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Climate warming enhances flower formation, earliness of blooming and fruit size in plum (*Prunus domestica* L.) in the cool Nordic environment

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ABSTRACT

The predicted and ongoing climate warming is expected to affect many aspects of plant development. We analysed data from a 31-year series of observations (1985–2016) on spring phenology and flowering and fruiting performance of three plum cultivars in an experimental orchard at Ås in southeast Norway (59° 40′N; 10° 50′E). Regression analyses revealed a trend of increasing March and April temperature during the study period that was highly significantly ($P < 0.001$) negatively correlated with the date of full bloom (FB). On average for all cultivars, blooming was advanced by 10 days over the study period. August and September temperature, which also increased significantly during the study period, was closely positively correlated with the amount of flowering in the subsequent spring and also interacted with early spring temperature in advancing blooming time. Investigation of the time of floral initiation in two of the studied plum cultivars revealed that the transition to reproductive development took place in early to mid-August. This finding strongly suggests that the close positive correlation between August-September temperature and the amount of flowering in plum observed in this and other studies, is causally linked to a specific physiological effect of elevated temperature on the flower bud formation process.

Increasing March and April temperatures during the last 30 years has advanced blooming and spring phenology in plum and the resulting extension of the growing season has led to increasing fruit size at harvest. We conclude that so far, the ongoing climate warming appears to have been positive for plum production in the cool Nordic environment. However, an increasing risk of frost associated with earlier blooming will represent a potential negative effect of continued warming.

1. Introduction

According to the Intergovernmental Panel on Climate Change (IPCC, 2014), the future climate is predicted to be warmer and wetter, and the changes will be particularly marked at high latitudes. Over the last decades, we can already observe ongoing climatic changes in agreement with these predictions. The most notable changes in Norway are more precipitation and increased frequency of floods, as well as milder winters and elevated spring and autumn temperatures. As a result, the length of the growing season has grown by several weeks in the fruit- and berry-production regions in Norway (Norwegian Meteorological Institute).

The climate has strong effects on many aspects of plant life such as phenology and productivity (Lambers et al., 2008; Schwartz and Hanes, 2010) that may have large consequences for food production and security (Olesen and Bindi, 2002; Kaukoranta et al., 2010). Especially in the Nordic climate, which is characterized by a cool and short growing season, vegetation may be highly sensitive to climate change, especially changes in temperature. The changes will be particularly critical for perennial and woody plants such as fruit trees, in which deviations in temperature can have lasting effects. Therefore, effort has been made in investigating and predicting the effects of a changing climate on performance and productivity of fruit trees, including the plum (e.g. Atkinson and Lucas, 1996; Døving, 2009, 2011; Hänninen and Tanino, 2011; Atkinson et al., 2013; Rivero et al., 2016). Analysis of long-term data observation series has proved very useful for such studies (Martínez-Lüscher et al., 2017, and references therein).

Many physiological processes in fruit trees are directly affected by temperature. Prominent among these are developmental processes such as flower bud formation (FBF) and induction and release of winter

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dormancy (Atkinson and Lucas, 1996; Ruiz et al., 2007; Horvath, 2009). In both pome fruits and stone fruits, FBF takes place in late summer and early autumn in the year preceding flowering and fruiting. Wells and Bukovac (2000) found that in Michigan, USA, the first morphological signs of flower initiation in the 'Stanley' plum cultivar took place in late June, 60 days after full bloom. They also found that the highest density of flowering nodes was present on second and third year-old wood. However, the effects of environmental factors on flower initiation is poorly known and understood in these species, and results are particularly scanty for plum (Gur, 1985). An unusual characteristic of plum and several other members of the Rosaceae family is that unlike other temperate trees, they are insensitive to short photoperiods for induction of growth cessation and winter dormancy (Nitsch, 1957; Heide and Prestrud, 2005; Heide, 2008). It is therefore generally considered that they are insensitive to photoperiod for flowering control as well.

However, regression analyses of data from a 40-year registration series (1934–1974) from a farmer's field in the fjord district of western Norway revealed that fruit yield was closely positively correlated with temperature in August-September in the previous year. For each 1 °C higher average temperature in these months, the yield increased by 27% (Måge, 1975). Likewise, regression analysis of yield variations for plums in three fruit cooperation districts in western Norway yielded a highly positive correlation between fruit yield and the July-August temperature in the previous year (Døving, 2009). Positive effects of autumn temperature on next year's flowering and fruiting was also demonstrated in 'Conference' pears in UK where artificial warming in October advanced flowering time and increased both yield and fruit number in the following season (Atkinson and Lucas, 1996). The importance of autumn temperature for flower initiation and subsequent fruit yield is also firmly documented for soft fruits such as *Rubus* and *Ribes* (Heide and Sønsteby, 2011; Sønsteby and Heide, 2011).

Another important developmental process that is directly controlled by temperature is the breaking of bud dormancy. It was early demonstrated that exposure of dormant buds to low temperatures in the 10 °C to −5 °C range for several weeks is required for dormancy release in a wide range of temperate tree species including fruit trees (Vegis, 1964). It should be noted that it is not notably low temperatures but temperatures slightly above freezing (0 – 5 °C range) which are optimal for the process. Dormancy release is not an all-or-none response, but is gradually attained by increasing duration of chilling as manifested by an increasing proportion of breaking buds and decreasing forcing time to budburst (Heide, 1993). Måge (1971) studied the duration of dormancy in fruit trees and bushes under outdoor conditions at Ås, Norway and found that plum buds had the longest dormancy period among a range of studied species, with dormancy release (75% buds sprouting within 20 days at 15 °C) by mid-March. After dormancy release, budburst is promoted by increasing temperatures (forcing period). However, because intermediate temperatures in the 5–15 °C range are partly effective for both dormancy release and progress to budburst, and since there is an overlapping period when both processes are progressing, budburst is markedly earlier after mild winters than after cold winters in the Nordic climate (Heide, 1993). Likewise, Martínez-Lüscher et al. (2017) reported that delayed chilling appeared to counteract flowering advances of apricot in southern UK.

Because of the strong positive correlations reported between fruit yield in plum and August-September temperature in the preceding year (Måge, 1975; Døving, 2009), we expected that also the amount of flowering might be similarly correlated with autumn temperature in the previous year. In light of the ongoing climate warming with elevated winter and spring temperatures, and the known effects of temperature on dormancy release and progress to budburst, we also hypothesized that budburst and flowering in plum might have advanced markedly over the last few decades. Accordingly, we analysed data from a 31-year series of observations (1985–2016) on the relationship between temperature and spring phenology and flowering performance of three plum cultivars in an experimental orchard at Ås in southeast Norway. In 2012, we also studied the time of growth cessation and floral initiation in two of the plum cultivars in the same orchard.

2. Materials and methods

2.1. Plant material and growing site

The study is based on data from registrations of the phenology and flowering and fruiting performance of the plum cultivars 'Ive', 'Mallard' and 'Victoria' grown in the experimental orchard of the Norwegian University of Life Sciences at Ås in southeast Norway (59° 40′N; 10° 50′E, 95 m a.s.l.) over the years 1985- 2016. The trees were grafted on 'Saint Julien A' rootstocks and planted in rows at a distance of 2.5 x 5 m. Each cultivar was represented by 8 trees in two replicates. They were pruned by renewal pruning in late winter every year during the study. In dry periods, the trees were sprinkle irrigated and when needed, fruitlets were thinned by hand in early July to an internal distance of ca. 5–8 cm along the length of the fruiting shoots in order to reduce variation in fruit load between years as much as possible. Fertilization and plant protection was performed according to standard plum growing practices in Norway. Effective pollination of the trees was secured by the location of a number of beehives at the edge of the orchard.

2.2. Data observations and collection

Days to full bloom (FB = 90% open flowers) was observed for each cultivar, but because of little variation between cultivars, the means for the three cultivars were usually used for the calculations. Abundance of flowering was estimated visually according to a scale from 0 (very low) to 5 (very high). The weight of 100 fruitlets was recorded at four sampling dates (every two weeks from 1 June to 15 August) and at fruit maturity (harvest). Earliness of flowering was recorded and presented as days to FB from 1 January (i.e. Julian days).

For determination of the time of growth cessation of the trees, we labeled five randomly selected shoots at the top and at the lower part of the tree, respectively, on each of two trees and monitored their growth increments by weekly measurements of shoot length. The shoots were located on the south side of the crown at approximately 180 cm above ground level. Buds for defining of the time of flower initiation were likewise sampled at weekly intervals from both spurs and the basal part of current season extension shoots on the same two trees. The severed buds were immediately dissected and examined for their stage of flower development under a stereo microscope using the scanning electron microscope images presented by Wells and Bukovac (2000) as reference. A 7-stage scale was used for classification of buds; stage 1 for vegetative buds, and stage 2 for the first morphological evidence of flower initiation, and stage 7 for fully differentiated flower buds with all flower parts present.

2.3. Statistics and calculations

Pearson correlations were calculated according to standard methods (Snedecor and Cochran, 1967). Despite of the well-known limitations of Pearson correlation analysis; i.e. a priori selection of window lengths, this simplistic linear approach was chosen because of its proven usefulness in analysis of long term phenological data series (Fitter and Fitter, 2002; Schleip et al., 2008; Fujisawa and Kobayashi, 2010; Wang et al., 2014).

For the evaluation of the relationship between temperature and the various developmental stages, the heat sums for the relevant periods in terms of growing degree days (GDD) were used. GDD was calculated by the following equation:

$$GDD = \frac{Tmax + Tmin}{2} - Tbase$$

Where ‘Tmax’ and ‘Tmin’ are the mean daily maximum and minimum temperatures, respectively, for the studied period, and base temperature ‘Tbase’ is the threshold temperature below which the specific process studied does not progress. To provide indication of the threshold temperature, GDD was calculated with base temperatures varying from 0 °C to 6 °C (GDD 0–6). The GDD and other temperature data used were obtained from The Norwegian Meteorological Institute (2016) and The Online Meteorological Service for Agriculture (2016). For validation of the multiple regression model (presented under section 3.1.), the same variables as used for the 1988–2008 period were used to develop a new model, which was then used to predict the FB date for the years 2009–2016 (cf. Døving, 2011).

For all statistical calculations, Excel® and a Minitab® Statistical Software programme package were used (Release 15, Minitab Inc., State College, PA, USA).

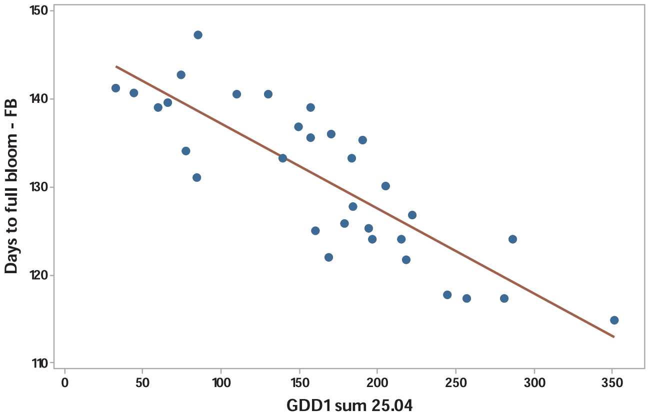

Fig. 2. Relationship between GDD1 temperature sum up to 25 April and Julian days to FB for the three studied plum cultivars.

3. Results

3.1. Time of blooming versus spring temperature

The mean date of FB for the three cultivars, together with the mean March, April and May temperature during the studied 31-year period are presented in Fig. 1. The mean date of FB was 16 May with a variation of 32 days (25 April in 1990 to 27 May in 1996). Analysis of the climate data revealed an increasing trend for mean March and April temperature, while no specific trend was observed for the mean May temperature. The increasing spring temperature was associated with an earlier mean date of FB for the plum cultivars resulting in ca. 10 days advancement of FB across the years 1985–2016. Thus, a strong negative correlation between early spring temperature and blooming time was observed ($r = -0.657$ and -0.644, respectively for March and April temperatures with $P < 0.001$).

A strong negative correlation between days to FB and cumulative GDD up to 25 April (the earliest flowering date observed) was also revealed (Fig. 2). Highly significant negative correlation coefficients for the relationship was calculated with $r = -0.827$; - 0.838; -0.838; -0.835; -0.819; -0.774, and 0.711, respectively, with base temperatures ranging from 0 °C to 6 °C. The best prediction of blooming time was obtained when base temperatures of 1 °C or 2 °C were used for the GDD calculations (Fig. 2). These results indicate that any March and April temperature above zero advances the flowering time in plum. Similar to spring temperature, also the temperature in September increased over the studied time period (Fig. 3), and as shown in Fig. 4, this trend was also negatively correlated with days to FB ($r = -0.447$; $P < 0.001$).

Based on the correlations between days to flowering and both September temperature and cumulative GDD sum up to 25 April with base temperature 1 °C (GDD1 sum 25.04.), the following multiple regression model for prediction of plum blooming time was calculated for the Ås location: **days to FB from 1 January = 154.80 – 0.0268 Sept. temp. – 0.0916 GDD1 sum 25.04.; $R^2 = 70.5$; SEE = 4.8.** This model gives a better prediction than GDD1 sum 25.04. used as a single variable. Fig. 5 presents the comparison between calculated and the actually observed days to blooming as means for the three studied plum cultivars. Because of the short time period between budburst and FB, days to budburst (green foliage showing) and days to FB was closely correlated as would be expected ($r = 0.987$; $P < 0.001$).

Since dormancy of plum winter buds is fully released at Ås by mid-March (Måge, 1971), it can be concluded that the flowering

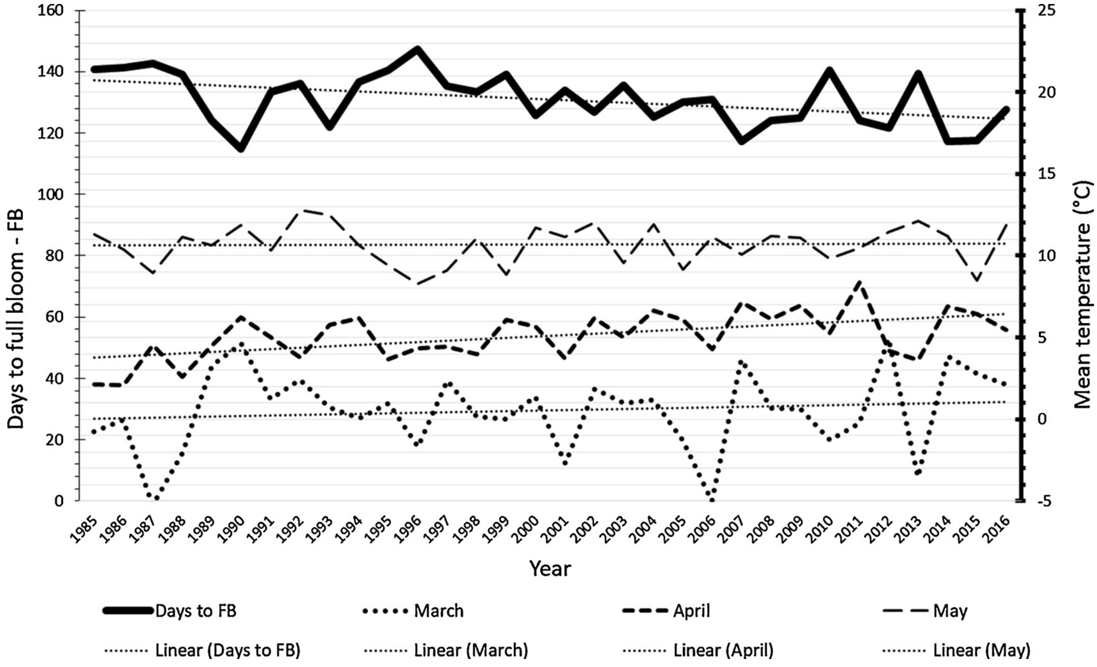

Fig. 1. Trends in March, April and May temperatures at Ås, Norway, and the corresponding trends in days to FB (Julian date) for the three studied plum cultivars over the years.1985–2016.

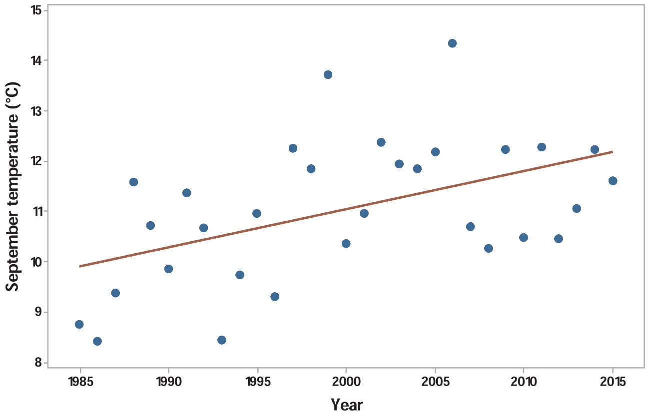

Fig. 3. Scatterplot and trend line for the average daily mean September temperature for each year across the 1985–2015 period.

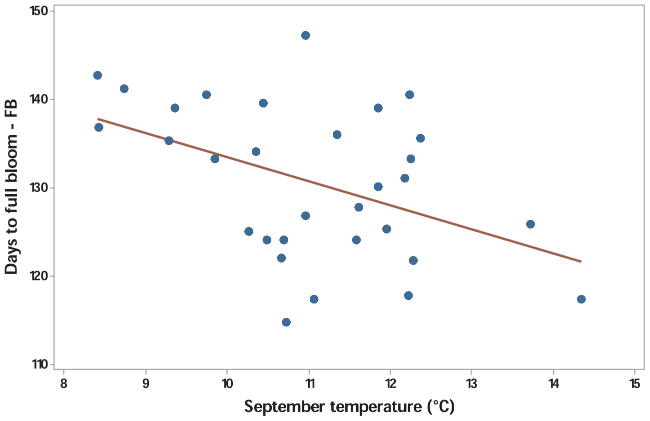

Fig. 4. Scatterplot and trend line for the relationship between average daily mean September temperature and days to FB in the subsequent year for the three studied plum cultivars.

Table 1
Correlation coefficients for the relationships between sums of temperature in August, September and August-September together versus the amount of flowering in the following year for three plum cultivars.

Cultivar	August	September	August-September
'Ive'	0.343	0.374*	0.415*
'Mallard'	0.523**	0.549***	0.621***
'Victoria'	0.113	0.234	0.197
All cultivars	0.339**	0.388***	0.420***

Levels of significance: * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

advancement effect of elevated spring temperature was causally and physiologically related to the forcing effect of elevated March and April temperatures. On the other hand, the causal effect of elevated September temperature is likely related to enhancement of the flower differentiation process that would render the flower buds to enter the winter at a more advanced state of development. This concurs with the earlier flowering in pears in response to artificial autumn warming reported by Atkinson and Lucas (1996).

3.2. *Amount of flowering versus previous year autumn temperature*

An overall positive correlation was observed between August, September and August plus September temperature and the amount of flowering in the subsequent spring (Table 1). The highest correlation coefficients were noted for 'Mallard', whereas none of the coefficients for the 'Victoria' correlation was significant at the 5% level. However, the overall correlation for all cultivars combined was highly significant (Table 1). The correlation with August and September temperature together was stronger than those for the separate months. The analysis also revealed a highly significant intercorrelation between the cultivars for the trend in the amount of flowering across the years ($r = 0.580$; $P < 0.001$). These results concur with the strong correlations that Måge (1975) and Døving (2009) observed between August–September temperature and fruit yield in the subsequent year in the main plum producing districts in Western Norway. On the other hand, while these authors observed a strong negative effect of high January and February temperature on fruit yield, there was no correlation between January-February temperature and the amount of flowering in our data from Ås

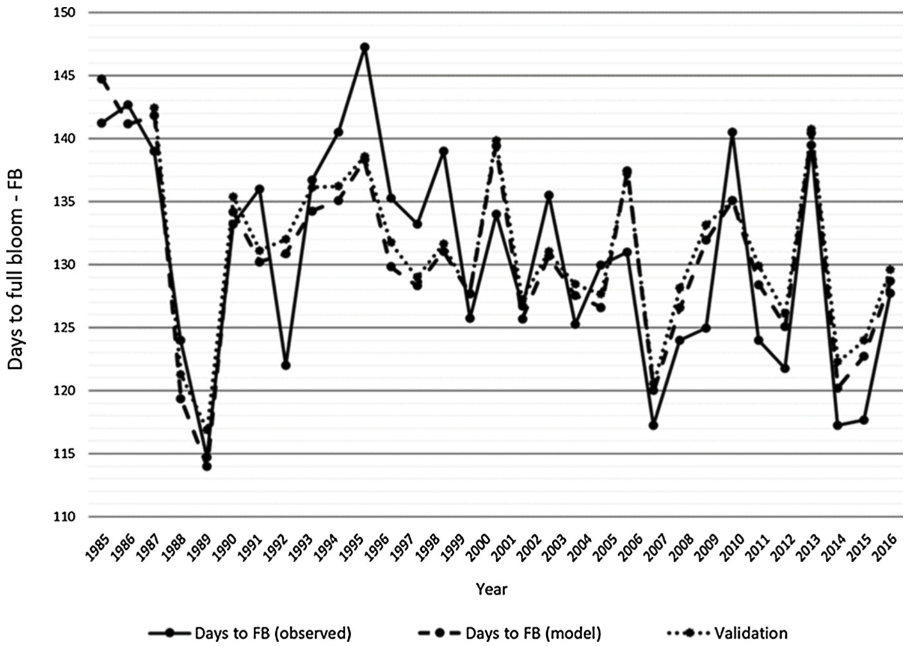

Fig. 5. Comparison between modelled, validated, and actually observed days to FB as means for the three studied plum cultivars over the years.1986–2016.

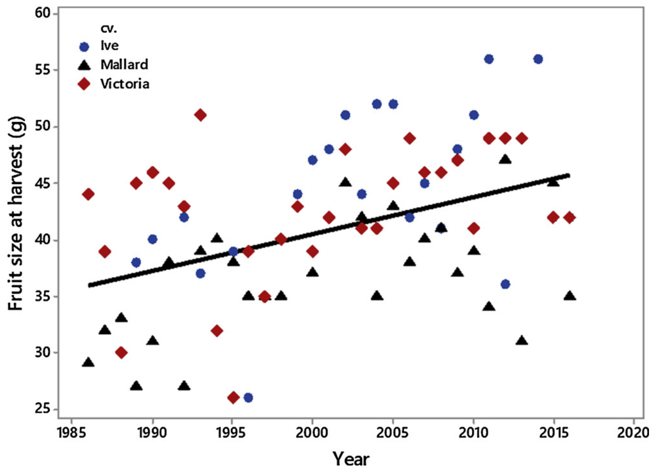

Fig. 6. Scatterplot and trend line for the mean fruit size at harvest for each year across the 1985–2016 period for the three studied plum cultivars.

(r = 0.231; $P = 0.210$).

3.3. Fruit size versus time of flowering

No significant correlation was observed between fruit size at harvest and the amount of flowering. The lack of correlation between these parameters indicates that the thinning management has been effective and sufficient. However, the statistical analysis revealed a strong positive intercorrelation between the cultivars for fruitlet weights at the various sampling dates (r = 0.830; $P =$ 0.001). A strong negative correlation between days to FB and fruitlet weight on 1 July (r = -0.761, $P < 0.001$), indicates that the length of the fruit development phase is the main factor determining fruitlet weight at any time during the summer. This concurs with the results of Måge and Grønnerød (2007). During the 31-year observation period (1985–2016), a general trend for increasing fruit size at harvest was also observed for all cultivars (Fig. 6). Since flowering was advanced by ca. 10 days during the same period (Fig. 1), while no significant trend for harvest time was observed, the total time available for fruit development also increased by ca. 10 days during the study period. In other words, when early flowering took place, a proportional increase in the length of the fruit growth and development period was observed (Fig. 7).

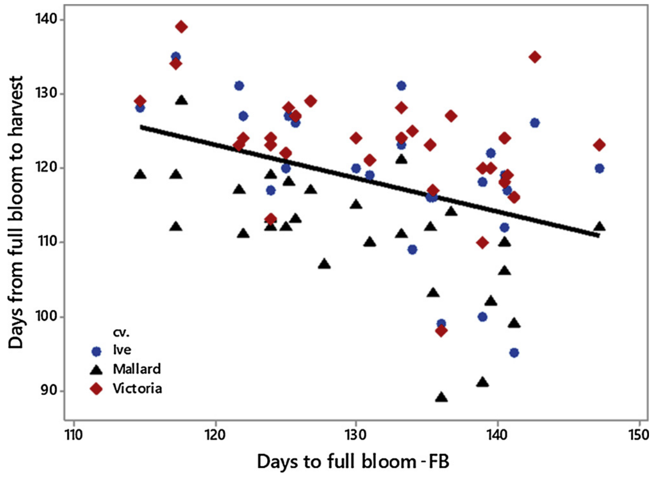

Fig. 7. Scatterplot and trend line for the relationship between days from FB to harvest and Julian date for FB for the three studied plum cultivars. Pearson correlation coefficients for 'Ive': r = -0.530, p = 0.006; 'Mallard': r = -0.598, p = 0.001; 'Victoria': r = -0.389, $P =$ 0.034, for all cultivars: r = -0.385, $P <$ 0.001.

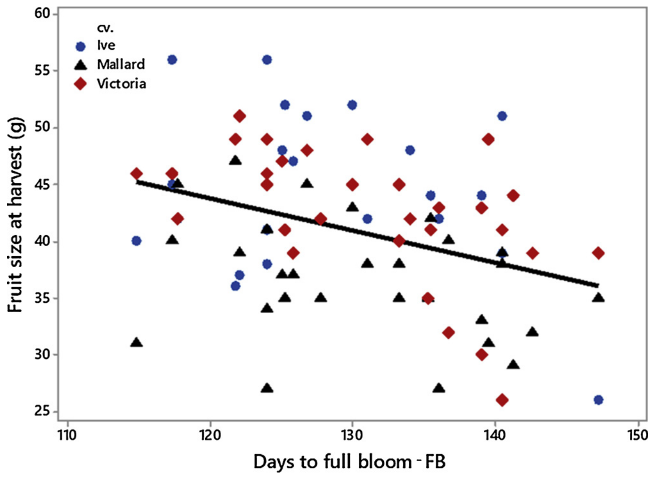

Fig. 8. Scatterplot and trend line for the relationship between fruit size at harvest and days to FB for the three studied plum cultivars.

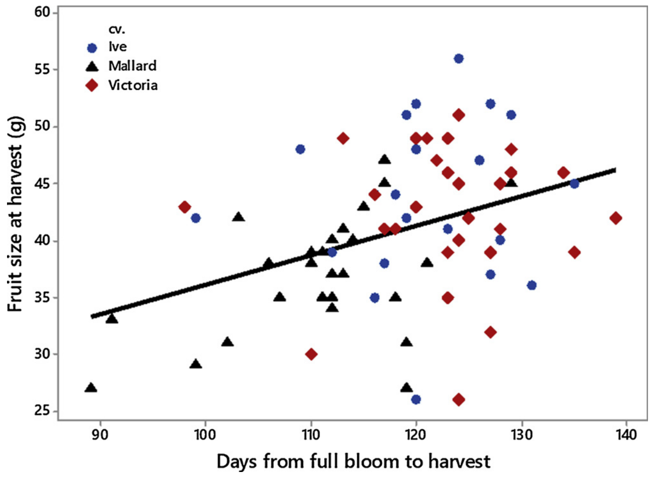

Fig. 9. Scatterplot and trend line for the relationship between days from FB to harvest and fruit size at harvest for the three studied plum cultivars. Pearson correlation coefficients for 'Ive': r = 0.533, p = 0.011; 'Mallard': r = 0.407, p = 0.032; 'Victoria': r = 0.331, $P =$ 0.201, for all cultivars: r = 0.367, $P =$ 0.001.

At the same time, late blooming was negatively correlated with fruit size at harvest for all cultivars as shown in Fig. 8 (r = -0.352; $P =$ 0.001). The highest correlation was noted for cv. Victoria (r = -0.517; $P =$ 0.003). There was thus a significant positive correlation between fruit size at harvest and the number of days from FB to harvest for all cultivars (Fig. 9). Since the period between blooming and fruit maturity (harvest) increased during the observed 31-year period, fruit size at harvest also increased across the years for all cultivars (Fig. 9).

3.4. Seasonal timing of shoot growth and floral initiation

Shoot growth of the plum cultivars gradually levelled off during July and came to a complete cessation by mid-August. Although the top shoot elongated twice as much as the less vigorous shoots positioned lower down the crown, their time of growth cessation was the same (Fig. 10). The first morphological evidence of floral initiation (stage 2) coincided with growth cessation in dissected spur buds but was few days ahead of growth cessation in buds from the basal part of the current season extension shoots. In both types of buds, floral initiation took place a few days earlier in 'Victoria' than in 'Mallard', while the further courses of flower bud differentiation was entirely parallel in the two cultivars. The flower differentiation process lasted for five weeks

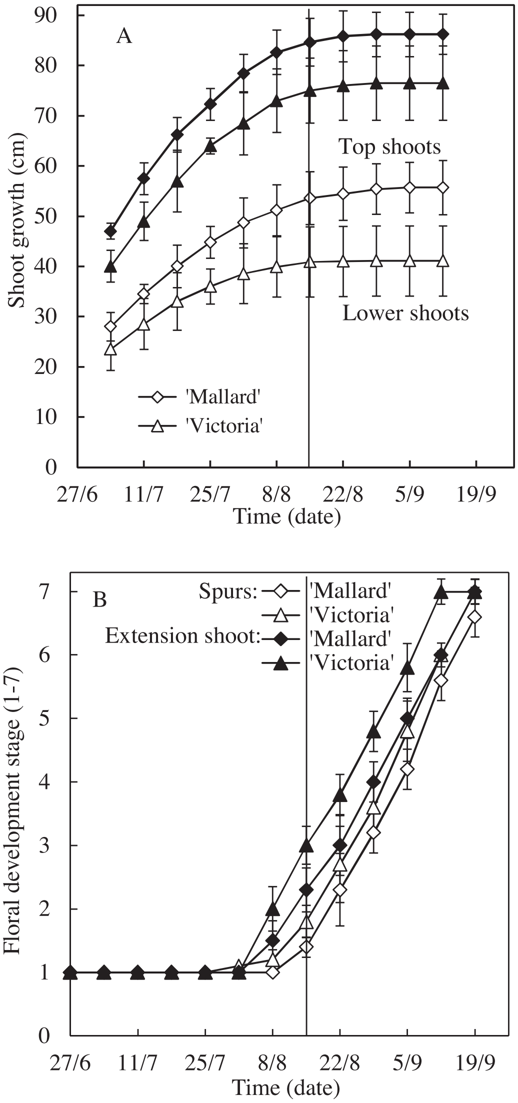

Fig. 10. Time courses of shoot elongation growth (Panel A) and the progress of flower bud initiation and differentiation in two plum cultivars grown in the experimental orchard at Ås, Norway (Panel B). The data are means ± SE of 5 shoots from each of two trees (A), and of 3 buds of each type from each of the same two trees (B).

and was not completed before mid-September (Fig. 10).

4. Discussion and conclusions

The results of these analyses are in close agreement with the findings of Måge and Grønnerød (2007) for the cultivars ‘Ive’, ‘Mallard’ ‘Opal’ and ‘Victoria’ for the 14-year period 1989–2003 at the same growing site. The results demonstrate that temperature is a powerful climatic factor for regulation of plum growth and development in the cool Nordic environment. The observed earlier blooming in plum in the wake of the ongoing climate warming concurs with the results of a similar analysis of blooming time in the apple cultivar ‘Gravenstein’ at Ås over a 70-year period (Rivero et al., 2016). Like the present results with plum, the analysis revealed a highly significant negative relationship (r = -0.98) between April and May temperature and days to FB which was reduced by 16 days during last 50 years with increasing temperature. The stronger weight of May temperature in apple versus March temperature in the present analysis of plum is apparently due to the approximately one month later flowering in apple. A parallel trend of advanced blooming was also reported for 12 other apple cultivars over the last 30-year period (1986–2016) by these authors. On average for all cultivars, FB was advanced by 9 days over this period. Regardless of variation in earliness among the cultivars, the advanced blooming response was unanimous among the cultivars. These results are also in close agreement with trends for budburst and blooming time reported for apple and a range of other temperate zone trees in Norway (Nordli et al., 2008). The positive correlation between blooming time and September temperature in the previous year further adds to the predictability of blooming time of plum. The physiological mechanism underlying such an advancement effect of September temperature on blooming time is probably an advancement effect on the flower bud differentiation process under warm September conditions.

The strong positive correlation between August-September temperature and the amount of flowering in the following spring is also in close agreement with the reports of Måge (1975) and Døving (2009) with plum. These results strongly suggest that relatively warm temperatures during these months are conducive to flower bud formation in plum trees and further contribute to explain the advancement effect of September temperature on flowering time. Closely similar effects were observed in the related sweet cherry (*Prunus avium*), in which August-September mean maximum temperature was strongly positively related to yield in the subsequent season (Døving, 2011). The results are particularly interesting in light of the negligible knowledge of the environmental control of flowering in plum trees (Gur, 1985).

The finding that floral initiation in the cultivars ‘Mallard’ and ‘Victoria’ took place at Ås in early to mid-August (Fig. 10), strongly support the suggestion that the widely documented positive relationship between August-September temperature and the magnitude of flowering and yield of plum trees in the following season is causally related to temperature enhancement of flower bud formation. However, the fact that September temperature contributed at least as much to increased flowering as did August temperature, indicates that the temperature enhancement effect was not limited to flower initiation but also included stimulation of the entire flower differentiation process, which lasted until mid-September. Coincidence of floral initiation with growth cessation suggests the two processes might be causally associated as has been shown for *Ribes* and *Rubus* species (Heide and Sønsteby, 2011; Sønsteby and Heide, 2011). The relatively weak correlation between autumn temperature and amount of flowering in’ Victoria’ (Table 1), suggests that this cultivar might be less dependent on elevated autumn temperatures for good flower formation than are the other two cultivars.

An interesting overall effect of warmer March and April temperatures and the associated longer period of fruit growth and development is that plum fruit weight at harvest has also increased in the wake of the observed climate warming. A possible causal mechanism behind this trend may be that early flowering is commonly followed by a period of low temperature. Therefore, fruit development have likely been slow under such conditions, and thus given rise to an overall extension of the period of fruit growth and development. This would also mean a prolonged period of accumulated solar radiation, and that may possibly be the physiological mechanism underlying the associated increase in fruit weight (cf. Monteith, 1977).

In conclusion, the observed positive correlation between August-September temperature and the abundance of flowering of plum trees in the subsequent year, together with the coincidence of flower initiation and differentiation during the same period, strongly suggest that the relationship is causally linked to temperature enhancement of the flower bud formation process. Furthermore, increasing March and April temperature during the last 30 years has advanced blooming and spring phenology in plum and the resulting extension of the growing season has led to increased fruit size at harvest. Thus, the ongoing climate warming appears so far, to have been beneficial for plum production in the cool Nordic environment. However, an increasing risk of spring frost associated with earlier blooming will represent a potential negative effect of continued warming.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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