

Morphological and Physiological Responses of Strawberry Plants to Water Stress

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Summary

The most of previous studies have been focused on the effect of water stress on plant yielding. However, the conditions in which plants grow from the moment of planting might affect their morphology and physiological response. The aim of this study was to examine the effect of water deficiency on growth and plant physiological response of strawberry (*Fragaria x ananassa* Duch. cv. 'Salut') under greenhouse conditions. The plants were grown in plastic containers filled with peat substratum. Water stress was imposed by reducing the irrigation according to substratum moisture readings. Water stressed plants had the lowest values of water potential and showed strong decrease in gas exchange rate. Also, biomass and leaf area were the lowest in this group of plants. No differences in the length of root system were observed between control and water stressed plants. The lack of water in growing medium resulted also in a decrease of density and reduction of dimensions of stomata on plant leaves. These changes contribute to optimising the use of assimilates and water use efficiency in periods when water availability is decreased.

Key words

Fragaria x ananassa Duch.; drought; growth; stomata; gas exchange

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Introduction

Drought is one of the most common limiting environmental factors affecting plant growth and productivity. Insufficient water supply leads to numerous morphological, physiological, and metabolic modifications occurring in all plant organs.

Water stress results in stomatal closure, decline in tissue water potential, reduction of transpiration and photosynthesis, alterations in assimilates partitioning, changes in hormonal balance (Starck et al., 1995) etc. Beside these physiological responses plants also undergo morphological changes. Modifications of plant growth and leaf anatomy under water stress conditions have been reported previously (Nautiyal et al., 1994; Palliotti et al., 2001).

Stomata control gas exchange between the interior of a leaf and the atmosphere. Therefore they mainly contribute to the ability of plants to control their water relations and to gain carbon (Hetherington and Woodward, 2003). It has been shown that environmental signals such as light intensity, carbon dioxide concentration and water availability may affect stomatal development by modifying their size and frequency (Knapp et al., 1994; Nautiyal et al., 1994; Dyki et al., 1998). The ability of a plant to live under stress has been shown to be related to stomatal density and size, since these were found to be related to the plant gas exchange (Aguirre et al., 1999). Therefore, it is possible that variations in stomatal characteristics may influence plant growth and productivity (Kundu and Tigerstedt, 1998).

Strawberry is a plant of large demand for water. This is due to a plant shallow root system, large leaf area and fruits with a high content of water. Influence of water stress on growth and yielding of strawberry plants have been reported (Chandler and Ferree, 1990; Gehrman and Lenz, 1991). However, these studies have been focused on plant response to water stress in short trials. There is little information on responses of strawberry plants to defined long term water stress.

Knowledge about long term 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 management and breeding programs (El-Jaafari, 2000). The aim of this study was to examine the response of strawberry plants to water deficit imposed from the moment of planting by evaluating morphological and ecophysiological parameters. Gas exchange parameters, stomatal characteristics, leaf area and root length were observed.

Material and methods

The experiment was carried out at the greenhouse of the Research Institute of Pomology and Floriculture, Skierniewice, Poland in 2005. Strawberry 'frigo' plants (cv. 'Salut') were planted in plastic boxes (18 dm³) filled with peat substratum (Degernes, Norway). Six plants were planted in each box. Plants were fertigated with nutrient solution according to Treder (2002) by CNL emitters (2 dm³ h⁻¹) (Netafim, Israel). Nutrient solution application was controlled by Akbar (AMGi, Spain) irrigation computer according to solar radiation intensity and growing medium moisture measurements. Two irrigation treatments were applied during the experimental period: 1) a control (optimal irrigation treatment) – plants were watered to 90 – 100% of water-holding capacity (WHC); 2) a water stress treatment – a moisture was maintained at a level of about 50% of WHC. Container capacity was determined according to water retention curves prepared for growing medium used in the experiment (Fonteno, 1996). Water stress conditions were obtained by reducing irrigation frequency. Both water regimes were applied to the plants at the beginning of the experiment and lasted for its whole period. Moisture of growing medium was controlled by ECH₂O capacitance probes connected to a data-logger (Decagon Devices, USA). The experiment was prepared in three replicates.

In order to monitor the water stress level the midday leaf water potential (Ψ) was measured on six plants from each combination using the SKMP-1400/40 (Skye Instruments, United Kingdom) pressure chamber. Midday gas exchange measurements were made at the same days as water potential ones on ten plants from each combination (two leaves per the plant) using LI-6400 (LI-COR, USA) portable system. Climatic parameters in a leaf chamber during the measurement (temperature, CO₂ concentration, irradiance) were set to be close to external ambient values. Measurements of gas exchange and water potential were conducted four times (every two weeks) during the plant growing cycle (four sampling dates). First measurements were made four weeks after the beginning of the experiment.

Fresh mass of plant organs, leaf area and root length were determined after the experiment was finished. Leaves from plants were collected and their area was measured using WinDIAS image analysis system (Delta-T Devices, United Kingdom). Root samples from each plant were removed and, after the cleaning, their length was measured using Scan Image Analysis System (Delta-T Devices, United Kingdom).

Examination of plant stomatal characteristics was determined by means of a light microscope on leaves collected about one week before the experiment was ac-

Table 1.
Growth related parameters of control and drought stressed strawberry (*Fragaria x ananassa* Duch. cv. 'Salut') plants

Treatment	Leaf fresh weight (g plant ⁻¹)	Total leaf area (cm ² plant ⁻¹)	Average leaf area (cm ²)	Root fresh weight (g plant ⁻¹)	Root length (cm plant ⁻¹)
Control	17.05 b	624.42 b	72.83 b	6.30 a	2291.13 a
Water deficit	8.57 a	360.36 a	57.84 a	5.66 a	1951.11 a

Means within columns with the same letter are not significantly different according to Duncan's multiple range test at $P \leq 0.05$.

completed. In order to calculate the number and stomata dimensions leaf samples were collected from the central leaflet of the main leaf at a place halfway between the main nerve and the right edge of the leaflet. Specimens for microscopic examination were prepared using the isolated epidermis method (Lisek et al., 2002). Strips of transparent tape were applied on the collected leaf pieces from both sides. The strips were then pulled apart leaving the epidermis of the abaxial and adaxial side of the leaf secured separately to the tape. The tape strips were rinsed and stained using toluidine blue. Stomata counting was performed at a magnification of 300x and dimensions of stomata were determined at a magnification of 600x. The number of stomata was expressed per 1 mm² of leaf area.

Data were analyzed by analysis of variance (ANOVA) and means were separated by Duncan's multiple range test, $P \leq 0.05$. All calculations were performed using Statistica 6.0 software (StatSoft, USA).

Results and discussion

Plants can survive drought conditions by avoiding tissue dehydration or by tolerating low tissue water potential. Avoidance of dehydration involves minimising water loss and maximising water uptake. As it is presented in the next part of our study, water loss is minimized by decreasing transpiration because of stomata closing. Some morphological changes observed during water stress also contribute to water conservation strategies.

Inhibition of growth (together with stomatal closure) is among the earliest responses of plants to drought (Boyer, 1970). Significant changes in plant morphological and leaf anatomical characteristics were observed in plants subjected to water stress. Both fresh mass and leaf area of stressed plants were reduced as compared to the control ones. However, no significant differences were observed in biomass and root length between control and stressed plants (Tab. 1).

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). A decrease of a leaf area reduces transpirational surface what is important in diminishing water loss during drought period, while an increase of investment in roots results in enhancement of root depth providing greater water uptake what is crucial for plant survival during drought. Higher root to shoot (leaf) ratio in water stressed plants was reported in many studies for different species (Gehrmann and Lenz, 1991; Buwalda and Lenz, 1992; Palliotti et al., 2001).

Stomatal characteristics are presented in figure 1. Strawberry leaves were found to be hypostomatous i.e. stomata were distributed across the one (abaxial) side of a leaf. The microscopic analysis showed that water deficit affected stomatal density and size of stomata. A significantly lower number of stomata and their reduced dimensions were found in plants grown under drought conditions. Differences in stomatal characteristics of leaves of the same species, depending on the environ-

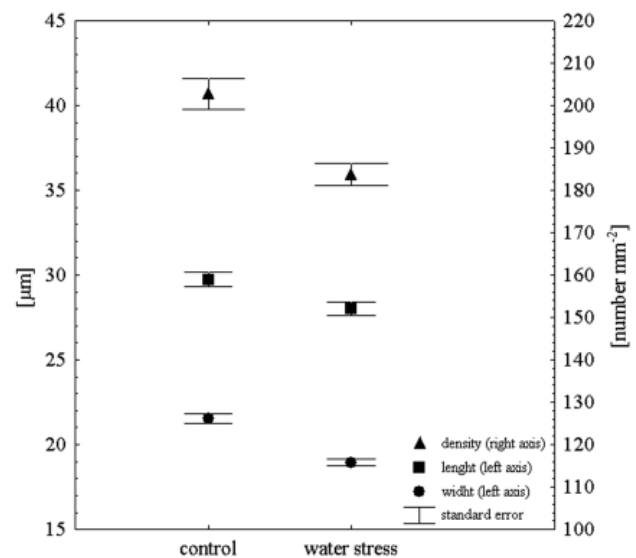


Figure 1.
Leaf stomatal characteristics of strawberry (*Fragaria x ananassa* Duch. cv. 'Salut') plants grown under different watering treatments

ment which the leaves developed in were presented in many studies (Knapp et al., 1994; Dyki et al., 1998).

There are conflicting results of different studies that show no consistent effect of drought conditions on stomatal characteristic. Some authors observed a decrease of stomatal frequency on leaves of different plant species grown under drought conditions, what is in agreement with our results (Nautiyal et al., 1994; Kumari et al., 1999). However, in other studies an increase of stomatal density with increasing moisture stress was presented (Manning et al., 1977; Dyki et al., 1998). Such contradictory results show that plants may respond to external factors in variety of ways. A variability problem of responses of plants grown in short-term field or growth chamber experiments was discussed by Royer (2001). Some authors suggested that higher stomatal density observed in their experiments was not an adaptive mechanism, but a consequence of a lesser leaf area in stressed plants (Manning et al., 1977; Bañon et al., 2004).

Gas exchange in plants takes place mainly through the stomata, and both photosynthesis and transpiration are affected by stomatal movements, geometry and frequency (Sharma, 1984; Kundu and Tigerstedt, 1998). During water deficit stomatal action is rapid and probably the most effective and adaptive mechanism. Lower number of stomata, less pore length and width would practically reduce transpirational losses (Thakur, 1990). Many xerophytic species, which are best adapted to arid conditions, most often show low densities of stomata on leaves (Bañon et al., 2004). According to the opinion presented by Stenglein et al. (2004) an ideal plant, which is resistant to drought, could have leaves with a lower density of smaller stomata.

Leaf water potential (Ψ) differences were observed between the well-watered and stressed plants. During the experimental period average Ψ values varied from -0.43 to -0.64 MPa for irrigated, and from -1.58 to -1.81 MPa for stressed plants. Differences between sampling dates were not statistically significant (data not shown). Differences in water potential between control and stressed plants observed during the experiment were similar (1.19, 1.12, 1.02 and 1.36 MPa for the following sampling dates). This means that during the whole experimental period plants were subjected to stress of a similar level of severity.

Under dry environment conditions plants develop different mechanisms to survive the drought period. These mechanisms are based on physiological and morphological responses. Difference in water potentials in soil-plant-atmosphere continuum is the driving force for a water movement through a plant. In situation when the soil water content is insufficient to provide the adequate plant supply, the water loss by transpiration re-

duces 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).

Response to water stress is dependent on the severity and duration of drought. Hsiao (1973) determined the level of water stress severity according to a decrease of plant water potential. According to this proposition, mild stress is considered to entail lowering of plant water potential by less than 1 MPa. Moderate stress refers to lowering water potential more than 1 but less than 1.5 MPa. If water potential is lowered more than 1.5 MPa, stress is severe. In our experiment, the differences of water potential between control and stressed plants were in the range of 1.02 – 1.36 MPa. According to above cited classification, these plants were subjected to moderate stress. Though such classification can not be applied to all plant species, it may be useful to assess the stress severity in certain period of time.

Generally, plants grown in soilless cultures under greenhouse conditions are exposed to quick and severe stress if the irrigation fails. This is due to a limited growing medium volume in which plants grow. Plants exhaust water reserves much faster compared to field conditions in such situation. In our study plants received reduced irrigation (based on the moisture readings) during the whole experimental period. No wilting of plants was observed even at the lowest recorded values of water potential (-1.81 MPa). It is in general accordance with observations of Sruamsiri and Lenz (1986) who suggested -1.7 MPa as onset of wilting and -2.5 MPa as onset of irreversible drought effects in strawberry plants.

Water deficit reduced all measured gas exchange related parameters (Tab. 2). Photosynthetic rate (A), transpiration rate (E), stomatal conductance (g) and intercellular CO_2 concentration (C_i) declined and remained at a similar level during the duration of the experiment. No significant differences were found between sampling dates for all gas exchange derived parameters measured on water stressed plants. However, such differences existed for g and E values recorded for well irrigated (control) plants, what in turn was caused by different climatic conditions in the greenhouse during the following sampling dates. The magnitude of photosynthetic rate decrease indicates that generally the photosynthetic apparatus was affected moderately by drought conditions.

Stomata play an important role in trade-offs between carbon gain and transpirational water loss because of their sensitivity to environmental and internal factors. When the soil is drying, some chemical signals (e.g. abscisic acid) synthesized in dehydrating roots are transported by the xylem to leaves controlling the stomatal behaviour (Davies and Zhang, 1991). The ability of plants

Table 2.
Gas exchange related parameters of control and drought stressed strawberry (*Fragaria x ananassa* Duch. cv. 'Salut') plants

Sampling date	A ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)		g ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)		C_i ($\mu\text{mol mol}^{-1}$)		E ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$)		WUE _i (A/g)	
	Control	Water deficit	Control	Water deficit	Control	Water deficit	Control	Water deficit	Control	Water deficit
	1	8.38 b	5.74 a	0.142 b	0.054 a	328 b	253 a	1.95 b	0.82 a	60.12 b
2	8.39 b	5.92 a	0.137 b	0.057 a	324 b	257 a	1.90 b	0.86 a	62.55 b	107.74 c
3	8.90 b	5.70 a	0.206 b	0.062 a	342 b	256 a	2.61 bc	0.99 a	60.12 b	91.82 c
4	9.42 b	5.52 a	0.240 c	0.066 a	357 b	256 a	3.17 c	1.09 a	41.12 a	104.23 c

A – photosynthetic rate, g – stomatal conductance, C_i – intercellular CO_2 concentration, E – transpiration rate, WUE_i – intrinsic water use efficiency; Means within a factor marked with the same letter are not significantly different according to Duncan's multiple range test at $P \leq 0.05$.

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). Plants react to water deficit by rapid closure of stomata to avoid transpirational water loss. As a consequence, a CO_2 diffusion into a leaf is restricted. Reduction of gas exchange rate of plants grown under conditions of water deficiency was reported previously (Chandler and Ferree, 1990; Naor et al., 1994). However, depression of photosynthesis under water stress conditions involves mechanisms at both the stomatal and non-stomatal (biochemical) levels (Escalona et al., 1999).

The question as to whether drought mainly limits photosynthesis through stomatal closure or metabolic impairments has not been finally answered (Cornic, 2000; Flexas et al., 2004). The relative part of stomatal limitation of photosynthesis depends on stress severity. Recently, most researchers have agreed that the stomatal closure is the main determinant for decreased photosynthesis under mild and moderate stress. Changes in photosynthetic reactions are considered as a prevailing factor which led to photosynthesis depression under severe water stress (Yordanov et al., 2003). According to Chaves et al. (2003) discrepancies in results concerning the contribution of stomatal and non-stomatal factors in photosynthesis inhibition may be explained by differences in the rate of imposition and severity of stress, developmental stage and plant condition, species studied and superimposition of other stresses.

The relationships between A and g and also between C_i and g (showed for the last sampling date) are presented in Figures 2 and 3. Under drought conditions stomatal conductance was more affected (reduced) than photosynthesis. Therefore C_i decreased, and a ratio of A/g (intrinsic water use efficiency) increased. Such results may indicate that stomatal closure was the dominant factor

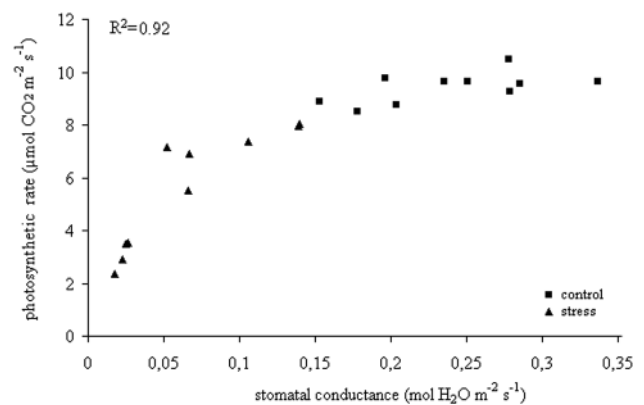


Figure 2.
Dependence of photosynthesis on stomatal conductance in strawberry (*Fragaria x ananassa* Duch. cv. 'Salut'). Each point represents average of two measurements

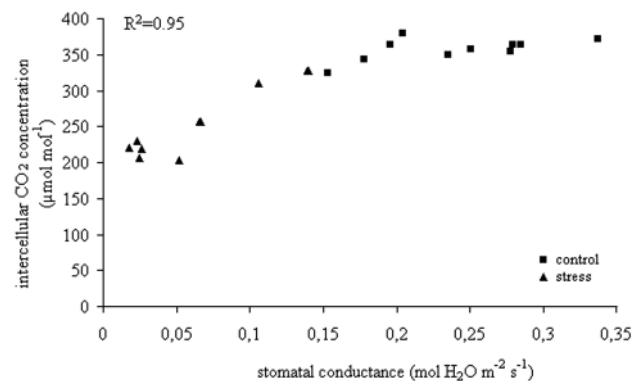


Figure 3.
Relationship between intercellular CO_2 concentration and stomatal conductance in strawberry (*Fragaria x ananassa* Duch. cv. 'Salut'). Each point represents average of two measurements

limiting the photosynthesis (Medrano et al., 2002; Flexas et al., 2004). Medrano et al. (2002) concluded that for grapevine g value of $0.05 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ is a threshold,

below which the predominance of non-stomatal limitation of photosynthesis occurs. Similar dependence was observed in our study. In several cases a decrease of g below the level of $0.05 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ was recorded. This decrease was not accompanied by reduction in C_i , what might indicate that non-stomatal components of photosynthesis limitation were also involved (Fig. 3).

Assimilation of carbon by plants incurs water costs. According to Boyer (1982) the ratio of carbon fixation to water loss (water use efficiency) is critical to plant survival, crop yield and vegetation dynamics. At a leaf level, water use efficiency can be defined as a ratio of photosynthetic rate to transpiration rate or to leaf conductance for water vapour (WUE_i - intrinsic water use efficiency) (Escalona et al., 1999).

The intrinsic water use efficiency (A/g) of water stressed plants was higher compared to well-irrigated ones (Tab. 2). This is in agreement with the results obtained by Flore et al. (1985) and Pietkiewicz et al. (2005) who observed the increase of WUE_i in different water stressed plant species. Chaves et al. (2003) conclude that most plants tend to show an increase in water use efficiency under conditions of mild and moderate water deficit. This increase results from the non-linear relationship between stomatal conductance and carbon assimilation. It means that water loss is restricted before, and more intensely than, the inhibition of photosynthesis. Such changes lead to optimization of carbon assimilation in relation to water supply. However, as it was shown in other studies, under severe drought conditions when depression of photosynthesis is stronger, WUE decreases (Lefi et al., 2004).

Conclusion

Presented results provide information about response of strawberry plants to water stress. Deficit irrigation induced a series of morphological and physiological responses and adaptations. In our research strawberry showed difference under water deficit treatments by reducing growth of the above part of a plant and by maintaining root system development. Modifications in stomatal density and size of stomata indicate that they play an important role in sensing environmental changes. These modifications contribute to optimising the use of assimilates and water use efficiency in periods when water availability is decreased.

In further study effect of various environmental factors (solar radiation, air humidity) on plant performance will be examined with special emphasis focused on modification of stomatal characteristics.

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