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Prohexadione-calcium Changes Morphological and Physiological Traits in Strawberry Plants and Preconditions Transplants to Water Stress

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Summary

Prohexadione-calcium (ProCa) applied as foliar spray, increases root to shoot ratio and reduces specific leaf area (SLA) in strawberry plants (*Fragaria* × *ananassa* Duch.). These effects may help treated plants to survive a transplant shock. Under mild water stress, ProCa caused a transient reduction in leaf stomatal conductance (g_s) in 'Camarosa' and 'Sweet Charlie' plants. This reduction in g_s was paralleled by a decrease in transpiration in treated plants, which was not attributable to differences in plant size or leaf area. Pressure volume curves of 'Sweet Charlie' plants revealed that ProCa application lowered leaf osmotic potential at both full and zero turgor, and increased the volumetric modulus of elasticity. ProCa treatment regulated the leaf morphology of strawberry and preconditioned strawberry plants to tolerate water stress. Under field conditions in the plasticulture fruit production system, newly transplanted bare-root strawberry plants had a progressively higher water potential (ψ_l) and g_s with a longer overhead irrigation. Plants treated with ProCa had a higher ψ_l and g_s than control plants at the same level of overhead irrigation. Application of ProCa to strawberry transplants may in part be able to replace overhead irrigation and at the same time maintain acceptable levels of fruit yield.

Key words. drought stress – pressure volume curves – osmotic potential – specific leaf area –turgor pressure.

Introduction

In Florida, USA, there are over 3,000 ha of plasticulture prepared annually for growing strawberry fruit crops in the fall. Most of these strawberry plants originate from northern Canadian nurseries and are transported by refrigerated trucks to Florida as bare-root plants. From nursery harvest, a bare-root can be transplanted into the plasticulture system in a few days, or it may take up to a couple of weeks. Transplantation usually takes place during a period of hot weather, and transplants will only survive if overhead irrigated for many hours during a period of two weeks.

Excessive water usage for agricultural crops is a concern in Florida and extensive overhead irrigation to ensure the survival of strawberry transplants is an added burden to an already overloaded water supply system. In recent years, various chemicals have been tested that could help to reduce overhead irrigation demands in plasticulture strawberries during the first two weeks of transplant establishment. Among these are "vapour guard", abscisic acid and prohexadione-calcium (Duval et al. 2001). Vapour guard is an anti-transpirant, which coats the leaves and forms a physical barrier and effectively reduces transpiration for at least 2 weeks in Chrysanthemum (Martin and Link 1973). Abscisic acid is a stress hormone, and when used as a foliar spray, can cause stomatal closure in plants and limit water loss (Salisbury and Ross 1992). ProCa is a gibberellin biosynthesis inhibitor which among other effects, decreases specific leaf area in strawberry plants and increases root to shoot ratio (Reekie and Hicklenton 2002).

Of the three methods under investigation, ProCa has shown the most promise when fruit yield is used as an indicator of transplant success. A study using 'Sweet Charlie' strawberry plants suggested that with ProCa application, the amount of overhead irrigation use for transplant establishment can be reduced without any detrimental effect on bare-root transplant survival in plasticulture or fruit yield (Duval et al. 2001). Other plant gibberellin inhibitors have shown similar effects. Triazoles, such as triadimefon, increased seed yield in soybeans and pea subjected to water stress (Fletcher and Nath 1984).

The precise mode of action of ProCa on strawberry plant water relations has not yet been studied. Additional knowledge in this area will aid in developing management practices that conserve irrigation water yet maintain a viable economic crop. The objectives of this study were to:

1) investigate the effect of ProCa on transpiration loss and stomatal conductance in strawberry plants under mild water stress in a controlled environment,
2) evaluate the effect of ProCa on changes in leaf water potential components using pressure volume (P-V) curves, and
3) study water potential and stomatal conductance (g_s) in bare-root transplants treated with ProCa and subjected to different amounts of overhead irrigation in a plasticulture fruit production system in Florida.

Materials and Methods

The effect of ProCa on transpiration in a controlled environment

Bare-root transplants of 'Camarosa' and 'Sweet Charlie' were planted in 3 L nursery pots containing a standard greenhouse soil mix (peat:sand:perlite, 8:3:3) and grown in controlled-environment (CE) growth chambers (model GR-36, Enconaire Systems, Ltd., Winnipeg, Man.). Day/night CE chamber temperatures were set at 24/17 °C. Plants were given a 14-hour photoperiod at 300 μmol m^{-2} s^{-1} PAR measured at plant level (LI-COR quantum sensor 188B, Lincoln, NE). Light was supplied by a mixture of cool-white fluorescent and incandescent lamps (75 % and 25 % input wattage, respectively). Plants were fertilized weekly with 15:15:18 ($N:P_2O_5:K_2O$) general purpose fertilizer alternating with calcium nitrate containing 150 mg L^{-1} nitrogen. Plants were rotated within and between growth chambers every week.

Runners began to form a month after planting. For each plant, all but one runner were removed. When the first daughter plant formed on the runner, it was placed in its own 15 cm diameter standard pot filled with standard greenhouse mix. The daughter plant was allowed to grow while still attached to its mother plant. Nine days later, the daughter had developed sufficient roots to be independent and it was severed from the mother plant. Twenty daughter plants of each cultivar were selected and divided into four groups of five plants. Each group received one of four foliar treatments of 0, 62.5, 125 and 250 mg L^{-1} aqueous ProCa solution prepared from a commercial formulation (Apogee®, BASF Corp., Research Triangle Park, N.C., 27.5 % active ingredient).

The transpiration experiment was a factorial design with two cultivars × four ProCa treatments. Immediately after ProCa application, each plant was watered and excess water was allowed to drain before the pot was sealed with double plastic bags tied around the plant crown to eliminate evaporation from the soil. The plants were then subjected to a dry down cycle after the initial weight of the pot was recorded. Water transpired was calculated by reweighing the plant every day at the same time and subtracting its current weight from its initial value. Leaf stomatal conductance (g_s) was measured daily on each plant using a LI-1600 steady state porometer (LI-COR Inc. Lincoln, NE) following standard protocols (McDermitt 1990). Measurements were taken on the abaxial surface of the last fully expanded leaf of each plant between 10.00 h and 12.00 h.

When the first group of plants of a given cultivar showed sign of wilting, all plants belonging to the same cultivar were harvested. Each plant was separated into leaf blades, petioles plus crown (stem) and roots. Leaf area was measured using a leaf area meter (LI-COR LI-3100, Lincoln, NE). All plant material was dried for 24 h at 70 °C in a forced air oven and then weighed. Specific leaf area (SLA) was calculated as the ratio of leaf area to leaf weight.

Repeated measures analysis of variance was performed using SAS (SAS Institute, Cary, NC) to detect effect of cultivar and ProCa concentration on transpiration and stomatal conductance (g_s) in strawberry plants over time. Plant weight data were subjected for analysis of variance using the GLM procedure of SAS to detect the effects of cultivar, ProCa concentration and their interactions. The Least Significant Difference (LSD) among means was calculated at the 5 % level.

Pressure volume curves in a controlled environment

Twenty 'Sweet Charlie' plants treated with 0, 62.5, 125 or 250 mg L^{-1} ProCa (five plants at each concentration) were grown under the same experimental conditions as described in the above experiment. Leaves born after treatment were identified and allowed to fully expand before they were used for pressure volume measurements. Pressure volume curves were determined for five water-saturated leaves (one per plant) from each ProCa concentration.

Leaves selected for measurements were excised in the CE growth cabinet and the petioles were re-cut under water. Each leaf was put in its own beaker filled with water. Leaves were completely enclosed in a plastic bag and allowed to re-hydrate for 48 h in darkness before measurements commenced. The pressure chamber technique was used to assess the P-V relationship (Wilson et al. 1979). Pressure was applied to the leaf at and beyond the initial balancing pressure to extract xylem water. The procedure was an alternating process of applying pressure to extract xylem water and reweighing the leaf to determine the corresponding water loss. Data for the initial water-saturated leaf weight, and the subsequent leaf weight corresponding to each xylem water potential (ψ) were used to construct a P-V curve depicting the relationship between the inverse of ψ and leaf relative water content (RWC) (Turner 1988). The P-V curves were used to determine osmotic potential at full (ψ_s^{100}) and zero (ψ_s^0) turgor, and the leaf volumetric elastic modulus (ε). SLA was calculated as the ratio of leaf area to leaf weight for each leaf.

Analysis of variance using the GLM procedure of SAS (SAS Institute, Cary, NC) was conducted to detect the effect of ProCa concentration on SLA, ψ_s^{100}, ψ_s^0, and ε.

Water relations post-transplant in the field

An aqueous ProCa solution of 62.5 mg L^{-1} a.i. at a rate of 102 g (a.i.) ha^{-1} was applied as a foliar spray to 'Sweet Charlie' strawberry plants on Sept. 5, 2003 in a nursery field in Nova Scotia (45 °26 ' N, 63 °27 ' W). Control plants were sprayed with water at the same rate. Plants were dug on Oct. 7, and transplanted on Oct. 10, 2003 into an annual hill plasticulture fruit production system at the Gulf Coast Research and Education Centre in Dover, Florida (28 °00 ' N, 82 °22 ' W). In Dover, plants were spaced 30 cm apart in a double row in plastic-mulched raised beds that were 60 cm wide, and separated by a 62 cm wide walk-way between beds. Treated and control

plants were set into separate plots each consisting of eight plants, and subjected to overhead irrigation of 10 h daily. There were three irrigation regimes of 4, 8 or 12 days of overhead irrigation, and each represented a complete block comprised of four treated and four control plots. Subsurface drip irrigation was implemented twelve days after transplantation.

Leaf water potential (ψ_l) was determined on six plants per treatment from each irrigation regime 8, 12 and 24 days after transplanting. Measurements were taken at pre-dawn, mid-day and dusk using a pressure chamber (PMS instrument Co. Ltd., Corvallis, OR). A leaf with its petiole was enclosed in a plastic bag prior to severing in the field to prevent evaporative water loss from the plant tissue. While still in the loosely sealed plastic bag, the leaf petiole was inserted into a pre-drilled rubber stopper. The rubber stopper and leaf were fitted into the pressure chamber, which was then pressurized with nitrogen at a rate not exceeding 0.025 MPa s^{-1} until xylem water returned to the cut surface of the petiole (the endpoint). To ensure accuracy, the cut surface was observed with the aid of a binocular microscope.

Stomatal conductance (g_s) was measured on six plants per treatment from each irrigation regime 12 days after transplanting and before subsurface irrigation was implemented. Measurement protocol was the same as in the transpiration experiment described above.

Analysis of variance using the GLM procedure of SAS (SAS Institute, Cary, NC) was conducted to detect the effect of overhead irrigation, ProCa treatment and their interactions on post-transplant ψ_l and g_s.

Results

The effect of ProCa on transpiration in a controlled environment

Foliar application of ProCa reduced transpiration in 'Camarosa' and 'Sweet Charlie' strawberry plants (Fig. 1). Transpiration was lowest in plants treated with the highest concentration of ProCa (250 mg L^{-1}). There was a progressive decrease in transpiration in 'Camarosa' plants with increases in ProCa concentration. But in 'Sweet Charlie', transpiration was similar in plants treated with all concentrations (including the control) except for 250 mg L^{-1} ProCa, which showed a lower transpiration rate. Transpiration rate was higher in 'Camarosa' than in 'Sweet Charlie'. This is reflected in the early wilting that occurred in the 'Camarosa' control plants (five days after water was withheld); it took 7 days for the control 'Sweet Charlie' plants to show any sign of wilting. Total water loss in untreated plants was 179 and 172 g $plant^{-1}$ in 'Camarosa' and 'Sweet Charlie', respectively. Final difference between the control and the 250 mg L^{-1} ProCa was 30 g $plant^{-1}$ for 'Camarosa' and 35 g $plant^{-1}$ for 'Sweet Charlie'.

In 'Camarosa', untreated plants had similar g_s values as those treated with 62.5 mg L^{-1} ProCa, but plants treated with 125 and 250 mg L^{-1} ProCa had lower g_s values (Fig. 2); the latter two treatments did not differ from each other in the first three measurement days. In both treatments, ProCa caused an initial decrease in g_s followed by a gradual recovery. On the 4th day, this recovery

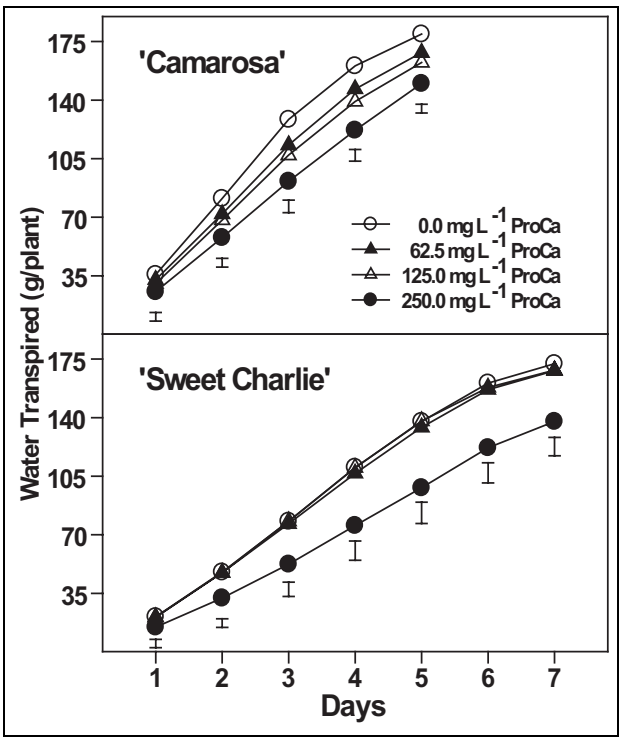


Fig. 1. Cumulative transpiration loss in 'Camarosa' and 'Sweet Charlie' strawberry plants treated with different concentrations of prohexadione-calcium (ProCa). Vertical bars represent ±1 SEM.

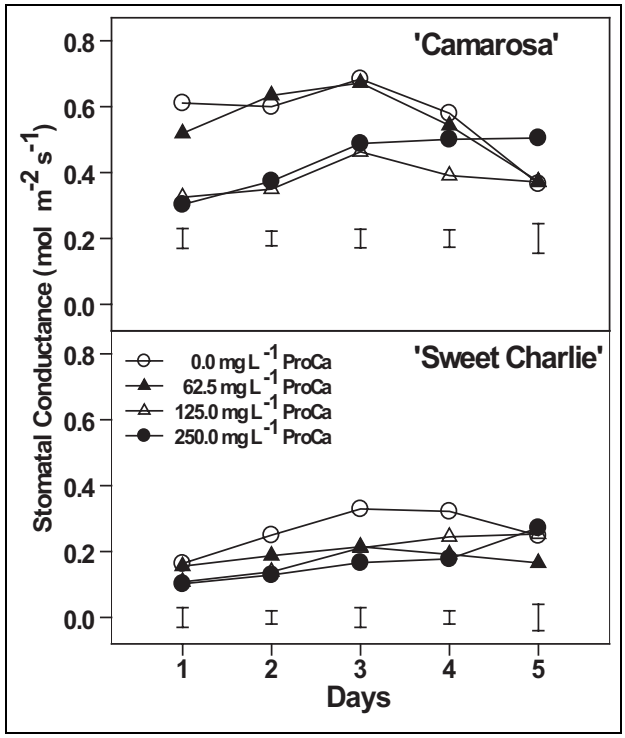


Fig. 2. Stomatal conductance of 'Camarosa' and 'Sweet Charlie' strawberry plants treated with different concentrations of prohexadione-calcium (ProCa). Measurements were taken on 5 consecutive days when water was withheld from the plants. Vertical bars represent ±1 SEM.

continued in plants treated with 250 mg L^{-1} ProCa, but declined in those treated with 125 mg L^{-1} ProCa. On the 5th day, g_s declined in all treatments except the 250 mg L^{-1} ProCa treatment and differences among treatments were no longer statistically significant.

'Sweet Charlie' plants had low g_s values over the entire course of the experiment (Fig. 2). In fact it became difficult to obtain meaningful measurements during the latter part of the experiment because g_s values were low and did not stabilize. Therefore g_s was not recorded on days 6 and 7. In 'Sweet Charlie', differences between ProCa-treated plants were not significant. Control plants did not differ from treated plants in g_s except on days 3 and 4 when values for control plants were higher.

In this short term experiment, ProCa treatment did not affect total plant weight or that of any of the component parts. Average dry weight of 'Camarosa' and 'Sweet Charlie' plants ranged from 2.48–2.66 g and 2.54–2.78 g, respectively. Specific leaf area ranged from 121.95–130.57 $cm^2\ g^{-1}$ in 'Camarosa' plants and from 141.65–154.10 $cm^2\ g^{-1}$ in 'Sweet Charlie' plants.

Pressure volume curves in a controlled environment

All the leaves in this experiment were born after treatment application and they were allowed to fully expand before being used for pressure volume measurements. ProCa application reduced SLA (Table 1). Control plants had the highest SLA, followed by those treated with 62.5 mg L^{-1}. Leaves treated with ProCa concentrations of 125 and 250 mg L^{-1} had the lowest SLA. ProCa application resulted in lower (more negative) values for ψ_s^{100} and ψ_s^0, and higher (more positive) values for ε compared to the control, but none of these parameters differed among the varying ProCa concentrations (Table 1). This is in contrast to the effects on SLA.

Water relations post-transplant in the field

With few exceptions, ProCa treated plants had a higher ψ_I than the corresponding control plants in the same irrigation treatment regardless of time of measurement (Fig. 3). This was most evident in plants with only 4 days of overhead irrigation; when measurements were taken on days 8 and 12 in this treatment, plants had been without any form of irrigation since day 4, although there was a rain event in the early hours of the 12th day. By day 24, these plants with overhead irrigation for 4 days, had received subsurface drip irrigation for 12 days, yet the ψ_I of the control plants was still relatively low. In comparison, their ProCa-treated counterparts had much higher ψ_I values. In some cases, these ProCa treated plants with 4 days

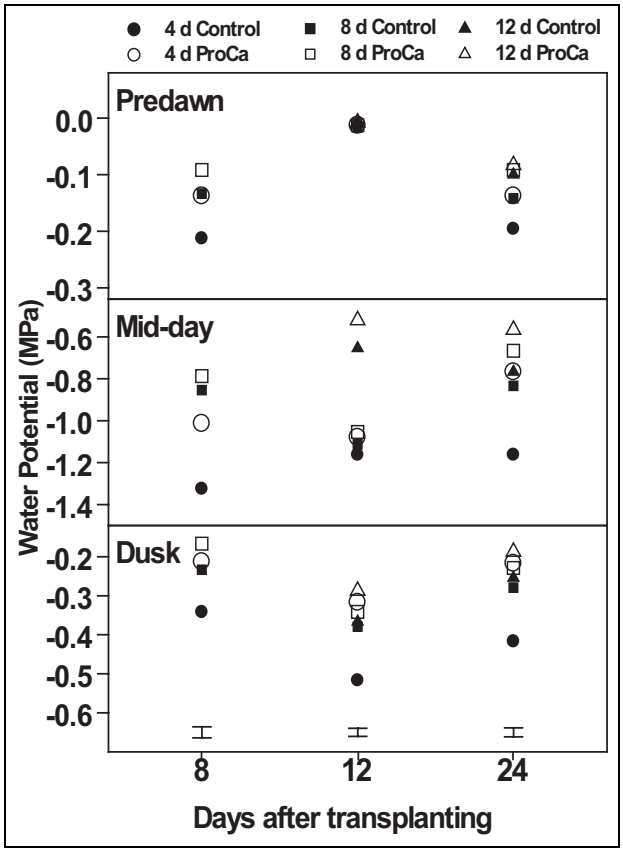


Fig. 3. Water potential of 'Sweet Charlie' strawberry bare-root plants treated with or without prohexadione-calcium. Plants were given either 4, 8 or 12 d of overhead irrigation, after which subsurface irrigation was supplied. Measurements were taken 8, 12, and 24 d after transplantation into plasticulture at predawn, mid-day and dusk. Vertical bars represent ±1 SEM. Note that the scales along the y-axis are different for the different periods during the day.

Table 1. Specific leaf area of the leaves generating the pressure volume (P-V) curves and the component data of water potential derived from the P-V curves obtained from 'Sweet Charlie' strawberry leaves treated with different concentrations of prohexadione-calcium (ProCa).

Measurement[Z]	Prohexadione–calcium concentration (mg L^{-1})			
	0.0	62.5	125.0	250.0
SLA ($cm^2\ g^{-1}$)	162.53 a	134.15 b	107.80 c	111.66 c
ψ_s^{100}(MPa)	−0.46 a	−1.25 b	−1.44 b	−1.54 b
ψ_s^0(MPa)	−1.27 a	−1.70 b	−1.84 b	−1.87 b
ε (MPa)	3.91 a	6.39 b	6.14 b	7.13 b

[Z]SLA is specific leaf area. ψ_s^{100} and ψ_s^0, are osmotic potentials at full and zero turgor, respectively, and ε is the volumetric modulus of elasticity.
a, b, c : Values followed by a common letter in a row are not significantly different at P<0.05

of overhead irrigation had a ψ_I similar to that of control plants with 8 days of overhead irrigation. Likewise, ProCa treated plants with 8 days of overhead irrigation had a ψ_I as high, or higher, than control plants with 12 days of irrigation when measurements were taken 24 days after transplanting. ProCa-treated plants that received 12 days of overhead irrigation had the highest ψ_I values. Measurements taken at dusk did not return to predawn ψ_I values on any measurement day.

In general, ProCa treatment and prolonged overhead irrigation increased g_s values measured 12 days after transplanting (Table 2). However, the effect of ProCa treatment on g_s varied depending on the duration of overhead irrigation. While the effect of ProCa on g_s was marked in plants with 4 days of overhead irrigation, its effect was small in the treatments with 8 or 12 days of overhead irrigation. On the other hand, prolonging the overhead irrigation progressively increased g_s.

Discussion

ProCa is a bioregulator, which affects gibberellin biosynthesis and it restricts cell elongation (Rademacher 2000), reduces leaf area, and decreases total plant weight; these effects can manifest within 2 weeks of application (Reekie et al. 2005). However, ProCa treated plants in the transpiration study had not yet experienced the effects by the end of the experiment long enough to express treatment-induced morphological changes. Given that there was no ProCa-induced plant weight or leaf area reduction, or decrease in SLA in the treated plants, any difference in transpiration loss among plants could not have been related to differences in plant size, leaf area or leaf morphology. Reduced transpiration in ProCa-treated plants, therefore, was likely a direct effect of a ProCa-induced decrease in g_s.

Table 2. Stomatal conductance of 'Sweet Charlie' strawberry bare-root plants treated with or without prohexadione-calcium. Plants were given either 4, 8 or 12 d of overhead irrigation, and measurements were taken 12 d after transplantation into plasticulture.

Overhead irrigation	Stomatal conductance (mol m^{-2} s^{-1})		
	Control	ProCa	Average
4-day	0.359	0.647	0.503
8-day	0.610	0.680	0.645
12-day	0.800	0.880	0.840
Average	0.590	0.736	
Significance :			
Overhead irrigation		**	
Treatment		**	
Overhead irrigation × Treatment		*	

*, **: Significant at P<0.05, P<0.01, respectively.

However, this effect may be dose dependent as demonstrated in 'Camarosa', where transpiration exhibited a gradient response to increasing ProCa concentrations. The two cultivars differed in this response; 'Sweet Charlie' plants required a higher ProCa concentration (250 mg L^{-1}) to reduce transpiration. The reason for the low g_s values in 'Sweet Charlie' plants could have been related to the relatively low light level in the CE growth cabinet. 'Sweet Charlie' plants may require a higher light intensity than 'Camarosa' to maximize their physiological functions; higher photosynthetic rates have been observed in 'Sweet Charlie' as compared with 'Camarosa' plants when light intensity is high (Reekie et al. 2005).

The ProCa induced reduction in g_s may be related to a possible increase in ABA content in the leaves, causing the stomata to partially close. It has been shown that ProCa can cause ABA levels to rise in wheat shoots (Grossmann et al. 1994). Nevertheless, the negative effect of ProCa on g_s in strawberry plants was transient. The partial stomatal closure was followed by a rebound in g_s. This was most obvious in plants treated with 250 mg L^{-1} ProCa. In 'Camarosa', g_s was reduced to 0.3 mol m^{-2} s^{-1} after ProCa was applied but increased to 0.5 mol m^{-2} s^{-1} by the end of the experiment. Likewise, g_s in 'Sweet Charlie' plants increased from 0.1 to 0.27 mol m^{-2} s^{-1} within the same timeframe. However, it is harder to assess plants treated with lower ProCa concentrations because most of them experienced water stress after water was withheld for three days; the decline in their g_s values by the end of the experiment was likely a direct response to soil water deficit that overrode any effect exerted by ProCa.

When gradually exposed to water stress over time, strawberry plants acclimate and develop adaptive mechanisms to cope with water deficits. A selection of *Fragaria chiloensis*, a drought resistant strawberry, can lower its ψ_s^{100} by accumulating solutes in leaves in response to drought stress (Zhang and Archbold 1993). Savé et al. (1993) found after several drought stress cycles, 'Chandler' strawberry plants osmoregulate, lowering their osmotic leaf potential (measured both at ψ_s^{100} and ψ_s^0) and increasing ε compared to well-watered strawberry plants. A decrease in SLA is found in water stressed strawberry leaves and may be partially responsible for the lowering of osmotic potential (Savé et al. 1993). Triazoles, which are GA inhibitors like ProCa, are known to protect plants from drought stress (Davis et al. 1988). Triazoles alter plant physiology (increase in stomatal diffusive resistance and water potential), plant chemistry (increase ABA levels and decrease ethylene content), and plant morphology (reduce leaf area and SLA) which may help to reduce drought stress in some plants (for reviews see Davis et al. 1988 and Fletcher et al. 2000). Our study showed that ProCa decreased SLA in strawberry leaves. These thicker leaves with smaller cells have a higher concentration of solutes and a lower osmotic potential due to the change in the ratio of symplasmic to apoplasmic water – an example of type 2 osmotic adjustment (Nilsen and Orcutt 1996). The P-V data showed treated plants had a lower ψ_s^{100} and ψ_s^0 and had the ability to develop a higher maximum turgor and maintain a positive turgor at lower leaf water potentials than control plants. Together with their higher ε, treated plants could minimize the change in tissue water content during water deficit while enhancing water uptake from the soil (Nilsen and Orcutt 1996).

Like triazoles, ProCa has the ability to change a strawberry leaf to a drought tolerant morphology and precondition plants for water stress. This may be one of the reasons for the higher ψ_l in ProCa-treated plants in plasticulture when they experienced water stress with reduced amounts of overhead irrigation. Another reason leading to improved water relations in ProCa-treated strawberry plants could be the increase in their root to shoot ratio, which may facilitate water uptake from soil. This higher ratio is the result of acceleration in root development and inhibition of shoot growth (Reekie et al. 2005). In addition to these drought tolerant traits, ProCa-treated bare-root plants in plasticulture had, on average, higher g_s values than control plants. It has been found that another GA inhibitor, paclobutrazol increases g_s in strawberry leaves (Archbold and Houtz 1988; Deyton et al. 1991). In forsythia, the increase in g_s was attributed to a possible increase in stomatal density (Thetford et al. 1995). However, in our plasticulture study, additional overhead irrigation increased g_s and diminished the difference in g_s between treated and control plants. It appears that g_s is more influenced by water availability than ProCa. But under mild water stress, osmotic adjustment can be an effective mechanism for maintaining turgor pressure, and may allow the stomata to stay open; this happens at water potentials that would have prohibited this if osmotic adjustment had not occurred (Nilsen and Orcutt 1996). This mechanism was well demonstrated in plants that received only 4 days of overhead irrigation – when measured on day 12 (after 8 d without any form of irrigation), the g_s in ProCa-treated plants was 80 % higher than their untreated counterparts.

Regardless of whether measurements were taken at predawn, mid-day or dusk, ψ_l values were generally higher in plants which received more overhead irrigation. The amount of overhead irrigation bare-root plants received in the first 12 d of plant establishment in plasticulture had a significant effect on overall plant water status, and may carry a longer term impact. Measurements taken on plant ψ_l 24 d after transplantation, when subsurface drip irrigation had already been implemented for 12 d, continued to show differences in ψ_l. However, ProCa alleviated water stress and exerted a positive influence on plant water relations much like the effect of irrigation. Compared to control plants of the same irrigation regime, treated plants had higher mid-day ψ_l , and there was less of a difference in their predawn ψ_l and dusk ψ_l which was indicative of a faster recovery from transplant stress. Therefore, application of ProCa to strawberry transplants may in part be able to replace overhead irrigation and at the same time maintain acceptable levels of fruit yield.

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