

# Repeated runner removal after harvest and floating row cover during fall affect carbohydrate status and yield potential of strawberry cvs. Polka and Wendy in the Northern climate

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We investigated the impact of repeated runner removal after harvest and row cover during fall on strawberry (*Fragaria × ananassa*) cvs. Polka and Wendy cropping potential in the joint project of the University of Helsinki and the Rural Advisory Services Finland. Field trials were carried out in 2017 to 2019 on strawberry farms in Southern Ostrobothnia, Finland, at 62°49'N. The treatment effects on the crown carbohydrate reserves, flowering, and yield were recorded. Runner removal three times in three-week intervals after harvest decreased the crown starch reserves but increased the length of the apical inflorescence initials as observed through flower mapping in November, and the numbers of inflorescences and flowers in cv. Polka. Floating row cover after flower induction in September to October hastened floral development in the fall and increased the numbers of inflorescences, flowers, and fruit in cv. Wendy. Although the effects may depend on a cultivar and weather conditions during fall, repeated removal of runners after harvest and covering plants with a floating row cover after flower induction are recommended to increase strawberry yield potential in the Northern climate.

**Key words:** floral development, flower mapping, *Fragaria × ananassa*, fruit yield, starch

## Introduction

Strawberry (*Fragaria × ananassa* Duch.) runners (stolons) are strong sinks for carbohydrates, water, and nutrients (Handley et al. 2009), and their removal is often a standard practice in production with the aim to decrease competition between the concurrently developing fruits and runners. However, the effect of runner removal is variable and depends on e.g. climate, cultivation system and a cultivar grown. In a short day (SD) cv. Toyonoka grown in subtropical annual winter production in Taiwan, yield is increased by weekly removal of runners during the first harvest cycle, but not during the second harvest cycle, when less runnering occurs due to the shorter day length and cooler temperatures (Lyu et al. 2014). Morrison et al. (2018) studied the effect of runner removal on yield of both SD and everbearing (EB) cultivars in winter production in greenhouses, but the results were variable. In Canada, runner removal on two everbearing cultivars had varying effects that were also dependent on the growing site, and the effects were not carried to next season (Hughes et al. 2017). Talton et al. (2020) observed increased yield in plants where runners were removed every two weeks in Florida. However, the effect was not consistent for all four cultivars studied (both SD and EB types). In matted row cultivation the situation is profoundly different; possible yield increases gained through runner removal would be counteracted by a reduced daughter plant density the following year and thereby decreased yield per area (Hancock et al. 1982, Pritts and Worden 1988).

While the majority of studies have focused on reducing the competition between the concurrently developing fruits and runners, the effect of runner removal on floral initiation and development has received less attention. Handley et al. (2009) observed in Maine, USA that repeated removal of SD cv. Honeyoe runners by hand or suppression with prohexadione-calcium starting on 10 August, increases the yield in the following year. The effects on floral development were not analyzed in the study. Recent literature also suggests that bi-weekly runner removal increases yield of EB strawberry cv. Favori, and specifically due to enhancement of continued floral initiation that occurs in everbearing cultivars after the first fruiting flush (Sønsteby et al. 2021). To the best of our knowledge, no published papers demonstrate the effect of runner removal after harvest on the development of flower initials in SD strawberry.

The influence of fall temperatures on strawberry yield potential has been noted in several studies (e.g. Døving and Måge 2001, Sønsteby and Heide 2008). High temperature after flower induction during the development of flower initials increases yield potential of strawberry. After analyzing several meteorological variables Døving and

Måge (2001) stated that the temperatures in August and September are the most significant variables in predicting strawberry yield in Norway (two research areas situated at 62 °N and at 64 °N) but affecting in the opposite ways; increased temperatures in August correlate with lower yields, while increased temperatures in September correlate with higher yields in the following year. Sønsteby and Heide (2008) reported that if the day temperature is 18 °C, the optimal night temperature for SD induction of flowering is 18 °C for cvs. Florence and Korona, and 15 °C for cv. Frida that is bred for Northern conditions. In line with this, the most effective temperature for SD induction of flowering for cv. Polka is 15 °C to 18 °C (Opstad et al. 2011). Lower than optimal temperatures extend the time period needed for the saturated flowering response in short day conditions (Sønsteby and Heide 2008, Opstad et al. 2011). According to Sønsteby et al. (2013), flowering and fruit yield in cvs. Korona, Polka and Sonata are increased through increasing the temperature above 15 °C in September, and the effect may be further intensified by fertilizer pulses applied after floral induction (Sønsteby et al. 2013). It is evident that the temperatures during the fall in Finland are lower than the optimal mentioned above. We hypothesize that floating row cover deployed in the fall, when the flower initials of strawberry are developing, would enhance floral development and increase yield potential through increased canopy temperature.

Carbohydrates accumulate in a strawberry crown during the growing season and are a prerequisite for successful overwintering and following yield production (Lieten et al. 1995). The major carbohydrates in strawberry crown are glucose, fructose, sucrose, and starch, which are accumulated in the crown during the vegetative phase and mobilized to other parts of the plant during blooming (Macías-Rodríguez et al. 2002). Carbon reserves in crown correlate with yield and high carbohydrate reserves may increase yield (Lieten et al. 1995, Acuña-Maldonado and Pritts 2008). Soluble carbohydrates on the other hand are crucial for frost hardening and successful overwintering of strawberry plants (Gagnon et al. 1990). In strawberry cvs. Redcoat and Bounty crowns the highest concentrations of sucrose and reducing sugars coincide with maximal frost hardiness in January (Paquin et al. 1989). Therefore, our interest was to examine, how runner removal affects sink-source balance of a strawberry plant and hence carbohydrate reserves in a crown. Furthermore, because floating row cover modifies temperature and light environment in vegetation, it also influences photosynthesis and respiration and consequently the carbohydrate balance of the plants.

The aim of our study was to evaluate the effect of 1) repeated runner removal after harvest and 2) fall row cover on strawberry floral development, carbohydrate reserves, and yield potential in farm environment in the Northern climate. The experiments reported here are a part of a three-year research project, which aimed at enhancing productivity and economical sustainability of open field strawberry production in Finland.

## Material and methods

### Experimental conditions and treatments

The experiments were conducted as a part of the joint project of the University of Helsinki and the Rural Advisory Services Finland on two strawberry farms in Lehtimäki (62°49'N, 23°56'E), Southern Ostrobothnia, Finland in 2017–18 and 2018–19. Temperatures recorded by the Finnish Meteorological Institute in Ähtäri Inha 29 km south from the experimental farms are presented in Figure 1. The effective temperature sum (threshold temperature +5 °C) was 960 °C d and 1483 °C d in growing seasons 2017 and 2018, respectively. Standard commercial strawberry management practices included black plastic mulch and fertigation through drip irrigation system.

The effect of runner removal was studied in the field, which was planted in May 2017 with SD cv. Polka frigo A++ plants. The experimental area of 34 × 6 m consisting of four adjacent rows was marked off in the field. The distance between the plants was 0.33 m in a row, and 1.3 m between the rows. The experimental design was a randomized complete block design (RCBD) with four blocks (four adjacent rows). The experimental units were 10 row meters each, consisting of 30 plants. There were three plots in each of the four rows, and 1 m between the plots in a row. The treatments were: R1 = runners were removed with pruning shears three times in three weeks intervals; 27 July, 17 August, and 7 September 2017 / 25 July, 15 August, and 4 September 2018, R2 = farm practice; runners removed with Reglone (a.i. diquat dibromide, Syngenta Group) on 27 August 2017 / 10 September 2018, and R3 = control, no runner removal.

The effect of floating row cover was studied in the field planted with SD cv. Wendy frigo A+ plants in May 2017. The distance between the plants was 0.25 m in a row, and 2 m between the rows. The experimental design was a randomized complete block design (RCBD) with five blocks (five adjacent rows) and the treatments (row cover,

uncovered) were replicated four times in each block. The experimental plots, which were 10 row meters each consisting of 40 plants, were randomly placed in the rows. There were eight plots in each of the five rows, and 1 m between the plots in a row. New experimental area was established in 2018. Floating row cover (Agrisoft, polypropylene 23 g m<sup>-2</sup>, Soft N.W. S.r.l., Italy) was installed on 28 August and 12 September in 2017 and 2018, respectively.

Flower mapping, crown carbohydrate analyses, and observations on winter injury, flowering and fruit yield were used to evaluate the treatment effects on strawberry yield potential.

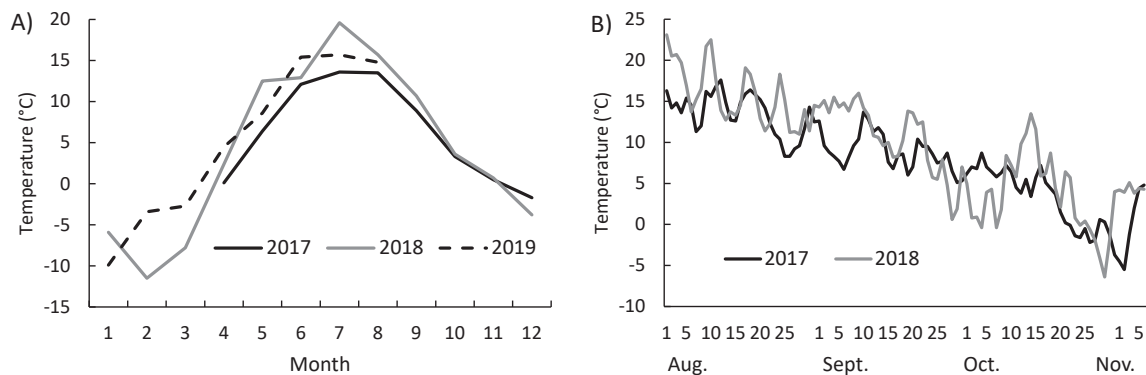


Fig. 1. Monthly average temperatures during the experiments in 2017 to 2019 (A) and daily average temperatures during August through 6 November in 2017 and 2018 (B) recorded in Ähtäri (Finnish Meteorological Institute, <https://en.ilmatieteenlaitos.fi/>)

### Flower mapping analyses

On 6 November 2017 and 2018, two randomly selected plants from each experimental plot in both experiments were harvested for flower mapping analyses. Leaves were removed from the plants except for a few youngest leaves, the roots were pruned to 2–3 cm, and the samples were immediately transported refrigerated to Planta-Logica (Wageningen, Netherlands) for dissection and flower mapping analyses. The variables retrieved from flower mapping data included: number of inflorescences per branch crown and per plant, length of the apical inflorescence of a branch crown, and the development stage (Taylor et al. 1997) of the top flower of the apical inflorescence. Number of inflorescences with top flower at development stage 5 (sepal and petal primordia initiated) or higher provides a more accurate estimate for the final number of inflorescences in a plant and was therefore also used in the analyses.

### Carbohydrate analyses

On 6 November in 2017 and 2018, three randomly selected plants from each experimental plot in both experiments were harvested for the carbohydrate analyses. Leaves were removed from the plants except for a few youngest leaves, the roots were pruned to 2–3 cm, and the samples were immediately transported to the University of Helsinki, where their carbohydrate concentrations were analyzed. The samples were washed, and the remaining roots and leaves removed. The crowns were immersed in liquid N and stored at  $-80^{\circ}\text{C}$  until freeze drying (Gamma 2-16 LSC, Martin Christ Gefriertrocknungsanlagen GmbH, Osterode, Germany) for 36 to 48 h. The samples were ground into fine powder with a sample mill (A10 Basic, IKA<sup>®</sup> –Werke GmbH & Co. KG, Staufen, Germany).

Starch samples (100 mg) were prepared by removing soluble carbohydrates by extraction with 80% EtOH three times followed by centrifugation at  $1740 \times g$  for 10 minutes. The starch remaining in the pellet was analyzed with the Megazyme Total Starch Assay kit (Megazyme, Bray, Ireland) according to the manufacturer's instructions. Corn starch was used as a standard. The method is based on an enzymatic reaction. The absorbance was read with a spectrophotometer (Shimadzu Spectrofotometer UV-1800, Shimadzu Corporation, Kyoto, Japan) at a wavelength of 510 nm, and the amount of starch in the sample was calculated using a Megazyme spreadsheet.

Sucrose, glucose and fructose were analyzed with the Megazyme Sucrose, D-Fructose and D-Glucose kit. The method is based on an enzymatic reaction. Samples were prepared by stepwise extraction of soluble carbohydrates into ethanol. Twenty mg of the ground sample was mixed with 4 ml of 80% EtOH, incubated for 30 minutes in a  $70^{\circ}\text{C}$  water bath and centrifuged at  $1600 \times g$  for 10 minutes. Supernatant was collected and the extraction was repeated twice so that the total volume of the sample was 10 ml. The samples were analyzed according to the kit

instructions. The absorbance was read with a spectrophotometer at a wavelength of 340 nm. The amounts of sucrose, glucose and fructose in the sample were calculated using the Megazyme spreadsheet.

### Overwintering, flowering, and fruit yield

Winter damage was visually assessed in May 2018 and 2019 on ten randomly selected plants per each experimental plot on a scale of: 1 = dead plant, 2 = > 50% of the crowns in a plant are injured, 3 = ≤ 50% of the crowns are injured, 4 = undamaged.

The number of flowers and inflorescences was recorded for 10 plants per experimental plot during peak flowering in 2018 and 2019. Fruit were harvested from 10 plants on each experimental plot every two to three days throughout the harvest season in 2018 and 2019. All the harvested fruit were weighed and counted, and the average yield per plant and fruit weight were calculated.

### Economics of the applied treatments

Economics of repeated runner removal after harvest and the use of fall row cover on strawberry were estimated using farm model approach (Koivisto 2004). In that approach a fictive strawberry farm with certain buildings, machinery, inputs use, outputs, and prices was generated. That fictive farm represents typical strawberry cultivation system in Finland. Using that farm model the economic effects of runner removal and fall row cover were simulated.

### Statistical analyses

The significance of the main effects (runner removal treatment and row cover) was statistically tested with the analysis of variance using MIXED procedure in statistical software SAS (version 9.4) for both years separately. Mean separation was performed with Tukey's test at a significance level of  $p < 0.05$ .

## Results

### Runner removal

To evaluate, whether runner removal increases strawberry yield potential, runners in cv. Polka plants were removed after harvest repeatedly (R1), once (R2), or left intact (R3). As the field was established in 2017, the plants produced very few runners during the first year of the experiment. Consequently, runner removal treatments had no effect on any of the measured variables, except sucrose content in a crown. The concentration of sucrose on 6 November 2017 was significantly lower in R1 (27 mg g<sup>-1</sup> DW) as compared to R2 (46 mg g<sup>-1</sup> DW) ( $p = 0.043$ ) and the same trend, although not significant ( $p = 0.075$ ) was observed in the concentration of soluble carbohydrates (Fig. 2A). Same time, flower mapping analysis revealed 1.5 inflorescence initials per branch crown and 7.5 per plant as an average across all treatments. The number of inflorescences with a top flower at development stage 5 or higher was 1.0 per branch crown and 5.0 per plant. The average length of the apical inflorescence was 2.1 mm, and the development stage of a top flower 5.5. No winter injury was observed in the field. During flowering, across all treatments the average of 7.9 inflorescences per plant were observed. The average yield per plant in 2018 was 360 g, and the average fruit weight 6.7 g.

In 2018 the plants produced an average of 36 runners (counted in R3 plots). Runner removal three times starting at the end of July (R1) decreased the concentration ( $p = 0.014$ ) and the amount ( $p = 0.030$ ) of starch in the crown as compared to treatments R2 and R3, while the concentration of soluble carbohydrates was increased in R1 as compared to R2 ( $p = 0.030$ ) (Fig. 2B). Total carbohydrate reserves per plant tended to be smaller in R1 (2.3 g) than in R2 (2.6 g) or R3 (2.8 g), but the difference was not significant.

While the concentration of total non-structural carbohydrates (TNSC) was similar between the years (115 mg g<sup>-1</sup> DW and 112 mg g<sup>-1</sup> DW), the greater proportion of carbohydrates was in a soluble form in 2017 (Fig. 2). The ratio of soluble carbohydrates to starch was 4.3 and 2.0 in 2017 and 2018, respectively. The total carbohydrate reserves in crown were 0.43 g plant<sup>-1</sup> in 2017, and greatly increased the following year being 2.54 g plant<sup>-1</sup>.

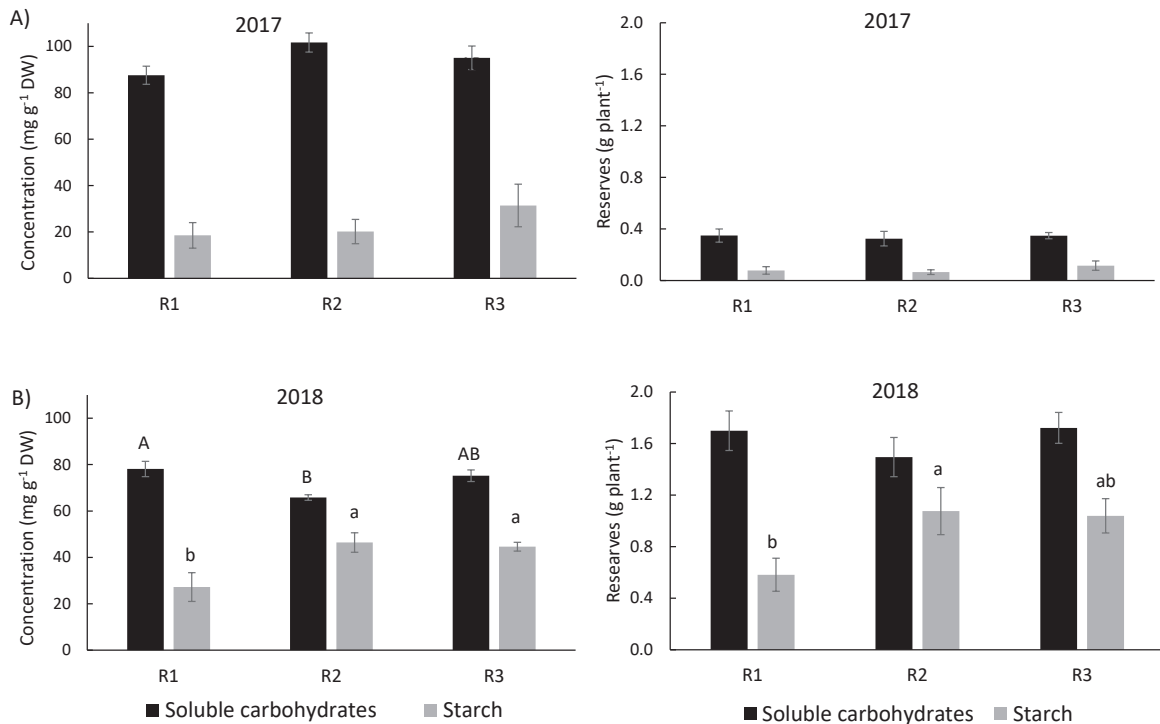


Fig. 2. Soluble carbohydrate and starch concentrations and reserves on 6 November 2017 (A) and 2018 (B) in the crowns of strawberry cv. Polka subjected to different runner removal treatments; R1 = runners removed three times in three weeks intervals beginning at the end of July, R2 = runners removed once on 27 August 2017 / 10 September 2018, R3 = control, no runner removal. Vertical bars represent ± SEM, n = 4. Values marked with the same letter are not significantly different at  $p < 0.05$  by Tukey's test.

While no treatment effects were observed on floral development in the first year, in November 2018 flower mapping analysis revealed that repeated runner removal increased the length of the apical inflorescence as compared to no runner removal (3.2 mm vs. 2.5 mm) ( $p = 0.028$ ). No other effects on floral development were observed through flower mapping analysis. The top flowers of apical inflorescences were, on an average, at the development stage 6 (the whorls of stamen primordia initiated). The total number of inflorescence initials was 1.2 per branch crown and 19.3 per plant. The number of inflorescences with a top flower at the development stage 5 or higher was 1.1 per branch crown and 17.8 per plant, on an average (Fig. 3). No treatment effect on the number of runner initials was observed, either.

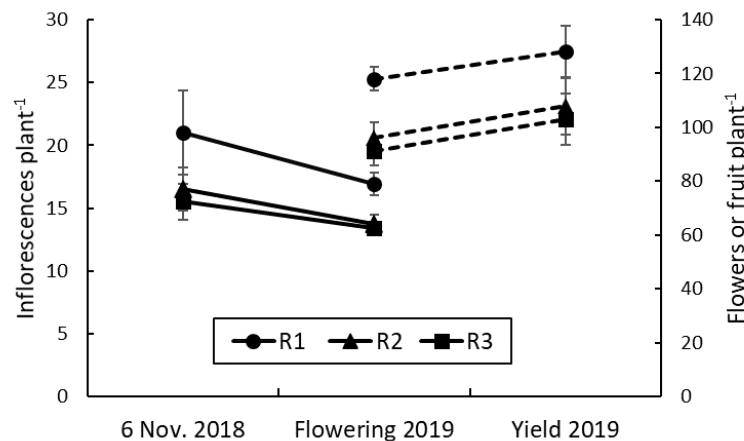


Fig. 3. Number of inflorescence initials (solid line) observed through flower mapping on 6 November 2018 (development stages 5 to 8) and during flowering in 2019, and the number of flowers and fruit (dotted line) per plant in strawberry cv. Polka in different runner removal treatments. R1 = runners removed three times; 25 July, 15 August, and 4 September 2018, R2 = runners removed on 10 September 2018, R3 = no runner removal. Vertical bars represent ± SEM, n = 4.

The average winter injury rating was 3.8 in 2019 and not affected by the treatments. Repeated runner removal increased the number of inflorescences ( $p = 0.023$ ) and flowers ( $p = 0.023$ ) during anthesis (Figs. 3 and 4) but had no effect on the number of flowers per inflorescence, which was 6.9. The average fruit yield per plant was 1087 g and not significantly different between the treatments, although there was a tendency to greater yield (21%), when runners were repeatedly removed in the previous year (Fig. 4). The average fruit weight was 9.7 g and not affected by runner removal.

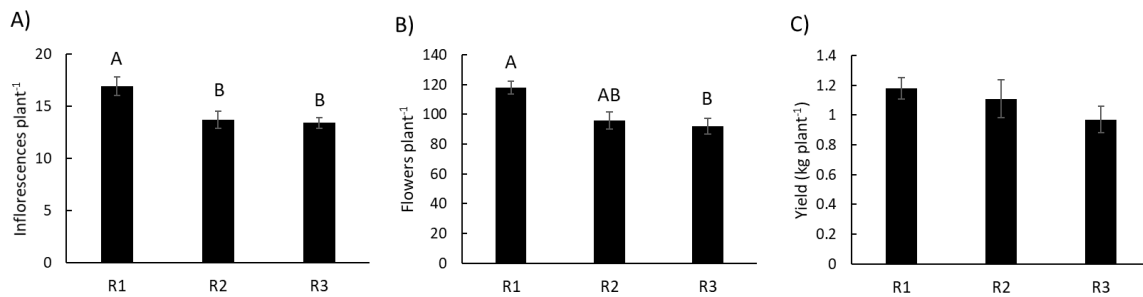


Fig. 4. Number of inflorescences (A) and flowers (B), and fruit yield (C) in strawberry cv. Polka in different runner removal treatments in June 2019. R1 = runners removed three times; 25 July, 15 August, and 4 September 2018, R2 = runners removed on 10 September 2018, R3 = no runner removal. Vertical bars represent  $\pm$  SEM,  $n = 4$ . Values marked with the same letter are not significantly different at  $p < 0.05$  by Tukey's test.

### Fall row cover

The effects of covering the plants of strawberry cv. Wendy with a floating row cover in the fall during the period, when flower initials are developing was studied in two years. Row cover was installed at the end of August or beginning of September.

### Carbohydrates

In November 2017 the concentration of TNSC was lower in the plants under row cover (95 mg g<sup>-1</sup> DW) than in control plants (106 mg g<sup>-1</sup> DW) ( $p = 0.032$ ). Covered plants also had lower starch reserves ( $p = 0.041$ ) (Fig. 5A). The following year, in November 2018, the concentration of TNSC was substantially higher, 154 mg g<sup>-1</sup> DW on an average, and not affected by row cover. However, the plants under row cover had lower concentrations of glucose ( $p = 0.023$ ), fructose ( $p = 0.004$ ), sucrose ( $p = 0.004$ ), and hence lower concentration of total soluble carbohydrates ( $p \leq 0.001$ ) than the uncovered plants (Fig. 5B). There was a trend of increased starch concentration under cover, but the difference was not statistically significant.

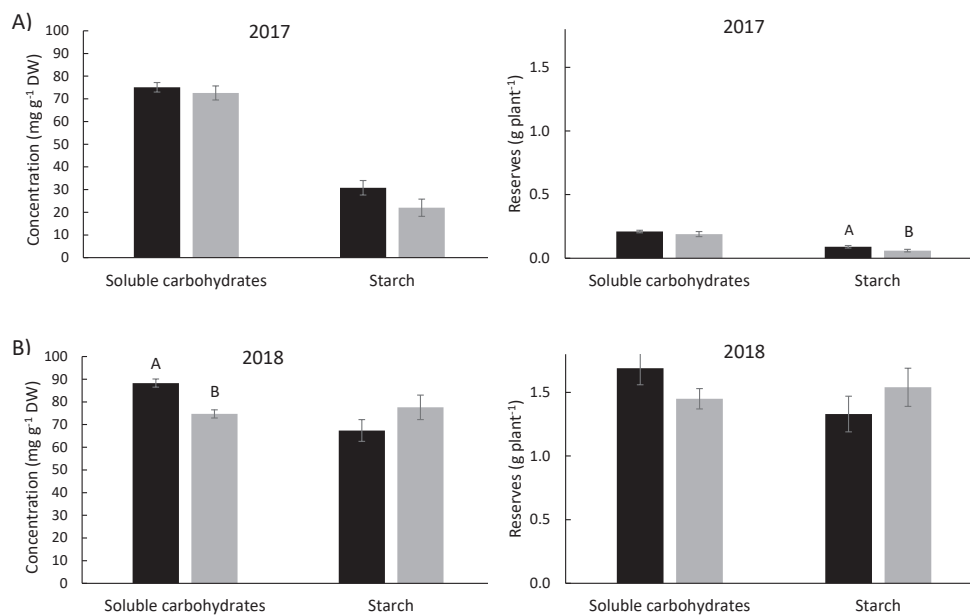


Fig. 5. Soluble carbohydrate and starch concentrations and reserves on 6 November 2017 (A) and 2018 (B) in strawberry cv. Wendy crowns with or without fall row cover installed on 28 August 2017 and 12 September 2018. Vertical bars represent  $\pm$  SEM,  $n = 5$ . Values marked with different letters are significantly different at  $p < 0.05$ .



While the difference in the concentration of soluble carbohydrates between the two years was small (74 vs. 81 mg g<sup>-1</sup> DW), the starch concentration was almost three times greater in 2018 than a year before (Fig. 5). The ratio of soluble carbohydrates to starch was 2.9 and 1.1 in 2017 and 2018, respectively. The total carbohydrate reserves in crown were about 3 g per plant in 2018, which was more than 10-fold that in the previous year.

### Floral development and fruit yield

In November 2017, no treatment effects were observed in flower mapping analysis. The average length of the apical inflorescences was 3.6 mm, and the developmental stage 6.0. The total number of inflorescence initials was 2.1 per branch crown and 4.2 per plant. The number of inflorescences with a top flower at the development stage 5 or higher was 1.0 per branch crown and 2.1 per plant, on an average. In spring 2018 no winter injuries were observed in the experimental field. While flower mapping analysis revealed no treatment effects, the final number of inflorescences and flowers were increased by floating row cover installed on 28 August in previous year (Table 1, Fig. 6). Inflorescences in covered plants also had more flowers. Row cover had no effect on total yield, but decreased the average fruit weight by 1.2 g, probably because there were more flowers in the inflorescences of the covered plants.

Table 1. Flowering and fruit yield in strawberry cv. Wendy with or without fall row cover installed on 28 August 2017 for 2017–2018, and 12 September 2018 for 2018–2019. Values are means of five replicates followed by  $\pm$  SEM.

	Control	Row cover	<i>p</i>
<b>2017–2018</b>			
Inflorescences plant <sup>-1</sup>	2.0 $\pm$ 0.1	2.2 $\pm$ 0.1	0.038
Flowers plant <sup>-1</sup>	9.3 $\pm$ 0.4	11.2 $\pm$ 0.5	0.001
Flowers inflorescence <sup>-1</sup>	4.6 $\pm$ 0.1	5.0 $\pm$ 0.1	0.015
Yield (kg plant <sup>-1</sup> )	0.15 $\pm$ 0.02	0.15 $\pm$ 0.01	n.s.
Fruit plant <sup>-1</sup>	9.2 $\pm$ 1.2	9.9 $\pm$ 0.6	n.s.
Fruit weight (g)	16.8 $\pm$ 0.3	15.6 $\pm$ 0.2	0.012
<b>2018–2019</b>			
Inflorescences plant <sup>-1</sup>	3.7 $\pm$ 0.2	4.3 $\pm$ 0.2	0.018
Flowers plant <sup>-1</sup>	20.8 $\pm$ 1.1	23.9 $\pm$ 1.2	0.014
Flowers inflorescence <sup>-1</sup>	5.6 $\pm$ 0.1	5.6 $\pm$ 0.1	n.s.
Yield (kg plant <sup>-1</sup> )	0.15 $\pm$ 0.01	0.17 $\pm$ 0.01	n.s.
Fruit plant <sup>-1</sup>	12.3 $\pm$ 0.6	15.3 $\pm$ 1.0	0.009
Fruit weight (g)	12.0 $\pm$ 0.4	11.0 $\pm$ 0.3	0.065

In November 2018 flower mapping revealed that the covered plants had more inflorescence initials with a top flower at development stage 5 or higher than the control plants (0.98 vs. 0.87 per branch crown) ( $p = 0.027$ ). The total number of inflorescences was 1.1 per branch crown and 7.5 per plant. The average length of the apical inflorescences was 3.8 mm, and the developmental stage 6.5. Lethally injured apical inflorescences were observed in 12% (range 6 to 18%) of plants in uncovered control plots, whereas no such damage was observed in covered plots. Eight days before sampling in the night between 28 and 29 October, temperature at soil ground fell to  $-14.2$  °C and the following night to  $-11.8$  °C (Finnish meteorological Institute, Ähtäri), which probably caused the damages. Consequently, we observed that fall row cover increased the numbers of inflorescences and flowers in the following season (Table 1, Fig. 6). When winter injury was assessed visually in the field in spring 2019, the average winter injury rating was 3.4 but not affected by the row cover during the previous fall.

Yield was not affected by the fall row cover treatment. However, the plants protected by row cover in previous fall produced three more fruit per plant, which was then also reflected in a slightly smaller fruit weight (Table 1, Fig. 6).

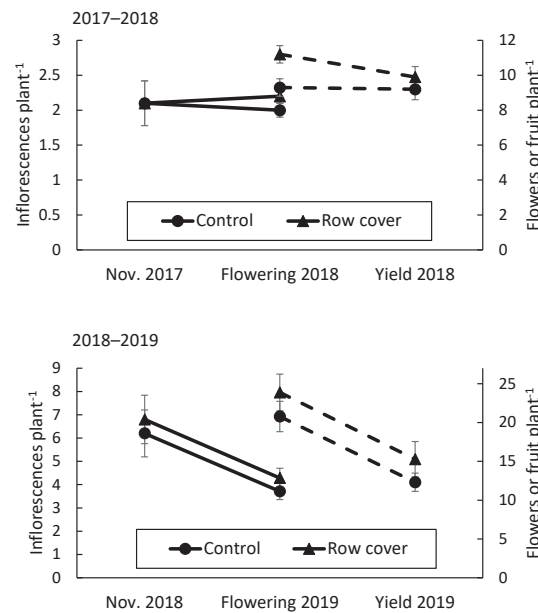


Fig. 6. Number of inflorescences (solid line) observed through flower mapping (development stages 5 or higher) on 6 November 2017 and 2018 and during flowering, and the number of flowers and fruit (dotted line) in strawberry cv. Wendy with fall row cover installed on 28 August 2017 for 2017–2018, and 12 September 2018 for 2018–2019, or uncovered (control). Vertical bars represent  $\pm$  SEM,  $n = 5$ .

## Economical viability

Economics of the studied treatments were estimated using a farm model approach. In the model, runner removal was made using tractor-driven cutting machine, which purchase price was 7000 € without value added tax (VAT). The yearly extra costs caused by runner removal consisted of fixed costs of cutting machine, fuel costs, and labor costs. The simulated value of extra costs was 430 € ha<sup>-1</sup>, which meant 86 kg ha<sup>-1</sup> yield addition to cover the extra costs, as the strawberry price was 5.04 € kg<sup>-1</sup> without VAT. Extra costs of the fall row cover consisted of labor cost and of the fixed costs of cover. Value of simulated extra costs was 143 € ha<sup>-1</sup>, which meant that 28 kg ha<sup>-1</sup> yield addition would be required to cover the extra costs. Both runner removal and fall row cover turned out to be economically feasible treatments, because the needed yield addition for covering the extra costs very likely realizes.

## Discussion

Runner removal three times in three-week intervals after harvest increased the number of inflorescences and flowers in strawberry cv. Polka. However, the treatment effects on yield were masked by large variation in the yield data. Runner removal in the beginning of September was too late to induce any beneficial effects on yield potential. This result is well in line with that reported by Handley et al. (2009) in Maine, USA, where runner removal three times (10 August, 24 August, and 7 September) increased the yield of cv. Honeoye in the following year as compared to runner removal only once on 7 September. In our experiment, runner removal did not influence winter survival of the plants, as has also been reported by Hughes et al. (2017) in Canada for everbearing strawberry cultivars. In November 2018 flower mapping analysis revealed that repeated runner removal increased the average length of the apical inflorescence initials by 0.7 mm as compared to no runner removal. Strawberry inflorescence initials grow about 1 mm per 1000 GDH, once they have reached the development stage 6 (GDH per day = (average 24-hour temperature – 4.5 °C) × 24) (Nauja Lisa Jensen, personal communication). Based on the temperatures recorded during August 2018, we may conclude that repeated runner removal resulted in a three-day earlier flower induction, or alternatively, that the inflorescence initials developed faster when the runners were removed.

In our experiment fall row cover increased the numbers of inflorescences and flowers in cv. Wendy. In Norway, increased temperatures in September have been observed to correlate with higher strawberry yields in the



following year (Døving and Måge 2001). On the other hand, in farm trials conducted in South-Western Finland, row cover installed at the end of September did not influence yield of cvs. Honeye, Polka and Sonata (Rantanen et al. 2021). Furthermore, we observed that fall row cover increased the proportion of inflorescences that had reached higher development stages by 6 November. Accordingly, Rantanen et al. (2021) report a non-significant trend of inflorescence initials being longer (2.5–3.4 mm) under fall row cover than without cover (2.3–2.9 mm) in late November. It must be noted that the focus in our study was specifically on row cover deployed in the fall with the aim to boost floral development, not the usage of thicker winter cover that is commonly used to protect strawberry plants from winter injury. However, fall cover also protected the inflorescence initials from injury during the sudden frost at the end of October in 2018.

The effective temperature sum was about 50% greater in 2018 as compared to 2017. The different temperature conditions during the two experimental years were reflected in floral development in the fall. On 6 November, the average lengths of the apical inflorescence initials of cv. Polka were 2.1 mm and 2.8 mm, and the respective development stages 5.5 and 6.0 in 2017 and 2018, respectively. In cv. Wendy, the inflorescence initials were 3.6 mm and 3.8 mm, and the development stages 6.0 and 6.5, on an average, in 2017 and 2018, respectively. According to Rantanen et al. (2021) the top flower of cvs. Polka and Honeye had reached the development stage 6 by the end of September in 2016 in Southern Finland.

In our experiment the concentration of TNSC in November was 112–115 mg g<sup>-1</sup> DW in cv. Polka and 101–154 mg g<sup>-1</sup> DW in cv. Wendy depending on a year. These values are in a range with those reported in the literature. In everbearing cv. Camarosa at the end of vegetative phase the concentration of TNSC was about 140 mg g<sup>-1</sup> DW in Mexico (Macías-Rodríguez et al. 2002), and up to about 100 mg g<sup>-1</sup> FW in Spain (López et al. 2002). Menzel and Smith (2012) reported 75–110 mg g<sup>-1</sup> DW TNSC at different growth stages in cv. Festival crowns in Australia. Cv. Elsanta crowns lifted on 4 December have 198 mg g<sup>-1</sup> FW starch and 339 mg g<sup>-1</sup> FW soluble carbohydrates (Lieten et al. 1995), while cv. Jewel crowns lifted in December contain about 30 mg g<sup>-1</sup> DW starch (Acuña-Maldonado and Pritts 2008). On the other hand, Sønsteby et al. (2016) reported that cv. Sonata runner plant crowns after 31 d of cultivation at 12 °C have 10.1–13.1 mg g<sup>-1</sup> DW starch and 6.6–8.1 mg g<sup>-1</sup> DW soluble carbohydrates. Differences in the reported values are affected partly by different cultivars, plant development stages, and growing conditions, but sometimes probably also by analytical procedures.

Contrary to our assumption, we did not observe a correlation between yield and crown carbohydrate reserves in our experiments. Strawberry crown is an important source of carbohydrates, and carbon reserves in crown correlate with yield (Lieten et al. 1995, Acuña-Maldonado and Pritts 2008). Under SD and low temperature conditions in the fall SD strawberries accumulate carbohydrates concurrently with floral initiation (Durner et al. 1984, Gast and Pollard 1991). Lowering temperatures promote the accumulation of starch in crown (López et al. 2002, Sønsteby et al. 2016), followed by its conversion into soluble carbohydrates, which has been observed to occur e.g. in Quebec from 4 to 25 November (Gagnon et al. 1990). Soluble carbohydrates are crucial for frost hardening and their concentration is related to the level of frost hardiness in strawberry plants (Paquin et al. 1989, Gagnon et al. 1990). In our experiment, freezing temperatures were experienced in both years during 10 d preceding sampling for carbohydrate analyses, presumably boosting the biochemical reactions associated with cold acclimation, such as conversion of starch into soluble carbohydrates. Notably in 2018, in the uncovered cv. Wendy plants that were exposed to lower temperatures and were hence presumably more prepared for winter than the uncovered plants, a greater proportion of TNSC was in soluble form as compared to starch. In New Hampshire, USA, row cover installed on 12 September only had influence on plant carbohydrate status in spring; during early growth crown concentration of total nonstructural carbohydrates was lower under cover than with no cover because of earlier spring growth (Gast and Pollard 1991).

In November 2017 covered plants had lower concentration of TNSC and lower starch reserves than the uncovered plants. We speculate that this was caused by the relatively cloudy weather during fall 2017, as the increased temperature under row cover increased respiration of the plants, but the scarcity of light limited photosynthesis. This is in line with the conclusions of Rantanen et al. (2021) from the farm trials in South-Western Finland. Weather in the fall 2018, on a contrary, was sunny, and both cultivars contained substantially more starch than in the previous year. Greater temperature sum in 2018 enhanced accumulation of carbohydrates, and the conversion of starch into soluble carbohydrates was retarded by relatively warm and sunny weather during fall.

Mother plant supports stolon and daughter plant growth until the daughter plant is autonomous, and able to produce enough photosynthates for its own growth. No direct evidence exists on, whether a daughter plant might be a source of carbohydrates when fully developed. According to Savini et al. (2008) stolon transport is bi-directional,

so physiologically daughter plants would be able to translocate assimilates to mother plants. As we observed the same trend of declining carbohydrate reserves following repeated runner removal in both years, it is tempting to speculate that runners translocate photosynthates into the mother plant after becoming photosynthetically independent. However, according to Acuña-Maldonado and Pritts (2008), young stolons do not assimilate much carbon.

Besides its commercial use, strawberry flower mapping analysis is a valuable tool in research focusing on floral development. It was especially useful for us, as we conducted experiments on commercial farms, where controlling environmental factors is more challenging than in a research environment. Flower mapping analysis facilitates uncovering effects that may later be masked by winter injury, adverse weather conditions at flowering, pest damage, etc. On the other hand, carrying out experiments on farms helps to realize the gap between scientific findings in a laboratory and their application in the field cultivation.

## Conclusions

Based on our results presented herein and the literature, repeated removal of strawberry runners after harvest may be recommended, since it increased the numbers of inflorescences, flowers, and fruit. Runner removal in the beginning of September was too late to induce any beneficial effects on yield potential. However, the effects may be cultivar dependent and affected by weather conditions during fall. Covering strawberry plants with a floating row cover after flower induction during floral development in September to October may increase yield potential, especially if there is enough sunlight to support photosynthesis under cover. The farm model and the used simulations are simplification of effects of these treatments, but they still indicated strong enough economic benefits.

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