Environmental regulation of dormancy, flowering and runnering in two genetically distant everbearing strawberry cultivars

R. Rivero[a,*], S.F. Remberg[a], O.M. Heide[b], A. Sønsteby[c]

[a] *Faculty of Biosciences, Norwegian University of Life Sciences, NO-1432 Ås, Norway*

[b] *Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway*

[c] *NIBIO, Norwegian Institute of Bioeconomy Research, NO-1431 Ås, Norway*

* Corresponding author.

E-mail address: rodmar.rivero.casique@nmbu.no (R. Rivero).

Environmental regulation of dormancy, flowering and runnering in two genetically distant everbearing strawberry cultivars

ABSTRACT

The environmental control of dormancy and its relation to flowering and runner formation is poorly understood in everbearing (EB) strawberry cultivars. We studied the topic by growing plants of the seed-propagated F1-hybrid 'Delizzimo' and the runner-propagated 'Favori' cultivar in daylight phytotron compartments under short day (SD) and long day (LD) conditions at temperatures of 6, 16 or 26 ℃ for 5 and 10 weeks. This was followed by forcing at 20 ℃ and 20-h photoperiod for 10 weeks with and without preceding chilling at 2 ℃ for 6 weeks. The results showed that dormancy in EB strawberry is regulated by a complex interaction of temperature, photoperiod and chilling in much the same way as known for seasonal flowering (SF) cultivars. Surprisingly, the EB cultivars exhibited the same SD dormancy induction response as SF cultivars, despite their opposite photoperiodic flowering requirements. However, at 26 ℃ the EB cultivars developed partial dormancy also under LD conditions. As known for SF cultivars, none of the EB cultivars became dormant at 6 ℃ regardless of daylength conditions, whereas they were increasingly sensitive to SD dormancy induction at intermediate and high temperatures. Similar to SF cultivars, the EB cultivars needed exposure to SD and relatively high temperatures for at least 10 weeks for attainment of the semi-dormant state that is typical for strawberry in general. As reported for SF cultivars, there was a close interrelation between the control of flowering, runner formation and dormancy also in the EB cultivars. 'Favori' had an obligatory LD requirement for flowering at 26 ℃ and was almost day neutral at 16 ℃, while 'Delizzimo' behaved as a quantitative LD plant at both temperatures, and both cultivars were completely day neutral at 6 ℃. Except for the stricter LD control of flowering in 'Favori', the overall environmental responses were quite similar in the two genetically distant cultivars. Chilling for six weeks at 2 ℃ was adequate for complete reversal of the constrained elongation of leaf petioles and flower trusses in dormant plants, but had little or no effect on the degree of flowering and runner formation.

Keywords: Chilling; Dormancy; *Fragaria x ananassa*; Photoperiod; Recurrent flowering; Temperature

1. Introduction

While the environmental regulation of flowering and dormancy has been extensively studied and is well understood in June-bearing or seasonal flowering (SF) strawberry genotypes (Darrow and Waldo, 1934; Guttridge, 1985; Heide et al., 2013), the environmental regulation of these processes is less studied in recurrent flowering or everbearing (EB) genotypes (Heide et al., 2013).

Most SF cultivars have proved to be basically short-day (SD) plants and are classified as facultative SD plants. At temperatures in the range 18-20 °C, they need SD for induction of flowering, while at lower temperatures, most cultivars also initiate flowers in long days (LD) (Ito and Saito, 1962; Heide, 1977; Heide et al. 2013). The critical photoperiod for SD induction is 14-15 h (Darrow and Waldo, 1934; Konsin et al., 2001), and the minimum number of SD cycles needed for induction is between 7 and 14 depending on the cultivar (Guttridge, 1985; Heide et al., 2013). However, the flower-inducing effect of SD is highly temperature dependent, it is optimal at intermediate temperatures and progressively declining at temperatures <12 °C and >21 °C (Guttridge, 1985; Heide et al., 2013). Because of this photoperiod x temperature interaction, flower initiation in SF strawberries takes place in response to the seasonally declining photoperiod and temperature conditions in late summer and autumn the year before flowering and fruiting.

While Darrow and Waldo (1934) in their classical paper concluded that "everbearing varieties of strawberries are long day plants, forming fruit buds under the long days of summer", the issue of photoperiodic control of flowering in EB has been a matter of debate. With the development and introduction of the new and successful everbearing cultivars in California in the 1980's, the notion developed that these are day-neutral plants (Galletta et al., 1981; Durner et al., 1984; Nicoll and Galletta, 1987; Durner and Poling, 1988; Galletta and Bringhurst, 1990; Dale et al. 2002). Apparently, the everbearing habit of these cultivars with year-round flowering may have been the reason for this notion. However, studies in both Japan (Nishiyama and Kanahama, 2000, 2002) and Norway (Sønsteby and Heide, 2007a, b) clearly demonstrated that the Californian everbearers are also highly sensitive LD plants and that, as in the SF cultivars, the photoperiodic response is highly dependent on the temperature conditions. It was therefore concluded that the EB cultivars are quantitative LD plants at intermediate temperatures and qualitative LD plants at high temperature, while at low temperatures only (< 15 °C) they are day-neutral. Later, the same response pattern was demonstrated also by other researchers with the so-called "strong day-neutral" cultivar 'Tribute' (Bradford et al., 2010).

In all studied *Fragaria* genotypes, there is an opposite relationship between flowering induction and runner formation in the axillary meristems, and both developmental processes are sensitive to environmental conditions (Brown and Wareing, 1965; Guttridge, 1985; Bradford et al., 2010; Hytönen and Elomaa, 2011; Heide et al., 2013; Hytönen and Kurokura, 2020). In SF cultivars, runners are produced almost exclusively in the vegetative phase of plant development, with long days and high temperatures promoting their formation (Darrow and Waldo, 1934; Heide, 1977; Durner et al., 1984; Bradford et al., 2010), and with a causal connection to gibberellin (GA) metabolism (Hytönen et al., 2009; Tenreira et al., 2017). The inhibition of GA biosynthesis has been demonstrated to enhance crown branching, inhibit runner formation and concomitantly increase flowering by increasing the number of potential sites for flower induction and differentiation (Hytönen and Elomaa, 2011; Tenreira et al., 2017). In EB cultivars in general, runner formation is less prolific than in SF cultivars (Sønsteby and Heide, 2007b) and this has been associated with the early floral initiation in shoot apices that results in enhanced crown branching capacity (Hytönen and Elomaa, 2011). As for SF, high temperatures are promotive for runner formation, while the effect of photoperiod varies among EB cultivars (Heide et al., 2013). Sønsteby and Heide (2007a, b) found that in EB cultivars runner formation was also enhanced by conditions that suppresses flowering, thus conforming the opposite relationship between flowering and runner formation in strawberry in general.

Under prolonged SD conditions, SF strawberries gradually enter a state of dormancy (Jonkers, 1965; Guttridge, 1985; Sønsteby and Heide, 2006). However, the dormant state is not absolute, but a state of semi-dormancy that is associated with strong restriction of vegetative growth (Guttridge, 1985; Sønsteby and Heide, 2006; Heide et al., 2013). Sønsteby and Heide (2006) found that although growth was strongly restricted with 5 weeks of SD, 10 weeks or more of SD exposure were required for induction of dormancy in the cultivars 'Elsanta' and 'Korona' and in addition, the dormant state is only attained at relatively high temperatures (cf. Kronenberg et al., 1976). This was recently confirmed for the cultivar 'Sonata' (Sønsteby and Heide, 2021). Release from dormancy and reversal of the restrained growth habit require several weeks of chilling at temperatures ranging from -2 °C to 7 °C, while 10 °C is only marginally effective (Guttridge, 1985; Lieten, 1997; Heide et al., 2013). However, prolonged exposure to LD conditions will also gradually break dormancy and bring about normal growth even in fully dormant plants (Lieten, 1997; Sønsteby and Heide, 2006). Apparently, since temperatures <10 °C are effective in breaking dormancy, continuous exposure to such low

temperatures seems to continuously nullify the dormancy-inducing effect of SD (Sønsteby and Heide, 2006).

Dormancy regulation and its environmental control have been less studied in EB cultivars. In their pioneering work, Darrow and Waldo (1934) reported that under SD conditions, EB cultivars cease growing and become dwarfed under natural summer conditions. This was confirmed by Sønsteby and Heide (2007a) with the seed-propagated F1 hybrid 'Elan', which was found to have a critical photoperiod of 15 h at 18 °C for maintenance of growth and floral initiation as well as runner formation. This agrees well with the critical photoperiod of 14 h at 30/25 °C day/night temperature reported by Nishiyama et al. (2006) for flower initiation in the EB cultivar 'Summerberry'. These responses are also widely confirmed in practice with the modern production system now commonly used in Europe for EB cultivars (Gallace et al., 2019). In this system, field-grown runners are cut in late August, and rooted and raised under natural decreasing temperature and daylength conditions during late summer and autumn. During this period, the plants initiate flower primordia and develop the typical constrained growth habit of semi-dormant strawberry plants. In order to overcome dormancy and reverse growth restriction, plants are usually cold-stored at -1.5 °C from December until planting in early spring in greenhouses and plastic tunnels for early production. Typically, such plants are accumulating from 1,500 to 3,000 chill-hours < 7 °C before planting. According to Gallace et al. (2019), this is far more than what is required for optimum yield and berry quality. Furthermore, chilling also delays re-initiation of new floral primordia in spring (Gallace et al., 2019). Apparently, this is the same physiological response as reported by Guttridge (1958) for SF cultivars which become insensitive to SD floral induction after winter chilling. However, since both flowering and dormancy are governed by a pronounced interaction of temperature and photoperiod also in EB cultivars (Heide et al., 2013; Hytönen and Kurokura, 2020), the entire photothermal environment must be considered when attempting to circumvent the negative effects of overchill.

Based on these considerations, the main purpose of the present study was to explore the interaction of photoperiod and temperature in controlling the onset and release of dormancy and its relation to flowering control in two genetically distant EB strawberry cultivars.

2. Materials and methods

2.1. Plant material and cultivation

All plant material used for the experiment was propagated in a greenhouse at the NIBIO Experimental Centre Apelsvoll, in South East Norway (60°40′N–10°50′E). Two commercially available everbearing strawberry (*Fragaria* x *ananassa* Duch.) cultivars were used for the experiment, the seed-propagated F1-hybrid cultivar Delizzimo (ABZ Seeds, Bovenkarspel, The Netherlands) and the runner-propagated cultivar Favori (Flevo Berry Holding B.V., The Netherlands). Young runner plants of 'Favori' were collected in late July from plants grown in a plastic tunnel at a commercial production nursery in South East Norway and rooted directly in 9 cm pots in a peat-based potting compost (Gartnerjord, LOG, Oslo) mixed with 10% (v/v) granulated perlite in a water-saturated atmosphere under a plastic enclosure at 10 h photoperiod and a minimum temperature of 24 °C. Seed of 'Delizzimo' were received directly from the breeder, and sown on 5 July in plug trays at 24 °C in 10 h photoperiod. After germination, seedlings were transplanted to 9 cm pots and raised under the same conditions as described above for 'Favori'. On 13 August, all plants were transferred to a phytotron at the Norwegian University of Life Sciences at Ås (59°40´N, 10°40´E) and exposed to 10-h short day (SD) and 20-h long day (LD) at temperatures of 6, 16 or 26 °C for 5 and 10 weeks. In the phytotron, all plants were grown during daytime (08:00-18:00 h) in natural daylight compartments and then moved to adjacent growth rooms from 18:00-08:00 h where they received either darkness for 14 h (SD) or 10 h low-intensity-light (~ 7 µmol m^{-2} s^{-1} PPF) from 70 W incandescent lamps for daylight extension (LD), so that the 4 h dark period was centered around midnight (22:00 h to 02:00 h). The daylight extension amounted to less than 2% of the total daily light radiation, all plants thus receiving nearly the same daily light integral in both photoperiods. In the daylight compartments, an additional 125 µmol quanta m^{-2} s^{-1} were automatically added by high-pressure metal halide lamps (400W Philips HPI-T) whenever the photosynthetic photon flux (PPF) in the compartments fell below 150 µmol quanta m^{-2} s^{-1} (as on cloudy days). The plant trolleys were positioned randomly in the daylight rooms during daily movement in and out of the adjacent photoperiodic treatment rooms. Temperatures were controlled to ± 1 °C and a water vapor pressure deficit of 530 Pa was maintained at all temperatures. Throughout the experimental period, the plants were irrigated daily to drip-off with a complete fertilizer solution [electric conductivity 1.3-1.5 mS cm^{-1}, 1:1 Kristalon™: Yaraliva™ (Yara, Norway)].

Half of the plants were grown under these conditions for 5 weeks and the other half for 10 weeks. After this preconditioning, half of the plants from each batch were forced directly in a greenhouse for 10 weeks with 20 h LD at 20 °C for recording of flowering and growth performance, while the other half was cold stored for 6 weeks in darkness at 2 °C before forcing under the same conditions. In addition to natural daylight conditions in the greenhouse, the

plants received an additional daily supply of 150 µmol m^{-2} s^{-1} from 400W Philips HPI-T lamps plus about 10 µmol m^{-2} s^{-1} from 70 W incandescent lamps for 20 h (02:00 h to 22:00 h) throughout the forcing period.

2.2. Experimental design and data observations

The experiment was conducted as a randomized block design with three randomized blocks of 5 plants of each cultivar in each treatment. During preconditioning, growth and flowering was monitored by weekly registration of the number of leaves, crowns and runners. At termination of the preconditioning treatments and before forcing or cold storage, the total number of leaves, runners, flowers, and petiole length of the last fully developed leaf were recorded. During forcing, flowering and growth performance were assessed by weekly recordings of the total number of leaves, runners and flowers in addition to the petiole and peduncle length of the three first developed leaves and inflorescences, respectively. Petiole length was measured from the base of the leaf to the trifoliate attachment zone and peduncle length was measured to the base of the primary flower at anthesis (i.e. peduncle + pedicel length). Runners and open flowers were removed weekly as they were recorded. The total number of leaves, runners, inflorescences, open flowers and flower buds were also recorded at termination of the 10-week forcing period.

Statistical analyses consisted of analysis of variance (ANOVA) run in Minitab v18.1 (Minitab Inc., State College, PA, USA). Prior to the analyses, homoscedasticity and normality assumptions were tested (Ryan-Joiner test for normality and Levene's test for homoscedasticity). Percentage values were always subjected to square root transformation before performing the ANOVA.

3. Results and discussion

3.1. Plant status after 5 and 10 weeks of preconditioning

The vegetative and generative plant development status of the two cultivars at termination of the 5- and 10-week preconditioning at varying temperature and daylength conditions are shown in Table 1, while the appearance of the plants after 10 weeks of preconditioning are shown in Fig. 1.

In general, all the plant growth parameters of both cultivars increased with increasing temperatures under both photoperiod treatments (Table 1). The initiation of new leaves was unaffected by photoperiod or cultivar, while it increased markedly with increasing temperature and duration of preconditioning, the main effect of both factors being highly significant ($P < 0.001$). On the other hand, petiole length increased with increasing temperature, photoperiod and duration of treatment in both cultivars. While the growth enhancement was greatest between 6 and 16 °C, it tended to level off at 26 °C in LD in plants preconditioned for 10 weeks. The main treatment effects of temperature, photoperiod and duration of treatment on petiole elongation, as well as their two- and three-factor interactions were all highly significant (Table 1).

No runner formation took place at 6 °C in either cultivar after 5 and 10 weeks of preconditioning in either daylength. At the higher temperatures, runnering was also rather sparse under all pretreatment conditions in 'Favori', while in 'Delizzimo' runner formation was abundant in SD, especially at 26 °C and with 10 weeks preconditioning. However, due to a highly significant temperature x photoperiod interaction, the main effect of photoperiod was not statistically significant for runner formation.

Although a few 'Favori' plants had started to develop inflorescences after 5 weeks in LD at the higher temperatures, no plants of any cultivar had reached anthesis at this stage. After 10 weeks preconditioning, however, both cultivars were flowering, and the process was enhanced by increasing temperature and photoperiod (Table 1). Of the 'Delizzimo' plants, 90% and 93% were flowering in LD at 16 and 26 °C, respectively, while none were flowering in SD. On the other hand, approximately two thirds of the 'Favori' plants, had open flowers after 10 weeks preconditioning in both daylengths at 16 °C. At 26 °C, however, no open flowers were found in 'Favori' in SD, while almost all plants flowered in LD. At 6 °C, no flowering was observed during the preconditioning.

In both cultivars, there were complex interrelations between flowering and leaf and runner production (Table 1). 'Favori' had a large increment in total leaf numbers (about 3 leaves per plant per week) between week 5 and week 10 at 26 °C in SD. This coincided with commencement of flowering in LD after 5 weeks. In 'Delizzimo' on the other hand, which did not flower after 10 weeks in SD at 26 °C, the increment in leaf numbers between week 5 and week 10 was rather small (about 3 leaves per plant) over the whole 5-week period in both SD and LD. This lower leaf production was associated with a large increment in the total number of runners (about 1.5 runners per plant per week) in SD at 26 °C. Furthermore, a lower rate of leaf and runner production in LD at 6 and 16 °C compared with 26 °C in both cultivars was

associated with over 90% flowering plants in LD in both cultivars at the highest temperature after 10 weeks preconditioning.

3.2. Effects of preconditioning during subsequent forcing

Figures 2, 3 and 4 show the weekly time courses of runner and flower production, and the percentage of flowering plants during preconditioning and the subsequent 10 weeks forcing period.

Overall, runner formation was much more abundant in 'Delizzimo' than in 'Favori' (Fig. 2). During preconditioning, no runners were formed in either cultivar at 6 °C, regardless of photoperiodic conditions, whereas runnering was enhanced by increasingly higher temperatures. In 'Delizzimo', there was little effect of photoperiod during the first 5 weeks of preconditioning at 26 °C, while SD enhanced runnering markedly in the second 5-week period. This shift coincided with the commencement of flower bud formation (cf. Fig. 3). At 16 °C however, there was no effect of photoperiod on runner formation in this cultivar. In 'Favori' plants, runner formation was generally low and only slightly enhanced by LD during preconditioning for 5 and 10 weeks (Fig. 2). Chilling had no marked effect on runner formation in any of the cultivars (Table S1). The transfer to forcing conditions (LD and 20 °C) resulted in commencement of runner formation also in plants preconditioned at 6 °C in both photoperiods, and in 'Delizzimo' plants pre-treated for 10 weeks, the effect was slightly enhanced by LD in both chilled and non-chilled plants. In 'Favori' plants pre-treated for 10 weeks in SD at 26 °C (and to a lesser extent at 16 °C), runnering increased strongly after transfer to the LD forcing conditions, an effect that was associated with suppression of flowering in SD (Figs. 2, 3). Marked differences in runner formation among EB cultivars was also reported by Sønsteby and Heide (2007b).

Flowers emerged earliest in plants of both cultivars when preconditioned for 10 weeks in LD at 16 and 26 °C (Fig. 3). With 5 weeks preconditioning, no flowering took place during the first 4 weeks of forcing, whereupon it increased steadily in both cultivars. LD and increasing temperatures progressively promoted the flowering process. In plants of both cultivars, 6 °C severely delayed the emergence of flowers. Regardless of photoperiod and treatment duration, it took 2 weeks for chilled plants and 5 weeks of subsequent forcing for non-chilled plants to reach anthesis. Chilling had no significant effect on the number of open flowers in plants preconditioned for 5 weeks, but reduced flowering markedly in plants of both cultivars when preconditioned for 10 weeks, especially in LD at 26 °C. The main effects of temperature,

268 photoperiod and duration of preconditioning were all highly significant in both cultivars (Table
269 S1).
270 With 10 weeks of preconditioning at 16-26 °C, plants of both cultivars started to flower
271 nearly simultaneously regardless of chilling treatment (Fig. 4). While 'Favori' plants had an
272 almost obligatory LD flowering requirement at 26 °C, 'Delizzimo' responded as a quantitative
273 LD plant. At 16 °C, however, both cultivars behaved as quantitative LD plants, while both were
274 day-neutral at 6 °C (Table 2, Fig. 3). These results are in general agreement with results
275 previously reported for other EB cultivars (Nishiyama and Kanahama, 2000, 2002; Sønsteby
276 and Heide, 2007a, b; Bradford et al., 2010). The marked SD suppression of flowering at high
277 temperature observed during the preconditioning period was maintained throughout the 10-
278 week LD forcing period, thus rendering the total numbers of flowers much higher in the plants
279 grown continuously in LD (Table 2, Fig. 3). However, while chilling for 6 weeks generally
280 advanced flower development (Fig. 4), it had no consistent effect on the abundance of
281 flowering (Fig. 3). Thus, while chilling slightly increased the number of inflorescences and
282 flowers in plants preconditioned for 5 weeks, it reduced flowering significantly in plants
283 preconditioned for 10 weeks (Table 2). This puzzling result was probably due to declining light
284 conditions in the greenhouse during forcing. Thus, since the experiment was conducted during
285 autumn and early winter, the daily light integral in the greenhouse was gradually declining
286 during the forcing period. Ideally, all plants should have been forced simultaneously under
287 identical light conditions, but regrettably, this was not possible with the capacity of the
288 controlled environment facilities available. However, this light effect was quantitative only,
289 whereas the quality response (flowering or non-flowering) was unaffected.
290 The difference in runner formation between 'Delizzimo' and 'Favori' shown in Fig. 2, was
291 largely related to the different propagation methods for the two cultivars. Thus, the seed-
292 propagated 'Delizzimo' plants had a so-called "juvenile runnering" period during which they
293 could not initiate flowers but instead initiated numerous runners (cf. Sønsteby and Heide,
294 2007a). In contrast, the 'Favori' runner plants were predisposed by their previous LD history,
295 which delayed runnering but resulted in a "flying start" of flower initiation. Although the
296 juvenility period for flowering is short in F1 strawberry seedlings, as shown in Fig. 3 for
297 'Delizzimo' and by Sønsteby and Heide (2007a) for the related F1 hybrid 'Elan', it provided
298 for a "flying start" of runnering in the seedlings in both SD and LD at 26 °C and to a lesser
299 extent at 16 °C. These differences were further augmented by the cultivar differences in
300 photoperiodic flowering requirements and the close interrelationship between flowering and
301 runner formation in strawberry plants. A related consequence of this was that runner formation

in ‘Delizzimo’ ceased as soon as floral initiation started (Figs. 2, 3). However, despite these differences, both cultivars exhibited strong stimulation of runner formation by SD and high temperature as previously reported for other EB cultivars (Sønsteby and Heide, 2007a, b). The results in Fig. 2 and Table S1 show that although chilling increased overall vegetative growth vigour, it had no significant effect on runner formation in either cultivar. Similar results were reported by Gallace et al. (2019) for the EB cultivar ‘Verity’, and by Sønsteby and Heide (2021) for the SF ‘Sonata’.

The dynamics of petiole elongation during forcing of ‘Delizzimo’ and ‘Favori’ plants are shown in Figs. 5 and 6, respectively (cf. Tables S2 and S3). Since chilling had no marked effect on petiole lengths in plants preconditioned at 6 °C regardless of photoperiod (cf. Table S4), the plants grown under such low-temperature conditions were apparently not dormant, even after 10 weeks exposure. Nevertheless, plants of both cultivars had slightly longer petioles in LD than SD, and the petiole lengths increased steadily in successively developing leaves. Nor was there any significant effect of chilling in plants of any cultivar when preconditioned at 16 °C for 5 weeks (indicating no dormancy). However, in plants of both cultivars preconditioned for 10 weeks at 16 °C, petiole lengths increased markedly after chilling of the SD-grown plants, thus indicating dormancy induction in SD. At both 6 and 16 °C, but not at 26 °C, was there a gradual increase in petiole length in successively developing leaves.

Neither in plants grown at 26 °C was there any clear effect of chilling on petiole length in plants preconditioned for 5 weeks (albeit a small increase in leaves #2 and #3 of ‘Favori’). However, in plants preconditioned for 10 weeks at 26 °C, there was a marked effect of chilling on petiole length of both cultivars with both photoperiods, particularly in SD. This indicates at least partial dormancy in both cultivars under these conditions. Unexpectedly, however, the petioles of successive leaves were longer in SD than LD both before and after the chilling treatment. The explanation for this is apparently that at this stage, the ‘Favori’ plants had started flowering in LD but not in SD (cf. Fig. 4). In particular, flowering plants of 'Favori' formed few new leaves at the base of the plant, instead forming new leaves on the peduncle axis. These leaves were not recorded, and accordingly, hardly any new leaves were available to measure. Accordingly, direct comparison between photoperiods was not possible in this case, while comparison of leaves before and after chilling (within photoperiods) is meaningful. It was clear, however, that in plants of both cultivars preconditioned at 16 and 26 °C for 10 weeks, chilling actually enhanced petiole elongation in the LD-grown plants as well. This suggests that intermediate and high temperatures have some dormancy-inducing effect in EB cultivars, even under LD conditions.

However, at 26 °C, and especially in LD, successively emerging leaves did not exhibit the usual trend of increasing growth (Figs. 5, 6). Rather, leaves #2 and #3 of both cultivars exhibited decreasing petiole lengths, followed again by increasing lengths in leaves of higher rank. The reason for this trend was probably that leaves of intermediate rank were formed and to an increasing degree developed during the preconditioning period at 26 °C, which was found to have a strong dormancy-inducing effect even in LD, while later leaves developed during forcing at 20 °C (cf. Table S2). Reversibility of this inhibition by chilling only took place for leaves preconditioned for 10 weeks. Note, however, that in the first developing and mature leaf #0, petiole length appeared to be fixed and therefore, not responsive to chilling.

The dynamics of peduncle elongation during forcing of 'Delizzimo' and 'Favori' plants are shown in Figs. 7 and 8, respectively (cf. also Tables S2 and S3). As for petiole length, there was no clear indication of dormancy in 'Delizzimo' plants preconditioned at 6 °C, regardless of photoperiod or duration of the preconditioning. On the other hand, in the runner-propagated 'Favori' plants which were influenced by their high temperature and LD prehistory, peduncle #1 was apparently initiated before the runner was severed from its mother plant, whereas peduncles #2 and #3 were probably initiated during preconditioning at 6 °C. Therefore, the length of the latter peduncles exhibited a decreasing trend similar to peduncles developed at 26 °C, and it may therefore be speculated that these plants were more or less fixed in a LD and high temperature flowering mode (confer the analogous discussion regarding runner formation in 'Favori' plants in Fig. 2).

At the higher temperatures, however, peduncle elongation was markedly constrained by SD in plants of both cultivars preconditioned for 10 weeks. In plants preconditioned at 16 °C for 10 weeks, the cultivars differed somewhat in their photoperiodic response. In 'Delizzimo', peduncle elongation was restricted to much the same length in SD and LD in non-chilled plants and chilling fully reversed the restriction in plants grown in both photoperiods. In 'Favori', on the other hand, peduncle elongation was only restricted under SD conditions, and chilling fully reversed the restriction to the same length as in LD-grown plants. However, in plants preconditioned at 26 °C for 10 weeks, peduncle elongation was strongly restricted by SD in both cultivars (the average peduncle lengths were <15 cm in both cultivars), and the restriction was fully reversed by chilling for 6 weeks. A puzzling result was, however, that in 'Favori' plants preconditioned in SD at 26 °C for 10 weeks, the peduncles elongated to a greater length after chilling than did peduncles developed in LD. The reason for this result was apparently that with the strict photoperiodic flowering response of 'Favori' at 26 °C (cf. Fig. 4), the

'Favori' plants were in different flowering modes in SD and LD. This was not the case for 'Delizzimo' plants, which flowered in both LD and SD at 26 °C.

The general conclusion that can be drawn from these results is that none of the cultivars developed the semi-dormant appearance at 6 °C, regardless of photoperiodic conditions and duration of exposure. The reason for this is apparently that, since 6 °C is within the range of temperatures that are fully effective in breaking dormancy in strawberry plants (Jonkers, 1965; Guttridge, 1985; Lieten, 1997; Heide et al., 2013), the dormancy-inducing effect of SD will be continuously nullified at such low temperature conditions (Sønsteby and Heide, 2006). Nor did 5 weeks exposure to SD or LD at higher temperatures induce dormancy, but only a temporary growth restriction in SD that was gradually reversed by transfer to high temperature and LD without any chilling treatment. However, with 10 weeks of exposure to SD at 16 °C and, in particular at 26 °C, plants of both cultivars developed the typical strawberry semi-dormant state (Figs. 5-8). This is in full agreement with results reported for SF cultivars (Kronenberg et al., 1976; Konsin et al., 2001; Sønsteby and Heide, 2006). In view of the opposite photoperiodic control of flowering in SF and EB strawberry, it was rather surprising that SD conditions induced dormancy in both groups. It is interesting to note that especially in 'Favori', there was a clear tendency to constrained leaf petiole growth at 26 °C even in LD. The results further showed that elongation of flower trusses was more vulnerable to growth restriction by SD and high temperature than was restriction of petiole elongation, and that 'Favori' was more sensitive to such growth restriction than was 'Delizzimo'.

A summary of vegetative and generative plant development states at the end of the 10-week forcing period is presented in Table 2. It is important to bear in mind, however, that at this stage, most of the preconditioning effects were probably "diluted out". This was especially the case for petiole and peduncle length of the last developed leaf and inflorescence, respectively. However, the data for total number of organs are interesting since they represent the total sum of organs formed during the entire experiment.

The total number of leaves produced increased significantly with increasing preconditioning temperature and length of the preconditioning period in both cultivars. Due to the well-known opposite relationship between flowering and leaf production in *Fragaria* genotypes (Brown and Wareing, 1965; Guttridge, 1985; Bradford et al., 2010; Hytönen and Elomaa, 2011; Heide et al., 2013; Hytönen and Kurokura, 2020), the total number of leaves produced was also significantly affected by photoperiod and/or the interaction of temperature x photoperiod, albeit with opposite trends in the two cultivars (stimulation by LD in 'Delizzimo' and by SD in 'Favori'). As a result, the abundantly flowering 'Favori' plants

grown continuously in LD and high temperature conditions, ended up with a very low leaf area. However, as shown in Table 1, leaf production was not affected by photoperiod during the initial period of vegetative growth. It should also be noted that, although chilling had no direct effect on leaf formation, it did reduce the total number of leaves when combined with 10 weeks preconditioning, due to declining daily light integral in the greenhouse during late forcing of these plants discussed above.

Even though LD significantly enhanced petiole length during preconditioning (cf. Table 1), this photoperiodic effect was no longer visible after 10 weeks forcing in LD, whereas the effect of temperature remained. In general, the petiole length of the last developed leaf increased significantly with increasing temperature in the 6-16 °C range, and, in most cases decreased slightly at 26 °C (Tables 2 and S1). The total number of runners produced during the entire experiment was significantly higher in 'Delizzimo' than in 'Favori' plants. In both cultivars, the number increased significantly with increasing temperature and duration of preconditioning while SD always enhanced runnering (cf. Table 1). Overall, chilling had no significant main effect on runner formation, nor was there any significant two- and three-factor interactions with chilling (Tables 2 and S1).

The total number of inflorescences and flowers per plant produced during the experiment was highest in LD and increased with increasing preconditioning temperature up to 16 °C in both cultivars while chilling had no significant effect (Tables 2 and S1). However, as discussed above for leaf formation, also the number of inflorescences and flowers declined after chilling in plants preconditioned for 10 weeks due to declining daily light integral during the late forcing of these plants. Overall, LD at 16 °C during preconditioning was optimal for flowering in both cultivars.

4. Conclusion

In summary, we conclude that dormancy in EB strawberry plants is regulated by a complex interaction of temperature, photoperiod, and chilling in much the same way as is known for SF cultivars, despite the opposite photoperiodic control of flowering and runnering in the two-cultivar groups. Like SF cultivars, EB cultivars do not become dormant at temperatures as low as 6 °C in either SD or LD while they are increasingly sensitive to SD dormancy induction at intermediate and high temperatures. Likewise, both groups of cultivars need exposure to SD and relatively high temperature conditions for at least 10 weeks for attainment of the semi-dormant state that is typical for strawberries in general. Although the LD control of flowering

at high temperature was stricter in the runner-propagated ‘Favori’ than in the seed-propagated F1 hybrid ‘Delizzimo’, the overall environmental responses were similar in the two genetically distant cultivars. Chilling in the dark at 2 °C for six weeks was adequate for complete reversal of the constrained elongation of leaf petioles and flower trusses of dormant plants but had little or no effect on the degree of flowering and runner formation.

References

Bradford, E., Hancock, J.F., Warner, R.M., 2010. Interactions of temperature and photoperiod determine expression of repeat flowering in strawberry. J. Amer. Soc. Hortic. Sci. 135, 102-107.

Brown, T., Wearing., 1965. The genetical control of the everbearing habit and three other characters in varieties of *Fragaria vesca*. Euphytica 14, 97–112 (1965).

Dale, A., Luby, J.J., Hancock, J.F., 2002. Breeding dayneutral strawberries for Northern North America. Acta Hortic. 567, 133–136.

Darrow, G.M., Waldo, G.F., 1934. Responses of strawberry varieties and species to duration of the daily light period. US Department Agriculture Tech. Bull. 453, 1-31.

Durner, E.F., Barden, J.A., Himelrick, D.G., Poling, E.B., 1984. Photoperiod and temperature effects on flower and runner development in day-neutral, June-bearing and everbearing strawberries. J. Amer. Soc. for Hortic. Sci. 109, 396–400.

Durner, E.F., Poling, E.B., 1988. Strawberry developmental responses to photoperiod and temperature: A review. Adv. Strawb. Prod. 7, 6–15.

Gallace, N., Lieten, P., Boonen, M., Bylemans, D., 2019. Reduced winter chill as a mean to improve the production potential of late day-neutral strawberry cultivars. Eur. J. Hortic. Sci. 84, 20-23.

Galletta, G.J., Draper, A.D., Swartz, H.J., 1981. New everbearing strawberries. HortScience 16, 726.

Galletta, G.J., Bringhurst, R.S., 1990. Strawberry management. In: Small Fruit Crop Management. (Galletta, G J. and Himelrick, D.G., Eds.). Prentice-Hall Inc., New York, USA. 83–156.

Guttridge, C.G., 1958. The effect of winter chilling on the subsequent growth and development of the cultivated strawberry plant. J. Hortic. Sci. 33, 119-127.

Guttridge, C.G., 1985. *Fragaria* × *ananassa*. In: CRC Handbook of Flowering. (Halevy, A., Ed.). Volume III. CRC Press Inc., Boca Raton, FL, USA. 16–33.

Heide, O.M., 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physiol. Plant. 40, 21–6.

Heide, O.M., Stavang, J.A., Sønsteby, A., 2013. Physiology and genetics of flowering in cultivated and wild strawberries–a review. J. Hortic. Sci. Biotech. 88, 1-18.

Hytönen, T., Elomaa, P., Moritz, T., Junttila, O., 2009. Gibberellin mediates daylength-controlled differentiation of vegetative meristems in strawberry (*Fragaria× ananassa* Duch). BMC Plant Biol. 9, 18.

Hytönen, T., Elomaa, P., 2011. Genetic and environmental regulation of flowering and runnering in strawberry. Genes, Genomes and Genomics 5, 56-64.

Hytönen, T., Kurokura, T., 2020. Control of flowering and runnering in strawberry. Hortic. J. 89, 96-107.

Ito, H., Saito, T., 1962. Studies on the flower formation in the strawberry plants. I. Effects of temperature and photoperiod on the flower formation. Tokohu J. Agric. Res.13, 191–203.

Jonkers, H., 1965. On the flower formation, the dormancy and the early forcing of strawberries. Meded. Landbouwhgesch. Wageningen 65; 1-71.

Konsin, M., Voipio, I, Palonen, P., 2001 Influence of photoperiod and duration of short-day treatment on vegetative growth and flowering of strawberry (*Fragaria x ananassa* Duch.). J. Hortic. Sci. Biotech. 76, 77-82.

Kronenberg, H.G., Wassenaar, L.M., Van De Lindeloof, C.E., 1976. Effect of temperature on dormancy in strawberry. Sci. Hortic. 4, 361–366.

Lieten, F., 1997. Effects of chilling and night-break treatment on greenhouse production of 'Elsanta'. Acta Hortic. 439, 633–639.

Nicoll, M.F., Galletta, G.J., 1987. Variation in growth and flowering habits of Junebearing and everbearing strawberries. J. Amer. Soc.Hortic. Sci. 112, 872–880.

Nishiyama, M., Kanahama, K., 2000. Effect of temperature and photoperiod on the development of inflorescences in everbearing strawberry (*Fragaria x ananassa* Duch.) plants. Acta Hortic. 514, 261–267.

Nishiyama, M., Kanahama, K., 2002. Effects of temperature and photoperiod on flower bud initiation of day-neutral and everbearing strawberries. Acta Hortic. 567, 253–255.

Nishiyama, M., Ohkawa, W., Kanayama, Y., Kanahama, K., 2006. Critical photoperiod for flower bud initiation in everbearing strawberry 'Summerberry' plants grown at high temperatures. Tohoku J. Agric. Res. 56, 1-8.

Sønsteby, A., Heide, O.M., 2006. Dormancy relations and flowering of the strawberry cultivars Korona and Elsanta as influenced by photoperiod and temperature. Sci. Hortic. 110, 57–67.

Sønsteby, A., Heide, O.M., 2007a. Quantitative long-day flowering response in the perpetual-flowering F1 strawberry cultivar Elan. J. Hortic. Sci. Biotech. 82, 266–274.

Sønsteby, A., Heide, O.M., 2007b. Long-day control of flowering in everbearing strawberries. J. Hortic. Sci. Biotec. 82, 875–884.

Sønsteby, A., Heide, O.M., 2021. Dynamics of dormancy regulation in 'Sonata' strawberry and its relation to flowering and runnering. CABI Agriculture and Bioscience, 2(1), 1-12.

Tenreira, T., Lange, M.J.P., Lange, T., Bres, C., Labadie, M., Monfort, A., Hernould, M. Rothan, C., Denoyes, B., 2017. A specific gibberellin 20-oxidase dictates the flowering-runnering decision in diploid strawberry. Plant Cell, 29, 2168-2182.

Acknowledgements

We thank Unni M. Roos, Signe Hansen and Kari Grønnerød for excellent technical assistance and Ge Bentvelsen at ASZ-seed for the gift of the 'Delizzimo' seed.

Table 1
Effects of photoperiod and temperature preconditioning for 5 and 10 weeks (w) on total number of leaves, petiole length of the last developed leaf, total number of runners and percentage flowering plants of 'Delizzimo' and 'Favori' strawberry plants.

Cultivar	Temperature (°C)	Photoperiod (h)	Total no. of leaves		Petiole length (cm)		Total no. of runners		Percentage of flowering plants	
			Weeks of preconditioning							
			5w	10w	5w	10w	5w	10w	5w	10w
Delizzimo	6	10	5.3	7.6	0.8	1.4	0.0	0.0	0.0	0.0
	16	10	9.6	16.4	4.4	9.5	4.6	6.4	0.0	0.0
	26	10	12.0	15.4	8.0	17.9	7.6	15.5	0.0	0.0
		Mean	*9.0*	*13.1*	*4.4*	*9.6*	*4.1*	*7.3*	*0.0*	*0.0*
	6	20	5.3	7.9	2.2	4.2	0.0	0.0	0.0	0.0
	16	20	9.3	13.8	12.0	22. 7	5.7	6.5	0.0	90.0
	26	20	10.8	18.1	15.1	21.4	7.3	10.2	0.0	93.3
		Mean	*8.5*	*13.3*	*9.7*	*16.1*	*4.3*	*5.6*	*0.0*	*61.0*
Favori	6	10	4.5	5.7	1.5	1.7	0.0	0.0	0.0	0.0
	16	10	8.4	16.4	5.5	7.3	0.3	0.3	0.0	65.2
	26	10	11.8	26.1	8.8	14.1	1.7	1.9	0.0	0.0
		Mean	*8.2*	*16.0*	*5.3*	*7.7*	*0.7*	*0.7*	*0.0*	*21.7*
	6	20	4.9	6.2	2.0	3.4	0.0	0.0	0.0	0.0
	16	20	8.0	17.3	10.5	18.3	1.2	1.2	0.0	53.5
	26	20	10.9	19.1	13.7	18.9	1.9	2.2	0.0	95.8
		Mean	*7.9*	*14.2*	*8.7*	*13.5*	*1.0*	*1.1*	*0.0*	*49.8*
Probability level of significance (ANOVA)										
Source of variation										

Temperature (T)	< 0.001	< 0.001	< 0.001	< 0.001
Photoperiod (P)	n.s.	< 0.001	n.s.	< 0.001
Cultivar (C)	n.s.	< 0.001	< 0.001	< 0.001
Precond. Duration (D)	< 0.001	< 0.001	< 0.001	< 0.001
T x P	n.s.	< 0.001	< 0.001	< 0.001
T x C	< 0.001	0.001	< 0.001	0.003
T x D	< 0.001	< 0.001	< 0.001	< 0.001
P x C	n.s.	0.003	0.001	n.s.
P x D	n.s.	< 0.001	< 0.001	< 0.001
C x D	0.002	< 0.001	< 0.001	< 0.001
T x P x C	< 0.001	n.s.	0 .001	< 0.001
T x P x D	n.s.	< 0.001	< 0.001	< 0.001
T x C x D	< 0.001	n.s.	< 0.001	0.001
P x C x D	n.s.	n.s.	0.001	< 0.001
T x P x C x D	<0 .001	n.s.	< 0.001	< 0.001

Values are significant different at $P \leq 0.01$ for the different temperature and photoperiod preconditioning. n.s., not significant. The data are means of three replicates, each with 5 plants.

Table 2

Effects of photoperiod and temperature on the formation of leaves, runners, inflorescences, and total flowers (buds + open) and on the petiole and peduncle lengths of the last developed leaf and inflorescence, respectively, in 'Delizzimo' and 'Favori' strawberry plants. Organ numbers per plant and lengths were recorded after 10 weeks (w) of forcing in 20 h photoperiod at 20 °C.

Cultivar	Temp. (°C)	Photop. (h)	Duration of precond. (w)	Leaves plant^{-1}		Petiole last dev. (cm)		Runners plant^{-1}		Inflorescences plant^{-1}		Total flowers plant^{-1}		Peduncle last dev. (cm)	
				Chill.	No-Ch.	Chill	No-Ch.	Chill	No-Ch.	Chill.	No-Ch.	Chill.	No-Ch.	Chill.	No-Ch.
Delizzimo	6	10	5	25.6	28.9	18.4	19.6	7.1	8.3	7.2	7.9	44.9	48.3	27.5	27.3
	16	10	5	28.7	30.8	21.5	20.3	12.1	12.8	8.1	8.2	70.2	63.3	28.9	29.4
	26	10	5	24.7	28.4	21.0	19.4	14.9	16.7	6.2	7.3	48.9	56.6	30.9	28.3
			Mean	*26.3*	*29.4*	*20.3*	*19.8*	*11.3*	*12.6*	*7.2*	*7.8*	*54.7*	*56.0*	*29.1*	*28.3*
	6	20	5	27.0	26.4	19.3	20.6	8.0	7.4	8.1	7.0	59.3	52.3	31.7	28.9
	16	20	5	37.4	39.7	21.4	20.2	11.2	12.9	11.8	14.3	84.5	109.6	29.7	29.8
	26	20	5	31.7	37.7	22.5	18.7	10.0	11.4	11.1	11.4	79.9	92.8	33.5	32.5
			Mean	*32.0*	*34.6*	*21.1*	*19.8*	*9.7*	*10.6*	*10.3*	*10.9*	*74.6*	*84.9*	*31.7*	*30.4*
	6	10	10	44.2	34.8	19.1	22.2	10.0	8.2	11.9	9.7	72.5	57.9	29.5	31.2
	16	10	10	54.4	40.5	20.6	23.8	9.7	14.4	15.2	12.6	108.1	97.7	34.5	32.8
	26	10	10	41.9	32.6	16.3	21.1	22.8	22.0	10.4	8.3	99.9	75.5	21.9	30.6
			Mean	*46.8*	*36.0*	*18.7*	*22.4*	*14.2*	*14.9*	*12.5*	*10.2*	*93.5*	*77.0*	*28.6*	*31.6*
	6	20	10	48.1	36.3	20.4	23.1	12.2	11.2	12.5	9.7	73.3	68.8	30.8	31.2
	16	20	10	45.3	44.1	19.6	26.3	8.6	12.7	18.0	17.7	141.3	132.5	26.2	35.1
	26	20	10	53.2	41.7	18.5	21.9	10.9	11.9	22.3	18.9	190.9	135.8	32.1	33.9
			Mean	*48.9*	*40.7*	*19.5*	*23.8*	*10.6*	*11.9*	*17.6*	*15.4*	*135.2*	*112.4*	*29.7*	*33.4*
Favori	6	10	5	21.2	23.6	15.5	15.6	2.8	2.5	6.7	9.2	66.1	80.2	26.5	31.3
	16	10	5	40.9	41.4	19.6	19.9	2.4	4.8	13.1	12.6	102.1	105.4	28.7	31.1
	26	10	5	45.8	37.5	19.0	16.8	3.1	1.8	9.7	10.0	70.6	110.0	30.7	31.7
			Mean	*36.0*	*34.2*	*18.0*	*17.5*	*2.8*	*3.1*	*9.8*	*10.6*	*79.6*	*98.5*	*28.7*	*31.4*
	6	20	5	25.4	27.1	14.2	16.9	1.9	3.6	8.9	9.3	91.9	87.0	25.9	31.9
	16	20	5	40.6	40.5	19.7	20.0	1.2	2.5	13.9	15.9	143.0	145.9	33.8	33.4
	26	20	5	27.1	26.6	15.2	11.0	2.4	1.8	11.5	13.8	126.9	130.3	26.1	25.4

		Mean	*31.0*	*31.4*	*16.4*	*16.0*	*1.9*	*2.6*	*11.4*	*13.0*	*120.6*	*121.1*	*28.6*	*30.2*
6	10	10	25.8	21.9	14.8	17.0	3.3	4.2	8.1	7.9	100.8	79.8	26.0	31.7
16	10	10	53.7	49.6	17.4	25.0	4.0	4.7	16.9	15.6	140.5	102.0	26.9	33.9
26	10	10	70.2	60.3	16.9	21.3	12.1	10.2	14.7	12.9	159.3	133.3	30.5	33.6
		Mean	*49.9*	*43.9*	*16.4*	*21.1*	*6.5*	*6.3*	*13.2*	*12.2*	*133.5*	*105.0*	*27.8*	*33.1*
6	20	10	25.6	23.0	15.9	15.5	3.5	3.9	8.4	8.3	93.4	83.3	27.8	26.1
16	20	10	62.4	56.3	19.1	23.4	1.9	1.8	27.7	23.8	222.5	201.7	33.6	34.6
26	20	10	30.5	30.4	13.2	16.1	3.3	2.4	17.0	13.8	293.1	170.1	25.4	30.1
		Mean	*39.5*	*36.6*	*16.1*	*18.3*	*2.9*	*2.7*	*17.7*	*15.3*	*203.0*	*151.7*	*28.9*	*30.3*

Data are mean values of three replicates of 5 plants each.

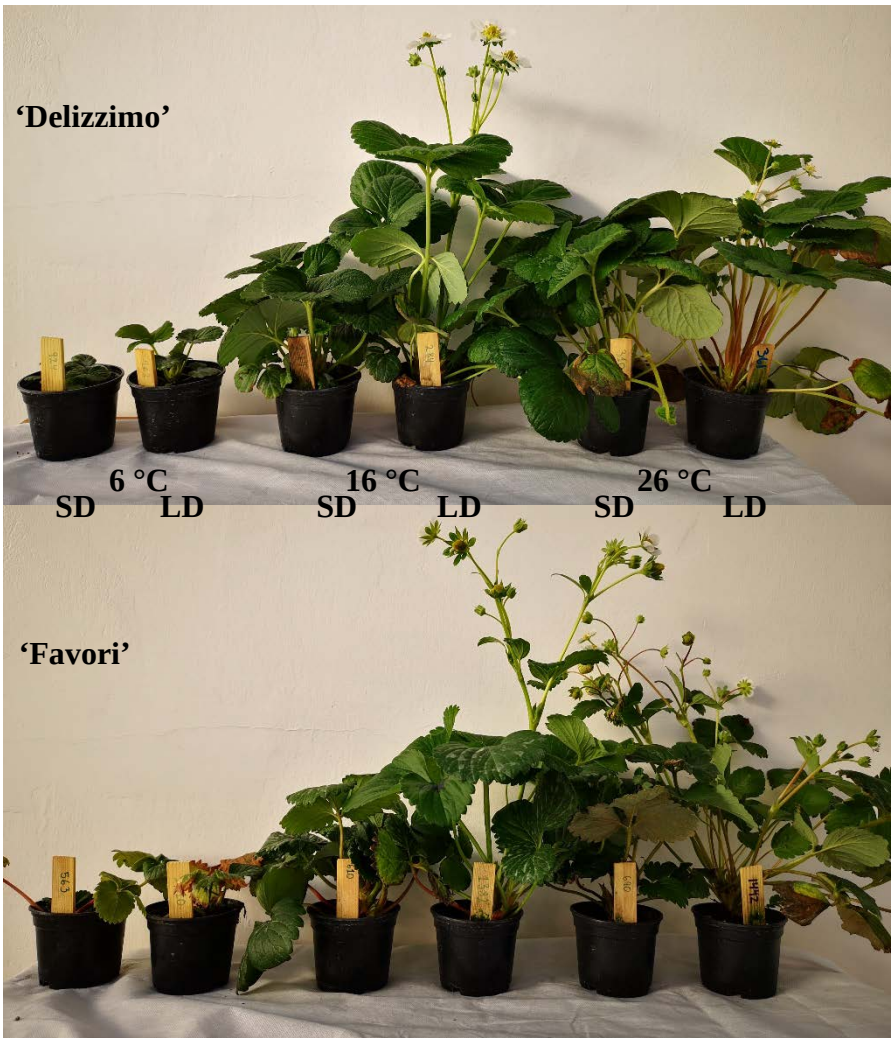

Fig. 1. The appearance of ‘Delizzimo’ and ‘Favori’ plants after 10 weeks of preconditioning at varying temperature and short day (10 h) and long day (20 h) as indicated. Photo on 24.10. 2019.

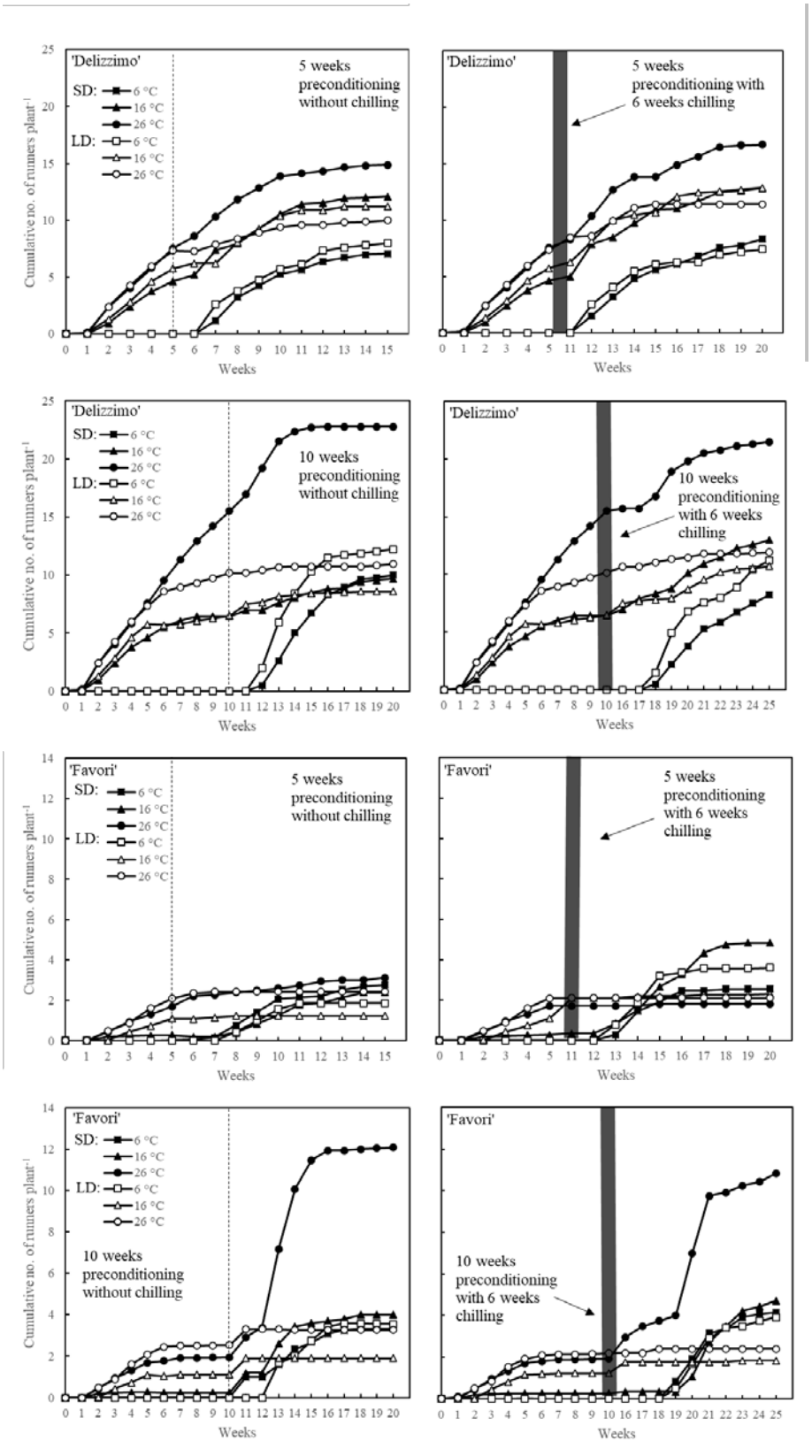

Fig. 2. Cumulative number of runners produced in 'Delizzimo' and 'Favori' strawberry plants during temperature and day length preconditioning for 5 or 10 weeks, followed by 10 weeks forcing in 20 h photoperiod at 20 °C. Plants in the right-hand panels were subjected to chilling at 2 °C for 6 weeks before forcing. Note the different scale on the Y-axis for two cultivars. Values are the means of three replicates of 5 plants each.

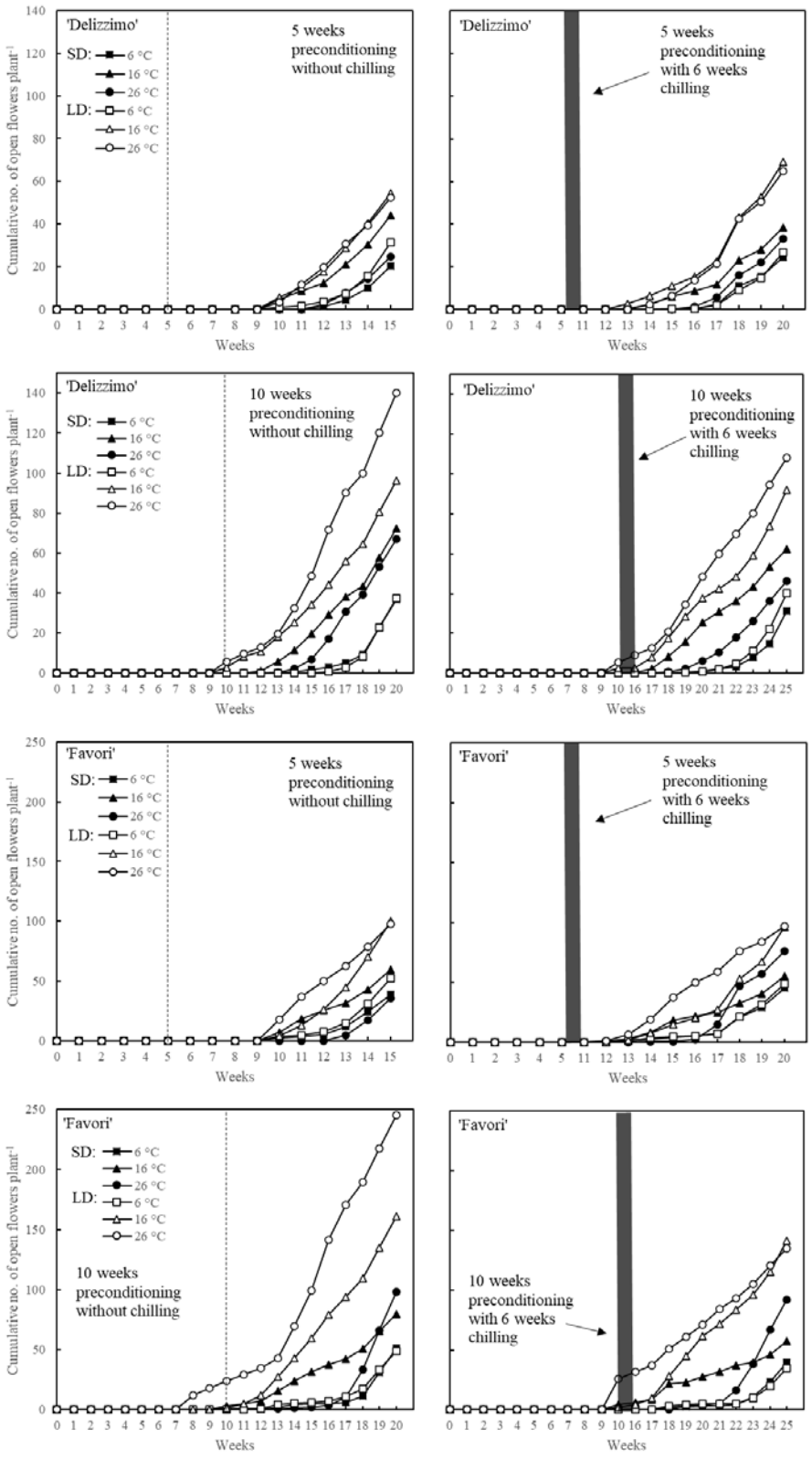

Fig. 3. Cumulative number of open flowers produced in 'Delizzimo' and 'Favori' strawberry plants during temperature and day length preconditioning for 5 or 10 weeks, followed by 10 weeks forcing in 20 h photoperiod at 20 °C. Plants in the right-hand panels were subjected to chilling at 2 °C for 6 weeks before forcing. Note the different scale on the Y-axis for two cultivars. Values are the means of three replicates of 5 plants each.

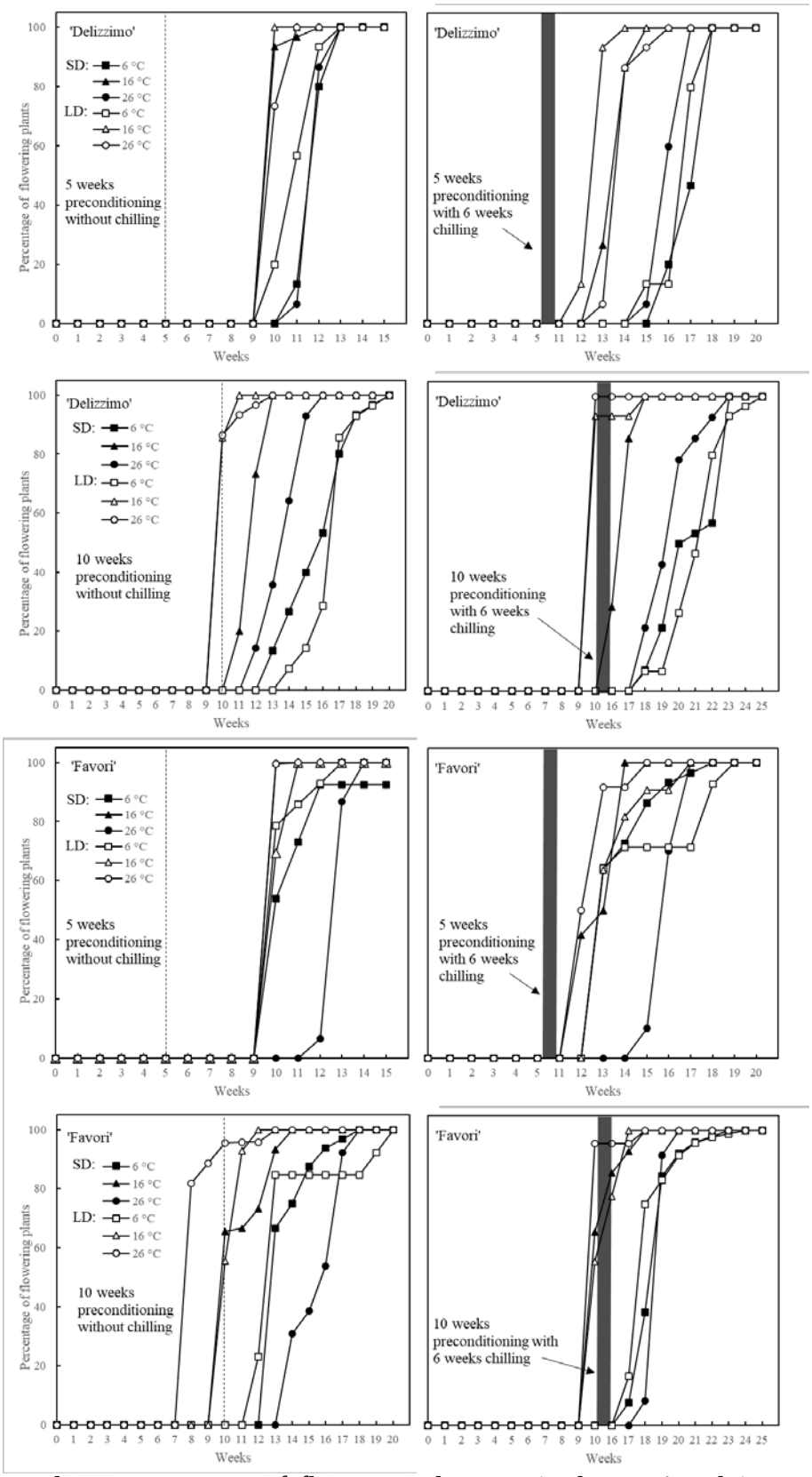

Fig. 4. Cumulative percentage of flowering plants in 'Delizzimo' and 'Favori' strawberry plants during temperature and daylength preconditioning for 5 or 10 weeks, followed by 10 weeks forcing in 20 h photoperiod at 20 °C. Values are the means of three replicates of 5 plants each.

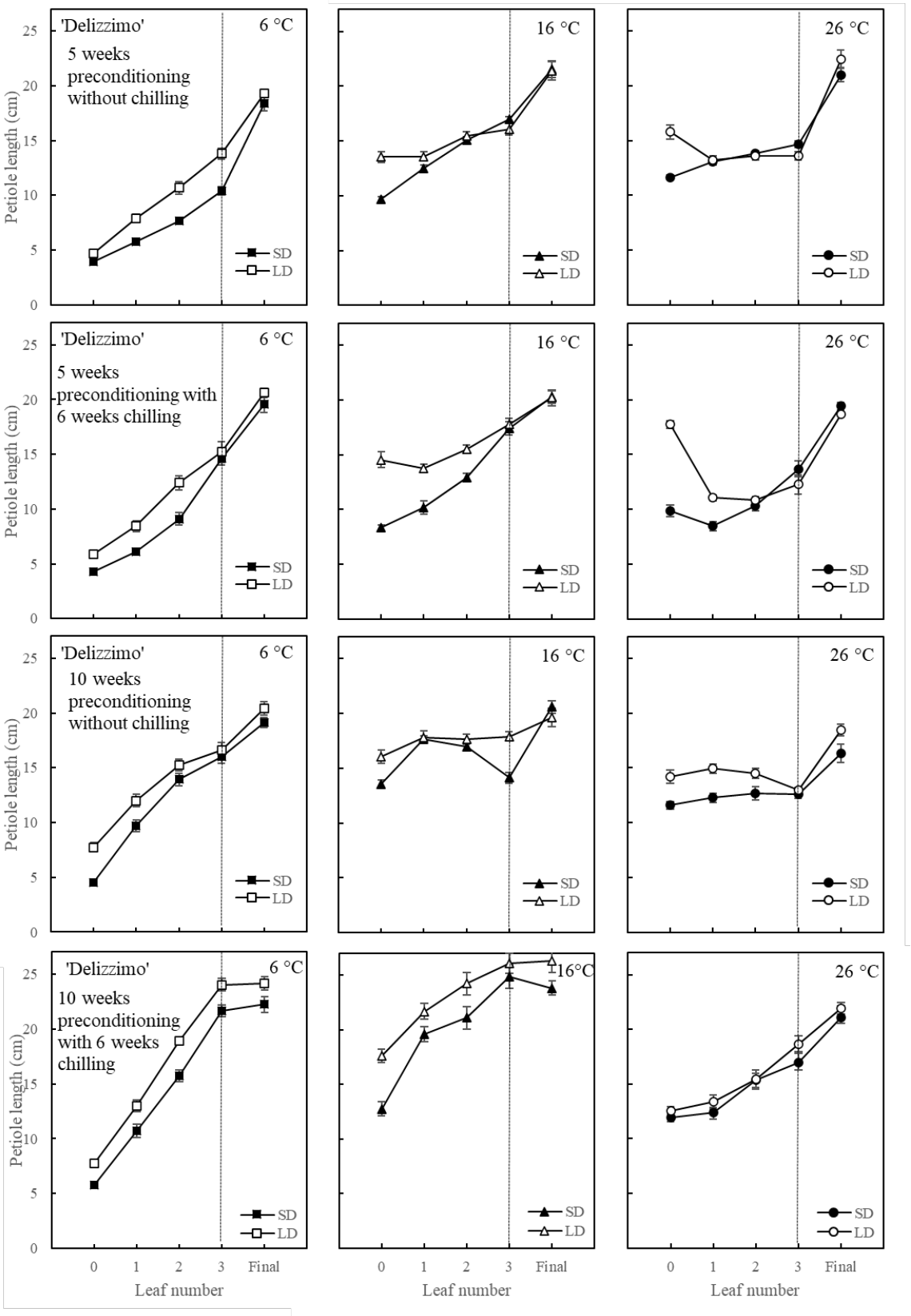

Fig. 5. Petiole length (cm) of the first four and the final developed leaves of 'Delizzimo' strawberry plants after 5 or 10 weeks of preconditioning and subsequent forcing for 10 weeks in 20 h photoperiod at 20 °C with and without preceding chilling. Values are the means ± SE of three replicates of 5 plants each.

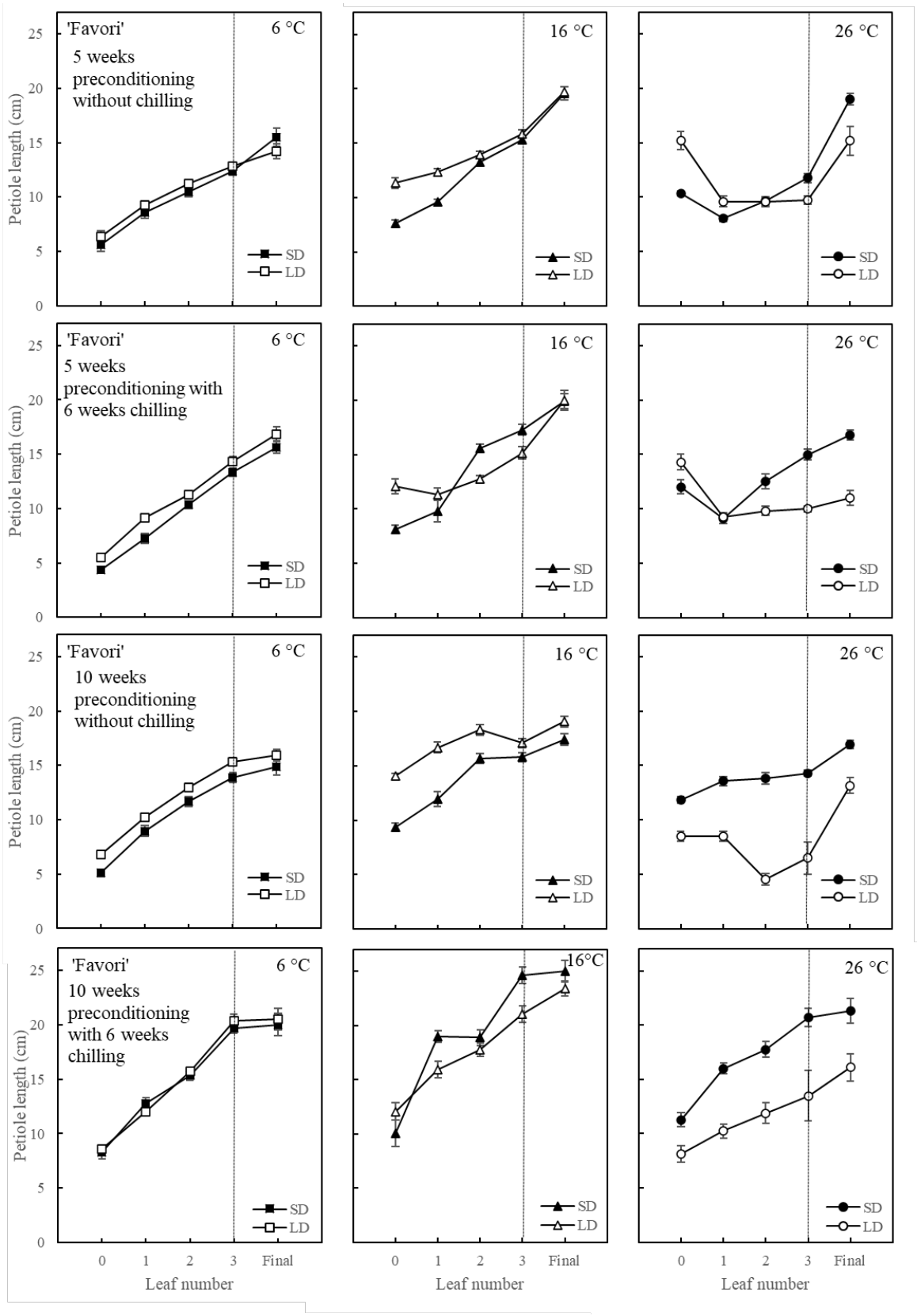

Fig. 6. Petiole length (cm) of the first four and final developed leaves of 'Favori' strawberry plants after 5 or 10 weeks of preconditioning and subsequent forcing for 10 weeks in 20 h photoperiod at 20 °C with and without preceding chilling. Values are the means ± SE of three replicates of 5 plants each.

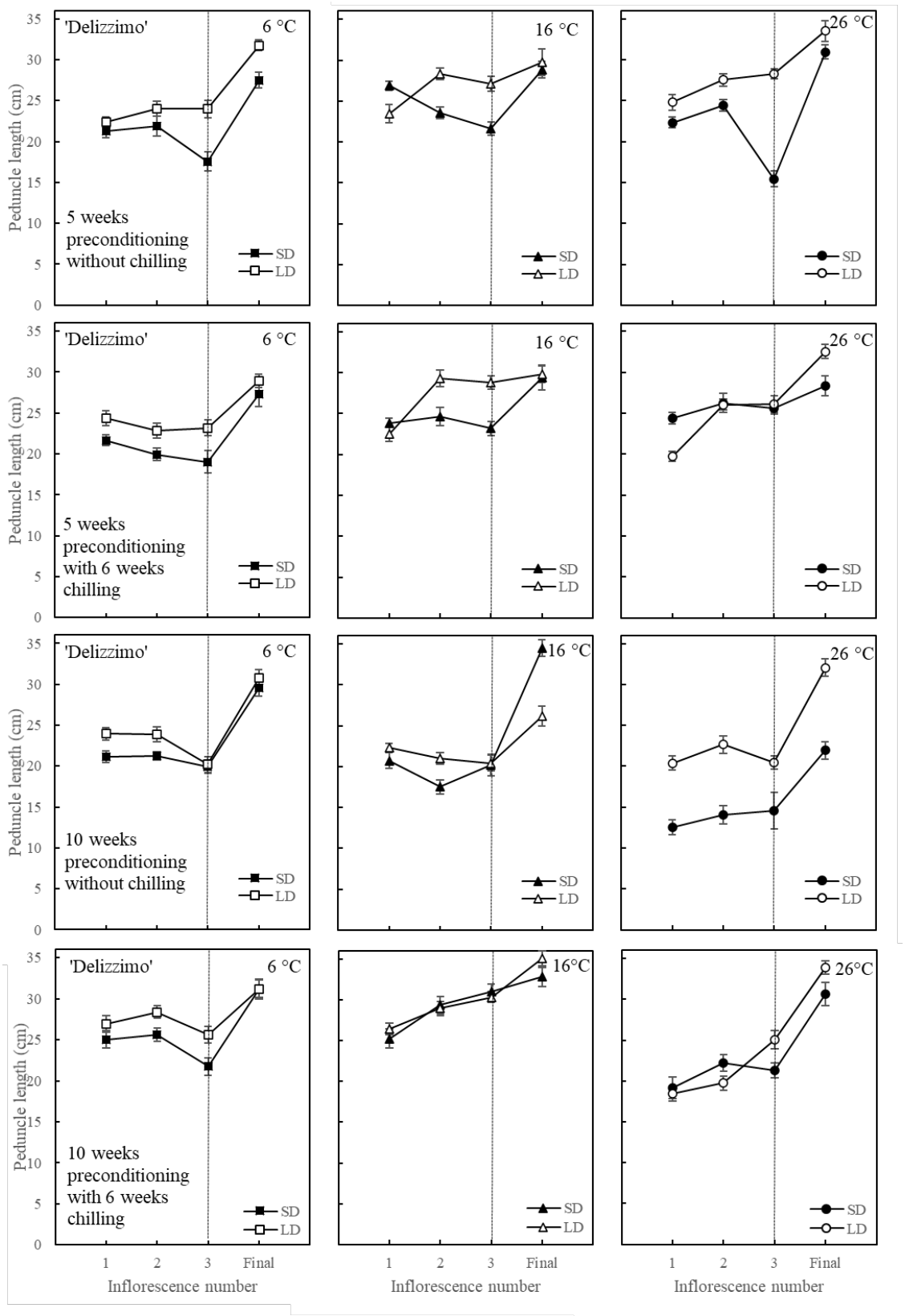

Fig. 7. Peduncle length (cm) of the first three developed inflorescences of 'Delizzimo' strawberry plants after 5 or 10 weeks of preconditioning and subsequent forcing for 10 weeks in 20 h photoperiod at 20 °C with and without preceding chilling. Values are the means ± SE of three replicates of 5 plants each.

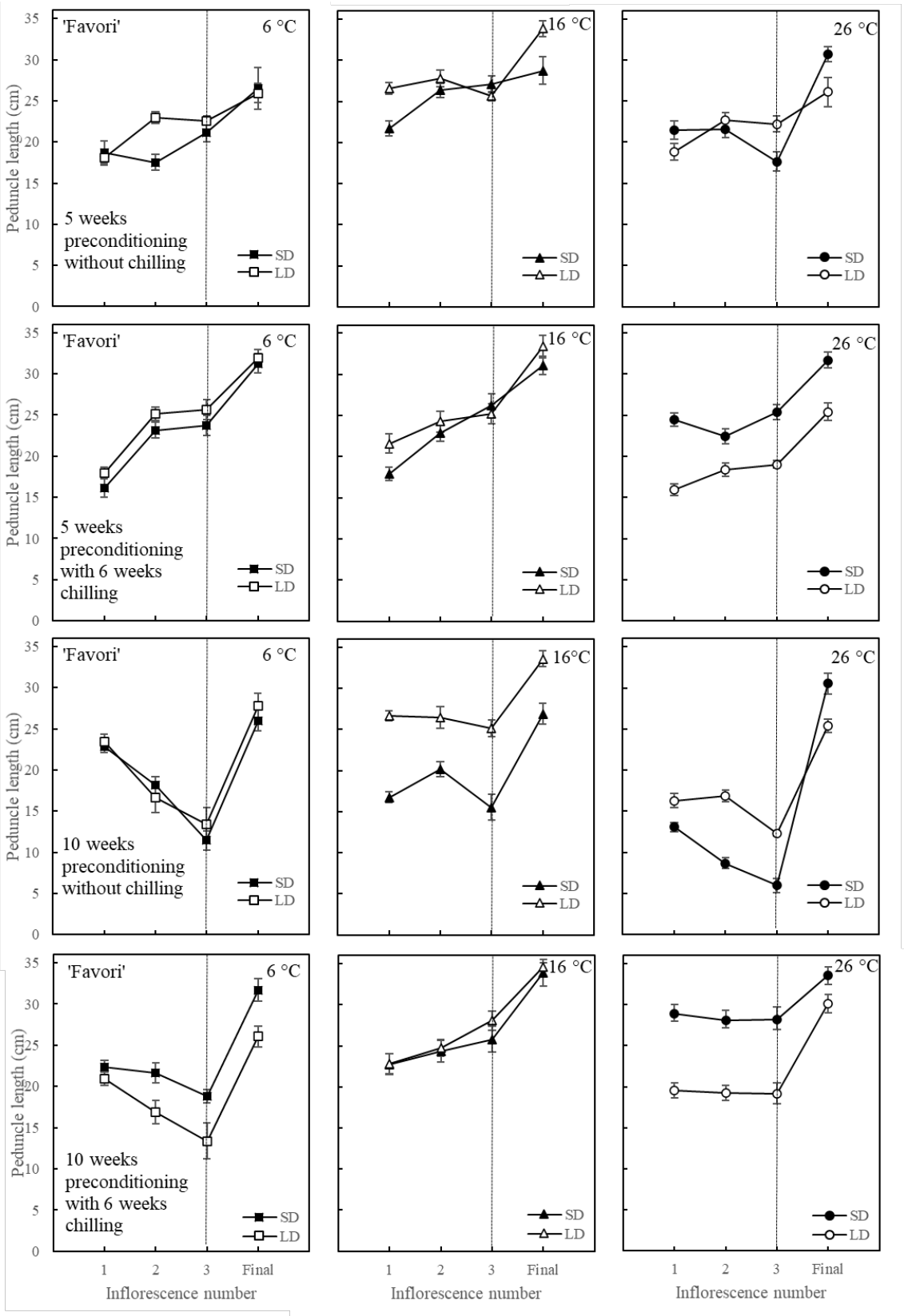

Fig. 8. Peduncle length (cm) of the first three developed inflorescences of 'Favori' strawberry plants after 5 or 10 weeks of preconditioning and subsequent forcing for 10 weeks in 20 h photoperiod at 20 °C with and without preceding chilling. Values are the means ± SE of three replicates of 5 plants each.