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RESEARCH

Growth analysis of the everbearing strawberry 'Delizzimo' under controlled temperature and photoperiod conditions

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Abstract

Background: There is limited information on the effect of environment on vegetative growth in everbearing (EB) strawberry (*Fragaria x ananassa* Duch.) and its comparison with the situation in seasonal flowering types.

Methods: We investigated the effects of photoperiod (daylengths of 10 and 20 h) and temperature (12, 19 and 26 ℃) on leaf growth, dry matter production and partitioning, concentrations of soluble sugars, starch, and chlorophyll in the F_1 hybrid 'Delizzimo' grown in a single experiment in daylight phytotron compartments in Norway.

Results: Plants grown in the long photoperiod (LD) and higher temperatures had greater leaf growth and higher dry matter production than those under short day (SD) and low temperature conditions. Growth decreased over the 39 days of the experiment. The changes in growth in the different environments were associated with changes in relative growth rate (RGR) and these were driven by changes in net assimilation rate (NAR) and leaf area ratio (LAR). The plants directed more dry matter to the leaves and crowns under LD and high temperature conditions and less dry matter to the roots, thus increasing the plant's shoot to root ratio. Long days decreased the concentrations of sugars and starch in most of the tissues, while the effect of temperature was more complex. Higher temperatures increased the concentrations of sugars in the leaves in LD, while starch accumulated in the roots under SD and low temperature conditions. Sucrose accumulated temporarily in the crowns at the time of flower bud formation in LD and higher temperatures.

Conclusions: The results of the experiment demonstrate that the effects of photoperiod and temperature on the vegetative growth of everbearing strawberry are similar to those reported for seasonal-flowering strawberry. Increases in temperature and photoperiod and the resulting enhancement of the RGR was associated with accumulation of soluble sugars (sucrose, glucose and fructose) in the above-ground parts of the plant, whereas low temperature and SD resulted in accumulation of starch in the roots.

Keywords: Carbohydrates, Everbearing strawberry, Flowering, *Fragaria x ananassa*, Growth, Photoperiod, Temperature

Introduction

The cultivated strawberry (*Fragaria x ananassa* Duch.) has a wide geographic distribution that demonstrates the broad adaptation of the species to different growing conditions (Hytönen 2009). Due to the economic importance of the crop, the environmental regulation of growth and flowering in strawberry plants has been explored in detail in the past decades and several authors have reviewed

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the literature on the subject (e.g. Guttridge 1985; Larson 1994; Battey et al. 1998; Taylor 2002; Heide et al. 2013; Hytönen and Kurokura 2020). Vegetative growth and the transition to reproductive development are mainly controlled by complex interactions of temperature, photoperiod and radiation (Heide et al. 2013). However, since yield is dependent upon the amount of dry matter produced and distributed to the different plant organs (Olsen et al. 1985), the quantification of plant productivity is an important link between yield and the physiological phenomena that determines it (Casierra-Posada et al. 2012).

Growth analysis is widely used to investigate how environmental factors affect plant growth, using simple, primary data such as weights of different plant fractions and leaf areas as inputs (Evans 1972; Hunt et al. 2002). The central parameter in these analyses is the relative growth rate (RGR), which describes the exponential growth phase of annual crop plants assuming that new growth is simply related to the existing biomass (Hunt 1990; Sønsteby et al. 2016). RGR represents the increase in plant weight per unit of existing weight over a given period, and has two components: Net assimilation rate (NAR), which is the increase in plant weight per unit of existing leaf area per unit time and Leaf area ratio (LAR), which is the ratio of leaf area to total plant weight at a given time:

$RGR = NAR \times LAR$, where,

$LAR = SLA \times LWR$,

$SLA =$ Specific Leaf Area (ratio of leaf area per unit leaf weight),

$LWR =$ Leaf Weight Ratio (ratio of leaf weight per unit total plant weight).

$RLAGR =$ Increase in leaf area per unit of existing area over a given period. The RLAGR is thus analogous to the RGR except that it is a specific expression on how leaf area is affected by the environment.

The advantage of growth analyses for the investigation of plant growth lies in the ease by which primary data such as dry weights, leaf areas and time are measured. Estimation of the relative growth components may also contribute to our understanding of the physiological processes defining plant production and fruit yield and facilitate the development of better crop management strategies (Fernandez et al. 2001; Casierra-Posada et al. 2012).

Growth analyses in cultivated strawberries have mainly been performed on field-grown plants to study the production and allocation of dry matter in response to seasonal changes in the environment during establishment and first year of the plant cycle (Olsen et al. 1985), in different cultivation systems (Strik and Proctor 1988a, 1988b; Fernandez et al. 2001). However, in field-grown plants it is laborious to extract roots, and therefore, root weights are often not included in the analysis. Under

field conditions, it is also difficult to separate the effects of temperature, photoperiod, solar radiation and precipitation which often vary in parallel. Only a few papers report on growth analyses under semi-controlled greenhouse conditions (Asgar et al. 2011; Casierra-Posada et al. 2012), and these were mainly focused on stress factors. To our knowledge, the only growth analyses of strawberry plants performed in fully controlled environment is the analysis by Sønsteby et al. (2016). The authors used young runner-propagated plants of the seasonal flowering (SF) cv. Sonata, grown in a daylight phytotron, where temperature, photoperiod, fertilization, and humidity were fully controlled during the entire experimental period.

As pointed out by Olsen et al. (1985), the growth of strawberry plants is also influenced by ontogenetic factors, and this makes the use of young, vegetative plants crucial in a growth analysis. As growth progresses, the leaves enter a state of negative carbon balance due to mutual shading and reduced photosynthesis of aging leaves (Sønsteby et al. 2016). Hunt (1990) also pointed out that as growth progresses, plant systems become more complex, with enlarged translocatory pathways that result in a lower rate of dry weight increase. The shift from vegetative to generative development also affects the production and allocation of photosynthates due to the large sink effect of developing flowers and fruits (Hunt 1990; Sønsteby et al. 2016).

The present study was motivated by the increasing interest in EB strawberry cultivars for commercial production, and the limited knowledge on the environmental control of vegetative growth of this type of cultivars. The main purpose of the study was to investigate the environmental control of vegetative growth in an EB strawberry by quantification of the production and distribution of dry matter and the concentrations of non-structural carbohydrates in the various parts of the plants during the early period of growth.

Materials and methods
Plant material and cultivation
Plants of the seed-propagated F_1 hybrid 'Delizzimo' (ABZ Seeds, Bovenkarspel, The Netherlands) were used for the experiment. Seeds were received directly from the breeder and sown on 16 March in sowing trays at a minimum temperature of 24 °C in 10-h photoperiod in a greenhouse at the NIBIO Experimental Centre Apelsvoll, in South East Norway (60°40′N, 10°40′E). On 26 March, the trays were transferred to the phytotron at the Norwegian University of Life Sciences at Ås, Norway (59°40′N, 10°45′E), and kept in a growth chamber in 10-h short day (SD) at 26 °C. On 14 April, seedlings were transplanted into 9 cm pots in granulated vermiculite and grown

further in a natural daylight phytotron compartment in SD at 26 °C until 30 April when the treatments were started.

The plants were then distributed to three natural daylight compartments maintained at 12, 19 and 26 °C where they were grown during daytime (0800–1800 h). For the rest of the day, the plants were moved to adjacent rooms from 1800 to 0800 h where they received either darkness for 14 h (10-h SD), or 10-h low-intensity-light ($\sim$ 7 μmol quanta m^{-2} s^{-1} photosynthetic photon flux (PPF)) from 70 W incandescent lamps for daylight extension (20-h LD). The 4-h dark period was centred around midnight (2200–0200 h). The daylength 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 (400 W Philips HPT-I) whenever the PPF fell below 150 μmol quanta m^{-2} s^{-1} (as on cloudy days). The plant trolleys were positioned randomly in the daylight rooms when moved to and from the adjacent photoperiodic treatment rooms, and the plants were randomly distributed on the plant trolleys. At the beginning, the young plants were placed a few cm apart, but the distance was adjusted after each harvest to give the best possible light conditions and avoid shading. Temperatures were controlled to $\pm$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 consisting of 1:1 (w:w) mixture of Kristalon™ (9-11-30% NPK + micronutrients) and Yaraliva™ (N 15.5% and Ca 19%) both from Yara International (Oslo, Norway) with an electric conductivity (EC) of 1.5 mS cm^{-1}.

Plants were harvested for growth analysis at start (day 0) and after 13, 26, and 39 days of growth. All the plants to be harvested were placed in the dark in a 5 °C cold room from 0800 h until harvest to reduce diurnal metabolic changes to a minimum during the day of harvest. The harvested plants were partitioned into green leaves (lamina), petioles, crowns, roots and flowers (when present). The roots were washed clean of vermiculite and each plant fraction was blotted on tissue paper and the fresh weight determined. Total leaf area of each sample was measured with a leaf area meter (LI-3100 Area Meter, LI- COR Biosciences, Lincoln, NE, USA).

The samples were placed loosely in open paper bags and dried in a forced-air drying oven at 100 °C for 60 min, and then further dried to constant weight at 70 °C. The initial heat treatment at 100 °C was used to inactivate carbohydrate-degrading enzymes (Acuña-Maldonado and Pritts 2013). The dried tissues were ground in a mill

(Thomas Wiley® Mini-Mill, A. H. Thomas Co., Scientific Apparatus, Phila., PA, USA) to pass through a 0.50 mm sieve and stored in vacuo in glass containers until analysed. The number of plants selected at each harvest was 10, 8, 6 and 5 after 0, 13, 26 and 39 days of growth, respectively. These varying plant numbers were used to compensate for the varying plant size at each harvest.

Relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR), were calculated as outlined by Radford (1967) and Evans (1972). The relative leaf area growth rate (RLAGR) was calculated in the same way as the RGR, except that leaf areas instead of weight data were used.

Determination of soluble sugars and starch concentrations

Soluble sugars and starch concentrations were measured at 26 and 39 days only. Approx. 100 mg dried plant material were weighed into an Eppendorf tube and soluble carbohydrates extracted with 80% ethanol using an ultrasonic bath (Model USC 200 TH, VWR, Leuven, Belgium) at 60 °C for 30 min with two repeated extractions with 2 ml each time. Three replicate samples were extracted for each treatment at day 26 and day 39. For each extraction, samples were centrifuged at 15,000 rpm for 3 min, and the supernatants from the two extractions combined. The ethanol was completely evaporated from the supernatant at 60 °C in a vacuum desiccator (Eppendorf AG 22,331, Hamburg, Germany). Afterwards, 2 ml MilliQ water (MQW) was added to the dry extract and the Eppendorf tube kept in the ultrasonic bath for 30 min at 60 °C. The extract was then centrifuged at 15,000 rpm for 3 min and the supernatant pipetted into HPLC (high pressure liquid chromatography) glass vials.

The extracts were run on a High Performance Liquid Chromatograph (Agilent 1200 series of HPLC, Agilent Technologies, Waldbronn, Germany) with a Refractive Index Detector to separate and identify soluble sugars. Sugars were separated using a column specialized for separating carbohydrates (Agilent Hi-Plex Ca USPL19, 4.0 * 250 nm, 8 μm; p/n PL1570-5810). For the mobile phase, 100% MQW was used as solvent. The flow rate was 0.3 ml min^{-1} and the column temperature was 80 °C. The sugar concentrations were determined by comparison with standard solutions of pure fructose, glucose and sucrose at concentrations of 0.5, 0.25, and 0.125%.

For starch determinations, 200 mg dried plant material was weighed into a 15 ml Sarstedt plastic centrifuge tube. Soluble sugars were extracted as described above and discarded with the supernatant. Starch in the pellet was solubilized by adding 2 ml dimethylsulfoxide (DMSO) and placing the tube on a boiling water bath for 5 min. Immediately, 2.9 ml MOPS buffer (pH 7) and 0.1 ml thermostable α-amylase (*Bacillus licheniformis*, Megazyme)

were added, and the tube incubated for 6 min on a boiling water bath. The tube was then placed on a 50 °C water bath and 4 ml sodium acetate buffer (pH 4.5) and 0.1 ml (20 units) amyloglucosidase (*Aspergillus niger*, Megazyme) were added and the tube incubated for 30 min at 50 °C. The glucose content after hydrolysis of starch was analysed by HPLC as described above. The amount of starch was estimated from standards of pure starch (100, 50, 25 and 10 mg) hydrolysed together with the samples.

Estimation of chlorophyll concentration
Total chlorophyll concentration was estimated optically by a leaf-clip sensor Dualex Scientific + (FORCE-A, Orsay, France) at start and after 13, 26, and 39 days of growth. Chlorophyll concentrations were assessed from apparent leaf transmittance (Cerovic et al. 2012). Measurements were performed on 5–6 plants in each treatment using the middle leaflet of the youngest fully developed leaf of each plant, with the adaxial leaf side facing the light source. The diameter cover by the sensor is about 6 mm (Cerovic et al. 2012). One point measurement was done on each plant.

Experimental design and data analysis
The experiment was conducted as a factorial split-plot design with temperatures as main plots and photoperiods as sub-plots. Each treatment had 3 replicates consisting of 10, 8, 6 or 5 plants grown on separate trolleys, and harvested after 0, 13, 26 and 39 days as explained above. The plants were randomly distributed on the plant trolleys. At the beginning, the young plants were placed a few cm apart, but the distance was adjusted after each harvest to give the best possible light conditions and avoid shading.

For the statistical analyses of the data, homoscedasticity and normality assumptions were tested prior to running of the generalized linear models (Ryan-Joiner test for normality and Levene's test for homoscedasticity). Analysis of variance (ANOVA) were performed with a MiniTab® Statistical Software program package (Release 18.1.0. Minitab. Inc., State College, PA, USA). Percentage values were always subjected to square root transformation before performance of the ANOVA. For the separation of the mean carbohydrate concentrations, 95% confidence intervals were calculated according to Cumming (2009) and are provided as supplementary figures (Additional file 1: Figs. S2 and S4).

Results
Growth analysis
Plant weight and leaf area increased with increasing temperature and photoperiod, the increases being exponential versus time, giving a linear time regression with the natural logs (ln) of weight and area (Figs. 1 and 2). The

LD-stimulation was larger at 12 °C than at the higher temperatures at all harvest times. An exception was present for leaf area, which had a slightly larger LD-promotion at 19 °C on day 13. At the later harvests, however, the daylength gap narrowed again at high temperature (Fig. 2).

RGR increased with increasing temperature (Table 1, Fig. 3), but generally decreased over time. The main effects of temperature and period of growth were statistically significant, as well as the two factor interactions between temperature and photoperiod and the three-factor interaction between temperature, photoperiod and growth period (Table 1). However, the main effect of photoperiod was not statistically significant. The temperature enhancement effect was largest between 12 and 19 °C at all harvest times (Table 1, Fig. 3).

Like the RGR, NAR increased with increasing temperature in LD, while in SD it reached a maximum at 19 °C and decreased again at 26 °C (Table 1, Fig. 3). While the main effect of photoperiod was non- significant, it had a highly significant interaction with both temperature and growth period, thus demonstrating its modifying effect on the NAR, especially during the early period of growth (Table 1).

Generally, LAR increased with increasing temperature, but the effect varied with photoperiod and the various periods of growth (Table 1). Thus, while LAR increased with increasing temperature in both photoperiods during the second and third periods of growth, it varied with photoperiod in a complex manner during the first period. This resulted in highly significant main effects of growth period and in the two- and three-factor interactions with photoperiod and temperature (Table 1).

RLAGR increased with increasing temperature during all periods of growth, and the effect was enhanced by LD, especially at 12 °C (Fig. 3). The main effects of temperature, photoperiod and period of growth, as well as their two- and three-factor interactions were all highly significant (Table 2). Although temperature had a large enhancement effect between 12 and 19 °C, the temperature effect levelled off above 19 °C. Comparison of RGR and RLAGR values shows that plant weight and leaf area were affected in much the same way and to the same extent by temperature and photoperiod.

Table 2 summarizes the results for the specific leaf area (SLA) and the leaf weight ratio (LWR) for each harvest day with the results for LAR included for comparison. SLA varied in a complex way with changes in both photoperiod, temperature and harvest day. SLA was enhanced by LD at day 13, but due to significant interactions between photoperiod and harvest day, photoperiod had the opposite effect at later harvests. LWR increased with increasing temperature and decreased over time at

Fig. 1 Time courses of total dry matter and leaf area increment of 'Delizzimo' strawberry plants during 39 days of growth. Values are the means ± SE of three biological replicates with 5–10 plants each
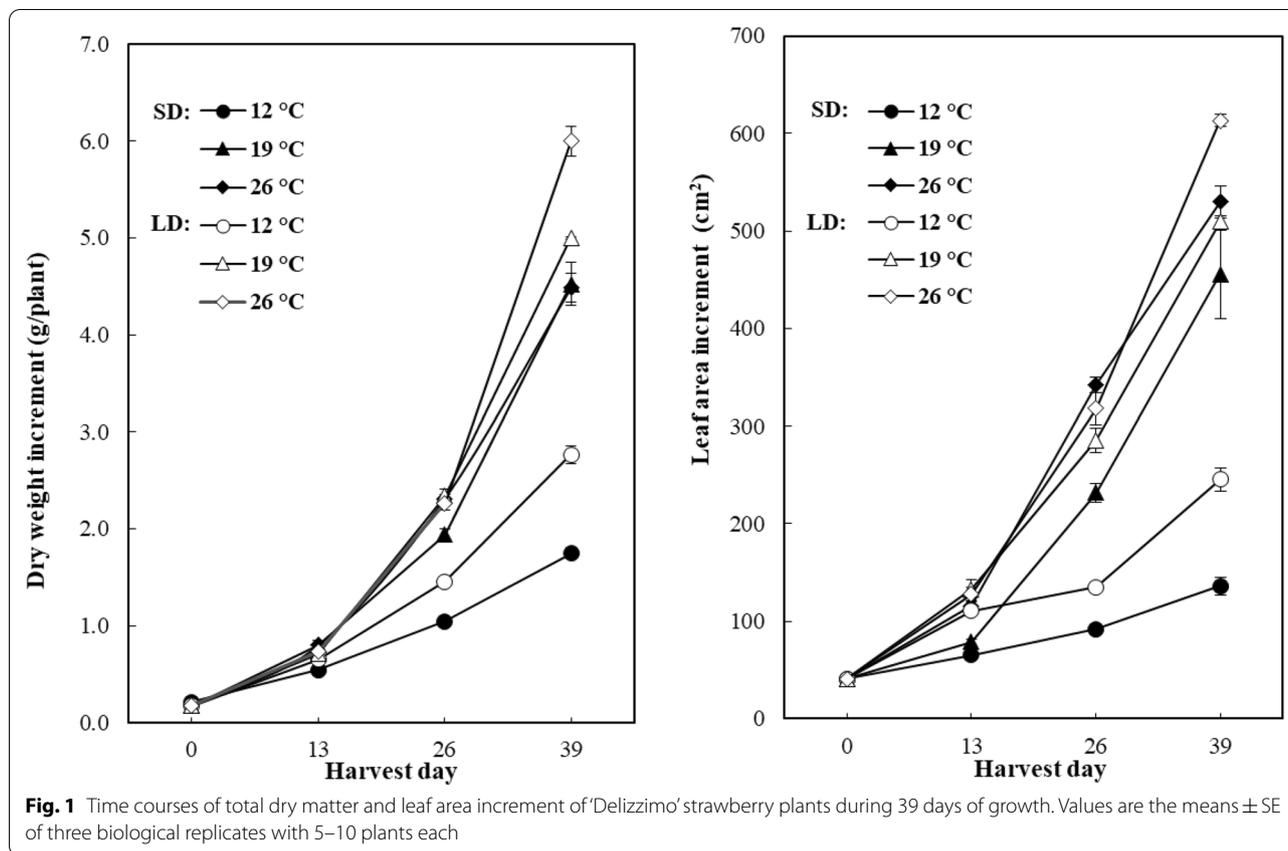
all temperatures. However, the effect of photoperiod varied with temperature, LWR being enhanced by LD at 12 and 19 °C, with the opposite effect at 26 °C (temperature by photoperiod interaction). The changes in LWR were associated with parallel changes in LAR.

Dry matter partitioning

While dry matter partitioning into the laminas increased with increasing temperature, the effect of photoperiod varied with temperature, increasing in LD at 12 °C, being neutral at 19 °C and decreasing at 26 °C (Table 3). Because of this strong interaction between temperature and photoperiod ($P \leq 0.001$), the main effect of photoperiod was not statistically significant for the laminas. In the petioles, dry matter partitioning increased with increases in both temperature and photoperiod, with no significant interaction. In contrast, allocation into crowns and roots decreased with increasing temperature and photoperiod, although in crowns only the main effect of temperature was statistically significant. At this stage of growth (after 39 days), the plants had initiated flowers in LD at 19 and 26 °C, and the weights of the entire inflorescence structures are presented in Table 3. Since increasing temperature and photoperiod enhanced the partitioning of dry

matter into the leaves (laminas and petioles) compared with the roots, the shoot to root ratio also increased under these conditions. The time changes in the shoot to root ratio are presented in Additional file 1: Fig. S1.

The proportional sizes of the plants' tops and roots after 39 days of growth are shown in Fig. 4. Both the photos and the data shown in Table 3, clearly illustrate that under increasing temperatures and daylength conditions, the plants partitioned a greater share of their production into aboveground organs, and less into the roots which were favoured by low temperature and SD conditions.

Non-structural carbohydrate concentrations and proportions

The concentrations of sucrose varied significantly with temperature, photoperiod, and day of harvest in all plant fractions, but with some variations between plant fractions and the two harvest days (Table 4, Additional file 1: Fig. S2). For all environmental conditions and at both harvests, there was a highly significant three-factor interaction, which renders the main effects subordinate. After 26 days, the concentration of sucrose at 12 °C was highest in LD, except for the roots, which had

Fig. 2 Linear regression for the natural log (ln) of total dry weight and leaf increment versus time as influenced by temperature and photoperiod (10 h SD, filled symbols and 20 h LD, open symbols) in 'Delizzimo' strawberry plants. The data are the means of three biological replicates, each consisting of five to ten plants depending on the date of harvest
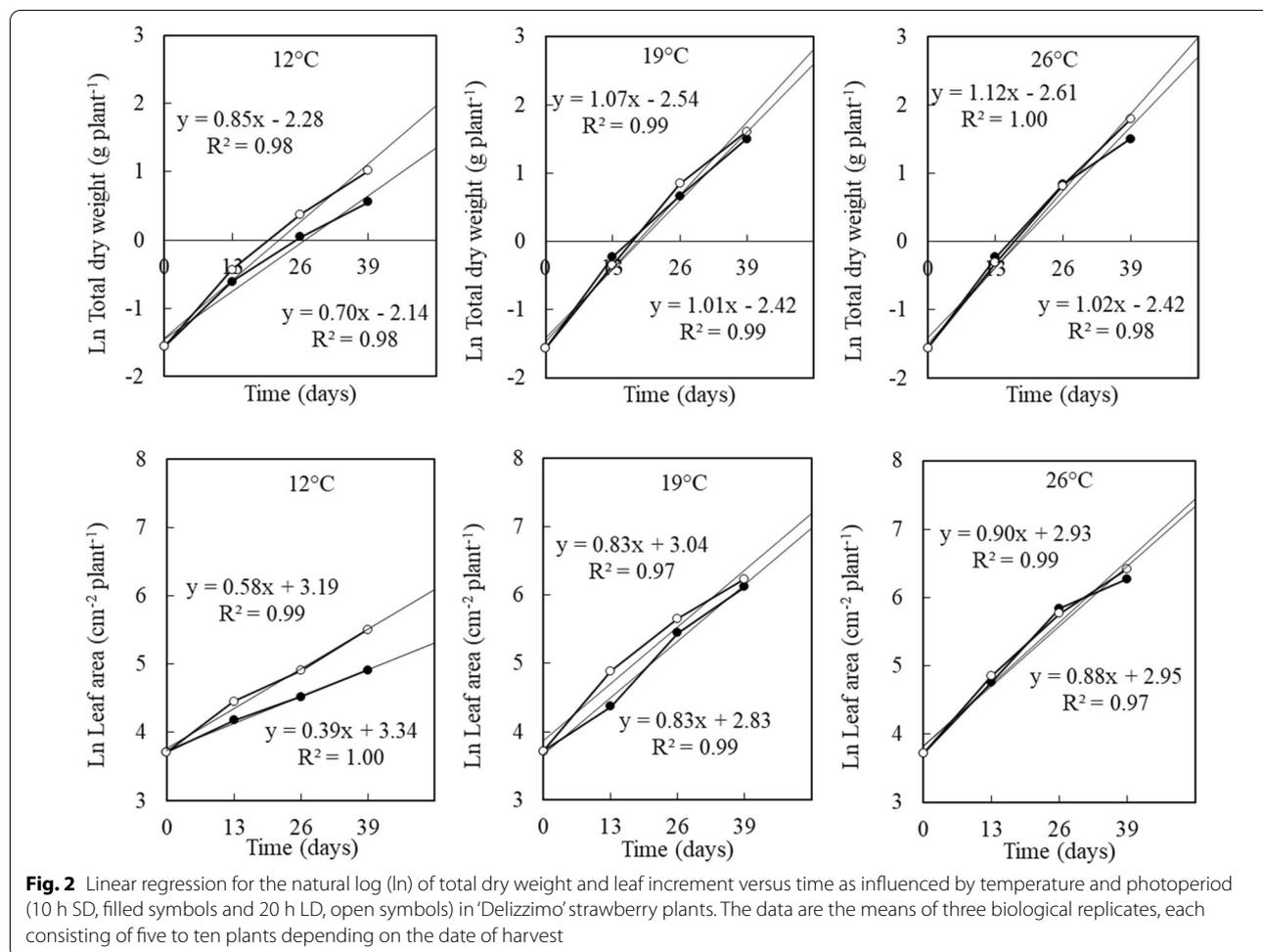
the highest concentration in SD, while at 19 °C, there were only minor variations between plant fractions and between SD and LD. At 26 °C on the other hand, a particularly high sucrose concentration was found in crowns in LD, which was not present after 39 days. However, at the latter time, a similar but smaller increase appeared in LD at 19 °C as well. These variations in sucrose concentration had important implications for the sucrose/glucose + fructose ratios (see Additional file 1: Fig. S3).

The average plant glucose concentrations increased with increasing photoperiod except for plants grown at 26 °C, while the effect of temperature was small and significant only for the 26-day harvest (Table 4). However, the effect was negligible in crowns and laminas, and as shown in Additional file 1: Fig. S2, it was mainly due to variations in the petioles. The concentration was also low in the roots, where it tended to decrease with increasing temperature.

For fructose, the concentration tended to increase in LD at low and intermediate temperatures (Table 4). At the plant fraction level, the concentration was relatively low in crowns, petioles and roots, and significantly higher in the laminas, in which the photoperiodic effect was also strongest (Additional file 1: Fig. S2). In the roots, fructose concentrations tended to decrease with increasing temperature in both photoperiods.

Although the total sugar concentrations generally tended to increase in LD at 12 and 19 °C in the aboveground parts of the plants, there was no such daylength effect at 26 °C in any of the plant fractions, and the effect was not always significant for all plant parts. Usually, the temperature and daylength effects were more pronounced in the day 26 harvest (Table 4, Additional file 1: Fig. S4). On the other hand, the total sugars concentration in the roots generally decreased with increasing temperature and photoperiod. At all temperatures and both photoperiods, except 12 °C/SD, total sugars were highest in the laminas and petioles, and lowest in the roots (Table 4, Additional file 1: Fig. S4).

The starch concentrations decreased strongly with increasing temperature in crowns and roots, the effect being particularly marked between 12 and 19 °C, while it

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Table 1 Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) and relative leaf area growth rate (RLAGR) of 'Delizzimo' strawberry plants as affected by photoperiod and temperature during a 39-day growth period

Temperature (°C)	Period (days)	Photoperiod (h)	RGR (g/g/day)	NAR (mg/cm²/day)	LAR (cm²/mg)	RLAGR (cm²/cm²/day)
12	0–13	10	0.073	0.488	0.149	0.035
		20	0.087	0.483	0.180	0.076
	0–26	10	0.062	0.509	0.121	0.031
		20	0.074	0.607	0.123	0.046
	0–39	10	0.054	0.495	0.109	0.031
		20	0.066	0.572	0.115	0.046
19	0–13	10	0.102	0.780	0.132	0.050
		20	0.094	0.496	0.190	0.090
	0–26	10	0.085	0.604	0.142	0.067
		20	0.093	0.648	0.143	0.075
	0–39	10	0.079	0.643	0.122	0.062
		20	0.081	0.662	0.123	0.065
26	0–13	10	0.102	0.625	0.165	0.080
		20	0.096	0.527	0.182	0.087
	0–26	10	0.092	0.569	0.162	0.082
		20	0.091	0.582	0.157	0.079
	0–39	10	0.078	0.574	0.137	0.066
		20	0.086	0.702	0.123	0.069
Probability level of significance (ANOVA)*						
Source of variation						
Temperature (A)			0.001	0.013	0.004	< 0.001
Photoperiod (B)			n.s	n.s	0.028	< 0.001
Growth period (C)			< 0.001	n.s	< 0.001	< 0.001
A x B			< 0.001	0.001	0.005	< 0.001
A x C			n.s	n.s	0.002	0.002
B x C			0.019	< 0.001	< 0.001	< 0.001
A x B x C			0.040	0.011	0.004	0.002

*The data are the means of three replicates, each with 10, 8, 6 and 5 plants at 0, 13, 26 and 39 days, respectively.

n.s not significant

was low and more or less constant across the treatments in laminas and petioles (Table 4, Additional file 1: Fig. S2).

The results in Additional file 1: Fig. S3 show the ratio of sucrose/glucose + fructose in the plants after 26 and 39 days of exposure to varying temperatures and photoperiods. Generally, the highest ratios were observed in the crowns and roots, and the lowest in the petioles and laminas; and except for the situation in crowns, the picture did not change markedly between the two harvest times. However, at day 26, the ratio in the crowns rose dramatically in LD at 26 °C compared with SD, and compared with lower temperatures in LD. On day 39 on the other hand, a similar, but smaller increase took place at 19 °C in LD compared with SD and with the other temperatures in LD. The results in Table 4 reveal that these transitional increases were mainly due to increases in the

sucrose concentration, whereas the concentrations of glucose and fructose remained relatively unchanged. In association with the elevated sucrose level at day 39 in SD at 19 °C, there was also a coincidental, but opposite transitional change in the sugar ratios in the petioles (Table 4, Additional file 1: Fig. S2).

Even larger changes took place in the total sugar/starch ratios at the various environmental conditions and harvest times (Additional file 1: Fig. S5). Generally, the ratio increased strongly in almost all plant fractions with increasing temperature, especially at day 26, but to a lesser extent also at day 39. Again, the highest ratios were generally observed in the laminas and petioles (except for some minor modifications for the latter at day 26), while the lowest ratios were found in the crowns and roots.

Fig. 3 Growth analysis parameters (RGR and NAR solid lines, RLAGR and LAR, dashed lines) for 'Delizzimo' strawberry plants grown in 10 h (SD, filled symbols) and 20 h (LD, open symbols) photoperiods at temperatures of 12, 19 and 26 °C. The results represent growth over the entire 39-days growth period. Values are the means ± SE of three biological replicates, each with five plants
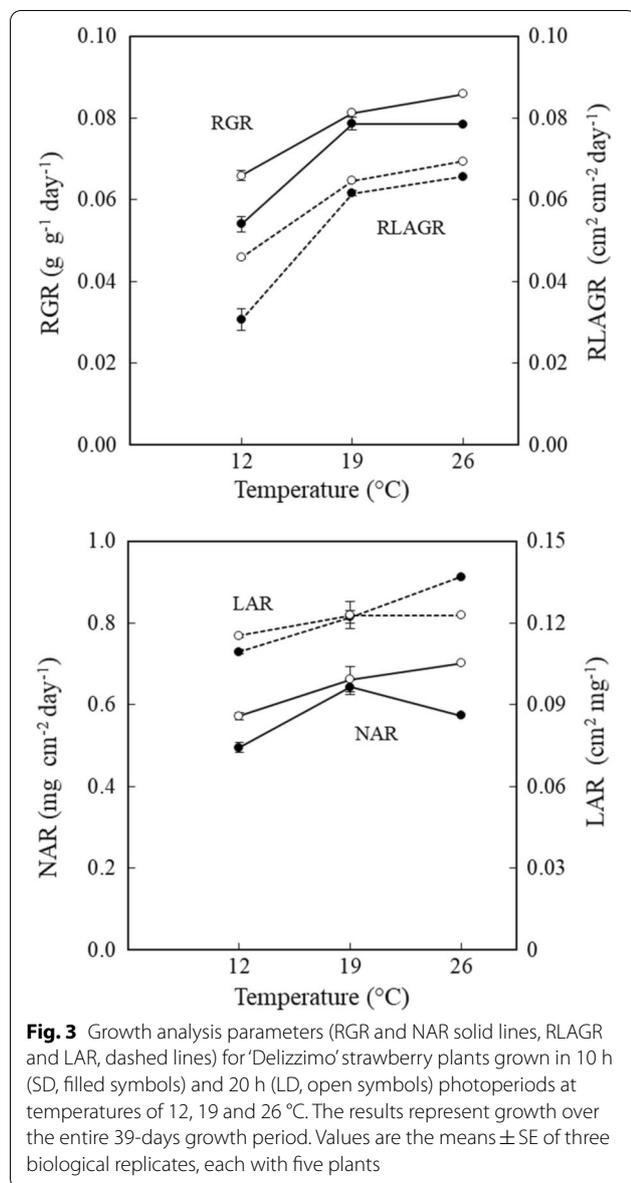
Chlorophyll concentrations

Concentrations of chlorophyll as estimated by the Dualex sensor increased with decreasing temperature and increasing growth period (Fig. 5). In general, the chlorophyll concentrations remained stable during the first 26 day and then increased rapidly. The concentration was highest in SD at 12 °C and decreased markedly with increases in both temperature and photoperiod. Throughout the 39-day experimental period, the lowest chlorophyll concentrations occurred in plants grown at 26 °C in LD.

Discussion

The results of the experiment demonstrate that despite of contrasting environmental control of flowering in SF and EB strawberry cultivars (Heide et al. 2013), the effect of photoperiod and temperature on vegetative growth is similar in the EB 'Delizzimo' (Fig. 1) and the SF 'Sonata' (Sønsteby et al. 2016). In both cultivars, plant dry weight and leaf area increased exponentially over time to increases in temperature and photoperiod, yielding linear time regressions with the natural log (ln) of plant weight and leaf area. Furthermore, in both cultivars the increases in growth rate were driven by changes in both net assimilation rate (NAR) and leaf area ratio (LAR) (Table 1). Except for minor modifications, the environmental regulation of dry matter partitioning was also surprisingly similar in the EB 'Delizzimo' and the SF 'Sonata'.

The present results with the EB 'Delizzimo' are also in general agreement with previous reports for SF strawberry cultivars and selections under field conditions (Olsen et al. 1985; Strik and Proctor 1988a). Generally, 'Delizzimo' had higher RGR than previously reported for SF cultivars. A maximum of 0.086 g/g/day obtained at 26 °C in LD is slightly higher than the values reported for the SF cultivar 'Sonata' by Sønsteby et al. (2016) for identical phytotron conditions and double the level for SF types reported by Olsen et al. (1985) and Strik and Proctor (1988a) for field conditions in midsummer of the first fruiting year. Important reasons for the differences are the small plants and the relative short experimental periods that deliberately were used for both plant types in the phytotron in order to study growth control during the vegetative plant state. Because of this, and since flowers and developing fruits are strong sinks for photosynthates in EB strawberry (Sønsteby et al. 2021), the differences between SF and EB types would probably have been more distinct if longer experimental periods had been used so that generative development would have represented a greater part of the experimental period. Hunt (1990) also concluded that the RGR decreases as plants become larger due to their increased anatomical and morphological differentiation and larger translocatory pathways. Hence, the RGR always decreased over time.

While Heide (1977) reported a temperature optimum of 18 °C for dry matter production in SF strawberry under autumn conditions, Sønsteby et al. (2016) reported a higher temperature optimum of 24 °C for 'Sonata' plants raised in spring and early summer. In the present experiment, RGR levelled off between 19 and 26 °C (Fig. 3), which indicates that 26 ℃ is supra-optimal for dry matter accumulation in 'Delizzimo'. This was directly supported by photosynthesis studies in three other EB cultivars under the same phytotron conditions, which showed that CO_2-uptake increased with increasing temperature to reach a plateau at 21 ℃ (Rivero et al. 2021b). The present results also confirmed a marked negative effect of SD and low temperature on the RGR that was associated with accumulation of starch in the roots. This is the first step in the sequence of events leading to winter preparation in

Table 2 Specific leaf area (SLA), leaf weight ratio (LWR) and leaf area ratio (LAR) of 'Delizzimo' strawberry plants at start of the experiment and as affected by photoperiod and temperature after 13, 26 and 39 days of cultivation

Temperature (°C)	Days	Photoperiod (h)	SLA (cm^2/mg)	LWR	LAR (cm^2/mg)
At start			0.278	0.702	0.195
12	13	10	0.204	0.588	0.120
		20	0.283	0.603	0.171
	26	10	0.172	0.511	0.088
		20	0.168	0.554	0.093
	39	10	0.171	0.457	0.078
		20	0.169	0.528	0.089
19	13	10	0.161	0.616	0.099
		20	0.298	0.630	0.188
	26	10	0.202	0.593	0.120
		20	0.202	0.605	0.122
	39	10	0.182	0.551	0.100
		20	0.183	0.555	0.102
26	13	10	0.232	0.635	0.147
		20	0.283	0.616	0.174
	26	10	0.233	0.635	0.148
		20	0.237	0.595	0.141
	39	10	0.194	0.610	0.118
		20	0.186	0.552	0.103
Probability level of significance (ANOVA)					
Source of variation					
Temperature (A)			0.003	< 0.001	0.002
Photoperiod (B)			< 0.001	n.s	0.002
Growth period (C)			< 0.001	< 0.001	< 0.001
A x B			0.031	< 0.001	0.005
A x C			< 0.001	< 0.001	0.001
B x C			< 0.001	n.s	< 0.001
A x B x C			< 0.001	< 0.001	< 0.001

*The data are the means of three replicates, each with 10, 8, 6 and 5 plants at 0, 13, 26 and 39 days, respectively

n.s not significant

strawberry plants, commonly referred to as the autumn syndrome (cf. Sønsteby et al. 2016).

The growth analysis revealed that the observed changes in RGR were driven by a combined effect of NAR and LAR, and that such changes were dependent on temperature and photoperiod together with duration of the growth period (Table 1). Similar results were reported by Sønsteby et al. (2016) for the SF 'Sonata' in which, however, the LAR was enhanced by increases in temperature only. The LD enhancement of RGR observed in the present study was most prominent at 12 °C for the whole period of growth (Fig. 3). At this temperature, LD also enhanced RLAGR significantly (*P* ˂0.001 for the whole period), whereas in 'Sonata', LD significantly enhanced RLAGR at all temperatures. This means that LD enhancement of leaf area expansion played a more general role in the temperature enhancement of RGR in 'Sonata' than

in 'Delizzimo'. A notable feature for all growth parameters, was the particularly large variation between treatments during the first 13 days of growth, and it is possible that this was a transitional response to the new growth conditions.

However, the driving forces for enhancement of RGR and dry matter accumulation observed in both SF and EB strawberries differ fundamentally from those reported for perennial temperate grasses, in which the changes in RGR and dry matter production in LD were mainly driven by a marked increase in LAR (Hay and Heide 1983; Heide et al. 1985; Hay 1990; Solhaug 1991). Hay (1990) concluded that the marked photoperiodic stimulation of growth in grasses is a consequence of a positive feedback system in which photosynthates produced by early emerging leaves under LD conditions are invested in larger leaves that intercept more photosynthetic active

Table 3 Effects of temperature and photoperiod on partitioning of dry matter production in 'Delizzimo' strawberry plants in a 39-day growth period. Flowers represent the entire inflorescence structure

Share of total plant dry matter (%)							
Temperature (°C)	Photoperiod (h)	Lamina	Petioles	Crowns	Roots	Flowers	Shoot:root ratio
12	10	45.7c	11.0d	7	36.3a	–	1.8c
	20	52.8b	14.4c	4.8	27.9b	–	2.6b
Mean		*49.3*	*12.7*	*5.9*	*32.1*	*–*	*2.2*
19	10	55.8b	14.1c	4.5	25.6b	–	2.9b
	20	55.5b	19.2b	4.4	16.5c	4.3	5.1a
Mean		*55.7*	*16.7*	*4.4*	*21.1*	*–*	*4*
26	10	61.0a	18.3b	4.2	16.5c	-	5.1a
	20	55.2b	22.6a	3.9	14.1c	4.3	6.1a
Mean		*58.1*	*20.4*	*4*	*15.3*	*–*	*5.6*
Probability level of significance (ANOVA)*							
Source of variation							
Temperature (A)			< 0.001	0.033	< 0.001	–	< 0.001
Photoperiod (B)			< 0.001	n.s	< 0.001	–	< 0.001
A x B			n.s	n.s	0.003	–	0.013

*Percentage data were transformed to the Arcsin ()$^{1/2}$ before the performance of ANOVA Values within the same column followed by different letters are significant different at $P \leq 0.05$ by Tukey's test for the different temperature and photoperiod treatments. The data are the means of three replicates, each with 5 plants.

n.s not significant

radiation which in turn enhances dry matter production. However, despite the different driving forces in grasses and strawberry plants, both plant types had a considerable increase in the shoot to root ratio when grown under LD conditions (cf. Sønsteby et al. 2016). Such photoperiodic responses have been discussed as important adaptations for plant establishment and development, as well as for winter survival. With increasing photoperiod and temperature during spring and early summer, dry matter production increases in aboveground plant parts, whereas late in the season, decreasing photoperiod and temperature will promote root growth and translocation of storage substances to the roots. Clearly, such seasonal responses will have large practical implication for growth and development of strawberry plants grown at different latitudes and altitudes.

In general, photoperiod and temperature influenced the accumulation of sugars and starch in opposite ways (Table 4, Additional file 1: Fig. S2). The high accumulation of total sugars observed in the laminas and petioles is consistent with an increased sugar availability under favourable growing conditions (i.e., intermediate and high temperatures in LD). The high sucrose concentrations found in the petioles, are consistent with mass transport of sucrose out of the leaves as sucrose is known as the main transport form of sugars in most plants (Lambers and Oliveira 2019). Likewise, the observed accumulation of starch in the roots under SD and low temperature conditions is generally found in strawberries

(Bringhurst et al. 1960; López et al. 2002; Acuña-Maldonado and Pritts 2013; Sønsteby et al. 2016) as a seasonal preparation for winter conditions. Lieten et al. (1995) and López et al. (2002), also demonstrated that high starch content in roots and crowns in the autumn is essential for winter survival under both field and cold-store conditions, and that the starch content decreases steadily during the winter.

An interesting finding of the experiment was the temporary increase in sucrose concentration in the crowns on day 26 in LD at 26 °C, and a similar increase on day 39 in LD at 19 °C (Table 4, Additional file 1: Fig. S2) that coincided with the commencement of flower initiation (confirmed by flower mapping, results not shown). Sucrose accumulation in apical buds has been associated with floral initiation in photoperiodic plants in general (Bernier et al. 1993), and in strawberry specifically (Eshghi et al. 2007). Although no such increases in sucrose were observed under flower-inducing SD conditions in 'Sonata' (Sønsteby et al. 2016), the present results suggest that sucrose accumulation may participate in the mediation of floral initiation in the EB strawberry.

SD and decreasing temperatures also increased chlorophyll concentration in the leaves, and similar results were reported by Sønsteby et al. (2016) and Rivero et al. (2021a). However, since dry matter accumulation was the least under these conditions, it indicates that chlorophyll content was not a limiting factor for photosynthesis in the strawberry plants.
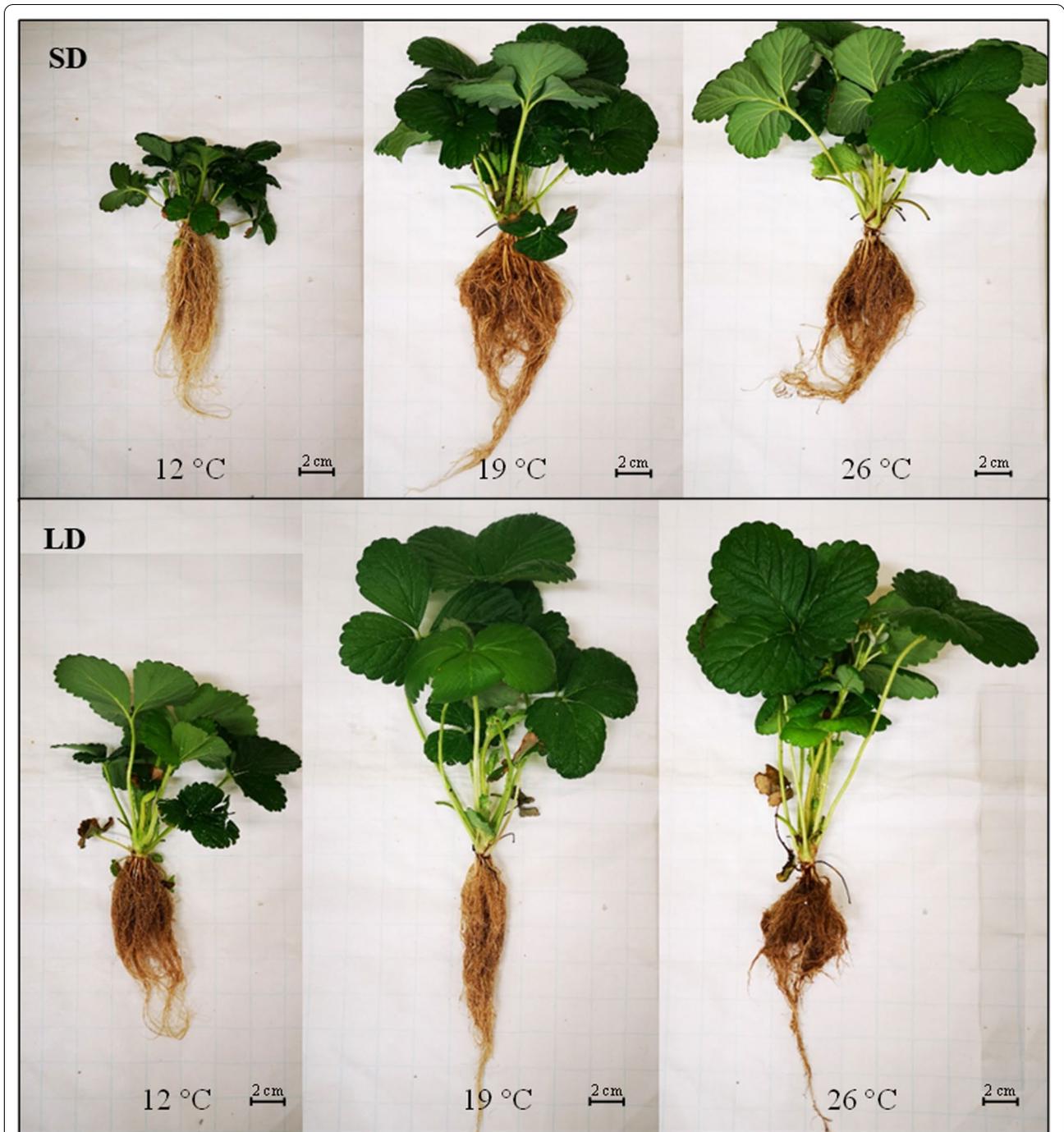
Fig. 4 Appearance of young 'Delizzimo' strawberry plants after 39 days of cultivation in 10 h SD and 20 h LD and temperatures of 12, 19 and 26 °C as indicated

We found the F_1 seedlings to be very useful experimental material for such an investigation. As F_1 progeny of inbred lines, they are genetically homogeneous and accordingly, they were not more variable than clonal material (runner plants). In addition, the seedlings have the advantage of not being developmentally preconditioned by their previous life history but are guaranteed of being initially vegetative and starts with a clean slate. This is particularly important for EB strawberries in which

Table 4 Effect of temperature, photoperiod and harvest day (day 26 and 39) on average tissue concentrations (mg/g DW) of non-structural carbohydrates (sugars and starch) in young plants of 'Delizzimo' strawberry. Values are means of three biological replicates with 5–6 plants each

Temperature (°C)	Photoperiod (h)	Plant fraction	Tissue concentrations (mg/g DW)									
			Sucrose		Glucose		Fructose		Total sugars		Starch	
			26 days	39 days	26 days	39 days	26 days	39 days	26 days	39 days	26 days	39 days
12	10	Lamina	17.5	15.0	33.0	31.6	68.5	62.9	119.0	109.4	16.8	14.3
		Petiole	11.1	10.7	46.6	47.4	37.9	30.7	95.6	88.8	26.9	25.1
		Crown	13.2	13.7	26.9	27.0	28.7	30.7	68.7	71.4	92.2	80.2
		Roots	21.8	21.1	28.0	29.2	29.1	31.1	78.9	81.4	106.3	135.1
		Mean	*15.9*	*15.1*	*33.6*	*33.8*	*41.0*	*38.8*	*90.6*	*87.7*	*60.6*	*63.7*
	20	Lamina	23.3	14.7	37.7	36.3	75.9	76.4	137.0	127.4	37.3	20.5
		Petiole	21.2	10.7	64.6	69.6	42.5	37.8	128.3	118.1	25.5	22.3
		Crown	22.6	14.1	27.5	29.6	34.4	36.5	84.5	80.2	67.4	61.9
		Roots	14.1	13.5	28.9	27.1	29.9	28.1	73.0	68.7	94.1	105.7
		Mean	*20.3*	*13.2*	*39.7*	*40.6*	*45.7*	*44.7*	*105.7*	*98.6*	*56.1*	*52.6*
19	10	Lamina	10.9	13.0	28.8	28.8	57.4	58.9	97.1	100.7	10.9	13.4
		Petiole	12.7	25.2	44.1	55.9	32.8	33.8	89.5	114.9	13.5	24.4
		Crown	8.9	16.7	26.6	26.6	27.5	31.1	62.9	74.4	17.7	46.2
		Roots	10.5	14.0	26.2	26.3	22.8	28.0	59.5	68.3	25.2	108.5
		Mean	*10.7*	*17.2*	*31.4*	*34.4*	*35.1*	*38.0*	*77.2*	*89.6*	*16.8*	*48.9*
	20	Lamina	9.8	12.3	34.5	33.0	70.6	66.3	114.9	116.6	18.1	14.2
		Petiole	11.7	13.9	61.0	72.7	39.7	42.7	112.4	129.3	18.2	22.7
		Crown	12.3	25.2	29.0	29.6	33.7	39.4	75.0	94.2	22.6	36.7
		Roots	10.3	10.9	22.5	23.9	16.9	23.6	49.7	58.5	21.0	47.0
		Mean	*11.0*	*15.6*	*36.8*	*39.8*	*40.2*	*43.0*	*88.0*	*98.4*	*19.4*	*30.2*
26	10	Lamina	13.7	11.2	33.2	33.1	61.9	60.7	108.9	105.0	8.9	13.1
		Petiole	11.0	12.9	55.8	65.9	39.7	40.0	106.4	118.7	11.3	13.3
		Crown	11.5	14.1	32.5	26.6	41.0	36.7	85.0	77.4	15.9	34.4
		Roots	8.5	11.1	23.6	26.6	18.3	24.0	50.4	61.6	12.4	34.6
		Mean	*11.2*	*12.3*	*36.3*	*38.0*	*40.2*	*40.3*	*87.7*	*90.7*	*12.2*	*23.8*
	20	Lamina	12.4	11.7	34.5	34.9	63.6	60.9	110.5	107.5	11.7	13.3
		Petiole	14.5	11.6	55.1	66.2	39.8	41.0	109.4	118.8	17.8	15.7
		Crown	32.2	13.9	27.0	31.8	34.9	43.1	94.1	88.8	34.0	27.7
		Roots	11.4	9.7	21.6	22.8	17.9	18.6	50.9	51.1	11.4	13.1
		Mean	*17.6*	*11.7*	*34.6*	*38.9*	*39.0*	*40.9*	*91.2*	*91.5*	*18.7*	*17.4*

Table 4 (continued)

Temperature (°C)	Photoperiod (h)	Plant fraction	Tissue concentrations (mg/g DW)									
			Sucrose		Glucose		Fructose		Total sugars		Starch	
			26 days	39 days	26 days	39 days	26 days	39 days	26 days	39 days	26 days	39 days
Probability level of significance (ANOVA)												
Source of variation												
Temperature(A)			< 0.001	< 0.001	0.004	n.s	< 0.001	n.s	< 0.001	n.s	< 0.001	< 0.001
Photoperiod (B)			0.001	0.036	0.001	< 0.001	< 0.001	0.041	< 0.001	0.016	n.s	< 0.001
Plant Fraction (C)			0.001	0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
A x B			0.003	n.s	< 0.001	0.009	< 0.001	0.05	< 0.001	0.043	0.003	0.002
A x C			< 0.001	< 0.001	0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
B x C			< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.001	< 0.001
A x B x C			< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.037	< 0.001	0.001	< 0.001	< 0.001

*The data are the means of three replicates, each with 6 and 5 plants after 26 and 39 days, respectively

n.s not significant

Fig. 5 Time course changes in chlorophyll concentrations in leaves of 'Delizzimo' strawberry plants estimated with the Dualex sensor. Values are means ± SE of three biological replicates with 5–6 plants each and three leaves of each harvested plant
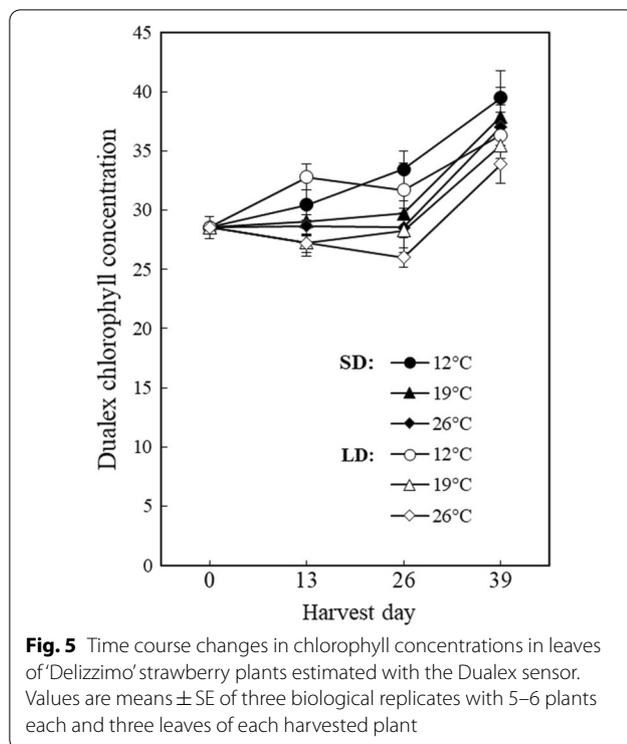
flower initiation takes place in the runners as soon as they emerge.

Conclusion

In summary, we conclude that despite of the contrasting environmental control of flowering in SF and EB strawberries, the EB 'Delizzimo' plants exhibited similar vegetative growth responses to variations in temperature and photoperiod as previously reported for SF genotypes. The increases in RGR observed in 'Delizzimo' seedlings under increasing temperature and daylength conditions were driven by a combined effect of NAR and LAR, in a similar manner as previously reported for the seasonal flowering 'Sonata' (Sønsteby et al. 2016), indicating mediations by both increased photosynthesis and expanded leaf area. Increases in temperature and photoperiod and the resulting enhancement of the RGR was associated with accumulation of soluble sugars (sucrose, glucose and fructose) in the above-ground parts of the plant, whereas low temperature and SD resulted in accumulation of starch in the roots that in nature is associated with declining growth and winter preparations in the autumn. The high accumulation of total sugars observed in the laminas and petioles was consistent with an increased sugar availability under favourable growing conditions, and a temporary rise in sucrose in the crowns coincided with the known commencement of floral initiation.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s43170-022-00110-w.

Additional file 1: Fig. S1. Time course changes in shoot/root ratio (DW basis) and leaf area in 'Delizzimo' strawberry plants during 39 days of cultivation. Values are the means ± SE of three biological replicates with 5 to 10 plants each. **Fig. S2.** Photoperiod x Temperature x Growth period interaction plots for the sucrose, glucose, fructose and starch content of the different plant fractions. Data are means of 10, 8, 6 and 5 plants depending on the harvest period. Vertical bars represent the 95% confidence interval for the means. **Fig. S3** Ratio of tissue concentrations of sucrose vs. glucose + fructose in 'Delizzimo' strawberry plants as affected by temperature and photoperiod treatments after 26 and 39 days of growth as indicated. Values are the means ± SE of three biological replicates with 5-6 plants each. **Fig. S4** Photoperiod x Temperature x Growth period interaction plots for the total soluble sugars content of the different plant fractions. Data are means of 10, 8, 6 and 5 plants depending on the harvest period. Vertical bars represent the 95% confidence interval for the means.

Author contributions

RR, SFR, OMH, KAS, AS: Conceptualization, methodology RR, AS: Data curation software RR, OMH, AS: Writing, original draft preparation RR: Investigation AS, SFR, OMH, KAS: Supervision, validation RR, SFR, OMH, KAS, AS: writing, reviewing and editing AS, SFR: Resources, funding acquisition, project administration. All authors read and approved the final manuscript.

Availability of data and materials

The datasets that were analysed during the study are available upon request from the authors.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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