 'Hedda', and 'Öjebyn' with growth cessation around 16 July, and then the cultivars 'Kristin' and 'Ben Tron' 2 weeks later (by 30 July). Last were the cultivars 'Narve Viking', 'Tiben', 'Ben Tirran', 'Ben Dorain', 'Ben Hope', 'Ben Avon', and 'Intercontinental', all of which showed growth cessation by 6 August (Figure 3). The overall annual shoot growth was determined mainly by the earliness of growth cessation, although growth vigour had an additional effect in cultivars such as 'Ben Tirran' and 'Tiben'.

DISCUSSION

The results in Figure 2 and Figure 3 show large differences in the seasonal timing of growth cessation and flower bud initiation in black currant cultivars of contrasting geographic origin. Most notable was the early cessation of growth and initiation of floral primordia in cultivars from high-latitudes. Thus, in the five Russian cultivars and in 'Sunderbyn II', cessation of growth and floral bud initiation occurred before mid-Summer, when the solar day-length at Apelsvoll was approx. 19 h and still increasing. All five Russian cultivars were released from the Polar Research Station at Apatity (67º30'N), and originated from crosses and selections of local, wild black currant populations from the Kola peninsula (Samuelsen and Nilsen, 2008). The cultivar 'Sunderbyn II' was also a selection from a wild black currant population found near the township of Sunderbyn (65º40'N), close to Luleå in Swedish Lapland (Hjalmarsson and Wallace, 2004). These six cultivars constituted a separate group having distinctly earlier cessation of growth and initiation of floral primordia than any of the other cultivars (Figure 2; Figure 3).

However, the cultivar 'Öjebyn', which is also putatively of high-latitude origin, was quite different and ceased growing and initiated floral primordia 5 – 6 weeks after the early group. This agrees with the results of Heide and Sønsteby (2011), who found no significant difference in the critical photoperiod of 'Öjebyn' and a range of other cultivars of more southerly origin. Nor was there any significant difference in the seasonal timing of growth cessation and floral initiation in these cultivars under controlled temperature and natural day-length conditions (Sønsteby and Heide, 2011; Sønsteby *et al.,* 2012). The cultivar 'Öjebyn' is of unknown origin, but is reported to have been found by chance near the Öjebyn Horticultural Experimental Station in the township of Öjebyn (65º20'N), near Piteå in Swedish Lapland (Hjeltnes, 2003; Hjalmarsson and Wallace, 2004). However, the present results, and those cited above, support the anecdotal notion that the cultivar 'Öjebyn' was not native to the high-latitude environment in which it was found (Hjalmarsson and Wallace, 2004; Heide and Sønsteby, 2011). The cultivar may have a lower-latitude origin and was subsequently naturalised to the high-latitude environment or, it could have originated from a "bumble bee cross" between a local plant and a cultivar from a lower-latitude grown at the Experimental Station. The intermediate earliness of the cultivar, as demonstrated in the present investigation, supports the latter possibility (Figure 2; Figure 3). Furthermore, the similar behaviour of 'Öjebyn' and the Norwegian cultivars 'Sunniva' and 'Hedda' was as expected, since the latter cultivars are selections from a

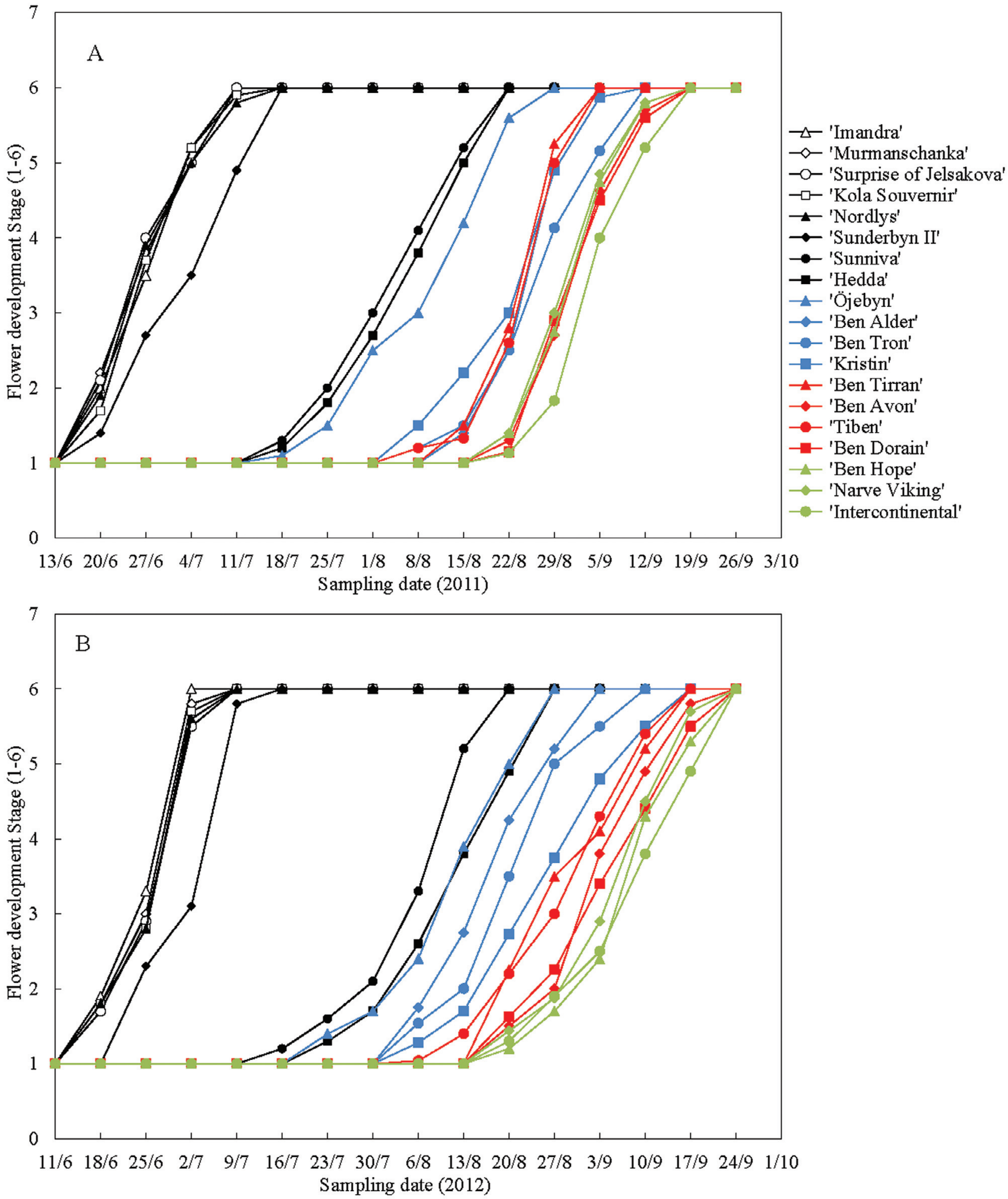

FIG. 2

Time-courses of flower bud initiation and differentiation in 19 black currant cultivars grown in the field at the Bioforsk Experimental Centre Apelsvoll, Norway (60º40'N) during the 2011 (Panel A) and 2012 (Panel B) growing seasons. Each datum point represents the mean of five buds from five different bushes.

cross between 'Öjebyn' and the Finnish cultivar 'Melalahti' (Hjeltnes, 2003).

The similar responses of the Norwegian 'Kristin' and the Scottish 'Ben Tron' are in agreement with earlier findings (Heide and Sønsteby, 2011; Sønsteby and Heide, 2011). This was not surprising, since 'Kristin' was selected from a cross between 'Ben Tron' and a 'Hedda' hybrid (Hjeltnes, 2003). This means that 'Öjebyn' is a grandparent of 'Kristin'. It is also of interest to note that 'Ben Tron' has 'Öjebyn' as one of its great grandparents, as a source of mildew resistance (Hjeltnes, 2003). Of similar earliness was the cultivar 'Ben Alder' which, together with 'Ben Tron', was earlier than the rest of the cultivars from the Scottish Crop Research Institute

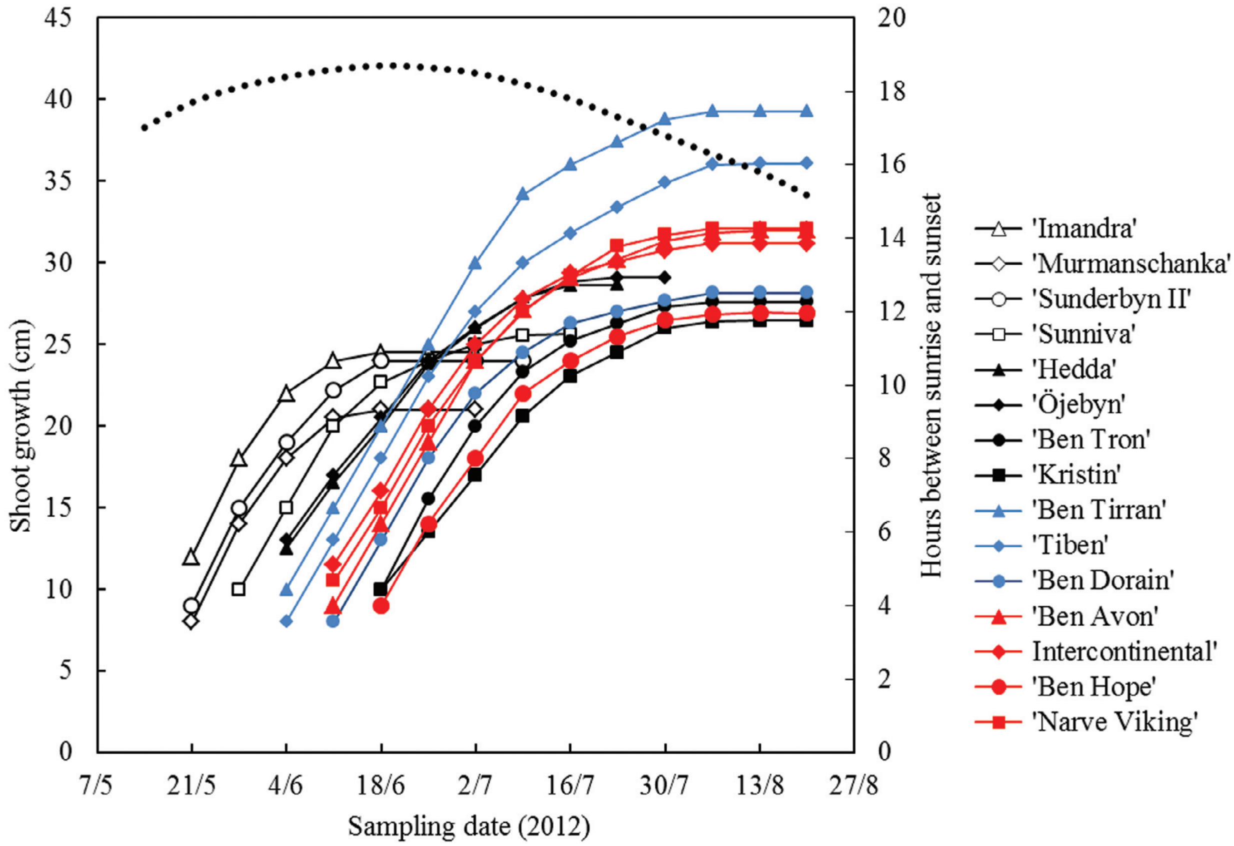

FIG. 3
Time-courses of shoot elongation growth in 15 black currant cultivars grown in the field at the Bioforsk Experimental Centre Apelsvoll, Norway (60°40'N). Seasonal changes in the natural photoperiod are indicated. Each datum point represents the mean of nine shoots from nine different bushes.

(SCRI). These two cultivars appeared well adapted to the Nordic environment and are important commercial cultivars in both Sweden and Norway (*cf.* Sakshaug, 1994). The other SCRI cultivars were all rather late, as were 'Narve Viking', 'Intercontinental', and 'Tiben' of South Norwegian, South Swedish, and Polish origins, respectively.

The seasonal timing of floral initiation, and the succession of cultivars in the process, were nearly identical in both years (Figure 2A, B), although the cooler July temperatures in 2012 slowed-down the floral differentiation process somewhat in the late cultivars in that year. The present results from field conditions at Apelsvoll (60º40'N), and earlier results from phytotron compartments with natural daylight conditions at Ås, Norway (59º40'N; Sønsteby and Heide, 2011; Sønsteby *et al.,* 2012), are in close agreement. The present results are also in good agreement with earlier findings from field observations at Ås by Kvam (1986) who reported that 'Hedda' and 'Öjebyn' had visible flower primordia by the first week of August, while cultivars of Dutch and British origin, followed 2 – 4 weeks later.

The present results are also in good agreement with results from related studies at other geographic locations. Since photoperiod is a function of both season and latitude, the timing of floral initiation in a photoperiod-sensitive plant such as black currant, will vary with latitude. As summarised by Tinklin *et al.* (1970), the timing of floral initiation in black currant cultivars has been shown to vary across Europe from mid-May/early-June at Bologna, Italy (44º30'N), to late-June/early-July in southern England (51ºN), and from early-August in southern Scandinavia (60ºN) to late September in the Arctic Circle at Rovaniemi, Finland (see Tinklin *et al.,* 1970; Sønsteby and Heide, 2011). This is in good agreement with the results for the late cultivars under the present conditions. It is notable, however, that the high-latitude Russian cultivars were almost as early at Apelsvoll, Norway (60º40'N) as the lower-latitude cultivars were at Bologna, Italy, approx. 16º further South. Such results highlight the importance of proper, latitude-specific selection in cultivated plants with a wide geographic distribution.

Overall, our results demonstrated a typical latitudinal cline in the photoperiodically controlled growth and flowering responses of black currant cultivars of varying geographic origin. The only exception was 'Öjebyn', but, as discussed above, this cultivar was obviously not of such high-latitude origin as previously reported. Such latitudinal clines in the seasonal timing of growth cessation are common and well-documented in a wide range of temperate woody plants (see Heide, 1974; Håbjørg, 1978, and references therein) and are of fundamental adaptive importance. Furthermore, the very early cessation of growth, even before mid-Summer, observed in the high-latitude black currant cultivars studied, suggests that these plants, like other woody plants of sub-Arctic origin, require almost continuous daylight (midnight-sun conditions) to maintain shoot growth (*cf.* Heide, 1974; Håbjørg, 1978). Thus, in a controlled environment experiment, it was found that a photoperiod of 20 h was not sufficient to support continuous growth in the high-latitude cultivars 'Imandra' and 'Murmanschanka' (Sønsteby and Heide, unpublished results). Clearly, the high-latitude Russian cultivars are genetically distant from the West-European commercial black currant cultivars and are uniquely adapted to the sub-Arctic environment. Preliminary trials with some of these cultivars at Tromsø (69º40'N) have given particularly promising results with 'Murmanschanka', which was reported to be high-yielding and early maturing with large berries on long trusses (Samuelsen and Nilsen, 2008). The high-latitude Russian cultivars also carry important resistance genes that make them of general interest for future black currant breeding.

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