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THE INFLUENCE OF CHILLING HOURS ON ROOT STARCH CONTENT, GROWTH AND YIELD OF STRAWBERRY TRAY PLANTS

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ABSTRACT

The chilling requirements of two strawberry cultivars (‘Sonata’, ‘Albion’) were assessed by evaluating the starch accumulation levels in the tray plants’ root system and their subsequent growth and yielding. The research was conducted in an experimental orchard and a greenhouse of the National Institute of Horticultural Research in Skierniewice, Poland, in 2017–2019 (2 cycles of obtaining planting material and growing plants). The tray plants (rooted tips) were grown in the natural field conditions until they were transferred in batches to a cold store (–2°C) on five different dates: 12 Oct., 30 Oct., 20 Nov., 11 Dec., and 3 Jan. (of the following year). The number of accumulated chilling hours less than 7°C was recorded for each transfer date, and the roots were analysed for starch content at the time of transfer. After the end of cold storage (3 months, standardised for all treatments), the plants were planted in pots and transferred to a greenhouse to assess growth and plant yielding. The obtained results indicate that chilling induces changes in the extent of starch accumulation. The highest starch accumulation in ‘Sonata’ roots was recorded when the plants received about 500 h of chilling (under Polish conditions accumulated in November/December). In the ‘Albion’ strawberry case, the maximum was found at the lower chilling level – about 300 h (middle of November). The highest fruit yields were produced by ‘Sonata’ plants, for which the number of chilling hours (0–7°C) was 500–800 h. In the case of ‘Albion’, the values were 2–3 times lower. A more extended period of keeping tray plants in field conditions (over 1000 h of chilling) resulted in a deterioration in fruit yield.

Key words: *Fragaria* × *ananassa*, chilling requirements, cold storage, protected cultivation, photoperiod

INTRODUCTION

The strawberry (*Fragaria* × *ananassa* Duchesne) is a cultivated species of significant economic importance in Poland. In recent years, the volume of strawberry fruit production has reached 170–200 thousand tonnes per year [FAO 2020]. The high yields, however, are obtained because of large land areas cultivated with this species, amounting to approximately 50 thousand hectares [FAO 2020]. Increasing competition in the market, low fruit yields, and the resulting gradual decline in income obtained from traditional strawberry plantations make it necessary to introduce modern cultivation technologies to enable a more significant intensification of production [Treder 2002, Paszko et al. 2014]. Development and implementation of new practices are necessary due to consumers’ growing interest in dessert fruit quality and the need to extend the period of strawberry supply in the market.

The quality of planting material plays a crucial role in intensifying strawberry production. Obtaining fruit outside the typical ripening season is possible through cultivation for early or delayed harvesting (controlled cultivation). Due to the relatively high investment

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costs (e.g. the cost of covers, energy, irrigation system), only the best quality planting material should be used in the controlled cultivation systems. It includes runner plants obtained from nursery plants during winter dormancy and tray plants (potted) obtained by rooting tips [Żurawicz and Masny 2005]. Both types of plants can be stored in a cold store (the so-called 'frigo' plants), increasing their availability and enabling growers to establish a crop at almost any time [Lieten 2002].

Strawberry cultivars can be categorised as June-bearers, everbearers, or day-neutrals based on photoperiodic responses, particularly flower bud formation. In June-bearing strawberry cultivars, flowering is induced by a short photoperiod (short-day cultivars), reducing vegetative growth. June-bearing strawberries form flower buds in late summer to early autumn when the day lasts less than 10 h per day. Everbearers can be generally classified as long-day plants because they initiate flower buds primarily when days exceed 12 h [Durner et al. 1984].

The chilling requirement is one of the most critical factors determining strawberry plants' successful growth and yielding. In temperate regions, strawberry plants accumulate a sufficient number of chilling hours and store carbohydrates in the roots and crowns, whereas the shoots remain dormant as a response to the short photoperiods and low temperatures during the autumn and winter [Durner et al. 1984, Maas 1986, Al-Madhagi et al. 2014]. The chilling requirement is the primary determinant of the initiation of strawberry flowers. Darnell et al. [2003] concluded that flower induction in strawberries is photoperiodically insensitive at low (10–15°C) and high (25°C) temperatures. Flowering is induced under any photoperiod at a low temperature, whereas a high temperature prevents flower-bud formation [Tanino and Wang 2008]. Inadequate (insufficient) chilling results in decreased plant vigour and reduced fruiting. However, excessive chilling may lead to delayed initiation of new flowers and reduced fruit yield [Voth and Bringhurst 1970, Craig and Brown 1977, Bringhurst and Galletta 1990, Robert et al. 1997, Meulenbroek and Lieten 2021].

The main factor determining the success of strawberry cultivation is keeping the planting material in the best condition during storage. Research by Treder et al. [2006] showed that assessing plug plants (potted plantlets) solely based on visual analysis or even morphological parameters is insufficient to fully determine their yielding potential or storage ability under cold conditions. Due to the relationship that exists between the amount of carbohydrates accumulated in plant tissues and the variation in climatic conditions (mainly temperature) during the strawberry runner plant production in nurseries, work is being undertaken to use this correlation to assess the vigour and productivity of the plants after storage [Lieten 1997, Schupp and Hennion 1997, Hicklenton and Reekie 1998, Al-Madhagi et al. 2018].

The accumulation of starch in the roots of strawberry plants is influenced by temperature; the total carbohydrate concentration in the tissues increases with the accumulation of chilling hours [Lieten 1997, Hicklenton and Reckie 1998, Klamkowski and Treder 2008]. Plants use starch as a source of carbon and energy [Smith 2001] to initiate root growth, the initial stage of leaf development and the early development of flowers [Schupp and Henion 1997, Nishizawa and Shishido 1998]. The accumulation of chilling by strawberry plants makes them better survive the stress of harvesting and subsequent transplantation. Nishizawa and Shishido [1998] and Schupp and Henion [1997] explain that by being subjected to the shortening of the day length and the lowering of the temperature, plants can reach full dormancy, which allows them to be stored for a long time in a cold store.

According to Lieten [1997], the entry of strawberry plants into dormancy and an increase in the starch content of their roots are closely correlated with the duration of autumn chilling. Our research [Klamkowski et al. 2008] confirmed it with the cultivar 'Elsanta' plants. The specific chilling requirements of different varieties of strawberries vary and should be evaluated in particular growing (climatic) conditions [Kronenberg and Wassenaar 1972, Craig and Brown 1977, Hancock 2000]. To optimise the quality and yielding of developing plants, it is crucial to understand the cultivar's inherent chilling requirement.

The study aimed to determine the chilling requirements of two strawberry cultivars by evaluating the levels of starch accumulation in the root system of tray plants and their subsequent growth and yielding during post-storage cultivation (after transplantation) under greenhouse conditions.

MATERIAL AND METHODS

Planting material, growing conditions and storage of tray plants. The research was conducted in an experimental orchard and a greenhouse of the National Institute of Horticultural Research in Skierniewice, Poland, in 2017–2019 (2 cycles of obtaining planting material and growing plants). The experiment was designed as a factorial RCBD with two factors: cultivars – 'Sonata' (June-bearing, released by Plant Research International B.V., NL) and 'Albion' (day-neutral, released by University of California, USA) and the chilling hours represented by the time of transferring plants from the field. The tray plants were obtained by rooting tips that had been taken from mother plants and planted in the 29th week of 2017 (first experimental series) and 2018 (second experimental series) in pots (9 × 9 × 10 cm) filled with a mixture of coconut (coir) substrate and sand (4 : 1). They were grown in the natural field conditions until they were transferred in batches to a cold store (–2°C) on five different dates: 12 Oct., 30 Oct., 20 Nov., 11 Dec., and 3 Jan. (of the following year). The number of accumulated chilling hours (0–7°C) was recorded for each transfer date [Warmund and Krumme 2005, Chhetri and Dolley 2018].

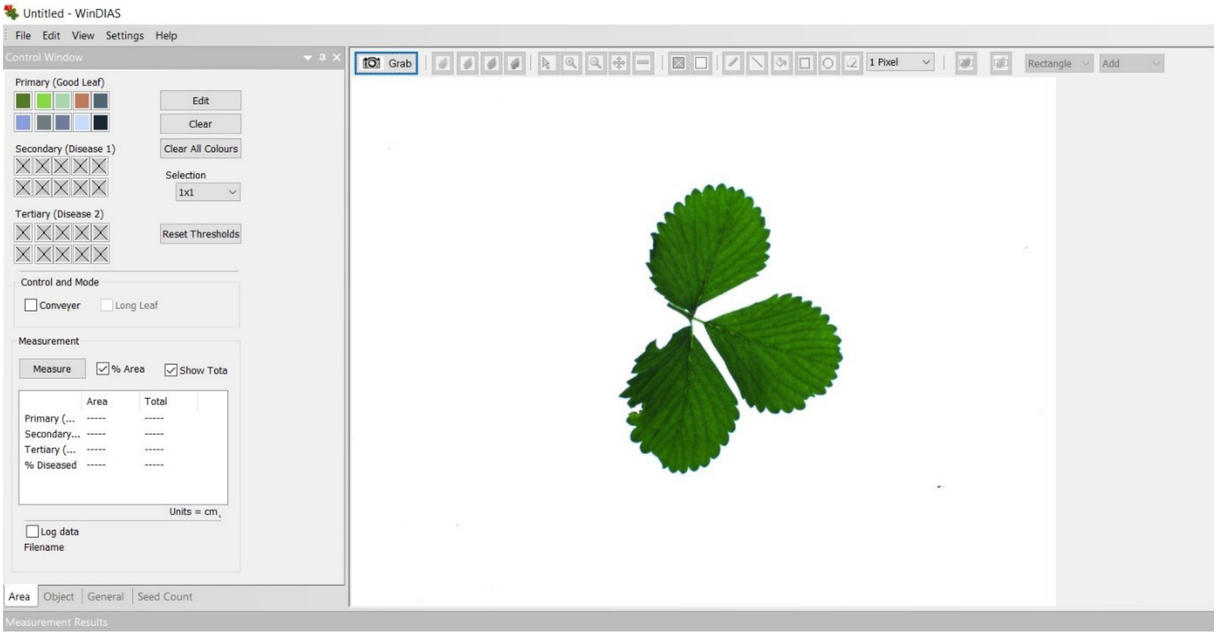
Starch content analyses. The roots of the plants were analysed for starch content just before transferring the tray plants into the cooling chamber. The amount of starch was determined by an enzymatic method using a commercial enzymatic kit from R-Biopharm [Boehringer Mannheim 1989]. The amount of glucose obtained after starch hydrolysis was determined spectrophotometrically. The analysis was performed on a randomly selected sample of 10 plants. Root samples (500 mg) were cut and homogenised in a mortar with dimethylsulfoxide (DMSO) and hydrochloric acid. The samples were incubated at 60°C in a water bath for 30 min. Then the solution was cooled to room temperature, and pH was adjusted to 4–5 (under vigorous shaking) and filtered. Glucose from starch hydrolysis by amyloglucosidase was phosphorylated by hexokinase and dehydrogenated to phosphorylated gluconate. The amount of NADPH formed in the above reaction was proportional to the amount of glucose. It was determined utilising its light absorbance at 365 nm [Boehringer Mannheim 1989].

Post-storage cultivation. The storage period lasted for three months (average storage period of strawberry planting material for early harvesting) in 1.5 L pots filled with a mixture of peat and coconut (coir) substrates (3 : 1) and transferred to a greenhouse (vegetation chambers) for the assessment of plant growth and yielding (Tab. 1). The growing conditions were as follow: PAR irradiance min. 150 µmol m^{-2} s^{-1}, photoperiod 16/8 h, temperature 20–22°C during light period, and 16–18°C during dark period. Irrigation was carried out based on the plant's water needs and estimated based on measurements of substrate moisture (using EC-5 dielectric probes, METER, USA). The fertiliser Granusol (MIVENA, The Netherlands) was used for fertigation.

During cultivation, the plants' inflorescences and yielding were assessed. After cultivating (12 weeks), the fresh weight of the plants' aerial part, the root system, and the total leaf surface area were measured. An image analysis system with WinDIAS software (Delta-T Devices, UK) was used to measure the leaf area (Phot. 1).

Table 1. Accumulation of chilling by tray plants before the storage period

Date of storage initiation	Date of transfer to the greenhouse	Accumulated chilling hours (≤7°C)	
		2017/2018	2018/2019
12 Oct.	9 Jan.	50	100
30 Oct.	29 Jan.	132	222
20 Nov.	19 Feb.	480	396
11 Dec.	12 Mar.	893	657
3 Jan.	30 Mar.	1245	985



Phot. 1. Image analysis system (leaf area measurements)

Data analysis. The data were statistically processed using the analysis of variance and regression. Duncan's multiple tests were used to assess the significance of differences between the means, with a significance level of 5%. Relationships between the accumulated amount of chilling and the root starch content were evaluated using polynomial regression models.

RESULTS AND DISCUSSION

The autumn and the beginning of winter in the years covered by the research (2017 and 2018) were notable for an unusual pattern of weather conditions. The average temperatures of the months in which the plants were grown were above zero and exceeded the multi-year average by a few degrees Celsius (Tab. 2). It was not until the end of the analysed period (January) that a decrease in temperature was registered (especially in the second year of the study). The minimum temperature in 2018/19 was –7°C in November and –11.7°C in December, a few degrees lower than the minimum temperatures recorded in 2017/18.

The dynamics of the accumulation of chilling hours (0–7°C) are presented in Figure 1, and the number of chilling hours received by the tray plants on successive dates before the start of the cold-storage period is shown in Table 1. Differences were found in the number of chilling hours that affected the different groups of tray plants. In the 2017/2018 season, the accumulation of chilling hours until mid-November was lower compared with the 2018/2019 season. However, starting from the second half of November, a more intense influence of chilling on plants was observed in the 2017/2018 season than in the 2018/2019 season. At the end of the analysed period, on the last date of transferring the plants to the cold store (3 Jan. 2018), the cumulative number of hours with a positive temperature lower than 7°C was 260 h greater than in 2019.

In strawberries, the chilling temperature is traditionally defined as hours below 5°C [Yanagi and Oda 1993], 7°C [Bigey 2002], or 8°C [Risser and Robert 1993, Tanini and Wang 2008]. The chilling requirement in Polish conditions is typically measured in terms of the number of hours during which temperature (positive) remains at or below 7°C (in some models corrected to 7.2°C) [Klamkowski et al. 2010]. Chilling hours are accumulated throughout the autumn/winter season and then added up [Luedeling 2012, Chhetri et al. 2018]. Other types of models for chilling quantification have also been developed. These models describe chilling effects using weighted accumulation of chilling units (e.g. the Utah Model and its variants) [Tanino and Wang 2008]. They have been adopted for warmer conditions, where the traditional models did not work well [Luedeling et al. 2009].

On average, the accumulation of starch in the roots of the 'Sonata' tray plants was more significant than in the cultivar 'Albion'. The differences in starch accumulation patterns in various cultivars were showed also by Al-Madhagi et al. [2014]. The correlations between the accumulated amount of chilling and the root starch content were evaluated using regression models (data from both seasons was used). In the 'Sonata' strawberry case, a third-order polynomial regression model provided the best-fit correlation between these two parameters. For 'Albion', it was a fourth-order polynomial regression model (Fig. 2). The highest accumulation of starch in 'Sonata' roots was recorded when the plants received about 500 h of chilling (0–7°C). This amount of chilling was accumulated in the middle of November 2017 and at the beginning of December 2018 (the difference between these 2 seasons was about 2 weeks). In the 'Albion' strawberry case, the maximum was found at the lower chilling level – about 300 h; for both years, it occurred in mid-November.

Several studies have shown that the quality of planting material and their storability are related to the sugar content in their organs (roots, crown), which in turn depends on the climatic conditions prevailing during cultivation [Cieśliński and Borecka 1989, Voth and Bringhurst 1990, Lieten 1997, Hicklenton and Reekie 1998, Lopez et al. 2002, Palha et al. 2002, Al-Doubibi et al. 2021]. Starch accumulation in plant organs occurs in low above-zero temperatures under suitable light conditions [Maas 1986]. In strawberry plants, intensive sugar accumulation in the roots and crowns occurs from late summer to early winter [Nishizawa and Hori 1989]. Studies have confirmed that during the storage period of planting material at

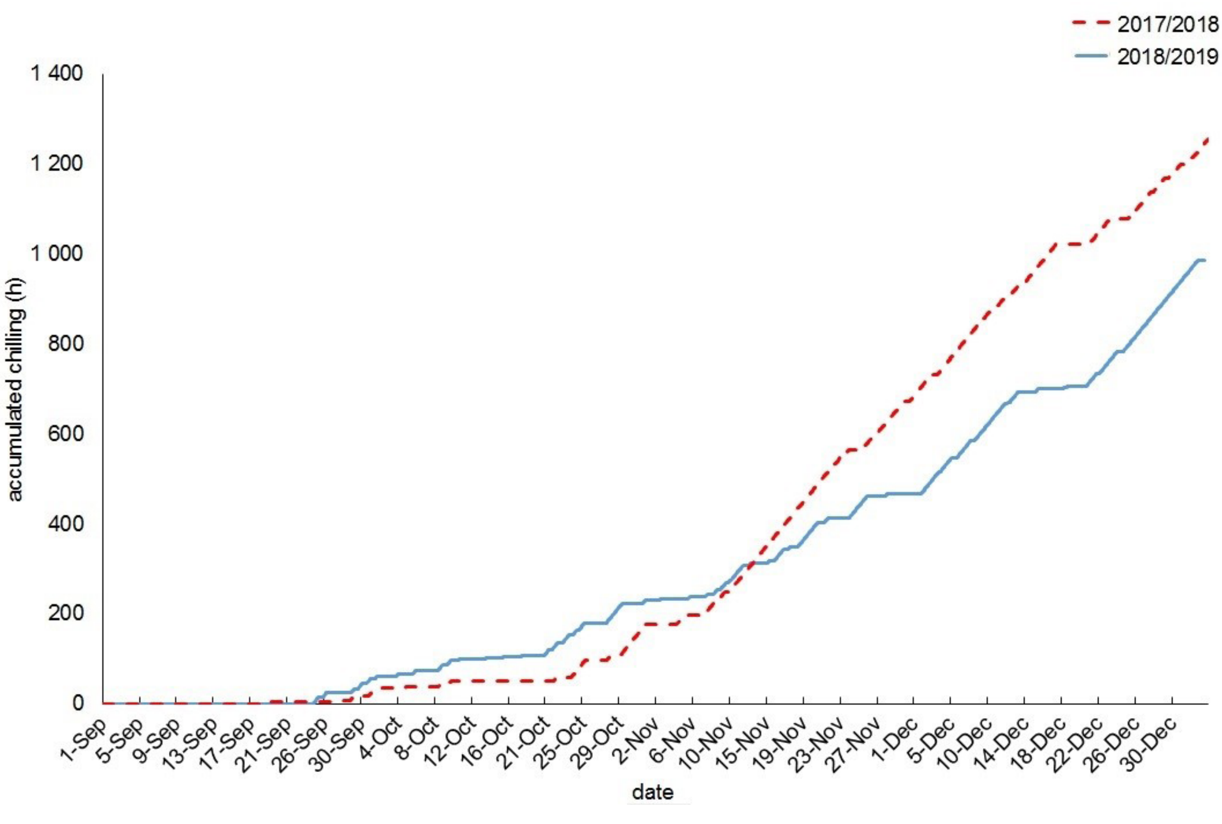


Fig. 1. Accumulated chilling for the 2017/2018 and 2018/2019 autumn/winter periods (1 Sep. – 3 Jan.)

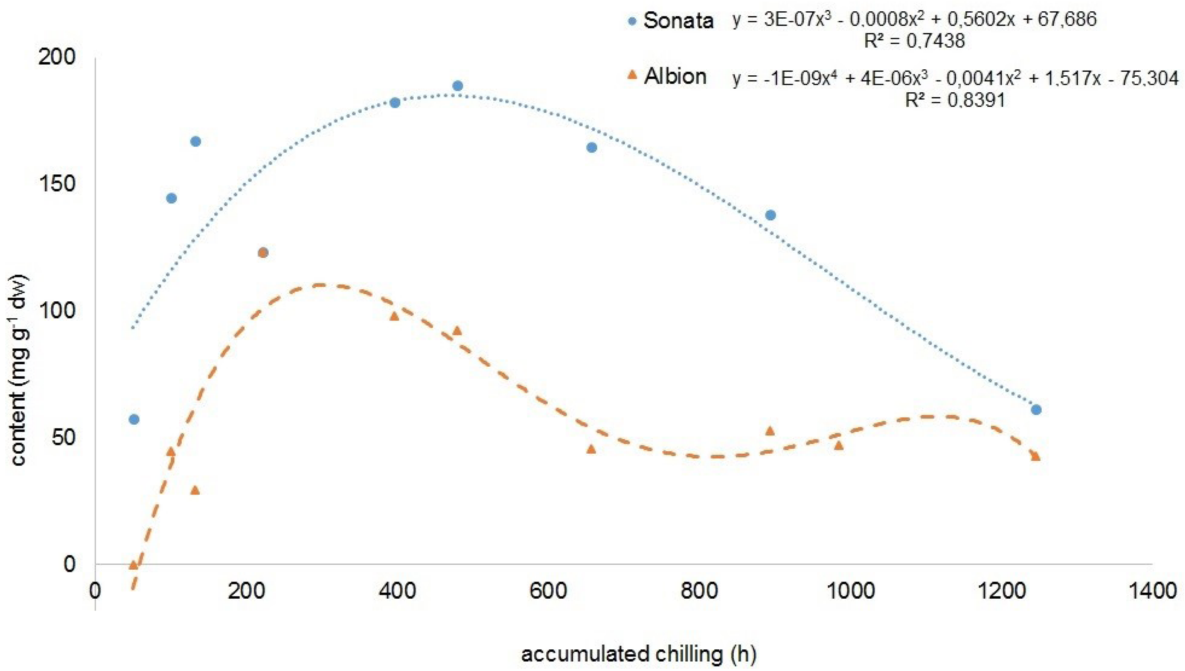


Fig. 2. Relationship between the accumulated amount of chilling and the root starch content (data from both seasons)

Table 2. Selected meteorological data for the years 2017–2019 covered by the study

Month	Average temperature (°C)			Temperature (°C)			
	2017/2018	2018/2019	Multi-year data*	Min 2017/2018	Max 2017/2018	Min 2018/2019	Max 2018/2019
Oct	10.0	10.1	8.3	0.5	22.7	–0.3	22.5
Nov	5.0	4.2	3.7	–1.0	13.2	–7.9	19.7
Dec	2.5	1.6	–0.2	–3.1	10.8	–11.7	8.1
Jan	0.9	–1.6	–1.1	–8.3	10.6	–10.3	6.5

* Based on data for 1991–2016. Source: weather station (iMetos, Pessl Instruments, Austria) located close to the experimental area

sub-zero temperatures, the starch content of the roots significantly decreases [Klamkowski et al. 2010]. Schupp and Hennion [1997] showed that the degradation of starch in strawberry (‘Elsanta’) roots occurred particularly intensely at the beginning of the period of storage of plants at sub-zero temperatures (for about a month after it started). The sucrose and simple sugars resulting from the hydrolysis of starch play a vital role in the mechanisms of plant defence against the effects of stress [Bigey 2002].

A characteristic for both cultivars is (after reaching the maximum value) the decrease in the starch content of the roots with progressive chilling (Fig. 2). In the study by Lieten [1995], a significant prolongation of the growing season resulted in a reduction in the starch content of strawberry roots (despite the greater extent of chilling), probably due to the negative temperatures recorded during this period. When determining the cumulative number of chilling hours, the chilling effect’s intensity should be considered. The chilling may be

Table 3. Selected morphological parameters and fruit yield of the strawberry cultivars 'Sonata' and 'Albion' in the first season (2017/2018)

Treatment	Fresh weight of aerial part (g plant^{-1})	Leaf number	Total leaf area (cm^2 plant^{-1})	Root fresh weight (g plant^{-1})	Number of inflorescences (plant^{-1})	Yield (g plant^{-1})
			Sonata			
12 Oct. (50 ch*)	14.93 cd	9.77 c	455.39 ab	11.43 d	1.98 c	96.62 d
30 Oct. (132 ch)	10.63 ab	6.50 ab	368.71 a	8.86 cd	2.17 c	117.28 de
20 Nov. (480 ch)	13.92 bc	6.25 ab	416.95 ab	6.76 bc	3.94 d	138.74 e
11 Dec. (893 ch)	24.95 f	6.00 ab	814.79 e	6.99 bc	4.01 d	142.27 e
3 Jan. (1245 ch)	18.60 de	5.92 ab	778.57 de	5.23 b	1.90 c	94.54 d
			Albion			
12 Oct. (50 ch)	9.93 ab	6.00 ab	448.89 ab	4.57 b	0.83 a	54.81 b
30 Oct. (132 ch)	13.83 bc	7.00 b	546.42 bc	5.82 bc	1.19 b	78.44 c
20 Nov. (480 ch)	11.59 abc	6.08 ab	330.39 a	4.32 b	1.20 b	70.02 c
11 Dec. (893 ch)	19.17 e	5.09 a	649.22 cd	3.86 b	0.99 ab	68.70 c
3 Jan. (1245 ch)	9.18 a	4.83 a	337.56 a	1.18 a	0.74 a	42.04 a

* Chilling hours. Means is average of 10 plants. Means marked with the same letters within columns do not differ significantly at α = 0.05

Table 4. Selected morphological parameters and fruit yield of the strawberry cultivars 'Sonata' and 'Albion' in the second season of 2018/2019

Treatment	Fresh weight of aerial part (g plant^{-1})	Leaf number	Total leaf area (cm^2 plant^{-1})	Root fresh weight (g plant^{-1})	Number of inflorescences (plant^{-1})	Yield (g plant^{-1})
			Sonata			
12 Oct. (100 ch*)	25.42 c	7.86 bc	954.24d	9.61 c	2.09 d	106.53 d
30 Oct. (222 ch)	24.40 c	8.50 cde	923.62 d	7.72 bc	1.59 c	94.36 c
20 Nov. (396 ch)	20.99 c	8.18 de	701.81 c	8.98c	2.94 e	106.45 d
11 Dec. (657 ch)	21.90 c	10.75 e	832.75 cd	7.92 bc	3.77 f	169.02 e
3 Jan. (985 ch)	12.21b	8.50 e	354.93 b	4.81ab	1.10 b	49.91 b
			Albion			
12 Oct. (100 ch)	12.18 b	4.81 a	352.50 b	5.30 ab	1.21 bc	80.33 c
30 Oct. (222 ch)	9.57 b	5.75 ab	254.04 ab	4.35 a	1.48 c	106.52 d
20 Nov. (396 ch)	9.83 b	6.30 abc	237.22 ab	2.30 a	1.65 c	96.19 c
11 Dec. (657 ch)	8.96 ab	8.33 cde	255.42 ab	3.36 a	0.99 b	47.06 b
3 Jan. (985 ch)	4.60 a	6.80 bc	108.59 a	2.01 a	0.26 a	14.47 a

* Chilling hours. Means is average of 10 plants. Means marked with the same letters within columns do not differ significantly at α = 0.05

interrupted by periods of higher temperatures. Such a situation happened during our study when, after a cold period, the temperature in October kept increasing above 20°C, and in November 2017, it was 13.2°C, while in 2018 as high as 19.7°C (Tab. 2). According to some reports [Bigey 2002, Darnel et al. 2003], such an increase in temperature may reduce the effect caused earlier by chilling. These inhibitory effects are analysed in some weighted modelling approaches quantifying effective chilling units [Tanino and Wang 2008]. It may be the reason for the differences in the level and patterns of starch accumulation in the roots of the tray plants observed in the 2017/18 and 2018/19 seasons, which is consistent with the earlier conclusions of Treder et al. [2006].

The analysis of morphological features of the plants after storage showed significant differences between the cultivars tested (Tabs 3 and 4). They differed in the average weight of plants and roots and the surface area of leaves. A much lower fresh weight characterised the plants of the cultivar 'Albion' assessed in 2017 compared with the cultivar 'Sonata'. The highest fresh weight of the aboveground part of plants and the surface area of leaves were recorded in both cultivars for the plants that had been transferred to the cold store on 11 Dec. 'Sonata' plants developed a much larger root system than those of the cultivar 'Albion'.

In the tests carried out in 2018, the cultivar 'Sonata' was characterised by a much more intense growth. Plants of this cultivar were recorded to have a greater fresh weight of the aboveground part and the root system and greater surface leaf area. The lowest values of morphological parameters (weight, leaf surface area) for both cultivars were recorded on 3 Jan., probably due to the prolonged period of low temperatures negatively affecting the condition of the tray plants. In the case of the other dates, no significant differences were found in the weight of the aboveground part and the root system and (for most combinations) in leaf surface area.

On average, the cultivar' Sonata' plants obtained more inflorescences and higher fruit yield. In 2017, the flowering and yielding were the lowest for the plants (of both cultivars) transferred to the cold store on the last day (3 Jan.). In the studies performed by Meulenbroek and Lieten [2021], strawberry plants (cv. 'Opera') exposed to excessive amounts of chilling gave lower yields and exhibited a delay in production. In the case of the 'Albion' cultivar, low fruit yields were also obtained from the plants placed in the cold store in the first half of October (12 Oct.). It may be related to the fact that there was no evidence of starch accumulation in the roots of those plants, resulting in their poor condition after storage. According to Lieten [1997], the entry of strawberry plants into a dormant stage and an increase in the starch content of the roots are closely correlated with the duration of autumn chilling. The most intensive flowering and the highest yielding were found to be the plants of the cultivar 'Sonata' from the planting stock that had been placed in the cold store in November–December, which was associated with a large amount of starch stored by the root system of these plants. No substantial differences in flowering time (beginning after planting) were recorded.

Similar observations were made in the subsequent growing season. A few inflorescences and low yields (from both cultivars) were obtained from the tray plants remaining in the field conditions until January. The highest yield (and the highest number of inflorescences) was obtained from the plants of the cultivar 'Sonata' that had been placed in the cold store in November–December, while in the case of the cultivar 'Albion' from those transferred in October–November. During those periods, starch accumulation in the roots was high, impacting the condition of the plants in the cold store.

The conducted research shows that the highest fruit yields of the cultivar 'Sonata' were obtained from those plants for which the amount of chilling was 500–800 h. In the case of 'Albion', the values were lower, at approximately 200–350 h. These values are lower than those recorded for other cultivars or different climatic conditions [Lieten 2009, Meulenbroek and Lieten 2021]. On the other hand, Bigey [2002] showed that some cultivars (e.g. from California breeding programs) could have relatively lower chilling requirements (<700 h). A more extended period of keeping the planting stock in the field (over 1000 h of chilling) resulted in a deterioration in yielding in the plants of both cultivars.

Evidence for a relationship between the storability of plants at sub-zero temperatures ('frigo'), the length of the chilling period and the starch content of their roots have been shown in several studies [Craig and

Brown 1977, Bringhurst and Galletta 1990, Robert et al. 1997, Klamkowski et al. 2008, 2010]. In California, daughter plants dug from the field in October did not store well in the cold store, and the starch content of their roots was very low. A delay in obtaining plantlets increased the starch content in their roots, resulting in a significant reduction in plants dying off during storage [Bringhurst et al. 1960]. Similar observations in Poland were made by Cieśliński and Borecka [1989], Treder et al. [2006] and Klamkowski et al. [2008, 2010]. Their works showed that daughter plants dug as late as December stored well (although this depended on the cultivar); a high starch content of the roots also characterised them.

CONCLUSIONS

The obtained results indicate that chilling induces changes in the extent of starch accumulation. A cool cultivation period is essential to obtain good quality strawberry planting material (tray plants). Poland's high weather variability is an obstacle to the precise determination of the relationship between the patterns of changes in starch accumulation in the roots of strawberry daughter plants, their storability and subsequent productivity. Our research shows that the highest fruit yields were produced by 'Sonata' plants, for which the number of chilling hours (0–7°C) was 500–800 h. In the case of the cultivar 'Albion', the values were 2–3 times lower. A more extended period of keeping tray plants in field conditions (over 1000 h of chilling) resulted in a deterioration in fruit yield.

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