

Water relations in Mango (*Mangifera indica* L.) trees

by

Michael Damaske

Submitted in partial fulfilment of the requirements for the degree

MInstAgrar: Horticulture

Department Plant Production and Soil Science

Faculty of Natural and Agricultural Science

University of Pretoria

Supervisor: Prof. P Soundy

Co-supervisor: Dr. N Taylor

February 2010

DECLARATION

I, the undersigned hereby declare that the dissertation submitted herewith for the degree Magister Institutionis Agrariae (Horticulture), to the University of Pretoria, contains my own original investigation except where acknowledged. This work has not been submitted for any degree at any university faculty.

Signed: _____

Date: _____

Michael A.C. Damaske

DEDICATION

I would like to dedicate this dissertation first and foremost to my heavenly father who has given me the ability to conduct the studies. Secondly, I dedicate this dissertation to my parents who have continuously encouraged and supported me in order to complete the studies, both financially and mentally.

ACKNOWLEDGEMENTS

I would like to thank my parents and my sister and her family for accommodating me during the time of my studies and for their continued support and encouragement.

I would like to thank my major advisor Dr E.W. Pavel for the continuous valuable guidance, advice, support and help offered to me to make this dissertation a success. Thanks to the Water Research Commission (WRC) for funding the project.

I would also like to thank Prof P. Soundy and Dr N Taylor for the guidance and advice and Prof P. Soundy for facilitating correspondence between myself and Dr E.W. Pavel during the final stages of the dissertation.

I would like to thank Khathu Oswald Neluheni for his good companionship during field trips and for his help in data collection.

I would like to thank the management of Bavaria Fruit Estate for the permission to stay on the estate and use their sanitary facilities during field trips. In particular, I would like to thank Mr Jaco Fivaz for the provision of nursery trees free of charge for the container experiments.

I would like to thank the management of Mariepskop Estate, especially Mr. Cobus Verster, for the permission to conduct the experiments on the estate and for the valuable advice and sharing of knowledge regarding orchard management practices.

ABSTRACT

Stem (Ψ_{stem}) and leaf (Ψ_{leaf}) water potential and stomatal conductance (g_s) were monitored in 6-7 year old, field-grown mango (*Mangifera indica* L. cvs 'Kent', 'Heidi' and 'Keitt') grafted onto 'Sabre' rootstock subjected to the following irrigation regimes during the season of 2002/2003: Co, control ($\pm 95\%$ of field capacity, FC); DI-1 and DI-2, continuous deficit irrigation ($\pm 79\%$ and $\pm 69\%$ of FC respectively); RDI, regulated deficit irrigation (like Co except that irrigation water was withheld for 2 weeks in Dec 2002/ Jan 2003 during the final stage of fruit growth); and Co-F, farm control, full irrigation when soil moisture was lower than -10 KPa). In Co Ψ_{stem} was more closely related to ambient air temperature ($r^2=0.88$) and ETo ($r^2=0.76$) than Ψ_{leaf} (ambient air temperature of $r^2=0.49$ and ETo of $r^2=0.27$ respectively). Stomatal conductance was mostly affected by relative humidity ($r^2=0.86$). Seasonal midday Ψ_{stem} was between -0.4 to -0.8 MPa, Ψ_{leaf} between -0.9 and -1.3 MPa and g_s ranged from 50 to 460 $\text{mmol m}^{-2}\text{s}^{-1}$. Cultivar differences in Ψ_{stem} and g_s were observed but appeared to be dominated by seasonal weather changes.

Potted 'Sabre' and 'Kent' trees appeared to be able to maintain Ψ_{stem} during periods of water stress by reducing g_s . However, after re-irrigation g_s in stressed trees did not recover as quick as Ψ_{stem} . While g_s in 'Sabre' showed some recovery, in 'Kent' it failed to show any significant recovery after re-irrigation.



TABLE OF CONTENTS

DECLARATION	iii
DEDICATION	iv
ACKNOWLEDGEMENTS	v
ABSTRACT	vi
TABLE OF CONTENTS	vii
GENERAL INTRODUCTION	1
1 LITERATURE REVIEW	4
1.1 Water relations in plants	4
1.2 Technologies to measure plant water status	9
1.3 Use of water potential and stomatal conductance to indicate water status and to detect water deficits in tree crops	13
2 CHARACTERISING WATER RELATIONS OF WELL-IRRIGATED MANGO TREES UNDER FIELD CONDITIONS	21
2.1 Introduction	21
2.2 Materials and Methods	23
2.2.1 Site description and experimental layout	23
2.2.2 Water potential and stomatal conductance measurements	24



2.2.3	Data analysis	25
2.3	Results and Discussion	25
2.3.1	Seasonal water potential and stomatal conductance	25
2.3.2	Seasonal cultivar comparison	28
2.4	Conclusions	36
3	FIELD AND CONTAINER GROWN MANGO TREE WATER RELATIONS AS AFFECTED BY IRRIGATION REGIMES AND SPATIAL VARIABILITY	38
3.1	Introduction	38
3.2	Materials and Methods	39
3.2.1	Site description and experimental layout	39
3.2.2	Measurements of water potential and stomatal conductance	41
3.2.3	Data collection and analysis	42
3.3	Results and Discussion	43
3.3.1	Comparison of seasonal water relations between different mango cultivars	43
3.3.2	Responses to water deficit of potted mango trees	47
3.4	Conclusions	63
4	SUMMARY	65
	REFERENCES	70

GENERAL INTRODUCTION

Water is a scarce commodity in South Africa and the agricultural industry in particular is a major consumer of water (Scotney and van der Merwe, 1994). Applying water to crops is a widely used practice mainly to stabilise production. However, it has been estimated that by the year 2020 South Africa would run out of surplus surface water (Bruwer and van Heerden, 1991). Predictions like these have increased, in recent years, the awareness of water as a valuable resource not only in South Africa but also in many areas around the world.

Water usage can be reduced in several ways, e.g. avoiding pipe leakages or limiting evaporation from water reservoirs like small dams, but the bulk of water used in agriculture is for the growing of crops, creating a need to improve the efficiency of crop water usage (Cochard, 2002). Therefore, to impact significantly on water consumption it is necessary to study crop water requirements and to determine the effect of deficit irrigation on crop growth and yield.

The Blyderiver irrigation scheme near Hoedspruit in the Limpopo Province of South Africa supplies water to over 10 000 ha of intensively cultivated land of which a substantial portion is planted with mango (Swart, 2000). In this area irrigation is essential for most crops in order to supplement the average annual rainfall of 400 to 500 mm mostly precipitating as thunderstorms from November to March, with great variability between months and years often leading to periodic droughts. For mango, 1000-1100 mm per year is required but may be reduced to 950 mm when stress is applied during vegetative bud initiation (Mostert and Kruger, 1998; Snyman, 1998).

The Blyderiver irrigation scheme was recently upgraded with a pipeline to replace the earth furrows in an attempt to limit losses due to seepage and illegal water use. Consumers are required to pay a water levy for the water supply and will therefore benefit from optimised irrigation scheduling, i.e. the ratio of the volume of water required and the volume of water applied (Barragan and Wu, 2001). It has become of primary importance that irrigation regimes are conducive to sustainable production of export quality fruit. Therefore, if the upgraded water supply system is going to be to the producer's advantage, irrigation scheduling may restrict vegetative growth but with the least possible effect on reproductive growth. It is therefore necessary to schedule irrigation in such a way that water stress is avoided during critical phenological stages like flowering, fruit set and rapid fruit growth.

Plant water status is a very sensitive indicator of the degree of water stress experienced by the plant and can respond very rapidly to water deficits (Day, 1981). Stem, leaf and predawn water potential (Ψ_{stem} , Ψ_{leaf} and Ψ_{pd}) and stomatal conductance (g_s) have been used extensively as measures of plant water status in fruit crops such as apple (Mills *et al.*, 1996; Mills *et al.*, 1997), prune (McCutchan and Shackel, 1992), and olive (Morigana and Fereres, 2002). Many plants have the ability to control their water status (Day, 1981). The control of stomatal conductance allows partial maintenance of tree water status by reducing transpiration or increasing water uptake (Tardieu, 1996). The water relations of trees may adapt to repeated water deficit over time leading to the maintenance of turgor at lower water potentials (Mielke *et al.*, 2000). If the mango tree water status could adapt to reduced irrigation levels, water could be saved while a viable yield, fruit quality, and tree health is maintained. However, water stress in well-irrigated crops may lead to decreased transpiration and an increased water vapour pressure deficit between

leaves and the immediate surrounding atmosphere affecting stomatal conductance (Calvet, 2000).

Despite the commercial value of mangoes published research results in mango under field conditions is limited, particularly in relation to water consumption (de Azevedo *et al.*, 2003). Most research on mango tree water relations was carried out in potted trees with the main focus on g_s and only to a lesser extent Ψ_{leaf} . However, well documented field research using Ψ_{stem} and g_s and their relation in mango growth has not been published to my knowledge. Stem water potential in prune has been shown to represent a more accurate indicator of plant water relations than Ψ_{leaf} (McCutchan and Shackel, 1992).

The objectives of this study were to characterise diurnal and seasonal patterns of water relations (Ψ_{stem} , Ψ_{leaf} and g_s) in well irrigated mango trees under field conditions, to compare water relations in different cultivars, and to evaluate responses of mango trees to different irrigation regimes with respect to their water relations.

1. LITERATURE REVIEW

1.1. Water relations in plants

Different irrigation regimes and their effect on water relations have been studied in many tree crops and other perennial and annual plants. The emphasis of most studies has mainly been on yield, vegetative growth and water relations in response to reduced water supply. Mangoes are frequently grown in areas where water supply limits optimum growth and production. Thus, information on the basic plant responses to reduced water status is important to optimise water use. Relatively little is known about the responses of mango trees to different irrigation regimes compared to other crops like deciduous crops, especially under field conditions (de Azevedo *et al.*, 2003). Many of the experiments relating to water relations of mango trees up to date were carried out under controlled glasshouse conditions (Pongsomboon *et al.*, 1992a; Pongsomboon *et al.*, 1992b; Núñez-Elisea and Davenport, 1994). Although these results may be of scientific value, they are of limited applicability to orchard conditions due to different environmental conditions prevailing within orchards.

Water stress can modify other aspects of the crops' environment besides their water status. For example, the ability to take up certain nutrients may decrease as the soil dries, depending on the amounts of nutrients in the soil (Day, 1981). The functioning of the soil-plant-atmosphere continuum, is therefore, very important (Behboudian and Singh, 2001) as the amount of plant available water in the soil and its absorption and movement within the plant may also affect the nutritional status of the plant.

Applying irrigation to crops could help in limiting the negative side effects of sub-optimal soil water levels often experienced under dryland conditions. On the contrary, over-irrigation would cause a leaching of nutrients leading to contamination of groundwater.

Many current irrigation recommendations for deciduous fruit trees have been based on an evaporative demand driven model of tree water requirements (Shackel *et al.*, 2000). Such recommendations were based on the assumption that tree water stress should be avoided, and that sufficient irrigation should be applied in order to satisfy the maximum tree water requirements under the given environmental conditions. Under conditions of limited water availability the overall plant productivity could be reduced in an attempt to reduce plant water demand (Kramer, 1983).

Under certain conditions and phenological stages in the plant growth cycle, a reduction in water supply may, however, not necessarily imply that the reproductive ability of a crop is negatively affected. However, it is very important that irrigation is well controlled in order to gain the full benefit of reduced irrigation; otherwise losses in tree productivity will most likely occur (Botes and Oosthuizen, 1994). Soil water holding capacity and deep root growth are important factors regarding the successful implementation of deficit irrigation (Fischer, 1994).

Plants need to adapt to prevailing conditions of water deficit during growth and development to avoid permanent injury. The main mechanisms of drought tolerance in perennial plants are osmotic adjustment and stomatal control resulting in maintenance of high water potential within the plant (Behboudian and Singh, 2001). Under conditions of water deficits, commonly occurring under agricultural situations,

plant water status is in many cases tightly controlled by the plant by stomatal conductance, root and leaf expansions and leaf senescence (Tardieu, 1996).

Plants, in general, experience diurnal and seasonal water deficits (Behboudian and Singh, 2001). The principle of water balance in plants is based on the amount of water taken up and the transpiration rate (Rutter, 1970). During the day, water absorption by roots often lags behind transpiration due to the resistances in water flow through the plant (Behboudian and Singh, 2001). Transpiration results in water loss from cells, leading to an increase in the suction pressure. This triggers the plant to adjust its water uptake, thereby balancing water usage (Rutter, 1970). Plant water deficit is usually replenished overnight, but may persist in dry soil (Behboudian and Singh, 2001) or soils with low temperature, poor aeration and drainage increasing the resistance of water to enter the root system (Rutter, 1970; Pavel and Fereres, 1998).

In trees, water shortage indirectly causes conditions that reduce transpiration, probably due to an increase in root resistance, leading to low leaf water potential and partial stomatal closure (Rutter, 1970; Pavel and Fereres, 1998). When repeatedly measuring plant water potential, short-term changes in water status may be observed that can be associated for example with increases in evaporative demand during the course of a day. It also partially reflects the ability of roots to extract soil water (Kramer, 1983).

The different methods of measuring plant water status use different principles and therefore, not all are equally well suited for all types of plants. The suitability largely depends on the plant characteristics including the presence or absence of latex or

resin, and woodiness (Pongsomboon *et al.*, 1992b). Several studies have shown that information on crop water status, required when planning irrigation programs, is provided more reliably by physiological (leaf and stem water potential, stomatal conductance) than by physical indicators (environmental factors like atmospheric temperature and vapour pressure deficit) (Remorini and Massai, 2003). Physical indicators are: leaf area, root/ shoot ratio, leaf size and shape, leaf orientation, leaf surface and size and position of stomata (Kozlowski and Pallardy, 1997). Visual symptoms in a variety of plants include changes in leaf colour, often coinciding with a change in leaf orientation and wilting. Eventually leaf rolling and necrosis may set in (Kramer, 1983). The oleoresin exudation pressure in pine and latex pressure in rubber trees are qualitative indicators of the water status. However, these methods only indicate the existence of water deficit but give no indication of its severity as its measurement is unpractical (Kramer, 1983).

Plant water status measured by leaf and stem water potential is a very sensitive indicator for the degree of water stress experienced by the plant (McCutchan and Shackel, 1992). It can react very rapidly in response to water deficits whether induced by low soil moisture or other environmental factors. Plant structure such as canopy size, water storage organs and leaf surface area, and transpiration rate also influences the water status of a plant (Day, 1981). During conditions of water stress in irrigated crops the canopy temperature is generally slightly higher due to decreased transpiration than in non-irrigated crops, which can easier deal with a water deficit. These differences may lead to decreased vapour pressure deficit in stressed crops, directly influencing stomatal conductance (Calvet, 2000).

Vapour pressure deficit (VPD) is the difference in vapour pressure between saturated and ambient air. It is the driving force for water to move from the leaf to the air. A large change in cell water potential causes only a small change in its vapour pressure (Behboudian and Singh, 2001). Stomatal movement affects transpiration only when the temperature and water vapour pressure gradient between the canopy and the atmosphere is very small (Behboudian and Singh, 2001). The effectiveness of stomata in controlling canopy transpiration depends on the state of air boundary layer resistance. Stomatal closure in response to air dryness regardless of the leaf water potential has been observed in various species (Behboudian and Singh, 2001). The effect of VPD seemed to be more severe in grapevine when well irrigated plants were subjected to water stress than plants subjected to deficit irrigation (Behboudian and Singh, 2001). Stomata of many plants can react within minutes to changing ambient humidity. They open wider in air with high humidity than in air with low humidity, and close in dry air. However, there is always a relation between temperature and humidity and other environmental factors (Weiers and Meidner, 1990).

The loss of turgor within the guard cells may lead to premature stomatal closure in the morning and is a relatively sensitive indicator of developing water stress. In general, stomatal response to temperature is usually optimal between 18 and 32°C and curves are rather shallow between 35-38°C, thereby showing no major effect on g_s if temperature changes by 1-2°C in that range (Weyers and Meidner, 1990). In well-irrigated, potted mango trees under controlled temperature, g_s rates were higher under warmer temperature regimes (20°C by night, 30°C by day) than under a cooler regime (10°C by night, 15°C by day) (Pongsomboon *et al.*, 1992b).

The duration and intensity of stress is of great importance since this affects the ability of trees to recover after stress exposure (Saliendra and Meinzer, 1989; Pavel and Fereres, 1998). Trees can adapt to stress conditions when subjected to periods of low water stress levels between irrigations. The duration of the intervals between stress periods can help plants to adapt to succeeding water stress conditions to a greater extent (Human et al., 1994). Comparative preconditioning studies in young apricot trees subjected to water stress through reduced irrigation volume by 75% and trees irrigated to field capacity with increasing irrigation frequency from once per day resulted in reduced water stress during stress periods (Ruiz-Sanchez *et al.*, 2000).

Plants of the same species and cultivar may react differently to the same water stress conditions if the conditions they were grown under differed. The increase in water deficit from sunrise towards midday is dependant on both species and environment. Plant adaptations due to repeated water stress might result in changes in critical stress threshold values over time (Walker and Nel, 1994). The osmotic potential in plants may decrease under prolonged stress conditions, leading to the maintenance of turgor at low water potentials, thereby adapting to water stress conditions.

1.2. Technologies to measure plant water status

Measurements of plant water status by compensation, psychrometry, sap flow, porometry and the pressure chamber methods are useful in establishing the degree of water stress in plants (Slavík, 1974; Kramer, 1983). The general principle of compensation method is based on the net water transfer between a test solution and the tissue sample. The difference of water potential is measured using a set of

uniform parallel tissue samples in a set of graded test solutions of known concentrations (Slavík, 1974). Compensation between the water potential of the sample and the osmotic potential of the test solution can take place either in liquid or in the vapour phase. The set of samples must be uniform and comparable in origin and size (surface) to increase accuracy (Slavík, 1974). The main disadvantage of this method is that a decrease of water potential estimates can occur with prolonged contact between sample and test solution, possibly due to irreversible changes of osmotic conditions at the cut surface (Slavík, 1974).

Psychrometric methods are used to measure water potential by determining the wet bulb depression in a closed gaseous system that is in equilibrium with the sample. Before use each psychrometer should be calibrated over a range of standard solutions of known water potential (Millar, 1971a). Isothermic conditions must be maintained, i.e. the sample, enclosed atmosphere, and thermocouple junction(s) (or thermostat) must all be at the same temperature, as water vapour pressure is greatly influenced by the prevailing temperature (Kramer, 1983). The wet bulb depression must be measured with an accuracy of 0.001°C (Slavík, 1974). The equilibration and subsequent measurement of a large number of samples is very time-consuming (Slavík, 1974) and water potential measurements below about $-7,5\text{ MPa}$ can be difficult (Kramer, 1983).

Stem heating methods were developed to measure the sap flow rate in a plant. In principle, a part of the stem is heated and then the heat loss over a given distance from the heater is detected. The greatest advantage of this method is probably the fact that water usage of the entire plant can be established contrary to the other methods discussed thus far where only the water potential of a relatively small plant

organ sample could be measured at a time (Kramer, 1983). It is important to differentiate between 'diffuse-porous' and 'ring-porous' trees when measuring sap flow. In 'diffuse-porous' trees the wood consists of vessels that are fairly uniform in size and distribution occupying 20-60% of the sapwood volume, e.g. apple, making them well suited for sap flow measurements (Weibel and de Vos, 1994). In 'ring-porous' wood, vessels occupy only about 5-20% of the sapwood volume mostly consisting of large early wood vessels. In contrast, certain softwoods may have up to seven growth rings that substantially contribute to sap conductance limiting the suitability for sap flow measurements (Weibel and de Vos, 1994). If trees with non-sap-conducting zones occur, it is difficult to establish the conductive, non-conductive, and intermediate zones. When sap-conducting bundles are twisted (instead of vertical only) it becomes even more complex to determine these zones. Sap flow in a particular stem area can also be related to the pattern of light interception of the canopy and thus becomes time-dependent (Weibel and de Vos, 1994). Similar responses to the daily pattern of light flux density and temperature were observed by Cohen *et al.* (1981) in citrus trees where leaf water potential (Ψ_{leaf}) decreased as leaves were warmed by the sun in the morning, while in shaded leaves Ψ_{leaf} remained high throughout the day.

Porometers provide quantitative measurements for the collective conductance of several thousand stomata together (Meidner, 1981). Null-point diffusion porometers introduce dry air to maintain a constant humidity thereby preventing moisture adsorption on the cuvette walls (Kramer, 1990). The ventilation of a closed leaf surface and the rapid mixing of the enclosed air enable more precise calculation of leaf conductance. A desiccant dries the air before entering the cuvette. A small fan ventilates the leaf surface and the humidity sensor (Slavík, 1974).

Measurements of water potential using the pressure chamber are instantaneous measurements; thus, the water potential of a plant is only measured at a specific point in time. Repeated measurements may be required to establish a trend in values over time (Slavík, 1974). The pressure chamber is portable and measurements are relatively fast compared to other techniques. It is well suited for accurate measurements of plant water status in most horticultural crops (Slavík, 1974). This makes the pressure chamber ideal for field research (Kramer, 1990). A leafy shoot or single leaf is detached from the plant as quickly as possible and enclosed in the steel pressure chamber with the cut end of the stem or petiole protruding. The chamber is then sealed and the atmospheric pressure around the enclosed leaf is increased by compressed air or nitrogen from a cylinder until a pressure is reached at which xylem sap appears at the cut surface of the shoot (Slavík, 1974; Kramer, 1983). There are several factors that may influence the readings and should be considered when taking measurements (Slavík, 1974; Kramer, 1983; Naor and Peres, 2001). Kramer (1983) indicated that the stem or petiole should only be cut once, as cutting again will change the volume of xylem that must be refilled by sap. The stem portions on the inside and outside of the chamber should be similar as it may influence the reading.

1.3. Use of stem water potential and stomatal conductance to indicate water status and to detect water deficits in tree crops

Variability in water potential depends on factors such as degree of soil saturation and relative air humidity. Diurnal variations normally vary between 1-2 MPa if exposed leaf water potentials (Ψ_{leaf}) are used in measurements and vary between plant species. Stem water potential is measured only on leaves that are still attached to the plant and enclosed in an aluminium foil covered plastic sheath for at least 90 minutes before measurements (Behboudian and Singh, 2001). Leaves for measuring stem water potential should preferably be near the stem or main scaffold on the lower part of the tree within the canopy. Thereby leaf-to-leaf variability is greatly reduced as the water status of the leaf is allowed to equilibrate with that of the stem to which it is attached (McCutchan and Shackel, 1992). By covering leaves in a dark and airtight bag the variations in air humidity can be significantly reduced thereby more stable and reliable readings can be obtained (Behboudian and Singh, 2001).

Water potential (Ψ) measurements in conifers with resin ducts and plants containing latex ducts are sometimes difficult or impossible to conduct because the exudate obscures the appearance of xylem sap (Kramer, 1983). Despite some limitations, water potential is probably the most commonly used plant-based technique for assessing the influence of irrigation treatments on tree water status (Marshal and Girona, 1997). Water potential of plants can be measured at different times of the day and on different locations within the plant canopy.

The accuracy of the results is influenced by the rate of pressure increase and on prevention of water loss from the plant material while it is being handled. Slavík (1974) suggested a stepwise pressure increase and rates generally used range from 0,01 MPa per second to 0,01 MPa every 4-5 seconds (Slavík, 1974). The amount of pressure that must be applied to force water out of the leaf cells into the xylem until it is refilled is regarded as being equal to the tension originally existing in the xylem sap and approximately equal to the water potential of the cells. This value is often termed xylem pressure potential (Kramer, 1983) and stem water potential (Ψ_{stem}) (McCutchan and Shackel, 1992), respectively. The xylem stem sap is then at atmospheric pressure. The measured pressure in this way compensates the original negative pressure in intact xylem vessels (Slavík, 1974).

Stem (Ψ_{stem}) and leaf water potential (Ψ_{leaf}) are often measured during midday to evaluate irrigation treatments. Leaf water potential has been widely used as a diurnal plant water status indicator showing the diurnal influence of evaporative demand (Ruiz-Sanchez, *et al.*, 1997; Giorio, *et al.*, 1999; Jensen, *et al.*, 2000). In some cases, Ψ_{leaf} has been found not to be sensitive enough (Behboudian and Singh, 2001). Leaf water potential is more dependent on environmental conditions and, therefore, is often characterised by greater variation than Ψ_{stem} under field conditions (McCutchan and Shackel, 1992; Jones, 1997).

Most trees exhibit a typical diurnal pattern where water potential is highest at predawn (Ψ_{pd}) and shortly thereafter. However, Ψ_{pd} may not indicate the soil-water status over the entire root zone as it tends to be biased towards the water status of

the wettest part (Behboudian and Singh, 2001). During the morning Ψ gradually decreases towards the warmest part of the day. Recovery takes place as temperatures decrease during the later parts of the afternoon. Stem water potential is often considered more sensitive to changes in soil water status than Ψ_{leaf} , with Ψ_{stem} usually being the first to react to changes in Ψ_{soil} (Sellés and Berger, 1990). Stem water potential is in many cases less variable than Ψ_{leaf} thereby providing the possibility of detecting smaller yet significant changes in Ψ_{soil} often before changes in stomatal conductance occur (McCutchan and Shackel, 1992), although it appears that the stomatal sensitivity to air humidity may depend on soil water content (Calvet, 2000). Stem water potential correlated better with g_s than did Ψ_{leaf} (Behboudian and Singh, 2001).

In potted 'Nam Dok Mai' mango trees kept under controlled air temperature conditions at around field capacity, Ψ_{leaf} followed a normal diurnal pattern with the greatest decrease in Ψ_{leaf} occurring between 06:00 and 08:00 hours in the morning (Pongsomboon *et al.*, 1992b). Leaf water potential ranged from -0.5 MPa to -1.64 MPa during the day (Pongsomboon *et al.*, 1992b). Frequently irrigated potted mango trees (cv. Tommy Atkins) maintained a morning Ψ_{leaf} of -0.33 MPa under glasshouse conditions. Leaf water potential dropped to -3.55 MPa when subjected to water stress for 25 days but decreased further to -3.78 MPa after an additional 11 days of stress coinciding with partial defoliation in about half of the stressed trees. Núñez-Elisea and Davenport (1994) concluded from their studies that Ψ_{leaf} as stress indicator proved to be efficient in potted water stressed trees. In two-year-old potted 'Kensington' mango trees cultivated in a glasshouse wilting occurred when Ψ_{leaf}

ranged between -1.2 MPa and -1.51 MPa after 21 days of water withholding (Pongsomboon *et al.*, 1992a). At -2.45 MPa leaves changed into a dull green colour and necrosis occurred in the older leaves at about -3.2 MPa. Irreversible damage was evident at -3.45 MPa and 44 days of water withholding (Pongsomboon *et al.*, 1992a).

When irrigation in a 5 year old peach orchard was reduced by 50% compared to the fully irrigated control, regular Ψ_{leaf} and Ψ_{stem} measurements showed a typical curve where Ψ was high at predawn, dropping rapidly after sunrise to its lowest level at about midday (Sellés and Berger, 1990). Both Ψ_{leaf} and Ψ_{stem} values increased as the evaporative water demand decreased during the afternoon. The reduced irrigation treatment had lower Ψ_{pd} values but otherwise the patterns for both treatments were similar. Plant water potentials responded very well to water applications, Ψ_{stem} reacted first followed by Ψ_{leaf} and Ψ_{pd} (Sellés and Berger, 1990). It, therefore, seemed that Ψ_{stem} was more dependent on soil water potential than Ψ_{leaf} . Similar diurnal responses in water potential are characteristic for most fruit trees (Sellés and Berger, 1990). Human *et al.* (1994) confirmed that stem water potential together with daily variations in trunk diameter were the most responsive to irrigation in peach.

In almond, midday Ψ_{stem} reflected differences in irrigation regimes (Shackel *et al.*, 2000). In prune and other deciduous tree crops it was found that the same quantity of irrigation, particularly at a deficit level, can result in very different levels of tree stress, depending on soil depth and possibly additional factors related to root health (Shackel, et al., 2000). Therefore to reliably manage deficit irrigation strategies such

as regulated deficit irrigation (RDI) under different soil conditions, it may be necessary to use a plant-based measure of stress, such as midday Ψ_{stem} as an irrigation guide (Shackel *et al.*, 2000).

The positive effect of the RDI strategy was also demonstrated in French prune where the expected midday Ψ_{leaf} for well irrigated trees was about -1.0 MPa (Lampinen *et al.*, 2001). By allowing a progressive decline in Ψ_{leaf} over the season to approximately -1.5 MPa towards harvest induced by reduced irrigation practices before harvest, excessive fruit drop was prevented. It, therefore, seemed to be an effective way to reduce irrigation and maintain economic returns in French prune (Lampinen *et al.*, 2001). In lemon trees, larger differences were found between different RDI treatments in Ψ_{pd} than in midday Ψ_{leaf} indicating that Ψ_{pd} was a more accurate indicator of the plant water status than Ψ_{leaf} (Domingo *et al.*, 1996).

Under tropical conditions midday Ψ_{leaf} of water stressed grapevines was about 0.1 to 0.2 MPa lower than in non-stressed plants (Araujo *et al.*, 1999). Water stress did not influence the typical diurnal fluctuations of Ψ with the highest values at predawn and the lowest just after midday (Araujo *et al.*, 1999; Pire and Ojeda, 1999). Stem water potential in non-irrigated vines decreased significantly to approximately 0.5 MPa more during the day than that of irrigated vines (Sipiora and Lissarrague, 1999). Predawn water potential in grapevine tended to rise rapidly with an increase in soil water content up to about 12% (Yuste *et al.*, 1999). Thereafter, an increase in soil water content was not reflected in Ψ_{pd} measurements. Predawn water potential appeared to provide a good estimation of plant water status, possibly even better than Ψ_{leaf} at midday (Yuste *et al.*, 1999). Choné *et al.* (2001) suggested that in

grapevine Ψ_{stem} was the most sensitive indicator for moderate and severe water deficits when compared to Ψ_{leaf} and Ψ_{pd} . Cultivar differences regarding Ψ_{leaf} have been reported for crops like grapevine (Pire and Ojeda, 1999) as well as avocado (Chartzoulakis *et al.*, 2002).

The importance of g_s and Ψ_{leaf} on each other has been demonstrated in numerous studies. In vines, there appeared to be a correlation between Ψ_{leaf} and g_s although g_s remained fairly constant for most of the afternoon, while leaf water potential had a tendency to increase (Sipiora and Lissarrague, 1999). Changes in ambient light could have been involved in the response of g_s .

Young apricot trees, subjected to drought conditions until water potential at predawn (Ψ_{pd}) reached -2.5 MPa, responded with rapidly decreasing g_s from the onset of stress and recovered slowly indicating that stomatal behaviour was not simply a passive response to water deficits (Torrecillas *et al.*, 1999). Stomatal control, lower transpiration through a smaller leaf area and epinasty appeared to have been the major factors for drought resistance in apricot (Torrecillas *et al.*, 1999).

In the case of sugarcane plants exposed to drying soil, control of g_s appeared to be primarily determined at the root rather than at the leaf level (Saliendra and Meinzer, 1989). Increasing soil water deficits resulted in stomatal closure, probably as drought avoidance mechanism, thereby maintaining a constant shoot water status (Saliendra and Meinzer, 1989).

In some instances there may be a delay in g_s adjustment in response to water deficits as reported by Moriana and Fereres (2002) in olive trees and in a pioneer shrub *Sorbus aucuparia* (Vogt and Lösch, 1999) where g_s was reduced only when water deficits approached moderate to severe levels. The slow response could be an effect of soil water potential, plant structure, and transpiration rate (Day, 1981). However, the fruit tree *Ziziphus rotundifolia* showed a substantial reduction in stomatal conductance (g_s) before changes in predawn water potential (Ψ_{pd}) were detected indicating that stomatal closure and enhanced efficient use of water were the first to respond to reduced water availability (Arndt *et al.*, 2001).

Overall, it seems that the use of water potential is a very good indicator in determining the water status of plants. However, stem water potential is considered to be more suitable as a tree water status indicator in prune than Ψ_{leaf} because of interactions between Ψ_{leaf} and g_s (McCutchan and Shackel, 1992). Being a plant-based measure of water stress, Ψ_{stem} may be used in irrigation scheduling whereby root health and other factors affecting soil water uptake are reflected (Shackel *et al.*, 2000). Stem water potential in grapevine appeared to be more sensitive to irrigation levels than leaf water potential (Behboudian and Singh, 2001). Being aware of and taking into account the factors that may influence measurements it might be a useful tool in irrigation management. Stem water potentials seem to react more reliably to changes in plant water status when compared to Ψ_{leaf} . The use of Ψ_{stem} in irrigation scheduling may be a useful tool in addition to soil moisture, as it more accurately reflects the water status of the plant which might be affected by environmental conditions (McCutchan and Shackel, 1992).

Mangoes, an important commercial tree crop worldwide, have been studied very little with respect to water relations over the season as well as in response to water deficit. The presence of latex in mango increases the difficulty of studying water relations in mango trees. To schedule irrigation based on plant parameters, such as stem and leaf water potential and stomatal conductance, it is necessary to study patterns of water relations in mango trees over the season under field conditions as well as their responses to water deficit.

2. SEASONAL PATTERN OF WATER POTENTIAL AND STOMATAL CONDUCTANCE IN MANGO TREES

2.1 Introduction

The growth of plants is reduced more often by water deficits than by any other factor. The first visible effects of water stress are cessation of growth, closure of stomata and wilting of young leaves and stems. Physiological processes of most plants are highly dependant on the plant water status. It is therefore of considerable importance to determine plant reactions to changes in water status. The changes in plant water status are dynamic, always reacting to changes in external weather and moisture conditions. In many cases changes in plant water potential are only visible long after these changes have started to affect physiological processes of the plant. By measuring certain critical processes in the plant, (for instance plant water potential and stomatal conductance) these effects on physiological processes may be detected at a much earlier stage. The effect of changes in environmental conditions on plants varies greatly between plant species and even between cultivars within species (Kozlowski and Pallardy, 1997). Some species and cultivars have characteristics to better deal with certain environmental conditions than others and therefore may be better adapted to certain regions than other species or cultivars of the same species, respectively (Kozlowski and Pallardy, 1997).

Transpiration as a physiological process is mainly affected by plant characteristics such as leaf structure, leaf area, root/shoot ratio, leaf size and shape, leaf orientation, leaf surface and stomatal degree of exposure and the responses of stomata (Kozlowski and Pallardy, 1997). Although some water vapour may escape through

lenticels in the bark and epidermis about 90% is lost through the stomata. External factors affecting transpiration consist mainly of leaf shape and structure and wind speed. Increasing wind directly affects transpiration as the boundary layer of vapour around the leaf is removed. Indirectly wind has a cooling effect (Kozlowski and Pallardy, 1997). Although there appears to be little effect of stomatal closure on transpiration in windless conditions, it becomes considerable once there is air movement around the leaf (Kozlowski and Pallardy, 1997).

Although leaf water status appears to have an overriding effect on stomatal aperture, the soil water status seems to have a very important influence particularly during long droughts when soil water potential becomes very low (Kozlowski and Pallardy, 1997).

Often there are clear decreases in water content of plants in sunny weather. Stomata are strategically placed between the dry atmosphere and wet leaf interior (Turner, 1991). Usually the plant has maximum water content early in the morning near sunrise, decreasing towards midday and increasing towards the afternoon and evening. There are also seasonal variations in water content evident in many hardwood tree species but is less evident under milder climates. There is evidence that delayed stomatal closure often is associated with species that are native to dry habitats and arid regions (Kozlowski and Pallardy, 1997).

Actual responses of plants vary considerably (Kozlowski and Pallardy, 1997). Diurnal and seasonal patterns of plants' water balance depend on a range of interactions between external factors and plant water relations. Leaf water potential can vary widely especially under well-irrigated conditions and variable solar radiation. Progressive drought results in a decline in plant water potential but diurnal variation

may be suppressed due to limited transpiration resulting from stomatal closure. Therefore, the objectives of this study were to determine patterns of water relations in well-irrigated mango trees (stem and leaf water potential and stomatal conductance) over the season.

2.2 Materials and Methods

2.2.1 Site description and experimental layout

Experiments were conducted with 6-7 year-old 'Kent', 'Heidi', and 'Keitt' (grafted on 'Sabre' rootstock) and 'Sabre' trees (grown from rooted cuttings) at the Westfalia-Moriah Estate (Hans Merensky Holdings) in the Hoedspruit area, Limpopo Province of South Africa (latitude: 24° 23' 54.11" S, longitude: 30° 51' 9.83" E) during the four 2002/2003 growing seasons. Trees were planted at a density of 1.5 x 6 m. Cultural management practices, such as pruning, thinning, fertilization, and pest control, were conducted as in a commercial orchard. Trees used in this study were chosen from the two controls of an irrigation experiment (details about irrigation scheduling are described in section 3.2.) and were, therefore, well-irrigated (control: 95 ± 3% of field capacity, farm control: -10 KPa) except for June and the first two weeks of July (control: 77 ± 12% of field capacity, farm control: -20 KPa) when a period of pre-flowering stress was implemented according to commercial practices. Twelve trees per replicate (four replicates randomly distributed within the one hectare orchard) were selected for data collection.

Climatic data, such as ambient air temperature, relative humidity, windspeed, and solar radiation, required for the calculation of evaporative demand, were collected from a weather station (Campbell Scientific Instruments, Logan, Utah, USA) located

within 5 km of the study site with a well-watered and short grass soil covering. Daily evaporative demand (ET_o) was calculated using a modified Penman-Monteith equation (Allen *et al.*, 1998). Annual rainfall amounted to 262 mm during the period of June 2002 until July 2003, while mean temperatures ranged from about 17°C in winter (June-July) to 26°C in summer (January-February)

2.2.2 Measurements of water potential and stomatal conductance

Stem water potential (Ψ_{stem}) and stomatal conductance (g_s) were measured in 'Kent' throughout the season in monthly intervals. In addition, from November 2002 on, leaf water potential (Ψ_{leaf}) was also determined. Both, Ψ_{stem} and Ψ_{leaf} , were measured using a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Stem water potential (Ψ_{stem}) measurements were taken on two to three leaves per tree near the main stem in the inner part of the canopy. Leaves were covered with a foil-lined plastic bag two hours before measurement to eliminate interactions between Ψ and stomatal conductance and to allow equilibration of Ψ_{leaf} with Ψ_{stem} as recommended by Moriana and Fereres (2002). Leaf water potential and g_s were measured on two to three exposed leaves on the outer part of the canopy.

Stem and leaf water potentials and stomatal conductance for diurnal curves were measured every 2-3 hours over a day, and seasonal measurements at midday were taken between 11:00 and 13:00 about once a month on 5-6 'Kent' trees.

A steady state porometer (LI-1600, Li-Cor, Inc., Lincoln, NE, USA) was used to measure stomatal conductance on three to five leaves per tree similarly exposed as

leaves used for Ψ_{leaf} measurements. All sample leaves were fully mature and necessary precautions as stipulated by Turner (1991) were observed.

2.2.3 Data analysis

Seasonal data of 'Kent' were analysed with ANOVA (F-test, one factor = season) as a completely randomised design with four replicates per treatment. Seasonal data of 'Kent' were analyzed with ANOVA (F-test, one factor = cultivar) as a completely randomised design with two cultivars per treatment and four replicates per treatment. Means were compared using the Tukey-Kramer and Tukey tests, respectively, at $P=0.05$.

2.3 RESULTS AND DISCUSSION

2.3.1 Factors influencing water potential and stomatal conductance

It is well known that environmental factors have a strong influence on water relations of plants. However, often there is an interaction amongst environmental factors themselves and plant water relations themselves. Furthermore, there are interactions between both environmental and plant factors. Thus, there is not always a clear relation between only one environmental factor and one plant factor. As there is limited control over these interactions under orchard conditions it is not always clear which factor is the most dominant at a specific point in time.

Stem water potential was poorly related to environmental factors ($r^2=0.19$ to $r^2=0.32$), such as leaf temperature, as measured by the porometer, and vapour pressure deficit (VPD) (data not shown). Good relations ($r^2=0.81$) between stem water

potential and VPD have been found in prune trees, and Ψ_{stem} appeared to be reasonably predictable in this respect (McCutchan and Shackel, 1992). In mango under orchard conditions good relations were found between Ψ and ambient temperature and ETo (Fig. 2.1 A and B). Stem water potential showed a stronger relation to the ambient air temperature ($r^2=0.88$) and ETo ($r^2=0.76$) than Ψ_{leaf} ($r^2=0.49$ and $r^2=0.27$ respectively). Reasons for this might be that leaves used for measuring Ψ_{stem} were enclosed prior to measuring Ψ whereas those used to measure Ψ_{leaf} were exposed to environmental conditions like wind or VPD prior to measuring. This could have affected the Ψ_{leaf} and thus could result in fluctuations that would have been less significant on enclosed leaves and this could explain the greater fluctuation in Ψ_{leaf} while ambient air temperature would be the same around enclosed and exposed leaves. Therefore it could be regarded that Ψ_{stem} is more responsive to changes in ambient temperature and ETo. It further indicates that there is less fluctuation in Ψ_{stem} than in Ψ_{leaf} thereby making Ψ_{stem} a potentially more reliable plant water stress indicator in mango. McCutchan and Shackel (1992) found that Ψ_{leaf} was not an accurate indicator of soil moisture and, therefore, often not clearly related to symptoms of plant water stress. Leaf water potential should not be regarded as an ideal parameter for detecting early phases of tree water stress (Remorini and Massai, 2003).

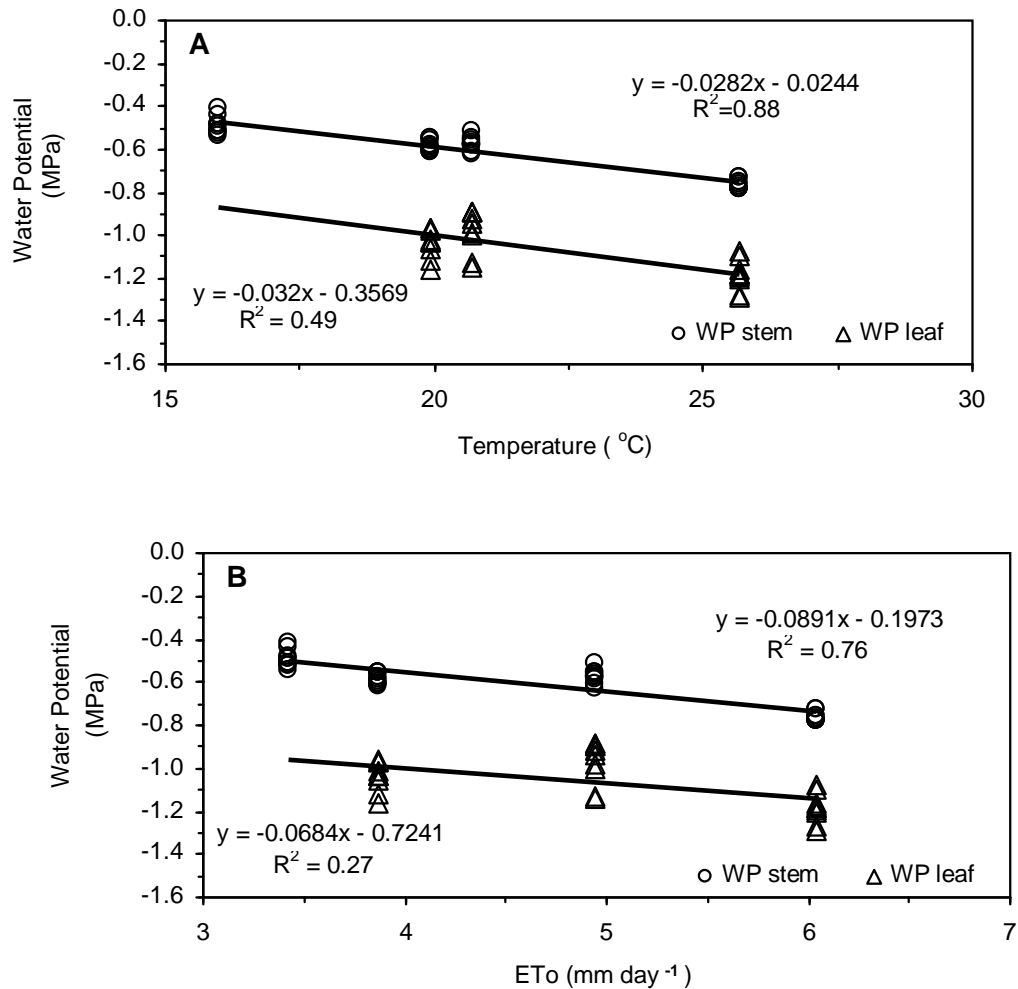


Fig. 2.1 Relationship between stem and leaf water potentials and temperature (A), and evaporative demand (ETo, B) at midday (12:30-15:00 h) of well irrigated 'Kent' 6-7 year-old mango trees over the season of 2002/2003 (Ψ_{stem} : n = 40; Ψ_{leaf} : n = 30).

Among the various environmental factors, relative humidity most strongly affected stomatal conductance ($r^2=0.86$) in mangoes (Fig. 2.2), while VPD and leaf temperature had only minor effects ($r^2=0.36$ and 0.21 , respectively). It might have been as a result of associated variable weather conditions. However in grapevine, stomatal conductance was strongly affected by VPD (Behboudian and Singh, 2001). The weak relation between temperature and g_s could in part explain why g_s was not strongly influenced by VPD. The good relationship between g_s and relative humidity could indicate that the regulation of g_s was of particular importance in preventing

excessive water loss under high evaporative demand and low relative humidity as suggested by Mielke *et al.* (2000) in eucalyptus.

However, the focus of this study was to describe the seasonal patterns of stem and leaf water potential and stomatal conductance in mangoes under subtropical field conditions.

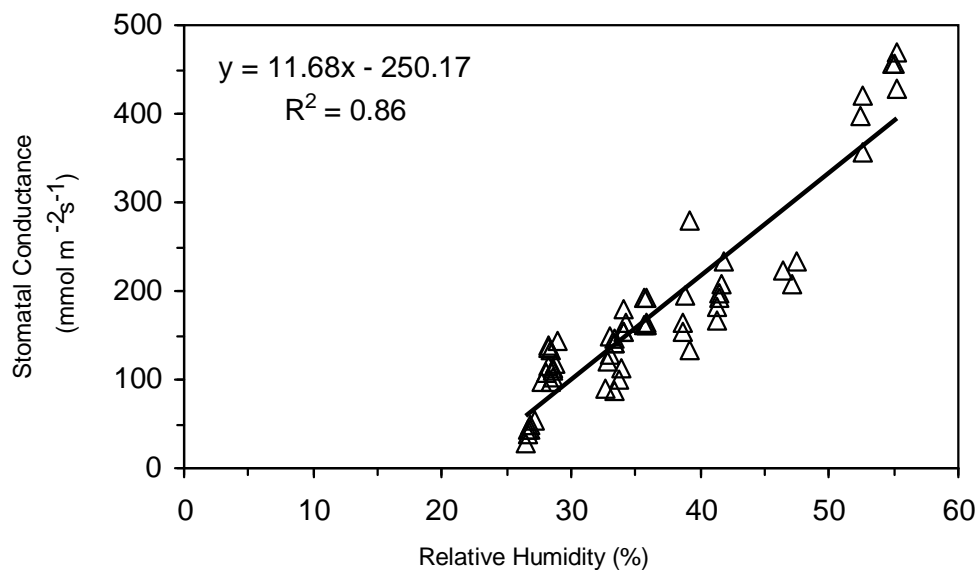


Fig. 2.2 Relationship between stomatal conductance and midday relative humidity of well irrigated 'Kent' 6-7 year-old mango trees over the season of 2002/2003 (n=175).

2.3.2 Seasonal and daily pattern of water potential and stomatal conductance

Midday stem water potential (Ψ_{stem}) fluctuated between -0.4 and -0.8 MPa over the season, but appeared to stabilise at around -0.6 MPa (Fig. 2.3A). The low value of Ψ_{stem} (about -0.77 ± 0.1 MPa) at the end of July 2002 was primarily attributed to a preceded period of reduced irrigation (pre-flowering stress) at the beginning of that

month. Low values of Ψ_{stem} during the warm summer months in December 2002 and January 2003 indicated light water stress most likely induced by high evaporative demands (ET_o ranged between 5.5 – 6.5 mm day⁻¹ over that period). Except for March and May 2003 (0.66 ± 0.02 and 0.61 ± 0.04 MPa, respectively), differences between Ψ_{stem} and leaf water potential (Ψ_{leaf}) were about 0.35 ± 0.01 MPa (Fig 2.3A). Similar magnitudes of differences between Ψ_{stem} and Ψ_{leaf} have been observed in prune (McCutchan and Shackel, 1992) and peach (Remorini and Massai, 2003). McCutchan and Shackel (1992) associated this difference with the Ψ gradient that may have been created by transpiration. In fruiting grapevine Ψ_{stem} ranged between -0.4 and -1.2 MPa while Ψ_{leaf} ranged between -1.2 and -1.6 MPa (Naor *et al.*, 1997). These values are considerably lower than observed in mango. Overall Ψ_{stem} appeared to have less variation than Ψ_{leaf} suggesting that Ψ_{stem} might be a more reliable indicator for plant water status in mango.

In fruiting grapevine, g_s appeared to increase as Ψ_{stem} increased (Naor *et al.*, 1997). This relation was also visible in mango at times during winter, spring and early summer but not so in later summer and autumn. The experimental trees under discussion were bearing fruit from September and were harvested at the end of February. The sudden elimination of a crop load after harvest could have affected this relation.

During late summer and early autumn midday Ψ_{stem} of -0.66 MPa and -0.6 MPa was recorded. Over the same period the highest g_s of the season, 392 and 453 mmol H₂O m⁻² s⁻¹ respectively, was recorded. Similar high g_s was observed in well-irrigated eucalyptus trees (447 mmol H₂O m⁻² s⁻¹) (Mielke *et al.*, 2000) and sessile oak (438

mmol H₂O m⁻² s⁻¹) (Aranda *et al.*, 2000). In fruiting grapevine, g_s ranged between 150 and 325 mmol H₂O m⁻² s⁻¹ (Naor *et al.*, 1997) while Behboudian and Singh (2001) recorded g_s as high as 900 mmol H₂O m⁻² s⁻¹ in grapevine.

Changes in g_s in banana were more influenced by soil water status than leaf water status (Turner and Thomas, 1998) in a manner similar to that observed in grapevines (Iacono *et al.*, 1998). In mangoes, the relation between Ψ_{leaf} and g_s was not existent (r²=0.02, data not shown) in contrast to field-grown olives (Giorio *et al.*, 1999) and other crops (Saugier and Katerji, 1991).

Relatively high stomatal conductances are not uncommon for mango, especially under conditions of favourable relative humidity (Pongsomboon *et al.*, 1992b; de Villiers, 2001). It has been well documented that stomata respond to changes in atmospheric humidity or vapour pressure deficit (McCutchan and Shackel, 1992; Takagi *et al.*, 1998; Mielke *et al.*, 2000) even when leaf water content remained constant (Lösch and Tenhunen, 1981). In conifers, stomatal aperture was also governed by ambient humidity when water status was favourable (Lösch and Tenhunen, 1981). It appeared that a similar scenario was prevailing in mango. In many plants, stomatal response to humidity occurred most often under saturating light conditions (Lösch and Tenhunen, 1981). As most measurements in this study took place under sunny conditions and, therefore, to a large extent under light saturated conditions, stomatal responses to relative humidity were very high in mangoes.

Flowering apparently did not affect relative water content of the trees since differences between diurnal curves of Ψ_{stem} and g_s in winter and spring (Fig. 2.4)

were minor in a manner similar to that found by Shivashankara and Mathai (2000) in mango.

In July 2002, low stomatal conductance rates (g_s) were associated with high stem water potentials as an effect of reduced water applications (Fig. 2.3B). In April 2003, the rise in g_s accompanied by a decrease in Ψ_{leaf} was most likely associated with pruning that opened the canopy thereby allowing more light to penetrate the canopy and probably causing the increase in stomatal conductance, while Ψ_{stem} was only slightly affected by the pruning measures. The fact that pruning resulted in a significant reduction in leaf transpiration surface might have enabled the tree to maintain a high transpiration rate throughout the day as the trees had adapted to supply a certain canopy area with water. Due to pruning the leaf area was reduced and therefore the tree might have had more capability to supply water to remaining leaves even when temperatures were high during midday as the relation between root and leaf surface had been temporarily disturbed. This relation normalised during the latter months as new vegetative growth occurred and cooler winter temperatures and lower relative humidity (Turner, 1991) associated with winter months could have limited transpiration. It is well known that tropical and sub-tropical plants generally have a higher temperature optimum for stomatal conductance than temperate species (Turner, 1991). The temperature optimum may be increased by growth at high temperatures and by acclimatisation. When water deficits and stomatal closure due to low humidity are avoided, stomata can continue to open at temperatures as high as 50°C (Turner, 1991). Earlier research has shown that g_s in cotton can reach up to 800 mmol m⁻²s⁻¹.

Leaf water potential also influences g_s . However, research in this respect is variable. Turner (1991) suggested that the reason being that Ψ_{leaf} is not the controlling factor for g_s in relation to plant hydration. He further suggested that g_s should be taken in conjunction with a measure of soil water status, root water status or the proportion of roots in dry soil. Gollan *et al.* (1986) showed convincingly that stomata conductance decreased as the soil water content decreased, despite the maintenance of a high Ψ_{leaf} by the application of pressure to the roots.

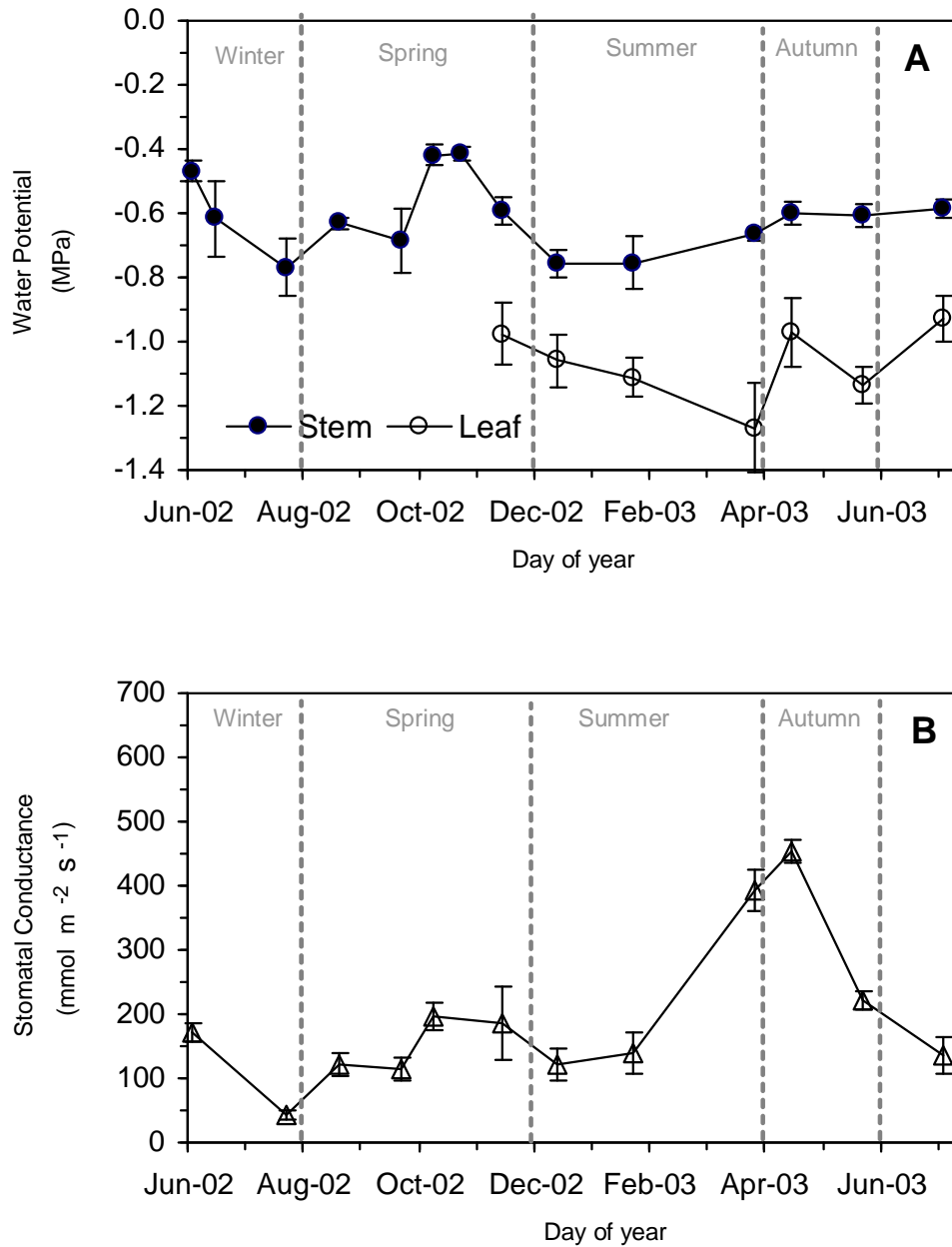


Fig 2.3 Seasonal patterns of mean stem and leaf water potentials (A) and stomatal conductance (B) of well-irrigated 6-7 year-old 'Kent' mango trees at midday under field conditions during 2002/2003 (each data point represents mean \pm SD of 3-6 replicate leaf samples).

Seasonal differences were reflected in the diurnal curves of Ψ_{stem} (Fig. 2.4A), Ψ_{leaf} (Fig. 2.4B), and g_s (Fig. 2.4C). Even under well-irrigated conditions, there were diurnal fluctuations in Ψ_{stem} of mango trees in a manner similar to that observed in beech (Kowalik *et al.*, 1997). Stem water potential followed a normal pattern across all seasons, decreasing towards midday and again increasing towards late afternoon. The differences between seasons may be attributed to annual changes in weather patterns. Water potential decreased from the morning to midday showing a maximum negative pressure between 12:00 and 14:00 h. In spite of a water potential recovery after 14:00 h, g_s continued to decline between 14:00 and 16:00 h only to recover after 16:00 h. This can be expected as stomatal closure limits water loss, thereby enabling the plant to show a recovery in water potential. It is well known that there is a decrease in plant water content near midday in sunny weather caused by resistance to movement of water from turgid plant tissue to transpiring leaves (Kozlowski & Pallardy, 1997).

During summer, diurnal curves of stem and leaf water potentials showed significantly the lowest values at most times over the day compared to the other seasons. Diurnal curves of Ψ_{stem} (Fig. 2.4A) and Ψ_{leaf} (Fig. 2.4B) exhibited similarity in spring and autumn whereas the diurnal curve for winter had the highest values across all seasons. Apparently, the lowest Ψ_{stem} values were between 14:00 and 15:00 h irrespective of season. Differences in stem water potentials between winter and summer in the morning were about 0.11 MPa but increased to about 0.35 MPa by midday.

Stomatal conductance during autumn seemed to be different to that of the other seasons (Fig. 2.4C). It was significantly higher during most of the day, only becoming similar to summer from 15:00 in the afternoon. A diurnal lowering in stomatal conductance was evident during summer and autumn. In contrast to the relatively flat curves for winter and spring which only differed significantly from each other in early morning. Similar diurnal patterns were recorded in *Fagus sylvatica* and *Quercus petraea* trees (Aranda *et al.*, 2000). It may have been linked to diurnal atmospheric influences (Marsal and Girona, 1997) conducive to high g_s at that time, such as high relative humidity and low ETo and low wind speed.

Except for winter, g_s (Fig. 2.4C) decreased during the course of the day in spring, summer, and autumn, as water deficit increased leading to partial stomatal closure in a manner similar to other crops (Lösch & Tenhunen, 1981). Stomatal conductance over the seasons showed that in winter, under cooler temperatures and late sunrise, there was an increase from the morning towards midday. In all other seasons, the maximum g_s was early in the day, decreasing as the day progressed. It could have been related to differences in time of sunrise over the seasons and changes in g_s generally associated therewith. However, g_s in the early morning was much higher during summer and autumn and spring. These seasonal changes were probably brought about by changes in time of sunrise, changes in ambient air temperature at a certain time over the seasons and probably changes in vapour pressure deficit.

Stomatal conductance rates in summer and autumn recovered slightly in the late afternoon. However, in spring and winter, g_s rates did not show a recovery during the afternoon but rather had a tendency to stabilize at around $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ for the greater part of the afternoon. During summer and autumn g_s showed a clear

decrease from late morning to late afternoon, after which signs of recovery became evident. Stomatal conductance was usually at its highest early in the morning during summer, spring, and autumn, when relative humidity was high and tree water status had recovered overnight. Low g_s rates early in the morning in winter may have been related to stress induced by low soil temperatures as was observed in field grown olives (EW Pavel, 2005: personal communication).

2.4 CONCLUSIONS

To conclude, it may be said that the results indicate that leaf water potential, stem water potential and stomatal conductance are governed by a range of environmental factors. However, only a few factors appear to have a determining influence on these processes, namely ambient temperature, evapotranspiration and relative humidity. Possible interactions between other plant and environmental factors may have lead to the other factors featuring less prominently during the study period.

Both stem and leaf water potentials responded well to plant water relations. However, stem water potential showed less fluctuation in relation to leaf water potential, thereby potentially making it a more reliable indicator of plant water status. Stomatal conductance in mango showed some seasonal variation related to seasonal variation in climatic conditions but it appeared to have been mainly influenced by relative humidity.

Future research should focus on interactions between environmental and plant factors and the influence they have on each other. It may then be useful to relate these factors to plant water status which could then be used in addition to soil water status to increase the accuracy of determining irrigation regimes.

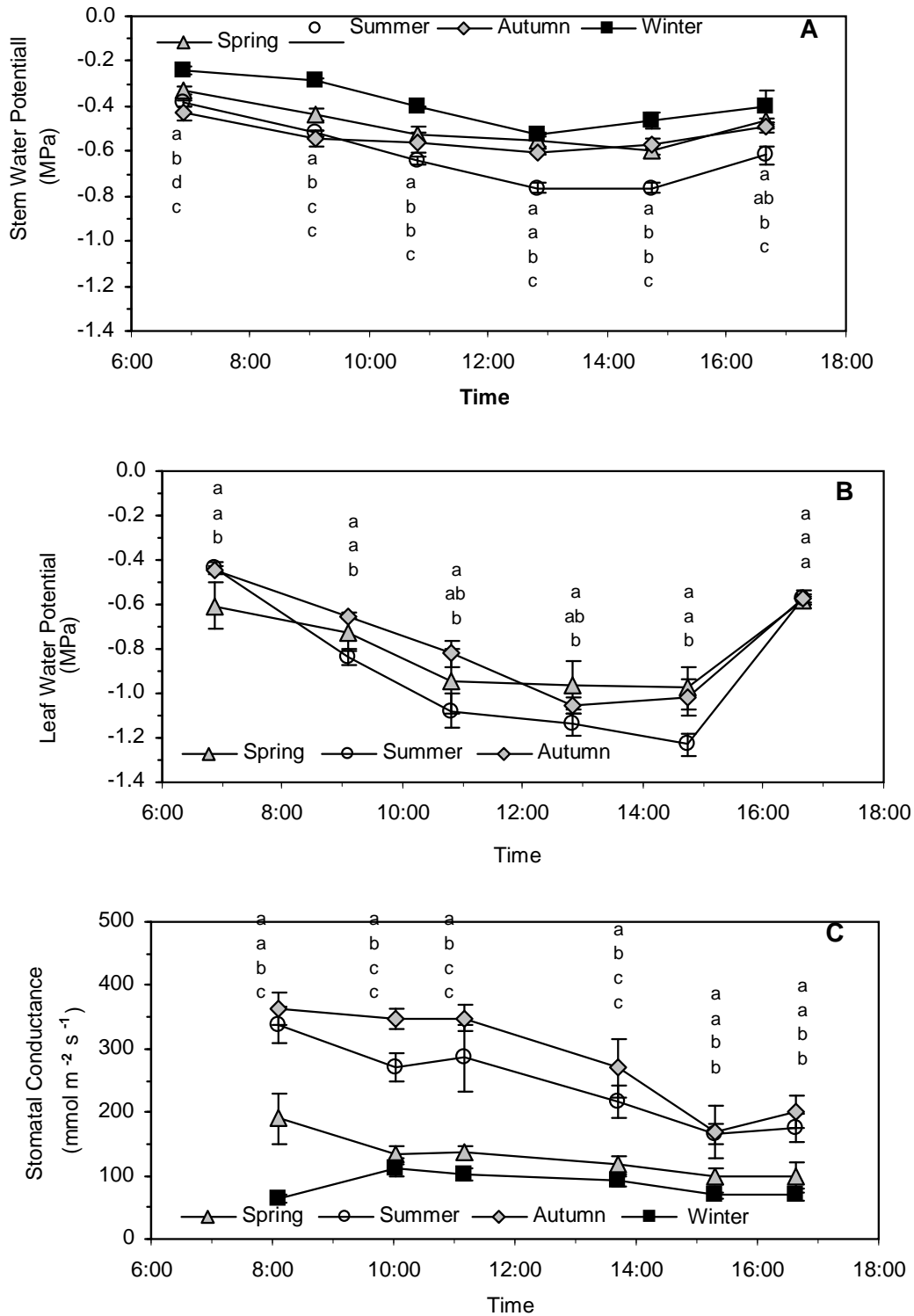


Fig. 2.4 Diurnal patterns of stem (A) and leaf water potential (B) and stomatal conductance (C) during spring (Aug-Nov 2002), summer (Dec 2002 – Mar 2003), autumn (Apr-May 2003), and winter (Jun-Jul 2002/2003), in 6-7 year-old, well irrigated ‘Kent’ mango trees (each data point represents mean \pm SD of 5 replicate leaf samples; different letters depict significant differences between seasons at each measurement)

date at $P = 0.05$). ETo: spring = 4.9 ± 1.6 , summer = 6.0 ± 1.5 , autumn = 3.9 ± 1.0 , and winter 3.4 ± 0.9 mm day⁻¹.

3. SEASONAL PATTERN OF WATER POTENTIAL AND STOMATAL CONDUCTANCE IN MANGO TREES

3.1 Introduction

Physiological processes of most plants are highly dependant on the plant water status. It is therefore of considerable importance to determine plant reactions to changes in water status. Studies conducted in a mediterranean climate on field grown non-irrigated evergreen sclerophylls indicated that there are seasonal differences in water potential and stomatal conductance that could be linked to soil water availability. While seasonal patterns between species were similar there appeared to be considerable differences in water potential and stomatal conductance rates (Rhizopoulou *et al.* 1991).

Cultivars in crops like grapevine and avocado are known to differ with respect to their plant water status when grown under similar conditions (Pire and Ojeda, 1999; Chartzoulakis *et al.*, 2002). These differences for mango cultivars have not yet been well documented, especially under field conditions. Responses of mango trees in terms of their water relations to soil drying have only been documented in potted trees under controlled conditions (Pongsomboon *et al.*, 1992a; Pongsomboon *et al.*, 1992b; Núñez-Elisea and Davenport, 1994). However, the applicability of such results may be very limited due to the different weather conditions persisting in the orchard.

Therefore, the objectives of this study was to determine water relations in mango trees (stem and leaf water potential and stomatal conductance) over the season, in different cultivars, and in potted trees in response to soil drying.

3.2 Materials and Methods

3.2.1 Site description and experimental layout

For the field trials the site is the same as described in 2.2.1. The one hectare orchard had a slight incline of about 2% from north to south. The soil type was classified as a sandy 'Glenrosa' with about 80% coarse sand up to an average depth of 90 cm with an underlying layer of semi-weathered Saprolite (de Villiers, 2001).

Soil moisture was measured weekly with a neutron hydroprobe (CPN 503, Campbell Pacific Nuclear Corp., CA, USA). Soil moisture measurement intervals were 10 cm from 0 – 90 cm depth at each replicate where access tubes were inserted to 1 m depth about 20 cm from the stem.

Trees were irrigated 3-5 times per day with two 4 L h⁻¹ emitters placed 30 cm on either side of the trunk in a single line drip system. Soil moisture was maintained at 73 ± 6% of FC from March until mid July 2002 and at 98 ± 6% of FC for the following two weeks. In August 2002 drippers were replaced by one micro-jet placed between two trees to improve water distribution within the root zone and since then soil moisture was maintained at 95 ± 3 % of FC.

In a commercially managed part of the orchard irrigation was scheduled according to tensiometers (Irrometer Co., Riverside, CA, USA) at 30 and 60 cm depths. Trees were irrigated once a day when soil moisture was lower than -10 kPa. In this part of the orchard 'Heidi' and 'Kent' tree water relations were compared from November 2002 to July 2003. In July 2003, 'Heidi', 'Kent' and 'Keitt', grafted onto 'Sabre' rootstock were compared under drip irrigation with one 8 L h^{-1} emitter per tree under the same irrigation management.

In winter (June 2002), sixteen one-year-old potted 'Sabre' trees, grown from root cuttings, were selected to measure responses to water deficit at Mariepskop Estate. Trees were planted in six-litre black planting bags. The growing medium consisted of composted pine bark, sand and red clay soil in a 5:4:1 ratio. Trees were placed outdoors similar to orchard conditions. All trees were well-irrigated daily to field capacity for 2-3 days prior to the start of the drying cycle to ensure similar tree water status in all trees. Excess free water drained through drainage holes at the bottom of the planting bags. Eight trees were irrigated at midday each day after measurements were taken (irrigated treatment), while the other eight trees were subjected to drought conditions and received no water during the drying cycle (non-irrigated treatment). The non-irrigated trees were measured until the leaves became necrotic or when the values of stem water potential became too low (>-4 MPa) to be measured with the pressure chamber.

In summer (February 2003) sixteen 'Sabre' trees rooted from cuttings and sixteen 'Kent' trees, grafted on 'Sabre' rootstocks, planted in plastic bags and kept under similar conditions as described above, were used in a drying and recovery cycle. Trees were well-irrigated for three days prior to the start of the experiment. On eight

trees of each cultivar irrigation was then withheld for five days, resuming irrigation thereafter on days six to nine to observe water stress recovery.

3.2.2 Measurements of water potential and stomatal conductance

Stem water potential (Ψ_{stem}) and stomatal conductance (g_s) were measured throughout the season. From November 2002 leaf water potential (Ψ_{leaf}) was also determined in the field-grown 'Kent' trees in addition to Ψ_{stem} . Both Ψ_{stem} and Ψ_{leaf} were measured using a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Stem water potential (Ψ_{stem}) measurements were taken on two to three leaves per tree near the main stem. The leaves were covered with an aluminium coated plastic bag two hours before measurement to eliminate interactions between Ψ and stomatal conductance as recommended by Moriana and Fereres (2002). Leaf water potential was measured on two to three exposed leaves on the outer part of the canopy. A steady state porometer (LI-1600, Li-Cor, Inc., Lincoln, NE, USA) was used to measure stomatal conductance on three to five leaves per tree similarly exposed as leaves used for Ψ_{leaf} measurements. All sample leaves were fully mature and dew free when measurements were taken.

Stem and leaf water potential and stomatal conductance for diurnal curves were measured every 2-3 hours and seasonal measurements at midday were taken between 11:00 and 13:00 h about once a month on 5-6 'Kent' trees. Comparisons between cultivars 'Heidi', 'Kent' and 'Keitt' over the season were conducted on four trees per cultivar.

For the study of tree responses to water deficit in the potted trees, Ψ_{stem} and g_s were determined on 3-4 trees per treatment. For Ψ_{stem} , 2-3 leaves per tree were measured, while 3-5 well exposed leaves per tree were used for g_s measurements.

3.2.3 Data analysis

Data were analyzed using analysis of variance (ANOVA, F-test) with one or more factors (irrigation, cultivar, season). Means were compared using the Tukey and Tukey-Kramer tests for equal and unequal sample sizes of treatments respectively, at a significance level of 5%.

Comparison of water relations between the different mango cultivars, 'Kent', 'Keitt', and 'Heidi', were analyzed with ANOVA (F-test, one factor = cultivar, two factors = cultivar and season). Means were compared using the Tukey-Kramer and Tukey tests respectively at $P=0.05$.

Data of the potted tree experiment were analysed with ANOVA (F-test, one factor = irrigation) as a completely randomised design with two irrigation treatments and four replicates per treatment. Means were compared using the Tukey-Kramer test ($P=0.05$).

3.3 RESULTS AND DISCUSSION

3.3.1 Comparison of seasonal water relations between different mango cultivars

In seasonal comparison under the same irrigation regime of stem water potential (Ψ_{stem}) between cultivars 'Kent', 'Keitt' and 'Heidi' (Fig. 3.1A) there were some significant differences. 'Kent' and 'Heidi' differed in all seasons except for spring. In summer, autumn and winter 'Heidi' Ψ_{stem} was about 0.1 ± 0.046 MPa lower than 'Kent'. 'Kent' and 'Keitt' only differed significantly during autumn and winter where 'Keitt' appeared to have a lower Ψ_{stem} . 'Keitt' and 'Heidi' showed significant differences during summer and autumn although not consistent as 'Heidi' was lower than 'Keitt' in summer and *vice versa* in autumn. However, considering the general trend over seasons all cultivars tended to be similar showing lowest Ψ_{stem} during summer and the highest Ψ_{stem} during autumn.

Stomatal conductance (g_s) between cultivars (Fig 3.1B) was generally inconsistent and insignificant except for 'Heidi' (spring) and 'Keitt' (autumn) where they differed significantly from the other cultivars. Also, there was no clear relationship between Ψ_{stem} and g_s in any particular cultivar. However, seasonal trends in g_s for all the cultivars appeared similar increasing from spring throughout summer to reach a peak in autumn of at least $300 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and decreasing towards around $200 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ in winter.

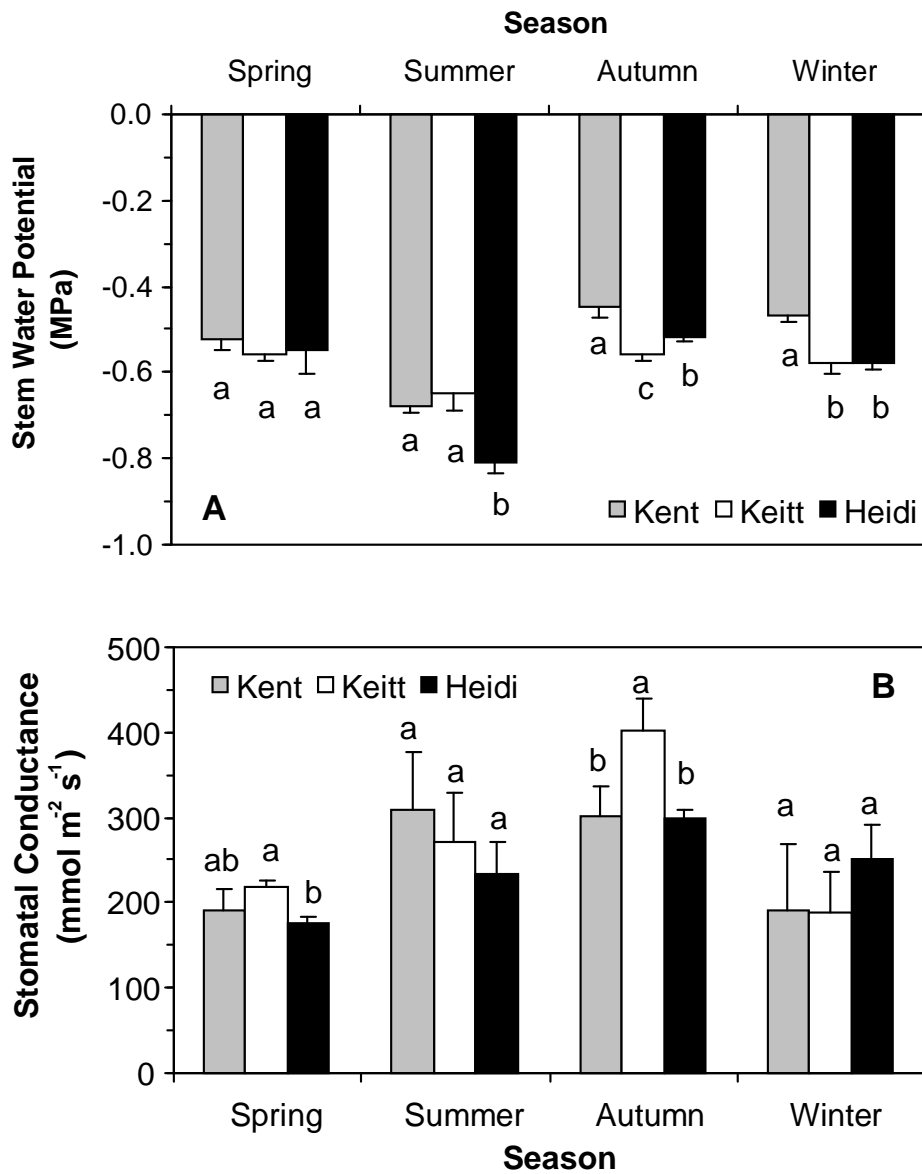


Fig 3.1 Mean stem water potential (A) and stomatal conductance (B) of well-irrigated 6-7 year-old ‘Kent’, ‘Keitt’, and ‘Heidi’ mango trees at midday under field conditions during spring (Oct/Nov 2002), summer (Jan/Mar 2003), autumn (Apr/May 2003), and winter (Jun 2002/Jul 2003) (each data point represents mean \pm SD of 4 replicate leaf samples; different letters depict significant differences between cultivars at $P=0.05$). E_{To} : spring = 4.9 ± 1.6 , summer = 6.0 ± 1.5 , autumn = 3.9 ± 1.0 , and winter 3.4 ± 0.9 mm day⁻¹.

When cultivar data for all seasons was pooled (Table 3.1), significant differences were found, with 'Kent' having the highest Ψ_{stem} , followed by 'Keitt' and 'Heidi'. The difference between the highest and lowest Ψ_{stem} was only 0.08 MPa, thus fairly close to each other.

Stomatal conductance data was also pooled but there were no significant differences between cultivars. Stomatal conductance ranged from 240 ± 53 to 270 ± 92 mmol H₂O m⁻² s⁻¹.

Combining all cultivar data for each season showed significant differences in Ψ_{stem} and g_s across all seasons (Table 3.1). In this instance it appeared that seasonal changes had a strong effect on all the cultivars. Differences in Ψ_{stem} ranged from -0.51 ± 0.05 MPa to -0.71 ± 0.08 MPa which is a 0.2 MPa difference, and 0.12 MPa more than between cultivars.

Stomatal conductance over the seasons ranged from 196 ± 23 to 334 ± 57 mmol H₂O m⁻² s⁻¹, a difference of 138 mmol H₂O m⁻² s⁻¹, which is also much larger than the difference between cultivars.

Judging by these results, it seemed that both cultivar and season had a significant effect on Ψ_{stem} and g_s . Due to the relatively small variation in Ψ_{stem} and g_s between cultivars compared to the larger variation between seasons, this probably indicates that there were significant interactions amongst the cultivars and seasons.

Table 3.1 Effect of cultivar ('Kent', 'Keitt', 'Heidi') and season (spring: Oct/Nov 2002; summer: Jan/Mar 2003; autumn: Apr/May 2003; winter: Jun 2002/Jul 2003) on mean stem water potential and stomatal conductance at midday in well-irrigated 6-7 year-old mango trees under field conditions (cultivar: n=16; season: n=12; different letters depict significant differences between cultivars and seasons at P=0.05). ETo: spring = 4.9 ± 1.6 , summer = 6.0 ± 1.5 , autumn = 3.9 ± 1.0 , and winter = 3.4 ± 0.9 mm day⁻¹.

Factor	Stem Water Potential		Stomatal Conductance	
	(MPa)		(mmol m ⁻² s ⁻¹)	
Cultivar				
Kent	-0.53 ± 0.10	a	249 ± 77	a
Keitt	-0.59 ± 0.04	b	270 ± 92	a
Heidi	-0.61 ± 0.12	c	240 ± 53	a
Season				
Spring	-0.54 ± 0.04	b	196 ± 23	c
Summer	-0.71 ± 0.08	c	272 ± 60	b
Autumn	-0.51 ± 0.05	a	334 ± 57	a
Winter	-0.54 ± 0.06	b	210 ± 61	c

The trees were all in close proximity to each other, therefore environmental conditions like shading and soil depth would have been similar. Considering both Ψ_{stem} and g_s , it becomes apparent that the trees probably had most favourable water relations during autumn, all responding in a similar manner with highest Ψ_{stem} and g_s . The fact that differences in Ψ_{stem} between cultivars were significant yet relatively small and g_s showed only insignificant differences may be attributed to the fact that

the cultivars are related. Both 'Kent' and 'Keitt' originate from the 'Turpentine' mango (Adato, *et al.*, 1995) and 'Heidi' being selected from a 'Kent' seedling (Human and Snyman, 1998). Therefore the fact that the cultivars are related might be the reason for the consistency in water relations and thus might be more significant. It might in part explain the apparent inconsistent significant differences between the cultivars which was probably as a result of tree differences.

Judging by the greater variation in g_s and the lesser variation in Ψ_{stem} it appeared that Ψ_{stem} was more accurate, less variable and therefore more sensitive than g_s , making Ψ_{stem} a potentially more reliable indicator of tree water relations.

Future research efforts should focus on greater detail and more regular measurements to get more clarity on the water relations of different cultivars in an effort to determine suitability of certain cultivars to different climatic growing conditions and water requirements.

3.3.2 Responses to water deficit of potted mango trees

Water withholding in non-irrigated one-year-old potted 'Sabre' seedling trees had its first significant impact on Ψ_{stem} (Fig. 3.2A) after ten days and on g_s (Fig. 3.2B) on day four, while Ψ_{stem} of well-irrigated trees remained stable between -0.5 and -1.0 MPa. It corresponded well with midday Ψ_{stem} in well-irrigated one year old potted olive trees which remained above -1.0 MPa (Pavel & Fereres, 1998). The earlier response of g_s in contrast to Ψ_{stem} indicates that trees might have tried to adapt to drought conditions by minimizing water losses through stomatal closure. Stem water potential on day 12 was fairly low (-2.9 ± 1.0 MPa) in non-irrigated trees and most leaves had

a wilted appearance with some leaves showing signs of necrosis along the outer edges. All leaves of irrigated trees were mature and no leaf rolling, abscission, chlorosis or necrosis was observed. The values are comparable to other findings considering that Ψ_{leaf} may be up to 0.4MPa or more lower than Ψ_{stem} as indicated in the previous chapter. Pongsomboon *et al.* (1992b) observed leaf necrosis and abscission under controlled conditions in two-year old potted 'Kensington' mango trees at Ψ_{leaf} of -3.2 MPa after 41 days, finally reaching -3.35 MPa after 46 days. They observed irreversible plant damage at -3.45 MPa. In 'Tommy Atkins' mango, Núñez-Elisea and Davenport (1994) managed to reach Ψ_{leaf} of -2.9 MPa after 14 days and Ψ_{leaf} of -3.55 MPa after 25 days during a drought cycle under controlled conditions that eventually reached -3.78 MPa after 36 days. However, contrary to Pongsomboon *et al.* (1992b), when irrigation was resumed the trees, in this study, managed to recover to produce vegetative and reproductive flushes in separate incidences.

Mango could endure very little stress compared to olive trees where water potential (Ψ) was as low as -10 MPa in field grown olive trees in the morning between 0700-0800 during summer but varied between -1.5 to -4 MPa during cooler months. Stomatal conductance was comparatively low throughout the year and varied between 5-30 in sun exposed leaves (Rhizopoulou *et al.* 1991).

On average, irrigated 'Sabre' mango trees exhibited Ψ_{stem} values of -0.58 ± 0.06 MPa at midday (Fig. 3.2A). Stem water potential of well irrigated peach ranged from above -0.3 MPa in the morning to -0.75 MPa at midday and from -0.3 MPa in the morning to -1.35 MPa at midday (1300) in severely stressed trees after two weeks of non-

irrigation (Berman and De Jong, 1997). In mango, significant differences in g_s were observed (Fig. 3.2B) when midday Ψ_{stem} was at about -1.0 MPa (Fig. 3.2A) on day four. In avocado significant differences in stomatal conductance between watered and stressed plants were first detected on day four after withholding water in ‘Fuerte’ and ‘Hass’ (Chartzoulakis *et al.* 2002).

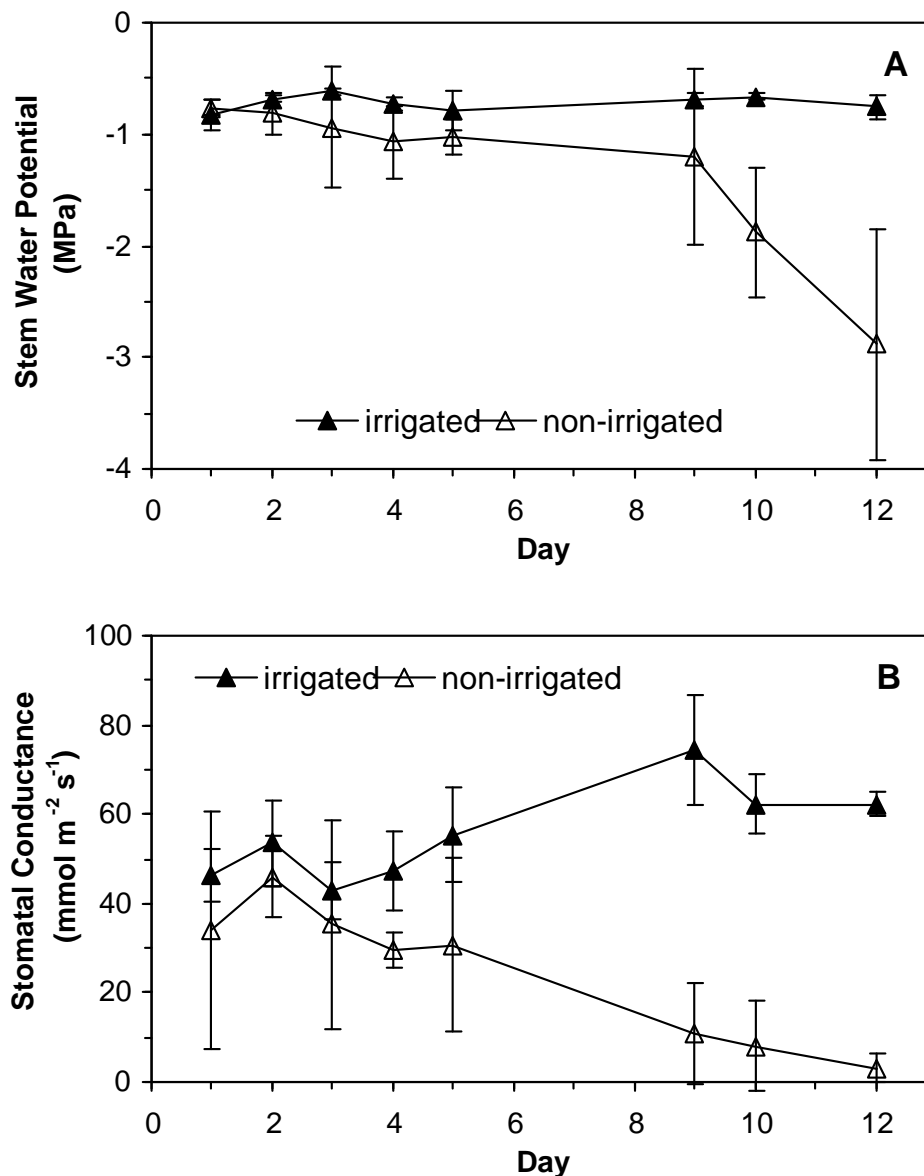


Fig 3.2 Midday stem water potential (A) and stomatal conductance (B) in irrigated and non-irrigated, 1 year-old, potted ‘Sabre’ seedlings during winter (Jun/Jul 2002) (data points depict mean \pm SD of 4 replicate leaf samples;

asterisks depict significant differences between treatments at $P=0.05$). $ET_o = 3.6 \pm 0.9 \text{ mm day}^{-1}$.

Stomatal conductance (g_s) in well-irrigated trees (Fig 3.2B) ranged between 40-60 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ from day one to five while non-irrigated trees over the same period was slightly lower though usually not significantly. Symptoms of water stress started showing from day four when g_s in non-irrigated trees started decreasing while g_s in irrigated trees showed an increase to above 60 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$. By day nine non-irrigated trees had a g_s of about 10 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and decreased further to nearly 0 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ by day 12.

Considering the response to water deficit, it appeared that g_s was the first to respond by showing signs of water stress by day four into the drying cycle. Responses in Ψ_{stem} only became significant six days later, dropping at a fast rate from about -1.2 MPa to nearly -3.0 MPa in a matter of two days. The delay in Ψ_{stem} decline was probably brought about by earlier stomatal closure as a measure to limit water losses. It appeared to be a very effective measure as this mechanism assisted in keeping Ψ_{stem} more or less constant for several days until stomatal closure was no longer sufficient to keep plant water relations at levels of irrigated trees.

The effect of water deficit was indicated by near stomatal closure from day 9 onwards (below 10 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) in non-irrigated trees in contrast to irrigated ones (62 - 74 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). Stress responses to severe water deficit are well known and have been documented for many crops. Well irrigated evergreen *Ziziphus rotundifolia* fruit trees usually have high transpiration rates, but showed selective defoliation in response to severe water deficit, with lower and inner leaves being shed first, followed by a more general abscission later in the drying cycle (Arndt *et al.*, 2001).

After re-irrigating, lemon Ψ_{leaf} recovered within two days but g_s failed to recover within the same time (Ruiz-Sanchez *et al.* 1997). In avocados, leaf anatomy changed in water-stressed leaves resulting in decreased palisade and total leaf thickness and intercellular spaces, and increased spongy cell density probably resulting in reduction of stomatal conductance. It has also been suggested that decreased leaf elasticity in combination with osmotic adjustment may be an efficient mechanism to enable plants to sustain stress conditions accounting for the decreased g_s (Chartzoulakis *et al.* 2002). It was also suggested by Rhizopoulou *et al.* (1991) that in olive sun exposed leaves have a lower g_s than shaded leaves. They concluded that exposed leaves are thicker primarily due to the thickness in palisade cell layers and it could therefore be that the tissue was more hydrated. Thus a drastic decrease in Ψ to below critical levels for stomatal closure is prevented under conditions of high evaporative demand. Stomatal closure in exposed leaves as opposed to shaded leaves may be attributed to higher evaporative demand (Rhizopoulou *et al.* 1991).

In summer (February 2003) another pot experiment was conducted on ‘Sabre’ and ‘Kent’ trees. This time the drying cycle was combined with a re-irrigation cycle to observe the recovery phase of the trees.

In ‘Sabre’ trees Ψ_{stem} (Fig 3.3A) of non-irrigated trees was significantly lower on day three but then, contrary to expectation, the irrigated treatment did not differ significantly for the remainder of the drying and re-irrigation cycles. Judging by Ψ_{stem} only, the trees did not show any signs of water stress whether irrigated or non-irrigated.

When g_s was taken into account (Fig 3.3B) it became evident that non-irrigated trees were affected by water deficit. Stomatal conductance declined from day two while g_s of irrigated trees appeared to increase. From day three the g_s of non-irrigated trees failed to reach levels of irrigated trees even though there appeared to be a marked recovery when irrigation was resumed on day six. The reduction in g_s probably limited the excessive decline in Ψ_{stem} , providing the plant with the ability to maintain its plant water status thereby assisting in the recovery of g_s when adequate water for uptake became available. In this instance it appeared that g_s recovered fairly easy although it failed to reach the levels of irrigated trees, even though levels were higher than at the start of the drying cycle.

No major differences were observed in Ψ_{stem} between irrigated and non-irrigated 'Sabre' trees during the stress and recovery periods (Fig. 3.3A).

Only on days five and six there were some significant differences, but the recovery of Ψ_{leaf} of non-irrigated trees within the stress period was probably a reaction of the reduced g_s during that time, thereby limiting water losses and enabling the tree to rehydrate. The early recovery of Ψ could be attributed to a response to stomatal closure and high root hydraulic resistance as experienced in potted olive trees subjected to low soil temperatures (Pavel and Fereres, 1998), and lemon trees subjected to flooding (Ruiz-Sánchez *et al.*, 1996).

Stomatal conductance (g_s) in non-irrigated 'Sabre' declined steadily from the second day after irrigation was suspended up to the fifth day (Fig. 3.3B). The decline was slower than in 'Kent' and never reached the low levels of non-irrigated 'Kent' trees

(Fig. 3.4B). Non-irrigated 'Sabre' trees reacted to irrigation within a short time showing a marked increase in g_s on the seventh day. However, non-irrigated 'Sabre' failed to recover to the same level as irrigated trees by day nine but nevertheless recovered to a slightly better g_s level than on day one. Concluding about the fast recovery of stomatal conductance after irrigation it appears that g_s in 'Sabre' was very sensitive to irrigation, possibly more than g_s in young olive trees that appeared to be insensitive to water deficits even though some treatment differences were observed (Morigana and Fereres, 2002).

The good stomatal conductance recovery of non-irrigated trees might be an indication of 'Sabre's ability to recover after the water stress period in contrast to g_s in 'Kent'. As 'Kent' trees had 'Sabre' rootstock it was unlikely that greater root damage would have occurred only in 'Kent' trees. Therefore, the ability to take up water through the roots should remain similar in both cultivars as the trees were standing in close proximity to each other for the duration of the experiment. It therefore seems that other factors besides irrigation could have been involved in the recovery rate of 'Kent' like the possibly greater resistance to sap flow as a result of the graft union. Alternatively, it could be genetic cultivar differences that played a role, similar to differences between 'Kent' and 'Sabre' in g_s as experienced under orchard conditions (section 3.3.1).

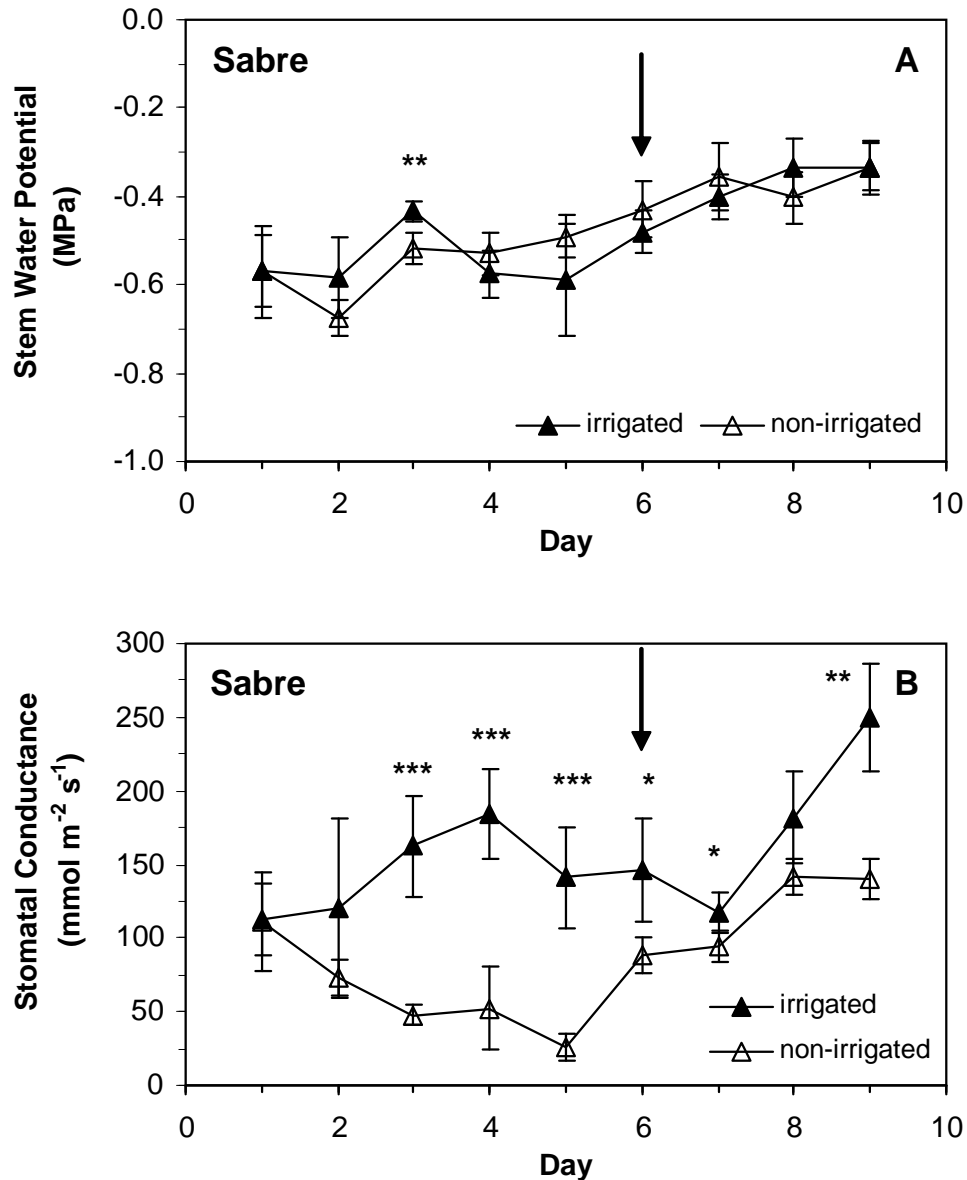


Fig 3.3 Mean stem water potential (A) and stomatal conductance (B) at midday in irrigated and non-irrigated, 1 year-old, potted ‘Sabre’ seedlings during summer (Feb 2003) (data points depict mean \pm SD of 4 replicate leaf samples; asterisks depict significant differences between treatments at $P=0.05$; arrow indicates the day of re-irrigation in the deficit treatment). $E_{To} = 6.1 \pm 0.9 \text{ mm day}^{-1}$.

In the same experiment, Ψ_{stem} of ‘Kent’ trees responded differently to Ψ_{stem} in ‘Sabre’ trees (Fig. 3.4A). During the first four days Ψ_{stem} in irrigated and non-irrigated trees appeared similar. However, on day five Ψ_{stem} of non-irrigated trees was significantly

lower. Upon re-irrigation on day six, Ψ_{stem} of non-irrigated trees significantly increased to a higher level than irrigated trees and remained equal or higher up to day ten, though not significantly so. Stem water potential (Ψ_{stem}) of irrigated 'Kent' trees remained very similar to that of non-irrigated 'Kent' trees with the exception of two days where significant differences were observed (Fig. 3.4A).

Stomatal conductance (Fig. 3.4B) became significantly lower on the second day and remained around $50 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ or lower for the duration of the trial. Stomatal conductance failed to recover following re-irrigation. It appeared that 'Kent' required a longer time to recover, appearing to be more severely affected by water stress than 'Sabre' even though Ψ_{stem} did indicate that internal plant water appeared to be normal. Recovery of Ψ_{stem} was probably aided by the low activity in stomatal conductance.

Stomatal conductance (g_s) of non-irrigated Kent decreased sharply from day two to day four (Fig. 3.4B), even though it appeared from Ψ_{stem} measurements that plants were not severely stressed. Stomatal conductance appeared to have been more sensitive than in other crops such as field quinoa where stomatal response only occurred when Ψ_{stem} was below -1.2 to -1.6 MPa (Jensen *et al.*, 2000). Stomatal conductance did not go above $50 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, even after irrigation, was resumed on day seven. Prolonged stomatal closure appeared to also occur in other crops. For example, in grapevines leaf water potential of irrigated and non-irrigated plants was similar, but stomatal conductance was significantly lower in the non-irrigated plants (Behboudian and Singh, 2001), and in pot-grown tomato prolonged stomatal closure allowed leaf water status recovery (Dell'Amico *et al.*, 2001).

It appeared that there might be cultivar differences between ‘Sabre’ and ‘Kent’ in that ‘Sabre’ seemed to have the ability to recover faster from water stress. It might also have to do with the fact that ‘Sabre’ was a clonal seedling while ‘Kent’ was grafted onto a ‘Sabre’ clonal seedling. The graft union might have had an effect on g_s as observed in vines where large differences were found in g_s values between grafted and ungrafted vines when subjected to water stress (Iacono *et al.*, 1998).

In the diurnal stem water potential of irrigated and non-irrigated ‘Sabre’ trees (Fig. 3.5A) on day three, irrigated trees were most of the day significantly higher than that of non-irrigated trees. On day four, both irrigated and non-irrigated trees were fairly similar, differing significantly only in the early afternoon.

On day three, irrigated ‘Sabre’ (Fig. 3.5A) had a significant higher Ψ_{stem} for most of the day. However, this difference gradually diminished over day four and five, showing no significance on day five between irrigated and non-irrigated trees. While predawn water potential on the three days appeared very similar (first measurement every day) (Fig. 3.5A), a similar scenario as in Ψ_{stem} was found in Ψ_{leaf} , although it appeared less consistent and greater variation occurred between measuring times. Just as in Ψ_{stem} irrigated ‘Sabre’ appeared less stressed than non-irrigated ‘Sabre’ on day four. On day five both treatments were inconsistent regarding the most stressed treatment. However, on day five it seemed that especially during the afternoon non-irrigated ‘Sabre’ was significantly less stressed than irrigated ‘Sabre’.

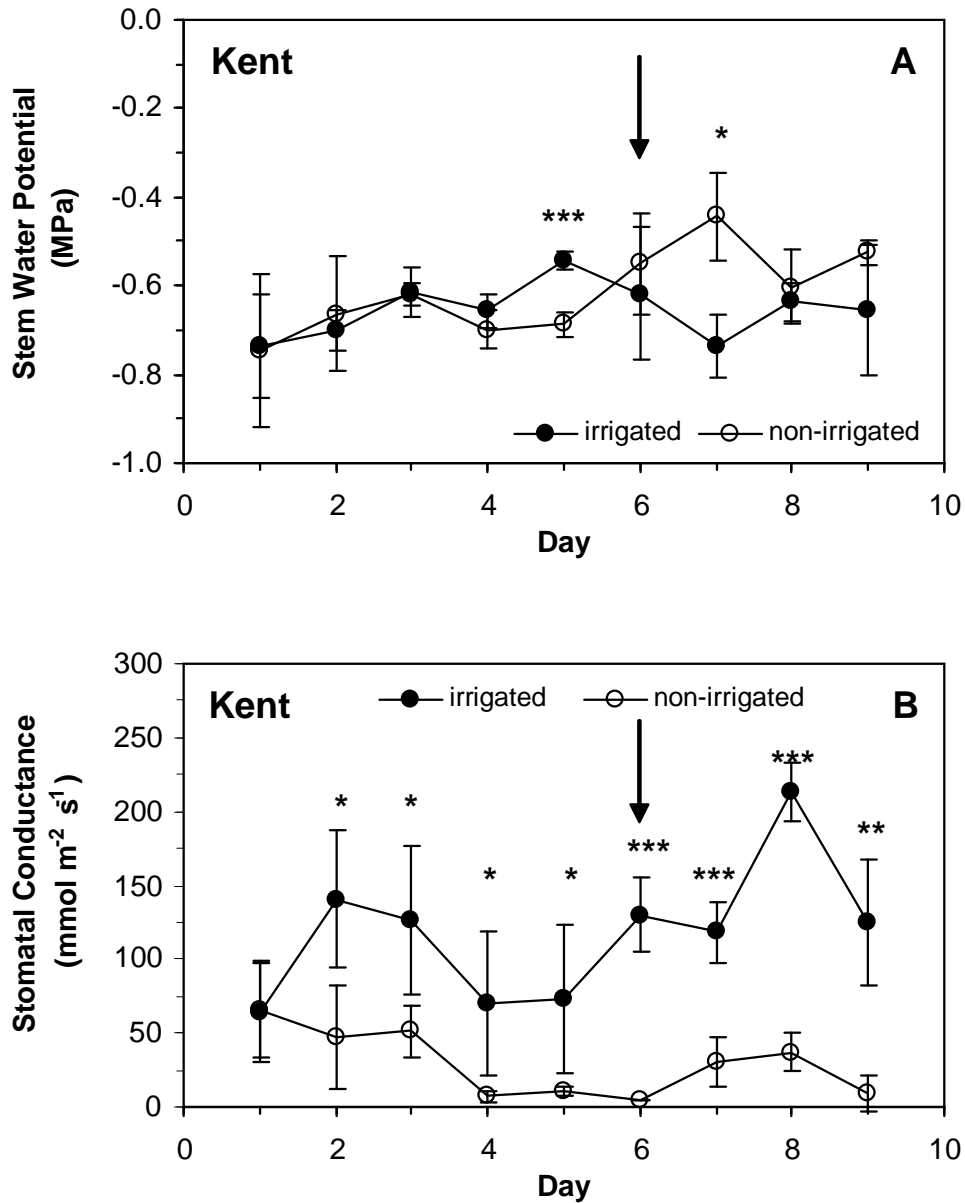


Fig 3.4 Mean stem water potential (A) and stomatal conductance (B) at midday in irrigated and non-irrigated, 1 year-old, potted ‘Kent’ mango trees during summer (Feb 2003) (data points depict mean \pm SD of 3-4 replicate leaf samples; asterisks depict significant differences between treatments at $P=0.05$; arrow indicates the day of re-irrigation in the deficit treatment). $E_{To} = 6.1 \pm 0.9 \text{ mm day}^{-1}$.

The apparently lower stress level (higher Ψ_{stem}) of non-irrigated ‘Sabre’ could have been brought about by stomatal closure (Fig. 3.5A), thereby limiting water losses. Although low g_s compared to irrigated ‘Sabre’ were already recorded in non-irrigated

'Sabre' on day four, the lowest values were recorded on day five, an indication that stomata were closed and therefore water losses were restricted.

Taking g_s into consideration (Fig. 3.5B) it appeared to be evident as to why there were so little differences in Ψ_{stem} between the treatments in 'Sabre' trees. Throughout day three to five g_s of non-irrigated trees was significantly lower compared to irrigated trees. Diurnal g_s of non-irrigated trees became progressively lower over the three days, probably enabling Ψ_{stem} to remain at similar levels as irrigated trees. While diurnal g_s curves of irrigated trees showed a big difference between highest and lowest value, the curves of non-irrigated trees were in a much smaller range and showing fairly flat diurnal curves. The flat curve for g_s on day five and very low peak for non-irrigated Sabre trees was probably as a result of water stress limiting water losses in an attempt to maintain a favourable tree water status.

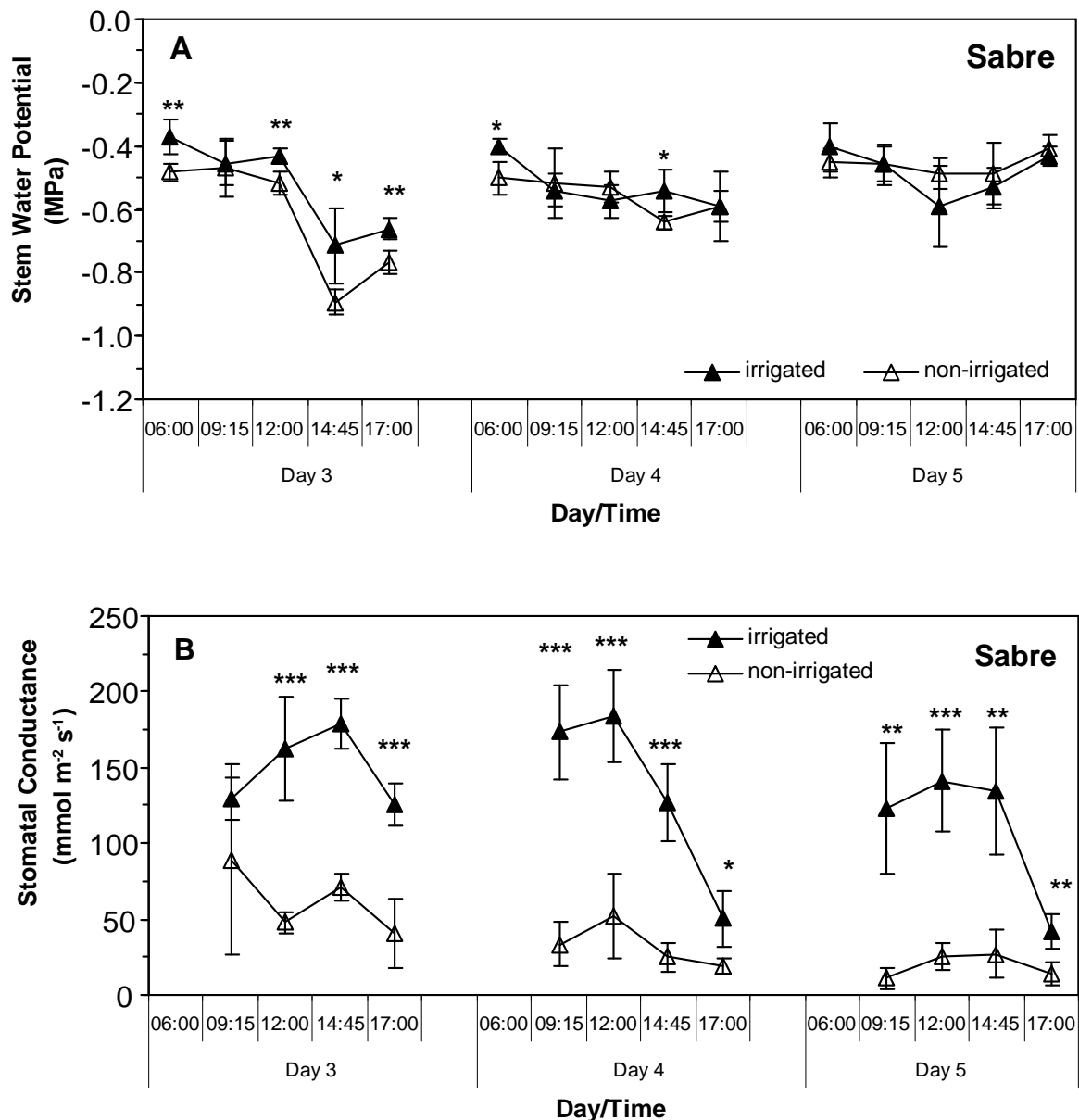


Fig 3.5 Diurnal pattern of mean stem water potential (A) and stomatal conductance (B) in irrigated and non-irrigated, 1 year-old, potted ‘Sabre’ mango seedlings on days 3-5 of the drying cycle in summer (Feb 2003) (data points depict mean \pm SD of 4 replicate leaf samples; asterisks depict significant differences between treatments at $P=0.05$).

Stem water potential in ‘Kent’ (Fig. 3.6A) between the treatments was irregular in the sense that both fluctuated in the same range over the days. Only on day five were there some significant differences between irrigated and non-irrigated trees. The non-irrigated trees started to show significant signs of water stress with leaves wilting.

Stem water potential in non-irrigated 'Kent' on day 3-5 generally appeared to be lower than irrigated 'Kent', although not always significantly so (Fig. 3.6A). It could have been an indication of the limited water availability from the soil. During the course of day 3 it appeared that non-irrigated 'Kent' trees Ψ_{stem} decreased significantly more than irrigated 'Kent', possibly as a result of water stress. During day 4 non-irrigated trees appeared significantly less stressed at times than irrigated trees regarding Ψ_{stem} , which was most likely caused by low g_s . On day 5 Ψ_{stem} showed a normal diurnal pattern, high in the morning decreasing towards midday and again increasing towards evening.

Through the course of the three days there were increasing differences of Ψ_{stem} between irrigated and non-irrigated trees early in the morning (Fig. 3.6A) (first data points at each day) probably as a result of the increased water deficit that developed in non-irrigated trees.

Diurnal measurements taken from day 3-5 showed that g_s in non-irrigated trees was usually significantly lower than in irrigated trees (Fig. 3.6B). In irrigated trees it appeared that g_s started off high in the mornings (day 3 and 4) and decreased as the day progressed, sometimes showing slight recovery towards the evening (day four). The unexpected rise in g_s of non-irrigated trees on day 4 may have been linked to similar responses in Ψ_{stem} . During day five g_s in irrigated 'Kent' trees showed a marginal increase towards midday but non-irrigated trees remained virtually unchanged throughout the day due to stomatal closure.

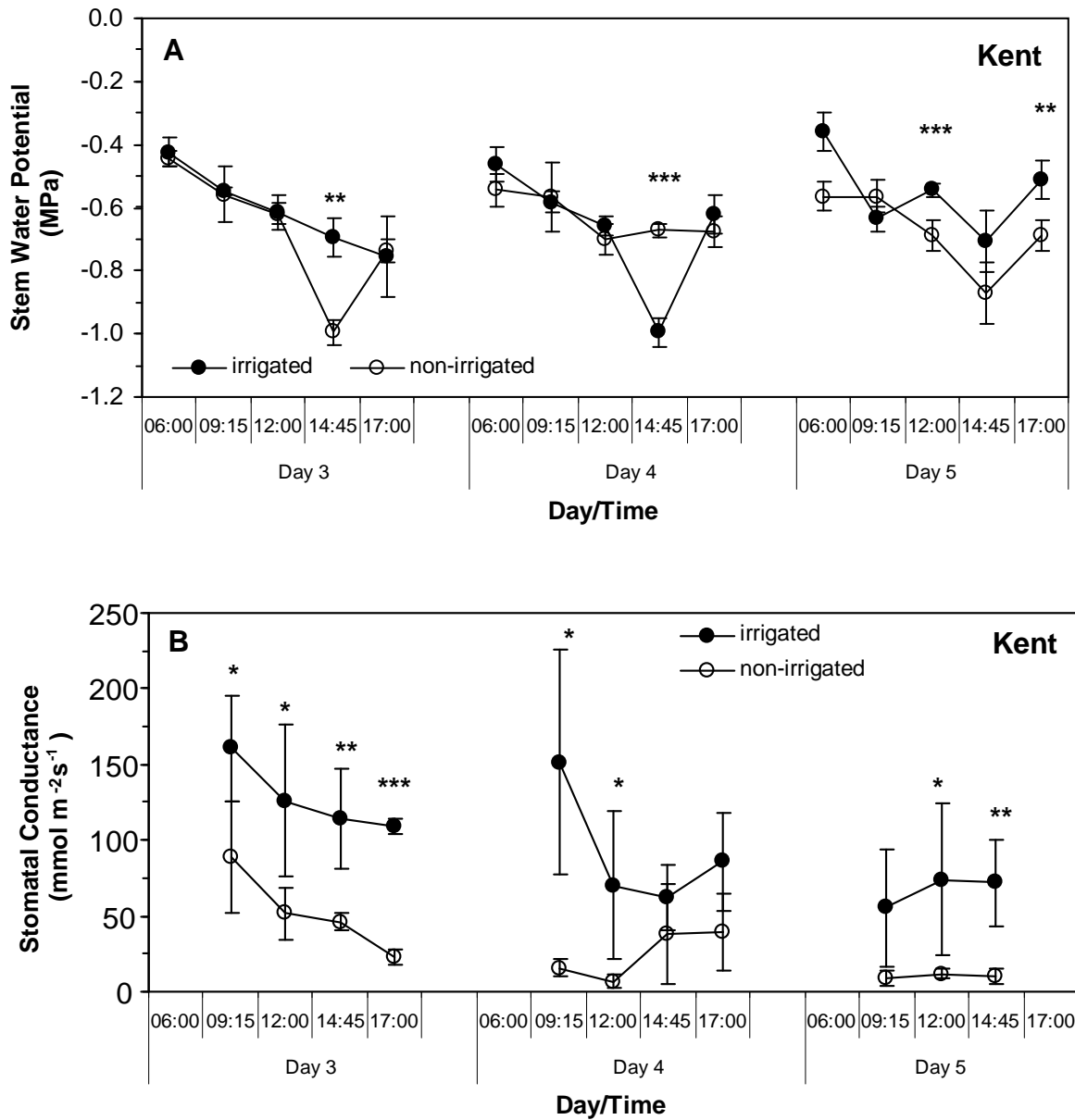


Fig 3.6 Diurnal pattern of mean stem water potential (A) and stomatal conductance (B) in irrigated and non-irrigated, 1 year-old, potted 'Kent' mango trees on days 3-5 of the drying cycle in summer (Feb 2003) (data points depict mean \pm SD of 4 replicate leaf samples; asterisks depict significant differences between treatments at $P=0.05$).

Similar to 'Sabre', g_s in 'Kent' was lower in non-irrigated trees than in irrigated trees.

Stomatal conductance gradually decreased over day three to five.

Taking a closer look at the diurnal Ψ_{stem} curves of 'Sabre' and 'Kent' on day three to five there appeared to be no consistent differences. A noticeable difference in 'Kent' was that g_s in irrigated trees on day three and four started high in the morning but declined during the course of the day, only showing some recovery in the late afternoon on day four. In 'Sabre', g_s increased from the morning towards midday and decreasing in the afternoon.

It might again indicate that 'Sabre' has a greater ability to maintain a favourable tree water status, suitable for g_s throughout the day. In 'Kent', it appeared that even in irrigated trees, g_s may have been limited by weather conditions prevailing throughout the day.

In contrast to irrigated 'Kent' trees, g_s in irrigated 'Sabre' trees showed a steady rise in the morning towards midday and then a decline towards dusk (Fig. 3.5B). This was in direct contrast to 'Kent', and may have been an indication that 'Sabre' could have had greater tolerance to water deficits, be it as a result of limited water supply or induced by weather conditions. This type of curve was evident in both irrigated 'Sabre' and to a lesser extent in non-irrigated 'Sabre' treatments suggesting that it could be a cultivar difference. It would have been expected to see a decline in non-irrigated 'Sabre' g_s towards midday, similar to irrigated 'Kent', but in contrast there was an incline in spite of the soil water limitations imposed on non-irrigated 'Sabre' trees. This pattern was evident in all three days when g_s was measured as a diurnal curve. Whenever measurements were taken, the results suggested that there were always significant differences in g_s between irrigated and non-irrigated 'Sabre'.

3.4. CONCLUSIONS

Stomatal conductance (g_s) showed a substantial degree of variation that appeared to be mainly caused by changes in relative humidity. Some other environmental factors also did influence g_s but their effect was usually inferior to that of relative humidity. Seasonal fluctuation of g_s seemed not to be an accurate reflection and consistent indicator of plant water status in the same degree as stem water potential (Ψ_{stem}). Seasonal variation was observed in both Ψ_{stem} and g_s . Stem water potential however appeared more consistent with changes in plant water status, and in that sense more predictable than g_s .

The effect of water withholding on potted 'Sabre' trees became evident only four days after irrigation had ceased. The deficit became evident in the significantly lower Ψ_{stem} and g_s values. This could have been an indication that g_s did react on changes in plant water status, but may be dominated by relative humidity when soil moisture or plant water status was near optimum. However, when water deficit developed, the plant water status could have played an increasing role in the regulation of stomatal conductance. 'Sabre' trees showed changes in Ψ_{stem} and g_s after only 11 days, an indication that Ψ_{stem} in mango did not decrease to severe levels of up to -10 MPa as reported for olive (Giorio *et al.*, 1999), but already showed necrosis at -2.8 MPa.

Stem water potential appeared to be a more reliable indicator of plant water status than Ψ_{leaf} and g_s . It appeared to be little influenced by seasonal changes although minor changes did occur between the seasons. These differences were most likely due to the influence of ET_0 and VPD on Ψ_{stem} .

Contrary to other previously published reports, it seemed that water potential could be measured in mango by using the pressure chamber, although caution should be exercised not to confuse latex exudation with the end point of water potential measurement.

By maintaining a high Ψ_{stem} , even though g_s may be low, it might give the plant the ability to recover quickly. When Ψ_{stem} would become lower than normal, it might take plants longer to resume normal physiological processes as Ψ_{stem} would firstly need to recover before g_s could recover. It appeared that both 'Sabre' and 'Kent' have an effective mechanism in g_s to be able to control tree water status by adjusting stomatal aperture. The ability to adjust g_s may be aiding mango trees to effectively adjust to periodic times of water stress. It is probably one of the mechanisms that makes mango suitable for cultivation under warm climatic conditions.

SUMMARY

To impact significantly on water consumption it is necessary to study crop water requirements and to determine the effect of deficit irrigation on crop growth and yield. Information on the basic plant responses to reduced water status is important to optimise water use. Plants need to adapt to prevailing conditions of water deficit during growth and development to avoid permanent injury. It has become of primary importance that irrigation regimes are conducive to sustainable production of export quality fruit. It is therefore necessary to schedule irrigation in such a way that water stress is avoided during critical phenological stages.

Plant water status is a very sensitive indicator of the degree of water stress experienced by the plant. Despite the commercial value of mangoes published research results in mango under field conditions relating to tree water relations is limited. The objectives of this study were to characterise diurnal and seasonal patterns of water relations (Ψ_{stem} , Ψ_{leaf} and g_s) in well irrigated mango trees under field conditions, to compare water relations in different cultivars.

To schedule irrigation based on plant parameters, such as stem and leaf water potential and stomatal conductance, it is necessary to study patterns of water relations in mango trees over the season under field conditions as well as their responses to water deficit. The first visible effects of water stress are cessation of growth, closure of stomata and wilting of young leaves and stems.

Low stomatal conductance rates (g_s) were associated with high stem water potentials as an effect of reduced water applications. Even under well-irrigated conditions, there were diurnal fluctuations in stem water potential of mango trees. Stem water potential followed a normal pattern across all seasons, decreasing towards midday and again increasing towards late afternoon. The differences between seasons may be attributed to changes in weather patterns. During summer, diurnal curves of stem and leaf water potentials showed significantly the lowest values at most times over the day compared to the other seasons.

Both stem and leaf water potentials responded well to plant water relations. However, stem water potential showed less fluctuation in relation to leaf water potential, thereby potentially making it a more reliable indicator of plant water status. Stomatal conductance in mango showed some seasonal variation related to seasonal variation in climatic conditions but it appeared to have been mainly influenced by relative humidity.

Physiological processes of most plants are highly dependant on the plant water status. Therefore, another objective was to determine water relations in mango trees (stem and leaf water potential and stomatal conductance) over the season, in different cultivars, and in potted trees in response to soil drying.

Seasonal trends in Stomatal conductance (g_s) between cultivars were very similar increasing from spring throughout summer to reach a peak in autumn. When stomatal conductance data was also pooled, no significant differences were found.

When stem water potential data for cultivars over all seasons was pooled significant differences were found, 'Kent' having the highest Ψ_{stem} , followed by 'Keitt' and 'Heidi'.

Combining all cultivar data for each season showed significant differences in Ψ_{stem} and g_s across all seasons. It appeared that seasonal changes had a strong effect on all the cultivars.

Judging by these results, it seemed that both, cultivar and season, had a significant effect on Ψ_{stem} and g_s . Due to the relatively small variation in Ψ_{stem} and g_s between cultivars compared to the larger variation between seasons indicates that there was probably significant interaction between the cultivars and seasons.

Responses to water deficit of potted mango trees showed an earlier response of g_s in contrast to Ψ_{stem} which might indicate that trees could have tried to adapt to drought conditions by minimizing water losses through stomatal closure.

During a drying and re-irrigation cycle of potted 'Sabre' and 'Kent' trees no major differences were observed in Ψ_{stem} between irrigated and non-irrigated 'Sabre' trees during the stress and recovery periods. Non-irrigated 'Sabre' trees reacted to irrigation within a short time showing a marked increase in g_s . However, g_s in non-irrigated 'Sabre' failed to recover to the same level as irrigated trees. Concluding from the fast recovery of stomatal conductance after irrigation it appeared that g_s in 'Sabre' was very sensitive to irrigation. The good stomatal conductance recovery of non-irrigated trees might be an indication of 'Sabre's' ability to recover after the water stress period.

Stem water potential (Ψ_{stem}) of irrigated 'Kent' trees remained very similar to that of non-irrigated 'Kent' trees. Ψ_{leaf} of non-irrigated 'Kent' was maintained at a similar level for the duration of the experiment, probably due to stomatal closure as reflected by low g_s . It appeared that g_s in 'Kent' required a longer time to recover, possibly being more severely affected by water stress than 'Sabre' even though Ψ_{stem} did indicate that internal plant water appeared to be normal. Ψ_{stem} recovery was probably aided by the low activity in stomatal conductance. Stomatal conductance (g_s) of non-irrigated Kent decreased even though it appeared from Ψ_{stem} measurements that plants were not severely stressed.

It appeared that there might be cultivar differences between 'Sabre' and 'Kent' in that 'Sabre' seemed to have the ability to recover faster from water stress. It might also have to do with the fact that 'Sabre' was a clonal seedling while 'Kent' was grafted onto a 'Sabre' clonal seedling. The graft union might have an effect on g_s .

In contrast to irrigated 'Kent' trees, g_s irrigated 'Sabre' trees showed a steady rise in the morning towards midday and then a decline towards dusk. This was in direct contrast to 'Kent', and may have been an indication that 'Sabre' could have had greater tolerance to water deficits, be it as a result of limited water supply or induced by weather conditions like relative humidity. Seasonal variation was observed in both Ψ_{stem} and g_s . Stem water potential however appeared more stable, and in that sense more predictable than g_s .

Contrary to other previously published reports it seemed that water potential could be measured in mango by using the pressure chamber, although caution should be practised not to confuse latex exudation with the end point of water potential measurement.

Judging by the greater variation in g_s and the lesser variation in Ψ_{stem} it appeared that Ψ_{stem} was more accurate, less variable and therefore more sensitive than g_s making Ψ_{stem} a potentially more reliable indicator of water relations. It appeared to be little influenced by seasonal changes although minor changes did occur between the seasons. These differences were most likely due to the influence of ET_0 and VPD on Ψ_{stem} .

REFERENCES

ADATO, A., SHARON, D., LAVI, U., HILLEL, J., & GAZIT, S. 1995. Application of DNA fingerprints for identification and genetic analysis of mango (*Mangifera indica*) genotypes. Journal of American Society for Horticultural Science, 120:259-264.

ALLEN, R.G., PEREIRA, L.S., RAES, D. AND SMITH, M. 1998. Crop evapotranspiration. Guidelines for computing crop water requirements. FAO Irrigation and Drainage paper No. 56. FAO, Rome, Italy.

ARANDA, I., GIL, L. & PARDOS, J.A. 2000. Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. Trees, 14:344-352.

ARAUJO, F.J., URDANETA, T., MARIN, M. & WILLIAMS, L.E. 1999. Effect of irrigation regime on photosynthesis and leaf water potential of *Vitis vinifera* L. (cv. Alphonse Lavallé) in Venezuela. Acta Horticulturae, 493:219-239.

ARNDT, S.K., CLIFFORD, S.C., WANEK, W., JONES, H.G. & POPP, M. 2001. Physiological and morphological adaptations of the fruit tree *Ziziphus rotundifolia* in response to progressive drought stress. Tree Physiology, 21:705-715.

BARRAGAN, J. & WU, I.P. 2001. Optimal scheduling of a micro-irrigation system under deficit irrigation. *Journal of Agricultural Engineering Research*, 80(2): 201-208.

BEHBOUDIAN, M.H. & SINGH, Z. 2001. Water relations and irrigation scheduling in grapevine. *Horticultural reviews*, 27:190-225.

BERMAN, M.E. & DEJONG, T.M. 1997. Crop load and water stress effects on daily stem growth in peach (*Prunus persica*). *Tree Physiology*, 17:467-472.

BOTES, J.H.F. & OOSTHUIZEN, L.K. 1995. An economic evaluation of a deficit irrigation scheduling strategy for wheat in the lower P.K. le Roux dam area. *Proceedings of the Southern African Irrigation Symposium*, 4-6 June 1991, Elangeni Hotel, Durban. Water Research Commission, Department of Water Affairs and Forestry. Pretoria, South Africa. Report No. TT 71/95, p. 381-389.

BRUWER, J.J. & VAN HEERDEN, P.S. 1995. Spotlight on irrigation development in the RSA: the past, present and future. *Proceedings of the Southern African Irrigation Symposium*, 4-6 June 1991, Elangeni Hotel, Durban. Water Research Commission, Department of Water Affairs and Forestry. Pretoria, South Africa. Report No. TT 71/95, p. 3-10.

CALVET, J.-C. 2000. Investigating soil and atmospheric plant water stress using physiological and micrometeorological data. *Agricultural and Forest Meteorology*, 103:229-247.

CASTRILLO, M., FERNANDEZ, D., CALCAGNO, A.M., TRUJILLO, I. & GUENNI, L. 2001. Responses of ribulose-1,5-bisphosphate carboxylase, protein content, and stomatal conductance to water deficit in maize, tomato, and bean. *Photosynthetica*, 39 (2): 221-226.

CHARTZOULAKIS, K., BOSABALIDIS, A., PATAKAS, A. & VEMMOS, S. 2000. Effects of water stress on water relations, gas exchange and leaf structure of olive tree. *Acta Horticulturae*, 537:241-247.

CHARTZOULAKIS, K., PATAKAS, A., KOFIDIS, G., BOSABALIDIS, A. & NASTOU, A. 2002. Water stress affects leaf anatomy, gas exchange, water relations and growth of two avocado cultivars. *Scientia Horticulturae*, 95(1-2): 39-50.

CHONÉ, X., VAN LEEUWEN, C., DUBOURDIEU, D. & GAUDILLÈRE, J.P. 2001. Stem water potential is a sensitive indicator of grapevine water status. *Annals of Botany*, 87(4):477-483.

COCHARD, H. 2002. Xylem embolism and drought-induced stomatal closure in maize. *Planta*, 215:466-471.

COHEN, Y., FUCHS, M. & GREEN, G.C. 1981. Improvement of the heat pulse method for determining sap flow in trees. *Plant, Cell and Environment*, 4: 391-397.

DAMATTA, F.M., CHAVES, A.R.M., PINHEIRO, H.A., DUCATTI, C. & LOUREIRO, M.E. 2003. Drought tolerance of two field-grown clones of *Coffea canephora*. *Plant Science*, 164:111-117.

DAY, W. 1981. Water stress and crop growth. In: Johnson, C.B. (ed) *Physiological processes limiting plant productivity*. The Camelot Press, Southampton, UK. p.199-215.

DE AZEVEDO, P.V., DA SILVA, B.B. & DA SILVA, V.P.R. 2003. Water requirements of irrigated mango orchards in northeast Brazil. *Agricultural Water Management*, 58:241-254.

DE JONG, T.M. 1983. CO₂ assimilation characteristics of five *Prunus* tree fruit species. *Journal of the American Society for Horticultural Science*, 108(2): 303-307.

DELL'AMICO, J., TORRECILLAS, A., RODRÍGUEZ, P., MORALES, D. & SÁNCHEZ-BLANCO, M.J. 2001. Differences in the effects of flooding the soil early and late in the photoperiod on the water relations of pot-grown tomato plants. *Plant Science*, 160(3):481-487.

DE VILLIERS, A.J. 2001. Seasonal growth patterns and water relations in response to reduced irrigation regimes in mango (*Mangifera indica* L.). M.Sc. (Agric) Horticulture Dissertation. University of Pretoria. Pretoria.

DOMINGO, R., RUIZ-SÁNCHEZ, M.C., SÁNCHEZ-BLANCO, M.J. & TORRECILLAS, A. 1996. Water relations, growth and yield of Fino lemon trees under regulated deficit irrigation. *Irrigation Science*, 16:115-123.

FISCHER, H.H. 1995. Scheduling of deficit irrigation for improved water use efficiency. Proceedings of the Southern African Irrigation Symposium, 4-6 June 1991, Elangeni Hotel, Durban. Water Research Commission, Department of Water Affairs and Forestry. Pretoria, South Africa. Report No. TT 71/95, p. 344-349.

GIORIO, P., SORRENTINO, G. & D'ANDRIA, R. 1999. Stomatal behaviour, leaf water status and photosynthetic response in field-grown olive trees under water deficit. *Environmental and Experimental Botany*, 42:95-104.

GOLLAN, T., PASSIOURA, J.B. & MUNNS, R. 1986. Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. *Australian Journal of Plant Physiology*, 13:459-464.

HIGGS, K.H. & JONES, H.G. 1991. Water relations and cropping of apple cultivars on a dwarfing rootstock in response to imposed drought. *Journal of Horticultural Science*, 66(3):367-379.

HUMAN, J.J., DE BRUYN, L.P. & PRETORIUS, J.P. 1995. Research on crop water stress as a key to increased water use efficiency. Proceedings of the Southern African Irrigation Symposium, 4-6 June 1991, Elangeni Hotel, Durban. Water Research Commission, Department of Water Affairs and Forestry. Pretoria, South Africa. Report No. TT 71/95, p. 120-130.

HUMAN, C.F., & SNYMAN, J.C., 1998. The cultivation of mangoes. ARC-ITSC, Nelspruit, South Africa.

IACONO, F., BUCCELLA, A. & PETERLUNGER, E. 1998. Water stress and rootstock influence on leaf gas exchange of grafted and ungrafted grapevines. *Scientia Horticulturae*, 75:27-39.

JENSEN, C.R., JACOBSEN, S.-E., ANDERSEN, M.N., NÚÑEZ, N., ANDERSEN, S.D., RASMUSSEN, L. & MOGENSEN, V.O. 2000. Leaf gas exchange and water relation characteristics of field quinoa (*Chenopodium quinoa* Willd.) during soil drying. *European Journal of Agronomy*, 13:11-25.

JONES, H.G. 1997. New concepts in plant water relations: relevance to horticultural production. *Acta Horticulturae*, 449:371-378.

KANG, S., HU, X., GOODWIN, I. & JERIE, P. 2002. Soil water distribution, water use, and yield response to partial root zone drying under a shallow

groundwater table condition in a pear orchard. *Scientia Horticulturae*, 92:277-291.

KOWALIK, P., BORGHETTI, M., BORSELLI, L., MAGNANI, F., SANESI, G. & TOGNETTI, R. 1997. Diurnal water relations of beech (*Fagus sylvatica* L.) trees in the mountains of Italy. *Agricultural and Forest Meteorology*, 84:11-23.

KOZLOWSKI, T.T. & PALLARDY, S.G. 1997. Transpiration and Plant Water Balance. *Physiology of Woody Plants*. Academic Press, Inc., New York. p.207-308.

KRAMER, P.J. 1983. *Water Relations of Plants*. Academic Press, New York.

KRAMER, P.J. 1990. A brief history of water stress measurement. In: Hashimoto, J., Kramer, P.J., Nonami, H. & Strain, B.R. (eds). *Measurement techniques in plant science*. Academic Press, Inc., New York. p. 45-68.

LAMPINEN, B.D., SHACKEL, K.A., SOUTHWICK, S.M. & OLSON, W.H. 2001. Deficit irrigation strategies using midday stem water potential in prune. *Irrigation Science*, 20:47-54.

LÖSCH, R. & TENHUNEN, J.D. 1981. Stomatal responses to humidity-phenomenon and mechanism. In: Jarvis, P.G. & Mansfield, T.A. *Stomatal physiology*. Cambridge University Press, Cambridge. p. 137-161.

MARSHAL, J. & GIRONA, J. 1997. Relationship between leaf water potential and gas exchange activity at different phenological stages and fruit loads in peach trees. *Journal of the American Society for Horticultural Science*, 122(3): 415-421.

MCCUTCHAN, H. & SHACKEL, K.A. 1992. Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French). *Journal of the American Society for Horticultural Science*, 117(4): 607-611.

MEIDNER, H. 1981. Measurements of stomatal aperture and responses to stimuli. In: Jarvis, P.G. & Mansfield, T.A. (eds). *Stomatal physiology*. Cambridge University Press, Cambridge. p. 25-49.

MIELKE, M.S., OLIVIA, M.A., DE BARROS, N.F., PENCHEL, R.M., MARTINEZ, C.A., DA FONSECA, S. & DE ALMEIDA, A.C. 2000. Leaf gas exchange in a clonal eucalypt plantation as related to soil moisture, leaf water potential and microclimate variables. *Trees*, 14:263-270.

MILLAR, B.D., 1971a. Improved thermocouple psychrometer for the measurement of plant and soil potential: thermocouple psychrometry and an improved instrument design. *Journal of Experimental Botany*, 22(73): 875-890.

MILLS, T.M., BEHBOUDIAN, M.H. & CLOTHIER, B.E. 1996. Water relations, growth, and the composition of 'Braeburn' apple fruit under deficit irrigation. *Journal of the American Society for Horticultural Science*, 121(2):286-291.

MILLS, T.M., BEHBOUDIAN, M.H. & CLOTHIER, B.E. 1997. The diurnal and seasonal water relations, and composition, of 'Braeburn' apple fruit under reduced water status. *Plant Science*, 126:145-154.

MORIANA, A. & FERERES, E. 2002. Plant indicators for scheduling irrigation of young olive trees. *Irrigation Science*, 21: 83-90.

MOSTERT, P.G. & KRUGER, J.A. 1998. Irrigation. In: de Villiers, E.A. (ed.). *The cultivation of mangoes*. ARC Institute for Tropical and Subtropical Crops, Private Bag X11208, Nelspruit, 1200, South Africa, p.80.

NAOR, A., GAL, Y. & BRAVDO, B. 1997. Crop load affects assimilation rate, stomatal conductance, stem water potential and water relations of field-grown Sauvignon blanc grapevines. *Journal of Experimental Botany*, 48(314):1675-1680.

NAOR, A. & PERES, M. 2001. Pressure-increase rate affects the accuracy of stem water potential measurements in deciduous fruit trees using the pressure-chamber technique. *Journal of Horticultural Science and Biotechnology*, 76(6): 661-663.

NÚÑEZ-ELISEA, R. & DAVENPORT, T.L. 1994. Flowering of mango trees in containers as influenced by seasonal temperature and water stress. *Scientia Horticulturae*, 58:57-66.

PAVEL, E.W. & FERERES, E. 1998. Low soil temperatures induce water deficits in olive (*Olea europaea*) trees. *Physiologia Plantarum*, 104: 525-532.

PIRE, R. & OJEDA, M. 1999. Effects of the irrigation regime on water relations of a table grape and two wine grape cultivars in a semiarid region in Venezuela. *Acta Horticulturae*, 493:97-102.

PONGSOMBOON, W., WHILEY, A.W. & SUBHADRABANDHU, S. 1992a. Development of water stress and stomatal closure in juvenile mango (*Mangifera indica* L.) stress. *Acta Horticulturae*, 321:496-503.

PONGSOMBOON, W., WHILEY, A.W. & SUBHADRABANDHU, S. 1992b. Effect of air temperatures on diurnal variation of water potential, conductance and CO₂ assimilation of mango (*Mangifera indica* L.). *Acta Horticulturae*, 321:472-481.

PRETORIUS, J.J.B. & WAND, S.J.E. 2003. Late-season stomatal sensitivity to microclimate is influenced by sink strength and soil moisture stress in 'Braestar' apple trees in South Africa. *Scientia Horticulturae*, 98: 157-171.

REMORINI, D. & MASSAI, R. 2003. Comparison of water status for young peach trees. *Irrigation Science*, 22:39-46.

RHIZOPOULOUS, S., MELETIOU-CHRISTOU, M.S. & DIAMANTOGLU, S. 1991. Water relations for sun and shade leaves of four mediterranean evergreen sclerophylls. *Journal of Experimental Botany*, 42:627-635.

RUIZ-SÁNCHEZ, M.C., DOMINGO, R., MORALES, D. & TORRECILLAS, A. 1996. Water relations of Fino lemon plants on two rootstocks under flooded conditions. *Plant Science*, 120:119-126.

RUIZ-SÁNCHEZ, M.C., DOMINGO, R., SAVE, R., BIEL, C. & TORRECILLAS, A. 1997. Effects of water stress and rewatering on leaf water relations of lemon plants. *Biologia Plantarum*, 39(4):623-631.

RUIZ-SANCHEZ, M.C., DOMINGO, R., TORRECILLAS, A. & PÉREZ-PASTOR, A. 2000. Water stress preconditioning to improve drought resistance in young apricot plants. *Plant Science*, 156:245-251.

RUTTER, A.J., 1970. Interactions of environment and crop in the water balance of tree crops. In: *Physiology of tree crops*. Second Long Ashton Symposium: 181- 192.

SALIENDRA, N.Z. & MEINZER, F.C. 1989. Relationship between root/soil hydraulic properties and stomatal behaviour in sugarcane. *Australian Journal of Plant Physiology*, 16:241-250.

SÁNCHEZ-BLANCO, M.J., RODRÍGUEZ, P., MORALES, M.A., ORTUÑO, M.F. & TORRECILLAS, A. 2002. Comparative growth and water relations of *Cistus albidus* and *Cistus monspeliensis* plants during water deficit conditions and recovery. *Plant Science*, 162(1):107-113.

SAUGIER, B. & KATERJI, N. 1991. Some plant factors controlling evapotranspiration. *Agricultural and Forest Meteorology*, 54 (2-4):263-277.

SAVÉ, R., BIEL, C., DOMINGO, R., RUIZ-SÁNCHEZ, M.C. & TORRECILLAS, A. 1995. Some physiological and morphological characteristics of citrus plants for drought resistance. *Plant Science*, 110:167-172.

SCOTNEY, D.M. & VAN DER MERWE, A.J. 1995. Irrigation: long-term viability of soil and water resources in South Africa. *Proceedings of the Southern African Irrigation Symposium*, 4-6 June 1991, Elangeni Hotel, Durban. Water Research Commission, Department of Water Affairs and Forestry. Pretoria, South Africa. Report No. TT 71/95, p. 50-59.

SELLÉS, G. & BERGER, A. 1990. Physiological indicators of plant water status as criteria for irrigation scheduling. *Acta Horticulturae*, 278:87-100.

SHACKEL, K., LAMPINEN, B., SIBBETT, S. & OLSON, W. 2000. The relation of midday stem water potential to the fruit growth and physiology of fruit trees under water limited conditions. *Acta Horticulturae*, 537:425-430.

SHIVASHANKARA, K.S. & MATHAI, C.K. 2000. Inhibition of photosynthesis by flowering in mango (*Mangifera indica* L.). A study by gas exchange methods. *Scientia Horticulturae*, 83:205-212.

SIPIORA, M.J. & LISSARRAGUE, J.R. 1999. Diurnal changes in vine water status and gas exchange parameters of *Vitis vinifera* L. cv. Tempranillo grapevines as influenced by irrigation and pruning level. *Acta Horticulturae*, 493:109-116.

SLAVÍK, B., 1974. Water in cells and tissues. In: Jacobs, J., Lange, O., Olson, J.S. & Wieser, W. (eds). *Methods of Studying Plant Water Relations*. Springer-Verlag, Berlin. p. 1-120.

SNYMAN, J.C. 1998. Climatic requirements. In: de Villiers, E.A. (ed.). *The cultivation of mangoes*. ARC Institute for Tropical and Subtropical Crops, Private Bag X11208, Nelspruit, 1200, South Africa, p.17.

SWART, H.J. 2000. Voorlegging aan die Blyderrivier besproeiingsraad raakende die laer Blyde besproeiingsnetwerk. Blyderriver Irrigation Board, P.O. Box 212, Hoedspruit, 1380, South Africa, Appendix B.

TAKAGI, K., TSUBOYA, T. & TAKAHASHI, H. 1998. Diurnal hystereses of stomatal and bulk surface conductances in relation to vapour pressure deficit in a cool-temperate wetland. *Agricultural and Forest Meteorology*, 91:177-191.

TARDIEU, F. 1996. Drought perception by plants: do cells of droughted plants experience water stress? *Plant Growth Regulation*, 20(2): 93-104.

TORRECILLAS, A., GALEGO, R., PEREZ-PASTOR, A. & RUIZ-SANCHEZ, M.C. 1999. Gas exchange and water relations of young apricot plants under drought conditions. *Journal of Agricultural Science*, 132:445-452.

TURNER, N.C. 1991. Measurement and influence of environmental factors on stomatal conductance in the field. *Agricultural and Forestry Meteorology*, 54:137-154.

TURNER, D.W. & THOMAS, D.S. 1998. Measurements of plant and soil water status and their association with leaf gas exchange in banana (*Musa* spp.): a laticiferous plant. *Scientia Horticulturae*, 77:177-193.

VOGT, U.K. & LÖSCH, R. 1999. Stem water potential and leaf conductance: a comparison of *Sorbus aucuparia* and *Sambucus nigra*. *Physical and Chemical Earth*, 24(1-2):121-123.

WALKER, S. & NEL, A.A. 1995. Crop indicators of water stress for use in irrigation scheduling: an overview. Proceedings of the Southern African Irrigation Symposium, 4-6 June 1991, Elangeni Hotel, Durban. Water Research Commission, Department of Water Affairs and Forestry. Pretoria, South Africa. Report No. TT 71/95, p. 131-135.

WEIBEL, F.P. & DE VOS, J.A. 1994. Transpiration measurements on apple trees with an improved stem heat balance method. *Plant and Soil*, 166: 203-219.

WEYERS, J.D.B. & MEIDNER, H. 1990. *Methods in Stomatal Research*. Longman Scientific & Technical, Essex. p. 26-33.

YUSTE, J., RUBIO, J.A., PELÁEZ, H.J., RUIZ, C. & LISSARRAGUE, J.R. 1999. Predawn leaf water potential and soil water content in vertical trellis under irrigated and non-irrigated conditions in 'Tempranillo' grapevines. *Acta Horticulturae*, 493:309-321.