

# Plant Growth, Water Relations, and Transpiration of Spiderplant [*Gynandropsis gynandra* (L.) Briq.] under Water-limited Conditions

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**ABSTRACT.** Plant growth and osmotic adjustment of spiderplant were investigated in a glasshouse and under field conditions. Two fast-growing genotypes (P-landrace and P-commercial) and a slow-growing landrace (G-landrace) were grown under soil water deficit and watered conditions. The fraction of transpirable soil water (FTSW) was used as an indicator of water availability in pots. In the greenhouse, transpiration was determined by changes in daily pot weights and the ratio of transpiration of plants in soil water deficit to watered treatments expressed as normalized transpiration ratio (NTR). Water use in the field experiment was determined by gravimetric methods. The fast-growing genotypes had a higher rate of soil drying due to a higher rate of leaf area development. They were also more sensitive to soil water deficit with NTR beginning to decline at FTSW of 0.55–0.77 as compared to 0.29 for the slow-growing landrace. Also, the fast growing genotypes had FTSW thresholds for the stem elongation rate of 0.35–0.55 as compared to 0.20 for the slow growing landrace. The rate of leaf development declined when 40% to 60% of available water in the soil was removed, regardless of genotype. Leaf area of plants under field conditions decreased when the soil moisture was <60% field capacity. Under severe soil water deficit stress in pots, plants partitioned more biomass to roots than above ground; however, biomass partitioning between leaves and stems was not influenced by soil water deficit. Spiderplant showed limited osmotic adjustment (OA) in the range of 0.10–0.33 MPa at the highest soil water deficit (FTSW = 0). Thus, spiderplant is mainly a drought avoiding species. To achieve maximum growth, it is necessary to keep FTSW above 0.6.

Spiderplant is an important traditional leafy vegetable crop grown and consumed in Kenya and most parts of Africa (Chweya and Eyzaguirre, 1999; Schippers, 2000). There is a lack of information concerning the adaptive responses of spiderplant to drought, but there are views that spiderplant is intolerant to water stress (Waithaka and Chweya, 1991).

Drought causes reductions of leaf area, dry matter production, decline in plant water status and transpiration. Reduced leaf area is a drought avoidance mechanism, aimed at reducing plant water consumption and hence conserving water during periods of drought (Jones, 1992). It is achieved through inhibition of leaf expansion and initiation, reduced branching and plant height as well as accelerated leaf senescence (Belaygue et al., 1996; Pic et al., 2002). Reduced leaf area decreases interception of solar radiation and consequently decreases biomass production for most crops (Delfine et al., 2000; Nam et al., 1998). Water deficits also influence dry matter partitioning in plants (Jones, 1992), including increasing ratios of root to shoot dry matter (Li et al., 1994).

One plant response to declining water potential is osmotic adjustment (OA), the accumulation of solutes within cells to maintain turgor under drought (Jones, 1992). This allows turgor dependent processes such as stomatal opening and expansive growth to continue during periods of water deficits (Jones, 1992). Crops reported to have a high OA (>0.8 MPa) include vegetable amaranth (*Amaranthus* L.), soybean [*Glycine max* (L.) Merr.], pigeonpea [*Cajanus cajan* (L.) Millsp.], peanut (*Arachis hypogea* L.), chickpea (*Cicer arietinum* L.), and sunflower (*Helianthus annuus* L.) (Angadi and Entz, 2002; Liu and Stützel, 2002a; Morgan, 1992; Turner et al., 2000). Those with low OA (<0.5 MPa) include lupin (*Lupinus cosentinii* Guss.), field pea (*Pisum sativum* L.), faba bean (*Vicia faba* L.), cowpea [*Vigna unguiculata* (L.) Walp.], tomato (*Lycopersicon esculentum* Mill.), and pepper (*Capsicum annuum* L.) (Kuang et al., 1990; Turner et al., 2000; Wullschlegel and Oosterhuis, 1991).

For many crops, transpiration declines after one-third of the extractable soil water remains in the root zone (Sadras and Milroy, 1996). However, some crops show decrease in transpiration at higher levels of extractable soil water (Henson et al., 1989). Decreases in transpiration that precede changes in the water status of the plant are attributed to a nonhydraulic root signal produced by roots growing in a drying soil (Davies et al., 1994).

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The objectives of this study were to evaluate the adaptive responses of selected spiderplant genotypes to soil water deficit stress in terms of leaf area development, dry matter production and partitioning, relative water content, osmotic adjustment, and transpiration. We hypothesized that there are soil moisture thresholds below which plant processes are affected and that genotypic differences exist in the adaptation of spiderplant to soil water deficit stress.

## Materials and Methods

**PLANT MATERIALS.** Two pot experiments were conducted in 2000 and 2002 at the Institute of Vegetable and Fruit Science, Univ. of Hannover, Germany (lat. 52°14'24" N, long. 9°43'48" E) and one field experiment in 2001 at the Jomo Kenyatta Univ. of Agriculture and Technology (JKUAT) farm, Kenya (lat. 1°10'48" S, long. 37°07'12" E). Spiderplant genotypes from two broad groups, one with purple stems and petioles (P-) and one with green stems and petioles (G-), were used: P-landrace and P-commercial genotypes, fast-growing and high-yielding purple stem and petiole landrace (farmer's field in western Kenya) and commercial (Kenya Seed Co., Nairobi, Kenya) genotypes were used in 2000. In 2001 and 2002, G-landrace, a slow-growing green stem and petiole landrace (Baobab Farm, Mombasa, Kenya) was included while P-commercial was dropped since its responses were similar to those of P-landrace. In addition, P-defoliated was a special treatment in the 2002 experiment in which P-landrace was defoliated daily to keep its leaf area similar to that of G-landrace. This was done to facilitate comparison of the responses from plants with similar leaf areas between the purple stem and petiole and green stem and petiole genotypes. The removed leaves were kept separately for each plant and were included in the total biomass.

**POT EXPERIMENTS.** Pot experiments were arranged in a completely randomized design with genotypes and water treatments as factors with three replications for each treatment at each harvest. Two water treatments were used in the pot experiments: soil water deficit and watered. Before the onset of the water treatments, soil moisture was kept high by daily watering of all pots. At the onset of the water treatments, soil moisture in all pots was raised to 100% and 90% water holding capacity (WHC) in 2000 and 2002, respectively. Plants in the soil water deficit treatment received no more water thereafter, while plants in the watered treatment were irrigated daily to maintain the soil moisture at 90% WHC in both years. Water treatments began at 21 d after sowing, just before the onset of flowering.

Pots made from PVC pipes, with 1 m length and a diameter of 0.2 m, were filled with loess soil (1.15 g·cm<sup>-3</sup> soil bulk density, 0.0016-0.00365% available nitrogen, pH of 7.4-7.5) obtained from the Ruthe research station, South of Hannover. Pot experiments were conducted in a glasshouse at 26 °C day and 20 °C night temperature and total photosynthetically active radiation of 49.6 kW/m<sup>2</sup> in 2000 and 37.9 kW/m<sup>2</sup> in 2002 without supplemental lighting. The relative humidity, which was not controlled, ranged from 50% to 70% in 2000 and 60% to 80% in 2002. About 10 seeds of the selected genotypes were sown directly into the pots on 29 May 2000 and 23 Apr. 2002. The pots were maintained well watered until water treatments were initiated. Emergence was observed after 4 d in both years. Seedlings were then thinned to one per pot 2 weeks after planting. Nitrogen was applied at rates of 0.5 and 1.0 g/plant N based on soil analysis results in 2000 and 2002, respectively, 3 weeks after planting by irrigating with 15N-3.1P-18.3K-3.6Mg fertilizer solution (Flory 9;

Planta GmbH, Regensatuf, Germany). The soil surface was then covered to a depth of ≈3 cm with quartz gravel to minimize soil evaporation.

Three plants per water treatment were harvested five times during the experiments: at the onset of water treatments, when average soil moisture contents had dropped to 70%, 60%, and 40% WHC and when transpiration of plants in the soil water deficit treatment was below 10% of that of watered plants. At each harvest plants were cut at the base and separated into petioles, stems and blades. Leaf area was measured using a leaf area meter (model 3100; LICOR, Lincoln, Nebr.). Roots were carefully removed from soil by hand and washed. Dry weight was determined for each plant part after being dried at 100 °C for 48 h. Root to shoot (petioles, stem, and blade dry weight combined) ratio was determined using dry weight from each harvest. The data were transformed to natural logarithms before analysis of variance (Hoffmann and Poorter, 2002; Poorter and Nagel, 2000).

Leaf production and stem elongation were determined daily by counting the number of leaves, and measuring the plant height using a meter ruler, respectively. Differences in numbers of leaves and plant height between two consecutive days were used to calculate leaf appearance (LAR) and stem elongation (SER) rates. Relative rates of leaf appearance and stem elongation, RLAR and RSER, were calculated as:

$$RLAR = \frac{LAR_d}{LAR_w} \quad [1a]$$

$$RSER = \frac{SER_d}{SER_w} \quad [1b]$$

where subscripts d and w refer to soil water deficit and watered treatments.

The plant available soil water was expressed as the fraction of transpirable soil water (FTSW) for each pot in the soil water deficit treatment. FTSW at day *i* for each pot was calculated as:

$$FTSW = \frac{\text{pot weight at day } i - \text{final pot weight}}{\text{initial pot weight} - \text{final pot weight}} \quad [2]$$

where initial pot weight refers to the weight of a pot at 100% WHC, while final pot weight refers to the weight of the pot when the transpiration of stressed plants was <10% of that of watered plants.

Water relations measurements were carried out at the onset of water treatments, and when average soil moisture contents had dropped to 70%, 60%, and 40% WHC in 2000, and to 80%, 70%, 60%, and 40% WHC in 2002. The last measurements in both years were taken when transpiration of the soil deficit plants had reached 10% of that of the watered ones. The measurements were done on the youngest fully expanded leaves between 1100 and 1500 HR. For determination of relative water content (RWC), the leaves were placed in distilled deionised water in a petri dish and left at 20 ± 2 °C in dim illumination for 24 h. The turgid weight was obtained after blotting; thereafter the leaves were dried at 100 °C to a constant weight to obtain the dry weight.

$$RWC = \frac{\text{fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \quad [3]$$

For measurement of osmotic potential 1-cm leaf disks were excised from young fully expanded leaves using a cork borer, wrapped in aluminium foil and immediately placed in liquid nitrogen. Osmotic potential (OP) was then measured at 22 °C with

a psychrometer (C52-chamber; Wescor Corp., Logan, Utah). To quantify osmotic adjustment, Ludlow's full-turgor adjustment method was used (Ludlow et al., 1983). In this method, bound water is neglected and the leaf osmotic potential at full turgor ( $OP_{100}$ ) of both soil water deficit and watered plants is given by:

$$OP_{100w} = OP_w \times RWC_w \quad [4]$$

$$OP_{100d} = OP_d \times RWC_d \quad [5]$$

where OP and RWC refer to measured osmotic potential and relative water content, respectively, and subscripts w and d designate watered and soil water deficit treatments, respectively.

The osmotic potential at full turgor was then subjected to analysis of variance by the GLM procedure of SAS (SAS Institute, Cary, N.C.). Osmotic adjustment (OA) was determined as:

$$OA = OP_{100w} - OP_{100d} \quad [6]$$

The RWC of plants in soil water deficit treatment was divided by that of watered plants to give the RWC ratio, which was then expressed as a function of FTSW.

Transpiration was determined by daily pot weight measurements using an electronic balance (capacity 64 kg  $\pm$  5 g, model QS 64B; Sartorius, Göttingen, Germany). In this case, the difference in weights between two consecutive days was considered as the water lost through transpiration. The transpiration data were analyzed using the double normalization procedure outlined by Ray and Sinclair (1998). First the transpiration ratio (TR) of each plant in the soil water deficit treatment was determined as:

$$\text{Transpiration ratio (TR)} = \frac{\text{transpiration of deficit plant}}{\text{average transpiration of watered plants}} \quad [7]$$

A second normalization was done so that TR of each plant was centered on a value of 1.0 when the soil water content in each pot was high (FTSW > 0.50). First, a mean TR was calculated for each plant for the period when soil moisture was high, and then the daily TR for each plant was divided by this mean TR to give a daily normalized transpiration ratio (NTR).

Statistical analysis was performed using the GLM procedure of SAS. Analyses of variance were executed for each date separately for plant leaf area. The relationships between relative parameters (i.e., RLAR, RSER, RWC ratio and NTR) and FTSW were developed using linear plateau regression using the non linear procedure of SAS as:

$$\begin{aligned} \text{Relative parameter} &= 1 && \text{if FTSW} > \text{FTSW}_t \\ \text{Relative parameter} &= 1 + A \times (\text{FTSW} - \text{FTSW}_t) && \text{if FTSW} < \text{FTSW}_t \end{aligned} \quad [8]$$

where A is the slope of the linear decline, and  $\text{FTSW}_t$  is the FTSW threshold at which the relative parameter began to decline.  $R^2$  values were calculated as:

$$R^2 = 1 - \frac{\text{SSE}}{\text{CSE}} \quad [9]$$

where SSE is the sum of squares of the residual and CSE is the total corrected sum of squares.

**FIELD EXPERIMENT.** A field experiment was set up in a split plot design with three replications. Water treatments were the main factors [i.e., soil water deficit, moderate stress (60% field capacity) and watered (80% field capacity)], while genotype was used as a subplot factor (i.e., P-landrace and G-landrace).

Amendments have been done to the soil by adding different soil types to the top horizon, which was previously gravelly clay over petroplinthite. The soils had bulk density of 1.20–1.47 g·cm<sup>-3</sup>, 0.20% total nitrogen and a pH of 6.0. Plastic sheets were placed in the soil at a depth of 1.0 m all round the main plots to limit lateral water movements. At the onset of water treatments, 21 d after sowing, all plots were thoroughly irrigated. Soil samples were taken 48 h later using a soil auger at depths of 0–20 and 20–40 cm to determine the gravimetric soil water content ( $G_w$ ) by drying at 105 °C for 48 h. Estimation of the amount of water necessary to maintain the soil moisture at 80% field capacity (FC) in the watered treatment was based on the soil water balance concept (Kramer and Boyer, 1995):

$$W = \text{SWC}_1 - \text{SWC}_2 \quad [10]$$

$$\text{SWC} = G_w \times \text{soil bulk density} \times d \quad [11]$$

where W refers to the amount of water to be applied,  $\text{SWC}_1$  is the soil water content of the 0–20 cm soil layer at 80% FC or 60% FC,  $\text{SWC}_2$  is the measured soil water content,  $G_w$  is gravimetric soil water content (%) in the soil layer and  $d$  is the thickness of the soil layer.

During watering, the calculated amount of irrigation water was applied carefully by hand to avoid runoff and deep drainage. In the moderate stress treatment, the soil was allowed to dry below 60% FC and was then rewatered using the same method described above for the watered treatment to maintain the soil moisture at 60% FC. In the soil water deficit treatment, no water was applied after the onset of the water treatments.

Subsequent soil water status was determined by measuring the gravimetric soil water content in 4- to 8-d intervals for the soil water deficit and moderate stress treatment before rewatering and in 2- to 3-d intervals for watered treatment and moderate stress treatment after rewatering. Soil sampling for gravimetric water determination on watered plots was always conducted just before watering. The same was done for moderate stress plots once rewatering had begun.

The subplots, each measuring 2  $\times$  2.5 m, were prepared by raising the soil  $\approx$  15 cm aboveground. About 10 seeds were sown directly on to the prepared plots at a spacing of 30 cm between and 20 cm within rows on 21 June 2001. The plots were well watered and covered by plastic sheets to maintain high moisture. Emergence was observed 3 and 5 d after sowing for P-landrace and G-landrace, respectively. Thinning was done 2 weeks after emergence to leave one seedling per hole. The crops were well watered daily by hand until the onset of water treatments. At this time, nitrogen and phosphorus were applied at rates of 52 kg·ha<sup>-1</sup> N (calcium ammonium nitrate, 26% N) and 40.2 kg·ha<sup>-1</sup> P (triple super phosphate, 20.1% P).

A rain shelter was constructed using timber and covered by a transparent plastic film at onset of water treatments. The film material used allowed transmission of 43% of incident solar radiation. Total photosynthetically active radiation during the experiment was 112.1 kW/m<sup>2</sup>, with an average relative humidity of 64.8%. During the day the shelter was kept open on all sides but was fully covered during rain events and at night. Seven harvests, based on the soil water status, were carried out. At each harvest, two to three plants in a central row from each plot were cut and divided into lamina, petioles and stems. Plant leaf area was measured on the lamina using a leaf area meter (model AAM-8; Hayashi Denko Co., Tokyo). All plant parts were then dried at 100 °C for 48 h and weighed to determine biomass.

Statistical analyses for the field experiment were performed using the GLM procedure of SAS. Analyses of variance were executed for each date separately for plant dry weight and leaf area, and means were separated by use of LSD ( $P < 0.05$ ). Partitioning of dry matter between leaves and stems was analyzed by expressing the ratio of dry weight of the leaf to that of the stem as a power function of plant height:

$$y = ax^{-b} \quad [12]$$

where  $y$  is the leaf to stem ratio,  $a$  and  $b$  are regression coefficients, and  $x$  is plant height.

This was based on the model of partitioning of new above-ground dry matter presented by Stützel et al. (1988), which recognizes the fact that as the plant leaf area increases, a greater proportion of new dry matter needs to be invested in structural material (mainly stems) to maintain the plant's integrity and strength.

## Results

**SOIL WATER EXTRACTION.** The decline in FTSW over time in the soil water deficit treatments was similar among the P-genotypes (P-landrace and P-commercial) in the pot experiment of 2000 (data not shown). In the 2002 pot experiment, P-landrace had higher water use rates than G-landrace resulting in a faster rate of soil drying under P-landrace (Fig. 1A). However, when P-landrace was defoliated (P-defoliated) to achieve similar leaf area development as G-landrace, it had similar water use patterns to the latter. In the field experiment, the gravimetric soil water contents over time were similar in the 0–20 cm and 20–40 cm depths, hence the mean of the two is considered (Fig. 1B and C). In the first week after the onset of soil water deficit, the gravimetric soil water content remained similar for P-landrace and G-landrace. This was followed by a more rapid decline in soil water content, faster for P-landrace than for G-landrace at both soil water deficit and moderate stress before rewatering.

**LEAF AREA DEVELOPMENT AND STEM ELONGATION.** There were no significant interactions between genotype and water treatments for the whole plant leaf area in either pot or field experiments. P-landrace had significantly higher plant leaf area than G-landrace (data not shown). Plants in the soil water deficit treatment had less leaf area 15–20 d after start of water treatments in pot experiments (2000, 2002), and greater than 30 d after the start of water treatments in the field experiment (2001) (Fig. 2A–C). Soil water deficit significantly reduced leaf appearance in pot experiments (Fig. 3A–C). The FTSW thresholds for leaf appearance rates showed no significant differences between genotypes. Soil water deficit also significantly reduced stem elongation of spiderplant in pot experiments (Fig. 4). G-landrace had a significantly lower FTSW threshold for stem elongation than the P-genotypes.

Plants in the soil water deficit treatments had higher root to shoot ratios 15 to 20 d after water treatments started (Fig. 5A and B). The leaf to stem ratio in 2001 declined with increasing plant height (Fig. 5C and D) but was not influenced by water treatments or genotype. This could be well described by a power function and there were no significant differences in the coefficients between soil water treatments and plant genotypes.

**WATER RELATIONS.** The difference in osmotic potential at full turgor (OP) between watered and soil water deficit plants was significant 24 d after start of water treatments in 2000, an OA

of 0.10 MPa (Fig. 6A). In 2002, the OA at endpoint was 0.33 MPa (Fig. 6B). The ratio of RWC between plants in soil water deficit and watered treatments was related to FTSW. The FTSW thresholds at which this ratio began to deviate from unity could not be determined precisely in the 2000 experiment due to the low number and uneven distribution of data points. It was, however, significantly lower than 1 for all FTSW below 0.6 (Fig. 6C). In

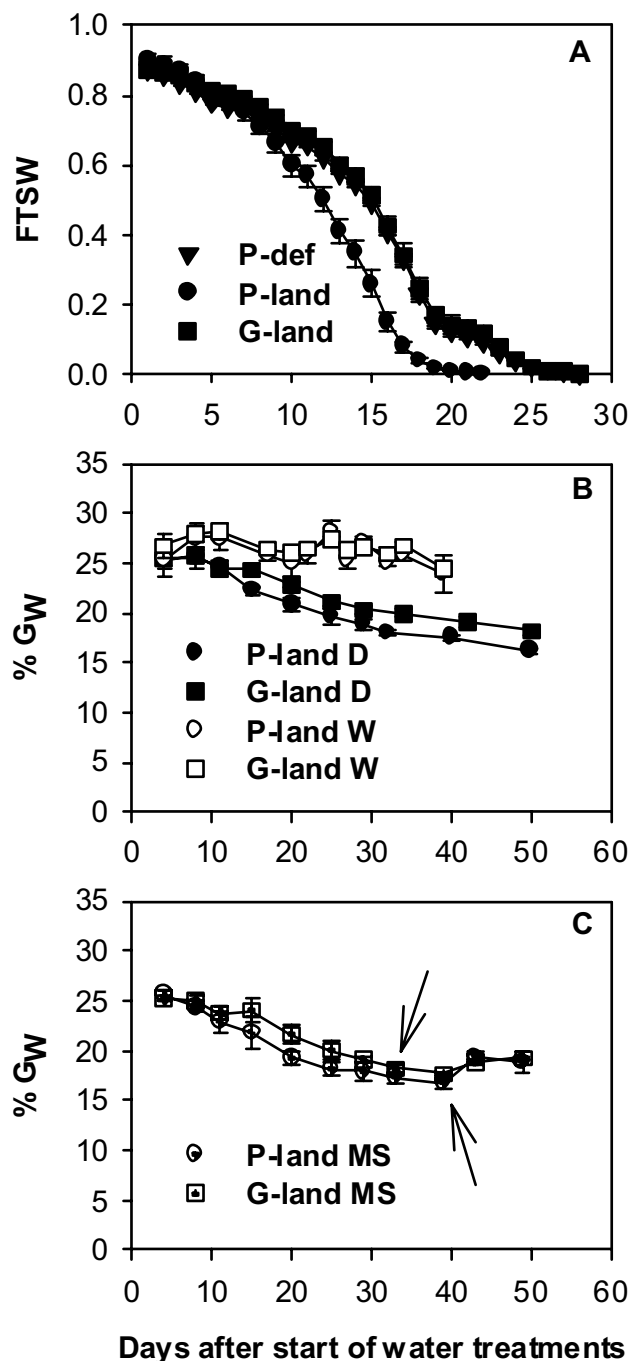


Fig. 1. Changes in the fraction of transpirable soil water (FTSW) and gravimetric soil water content (%  $G_w$ ) at 0–40 cm depths for spiderplant genotypes purple stems and petioles defoliated (P-def), purple stems and petioles landrace (P-land) and green stems and petioles landrace (G-land) grown in the glasshouse under soil water deficit conditions in 2002 (A), and at soil water deficit–D, watered–W, and moderate stress–MS under field conditions in 2001 (B, C). Arrows in the MS treatment (C) indicate the rewatering dates for P-land (upper) and G-land (lower). Vertical bars show SE ( $n = 3-6$ ).

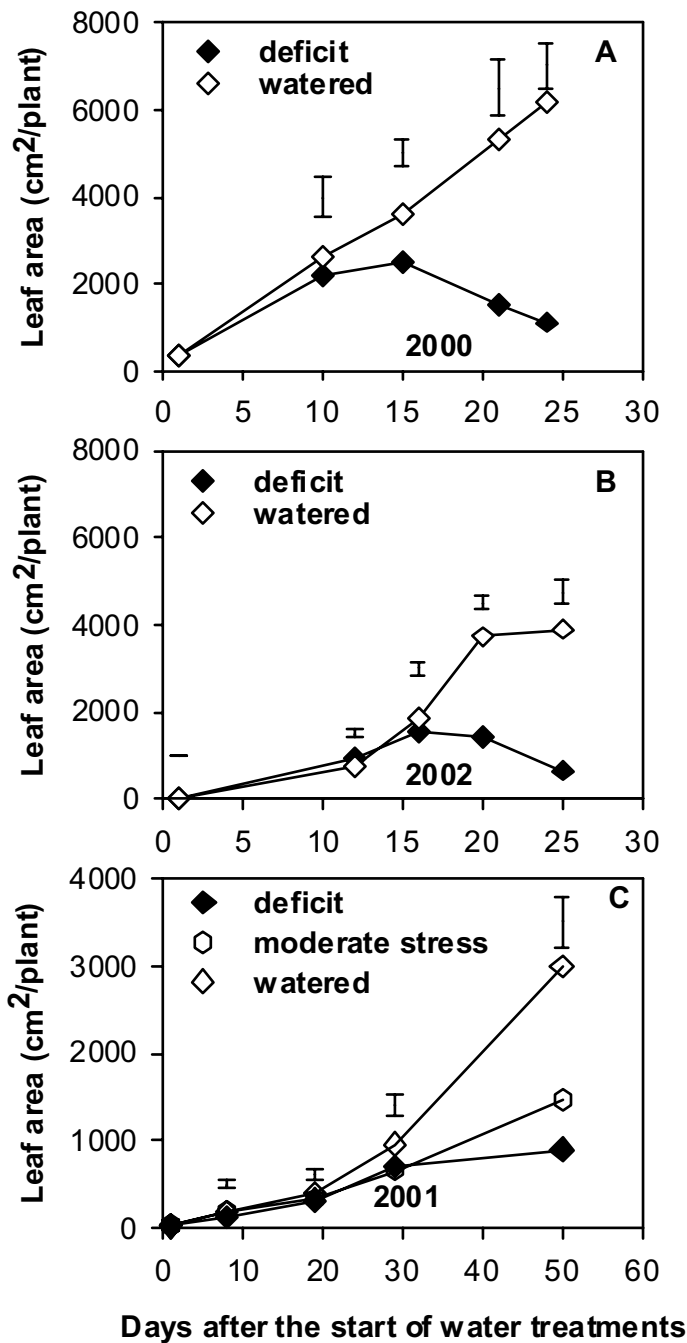


Fig. 2. Plant leaf area of spiderplant grown in the glasshouse (A, B) and in the field (C) as influenced by water treatments, soil water deficit (deficit), watered and moderate stress (means across genotypes). Vertical bars show  $LSD_{0.05}$ .

the 2002 experiment, the RWC ratio fell below 1 at lower FTSW values than in 2000 with no significant differences between the genotypes (Fig. 6D and Table 1).

**TRANSPIRATION.** The effect of soil water deficit on transpiration was similar for P-landrace and P-commercial genotypes in 2000. In pot experiments, P-landrace and P-commercial had significantly higher FTSW thresholds at which NTR began to decline than G-landrace (Fig. 7). However, when defoliated, P-landrace had an FTSW threshold similar to that of G-landrace.

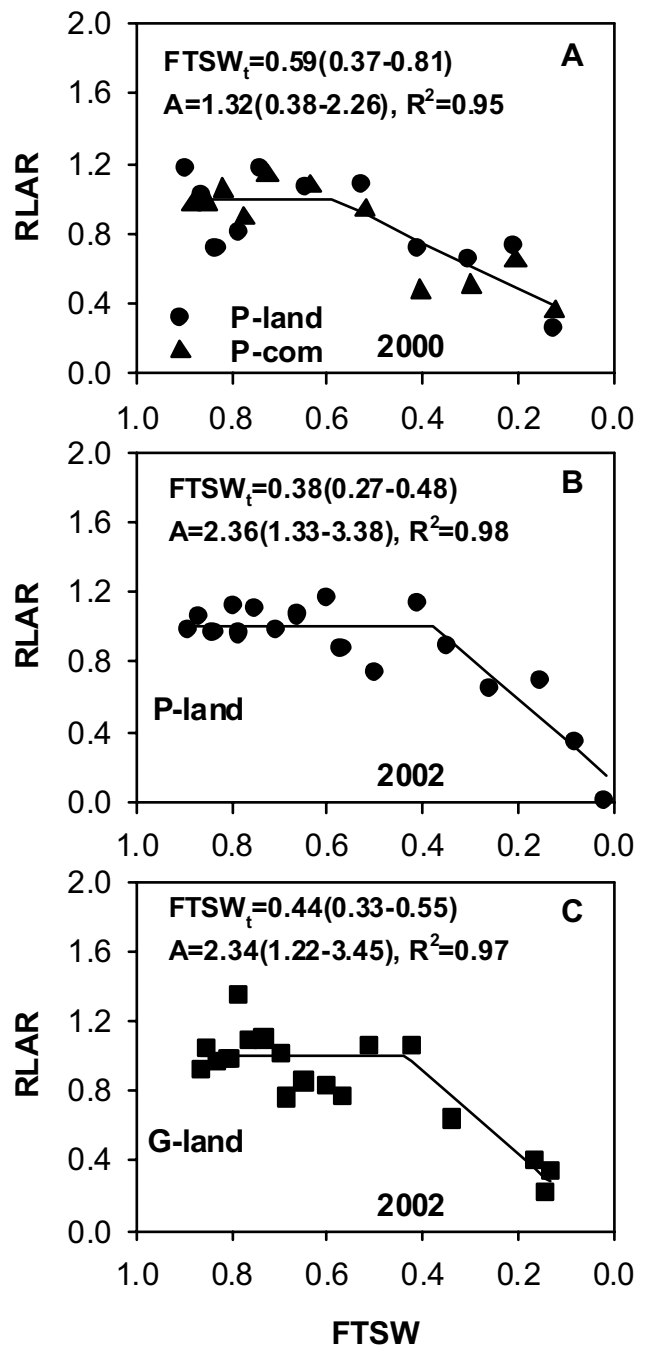


Fig. 3. The relative leaf appearance rate (RLAR) as a function of FTSW for spiderplant genotypes purple stems and petioles landrace (P-land), purple stems and petioles commercial (P-com), and green stems and petioles landrace (G-land) (A–C) in 2000 and 2002. Lines show plateau regression functions. The fraction of transpirable soil water threshold ( $FTSW_t$ ) and slope of the decline (A) with their 95% confidence intervals (in parentheses) are shown in the figure.

## Discussion

This study was conducted to evaluate the adaptive responses of selected spiderplant genotypes to soil water deficit. The hypothesis was that plant processes such as leaf area development, dry matter production and partitioning, osmotic adjustment, and transpiration were affected once the soil moisture fell below certain thresholds and that there existed genotypic differences in the adaptation of spiderplant to soil water deficit.

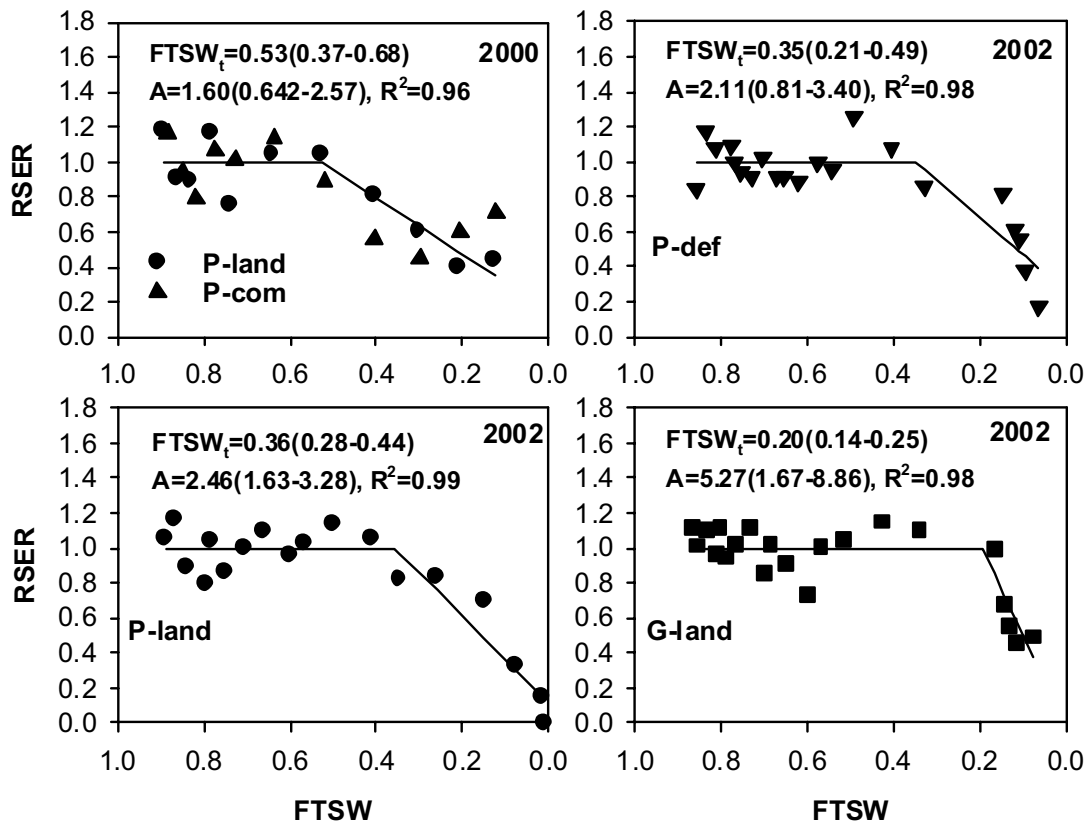


Fig. 4. Relative main stem elongation rate (RSER) as a function of FTSW for spiderplant genotypes purple stems and petioles landrace (P-land), purple stems and petioles commercial (P-com), purple stems and petioles defoliated, (P-def) and green stems and petioles (G-land) grown in the glasshouse in 2000 and 2002. Lines show plateau regression functions. The fraction of transpirable soil water threshold ( $FTSW_t$ ) and slope of the decline ( $A$ ) with their 95% confidence intervals (in parentheses) are shown in the figure.

Water use by spiderplant under soil water deficit conditions depended largely on leaf area. When P-landrace and P-commercial had similar leaf area (2000 pot experiment) they showed similar patterns of water use. When P-landrace had greater leaf area than G-landrace (2002 pot experiment), P-landrace used more water than G-landrace. But when P-landrace had similar leaf area (P-defoliated) as G-landrace, it had a similar rate of soil drying. Similar dependencies of water extraction on leaf area have been found for other crops [e.g., sorghum (*Sorghum bicolor* (L.) Moench.)] (Salih et al., 1999).

Leaf area development is directly related to the yield of spiderplant since the edible part is the leaf. It also affects dry matter production and plant growth through the role of leaf area in light interception (Jones, 1992). Severe soil water deficit ( $FTSW < 0.40$ ) caused a reduction of stem elongation rates resulting in smaller plant heights and hence implying reduced branching. Consequently, there was a decline in leaf appearance rates as shown by the FTSW thresholds especially in 2002. This, together with leaf senescence and shedding that were observed under severe stress resulted in a rapid decline of plant leaf area. The overall effect was a drastic reduction of transpiration. This mechanism of water conservation is part of a drought avoidance strategy (Jones, 1992). Although the stem elongation rate of P-landrace declined at significantly higher FTSW thresholds than G-landrace, there were no genotypic differences in the leaf appearance FTSW thresholds.

The increase in root to shoot ratio under severe stress was mainly due to differential sensitivity of the root and shoot biomass production to soil water deficit. At maximum stress ( $FTSW = 0$ ),

the root biomass was reduced by 28% to 32% as compared to 42% to 45% for shoot biomass. This differential sensitivity has also been reported in crops such as wheat (*Triticum aestivum* L.) (Blum and Sullivan, 1997) and beans (*Phaseolus vulgaris* L.) (Boutraa and Sanders, 2001). On the other hand, the leaf to stem ratio declined as plant size increased. This is in line with the concept that increasing plant height necessitates an increase in structural material to maintain its stability (Stützel et al., 1988). This relationship between leaf to stem ratio and plant size was not influenced by soil moisture status in this study, implying that the partitioning of new above-ground dry matter was directly dependent on plant size rather than soil moisture.

In the early stages of the drying cycle, the RWC was generally high (above 0.71). As the FTSW declined below 0.4–0.6, RWC declined and the plants lost turgor at RWC values of 0.54–0.57. Osmotic adjustment (OA) by 0.10–0.33 MPa for spiderplant is relatively low compared with values of  $>0.8$  MPa for crops such as vegetable amaranth (Liu and Stützel, 2002a) and soybean (Turner et al., 2000), suggesting that spiderplant relies less on osmotic adjustment for its adaptation to drought. Moreover, this OA could not sustain turgor in spiderplant leaves beyond a RWC of 0.54–0.57, at which point the plants were persistently wilted and marked the endpoint of the pot experiments. This is in the range of leaf water status at permanent wilting point for other crop species with similar low OA capacity (Ludlow et al., 1983; Wullschlegel and Oosterhuis, 1991). Bolanos and Edmeades (1991) considered that an OA of 0.4 MPa and above was necessary to justify the inclusion of a cultivar in a crossing program for maize (*Zea mays* L.).

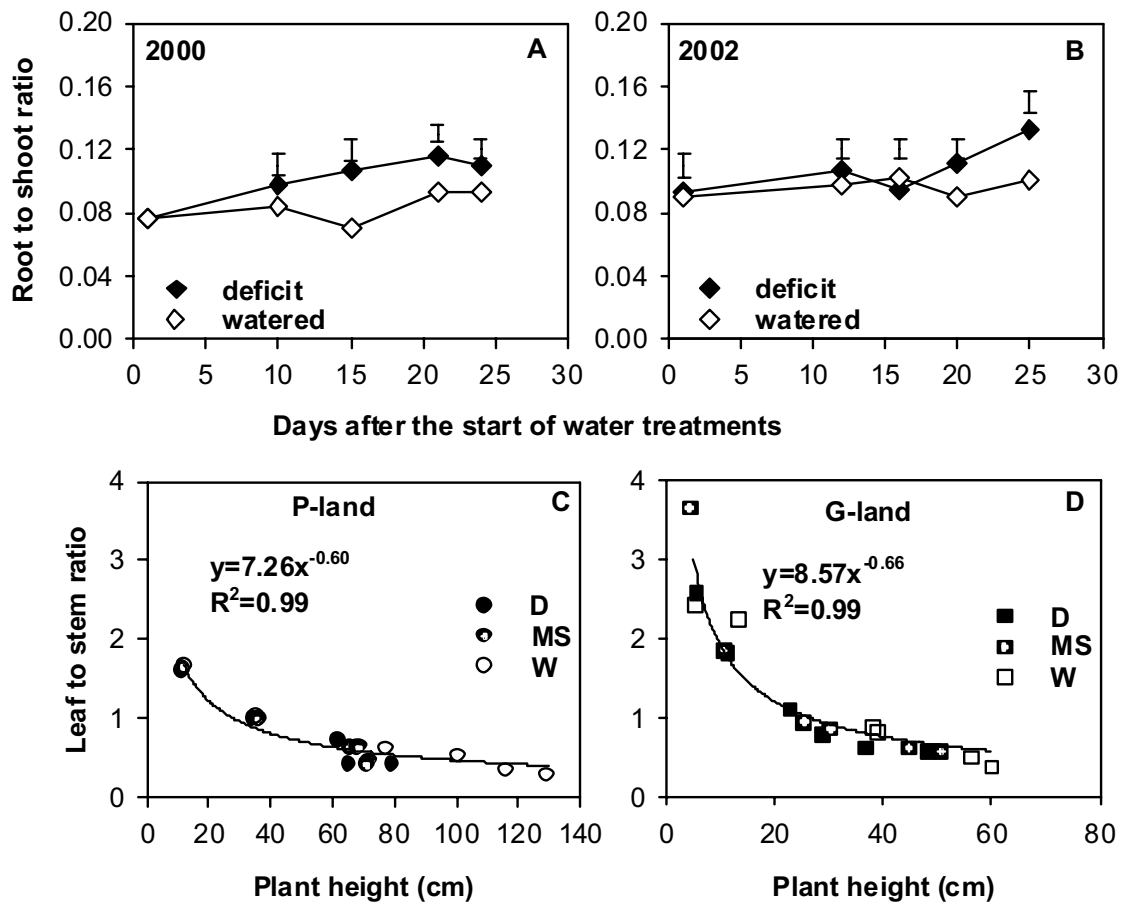


Fig. 5. The root to shoot ratio of spiderplant grown in the glasshouse under soil water deficit and watered conditions (means across genotypes) in 2000 and 2002 (A, B), and the relationship between leaf to stem ratio and plant height of spiderplant genotypes purple stems and petioles landrace (P-land) and green stems and petioles (G-land) grown at soil water deficit–D, moderate stress–MS, and watered–W treatments under field conditions in 2001 (C, D). Vertical bars show  $LSD_{0.05}$ .

P-genotypes showed higher FTSW thresholds for transpiration (0.55–0.77) than G-landrace (0.29). The latter was comparable to the widely reported threshold range of 0.3–0.4 for decline in transpiration in crops such as maize (Ray and Sinclair, 1997, 1998), various legumes (Sinclair and Ludlow, 1986), and vegetable amaranth (Liu and Stützel, 2002b), whereas the thresholds for P-genotypes were similar to those reported for a sensitive maize hybrid (Ray and Sinclair, 1997).

The higher sensitivity of transpiration of P-landrace and P-commercial to soil water deficit as compared with G-landrace related to leaf area development. The faster leaf area development in P-landrace led to a higher rate of soil drying causing it to reach the endpoint 4–6 d earlier than the G-landrace and P-defoliated. The rate of soil drying has been shown to have no direct effect on the relationship between normalized transpiration ratio (NTR) and fraction of transpirable soil water (FTSW) in grain legumes (Sinclair and Ludlow, 1986). However, a high rate of soil drying in combination with a large pot size such as the one used in this study can exacerbate soil moisture gradients with the soil water content being highest in the lower layers (Jensen et al., 1989). Whereas pot size may not directly influence the NTR–FTSW relationship as has been shown in maize and soybean (Ray and Sinclair, 1998), root distribution in large pots may be inhomogeneous resulting in steeper water potential gradients between soil and roots, which may have affected the NTR–FTSW relationship.

There is a possibility that the rooted depth in both purple stem and petiole and green stem and petiole genotypes was similar

at the early stages of plant growth as observed during harvests. With a higher rate of soil drying, the P-genotypes had part of their roots exposed to drying soil in the upper layers, a phenomenon referred to as top-root drying (Blum and Sullivan, 1997), which might have induced ABA mediated stomatal closure and thus a reduction of transpiration, even though moisture was still high at lower layers.

The higher FTSW thresholds for transpiration of P-genotypes in 2000 as compared with 2002 could be attributed to the lower evaporative demand in 2002. In 2000, relative humidity (RH) was in the range of 50% to 70% and total photosynthetically active radiation was 49.6 kW/m<sup>2</sup> during the experimental period, while in 2002, the RH range was 60% to 80% with a total photosynthetically active radiation of 37.9 kW/m<sup>2</sup>. A high evaporative demand can cause plant leaf responses even when the soil moisture is high. This has been associated to the soil hydraulic resistance (Franks and Farquhar, 1999). Furthermore, it is thought that plants can sense soil and atmospheric water status independently (Sadras and Milroy, 1996).

## Conclusion

Our results show that spiderplant adapts to soil water deficit stress mainly by regulating transpiration through reduction of leaf area, and possibly stomatal conduction. Maintaining the available soil water above 0.6 FTSW for P-landrace and P-commercial, and above 0.4 FTSW for G-landrace (50% to 60% water holding

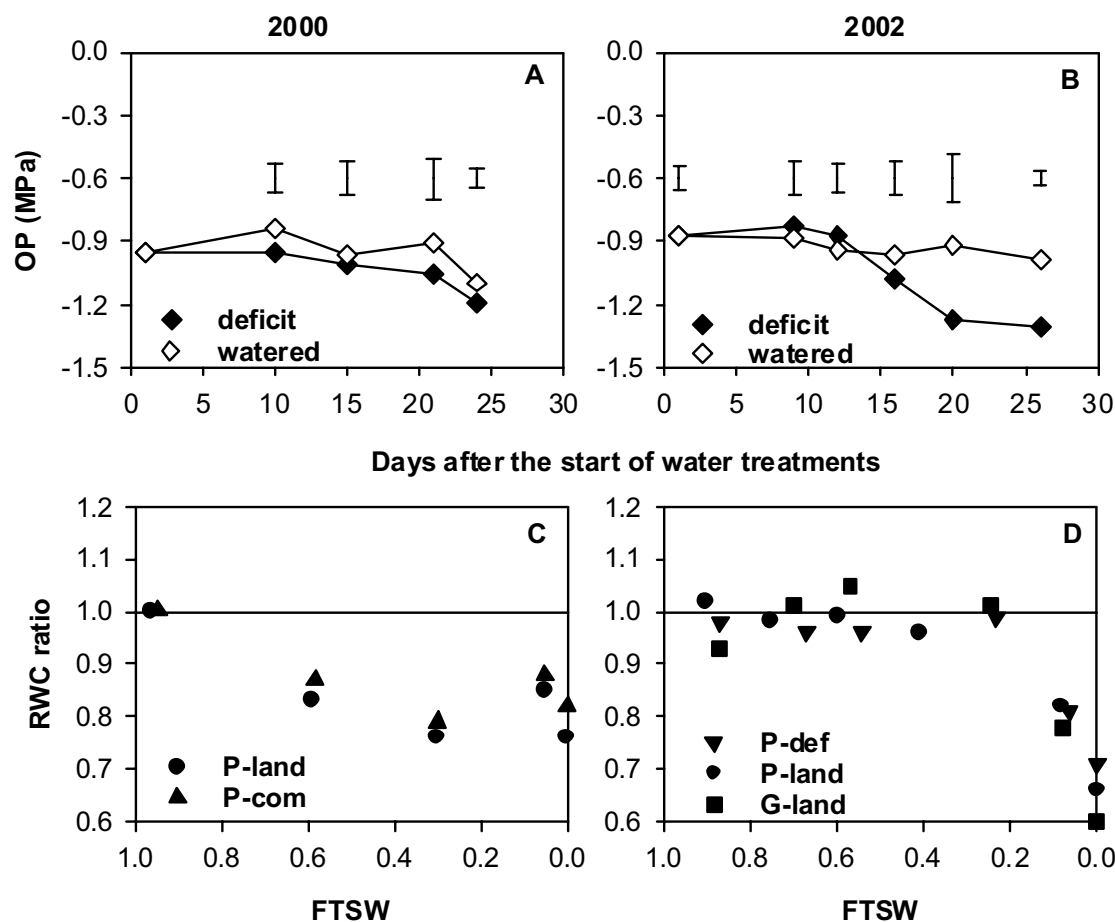


Fig. 6. The osmotic potential at full turgor (OP) of spiderplant grown under soil water deficit (deficit) and watered conditions (means across genotypes) (A, B) and the scatter diagrams of the ratio of relative water content (RWC) of plants in soil water deficit to watered treatments as functions of fraction of transpirable soil water (FTSW) for spiderplant genotypes purple stems and petioles landrace (P-land), purple stems and petioles commercial (P-com), purple stems and petioles landrace (P-landrace), and green stems and petioles landrace (G-landrace) grown in the glasshouse in 2000 and 2002. Vertical bars show  $1SD_{0.05}$ . Lines in c and d show ratio = 1. Regression coefficients are shown in Table 1.

Table 1. The fraction of transpirable soil water threshold value for relative water content (RWC) ratio decline (FTSW<sub>t</sub>) and the slope of the decline (A) obtained from plateau regression analysis for spiderplant genotypes purple stems and petioles defoliated landrace (P-defoliated), purple stems and petioles landrace (P-landrace), and green stems and petioles landrace (G-landrace) grown in the glasshouse in 2002. The 95% confidence intervals are shown in parentheses.

Genotype	A	FTSW <sub>t</sub>	R <sup>2</sup>
P-defoliated	1.18 (0.67–1.65)	0.24 (0.17–0.31)	0.98
P-landrace	0.65 (0.28–1.03)	0.45 (0.26–0.65)	0.98
G-landrace	2.31 (0.21–4.40)	0.17 (0.05–0.30)	0.98

capacity) is necessary to obtain maximum leaf area development and dry matter production. Under field conditions, it is necessary to keep soil moisture above 60% field capacity.

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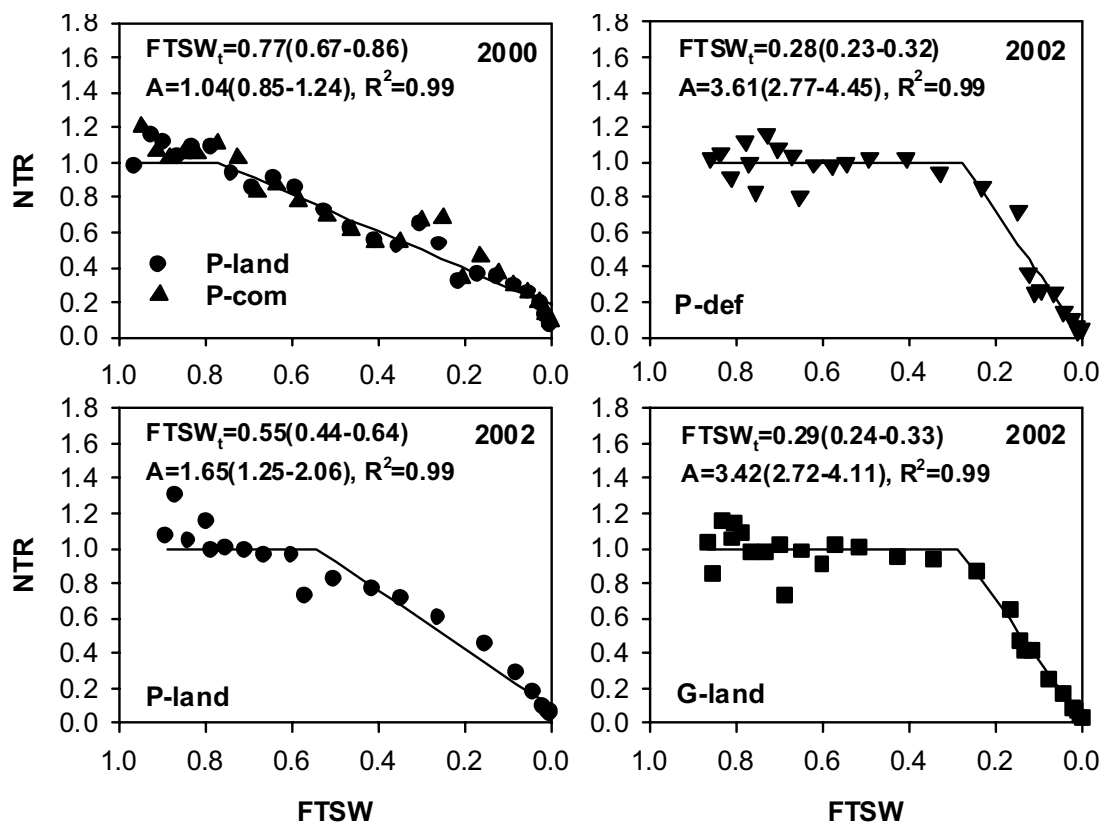


Fig. 7. Normalized transpiration ratio (NTR) as a function of fraction of transpirable soil water (FTSW) for spiderplant genotypes purple stems and petioles landrace (P-land), purple stems and petioles commercial (P-com), purple stems and petioles defoliated, (P-def) and green stems and petioles (G-land) grown in the glasshouse in 2000 and 2002. Lines show plateau regression functions. The fraction of transpirable soil water threshold (FTSW<sub>t</sub>) and slope of the decline (A) with their 95% confidence intervals (in parentheses) are shown in the figure.

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