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## DIVERSIFIED RESPONSE TO DROUGHT OF LIGHT EXPOSED AND SHADED LEAVES OF POTTED GRAPEVINE, PEACH AND PEAR TREES

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### ABSTRACT

The short-term physiological and morphological response of potted pear, peach and grapevine were studied as a function of soil water supply and light availability. Plants were stressed by withholding water for 13 days prior to rewatering. Shading was imposed after full lamina development by covering with a neutral density cloth (photon flux density, PFD, less than  $50 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) half the leaves of each tree. Soil water content (SWC) was monitored by time domain reflectometry (TDR) and leaf physiology assessed as photosynthetic rate ( $A$ ), conductance ( $g_l$ ), total ( $\psi_w$ ) and stem ( $\psi_{st}$ ) water potential. Shading decreased  $A$  rates to the compensation point regardless SWC. Rates began to decline sharply eight days into stress in all species at about 50% SWC of watered pots; the decrease was less pronounced in pear. A significant species x water regime interaction occurred on the same date, with higher  $g_l$  in stressed peach and grape than in the control. Within species, total leaf  $\psi_w$  was more affected by water stress than by light regime and no interactions were found.  $\Delta\psi$ , equal to  $\psi_{st} - \psi_w$ , at the stress peak in the shaded portion of the plant, was higher in pear than in peach and grapevine. Accelerated leaf shedding observed in stressed and shaded pear trees might be interpreted as an adaptive mechanism to counter the effects of poor water loss control, leading to very low water use efficiency. Peach and grapevine plants showed better stomata control, their response being less pronounced in the shaded portion of the canopy with respect to that well-lit.

**Key Words:** *Pyrus communis*, *Prunus persica*, *Vitis vinifera*, water stress, light exposure, assimilation, stomatal conductance, water potential

## INTRODUCTION

Light is one of the most important environmental factors determining the morphology and physiology of leaves in woody plants. Light availability changes over time, latitude and local climatic conditions. Distribution inside the canopy depends on the whole-tree structure and is dynamic during the growing season. Light penetration in the internal part of the tree is rather uniform at bud break. Despite this uniformity, the early leaf development can be affected by previous year's light availability. In apple, spur-leaf dry weight per unit of leaf area is lower in the interior parts of the canopy, and on spurs differentiated in heavy shade (Tustin et al., 1992). Internal parts of the tree thus have less growth, even if well-lit early in the season. As more shoots emerge and start growing, light distribution tends to become less uniform and shading of the interior leaves increases, although these can benefit from sun flecks (Kriedemann et al., 1973; Lakso and Barnes, 1978).

The physiological response of mature leaves to shade is likely mediated by transpiration, as nutrient and hormone partitioning to single leaves is dependent on the transpiration stream. Leaves exposed to high light usually transpire the most and receive greater amounts of resources than those shaded (Neuman and

Stein, 1983). Water loss depends on the vapour pressure gradient between leaves and air and is partially controlled by stomata closure and boundary layer resistance. Jarvis (1985) suggested that trees do not have an efficient leaf boundary layer even inside the canopy, given the high degree of air mixing within canopy. Moreover, under shaded conditions, stomatal conductance is considerably reduced (Neri and Scudellari, 1994). As a result, in apple, transpiration is reduced by about 50% in shaded leaves (Marangoni et al., 1992). Thus, it can be argued that under non limiting soil moisture, transpiration can promote a sufficient import of nutrients by shaded leaves to prevent their abscission.

A question then arises, what happens to the leaves in both shaded and sunny part of the canopy if water becomes a limiting factor. The leaves have enormous differences in morphology as it was reported by Björkman (1981). It has been suggested that the upper leaves in the crown are more xeromorphic than those lower (Zimmermann and Brown, 1971), even under favourable water regimes, and these differences become greater under drought stress. The physiological mechanism at work in this response have not yet been fully elucidated, although an increased abscission of shaded leaves or a reduction in size of the exterior leaves to allow more light penetration in the inner canopy

can be envisaged. The former mechanism likely applies to trees under adequate soil moisture and then drought; the latter may be typical of plants developed under sub-optimal soil water supply.

Transpiration plays an important role in the energy balance of each leaf, which is mostly affected by net radiation (Jones, 1983). It is also an important factor for temperature regulation, especially in well-lit leaves, which need a higher latent heat flux to prevent an extreme temperature increase. If not controlled, this increase can lead to leaf spot necrosis, desiccation, and abscission. This is more likely to happen in large-leaved species like grapevine or kiwifruit, although osmotic adjustment can help to overcome it (Lakso, 1994). The present study with potted grapevine, peach and pear plants investigated differential morphological and physiological adaptations of mature well-lit and shaded leaves, all developed under high light, to drought and subsequent rewatering.

## MATERIAL AND METHODS

*Plant material.* Eight potted plants for each of the three species, the 2-yr-old pear 'Bartlett/seedling', the 3-yr-old peach 'Weimberger/-PSA5 seedling', and the 3-yr-old own-rooted grapevine 'Chardonnay' were employed. Pear and peach trees

were grown in 19-liter (l) black polyethylene pots and the grapevines in 32-liter green polyethylene pots in 70-30% peat-sand medium. All pots were wrapped with aluminium foil to reduce root-zone heating.

The peach and pear trees were pruned during the rest period to a few good lateral limbs; the vines were pruned to several three-node spurs for a total bud charge of about 12-15 buds per vine. All fruits on the trees had been removed prior to the trial.

The pots were arranged in four rows of 6 plants each, with two trees per species in each row. A wire trellis was placed along each row and fitted with a neutral density cloth (5% transmission) to allow shading of about 50% of each plant. The trees were trained so as to shade whole shoots 15 days before water stress, i.e. when the shoots had stopped growing and all their leaves were mature and well-lit.

Drip-irrigation lines, with one emitter per pot for pear and peach and two for grapevines provided water as needed until the beginning of stress (July 21), when irrigation was withheld in all pots in 2 of 4 rows until rewatering the stressed trees on August 4.

*Gas exchange.* The assimilation rate (A) and leaf conductance (g) of two mature leaves were measured on each plant, one leaf from the well-lit portion and one from the shaded part of the tree. Measurements were taken on 21, 24, 27 and 29 July and on 3, 6, and 10 August, i.e. 0, 3, 6, 8

and 13 days after withholding irrigation and 2 and 4 days after rewatering with an ADC LCA2 unit (Hoddesdon, UK), fitted with a broad leaf chamber. The measurements were usually taken between solar noon and 14:00 hr under saturating photosynthetic flux density (PFD). To avoid excessive heating, the chamber was held in the shade between subsequent measurements.

*Water relations.* Air vapour pressure deficit (VPD) was computed daily from local weather station data, using mean values of air temperature and relative humidity. Soil water content (SWC) was measured by a time domain reflectometry (TDR) device, (Soil-moisture Corp. Model 6050 X1 Trase, Santa Barbara, CA) at 2-4 day intervals throughout the experiment. Two readings per pot were usually taken 3 hours after irrigation of the control plants.

TDR readings were performed using 30 cm long wave guides to provide sampling throughout the soil profile. On 0 and 11 days after stress imposition, pre-dawn water potential ( $\psi_{pd}$ ) was estimated, on two leaves per tree, one from the well-lit and one from the shaded portion of the canopy. Total leaf water potential ( $\psi_w$ ) was estimated with a pressure chamber (Soil Moisture Corp., Model 3005, Santa Barbara, CA) on one of the same leaves and on the same dates in sunny conditions when photosynthesis was measured.

Stem water potential ( $\psi_{st}$ ) was estimated on a leaf adjacent to one of those previously sampled for  $\psi_w$  at the beginning of and at stress peak and 2-6 days after rewatering in the well-lit and in the shaded parts of the tree. Each leaf was covered completely with aluminium foil, to stop transpiration and allowed 30 minutes' equilibration before measurement.

*Statistical analysis.* The experimental design was a split-split-plot with two blocks. Treatments were two levels of water supply (watered vs stressed) as the main plot, three fruit species (pear, peach and grapevine) as the subplot, and two light regimes (well-lit vs shaded) as the sub-subplot. For each water supply-light regime combination four trees per species were used. Due to severe leaf damage and drop manifested at stress peak, the data taken on this date and 2 and 6 days after rewatering had missing values that considerably increased variability.

## RESULTS AND DISCUSSION

Shade without water stress in this short-term experiment induced no detectable morphological modifications. Leaf wilting, necrosis and abscission in the well-watered trees did not occur in light nor shade. At the stress peak, the shaded part of the trees showed greater apparent response than the sunlit part, although symptoms varied between species. The shaded part of the pear trees

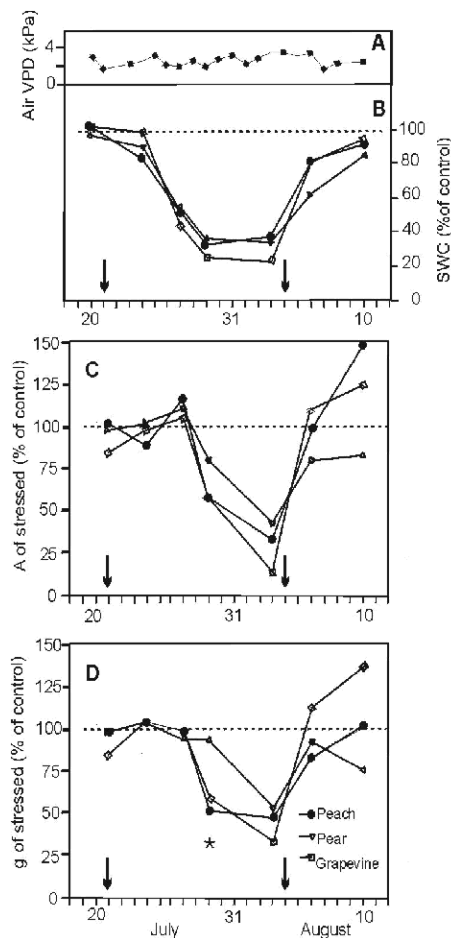
evinced almost total defoliation, much earlier and more severe than the corresponding well-lit part. At the peak of stress, two out of four trees were dying. Shaded and stressed peach leaves wilted earlier than those well-lit and then abscised, although these symptoms were less severe than in pear. Similarly to peach, grapevine had shaded-leaf yellowing and necrosis and less pronounced abscission.

*Air VPD, soil moisture and gas-exchange.* The evaporative demand during water stress was generally high and showed a maximum of 3.6 kPa at the stress peak (Fig. 1A). Water-use dynamics during stress were similar among the tested species. SWC sharply decreased 6 days after withholding irrigation (Fig. 1B), recorded the minimum two days later and thereafter remained fairly constant until rewatering. Grapevine pots showed the lowest SWC (22% of control) at stress peak.

Pre-dawn leaf water potential 11 days after withholding irrigation was -2.1, -2.3 and -1.1 MPa for the pear, peach and grapevine as compared to -0.36, -0.48 and -0.20 MPa, respectively, in watered controls. The differences among species were much greater than those estimated by TDR in soil water content, a likely consequence of diversified root resistance to water movement.

Because of the marked shade tested (PFD levels never exceeded  $50 \mu\text{mol m}^{-2}\text{s}^{-1}$ ), the A rates for all species in the shade-treatments were

close to the compensation point, regardless of water shortage severity (data not shown). This rules out the possibility of sustained osmotic adjustment being dependent on the photosynthates in shaded leaves, although imports of osmoticum or passive adjustment may still occur. Heavy shading also prevented A from responding to the water stress.



**Figure 1.** Air-VPD (A), relative (% of control) soil water content (B), assimilation rate (C), and leaf conductance (D) recorded in stressed potted pear, peach, and grape-vine plants. The asterisk (\*) in Figure 1D

indicates a significant species x water regime interaction ( $p \leq 0.05$ ). Arrows indicate date of water withholding (July 21) and rewatering (August 4)

This resulted in a confounding effect on the interactions of light x water regime within species, which primarily reflected variations due to the water supply. When the A of stressed trees was plotted per species as percentage of watered trees, the maximum rates remained at a 50% SWC of control, while an abrupt decrease occurred at lower SWCs (Fig. 1C). Interestingly, at the stress peak a certain photosynthetic capacity (ranging from 20-40% of control by species) was maintained by the stressed trees, likely as a result of different susceptibility of individual plants to the increasing soil water deficit. The A rates recovered promptly upon rewatering in peach and grapevine plants but not until 6 days after rewatering in the pear trees (Fig. 1C).

Trends of leaf conductance were similar to A up to 6 days after withholding irrigation (Fig. 1D), although no significant reductions in  $g_l$  occurred within species despite a drop in SWC of about 50%. A significant interaction between species and water regime was recorded two days later when stressed pear leaves had  $g_l$  values similar to those of well-watered control ( $156 \text{ mmol m}^{-2}\text{s}^{-1}$  vs  $168 \text{ mmol m}^{-2}\text{s}^{-1}$ ); both stressed peach and grapevine leaves showed considerably lower leaf conductances than watered ones ( $80$  vs  $156 \text{ mmol m}^{-2}\text{s}^{-1}$  and  $83$  vs  $142 \text{ mmol m}^{-2}\text{s}^{-1}$ ,

respectively). Since on the same date the 2nd order interaction (stress x species x light regime) was not significant, the above holds regardless of light exposure. The  $g_l$  of stressed pear leaves dropped to values similar to those detected for the two other species 13 days after stress and recovered promptly after rewatering.

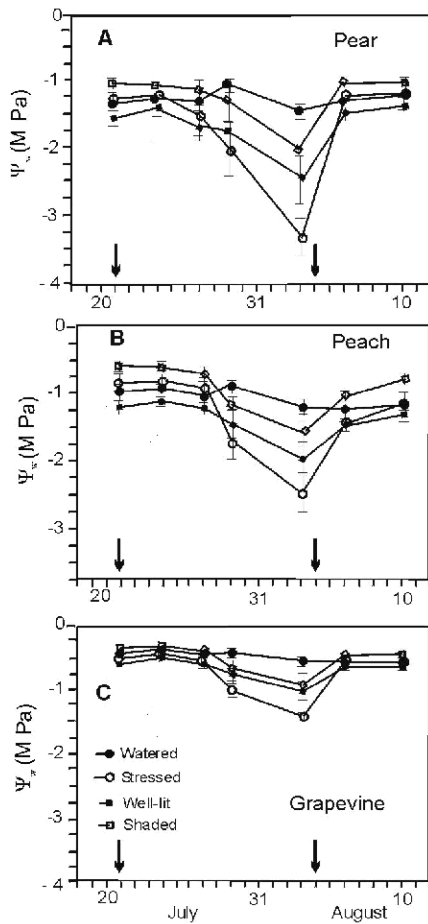
The longer period of wide stomata opening during water shortage can be linked to the morphological response of pear trees, which in shade showed very rapid leaf senescence and abscission. This may be the consequence of the combined effects of carbon starvation induced by the inhibition of photosynthesis and poor water loss control under severe drought and strong VPD, resulting in rapid dehydration. Thus, an inherent plant adaptation would be to get rid of those leaves having very low water-use efficiency by accelerating abscission. It may be argued, however, that high  $g_l$  should maintain high cytokinin import thus, delaying senescence (Thimann, 1980). Yet it is true that well-lit and shaded leaves coexisted on the same plants in the present study, so the competition exerted by the former may have been a dominant factor. Further, cytokinin synthesis and translocation can be greatly limited by severe water stress.

Shaded and stressed peach and grape leaves showed a more efficient control of water loss than pear leaves, as indicated by the earlier reduction of  $g_l$ . However, this stomata sensitivity lowered in both species the benefit

from evaporative cooling (maximum air temperature always higher than 30°), thus increasing the risk of overheating and leaf burning. Such risk is inherently higher in large-sized leaves whose heat transfer by convection with the surrounding air is lowered due to higher leaf boundary resistance (Lakso, 1990). This mechanism would explain why the necrotic areas found in the

stressed grape leaves were much more extensive than in peach.

*Leaf water potentials.* Like the A rates, a lag of several days was found in all species between the onset of the sharp SWC decrease and the drop of leaf water potential of stressed trees (Fig. 2 A, B and C). At stress peak, all the non-irrigated plants showed the lowest negative values of  $\psi_w$  (-3.3 MPa in pear, -2.7 MPa in peach, -1.4 MPa in grapevine), which is critical for leaf functioning and plant survival. By comparison, field-grown peaches of ‘Elberta’ showed a sequence of symptoms leading in most cases to death after experiencing  $\psi_w$  around -3.0 MPa, whereas at similar leaf water potentials ‘Bartlett’ trees survived despite their showing severe stress symptoms (Proebsting and Middleton, 1980). In grapevine, full stomata closure usually occurs beyond the threshold of -1.5 MPa (Smart and Coombe, 1983). The trends of light and shade treatments within species were fairly parallel, showing comparable decreases at peak and similar increases after rewatering (Fig. 2A, B and C).



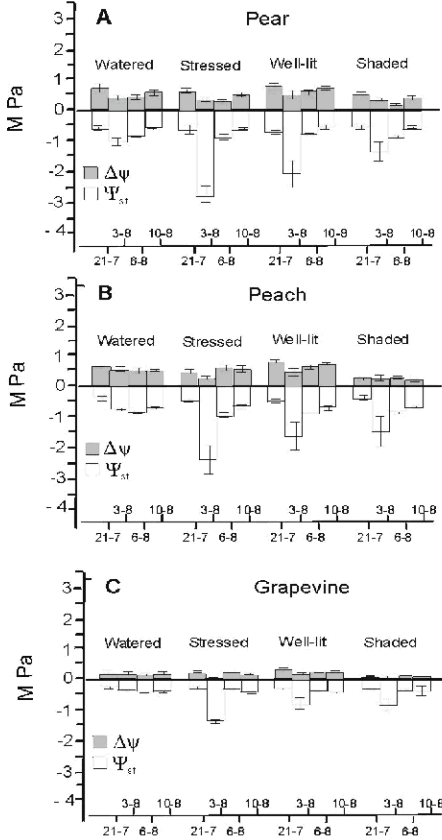
**Figure 2.** Main effects on leaf water potential (watered vs stressed, unshaded vs shaded) for pear (A), peach (B) and grapevine (C) plants. Vertical bars at each date indicate standard error (SE) of means. Symbol size on some dates exceeds SE

Stem water potential ( $\psi_{st}$ ) for main effects within species (Fig. 3A, B and C) showed a dramatic decrease along the stress period, and a rapid recovery after rewatering, in all species. While the difference between leaf water potential and stem water potential ( $\Delta\psi = \psi_w - \psi_{st}$ ) was high and fairly stable in well watered plants, it became much lower in

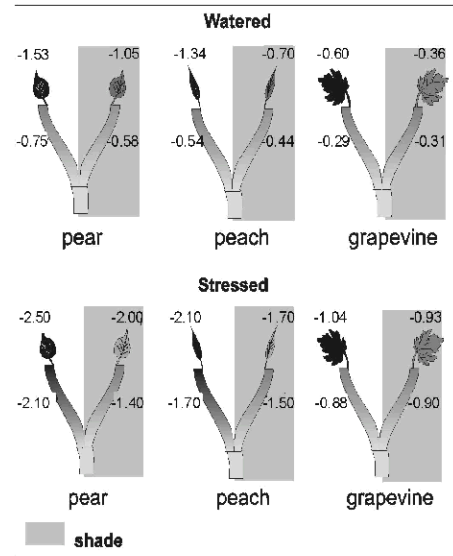
stressed plants, reaching values close to zero in grapevines at the stress peak. Noteworthy, too, on the same date in the shaded portion of water stressed plants the highest  $\Delta\psi$  was in pear (0.6 MPa), followed by peach (0.2 MPa) and grapevine (0.03 MPa; Fig. 4). Since the  $\Delta\psi$  is usually highly correlated to transpiration

(Jones et al., 1985), it appears again that pear under extreme stress lacks an effective mechanism to control water loss. The full recovery of  $\Delta\psi$  was reached 2 days after rewatering for grapevine and peach, and 6 days for pear.

### CONCLUSIONS



**Figure 3.** Stem water potential and stem-to-leaf gradient of water potential ( $\Delta\psi$ ) as per the main effects (watered vs stressed, unshaded vs shaded) at initial (21 July) and stress peak (3 August) and 2-6 days after rewatering (6-10 August, respectively) in pear (A), peach (B) and grapevine (C) plants. Vertical bars at each date indicate standard error (SE) of means



**Figure 4.** Leaf and stem water potentials (in MPa) in watered and stressed plants in sunny and shaded parts of the canopy at the peak of stress

Light played an important role in the competition for water of shaded and well-lit leaves under drought conditions in all the species, reducing the adaptive response of the former leaves to stress. As a consequence, leaf wilting, necrosis, and abscission occurred earlier in the shaded parts of the stressed trees. Pear showed the highest sensitivity



to stress effects. This response may be due to (a) species and varietal susceptibility and (b) pear's osmoregulation.

Certain pear cultivars, including 'Bartlett', are reported to have a weak stomata control (Bonany et al., 1991; Mitchell et al., 1994), which may result, under heavy stress conditions, in severe leaf burning and abscission. This may have contributed to the heavy loss of foliage in the shaded, water stressed limbs. Although leaf water potential components were not measured in this trial, maintenance of  $g_l$  does not rule out that this species may have undergone passive osmotic adjustment, which might have enabled it to maintain sufficient turgor, and allow partial stomata opening.

While responses to water stress of field-grown plants may differ from those of potted ones, the results of the present study suggest that under drought conditions peach, pear, and grapevine anticipate the stress response to drought in the internal shaded part of the canopy as it was found in cherry (Neri and Scudellari, 1994) and also in *Robinia pseud-acacia* and *Tilia* spp. (unpublished observations). Therefore, in drought conditions the choice of the training system and the canopy management strategies (e.g. summer pruning) should emphasize the need to maximize the ratio of well-lit vs shaded leaves. More sparse, vase-shaped canopies, Tatura trellis, thin horizontal or vertical wall-

shaped trees, well-trained spindles or central axes with reduced internal shading and wider spacing could strongly enhance water use efficiency.

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## ZRÓŻNICOWANA REAKCJA NA SUSZĘ OŚWIETLONYCH I ZACIENIONYCH LIŚCI UPRAW POJEMNIKOWYCH WINOROŚLI, BRZOSKWINI I GRUSZY

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### S T R E S Z C Z E N I E

Przedmiotem badań była fizjologiczna i morfologiczna reakcja uprawianych w pojemnikach gruszy, brzoskwini i winorośli w odniesieniu do stanu nawodnienia podłoża i dostępu światła. Rośliny poddano stresowi suszy przez wstrzymanie podlewania przez 13 dni. Po całkowitym wykształceniu blaszek liściowych na połowę liści każdej rośliny założono zacinienie z tkaniny o neutralnej gęstości (PFD – gęstość strumienia fotonowego – poniżej  $50 \mu\text{mol m}^{-2}\text{s}^{-1}$ ). Zawartość wody w podłożu (SWC) była monitorowana za pomocą reflektometrii czasowej (TDR), a stan fizjologiczny liści oceniano na podstawie tempa fotosyntezy ( $A$ ), przewodności szparkowej ( $g_s$ ) oraz potencjału wodnego liści ( $\psi_w$ ) i pędu głównego ( $\psi_{st}$ ).

Niezależnie od zawartości wody w podłożu (SWC) zacinienie obniżyło tempo fotosyntezy ( $A$ ) do punktu kompensacji. Silny spadek tego tempa nastąpił po ośmiu dniach stresu suszy u wszystkich trzech gatunków roślin przy dwukrotnie niższej zawartości wody w podłożu (50% SWC) w stosunku do roślin podlewanych. Spadek ten był stosunkowo najslabiej zaznaczony u gruszy. Wyraźna reakcja na stan nawodnienia wystąpiła u badanych gatunków roślin tego samego dnia, przy wyższej wartości  $g_s$  u poddanych stresowi brzoskwini i winorośli w porównaniu z kontrolą.

U badanych upraw całkowity potencjał wodny liści ( $\psi_w$ ) był bardziej podatny na stres suszy niż na poziom naświetlenia i nie stwierdzono tu wystąpienia interakcji. Wartość  $\Delta\psi$  ( $\psi_{st} - \psi_w$ ) w czasie największego stresu u zacinionej części rośliny była wyższa u gruszy niż u brzoskwini i winorośli. Wcześniejsze zrzucanie liści w części zacinionej u poddanej stresowi gruszy może być wynikiem mechanizmu adaptacyjnego do warunków niedostatecznego nawodnienia, prowadzącego do znacznego obniżenia efektywności wykorzystania wody. Brzoskwinia i winorośl wykazały lepszą regulację aparatów szparkowych, stąd u nich reakcja na suszę była słabsza w zacinionej części rośliny w porównaniu do części oświetlonej.

**Słowa kluczowe:** *Pyrus communis*, *Prunus persica*, *Vitis vinifera*, stres wodny, naświetlanie, asymilacja, aparat szparkowy, potencjał wodny