Effects of Water Stress on the Growth of Spiderplant (*Gynandropsis gynandra* (L.) Briq.) and African Nightshade (*Solanum* spp.), Two Traditional Leafy Vegetables in Kenya

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Kurzfassung

Auswirkungen des Wasserstresses auf das Wachstum der Spinnenpflanze (*Gynandropsis gynandra* (L.) Briq.) und des afrikanischen Nachtschattens (*Solanum* spp.), zwei traditionelle Blattgemüse in Kenia.

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Die Spinnenpflanze (*Gynandropsis gynandra* (L.) Briq.) und der afrikanische Nachtschatten (*Solanum* spp.) sind zwei wichtige Blattgemüse, die zahlreichen ländlichen Gemeinden in Kenia als Nahrungsmittel dienen. Sie sind bedeutende Nährstoffspender und besitzen medizinischen Wert. Unregelmäßige Regenfälle, Dürreperioden und die Notwendigkeit des Anbaus in Trockenzeiten machen Bewässerung notwendig, damit diese Gemüse erfolgreich vermarktet werden können. Es liegen jedoch nur vage Informationen zum Wassemanagement dieser Feldgemüse vor. Darüber hinaus ist es zur Entwicklung einer Strategie des Wassermanagements zur Optimierung der Produktion bei minimalen Bewässerungskosten unumgänglich zu wissen, wie sich diese Pflanzen an Trockenstress anpassen. Hauptziel dieser Arbeit war daher die Bewertung der Mechanismen zur Anpassung an Trockenstress bei der Spinnenpflanze und dem afrikanischen Nachtschatten, sowie deren Relation zum Ertrag dieser Pflanzen.

Pflanzenwachstum, relativer Wassergehalt, osmotisches Potential, Wasserpotential und Transpiration von drei Genotypen der Spinnenpflanzen, P-landrace und P-commercial (schnell wachsend), und G-landrace (langsam wachsend) wurden unter trockenen und gewässerten Bedingungen im Gewächshaus untersucht. Als Indikator für verfügbarkeit von Wasser wurde der Teil des transpirierten Bodenwassers (FTSW) verwendet. Die Transpiration wurde anhand der täglichen Veränderung des Gefäßgewichts bestimmt und das Transpirationsverhältnis zwischen trockenen und gewässerten Pflanzen wurde als normalisiertes Transpirationsverhältnis (NTR) ausgedrückt.

Die Geschwindigkeit der Bodenaustrocknung hing überwiegend von der Geschwindigkeit des Blattflächernwachstums ab. P-landrace und P-commercial besaßen eine höhere Rate der Blattflächenausbildung und eine höhere

Geschwindigkeit der Bodenaustrocknung. Infolgedessen sind sie gegen Trockenstress anfälliger, wobei das normalisierte Transpirationsverhältnis (NTR) bei FTSW Grenzwerten von 0,55-0,77 im Vergleich zu 0,29 bei G-landrace zurückging. Die Blattausdehnung bei P-landrace und P-commercial war ebenfalls empfindlich gegenüber Dürre, bei einem ähnlichen FTSW Grenzwert wie NTR. In ähnlicher Weise zeigte das Blatterscheinen bei allen Genotypen eine hohe Empfindlichkeit gegenüber Dürre bei FTSW Grenzwerten von 0,38-0,59. Beim Längenwachstum des Stengels besaß aber G-landrace im Vergleich zu P-landrace und P-commercial einen geringeren FTSW Grenzwert. Die osmotische Anpassung (OA) war bei allen Genotypen ähnlich und reichte von 0,10-0,33 MPa. Dürre führte zu einer Reduzierung in spezifischen Blattfläche (SLA), die bei Absinken des FTSW unter 0,4 mit Abwerfen der älteren, größeren Blätter einherging. Das Wurzel/Schößling-Verhältnis erhöhte sich bei beiden Genotypen unter schweren Stressbedingungen im wesentlichen wegen der relativ höheren Verringerung der Trockenstoffe des Schößlings im Vergleich zur Wurzel. Dürre erhöhte auch die Transpirationseffizient aller Genotypen.

Eine ähnliche Studie wurde für Genotypen von zwei afrikanischen Nachschattenarten, *Solanum villosum* und *S. sarrachoides* durchgeführt. Die Blattausdehnung, das Stengelwachstum und das normalisierte Transpirationsverhältnis waren gleichermaßen sensibel gegenüber Trockenheit bei FTSW Grenzwerten von 0,46-0,64. Zwischen den Genotypen bestanden keine signifikanten Unterschiede. Die osmotische Anpassung war ohne Unterschied zwischen den Genotypen im Bereich von 0,16-0,19 MPa begrenzt. Ähnlich zum Fall der Spinnenpflanze, waren spezifische Blattfläche unter schwerer Belastung reduziert (FTSW<0,4), was wahrscheinlich das Ergebnis des Abwerfens älterer und größerer Blätter war. Ferner lag bei afrikanischen Nachtschatten unter Dürrebedingungen ein erhöhtes Wurzel/Sproß-Verhältnis und Transpirationseffizienz vor.

Um die Wasseraufnahme und das Pflanzenwachstum von Spinnenpflanzen und afrikanischen Nachtschatten unter unkontrollierten Bedingungen und nicht begrenzten Bodenvolumen im Gegensatz zu den Gewächshausexperimenten untersuchen zu können, wurde eine Feldstudie durchgeführt. Sowohl bei

Spinnenpflanzen als auch bei afrikanischen Nachtschatten war die Ausbildung der Blattfläche und die Trockenstoffproduktion deutlich verringert, wenn die Bodenfeuchtigkeit unter 60% Feldkapazität sank, was mit den Gewächshausexperimenten vergleichbar war. Bei dem afrikanischen Nachtschatten *S. sarrachoides* kam es zu einer höheren Blattausbildung und Trockenstoffproduktion als beim *S. villosum*. Die Partitionierung der Trockenstoffe zwischen Blatt und Stengel lag bei Spinnenpflanze und afrikanischem Nachtschatten aufgrund von Potenzfunktionen im Verhältnis zur Pflanzenhöhe und wurde nicht direkt durch Dürre beeinträchtigt.

Aus den Gewächshausexperimenten lässt sich schließen, dass sowohl Spinnenpflanze als auch afrikanischer Nachtschatten auf Dürre durch reduzierte Transpiration infolge geringerer Blattausbildung reagierten und nur begrenzte osmotische Korrektur aufwiesen. Bei der Spinnenpflanze war die Empfindlichkeit der Transpiration und Stengelausdehnung gegenüber Dürre vom jeweiligen Genotyp beeinflusst, hauptsächlich wegen den Unterschieden in der Geschwindigkeit der Blattflächenausbildung und Pflanzenhöhe. Die Genotypen der afrikanischen Nachtschatten zeigten andererseits in den beobachteten Prozessen ähnliche Reaktionen auf Dürre. Um generell eine hohe Blattausbildung, Blatterscheinen, Stengelausdehnung und damit einen hohen Ernteertrag bei Spinnenpflanze und afrikanischem Nachtschatten zu erzielen, muss der FTSW auf über 0,5-0,6 (etwa 60% Wasserhaltekapazität) gehalten werden. Unter Feldbedingungen muss die Bodenfeuchtigkeit auf über 60% der Feldkapazität gehalten werden, um eine Reduzierung der Blattflächen und Trockenstoffproduktion bei Spinnenpflanze und afrikanischem Nachtschatten zu verhindern. Beim afrikanischen Nachtschatten könnte *Solanum sarrachoides* wegen seines Potentials hoher Blatterträge für die Produktion und Nutzung zur Sortenverbesserung empfohlen werden.

Schlüsselworte: Blattflächernwachstum, normalisiertes Transpirationsverhältnis, osmotische Anpassung

Abstract

Effects of Water Stress on the Growth of Spiderplant (*Gynandropsis gynandra* (L.) Briq.) and African Nightshade (*Solanum* spp.), Two Traditional Leafy Vegetables in Kenya.

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Spiderplant (*Gynandropsis gynandra* (L.) Briq.) and African nightshade (*Solanum* spp.) are important leafy vegetable crops consumed by various rural communities in Kenya. They are important sources of nutrients and have medicinal value. Unreliable rainfall, intermittent droughts and the need for production during dry season necessitate irrigation for successful commercialization of these crops. However, there is only scanty information on the water management of these crops. Moreover, understanding the adaptation of these crops to drought is crucial in devising water management strategies that will maximize production at minimal irrigation costs. The main objective of this work therefore was to evaluate the mechanisms of adaptation to drought in both spiderplant and African nightshade and to relate them to productivity of these crops.

Plant growth, relative water content, osmotic potential, water potential and transpiration of three spiderplant genotypes, P-landrace and P-commercial (fast growing) and G-landrace (slow growing) were investigated under droughted and watered conditions in a glasshouse study. The fraction of transpirable soil water (FTSW) was used as an indicator of water availability. Transpiration was determined by changes in daily pot weights and the ratio of transpiration of droughted to watered plants expressed as normalized transpiration ratio (NTR).

The rate of soil drying depended largely on the rate of leaf area development. P-landrace and commercial genotypes had a higher rate of leaf area development and a higher rate of soil drying. Consequently, they were more sensitive to drought stress with normalized transpiration ratio (NTR) beginning to decline at FTSW thresholds of 0.55-0.77 as compared to 0.29 for G-landrace. Leaf expansion for P-landrace and commercial genotypes was equally sensitive to drought stress with similar FTSW threshold as NTR. Similarly, leaf appearance showed high sensitivity to drought stress with FTSW thresholds of 0.38-0.59 for all the genotypes. However, for stem elongation, G-landrace had a lower FTSW threshold as compared to P-landrace and commercial. Osmotic adjustment (OA) was similar in all genotypes and ranged from 0.10-0.33 MPa. Drought stress caused reduction of specific leaf area (SLA), which coincided with leaf senescence and shedding as the FTSW declined below 0.4. The root to shoot ratio similarly increased in both genotype groups under severe stress mainly due to relatively higher reduction of dry matter production of the shoot as compared to the root. Drought stress also increased transpiration efficiency in all the genotypes.

A similar study was conducted for the genotypes of two African nightshade species, *Solanum villosum* and *S. sarrachoides*. Leaf expansion, stem elongation and normalized transpiration ratio were equally sensitive to drought stress with FTSW thresholds of 0.46-0.64. There were no significant differences between genotypes. Osmotic adjustment was limited, in the range of 0.16-0.19 MPa, with no differences between the genotypes. Similar to the case of spiderplant, specific leaf area was reduced under severe stress (FTSW<0.4) probably as a result of shedding of older and larger leaves. In addition, there were increases in the root to shoot ratio and transpiration efficiency in African nightshade under droughted conditions.

A field study was also conducted to investigate the water use and plant growth of spiderplant and African nightshade under uncontrolled conditions and unlimited soil volumes in contrast with the glasshouse pot experiments. Leaf area and dry matter production for both spiderplant and African nightshade were significantly reduced as the soil moisture declined below 60% field capacity, which was comparable to results from pot experiments. For African nightshade, *S. sarrachoides* had higher leaf area and dry matter production as compared to *S. villosum*. Dry matter partitioning between the leaf and stem was related to plant height through power functions in both spiderplant and African nightshade, and was not directly affected by drought stress.

From the glasshouse experiments, it can be concluded that both spiderplant and African nightshade responded to drought mainly by reducing transpiration through reduced leaf area development and showed only limited osmotic adjustment. For spiderplant, the sensitivity of transpiration and stem elongation to drought was influenced by the genotype, mainly due to differences in leaf area development rate and plant height. African nightshade genotypes on the other hand, showed similar responses to drought in the processes considered. In general, to maintain high leaf expansion, leaf appearance, stem elongation and hence, high yield in both spiderplant and African nightshade, the FTSW needs to be kept above 0.5-0.6 (about 60% water holding capacity). Under field conditions, the soil moisture should be maintained above 60% field capacity to prevent reductions of leaf area and dry matter production in both spiderplant and African nightshade. For African nightshade, *Solanum sarrachoides* could be recommended for production and use for variety improvement due to its potential for high leaf yields.

Key words: Leaf area development, normalized transpiration ratio, osmotic adjustment

Contents

List of Abbreviations

Abbreviation	Description	Units
ABA	Abscisic acid	-
CT	Cumulative transpiration	kg/plant
DM	Dry matter produced	g/plant
FTSW	Fraction of transpirable soil water	-
G_W	Gravimetric soil water content	%
NTR	Normalized transpiration ratio	-
OA	Osmotic adjustment	MPa
OP	Osmotic potential at full turgor	MPa
RLAR	Relative leaf appearance rate	-
RLER	Relative leaf expansion rate	-
RSER	Relative stem elongation rate	-
RWC	Relative water content	-
SLA	Specific leaf area	cm^2/g
TE	Transpiration efficiency	g DM/kg water transpired
TR	Transpiration ratio	-
W_L	Dry weight of leaf blades	g/plant
W_S	Dry weight of stem	g/plant
WP	Leaf water potential	MPa

1.0 General Introduction

Spiderplant (*Gynandropsis gynandra* (L.) Briq.) and African nightshade (various *Solanum* species) are important traditional leafy vegetables consumed by various rural communities in Kenya (Onyango et al., 1999; MOALD&M, 1997). The consumption of both vegetables in urban areas is on the rise probably due to rural-urban migration, necessitating market gardening. Moreover, these crops are grown and consumed as leafy vegetables in various parts of Africa and South East Asia (Edmonds and Chweya, 1997; Madisa et al., 1997; Humphry et al., 1997; Mingochi et al., 1997; Chweya and Eyzaguirre, 1999).

These vegetables are good sources of nutrients such as vitamin A, vitamin C, as well as minerals, especially micronutrients such as Fe (Mwajumwa et al., 1991; Chweya, 1985). Besides, these vegetables provide variety in the family diet and help to ensure household food security (Mingochi et al., 1997). Spiderplant and African nightshade are also used for medicinal purposes (Edmonds and Chweya, 1997; Kokwaro, 1993). However, they also contain anti-nutrients such as glucosinolates and nitrates, and phenolic compounds and oxalates, which give the crops an astringent taste (Edmonds and Chweya, 1997).

Growers of spiderplant and African nightshade obtain yields of 1.5-3.0 tons/ha (MOALD&M, 1995; 1998), which are low compared to potential yields of 20-30 tons/ha (Chweya and Mnzava, 1997; Edmonds and Chweya, 1997). The main reasons for the low yields are poor agronomic practices, which include lack of fertilizer use, irrigation and improved varieties. Production of these crops is mainly rainfed. The rainfall is erratic and hence exposes the crops to episodes of drought. Irrigation is therefore necessary to maximize the leaf yields and nutrient content for successful commercialization of these crops. This calls for efficient water management practices considering that water is scarce and the costs of irrigation are high.

Water stress affects various plant processes with the main ones being leaf area development, dry matter partitioning, water relations and transpiration (Fig. 1).

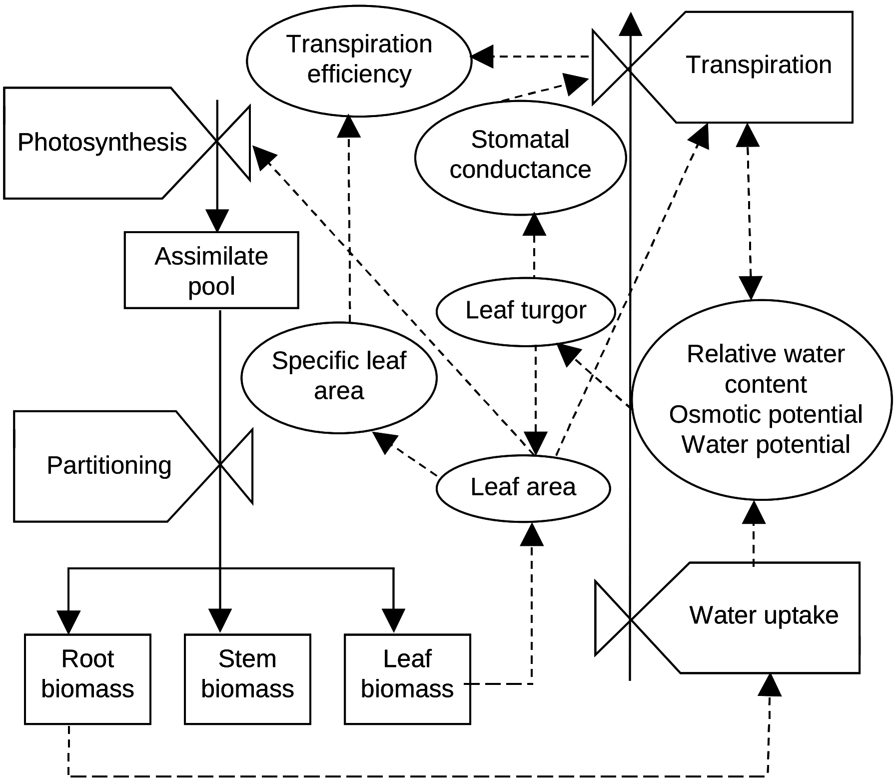

Fig. 1 A schematic presentation of plant processes that are affected by water stress.

Leaf Area Development

Reduction of leaf area is a drought avoidance mechanism, which reduces plant water use rate and hence conserves water during periods of drought (Jones, 1992; Ludlow and Muchow, 1990). This reduction of leaf area is attributed to inhibition of individual leaf expansion and reduced total number of leaves per plant (Belaygue et al., 1996; Chartzoulakis et al., 1993). Reduction of the number of leaves per plant under water deficits can be brought about by reduction of leaf appearance rate, branch formation in species that do branch (or tiller), leaf number per branch, plant height as well as accelerated leaf senescence (Belaygue et al., 1996; Carberry et al., 1993a, b; Pic et al., 2002; Marcelis et al., 1998; Gupta et al., 2001). The extent of reduction of leaf appearance rate depends on the timing and duration of the stress period (Belaygue et al., 1996).

The reduction of individual leaf area involves inhibition of expansive growth of the leaf. Expansive growth results from cell division and enlargement, which involves extensibility of the cell wall under turgor pressure (Pugnaire et al., 1999). Under limited water supply, turgor pressure reduces and growth depends on the rate of water supply (Jones, 1992). In this way, water deficits or other environmental factors such as air humidity that reduce turgor pressure also reduce expansive growth (Turner, 1997; Serpe and Mathews, 2000).

Leaf expansion in a drying soil can be reduced before any measurable decline in leaf water status in some crops (Saab and Sharp, 1989; Dodd et al., 2002). This has been attributed to a non-hydraulic signal produced when roots are growing in a drying or compacted soil, which act to inhibit leaf expansion (Saab and Sharp, 1989; Roberts et al., 2002). The hormone ABA is known to play a major role in this signal, but other hormones, ions and growth inhibitors are known to be involved (Munns, 1992; Davies et al., 2002b). Leaf expansion can also be inhibited by other environmental factors that reduce plant water status, for instance, high evaporative demand (Tardieu et al., 2000; Salah and Tardieu, 1996; Van Volkenburgh, 1999).

Dry Matter Partitioning

By limiting leaf area development, water deficits reduce radiation interception by plants and consequently less biomass is produced as has been reported in most crops (Sadras et al., 1993; Jones, 1992; Singh, 1991; Delfine et al., 2000; Nam et al., 1998; Turc and Lecoeur, 1997). Furthermore, the reduction of stomatal conductance by water deficits leads to reduced carbon assimilation and consequently low biomass production (Delfine et al., 2000; 2001; Medrano et al., 2002; Kumar et al., 1994). Water deficits can also negatively affect the photosynthetic machinery of the plant for instance through inactivation of enzymes (Chaves et al., 2002; Lawlor, 2002; Medrano et al., 2002). This inactivation can be due to an increase in leaf temperature beyond certain threshold, for instance 30°C in maize (Crafts-Brandner and Salvucci, 2002), resulting from reduced transpirational cooling that accompanies reduction of transpiration under water stress (Jones, 1992). Alongside reduced dry matter production, drought also influences dry matter partitioning (Jones, 1992). Many studies indicate that relatively more dry matter is partitioned to the root as compared to the shoot in plants facing drought (Li et al., 1994; Arora and Mohan, 2001; Lehto and Grace, 1994; Wilson, 1988; Wien, 1997). Increase in root to shoot ratio under drought has also been attributed to the fact that shoot growth is more sensitive to increasing soil moisture stress than root growth (Kramer and Boyer, 1995) as has been shown in cowpea (Sangakkara, 1998), French beans (Sangakkara et al., 1996a, b), soybean (Huch et al., 1986) and various C_4 grasses (Fernandez et al., 2002).

Water Relations

The water balance of plants is determined by the difference between transpiration and root uptake (Sinclair and Ludlow, 1985). Under well watered conditions, water is freely available from soil and stomatal conductance is maximum; thus environmental conditions around the shoot determine the rate of transpiration. At this stage, the relative water content (RWC) is maintained above 0.75 (Sinclair and Ludlow, 1986). In a drying soil, the soil hydraulic conductivity declines with the decline in volumetric water content and the rate of water uptake from the soil cannot match the potential transpiration rate. Consequently, stomatal conductance declines in an attempt to balance transpiration rate and the rate of uptake of soil water thus, maintaining RWC above 0.60. Under severe stress, there is stomatal closure and further decline in the plant water status leads to eventual death of the plant (Sinclair and Ludlow, 1986).

Declining plant water status under increasing soil water deficits has detrimental effects on various physiological processes and eventually plant productivity. Lawlor, 2002 has reported that decreasing RWC in a drying soil leads to a decline in stomatal conductance as well as CO_2 assimilation, with these two approaching zero at RWC of 40%. This has been attributed to impaired metabolism (Lawlor, 2002) for example through reduced activity of enzymes involved in assimilation such as Ribulose-1, 5-biphosphate carboxylase/oxygenase (Pary et al., 2002).

Osmotic adjustment (OA) resulting from accumulation of solutes within cells in response to declining water potential helps to maintain turgor of shoot and roots during drought (Jones, 1992; Angadi and Entz, 2002; Flower et al., 1990; Morgan, 1992; McCree and Richardson, 1987; Wright et al., 1997). This allows turgor dependant processes such as stomatal opening and expansive growth to continue at reduced rates under declining water potentials (Jones, 1992; Ludlow and Muchow, 1990). Osmotic adjustment would be of great importance to spiderplant and African nightshade provided that it enables leaf expansion to continue under drought. However, Wullschleger and Oosterhuis (1991) have reported that in bean and pepper, OA was not associated with the maintenance of leaf growth. Similarly, Flower et al. (1990) found that leaf area in sorghum lines with high and low OA capacity was reduced similarly under drought. Other beneficial effects of OA under drought include reduced rate of leaf senescence, enhanced root growth, which enhances water uptake and subsequently yield improvement (Ludlow and Muchow, 1990; Tollenaar and Wu, 1999).

Conversely, OA reduces the ability of the plants to avoid dehydration in the event of terminal drought through the delay in leaf senescence and stomatal closure (Ludlow and Muchow, 1990). In this case, there will be continued water use by the plants leading to progressive decline in leaf water potential, probably causing plant death (Sinclair and Muchow, 2001). The capacity for plants to adjust osmotically when subjected to water deficits is genetically determined, but the extent of OA is an inducible trait (Ludlow and Muchow, 1990). Thus, full expression of the extent of OA requires that drought be imposed slowly (Jones, 1992; Nguyen et al., 1997; Ludlow et al., 1985). Rapid depletion of soil water due to small soil volume or rapidly growing plants leads to lower OA than would be expected as has been observed in wheat and sorghum (Machado and Paulsen, 2001). Thus, the effects of water deficit on plant performance are expected to be minimized under field conditions where plants have access to large volumes of soil as compared to pots (Ludlow et al., 1985).

Water Use

Plant water use is closely correlated with leaf area development rate. Plant species or genotypes with high leaf area development rate also show a high water use rate (Salih et al., 1999). Rajendrudu et al., 1996 reported that high leaf area development rate in spiderplant was associated with high transpiration rate, which was detrimental to the plant’s leaf water status. Thus, high water use may lead to lack of tolerance to water deficits in the event of a drought. Reduction of plant leaf area is therefore, important for the plant’s survival under drought (Sinclair and Muchow, 2001). Water use is also influenced by environmental factors such as radiation, relative humidity and temperature (Salas et al., 2000; Jones, 1992).

The general agreement from studies on many crops is that plant physiological activity is reduced after about two thirds of the extractable soil water in the root zone has been used (Turner, 2000). In this way, transpiration under drought usually declines only when a third of the available water is left in the root zone for many crops (Sadras and Milroy, 1996; Moreshet et al., 1996). Exceptions to this general trend in which transpiration shows higher sensitivity to soil water status have been reported (Henson et al., 1989a; Ameglio et al., 2000). This has been attributed to a non-hydraulic root signal, which entails chemical “messages”, mainly hormones produced in roots growing in a drying soil (Davies et al., 1994; 2002b; Chaves et al., 2002). These provide the shoot with a measure of the water availability and in this way, plants growing in dry soil can reduce their transpiration even with only small changes in soil water potential and before changes in leaf water status (Davies et al., 1994, 2002b).

Abscisic acid (ABA) has been shown to be an essential component of the root signals (Hussain et al., 1999; Davies et al., 1994, 2002b; Henson et al., 1989b; Hartung et al., 2002; Roberts et al., 2002; Bahrun et al., 2002, Masia et al., 1994; Shashidhar et al., 1996; Puliga et al., 1996; Rodrigues et al., 1995; Tardieu and Simonneau, 1998). ABA is known to cause stomatal closure under water stress as well as performing the major role of integrating other plant responses to water stress and other types of environmental stresses (Jones, 1992; Pugnaire et al., 1999; Davies et al., 2002b; Turner et al., 2000).

Transpiration efficiency (TE), the ratio of dry matter produced to total water transpired, is an important aspect involved in adaptation of plants to drought (Jones, 1992; Ehdaie, 1995). Under increasing water deficits, leaf conductance declines leading to reduction of transpiration (Mojayad and Planchon, 1994; Ghannoum et al., 2001). Partial stomatal closure reduces transpiration more than photosynthesis resulting in increases in TE (Nobel, 1999). Increased TE under drought implies that more dry matter is produced for every unit of water used, and this is desirable especially if this dry matter is part of the economic yield (Howell, 2000) e.g. the leaf in the case of spiderplant and African nightshade. Under field conditions, water use involves transpiration and evaporation, hence the term water use efficiency is more appropriate than TE, which involves transpiration alone (Turner, 2000).

Transpiration efficiency depends on the balance between CO_2 assimilation and transpiration, hence is influenced by the photosynthetic pathway. The difference between C_4 and C_3 pathways is that in C_4, CO_2 is concentrated around the site of fixation, resulting in more photosynthesis per unit of water (Kramer and Boyer, 1995). On the other hand, CAM plants concentrate CO_2 by temporarily fixing it at night in organic acids from which it is released the next day for photosynthesis, during which time the stomata are closed and water is conserved. Thus, the magnitude of water use efficiency is expected to be highest in CAM and lowest in C_3 plants (Jones, 1992; Kramer and Boyer, 1995). Genotypic differences in water use efficiency have been reported in various crops (Donatelli et al., 1992; Turner, 1997; Ludlow and Muchow, 1990).

The objectives of this study therefore were to evaluate the adaptive responses of spiderplant and African nightshade and to establish relationships describing the effects of drought on leaf area development, dry matter partitioning, relative water content, osmotic potential, water potential and transpiration under controlled conditions in a glasshouse. In addition, the study also aimed at identifying differences in the adaptation between selected genotypes. A field study was carried out in Kenya, following the glasshouse experiments, to assess the responses of both crop species to drought under uncontrolled conditions with unlimited soil volumes.

In this thesis, chapters two and three address the effect of water stress on plant processes for spiderplant and African nightshade, respectively, under controlled conditions. Chapter four focuses on the responses of both vegetables under field conditions.

2.0 Plant Growth, Water Relations and Transpiration of Spiderplant (*Gynandropsis gynandra* (L.) Briq.) under Water-Limited Conditions

Abstract

Plant growth, relative water content, osmotic potential, water potential and transpiration of spiderplant (*Gynandropsis gynandra* (L.) Briq.) were investigated in a glasshouse study. Two fast growing genotypes (P-landrace and P-commercial), and a slow growing landrace (G-landrace) were grown under droughted and watered conditions. The fraction of transpirable soil water (FTSW) was used as an indicator of water availability. Transpiration was determined by changes in daily pot weights and the ratio of transpiration of droughted to watered plants expressed as normalized transpiration ratio (NTR). The rate of soil drying depended largely on the rate of leaf area development. The fast growing genotypes had a higher rate of soil drying due to a higher rate of leaf area development. Consequently, they were more sensitive to drought stress with NTR beginning to decline at FTSW thresholds of 0.55-0.77 as compared to 0.29 for the slow growing genotype. Leaf expansion in the fast growing genotypes was equally sensitive to drought stress with an FTSW threshold of 0.56. In both genotype groups, leaf appearance was similarly affected by drought stress, with FTSW thresholds of 0.38-0.59. On the other hand, 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.

In all the genotypes, the relative water content (RWC) remained relatively unchanged at the onset of drought, but declined as FTSW fell below 0.3-0.4. Also, osmotic adjustment (OA) was similar in all genotypes and ranged from 0.10-0.33 MPa at the highest drought stress (FTSW = 0). Under severe stress (FTSW<0.40), there were significant reductions of plant leaf area, specific leaf area (SLA) and dry matter production. On the other hand, root to shoot ratio increased under severe stress in both genotype groups. There was an increase in transpiration efficiency of 16-21% for fast growing genotypes and 8% for the slow growing landrace. Thus, spiderplant is mainly a drought avoiding species. In general, it is necessary to keep FTSW above 0.6 in order to maintain leaf expansion, stem elongation, plant water status and transpiration high, and hence to achieve high leaf yields.

2.1 Introduction

Spiderplant (*Gynandropsis gynandra* (L.) Briq.) is an important traditional leafy vegetable crop in Kenya. It forms a substantial part of the diets of most low and middle level income earners in various parts of the country (MOALD&M, 1997). Moreover, it is grown and consumed as a leafy vegetable in most parts of Africa (Schippers, 2000; Chweya and Eyzaguirre, 1999). Production of spiderplant is mainly rainfed leading to exposure of the crop to varying degrees of drought due to unreliable rainfall.

There is only limited information concerning the adaptive responses of spiderplant to drought. The general view is that spiderplant is intolerant to water stress (Waithaka and Chweya, 1991; Chweya and Mnzava, 1997). It exhibits high transpiration rates due to a high leaf area development rate (Rajendrudu et al., 1996). This makes it prone to deterioration in the plant's water status leading to reduced leaf area development and plant growth.

Drought causes reductions of leaf area, dry matter production, decline in plant water status and transpiration. The reduction of leaf area is a drought avoidance mechanism, aimed at reducing plant water use rate and hence conserves 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; Chartzoulakis et al., 1993; Carberry et al., 1993a, b; Pic et al., 2002; Marcelis et al., 1998; Gupta et al., 2001). Reduction of leaf area leads to reduction in the amount of solar radiation intercepted by the crop and consequently less biomass is produced as has been reported in most crops (Turc and Lecoeur, 1997; Sadras et al., 1993; Jones, 1992; Singh, 1991; Delfine et al., 2000; Nam et al., 1998). Furthermore, water deficits cause reduction of stomatal conductance (Jones, 1992), and this leads to reduced carbon assimilation and consequently low biomass production (Delfine et al., 2000; 2001; Medrano et al., 2002; Kumar et al., 1994). Water deficits also influence dry matter partitioning in plants (Jones, 1992). Studies have shown that more dry matter is partitioned to the root as compared to the shoot in plants facing drought (Li et al., 1994; Arora and Mohan, 2001; Lehto and Grace, 1994; Wilson, 1988; Wien, 1997).

In a drying soil, the soil hydraulic conductivity declines and the rate of water uptake from soil by plants cannot match the potential transpiration rate. Stomatal conductance declines, keeping transpiration rate similar to the rate of uptake of soil water, thus maintaining water balance of the plant (Sinclair and Ludlow, 1985). However, under severe stress, the ability of stomates to compensate for declining rate of uptake from the soil gets exhausted leading to deterioration in plant water balance. This causes loss of turgor and has detrimental effects on various physiological processes and eventually plant productivity (Jones, 1992).

Plants respond to declining water potential by accumulation of solutes within cells i.e. osmotic adjustment (OA), in order to maintain turgor of shoot and roots under drought (Jones, 1992). This allows turgor dependant processes such as stomatal opening and expansive growth to continue during periods of water deficits (Jones, 1992; Ludlow and Muchow, 1990). The involvement of OA in maintenance of positive turgor under drought has been reported in crops such as sunflower (Angadi and Entz, 2002), sorghum (Flower et al., 1990), soybean (Morgan, 1992), sugarbeets (McCree and Richardson, 1987) and mustard (Wright et al., 1997).

For many crops, transpiration declines only after a third of the extractable soil water in the root zone has been left (Sadras and Milroy, 1996). However, cases of crops showing a decline in transpiration at higher levels of extractable soil water have been reported (Henson et al., 1989a; Ameglio et al., 2000). This decline precedes changes in the water status of the plant, and is hence attributed to a non-hydraulic root signal produced by roots growing in a drying soil (Davies et al., 1994; 2002b; Chaves et al., 2002).

Increase in transpiration efficiency under drought has been reported in various crops (Jones, 1992). It is attributed to the fact that partial stomatal closure under increasing water deficits leads to more decline in transpiration as compared to dry matter production (Nguyen et al., 1997; Nobel, 1999). In spiderplant, an increase in leaf (edible part) TE would be more desirable as compared to the total plant TE.

The objective of this study therefore was to evaluate the adaptive responses of selected spiderplant genotypes to drought in terms of leaf area development, dry matter production and partitioning, relative water content, water potential, osmotic potential and transpiration. The study aimed at establishing the thresholds of plant available water at which the various parameters began to decline during the drying cycle and to show the effect of drought on dry matter partitioning and transpiration efficiency for spiderplant. In addition, the study also aimed at evaluating any differences in the adaptation between genotypes.

2.2 Materials and Methods

Experimental Design

Two pot experiments were conducted in 2000 and 2002 in a glasshouse at the Institute of Vegetable and Fruit Science, University of Hannover, Germany. Each was a factorial experiment laid out in a completely randomized design with three replications. Two broad groups of spiderplant genotypes were used (Table 1).

Table 1. Summary of the experimental factors for the spiderplant glasshouse experiments in 2000 and 2002 at Hannover (Germany).

Factor	Level	Description
Genotypes	P-landrace (P-land)	Fast growing and high yielding purple stem and petiole landrace
	P-commercial (P-com)	Fast growing purple stem and petiole commercially available genotype
	G-landrace (G-land)	Slow growing green stem and petiole landrace
	P-defoliated (P-def)	P-landrace defoliated to match leaf area of G-landrace
Water levels	Droughted	No watering after start of the treatments
	Watered	Rewatered daily to 90% water holding capacity (WHC)

P-landrace and P-commercial genotypes were used in 2000. In 2002, G-landrace was included, while P-commercial was dropped since its responses were similar to those of P-landrace. 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 of 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.

Water Treatments

Two water levels were used, droughted and watered. The treatments began at 21 days after sowing in both years, just before onset of flowering. At the onset of the treatments, soil moisture in all pots was raised to 100% and 90% water holding capacity (WHC) in 2000 and 2002, respectively. Droughted pots thereafter received no more water, while watered pots were watered daily to maintain the soil moisture at 90% WHC in both years

Sowing and Cultivation Details

Pots made from PVC pipes, 1 m in length and 0.20 m in diameter were filled to a soil bulk density of 1.15 g/cm^3 with loess soil obtained from the Ruthe research station, South of Hannover. The pot water holding capacity (WHC) was 0.30 and 0.28 w/w in 2000 and 2002, respectively. The experiments were conducted in a glasshouse at 26°C day and 20°C night. The weather data were obtained from the weather station in the Institute of Vegetable and Fruit Science, University of Hannover. Seeds of the selected genotypes were sown directly into the pots on 29th May 2000 and 23rd April 2002. The pots were maintained well watered and emergence was observed after four days in both years. Seedlings were then thinned to one per pot two weeks after planting. Nitrogen was applied at rate of 0.5 and 1.0 g N/plant based on soil analysis results in 2000 and 2002, respectively three weeks after planting by irrigating with fertilizer Flory 9 (15% N: 7% P_2O_5: 22% K_2O: 6% MgO). The soil surface was then covered to a depth of about 3 cm with quartz gravel to minimize soil evaporation.

Dates for Harvesting and Sampling for Water Relations Measurements

Five harvests were carried out in both years; at the onset of water treatments, at average soil moisture contents of 70, 60 and 40% WHC and lastly when transpiration in droughted plants was below 10% of that in watered plants. Sampling for water relations measurements was carried out starting from the onset of water treatments, and at average soil moisture contents of 70, 60, 40% WHC in 2000 and 80, 70, 60 and 40% WHC in 2002. The last measurement in both years was carried out when transpiration of droughted plants was below 10% of that of the watered ones. The corresponding days after the start of water treatments at which these harvests and water relations measurements were done are shown in Table 2. In 2002, the time taken to reach specified soil moisture levels for harvesting and sampling for water relations measurements was different between P-landrace, P-defoliated and G-landrace.

Table 2. Dates for harvesting and sampling for water relations' measurements for spiderplant glasshouse experiments in 2000 and 2002. The duration range in 2002 shows time for P-landrace (lower range value) and, P-defoliated and G-landrace (upper range value).

Harvest/sample No.	**Days after the start of water treatments**		
	2000	**2002**	
	Harvest/ water relations	**Harvest**	**Water relations**
1	1	1	1
2	10	10-14	7-10
3	15	13-18	10-14
4	21	17-23	13-18
5	24	22-28	17-23
6	-	-	24-28

Measurements

During the experiment, measurements were made to quantify leaf area development, plant growth, plant water status and transpiration (Table 3).

Table 3. Summary of the measurements done in the spiderplant glasshouse experiments of 2000 and 2002 at Hannover (Germany).

Measurement	**Equipment/Method**
Leaflet length and width (in 2002 only)	Meter rule
Leaf number	Counting of all leaves on the plant
Main stem length	Meter rule
Plant leaf area	Leaf area meter, Model LICOR 3100 (LI-COR Inc., Lincoln, NE, USA)
Leaf water potential	Pressure chamber
Osmotic potential	C52-chamber, Wescor-Corp
Pot weight	Weighing balance, model QS 64B, capacity 64 kg±5 g (Sartorius, Germany)

Soil Water Status

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

$$\mathrm{FTSW} = \frac{\text{pot weight at day i} - \text{final pot weight}}{\text{initial pot weight} - \text{final pot weight}} \qquad (1)$$

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

Plant Growth

Leaf length (L) and width at the widest part of the blade (W) of the central leaflet of leaf numbers 10, 11 and 12 from the base, number of leaves and plant height were determined daily on 5-7 plants for each treatment until increases in these parameters stopped in droughted plants. The leaflet area (LA) was estimated as the product of L and W. A linear relationship between LA and actual leaf area (measured by a leaf area meter Model LI-COR 3100) was established on individual leaves (n=68 and 113 for P-genotypes and G-landrace, respectively) using the linear regression procedure (SAS, 1999). The differences in LA, number of leaves and plant height between two consecutive days were taken as the leaf expansion, leaf appearance and stem elongation rates (LER, LAR and SER), respectively. Relative rates were calculated as:

$$\mathrm{RLER} = \frac{\mathrm{LER_d}}{\mathrm{LER_w}} \qquad 2a$$

$$\mathrm{RLAR} = \frac{\mathrm{LAR_d}}{\mathrm{LAR_w}} \qquad 2b$$

$$\mathrm{RSER} = \frac{\mathrm{SER_d}}{\mathrm{SER_w}} \qquad 2c$$

where RLER, RLAR and RSER are the relative leaf expansion, leaf appearance and main stem elongation rates and subscripts d and w refer to watered and droughted treatments.

The relative rates were then expressed as functions of FTSW.

Plant leaf area and biomass were determined during the destructive harvesting. Plants were cut at the base and separated into petioles, stems and blades. Roots were carefully picked by hand and washed. All plant parts were then dried at 100°C for 48 hours and weighed. Specific leaf area (SLA) was determined at individual harvests by dividing plant leaf area and dry weight of leaf blades (Hunt, 1982)

Root to shoot ratio was expressed in terms of dry weights at each harvest. The data were transformed to natural logarithms before analysis of variance (Poorter and Nagel, 2000; Hoffmann and Poorter, 2002).

Water Relations

Water relations' measurements were done on young fully expanded leaves between 11.00 and 15.00h. For 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 hours. The turgid weight was obtained after blotting; thereafter the leaves were dried at 100°C to a constant weight to obtain the dry weight (Cohen et al., 1999). RWC was then calculated as:

$$\mathrm{RWC} = \frac{\text{fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \tag{3}$$

For measurement of osmotic potential, leaf discs of 1 cm diameter obtained using a cork borer from young fully expanded leaves were put in aluminium foil and immediately kept in liquid nitrogen. Osmotic potential was then measured at 22°C with a psychrometer (C52-chamber, Wescor-Corp). 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 droughted and watered plants is given by:

$$\mathrm{OP}_{100\mathrm{w}} = \mathrm{OP}_{\mathrm{w}} \times \mathrm{RWC}_{\mathrm{w}} \tag{4}$$

$$\mathrm{OP}_{100\mathrm{d}} = \mathrm{OP}_{\mathrm{d}} \times \mathrm{RWC}_{\mathrm{d}} \tag{5}$$

where OP_{w} and OP_{d} refer to measured osmotic potential for watered and droughted plants, respectively.

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

$$\mathrm{OA} = \mathrm{OP}_{100\mathrm{w}} - \mathrm{OP}_{100\mathrm{d}} \tag{6}$$

Leaf water potential (WP) was measured by the pressure chamber method. A young fully expanded leaf was cut and immediately placed in the pressure chamber and pressure at which a drop of water formed at the cut end of the leaf was recorded as the leaf water potential. The RWC of droughted plants was divided by that of watered plants to give RWC ratio, which was then expressed as a function of FTSW.

Transpiration

Transpiration was determined by daily pot weight measurements. In this case, the difference in weights between two consecutive days was considered as the water lost through transpiration. The transpiration data was analysed using the double normalization procedure outlined by Ray and Sinclair (1998). First the ratio of transpiration in droughted to watered plants was determined as shown in equation 6.

$$\text{Transpiration ratio (TR)} = \frac{\text{transpiration of droughted plants}}{\text{average transpiration of watered plants}} \qquad (7)$$

A second normalization was done so that the TR rate 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 pot for the period when soil moisture was high, and then the daily TR for each pot was divided by this mean TR to give a daily normalized transpiration ratio (NTR). Transpiration efficiency (TE) was determined as the slope of the linear function between dry matter produced (DM) and cumulative transpiration (CT).

Data Analyses

Statistical analysis was performed using the GLM procedure of SAS (SAS, 1999). An ANOVA was executed with factorial design for each date separately. The relationships between relative parameters, i.e. RLER, RLAR, RSER, relative water relations and NTR, and fraction of transpirable soil water (FTSW) were developed using plateau linear regression using the non linear procedure of SAS as shown in equation 7.

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

where A is the slope of the linear decline, and FTSW_t is the FTSW threshold at which the relative parameter began to decline.

R^2 values were calculated as:

$$R^2 = \frac{SSE}{CSE} \tag{9}$$

where SSE is the sum of squares of the residual, CSE is the corrected sum of squares.

2.3 Results

Soil Water Extraction

The decline in FTSW over time in the droughted treatments was similar among the P-genotypes (P-landrace and commercial) in 2000. In the 2002 experiment, P-landrace had higher water use rate than G-landrace and this resulted in the P-landrace having a faster rate of soil drying (Fig. 2a). However, when P-landrace was defoliated (P-defoliated) to have similar leaf area development as G-landrace, the two had similar water use patterns.

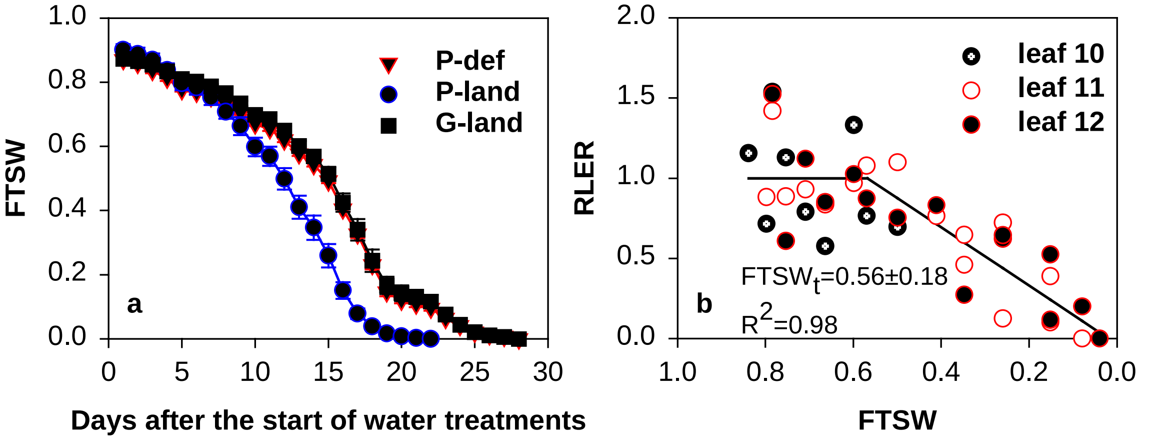

Fig. 2. The decline in fraction of transpirable soil water (FTSW) of genotypes P-defoliated (P-def), P-landrace (P-land) and G-landrace (G-land) under droughted conditions (a) and the relative leaf expansion rate (RLER) of P-landrace as a function of FTSW (b) for spiderplant grown in the glasshouse in 2002. Points are means of FTSW and RLER (n=5-6), vertical bars show standard errors (a), $FTSW_t$=threshold ± 95% confidence interval and line=plateau regression function (b).

Leaf Area Development and Stem Elongation

Expansion of the selected leaves for P-landrace was significantly reduced by drought (Fig. 2b). In contrast, the selected leaves for G-landrace and defoliated P-landrace expanded to completion before any noticeable effect of drought.

However, the whole plant leaf area showed no significant interactions and hence only main effects are considered for both years. Droughted plants began having significantly lower leaf area at harvest three in 2000 and harvest four in 2002 (Fig. 3a, b). Plant leaf area was similar between P-landrace and P-commercial genotypes. However, in the 2002 experiment, P-landrace had significantly higher plant leaf area than G-landrace and P-defoliated in the early stages of growth (Fig. 3c). Plant leaf area in the droughted treatment was only 17-18% of that in watered treatment for all genotypes at harvest five in both years.

Drought significantly reduced leaf appearance in both years (Fig. 3d-f). The FTSW thresholds for leaf appearance rate showed no significant differences between genotypes (Table 4). Specific leaf area (SLA) of watered plants remained high and was more or less constant for all the genotypes in both years. Under droughted conditions, SLA was equally high until harvest three in 2000 and harvest four in 2002, after which it declined significantly (Fig. 4a, b). This coincided with FTSW values falling below 0.4 for P-landrace and commercial, and 0.2 for G-landrace and P-defoliated as shown by the relationship of the SLA of droughted to watered plants (relative SLA) and FTSW (Fig. 4c, d). Drought significantly reduced stem elongation of spiderplant in both years (Fig. 5). G-landrace had a significantly lower FTSW threshold for stem elongation than the P-genotypes (Table 4).

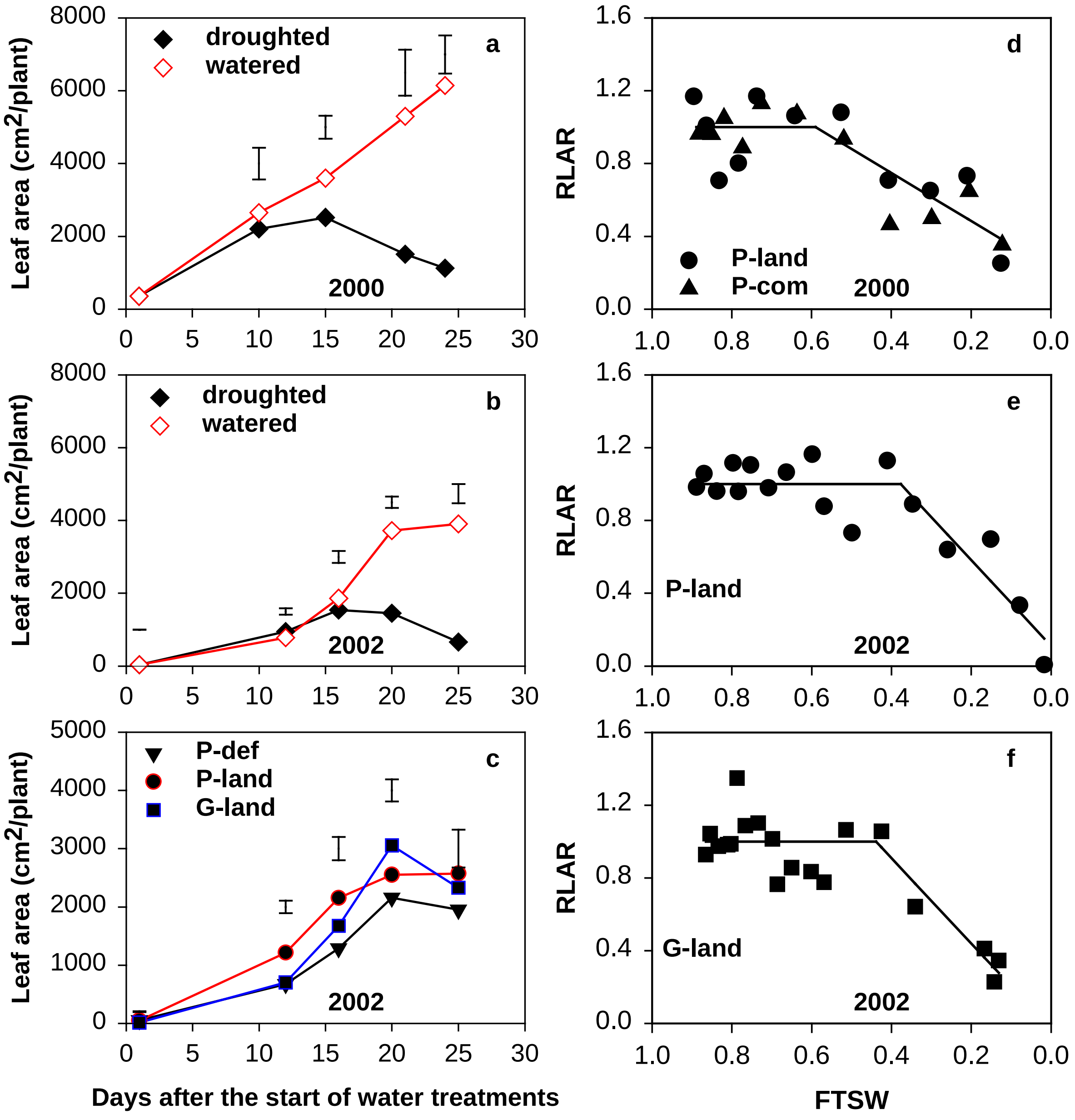

Fig. 3. Plant leaf area of spiderplant grown in the glasshouse as influenced by water levels (means across genotypes) (a, b) and genotypes (means across water levels) (c) and relative leaf appearance rate (RLAR) as a function of FTSW for spiderplant genotypes (d-f) in 2000 and 2002. Vertical bars show $LSD_{0.05}$ and days after the start of water treatments for 2002 are averages shown in Table 2. Lines in d, e and f show plateau regression functions (regression coefficients are shown in Table 4).

Table 4. The fraction of transpirable soil water threshold for leaf appearance and stem elongation rates decline ($FTSW_t$) and the slope of the decline (A) for spiderplant grown in the glasshouse in 2000 and 2002. The 95% confidence intervals are shown in parentheses.

Year	**Genotype**	**Slope (A)**	**$FTSW_t$**	**R^2**
Leaf appearance				
2000	P-landrace /commercial	1.32 (0.38-2.26)	0.59 (0.37-0.81)	0.95
2002	P-landrace	2.36 (1.33-3.38)	0.38 (0.27-0.48)	0.98
	G-landrace	2.34 (1.22-3.45)	0.44 (0.33-0.55)	0.97
Stem elongation				
2000	P-landrace /commercial	1.60 (0.64-2.57)	0.53 (0.37-0.68)	0.96
2002	P-defoliated	2.11 (0.81-3.40)	0.35 (0.21-0.49)	0.98
	P-landrace	2.46 (1.63-3.28)	0.36 (0.28-0.44)	0.99
	G-landrace	5.27 (1.67-8.86)	0.20 (0.14-0.25)	0.98

Dry Matter Partitioning

The root to shoot ratio was significantly higher in droughted than watered plants from harvest three in 2000 and harvest four in 2002 (Fig. 6a, b).

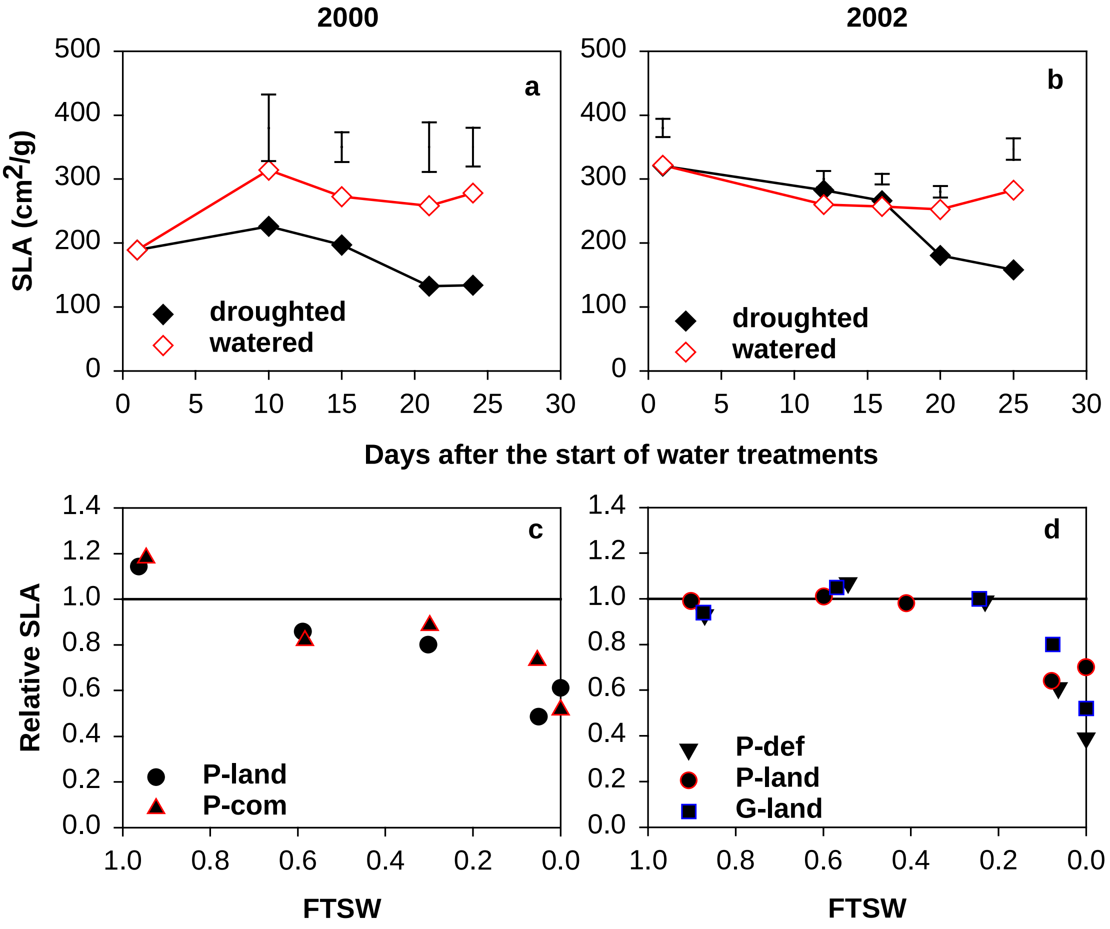

Fig. 4. Specific leaf area (SLA) of spiderplant (means across genotypes) grown in the glasshouse under droughted and watered conditions (a, b) and the scatter diagrams of relative SLA of genotypes P-landrace (P-land), P-commercial (P-com), P-defoliated (P-def) and G-landrace (G-land) as functions of FTSW (c, d) in 2000 and 2002. Vertical bars in a and b show $LSD_{0.05}$ and lines in c and d show relative SLA=1. Days after the start of water treatments for 2002 are averages shown in Table 2.

Water Relations

There were no significant interactions or genotype effects for the water relations of spiderplant, hence only the water treatment effects are considered. Drought reduced the relative water content (RWC) significantly, from 10 and 20 days after the start of water treatments in 2000 and 2002, respectively for all spiderplant genotypes (Fig. 7a, b). The difference in the osmotic potential at full turgor (OP) between watered and drought plants was significant at 24 days after the start of water treatments in 2000, giving an OA of 0.10 MPa (Fig. 7c). Similarly, OA was observed in the 2002 experiment, significant from 20 days after the start of water treatments (Fig. 7d). In this case, OA at the end point was 0.33 MPa. The ratio of RWC between droughted and watered was related to FTSW. The FTSW thresholds at which these ratio changed from unity could not be determined precisely in the 2000 experiment due to few and unevenly distributed data points. In general however, the relationship show that RWC ratio changed as FTSW fell below 0.6 (Fig. 7e). In the 2002 experiment, the FTSW thresholds at which the RWC ratio changed was relatively lower and showed no significant differences between the genotypes (Fig. 7f and Table 5).

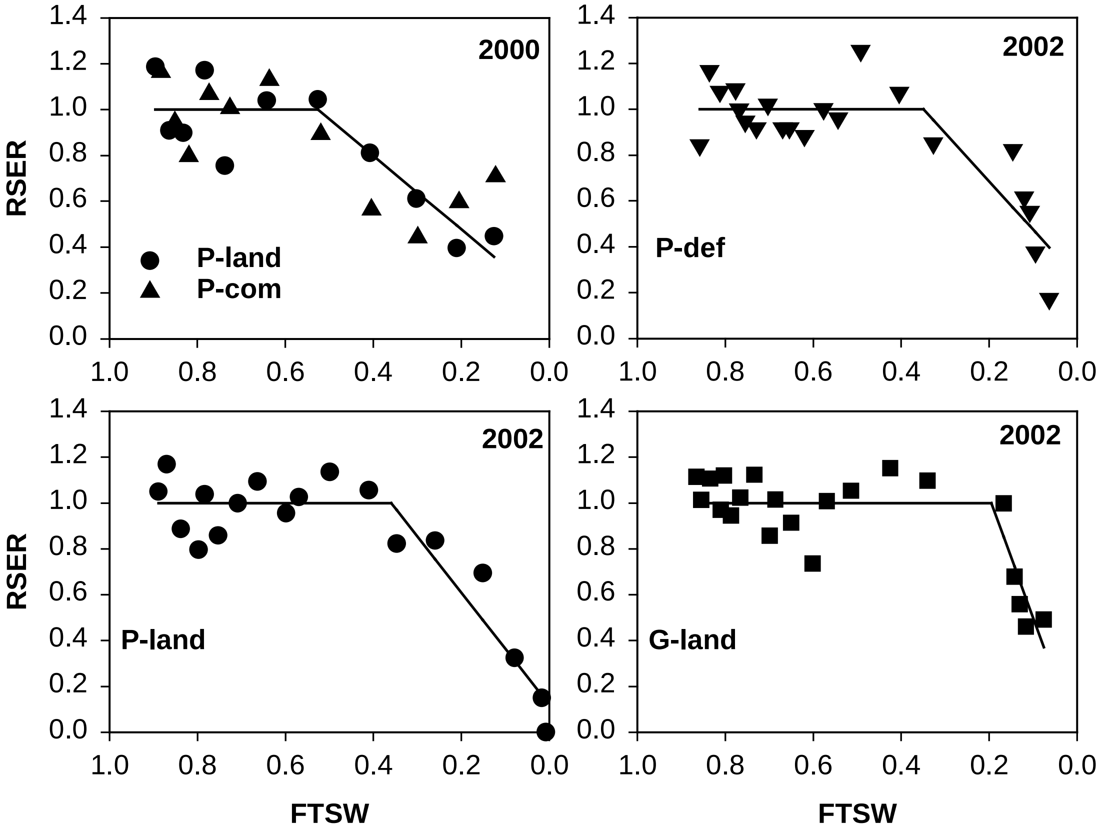

Fig. 5. Relative main stem elongation rate (RSER) as a function of FTSW for spiderplant genotypes P-landrace (P-land), P-commercial (P-com), P-defoliated (P-def) and G-landrace (G-land) grown in the glasshouse in 2000 and 2002. Lines show plateau regression functions (regression coefficients are shown in Table 4).

Water potential (WP) is shown for the 2000 experiment only due to unrealistic values obtained in 2002. Drought caused a decline in WP, significantly from 10 days after the start of water treatments in 2000 (Table 6).

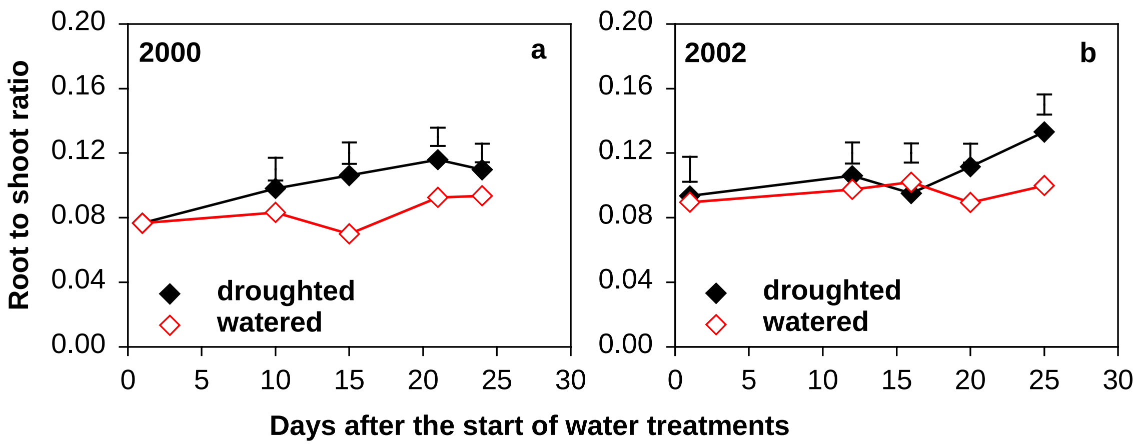

Fig. 6. The root to shoot ratio of spiderplant grown in the glasshouse under droughted and watered conditions (means across genotypes) in 2000 (a) and 2002 (b). Vertical bars show $LSD_{0.05}$ and days after the start of water treatments for 2002 are averages shown in Table 2.

Table 5. The fraction of transpirable soil water threshold value for RWC ratio decline ($FTSW_t$) and the slope of the decline (A) for spiderplant genotypes grown in the glasshouse in 2002. The 95% confidence intervals are shown in parentheses.

Genotype	**Slope (A)**	**$FTSW_t$**	**R^2**
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

Transpiration and Transpiration Efficiency

The effect of drought on transpiration was similar between P-landrace and P-commercial genotypes in 2000. In both years, P-landrace and P-commercial had significantly higher FTSW thresholds at which NTR began to decline as compared to the G-landrace (Fig. 8 and Table 7). However, when defoliated, P-landrace had FTSW threshold similar to that of G-landrace.

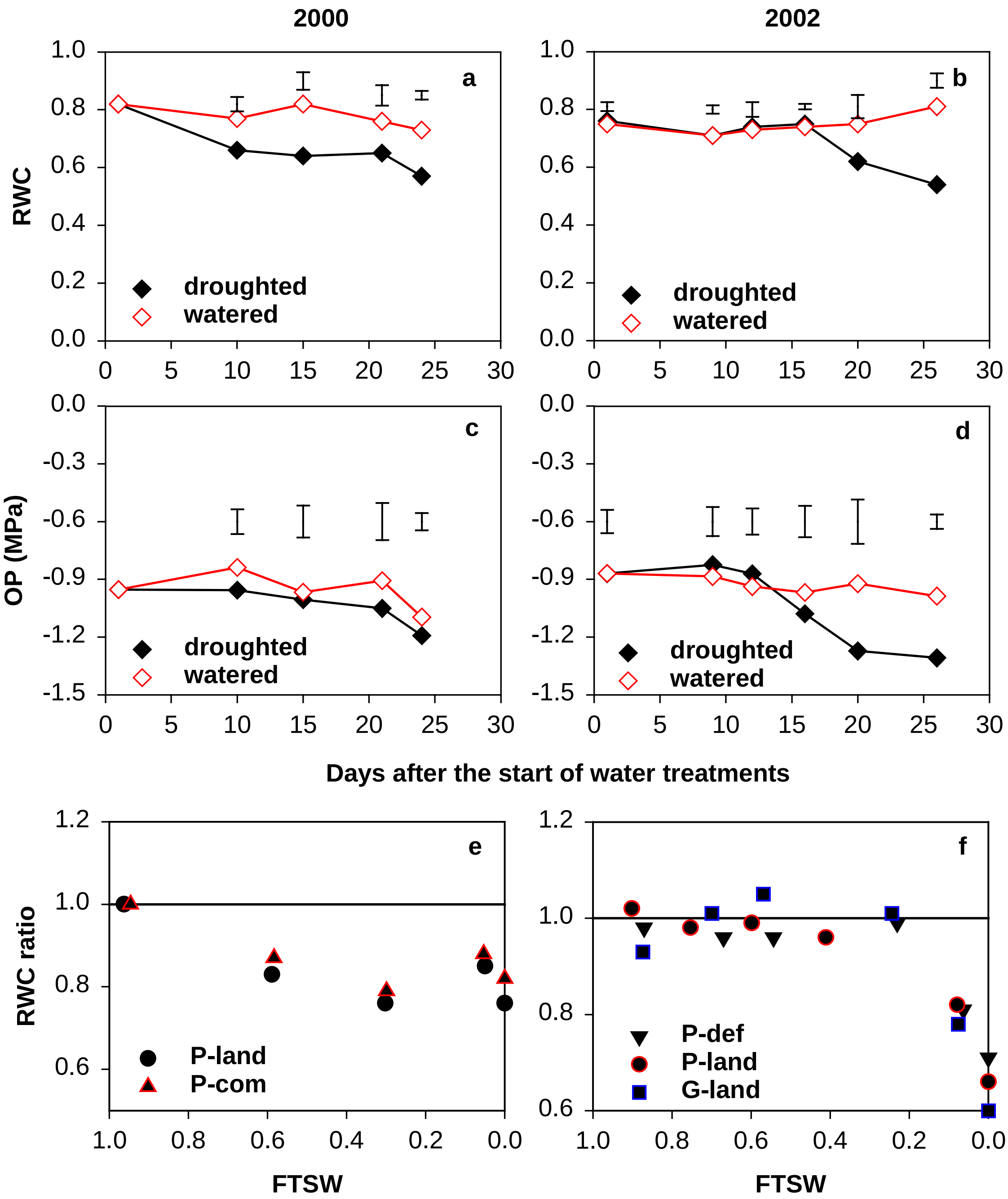

Fig. 7. The relative water content (RWC) and osmotic potential at full turgor (OP) of spiderplant grown under droughted and watered conditions (means across genotypes) (a-d) and the scatter diagrams of the ratio of RWC of drought to watered plants as functions of FTSW for spiderplant genotypes P-landrace (P-land), P-commercial (P-com), P-defoliated (P-def) and G-landrace (G-land) (e, f) grown in the glasshouse in 2000 and 2002. Vertical bars show $LSD_{0.05}$ and days after the start of water treatments for 2002 are averages shown in Table 2, lines in e and f show ratio=1.

In both years, transpiration efficiency (TE) was higher in the droughted as compared to the watered treatment for all genotypes, being significant only for the P-genotypes (Fig. 9 and Table 8). The P-genotypes increased their TE under drought by 21% in 2000 and 16% in 2002 as compared to watered conditions. On the other hand, G-landrace showed an increase of only 8%. Overall, both purple stem and petiole, and green stem and petiole genotypes had similar transpiration efficiencies at similar water levels.

Table 6. The leaf water potential (WP) (means across genotypes) of spiderplant grown in the glasshouse in 2000.

WP (-MPa)					
Days after the start of water treatments					
Water level	**1**	**10**	**15**	**21**	**24**
Droughted	0.86	0.97a	1.28a	1.44a	2.01a
Watered	0.86	0.61b	0.51b	0.46b	0.64b
$LSD_{0.05}$	-	0.14	0.11	0.16	0.12

Means followed by the same letter within the column are not significantly different ($P<0.05$).

2.4 Discussion

Water Use

Water use under droughted conditions depended largely on leaf area. In 2000, both P-landrace and P-commercial had similar leaf area development and consequently similar water use patterns. However, in 2002, G-landrace had smaller leaf area at onset of water treatments and had a slower leaf area development in the early stages of the experimental period. It therefore had lower soil drying rate when compared with P-landrace at similar dates. The P-defoliated had similar soil drying rate as G-landrace. Turner et al. (1987) have similarly reported that in lupins, species with large leaf area showed a faster rate of soil drying.

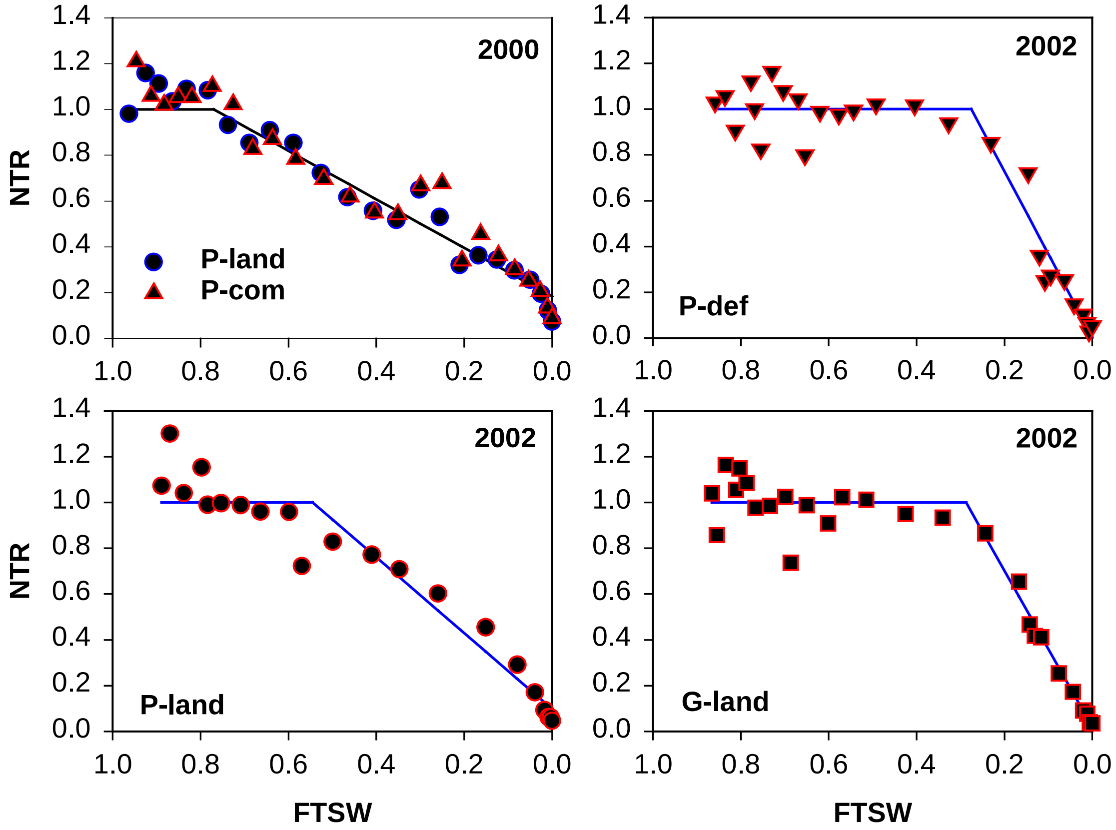

Fig. 8. Normalized transpiration ratio (NTR) as a function of fraction of transpirable soil water (FTSW) for spiderplant genotypes P-landrace (P-land), P-commercial (P-com), P-defoliated (P-def) and G-landrace (G-land) grown in the glasshouse in 2000 and 2002. Lines show plateau regression functions (regression coefficients are shown in Table 7).

Table 7. The fraction of transpirable soil water threshold value ($FTSW_t$) at which normalized transpiration ratio (NTR) began to decline and the slope of the decline (A) for spiderplant grown in the glasshouse in 2000 and 2002. The 95% confidence intervals are shown in parentheses.

Year	**Genotype**	**Slope (A)**	**$FTSW_t$**	**R^2**
2000	P-landrace/P-commercial	1.04 (0.85-1.24)	0.77 (0.67-0.86)	0.99
2002	P-defoliated	3.61 (2.77-4.45)	0.28 (0.23-0.32)	0.99
	P-landrace	1.65 (1.25-2.06)	0.55 (0.44-0.64)	0.99
	G-landrace	3.42 (2.72-4.11)	0.29 (0.24-0.33)	0.99

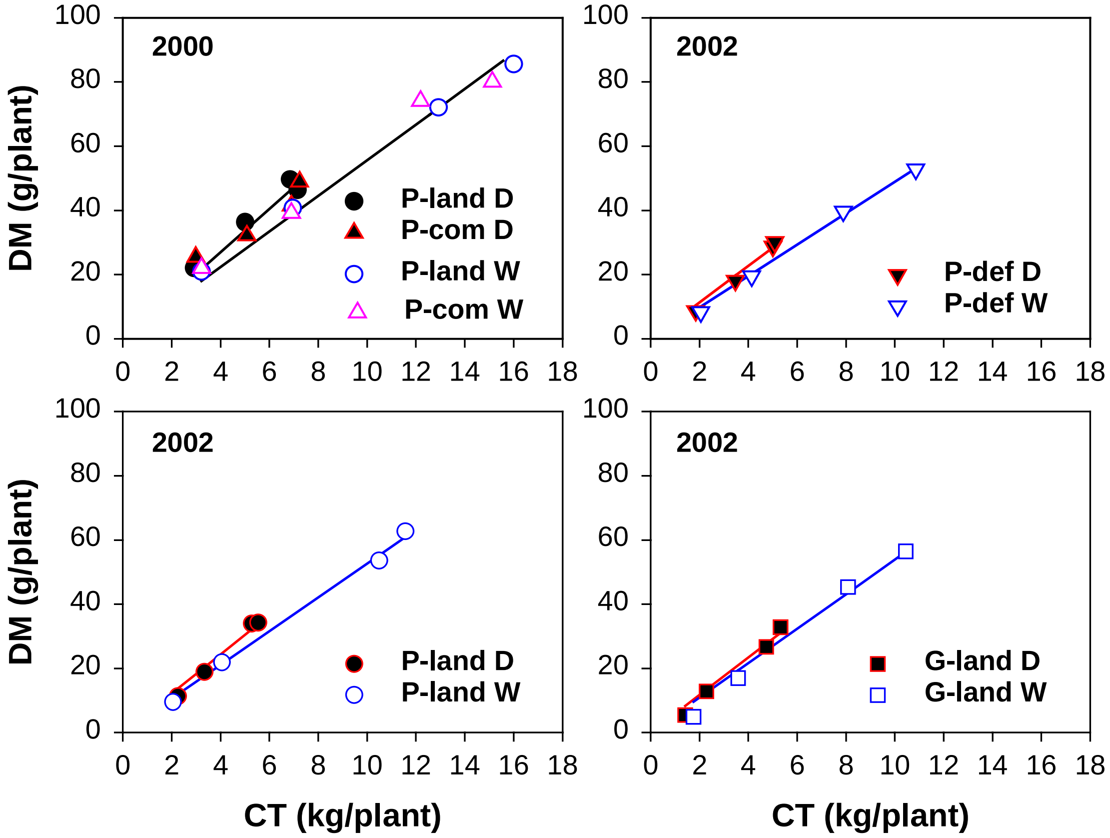

Fig. 9. The relationship between plant dry matter produced (DM) and cumulative transpiration (CT) of spiderplant genotypes P-landrace (P-land), P-commercial (P-com), P-defoliated (P-def) and G-landrace (G-land) grown in the glasshouse under droughted (D) and watered (W) conditions in 2000 and 2002. Lines are linear functions (regression coefficients are shown in Table 8).

Leaf Area Development

Leaf area development directly affects 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). The expansion of selected leaves for P-defoliated and G-landrace was completed before any measurable effect of drought due to a slower rate of soil drying in these genotypes. On the other hand, the higher rate of soil drying for P-landrace led to relatively higher FTSW threshold at which expansion of selected leaves declined under droughted conditions. This threshold was comparative to that for transpiration suggesting that the two processes showed equal sensitivity to drought in this genotype. Similar results have been reported for crops such as maize (Muchow and Sinclair, 1991), pea (Lecoeur and Sinclair, 1996), legumes such as soybean, cowpea and blackgram (Sinclair et al., 1987). However, leaf expansion has been reported to be more sensitive to drought, preceding declines in stomatal conductance and transpiration in other crops (Munns and Sharp, 1993; Liu, 2000; Rosenthal et al., 1987; Soltani et al., 1999).

Table 8. The slope (A), its standard error (SE) and R^2 for the linear relationship between plant dry weight and cumulative transpiration of spiderplant genotypes grown in the glasshouse in 2000 and 2002.

Year	**Genotype**	**Water level**	**Slope (A)**	**SE**	**R^2**
2000	P-landrace/commercial	Droughted	6.74a	0.20	0.99
		Watered	5.57b	0.17	0.99
2002	P-defoliated	Droughted	5.66a	0.20	0.99
		Watered	4.88b	0.09	0.99
	P-landrace	Droughted	6.09a	0.23	0.99
		Watered	5.26b	0.10	0.99
	G-landrace	Droughted	5.82a	0.27	0.99
		Watered	5.38a	0.23	0.99

Slopes followed by the same letter within a genotype are not significantly different ($P<0.05$).

The decline in leaf expansion of P-landrace preceded the decline in RWC, although the FTSW thresholds had overlapping 95% confidence intervals. Reduction of leaf growth in drying soil before changes in water status is usually attributed to non-hydraulic root signals (Kuang et al., 1990; Munns et al., 2000; Saab and Sharp, 1989; Bacon et al., 1998; Puliga et al., 1996). In this study, the evidence for such signals is not strong. Thus, the reduction of leaf expansion could have been partly due to hydraulic signals as has been reported by various authors (Salah and Tardieu, 1997; Volkmar, 1997; Passioura and Munns, 2000; Puliga et al., 1996; Sadras et al., 1993; McCree and Richardson, 1987; Melkonian and Wolfe, 1995).

The reduction of plant leaf area before onset of leaf senescence and shedding (FTSW>0.40) was mainly due to the reduction of leaf appearance and stem elongation rates, and the rate of expansion of the leaves initiated after onset of drought. Severe drought stress (FTSW<0.40) caused a rapid decline in the plant leaf area mainly due to leaf senescence and shedding. The overall effect was a drastic reduction of transpiration. This is usually associated with water conservation and is part of drought avoidance mechanisms (Dosmann et al., 1999). This sequence of events as the stress intensified is similar to what has been reported by Borell et al. (2000) and Rosenthal et al. (1987). The reduction of SLA under drought observed in this study coincided with leaf shedding as the stress intensified. This implies that the reduction was mainly due to shedding of old leaves leaving new leaves, which were smaller and thicker (Husain et al., 1990).

The stem elongation rate of P-landrace similarly declined at higher FTSW thresholds and hence was more sensitive to drought as compared to that of G-landrace. This could have been due to the fact that G-landrace plants were shorter than P-landrace.

Dry Matter Partitioning

The increase in root to shoot ratio under severe stress was mainly due to differential sensitivity of the root and shoot biomass production to drought. At maximum stress (FTSW=0), the root biomass reduced by 28-32% as compared to 42-45% for shoot biomass. This differential sensitivity has also been reported in crops such as wheat (Blum and Sullivan, 1997), cowpea (Sangakkara, 1998) and beans (Boutraa and Sanders, 2001).

Water Relations

Measures of relative water content (RWC), osmotic potential at full turgor (OP) and water potential (WP) are indices of plant water status, which are useful in monitoring the development of stress in plants growing under droughted conditions (Jones, 1992). In the early stages of the drying cycle, the RWC was generally high (above 0.71). As the FTSW declined below the thresholds, the plants lost turgor with RWC reaching lowest values (0.54-0.57) when all the plant available water had been used up. Similar results have been reported for peanut (Erickson et al., 1991; Awal and

Ikeda, 2002), vegetable amaranth (Liu, 2000), soybean (Luquez and Guiamet, 2002) and oilseed rape (*Brassica napus* L.) (Jensen et al., 1996).

The osmotic adjustment (OA) values of 0.10-0.33 MPa for spiderplant are relatively low compared to values for crops with high OA capacity. This low value of OA suggests that spiderplant relies less on osmotic adjustment for its adaptation to drought. Moreover, this OA could not sustain turgor in spiderplant leaves beyond water potential of -2.01 MPa and RWC of 0.54-0.57. This is in the range of leaf water status at permanent wilting point for other crop species with similar low OA capacity (Moustafa et al., 1996; Kumar and Elston, 1992; Ludlow et al., 1983; Allen, et al., 1998; Premachandra et al., 1995; Awal and Ikeda, 2002; Blum, 1989; Jensen et al., 1996; Davies et al., 2002a; Wullschleger and Oosterhuis, 1991; Shackel and Hall, 1983; McCree and Richardson 1987). Plant species with a higher degree of OA are able to tolerate lower leaf water potentials as has been shown in vegetable amaranth (Liu, 2000), sorghum (Girma and Krieg, 1992) and wheat (Entz and Fowler, 1990; Gesch et al., 1992). 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.

Transpiration

Reduction of transpiration under droughted conditions is usually correlated with reduction of dry matter production since cumulative transpiration is linearly related to dry matter production (Jones, 1992). P-genotypes showed relatively higher FTSW thresholds for transpiration (0.55-0.77) as compared to G-landrace (0.29). The latter was therefore comparable to the widely reported threshold range of 0.3-0.4 for decline in transpiration for crops such as maize (Muchow and Sinclair, 1991; Ray and Sinclair, 1997; 1998; Ray et al., 2002), wheat (Sadras and Milroy, 1996), sorghum (Rosenthal et al., 1987; Sadras and Milroy, 1996; Nable et al., 1999), various legumes (Sinclair and Ludlow, 1986; Sinclair et al., 1998, Lecoeur and Sinclair, 1996), vegetable amaranth (Liu and Stützel, 2002) and cotton (Rosenthal et al., 1987). On the other hand, the thresholds for P-genotypes were similar to those reported for a sensitive maize hybrid (Ray and Sinclair, 1997), field chickpea (Soltani et al., 1999) and sugarcane (Nable et al., 1999).

The higher sensitivity of transpiration in P-landrace and commercial genotypes to drought as compared to the G-landrace was related to leaf area development as clearly shown by the similarity between P-defoliated and G-landrace. The faster leaf area development in P-landrace led to a higher rate of soil drying causing it to reach the endpoint 4-6 days 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 the normalized transpiration ratio (NTR) and the 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 uneven and this may have important effects on the NTR-FTSW relationship (Lecoeur and Sinclair, 1996).

The rooted depth in both purple stem and petiole and green stem and petiole genotypes was similar at the early stages of the plant growth as observed during harvests. Consequently, water uptake was probably occurring at similar depths (Penning de Vries et al., 1989). 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). Soil drying reduces the hydraulic conductivity of soil (Li et al., 2002) leading to the reduction of soil water supply to the plant (Sinclair and Ludlow, 1986). This means that the P-genotype plants suddenly could not obtain sufficient water in the root zone to satisfy transpiration requirement and had to adapt by reducing transpiration even though moisture was still high at lower layers (Cantore et al., 2000; Jones and Tardieu, 1998). Thus, the higher FTSW thresholds for P-landrace could have been due to non-hydraulic root signals. However, the evidence for these signals was not strong since the thresholds for decline in transpiration and RWC were not statistically different.

The higher FTSW thresholds for transpiration of P-genotypes in 2000 could be attributed to the higher evaporative demand as compared to 2002. In 2000, the relative humidity (RH) was in the range of 50-70% and the total radiation was

99190.5 W/m^2 during the experimental period, while in 2002, the RH range was 60-80% with a total radiation of 75743.0 W/m^2 (Appendix 1). Plants can respond to a high evaporative demand by generation of hormonal signals and hence cause leaf responses, which may not be related to the soil water status (Sadras and Milroy, 1996; Franks and Farquhar, 1999). Leaf responses under high evaporative demand can also be due to increased sensitivity to ABA and also increased ABA delivery rate to leaves via a more rapidly moving transpiration stream (Davies et al., 2002b). However, there are also reports of high evaporative demand causing no leaf responses (Ray et al., 2002).

P-genotypes showed the potential to significantly increase their transpiration efficiency (TE) under drought as compared to G-landrace. Increase in TE is a drought adaptation mechanism that leads to production of more dry matter per unit of water transpired (Jones, 1992). TE depends on the balance between photosynthesis and transpiration both of which depend on stomatal conductance (Nobel, 1999; Ludlow and Muchow, 1990). Stomatal conductance is sensitive to water stress and this is partly responsible for the reduction of both photosynthesis and transpiration under drought (Jones, 1992). Under moderate stress, stomatal conductance can reduce at little cost to assimilation rate as has been found in wild rice species (Nguyen et al., 1997). This results in a higher dry matter production relative to transpiration, hence a higher TE under drying soil as compared to under well-watered conditions.

Increases in TE or the wider term, water use efficiency, have been reported by various authors (De Costa and Linyanage, 1997; Clifton-Brown and Lewandowski, 2000; Arndt et al., 2000; Davies et al., 2002a; Fernandez et al., 2002; Li et al., 2000; Johnson and Tieszen, 1994). However, Liu and Stützel (2002) have reported no effect of drought on TE of vegetable amaranth.

Differences between the genotypes were limited mainly to leaf area development in the early stages of growth and could have been due to differences in seed size. The seed size of P-genotypes was almost double that of G-landrace (the weight of 1000 seeds was 1.42±0.02 g for P-genotypes and 0.63±0.01g for G-landrace, n=3). A larger seed size is usually associated with greater vigour of the plant in the seedling stages. Thus, seedlings from large seeds are usually bigger in sizes as compared to those from small seeds (Karaki and Ghazi, 1999; Chastain-Thomas et al., 1995). In this case, large seeds have a higher initial capital of food reserves as compared to small seeds, hence the higher growth rate of seedlings (Bhattacharjee et al., 2000).

2.5 Conclusion

Drought significantly reduced the rates of leaf expansion, leaf appearance and stem elongation of spiderplant. The onset of reduction of leaf expansion occurred after about 40% of the transpirable soil water had been used for P-landrace. The response of leaf appearance rate to drought was similar between the genotypes, beginning to decline after about 40-60% of the transpirable soil water had been used. Stem elongation on the other hand was less sensitive to drought for the green stem and petiole genotype, starting to decline after about 80% of the transpirable soil water had been used as compared to 40-60% for the purple stem and petiole genotype. Drought also reduced SLA and enhanced leaf senescence and shedding, with both occurring simultaneously after the plants had used up 70% of the transpirable soil water.

Plant dry matter production was reduced under severe drought after the plants had used up about 70% of the transpirable soil water. This was accompanied by an increase in root to shoot ratio. Osmotic adjustment was limited with values of 0.10-0.33 MPa at maximum stress (FTSW=0). Purple stem and petiole genotypes were more sensitive to drought with their transpiration beginning to decline after 20-40% of the transpirable soil water had been used as compared to 70% for green stem and petiole genotype. At the same time, drought caused increases in TE for both genotypes.

It can therefore be concluded that spiderplant adapt to drought mainly by regulating transpiration through reduction of leaf area and possibly stomatal conductance. Fast growing genotypes (P-landrace and commercial) tend to exhaust soil moisture in the root zone more rapidly as compared to the slow growing genotype (G-landrace). Consequently, under drought the fast growing genotypes are expected to reduce their leaf growth and transpiration early in order to slow down the development of water deficit. To prevent decline in leaf growth, it is necessary to keep the fraction of transpirable soil water (FTSW) above of 0.6 for P-landrace and commercial and 0.4 for G-landrace (50-60% water holding capacity). This will also keep transpiration and plant water status high, prevent reduction of dry matter production and lead to higher leaf yields.

3.0 Plant Growth, Water Relations and Transpiration of Two Species of African Nightshade (*Solanum villosum* Mill. subsp. *miniatum* (Bernh. Ex Willd.) Edmonds and *S. sarrachoides* Sendtn.) under Water-Limited Conditions

Abstract

The adaptation to drought stress of two African nightshade species, *Solanum villosum* and *S*. *sarrachoides* was investigated in a glasshouse study. Two genotypes of *S*. *villosum* (landrace and commercial) and one accession of *S*. *sarrachoides* were grown under droughted and watered conditions. The fraction of transpirable soil water (FTSW) was used as an indicator of stress. Transpiration was determined by changes in daily pot weights and the ratio of transpiration of droughted to watered plants expressed as normalized transpiration ratio (NTR). Leaf expansion, stem elongation and normalized transpiration ratio began to decline early in the drying cycle with FTSW thresholds of 0.46-0.64. Significant reductions in the plant leaf area occurred under severe stress (FTSW<0.40) and were attributed to inhibited leaf expansion and stem elongation as well as leaf shedding and senescence. Similarly, the specific leaf area (SLA) was also reduced under severe stress. Dry matter production was reduced at the same time as reduction of plant leaf area. This reduction was relatively higher in the shoot than the root leading to increased root to shoot ratio.

The relative water content (RWC), osmotic potential and water potential (WP) also declined under severe stress. The resultant osmotic adjustment (OA) was in the range of 0.16-0.19 MPa and could not maintain positive turgor below WP of -1.80 to -2.04 MPa. Under severe stress, there was an increase in transpiration efficiency (TE) of 11-17%. The responses evaluated were similar in the three genotypes suggesting similar strategies of adaptation to drought stress. It is concluded that the three African nightshade genotypes have limited OA capacity and adapt to drought mainly by regulating transpiration. This was achieved by reduction of leaf area leading to a decline in the transpiration but had the undesirable effect of reduced dry matter production. In general, it is necessary to maintain FTSW above 0.5-0.6 to prevent decline in leaf expansion, stem elongation and transpiration, and to maintain the plant water status high. This will lead to higher leaf yields.

3.1 Introduction

African nightshade refers to a loose grouping of *Solanum* species that are grown and consumed as leafy vegetable crops in Kenya and various parts of Africa (Chweya and Eyzaguirre, 1999; Edmonds and Chweya, 1997). These species are also widespread in other parts of the world where they are treated as weeds (Hermanutz and Weaver, 1991; Tan and Weaver, 1997). The species of African nightshade utilized by some rural communities in Kenya include *Solanum villosum* Mill. subsp. *miniatum* (Bernh. Ex Willd.) Edmonds and *S. sarrachoides* Sendtn. (Schippers, 2000; Edmonds and Chweya, 1997).

Agronomic studies to develop optimal cultivation practices for improved yield and nutritive quality of these crops have concentrated mainly on fertilizer use (Khan et al., 1995, 2000; Murage, 1990). There is only sketchy information concerning water management of African nightshade. The general assumption is that it is intolerant to water stress (Edmonds and Chweya, 1997). Related species have been shown to be highly sensitive to water stress, experiencing more than 50% reduction of the height, leaf area and biomass when watering to water holding capacity was done biweekly instead of weekly (McGiffen, et al., 1992).

Leaf expansion is brought about by cell division and enlargement, which involves the extensibility of cell wall under turgor pressure (Pugnaire et al., 1999). Thus, water deficits or other environmental factors that reduce turgor pressure also reduce expansive growth of the leaf and plant as a whole (Turner, 1997; Serpe and Mathews, 2000). Nevertheless, leaf expansion in a drying soil has also been reported to reduce before any changes in turgor and this has been attributed to a non-hydraulic root signal (Saab and Sharp, 1989; Dodd et al., 2002; Roberts et al., 2002). The hormone ABA has been shown to be a major component of this signal (Davies et al., 2002b). Other possible root signals include precursors of ABA, other hormones e.g. cytokinins and xylem sap compounds and ionic composition (Holbrook et al., 2002; Bahrun et al., 2002). Water deficits also cause reduction of leaf initiation (Belaygue et al., 1996; Carberry et al., 1993a) and enhanced leaf senescence (Carberry et al., 1993b; Pic et al., 2002). Thus, plants respond to water deficits by reducing the leaf area, which reduces the plant water use rate and hence conserves water during periods of drought (Jones, 1992; Ludlow and Muchow, 1990).

Under moderate water stress, leaf expansion is inhibited relatively more than photosynthesis leading to carbon accumulation and hence reduced specific leaf area SLA (Tardieu et al., 1999; Sangakkara et al., 2001). Reduction of SLA can also be brought about by shedding of old leaves under severe drought since the new leaves are usually smaller and thicker (Husain et al., 1990).

Water stress inhibits dry matter production largely through its inhibitory effects on leaf area development and consequently reduced light interception (Jones, 1992; Nam et al., 1998). Moreover, water stress reduces stomatal conductance leading to reduced carbon assimilation and consequently low biomass production (Delfine et al., 2000; 2001; Medrano et al., 2002; Kumar et al., 1994). Water stress reduces transpiration and hence transpirational cooling, consequently leading to increase in leaf temperature (Jones, 1992). Increase in leaf temperature beyond certain thresholds leads to inactivation of photosynthetic enzymes and hence inhibited dry matter production (Chaves et al., 2002; Lawlor, 2002; Medrano et al., 2002).

Partitioning dry matter preferentially to the roots as compared to the shoots is a commonly reported drought adaptation mechanism in plants (Jones, 1992; Li et al., 1994; Arora and Mohan, 2001; Lehto and Grace, 1994; Wilson, 1988; Wien, 1997). In addition, plant shoot has been shown to be more sensitive to drought as compared to the roots, hence the increase in root to shoot ratio as has been reported in many crops (Kramer and Boyer, 1995; Sangakkara, 1998; Sangakkara, et al., 1996a, b; Huch et al., 1986; Fernandez et al., 2002).

In a drying soil, the leaf water potential as well as the relative water content of plants declines leading to loss of turgor. This leads to reduced leaf growth and hence dry matter production. In addition, it causes stomatal closure and hence reduced CO_2 assimilation (Lawlor, 2002). Plants respond to declining water potential under drought through osmotic adjustment (OA) as a result of accumulation of solutes within cells to help maintain turgor of shoot and roots (Jones, 1992). This allows turgor dependant processes such as stomatal opening and expansive growth to continue at reduced rates under declining water potentials (Jones, 1992; Ludlow and

Muchow, 1990). However, OA reduces the plant's ability to avoid dehydration in the event of terminal drought (Ludlow and Muchow, 1990). In this case, there will be continued water use by the plants leading to progressive decline in the leaf water potential. This increases the possibility of such plants reaching lethal water status that will cause plant death (Sinclair and Muchow, 2001).

Drought affects transpiration of plants partly through its inhibition of leaf area development (Jones, 1992). In many crops, transpiration is reported to decline only after the plant has used up two thirds of the available water (Sadras and Milroy, 1996). Thus, plant physiological activity is maintained until after two thirds of the extractable soil water in the root zone has been used (Turner, 2000). Exceptions to this general trend in which transpiration showed higher sensitivity to soil water status have been reported (Henson et al., 1989a; Ameglio et al., 2000). This has been attributed to a non-hydraulic root signal produced by roots growing in a drying soil (Davies et al., 1994; 2002b; Chaves et al., 2002).

Increase in transpiration efficiency is another important mechanism of drought adaptation in plants (Jones, 1992; Ehdaie, 1995). Under increasing water deficits, leaf conductance declines leading to reduction of transpiration (Mojayad and Planchon, 1994; Ghannoum et al., 2001). It is thought that stomatal conductance in some plant species can be luxurious (Nguyen et al., 1997). In such cases, drought can cause relatively more inhibition of transpiration than dry matter production, hence more dry matter is produced per unit of water transpired (Nobel, 1999).

The objective of this study therefore was to evaluate the adaptive responses of selected African nightshade to drought in terms of leaf area, dry matter production, relative water content, water potential, osmotic potential and transpiration. The study aimed at establishing the thresholds of plant available water at which the various parameters began to decline during the drying cycle and to show the effect of drought on dry matter partitioning and transpiration efficiency for African nightshade. In addition, the study also aimed at evaluating any differences in the adaptation between genotypes.

3.2 Materials and Methods

Experimental Design

Two pot experiments were conducted in 2000 and 2002. Each was a factorial experiment laid out in a completely randomized design with three replications. Two genotypes of *Solanum villosum* and one accession of *Solanum sarrachoides* were used (Table 9).

Table 9. Summary of the experimental factors for the African nightshade glasshouse experiments in 2000 and 2002 at Hannover (Germany).

Factor		**Description**
Genotypes	Landrace (land)	Glabrous landrace of *Solanum villosum* cultivated in Western Kenya
	Commercial (com)	Commercially available *Solanum villosum*, produced by Kenya seed company.
	Accession (acc)	An accession of *Solanum sarrachoides* obtained from Genebank of Kenya (GBK 028726) and also from IPK Genebank, Gatersleben, Germany (Sol 262/97), originating from Eastern Kenya.
Water levels	Droughted	No watering after start of the treatments
	Watered	Rewatered daily to 84-90% water holding capacity (WHC)

The landrace and commercial genotypes of *S. villosum* were used in 2000, while the *S. sarrachoides* accession was included in the 2002 experiment.

Water Treatments

The two water levels, droughted and watered began at 31 and 30 days after sowing in 2000 and 2002, respectively. At the onset of the treatments, the soil moisture was raised to 84 and 90% water holding capacity in 2000 and 2002, respectively. Thereafter, droughted pots received no more water while watered pots were maintained at their respective WHC.

Sowing and Cultivation Details

The pots used were the same as those described for spiderplant in Chapter 2. The pots were filled with loess soil obtained from the Ruthe research station, South of Hannover, to a soil bulk density of 1.25 and 1.18 g/cm^3 in 2000 and 2002, respectively. The pot water holding capacity was 0.28 and 0.27 w/w in 2000 and 2002, respectively. The experiment was conducted in a glasshouse at 26°C day and 20°C night. The weather data were obtained from the weather station in the Institute of Vegetable and Fruit Science, University of Hannover. Seeds of the selected genotypes were sown directly into the pots on 30th July 2000 and 15th July 2002. The pots were maintained well watered and emergence was observed after seven days in 2000 and five days in 2002. Seedlings were then thinned to one per pot two weeks after planting.

Based on soil analysis results, nitrogen was applied at a rate of 1.5 and 1.0 g N/plant in 2000 and 2002, respectively, three weeks after planting by irrigating with fertilizer Flory 9 (15% N: 7% P_2O_5: 22% K_2O: 6% MgO). The soil surface was then covered to a depth of about 3 cm with quartz gravel to minimize soil evaporation.

Dates for Harvesting and Sampling for Water Relations Measurements

Four harvests were carried out in both years; at the onset of water treatments, at average soil moisture contents of 60 and 40% WHC and lastly when the transpiration of droughted plants was below 10% of that of watered plants. Sampling for water relations measurements were carried out at the onset of water treatments, at 60% and 40% WHC in 2000, and 70%, 60% and 40% WHC in 2002. The last sampling in both years was done when the transpiration of droughted plants was below 10% of that of watered plants. The dates at which the harvesting and sampling for water relations' measurements were done are shown in Table 10.

Measurements

Measurements to quantify plant growth, relative water content, osmotic potential, water potential and transpiration as well as the determination of FTSW were all done as described for spiderplant (Chapter 2).

Leaf Expansion

At the onset of water treatments, 5-7 plants for each genotype and water level were marked for the daily measurements of leaf length and width, and plant height until the increases in droughted plants stopped. Leaves were numbered from the base and measurements of the length (L) and the width (W) at the widest part done on leaf numbers 14 and 15 in 2000, and 11, 12 and 13 in 2002. A linear relationship was established between the product of the length and width and the actual leaf area (measured by a leaf area meter Model LI-COR 3100) on individual leaves (n=184 and 90 for *S*. *villosum* genotypes and *S*. *sarrachoides* accession, respectively) using linear regression procedure (SAS, 1999).

Table 10. Dates for harvesting and sampling for water relations' measurements for the African nightshade glasshouse experiments in 2000 and 2002.

Harvest/sample No.	**Days after the start of water treatments**			
	2000		**2002**	
	Harvest	**Water relations**	**Harvest**	**Water relations**
1	1	1	1	1
2	9	9	10	9
3	16	16	15	11
4	24	24	22	16
5	-	27	-	22

Leaf expansion, stem elongation, plant leaf area, plant biomass, relative water content, osmotic potential, water potential and transpiration were determined as described for spiderplant (Chapter 2). Dry matter partitioning was analysed as the ratio of the dry weight of roots to shoots at each harvest. The data were transformed to natural logarithms before analysis of variance (Poorter and Nagel, 2000; Hoffmann and Porter, 2002). Transpiration efficiency was determined as ratio of dry matter produced (DM) to the cumulative transpiration (CT) between individual harvests. Data analyses were done as described for spiderplant (Chapter 2).

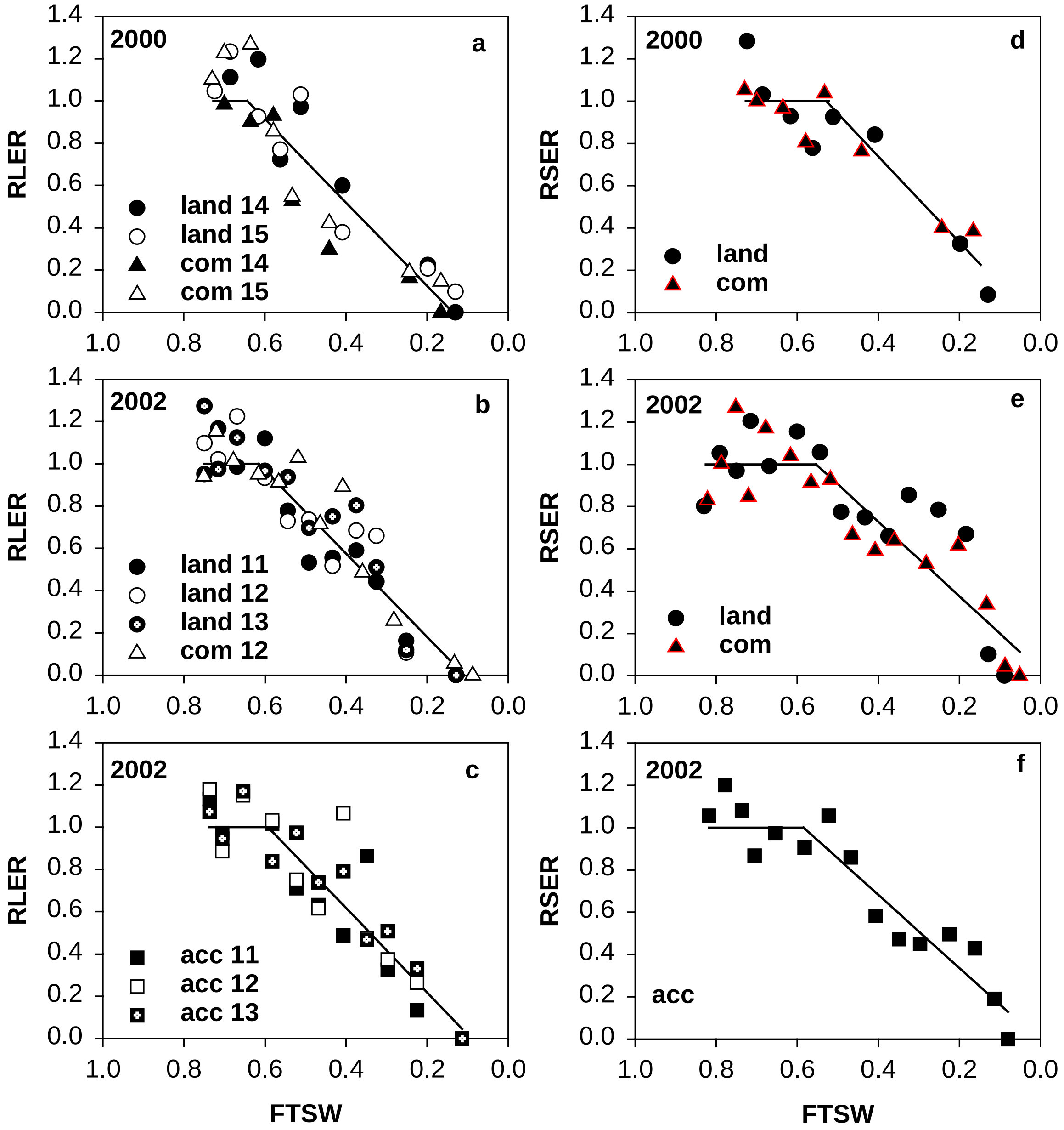

Fig. 10. The relative leaf expansion rate (RLER) of leaf numbers 11-15 (a-c) and the relative mainstem elongation rate (RSER) (d-f) as functions of FTSW for African nightshade genotypes landrace, (land) commercial (com) and the accession (acc) grown in the glasshouse in 2000 and 2002. Lines show plateau regression functions (regression coefficients are shown in Table 11).

3.3 Results

Leaf Area Development and Stem Elongation

The rate of soil drying was similar between the genotypes in both years. Leaf expansion of droughted plants began to decline relative to the expansion of watered plants at relatively high FTSW values with no significant differences between genotypes in both years (Fig. 10a-c and Table 11). Stem elongation of droughted plants began to decline relative to that of watered plants at FTSW thresholds comparable to those of leaf expansion for all the genotypes (Fig. 10d-f and Table 11).

Table 11. The fraction of transpirable soil water threshold for leaf expansion and stem elongation decline ($FTSW_t$) and the slope of the decline (A) for landrace and commercial genotypes (land/com pooled) and the accession (acc) grown in the glasshouse in 2000 and 2002. The 95% confidence intervals are shown in parentheses.

Leaf expansion				
Year	**Genotype**	**Slope (A)**	**$FTSW_t$**	**R^2**
2000	Land/com	1.97 (1.41-2.54)	0.64 (0.56-0.73)	0.99
2002	Land/com	1.97 (1.57-2.37)	0.62 (0.56-0.68)	0.99
	Acc	1.99 (1.44-2.54)	0.59 (0.47-0.62)	0.99
Stem elongation				
2000	Land/com	2.03 (1.12-2.93)	0.53 (0.42-0.64)	0.98
2002	Land/com	1.76 (1.50-2.38)	0.55 (0.44-0.67)	0.97
	Acc	1.73 (1.23-2.23)	0.58 (0.49-0.68)	0.99

In 2000, only water level had significant effects on plant leaf area. Droughted plants had lower leaf area, significant from 9 days after the start of water treatments. At the end of the experiment, droughted plants had a leaf area of 20-26% of that in watered plants for both landrace and commercial genotypes of *S. villosum* (Fig. 11a, b). In 2002, significant differences between leaf area of droughted and watered plants began at 15 days after the start of water treatments. At the end point, interactions between the genotypes and the water levels were significant. In this case, the leaf area differed significantly between the genotypes only under watered treatment in the order of the accession>landrace>commercial. Leaf area of droughted plants at this end point was only 12% of that in watered plants for the accession and landrace, and 15% for commercial genotype.

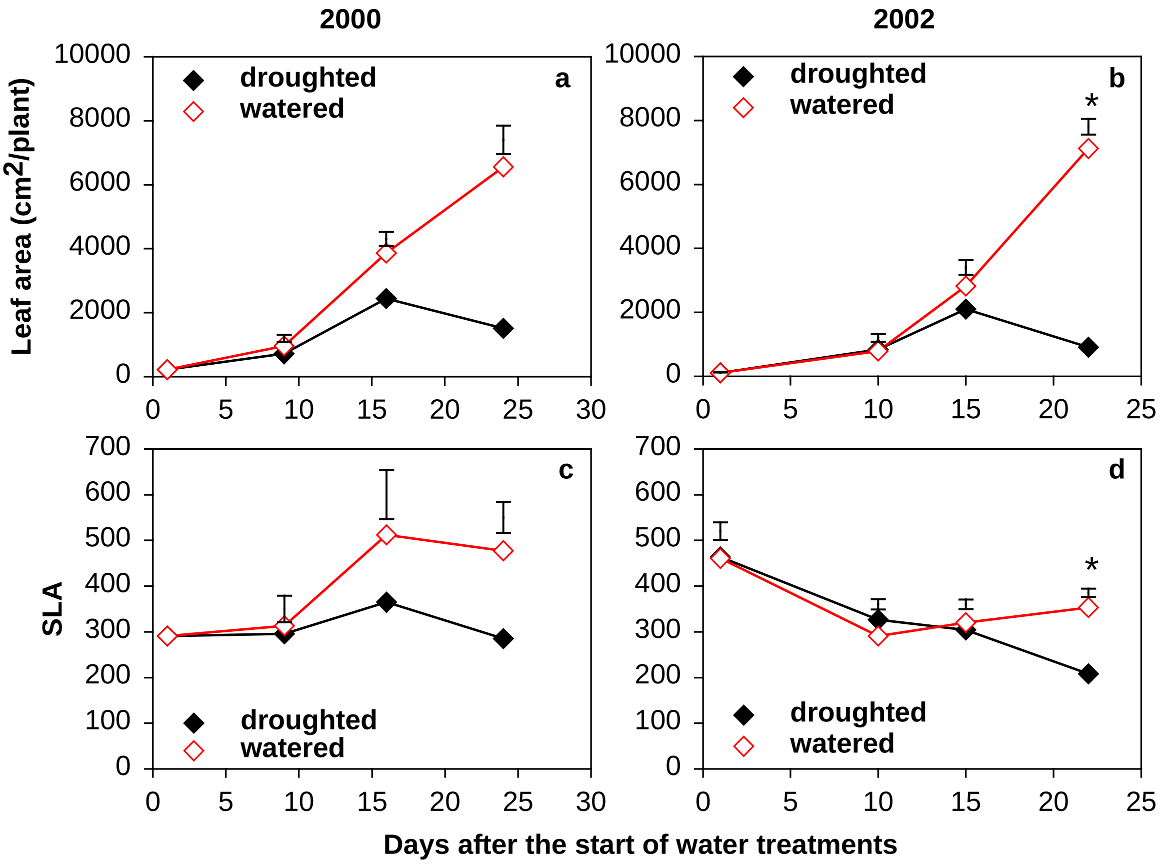

Fig. 11. Plant leaf area (a, b) and SLA (c, d) of African nightshade grown in the glasshouse as influenced by water levels (means across genotypes) in 2000 and 2002. Vertical bars show $LSD_{0.05}$, data points with asterisk show significant interactions described in text.

SLA at individual harvests was reduced by drought, significant from 16 days after the start of water treatments in 2000, with no significant differences between genotypes (Fig. 11c, d). However, in 2002, there were significant interactions between genotype and water level in which the SLA differed only under watered treatments in the order accession>commercial>landrace.

Dry Matter Partitioning

There was no clear trend in the root to shoot ratio in 2000 while in 2002, droughted plants had higher root to shoot ratio, significant from 10 days after the start of water treatments (Fig. 12).

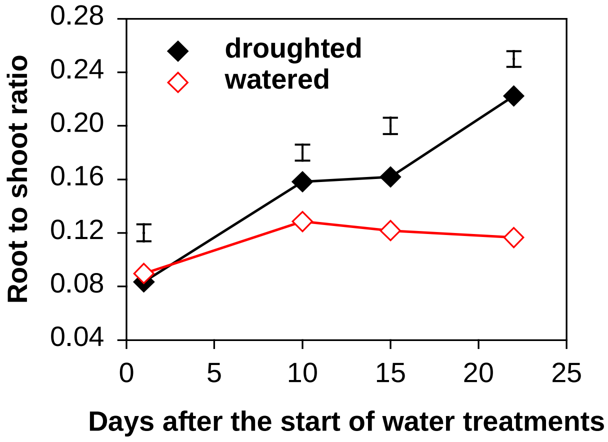

Fig. 12. The root to shoot ratio of African nightshade grown in the glasshouse under droughted and watered conditions (means across genotypes) in 2002. Vertical bars show $LSD_{0.05}$.

Water Relations

No significant interactions or effects of genotypes were observed in the water relations of African nightshade and hence only the water level effects are considered. RWC remained high in both droughted and watered plants until 16 days after the start of water treatments in both years after which it declined significantly in droughted plants (Fig. 13a, b). Droughted plants had lower osmotic potential at full turgor (OP), significant from 16 days after the start of water treatments in both years (Fig. 13c, d). The resultant osmotic adjustment (OA) was 0.16 MPa in 2000 and 0.19 MPa in 2002 at maximum stress (FTSW=0). Water potential (WP) followed the same trend as that of RWC and OP (Fig. 13e, f). RWC, OP and WP of watered plants remained more or less constant over the experimental period in both years.

The ratio of RWC, OP and WP of droughted plants to that of watered plants (RWC, OP and WP ratios) remained close to 1.0 until FTSW fell below about 0.2-0.4, after which it changed rapidly in both years (Fig. 14a-f).

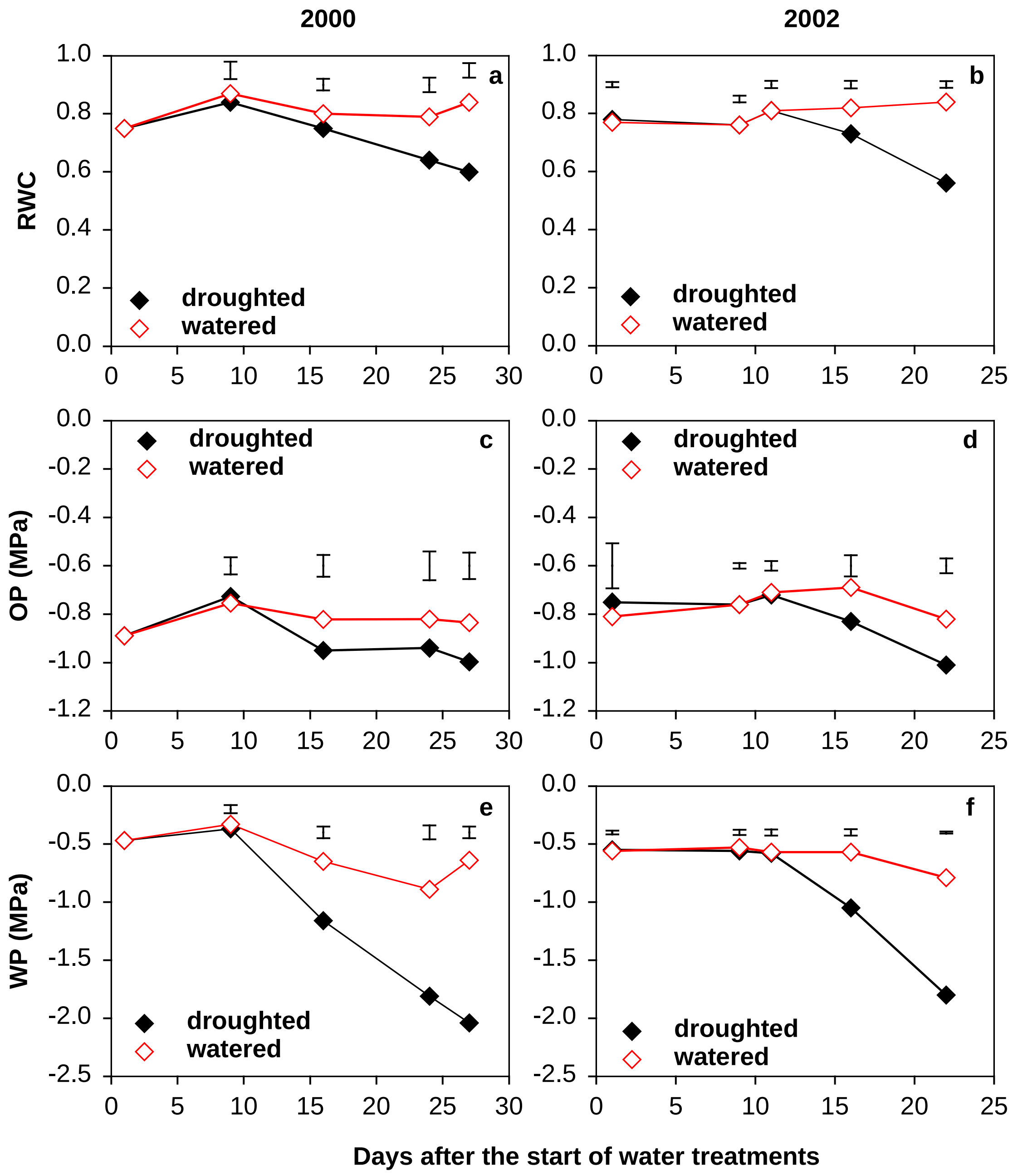

Fig. 13. Relative water content (RWC) (a, b), osmotic potential at full turgor (OP) (c, d) and water potential (WP) (e, f) of African nightshade grown in the glasshouse under droughted and watered conditions in 2000 and 2002. Data points are means across the genotypes and vertical bars show $LSD_{0.05}$.

Transpiration and Transpiration Efficiency

The relationship between NTR and FTSW fitted well to the plateau regression function (Fig. 15a-c). The FTSW thresholds for the NTR decline were similar between genotypes and similarly the threshold for both years were comparable

(Table 12). Transpiration efficiency was significantly higher in the droughted than watered treatment at 24 and 22 days after the start of water treatments in 2000 and 2002, respectively (Table 13). The increase in the droughted plants was about 17% and 11% in 2000 and 2002, respectively.

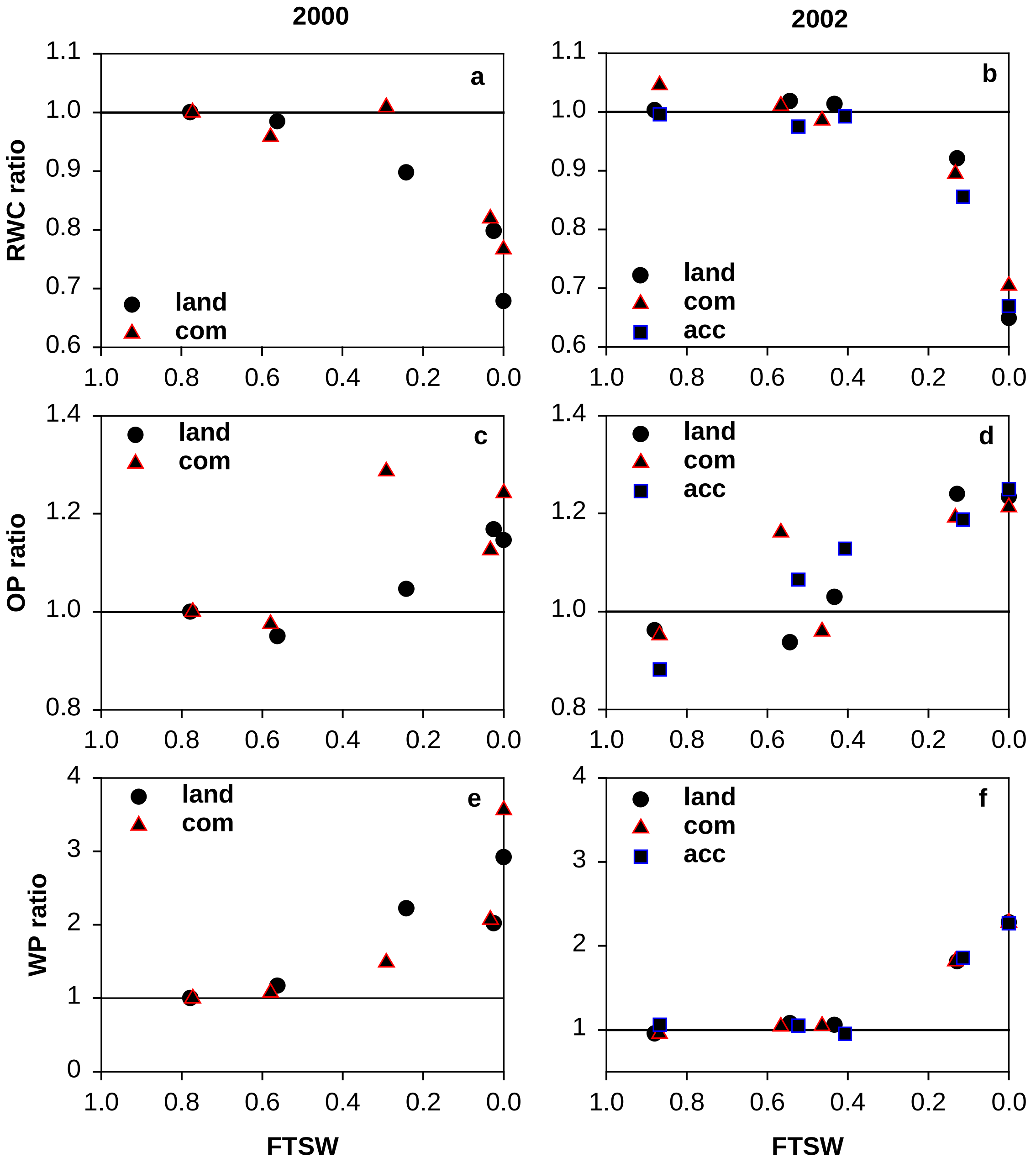

Fig. 14. Scatter diagrams of the ratio of relative water content (a, b), osmotic potential at full turgor (c, d) and water potential (e, f) of droughted to watered plants as functions of the fraction of transpirable soil water (FTSW) for African nightshade genotypes grown in the glasshouse in the years 2000 and 2002. The lines show ratio=1.

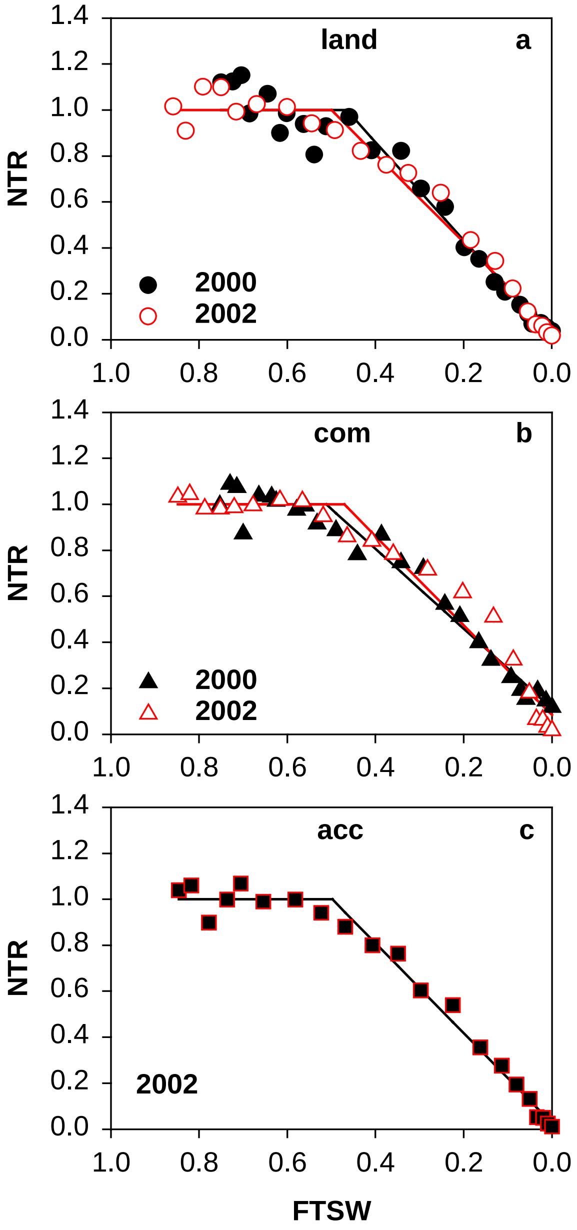

Fig. 15. Normalized transpiration ratio (NTR) as a function of fraction of transpirable soil water (FTSW) for African nightshade genotypes landrace (land) (a), commercial (com) (b) and accession (acc) (d) grown in the glasshouse in 2000 and 2002. Points are measured data while lines are plateau regression functions (regression coefficients are shown in Table 12).

3.4 Discussion

Leaf Area Development and Stem Elongation

Leaf area plays an important role in light interception and hence influences dry matter production and plant growth (Jones, 1992). Leaf area development therefore has direct effects on the yield of leafy vegetables such as African nightshade. Leaf expansion in this study declined relatively early in the drying cycle, with the FTSW threshold range of 0.59-0.64. The lack of significant differences in the thresholds between genotypes could be attributed to the fact that the genotypes had similar leaf areas under droughted conditions and hence similar rate of soil drying. Such high sensitivity of leaf expansion to drought has also been reported in various other crops under glasshouse such as chickpea (Soltani et al., 1999) and sunflower (Sadras et al., 1993). Although no precise FTSW thresholds for decline in water status were determined in this study, the general range of 0.20-0.40 was lower than the thresholds for leaf expansion. The decline in leaf expansion therefore seems to have preceded changes in relative water content and water potential suggesting presence of root signals.

Table 12. The fraction of transpirable soil water threshold value ($FTSW_t$) at which normalized transpiration ratio (NTR) began to decline and the slope of the decline (A) for African nightshade genotypes grown in the glasshouse in 2000 and 2002. The 95% confidence intervals are shown in parentheses.

2000			
Genotype	**Slope (A)**	**$FTSW_t$**	**R^2**
Landrace	2.14 (1.85-2.42)	0.46 (0.42-0.51)	0.99
Commercial	1.74 (1.53-1.95)	0.51 (0.47-0.55)	0.99
2002			
Landrace	1.92 (1.71-2.12)	0.50 (0.46-0.54)	0.99
Commercial	1.95 (1.67-2.22)	0.47 (0.42-0.51)	0.99
Accession	1.95 (1.78-2.13)	0.50 (0.47-0.53)	0.99

In the early stages during the drying cycle, the root size was small and it can be assumed that roots were extracting water mainly from the upper soil layer leading it to dry ahead of the lower layers. It is therefore probable that roots in the upper drying soil produced non-hydraulic signals that acted to inhibit leaf expansion, while roots extracting water from lower soil layers maintained the plant water status high. Reduction of leaf growth in the absence of changes in turgor has been reported in various studies (Munns et al., 2000; Ismail et al., 2002) and is usually attributed to signals from roots growing in a drying soil overriding water relations (Kuang et al., 1990; Saab and Sharp, 1989; Bahrun et al., 2002).

Table 13. Transpiration efficiency (TE) of African nightshade (means across genotypes) grown in the glasshouse in 2000 and 2002.

TE (g plant dry matter produced/ kg water transpired)			
2000			
Water level	**Days after the start of water treatments**		
	9	**17**	**24**
Droughted	3.55a	4.38a	4.63a
Watered	3.62a	5.35a	3.93b
$LSD_{0.05}$	0.99	1.24	0.53
2002			
	10	**15**	**22**
Droughted	2.31a	3.38a	3.92a
Watered	2.57a	3.17a	3.52b
$LSD_{0.05}$	0.70	0.51	0.30

Means followed by the same letter within the column are not significantly different ($P<0.05$).

Although there was some evidence of root signals regulating leaf growth of African nightshade in this study, the same cannot be assumed to be the case under field conditions or even when the stress begins at different stages of crop development.

The presence or absence of root signals in regulating leaf growth in plants growing in a drying soil could be influenced by soil volume that the plants are able to exploit. It is thought that root signals are more pronounced in pots as compared to the field due to the small soil volume available for plant exploitation and high resistance the root experience at pot walls (Sadras et al., 1993).

Stem elongation in all the genotypes responded in the same way as leaf expansion and the resulting reduction of plant height under droughted conditions contributed further to reduction of plant leaf area through inhibited branching. Furthermore, leaf shedding and senescence under severe stress (FTSW=0.2-0.4) caused large reductions of plant leaf area in all the genotypes.

The specific leaf area (SLA) was reduced by drought in the same way for all the genotypes. The reduction coincided with period of severe stress and hence may have been due to leaf senescence and shedding especially of old large sized leaves leaving small thick young leaves (Husain et al., 1990).

Dry Matter Partitioning

The reduction of leaf area under drought resulted in inhibited dry matter production and changes in dry matter partitioning. Reduction of leaf area leads to reduction of light interception, which is known to be linearly related to dry matter production (Jones, 1992). Similarly, reduced transpiration due to drought leads to inhibited dry matter production since cumulative transpiration is also known to be linearly related to dry matter production in most crops (Turner, 2000; Jones, 1992). Under severe stress (FTSW<0.4), the water status of droughted plants declined resulting in loss of turgor and probably further closure of the stomata. This is known to cause reduction of carbon assimilation (Chaves et al., 2002). Leaf shedding while acting to reduce transpiration in an effort to promote survival, most likely exacerbated the reduction of carbon assimilation. Thus, biomass production was inhibited in both shoots and roots.

However, relatively larger reductions of biomass production were observed in shoots than roots in 2002, which resulted in higher root to shoot ratio under drought. However, lack of similar results in 2000 means that no strong conclusion can be drawn on the effect of drought dry matter partitioning between root and shoot in the African nightshade genotypes studied.

Water Relations

Relative water content (RWC), osmotic potential at full turgor (OP) and water potential (WP) are measures of plant water status, which are useful in monitoring the development of stress in plants growing under droughted conditions. In this study, the RWC, OP and WP all remained relatively unchanged until FTSW range of 0.2-0.4. Below this soil moisture level, RWC declined rapidly to 65-77% of that in watered treatment; OP decreased by about 15-24% compared to watered treatment, while WP declined two to three folds. This pattern of change in plant water status with declining soil moisture has been reported in many other crops (Qian and Fry, 1997; Gesch et al., 1992; Henson et al., 1989a; Erickson et al., 1991; Jensen et al., 1989; Machado and Paulsen, 2001).

With an osmotic adjustment (OA) in the range of 0.16-0.19 MPa at the highest stress level (FTSW=0), it appears that the genotypes of the African nightshade studied have only limited OA capacity. This OA could not keep turgor positive below WP of -1.8 to -2.04 MPa and RWC of 0.56-0.60, hence the wilting and leaf shedding observed. Similar results have been reported in genotypes of other crops with similar low OA capacity (Entz and Fowler, 1990). This contrast with crop species that are able to withstand low WP for instance up to -3.7 MPa reported in winter wheat (Gesch et al., 1992).

A low OA could also be due to diurnal water deficits developing in well-watered plants caused by environmental aridity (Bolanos and Edmeades, 1991). Similarly, it has been reported that water potential of well-watered plants can decline with ontogeny due to increasing demand for water as the leaf area increases (Allen, et al., 1998; Flower et al., 1990). In this study both WP and RWC in the watered plants was maintained in the range that well-watered plants are expected to maintain (Sinclair and Ludlow, 1985). Thus, the possibility that water deficits developed in watered plants to levels that could substantially reduce the magnitude of OA in this study was minimal.

Transpiration

Decline in the cumulative transpiration under drought conditions is usually correlated with reduction of dry matter production since both are linearly related (Jones, 1992). The sensitivity of transpiration to drought was similar in the African nightshade genotypes, with FTSW thresholds at which NTR began to decline during the drying cycle of 0.46-0.51. This suggests that in the event of terminal drought which starts in early vegetative stage of plant growth, transpiration starts to decline once about 50% of the available soil water has been used up. Moreover, these FTSW thresholds for transpiration were similar to those reported for P-landrace spiderplant (Chapter 2). There is a general agreement in the literature that evapotranspiration in many crops reduces only when two thirds of the extractable soil water in the root zone has been used (Turner, 2000; Sadras and Milroy, 1996). Decline in transpiration seem to have preceded decline in the plant water relations in this study. This suggests the presence of non-hydraulic root signals in regulating transpiration.

Decline in transpiration can also be due to reduced leaf expansion under moderate stress as well as leaf shedding under severe stress (Jones, 1992; Rosenthal et al., 1987; Borell et al., 2000). Transpiration efficiency (TE) increased by 11-17% under severe stress (FTSW=0). Increase in TE is a general adaptation to stress reported in various crops (Jones, 1992; Clifton-Brown and Lewandowski, 2000; Nguyen et al., 1997; Pugnaire et al., 1999). This can be explained by the fact that TE depends on the balance between photosynthesis and transpiration (Jones, 1992). Partial stomatal closure under stress reduces transpiration more than CO_2 assimilation, hence increases TE (Nobel, 1999). In this study no genotypic variation in TE was observed. However, these results are not conclusive and more genotypes of *Solanum* species need to be tested considering that genotypic variability in TE has been reported in other crops (Turner et al., 2000; Donatelli et al., 1992; Ludlow and Muchow, 1990).

Responses of the genotypes in terms of the FTSW thresholds for decline in leaf expansion, stem elongation and normalized transpiration were comparable between the years. This could be attributed to similar climatic conditions especially radiation in both years (Appendix 2).

3.5 Conclusion

Drought caused a reduction of leaf expansion, stem elongation rate and plant leaf area. Leaf expansion, stem elongation and transpiration were the most sensitive processes, beginning to decline earlier in the drying cycle as compared to plant leaf area, dry matter production, relative water content and water potential, which declined under severe stress. Severe stress induced osmotic adjustment, which was however only 0.16-0.19 MPa at maximum stress when all transpirable soil water had been used. At the same time, there was increased root to shoot ratio and an increase in the transpiration efficiency (TE).

It can therefore be concluded that the African nightshade genotypes studied adapt to drought stress mainly by avoidance mechanism through reduction of expansive growth and transpiration in order to conserve water as well as increase in root to shoot ratio and TE under severe stress. They have only limited OA. Thus, maintaining the soil moisture at 50-60% of the transpirable soil water (about 60% water holding capacity) would be sufficient to prevent decline in leaf expansion, stem elongation and transpiration and sustain relatively high dry matter production. This will translate into relatively high leaf yields.

The *Solanum villosum* genotypes landrace and commercial originate from western Kenya while the accession of *S. sarrachoides* originates from Eastern. However, the specific localities in which these genotypes are found share similarities in altitude, rainfall and temperature conditions. This could explain the largely similar responses of the genotypes to drought. However, under well watered conditions, there was evidence of higher leaf yields for the accession as compared to the other genotypes.

4.0 Plant Water Use and Growth of Spiderplant (*Gynandropsis gynandra* (L.) Briq.) and African Nightshade (*Solanum* spp.) at Different Soil Moisture Regimes under Field Conditions

Abstract

The water use, expansive growth, dry matter production and partitioning of spiderplant and the two African nightshade species were investigated under field conditions. The spiderplant study involved two genotypes, a fast growing landrace (P-landrace) and a slow growing one (G-landrace), while for the African nightshade study, the commercial genotype of *S*. *villosum* Mill. Subsp. *miniatum* (Bernh. Ex Willd.) and a genebank accession of *S*. *sarrachoides* (Sendtn.) were used. For both spiderplant and African nightshade three water treatments, droughted, moderate stress and watered, were applied.

Leaf area and dry matter production for both spiderplant and African nightshade was significantly reduced as the soil moisture declined below 60% field capacity. The responses were similar for the genotypes studied in both spiderplant and African nightshade. Dry matter partitioning between the leaves and the stems for both spiderplant and African nightshade was related to the plant height and could be described by power functions. This relationship was not influenced by drought stress.

In African nightshade, the accession produced more dry matter at all soil water levels as compared to the commercial genotype while both had similar water use under droughted and moderate stress conditions. This suggests that the accession had a higher water use efficiency compared to commercial genotype. In both spiderplant and African nightshade, rewatering to maintain a moderate stress caused some recovery in leaf growth and dry matter production. While there were no clear differences in this recovery for spiderplant genotypes, the African nightshade accession showed more recovery than the commercial genotype.

It is therefore concluded that both spiderplant and African nightshade require soil moisture above 60% FC for maximum expansive growth and dry matter production. In the event of intermittent drought only the *S*. *sarrachoides* accession is expected to have good recovery when rains come late in the growing season.

4.1 Introduction

Spiderplant and African nightshade have been grown and consumed in Kenya for along time, but their integration into mainstream agriculture has been slow. Consequently, no work has been done to asses their response to drought under field conditions. In the previous two chapters of this work, experiments were conducted in pots under controlled conditions. One fundamental difference between pot and field studies is the volume of soil that plants are able to exploit. Unlike in the field, pot-grown plants have access only to small volumes of soil and hence water deficits develop rapidly once watering is stopped (Ludlow et al., 1985). Ray and Sinclair (1998) have demonstrated that the rate of soil drying increased with decreasing soil volume available for exploitation by the plants.

Under field conditions, the rate of soil drying in the event of a drought is slow, which accords sufficient time for the occurrence of acclimation processes such as osmotic and stomatal adjustment. This is in contrast with the rapid soil drying associated with pot grown plants (Jones, 1992; Ludlow et al., 1985). Thus, the effects of water deficit on plant performance are expected to be minimized under field conditions (Ludlow et al., 1985). It should be noted however, that the timing of the occurrence of drought in the field influences plant responses. In cases of droughts occurring early, when the root size is still small, the plants may be unable to utilize moisture in deep soil layers. For instance, Lecoeur and Sinclair (1996) found that pea plants did not exploit water at the bottom layers in the soil profile.

Another major difference between pot and field grown plants concerns root growth. Under field conditions, root length density is known to decrease with soil depth (Salih et al., 1999; Li et al., 2002; Husain et al., 1990; Penning de Vries et al., 1989). This contrasts with pot grown plants where root length density may increase with depth (Henson et al., 1989a). Also, roots growing in pots find resistance to penetration at pot walls and this could lead to production of stronger root signals as compared to field grown plants (Sadras et al., 1993). Temperature under field conditions can be highly variable and exposure of plants to temperature extremes could influence their leaf growth and transpiration responses under water stress (Lecoeur and Sinclair, 1996).

Determination of the upper limit (field capacity) and lower limit (permanent wilting point) of soil water content is necessary to be able to estimate plant available soil water under field conditions. This is usually difficult and ambiguous (Sinclair et al., 1998). For instance, discrepancies have been reported between the lower limit of soil water availability measured in the field and in the laboratory, and Savage et al. (1996) have discussed the possible reasons. Briefly, they attributed the discrepancies to the treatment of soil between the time when the samples are taken and when the laboratory measurements are done. The necessity of determining the upper and lower limits of soil water content can be avoided by relating plant responses directly to the soil water content instead of plant available water (Sinclair et al., 1998; Moreshet et al., 1996).

Droughts in the field can occur at any stage of plant growth and they could be terminal, which leads to development of severe water deficits, or intermittent in which case the water deficits are relieved by precipitation (Nleya et al., 2001). Reduction of leaf area in response to drought leads to reduced light interception and hence inhibited biomass production (Jones, 1992). In the early stages of drought, stomatal closure occurs leading to lower intercellular CO_2 and reduced photosynthesis (Chaves et al., 2002; Awal and Ikeda, 2002). However, the biochemistry of the photosynthetic machinery is not affected (Delfine et al., 2000). Thus, when water stressed plants are rewatered, as is the case for intermittent drought, they are expected to resume physiological activity. This recuperative plasticity is a desirable trait under situations of unpredictable rain and has been shown to increase yield in some pinto bean cultivars (Nleya et al., 2001).

Studies in Chapters 2 and 3 were pot experiments conducted under controlled temperature in the glasshouse. It was therefore necessary to ascertain as to whether the responses observed under glasshouse could be replicated under unlimited soil volume and uncontrolled temperature. A field study was therefore conducted for both spiderplant and African nightshade with the objective of assessing water use, plant growth and dry matter partitioning at soil moisture regimes that simulate terminal drought, intermittent drought and well watered conditions.

4.2 Materials and Methods

Experimental Design

Two field experiments one for each crop were carried out at Jomo Kenyatta University of Agriculture and Technology (JKUAT) farm at Juja-Kenya (1525 m above sea level) between August and October 2001. The soils have been classified as eutric cambisols (FAO/UNESCO, 1974). They are well-drained, moderately deep to deep, dark brown in colour, friable and gravelly clay over petroplinthite. However, amendments have been done involving adding new soils to horizon A., hence the current soils could be classified under Anthrosols (FAO/UNESCO, 1988; Muchena et al., 1978). The weather data were obtained from Meteorology department at Thika (1548 m above sea level).

Genotypes with diverse characteristics were selected in screening trials, for use in the spiderplant and African nightshade experiments. Each experiment was carried out as a split plot in a completely randomised block design with 3 replications. The main plots comprised of three water levels, while the split plots consisted of two genotypes (Table 14). Plastic sheets were placed in the soil to a depth of 1.0 m all round the main plots to limit lateral water movements. Saeed and El-Nadi (1997) used iron sheets to achieve a similar effect.

Table 14. Summary of the experimental factors for the spiderplant and African nightshade experiments in 2001 at JKUAT farm, Juja (Kenya).

Factor		Description
Spiderplant genotypes	P-landrace (P-land)	Fast growing and high yielding purple stem and petiole landrace
	G-landrace (G-land)	Slow growing green stem and petiole landrace
African nightshade genotypes	Commercial (com)	*Solanum villosum* commercial genotype obtained from Kenya Seed Company
	Accession (acc)	*Solanum sarrachoides* accession, GBK 028726 from Genebank Kenya, originating from Eastern Kenya.
Water levels	Droughted (D)	No watering after onset of drought
	Moderate stress (MS)	Watered to maintain about 60% field capacity (FC)
	Watered (W)	Watered to maintain about 80% FC

Water Treatments and Soil Water Measurement

Three soil water levels, droughted, moderate stress (maintenance of 60% field capacity) and watered (maintenance of 80% field capacity) were established at 21 days after sowing for spiderplant and 18 days after transplanting for African nightshade. At the onset of water treatments, all plots were thoroughly irrigated. 48 hours later soil samples were taken by a soil auger at depths of 0-20 and 20-40 cm, and the gravimetric soil water content (G_W) determined by drying at 105°C for 48 hours. Most water extraction has been shown to be concentrated in these soil layers for various crops (Girona et al., 2002; Li et al., 2002; Pearce et al., 1993). 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; Hamer, 1997; Brisson et al., 2001). The following expressions were used:

$$W = SWC_1 - SWC_2 \tag{9}$$

$$SWC = G_W \times \text{soil bulk density} \times d \tag{10}$$

where W refers to the amount of water to be applied, SWC_1 is the soil water content for 0-20 cm soil layer at 80% FC, SCW_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 estimated amount of 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 then rewatered using the same method described above for the watered treatment to maintain the soil moisture at 60% FC. In the droughted treatment, no watering was done after the onset of the drying cycle.

Subsequent soil water status was determined by measuring the gravimetric soil water content at 4-8 days interval for droughted treatment and moderate stress treatment (before rewatering) and 2-3 days interval for watered treatment and moderate stress treatment (after rewatering). Sampling soil for gravimetric water determination on watered plots was always done just before watering. The same was done for moderate stress plots once rewatering had began.

Crop Establishment

Spiderplant

The sub-plots, each measuring 2 m × 2.5 m were prepared by raising the soil about 15 cm above the ground. Seeds were sown directly on to the prepared plots at a spacing of 30 cm between and 20 cm within rows on 21st June 2001. The plots were well watered and covered by plastic sheets to maintain high moisture. Emergence was observed three and five days after sowing for the P-landrace and G-landrace, respectively. Thinning was done two 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 the rates of 52 kg N/ha and 92 kg P_2O_5/ha.

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. However, the shelter was kept open on all sides by rolling the plastic film up during the day, but was fully covered in the event of rain and at night.

African Nightshade

Seeds were sown on trays on 28th June 2001. Emergence was observed 7 and 12 days after sowing for *S. villosum* commercial genotype and *S. sarrachoides* accession, respectively. The seedlings were then transplanted into plastic pots (10 cm diameter). The sub-plots were prepared as described above for spiderplant. Transplanting to the field was done on 6th August 2001 at a spacing of 40 cm between rows and plants. The crops were watered daily by hand before water treatments began. At the onset of the treatments, nitrogen and phosphorus were applied at the rates of 90 kg N/ha and 92 kg P_2O_5/ha. A rain shelter was constructed and used as described for spiderplant above.

Harvests and Plant Growth Measurement

Seven harvests, based on the soil water status, were carried out for both spiderplant and African nightshade (Table 15). At each harvest for spiderplant, 2-3 plants in a central row from each plot were cut at the base and divided into blades, petioles and stems. Plant leaf area was measured using a leaf area meter (model AAM-8, Hayashi Denko Co. LTD., Japan). The number of leaves and height of the main stem were determined. The plant parts were then dried at 100°C for 48 hours and weighed.

The same procedure was repeated for African nightshade except that only one plant was cut from each plot in the first six harvests. At the seventh harvest, six plants were cut from each plot, but only one was used to determine leaf area.

Table 15. The harvest dates and corresponding soil water status (field capacity, FC) of the top 0-20 cm layer for the spiderplant and African nightshade experiments in 2001.

Spiderplant		**African nightshade**	
FC (%)	**Days after the start of water treatments**	**FC (%)**	**Days after the start of water treatments**
80	1	80-90	1
75-80	8	70-75	15
65-70	19	55-60	22
60-65	29	50-55	28
55-60	36	45-50	35
50-55	43	40-45	42
45-50	50	≈40	51

Data Analyses

Analysis of variance was executed with a split plot design for all the measured parameters separately for each date using the GLM procedure of SAS (SAS, 1999). Significance was measured at $P<0.05$. The increases in leaf area and dry matter between successive harvests for droughted plants were expressed relative to corresponding increases for watered plants and plotted against the gravimetric soil water content of droughted plots. Partitioning of dry matter between leaves and stems was analysed by expressing the leaf to stem ratio as a power function of plant height:

$$y = ax^{-b} \qquad 11$$

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 need to be invested in structural material (mainly stems) to maintain the plant's integrity and strength.

Table 16. Soil bulk densities and, the gravimetric soil water content (G_W) at field capacity (FC) and permanent wilting point (PWP), as determined on the field and in the laboratory (lab) for soils at the experimental sites on the JKUAT farm Juja (Kenya). Values in parentheses show ±SE.

Spiderplant				
Depth (cm)	**Bulk density (g/cm^3)**	**% G_W at FC (Field)**	**% G_W at FC (Lab, -0.33 bars)**	**% G_W at PWP (Lab, -15 bars)**
0-20	1.21 (0.08)	31.42 (0.75)	30.75 (3.36)	19.53 (0.64)
20-40	1.47 (0.01)	32.58 (2.50)	30.82 (2.75)	19.92 (0.65)
African nightshade				
0-20	1.20 (0.05)	29.21 (1.01)	35.83 (2.56)	23.34 (0.59)
20-40	1.40 (0.06)	34.91 (0.58)	35.29 (1.57)	24.69 (0.40)

4.3 Results

Soil Characteristics

The important soil characteristics at the experimental sites are shown in Table 16. The gravimetric soil water contents at field capacity determined on the field were similar to the ones determined in the laboratory. On the other hand the soil water contents at permanent wilting point determined in the laboratory were unrealistically high considering that they corresponded to 60-70% FC. Thus, plant available soil water was not computed, instead only gravimetric soil water content is shown.

Spider Plant

Plant Water Use

Changes in the gravimetric soil water content over time were similar between 0-20 cm and 20-40 cm depths, hence only the mean of the two is considered. In the first week after onset of drought, the gravimetric soil water content remained similar between P-landrace and G-landrace. This was followed by a more rapid decline in soil water content, with the rate being higher for P-landrace than G-landrace at both droughted and moderate stress before rewatering (Fig. 16a, b). Soil water content under the watered treatment was generally maintained around 25% (80% FC) (Fig. 16a).

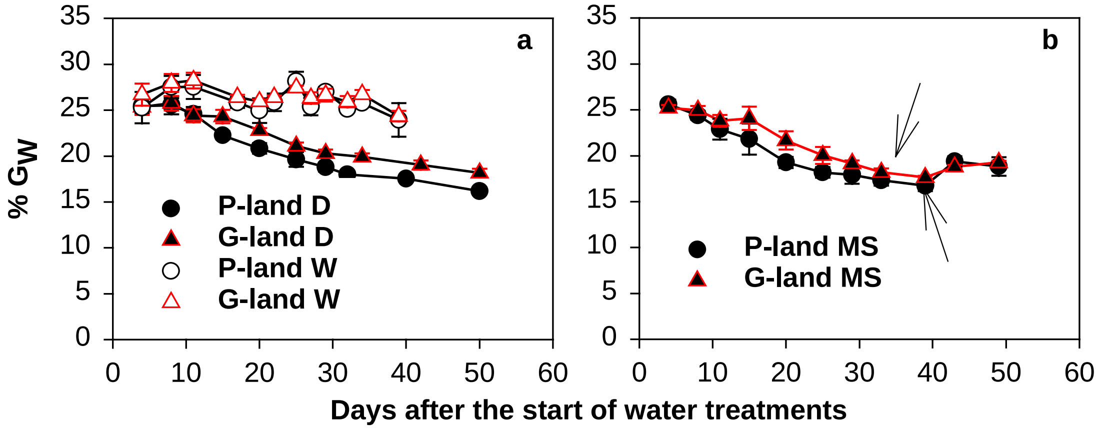

Fig. 16. The gravimetric soil water content (% G_W) at 0-40 cm depths for spiderplant genotypes P-landrace (P-land) and G-landrace (G-land) grown at three water levels, droughted, D and watered, W (a), and moderate stress, MS (b) under field conditions in 2001. Arrows in the MS treatment (b) indicate the rewatering dates for P-landrace (upper) and G-landrace (lower). Vertical bars show SE (n=3).

Leaf Area Development and Plant Height

The magnitude of plant leaf area was in the order of watered>moderate stress>droughted treatments, with the differences being significant at 50 days after the start of water treatments. At the end of the experiment, plant leaf area in droughted and moderate stress treatments was about 30% and 50%, respectively, of that in the watered plants (17a).

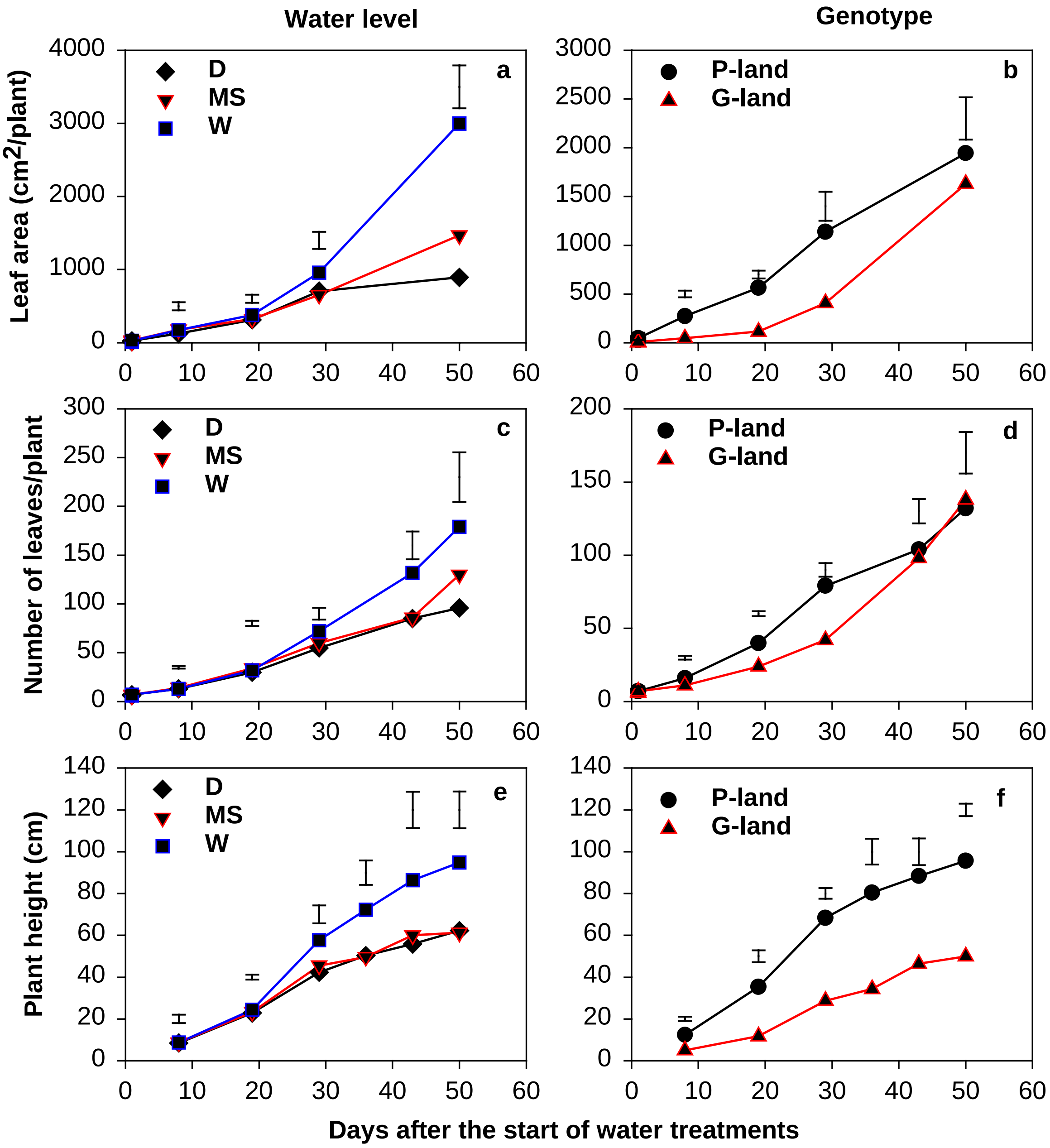

Fig. 17. Plant leaf area (a, b), number of leaves (c, d) and plant height (e, f) of spiderplant as influenced by water levels (means across genotypes), droughted (D), moderate stress (MS) and watered (W) and genotypes (means across water levels) P-landrace (P-land) and G-landrace (G-land) under field conditions in 2001. Vertical bars show $LSD_{0.05}$.

P-landrace maintained a higher plant leaf area than G-landrace, significant at all dates except at 50 days after the start of water treatments (Fig. 17b). On average, the leaf area of G-landrace plants across the soil water levels was about 16% of that of P-landrace at start of water treatments and about 84% at the end of the experimental period. Number of leaves per plant followed the same pattern as leaf area, with significant differences between soil water levels and genotypes from 29 days after the start of water treatments (Fig. 17c, d). Further, watered plants had greater heights, significant from 29 days after the start of water treatments (Fig. 17e). P-landrace had a significantly greater plant height than G-landrace at all harvest dates (Fig. 17f).

Dry Matter Production and Partitioning

The leaf and stem dry weights followed the same pattern as that of leaf area. The dry weights were in the order of watered>moderate stress>droughted (data not shown). P-landrace plants had significantly higher shoot dry weights than G-landrace (Fig. 18a).

The ratio of dry matter production of droughted to watered plants for spiderplant remained high until a soil moisture content of 18-20%. Decline in the gravimetric soil water content below this range was accompanied by a rapid decline in the dry matter production (Fig. 18b). The leaf to stem ratio declined with increasing plant height (Fig. 19). This could be well described by a power function and there were no significant differences in the coefficients between soil water levels and plant genotypes.

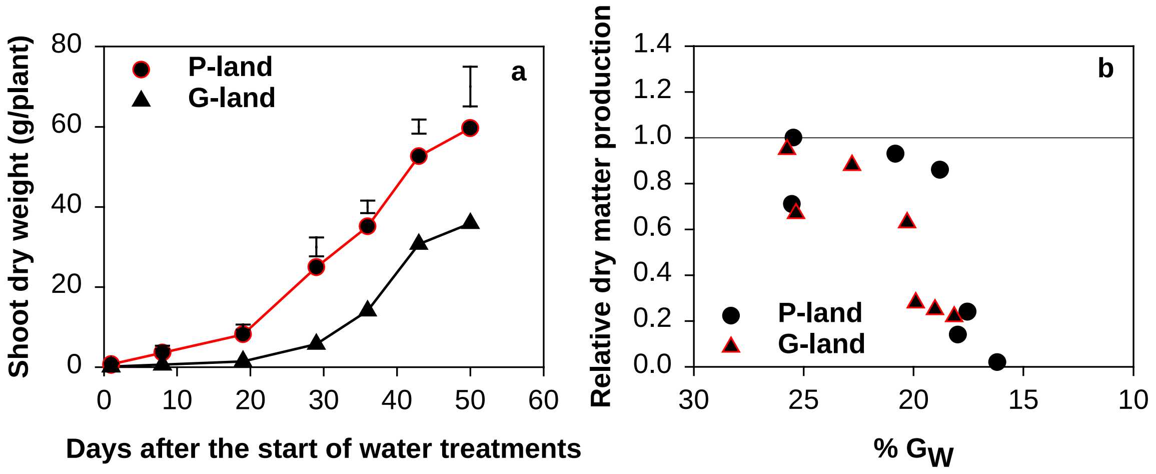

Fig. 18. Shoot dry weight of spiderplant as influenced by genotypes (means across water levels) (a) and the scatter diagram of dry matter production of droughted relative to watered plants as a function of the gravimetric soil water content (% G_W) (b) for genotypes P-landrace (P-land) and G-landrace (G-land) grown under field conditions in 2001. Vertical bars show $LSD_{0.05}$.

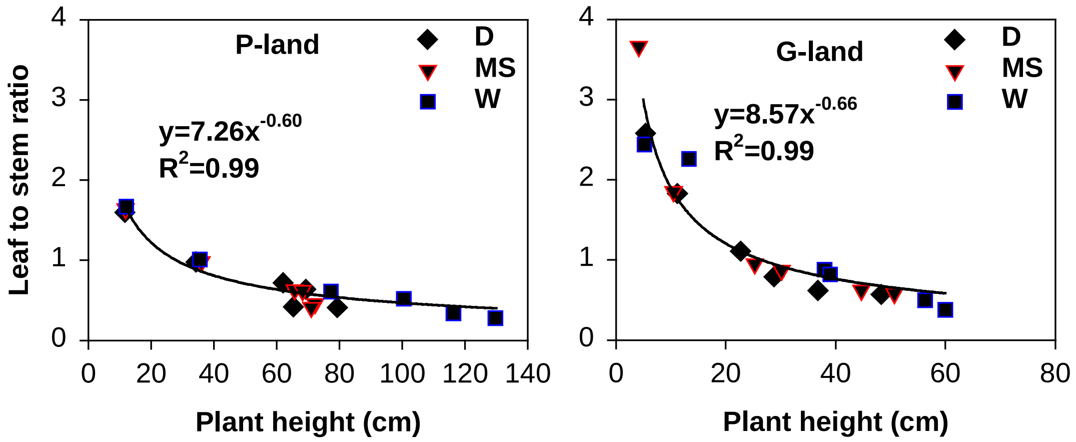

Fig. 19. The relationship between leaf to stem ratio and plant height of spiderplant genotypes P-landrace (P-land) and G-landrace (G-land) grown at three water levels, droughted (D), moderate stress (MS) and watered (W) under field conditions in 2001. Points are measured data and lines are power functions shown.

African Nightshade

Plant Water Use

The gravimetric soil water contents at 0-20 cm and 20-40cm depths were similar, hence only the mean of the two is considered. The decline in soil water content under the droughted treatment was similar in both the *S. sarrachoides* accession and *S. villosum* commercial genotypes (Fig. 20a). The soil water content declined rapidly from onset to 28 days after the start of water treatments beyond which the decline was less rapid. A similar observation was made for moderate stress treatment before rewatering (Fig. 20b). Variability was high in the soil water content results under watered treatment (Fig. 20a). However, the soil water content was maintained around 25% (75% FC) for both genotypes in the early stages of growth. In the later stages, the soil moisture content for commercial plants at both depths remained significantly lower than that for the accession plants.

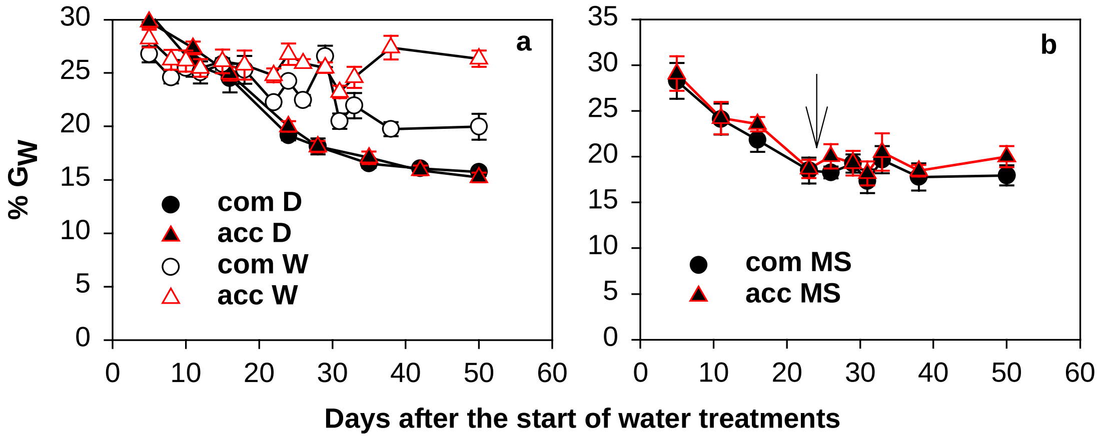

Fig. 20. The gravimetric soil water content (% G_W) at 0-40 cm depth for African nightshade genotypes commercial (com) and accession (acc) grown at three water levels, droughted, D and watered, W (a), and moderate stress, MS (b) under field conditions in 2001. The arrow in the MS treatment indicates the rewatering date. Vertical bars show SE (n=3).

Leaf Area Development and Plant Height

Watered plants had significantly higher leaf area for both the accession and the commercial genotype at 22 and 29 days after the start of water treatments. Beyond this time, there were significant interactions between genotype and soil moisture in which accession plants exhibited a significantly higher leaf area compared to the commercial genotype at the corresponding soil water levels (Fig. 21a, b). Plants in the moderate stress treatment initially had similar leaf area as droughted ones, but after rewatering, their leaf area increased significantly, although it remained lower than that in the watered treatment for both genotypes.

Specific leaf area (SLA) declined almost linearly over time in the droughted treatments but remained more or less constant in the watered treatment, with the difference being significant from 28 days after the start of water treatments (Fig. 21c, d). Initially, SLA for the moderate stress treatment was similar to that of droughted ones, but after rewatering, it was similar to that in the watered treatment. The accession maintained a higher SLA than the commercial genotype, significant at 35 and 42 days after start of water treatment. Plant height was greater in watered than the other treatments, significant from 22 days after the start of water treatments (Fig. 21e). At 51 days after the start of water treatments, the moderately stressed plants increased their heights significantly for the accession. Considering the effect of genotypes, commercial plants maintained a significantly greater plant height than those of the accession at corresponding soil water levels at all harvest dates except 51 days after the start of water treatments (Fig. 21f). The ratio of leaf area increase of droughted to watered plants declined linearly with soil water content (Fig. 22e).

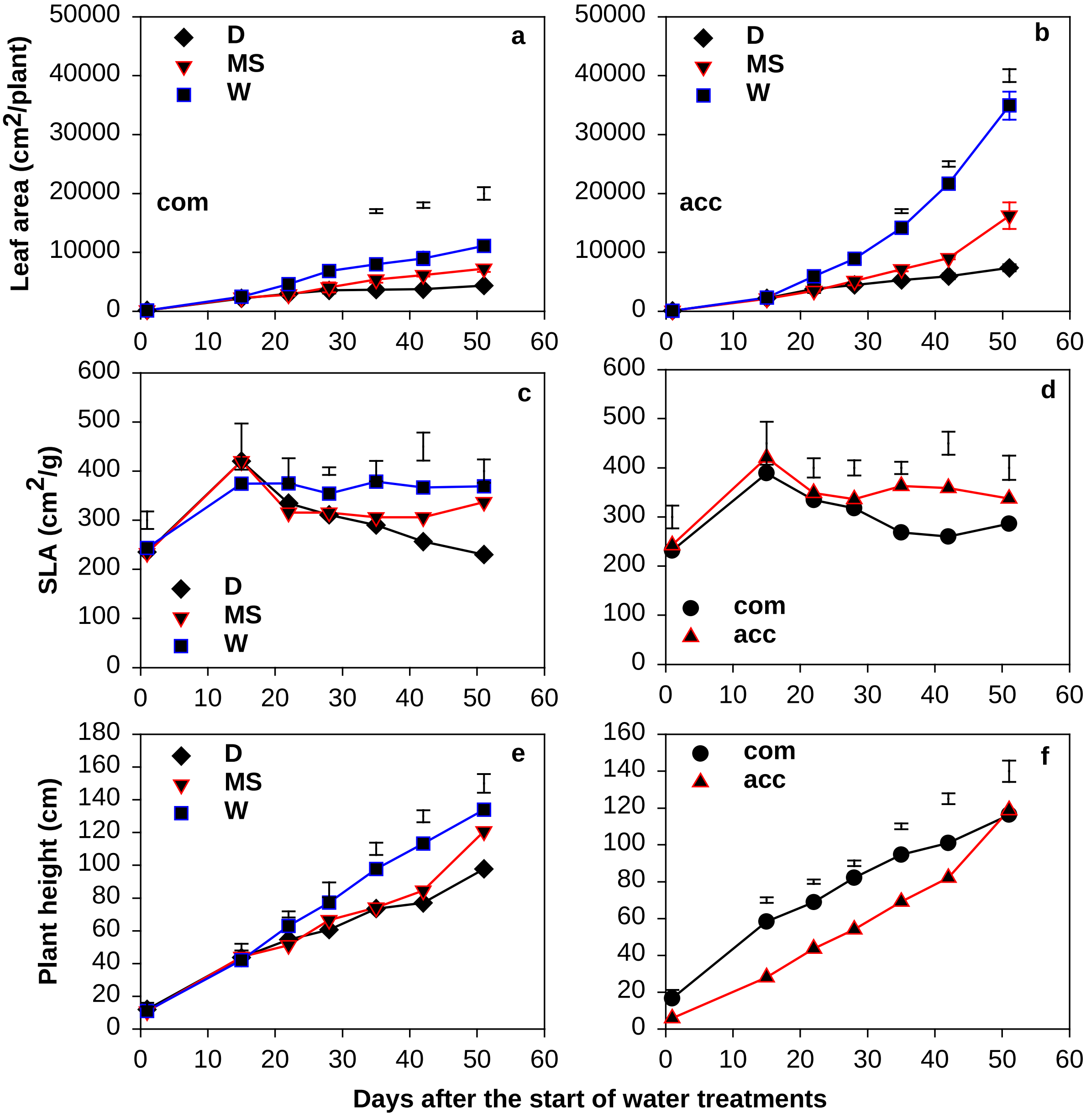

Fig. 21. Plant leaf area of genotypes commercial (com) and accession (acc) at three water levels, droughted (D), moderate stress (MS) and watered (W) (a, b), the SLA and plant height as influenced by water levels (means across genotypes) (c, e) and genotypes (means across water levels) (d, f) for African nightshade grown under field conditions in 2001. Vertical bars above the lines show $LSD_{0.05}$ for interactions (a, b) and for means (c, d, e, f), while those on lines show SE (n=3).

Dry Matter Production and Partitioning

Watered plants had higher leaf and stem dry weights, significant from 22 to 35 days after the start of water treatments. Beyond this time, interactions between water level and genotype were significant. In the interactions, the dry weights were higher in accession as compared to the commercial genotype at corresponding soil water levels, and the order of magnitude was watered>moderate stress>droughted for both genotypes (Fig. 22a-d). Decline in dry matter production for African nightshade coincided with a soil moisture content of 19-20%. Below this soil water level, the dry matter production in droughted plants relative to watered ones declined linearly with decline in soil moisture content (Fig. 22f).

The leaf to stem ratio was correlated with plant height and could be explained by a power function with no significant differences in the regression coefficients between soil water levels (Fig. 23).

4.4 Discussion

Spiderplant

Plant Water Use

Under drought, P-landrace showed a higher water extraction at 0-40 cm depth as compared to G-landrace. These results could be explained in two ways. Firstly, water extraction in a given soil layer depends on root length density as well as soil extraction efficiency (Moreshet et al., 1996; Penning de Vries et al., 1989). Although root growth was not determined in this study, it is possible that P-landrace had a higher root length density or had a higher soil water extraction efficiency. Secondly, the differences in soil water extraction could be explained by canopy characteristics. P-landrace had higher leaf area and produced a higher aerial dry matter than G-landrace especially in the early stages of growth. This implied a higher transpiration rate as compared to G-landrace, which showed a slower rate of leaf area development. Similarly, Angadi and Entz (2002) attributed low water extraction by a dwarf cultivar of sunflower as compared to a standard height cultivar to its lower leaf area. Salih et al. (1999) also found that the sorghum cultivar with the higher leaf area also had higher transpiration rates.

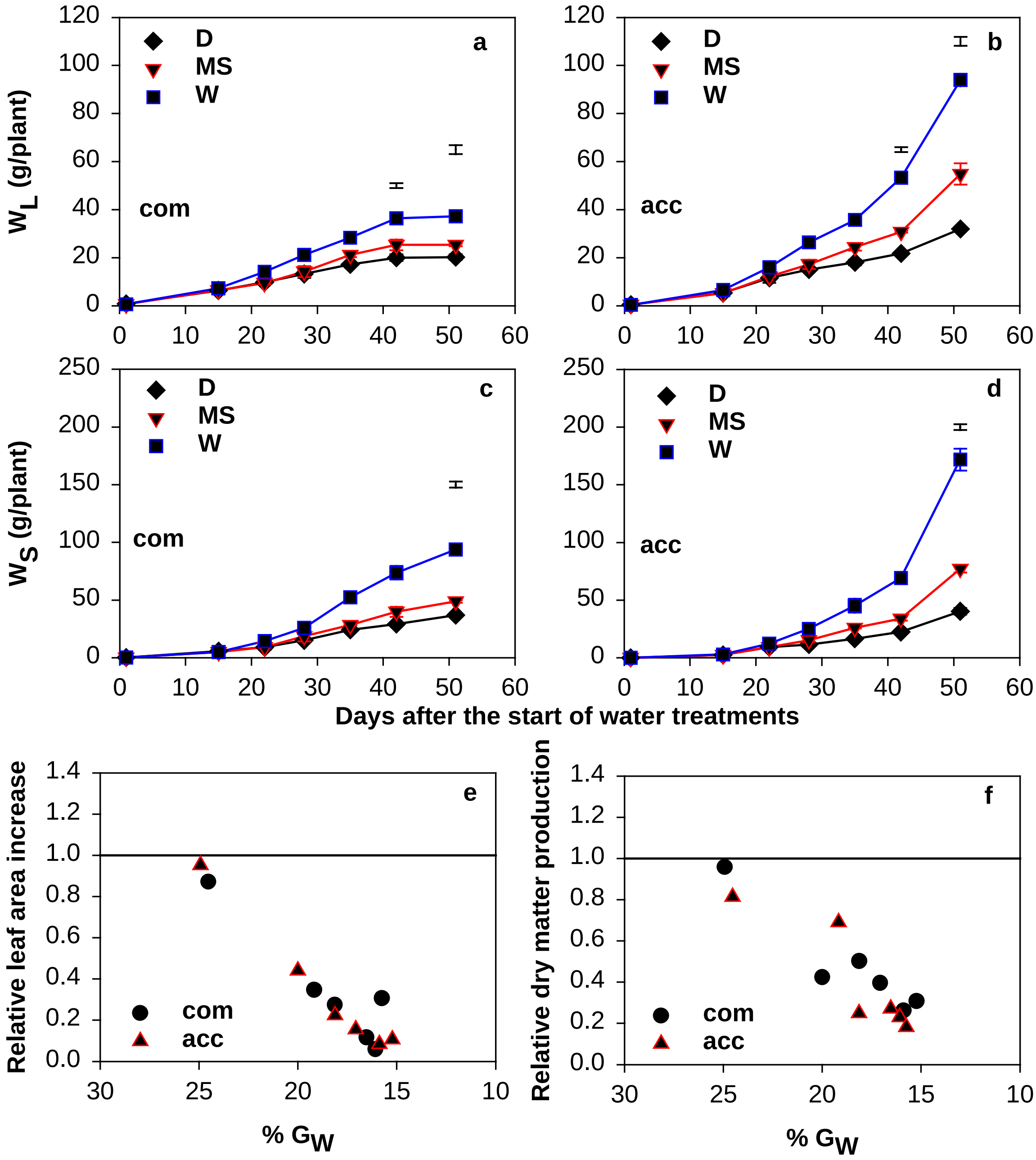

Fig. 22. Dry weights of the leaves (W_L) (a, b) and stems (W_S) (c, d) of genotypes commercial (com) and accession (acc) grown at three water levels, droughted (D), moderate stress (MS) and watered (W), and the scatter diagrams of leaf area and dry matter production of droughted relative to watered plants as functions of the gravimetric soil water content (% G_W) (e, f) for African nightshade under field conditions in 2001. Vertical bars above the lines show interaction $LSD_{0.05}$, while bars on the lines show SE (n= 3).

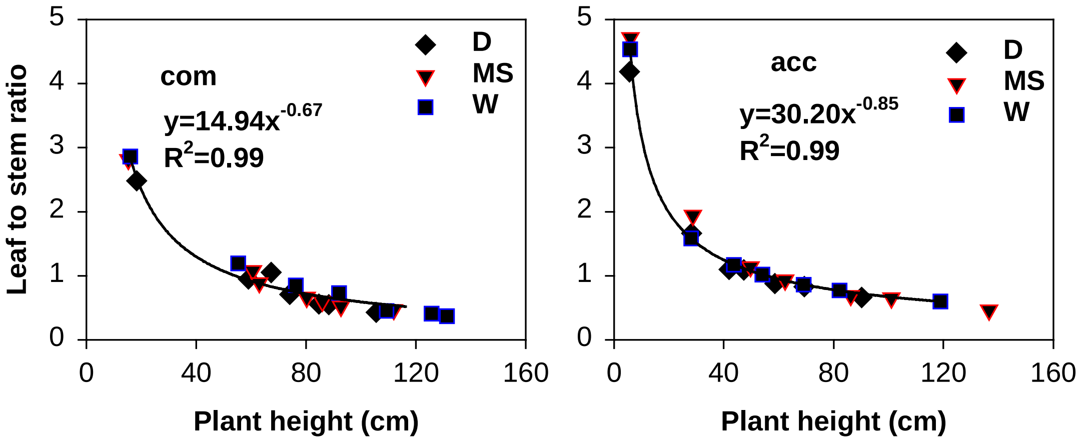

Fig. 23. The relationship between leaf to stem ratio and plant height of African nightshade genotypes commercial (com) and accession (acc) grown at three water levels, droughted (D), moderate stress (MS) and watered (W) under field conditions in 2001. Points are measured data and lines are power functions shown.

With a higher rate of water use, there is a possibility that P-landrace can exhaust soil moisture in the event of a long drought spell earlier than G-landrace. This is a disadvantage, as the plants may not benefit from late rains.

Expansive Growth, Dry Matter Production and Partitioning

Expansive growth in terms of leaf area, number of leaves, plant height and shoot dry matter were reduced by drought to similarly extents in both P-landrace and G-landrace in older plants. This reduction began as the soil water content decreased below 60% FC. It should be noted that P-landrace had a rapid expansive growth rate at the young stages as compared to G-landrace but that this was reversed in the older plants, leading to minimal differences in plant sizes under corresponding soil moisture regimes. The only exception to this was plant height, which remained smaller in G-landrace.

Rewatering of moderately stressed plants resulted in some recovery in expansive growth in terms of leaf area, number of leaves and shoot dry matter but not plant height in both genotypes. Boutraa and Sanders (2001) have reported a similar recovery in beans. At the end of the experiment, plants in the moderate stress treatment had more leaf area (60-70%) and shoot dry weight (30-50%) as compared to droughted plants but remained about 50% of that in watered plants. There was a delay in raising the soil water content to about 60% FC in the moderate stress treatment after onset of rewatering. This could be attributed to the low leaf area after the stress period, which meant that the plants maintained a low ground cover (leaf area index<2). Soil evaporation on rewatering was therefore considerably high. According to Jones (1992), evaporation from wet soil can be as much as half the total when leaf area index is below 2.

As expected, the leaf to stem ratio declined with increase in plant size. This is in line with the concept that increasing plant size necessitates increase in structural material to maintain integrity and strength (Stützel et al., 1988; Marcelis, 1993) and hence an increase in the stem fraction relative to the leaf. 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.

African Nightshade

Plant Water Use

The two African nightshade species exhibited similar soil water extraction patterns at 0-40 cm depths under droughted and moderate stress treatments. This implied that accession plants had higher water use efficiency considering that they produced more dry matter than commercial plants under these conditions. Assuming that the soil water available to both genotypes was the same, the accession plants were more efficient in maximising assimilation in relation to the water available, which is a desirable trait in dry environments (Jones, 1992).

Under the watered treatment, the water use was similar between the genotypes in the early stages. In mature plants, differences in the soil water content between the two genotypes under watered treatment were pronounced. Despite receiving proportionately more water, soils in the commercial genotype plots remained drier as compared to the accession plots. This difference in the water use could be attributed to the differences in canopy characteristics between the two genotypes. Mature accession plants had a more spreading growth habit, forming a series of interlocking lateral branches, which together with the higher leaf area formed a compact canopy. This meant little or no soil evaporation as well as low transpirational loss from canopy due to reduced windspeed and light penetration and high relative humidity (Jones, 1992). This contrasts with the commercial plants, which had a more erect growth habit, usually associated with a rough canopy, and in addition lower leaf area, all leading to higher soil evaporation and canopy transpiration losses (Jones, 1992).

Expansive Growth, Dry Matter Production and Partitioning

In both species, leaf area development, plant height and dry matter production were reduced in droughted plants as the soil moisture declined below 60% FC. In general, the decline in leaf area development and dry matter production was linearly related to soil water content for both species. However, the soil water content thresholds at which the declines began could not be precisely established due to few data points. SLA was also reduced by drought in both species after the soil moisture declined below 60% FC. This could be attributed to senescence and shedding of older leaves, leaving small and thick young leaves (Husain et al., 1990).

The two plant species had different growth characteristics at different stages. In the seedling stages, commercial plants had a higher aerial dry matter, plant height and leaf area. This changed as the accession plants exhibited a higher rate of expansive growth thus having higher leaf area, aerial dry matter and similar plant height as the commercial plants in the mature stage at all the soil water levels. For instance, at the last harvest, leaf area of commercial plants was just about 59%, 45% and 32% of that in accession plants at droughted, moderate stress and watered treatments, respectively. Dry matter production was equally lower in commercial plants at all the soil water levels. This lower expansive growth and dry matter production in commercial plants could be attributed partly to the fact that flowering and fruit development was more pronounced in the mature stages in this species.

The rapid increase in leaf area of accession under watered conditions contributed to the higher dry matter production observed as compared to commercial plants under similar conditions due to the role of leaf area in light interception (Jones, 1992). Also, the fact that accession plots maintained a high soil moisture under watered treatment meant that these plants had unlimited water supply most of the time hence the rapid increase in growth. Commercial plants on the other hand experienced some stress in between the waterings and this could have contributed to the low leaf area increase and hence low dry matter production.

Rewatering in the moderate stress treatment resulted in a more rapid recovery in leaf area, plant height and dry matter production of accession as compared to the little recovery shown by commercial genotype. The difference in the recovery between the two genotypes could be attributed to canopy and phenological characteristics. At the time of rewatering, accession plants had a higher leaf area and hence lower soil evaporation than commercial plants. Moreover, flowering and fruit set had began in both species but was more pronounced in the commercial genotype. Plants are known to have preferential diversion of photosynthates to the reproductive parts at the expense of vegetative parts (Marcelis, 1993). Whereas flowers are generally poor competitors for available assimilates, fruits are strong sinks (Marcelis, 1993; Wien, 1997). Ayodele (2000) alluded to these reasons in explaining his findings, in which stress occurring during the reproductive stage of both grain and vegetable caused severe reduction in growth than stress occurring earlier.

The difference in the recovery from stress has important implication on the production of these two species. It would seem that precipitation later in the season after an early spell of drought would be beneficial only to the accession. Nleya et al. (2001) have shown that recovery from stress gave yields in indeterminate late maturing cultivars of pinto bean as compared to the determinate early maturing ones.

Similar to the case of spiderplant, leaf to stem ratio was a function of plant size and this function was similar under all water levels.

4.5 Conclusion

Water use under droughted conditions was related to plant size as shown in spiderplant. P-landrace having a larger shoot size tended to have a higher water use as compared to G-landrace. Thus, in the event of terminal drought, P-landrace is expected to exhaust the soil moisture faster than G-landrace. Expansive growth for both spiderplant and African nightshade was significantly reduced as the soil moisture declined below 60% field capacity. The responses were similar for the genotypes studied in both crops. Dry matter partitioning between leaf and stem was related to plant height and could be described by power functions for both spiderplant and African nightshade. This relationship was not influenced by soil moisture.

In African nightshade, the accession showed higher expansive growth at all water levels as compared to the commercial genotype while both had similar water use. This suggests that the accession had a higher water use compared to commercial genotype. In both spiderplant and African nightshade, rewatering to maintain a moderate stress caused some recovery in expansive growth. While there were no clear differences in this recovery for spiderplant genotypes, the accession showed more recovery than commercial genotypes for African nightshade.

Thus, under field conditions, both spiderplant and African nightshade respond to drought mainly by an early reduction of expansive growth in an attempt to reduce water use. This is similar to the results obtained in the pot experiments. It is therefore concluded that to prevent significant reductions of expansive growth and maintain high yields under field conditions, both Spiderplant and African nightshade should be grown at soil moisture above 60% FC. In the event of intermittent drought only the *S. sarrachoides* accession is expected to have good recovery when rains come late in the growing season.

5.0 Final Discussion

Pot experiments showed that the selected genotypes of both spiderplant and African nightshade responded to drought mainly by reduction of leaf area, which led to reduction of transpiration. Similar results were obtained in the field experiments. Reduction of leaf area is a drought avoidance mechanism, which aims at slowing down the development of water deficits (Jones, 1992). Leaf expansion, leaf appearance, stem elongation and transpiration in African nightshade and the fast growing genotypes of spiderplant all began to decline at fraction of transpirable soil water (FTSW) thresholds higher than the commonly reported range of 0.3-0.4 (Sadras and Milroy, 1996). In contrast, the FTSW threshold for transpiration and stem elongation in the slow growing spiderplant genotypes was within this common range.

The decline in expansive growth of African nightshade and the fast growing genotypes of both spiderplant at relatively high FTSW thresholds seems to suggest the presence of non-hydraulic root signals regulating the plant’s response to drought. Reduction of leaf expansion in a drying soil before any measurable decline in leaf water status, attributed to non-hydraulic signals, has been shown in various crops growing in a drying soil (Saab and Sharp, 1989; Roberts et al., 2002; Kuang et al., 1990; Munns et al., 2000; Bacon et al., 1998; Puliga et al., 1996; Pugnaire et al., 1999; Dodd et al., 2002; Turner, 1997; Munns, 1988). Drought has been reported to reduce leaf appearance rate to varying extents in crops such as barley (Teulat et al, 1997), faba bean (Husain et al., 1990), maize (Alvino et al., 1999), kiwi (Chartzoulakis et al., 1993) and clover (Belaygue et al., 1996). This contrasts with reports of no effects in pea (Lecoeur et al., 1995), wheat (Krenzer et al., 1991), or relatively low FTSW thresholds for various genotypes of vegetable amaranth (Liu, 2000), sorghum (Rosenthal et al., 1987), and soybeans (Hoogenboom et al., 1987b).

Under severe stress, (FTSW<0.40), the relative water content, osmotic potential and water potential of both spiderplant and African nightshade declined rapidly (Chapters 2 and 3). This resulted in only limited osmotic adjustment of 0.10-0-33 MPa for spiderplant, and 0.16-0.19 for African nightshade. Similarly, severe stress (FTSW<0.4) caused leaf senescence and shedding, which coincided with significant decline in dry matter production. Severe drought stress resulted in reduced specific leaf area (SLA) for spiderplant and African nightshade in pot experiments (Chapters 2 and 3). This could be attributed to the shedding of old, large leaves, with the new leaves being smaller and thicker (Husain et al., 1990). SLA is known to be negatively correlated with water use efficiency (WUE) since thicker leaves usually have a higher density of chlorophyll per unit leaf area and hence have greater photosynthetic capacity than thinner leaves (Craufurd et al., 1999; Wright et al., 1994).

In both spiderplant and African nightshade, production of the shoot biomass was more sensitive to drought as compared to that of the root, resulting in increased root to shoot ratio (Chapters 2 and 3). Similar results have been reported for crops such as wheat (Blum and Sullivan, 1997), cowpea (Sangakkara, 1998) and beans (Boutraa and Sanders, 2001), French beans (Sangakkara et al., 1996a, b), soybean (Huch et al., 1986) and various C_4 grasses (Fernandez et al., 2002). Root growth expressed in terms of dry weight is routinely reported to decrease as opposed to root length, which is reported to increase when plants are exposed to drought (Blum and Sullivan, 1997; Chaves et al., 2002; Rodrigues et al., 1995; Hoogenboom et al., 1987a; Sangakkara et al., 1996b; Sangakkara et al., 2001; Huck et al., 1986). The increase in root to shoot ratio under drought could also be partly explained by increase in the dry matter allocation to roots at higher stress levels. Water deficit leads to reduced water uptake and probably also reduced nutrient uptake since mass flow of nutrients is hampered in dry soil (Marschner, 1986) and the plant responds by increasing assimilates allocation to the roots as opposed to the shoot (Poorter and Nagel, 2000). However, the increases in root to shoot ratio in both spiderplant and African nightshade are comparatively lower than those reported for crops grown under nitrogen stressed conditions (Andrews et al., 1999; Vavrina et al., 1998).

The magnitude of osmotic adjustment (OA) in both spiderplant and African nightshade from pot experiments was low and comparable to crops reported to have low OA capacity (Moustafa et al., 1996; Kumar and Elston, 1992; Ludlow et al., 1983; Allen, et al., 1998; Premachandra et al., 1995; Awal and Ikeda, 2002; Blum, 1989; Jensen et al., 1996; Davies Jr., et al., 2002; Wullschleger and Oosterhuis, 1991). Thus, both vegetables cannot sustain positive turgor under severe drought unlike the case for crops such as sunflower (Angadi and Entz, 2002), sorghum (Flower et al., 1990), soybean (Morgan, 1992), sugarbeets (McCree and Richardson, 1987) and mustard (Wright et al., 1997).

The decline in transpiration at relatively high FTSW thresholds for African nightshade genotypes and the fast growing genotypes of spiderplant in the pot experiments also suggest the presence of non-hydraulic root signals. These genotypes exhibited a high rate of leaf area development, and hence high soil drying rate. The effect of root signals in causing an early decline in transpiration and stomatal conductance during soil drying has been reported in crops such as sugarcane (Nable et al., 1999), tomato (Wilkinson et al., 1998; Holbrook et al., 2002), sunflower (Masia et al., 1994; Shashidhar et al., 1996; Cellier et al., 1998), rice (Nguyen et al., 1997) wheat (Nan et al., 2002) and lupins (Henson et al., 1989b; Gallardo et al., 1994; Rodrigues et al., 1995).

Under field conditions (Chapter 4), soil water extraction was higher for genotypes with a higher leaf area development as observed for spiderplant. Expansive growth and dry matter production was significantly reduced as the soil water content fell below 60% field capacity for both vegetable crops. SLA was also reduced by drought stress especially for African nightshade. Rewatering in the moderate stress treatment resulted in recovery in leaf area, plant height and dry matter production but the extent depended on the genotype. Partitioning of dry matter between the leaf and stem for both spiderplant and African nightshade was related to plant height through a power function, with no significant effect of drought stress.

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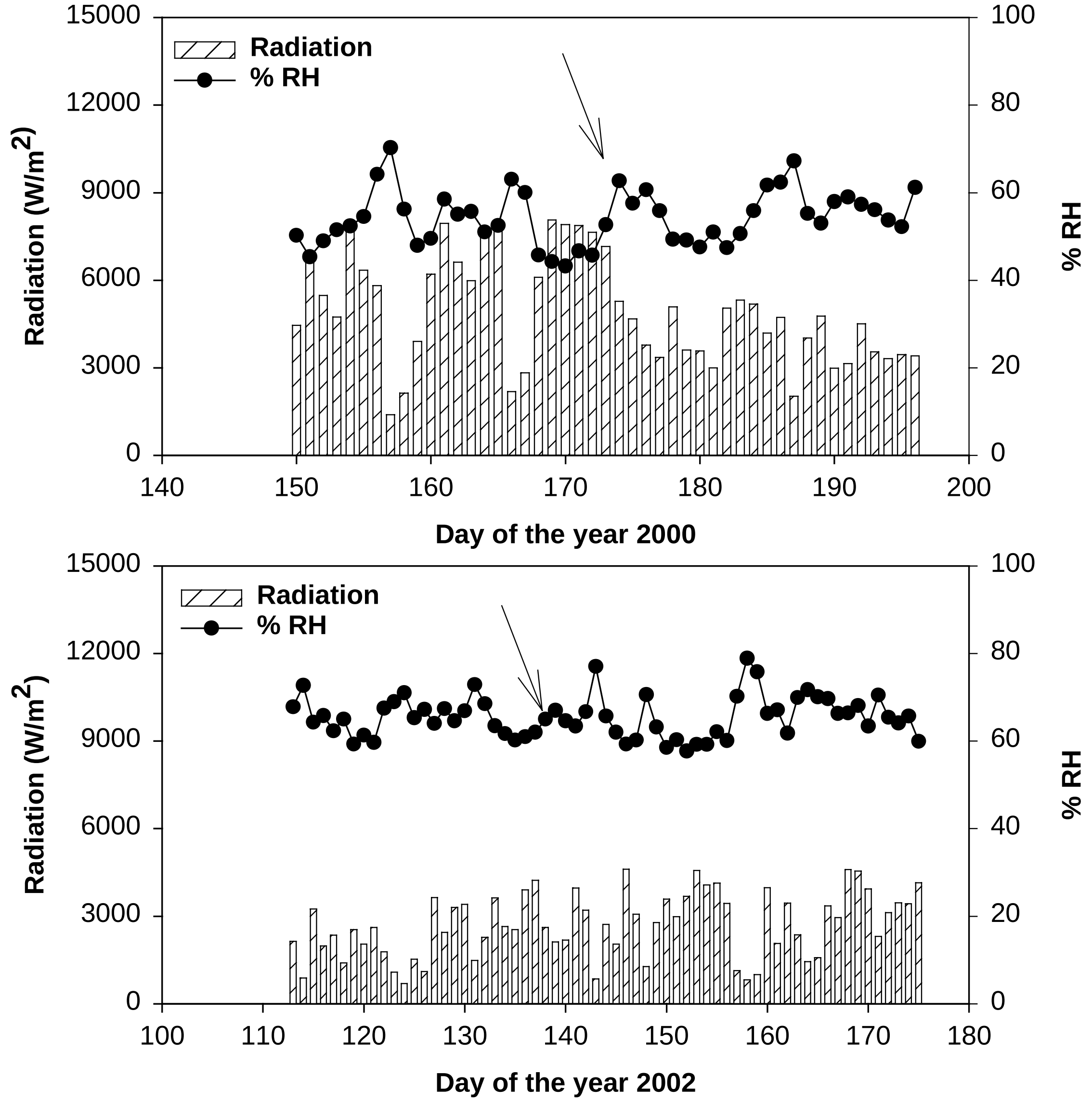
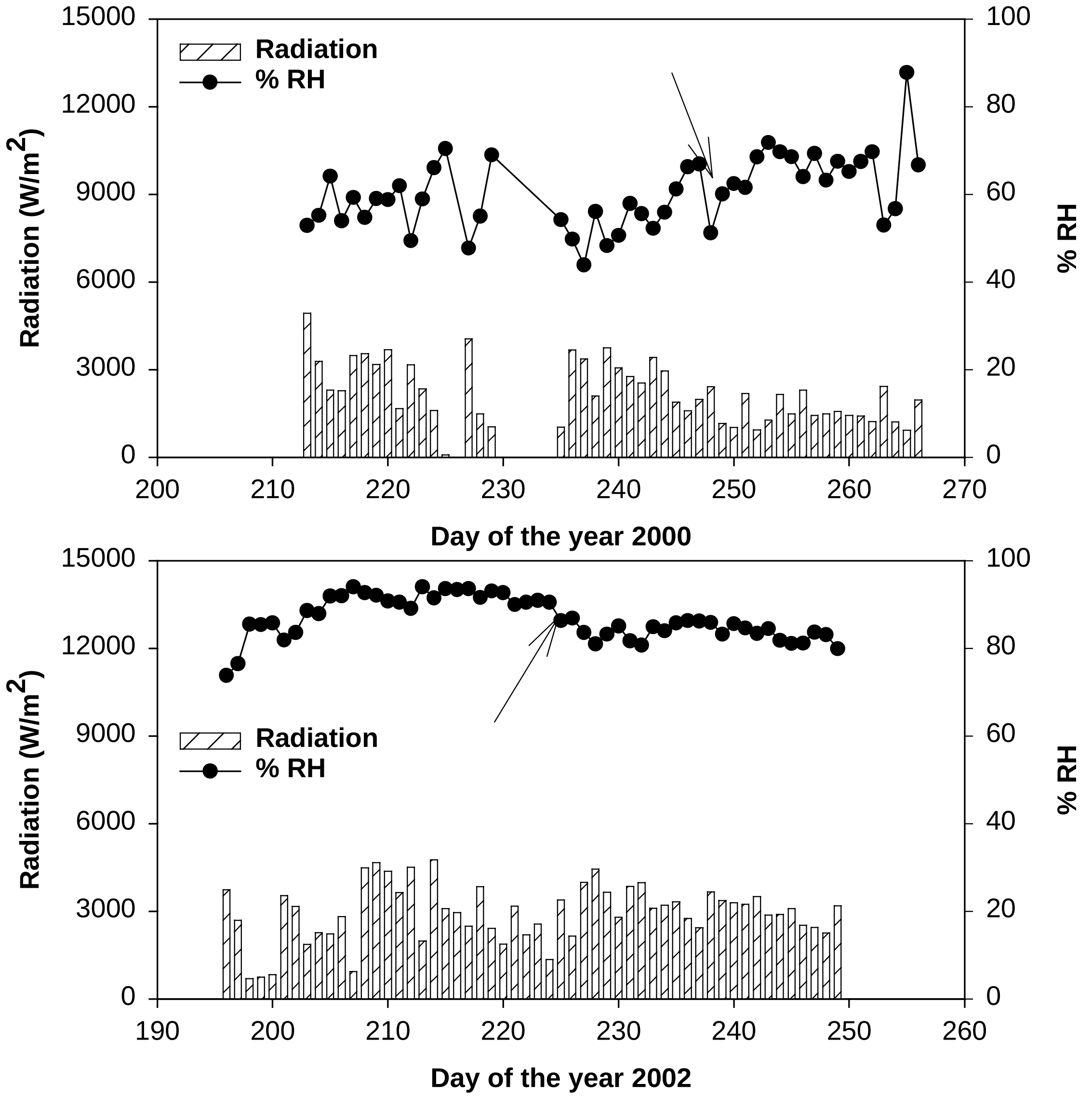
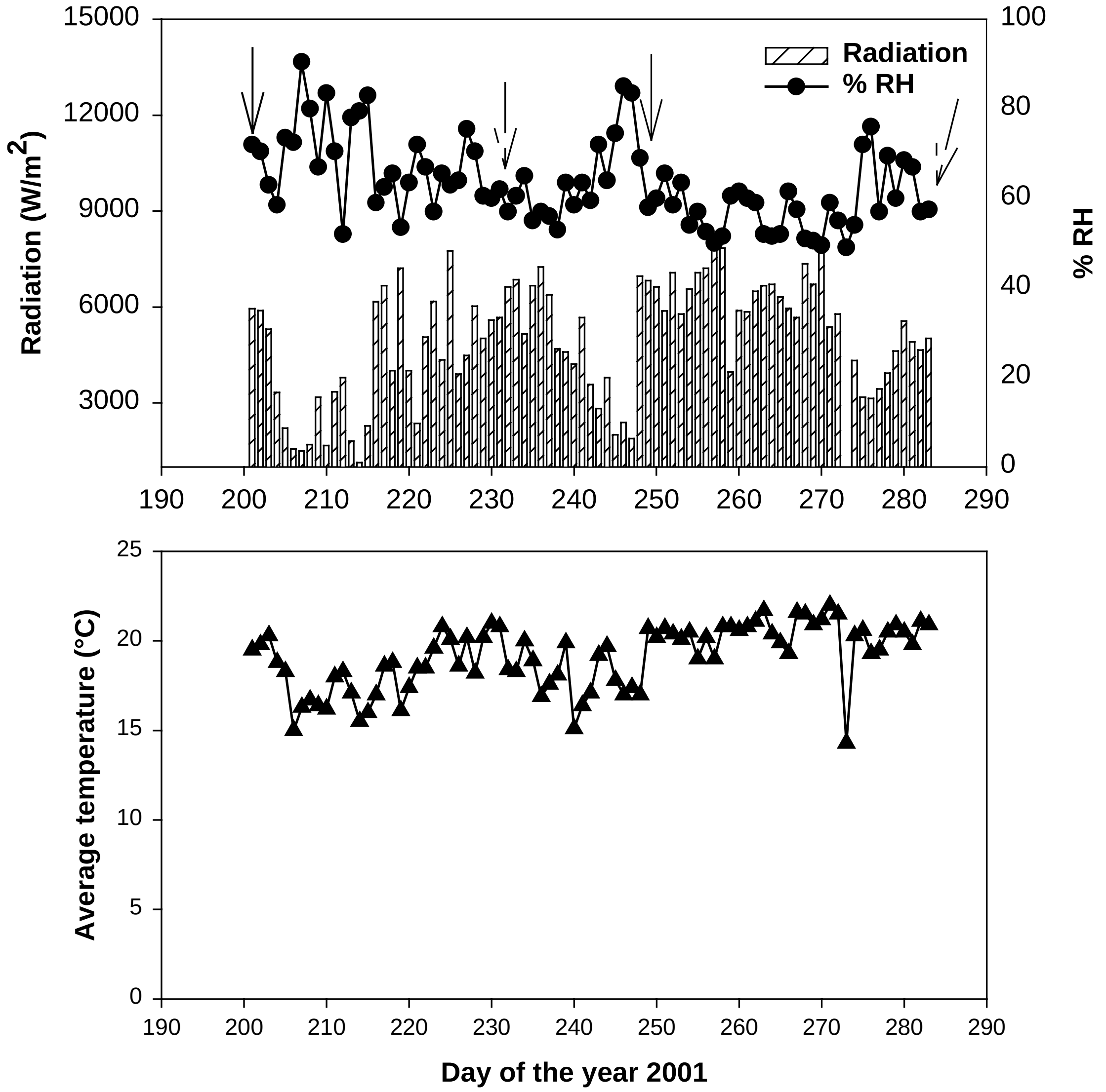
7.0 Appendices



Appendix 1. Climatic conditions during the spiderplant glasshouse experiments in 2000 and 2002 at Hannover (Germany), the arrows show the onset of water treatments



Appendix 2. Climatic conditions during the African nightshade glasshouse experiments in 2000 and 2002 at Hannover (Germany), the arrows show the onset of water treatments



Appendix 3. Climatic conditions during the field experiments in 2001 at Juja (Kenya), arrows from left to right show onset and end of water treatments for spiderplant (solid arrows) and African nightshade (broken arrows)

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides Statt, daß ich die vorliegende Arbeit selbständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe sowie daß diese Arbeit noch nicht als Dissertation oder andere Prüfungsarbeit vorgelegt worden ist.

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