Water Relations of a *Fragaria chiloensis* and a *F. virginiana* Selection during and After Water Deficit Stress

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Abstract. A comparative study was performed to elucidate changes in the water relations of *Fragaria chiloensis* (L.) Duch. 'BSP14' (FC) and *F. virginiana* (L.) Duch. 'NCC85-13V' (FV), grown in containers in a greenhouse, in response to imposed water deficit stress and subsequent recovery. At incipient wilting, a reduction in osmotic potential at full turgor (Ψ_{π}^{100}) of 0.42 MPa occurred in leaves of FC, while no change was found in FV. Leaf water potential (Ψ) isotherms revealed that as leaf Ψ and relative water content (RWC) declined, stressed FC plants maintained a higher turgor potential (Ψ_p) and lower osmotic potential (Ψ_{π}) than nonstressed (control) plants, while there was no effect of drought stress on these relationships in the FV plants. From the isotherms, turgor loss was estimated to occur at a lower leaf Ψ and RWC in stressed FC plants than either in control FC plants or stressed and control FV plants. During a diurnal phase 36 hours after wilting, leaf Ψ , Ψ_p , and RWC of the FC selection were generally lower in stressed than in control plants, with differences ranging from 0.14 to 0.74 MPa, 0.28 to 0.47 MPa, and 1% to 8%, respectively. In the FV selection, Ψ_p was 0.09 to 0.31 MPa lower in stressed than in control leaves, while the other characteristics were not affected. Leaf Ψ_p of stressed FC plants was 0.09 to 0.27 MPa higher than controls during the dark period, but was similar during the day. When plants of both species were grown and stressed in the same container, FV plants wilted $\approx$ 4 days earlier than FC plants, and foliar Ψ_{π}^{100} of FC was 0.35 MPa lower than that of FV at incipient wilting. The isothermal relationships between leaf Ψ and Ψ_{π}^{100} indicated FC had a $\Psi_{\pi}^{100} \approx 0.25$ MPa lower than FV at a $\Psi < 1.5$ MPa. This study provided evidence for greater osmotic adjustment in response to imposed water deficit stress in a selection of *F. chiloensis* than in one of *F. virginiana*.

Water availability has a significant impact on strawberry plant growth and yield (Dwyer et al., 1987; Gehrman, 1985; Renquist et al., 1982a, 1982b). In the genus *Fragaria*, there may be great variation in drought resistance among cultivars and wild species (Archbold and Zhang, 1991; Chandler and Ferree, 1990; Darrow and Dewey, 1934; Mazhorov, 1978). Commercial strawberry cultivars (*F. $\times$ ananassa* Duch.) are direct or indirect hybrids of the putatively drought-resistant *F. chiloensis* Duch. and the drought-susceptible *F. virginiana* Duch. The mechanism(s) for drought resistance in *Fragaria* is not clear.

The reduction of leaf turgor potential (Ψ_p) that accompanies the loss of water from leaf tissue directly affects many important morphological and physiological processes, such as leaf enlargement, stomatal aperture, photosynthesis, and N assimilation (Hsiao, 1973; Hsiao et al., 1976; Kramer, 1983; Turner and Jones, 1980). As leaf water potential declines, strawberry photosynthetic rate declines, indicating sensitivity to drought stress (Sruamsiri and Lenz, 1986). Many plant species adjust to water deficits and maintain leaf Ψ_p as leaf water potential (Ψ) declines. The relationship between leaf Ψ and Ψ_{π} may be altered by drought stress preconditioning so that previously stressed plants may have a lower leaf Ψ at zero turgor than nonstressed ones (Jones and Turner, 1978; Turner, 1986; Turner and Jones, 1980). This situation leads to a reduction in the critical leaf Ψ or relative water content (RWC) at which physiological and morphological processes are

affected (Farquhar and Sharkey, 1982; Turner, 1986; Turner and Jones, 1980).

Osmotic adjustment, the active accumulation of leaf solutes lowering leaf osmotic potential (Ψ_{π}), is a process by which many species respond and adjust to drought and/or salinity (Barlow, 1986; Hsiao, 1973; Morgan, 1984; Turner, 1986; Turner and Jones, 1980). Osmotic adjustment allows the aforementioned turgor-regulated processes to continue at progressively lower leaf Ψ and maintains water extraction from the soil as the root Ψ decreases (Ludlow and Muchow, 1990; Turner, 1986). Following adjustment, the leaf can maintain photosynthesis at lower leaf Ψ (Jones and Rawson, 1979); thus, the supply of assimilates to actively growing sites can continue.

Renquist et al. (1982c) reported that osmotic adjustment was exhibited in 'Olympus' strawberry. Diurnal leaf Ψ_p was maintained, while Ψ and Ψ_{π} declined in nonirrigated plants in the field. They concluded that the maintenance of leaf Ψ_p in nonirrigated plants, despite lower Ψ , was due to diurnal osmotic adjustment in the leaves. However, the maintenance of leaf Ψ_p could also be due to increased elasticity of the leaf cell walls (Elston et al., 1976; Kim and Lee-Stadelmann, 1984; Turner and Jones, 1980). Osmotic adjustment cannot be confirmed unless the reduction of Ψ_{π} , due to the accumulation of osmotically active solutes is verified. By using the pressure-volume technique and establishing the foliar water content to Ψ_{π} relationships for well-watered and water-stressed plants, O'Neill (1983) concluded that osmotic adjustment occurred in water-stressed plants of a *F. virginiana* selection. *Fragaria chiloensis* is reportedly much more drought-resistant than *F. virginiana*; however, little information is available on the comparative drought stress physiology of either species under similar water deficit

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Abbreviations: FC, *Fragaria chiloensis* (L.) Duch. 'BSP14'; FV, *Fragaria virginiana* (L.) Duch. 'NCC85-13V'; RWC, relative water content; Ψ , water potential; Ψ_p , turgor potential; Ψ_{π} , osmotic potential; Ψ_{π}^{100} , osmotic potential at full turgor.

induction conditions. Morphological adaptations, hypothesized as the source of drought response variation (Darrow, 1966), are not solely responsible for the differences in drought resistance between selections of these and other *Frugaria* species (Archbold and Zhang, 1991).

Increasing drought stress resistance in cultivated varieties may be possible via breeding and biotechnological methods, but only when those traits conferring resistance have been determined. Preliminary observations indicated that a *F. chiloensis* selection, 'BSP14', had greater drought resistance than a *F. virginiana* selection, 'NCC85-13V' (Archbold and Zhang, 1991), fitting the reported drought-resistance classification of each species (Darrow, 1966). The objectives of this study were to characterize the water relations of the drought-resistant *F. chiloensis* selection and the drought-susceptible *F. virginiana* selection during and after imposed water deficit stress to determine if osmotic adjustment occurs in either species.

Materials and Method

Plant materials and stress imposition. Plants of *F. chiloensis* 'BSP14' (FC) were obtained from the National Germplasm Repository in Corvallis, Ore. Plants of *F. virginiana* 'NCC85-13V' (FV) were obtained from Ronald Goldy, North Carolina State Univ., Raleigh. Plants were propagated by runner cuttings and were 4 months old when the experiments were started. They were maintained in containers (2.4 l, 15 cm diameter) containing Pro-Mix BX (Premier Brands, Stamford, Conn.), unless indicated otherwise. All plants were watered daily and received a 200 ppm 20N-20P-20K fertilizer solution weekly until the experiments started. The greenhouse was at $21 \pm 6^\circ\text{C}$ with ambient light levels during the experiments. To induce water deficit stress, water was withheld from plants until at least 50% of the plants of a selection exhibited incipient wilting at midday, or loss of leaf petiole turgor. All plants were then re-watered daily during the recovery period. Control plants were watered daily.

Leaf sampling and measurement of water relation components. Leaf Ψ was measured on the most recent fully expanded, mature leaf of each test plant using a pressure chamber (Model 610, PMS Instruments, Corvallis). Leaves were sampled between 1000 and 1200 HR unless otherwise indicated. The procedure was basically the same as that described by Turner (1988). Briefly, the leaf was cut at the petiole base and immediately placed in the pressure chamber with ≈ 0.5 cm of the cut end of the petiole protruding through the rubber stopper used to seal the chamber. The pressure in the chamber was gradually increased by applying compressed N_2 gas until the sap returned to the cut end of the main xylem vessels, monitored with a magnifying lens. The pressure inside the chamber was recorded and released before the leaf was removed. Once removed from the pressure chamber, the leaf was immediately sealed in a plastic bag, placed in a Dewar flask containing ice-cold tap water to minimize water loss from the leaves, and transported to the laboratory. In the laboratory, the three leaflets of each sampled leaf were used for measurements of Ψ_p , Ψ_{π}^{100} , and RWC, respectively. For measurement of Ψ_p , one leaflet from each sampled leaf per test plant was placed in an aluminum sample cup, sealed with Parafilm, and frozen at -20°C . It was thawed for 2 h inside the sealed cup at room temperature, and the cup was then placed in a Decagon SC-10 thermocouple psychrometer connected to a NT-3 nanovoltmeter (Decagon Devices, Pullman, Wash.). Voltage readings were taken after a minimum 2-h temperature equilibration. Voltage (μV) was converted to MPa by the use of a regression of voltage against a series of KC1 standards of known

Ψ_p . The leaf Ψ_p was calculated as the difference between Ψ and Ψ_{π} , or $\Psi_p = \Psi - \Psi_{\pi}$.

The two remaining leaflets from each sampled leaf, one of which had been weighed, were floated on distilled deionized water for 12 h in a covered petri dish at ambient laboratory temperature. They were then blotted dry and one was used for the measurement of Ψ_{π}^{100} in the same way as for Ψ_p . For determination of RWC, the remaining leaflet was reweighed to get turgid weight (TW), then oven-dried for 16 h at 80°C . RWC was calculated as follows: $\text{RWC} = ((\text{FW} - \text{DW}) \div (\text{TW} - \text{DW})) \times 100$, where FW was initial fresh weight and DW was the oven-dry weight (Turner, 1988).

Rapid stress induction and recovery. Four single-plant replicates of each species and treatment at each sampling date were used. Starting on day 0, the final watering date, the most recent fully mature leaf of each plant was sampled on each of four dates until incipient wilting. Sampling intervals of 2 days started on day 3 for FC plants and were daily starting on day 2 for FV plants. Stressed plants were watered for a recovery period equal to half the length of the wilting cycle for each species, then sampled. The experiment was conducted in May 1989.

Characterization of leaf Ψ isotherms. From both control and stressed plants of each species, following an experiment as described above, a recently matured leaf was sampled from 14 to 18 individual plants at incipient wilting. Intact leaves were floated on distilled deionized water to achieve full turgor as for the measurement of RWC. After being blotted dry, the leaves were placed on a laboratory bench to undergo desiccation at ambient temperature ($23 \pm 2^\circ\text{C}$) and light intensity ($10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). During desiccation, Ψ , Ψ_p , and RWC were determined on randomly selected leaves as described previously. From these data, plots of Ψ , Ψ_p , and Ψ_{π} against RWC as well as plots of Ψ_p and Ψ_{π} against Ψ were made as described by Jones and Turner (1978).

Poststress diurnal phase. Plants of each selection were stressed once as described above. One recently matured leaf was removed from each of four single-plant replicates for each selection and treatment at each sampling time. Thirty-six hours after re-watering, starting at 0000 HR, light intensity, Ψ , Ψ_p , and RWC were measured at 2-h intervals. The experiment was conducted in May 1989.

Slow stress induction. Two runner plants of each selection were rooted opposite one another in the same container (15 l, 27 cm diameter) containing washed sand (U.S. Sand, Ottawa, Ill.). There were six replicate pots at each sampling date. After 50 days, starting 15 Sept. 1989, water was withheld from the plants. The date of incipient wilting was recorded for each plant. Starting at day 73, 23 days after withholding water, one fully mature leaf per plant was sampled at 1000 HR at 4- to 8-day intervals to measure leaf Ψ and Ψ_{π}^{100} . Leaves were sampled from each plant until the final plant in each pot reached wilting. The mean value of leaf Ψ and Ψ_{π}^{100} from the pair of plants of each species in each pot was recorded as the response.

All treatments within each experiment were randomly arranged on a greenhouse bench under ambient conditions. Significant differences between control and stress plant means were determined by *t* test. Linear or quadratic functions were fitted to isotherm data if the relationship was significant ($P > 0.05$).

Results

Rapid stress induction and recovery. At least 50% of stressed FV plants exhibited incipient wilting 3 days after withholding of water, while those of FC wilted on day 9. For FC, leaf Ψ of stressed plants did not differ from control plants during the first 4 days after watering ceased (Fig. 1A). By day 7, leaf 4 was 0.29 MPa below

Fig. 1. Leaf Ψ (A,B), Ψ_{π} (C,D), and Ψ_{π}^{100} (E,F) of control and stressed *F. chiloensis* (A,C,E) and *F. virginiana* (B,D,F) plants during and after drought stress. Plants were re-watered starting the day indicated by the arrow. Each data point represents the mean of four measurements. Bars indicate the SE of the mean and are not shown if they are smaller than the symbols. An asterisk (*) indicates a significant difference between control and stressed plant means by *t* test at $P \leq 0.05$.

controls and decreased to -2.23 MPa, 1.56 MPa below controls, when plants started to wilt. The leaf Ψ of the FV selection declined to -1.69 MPa, 1.1 MPa below controls, on day 3 when stressed plants started to wilt (Fig. 1B). Leaf Ψ returned to control levels during recovery for both species. In FC, leaf Ψ_{π} of stressed plants was consistently below controls after 3 days of stress and through recovery (Fig. 1C). In FV, the Ψ_{π} of stressed plants did not differ from control plants at incipient wilting and through recovery (Fig. 1D). In FC, leaf Ψ_{π}^{100} was 0.19 MPa below the control value before wilting (Fig. 1E). The Ψ_{π}^{100} at incipient wilting was 0.42 MPa lower than controls. After recovery, leaf Ψ_{π}^{100} returned to control levels. For stressed FV plants, however, leaf Ψ_{π}^{100} was higher than controls 1 day before wilting, but was 0.2 MPa lower than controls after the recovery period (Fig. 1F).

Leaf Ψ isotherms. The relationships of leaf Ψ_{π} and Ψ_p with RWC for the FC selection were altered by a prior drought stress, while leaf Ψ was not (Fig. 2 A, C, and E). As leaf water content declined, leaf Ψ_p was higher and leaf Ψ_{π} was lower in the stressed than in control plants. For example, at 30% water loss, or a RWC of 70%, estimates of leaf Ψ , Ψ_{π} , and Ψ_p were -2.19, -1.63, and -0.52 MPa, respectively, for control plants, whereas they were -1.76, -2.55, and 0.16 MPa, respectively, for stressed plants of FC. At a Ψ_p of zero, RWC was 84% and 60% for control and stressed plants, respectively. The relationships of leaf Ψ , Ψ_{π} , and Ψ_p with RWC for FV were not altered appreciably by stress (Fig. 2 B, D, and F). Stressed FV plants wilted at a leaf Ψ of -1.65 MPa and a RWC of 82%.

The relationships of leaf Ψ_{π} and Ψ_p with Ψ in FC were also altered by prior stress (Fig. 3 A and C). Leaf Ψ_p reached zero when the leaf Ψ was -1.4 and -2.8 MPa for control and stressed plants, respectively. These relationships were not appreciably altered in the FV selection (Fig. 3 B and D).

Fig. 2. Relationships of leaf Ψ (A,B), Ψ_{π} (C,D), and Ψ_p (E,F) with leaf RWC for control and stressed *F. chiloensis* (A,C,E) and *F. virginiana* (B,D,F) plants after drought stress. Measurements were made on 14 to 18 leaflets from separate plants during desiccation after the leaflets were rehydrated to full turgor. Each data point represents one measurement or a single leaf.

Poststress diurnal phase. The leaf Ψ of stressed FC plants was generally lower than controls over the diurnal period (Fig. 4A). During the dark period, leaf Ψ of stressed FC plants averaged -0.4 MPa, ≈ 0.2 MPa below that of controls. By 1000 hr it had dropped sharply, to a low of -1.37 MPa, 0.74 MPa below that of the controls, which had also declined from predawn values. Leaf Ψ remained below -1.0 MPa through 1600 hr until increasing to -0.7 MPa by 1800 hr. For FV, leaf Ψ showed similar diurnal variation, but values for stressed plants were lower than those of control plants at 1200 hr only (Fig. 4B).

Leaf Ψ_{π} of stressed plants of both species was consistently lower

Fig. 3. Relationships of leaf Ψ_p (A,B) and Ψ_{π} (C,D) with leaf Ψ for *F. chiloensis* (A,C) and *F. virginiana* (B,D) plants following drought stress. Measurements were made on 14 to 18 leaflets from separate plants during desiccation after the leaflets were rehydrated to full turgor. Each data point represents one measurement or a single leaf at a RWC.

Fig. 4. Diurnal changes in leaf Ψ (A,B), Ψ_{π} (C,D), Ψ_p (E,F), and RWC (G,H) of control and previously stressed *F. chiloensis* (A,C,E,G) and *F. virginiana* (B,D,F,H) plants. Measurements were made 36 h after the stressed plants were re-watered. Each data point represents the mean of four single plant replicates. Bars indicate the SE of the mean and are not shown if they are smaller than the symbols. An asterisk (*) indicates a significant difference between control and stressed plant means by t test at $P \leq 0.05$.

than that of controls, but the magnitude of the difference was consistently greater for FC than for FV (Fig. 4 C and D). The mean leaf Ψ_{π} of stressed FC plants was 0.4 MPa below the control mean, with a maximum difference of 0.47 MPa at 1200 HR and a minimum difference of 0.28 MPa at 2000 HR. For FV, the mean difference in leaf Ψ_{π} between the control and stressed plants was 0.19 MPa with a maximum difference of 0.31 MPa at 1600 HR and a minimum difference of 0.09 MPa at 1400 HR. The mean predawn leaf Ψ_p of stressed plants, between 0000 and 0630 HR, was 0.38 and 0.17 MPa lower than that of control plants for the FC and FV selections, respectively.

The pattern of diurnal change in leaf Ψ_p of control and stressed plants of both species was similar to that for leaf Ψ (Fig. 4 E and F). For the FC selection, the mean predawn leaf Ψ_p of stressed plants, between 0000 and 0630 HR, was 0.21 MPa higher than that of controls. From 0800 through 1600 HR, the leaf Ψ_p of stressed plants fell below that of controls, ranging from 0.54 to 0.85 MPa for stressed plants, and from 0.82 to 1.01 MPa for controls. The lowest value, 0.54 MPa, occurred at 1000 HR, when leaf Ψ was at its lowest. For FV, the mean predawn leaf Ψ_p of stressed plants was 0.15 MPa higher than that of controls. The minimum leaf Ψ_p was 0.67 MPa for stressed and 0.49 MPa for control plants, occurring at 1400 and 1600 HR, respectively.

There was diurnal variation in leaf RWC of both species (Fig. 4 G and H). During the dark period, leaf RWC was $>90\%$ for control and stressed plants of both species. During the day, leaf RWC reached its lowest levels. The leaf RWC of the stressed FC plants averaged 5% lower than that of control plants throughout the 24-h period. For FV, the diurnal fluctuation of leaf RWC was similar to that of FC, but there was no difference between control and stressed plants, nor were the leaf RWC's of stressed FV plants as low as those for the FC selection.

Slow stress induction. When grown and stressed in the same pot, the mean time to incipient wilting was 31 ± 2 and 35 ± 2 days for the FV and FC selections, respectively. No difference in the rate of leaf Ψ decline was observed between the selections (Fig. 5A). Foliar Ψ_{π}^{100} was similar until 37 days after withholding water, when it was ≈ 0.35 MPa lower in FC than FV (Fig. 5B). The isothermal relationship between leaf Ψ_{π}^{100} and Ψ showed that the Ψ_{π}^{100} of FC was ≈ 0.25 MPa lower than that of FV, when leaf Ψ was lower than -1.5 MPa (Fig. 6).

Discussion

The diurnal phase measurements showed that between 1000 and 1200 HR, leaf Ψ_{π} was lower for stressed than for control plants of both species (Fig. 4). Differences between control and stressed plants at midday were greater than predawn differences, in contrast to results of a study of the *Fragaria* $\times$ *ananassa* Duch. cultivar Olympus (Renquist et al., 1982c). Leaf Ψ_{π} at midday likely reflected both diurnal and stress-induced osmotic adjustment (Jones

Fig. 5. Leaf Ψ (A) and leaf Ψ_{π}^{100} (B) of *F. chiloensis* and *F. virginiana* under slowly induced water deficit stress. Two plants each of both species were grown in the same pot. Water was withheld from the plants 50 days after rooting, and measurements of leaf Ψ and Ψ_{π}^{100} started 23 days after withholding water. Each data point is the mean of six single plant replicates SE.

Fig. 6. Relationship between leaf ψ_{π}^{100} and ψ of *F. chiloensis* and *F. virginiana* under slowly induced water deficit stress. Two plants each of both species were grown in the same pot. Water was withheld from the plants 50 days after rooting, and measurements of leaf ψ and ψ_{π}^{100} started 23 days after withholding water began. An asterisk (*) indicates that the correlation between leaf ψ and ψ_{π}^{100} is significant at $P \leq 0.05\%$, t test. Each data point represents the mean value for both plants of a species in a pot and six replicate pots.

et al., 1985). Since the stressed plants exhibited lower leaf ψ_{π} regardless of the sampling time, and control and stress plants exhibited similar patterns of change, a diurnal ψ_{π} adjustment of 0.5 MPa in the FC selection and 0.2 MPa in FV selection was observed.

The water relations data in this study provided evidence for greater foliar osmotic adjustment in the FC selection 'BSP14' than in the FV selection 'NCC85-13V' in response to water deficit stress. The lower predawn leaf ψ_{π} in stressed than in control plants 36 h after re-watering following wilting (Fig. 4 C and D), and the reduction of leaf ψ_{π}^{100} by rapidly or slowly induced stress (Fig. 1 E and F; Fig. 5), demonstrated greater osmotic adjustment in FC. The isothermal relationships of ψ_{π} with leaf RWC and ψ , useful in determining leaf water relations components as stress progressively increases, showed that at a given leaf RWC or ψ , ψ_{π} and ψ_{π}^{100} were lower in stressed than in control plants, and the difference in ψ_{π} was much greater in FC than in FV (Fig. 2 C and D; Fig. 3 C and D; Fig. 6). The maintenance of turgor in stressed FC plants resulted, at least in part, from this net lowering of leaf ψ_{π} , i.e., osmotic adjustment, similar to that reported for many species (Hsiao, 1973; Jones and Turner, 1980; Morgan, 1984; Turner and Jones, 1980). These results confirmed conclusions from previous studies reporting osmotic adjustment of cultivated and wild strawberry based on a decline of leaf ψ_{π} (O'Neill, 1983; Renquist et al., 1982c). The greater degree of osmotic adjustment that occurred in FC in response to water deficits may be a primary mechanism by which FC was characterized as more drought-resistant than FV (Darrow and Dewey, 1934).

The magnitude of osmotic adjustment is often measured as the change in osmotic potential at full turgor (Turner and Jones, 1980). Under rapidly induced water stress, the FC selection showed osmotic adjustment of 0.42 MPa, but the FV selection did not adjust (Fig. 1 E and F). When water deficits were slowly imposed on both species at the same rate, both species exhibited osmotic adjustment, but the magnitude was ≈ 0.35 MPa greater in FC than in FV (Fig. 5B). The maximum osmotic adjustment in FC leaves was 0.19 MPa, as observed in the diurnal phase (Fig. 1 D). Repeated stresses on FV resulted in no greater osmotic adjustment (Archbold and Zhang, 1991; Zhang and Archbold, 1992). The adjustment in FC leaves ranged from 0.20 to 0.42 MPa (Fig. 1E; Fig. 5B), similar to other species (Bitman and Simpson, 1989; Johnson et al., 1984;

Morgan, 1984; Turner et al., 1987). The degree of osmotic adjustment, measured by thermocouple psychrometry in this study, was likely underestimated because dilution of symplastic solution with apoplastic water occurred during the freeze-thaw process (Jones and Turner, 1978; Turner, 1988). Thus, both selections could have had a somewhat greater osmotic adjustment than reported.

The magnitude of leaf osmotic adjustment in the FV selection used by O'Neill (1983) was 0.5 MPa or greater, much greater than reported here. This difference is substantial but may be due to several causes. In the prior report (O'Neill, 1983), the plants had been grown in the field and transplanted into containers in the greenhouse before the treatments started, whereas in our study, the plants were maintained in the greenhouse continuously. Renquist et al. (1982c) reported that field-grown 'Olympus' strawberry demonstrated osmotic adjustment in the field, but not when container-grown in a growth chamber. Another cause for the disparity may be that the selection used in our study responded differently from that used by O'Neill (1983). The selection used in the prior study may have been very drought resistant. Variation in the degree of osmotic adjustment among cultivars or selections within a species has been observed with *Fragaria* species (Archbold, unpublished data) as well as with other species (During, 1985; Morgan, 1977; Morgan, 1983; Turner et al., 1987; Wright et al., 1983). Experimental conditions may also influence the degree of osmotic adjustment. In our studies, the magnitude of osmotic adjustment in different experiments varied for both selections because the experiments were conducted under varying light and temperature conditions. Preliminary attempts at pressure-volume analyses, the technique used by O'Neill, caused unreliable estimates of ψ_{π}^{100} due to crushing of the petiole. Similar problems have also been encountered with lupins (*Lupinus* spp. L.) (Turner, 1988; Turner et al., 1987). O'Neill's (1983) results, obtained using pressure-volume curves, therefore, may have been similarly affected, since petiole examination was not reported. The methodology used to estimate ψ_{π}^{100} in the two studies, pressure-volume analysis vs. psychrometry following rehydration, may also contribute to the contrasting results. The degree of osmotic adjustment reported by O'Neill, up to 0.9 MPa, appears excessive in view of the values reported for other species (Turner and Jones, 1980).

During a rapidly induced drought stress, plants of FV wilted at a leaf ψ 1.10 MPa and ψ_{π} 0.7 MPa higher than did those of FC (Fig. 1 A and B). This difference indicated that the FC selection tolerated a lower leaf ψ , i.e., greater water stress, than the FV selection before wilting. The lower leaf ψ at incipient wilting likely resulted from the higher degree of leaf osmotic adjustment in the FC selection than the FV selection. Determining the leaf ψ and ψ_{π} at which photosynthesis is affected in stressed plants of selections of the two species may be valuable information. Before incipient wilting, photosynthesis was impaired in *F. ×ananassa* plants as water deficit stress increased (Sruamsiri and Lenz, 1986). Another characteristic indicating the superior drought resistance of the FC selection was the leaf RWC at zero turgor from the isothermal relationships (Fig. 2 E and F). Plants of FV started to wilt at a mean leaf RWC 13% higher than those of FC, suggesting that FC could tolerate more cellular water loss than the FV plants (Fig. 2 E and F). These RWC values do not take into account possible differences in water partitioning between symplastic and apoplastic compartments.

The rate of stress induction differed in the experiments when the plants were grown in separate containers, and was more rapid for FV than for FC. This difference may affect the ability of plants to osmotically adjust (Jones and Rawson, 1979; Morgan, 1984). However, when the FC and FV selections were grown and stressed

in the same pot, the FV plants wilted ≈ 4 days earlier than the FC plants. This difference indicated that FV lost turgor earlier than FC, even though they were exposed to the same soil water status. Thus, the rate of stress imposition had no effect on the ability of FV to respond. The inability to adequately osmotically adjust hindered FV from remaining turgid as long as FC. Evidence for net solute accumulation in stressed plants of these two species has been obtained (Zhang and Archbold, 1992). Kim and Lee-Stadelmann (1984) stated that the plant cell has two major mechanisms for avoiding water stress damage: 1) osmotic adjustment, and 2) a high cell wall elasticity. Both mechanisms will eventually have the same effect, i.e., avoidance of mechanical stress on the protoplasm layer and, especially, the cell membrane. The FC selection used in this study, which was more drought resistant than FV, exhibited at least one of these mechanisms, superior osmotic adjustment, while the FV selection had a negligible ability to respond in kind. The work of Darrow and Dewey (1934) reporting species differences in drought stress resistance may have been derived from comparison of selections similar to those in this study. Since these and other native *Fragaria* selections are being used in breeding and cultivar development programs, identifying and characterizing selections with superior drought resistance traits may provide a basis to develop drought resistant cultivars.

Literature Cited

- Archbold, D.D. and B. Zhang. 1991. Drought stress resistance in *Fragaria* species, p. 138-144. In: A. Dale and J.J. Luby(eds.). The Strawberry into the 21st Century. Timber Press, Portland, Ore.
- Barlow, E.W.R. 1986. Water relations of expanding leaves, p. 45-58. In: N.C. Turner and J.B. Passioura (eds.). Plant growth, drought and salinity. CSIRO, Melbourne, Australia.
- Bitman, S. and G.M. Simpson. 1989. Drought effects on water relations of three cultivated grasses. *Crop Sci.* 29:992-999.
- Chandler, C.K. and D.C. Ferree. 1990. Response of 'Raritan' and 'Surecrop' strawberry plants to drought stress. *Fruit Var. J.* 44:183-185.
- Darrow, G.M. 1966. The Strawberry: History, breeding, and physiology. Holt, Rinehart, and Winston, New York.
- Darrow, G.M. and G.W. Dewey. 1934. Studies on the stomata of strawberry varieties and species. *Proc. Amer. Soc. Hort. Sci.* 32:440-447.
- During, H. 1985. Osmotic adjustment in grapevines. *Acta Hort.* 171:315-322.
- Dwyer, L.M., D.W. Stewart, L. Houwing, and D. Balchin. 1987. Response of strawberries to irrigation scheduling. *HortScience* 22:42-44.
- Elston, J., A.J. Karamanos, A.H. Kassam, and R.M. Wadworth. 1976. The water relations of the field bean crop. *Phil. Trans. Royal Soc. London Ser. B.* 273:581-591.
- Farquhar, G.D. and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis. *Annu. Rev. Plant Physiol.* 33:317-345.
- Gehrmann, A. 1985. Growth, yield, and fruit quality of strawberries as affected by water supply. *Acta Hort.* 171:463-469.
- Hsiao, T.C. 1973. Plant responses to water stress. *Annu. Rev. Plant Physiol.* 24:519-570.
- Hsiao, T.C., F. Acevedo, E. Fereres, and D.W. Henderson. 1976. Stress metabolism, water stress, growth, and osmotic adjustment. *Phil. Trans. Royal Soc. London Ser. B.* 273:479-500.
- Johnson, R.C., H.T. Nguyen, and L.I. Croy. 1984. Osmotic adjustment and solute accumulation in two wheat genotypes differing in drought resistance. *Crop Sci.* 24:957-962.
- Jones, H.G., A.N. Lakso, and J.P. Syvertsen. 1985. Physiological control of water status in temperate and subtropical fruit trees. *Hort. Rev.* 7:301-344.
- Jones, M.M. and H.M. Rawson. 1979. Influence of rate of development of leaf water deficits upon photosynthesis, leaf g, water use efficiency, and osmotic potential in sorghum. *Physiol. Plant.* 45: 103-111.
- Jones, M.M. and N.C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. *Plant Physiol.* 61:122-126.
- Kim, J.H. and O.Y. Lee-Stadelmann. 1984. Water relations and cell elasticity quantities in *Phaseolus vulgaris* leaves. *J. Expt. Bot.* 35:841-858.
- Kramer, P.J. 1983. Water deficits and plant growth, p. 342-415. In: P.J. Kramer (ed.). Water Relations of Plants. Academic Press, New York.
- Ludlow, M.M. and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. *Adv. Agron.* 43:107-153.
- Mazhorov, E.V. 1978. Comparative drought resistance of strawberry from different ecologico-geographical zones. *Vses. Ordena Linina Inst. Rastenievodstva imeni N.I. Vavrilova.* 86:18-21. (*Hort. Abstr.* 1980. 50:425)
- Morgan, J.M. 1977. Differences in osmoregulation between wheat genotypes. *Nature* 270:235.
- Morgan, J.M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agr. Res.* 34:637-651.
- Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. *Annu. Rev. Plant Physiol.* 35:299-319.
- O'Neill, S.D. 1983. Role of osmotic potential gradients during water stress and leaf senescence in *Fragaria virginiana*. *Plant Physiol.* 72:931-937.
- Renquist, A.R., P.J. Breen, and L.W. Martin. 1982a. Vegetative growth response of 'Olympus' strawberry to polyethylene mulch and drip irrigation regimes. *J. Amer. Soc. Hort. Sci.* 107:369-372.
- Renquist, A.R., P.J. Breen, and L.W. Martin. 1982b. Effect of polyethylene mulch and summer irrigation regimes on subsequent flowering and fruiting of 'Olympus' strawberry. *J. Amer. Soc. Hort. Sci.* 107:373-376.
- Renquist, A.R., P.J. Breen, and L.W. Martin. 1982c. Influence of water status and temperature on leaf elongation in strawberry. *Scientia. Hort.* 18:77-85.
- Sruamsiri, P. and F. Lenz. 1986. Photosynthesis and stomatal behaviour of strawberries. IV. Effects of water deficiency. *Gartenbau.* 51:84-92.
- Turner, N.C. 1986. Crop water deficits: A decade of progress. *Adv. Agron.* 39:1-51.
- Turner, N.C. 1988. Measurement of plant water status by the pressure chamber technique. *Irr. Sci.* 9:289-308.
- Turner, N.C. and M.M. Jones. 1980. Turgor maintenance by osmotic adjustment: A review and evaluation, p. 155-172. In: N.C. Turner and P.J. Kramer (eds.). Adaptation of plants to water and higher temperature stress. Wiley-Interscience, New York.
- Turner, N.C., W.R. Stem, and P. Evans. 1987. Water relations and osmotic adjustment of leaves and roots of lupins in response to water deficits. *Crop Sci.* 27:977-983.
- Wright, S.T.C., R.C.G. Smith, and J.M. Morgan. 1983. Differences between the grain sorghum genotypes in adaptation to drought stress. III. Physiological responses. *Aust. J. Agr. Res.* 34:637-651.
- Zhang, B. and D.D. Archbold. 1992. Solute accumulation in leaves of *Fragaria chiloensis* and *F. virginiana* responds to water deficit stress. *J. Amer. Soc. Hort. Sci.* 118:280-285.