

EFFECTS OF LONG-TERM WATER STRESS ON LEAF GAS EXCHANGE, GROWTH AND YIELD OF THREE STRAWBERRY CULTIVARS

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Abstract. Drought is one of the most common limiting environmental factors affecting plant growth and productivity. Strawberry is a plant of large demand for water along with a high susceptibility to drought. In the present study, the response of three strawberry cultivars ('Elsanta', 'Honeoye', 'Grandarosa') grown under greenhouse conditions to water deficiency was examined by evaluating the yield and morphological (leaf and root development) and physiological (leaf gas exchange, leaf water potential) parameters. Plants were subjected to two different water regimes: optimal irrigation (control, water potential in the growing medium was maintained at the level of -10 kPa), and reduced irrigation (stress treatment, water potential in the growing medium was maintained at the level of -30 kPa). Genotypes differed in their response to water deficiency. Cultivar 'Elsanta' presented high rates of net photosynthesis with high value of water use efficiency (a ratio of photosynthetic rate to transpiration rate) under water shortage conditions. Water stress affected plant vigor. The weight and total leaf area of the stressed 'Honeoye' plants were considerably reduced as compared to these of the control. No significant differences in weight and root length were observed between the well-irrigated and stressed 'Elsanta' plants, while the root development in two other cultivars was retarded. Under water deficiency conditions 'Elsanta' gave the highest yield whereas 'Honeoye' the lowest. Among examined cultivars, 'Elsanta' appeared to be more drought tolerant which was reflected by both growth and yield parameters.

Key words: *Fragaria ananassa*, photosynthetic rate, transpiration, growth, water stress

INTRODUCTION

Drought is one of the most common environmental stresses affecting productivity of agricultural crops in many regions of the world. Along with climate changes, the mean

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global temperatures are expected to rise over the next decades, leading to an increase in global aridity and crop demand for water [Feng and Fu 2013]. The problem of drought and its impact on agriculture and water supplies has become prevalent in many countries, including Poland [Treder et al. 2009, 2013].

Water availability is a limiting factor for a wide range of physiological processes in plants. Water stress results in stomatal closure, decline in tissue water potential, reduction of transpiration and photosynthesis, alterations in assimilate partitioning and changes in hormonal balance [Starck et al. 1995]. Beside these physiological responses plants also undergo morphological modifications. Changes in the distribution of assimilates can reduce vegetative growth and retard the development of plant reproductive organs [Singer et al. 2003]. Modifications of plant growth and leaf anatomy under water stress conditions have been reported in many studies [Nautiyal et al. 1994, Palliotti et al. 2001, Klamkowski and Treder 2008].

Strawberry is a plant of large demand for water. This is due to a shallow root system, large leaf area and fruits with a high content of water. Cultivation of strawberry requires irrigation, and a proper scheduling of irrigation is necessary to achieve the most efficient water use [Treder et al. 2009]. Generally, plants grown in soilless culture under greenhouse conditions are exposed to a sudden and severe stress when irrigation fails. This is because the volume of the substrate in which the plants are growing is limited. Water reserves are therefore quickly exhausted, and the plants suffer from drought. Irrigating greenhouse crops according to measurements of growing medium moisture prevents plants from damages caused by insufficient water supply [Treder et al. 2013].

The severity of drought damage depends on stress duration. Influence of water stress on growth and yielding of strawberry plants have been previously reported [e.g. Gehrmann and Lenz 1991, Liu et al. 2007, Kim et al. 2009]. Genotypic differences in drought tolerance have been observed for various crop species [Bota et al. 2001, Herralde et al. 2001], but to date variation between strawberry cultivars in response to limited water availability has been little explored. There is also insufficient information on response of strawberry plants subjected to long-term water stress. Knowledge about plant responses to drought and drought tolerance mechanisms can contribute to improving the comprehension of plant adaptations to extreme conditions and could be relevant to breeding programs for acquisition cultivars with high yield potential and tolerance to water deficit.

The aim of this study was to examine the response of strawberry plants to water deficit imposed from the moment of planting by evaluating productivity and selected morphological and physiological parameters.

MATERIAL AND METHODS

The experiment was carried out in a greenhouse of the Research Institute of Horticulture in Skierniewice, Poland. Three strawberry cultivars were the object of investigation: 'Elsanta', 'Honeoye', 'Grandarosa'. On 11 April 2013 potted transplants (plugs) [Treder et al. 2007] were planted in plastic containers (18 dm³) filled with a 3:1 mixture of peat and coco substrate. Plants were subjected to two different water regimes: optimal irrigation (water potential in the growing medium was maintained at a level (-)10 kPa,

control), and reduced irrigation (water potential in the growing medium was maintained at a level (-)30 – (-)40 kPa, stress treatment). Both water regimes were applied to the plants at the beginning of the experiment and lasted for its whole period (3 months). A drip system (2 l h⁻¹ drip emitters, Netafim, Israel) controlled by a computer according to growing medium moisture measurements was used to manage irrigation regimes. The moisture content and water potential of the growing medium were monitored with capacitance probes (5TE and MPS-2, Decagon Devices, USA) [Klamkowski and Treder 2008]. The experiment was prepared in four replicates, each comprising one container with four plants.

Measurements of the leaf water potential and leaf gas exchange (net photosynthesis and transpiration) were performed twice during the experimental period (two sampling times: thirty and sixty days after the onset of the experiment). The gas exchange rate was measured on 20 young, fully expanded leaves from each combination using an LCpro+ portable photosynthesis system (ADC BioScientific, UK). The system measures photosynthesis and transpiration on the basis of differences in CO₂ and H₂O concentrations between the air incoming and outgoing a leaf cuvette [Long et al. 1996]. Temperature, CO₂ concentration, and irradiance in the leaf cuvette during analysis were set to approximate ambient conditions. Measurements of the midday leaf water potential were made on 5 leaves from each combination using the SKMP-1400/40 pressure chamber (Skye Instruments, UK) [Turner 1988].

Harvests were performed several time during growing season when fruit reached the ripe stage. Morphological characterization involved measurement of leaf and root weight, total leaf area and root length. Measurements were performed at the end of the experiment. The leaf surface area was measured using a WinDIAS image analysis system (Delta-T Devices, UK) [Jonckheere et al. 2003]. Root samples from each plant were collected and cleaned. The total root length was measured using a scanner and a WhinRhizo image analysis software (Regent Instruments, Canada) [Bauhus and Messier 1999].

All data were statistically elaborated using analysis of variance, followed by means separation using Duncan's multiple-range t-test at $P < 0.05$. The standard error of the mean was calculated and used to indicate error ranges on graphs. All calculations were performed with the help of the Statistica software package (StatSoft, Poland).

RESULTS AND DISCUSSION

The physiological state of the strawberry plants was assessed by measuring water potential and gas exchange rate in the leaves. In the situation when the water content in a growing medium is insufficient to provide the adequate plant supply, the water loss through transpiration reduces the water potential in tissues. Such reaction was observed in many plant species both under field and protected conditions [Valancogne et al. 1997, Blanke and Cooke 2004]. In the present study differences in leaf water potential were observed between the well-watered and stressed plants. During the experimental period average water potential values varied from -1.51 to -2.09 MPa for irrigated, and from -2.21 to -2.71 MPa for stressed plants (data not shown). Differences in water potential between the control and stressed plants observed during the experiment were similar and

reached 0.62, 0.65, 0.70 MPa for ‘Elsanta’, ‘Grandarosa’ and ‘Honeoye’ respectively. According to the classification proposed by Hsiao [1973], the plants from all cultivars were subjected to stress of a similar (mild) level of intensity.

Most higher plants possess mechanisms to avoid or to endure drought conditions, and they also have developed mechanisms to regulate their water use efficiency [Chaves et al. 2003]. One of the first responses of plants to drought is stomatal closure. The stomata regulate gas exchange between the inside of the leaf and the atmosphere. Therefore, they are the main means of regulating water relations and carbon assimilation in plants [Hetherington and Woodward 2003]. Stomatal closure protects plants against excessive water loss, but also restricts the diffusion of CO₂ into the leaves [Chaves et al. 2003]. In the present study the leaf gas exchange parameters in the control plants did not show significant differences among the examined cultivars (fig. 1–4). One exception was ‘Elsanta’ for which lower rate of transpiration was recorded in both sampling dates. As water stress developed, the rate of gas exchange decreased in all cultivars. The strongest decrease in net photosynthesis was observed for ‘Honeoye’ (by more than 90% compared to control), followed by ‘Grandarosa’ and ‘Elsanta’. Higher reduction in transpiration was recorded for ‘Grandarosa’ and ‘Honeoye’ than for ‘Elsanta’. Limitation in gas exchange rates has been observed in many fruit crops grown under drought conditions [Jorba et al. 1985, Klankowski and Treder 2002, 2011].

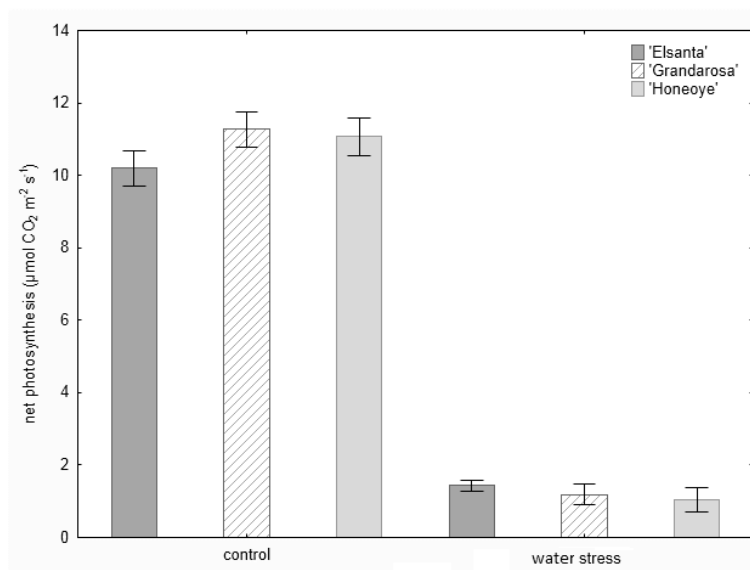


Fig. 1. Photosynthetic rate of control and water-stressed strawberry plants (30 days after the onset of the experiment, means \pm SE)

Depression of photosynthesis under water stress conditions involves mechanisms at both the stomatal and non-stomatal (biochemical) levels [Escalona et al. 1999]. A decrease in stomatal conductance is the major limitation to photosynthesis during mild to moderate drought stress [Flexas and Medrano 2002]. From the obtained results, it could be stated that

strawberry cultivars responded to water deficiency by stomatal closure (strong reduction in transpiration) rather than metabolic limitations. Similar observations on strawberry were made by Grant et al. [2010] and by Ghaderi and Siosemardeh [2011].

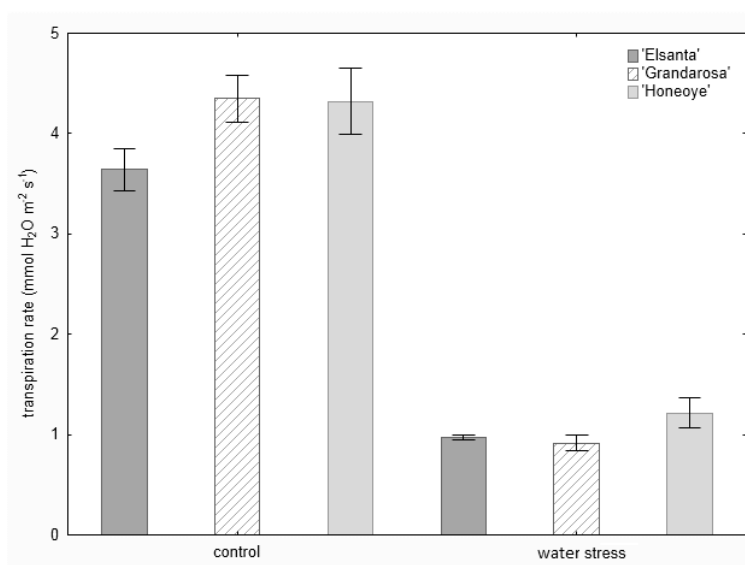


Fig. 2. Transpiration rate of control and water-stressed strawberry plants (30 days after the onset of the experiment, means \pm SE)

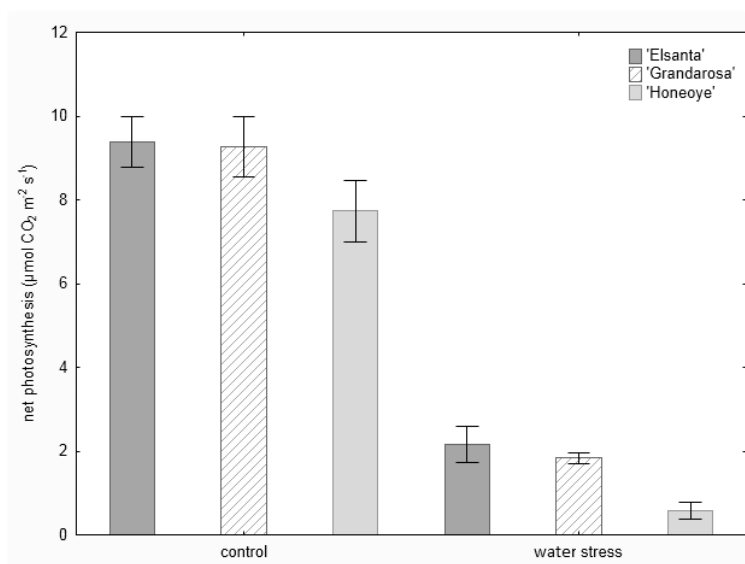


Fig. 3. Photosynthetic rate of control and water-stressed strawberry plants (60 days after the onset of the experiment, means \pm SE)

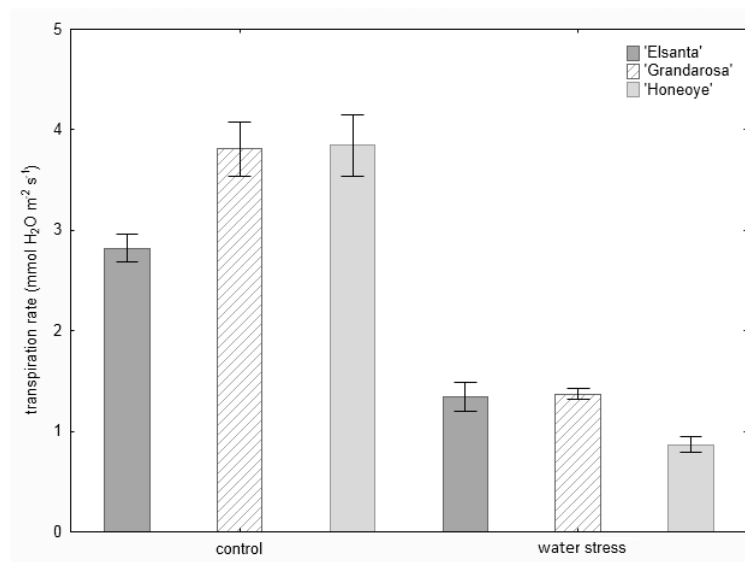


Fig. 4. Transpiration rate of control and water-stressed strawberry plants (60 days after the onset of the experiment, means \pm SE)

The ability of plants to regulate gas exchange through stomata allows them to control water relations and carbon assimilation, and the aperture of the stomatal pore reflects a compromise between the photosynthetic requirement for carbon dioxide and the availability of water [Jarvis et al. 1999]. A water-use efficiency (WUE) was calculated in order to integrate the results on changes in gas exchange rates. At the leaf level, WUE can be determined as a ratio of photosynthetic rate to transpiration rate or to leaf conductance for water vapour [Sinclair et al. 1984, Pietkiewicz et al. 2005]. According to Boyer [1982] the ratio of carbon fixation to water loss (i.e. water use efficiency) is critical to plant survival, crop yield and vegetation dynamics. WUE has been used in many experiments on water relations and drought resistance in various crop species [Flore et al. 1985, Escalona et al. 1999, Klamkowski and Treder 2008].

In the present study, WUE varied significantly depending on the examined cultivar and water availability (tab. 1). It was found that in the case of cultivar 'Elsanta' (both sampling dates) and 'Grandarosa' (the second sampling date), WUE of the stressed plants was higher compared to 'Honeoye'. Such results might indicate increased capacity for water saving by these two cultivars (especially 'Elsanta') in comparison to 'Honeoye' [Ghaderi and Siosemardeh 2011]. According to Escalona et al. [1999] high WUE reflects an ability to maintain photosynthetic capacity under water deficiency conditions and a higher resistance to drought [Bota et al. 2001].

The linkage between water availability and plant growth is well documented in a wide range of species including strawberry plants [Gehrmann 1985, Chandler and Ferree 1990, Gehrmann and Lenz 1991]. Alterations in biomass distribution patterns resulting in growth modifications are generally considered as important acclimation mechanisms to drought conditions [Buwalda and Lenz 1992, Starck 1995]. Growth

inhibition is one of the earliest responses of plants to water deficiency [Boyer 1970, Hsiao 1973]. In our study, changes in some morphological parameters in the plants subjected to water deficiency were observed (tabs 2, 3). The highest number of leaves per plant was recorded in cultivar ‘Grandarosa’, but no significant influence of water regime on this parameter was observed. The weight and total leaf area of the stressed ‘Honeoye’ plants were considerably reduced as compared to these of the control ones. Strong reduction in leaf area for ‘Honeoye’ grown under deficit irrigation in the field conditions was also reported by Liu et al. [2007]. No significant differences in weight and root length were observed between well-irrigated and stressed ‘Elsanta’ plants, while the root development in two other cultivars (especially ‘Honeoye’) was retarded (tab. 3). An increase of investment in roots results in enhancement of root depth. This type of response to water shortage conditions enables ‘Elsanta’ plants to increase water uptake during drought period [Klamkowski and Treder 2008, Prokic and Stikic 2011].

Table 1. Water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of control and water-stressed strawberry plants (two sampling times)

Cultivar	Treatment			
	30 days after the onset of the experiment		60 days after the onset of the experiment	
	control	water stress	control	water stress
Elsanta	2.88 c	1.47 b	3.33 e	1.50 b
Honeoye	2.60 c	0.83 a	2.00 c	0.59 a
Grandarosa	2.64 c	1.19 ab	2.48 d	1.35 b

Means in the columns followed by the same letter are not significantly different according to Duncan’s multiple-range t-test at $P < 0.05$. Analysis performed separately for each sampling date

Table 2. Growth related parameters of control and water-stressed strawberry plants (measurements performed at the end of the experiment)

Cultivar	Fresh weight of leaves (g plant^{-1})		Total leaf area ($\text{cm}^2 \text{ plant}^{-1}$)		Number of leaves (no. plant^{-1})	
	control	water stress	control	water stress	control	water stress
Elsanta	19.90 a	18.51 a	580.89 a	543.75 a	26.18 ab	22.00 a
Honeoye	29.10 b	18.78 a	980.50 c	623.75 ab	28.90 abc	23.75 ab
Grandarosa	26.15 ab	19.06 a	837.87 bc	670.12 ab	34.40 c	31.36 bc

Means in the columns followed by the same letter are not significantly different according to Duncan’s multiple-range t-test at $P < 0.05$

In our previous study [Klamkowski and Treder 2008] cultivar ‘Elsanta’ exhibited significant reduction in leaf area under drought conditions. Similar observations were reported by Grant et al. [2010]. In their experiment the root to shoot ratio increased under water limitation, which was attributed to a large decrease in leaf weigh with relatively little reduction in root weight. Such modifications can be recognized as an acclimation response of strawberry to limited water availability [Grant et al. 2010]. In the study described here, the leaf development of well-irrigated and stressed ‘Elsanta’ (and ‘Grandarosa’) was similar, possibly as a result of low intensity of stress the plants

experienced during the experimental period. A significant reduction in the leaf area observed in ‘Honeoye’ (along with the strong limitation of root growth) may indicate high susceptibility of this cultivar to water deficiency. The evaluation of plant yielding seems to confirm this finding.

Table 3. Fruit yield and growth related parameters of control and water-stressed strawberry plants (measurements performed at the end of the experiment)

Cultivar	Fresh weight of roots (g plant ⁻¹)		Root length (cm plant ⁻¹)		Yield (g plant ⁻¹)	
	control	water stress	control	water stress	control	water stress
Elsanta	10.28 b	8.03 ab	3287.12 bcd	2162.83 ab	515.61 e	380.75 d
Honeoye	10.46 b	6.26 a	4202.17 d	2762.55 abc	129.59 b	52.57 a
Grandarosa	11.25 b	7.84 ab	3550.43 cd	1915.50 a	377.96 d	200.22 c

Means in the columns followed by the same letter are not significantly different according to Duncan’s multiple-range t-test at $P < 0.05$

Photosynthesis is an important factor that determines plant productivity. The ability to maintain photosynthesis during drought stress, is indicative of the potential to sustain productivity under water-limited conditions. In the present study, limited irrigation resulted in a significant decrease in the berry yield (tab. 3). The highest yield (both under conditions of optimal and reduced water availability) was obtained from the cultivar ‘Elsanta’. The losses in yield in response to stress treatment were: 26% for ‘Elsanta’, 47% for ‘Grandarosa’, and 59% for ‘Honeoye’.

In the experiment performed by Grant et al. [2010] ‘Elsanta’ grown under drought stress conditions showed significant decrease in yield. However, it was still equal to or even greater than the yields of other cultivars grown under well-watered conditions. Drought resistance, important for plant survival under water deficiency conditions, can result in inhibition of yield potential, as high yield is associated with high photosynthesis, which is in turn associated with high stomatal conductance (and hence transpiration) [Grant et al. 2010]. According to Bota et al. [2001], cultivars which are more resistant to drought (presenting high WUE values when water availability is decreased) are usually less productive under favorable conditions. Similar observations were made by Chandler and Ferree [1990] on two strawberry cultivars. In our previous [Klankowski and Treder 2008] and current investigations ‘Elsanta’ out-yielded other cultivars both under conditions of optimal and limited irrigation.

CONCLUSIONS

Genotypic differences in drought tolerance of strawberry have been observed. Among the cultivars tested, ‘Elsanta’ emerged as the most adaptable to water shortage. This cultivar presented high value of water use efficiency both under favorable and water deficiency conditions. Morphological and physiological adaptations allowed ‘Elsanta’ plants to maintain growth and productivity when water availability was decreased. The plants of cultivar ‘Honeoye’ showed the lowest tolerance to water shortage.

Drastic reduction in growth and losses in yield in response to low water availability confirms low usefulness of this genotype to cultivation in water-limited environments.

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WYMIANA GAZOWA LIŚCI, WZROST I PLONOWANIE TRZECH ODMIAN TRUSKAWKI ROSNĄCYCH W WARUNKACH DŁUGOTRWALEGO DEFICYTU WODY

Streszczenie. Niedobór wody jest jednym z ważniejszych czynników ograniczających plonowanie roślin uprawnych. Truskawka jest zaliczana do roślin o dużym zapotrzebowaniu na wodę i wysokiej wrażliwości na jej deficyt. W doświadczeniu określono reakcję na deficyt wody trzech odmian truskawki: ‘Elsanta’, ‘Grandarosa’, ‘Honeoye’. Rośliny były uprawiane w szklarni w pojemnikach wypełnionych mieszaniną substratu torfowego i kokosowego. Zastosowano dwie kombinacje nawodnienia: (i) optymalne nawadnianie – potencjał wody w podłożu utrzymywany był na poziomie -10 kPa (kontrola), (ii) deficyt wody – potencjał wody utrzymywany na poziomie -30 kPa. Rośliny stresowane otrzymywały obniżone dawki wody w ciągu całego cyklu uprawowego. Wykonywano pomiary intensywności wymiany gazowej oraz potencjału wody liści. Ponadto oceniono wzrost roślin oraz ich plonowanie. Deficyt wody w podłożu ograniczył natężenie wymiany gazowej oraz potencjał wody w liściach roślin. Pomiędzy badanymi odmianami stwierdzono istotne różnice w tolerancji na suszę. U roślin odmiany ‘Elsanta’ rosnących w warunkach deficytu wody stwierdzono wysokie wartości efektywności wykorzystania wody (określonej jako stosunek natężenia fotosyntezy do natężenia transpiracji). Niedobór wody wpłynął na wzrost roślin. Jedynie w przypadku odmiany ‘Honeoye’ stwierdzono znaczącą redukcję masy i powierzchni liści roślin poddanych działaniu stresu (w porównaniu do kontroli). Nie wykazano istotnych różnic w masie i długości systemu korzeniowego roślin odmiany ‘Elsanta’ rosnących w warunkach zróżnicowanego zaopatrzenia w wodę. W przypadku pozostałych odmian rozwój systemu korzeniowego roślin stresowanych był zahamowany. Największy plon uzyskano z roślin odmiany ‘Elsanta’, najmniejszy z ‘Honeoye’. Uzyskane wyniki wskazują, że spośród ocenianych odmian największą tolerancją na suszę charakteryzowały się rośliny odmiany ‘Elsanta’.

Słowa kluczowe: *Fragaria ananassa*, wzrost, fotosynteza, transpiracja, stres wodny

Accepted for print: 26.07.2015

For citation: Klamkowski, K., Treder, W., Wójcik, K. (2015). Effects of long-term water stress on leaf gas exchange, growth and yield of three strawberry cultivars. *Acta Sci. Pol. Hortorum Cultus*, 14(6), 55–65.