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Physiological Responses of Carambola Trees to Soil Water Depletion

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***Abstract*. Two-year-old 'Arkin' carambola (*Averrhoa carambola* L.) trees were grown in containers in a greenhouse and the field in a very gravelly loam soil. Trees in the field were subjected to four soil water depletion (SWD) levels which averaged, 10.5%, 26.5%, 41.0%, and 55.5% and trees in the greenhouse were maintained at field capacity or dried continuously to produce a range of SWD levels. The relationships between SWD and leaf (Ψ_L) and stem (Ψ_s) water potential, net CO_2 assimilation (A_{CO_2}), stomatal conductance of water (g_s) and transpiration (E) were determined. Coefficients of determination values between physiological variables were higher for trees in the greenhouse than in the field, which may have been due to greater fluctuations in vapor pressure deficit (VPD) in the field. Soil water depletion levels above 50% caused a reduction in Ψ_s that subsequently decreased g_s. This reduction in Ψ_s was correlated with a linear reduction in E and a considerable decline in A_{CO_2} when g_s fell below about 50 mmol·m^{-2}·s^{-1}. Leaf gas exchange parameters were better correlated with Ψ_s than with SWD level. Therefore, Ψ_s may be a better predictor of carambola tree water status than SWD in a well-drained, very gravelly loam soil.**

Carambola (*Averrhoa carambola* L.), a tropical fruit tree native to southeastern Asia, responds to water deficits by the 'avoidance' strategy (Neuhaus, 2003). This strategy involves minimizing water loss by stomatal control, leaf movement, reducing leaf area, and leaf abscission (Ludlow, 1998). The lethal leaf water potential (Ψ_L) level for carambola is about –2.9 MPa and the lethal leaf relative water content (RWC) is about 56% (Ismail et al., 1994). Carambola responses to soil water deficit can be divided into four phases (Neuhaus, 2003): 1) minimizing water loss by stomatal closure, initial osmotic adjustment, and leaflet movement from a horizontal to vertical orientation; 2) increasing root to shoot ratio via leaf and fruit abscission, and increasing proline levels for leaf osmotic adjustment; 3) reaching a stage of irreversible damage caused by chlorophyll degradation, root growth inhibition, and further leaf and fruit shedding; and 4) tree death. Rewatering the trees during phase 2 resulted in plant recovery within a few days (Salakpetch et al., 1990).

Leaf water potential of orchard and container-grown carambola trees decreased with increasing drought stress (Ismail and Noor, 1996; Ismail et al., 1994, 1996). Ismail et al. (1994) found a difference in Ψ_L of up to –2.2 MPa between stressed and well-watered carambola trees. Salakpetch et al. (1990) observed that Ψ_L of drought-stressed carambola trees (–2.0 MPa) returned to the prestress level (–0.6 MPa) upon rewatering. Net CO_2 assimilation of carambola also decreased with increased drought stress. Net CO_2 assimilation of 6-month-old, container-grown carambola trees was 3.13 µmol·m^{-2}·s^{-1} for nonstressed compared to 0.24 to 1.83 µmol·m^{-2}·s^{-1} for drought-stressed trees (Ismail et al., 1994). Net CO_2 assimilation decreased when Ψ_L fell below –0.80 MPa (Ismail et al., 1994; Razi et al., 1992). The decrease in A_{CO_2} was concomitant with reduced stomatal conductance.

In southern Florida, carambola trees are grown in a very gravelly loam soil classified in the Krome series. This soil has an alkaline pH (7.4 to 8.4), a very low water holding capacity (0.08 to 0.12 cm·cm^{-1} of soil) and a rapid permeability rate (1.5 to 5.1 cm·h^{-1}) (Li and Klassen, 2001). In orchards in southern Florida with Krome very gravelly loam soil, the shallow water table is only 1 to 2 m below the surface. Thus, due to capillary and lateral water movement through the soil it is difficult to maintain sustained periods of very low soil water content (Al-Yahyai et al., 2005). Little is known about the physiological responses of young carambola trees to drought stress in very gravelly loam soils. The first objective of this study was to compare the effect of varying soil water depletion levels on Ψ_L, Ψ_s and leaf gas exchange of carambola trees in a very gravelly loam soil in southern Florida growing in containers in a greenhouse and the field. The second objective was to determine relationships among the various gas exchange and water potential parameters.

Materials and Methods

Experimental site and plant material. Two-year-old 'Arkin' carambola trees grafted onto Golden Star rootstock were planted in 95-L containers in the field or a greenhouse. The containers were filled with Krome very gravelly loam soil (loamy-skeletal, carbonatic, hyperthermic, Lithic Udorthent, Nobel et al., 1996) that was excavated from a site next to a mature orchard. Fertilizer application and pest management followed standard practices for commercial carambola production in Florida (Crane, 1994).

Trees were irrigated using microsprinklers with a 360° wetting area (Maxijet, Dundee, Fla.) providing 89 L·h^{-1}. In field containers, trees were irrigated at various times and rates to provide a range of SWDs over the course of the experiments. The ranges were determined from a preliminary study (Al-Yahyai, unpublished data) and based on the SWD from soil field capacity (FC) to leaf yellowing, which was the first visual sign of drought stress. Containers were placed on metal bases above the ground to prevent capillary water movement from the shallow (1 to 2 m below the soil surface) water table.

Soil water measurements and treatments. Soil water depletion was determined by continuously measuring soil water content using multisensor capacitance probes (EnviroSCAN, Sentek PTY Ltd., Kent Town, Australia) placed 20 cm from the trunk. The sensors recorded soil water content every 30 min at depths of 10, 20, and 30 cm. The data were stored in a datalogger and later downloaded to a computer for analysis. Soil water content measurements from sensors placed at the three depths were summed, plotted and used to calculate SWD. Installation of the system in Krome soils was previously described by Al-Yahyai et al. (2003) and Núñez-Elisea et al. (2001), and technical multisensor capacitance probe specifications were described by Paltineanu and Starr (1997). Irrigation in the field was initiated when SWD averaged one of the following four levels: 10.5%, 26.5%, 41.0%, and 55.5%. Trees in containers in the greenhouse were divided into two treatments: 1) soil water was maintained at FC and 2) trees were not irrigated over the entire experiment to achieve high levels of SWD.

Leaf gas exchange and water potential measurements. Net CO_2 assimilation, stomatal conductance of water vapor (g_s), transpiration (E), Ψ_s, and Ψ_L were determined periodically for trees in the field on three mature leaves per tree and three trees per treatment between 1100 and 1400 HRS. Net CO_2 assimilation, g_s, E, Ψ_s, and Ψ_L for trees in the greenhouse were determined three times per week for 6 consecutive weeks from 18 Oct. to 2 Dec. 2002 as the SWD increased. Three mature leaves per tree were randomly selected for leaf gas exchange and water potential measurements from 1100 to 1400 HR. The number of leaves measured per tree and measurement time had been determined in preliminary experiments. Net CO_2 assimilation, E, and g_s were determined with a portable infrared gas analyzer (CIRAS II; PP Systems Ltd., Herts, U.K.). Measurements were made on the terminal leaflet (Carambola has a compound leaf.) of fully sunlit leaves at a photosynthetic photon

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flux (PPF) of 1000 $\mu mol\cdot m^{-2}\cdot s^{-1}$, which is above the saturation point for photosynthesis of carambola (Marler et al., 1994), and reference CO_2 of 375 $\mu mol\cdot mol^{-1}$ at a flow rate of 200 $mL\cdot min^{-1}$.

Leaf and stem water potentials were measured on the same leaves used for gas exchange measurements using a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, Calif.). Stem water potential was determined using a fully matured leaf enclosed in a reflective plastic bag for 1 h to suppress E and allow Ψ_s to equilibrate with Ψ_L (Begg and Turner, 1970; McCutchan and Shackel 1992; Shackel et al., 1997).

Experimental design and statistical analysis. Field containers were arranged in a completely randomized design with three individual tree replications per treatment. The greenhouse experiment was set up to measure different leaves on the same six trees over time as the SWD increased. Linear regression analysis was performed with SigmaPlot software (SYSTAT Software Inc., Richmond, Calif.) and nonlinear regression analysis was performed with TableCurve 2D software (SYSTAT Software Inc.).

Results and Discussion

Stem water potential of trees in containers in the greenhouse remained above –1.0 MPa as SWD increased from 0% to 58%, above which there was a gradual, nonlinear decrease in Ψ_s (Fig. 1a). A similar trend was observed in field trees with a gradual decline in Ψ_s when SWD reached about 44% (Fig. 1b). Similarly, Salakpetch et al. (1990) found that leaves of 2-year-old carambola trees in containers wilted when midday Ψ_L reached –2.0 MPa 10 d after withholding water. Leaf water potential returned to its original level (–0.6 MPa) 2 to 3 d after rewatering (Salakpetch et al., 1990). The ability of carambola trees to regulate their water potential levels was attributed to osmotic adjustment through increased levels of proline (Ismail et al., 1994) and a reduction in g_s (Ismail et al., 1994, 1996; Razi et al., 1992).

Stomatal conductance of container-grown carambola trees was more closely correlated with Ψ_s (Fig. 3a) than SWD (Fig. 2) in the greenhouse but not in the field (Fig. 3b). These findings are in agreement with studies that found Ψ_s to be a good indicator of drought stress of fruit trees and thus useful for irrigation management (Naor, 2000; Shackel et al., 1997; Stern et al., 1998).

A reduction in Ψ_s below about –1.0 MPa resulted in reduced g_s for trees in containers in the greenhouse (Fig. 3a) and in the field (Fig. 3b), although the critical point was not as clearly defined in the field as in the greenhouse. Similarly, Razi et al. (1992) reported a decline in g_s in carambola trees as a consequence of a decrease in Ψ_L. Differences between greenhouse and field trees in the response of physiological variables to SWD were possibly due to greater climatic variability in the field than in the greenhouse. For example, vapor pressure deficit was more variable in the field [coefficient of variation (CV) = 29%] than in

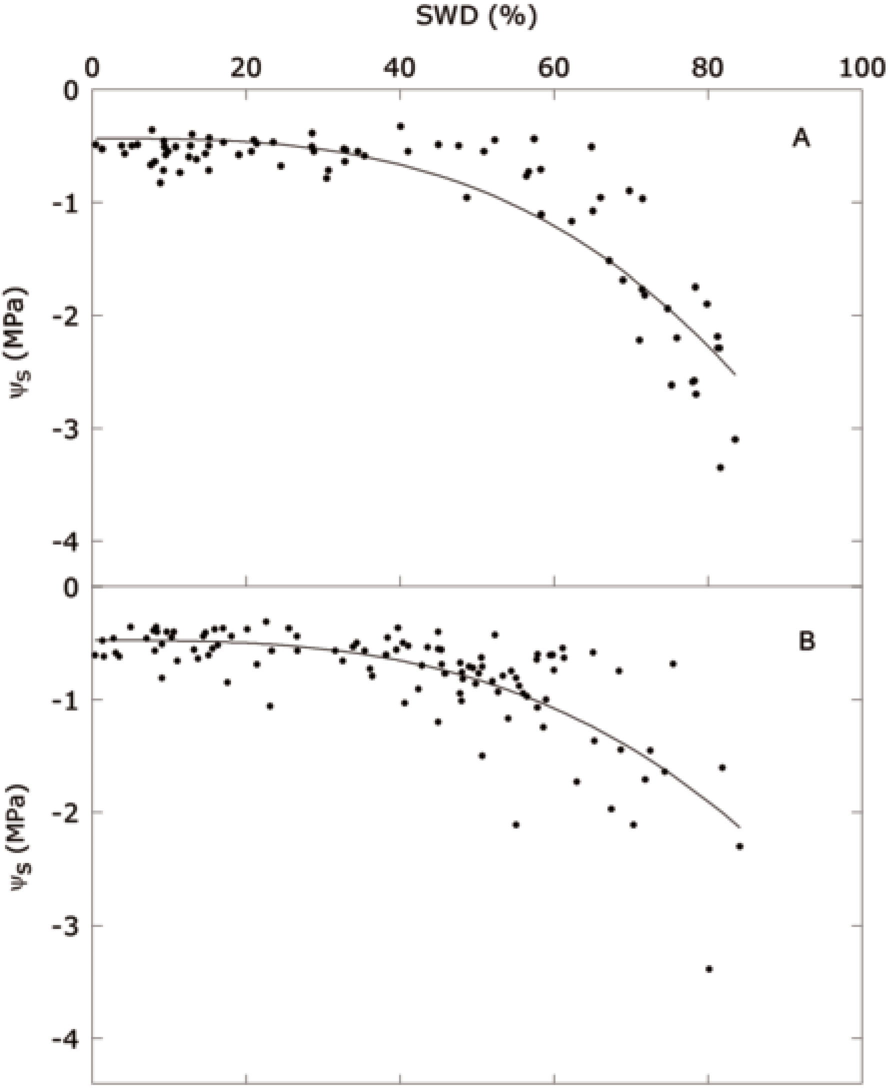

Fig. 1. Soil water depletion (SWD) and stem water potential (Ψ_s) of carambola trees in containers (**A**) in a greenhouse; $y = -0.44 - (3.59e^{-06})\, x^3$, $r^2 = 0.82$ and (**B**) in the field; $y = -0.48 - (2.79e^{-06})\, x^3$, $r^2 = 0.56$.

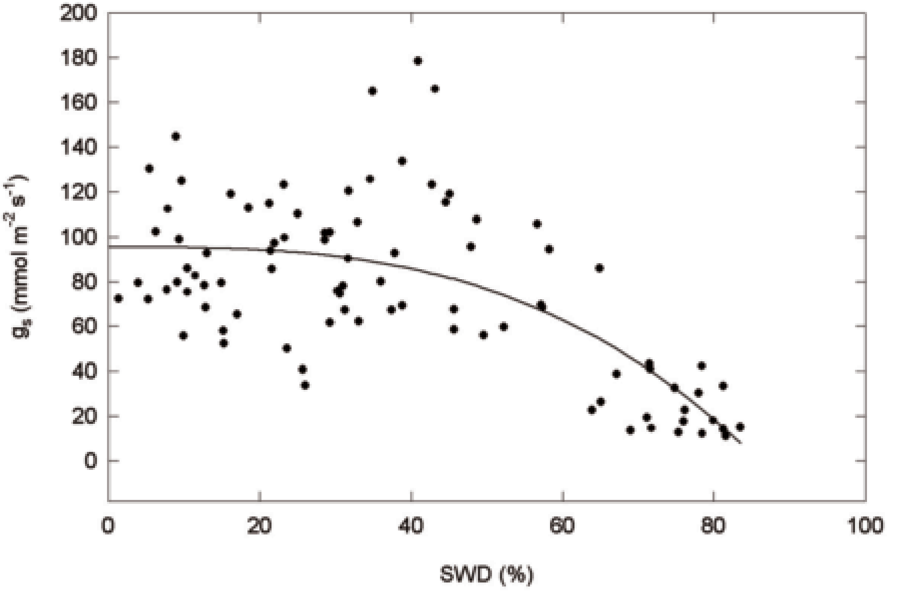

Fig. 2. Soil water depletion (SWD) and stomatal conductance to water vapor (g_s) of carambola trees in containers in a greenhouse; $y = 95.46 - 0.0002\, x^3$, $r^2 = 0.46$.

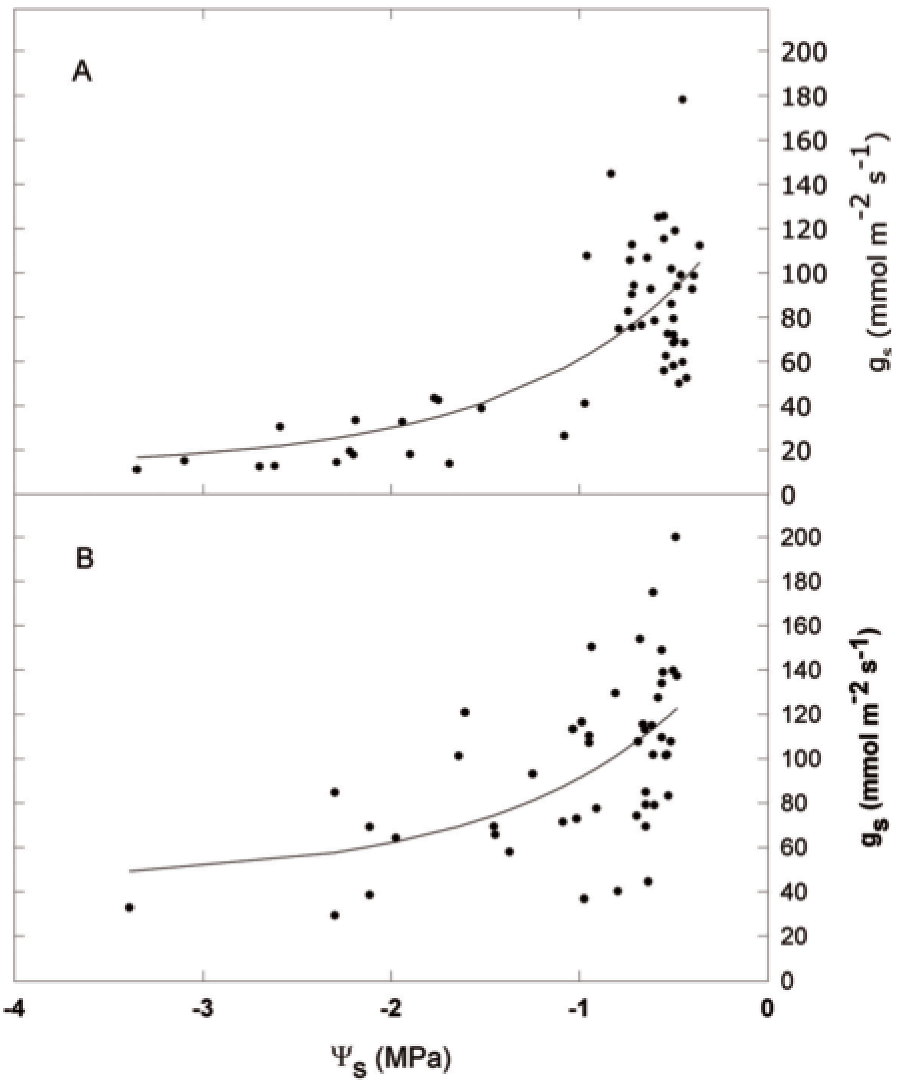

Fig. 3. Stem water potential (Ψ_s) and stomatal conductance to water vapor (g_s) of carambola trees in containers in an (**A**) greenhouse; $y = 11.88 + 132.94\ e^x$, $r^2 = 0.54$ and (**B**) the field; $y = 44.76 - 41.57/x$, $r^2 = 0.32$.

the greenhouse (CV = 17%) and VPD often has a significant effect on g_s.

Reductions in E were related to reductions in Ψ_s for carambola trees in the greenhouse (Fig. 4a) and in the field (Fig. 4b). This curvilinear response of carambola trees differs from previous results of Razi et al. (1992) who found a linear relationship between Ψ_L and E in carambola trees. This difference in response is possibly due to differences in soil properties in the two studies.

Net CO_2 assimilation decreased as Ψ_s declined below about –1.0 MPa in trees grown in containers in the greenhouse (Fig. 5a), but the critical value in the field was not clear from the data (Fig. 5b), and the r^2 value was quite low. At –2.0 MPa, A_{CO_2} approached zero and became negative at about –3.0 MPa. Similarly, Razi et al. (1992) observed that A_{CO_2} of carambola trees decreased when leaf water potential fell below –0.85 MPa. Maximum A_{CO_2} values in this study, about 10.0 µmol m^{-2}s^{-1}, especially for field trees were considerably greater than those reported by Ismail et al. (1994) of only 3.13 µmol m$^{-2}\cdot$s^{-1}. We assume that environmental factors were much different in the two studies.

The reduction in A_{CO_2} with decreasing Ψ_s was presumably due to a direct nonlinear effect of g_s for trees in the greenhouse (Fig. 6a) and in the field (Fig. 6b). Ismail et al. (1994) also reported that increased stomatal resistance in young carambola trees limited CO_2 uptake during drought stress. A reduction in A_{CO_2} for carambola trees in the greenhouse and the field in Krome soils occurred when g_s fell below about 50 mmol$\cdot$m$^{-2}\cdot$s^{-1}, although there was considerable variation in the data. We also constructed A_{CO_2}/Ci curves (data not shown) which were inconclusive for determining the relative contributions of stomatal and nonstomatal conductivities to net carbon assimilation.

The positive linear correlation between g_s and E (data not shown; $r^2 = 0.76$ and 0.75 in the greenhouse and field, respectively) suggests that partial stomatal closure was essential to conserve water by reducing E. This partial stomatal closure resulted in a gradual decline in A_{CO_2} as soil water was initially depleted.

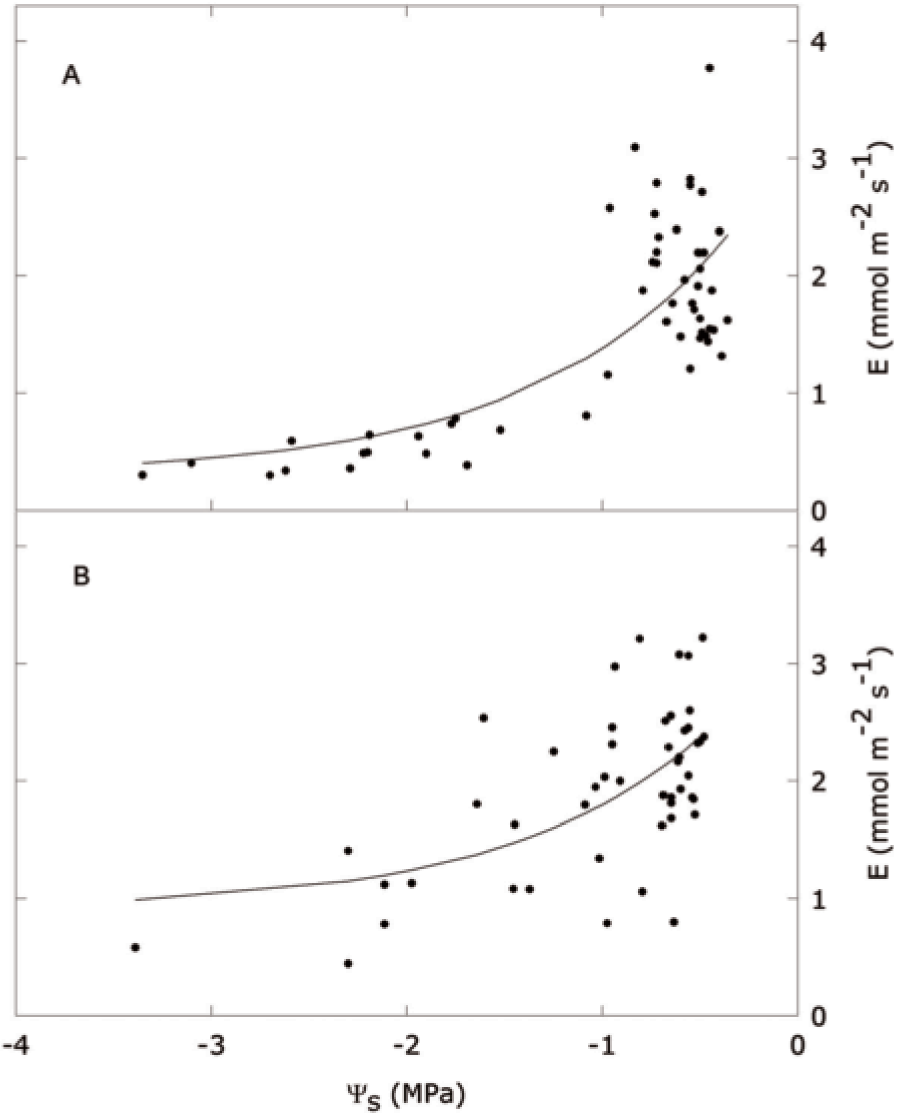

Fig. 4. Stem water potential (Ψ_s) and transpiration (E) of carambola trees in containers in an (**A**) greenhouse; y = 0.30 + 2.94 e^x, $r^2 = 0.55$ and (**B**) the field; y = 1.03 + 2.11 e^x, $r^2 = 0.28$).

However, as SWD increased and plant drought stress increased, a further decline in g_s (below 50 mmol·m^{-2}·s^{-1}) resulted in sharp decline in A_{CO_2}. This perhaps was an avoidance mechanism by carambola trees to conserve water by reducing E, while at the same time maintaining moderate A_{CO_2} levels during periods of occasional or short-term drought stress. A SWD <50% in Krome soils did not affect tree gas exchange.

It has been suggested that Ψ_L is a less reliable variable for making irrigation scheduling decisions for fruit trees than Ψ_s due to the inherent variability of Ψ_L under field conditions (Garnier and Berger, 1985; McCutchan and Shackel, 1992; Naor, 2000). Enclosing leaves in a reflective, dark plastic bag for 1 to 2 h before water potential measurements reduces E until an equilibrium is achieved between the Ψ_L and the Ψ_S (Begg and Turner, 1970), thus providing a more precise method of determining tree water status (Garnier and Berger, 1985; McCutchan and Shackel, 1992; Naor, 2000; Shackel et al., 1997). In this study, Ψ_L and Ψ_s from the same branch were measured within 2 min of each other to determine their relationship. There was a strong linear relationship between Ψ_L and Ψ_s for trees in the greenhouse ($r^2 = 0.97$ and in the field ($r^2 = 0.97$) and values were very similar suggesting that either method could be used to measure water potential of carambola leaves. However, Ψ_s may be better indicator of drought stress of carambola trees in Krome very gravelly loam soil than SWD as determined from measurements of soil water content.

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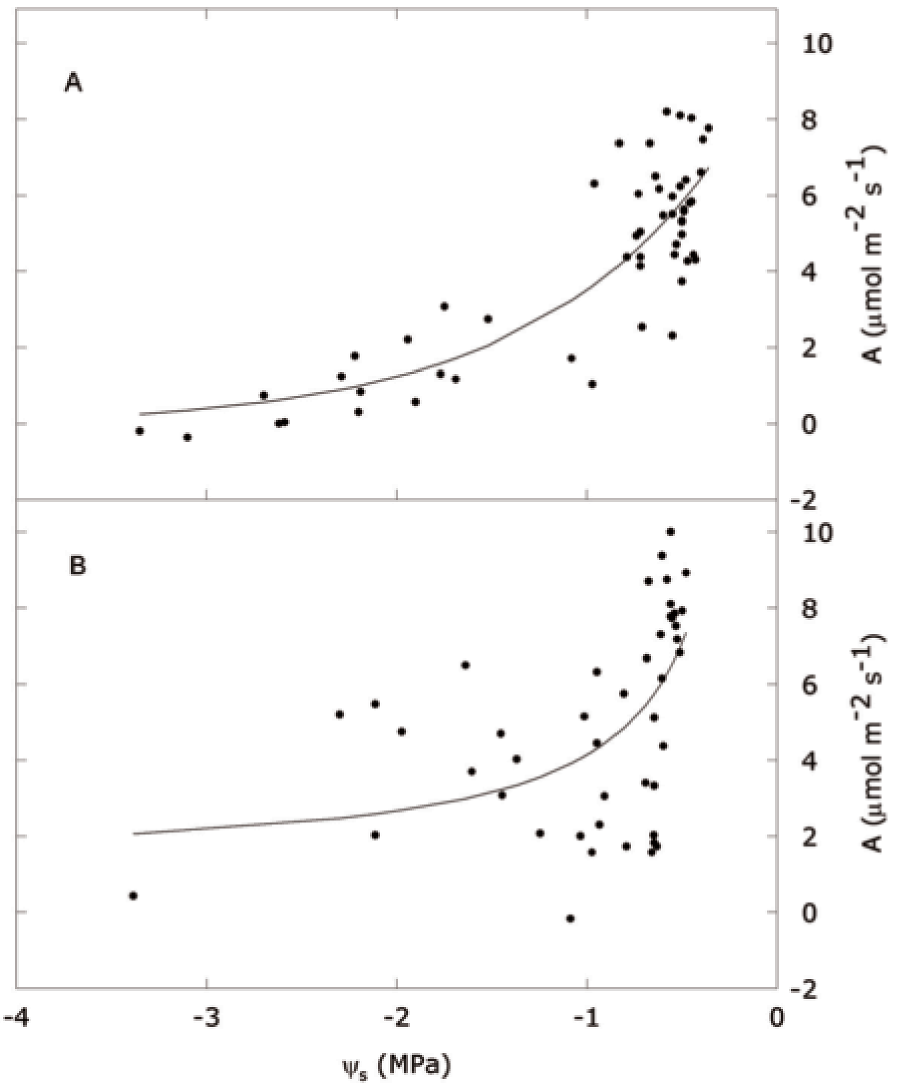

Fig. 5. Stem water potential (Ψ_s) and net CO_2 assimilation (A) of carambola trees in containers (**A**) in a greenhouse; $y = -0.09 + 9.76\ e^x$, $r^2 = 0.70$ and (**B**) in the field; $y = 1.19 - 2.95/x$, $r^2 = 0.31$).

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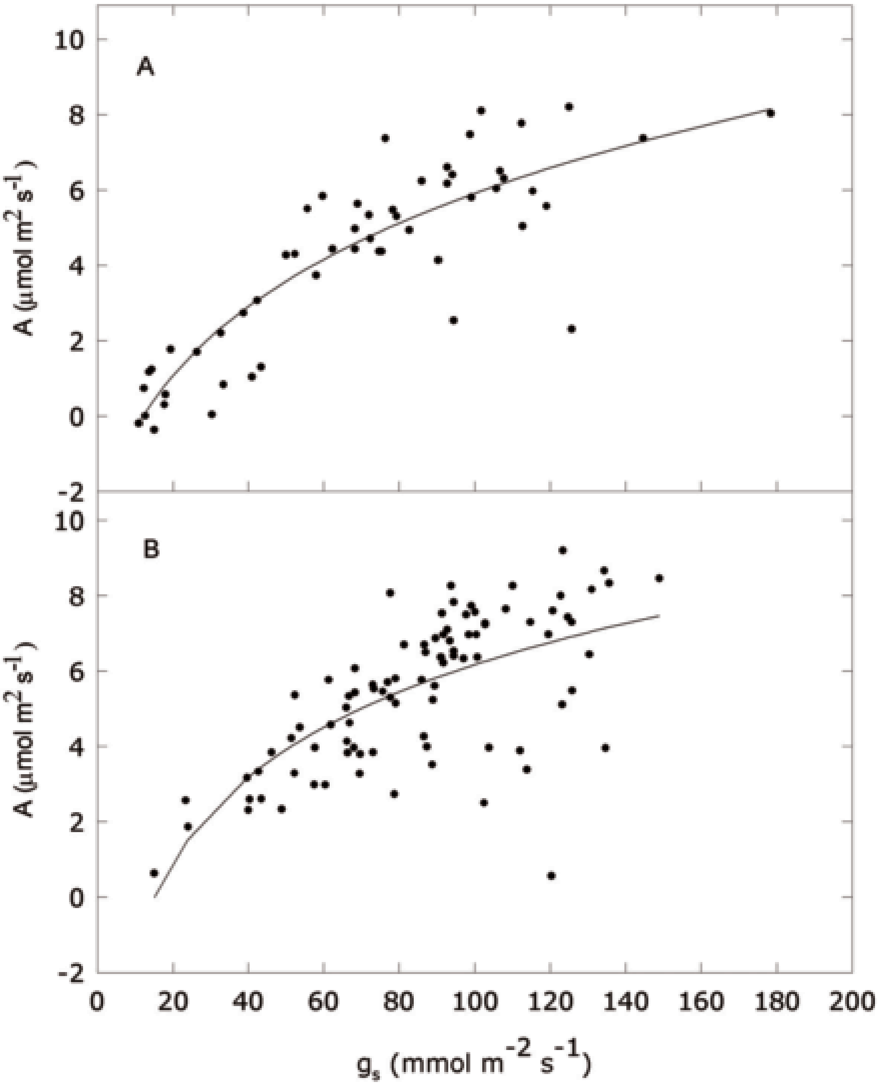

Fig. 6. Stomatal conductance (g_s) and net CO_2 assimilation (A) of carambola trees in containers (**A**) in a greenhouse; $y = -2.46 + 0.39 (\ln x)^2$, $r^2 = 0.75$ and (**B**) in the field; $y = -2.24 + 0.40 (\ln x)^2$, $r^2 = 0.45$.

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