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Extreme short-day induction requirements for flowering strawberry cultivar 'Malwina'

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16 **ABSTRACT**

17 We studied short-day induction of the strawberry cultivar ‘Malwina’ under both phytotron and
18 field conditions. Flowering was assessed by crown dissection of treated plants and subsequent
19 flowering performance. Serial dissections revealed no visible changes in crown apices during
20 the first 4 weeks of short day (SD) at 18°C in the phytotron, while after 6 weeks, all plants had
21 formed rudimentary flower primordia with visible sepals. At 9°C, the same stages were reached
22 after 8 and 10 weeks of SD, respectively. When subsequently forced in long day (LD) at 20°C,
23 no substantial flowering took place after less than 6 weeks SD treatment at 18°C, while full
24 flowering required 10 weeks of SD induction. At 9°C, full flowering was not obtained even
25 after 10 weeks of SD treatment. Under field conditions, the ‘Malwina’ plants did not reach
26 floral development stage 2 before 22 October, approximately a month after ‘Frida’ and ‘Sonata’
27 which reached this stage on 21 September, and three weeks after ‘Florence’. SD exposure
28 resulted in repeated crown branching in ‘Malwina’ and we suggest that early spontaneous
29 abortion of the emerging floral primordium takes place under unsaturated SD induction
30 conditions, thus causing crown branching and hence, delayed floral initiation and development.
31

32 **KEYWORDS**

33 Floral initiation; ‘Malwina’ strawberry; photoperiod; SD requirement; temperature

Introduction

Because of the economic importance of the cultivated strawberry (*Fragaria* x *ananassa* Duch.), the flowering physiology of the species has been extensively researched and reviewed. Most seasonal flowering (June-bearing) strawberry cultivars are classified as facultative short day (SD) plants. At temperatures bove 18-20°C, they require exposure to SD for induction of flowering, while at lower temperatures, most cultivars also initiate flowers in long days (LD) (Guttridge, 1985; Heide et al., 2013). However, the flower-inducing effect of SD is highly temperature dependent and is optimal at intermediate temperatures, while at temperatures < 12°C and > 21°C, short day induction efficiency is progressively declining (Guttridge, 1985; Heide et al., 2013). The critical photoperiod for SD induction is about 14-15 h, depending on the cultivar (Darrow & Waldo, 1934; Konsin et al., 2001). Therefore, under natural environment conditions, floral initiation takes place in late summer and early autumn when photoperiod and temperature become conducive for floral induction (Guttridge, 1985; Heide et al., 2013).

The minimum number of SDs required for induction of flowering is between 7 and 14, but can vary considerably in response to temperature conditions, length of the photoperiod, and daily light integral (Guttridge, 1985; Heide et al., 2013). With extension of the SD period beyond the critical length, the number of initiated flowers increases linearly with the additional number of SD cycles, at least up to 49 cycles, while further initiation ceases immediately when the plants are transferred to LD conditions (Konsin et al., 2001; Heide et al., 2013). For commercial greenhouse production, SD periods of 3-5 weeks duration are usually recommended. However, the SD requirement can vary considerably among cultivars, early cultivars generally needing the lowest number of SD cycles (Heide et al., 2013). In an experiment with six cultivars of distant origin, Sønsteby and Heide (2017) found that 4 weeks of 10-h SD at intermediate temperatures induced profuse flowering in all cultivars except the late-flowering and late-maturing 'Malwina' (Stoppel, 2012), which produced only a few flowers in a single plant at 15°C. By comparison, the cultivar 'Florence', which is also known to be slow-responding and late flowering (Opstad et al., 2011), produced profuse flowering with the 4-week induction period at both 15 and 21°C. After autumn-planting and overwintering in the field, flowering and fruit ripening was also delayed by 2-3 weeks in 'Malwina' compared with 'Florence' and even more so compared with the other cultivars (Sønsteby & Heide, 2017).

Basically, there are two principally different response patterns that can explain such a delayed flowering response: 1) the plants have an exceptionally short critical photoperiod for

floral induction which under natural light conditions postpones the date when the critical daylength is reached, or 2) the plants have a normal critical photoperiod but require an exceptionally large number of SD cycles for initiation of flowering. Since the 10-h photoperiod used in the cited experiment by Sønsteby and Heide (2017) is 4-5 h shorter than the critical photoperiod commonly found in seasonal flowering strawberry cultivars (Guttridge, 1985; Heide et al., 2013), the results strongly support the second alternative.

In order to learn more about this unusual flowering behaviour, we have studied flower induction in 'Malwina' strawberry in more detail under both phytotron and field conditions.

Materials and methods

Plant materials and handling

For the phytotron experiment, stock plants were dug in the field in early August at the NIBIO Experimental Centre Apelsvoll in South East Norway (60º40'N, 10º40'E, 250 m above sea level) and brought into a heated greenhouse maintained at minimum 21°C and 20 h photoperiod. Runners were collected from these plants on 6 September and rooted in 9 cm plastic pots in a peat based potting compost (Gartnerjord, LOG, Oslo, Norway with 10% added granulated perlite) under saturated atmosphere and the same temperature and light conditions. On 4 October, when the plants were well rooted, they were moved into the daylight phytotron of the Norwegian University of Life Sciences at Ås, Norway, where they were exposed to 10-h photoperiod at 9 and 18°C for 4, 6, 8, or 10 weeks. In the phytotron, the plants received natural daylight supplemented by 150 µmol quanta m^{-2} s^{-1} artificial light supplied by 400 W Philips HPI-T lamps from 0800 h to 1800 h. Control plants were exposed to 20 h photoperiod established by daylength extension with 80 W incandescent lamps. Temperatures were controlled to ± 1.0°C, and a water vapour pressure deficit of 530 Pa was maintained at both temperatures throughout day and night.

For the field experiment, over-wintered plug plants were received from an authorized producer and planted in the field at Apelsvoll in early June 2018 on raised beds with black polyethylene mulch at a spacing of 25 cm x 40 cm x 160 cm. Flowers were removed as they appeared, while runners were allowed to grow until 3 September when all runners were removed. For comparison, the well-known cultivars 'Florence', 'Frida' and 'Sonata' were included in the experiment. These plants were rooted current year runners which were planted in the field in early August 2018. Otherwise, the plants were treated as described above for the 'Malwina' plants.

Starting on 17 August, the progress of the floral initiation process of the plants was monitored by sampling and dissection of crowns at approximately 10-day intervals. Starting on 1 October, samples of plants were also dug at monthly intervals and forced in a greenhouse at 21°C and 20 h photoperiod for assessment of flowering performance. Furthermore, two groups of 15 plants were overwintered in the field, of which one group was dug in late April of the following spring for forcing in the greenhouse as ascribed above, while the other group was allowed to flower and fruit in the field for assessment of flowering and yield performance. Temperature conditions at Apelsvoll in the 2018-2019 autumn and winter season are shown in Figure 1.

Experimental design, data collection and analyses

The experimental design of the phytotron experiment was a split plot with temperatures as main plots and photoperiods as subplots. Each treatment had three replications, each with 14 plants on a separate trolley (9 plants for dissection and 5 for flowering performance). Plant growth and development during SD treatment was monitored by counting of the numbers of leaves, runners and crowns and by measurement of petiole length of the last fully developed leaf in each plant at completion of each treatment duration. On each occasion, 9 plants in each treatment were dissected for assessment of the flower development status of the main crown as described by Opstad et al. (2011), while 5 plants in each treatment were transplanted to 12 cm pots and set to flower in a heated greenhouse at 20°C and 20 h photoperiod. Flower development status of the dissected plants was scored according to a six-stage scale where stage 1 denotes entirely vegetative apices, and stage 2 the first visible sign of transition to generative development, while stage 6 denotes fully differentiated primary flower primordia (cf. Opstad et al., 2011). Flowering performance of the forced plants was recorded after 10 weeks of forcing of plants from each treatment.

The field experiment had three replicate beds with 60 plants each of each cultivar. At each sampling date, 2 plants from each replicate bed were dissected and examined for flowering status ($n = 6$). The dissections followed the same procedures as described above for the phytotron experiment. For assessment of flowering performance in the greenhouse and in the field, 5 plants from each replicate bed were used ($n = 15$).

Experimental data were subjected to analysis of variance (ANOVA) by standard procedures using a MiniTab® Statistical Software program package (Release 15, Minitab Inc., State College, PA, USA). Percentage values were always subjected to an arc sin transformation before performance of the ANOVA.

Results

Phytotron experiment

Runner formation declined sharply when the plants were transferred to SD and ceased almost completely after 4 weeks at both 18 and 9°C, while production of leaves continued at more or less constant, but temperature dependent rates in SD (Figure 2). This was accompanied by a strong and parallel decline in petiole length of the new-formed leaves at both temperatures. On the other hand, little crown branching took place during the first 8 weeks of SD, where after it started to increase at both temperatures.

Serial dissections of crowns revealed no visible changes in the crown apices during the first 4 weeks of SD at 18°C, while after 6 weeks, all plants had formed rudimentary flower primordia with visible sepal primordia (stage 2) (Figure 3). With continued SD, there was a more or less linear progress in flower primordia development all the way up to stage 6 after 10 weeks of SD. At 9°C, the first visible changes were observed in one half of the plants after 8 weeks, whereas floral stage 2 in all plants was not reached until 10 weeks of SD treatment.

The flowering performance of the plants when forced in LD at 20°C is shown in Table 1. The results show that although a single plant from 18°C formed a few flowers after 4 weeks of SD treatment, no substantial flowering took place with less than 6 weeks of SD treatment, while 100% flowering required 10 weeks of SD. Among the plants from 9°C, a couple of plants flowered with 6 weeks of SD, while full flowering was not obtained even after 10 weeks of SD treatment. The number of inflorescences and flowers per plant were always higher in plants exposed to SD at 18°C than in those at 9°C, and at both temperatures the numbers increased steadily with increasing length of SD treatment. With marginal SD induction, a few plants from both temperatures developed pronounced phyllody as shown in Figure 4. In plants from both temperatures, the time to anthesis decreased in parallel with increasing length of SD treatment. The trend of change was the same at both temperatures, but with a delay of approximately two weeks at 9 °C. Although the plants at 18°C had twice as many crowns as those at 9°C after 10 weeks of SD (Figure 2), the difference had evened out during the forcing period (Table 1).

Field experiment

Also under field conditions, 'Malwina' initiated floral primordia very late, and much later than the other cultivars (Figure 5). Thus, visible floral primordia at stage 2 was not observed until 22 October in 'Malwina', 3 weeks after 'Florence' and 5 weeks after 'Frida' and 'Sonata'. Further floral differentiation progressed in parallel in the four cultivars, so that at the last sampling on 9 November, 'Malwina' was still at floral stage 3.5 only, whereas 'Frida' and

169 'Sonata' had fully differentiated terminal flowers on their primary inflorescences, a floral stage
170 that was not reached in the 'Malwina' plants until in the following spring. Crown branching
171 increased rapidly in all cultivars during the first and second week of September, where after it
172 gradually levelled off in parallel with the decreasing autumn temperature (Figure 6). The
173 number of crowns was always highest in the 'Malwina' plants.
174 Greenhouse forcing of 'Malwina' plants dug in the field on 1 October produced similar
175 results (Table 2). Although most plants eventually flowered, it took more than 12 weeks of
176 forcing in LD at 20°C and the plants produced only one or two inflorescences each. When dug
177 on 1 November, all 'Malwina' plants flowered, but still only after nearly 11 weeks of forcing,
178 compared with 5-6 weeks in 'Frida' and 'Florence'. However, flowering was still rather sparse
179 in 'Malwina', with only 3 inflorescences and a total of 16 flowers per plant, compared with 6-
180 7 inflorescences and 45-60 flowers per plant in 'Frida' and 'Florence'. Also, in plants that were
181 overwintered in the field and dug and set to forcing on 23 April (when the soil had thawed),
182 flowering was still 10 to 15 days later in 'Malwina' than in the other cultivars. However, while
183 the number of inflorescences and flowers per plant decreased in 'Frida' and 'Florence' plants
184 forced in spring, it increased slightly in 'Malwina', indicating that continued flower initiation
185 had compensated for losses of flower primordia during the winter (Table 2). Furthermore, the
186 losses of flower primordia were largely eliminated in all three cultivars when the plants were
187 allowed to flower in the field under cooler temperature conditions. This response was most
188 pronounced in 'Frida' where greenhouse forcing in spring reduced flowering by nearly 50%
189 compared with November forcing or spring flowering in the field (Table 2). Another marked
190 difference between the cultivars was that while 'Frida' and 'Florence' plants developed 5-10
191 crowns, the 'Malwina' plants on average produced nearly 20 crowns plant^{-1} by the time of
192 flowering (Table 2).
193 The yield of the field-grown plants presented in Figure 7, show disappointingly low yields
194 of 'Malwina' compared with the other cultivars. Thus, the yield was only 54% of that of the
195 Norwegian cultivar 'Frida', and 62% of that of 'Sonata'. As usual, the date of 50% harvest was
196 delayed by approximately 3 weeks compared with these two cultivars.
197
198 **Discussion**
199 The results confirm our earlier results (Sønsteby & Heide, 2017) showing that the strawberry
200 cultivar 'Malwina' has an extreme SD induction requirement for flower initiation. Whereas
201 most other SD cultivars produced advanced flower primordia and attained saturated flowering

with 4 weeks of SD induction under optimal temperature conditions of 18-21°C (Guttridge, 1985; Konsin et al., 2001; Heide et al., 2013; Sønsteby & Heide, 2017), 'Malwina' required 10 weeks of SD under the same conditions for a similar flowering response. At suboptimal temperatures of 9°C, 'Malwina' produced only partial flowering even with 10 weeks of 10-h SD treatment (Figure 2, Table 1). Similarly, under field conditions at Apelsvoll in South East Norway, most SD cultivars developed visible flower primordia around mid-September (Opstad et al., 2011), whereas this stage was delayed for another 5 weeks till about 20 October in 'Malwina' (Figure 5). Even the relatively late-flowering and late-maturing cultivar 'Florence', which is commonly used for extension of the strawberry marketing season, initiated floral primordia 3 weeks ahead of 'Malwina'. This extreme SD induction requirement is apparently the main reason for the exceptionally late flowering and fruit maturation experienced in 'Malwina' under both experimental and commercial production conditions (Sønsteby & Heide, 2017). On the other hand, the slow response to the near-optimal SD photoperiod of 10 h is not compatible with the possibility that an exceptionally short critical photoperiod is the reason for the late flowering of the cultivar. Rather, the prompt cessation of runner formation and strong restriction of petiole length after 4 weeks of SD exposure (Figure 2), indicate normal SD signalling.

This unusual physiological behaviour may morphologically be associated with the excessive branching of the crown axis of 'Malwina' (Tables 1, 2; Figure 6). Normally, crown branching is the result of terminal flower formation and lateral displacement of the leading shoot (cf. Guttridge, 1985). However, in 'Malwina' the crowns had been branching repeatedly before the first inflorescence appeared. This suggests the occurrence of an early spontaneous abortion of the emerging floral primordium. Possibly, this could be caused by some sort of cultivar specific malfunction of the apical meristem. This would have the same effect as a soft pinch in causing outgrowth of subtending lateral meristems. In some ornamental SD plants such as poinsettia *(Euphorbia pulcherrima*), a marginal SD induction has in fact been used to bring about symmetrical branching of the stem (Rünger, 1967). The excessive and repeated branching of 'Malwina' (Figure 6, Table 2), provides strong support for the hypothesis. It may be argued that the results of the field experiment are not directly comparable due to different planting dates (early June and August, respectively). However, it is not likely that earlier planting of 'Malwina' should result in delayed flowering. Furthermore, coincidence in the timing of crown branching in all cultivars (Figure 6), together with several weeks difference in floral initiation (Figure 5) tend to exclude the possibility that different planting dates could be the reason for the differences in flowering time.

However, since the strawberry plant in fact appears to be a negative LD-plant rather than a regular SD-plant with a direct response to SD (cf. Guttridge, 1985), an alternative perspective of the results could also be suggested. Thus, by the use of donor-receptor pairs of runner plants connected by the stolon, Guttridge (1959) found that donor plants in LD delayed and sometimes inhibited flower formation in receptor plants in SD, while donors in SD failed to induce flowering in receptors in LD. Further spectral evidence for induction of flowering in strawberry by release from LD inhibition was provided by studies on the sensitivity of strawberry plants to R and FR irradiation indicating the temporal sensitivity of a LD-plant (Vince-Prue & Guttridge, 1973). It might therefore, be argued that the rapid cessation of runner formation and petiole elongation upon transfer to SD indicates that the photoperiodic response involved is a promotion of runnering by LD. However, the repeated branching of the crown in 'Malwina' plants during SD induction demonstrate that the mechanism involved is an impairment of the apical development taking place downstream of the triggering photoperiodic response.

Whatever the explanation, since flower initiation eventually took place also in the 'Malwina' plants, it is evident that an extended period of SD exposure is able to trigger and support the normal development of the inflorescence primordium also in this cultivar.

In commercial production, the late flowering characteristic of 'Malwina' has been of interest mainly for extension of the marketing season. However, the excessive crown branching of the cultivar (Table 2) results in shoot crowdedness and competition for space and light, and possibly constrained yields. Low yields of 'Malwina' has in fact been experienced by strawberry growers in both Norway and Finland (J. Haslestad, Norwegian Agricultural Advisory team), as well as in the present experiment, where 'Malwina' yielded only 55 to 60% of 'Frida' and 'Sonata', respectively. The destiny of 'Malwina' in commercial production therefore seems rather uncertain at present.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Table 1. Flowering performance of 'Malwina' strawberry plants exposed to varying durations of SD treatment at 9 and 18°C and subsequently forced in LD at 20°C for 10 weeks. The data are means of three replicates with 5 plants each.

Temperature (°C)	Weeks of treatment	Flowering plants (%)	Days to anthesis	Infloresc. plant^{-1}	Flowers plant^{-1}	Flowers inflor^{-1}	Crowns plant^{-1}
9	0	0.0	>100	0.0	0.0	0.0	-
	4	0.0	>100	0.0	0.0	0.0	4.0
	6	13.3	96.2	0.1	1.0	1.0	6.5
	8	73.3	75.0	1.9	13.9	5.6	7.3
	10	73.3	71.0	2.3	16.5	5.2	8.1
Mean		*32.0*	*88.4*	*0.9*	*6.5*	*2.4*	*7.5*
18	0	0.0	>100	0.0	0.0	0.0	-
	4	6.7	99.8	0.3	0.7	0.2	6.0
	6	80.0	76.9	5.0	12.8	2.0	7.8
	8	86.7	70.8	6.0	23.2	3.3	7.9
	10	100	59.5	7.5	38.1	4.9	6.1
Mean		*54.7*	*81.4*	*3.8*	*14.9*	*2.1*	*7.3*
Probability level of significance (ANOVA)							
Source of variation							
Temperature (A)		0.059	ns	0.03	ns	ns	Ns
Weks. of treatment (B)		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
A x B		0.002	0.003	<0.001	0.03	ns	0.001

Table 2. Flowering performance of field-grown strawberry cultivars after lifting at different times and forcing in a greenhouse at 20°C and 20 h photoperiod for 11 ('Frida' and 'Florence') or 14 weeks ('Malwina'). The flowering performance of plants flowering in the field in the spring 2019 is also included. The data are means of three replicates, each with 5 plants of each cultivar.

Cultivar	Date of lifting/ start forcing	Flowering plants (%)	Days to flower emergence	Days to anthesis	Infloresc. plant^{-1}	Flowers plant^{-1}	Crowns plant^{-1}
'Malwina'	1 Oct. 2018	89	77.3	87.7	1.8	14.4	17.6
	1 Nov. 2018	100	63.2	75.9	3.2	15.7	21.3
	23 Apr. 2019	100	27.6	39.2	3.5	21.7	16.7
	Field flowering	100	-	66.1*	4.9	36.9	19.2
'Frida'	1 Oct. 2018	-	-	-	-	-	-
	1 Nov. 2018	100	23.3	33.2	7.1	44.9	5.1
	23 Apr. 2019	100	13.2	22.5	3.9	23.2	7.8
	Field flowering	100	-	52.3*	7.9	45.3	10.0
'Florence'	1 Oct. 2018	-	-	-	-	-	-
	1 Nov. 2018	100	31.5	45.3	6.2	59.6	4.5
	23 Apr. 2019	100	18.2	28.5	4.8	31.0	9.7
	Field flowering	100	-	59.1*	5.6	33.1	9.0

*Days from 23 April

FIGURE LEGENDS

Figure 1. Temperature conditions at the NIBIO Experimental Centre Apelsvoll during late summer and autumn in 2018 and winter and spring 2019 (1 August 2018 – 1 July 2019).

Figure 2. Plant growth and development of 'Malwina' strawberry plants during 10 weeks of SD treatment at 9 and 18°C. The data are means of three replicates with 5 plants each ± SE.

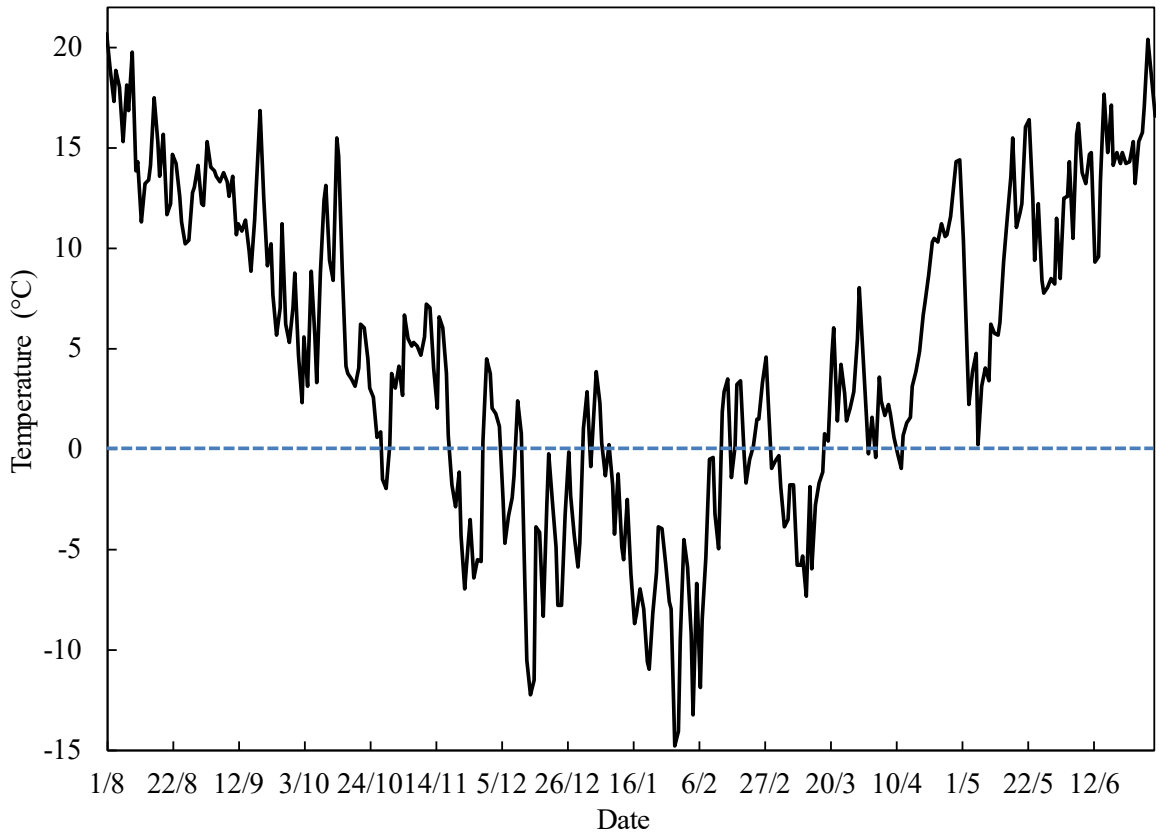
Figure 3. Time courses of successive floral development stages of 'Malwina' strawberry plants as affected by increasing duration of SD treatment in the phytotron at 9 and 18°C. The data are means of three replications with 9 plants each ± SE.

Figure 4. Abnormal flower development (phyllody) in 'Malwina' strawberry plants after marginal SD induction of 6 weeks at 9°C.

Figure 5. Time courses of successive floral development stages of four strawberry cultivars under natural field conditions at Apelsvoll. The data are means of three replicates with two plants each of each cultivar ± SE.

Figure 6. Time courses of cumulative crown branching of four strawberry cultivars under natural field conditions at Apelsvoll. The data are means of three replicates with two plants each of each cultivar ± SE.

Figure 7. Time courses of cumulative berry yield in four strawberry cultivars in 2019. Data are the means of 3 replicate plots with 0 plants per plot of each cultivar ± SE.



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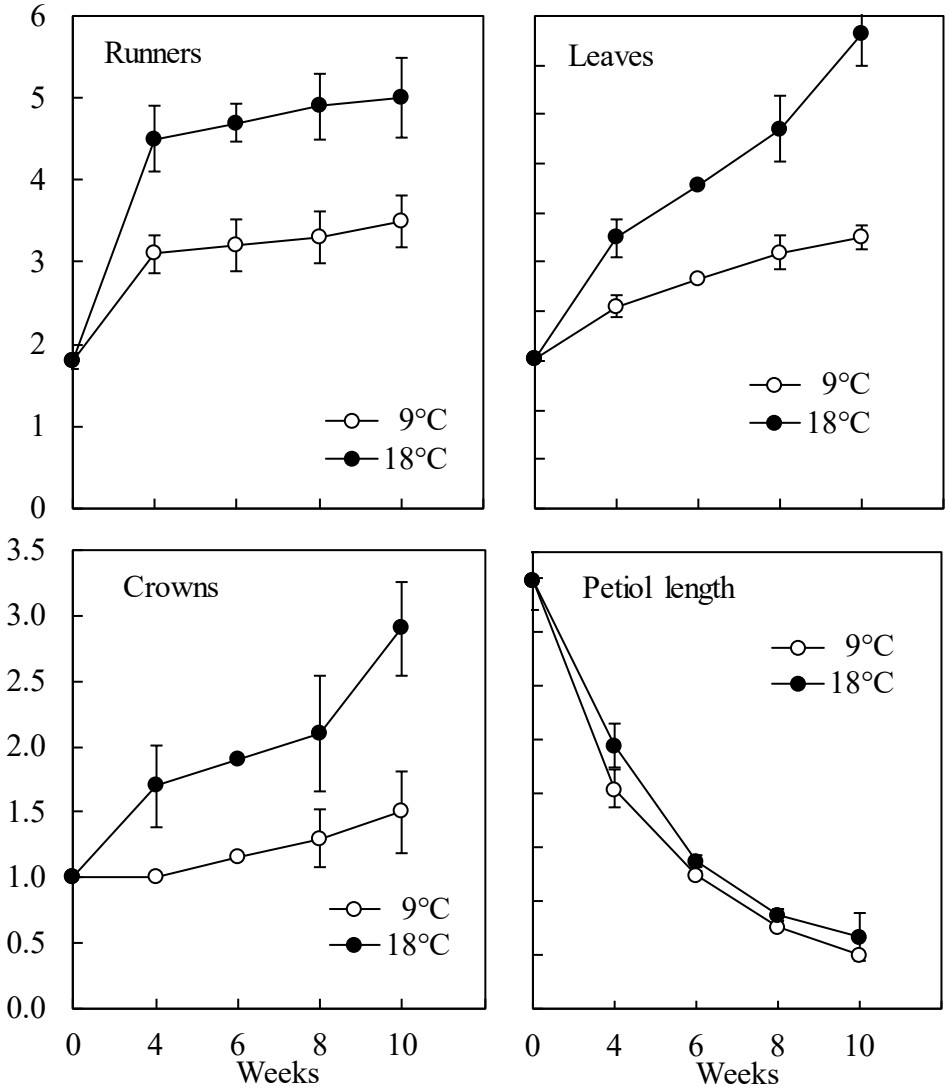

Figure 2. Plant growth and development of 'Malwina' strawberry plants during 10 weeks of SD treatment at 9 and 18°C. The data are means of three replicates with 5 plants each ± SE.

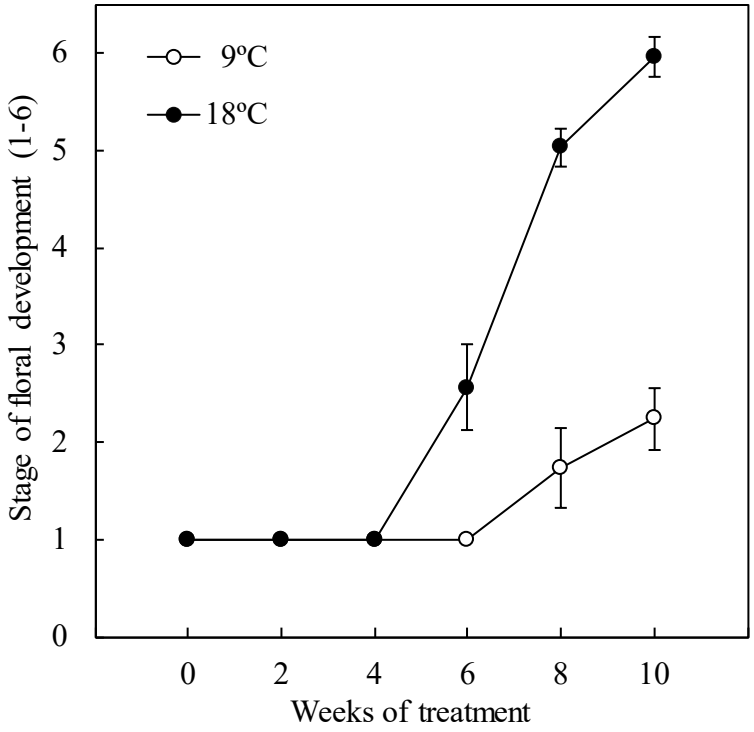

Figure 3. Time courses of successive floral development stages of 'Malwina' strawberry plants as affected by increasing duration of SD treatment in the phytotron at 9 and 18°C. The data are means of three replications with 9 plants each ±SE.

Figure 4. Abnormal flower development (phyllody) in ‘Malwina’ strawberry plants after marginal SD induction of 6 weeks at 9℃.

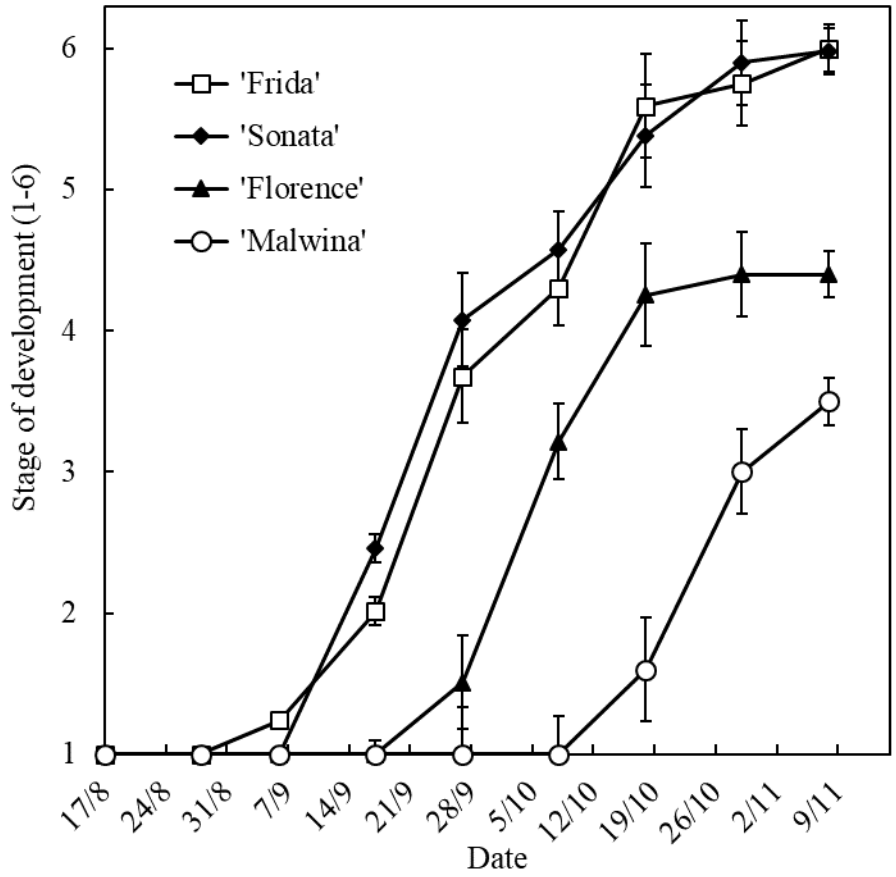

Figure 5. Time courses of successive floral development stages of four strawberry cultivars under natural field conditions at Apelsvoll. The data are means of three replicates with two plants each of each cultivar ± SE.

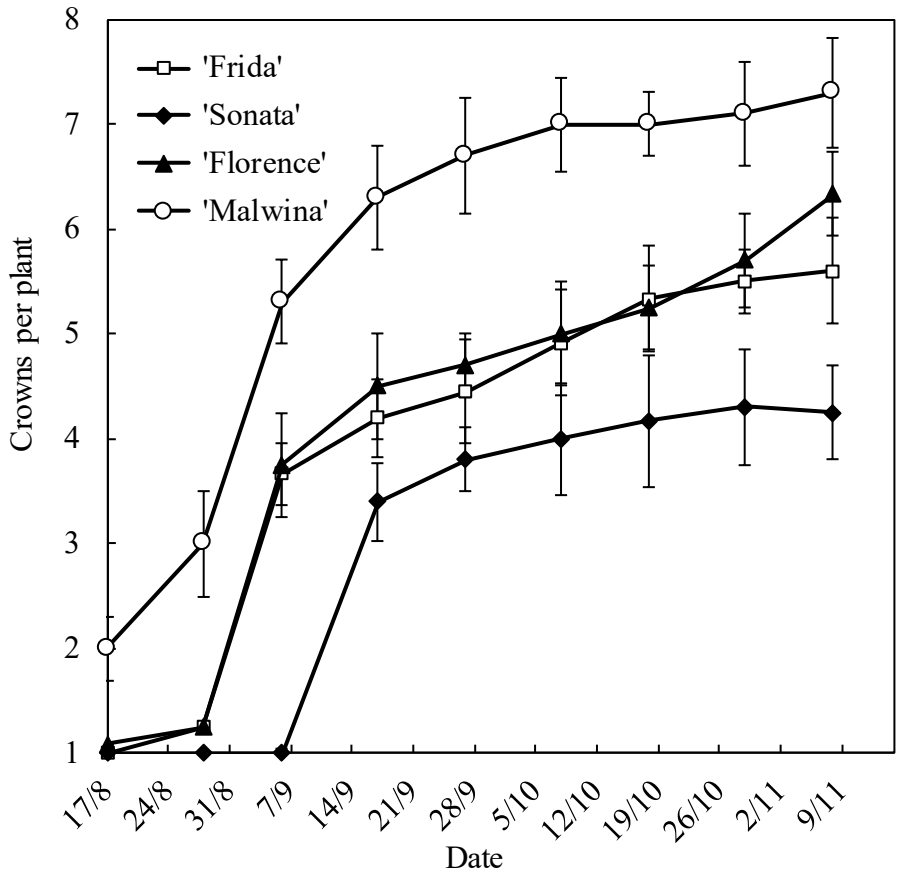

Figure 6. Time courses of cumulative crown branching of four strawberry cultivars under natural field conditions at Apelsvoll. The data are means of three replicates with two plants each of each cultivar ± SE.

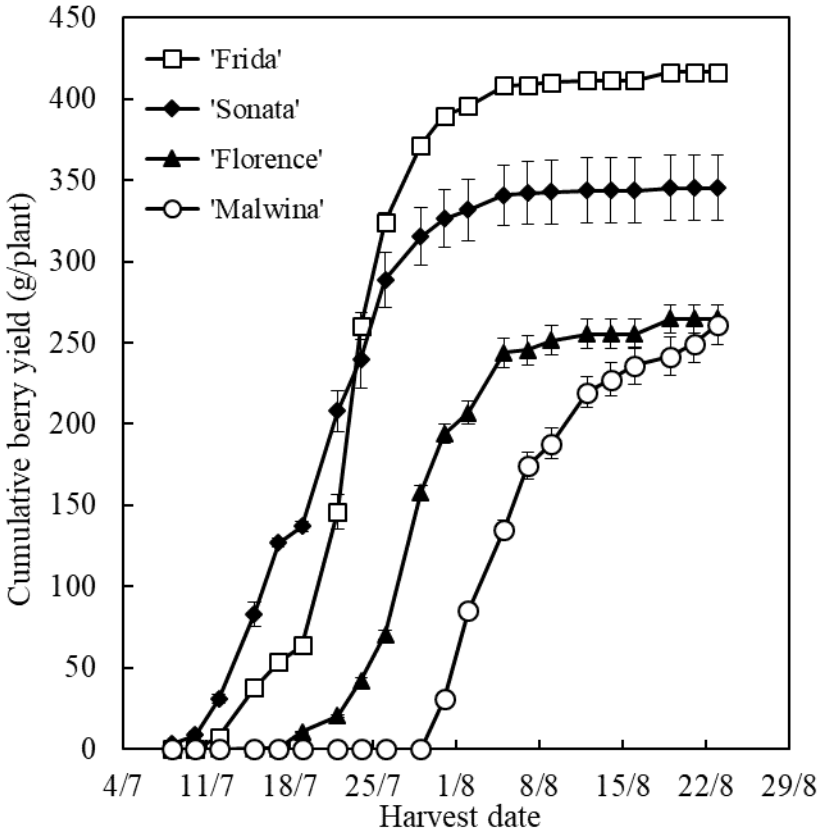

Figure 7. Time courses of cumulative berry yield in four strawberry cultivars in 2019. Data are the means of 3 replicate plots with 20 plants per plot of each cultivar ± SE.