


Stomatal oscillations and the response of citrus trees to different irrigation strategies in northern Zimbabwe

Sebinasi Dzikiti

UNIVERSITEIT GENT

FACULTEIT BIO-INGENIEURSWETENSCHAPPEN

Promoters: Prof. Dr. Raoul LEMEUR
Dr. ir. Kathy STEPPE
Department of Applied Ecology and Environmental Biology
Laboratory of Plant Ecology
Ghent University

Dean: Prof. Dr. ir. Herman VAN LANGENHOVE

Rector: Prof. Dr. Paul VAN CAUWENBERGE

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Thesis submitted in fulfillment of the requirements
for the degree of Doctor (PhD) in Applied Biological Sciences

Stomatale oscillaties en de respons van citrusbomen op verschillende irrigatiestrategieën in het noorden van Zimbabwe

Illustrations on the cover:
Front: experimental set up at the University of Zimbabwe; stem sap flow sensor on a mature orange tree; dendrometer measuring fruit growth; automatic weather station at the trial site at Mazowe Citrus Estate, Zimbabwe
Back: young citrus orchard in northern Zimbabwe

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Ghent, September 2007

Sebinasi

Contents

List of symbols and abbreviations

Abbreviations

ABA	abscisic acid
BA	basal area
CR	capillary rise
DOY	julian day of year
DP	deep percolation
ET	crop evapotranspiration
ET_c	evapotranspiration under standard conditions
ET_{cadj}	evapotranspiration under non-standard conditions
ET_o	potential evapotranspiration
E_{pan}	pan evaporation
I	irrigation
ITCZ	inter-tropical convergence zone
LAI	leaf area index
MCE	Mazowe Citrus Estate
MDS	maximum diameter shrinkage
PAR	photosynthetically active radiation
P_r	precipitation
PRD	partial rootzone drying
PRD100	partial root zone drying with 100 % ET replacement
PRD50	partial root zone drying with 50 % ET replacement
RAW	readily available water
RDI	regulated deficit irrigation
RDI50	regulated deficit at 50 % ET replacement
RH	relative humidity
RO	run off
RSA	relative sapwood area
SAI	sapwood area index
SF	scaling factor
TA	titratable acids
TAW	total available water
TDP	thermal dissipation probes

TSS	total soluble solids
VPD	vapor pressure deficit of the air
W_r	water content in the root zone

Roman symbols

Symbol	Description	Unit
a	branch leaf area of potted trees	(m^2)
A	total leaf area of the potted trees	(m^2)
a_p	stomatal pore width	(µm)
A_s	conducting sapwood area	(cm^2)
A_{st}	stem cross sectional area	(cm^2)
C	plant capacitance	(kg MPa^{-1})
c_p	specific heat of the air at constant pressure	(J kg^{-1} K^{-1})
d	zero plane displacement	(m)
Δd	stem diameter fluctuation	(µm)
E	transpiration rate by the whole canopy	(g h^{-1})
E_L	branch sap flow rate	(g h^{-1})
e_s	saturation vapor pressure	(kPa)
e_a	vapor pressure of the air	(kPa)
F	stem sap flow rate	(g h^{-1})
f	recharge/discharge of internal storage pools	(g h^{-1})
F_{LA}	sap flow rate per unit leaf area	(g h^{-1})
G	soil heat flux	(W m^{-2})
g_s	stomatal conductance	(mmol m^{-2} s^{-1})
h	sadius of the heartwood of a tree stem	(cm)
J_s	stem sap flux density measured with a TDP	(g m^{-2} h^{-1})
k	von Karman constant	(-)
K	dimensionless flow constant for computing sap velocity in TDPs	(-)
K_c	crop coefficient	(-)
K_p	pan coefficient	(-)
K_{sh}	radial sheath conductance of heat balance sap flow gauges	(W mV^{-1})
k_{st}	thermal conductivity of wood	(W m^{-1} K^{-1})
m	cell mechanical advantage	(-)

n	number of drip emitters	(-)
N	sample size for computing the standard error in the mean	(-)
P	atmospheric pressure	(kPa)
P_e	epidermal cell turgor pressure	(kPa)
P_g	guard cell turgor pressure	(kPa)
P_i	PAR outside the rain shelter	(µmol m^{-2} s^{-1})
P_{in}	power input to the heat balance sap flow gauge	(W)
q_f	heat transport by the moving sap stream	(W)
q_r	radial heat transport from the heat balance sap flow gauge	(W)
q_v	axial heat transport on the heat balance sap flow gauge	(W)
R	sapwood radius	(cm)
r_a	aerodynamic resistance	(s m^{-1})
R_i	PAR inside the rain shelter	(µmol m^{-2} s^{-1})
r_l	stomatal resistance	(s m^{-1})
R_{net}	net radiation	(W m^{-2})
R_s	solar radiation	(W m^{-2})
r_s	bulk surface resistance	(s m^{-1})
R_x	plant hydraulic resistance	(h MPa kg^{-1})
ΔS	change in internal water storage	(g h^{-1})
dT_m	maximum temperature difference between TDP probes	(°C)
$\sum R_s$	daily total solar radiation	(W m^{-2})
ΔT_a	voltage difference across the upper pair of thermocouples in the heat balance sap flow gauge	(V)
ΔT_b	voltage difference across the lower pair of thermocouples in the heat balance sap flow gauge	(V)
ΔT_r	radial voltage difference across the heat balance	(V)
T_a	air temperature	(°C)
t_e	equilibration time for heat pulse	(s)
T_l	leaf surface temperature	(°C)
T_{max}	maximum air temperature	(°C)
T_{mean}	average air temperature	(°C)
T_{min}	minimum temperature	(°C)
T_s	soil temperature	(°C)
U_e	molar flow at the inlet of the infrared gas analyzer	(mmol s^{-1})
u_z	wind speed at height z	(m s^{-1})

V	sap velocity	(cm h^{-1})
V_c	heat pulse velocity corrected for wounding	(cm h^{-1})
$\sum VPD$	daily total vapor pressure deficit of the air	(kPa)
V_w	volume of water applied by irrigation	(m^3)
W	tissue water content	(g)
Δx	distance between thermocouple junctions in heat balance sap flow gauges	(m)
X_d	downstream distance of temperature probe in heat pulse sap flow gauges	(m)
X_e	partial pressure due to water molecules	(kPa)
X_u	upstream distance of temperature probe in heat pulse sap flow gauges	(m)
z_h	height of humidity measurement	(m)
z_m	height of wind speed measurement	(m)
z_{oh}	roughness length for heat and vapor transfer	(m)
z_{om}	roughness length for momentum transfer	(m)

Greek symbols

Symbol	**Description**	**Unit**
α	standard error in the mean transmittance to PAR	(µmol m^{-2} s^{-1})
Δ	slope of the saturation vapor pressure vs temperature graph	(kPa $°C^{-1}$)
ρ_a	density of air	(kg m^{-3})
θ	volumetric soil water content	(m^3 m^{-3})
τ	transmittance to PAR	(-)
π_g	guard cell osmotic potential	(MPa)
π_e	epidermal cell osmotic potential	(MPa)
γ	psychrometric constant	(kPa $°C^{-1}$)
λ	latent heat of vaporization	(J kg^{-1})
ψ_e	epidermal cell water potential	(MPa)
ψ_g	guard cell water potential	(MPa)
ψ_l	leaf water potential	(MPa)
ψ_s	soil water potential	(kPa)

Introduction and structure of the thesis

Background and justification

In Zimbabwe, as elsewhere in Southern Africa, the economy is heavily dependent on agriculture which accounts for approximately 20 % of the gross domestic product (GDP). This figure rises to 60 % when agriculture-based industries, including services, are taken into account (Horticultural Promotion Council of Zimbabwe, 2000). Approximately 45 % of the total export earnings in Zimbabwe are agriculture related with horticultural exports comprising a substantial proportion. Citrus products (fresh fruit, juice and oil) account for approximately 55 % of the horticultural exports by volume and 10 % by value. Most of the citrus fruit (~ 60 %) is exported as fresh fruit to the European and the Middle East markets. The favorable climatic conditions characterized by warm temperatures ensure that the Zimbabwean fruit enters the market up to four weeks earlier than South Africa, which is the main regional competitor. In addition, the Zimbabwean citrus industry can supply the fruit over an extended period due to the relatively longer growing season which allows a wider range of citrus cultivars to be grown.

Despite the immense potential for citrus production in Zimbabwe, the availability of adequate water throughout the year is a major factor limiting production since citrus is an evergreen crop. The rising competition for water between the urban domestic users, industrial, recreational, wildlife and other irrigation users results in less water being available for citrus irrigation. This problem is exacerbated by the increasing frequency and severity of droughts in Southern Africa in recent years (Makarau and Jury, 1997), presumably associated with the effects of global climate change. The intense competition for water is clearly evident in northern Zimbabwe, in the Mazowe catchment (~ 40 km north of Harare), where one of the major citrus producing farms, the Mazowe Citrus Estate (MCE), is located (Fig 1). In addition, there are also many large scale farms producing a range of horticultural crops all year round, e.g. flowers, potatoes vegetables and cereals, mainly maize and wheat. The bulk of the water for all these crops is withdrawn from the Mazowe Dam (Fig 1). Mazowe Citrus Estate, with 800 ha under citrus trees, uses approximately 41.5 % of the total annual water allocation to the farmers.

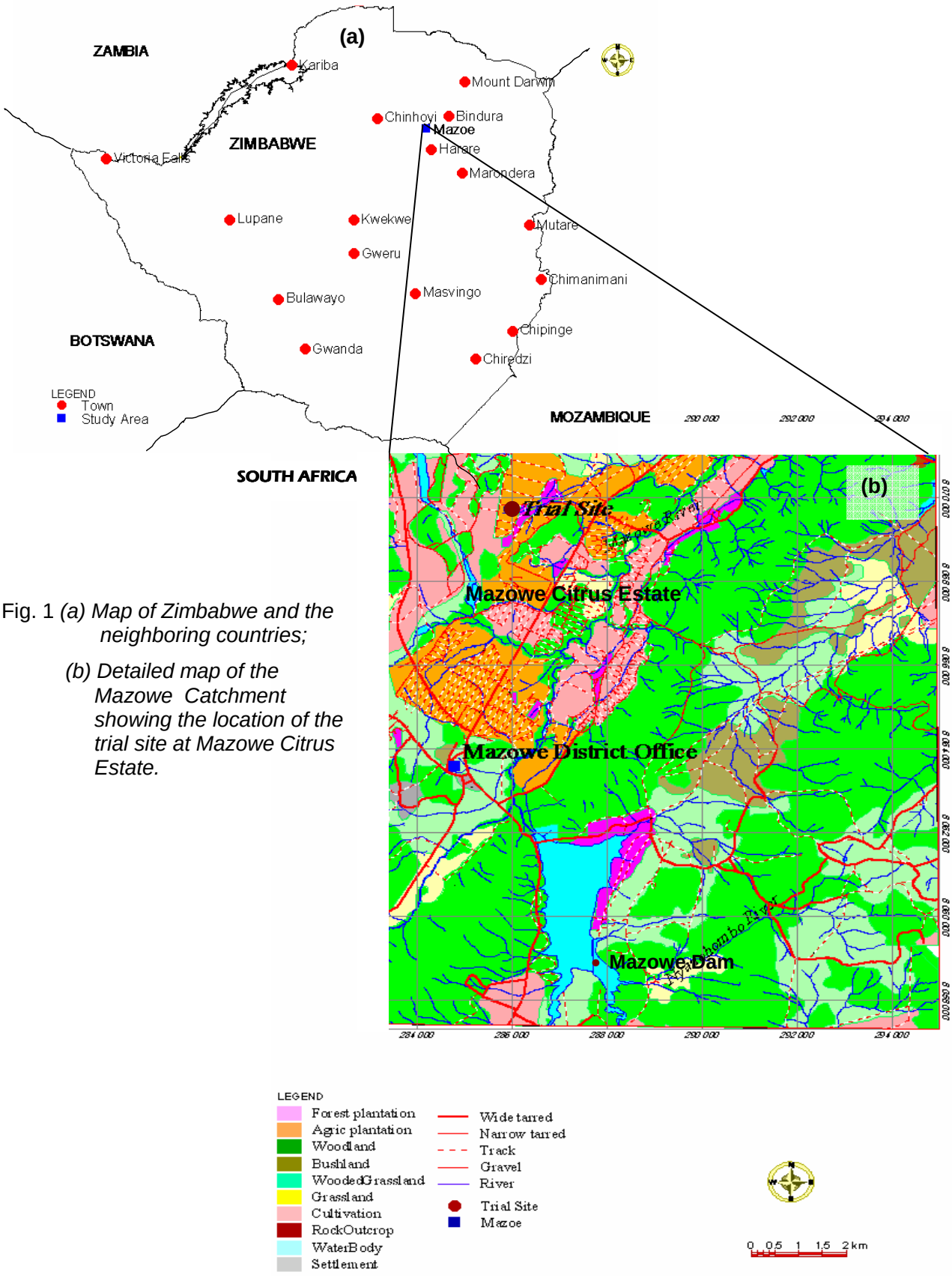


Fig. 1 *(a) Map of Zimbabwe and the neighboring countries;*

(b) Detailed map of the Mazowe Catchment showing the location of the trial site at Mazowe Citrus Estate.

However, this quantity of water is not always guaranteed due to the increasing frequency of droughts leading to acute shortages. Fluctuations in the level of the Mazowe Dam in the last 36 years are shown in Fig 2. These variations are closely related to the incidences of drought due primarily to the El Niño and Southern Oscillation events (Wouters, 2004). Flood irrigation was the method used by the citrus growers in the early years of establishment of the orchards. To improve the water use efficiency, new methods e.g. the basin type, microjet and now the drip irrigation systems have been introduced over the years. For example, under the flood irrigation, in excess of 20 Ml of water was needed to irrigate a hectare of citrus. However, only 8.0 Ml is now needed per hectare under the drip irrigation system. In addition, yields have been significantly increased under the drip system.

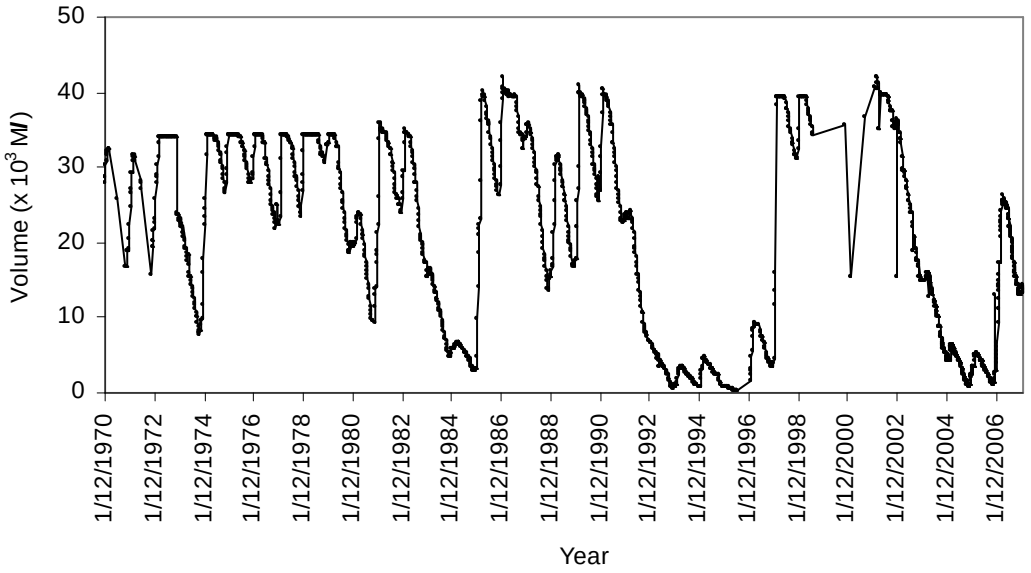


Fig 2 *Variations in the volume of water in the Mazowe Dam in the last 36 years. At full capacity, the dam holds approximately 39000 Ml of water (Source: Zimbabwe National Water Authority).*

Recent research on the irrigation of fruit trees has shown that even more water savings can be achieved under drip irrigation, e.g. by imposing controlled levels of drought stress in the rootzone of the trees at certain stages of growth with minimal yield losses (Chalmers *et al*., 1981). Under these conditions, a shift in resource allocation from vegetative growth to reproductive development has been reported (Chalmers *et al*., 1981; Bacon, 2004; Jones, 2004). Consequently, certain horticulturally important attributes of the fruit, e.g. the internal quality and the control of excessive vegetative growth, can be improved. This irrigation technique is called the regulated deficit irrigation (RDI) strategy. Excessive vegetative growth requires frequent pruning which is both expensive in terms of the labor and equipment

requirements and has negative effects on the tree itself through injury. But the timing of the application of RDI has proved to be critical as water stress during fruitset can have catastrophic effects on yield (Goldhammer and Salinas, 2000). Another method requiring less water application and with potentially beneficial effects on yield and fruit quality is the partial rootzone drying (PRD) method (Dry *et al*., 1996). This strategy uses the root to shoot chemical signaling mechanisms (Davis *et al*., 2001) of the plant when part of the root system is alternately subjected to drying soil.

Apart from the few publications by Goldhammer and Salinas (2000) on the application of the RDI strategy on citrus, literature on the application of the RDI and PRD strategies to citrus trees, especially in the semi-arid tropics, is sparse. In addition, it has been reported with other crops that the suitability of these techniques depend on the crop, soil and local climatic conditions (Chalmers *et al*., 2004). Thus, before these techniques can be recommended for citrus irrigation in Zimbabwe, thorough investigations are required on their effects both on tree water relations and productivity of the orange trees.

Set up of the research

To accomplish this goal, two experimental set ups were established. The first set of experiments were conducted in the open air laboratory on the roof of the Physics Department, University of Zimbabwe with young Navel orange trees [*Citrus sinensis* (L.) Osbeck] grown in pots. This sort to study, in detail, the water relations of the orange trees under semi-arid conditions but with certain aspects of the plant's environment, e.g. the edaphic environment, controlled. In addition, preliminary responses of the Navel orange trees to the two watering strategies (RDI and PRD) were established.

The second experimental set up was established with field-grown orange trees in the orchard at Mazowe Citrus Estate where up scaling of the laboratory observations to field conditions were done. Results of the application of these irrigation strategies in northern Zimbabwe were evaluated over three growing seasons, namely 2004/05, 2005/06 and 2006/07.The two experimental phases (i.e. the laboratory and field experiments) are presented in the thesis as Parts A and B, respectively as will be detailed below.

Objectives of the thesis

The specific objectives of the laboratory experiments (Part A) were firstly, to study in detail, the water relations of the Navel orange trees when subjected to drought stress applied in different ways. This gave insights on the response of the trees to the RDI and the PRD

irrigation strategies with the soil water conditions controlled. Different stress detection variables, e.g. variations in the sap flow totals over specific time intervals, stem growth rate, stem diameter variations and the leaf to air temperature differences, were evaluated for potential use in water management in citrus orchards. Secondly, the dynamic flow of water in the Navel orange trees as affected by the hydraulic properties of the transpiration stream were investigated to better understand and explain the water relations of the orange trees. A dynamic water transport model was developed and used to derive typical values of the hydraulic parameters of the transpiration stream of the orange trees.

The objectives of the second part of the experimental campaign (Part B) were to evaluate the responses of mature trees in a commercial orchard to the RDI and PRD strategies. Particularly, the effects on tree-water relations and on yield quality and quantity were investigated. Up scaling of the sap flow data from single tree level to the orchard was done to estimate the seasonal and annual total transpirational losses under different irrigation regimes. Water use efficiency, defined in this study as the ratio of the total yield by the whole orchard to the total transpirational losses was derived for the different irrigation methods. This information is useful for assisting growers in identifying techniques that can potentially maximize the water use efficiency in citrus irrigation in the semi-arid tropics.

Thesis outline

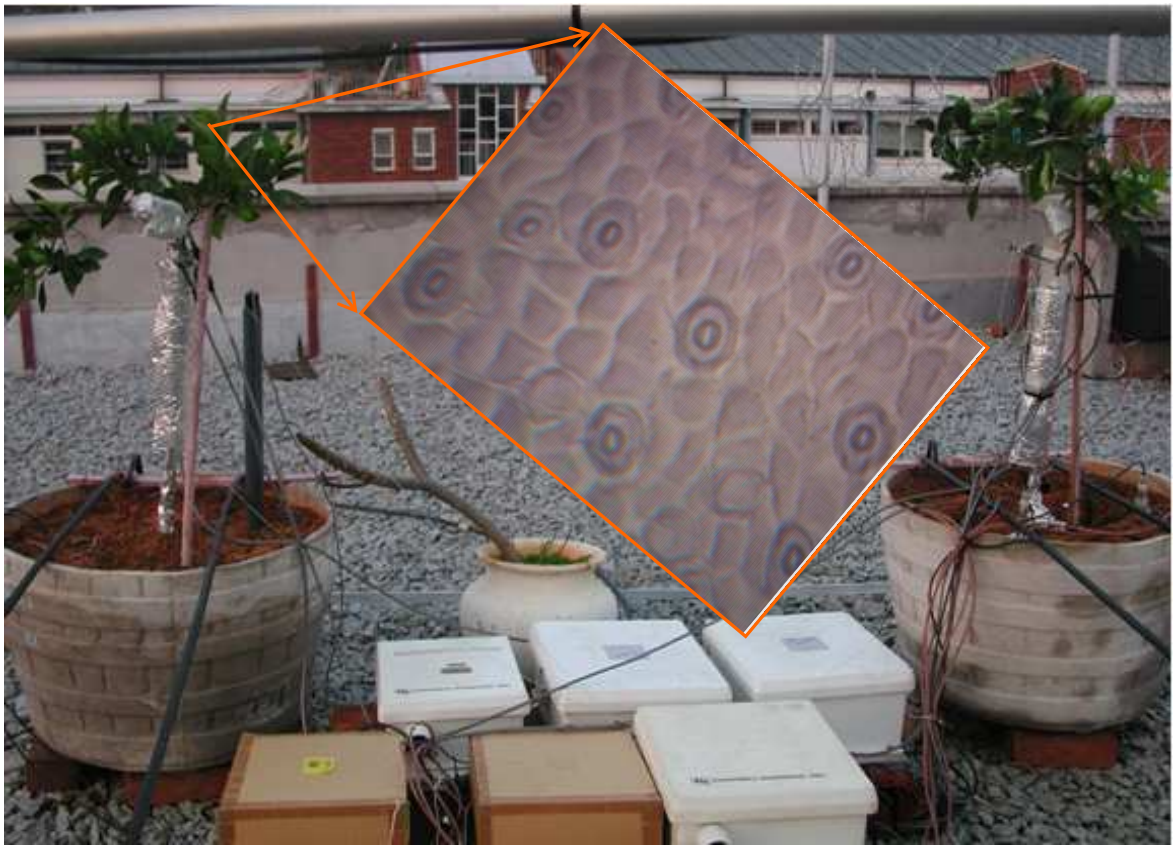
The thesis comprises of five distinct chapters, each covering a specific topic. Part A comprises Chapter 1 to Chapter 3. In Chapter 1, the responses of the young potted Navel orange trees to drought stress applied in different ways are discussed. These responses are detected in terms of changes in the sap flow rates, stem diameter variations, stem growth rates and the leaf to air temperature variations. A literature review is given in which these stress detection signals can be used for irrigation scheduling. Most importantly, insights into the response of the Navel orange trees to the RDI and PRD irrigation strategies are gained. Chapter 2 also deals with the potted tree experiments. In this chapter, the role of the whole-tree water balance in the generation of stomatal oscillations, which characterize the water relations of Navel orange trees, is explored. A dynamic water transport model is developed and typical values of the hydraulic parameters of the transpiration stream of the Navel orange trees budded on the Troyer citrange rootstock are presented. In Chapter 3, the dynamics of water uptake by Navel orange trees budded on two rootstocks with contrasting water uptake capabilities, namely the Rough lemon and the Troyer citrange, are discussed. The efficiency of water uptake by these rootstocks are then related to the different forms of stomatal oscillations that characterized these rootstocks. Evidence that the root hydraulic resistance

plays an important role in the efficiency of water supply to the leaves and modifies the form of the stomatal cycling is given.

Part B comprises Chapter 4 and Chapter 5. Chapter 4 discusses the effect of the RDI and PRD irrigation strategies on tree water relations, yield quality and quantity and root development. These investigations were done on mature trees in the orchard at Mazowe Citrus Estate. Literature review of the root to shoot chemical signaling mechanisms and its utilization in the different irrigation strategies is given. Chapter 5 begins with a discussion of the different methods for quantifying the transpiration rates of fruit trees. Up scaling of the sap flow rates measured on individual trees subjected to different irrigation treatments to orchard level and from one day to season and annual levels is done. Typical values of the water use efficiencies under the different irrigation regimes are presented. Chapter 6 gives the conclusions and future perspectives on the subject of stomatal oscillations and recommendations on the optimal irrigation strategy for citrus production at Mazowe Citrus Estate.

PART A

STOMATAL OSCILLATIONS AND THE RESPONSE OF POTTED NAVEL ORANGE TREES [*CITRUS SINENSIS* (L.) OSBECK] TO DROUGHT STRESS



Chapter 1 Sap flow dynamics of young potted Navel orange trees [*Citrus sinensis* (L.) Osbeck] under uniform and alternating partial drought stress

Parts of this chapter are published in:

Dzikiti S, Steppe K, Lemeur R, Milford JR. 2006. Water use by young Navel orange trees [*Citrus sinensis* (L.) Osbeck] in Zimbabwe. Acta Hort. 707, 135-141.

1.1 Introduction

Efficient management of water in any cropping situation requires accurate quantitative information on water use. This information is important in the irrigation scheduling of perennial crops like citrus trees grown in the arid and seasonally arid climates. In these regions, citrus production relies heavily on irrigation. Citrus irrigation is also increasingly being employed in plantations in the humid and sub-humid climates to maintain yields that are often reduced by long rainless periods. A typical example of the usefulness of irrigation in the sub-humid climates is by Koo (1979) who found an increase in the yield of Valencia orange fruit of 22 % with 276 mm yr^{-1} irrigation added to 1160 mm yr^{-1} of rain.

Over-watering or under-watering has negative consequences on citrus growth and production. For example, a decay of the fibrous or larger roots can occur under water logging conditions due to the formation of hydrogen sulphide by sulphur-fixing bacteria which are abundant under these conditions. This leads to a deterioration of tree health (Davis and Albrigo, 1994; Spiegel-Roy and Goldschmidt, 1996). Despite these risks and the general shortage of water in many regions, actual management practices in citrus orchards generally tend towards excessive water use due to fears of a decline in growth and production (Marsh, 1958; Davies and Albrigo, 1994; Germanà and Sardo, 2004; Rana *et al*., 2005). This situation is, to a large extent, caused by the large uncertainties in irrigation scheduling not only in citrus plantations, but in most crop production systems (Clyma, 1996; Naor, 2004).

Jensen (1975), reviewing a decade of emphasis on irrigation scheduling, observed that scheduling involved the farmer in too much information and too many decisions, a situation which still holds at present. The automation of irrigation scheduling is a viable solution to this problem and is receiving a lot of attention (Jones, 2004). In addition, models which estimate

the rates of transpirational losses are also increasingly being used in these automated systems (Santini and Romano, 1996). Use of these models somewhat adds to the uncertainty in irrigation scheduling since transpiration rates are often not estimated accurately (Bauerle *et al*., 2002) especially for drought stressed trees.

Precise irrigation scheduling is a crucial component of the recently developed irrigation strategies such as the deficit irrigation (Chalmers *et al*., 1981) and the partial rootzone drying techniques (Cohen *et al*., 1985; Dry *et al*., 1996). In these methods, controlled levels of drought stress are maintained in the root zone. Chalmers *et al*. (1981) observed that by maintaining a slight water deficit in the rootzone of peach trees, the partitioning of carbohydrates to the reproductive structures such as the fruit and also the control of excessive vegetative growth can be improved. Excess water application reverses these advantages while severe drought stress often leads to severe yield losses.

The objectives of this chapter are to investigate the response of young pot grown Baianinha Navel orange trees [*Citrus sinensis* (L.) Osbeck] to drought stress applied in different ways. This provided insights in the response of these trees to the deficit irrigation strategies. Based on a detailed knowledge of these responses, up scaling of the potted tree experimental results was done to evaluate the potential application of the deficit irrigation strategies in the orchards with mature citrus trees. Details of the field experiments are given in Chapter 4 of this thesis. In addition, potential plant-based stress indicators for the irrigation scheduling of Navel orange trees growing on Rough lemon rootstocks [*Citrus Jambhiri* (Lush.)] in the semi-arid tropics were explored and their typical threshold values proposed. To date, researchers have not yet addressed the question of transferability of thresholds for irrigation scheduling (Naor, 2004). Thus different thresholds might be needed for different climatic regions because the differences in the climatic conditions can alter the relationship between tree water status and the amount of assimilates available for the accumulation of dry matter. To date, attempts have been made to use these plant-based irrigation scheduling techniques on horticultural crops, and most progress has been made in the protected cropping sector (Jones, 2004), but there is need for these to be validated on high value perennial crops, like citrus.

1.2 Irrigation scheduling of fruit trees

1.2.1 Soil-based irrigation scheduling

Irrigation scheduling was first introduced in the 1960s and was defined as the method of measuring soil water status for deciding when to irrigate (Clyma, 1996). Today, irrigation scheduling is understood to involve not only deciding when to irrigate but also how much water to apply. Severe drought stress deleteriously affects both the vegetative growth and yield of citrus trees while moderate stress has been found to favour reproductive development (Chalmers *et al*., 1981; Spiegel-Roy and Goldschmidt, 1996; Dariusz, 1997). Yield is thus a function of both the amount and timing of irrigation. Conventional approaches to irrigation scheduling are based on the estimation of the soil water status.

Soils on which citrus trees are commonly grown have a porosity ranging from 40 to 55 % (Marsh, 1958). These pores hold water and air that are necessary to citrus roots. Water is held in the pores by attraction between the water molecules and the surrounding solid particles. The relationship between the soil matric potential and the soil water content is called the water retention curve as shown in Fig 1.1. At low water content, water is spread as a thin film over the surfaces of all the soil particles. A larger suction is needed to extract the water molecules. The thinness of the film is dependent on the amount of water present and the total surface area of all the solid particles. Fine-textured (clay) soils for example, have greater particle surface area than course-textured (sandy) soils such that a given amount of water is spread in thinner films in sandy soils. In the process of water use by plants, first the medium and eventually the smaller pores lose water. Water films gradually become thinner and more energy (larger suction) is needed to extract the water than when the soil is saturated (all the pores filled with water).

Water status is quantified in fruit tree orchards through measurements of either the soil water content or soil water potential using a range of devices e.g. neutron and capacitance probes (Payne and Brück, 1996; Fares and Alva, 2000) or tensiometers (Isbérie, 1996). For operational use, tensiometers are most commonly used for scheduling irrigations in citrus plantations (Marsh, 1958).

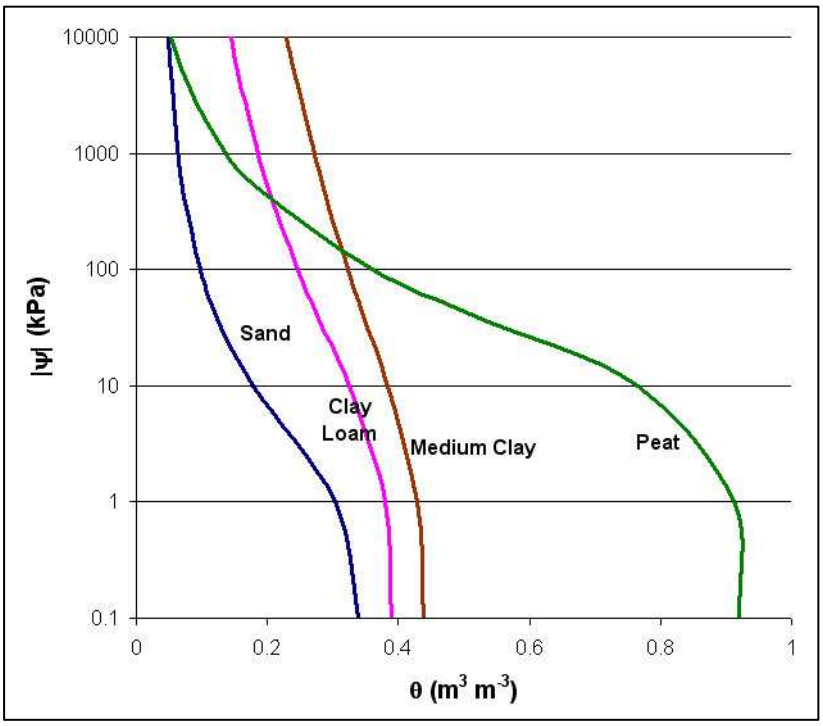


Fig 1.1 *Typical water retention curves for different soil types. The quantity in the x-axis (θ) represents the water content while the y-axis (ψ) represents the soil water potential.*

The tensiometer is a closed, water filled tube with a hollow, ceramic tip at one end and a vacuum gauge at the other as shown in Fig 1.2. The ceramic tip is permeable, and the water in the tube saturates it. The tip is placed in contact with the soil in the root zone. Because the soil is normally not saturated, water is drawn from the tip into the soil. As water moves from the tube into the soil, a partial vacuum is created and measured by the gauge. In modern versions of the tensiometers, this vacuum can be detected by means of electronic transducers which normally convert it to a voltage signal. Tensiometers operate in the wetter portion of the soil-water spectrum (approximately 0 to -80 kPa). This covers the range of greatest interest to most citrus growers because firstly saturation is a dangerous condition for citrus trees which should be known and secondly, in most orchards irrigation is desirable to avoid the adverse effects in severe weather before a soil water potential of -80 kPa is reached in the rootzone. The tensiometers are often used in pairs, one in the rootzone (~ 30 cm depth) used for routine scheduling and the other beyond the rootzone (~ 60 cm) as an indicator for drainage beyond the region of active root water uptake. However, susceptibility to frost and the need for regular degassing are major drawbacks associated with the use of manual tensiometers shown in Fig 1.2. The use of neutron probes and capacitance sensors has largely been limited for research purposes only.

The soil water status can also be estimated by calculation using a water balance approach. Here, the change in soil moisture content (W_r) over a specific period is given as the difference between the inputs (irrigation plus precipitation) and the losses (runoff plus drainage plus evapotranspiration) as illustrated in Fig 1.3.

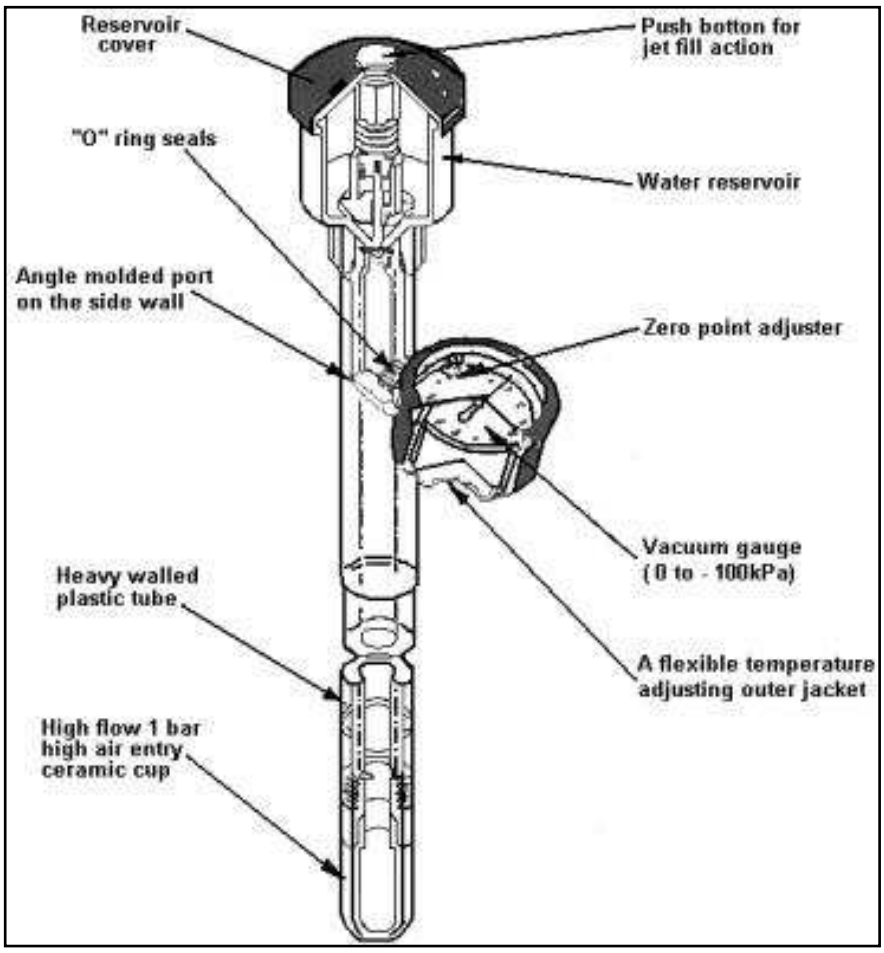


Fig 1.2 *Cross-section of a tensiometer. Essential parts include the porous ceramic cup, connecting tube, vacuum gauge and a movable stopper or cap.*

The total available water (TAW) is the difference between the water content at field capacity (maximum water holding capacity of the soil) and at the permanent wilting point (lowest soil water content before irreversible wilting occurs). Irrigation is then managed by allowing a certain level of moisture depletion in the rootzone e.g. 33 % of TAW for citrus trees. Although the water balance approach is not very accurate, it has generally been found to be sufficiently robust under a wide range of conditions (Jones, 2004). The main disadvantage of this approach, however, is that the errors are cumulative over time and thus a recalibration of the calculated water balance is necessary using actual soil measurements or other techniques.

Generally, soil water-based approaches have the potential limitation that many features of the plant's physiology respond directly to changes in the water status in the plant tissues rather than to changes in the bulk soil water status (Intrigliolo and Castel, 2004; Naor, 2004).

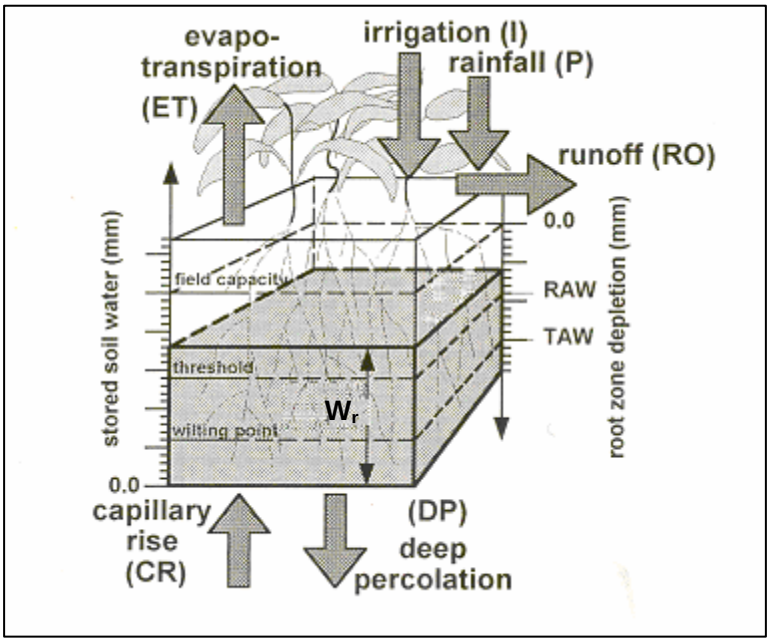


Fig 1.3 *Components of the water balance in the root zone for irrigation scheduling (adapted from Raes, 2001).*

Drought stress and yield declines have been observed before the soil water depletion reached the threshold values. Furthermore, the soil water suction readings have been reported to be more variable than the midday stem water potential in apple (Naor *et al*., 1995), nectarine and pear (Naor *et al*., 2000). Thus getting representative measurements is somewhat problematic and plant based stress-indicators are preferable for fruit trees. Consequently, current research emphasis on the irrigation scheduling of fruit trees is on exploring the possibility of plant-dependent irrigation scheduling, e.g. measurements of plant water status (i.e. leaf or stem water potential) or other plant processes that are known to respond sensitively to water deficits like the sap flow rate and stem diameter variation (Cornelius *et al*., 1996; Isbérie *et al*., 2004). A review of the possible stress indicators for fruit trees and for citrus in particular is given below.

1.2.2 Plant-based water stress indicators

1.2.2.1 Visible symptoms

This is probably the simplest means of determining the irrigation needs of citrus trees. Furr and Taylor (1939) observed the curling of immature leaves on succulent, elongated shoots as the first visible sign of stress. According to these authors, cessation of shoot elongation occurred at about the same time. With further soil drying, young leaves showed severe distortion and old leaves began to drop. As expected, citrus experts have expressed various reactions to the method of determining irrigation need based on visible tree symptoms. For example, Koo (1979) reported that this practice, common to Florida, of waiting to irrigate until trees show a visible stress was uneconomic, while properly timed irrigation was profitable. Lyon (1958) noted that a tree on sweet orange rootstock showed stress earlier than on other rootstocks and an early sign of stress was a retardation of fruit growth. Slowing of shoot growth came later and is not a useful indication of water need of the citrus trees. In addition, recent experiments have shown that by the time wilting is apparent, a substantial proportion of the potential yield may already have been lost (Dariusz, 1997; Jones, 2004).

1.2.2.2 Plant water status

Trees have a large rootzone, and the availability of soil moisture varies within the rootzone of each tree, because of the non-uniform water application and the variability in the soil hydraulic properties. Trees can adapt the distribution of their water absorbing roots to compensate for the variability in soil moisture availability by increasing the density of the root system where moisture is highly available. For this reason and those mentioned above, plant water status is a better indicator for drought stress than soil based approaches and thus is a better guide for irrigation scheduling. But a fundamental question still remains regarding where on the plant the stress should be measured. Presumably, a rigorous and sensitive measure of the plant water status should be used, e.g. the bulk leaf water potential (Jones, 2004).

However, the fact that plant water status and, especially the leaf water potential, is usually controlled to some extent by means of stomatal movements is problematic in that other factors e.g. the so-called root to shoot chemical signalling have a strong effect on stomatal movements (Dariusz, 1997; Mingo and Davies, 2001). A further problem relating the use of the leaf water potential as a measure for irrigation scheduling are the rapid fluctuations which occur in this variable, for example, due to sudden changes in the environmental conditions by passing clouds (Jones 1990b). This makes the use of the leaf water potential as an indicator for irrigation need unsatisfactory.

Given these concerns regarding the use of the leaf water potential for irrigation scheduling, some researchers have proposed the use of a more stable variable, the xylem water potential or stem water potential (Jones, 2004). For fruit trees, this is estimated either from the water status estimates of leaves that are under deep canopy shade or enclosed in darkened plastic bags. These methods are thought to be preferable because they approach closely the stem/xylem water potential which is more stable than the leaf water potential. But they then miss out on the potential advantages of plant-based methods. Another possible measure is the pre-dawn leaf water potential, which should approximately be equal to the soil water potential. Unfortunately, this has often been found to be insensitive to variations in soil moisture content and frequent measurements are difficult to obtain. Lastly, all these variables are not suitable for automation and they are destructive and thus other stress indicators have to be considered as well.

1.2.2.3 Fruit and trunk diameter changes

Stem and fruit diameters fluctuate diurnally in response to changes in the water content of the different organs. The diurnal dynamics of changes in diameter, especially of fruits have been used to derive rather more sensitive indicators of irrigation need, where the magnitude of the daily shrinkage has been used to indicate water status (Jones, 2004). In addition, comparisons of diameters at the same time on succeeding days give a measure of growth rate and the trend in growth can also be used as an indicator for stress. Growth of Valencia oranges in Arizona from plots irrigated at two different frequencies over a $2^1/_2$ month period are as shown in Fig 1.4. Rapid fruit growth occurred after each irrigation of the dry plot although the final fruit size was smaller compared to the wet plot.

According to Marsh (1958), if fruit growth records are to be used as a guide for irrigation, five to ten fruit per tree on several trees distributed throughout the orchard must be tagged and measured regularly. When the growth rate slows down and the growth curve tends towards a more nearly horizontal line, fruit growth is slowing. If the line becomes horizontal, fruit growth has ceased and if the line turns downwards, then the fruit will be shrinking. According to Furr and Taylor (1939), if water is applied soon after the first significant decrease in growth rate the ultimate fruit size will not be reduced because the growth rate accelerates for a few days after irrigation. If water is withheld until growth ceases, however, the final fruit size is reduced. Although changes in growth rate provide a particularly sensitive measure of plant drought stress, such daily measurements are not particularly useful for the control of high frequency irrigation systems. Moreover, the uncertainty about the representativity of the fruits that are selected for size measurements pose another difficulty.

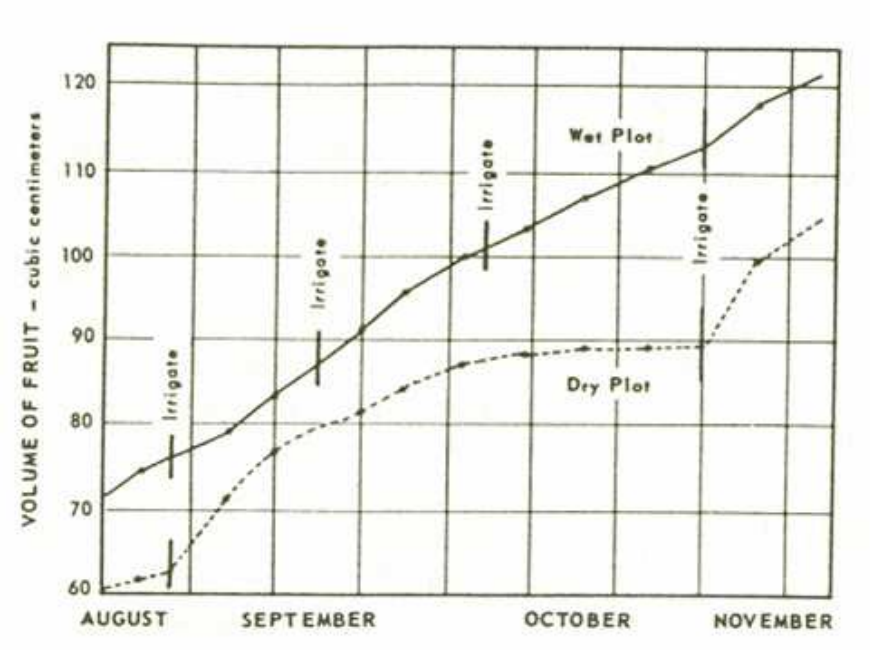


Fig 1.4 *Effect of irrigation on the growth of Valencia oranges (Marsh, 1958).*

Maximum daily trunk shrinkage in fruit trees has been reported to be a more sensitive indicator than the midday stem water potential (Fereres *et al*., 1999; Goldhammer *et al*., 1999a; Cohen *et al*., 2001). But at the same time, the maximum diameter shrinkage is more variable than midday stem water potential. It was observed that for apple trees and plum trees under different irrigation treatments, midday stem water potentials showed significant differences more frequently than the maximum daily trunk shrinkage. This suggests that one should take both the sensitivity and variability of drought stress indicators into consideration in selecting the optimal drought stress indicator (Naor, 2004).

1.2.2.4 Sap flow measurements

For drip irrigated fruit trees, the water requirements arise primarily from the water loss through transpiration (Cohen, 1991; Cornelius *et al*., 1996; Andreu *et al*., 1997). Irrigation scheduling in this case seeks to replace the water lost by transpiration. The technical problem with this approach has been the lack of a suitable method to monitor transpiration continuously under field conditions. The development of reliable techniques for measuring sap flow in recent years (Sakuratani, 1981; Granier, 1987) has seen the development of transpiration-based irrigation systems.

One such system is the Dynamax Flow-4^{TM} system (Cornelius *et al*., 1996) which uses four heat balance sap flow sensors (theory explained in the next section) connected to four

trees selected to represent the average tree size in the orchard. This system automatically replaces the water actually used as transpiration, calculated as the cumulative total sap flow over a given interval plus some minor, but essential corrections for distribution inefficiency, salinity control and surface evaporation. In addition to the ease of automation of sap flow sensors for irrigation scheduling and control, the use of cumulative transpiration for the replacement of the soil water was found to be closely related to the accumulated dry matter in fruit trees (Kramer and Boyer, 1995) and thus yield estimates can also be inferred from such a system.

However, some important questions still need to be answered regarding the use of this method for irrigation scheduling. For example, how many gauges are needed to obtain representative transpiration rates in an orchard which is several hectares in size? Setting up the control points at which irrigation should be turned on or off is also a difficult task. In addition, appreciable technical skill is needed both in the selection of the trees and in the operation of the sap flow gauges to obtain accurate measurements. The Flow-4^{TM} system described above has been used to schedule irrigation for periods as short as hourly intervals (Cornelius *et al*., 1996), thus neglecting tree capacitance effects which cause sap flow to lag behind the transpiration (Steppe and Lemeur, 2004; Dzikiti *et al*., 2007).

Despite the problems and uncertainties associated with the direct use of sap flow gauges in scheduling irrigation of fruit trees, it still remains one of the best options for automated irrigation scheduling and control since they can be readily connected to automatic data acquisition systems (Li *et al*., 2002; Cifre *et al*., 2005). This is particularly important in high frequency irrigation systems such as those used in drip irrigated plantations in the semi-arid and arid tropics. For example, in citrus orchards in Zimbabwe, irrigation is applied daily either continuously for several hours by some growers or in pulses whose duration range from a few minutes to an hour by other growers. The pulses are applied several times during the course of the day. Uncertainties in the exact amounts of water needed by the trees and thus the duration of each irrigation are large and growers rely to a large extent on visual observations of the tree water status (Dupont, personal communication).

Use of accurate models to simulate the sap flow rates of fruit trees using readily available meteorological data as inputs would greatly reduce the sampling and management problems mentioned above. But a thorough knowledge of the dynamics of sap flow in the trees is needed to develop these models. In addition, data are needed for the calibration and validation of the models. Literature describing the daily dynamics of sap flow in detail for citrus trees is sparse (Rana *et al*., 2005; Dzikiti *et al*., 2006). In addition, few attempts have been

made to identify appropriate plant-based stress indicators for citrus trees especially under the semi-arid tropical conditions. Consequently an experimental set-up is described in this chapter to investigate in detail the sap flow dynamics of a typical citrus cultivar, the Navel orange tree, commonly grown in Southern Africa. Responses of the citrus trees to deficit irrigation strategies are also investigated in this set-up.

1.3 Materials and methods

1.3.1 Experimental set-up

This study was conducted during two spring seasons (August – October) in 2003 and 2004, respectively, in Zimbabwe. The experimental set-up was mounted on the open – air laboratory on the third floor of the Department of Physics building, University of Zimbabwe (17.79° S, 31.04° E, elevation 1450 m a.s.l). The site comprised a wide open space with dimensions of approximately 25 x 10 m (length x width) bounded to the north, east and west by a continuous wall approximately one and half meters tall. To the south of the site was another wall, which formed part of a storeroom measuring up to two and half meters tall. Several layers of closely packed, dark coloured granite stones about 4 cm mean size uniformly covered the floor to a depth of approximately 10 to 15 cm.

Six, 2-year-old Navel orange trees [*Citrus sinensis* (L.) Osbeck] of the Baianinha selection budded onto a rough lemon [*Citrus jambhiri* (Lush.)] rootstock were used for the experiment. The rough lemon rootstock on the one hand is commonly used in many citrus plantations in the arid and semi–arid regions because of its deep root system which enhances the chances of survival of the trees during periods of water shortage. The oranges from the Navel cultivar on the other hand mature early under the warm climatic conditions in northern Zimbabwe and thus reach the export markets in Europe and the far–east Asia earlier than oranges from regional competitors (Dupont, personal communication).

Typical distributions of the citrus cultivars (scions) used at one of the major citrus producing farms in Zimbabwe, the Mazowe Citrus Estate and the corresponding rootstocks are shown in Fig 1.5. Attributes of each rootstock will be described in detail in Chapter 3. The rough lemon rootstock constitutes approximately 27 % of all the rootstocks used at Mazowe Citrus Estate, while the Navel scion comprises over 40 % of the varieties planted. Thus, this Navel on rough lemon scion–rootstock combination is of economic value to Zimbabwe.

The trees which were 90–100 cm tall, were planted in six asbestos pots measuring 70 cm x 50 cm (diameter x depth). Five of the pots were partitioned into two equal sections vertically through the middle using a thick polyethylene plastic material. This plastic was

sealed against the walls of the pots using window putty to form an impermeable barrier for water between the different compartments of the pots. This set-up allowed the creation of independent soil water regimes in a typical split root system to investigate the responses of the young trees to the partial root zone drying method. In the five pots, the trees were planted with roughly equal root volumes either side of the plastic barrier. Figure 1.6 shows a typical plant pot with a young tree. The pot which was not partitioned was used as the control.

The top soil used in the pots belongs to the Banket 5E.2 series (Local classification), being dark red in colour and with a high clay percentage. Some salient properties of the soil derived by Hussein (1982) are shown in Table 1.1. The growing medium was obtained from the trial site of the Mazowe Citrus Estate (MCE), Zimbabwe. After planting, the soil water content inside the pots was kept close to field capacity (45 % v/v). Standard fertilizer application programmes for citrus were followed to maintain the young trees. Approximately 5 g of ammonium nitrate granules (NH_4NO_3) with 28 % nitrogen were given to each tree per week. In addition, approximately 5 ml of micronutrients (namely zinc, copper, boron and manganese) were administered to each tree once every six weeks by foliar application.

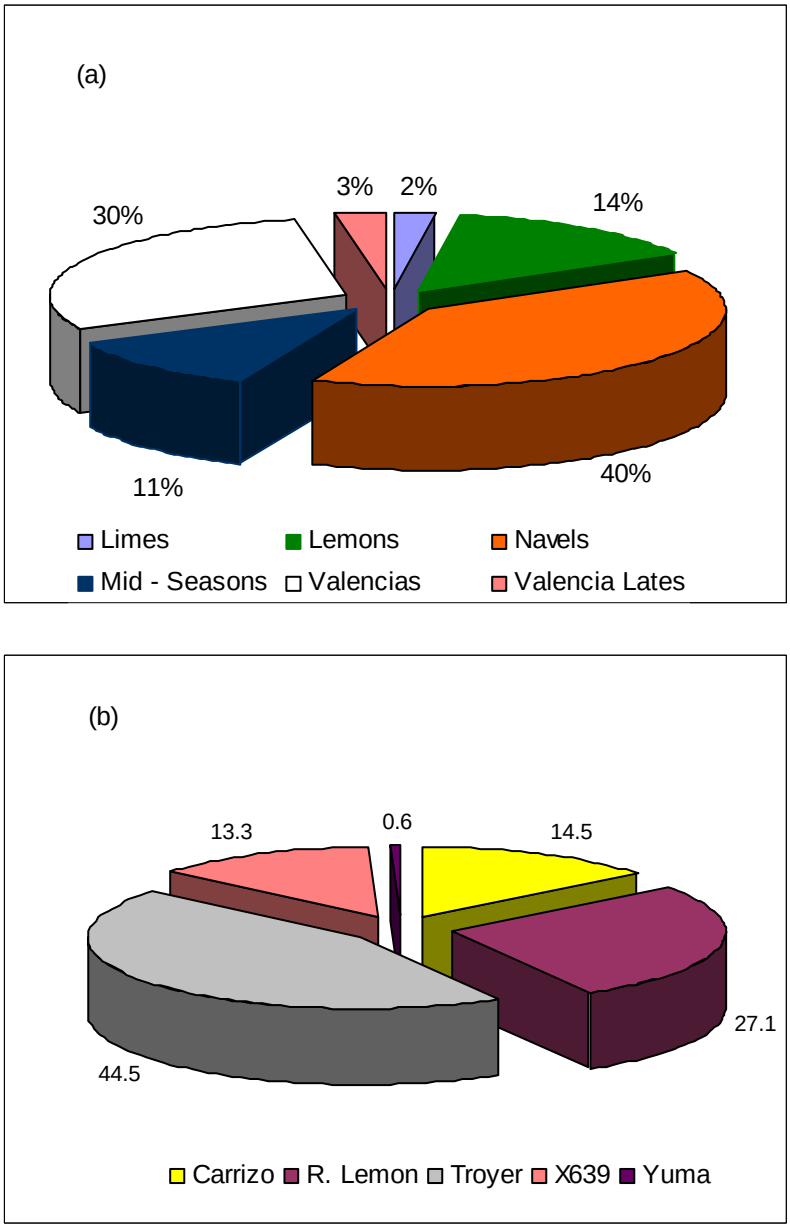


Fig 1.5 (a) *Distribution of the citrus trees by cultivar (b) the rootstocks in common use at Mazowe Citrus Estate, Zimbabwe.*

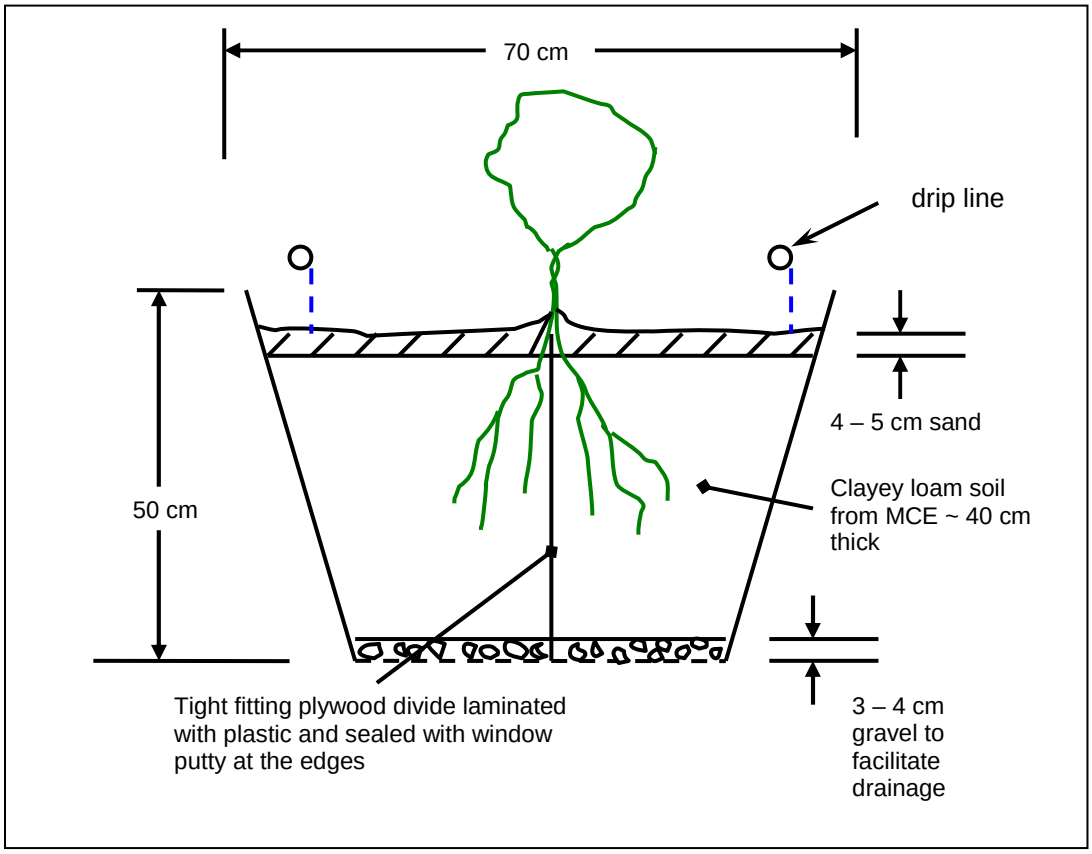


Fig 1.6 *Split-root set-up to create independent wet and dry soil moisture regimes in the root zone of the young orange trees. This set-up was established on five trees to investigate the effects of the partial rootzone drying irrigation strategy.*

To exclude rain from the treatments during the rainy season (late October to early April the following year), the young trees were planted under a shelter measuring 7 m x 4 m x 2 m (length x width x height). Transparent polyethylene plastic approximately 200 μm thick was used as the cover material at the top of the shelter. The sides of the shelter were left open to allow free circulation of air. Water was applied using two standard 15 mm drip irrigation lines (Netafim^{TM}) one either side of each tree using button - type drip emitters delivering approximately 2 litres of water per hour. The water was obtained from a nearby tap. An overview of the whole set-up is shown in Fig 1.7.

Table 1.1 *Characteristics of the soil at Mazowe Citrus Estate, Zimbabwe trial site (Hussein, 1982). The trial site was used for the field experiments described in other sections of this thesis and the soil medium (mainly top soil) for the laboratory experiments was obtained from this site.*

Soil property	Top soil	Subsoil
Sample depth (mm)	0 - 150	600 – 750
Clay (%)	63	81
pH ($CaCl_2$)	6.6	5.7
Bases exchange (me %)	27.5	15.9
Cation exchange (me %)	33.2	18.1
E/C value (%)	53	22
S/C value (%)	44	20
Bulk density (kg m^{-3})	1330	1350
Available water capacity (mm/100mm)	14.9	14.3

1.3.2 Experiments

Experiment 1: *Effects of drought stress applied uniformly to the rootzone on water use by the young orange trees*

The response of the young potted trees to drought stress induced by withholding water for several days was conducted during the hot and dry season (spring) in Zimbabwe. Demand for irrigation water is at its peak during this time of year and thus understanding the water requirements of the trees is crucial. Of the six potted trees, only two were instrumented and their response to drought stress quantified with one of the trees having a non-split root system. In particular, the effects of drought stress on the transpiration rates, liquid phase water transport, stem diameter variations and leaf surface temperature dynamics were investigated. Potential application of these variables as stress indicators is discussed.

In a typical experiment, on 4 October 2003 [Julian day of year (DOY), 274] the trees were watered to field capacity with the mean volumetric soil water content in the pots being about 44 %. Then the trees were subjected to a drying cycle until 8 October 2003 (DOY 279) when the mean volumetric soil water content in the pots was less than 35 %. Significant drought stress had developed in the root zone of the trees in this time. Clear sky conditions prevailed from the start to the end of the drying cycle. The clear skies occurring over a sustained period are typical of spring conditions in Southern Africa. In the absence of growth chambers, as was

the case in this study, these conditions offered an opportunity for comparing events over many days without the influence of clouds.

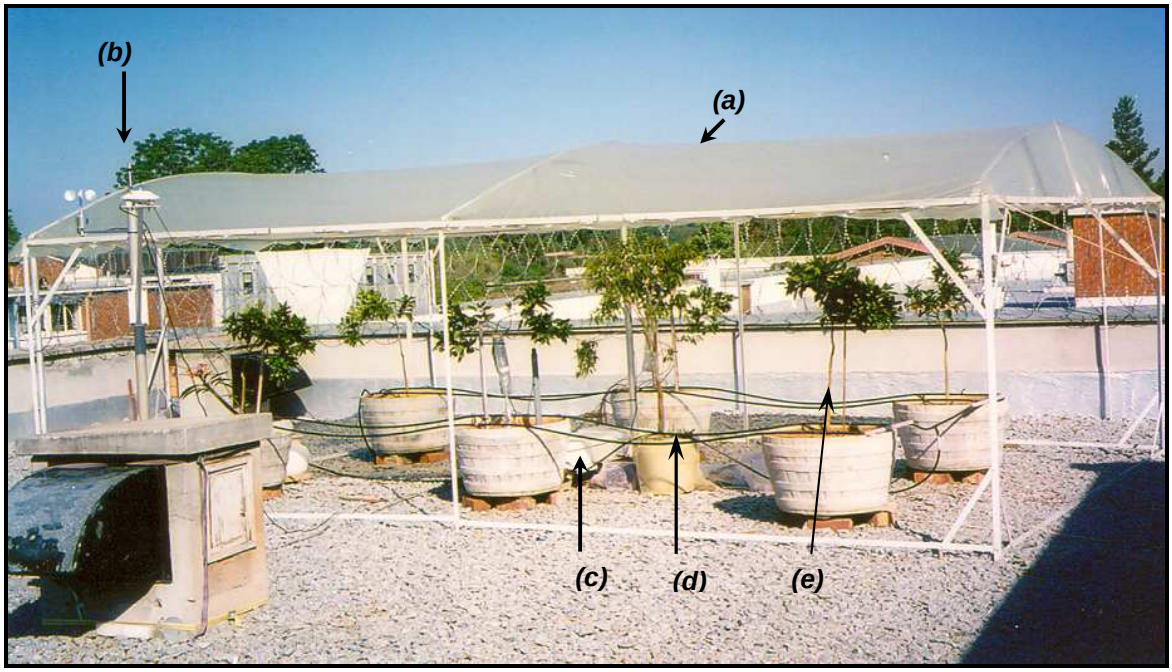


Fig 1.7 *Experimental set-up to study the response of the young Navel orange trees to environmental variables and to drought stress. (a) Covering plastic to keep out rain during the experiments; (b) Sensors on the automatic weather station outside the rain shelter; (c) CR23X Campbell Scientific data loggers for recording signals from all the sensors; (d) Drip irrigation lines for watering the trees, and (e) The young Navel orange trees in asbestos pots.*

Experiment 2*: Response of potted Navel orange trees to partial drought stress in the rootzone*

The response of the young Navel orange trees to partial drought stress alternated fortnightly was investigated during August to September 2004. One of the trees was planted with a split root system as described above while the control tree was planted without splitting the root system. The control tree will be called Tree A, while the split root tree will be called Tree B, henceforth.

Sap flow sensors and dendrometers (for monitoring growth) were installed only on the stems of the model trees on 24 August 2004 (DOY 237) and they remained on the trees for

several days. Both trees received equal volumes of irrigation daily (i.e. 4 litres per tree) applied using two drip irrigation lines. On 1 September 2004 (DOY 244) Tree B received 50 % irrigation (2 litres) applied to half of the rootzone while the other half of the root zone remained dry. Tree A continued to receive full irrigation (4 litres). For Tree B, the watered and the dry sides were switched at 14 day intervals although the sap flow sensors were allowed to remain on the trees only for part of the time. The trees showed signs of stress when subjected to prolonged exposure to the sap flow gauges, for example, for periods exceeding three weeks.

1.3.3 Microclimatic data collection

The microclimate was monitored using two automatic weather stations, one inside and the other outside the shelter. The photon flux density of the photosynthetically active radiation (PAR) incident on the crown of the young trees and outside the rain shelter was measured using two PAR sensors (LI-190SZ, LI-COR Radiation Sensors, Nebraska, USA). The PAR sensor inside the rain shelter was fixed on a horizontal levelling holder in the middle of the structure immediately above the crown of the trees. Net radiation inside the shelter was monitored using a net radiometer (Radiation Energy Balance Systems, Seattle, USA) located between the tree rows in a north-south orientation. This radiation component was only measured inside the shelter. Wind speed was measured using an AL100 cup anemometer (Vector Instruments, Rhyl, UK) at 2 m height above the surface. Measurements of air temperature and humidity in the rain shelter were obtained using an HMP35AC probe (Campbell Scientific Ltd, Shepshed, UK) inserted in a 12-plate Gill radiation shield (Vaisalla, Ltd, Helsinki, Finland) at screen height (~1.5 m above the surface). All the sensors were connected to a CR23X datalogger (Campbell Scientific Ltd, Shepshed, UK) programmed with a scan interval of 5 s and all signals averaged every 5 min.

1.3.4 Characterisation of the radiation microclimate under the rain shelter

Apart from keeping the rain out of the treatments, the presence of the plastic shelter above the young orange trees also modified the radiation microclimate around them. Thus characterisation of the optical properties of the covering material was essential to relate the radiation regime inside the rain shelter to the outside. Of importance to the growth of the orange trees was the transmittance (τ) to the photosynthetically active radiation in the spectral range 400–700 nm. This was quantified using two quantum sensors, one inside and the other outside the rain shelter, as described above. Seven model days with clear skies were selected (9 to 15 September 2003: DOY 252 to 258) to derive the transmission coefficient of the plastic.

If PAR_i is the PAR flux (µmol m^{-2} s^{-1}) measured inside the rain shelter in the i^{th} interval and PAR_o the corresponding PAR flux measured outside the shelter then the transmittance for a given day can be calculated as:

$$\tau = \frac{\sum_i PAR_i}{\sum_i PAR_{o_i}} \qquad (1.1)$$

where the summation was evaluated from sunrise (0600 h) to sunset (1800 h, Local Time = GMT + 2 h) for each day. Table 1.2 shows typical values of the transmission coefficients. If $\bar{\tau}$ is the average transmittance for all the seven days then the standard error in the mean transmittance calculated as:

$$\alpha = \sqrt{\frac{\sum_i (\tau_i - \bar{\tau})^2}{N(N-1)}} \qquad (1.2)$$

is $\pm$ 0.3 % where τ_i is the transmittance for a given day and N the total number of days. The transmittance of the plastic covering material used, taken as the mean value for the seven days was 73.9 $\pm$ 0.3 %.

Table 1.2 *Transmittance (τ) to the photosynthetically active radiation by the polyethylene plastic cover on the rain shelter above the young orange trees expressed as a percentage.*

DOY	Daily PAR total (inside) (mol m^{-2})	Daily PAR total (outside) (mol m^{-2})	τ (%)
252	65.1	47.6	73.2
253	51.9	37.8	72.8
254	67.7	50.9	75.2
255	72.1	53.2	73.8
256	75.4	55.7	73.9
257	76.2	56.5	74.1
258	74.1	54.8	74.1

1.3.5 Physiological data collection

1.3.5.1 Sap flow: Heat balance method

The dynamic flow of water through the young trees monitored simultaneously at root, stem and branch level, was measured using the heat balance sap flow gauges (Dynamax, Houston. TX, USA). Figure 1.8 shows a typical representation of the heat balance sap flow sensor. In this technique, a known constant power, P_{in}, is applied to the plant segment encircled by a small flexible heater, typically a few centimetres in width, wrapped around the organ where sap flow is to be measured (Smith and Allen, 1996). The energy balance equation for that segment is then solved for the amount of heat taken up by the moving sap stream under steady state conditions. This energy is then used to calculate the mass flow of sap. Given the need for steady state conditions, it is essential that the heater is the sole source of energy and thus insulation of the gauge to cut out energy inputs from the environment is crucial.

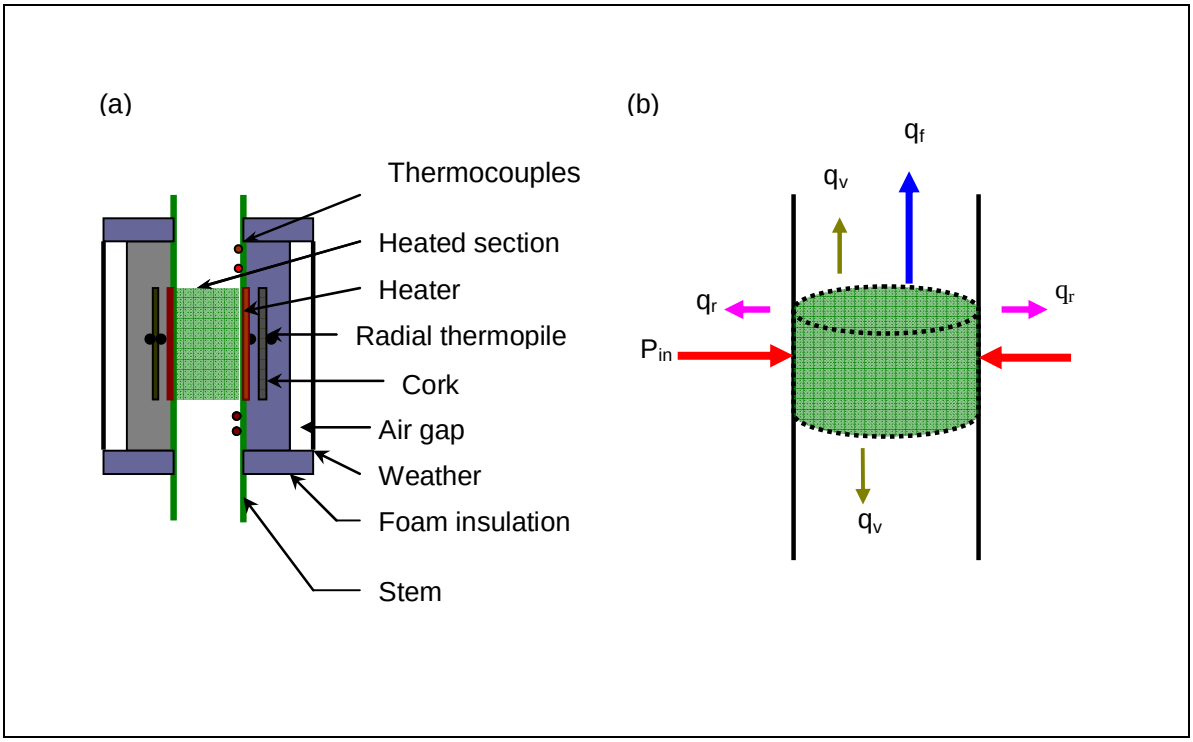


Fig 1.8 *Schematic representation of the heat balance sap flow gauge (Dynamax, Houston, TX, USA). (a) Vertical section through the stem heat balance sap flow gauge. (b) Energy balance components of the heat balance sap flow sensor connected to a plant stem. Refer to text for symbols.*

Suppose the power input to the plant organ (e.g. the stem in Fig 1.8) is P_{in}, then the heat balance of the stem according to Sakuratani (1981) and Baker and van Bavel (1987) can be written as

$$P_{in} = q_v + q_r + q_f \tag{1.3}$$

where q_v is the rate of vertical heat loss by conduction, q_r is radial heat loss by conduction and q_f is heat uptake by the moving sap stream. The value of q_f is obtained by subtracting q_v and q_r from P_{in} which all can be measured. If ΔT_a and ΔT_b are the temperature gradients measured by the axial thermocouples above and below the heater and ΔT_r is the radial temperature gradient, then applying Fourier's law for one dimensional heat flow, q_v is calculated using

$$q_v = A_{st} k_{st} \left(\frac{\Delta T_b - \Delta T_a}{x} \right) \tag{1.4}$$

where A_{st} is the cross sectional area of the heated section, k_{st} is the thermal conductivity and x is the distance between the two thermocouple junctions on each side of the heater. The radial component of the stem heat balance, q_r, is determined from ΔT_r using

$$q_r = K_{sh} \Delta T_r \tag{1.5}$$

where K_{sh} is the effective thermal conductance of the sheath of materials surrounding the heater. The value of K_{sh} is unknown and depends on the thermal conductivity of the insulating sheath and stem diameter. This is determined from the energy balance equation during periods when q_f is zero. This condition is approached at predawn.

Sources of error in sap flow measurements using the heat balance technique include the influence of the changes in the heat storage of the gauged section of the plant which is often neglected and errors in the determination of K_{sh} among others. Most reliable methods for checking the accuracy of sap flow measurements are expensive and time consuming, e.g. use of lysimeters. A cheap and user-friendly technique for establishing the error margins of the heat balance sap flow measurements especially on small stems is described in the next section.

1.3.5.2 Accuracy of the heat balance sap flow sensors

This technique requires the use of a freshly cut stem of the appropriate dimensions for the gauge being used. Since water movement through the transpiration stream is driven by the water potential gradients between the soil and the leaves, it is possible to artificially induce water flow through the excised stem. In the set-up shown in Fig 1.9, water is pushed through the conducting conduits of the tree stem using a high pressure water source (e.g. a water tap) connected to one end of the stem. Water, forced through the excised stem drips-off at the other end and its mass is measured at the intervals at which the sap flow gauge is programmed to produce an output.

By comparison of the mass of water collected in the container (beaker in this case) and the output from the sap flow gauge, it is possible to establish the error margins of the sap flow measurements since the actual mass flow will be known. Since the operation of the heat balance sap flow gauge does not require the exact pathway for water flow to be defined as is the case e.g. with the thermal dissipation probes (Granier, 1987), it is possible to use such a set-up to check the accuracy of sap flow measurements.

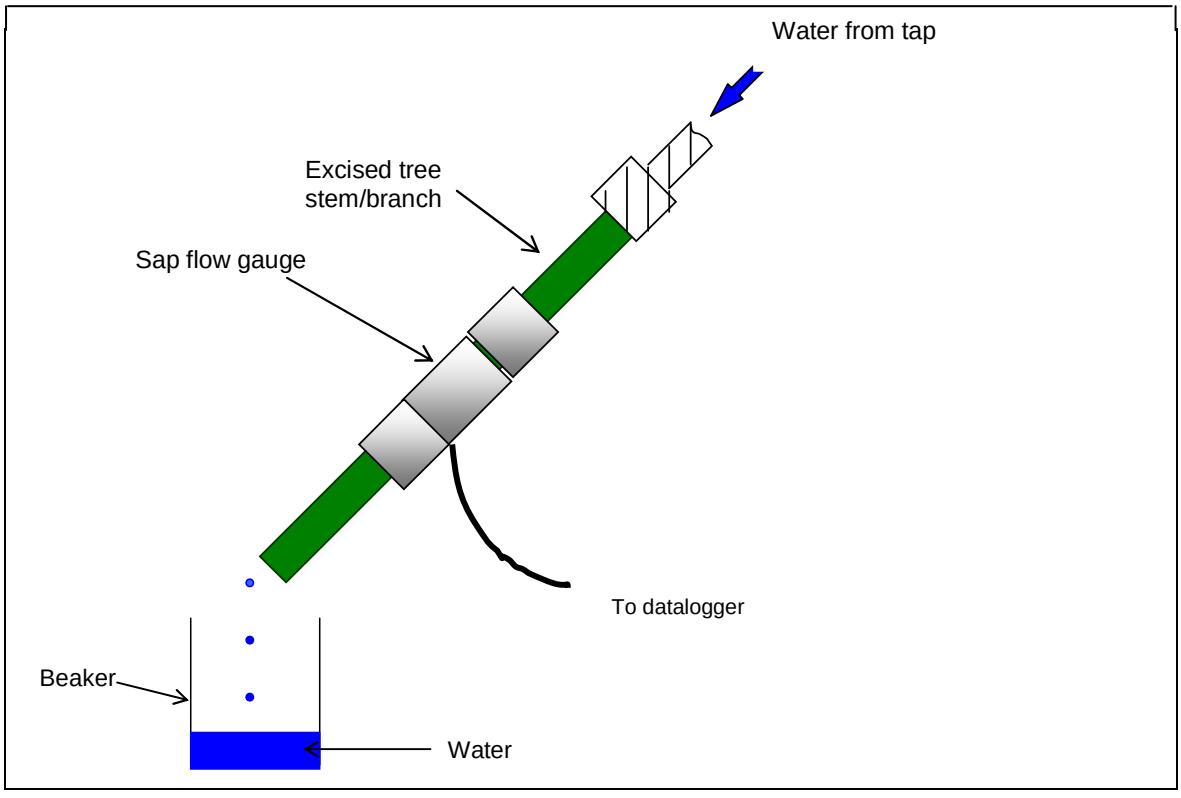


Fig 1.9 *Set-up of the cut-stem experiment to establish the accuracy of sap flow measurements using heat balance sap flow gauges. An excised orange tree stem was used under laboratory conditions.*

1.3.5.3 Sap flow measurements on the young potted trees

The two trees which were instrumented in the experiments described above were healthy and actively growing. The SGA9, SGA5 and SGA2 heat balance sap flow sensors (Dynamax, Houston, TX, USA) installed on the stem, a branch and a root respectively, of the trees were used for monitoring the sap flow dynamics. Operating instructions by Baker and van Bavel (1987) were followed during sensor installation. The diameters at the stem and branch installation points were 9.4 and 5.7 mm for the first tree and 8.6 and 5.3 mm for the second tree, respectively (see Fig 1.10). Branch sap flow was measured as close as possible to the leaves of the trees so that it approximated the transpiration rate (Meinzer *et al*., 2004; Steppe and Lemeur, 2004), assuming that water storage between the gauge and the leaves is negligible. Thin plastic films were wound around the plant section on which the sap flow gauges were connected to ensure that possible stem/branch transpiration did not affect the readings.

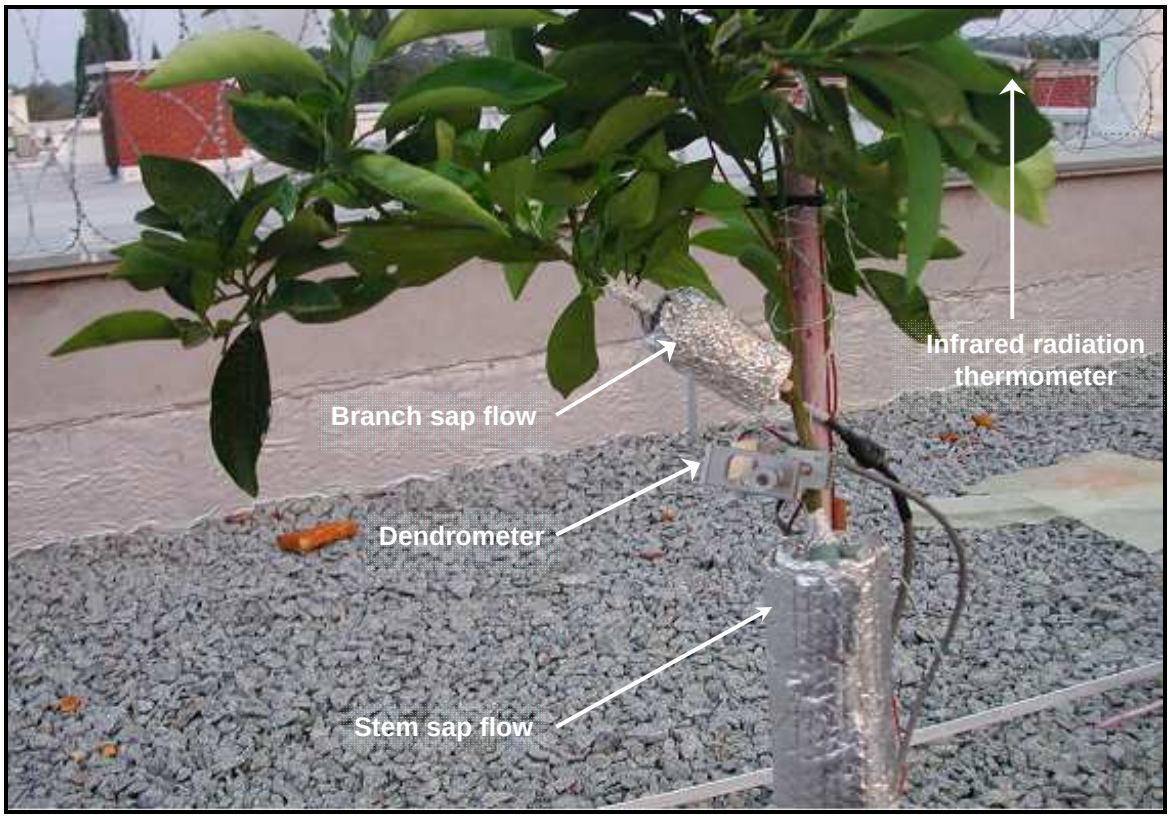


Fig 1.10 *Sensors to monitor the dynamic flow of water through the young Navel orange trees. All the sensors were connected to a CR23X datalogger (Campbell Scientific Ltd, Shepshed, UK) programmed to average all the signals at 5 min intervals.*

By carefully excavating the root of appropriate diameter and cleaning it, it was possible to install a heat balance sap flow sensor on the root for sap flow monitoring. SGA2 sap flow sensors were connected to the roots with a mean diameter of 2.6 mm as shown in Fig 1.11. Care was taken to avoid disturbance of the root-hairs, which are responsible for soil water uptake. Double layers of aluminium foil were wrapped around the root sap flow gauge to minimise extraneous thermal gradients. Then the root was carefully returned to the soil. The sap flow sensors were regularly moved from one tree to another to avoid damage due to prolonged exposure.

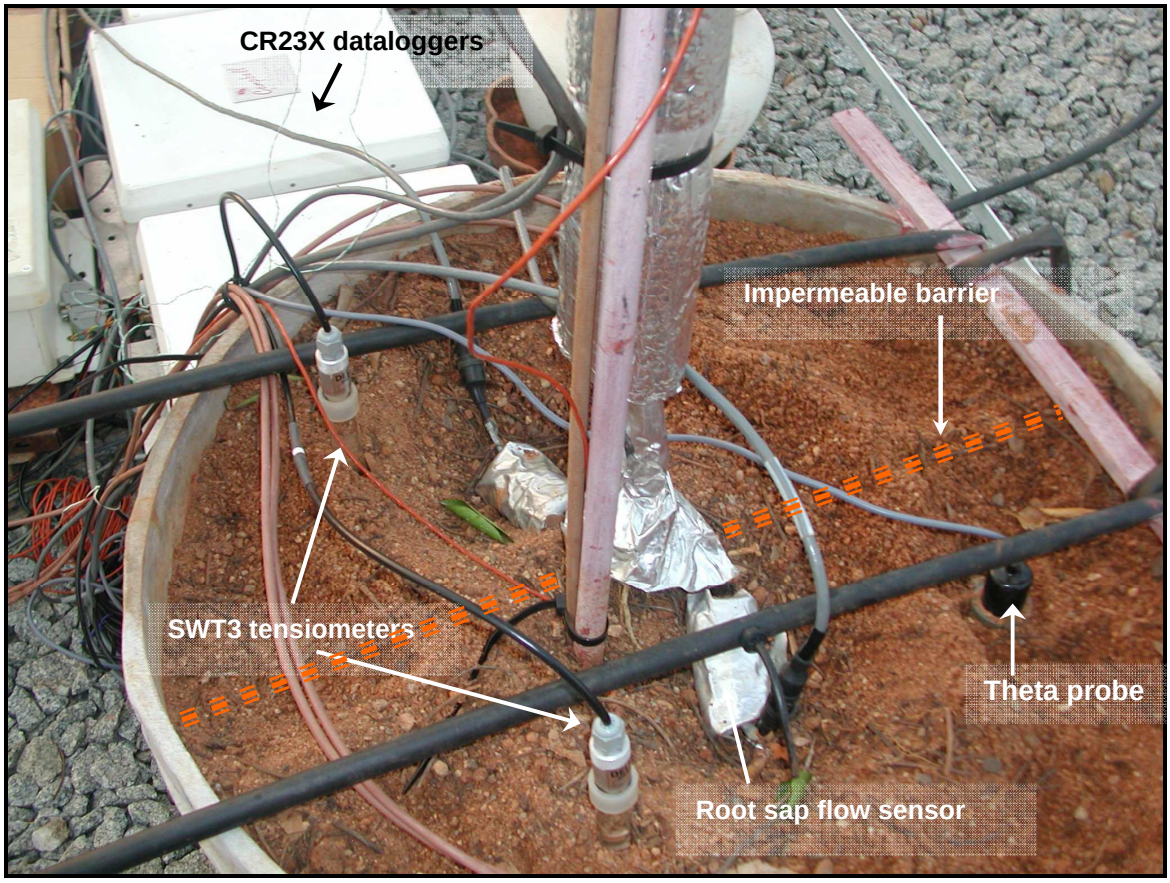


Fig 1.11 *Measurement of root sap flow, volumetric soil water content (theta probe, Delta-T Devices, Cambridge, UK) and soil water potential (SWT3, automated tensiometers, Delta-T Devices, Cambridge, UK) in the root zone of the young Navel orange trees.*

1.3.5.4 Stem diameter and leaf surface temperature measurements

Stem diameter was monitored midway between the branch and stem sap flow sensor (Fig 1.10) using the DEX 70 and DEX 20 dendrometers (Dynamax Houston, TX, USA). Leaf

surface temperature was measured on healthy and fully expanded leaves using K-type infrared radiation thermometers (Ecotechnic, Belgium) placed a few centimetres above the surface of the leaf (Fig 1.10). Large leaves, approximately 7 cm by 5 cm mean length and width were selected to enable the infrared radiation thermometer to be positioned at a sufficiently large distance to reduce its effect on the leaf microclimate and care was taken to ensure that only the leaf surface remained in the field of view of the sensor. The infrared thermometer was calibrated using a black body in a constant temperature water bath in the laboratory before use. All the sensors were connected to two CR23X dataloggers (Campbell Scientific Ltd, Shepshed, UK) with the same logging frequencies as mentioned above.

1.3.5.5 Soil measurements

Four heavy-duty thermistors, (Model 107, Campbell Scientific Ltd, Shepshed, UK) were used to monitor soil temperature with two sensors in each pot at approximately 5 and 20 cm depth, respectively. Two tensiometers (SWT3, Delta - T Devices Ltd, UK) inserted in the middle of the rootzone (25 cm depth) and 15 cm away from the stem were used to monitor the soil water potential. In addition, the volumetric soil water content was also monitored using a theta probe (Delta-T Devices, Ltd, UK) at 25 cm depth in each plant pot (Fig 1.11). A summary of all the sensors used in this and in other sections of this thesis including the accuracy of each instrument is given in Table 1.3.

Table 1.3 *Summary of the sensors used in the experiments in all chapters of this thesis and their accuracy as stated by the manufacturers.*

Measured variable	Symbol	Units	Accuracy	Sensor type	Manufacturer
Photosynthetically active radiation	PAR	µmol m^{-2} s^{-1}	± 10 µmol m^{-2} s^{-1}	LI-190SZ quantum sensor	LI-COR Inc, NE, USA
Net radiation	R_{net}	W m^{-2}	-	Q-7.1* Net radiometer	Radiation Energy Balance Systems, Seattle, USA
Solar radiation	R_s	W m^{-2}	± 10 W m^{-2}	CM11 pyranometer	Kipp and Zonen, The Netherlands
Air temperature	T_a	℃	± 0.1 ℃	HMP 45 AC	Campbell Sci, Inc, UK
Relative humidity	RH	%	± 5 %	HMP 45 AC	Campbell Sci, Inc, UK
Wind speed	-	m s^{-1}	± 0.15 m s^{-1}	A100 L 2 cup anemometer	Vector Instruments, N Wales, UK
Wind direction	-	°	±5°	Wind sentry	RM Young, Inc, UK
Leaf temperature	T_l	℃	± 0.1 ℃	Infrared thermometer (1:1 field of view)	Ecotechnic, Be
Leaf area	-	m^2	± 10 %	Leaf area meter	Delta-T Devices, Ltd, UK
Leaf area index	LAI	m^2 m^{-2}	± 10 %	Sunscan Ceptometer	Delta-T devices, Ltd, UK
Stem diameter fluctuation	Δd	µm	±7 µm	DEX 20, 70 and 100 dendrometers	Dynamax Inc, Houston, Texas, USA
Sap flow	-	cm h^{-1}	± 10 %	Dynamax, TDP 30	Delta-T devices Ltd, Cambridge, UK
		g h^{-1}	± 10 %	Dynagage, SGA2, 5 and 9; SGB 19, 25 and 35	Dynamax, Inc, Houston, USA.
Soil temperature	T_s	℃	± 0.1 ℃	T-Type thermo-couples	Campbell, Sci, Ltd, UK
Soil moisture content	θ	m^3 m^{-3}	0.05 m^3 m^{-3}	Theta probe	Delta, Devices Ltd, Cambridge, UK
Soil water potential	ψ_s	hPa	± 30 hPa	SWT3 tensiometer	Delta-T Devices, UK

1.4 Results and discussion

1.4.1 Establishing the error margins of heat balance sap flow gauges

A typical comparison of the output from the heat balance sap flow gauge and the actual mass flow of water is shown in Fig 1.12. The rate of water flow through the excised stem was varied by changing the pressure of water coming out of an ordinary tap. The heat balance sap flow gauge installed on the excised stem of an orange tree estimated the rate of water flow to within 10 % of the true values. This figure is within the error limits provided by the manufacturers but established using more sophisticated equipment, e.g. lysimeters (Dynamax heat balance sap flow manual). No significant corrections for the changes in the heat storage by the stems were needed.

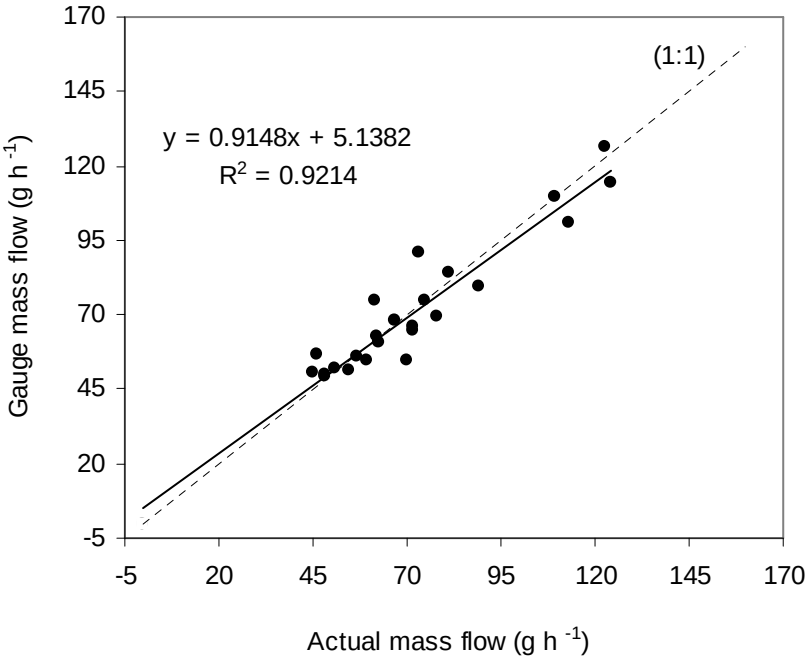


Fig 1.12 *Comparison of the water flow as recorded by a heat balance sap flow sensor installed on an excised citrus stem with the actual mass of water that passes through the stem.*

1.4.2 Sap flow dynamics of well-watered young orange trees

The typical diurnal course of the microclimatic variables under the rain shelter over a period of three days from 4 to 6 October 2003 (DOY 274 - 276) is shown in Fig 1.13 below. The trees were well-watered on 5 October (DOY: 275) as described in experiment 1 above. Clear skies coupled with dry atmospheric conditions with the relative humidity ranging from approximately 50 % at 0500 h (Local time: GMT + 2 h) down to approximately 15 % after midday at 1400 h characterised the experimental period. The small fluctuations in the PAR around midday were

due to the effect of the obstruction of radiation due to structural components of the rain shelter on the plastic covering material. Wind speed was generally low with a daily average of approximately 1.2 m s^{-1}.

Despite the clear sky conditions (Fig 1.13a), sap flow followed cyclic oscillations as shown in Fig 1.13e. The periodicity of the oscillations varied from approximately 55 $\pm$ 5 min in the morning and late afternoon to approximately 35 $\pm$ 5 min around midday. In addition, no sudden changes in the atmospheric evaporative demand, e.g. due to fluctuations in the vapour pressure deficit of the air was observed. Apart from the influence of the climatic factors, rapid closure of the stomatal aperture has been attributed to sudden changes in root surface temperature (Ali *et al*., 1996), but no such change in root temperature occurred as shown in Fig 1.13c suggesting that some other mechanisms were responsible for the oscillatory response to the environmental variables. The oscillations were observed all the time under natural climatic conditions. Clearer illustrations of the microclimatic conditions and the sap flow dynamics at roots, stem and branch level of the young orange trees are shown in Fig 1.14 and 1.15, respectively, for parts of a single day.

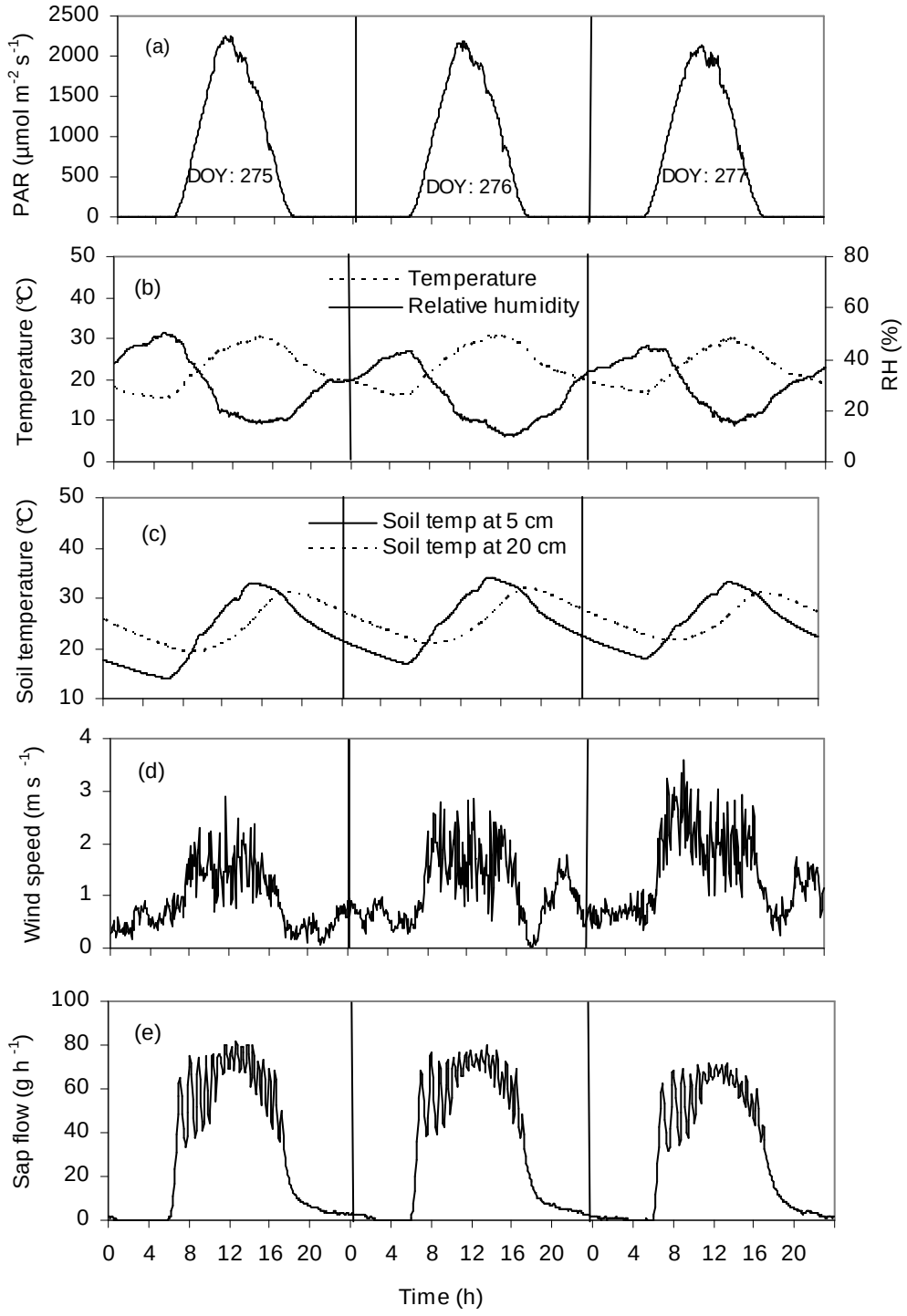


Fig 1.13 *The course of (a) the photosynthetically active radiation (PAR), (b) air temperature and relative humidity (RH), (c) soil temperature in the pots at 5 and 20 cm depth, (d) wind speed and (e) stem sap flow for a typical young potted orange tree over a period of three days (DOY 275 – 277).*

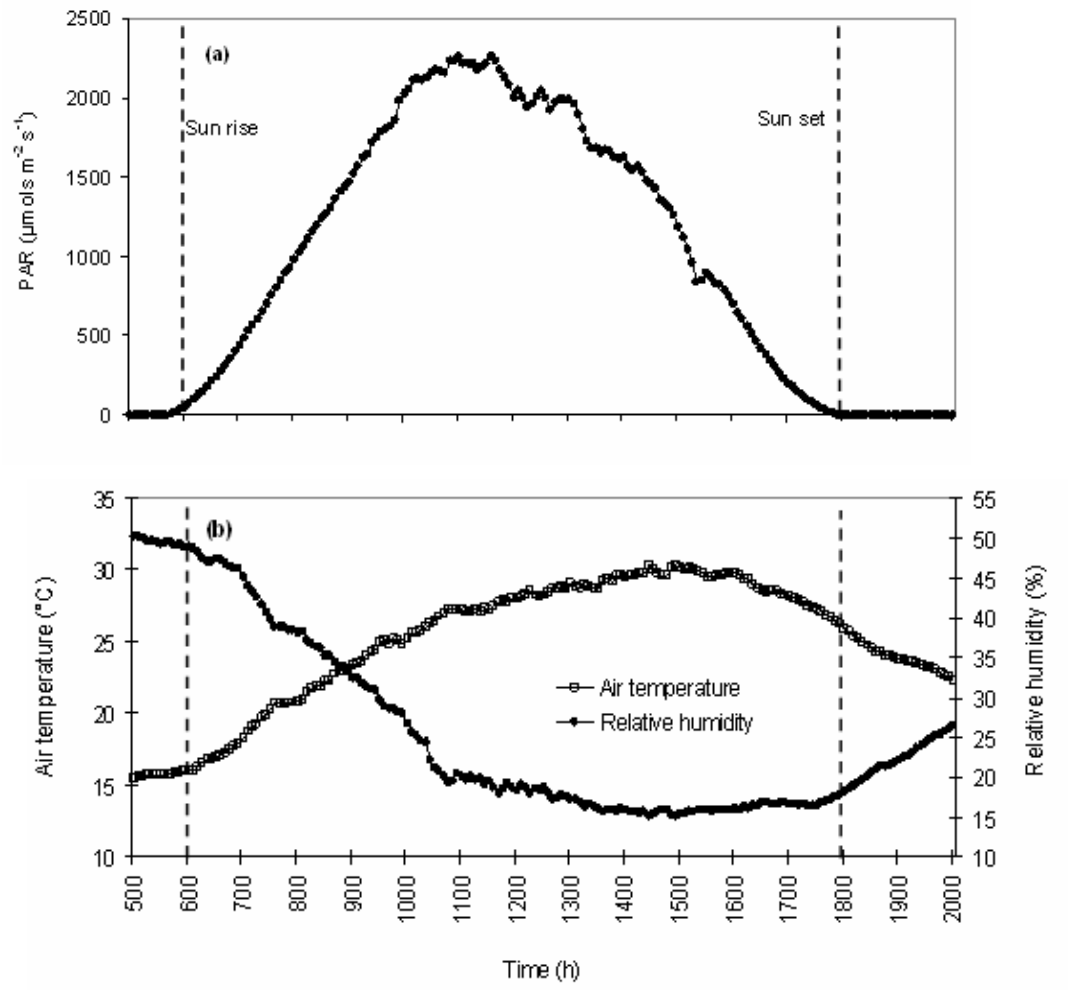


Fig 1.14 *The course of the driving microclimatic variables for sap flow on DOY 275 when the trees were not under drought stress. (a) Flux of the photosynthetically active radiation (PAR) incident on the crown of the young trees; (b) air temperature (open squares) and relative humidity (closed circles) measured under the rain shelter at screen height (~1.5 m).*

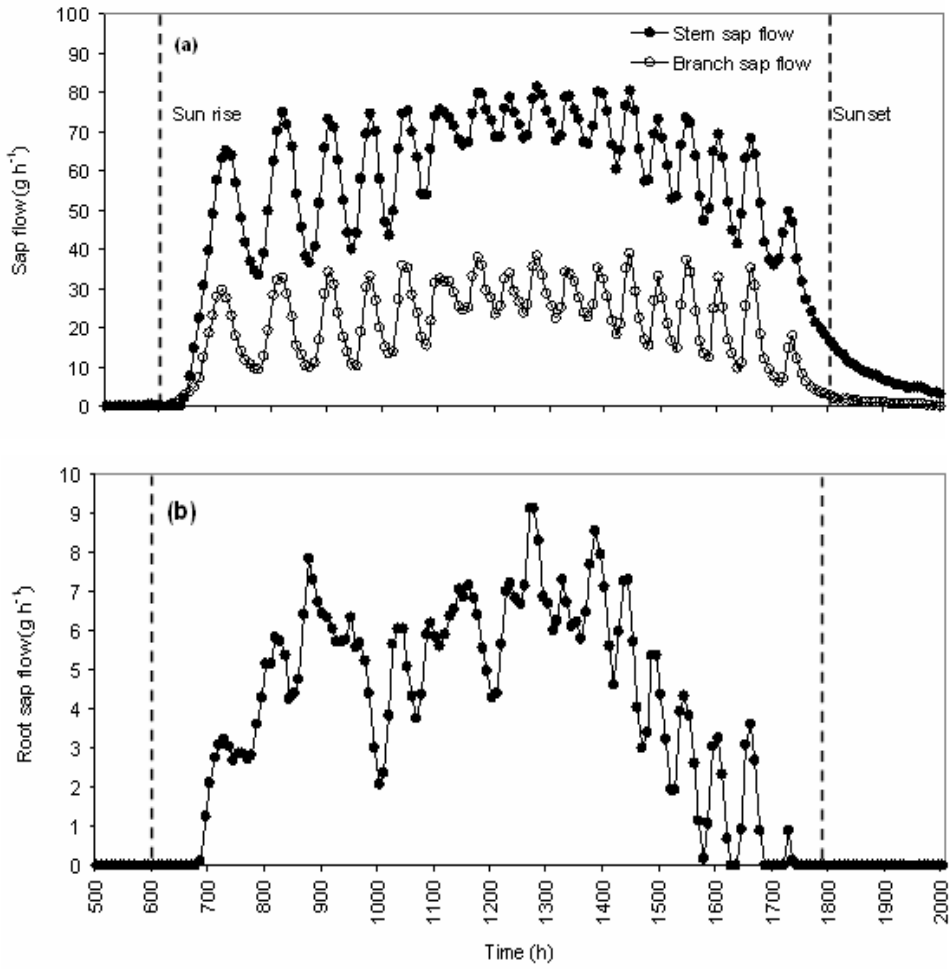


Fig 1.15 *(a) The typical course of sap flow measured at stem and branch level by a well watered Navel orange tree on a clear day, DOY 275. Open circles represent branch sap flow, while stem sap flow is shown by closed circles. (b) The corresponding course of root water uptake inferred from sap flow measurements on a clear day. Note the difference in the vertical scale of the two graphs.*

Although this phenomenon of stomatal oscillations was first discovered many decades ago (Barrs, 1971; Farquhar and Cowan, 1974; McBurney and Costigan, 1984), and in citrus (Lang *et al*., 1969; Davis and Albrigo, 1994; Spiegel-Roy and Goldschmidt, 1996) the exact cause of this cycling still remains debatable. This subject will be discussed in detail in Chapter 2 of this thesis. Changes in the boundary layer resistance due to the effect of wind gusts did not fully explain the sensitive stomatal behaviour. For example, Fig 1.16 shows a regression of the sap flow against the wind speed during the day-time (sunrise to sunset) for a period of

three days. The very weak coefficient of determination suggests that the oscillations in sap flow cannot be fully explained from the effects of the variations in the wind speed alone.

More importantly, however, the wider eco-physiological implications of this cyclic opening and closure of the stomata on plant functioning and productivity are not yet fully explained (Upadhyaya *et al*., 1988). Nevertheless, the effects on the water relations and potential plant-based stress indicators for the scheduling of irrigation of orange trees will be explored here. A direct consequence of the partial closure of the stomata during parts of the day is that total transpirational loss by the trees is significantly reduced. Assuming negligible water storage between different plant organs (e.g. the stem, branches and leaves), the stem sap flow rate could be equated to the transpiration rate (Fredrick, 1997; Steppe and Lemeur, 2004). It can be concluded therefore that for the greater part of the day, the transpiration rate of Navel orange trees oscillated about a mean value reached as early as, say, 0800 to 0900 h (Local Time) implying that the Navel orange trees are generally low transpiring species. This is clearly illustrated in Fig 1.17 where the daily evolution of sap flow expressed per millimetre depth of the soil in the pots is compared with the daily course of the evapotranspiration calculated according to the equation by Allen *et al*. (1998). The cumulative total sap flow over the whole day was approximately one third of the potential evapotranspiration under the rain shelter.

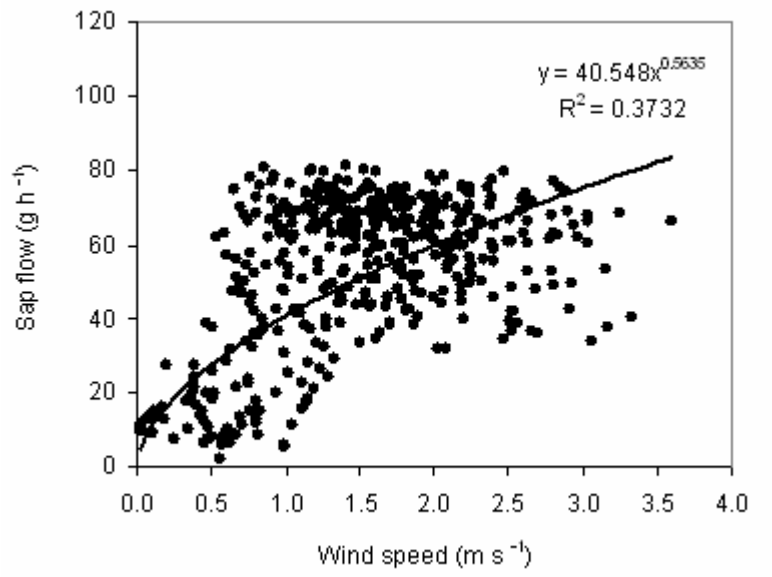


Fig 1.16 *Effect of the changes in wind speed on the daytime sap flow for a period of three days from 4 to 6 October 2003 (DOY: 274-276).*

In addition, the sap flow measurements at various levels within the trees revealed that the oscillations occurred throughout the transpiration stream. This tendency to oscillate was not a localised phenomenon, occurring only in the leaves as has been widely reported (McBurney and Costigan, 1984; Naidoo and von Willert, 1994; Kaiser and Kappen, 2001). The amplitude of the oscillations had larger values in the morning and late afternoon than in the middle of the day. It is not clear whether this variation in the periodicity and amplitude of the oscillations was induced by the shelter under which the trees were growing or by the plant internal functioning, especially the rootstock attributes (see Chapter 3). The trees tended to receive more solar radiation in the morning and late afternoon when the sun penetrated through the open sides of the shelter. What was plainly evident, however, is the fact that the oscillations themselves were generated from the plant since the key driving environmental factors shown in Fig 1.14 and Fig 1.16 were not well correlated with the observed oscillations, at least for short intervals.

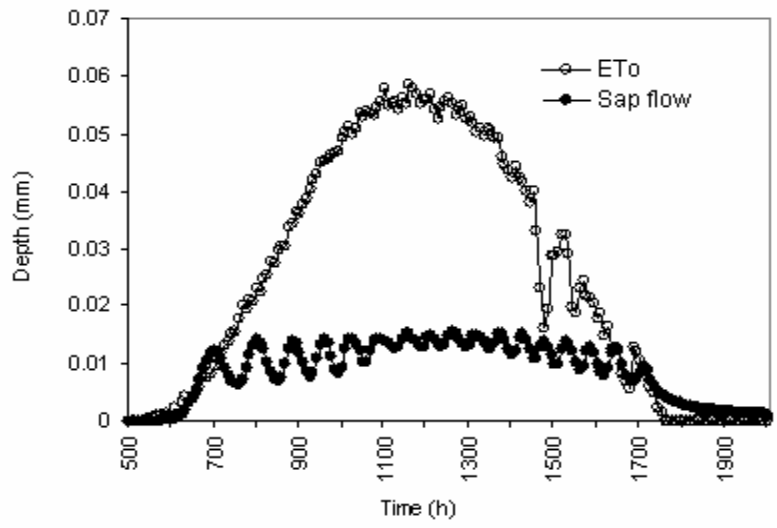


Fig 1.17 *Comparison of the daily course of stem sap flow of a well-watered young potted Navel orange tree with the potential evapotranspiration (ET_o) under the rain shelter. Water extraction by the trees was assumed to be occurring from an area equal to the surface area of the plant pot.*

Increasing time lags in the onset of sap flow of approximately 10, 15 and 50 min referenced to sunrise in Fig 1.15 were evident on the branch, stem and roots, respectively. Such time delays in the commencement of water uptake and its flow in different plant organs were also observed in young trees of different species, e.g. ornamental plants (Fredick, 1997), oak and beech trees (Steppe and Lemeur, 2004). Despite the cyclical oscillations, the daily total transpiration, calculated as the time integral of stem sap flow over the whole day was related with the daily total radiation intercepted by the crown of the trees as shown in Fig 1.18, but in a curvilinear trend.

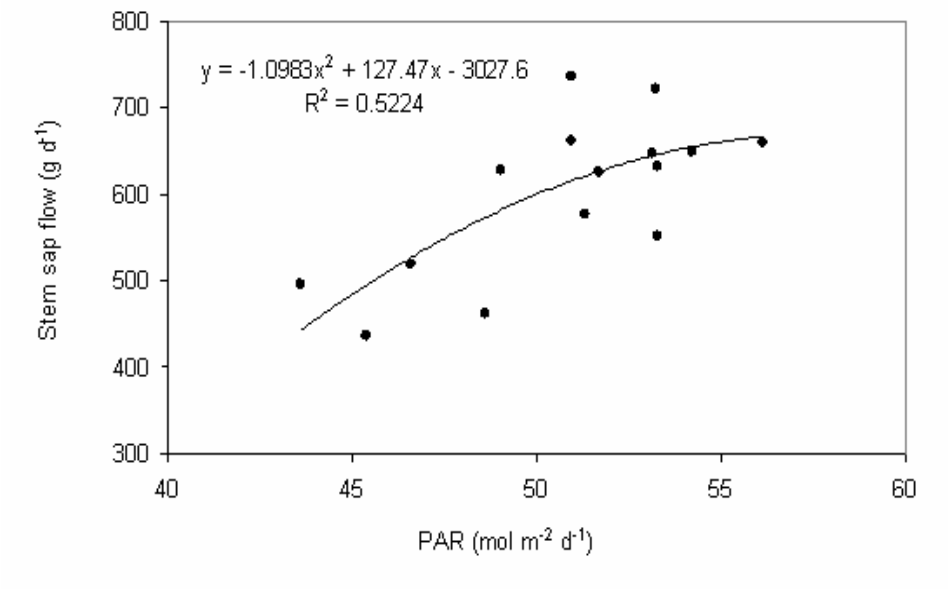


Fig 1.18 *Effect of the daily total intercepted photosynthetically active radiation (PAR) on the daily total sap flow of the Navel orange tree over a period of two weeks. A curvilinear, rather than a linear, relationship exists showing a strong stomatal control on transpiration at high irradiances.*

The curvilinear trend however, most likely reflected the occurrence of a strong stomatal control of transpiration since the daily total transpiration increased at a slower rate at higher daily irradiances. The influence of the leaf to air vapour pressure deficit on sap flow showed a hysteresis effect as shown in Fig 1.19. The data for this day was split into two periods, morning (0600 – 1330) and afternoon (1335 – 1800 local time). The morning period was generally associated with increasing sap flow rates, while the afternoon was characterised by decreasing sap flow rates. It is plainly evident that for this clear day (DOY 275), for the same VPD, the sap flow rates were different in the morning and in the afternoon. Although it is difficult to fully explain the cause of the hysteresis effect, one possibility is the development of

embolisms in the xylem vessels, but this cannot be fully confirmed from these results. When air bubbles develop in the xylem vessels, they impair water uptake thus temporarily making the vessels dysfunctional (Vogt, 2001).

The relationship between the sap flow measured at stem and branch level above can be used to explain other physiological responses by the Navel orange trees, e.g. the diurnal evolution of the stem diameter based on tree level water balance. However, the up-scaling strategy for branch sap flow to whole tree level is discussed first.

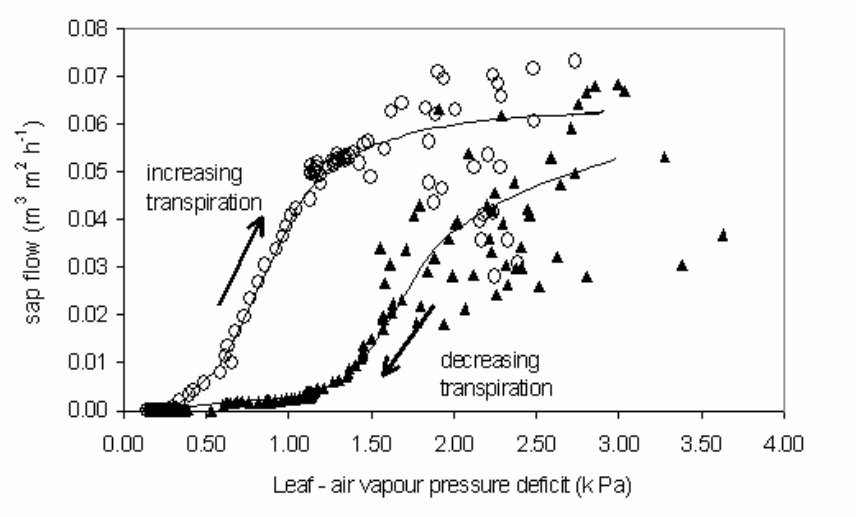


Fig. 1.19 *Effect of the leaf to air vapour pressure deficit on the course of sap flow expressed per unit leaf area. Different sap flow rates are obtained for the same vapour pressure deficit. Open circles represent stem sap flow for the first half of the day (0800 – 1400 h) while the closed triangles represent sap flow for the second half of the day (1405 – 1800 h).*

1.4.3 Scaling up branch to whole tree level sap flow

The most widely used scaling factor for branch sap flow is the leaf area (Fredrick, 1997; Samson, 2001). For instance, if 'E_L' (in g h^{-1})' is the branch sap flow measured at time i, ''a'' and A are the branch and whole tree leaf areas in square meters, then by normalisation of the branch sap flow with leaf area, stem sap flow ''F (in g h^{-1})'' can be estimated from

$$F = \frac{E_L}{a} A \qquad (1.6)$$

This equation assumes that the normalised branch sap flow is uniform throughout the tree which may not be the case for big trees where there is mutual shading of the leaves.

In the absence of reliable leaf area measurements as was the case in this study, the up scaling approach by Meinzer *et al* (2004) was adopted. It is generally accepted that over long periods e.g. a day or more, total stem sap flow closely approximates whole tree transpiration, E (Samson, 2001; Jones, 2004). According to this approach, the scaling factor (SF) for branch sap flow to tree level is given by

$$SF = \frac{\sum_i F}{\sum_i E_L} \qquad (1.7)$$

where the summations are evaluated over the whole day. Since sap flow was measured on only one branch and on the other hand the daily total transpiration was known from the daily total stem sap flow, a further assumption was made in deriving the above scaling factor that all the sap flow which occurred in the branches was via the gauged branch. Hence, a scaling factor with the magnitude shown in equation 1.7 is feasible.

1.4.4 Stem diameter dynamics

The diurnal evolution of trunk diameter can be used as an indicator for plant water status as described in section 1.2.2.3. Stem diameter changes are known to be a function of two main processes namely, a reversible component due to variations in the water content of the plant cells and an irreversible component due to growth as illustrated in Fig 1.20 for a young citrus stem.

This shrinkage in trunk diameter at sunrise and expansion late in the day has been observed on other fruit trees e.g. apple (Lakso *et al*., 1995); pear (Naor *et al*., 2000) and plum (Intrigliolo and Castel, 2004). A more detailed trend in the diurnal evolution of the stem diameter for the young orange trees is shown in Fig 1.21 for a typical clear day, DOY 275.

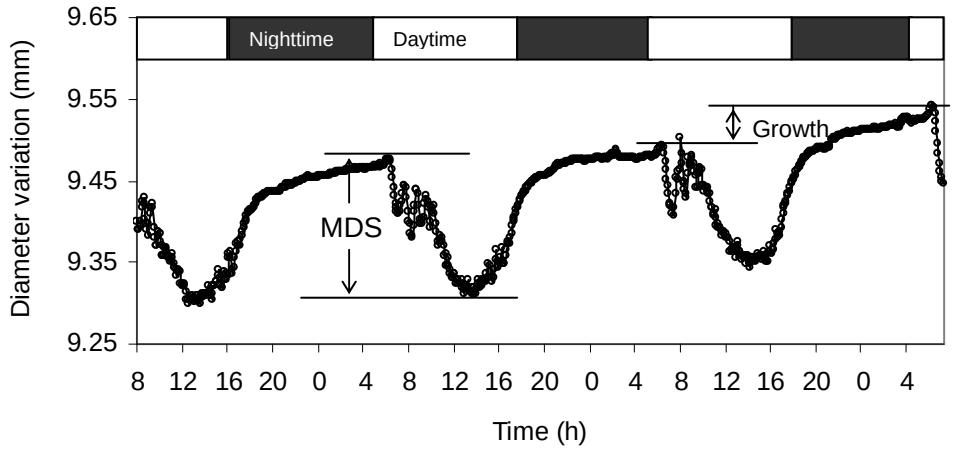


Fig 1.20 *The typical diurnal evolution of the stem diameter of a young potted Navel orange tree over a period of three days.*

The shrinkage in the stem diameter immediately after sunrise occurred due to the utilisation of the internally stored water when whole-tree transpiration, E exceeded water uptake (stem sap flow, F). This situation arose due to the existence of a hydraulic resistance and capacitance in the vascular system of the trees leading to a time lag between water loss and uptake. Cyclic oscillations with the same period as the sap flow were observed in the stem diameter (Fig 1.21c) during the whole day. A larger stem size was reached before sunrise the following day (Fig 1.20). The difference in the maximum stem size between successive days gives the stem growth, while the slope of the graph of stem growth against time gives the stem growth rate. The stem growth rate has been used as indicator for irrigation need in fruit trees, e.g. in almond trees (Fereres and Goldhammer, 2003). Another stress indicator is the maximum daily shrinkage (MDS) of the stem and has been tested on plum (Intrigliolo and Castel, 2004), olive trees (Moriana and Fereres, 2002) and ornamental plants (Fredrick, 1997). When water supply becomes limited, the trees rely more on their internal storage reserves. Water is transported not only from the soil but also radially into the xylem vessels from the bark and other tissues surrounding the xylem vessels to avoid a precipitous decline in the plant water status.

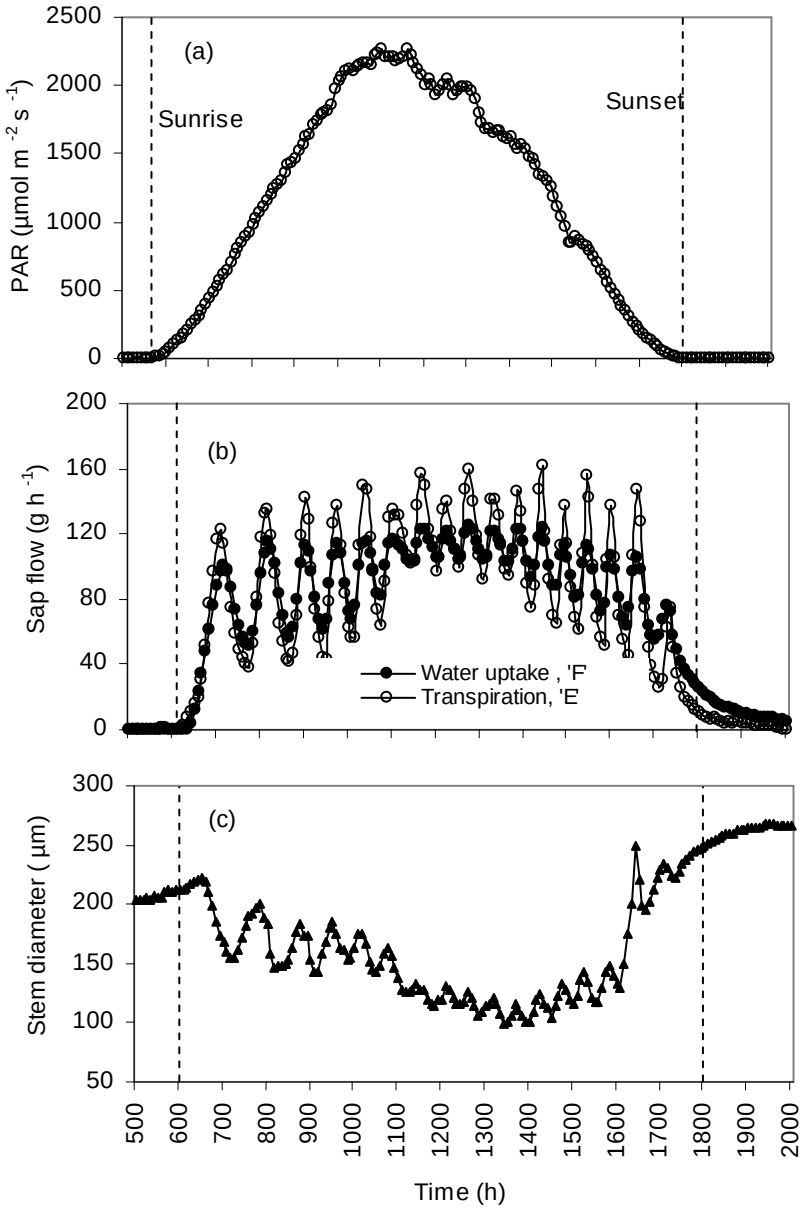


Fig 1.21 *(a) Course of the photosynthetically active radiation (PAR) incident on the crown young trees on DOY 275; (b) Relationship between water uptake, (F) and water loss, (E) by the stem section between the branch and stem sap flow sensors. (c) Course of the stem diameter fluctuation for the well watered tree.*

1.4.5 Dynamics of leaf surface temperature

Leaf surface temperature plays an important role in the productivity of most citrus trees (Spiegel-Roy and Goldschmidt, 1996; Jifon and Syvertsen, 2003). Maximum net CO_2 assimilation of most citrus cultivars saturates at relatively low PAR levels (600 – 700 µmols m^{-2} s^{-1}), which is only 24 – 30 % of full sunlight (2000 – 3000 µmol m^{-2} s^{-1})

during the dry season in Zimbabwe. The excess radiation predisposes the trees to photoinhibition, heat stress and stomatal closure resulting in the reduction of photosynthesis. Optimal photosynthetic rates occur at leaf surface temperatures of approximately 25 ℃ while temperatures in excess of 35 °C can severely reduce the photosynthetic rate for citrus trees due to reduced enzyme activity (Spiegel-Roy and Goldschmidt, 1996). Under field conditions, sustained high temperatures above this threshold can lead to severe abscission of young fruitlets during the fruit set stage due to a reduced supply of assimilates.

The diurnal course of the leaf surface temperature was strongly correlated to the trend in the branch sap flow. As shown in Fig 1.22, leaf surface temperature was always in anti-phase to the transpiration peaks and dips which determine the rate of evaporative cooling of the leaf. When transpiration was on the declining phase, leaf surface temperature rose and vice versa. When compared to air temperature measured at screen height, Fig 1.23 shows that throughout the day leaf surface temperature was higher than the air temperature due to the reduced evaporative cooling owing to the low transpiration rates. Under clear sky conditions, the leaf temperature was observed to rise as much as 9 °C higher than the air temperature. For a large part of the day, the leaf temperature was above the upper limit of optimal photosynthetic activity (35 °C) and the implications of this on plant growth and productivity are uncertain.

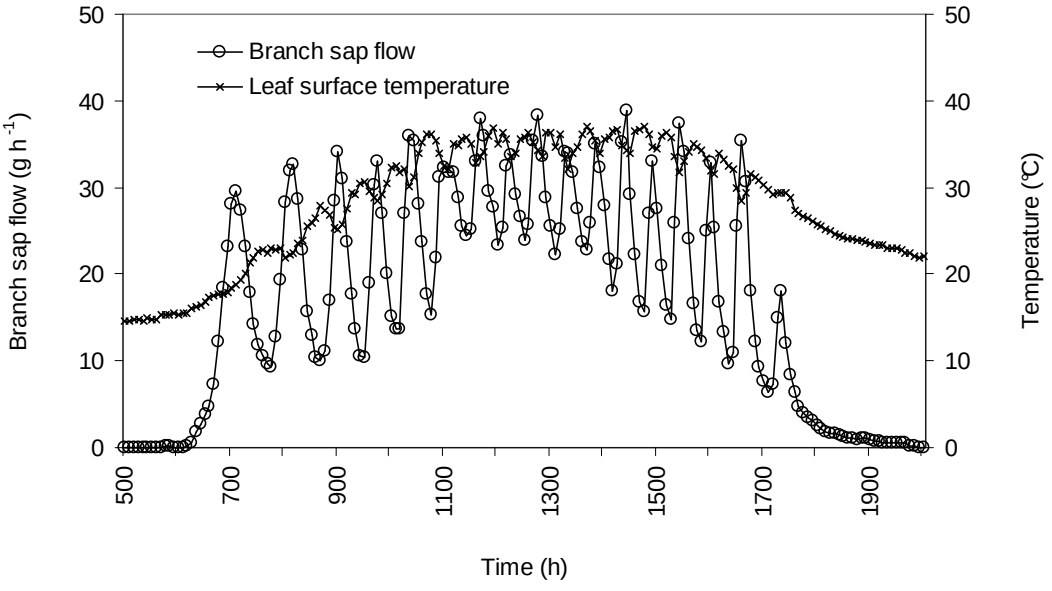


Fig 1.22 *Effect of the diurnal course of sap flow on the leaf surface temperature of the young Navel orange trees on a typical clear day. Leaf surface temperature also oscillated but in anti-phase to transpiration oscillations (Data is for DOY 275).*

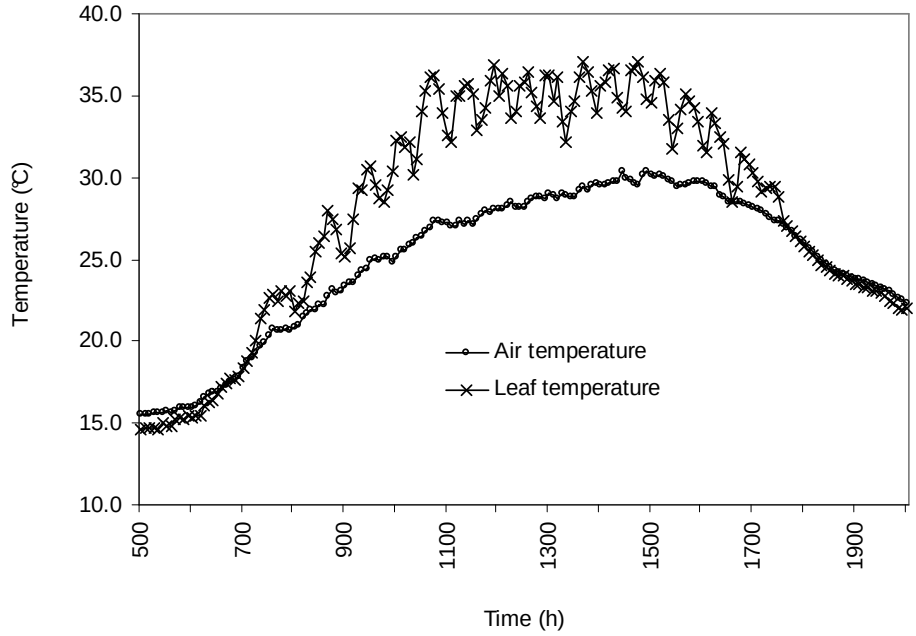


Fig 1.23 *Relationship between the air and leaf surface temperature of the young potted citrus trees. The citrus leaf is much warmer than the air during the day because of the reduced evaporative cooling owing to the low transpiration rates.*

1.4.6 Response to drought stress applied uniformly to the rootzone (Experiment 1)

Experiments to investigate the response of the young Navel orange trees to uniform soil drying were conducted as described in *Experiment 1*. The variation of the microclimatic conditions and the soil water potential during a typical drying cycle from 4 to 8 October 2003 (day of year, DOY 274 to 279) is shown in Fig 1.24. Plant response was analysed in detail on two model days with different soil moisture regimes. The selected days are DOY 275 when the trees were well-watered and DOY 278, when they were under drought stress. The key driving microclimatic variables on these two model days were comparable as summarised in Table 1.4. Thus plant responses could be compared with drought stress being the major cause of any difference observed.

Table 1.4 *Comparison of the microclimatic conditions on two model days (DOY 275 and 278) during the drying cycle. All the climatic variables were measured with the automatic weather station inside the shelter. The microclimatic conditions on these two days were not statistically different for all the variables ($p<0.05$).*

Climatic variable	DOY 275	DOY 278
PAR (mol m^{-2} d^{-1})	53.2	53.3
Mean air temperature (℃)	25.9	24.3
Maximum air temperature (℃)	30.4	28.9
Mean daytime VPD (kPa)	2.68	2.40

Figure 1.24 shows that soil drying caused a reduction in the daily total water use. The area under the sap flow graphs gradually decreased indicating that the daily total transpiration was also declining from DOY 275 when the trees were well watered until DOY 278 when drought stress had developed. On re-watering on DOY 279 water use immediately increased signalling that soil moisture content was the main variable influencing the trend in transpiration.

These measurements reveal that despite the already high resistance to water transport as a result of the cyclic opening and closure of the stomata round the day, a further reduction in daily transpiration can still be detected using the heat balance sap flow gauges on the orange trees. Thus these devices can potentially be used for the automated irrigation scheduling and control in young citrus plantations using models/algorithms that integrate the sap flow rates to total water use at selected intervals. Transpiration reduction sort, for example, by the deficit irrigation techniques can also be achieved. Drastic stomatal closure inevitably has adverse implications on CO_2 uptake thus affecting tree growth and productivity. In the case of the deficit irrigation methods, soil suctions of approximately 20 hPa can be maintained as the trees will clearly not be under severe drought stress (Fig 1.24). The implications of the drought stress on the functioning of the young orange trees are explored further in sections that follow.

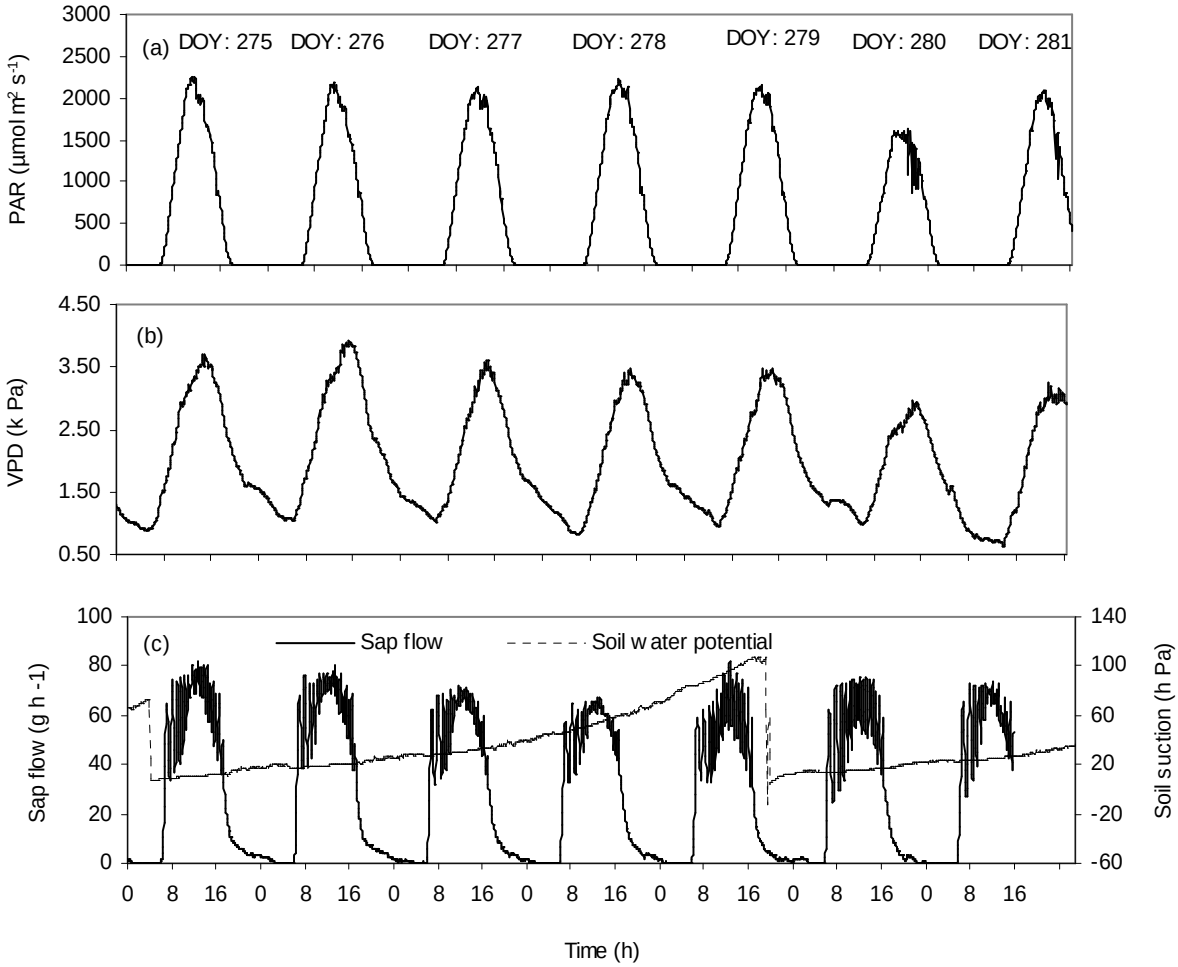


Fig 1.24 *(a) Diurnal course of the photosynthetically active radiation incident on the crown of the young trees and (b) the course of the vapour pressure deficit of the air from Julian day 274 to 281, (October 2003). (c) Typical variations in the sap flow rate (full lines) with the soil water potential (dotted line) during the drying cycle.*

Due to the fact that water uptake by plants often lags behind water loss (transpiration), plants derive some of the water from their internal storage reservoirs (Samson, 2001; Sevanto, 2003; Meinzer *et al*., 2004; Steppe and Lemeur, 2004). This is more significant in larger trees as well as trees under drought stress. The amount of water extracted from the internal reserves has a bearing on the diurnal course of the stem diameter. For instance, when more water is extracted from the internal storage reserves, stem diameter shrinks by a larger proportion (Ferreira *et al*., 1996; Fredrick, 1997) and this shrinkage can be used as an indicator for drought stress and has potential utility in water management using automated irrigation scheduling systems (Jones, 2004).

When transpiration exceeded water uptake, water had to be withdrawn from the internal reserves to meet the atmospheric evaporative demand. This condition was accompanied with a shrinkage of the stem diameter as shown in Fig 1.21c. The use of water from the internal reserves (ΔS, cm^3) was calculated from the cumulative total from 0800 to 1600 h each day only when $F < E$ i.e.

$$\Delta S = \sum_{i} (F - E) \qquad (1.8)$$

where F is the stem sap flow rate corresponding to the water uptake at a given time and E is the transpiration rate by the whole tree for that time. Table 1.5 shows the relationship between the total transpiration and changes in internal storage as the soil dried. The negative values of the sum of changes in internal water storage indicate a net use of water from the tree contributing to the transpirational losses. As the soil continued to dry, it is evident that the total water use during the period 0800 to 1600 h declined, while the amount of water extracted from the internal reserves increased. This in turn led to an increase in the maximum daily shrinkage (MDS) of the stems except for DOY 276. A disturbance occurred on the dendrometer readings leading to an anomalously large maximum daily shrinkage of the stem diameter. Generally, the maximum daily shrinkage increased by up to 18 % of its well-watered value when the soil suction reached approximately 40 hPa. When the trees were under severe drought stress on DOY 278, the maximum daily shrinkage had increased by approximately 33 % of its well-watered value with the soil suction of about 68 hPa in the root zone. These values translate to approximately 0.5 % increase in MDS for every 1 hPa drop in soil suction. Thus despite the active stomatal control of water use by Navel orange trees, the MDS is a potentially useful measure of the water status of the young orange trees.

Table 1.5 *Total transpiration and the sum of changes in internal water storage by the young orange trees from 0800 to 1600 h during a typical drying cycle from DOY 275 - 279.*

DOY	Transpiration (cm^3)	ΔS (cm^3)	Maximum stem diameter shrinkage (± 7 μm)	Soil water status
275	554.22	-21.6	120	Well-watered
276	569.22	-33.1	*207*	↓
277	528.23	-39.9	142	
278	510.22	-48.4	160	Stressed
279	473.35	-8.2	161	Well-watered

Given the fact that transpiration rates decrease quite significantly due to the imposition of drought stress as shown in Fig 1.24, one would expect that a further reduction in evaporative cooling should lead to much higher canopy temperatures for citrus (Jones, 1992). But this was not the case as shown in Fig 1.25 if the leaf position is not manipulated. The gradual drop in the leaf surface temperature was a result of the curling of the leaves as the level of drought stress became severe. In fact, the trend in leaf surface temperature measurements using the infrared thermocouples became distorted and K-type thermocouples clipped on the lower shaded side of the leaves using plastic paper clips had to be used. After re-watering on DOY 279, leaf surface temperature began to creep upwards again as the leaves unfolded. Curling of the leaves reduced the maximum leaf-air temperature difference from approximately 9 ℃ down to less than 1 ℃. Whether the reduction in th e leaf to air temperature difference with increasing drought stress for the orange trees can be used as a stress indicator is unclear for now. After irrigation e.g. on days 280 and 281 the leaf – air temperature difference remained low because it took some time for the leaves to fully recover from water stress and to uncoil.

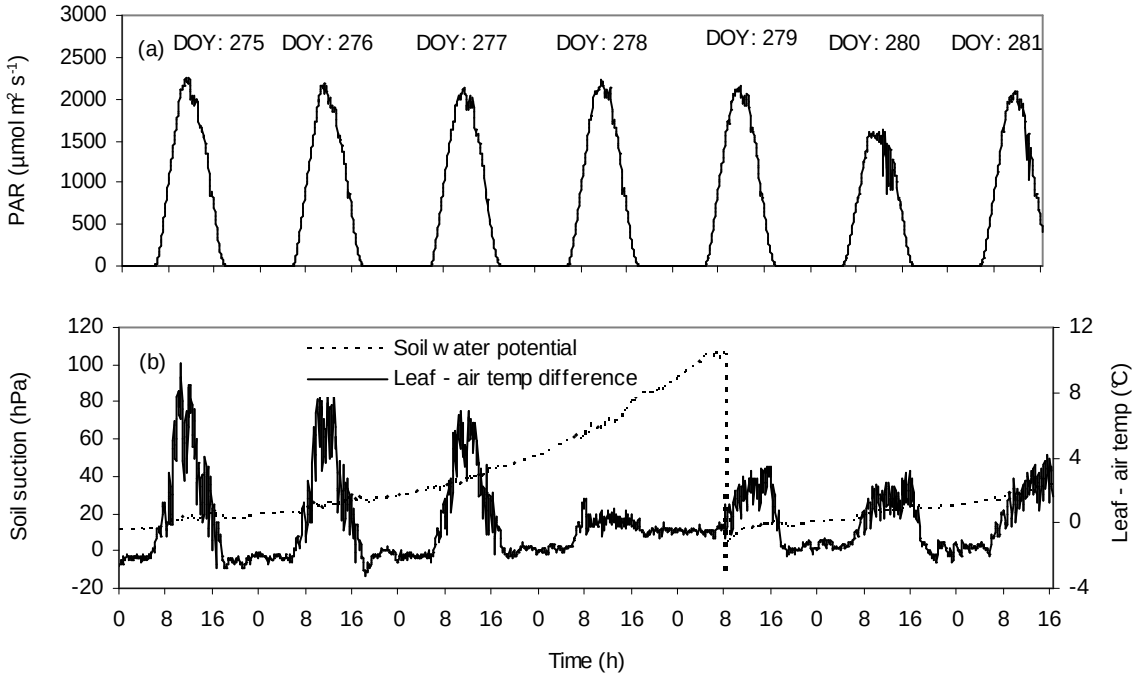


Fig 1.25 *Effect of the soil drying on the leaf to air temperature difference over a period of 7 days. Leaf temperature was measured using a K-type thermocouple stuck with a plastic paper clip below the leaf. Measurements from the infrared radiation thermometer could not be used due to leaf curling.*

1.4.7 Response to alternating partial drought stress (Experiment 2)

Alternating the partial drought stress in the rootzone of plants is employed in recent irrigation techniques such as the partial rootzone drying (PRD). In this method, water is applied to half of the rootzone of the plant (usually 50 % of the control) while keeping the other part of the root zone dry. The wet and dry regions are alternated at 10 to 14 day intervals to ensure that the root to shoot chemical signals that control the stomatal aperture are maintained (Dry *et al*., 1996; Mingo and Davies, 2001).

This split root experiment was designed to investigate the response of the young Navel orange trees to a typical partial rootzone drying strategy in an environment where the driving variables could be controlled to some extent. Under orchard conditions, the interaction of the different variables (e.g. the effect of neighbouring plants and the non-uniformity of the irrigation system) introduce some complexity to the results. The responses in terms of changes in water consumption patterns and stem growth due to partial stressing were evaluated. The detailed description of the experiment is given in section 1.3.1. Figure 1.26 illustrates the changes in sap flow rates in the two experimental trees, Tree A and Tree B, respectively. When the trees were well-watered, from DOY 238 till DOY 244, the daily total sap flow rates were similar.

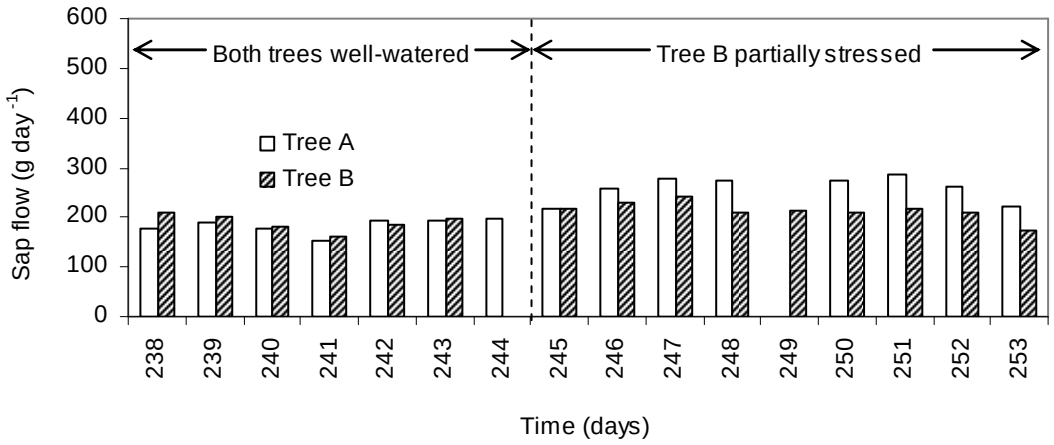


Fig 1.26 *Effect of the partial drought stress on the daily total sap flow of two potted orange trees. Both Tree A (open rectangle) and Tree B (hashed rectangle) were well watered from DOY 238 till 244 (4 litres a day). From DOY 245, Tree B received 50 % less irrigation applied to half of the root zone only. An error margin of 10 % is assumed for the sap flow measurements.*

However, when Tree B was partially stressed, from DOY 245 onwards, daily total water use declined compared to the well-watered tree (Tree A). The reduction in sap flow rates was more apparent as the level of stress on the dry side of the rootzone increased e.g. on DOY 253. More importantly, the reduction in the daily total sap flow was not accompanied with a reduction in stem growth rate as shown in Fig 1.27. This observation suggests that partially stressing the rootzone of the orange trees did not have a short-term effect on stem growth although the transpiration rates were suppressed and thus it has the potential of increasing the water use efficiency of the orange trees.

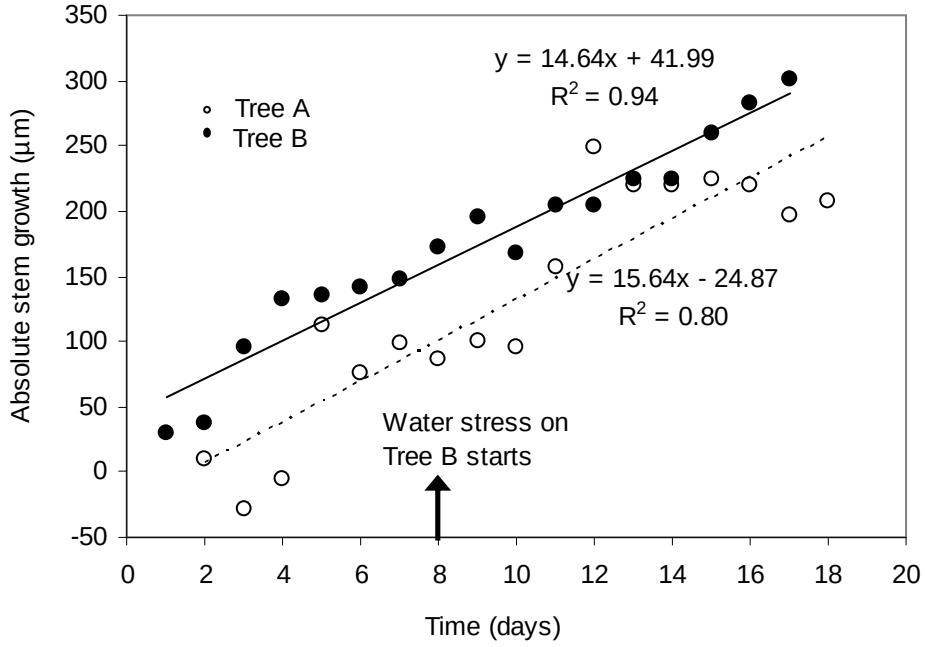


Fig 1.27 *Effect of the partial drought stress on stem growth of the potted orange trees. Open circles show the course of the cumulative absolute growth for Tree A and closed circles cumulative absolute growth for Tree B. Growth is expressed as a function of time in days starting from DOY 238 and ending with DOY 256. The slope of the graph, which is a measure of the growth rate of the trees was not significantly different (p<0.05).*

1.5 Conclusions

Although a lot of water is often used for irrigating citrus trees in the seasonally arid tropics, measurements on the Baianinha Navel variety of orange trees [*Citrus sinensis* (L.) Osbeck] revealed that these trees do not use a lot of water. There is a very strong stomatal control on water use depending on environmental conditions. This control on water use arises from the cyclical oscillations in the stomatal conductance; a phenomenon that is yet to be fully explained (Loesch, 2001 and Wang *et al*., 2001; Yang *et al.*, 2003; Buckley, 2005; Steppe *et al*., 2006b).

It is also important to note that despite these low transpiration rates, these trees need adequate water supply in the rootzone to prevent severe reductions in stomatal conductance which may lead to reductions in growth and production. Consequently the need for efficient soil water management in citrus plantations is unquestionable as too much or too little water may lead to adverse effects. Too much water, leading to water logging, causes a deterioration of root health due to the effects of anaerobic bacteria which release excess sulphur dioxide

while too little water causes even smaller stomatal apertures presumably leading to reduced CO_2 up take and, hence, less growth and production.

Regarding water management, plant based responses are increasingly being used for scheduling irrigation of horticultural crops (Naor and Cohen, 2002; Jones, 2004). For the Navel orange trees budded on rough lemon rootstocks studied here, it appears that the stem diameter variations is the most sensitive measure of plant water status, while the leaf to air temperature differences are affected by the curling of the leaves. Despite the stomatal oscillations, the dynamics of sap flow also seemed to be very sensitive to soil drying and thus they can be potentially used to establish irrigation need. Models/algorithms or spreadsheets are often needed to compute the time integrals of accumulated sap flow over selected intervals. Over sufficiently long periods e.g. daily time steps or longer the transpirational losses will be equal to the cumulative sap flow over that period.

Experiments with drought stress showed that transpiration rates, inferred from sap flow measurements, were significantly reduced under partial drought stress while the stem growth rate was not changed. We can conclude based on these potted tree experiments that there is a possibility of improved water use efficiency by the citrus trees using techniques such as the partial rootzone drying irrigation strategy as demonstrated in this study. However, the commercial utility of this approach on citrus trees still needs to be validated with field-grown trees in orchards. Given the fact that the growth measurements in this study were based on stem measurements, fruit response to partial stress may be different from the stem response and thus further experiments on the effects of partial stress on yield are crucial. The data presented in this Chapter will, however, be useful for the calibration and validation of models for resource management in young citrus orchards. Given the need to fully understand the water relations of these economically important trees, the yet not-fully-understood phenomenon of stomatal cycling is investigated further in the next chapters.

Chapter 2 Temporal non-synchronization between water uptake and loss causes stomatal oscillations in young orange trees [*Citrus sinensis* (L.) Osbeck]

Parts of this chapter are published as follows:

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2. **Dzikiti S, Steppe K, Lemeur R, Milford JR.** 2007. Whole-tree level water balance and its implications on stomatal oscillations in orange trees under natural climatic conditions. Journal of Experimental Botany 58,1893 – 1901.

2.1 Introduction

Though stomatal oscillations were first discovered three to four decades ago (Lang *et al*., 1969; Barrs, 1971; Farquhar and Cowan, 1974), they remain a subject of scientific interest because it is difficult to fully explain the mechanisms leading to the oscillations. Thus it remains difficult to develop mechanistic models to describe the water relations of plants undergoing stomatal cycling e.g. citrus trees in response to environmental variables (Upadhyaya *et al*., 1988). This is despite the growing need for such modelling tools in the management of resources and in yield prediction especially in capital intensive cropping systems (Jones, 2004) such as in citrus plantations. The early maturing Navel variety of orange trees [*Citrus sinensis* (L.) Osbeck] are commonly budded on the Troyer citrange rootstock [*Citrus sinensis* x *Poncirus trifoliata* L. Raf] which produces trees with less vegetative vigour and good quality fruit (Spiegel-Roy and Goldschmidt, 1996). Stomatal oscillations, which characterise the water relations of this scion-rootstock combination of orange trees, are interpreted and documented in the present chapter.

Recent evidence suggests that stomatal oscillations arise from responses of the stomata to leaf level water balance involving the juxtaposition of opposing positive and negative feedback loops (Buckley, 2005; Steppe et al., 2006b). The positive feedback loop has been identified with the effect of the epidermal mechanical advantage on passive stomatal hydromechanics. Loss of turgidity by the epidermal cells due to transpiration enhances stomatal opening (Shackel and Brinckmann, 1984; Franks, 2004). But this ‘wrong way’

response is subsequently followed by an exponential transition to a new steady-state conductance that partially counteracts the perturbation involving guard cell movements in the negative feedback loop. It is possible that this two-phase pattern repeats itself producing oscillations that may persist for a while before damping out or may even occur indefinitely (Buckley, 2005).

While most studies on stomatal oscillations have focused on events at leaf level (McBurney and Costigan, 1984; Reich, 1984; Naidoo and von Willert, 1994; Zipperlen and Malcolm, 1997; Yang *et al*., 2003), the positive feedback described above can also arise e.g. from xylem cavitation in response to increased tension in any part of the hydraulic vascular system of the plant (Buckley, 2005). Cavitation causes a decrease in the hydraulic conductance by reducing the number of active xylem vessel elements. Water flow is impeded causing a decrease in the water status of the leaves, hence, amplifying the 'wrong-way' response. An important precondition for stomatal oscillations to be generated in this way is that cavitation repair has to occur at short intervals of the same order of magnitude as half the period of the oscillations. But evidence for this rapid reversal remains sparse (Vogt, 2001; Bucci *et al*., 2003; Brodribb and Holbrook, 2004).

Since the stomata are coupled hydraulically to each other and to other compartments of the transpiration stream, the role of the whole-tree level water balance in the generation of stomatal oscillations is investigated in this study. Despite the increasing availability of estimates of water storage capacity in trees, relatively little is known about the daily dynamics of discharge and recharge of stored water and their consequences for stomatal regulation of water use (Meinzer *et al*., 2003). In this study, the dynamics of water uptake by the roots, supply to the leaves and loss through transpiration by young orange trees are inferred from simultaneous measurements of sap flow on different organs of the trees; the stomatal conductance and leaf water potential. Tree level water balance is evaluated using a simple water balance model from which the hydraulic parameters of the water transport pathway are derived and related to events at leaf level. Despite the role of hydro-passive mechanisms in generating stomatal oscillations, it appears that changes in the whole-tree level water balance are also important in triggering the stomatal oscillations. A better understanding of the mechanistic basis of stomatal control is necessary to improve the theoretical foundation for predictive models and manipulative experiments. A review of the current state of knowledge regarding stomatal movements is given below including the different theories of stomatal oscillations. Finally, an attempt to explain why the stomata should behave in such a dynamic way, based on the hydraulic properties of the transpiration pathway of the orange trees, is given.

2.2 Background: Stomata

Stomatal pores are microscopic openings on the surface of a leaf which permit CO_2 and water vapor exchange between the leaf interior and the environment (Fig 2.1). Carbon dioxide enters the leaf through open stomata and is utilized in photosynthesis. Water vapor diffuses out of the leaf when stomatal pores are open. Thus, stomata play a crucial role of permitting sufficient entry of CO_2 while avoiding excessive water loss. Stomata change their width 'a_p' (Fig 2.1) continuously in response to changes in the surrounding environment.

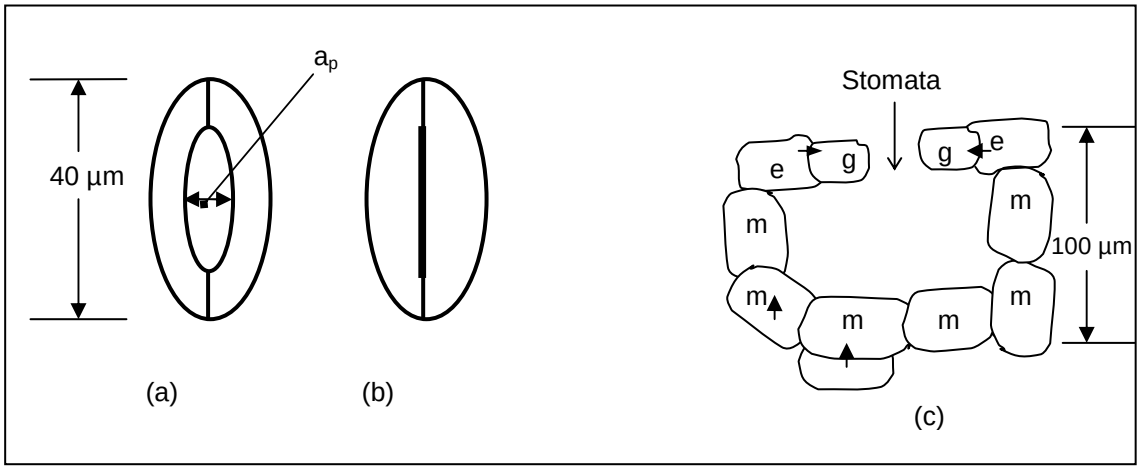

Fig 2.1 *Stomatal apparatus: (a) pore open, (b) pore closed, (c) cross sectional view with arrows representing various water fluxes; g, guard cell; e, epidermal cell; m, mesophyl cell (from Upadhyaya et al., 1988).*

While it is clear that stomata play a critical role in regulating water loss from vegetation, what is not clear is how this regulation is achieved (Cowan, 1977; Franks, 2004; Buckley, 2005). Stomata appear to respond to changes in many aspects of the soil-plant-atmosphere hydraulic continuum, but there is little agreement regarding the mechanism(s) by which the stomata sense these changes. As a consequence, phenomenon such as that of stomatal oscillations and stomatal patchiness remain not fully explained (Franks, 2004; Buckley, 2005). The phenomenon of stomatal oscillations will be described in greater detail in sections that follow. The fact that within the same leaf and under identical environmental conditions, stomata open and close with vastly different phase relations is the so-called stomatal patchiness. More importantly, stomatal oscillations appear to be a common feature of many plants having been observed in more than 30 different species, many of them being high value agricultural crops e.g. some cultivars of beans, cotton, citrus and sunflower among others.

2.2.1 Stomatal mechanics

It is widely accepted that the opening and closing of stomatal pores results primarily from increasing or decreasing guard cell turgor, P_g. The stomatal pore is bounded by guard cells as shown in Fig 2.1, which cause the pore to open when the cells gain turgidity and to close when the cells lose turgidity. In addition, the stomatal pore size 'a_p' may be influenced by changes in the turgor of the surrounding epidermal or subsidiary cells, P_e. This observation follows studies which have shown that when the humidity around a leaf is reduced, the stomatal conductance increases for a short time, typically 5-15 min and then declines for another 20-75 min, ultimately approaching a steady conductance (Shackel and Brinkman, 1984; Nonami *et al*., 1990; Buckley, 2005). A similar effect characterized by an initial opening of the stomata then followed by a closing one was observed after leaf excision (Darwin, 1898). The only difference is that the stomata closed completely in the case of leaf excision.

The enlargement of the stomatal aperture 'wrong way response' following a change in some factor of the plant's environment that increases transpiration was attributed to a decline in epidermal turgor pressure (Shackel and Brinkman, 1984; Nonami *et al*., 1990). An increase in the epidermal turgor pressure can push guard cells closer together to reduce the pore size and decreasing the epidermal turgor can act in the reverse as illustrated in Fig 2.2.

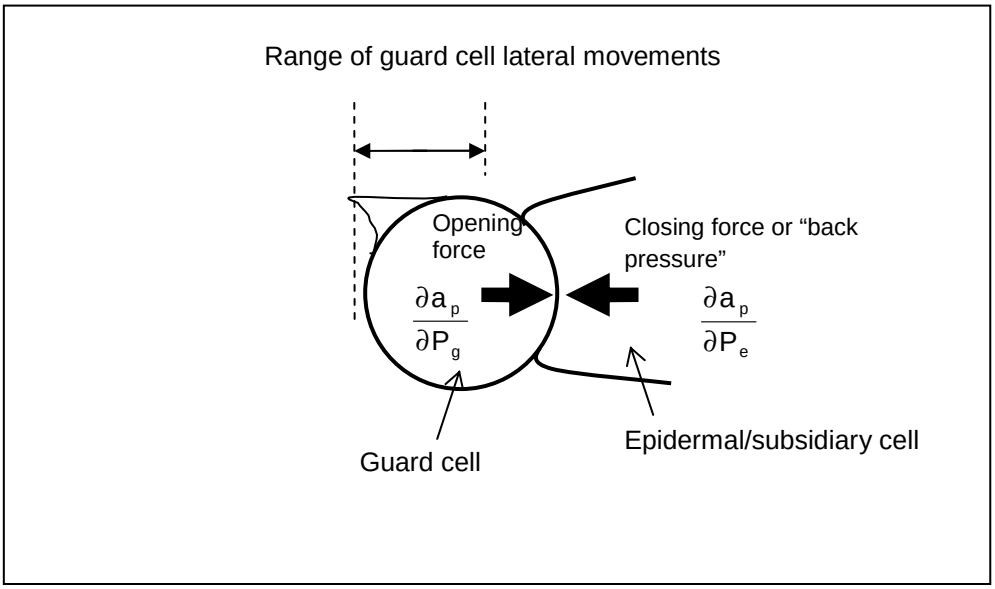

Fig 2.2 *Interacting mechanical forces in the vicinity of the guard cells showing the opposing effects of the guard and epidermal cell turgor pressures on stomatal aperture.*

At any instant, P_g and P_e (all in MPa) are defined by:

$$P_e = \Psi_e + \pi_e \tag{2.1}$$

and

$$P_g = \Psi_g + \pi_g \tag{2.2}$$

where π_g and π_e are guard cell and epidermal cell osmotic pressures (MPa), respectively. Ψ_g and Ψ_e are the guard and epidermal cell water potentials. In the short-term, π_e is kept relatively constant, and P_e changes passively with Ψ_e (Buckley, 2005). In contrast, π_g is actively regulated by guard cells in direct response to both internal (within the leaf) and external (environmental) stimuli. As a consequence, the guard cell turgor and, hence, the stomatal aperture change relatively quickly in response to stimuli that alter π_g or Ψ_g. A typical relationship between P_g, P_e and *a* showing how P_e can reduce stomatal pore size for a species whose stomatal responses is well documented (*Tradescantia virginiana*) is shown in Fig 2.3 (Franks *et al*., 1998).

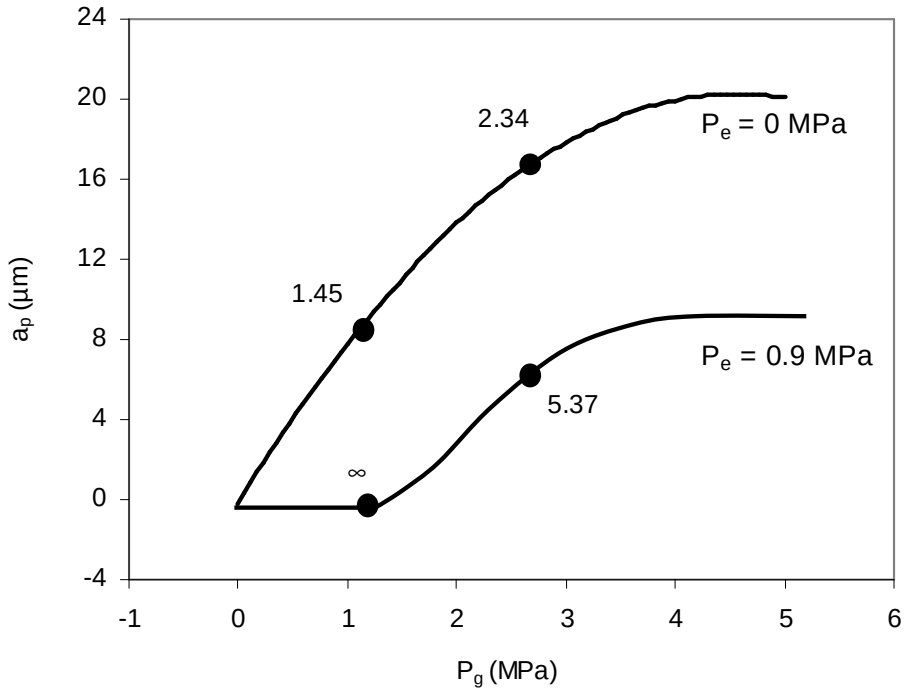

Fig 2.3 *Typical relationship between stomatal pore width 'a_p' and guard cell hydrostatic pressure 'P_g' at different epidermal turgor pressures (P_e; 0 and 0.9 MPa) as measured directly using a pressure probe (Adapted from Franks et al., 1998).*

According to this example, the reduction in aperture 'a_p' due to P_e ranges from 100 % at low P_g to about 50 % at high P_g although the effect may not be this great across different species (Franks, 2004). In fact, the wide variation in overall structure and the physical arrangement of guard cells relative to the adjacent epidermal cells in different species suggests that the magnitude of the mechanical interaction between the two sets of cells is likely to vary considerably across species. The mechanical relationship, 'm', (also called the mechanical advantage) between the guard and epidermal cells is specific to a given combination of P_g and P_e, and for any such combination it is best defined by the ratio of the sensitivities of *a* to P_e at constant P_g and *a* to P_g at constant P_e (Cook *et al*., 1976):

$$m = -\frac{\left(\frac{\partial a}{\partial P_e}\right)_{P_g}}{\left(\frac{\partial a}{\partial P_g}\right)_{P_e}} \qquad (2.3)$$

The negative sign makes 'm' a positive quantity since P_e and P_g have opposing effects on '*a*'. When m>1 (the usual case), there will be a net reduction in the stomatal aperture for the same increase in P_g and P_e. Under these conditions, the epidermal cells are said to have a

mechanical advantage over the guard cells. The larger the value of m, the more difficult it is for the guard cells to open against the opposing force of the adjacent epidermal cells. If there is no mechanical interaction between the guard and epidermal cells then m = 0.

Consequently, the following conclusions can be drawn about the relationship between the turgor pressures and the size of the stomatal aperture: (1) in the absence of any mechanical interaction with epidermal cells, the relationship between *a* and P_g approximates an exponential decay function as shown in Fig 2.3, and (2) in the presence of mechanical interaction with epidermal cells, the relationship between *a* and P_g is sigmoidal.

While the initial opening of the stomata following an increase in transpiration 'wrong-way response' can be explained, the mechanisms involved in the gradual closing movement of the stomata towards a steady state value 'right way response' remains debatable. Buckley (2005), however, argued that any mechanism leading to this closing effect must decouple the guard and the epidermal turgor in the steady state. For this to happen, two hypotheses were suggested. According to one hypothesis, the reduced water status following an initial increase in transpiration causes a decrease in the water status of both the guard and epidermal cells by similar amounts. So the stomatal aperture increases and this is followed by the active adjustment of the guard cell osmotic pressure which reduces guard cell turgor enough to produce the closing movement 'right-way response'. The second hypothesis supposes that guard cells are separated from epidermal cells by a large water potential gradient, probably caused by a large hydraulic resistance or by the accumulation of osmolytes in the guard cell apoplast. Thus, an increase in evaporation rate reduces guard cell turgor more than epidermal turgor and the aperture declines. However, credible experimental evidence to justify these two hypotheses is still sparse although the possibility remains that the hydraulic resistance from epidermal to guard cells is dynamically and actively regulated in such a way as to produce a wrong- way and subsequent steady-state response (Buckley and Mott, 2002b).

2.2.2 Stomatal hydraulics

Stomata are connected hydraulically to each other throughout the leaf (Raschke, 1970) and to the rest of the transpiration stream through the xylem vessels in the leaf petiole (Fig 2.4). This connectivity has been demonstrated by many researchers in experiments where a perturbation introduced on one part of the leaf, e.g. by imposing irradiance (Buckley and Mott, 2000) or a step change in the vapor pressure deficit (VPD) of the air (Nonami *et al*., 1990), caused the stomata on the same leaf but distal from the perturbation to respond despite no local change in either the irradiance or VPD. Thus the behavior of individual stomata is

strongly influenced by developments elsewhere in the transpiration stream. This is substantiated by the fact that plants behave in such a way that their water status is maintained above a certain threshold value by ensuring that their stomatal conductance somewhat matches the hydraulic conductance of the transpiration stream (Meinzer *et al*., 2003). For instance, trees with high stomatal conductances generally tend to have high hydraulic conductances as well so that water demand by the leaves is matched with water supply. Limiting water supply to the leaves e.g. by transverse cuts to the xylem vessels or by inducing air embolisms causes the stomatal conductance to decrease (Sperry *et al*., 1993).

The total leaf transpiration rate which is driven by the atmospheric evaporative demand also includes a component that bypasses the stomatal pores and diffuses directly across the epidermal cuticle to the atmosphere. It is also possible that part of this cuticular transpiration occurs directly from the externally exposed cuticle of the guard cells (Maier-Maercker, 1979), although this component has proven to be difficult to quantify (Franks, 2004). The overall contribution of cuticular transpiration to stomatal response remains uncertain. For example, in the event of substantial cuticular transpiration happening, then this would provide a mechanism for regulating leaf transpiration regardless of the leaf water status thus allowing leaf transpiration rates to decline even if the atmospheric evaporative demand is rising.

Another unresolved question relates to the pathway taken by the transpiration stream once it leaves the xylem and flows towards the stomatal pores. Specifically, how far the waxy cuticle of the leaf surface extends into the throat of the stomatal pore or even further into the substomatal cavity is not clear. Meidner (1986) and Cowan (1977) showed that for a uniformly wet substomatal chamber, most of the transpiration occurred from wet surfaces closest to the stomatal pore. The presence or absence of the waxy cuticle around the guard cells would affect the turgor relations between the guard and the surrounding epidermal cells as well as the hydraulic conductance between the soil and the respective cells.

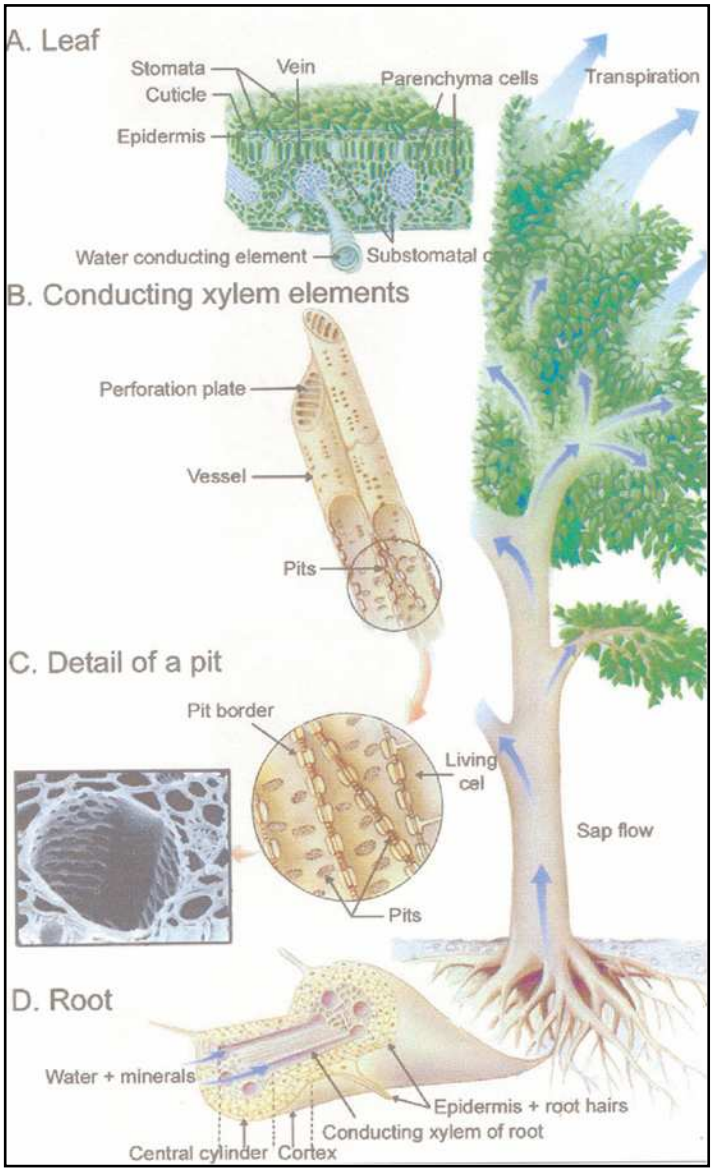

Fig 2.4 *Components of the transpiration pathway for a typical tree from the roots to the leaves (adapted from Steppe, 2004). The detailed characteristics of each component are shown on the left hand side of the diagram.*

2.2.3 Theories of stomatal oscillations

Stomatal oscillations are defined as the phenomenon of cyclic opening and closing movements of stomata (Barrs, 1971). Based on the work of Apel (1967), Barrs (1971) proposed a tentative grouping into water-based and CO_2-based oscillations. Short-period stomatal oscillations (less than 10 min) with small amplitudes are associated with the control of CO_2 status and appear to be dependent on the external carbon dioxide concentration; while slower oscillations (30 - 50 min) with larger amplitudes are associated with the control of plant

water status. Metabolically induced stomatal movements are generally termed hydro-active while those due to the plant water status are called hydro-passive movements. Upadhyaya *et al.* (1981), proposed the scheme shown in Fig 2.5 for the generation of the CO_2-based and the water status based stomatal oscillations.

2.2.3.1 Hydro-active stomatal oscillations

According to the scheme in Fig 2.5, CO_2 entering the stomatal pore by diffusion is absorbed by the wet cell walls of the guard cells. According to Upadhyaya *et al*. (1981) dissolved CO_2 diffuses through the cell liquid to carboxylation sites where malic acid is produced in the case of plants with the crassulacean acid metabolism (CAM) photosynthetic pathway. The H^+ ions of the dissociated malic acid are actively pumped across the guard cell membrane, increasing the negative electrical charge inside the guard cell. In response to this, K^+ ions passively diffuse into the guard cell from the neighbouring subsidiary cells. The osmotic content of the guard cell is now increased causing water to flow passively into the guard cell. The resulting increase in the turgor causes the stomatal pore width to increase. This continues until the H^+ pump reaches its maximum capacity, after which the H^+ ions begin to accumulate inside the guard cell and the resulting pH change forces the K^+ ions to passively diffuse out of the guard cell. The water follows and the K^+ ion transport and the guard cell turgor drops causing the stomatal pore width to decrease. An important assumption built into this CO_2 scheme is that both the initiation and the cessation of the H^+ pump are dependent on the water status of the mesophyll cells. This is based on the premise that the abscisic acid (ABA) is produced in the mesophyll under drought stress and upon arriving at guard cells causes solute loss. Thus it appears that the plant water status is essential in the initiation of the CO_2 based stomatal oscillations.

2.2.3.2 Hydro-passive stomatal oscillations

According to this theory, water vapor evaporating from the wet mesophyll cell walls diffuses through the stomatal pore to the leaf exterior. This water is replaced both by a flux brought to the leaf mesophyll from the roots via the vascular system as well as by water diffusing passively from the guard cells to the mesophyll cells. The resulting decrease in the turgor in the guard cells causes the stomatal pore width to decrease. A smaller pore width slows the rate of evaporation and causes water to accumulate in the mesophyll cells. In response to this accumulation, water diffuses back to the guard cells increasing their turgor and increasing the pore width. This pattern then repeats itself to generate the oscillations (Upadhyaya *et al*., 1981).

More recent evidence, however, suggests that rather than the oscillations arising from fluctuations in the water content in the substomatal cavity, the oscillations arise from responses of the stomata to water balance involving the juxtaposition of opposing positive and negative feedback loops (Buckley, 2005). The positive feedback loop has been identified with the effect of the epidermal mechanical advantage on passive stomatal hydromechanics. As already illustrated above, loss of turgidity by the epidermal cells due to transpiration enhances stomatal opening. But this ‘wrong way’ response is subsequently followed by an exponential approach to a new steady-state conductance that partially counteracts the perturbation involving guard cell movements in the negative feedback loop. According to Buckley (2005), the negative feedback loop is metabolically mediated involving an active regulation of the guard cell osmotic potential. It is possible that this two-phase pattern repeats itself producing oscillations that may persist for a while before damping out or may even occur indefinitely. According to this new hypothesis, both the hydro-active and hydro-passive movements are involved in the generation of the oscillations.

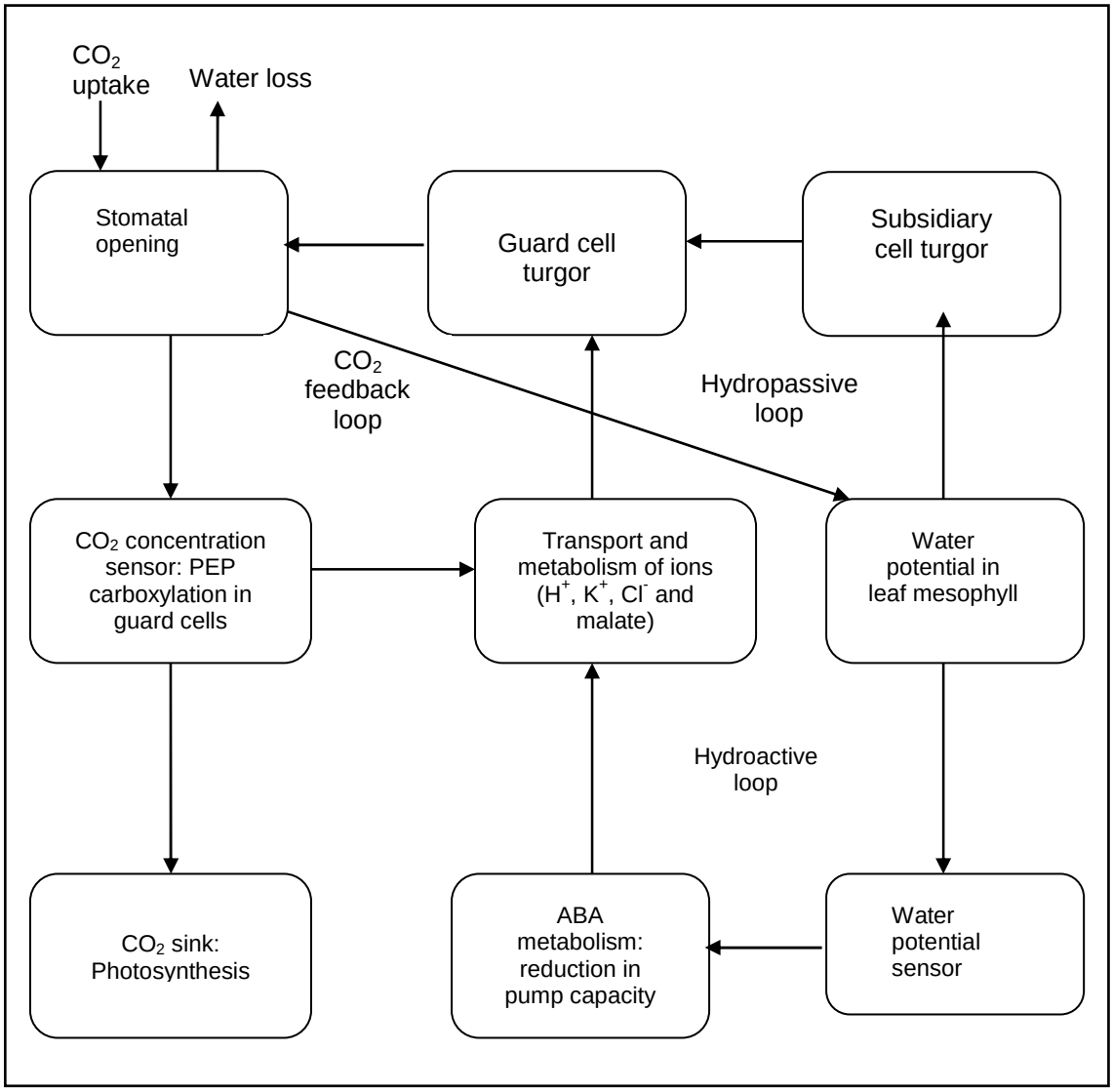

Fig 2.5 *Schematic representation of a typical model for stomatal oscillations in C_4 plants involving both the hydro-active and hydro-passive feedback loops (adapted from Upadhyaya et al., 1988).*

2.3 Materials and methods

2.3.1 Orchard experimental site

Cyclic oscillations in sap flow were observed during an irrigation experiment in a commercial orchard at Mazowe Citrus Estate (MCE), Zimbabwe (17°27' S, 30°59' E, 1189 m above sea level) in November 2004 (see Chapter 3). The orchard, which covers approximately 2 ha under drip irrigation, is situated on a gentle sloping terrain about 40 km to the north of Harare, Zimbabwe (Fig 1). The trees were four-year-old Navel orange trees

[*Citrus sinensis* (L.) Osbeck] of the Bahianinha selection budded onto a Troyer citrange rootstock [*Citrus sinensis* x *Poncirus trifoliata* L. Raf]. The growing medium was the dark red clayey loam soil whose physical and chemical characteristics were summarized by Hussein (1982).

The microclimate was monitored using an automatic weather station located to the southwest of the orchard approximately 70 m from the edge (Fig 2.6). A CM11 pyranometer (Kipp and Zonen, The Delft, Netherlands) installed horizontally on a levelling fixture measured the solar radiation incident on the crown of the trees, while wind speed was monitored using an AL100 cup anemometer (Vector Instruments, Rhyl, UK) at 2 m height. Air temperature and humidity were monitored using an HMP35AC probe (Campbell Scientific Ltd, Shepshed, UK) inserted in a 12-plate Gill radiation shield (Vaisala Ltd, Finland) at ~1.5 m above the ground. Signals from all the sensors were recorded automatically at 5 s intervals and 5 min averages were stored on a datalogger (CR23X, Campbell Scientific Ltd, Shepshed, UK).

Fig 2.6 *Automatic weather station to monitor the orchard microclimate at the trial site at Mazowe Citrus Estate, Zimbabwe. The orchard with four-year-old Navel orange trees can be seen in the background.*

2.3.2 Physiological measurements on orchard trees

Branch level sap flow rates were measured on fully exposed branches of four trees in the orchard using SGB19 heat balance sap flow sensors (Dynamax, Houston, USA). The mean branch diameter on which the sap flow gauges were installed was about 18.4 ± 0.5 mm (Fig 2.7). Operating instructions by Baker and van Bavel (1987) were followed during sensor installation, and weather shields were also installed round each sensor. In addition, all the sensors and the exposed parts of the branches were wrapped in a double layer of aluminium foil to minimise the effects of spurious temperature gradients due to radiant heating. The sensors were connected to two dataloggers (CR23X, Campbell Scientific Ltd, Shepshed, UK) with similar logging frequencies as the climatic data.

Fig 2.7 *Heat balance sap flow gauge (SGB19; Dynamax Houston, USA) installed on a branch of a four-year-old Navel orange tree at Mazowe Citrus Estate, Zimbabwe.*

2.3.3 Potted tree experimental site

A detailed experiment to further investigate the cyclic oscillations in sap flow observed in the orchard at MCE was set-up outdoors on the flat roof of the Physics Department, University of Zimbabwe, Harare. Details of the experimental set-up are given in Chapter 1 of this thesis. Plant material comprised six two-year-old orange trees of the same citrus cultivar

scion-rootstock combination as in the orchard. The trees were planted in asbestos pots also as described in Chapter 1, only that a different root stock-scion combination was being used.

Two healthy and actively growing trees were selected for the experiments and instrumented to investigate the phenomenon of stomatal cycling in detail. All six trees could not be investigated simultaneously due to limitations in the number of sensors. Henceforth, these two model trees are referred to as Tree 1 and Tree 2, respectively.

2.3.4 Physiological measurements on potted trees

Measurements of sap flow on the potted trees were made using SGA9 and SGA5 heat balance sap flow sensors (Dynamax, Houston, USA) installed on the stem and the branch, respectively, of each of the two young model trees. The mean diameters at the stem and branch sensor installation sections of the potted trees were 11.3 and 6.5 mm for Tree 1 and 11.6 and 5.4 mm for Tree 2, respectively. Care was taken to avoid the dead wood at the bud union for the installation of the stem sap flow gauges. A strip of thin plastic was wrapped around the sections where the sensors were to be installed to ensure that possible transpiration by the green parts of the young trees did not affect the signals. Weather shields and a double layer of aluminium foil were installed around the gauges. In addition, the exposed parts of the stems below the stem sap flow sensors were wound with aluminium foil to the soil surface to minimise the effects of exogenous heating on the stem especially early in the morning and at sunset.

Stem diameter variations were monitored between the branch and stem sap flow sensors using dendrometers (DEX 70 and DEX 20, Dynamax, Houston, USA) on Tree 1 and Tree 2, respectively. The accuracy of the dendrometers was ± 10 µm. All the sensors were connected to two dataloggers (CR23X, Campbell Scientific Ltd, Shepshed, UK) programmed with a 5 s scan interval and all signals averaged every 5 min.

To get a clear relationship between the stomatal conductance and leaf water potential during the oscillations, the experiments were conducted on cloudless days. These conditions were not difficult to achieve as the transition period from winter to spring in Southern Africa is characterised by cloudless conditions over many days. Consequently, the period from 5 to 7 July 2005 (Julian day of year [DOY] 186-188) was chosen for intensive measurements of the plant variables. However, the most complete data for the simultaneous measurements of the stomatal conductance and the leaf water potential is available for 6 July 2005 (DOY 187).

Stomatal conductance was measured using the AP4 porometer (Delta-T Devices, Burwell, Cambridge, UK) as shown in Fig 2.8. The technique used in the AP4 porometer consists of enclosing the leaf in a small air chamber equipped with a humidity sensor and subsequent measurement of the time (called the transit time) it takes for a leaf to release sufficient water vapour to change the relative humidity in this chamber by a fixed amount. The cycle is then repeated to guarantee reproducibility. This is compared with a calibration plate of known resistance to give the stomatal resistance of the leaf. The AP4 automatically converts the readings into calibrated values of conductance or resistance.

In this experiment, the stomatal conductance was measured on four leaves in Tree 1 and on one leaf in Tree 2. The selected leaves were healthy, mature, fully expanded and exposed to solar radiation. One leaf was sampled on Tree 2 to check on the results from Tree 1. Stomatal conductance measurements were taken in continuous cycles such that each leaf was sampled at least once every 5 min on average except during calibrations. To ensure accurate measurements, a new calibration curve was fitted every time when a change in cup temperature of 2 ℃ on average occurred since the instrument's calibration is strongly temperature dependent. During the porometer measurements care was taken that the temperature difference between leaf and cup was minimal (less than 0.5 ℃). Additional leaf surface temperature measurements were taken on a representative leaf using a fine K-type thermocouple firmly fixed on the abaxial side of the leaf using a plastic paper clip. This provided an independent check of the leaf to cup temperature difference. A rigorous temperature correction was not applied to the stomatal conductance values as proposed by Verhoef (1997) since only the trend rather than the absolute values of the stomatal conductance was important in this Chapter. In addition, no quantitative derivations were made from the absolute values of the stomatal conductance.

Fig 2.8 *Set-up showing the measurement of the stomatal conductance of the leaves of a young Navel orange tree using the AP4 porometer (Delta-T Devices, Burwell, Cambridge, UK).*

Leaf water potential was measured only for the potted Tree 1 using a thermocouple psychrometer. Details of the operation of the thermocouple psychrometer can be found in Steppe (2001). The selected leaves were in the vicinity and under similar conditions to those used for porometer measurements. The thermocouple psychrometer comprised four standard C-52 sample chambers (Wescor Inc, Logan, UT, USA) connected to a microvoltmeter (HR-33T, Wescor, Inc, USA). Chambers were kept at a constant temperature inside a white datalogger enclosure box which was well insulated and kept inside the laboratory. Leaf samples, collected with an ordinary 6 mm paper punch were immediately wrapped with an aluminium foil and put in an air-tight plastic bag and taken indoors. The samples were loaded into the sample chambers within ten minutes of being collected at most. Measurements were made in the psychrometric (wet bulb depression) mode. The psychrometers were calibrated with NaCl solutions over the range 0 to -4.55 MPa. In order to determine the dynamics of the leaf water potential, measurements were taken at 10 min intervals. With four C-52 sample chambers, equilibration intervals were limited to 40 min. As a consequence, water potential measurements could not be replicated.

2.3.4.1 Equilibration test for the citrus leaves

An additional test was conducted to establish whether an equilibration period of 40 min was long enough for the citrus leaves given the fact that these leaves have a well developed

cuticle. This was done following the approach by Steppe *et al*., 2006b were the wet bulb depression from the four sample chambers each loaded with a disc from the same leaf was monitored. This trial run was repeated on several occasions and it was confirmed that equilibration was indeed reached in 40 min as shown in Fig 2.9.

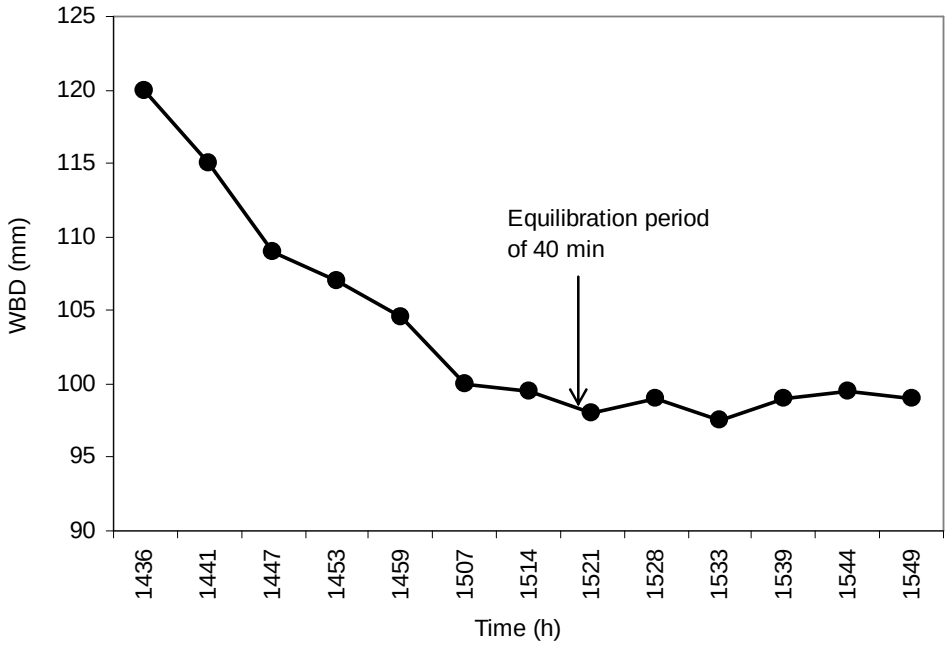

Fig 2.9 *A typical mean wet bulb depression (WBD) from four sample chambers loaded with a citrus leaf. Equilibration was reached after approximately 40 min since the wet bulb depression remained constant after this interval.*

2.3.5 Whole–tree sap flow, hydraulic resistance and water storage

The dynamics of the sap flow rate near the base of the stem (F) as affected by changes in the transpiration rate (E) of the whole crown due to stomatal oscillations can be described using a simple water balance model. The rate of change of the water stored in the tissues of the tree (W, kg) is related to the difference between water uptake (F, kg h^{-1}) and loss (E, kg h^{-1}) by

$$f = \frac{dW}{dt} = F - E \qquad (2.4)$$

In this equation we assume that there is a negligible capacitance in the roots such that the stem sap flow rate (F) equals the root water uptake. To estimate the total transpiration E, branch sap flow can be scaled up to whole-crown level using the approach by Meinzer *et al.* (2003). In this method, the scaling factor is calculated as the ratio of the daily total sap flow at

stem level to that at branch level (equation 1.7). Multiplying the branch sap flow rate by this factor gave an estimate of the whole-crown sap flow rate. Whole-tree transpiration rate (E) was then estimated from the whole-crown sap flow rate by imposing a 20 min time lead ahead of the whole-crown sap flow rate since the stomatal conductance led the branch sap flow by this factor (see below).

Given the fact that the stem sap flow (F) is driven by the water potential gradient between the soil and the leaves, a typical Ohm's law analogue can be used to describe the stem sap flow according to Jones (1992)

$$F = \frac{\Psi_s - \Psi_l}{R_x} \qquad (2.5)$$

where Ψ_s is the soil water potential measured in the root zone of the trees (MPa), Ψ_l the leaf water potential (MPa) and R_x the hydraulic flow resistance of the whole – tree (h MPa kg^{-1}). The hydraulic resistance is initially assumed to be constant in this equation. To describe the non-steady nature of the flow due to the temporal imbalances between water uptake and loss, the capacitance (C, kg MPa^{-1}) of the tree, which is a measure of their ability to store water, was defined as the ratio of the change in the tissue water content to the change in the driving water potential difference between the soil and the leaves

$$C = \frac{dW}{d\psi} \qquad (2.6)$$

The model was formulated as an electrical circuit analogue (Philips *et al*., 1997; Lhomme *et al*., 2001; Steppe *et al*., 2006a) developed using the Model-Maker Version 3 software package (Cherwell Scientific Ltd, UK). A schematic representation of the dynamic model for water transport is shown in Fig 2.10. Further model details are given in appendix 2.1.

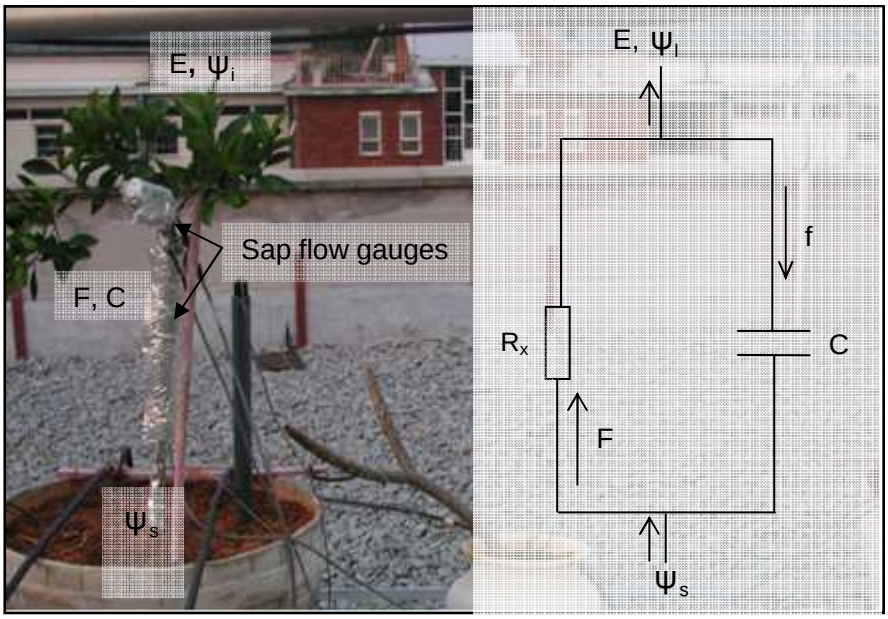

Fig 2.10 *The picture of the set-up showing the positions of the different variables in the transpiration stream (left hand side) and the corresponding electrical analogue for the dynamic model for sap flow at the base of the potted Navel orange trees (right hand side).* F *represents sap flow measured at the base of the tree,* E *the transpiration rate by the whole-tree,* f *the recharge/discharge of water by the storage compartments with a capacitance* C*.* R_x *is the hydraulic resistance of the stem,* ψ_l *is the leaf water potential and* ψ_s *the soil water potential, respectively.*

2.4 Results and discussion

2.4.1 Oscillations in sap flow under natural climatic conditions

The typical course of branch sap flow for the Navel on Troyer orange trees growing in the commercial orchard at Mazowe Citrus Estates, Zimbabwe is shown in Fig. 2.11b. Although predominantly clear sky conditions prevailed (Fig. 2.11a) and no sudden changes in the difference between the air's actual and potential saturated value (VPD henceforth) occurred, sap flow followed cyclic oscillations. No specific disturbance in the trees' environment was needed to generate the oscillations as is commonly reported elsewhere (Naidoo and von Willert, 1994; Reich, 1984; Upadhyaya *et al*., 1981; Cowan, 1977).

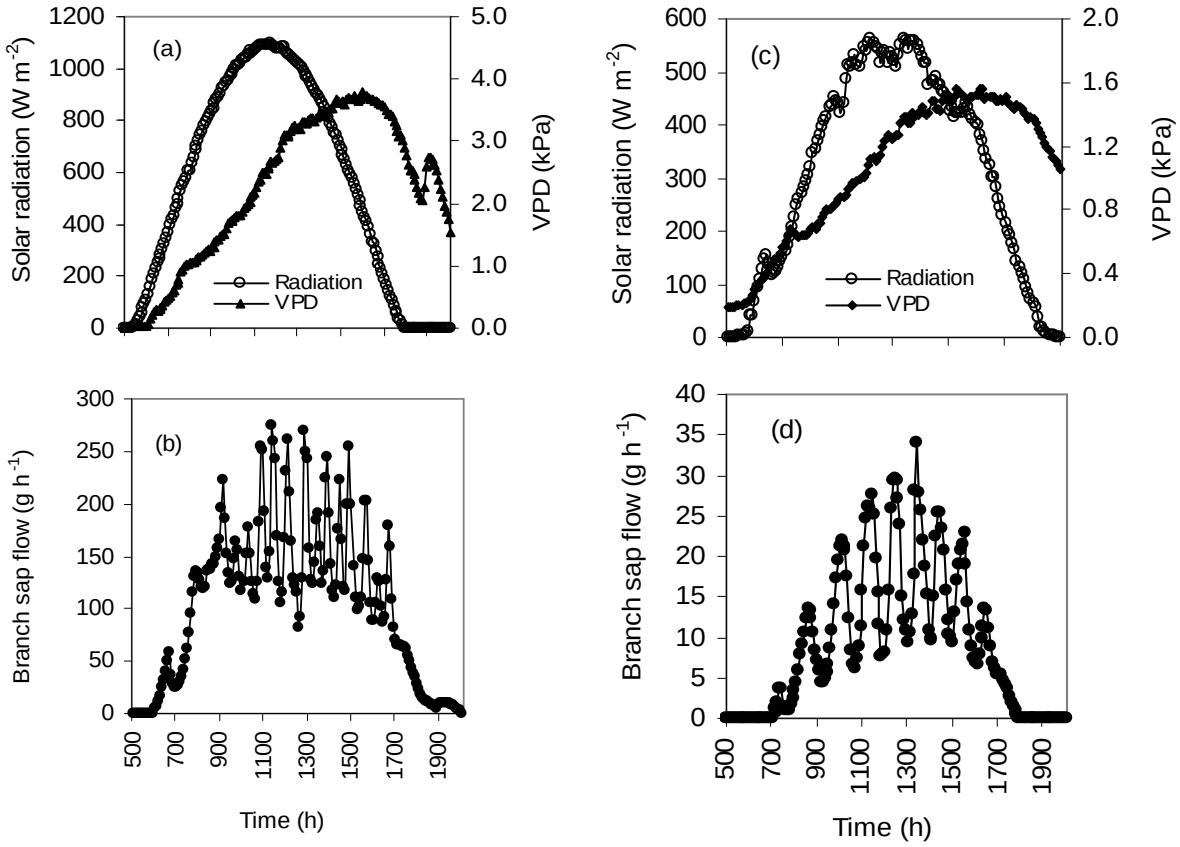

Fig 2.11 *The diurnal course of the solar radiation (open circles), vapour pressure deficit (VPD) of the air (closed triangles, Fig 2.11a) and branch sap flow of a four-year-old orange tree (Fig 2.11b) during a typical clear day on 3 November 2004 (DOY 307) at Mazowe Citrus Estate, Zimbabwe. Figures 2.11c and 2.11d show the same variables for a young potted orange tree under the rain shelter on 6 July 2005 (DOY 187). The cyclic oscillations in sap flow occurred both under field and laboratory conditions and each data point on the graphs is a five minute average.*

A clearer diurnal trend in sap flow was observed with the young orange trees grown in pots (Fig. 2.11d). Despite the small fluctuations and the relatively low intensities of the key driving climatic variables during the Southern African winter (Fig. 2.11c), well defined and sustained cyclic oscillations in sap flow were observed. Oscillations in the orchard on bigger trees were faster than for the young potted trees probably because of the differences in the hydraulic properties of the trees which are known to vary with tree size for a given species (Meinzer *et al*., 2004).

2.4.2 Stomatal conductance and sap flow of potted orange trees

Like the sap flow, stomatal conductance followed cyclic oscillations as expected (Fig 2.12). Seven clear oscillations were observed in approximately 8 h giving a mean period of 70 min per oscillation in both trees. Since the stomatal movements and water flow through the different compartments of the transpiration stream are hydraulically coupled, the stomatal conductance, branch and stem sap flows all oscillated with an identical period. Most work reported in literature has shown oscillations with a maximum period of up to 50 min obtained mostly under controlled climatic conditions (Jarvis *et al*., 1999; Wang *et al*., 2001).

The stomatal conductance measured in this campaign, ranged from 5 to 130 mmol m^{-2} s^{-1} for Tree 1 and from 5 to 175 mmol m^{-2} s^{-1} for Tree 2, respectively. Levy and Kaufmann (1976) reported oscillations in stomatal conductance varying between 4 and 42 mmol m^{-2} s^{-1} for four-year-old citrus trees growing under controlled greenhouse conditions and with root systems at different temperatures. Moreover, the measured stomatal conductance in this experiment with the Navel on Troyer scion–rootstock combination was higher after sunset (~1730 h Local Time; GMT + 2 h) with a mean value of approximately 11 mmol m^{-2} s^{-1} for both trees compared to the lowest average value of 5 mmol m^{-2} s^{-1} reached during the day. A closer inspection of the course of the stomatal conductance in Fig 2.12 also reveals that the stomata tended to stay partially closed for significant periods of each cycle and only opened fully for shorter intervals. Direct measurements of the stomatal aperture by Kaiser and Kappen (2001) working with *Sambucus nigra* L. plants showed that during oscillations the stomatal aperture varied between the slightly open and the closed states with a tendency of the stomatal aperture to overshoot the optimal size during opening but only for short periods. This observation explains the rapid increase in the stomatal conductance in the present study which occurred when the stomata were opening, as shown in Fig. 2.12.

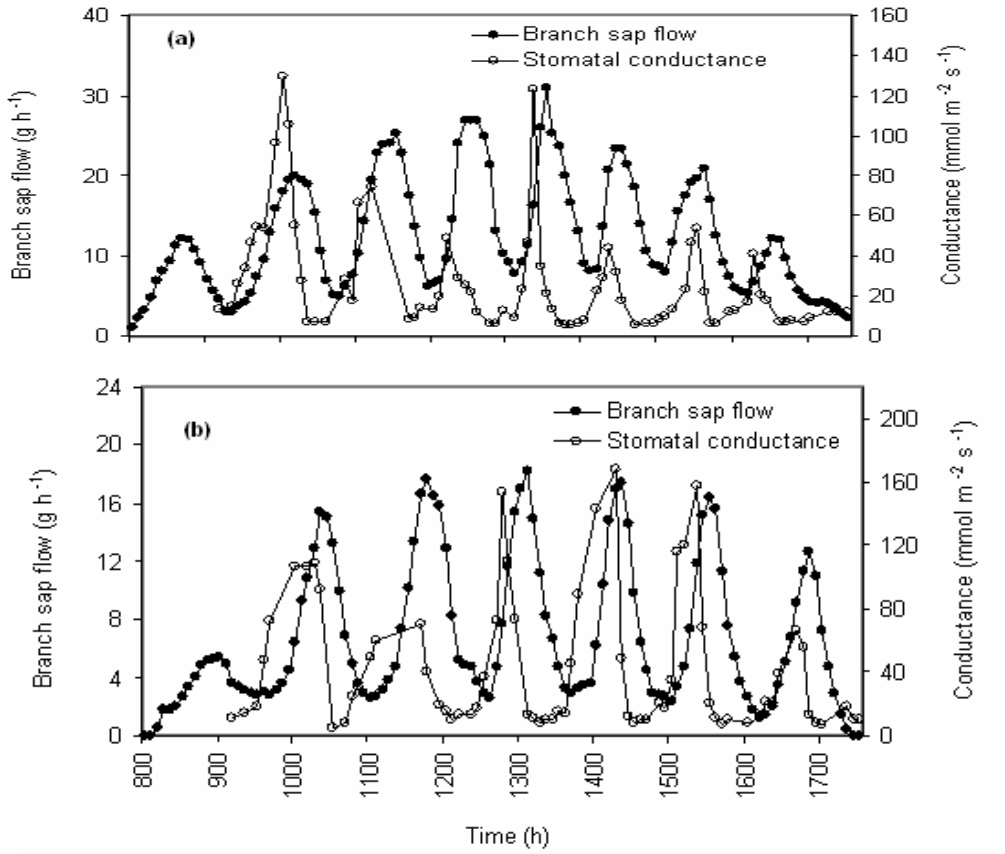

Fig 2.12 *Evolution of the stomatal conductance and branch sap flow of the young potted trees, Tree 1 (a) and Tree 2 (b), respectively, during a typical clear day (6 July 2005; DOY 187). Stomatal conductance was measured regularly from 0910 until 1805 h (Local Time, GMT + 2h) using the hand-held AP4 porometer (Delta–T Devices, UK). The stomatal conductance after sunset was higher than the minimum reached during the day due to the oscillations.*

Branch sap flow for both Tree 1 and Tree 2 ceased at sunset while stem sap flow occurred until 2000 h. The continued stem sap flow occurred to replenish the internal water reserves depleted when water loss from the tree exceeded water uptake during the day. For Tree 1 on DOY 187, for example, total transpiration calculated as the time integral of branch level sap flow scaled up to tree level from sunrise (~ 0600 h) to sunset (~ 1730 h) as described above was approximately 712.4 cm^3. Of this amount, about 103.3 cm^3, i.e. approximately 14 % of the total transpiration was extracted from the internal storage reserves while 76.9 cm^3 was used to replenish the internal storage reserves during the same period. When whole-tree water loss (total transpiration) exceeded water uptake (stem sap flow) at any instance, then the balance of water had to be withdrawn from the internal water storage reserves. The contribution of the internally stored water to transpiration was thus calculated as the time integral for all the instances when the difference between stem sap flow and transpiration was

negative and the converse was applied for the refilling of the internal storage pools. Consequently, a deficit of 26.4 cm^3 calculated as the difference between water withdrawn from the internal storage and that used to replenish the internal reserves occurred at the end of the day. This had to be refilled after sunset through continued water uptake when transpiration had ceased. It is important to note that, while discharge of water from the internal storage occurs mainly in the morning and recharge in late afternoon on clear days for most species (Meinzer *et al*., 2004; Steppe, 2004), more frequent recharge and discharge cycles occurred several times throughout the day for the orange trees.

2.4.3 Dynamics of the leaf water potential

Stomata respond to environmental variables so as to maintain the water potential above a certain critical limit to avoid catastrophic declines in the water potential. For the Navel on Troyer scion-rootstock combination used in this study, the dynamics of leaf water potential were described using equation 2.5 above in a typical whole-tree water balance model. The model calibration procedure involved systematically adjusting the values of the hydraulic parameters (R_x and C) and the soil water potential (ψ_s) to minimise the squared differences between the measured and the modelled stem sap flow and the leaf water potential, weighted by the squares of the errors in the measurement of each quantity as

$$\chi^2 = \sum \frac{(\text{model} - \text{data})^2}{\text{error}^2} \qquad (2.7)$$

where χ is the variable being minimized.

This was achieved using the Marquardt iterative method within the Model-Maker software package. Errors of 10 % for the stem sap flow measurements (Baker and van Bavel, 1987) and a larger error of 20 % for the unreplicated and variable leaf water potential measurements were used for the model optimisation. Data collected on 6 July 2005 was used for calibrating the model.

Typical values of the hydraulic parameters R_x and C that gave the best fit for the young orange trees on Troyer rootstock are shown in Table 2.1. The soil water potential at the surface of the roots was predicted to be approximately -0.5 MPa. In addition, the hydraulic resistance estimated by the model (47.9 h MPa kg^{-1}) was considerably larger than the one estimated from the inverse of the slope of the linear regression of stem sap flow against the water potential graph (31.0 h MPa kg^{-1}) in Fig. 2.13, albeit with a low coefficient of

determination (R^2 = 0.36). Contrary to the earlier assumption made on R_x in the model formulation above, Fig. 2.13 shows that the stem resistance to water transport in the young orange trees was in fact not constant throughout the day and this is a potential source of uncertainty in the model performance.

Table 2.1 *Comparison of the hydraulic parameters (R_x and C) of three young tree species namely, citrus (Baianinha Navel budded on Troyer citrange rootstock), beech and oak trees on typical clear days. Estimates of the hydraulic parameters for beech and oak trees were obtained from Steppe (2004). The stem diameters were measured adjacent to the point of stem sap flow gauge installation.*

Parameter	Citrus	Beech	Oak
R_x (h MPa kg $^{-1}$)	48 ± 3	39.7 ± 0.4	17.2 ± 0.1
C (kg MPa $^{-1}$)	0.28± 0.02	0.0016 ± 0.0003	0.0031 ± 0.0007
Internal storage use (%)	14.0	2.2	3.4
Stem diameter (mm)	11.3	18.0	17.9

Typical estimates of R_x and C from *in situ* measurements on intact young beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) trees (Steppe, 2004) are also shown in Table 2.1. These young trees were growing outdoors and were comparable in size to the orange trees investigated here. Additional estimates of the capacitance from *in situ* measurements on intact trees, larger in size than the young orange trees studied here are in the range 0.4 – 2.0 kg MPa^{-1} (Meinzer *et al.,* 2003).

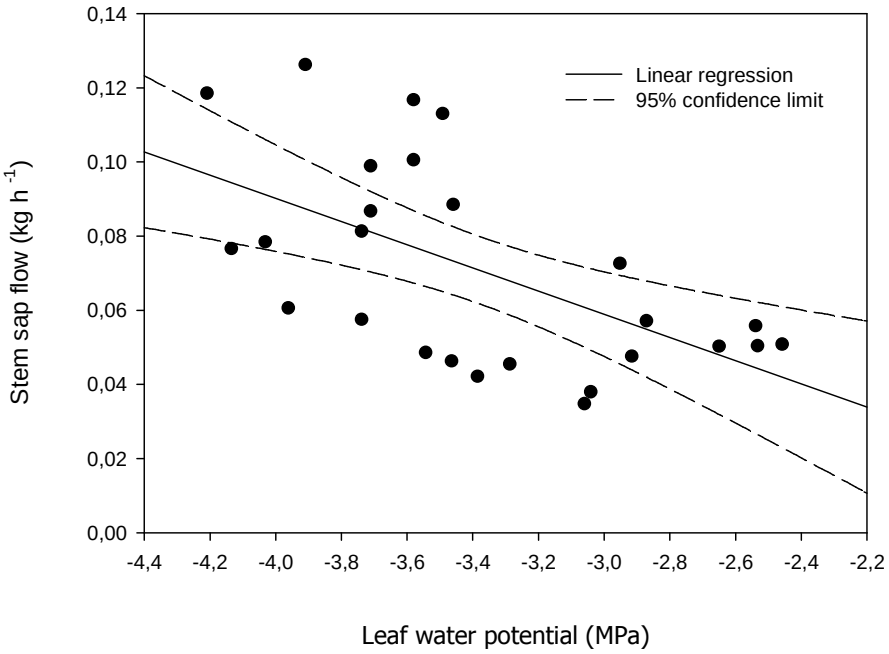

Fig 2.13 *Relationship between changes in the leaf water potential and stem level sap flow. The inverse of the slope of this graph is a measure of the hydraulic resistance of the stem and this appeared to vary throughout the measurement period. Dotted lines indicate the 95 % confidence limits.*

Figure 2.14a illustrates the performance of the model in predicting the leaf water potential of the young orange trees while Fig. 2.14b shows the course of sap flow at the base of the stem using the data for DOY 187. Despite the tendency by the model to predict slightly lower values than the measured ones at low water potentials, both quantities followed cyclic oscillations with an identical period to the sap flow indicating that the oscillations in leaf water status were somewhat related to the dynamics of water transport. An improved fit of the model to the measured data could be obtained by including, for example, a variable hydraulic resistance function. Model validation was done using the data for DOY 185 to 186 (not used for model parameterisation) as shown in Fig. 2.15. The model predicted the stem sap flow of the orange trees to within 10 % of the true values.

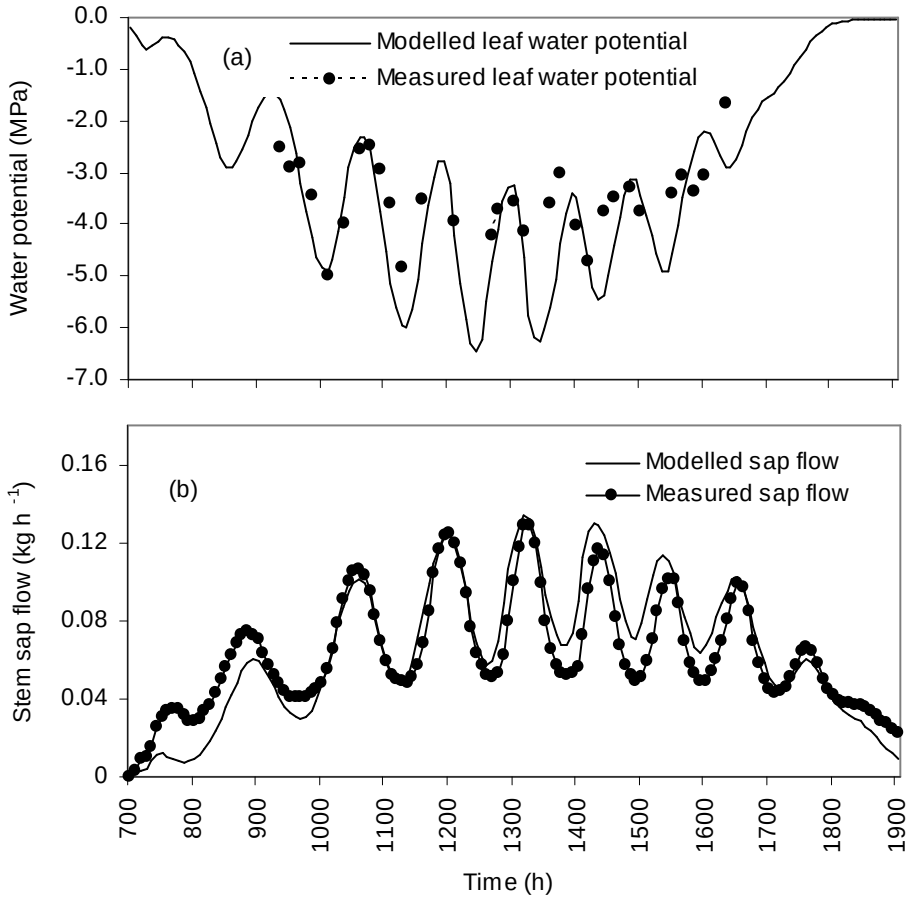

Fig 2.14 *(a)Comparison of the measured (full circles) and the predicted leaf water potential (continuous line) on 6 July 2005 (DOY 187). Leaf water potential measurements were taken from 1040 till 1740 h (Local Time, GMT + 2h). Given the long intervals between the leaf water potential measurements (10 – 20 min), interpolation was done with the aid of the water balance model. (b) Comparison of the predicted (continuous line) and measured (full circles) stem sap flow of the young orange trees.*

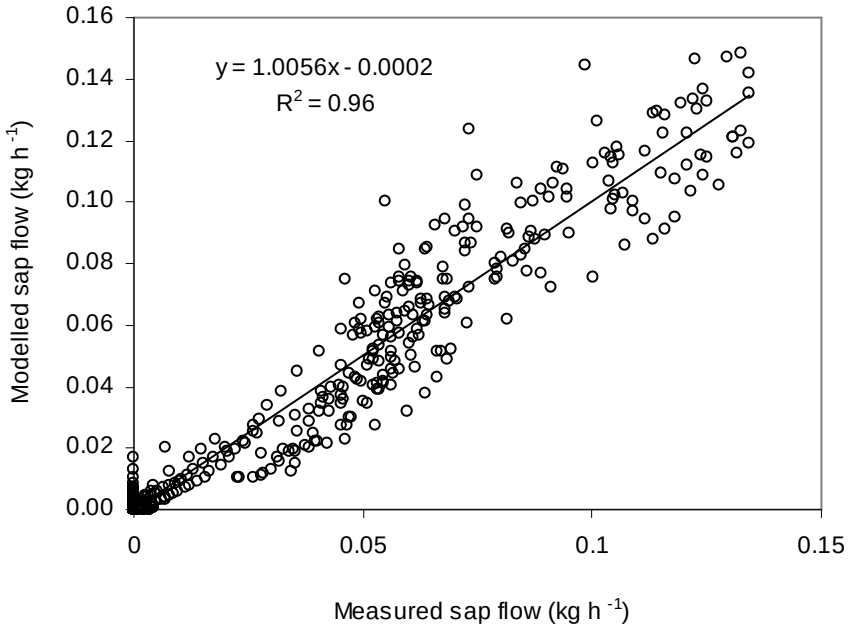

Fig 2.15 *Validation of the water balance model using sap flow data collected over a period of two days (DOY: 185 - 186).*

It is apparent from Table 2.1 that the hydraulic resistance of this scion-rootstock combination of orange trees is marginally larger than that of other trees, notably three-year-old oak and beech trees, while the capacitance is more than hundred times higher for the orange trees than for young beech and oak trees. Studies on different tropical trees (Goldstein *et al.,* 1998) showed that species with high water storage capacities tended to rely more on their internally stored water to sustain high transpiration rates. This was indeed true for the young orange trees where the high capacitance led to a larger utilisation of internally stored water during transpiration (14.0 %) compared to young beech (2.2 %) and oak (3.4 %), respectively, on typical clear days. In addition, the humidity dependence of sap flow for the orange trees both at branch (Fig 2.16a) and stem level (Fig 2.16b) over a single day (DOY 187) showed a significant hysteresis effect which is a further indication of the high capacitance. In Fig 2.16, the VPD was increasing (route 1) from sunrise (~0620 h) untill 1400 h and decreasing (route 2) from 1405 h until sunset (~1730 h). The hysteresis effect can also occur due to xylem cavitation (Brodribb and Holbrook, 2004; Buckley, 2005), but the occurrence of this phenomenon cannot be fully ascertained at present.

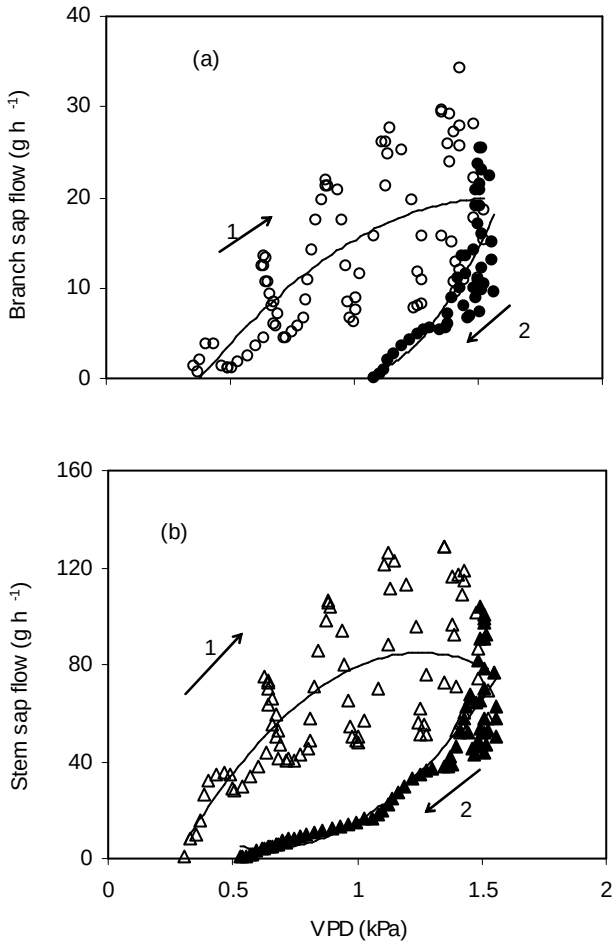

Fig 2.16 *Relationship between sap flow at branch (a) and stem level (b) with the vapour pressure deficit (VPD) of the air for Tree 1 during the increasing (route 1) and decreasing (route 2) VPD on DOY 187. The increasing VPD (open circles Fig 2.16a and open triangles Fig 2.16b) was from 0600 to 1400 h, while the decreasing VPD (closed circles Fig 2.16a and closed triangles Fig 2.16b) was from 1405 to 1800 h.*

Despite the high capacitance, which should ensure an abundant source of water to meet the atmospheric evaporative demand, the fact that the leaf water potential of these orange trees dropped at regular intervals throughout the day (Fig 2.14a) suggested the occurrence of periodic water deficits in the leaves as further proven below.

2.4.4 Tree level water balance, leaf water potential and stem diameter variation

The dynamics of water uptake by the roots can be inferred from stem sap flow measurements, assuming there is no capacitance in the roots, while the transpiration rates provide information on water loss from the tree. The difference in the daily courses of water uptake and loss gives the dynamics of the internal water storage of the trees. Figure 2.17 shows that for the young orange trees. The imbalance between water supply by the roots and demand by the leaves strongly influenced the course of the measured leaf water potential. When water loss exceeded uptake, leaf water potential dropped (more negative), while high leaf water potentials (less negative) were associated with water uptake exceeding loss.

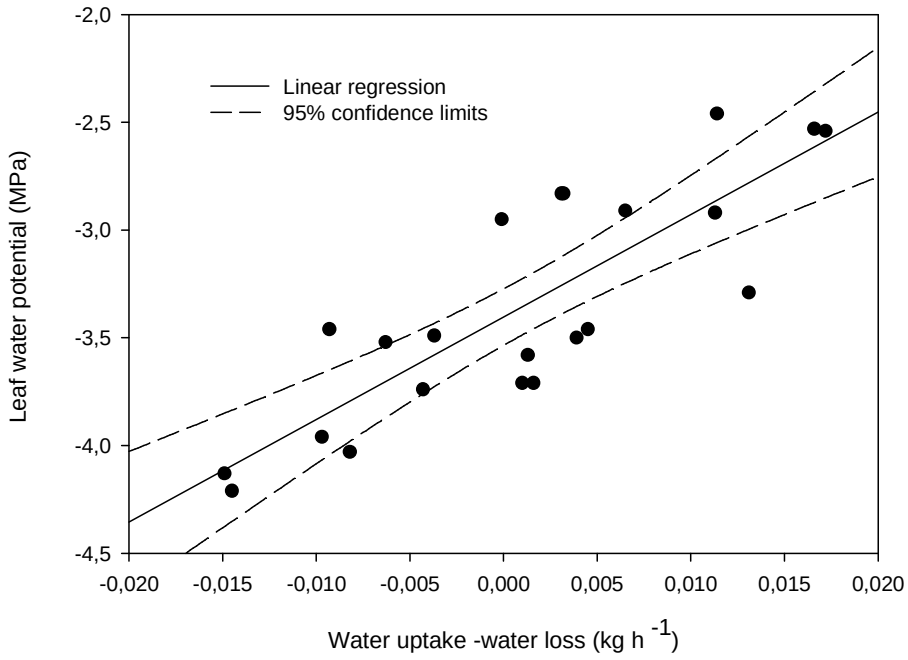

Fig 2.17 *Effect of the imbalance between water uptake (stem sap flow) and water loss (branch sap flow scaled to the whole crown) on the course of leaf water potential of the young orange trees during a typical clear day. It is evident that the course of leaf water potential was strongly dependent on the water supply to the leaves. Measurements used in the graph were taken between 1130 and 1630h on DOY 187. Dotted lines are 95 % confidence limits.*

Further independent evidence of the occurrence of temporal internal water deficits due to changes in internal water storage is shown by the evolution of the stem diameter in Fig 2.18. The cyclic changes in the internal water storage were accompanied by the oscillations in stem diameter with an identical period of approximately 70 min but phase shifted (Fig 2.18b). Stem

diameter variations lagged behind the changes in the internal water storage by approximately 15 to 20 min as shown in Fig 2.19d. According to Génard *et al.* (2001), the time lag between the rate of change in the stored water and the stem diameter could be due to a high radial hydraulic resistance between the water storage compartments in the stem (e.g. the bark) and the conducting xylem tissue. For young oak and beech trees, for example, this time lag was found to be negligible (Steppe and Lemeur, 2004). However, for the orange trees studied here, the large time lag suggests the existence of a high radial resistance. The possible implication of this high resistance is that the water stored in the stem tissues (e.g. the bark) is not readily available to replenish the water deficits that will have occurred in the xylem vessels in the short-term. This leaves the soil as the most important water source to maintain the leaf water status in the short-term but this too takes time. The high capacitance seems to be in the leaves than elsewhere in the transpiration stream.

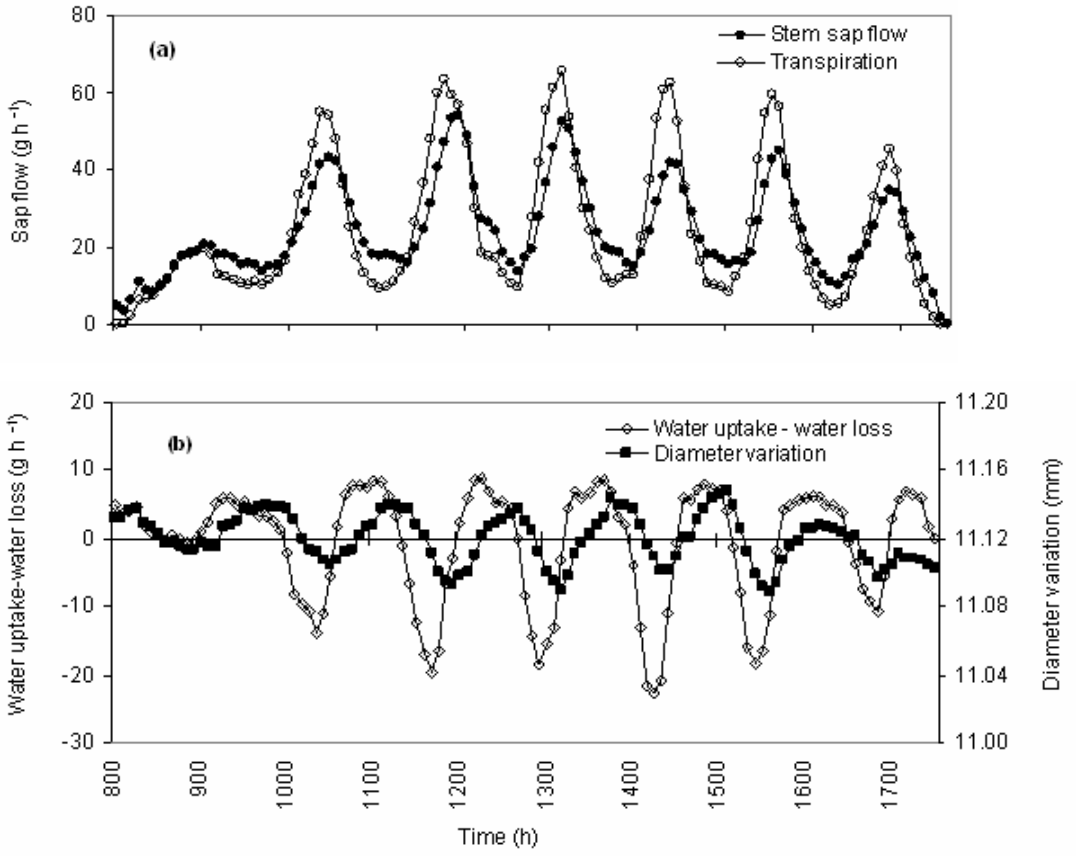

Fig 2.18 *Effect of the changes in the internal water storage of the young orange tree on stem diameter on a typical clear day (DOY 187). (a) Time series of transpiration (water loss) and stem sap flow (water uptake). (b) The difference between water uptake and loss influences the evolution of the stem diameter.*

2.4.5 Time lags and their effects on oscillations

Comparison of the stomatal conductance and branch sap flow in Fig 2.12 reveals that branch sap flow lagged behind the stomatal conductance by approximately 20 min as clearly illustrated in Fig 2.19a. The time lags were determined by cross-correlation of the two variables by imposing systematic time shifts (Philips *et al.*, 1997). Stem sap flow best matched branch sap flow by imposing a 5 min time lag in stem sap flow as shown in Fig 2.19b. Consequently, the time lag between transpiration and water uptake by the young trees was at least 25 min. The internal water deficits arising from these time lags seemed to be an essential feature for the occurrence of the oscillations, as hypothesized by Lang *et al.* (1969). In addition, the occurrence of a higher time lag between the stomatal conductance and branch sap flow than between the branch and stem sap flows suggested that the high resistance to water transport or high capacitance is most probably downstream of the branch.

As shown in Fig 2.20 the cyclic oscillations in leaf water potential were accompanied by oscillations in the stomatal conductance. The maximum conductance and minimum leaf water potential were out of phase by approximately 20 min (Fig 2.19c). Stomates started opening when leaf water potential was high (less negative) and started closing when leaf water potential was low (more negative). While the exact mechanism of stomatal movements is still unresolved, generally these can be explained based on two approaches (Buckley, 2005; Steppe *et al*., 2006b). The first mechanism involves the effect of a hydro-passive, positive feedback response, which is purely hydraulic and causes stomata to open when increased transpiration reduces the turgor pressure in the guard and epidermal cells. Loss of turgor pressure from the guard cells causes closure of the stomatal aperture, while the aperture tends to open due to loss of turgor pressure in the epidermis. Any increase in transpiration, for example due to an increase in the atmospheric evaporative demand, lowers the epidermal turgor pressure more than the guard cell turgor and thus supports stomatal opening through the mechanical advantage of the epidermis (Kaiser and Kappen, 2001; Franks, 2004; Buckley, 2005). The reverse effect acts when stomata close.

The second possible mechanism is the hydro-active, negative feedback response where an increase in transpiration acts as a closing stimulus. It involves an active (i.e. bio-chemically mediated) physiological response of guard cells to perturbations of the leaf water potential. With increased transpiration, active regulation of guard cell osmotic pressure will reduce guard cell turgor and cause stomatal closure. This physiological response of guard cells lags behind the stimulus (probably leaf water potential) and is responsible for the relatively slow turgor mechanism (Kaiser and Kappen, 2001). The hydraulic effect acts more rapidly and precedes the slower physiological feedback response, which acts in the opposite direction

(Buckley, 2005). However, for the orange trees studied here, the dynamics of water supply to the leaves appear to have a direct bearing on the sensitive stomatal movements observed through the rapid fluctuations in the bulk leaf water potential.

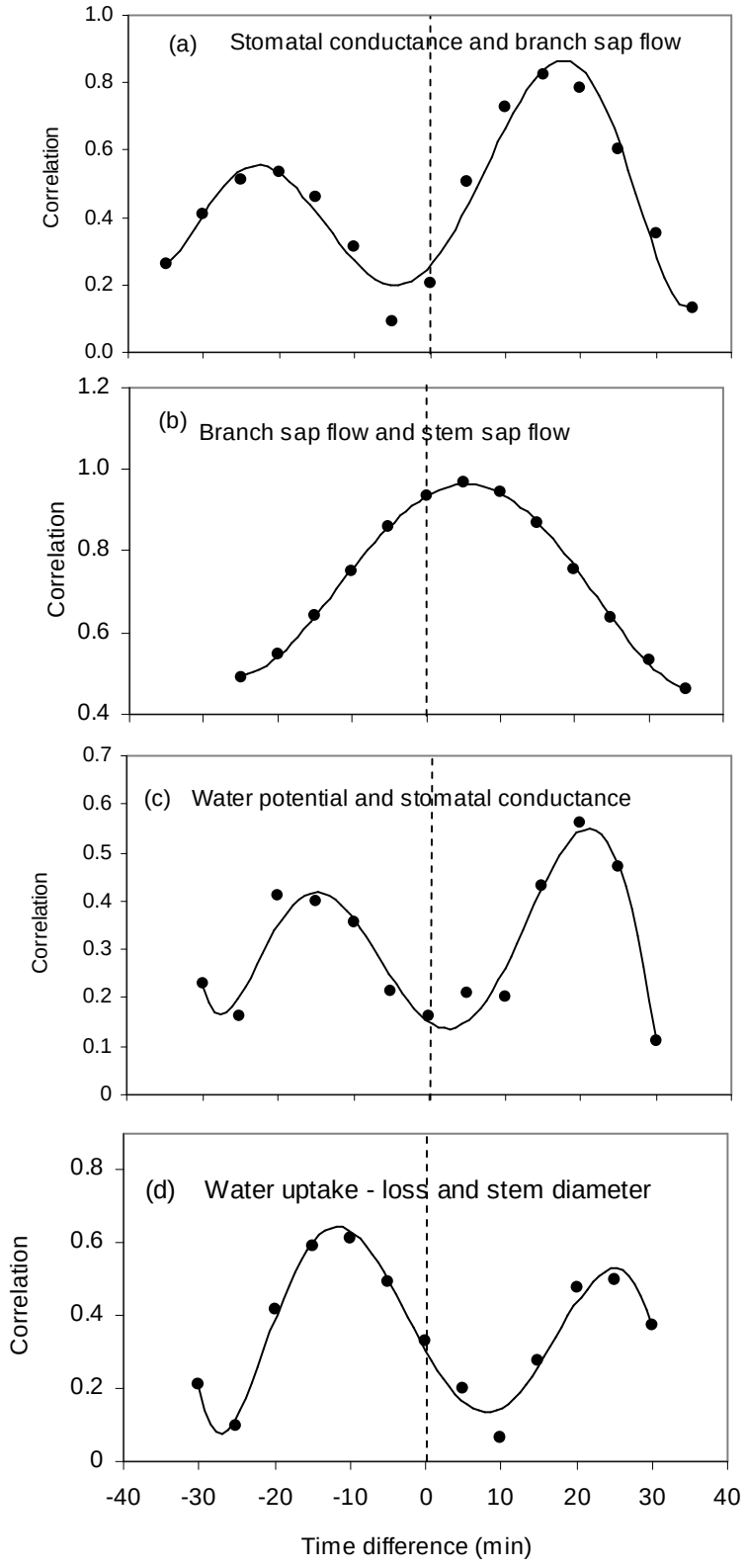

Fig 2.19 *Phase relationships of different water transport variables as influenced by stomatal oscillations. (a) Cross-correlation between the stomatal conductance and the branch sap flow. Stomatal conductance had a phase lead of approximately 20 min compared with branch sap flow. (b) The phase relationship between the branch and stem sap flow rates with the branch sap flow leading the stem sap flow by approximately 5 min. (c) Correlation between the stomatal conductance and the leaf water potential. Leaf water potential had a phase lead of approximately 20 min over the conductance. (d) This shows the oscillations in stem diameter lagging behind the difference between water uptake and loss by the stem by approximately 15 min. Negative values of time in the x-axis depict time lags, while positive ones show time leads. Only the larger peak correlation coefficient was considered in the analysis and the differences in the peaks in (a), (c) and (d) were significant at $P<0.05$.*

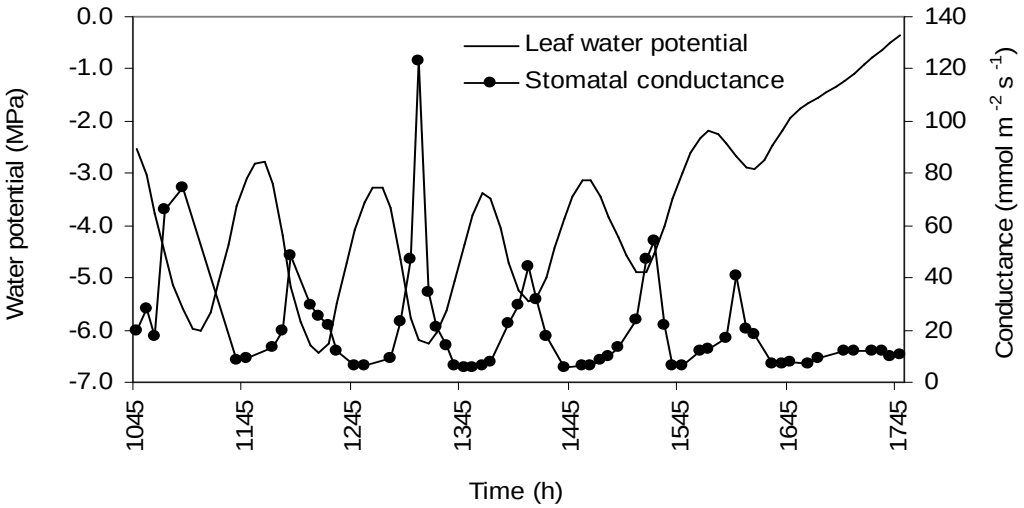

Fig 2.20 *Comparison of the diurnal course of the measured stomatal conductance and the modelled leaf water potential for Tree 1 on 6 July 2005 (DOY 187). The peak in the stomatal conductance clearly lagged behind that of the leaf water potential by approximately 20 min, but with an identical period. This showed that water supply to the leaves influenced the size of the stomatal aperture, but with a significant time lag.*

2.5 Conclusions

The creation of transient internal water deficits due to the imbalance between water supply and demand seem to have an important role in the generation of the stomatal oscillations. It is probable that these oscillations occur to prevent the excessive depletion of the leaf water status due to limitations in water supply. While for most trees, the high capacitance confers elasticity to their hydraulic system by availing the internally stored water to meet the atmospheric evaporative demand, it appears that the replenishment of the internally stored water once utilised is much slower for these orange trees leading to fluctuations in the internal storage and, hence, the bulk leaf water potential. Increasing the stem capacitance in the model by arbitrary values to ensure abundant water supply for transpiration by the trees, we observed that the oscillations tended to dissipate as shown in Fig 2.21. This observation suggests that drastic reductions in internally stored water occur in the citrus trees such that an even larger capacitance would be needed to ensure normal non-oscillating leaf water potential changes.

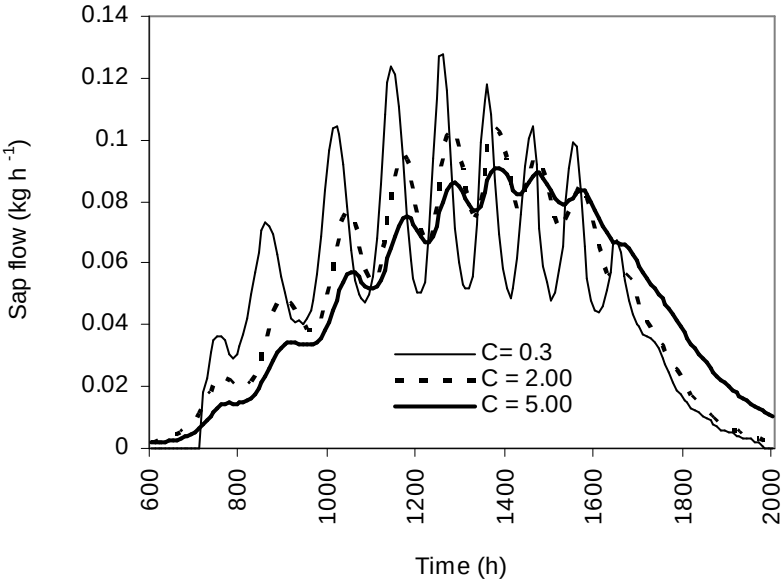

Fig 2.21 *Effect of changing the whole tree capacitance on the oscillations in stem sap flow. At higher capacitances, the tendency to oscillate was reduced.*

The slow supply of water to the leaves suggested the existence of a high hydraulic resistance somewhere in the transpiration stream. In addition, we are uncertain of the overall importance of the radial transfer of water from the stem tissues into the xylem vessels of citrus trees. While the large time lag in water transport downstream of the branch suggested the occurrence of a high resistance in the leaves, it is also highly probable that this high resistance could be elsewhere in the transpiration stream e.g. in the roots. This is supported by the cyclic changes in stem diameter, which proved that the deficits were not localised to the leaves but they occurred throughout the transpiration stream. The possibility of an additional high resistance occurring in the roots is explored in the next chapter.

Comparative work of the root hydraulic resistance for citrus in relation to other trees is important to provide insights into the suspected water uptake difficulties by citrus trees leading to the cyclic opening and closure of the stomata. Related to this, is the need to thoroughly investigate the possible occurrence of cavitation and its rapid reversal as a possible source of the high resistance. Recent studies conducted in intact plants using cryogenic scanning electron microscopy have shown that the number of embolized vessels can decrease during the daytime, suggesting that embolism repair can occur concurrently with transpiration (Tyree *et al*., 1999; Bucci *et al*., 2003). In addition, recent studies by Brodribb and Holbrook (2004) showed a rapid reversal of the xylem cavitation during the daytime.

Chapter 3 Rootstock effects on stomatal oscillations of orange trees [*Citrus sinensis* (L.) Osbeck]: measurements and modelling

Parts of this chapter have been submitted to Acta Horticulturae as proceedings of the 8th International Symposium on Modelling in Fruit Research and Orchard Management held in Switzerland from 1 – 5 July 2007.

Dzikiti S, Steppe K, Lemeur R, Milford JR. Modelling the water transport dynamics in young Navel orange trees budded on rootstocks commonly grown in northern Zimbabwe

3.1 Introduction

Until the mid 1800s, citrus trees were propagated from seeds. The grave damage to seedling orange trees by disease, especially *Phytophtora* foot rot, led to a shift in favour of grafted (or budded) trees where the top part, which bears fruit, is genetically different from the rootstock (Spiegel-Roy and Goldschmidt 1996). Citrus cultivars (scions) are budded onto rootstocks with desirable attributes such as resistance to disease, cold, drought and their effects on tree size and yield. A summary of common citrus rootstocks is presented in Table 3.1.

For example, citrus producers in the warmer but seasonally arid northern parts of Zimbabwe prefer growing the Navel variety of orange trees whose fruit matures several weeks earlier than that from the relatively cool parts of Southern Africa. The Navel orange scions are commonly budded on two rootstocks namely, the Rough lemon [*Citrus jambhiri* (Lush)] and the Troyer citrange [*Citrus sinensis* x *Poncirus trifoliata* (L.) Raf] or some close relative of these two rootstocks. The Rough lemon rootstock has a deep root system and it produces large trees with high mean yield per tree but with fruit of low internal quality. Trees on this rootstock are generally drought tolerant. Orange trees grafted on the shallow rooted Troyer citrange rootstock are smaller in size, yield per tree is relatively low but of higher internal quality than those on Rough lemon.

It has been outlined by Castle (1995) that the internal quality of citrus fruit is strongly dependent on the rootstock effects on the water relations of the trees. For example, Valencia orange trees on the vigorous rough lemon rootstock tended to maintain high leaf water

potentials but produced fruit with low soluble solids and low juice content than less vigorous rootstocks (Albrigo, 1977). The exact mechanism by which these fruit quality attributes are achieved is not clear. But it is thought that indirect effects e.g. the high yields and excessive vegetative growth for trees on rough lemon rootstock result in fewer assimilates being availed to the fruit due to high competition. Another possible and indirect reason for the low soluble solid content of trees on rough lemon is the excessive mutual shading of leaves and fruit which causes lower photosynthetic rates and, thus, less accumulation of solids.

In the previous chapters, it was shown that the water relations of the Navel orange trees are characterized by cyclic oscillations and plant water status plays an important role in the generation of the oscillations (Dzikiti *et al*., 2007). However, it is not clear whether the roots have a significant role in delaying the availing of water to the evaporation sites in the leaves leading to transient water deficits. In this chapter, we investigate this possibility by evaluating the water relations of Navel orange trees budded on two rootstocks with contrasting water uptake capabilities namely, the Rough lemon and the Troyer citrange rootstocks.

We argue based on whole-tree level water balance of the Navel orange trees that firstly, in addition to a high resistance downstream of the branch, another high resistance, probably in the roots contributes to the overall inefficiency in water transport to the leaves thus increasing the imbalance between water supply to and demand in the leaves. Finally, we demonstrate that by keeping a low leaf water potential, for example, by imposing a severe soil drought stress, small stomatal apertures are maintained with a limited tendency to overshoot the optimal size so that the oscillations die out. Typical values of the hydraulic parameters of the transpiration stream of the orange trees on the two rootstocks are estimated with the aid of the whole-tree level water balance model described in Chapter 2 and applied to trees on the different rootstocks.

Table 3.1 *Characteristics of the principal citrus rootstocks (adapted from Spiegel-Roy and Goldschmidt, 1996)*

Common name	Botanical classification	Main characteristics
Sour orange	*Citrus aurantium*	Cold tolerance; foot rot tolerance; good compatibility; vigorous; high fruit quality; often relatively low yields.
Rough lemon	*Citrus jambhiri*	Deep rooted large trees; high susceptibility to *Phytophtora*; blight; low fruit quality; high early yields.
Volkamer lemon	*Citrus volkmeriana*	Similar to Rough lemon; cold hardier, more tolerant to *Phytophtora parasitica*.
Rangpur Lime	*Citrus reticulate var austere x Citrus limon*	High early yields; salt tolerance; fruit quality mediocre; sensitve to *Phytophtora.*
Alemow	*Citrus macrophylla*	High early yields; susceptible to tristeza; xyloporosis; fruit quality moderate to low; sensitive to cold; blight.
Sweet orange	*Citrus sinensis*	Tolerant to trisfteza; fruit quality high; very susceptible to Phytophtora; moderate to high blight tolerance.
Cleopatra mandarin	Citrus sinensis x Poncirus trifoliata *Citrus reticulate*	Small fruit size; salt tolerance; fruit quality high; slow growth in nursery; tolerant of high pH.
Carrizo citrange	*Citrus sinensis* x *Poncirus trifoliata*	High yield and good fruit quality; susceptibility to exocortis; tolerant to burrowing nematode.
Troyer citrange	*Citrus sinensis x Poncirus trifoliata*	Similar to Carrizo; no resistance to burrowing nematode; relatively good tolerance to cold.

3.2 Materials and methods

3.2.1 Experimental site and plant material

To study the water transport dynamics in Bahianina Navel orange trees [*Citrus sinensis* (L.) Osbeck] budded on two different rootstocks namely, the deep rooted Rough lemon [*Citrus jambhiri* (Lush)] and the shallow rooted Troyer citrange [*Citrus sinensis* x *Poncirus trifoliata* L. Raf], an experimental set-up was established outdoors on the flat roof of the Physics Department, University of Zimbabwe, Harare (17°79'S , 31°04'E, elevation 1450 m above sea level). The measurements were conducted during 2003/4 and 2005/6, respectively.

Plant material comprised six young Navel orange trees budded on Rough lemon rootstocks for the experiments in 2003/4 and on Troyer citrange rootstocks in 2005/6. The trees were planted in asbestos pots, approximately 70 cm diameter and 50 cm deep as described in Chapter 2. Navel orange trees on Rough lemon rootstock were planted in the pots on 13 December 2002 while the trees on Troyer rootstock were planted on 18 July 2004. The growing medium in the pots was the clayey loam soil as already described in Chapters 1.

Two healthy and actively growing trees budded on the Rough lemon rootstock (2003/4) and the Troyer citrange rootstock (2005/6) were selected for the experiments and instrumented to study their response to environmental variables in detail. All six trees could not be investigated simultaneously due to limitations in the number of sensors. Microclimatic measurements were taken as described in Chapter 1. In addition, measurements were taken before the trees outgrew the pots and the restriction on the root volume was minimal.

3.2.2 Physiological measurements on potted trees

Measurements of sap flow on the potted trees were made using SGA9 and SGA5 heat balance sap flow sensors (Dynamax, Houston, TX, USA) installed on the stem and the branch, respectively, of each of the two young model trees. Mean diameters of the stem and the branch at the sensor installation positions were 9.0 $\pm$ 0.2 mm and 5.5 $\pm$ 0.2 mm for the Rough lemon rootstock in 2003/4. In 2005/6, with the trees grafted on Troyer rootstock, mean diameters at stem and branch level were 11.5 $\pm$ 0.2 mm and 6.0 $\pm$ 0.2 mm, respectively. Care was taken to avoid the dead wood at the bud union for the installation of the stem sap flow gauges. A strip of thin plastic was wrapped around the sections where the sensors were to be installed to ensure that possible transpiration by the green parts of the young trees did not affect the signals. Weather shields and a double layer of aluminium foil were installed around the gauges. In addition, the exposed parts of the stems below the stem sap flow sensors were covered with aluminium foil to the soil surface to minimize the effects of exogenous heating on

the stem especially early in the morning and at sunset. No measurements of root sap flow were taken on these days due to sensor malfunction.

Stem diameter variations were monitored midway between the branch and stem sap flow sensors using dendrometers (DEX 70 and DEX 20, Dynamax, Houston, TX, USA). The accuracy of the dendrometers was ± 10 µm. All the sensors were connected to two dataloggers (CR23X, Campbell Scientific Ltd, Shepshed, UK) programmed with a 5 s scan interval and all signals averaged every 5 min. To unravel the effect of the relationship between water uptake by the roots of the orange trees and loss by the leaves on plant water status, leaf water potential was measured on clear days (on 7 February 2004, Julian day of year: DOY 32, for Rough lemon rootstock and on 6 July 2005, DOY: 187, for Troyer citrange rootstock) using a thermocouple pyschrometer. Both days were cloudless and typical of the seasons. The thermocouple psychrometer comprised four standard C-52 sample chambers (Wescor Inc, Logan, UT, USA) connected to a microvoltmeter (HR-33T, Wescor, Inc, USA) operated as described in Chapter 2. Leaf water potential measurements were taken at hourly intervals from 0400 to 2000 h in February 2004 and at 10 – 20 min intervals from 1000 to 1730 h (Local time = GMT + 2 h) in July 2005. Additional measurements of the leaf water potential and the stomatal conductance were taken on 11 September 2005 [DOY: 254] with the trees on Troyer citrange rootstock under severe drought stress. The stomatal conductance was measured using the AP4 porometer in continuous cycles also as described in Chapter 2.

3.2.3 Comparison of the hydraulic characteristics of the two citrus rootstocks

The differences in the hydraulic properties of the Navel orange trees budded on the two rootstocks can be unravelled using the simple, dynamic whole tree-level water balance model (Philips *et al*., 1997; Steppe *et al.,* 2006a; Dzikiti *et al*., 2007) already described in Chapter 2. Model calibration for the Navel orange trees on Rough lemon rootstock was done using the data for 7 February 2004 (DOY: 32) and validated using the sap flow data collected on 2 October 2003 (DOY 275) for the same rootstock. For the trees on Troyer citrange rootstock, model calibration was done using the data collected on 6 July 2005 (DOY: 187) and validated using the data of 8 September 2005 (DOY: 251). The Marquadt iterative tool within the Model-Maker software package was used to derive the best values of the hydraulic parameters (R_x and C) and minimized the squared differences between the measured and the modelled leaf water potential and the stem sap flow rates, respectively, weighted by errors of 10 % for the stem sap flow and 20 % for the leaf water potential measurements.

3.3 Results and discussion

Active stomatal control of transpiration by the Navel orange trees budded on both the Rough lemon and the Troyer citrange rootstocks was apparent from the evolution of sap flow which followed cyclical oscillations as shown in Fig 3.1. This was despite the fact that the key climate factors driving transpiration, namely the radiation and the vapour pressure deficit of the air were not changing rapidly (Fig 3a and d). The fact that the oscillations occurred on both rootstocks suggested that a high resistance to water transport (e.g. in the leaves of the Navel scion itself) was probable as discussed in Chapter 2. Oscillations from the trees on Troyer citrange rootstock had a period of between 70 and 75 min (Fig 3.1b) with a large and nearly constant amplitude. This contrasted with the oscillations from the trees budded on Rough lemon rootstock which had a shorter and variable period of oscillation ranging from 55 min in the morning and late afternoon to 35 min around midday (Fig 3.1e) and a variable amplitude. The larger and sustained oscillations for trees grafted on Troyer citrange rootstock suggested that the stomata closed much more than on the Rough lemon rootstock.

Stem diameter also followed cyclic oscillations with an identical period to that of sap flow for both rootstocks (Fig 3.1c and f), respectively. However, the relationship between the stem diameter oscillations and the sap flow oscillations was dependent on the difference between water uptake by the roots (F) and loss by the leaves (E) as clearly illustrated in Fig 3.2. Many researchers have reported an increased tendency to produce stomatal oscillations when the vapour pressure deficit (VPD) of the air increased (Naidoo and von Willert, 1994; Kaiser and Kappen, 2001; Buckley 2005), while others attributed the oscillations solely to the effects of chemical ions on the guard cell osmotic potential, e.g. the Ca^{2+} ions (Upadhyaya *et al*., 1988; Yang *et al*., 2003). But the high correlation between the evolution of the leaf water potential and the balance between water uptake and loss (Fig 2.17; for the Troyer) suggests that rather than directly responding to the changes in the ambient humidity per se as proposed by the authors above, the stomata respond to the changes in the whole-tree (or local) water balance induced by the high VPD. When high transpirational water losses are not matched with a rapid water uptake, then stomatal closure is inevitable to avoid a catastrophic decline in the leaf water potential (Carlson and Lynn, 1991; Goldstein *et al*., 1998). This is illustrated by the fact that the extent of stomatal closure was not as pronounced in the Rough lemon rootstock, which is known to be more efficient in terms of water uptake than the Troyer citrange rootstock. This fact is clearly illustrated in Fig 3.1 which shows that the sap flow per unit leaf area was nearly twice as large in the rough lemon rootstock (e) than the Troyer citrange rootstock (b). This agrees with the observations by Albrigo (1977) who observed a consistently high plant water status for orange trees budded on the Rough lemon rootstock

than other rootstocks. The leaf area was approximately 0.62 m^2 for orange trees on the Troyer citrange rootstock and 0.47 m^2 for trees on the Rough lemon rootstock.

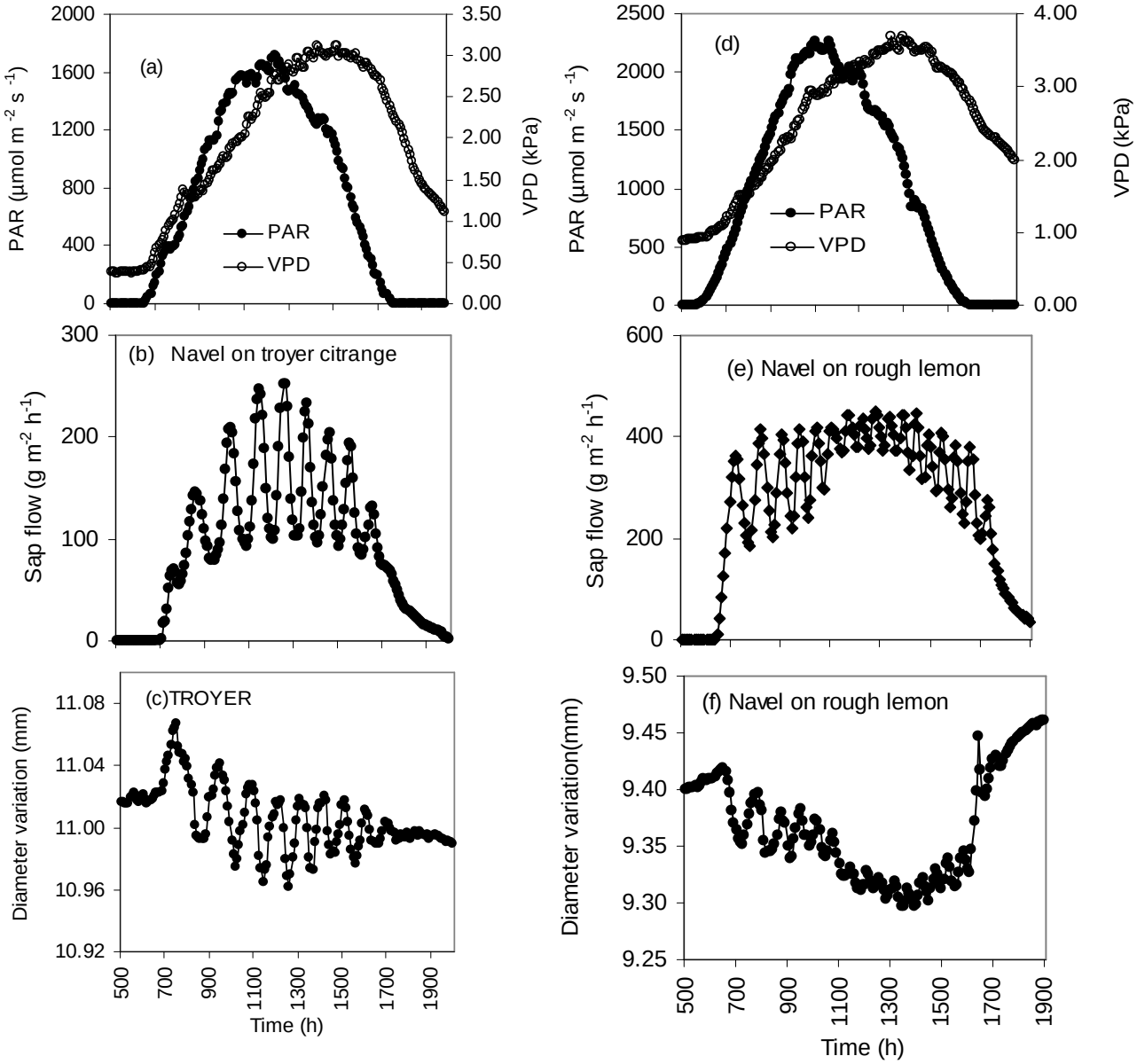

Fig 3.1 *Comparison of the diurnal characteristics of the oscillations in two year old Navel orange trees budded on the Troyer citrange and the Rough lemon rootstocks. (a) and (d) shows the diurnal course of the driving climatic variables, the photosynthetically active radiation (PAR) and the vapour pressure deficit of the air (VPD) for sap flow on typical clear days in September 2005 and October 2003, respectively. The courses of the stem sap flow rate for trees budded on Troyer citrange and on Rough lemon rootstocks, are shown in (b) and (e). The corresponding evolution of the stem diameter is shown in (c) for trees on Troyer*

citrange and (f) for trees on Rough lemon rootstock. The data are five minute averages presented in local time (GMT + 2 h).

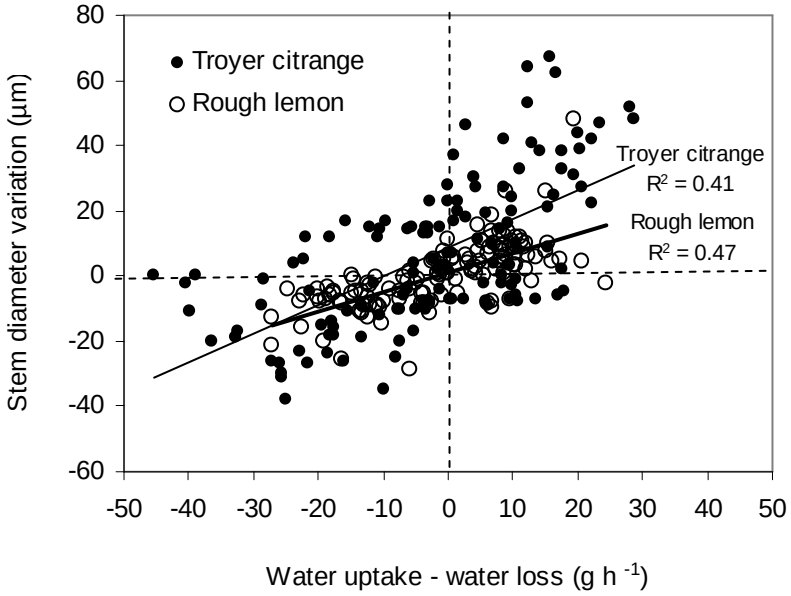

Fig 3.2 *Effect of the imbalance between water uptake and loss on the variations in stem diameters of young Navel orange trees on Troyer citrange rootstock (closed circles) and Rough lemon rootstock (open circles). Transient changes in the internal water content of the trees due to the imbalance between water uptake and loss are closely correlated with the changes in stem diameter.*

Further restricting water uptake by imposing a severe drought stress on both rootstocks caused the oscillations to diminish as illustrated by the course of stem sap flows in Fig 3.3. Drought stress was imposed by allowing the soil to dry over several days. This stress led to small stomatal apertures (low transpiration rates) with a reduced tendency to overshoot the optimal aperture size. For example, trees on Troyer citrange rootstock showed a more drastic reduction in the amplitude of the oscillations (Fig 3.3b) than those on Rough lemon rootstock (Fig 3.3d) because the roots of the Rough lemon rootstock can scavenge for water better than those of the Troyer citrange rootstock. Thus the roots of the Rough lemon were still able to supply water to the leaves, albeit in smaller quantities, and the oscillations did not completely dissipate.

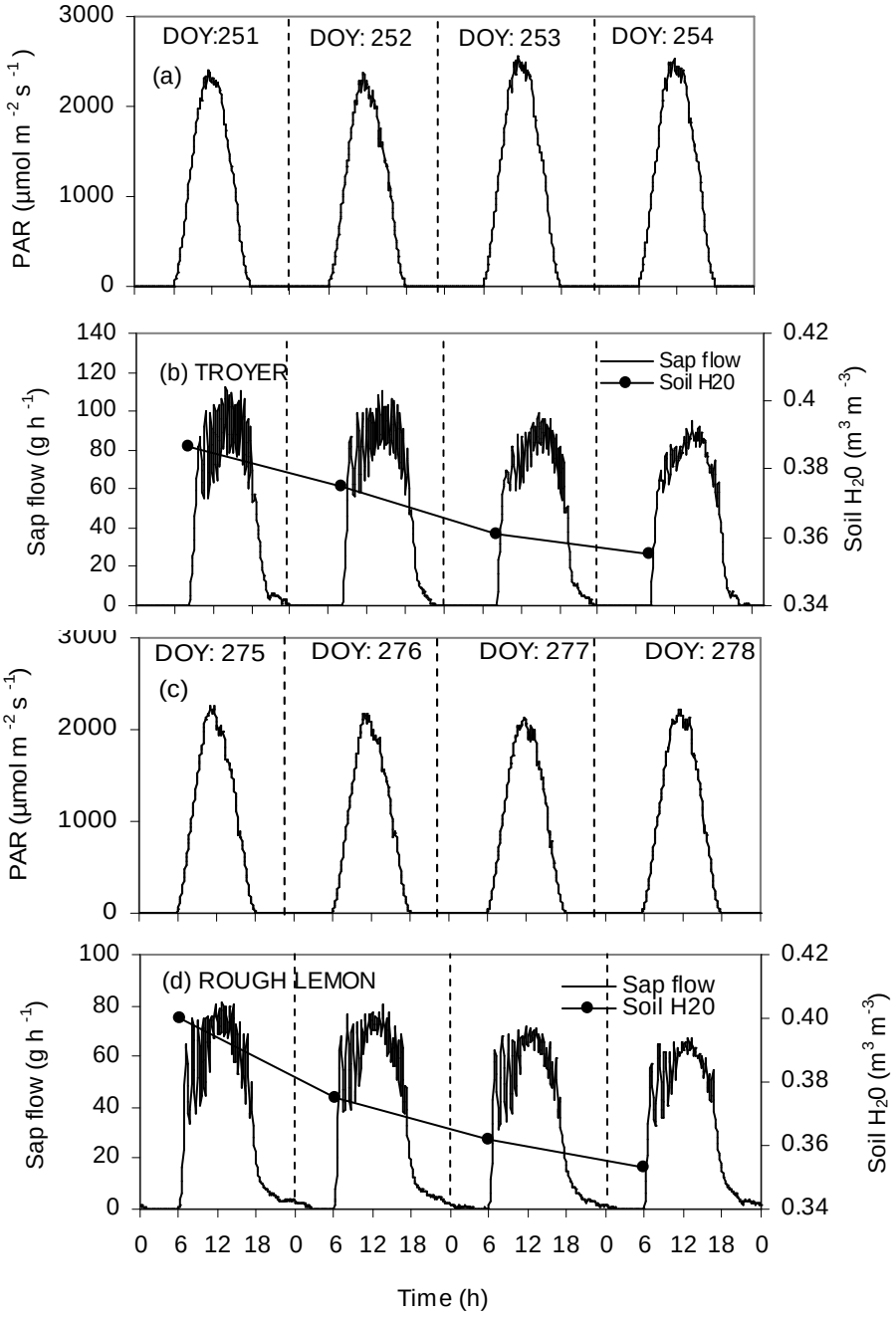

Fig 3.3 *Restricting water supply to the leaves by imposing drought stress in the root zone leads to consistently small stomatal apertures and a limited tendency of the aperture to overshoot the optimal size and thus eliminating the oscillations. Results are presented for stem sap flow of trees on Troyer citrange rootstock (b) and the Rough lemon rootstock (d) over a four day drying cycle in Zimbabwe with clear sky conditions (a and c). The data are five minute averages presented in local time (GMT + 2 h).*

The fact that low stomatal apertures were maintained was confirmed by the comparison of the stomatal conductances of a well-watered and a water-stressed tree shown in Fig 3.4. In the

severely water-stressed orange tree, the stomatal conductance showed a narrow range of variation from 10 to slightly over 50 mmol m^{-2} s^{-1} with an average value lower than 50 mmol m^{-2} s^{-1}. The range of variation in the well-watered tree on the other hand was from around 10 to over 150 mmol m^{-2} s^{-1}. These measurements were taken on a clear day in spring in Zimbabwe.

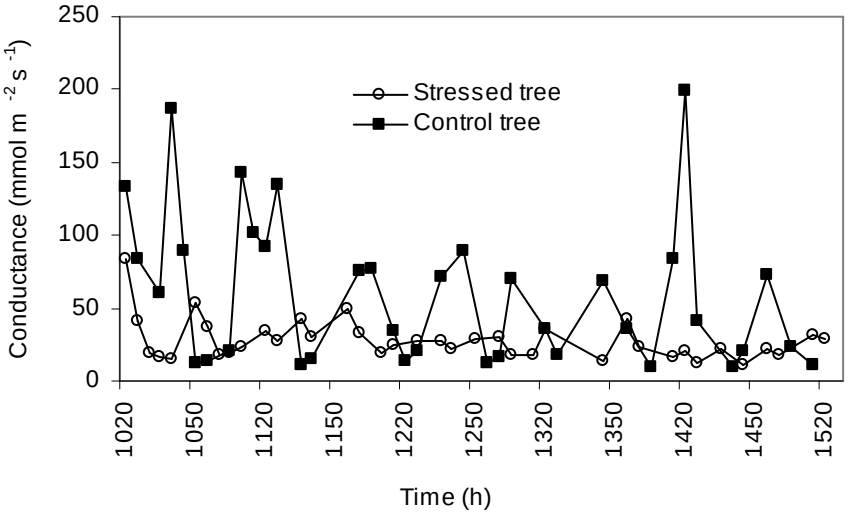

Fig 3.4 *Comparison of the stomatal conductance of a well-watered tree (closed circle) and a severely water-stressed Navel on Troyer orange tree on 11 September 2005 [DOY 254]. The stomatal conductance was consistently low for the drought stressed tree implying the maintenance of low stomatal apertures.*

A plot of the evolution of the stomatal conductance with the leaf water potential for a drought stressed tree is shown Fig 3.5. In the drought stressed tree, the leaf water potential oscillated about a low value of approximately -4.0 MPa and it exceeded a high value of -3.0 MPa only on few occasions. Whether the consistently low stomatal conductance with a limited tendency to overshoot to larger values was a direct result of the low leaf water potentials cannot be fully ascertained, but a cause and effect between these variables is probable (Franks, 2004; Buckley, 2005). The suppression of the oscillations due to the restricted water supply to the leaves are clearly seen when the stomatal conductances for a well-watered and a water-stressed Navel orange tree are compared with the branch sap flow as shown in Fig 3.6.

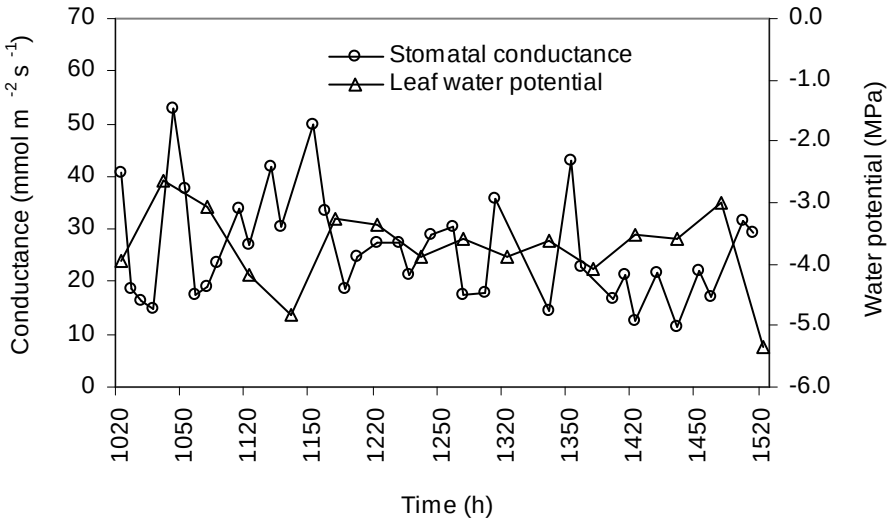

Fig 3.5 *Evolution of the stomatal conductance (open circles) and the leaf water potential (closed triangles) of a drought stressed Navel orange tree budded on a Troyer citrange rootstock.*

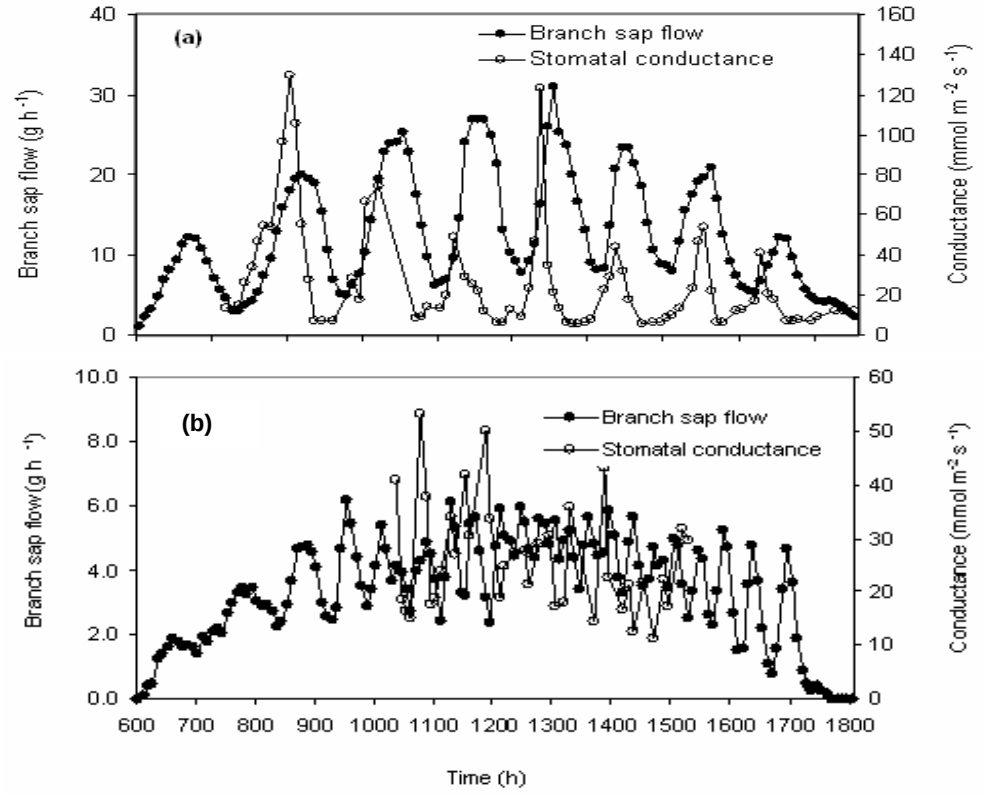

Fig 3.6 *Effect of severe drought stress on the relationship between the branch sap flow and the stomatal conductance. Results for a well-watered tree on Troyer citrange rootstock are shown in (a), while (b) shows the relationship for a drought-stressed tree also on Troyer citrange rootstock.*

The contribution of the internal storage pools to the daytime transpiration from sunrise to sunset, calculated as explained in Chapter 2 revealed important differences between the rootstocks which can be linked to the oscillatory behaviour. When the trees were well-watered (42 % v/v soil water content), less than 4 % of the total daytime transpiration came from the internal water storage pools for the Rough lemon rootstock compared to 10 % for the Troyer citrange rootstock. When subjected to moderate drought stress of approximately 38 % (v/v), a little over 5 % of the transpiration of the orange trees on Rough lemon came from the internal reserves, while as much as 22 % was derived from the internal storage pools for trees on the Troyer citrange rootstock as illustrated in Fig 3.7.

Navel orange trees on Troyer citrange rootstock thus extract approximately four times more water from their internal reserves to meet the transpirational demand at moderate drought stresses than those on Rough lemon rootstock. This heavy reliance on the internal storage for transpiration further indicates the inefficiency in water uptake by the Troyer citrange rootstock. The fact that the Navel orange trees on Troyer citrange rootstock give fruit with a better internal quality than those on Rough lemon rootstock is hardly surprising given the need for mild drought stress to improve the internal quality of citrus fruit (Castle 1995; Spiegel-Roy and Goldschmidt 1996). Trees on the Troyer citrange rootstock already experience drought stress even when a slight drop in soil water content occurs. The decline in the use of water from the internal storage at high drought stresses (Fig 3.7) was a result of the drastically suppressed oscillations causing a limited overshooting transpiration response (Fig 3.3b).

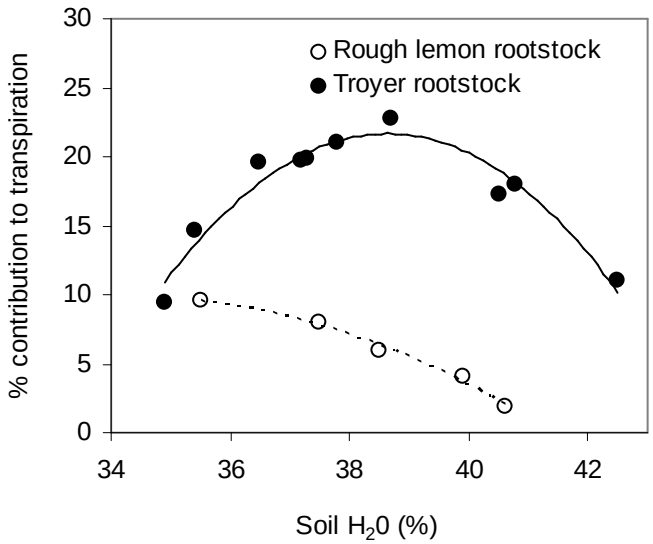

Fig 3.7 *Effect of soil drying on the utilization of the internally stored water by Navel orange trees on the Troyer citrange and the Rough lemon rootstock.*

Model estimates of the values of the hydraulic parameters (R_x and C) for the Navel orange trees on the two rootstocks are shown in Table 3.2. While the hydraulic resistances of the trees on the two rootstocks, 48 ± 3 h MPa kg^{-1} for the Troyer citrange and 57 ± 10 h MPa kg^{-1} for the Rough lemon, are not significantly different, these are substantially higher than those for two-year old intact oak (*Quercus robur* L., R_x = 17.2 ± 0.1 h MPa kg^{-1}) and beech (*Fagus sylvatica* L., R_x = 39.7 ± 0.4 h MPa kg^{-1}) trees, according to Steppe (2004).

Table 3.2 *Hydraulic model parameters (R_x and C) that gave the best estimates of the stem sap flow rate in young Navel orange trees budded on two rootstocks, namely the Rough lemon and the Troyer citrange rootstocks, respectively. The parameters were derived using the dynamic water transport model applied to the different rootstocks.*

Parameter	Navel/ Rough lemon	Navel/ Troyer citrange
R_x (h MPa kg^{-1})	57 ± 10	48 ± 3
C (kg MPa^{-1})	0.18 ± 0.06	0.28 ± 0.02
Stem diameter (mm)	9.4 ± 0.1	11.3 ± 0.1

The higher resistances in the citrus rootstocks suggest greater water uptake difficulties than in the other two species. This most probably contributes to the tendency to produce oscillations. However, the relative magnitudes of the resistances between the citrus rootstocks themselves are not conclusive. This may be because the measurements on the Rough lemon rootstock were done when the trees were relatively smaller than for the Troyer rootstock. The hydraulic resistance is known to be a function of tree size (Meinzer *et al*., 2004) with smaller trees having a larger resistance than bigger ones, while the capacitance follows the opposite trend (Table 3.2). Application of these model parameters to estimate the stem sap flow rates using the transpiration measurements on 2 October 2003 (DOY: 275) for the Rough lemon rootstock showed that the stem sap flow could be estimated to within 10 % of the true values as shown in Fig 3.8, illustrating that the water transport dynamics in the orange trees can be described using these parameters.

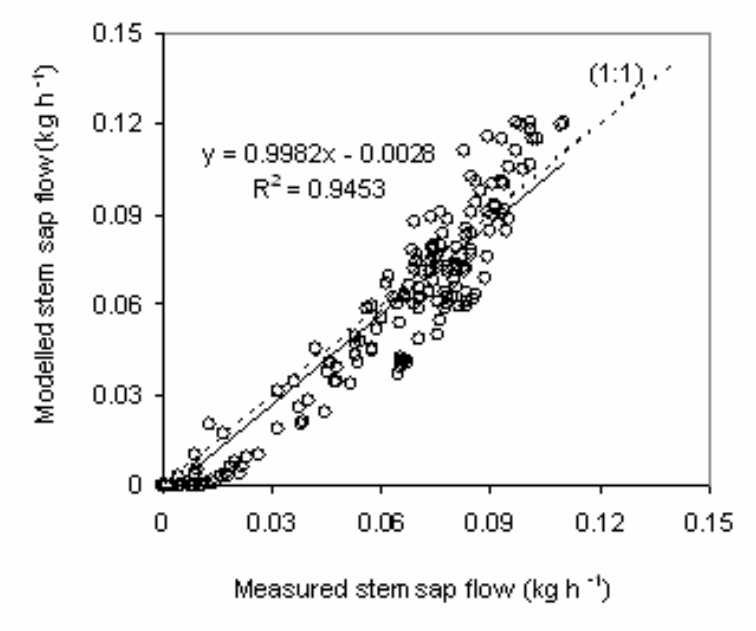

Fig 3.8 *Simulation of the stem sap flow of young Navel orange trees budded on Rough lemon rootstock using the dynamic water transport model and the hydraulic parameters shown in Table 3.2.*

3.4 Conclusions

The results presented in this chapter and the preceding one demonstrate that plant water status is indeed the main factor triggering stomatal oscillations in orange trees. The extent of stomatal cycling appears to be strongly dependent on either the tree-level and/or the local leaf-level water balance as affected by the balance between water supply to and demand in the leaves. While a high resistance downstream of the branch maybe a crucial factor in the generation of the stomatal oscillations as illustrated in the preceding chapter, the stomatal oscillations appear to be highly sensitive to the root resistance. This was clearly illustrated by the form of the stomatal oscillations when different citrus rootstocks were used on the same scion. The oscillations from trees on the Rough lemon rootstock, which is known to be efficient in water uptake, were less pronounced than those in the Troyer citrange rootstock which is less efficient in water uptake. The water uptake difficulties were illustrated by the heavy reliance on the internal water storage by young orange trees budded on the Troyer citrange rootstock which was comparable and in some cases greater than that in mature intact trees (Meinzer *et al*., 2003 and 2004).

However, the fact that the oscillations still occurred on the trees budded on the Rough lemon rootstock suggested that the root resistance was still high even for this rootstock compared

with other trees. This was confirmed by an even larger time lag in water uptake of approximately 35 min between the roots and the stem sap flow in young Navel orange trees budded on the Rough lemon rootstock as shown in Fig 1.15. The sensitivity of the oscillations to water availability in the leaves as affected by the root resistance was further demonstrated by the responses to drought stress. As the water became less available in the roots, the stomatal apertures remained small with a limited tendency to overshoot the optimal size, probably because the guard cells rarely attained full turgidity which seemed to trigger the overshooting response. Why the root resistance of citrus rootstocks could be generally high is unclear, but a reduced surface area for water absorption presumably due to few root hairs may be an important factor. Interestingly, the presence of the fibrous root hairs which are responsible for water uptake in citrus has been controversial for many decades (Spiegel-Roy and Goldschmidt, 1996) but was convincingly demonstrated by Castle and Krezdorn (1979). But their abundance and activity with respect to water uptake still need to be clarified (Cavazza *et al*., 1985; Spiegel-Roy and Goldschmidt 1996). Too few root hairs limit the efficiency of water uptake and, thus, it is difficult for the tree to meet the atmospheric evaporative demand.

Buckley (2005) suggested the occurrence of cavitation and its rapid reversal as a possible cause of the existence of a fluctuating hydraulic resistance leading to transient changes in the efficiency of water transport to the leaves, thus, possibly causing the stomatal oscillations. This possibility is supported by recent experimental evidence of cavitation repair under tension of the xylem vessels by Brodribb and Holbrook (2004), but convincing evidence to link this with the stomatal movements associated with the oscillations is largely missing.

PART B

RESPONSE OF ORANGE TREES TO THE PARTIAL ROOTZONE DRYING IRRIGATION STRATEGY AT MAZOWE CITRUS ESTATE

Chapter 4 Partial rootzone drying of drip irrigated 'Navel' orange trees [*Citrus sinensis* (L.) Osbeck] under semi-arid tropical conditions

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Dzikiti S, Steppe, K and Lemeur R. Partial Rootzone Drying of Drip Irrigated 'Navel' Orange Trees [*Citrus sinensis* (L.) Osbeck] under Semi-Arid Tropical Conditions

4.1 Introduction

The conventional irrigation strategy at Mazowe Citrus Estate, northern Zimbabwe, and indeed in most orchards elsewhere, involve the full replacement of water lost through evapotranspiration at daily time steps. Evapotranspiration estimates in these orchards are commonly obtained from class A evaporation pan readings or from climate data. Recent studies (Chalmers *et al*., 1981; Loveys *et al*., 1998) have shown that some important horticultural aspects of fruit trees such as the control of excess vegetative vigour, crop load and fruit quality can be improved when only a fraction of the evapotranspirational loss is replaced (Ferreira *et al*., 1996; Teviotdale *et al*., 2001; Jones, 2004). The practice of maintaining a controlled level of drought stress in the rootzone by replacing only part of the total evapotranspirational loss is called deficit irrigation.

This chapter seeks to investigate the potential benefits of deficit irrigation strategies to the productivity of Navel orange trees growing in the seasonally arid tropics in northern Zimbabwe. A particular deficit irrigation strategy of interest in this study is the partial rootzone drying (PRD) irrigation strategy (Loveys *et al*., 1998). An important advantage of the PRD strategy over other deficit irrigation methods is that it does not require the maintenance of precise soil water conditions. Thus, it can be readily implemented in plantations without elaborate environmental monitoring devices as is the case at Mazowe Citrus Estate. Significant water savings have been reported for different crops under the PRD technique (Dry *et al*., 1996; Kang *et al*., 1998; Mingo and Davies, 2001). But inconsistent results have also been observed in a number of cases depending on the crop, soil and even the local climatic conditions. For example, Kang *et al*, (2002) showed that 23 to 52 % water savings could be achieved for flood irrigated pears (*Pyrus communis* L.) under PRD without loss of yield or fruit size. But O'Connell

and Goodwin (2004), also working on pears under microjet irrigation, observed that the pear trees were in fact, under drought stress due to PRD with significant reductions in stem water potential. Recent studies with wine grapes (Vitis *vinifera* L.) (Chalmers *et al*., 2004) and red grapes (Bravdo *et al*., 2004) under semi-arid conditions showed no PRD responses (see below) by the trees. Such varied results reveal the importance of crop and even soil specific investigations with respect to the PRD method under different climatic conditions.

The response of the orange trees to the PRD strategy will be compared with their responses to other well-documented deficit irrigation methods such as the regulated deficit irrigation (RDI) (Domingo *et al*., 1996; Goldhamer and Salinas 2000). In addition, recommendations for the yet unresolved question of the appropriate control for drip irrigated fruit trees (Bravdo *et al*., 2004; Chalmers *et al*., 2004) are made for drip irrigated Navel orange trees growing in northern Zimbabwe. There is currently no consensus among fruit growers whether to use one drip line per row of trees or to use two drip lines with one line running either side of the tree row as the standard practice (Chalmers *et al*., 2004). Some of the heaviest criticism of the partial rootzone drying strategy arises from this lack of standardisation in the irrigation criteria. Some authors simply argue that, with two drip lines, more water than needed was already being applied and so the absence of a yield drop due to PRD where one drip line at a time is used is expected (Bravdo *et al*., 2004). The controversy concerns not only the amount of water being applied, but also the effects of the watering regimes on root growth and development. The fibrous feeder roots responsible for water and nutrient uptake in most fruit trees (including citrus) tend to grow in the irrigated zones (Spiegel-Roy and Goldschmidt, 1996). An efficient root system is essential to ensure adequate water and nutrient supply to the reproductive sites in the canopy. For example, most fruit tree growers in Australia employ double drip lines as their standard practice, while most growers e.g. in Israel and some parts of the USA use single drip lines (Bravdo *et al*., 2004). At Mazowe Citrus Estate, Zimbabwe, one drip line is also being used for trees of all ages and the effects on tree growth and productivity are not yet quantified. This chapter begins with a review, firstly of the annual growth cycle of citrus trees in the southern hemisphere and then the theoretical background of the deficit irrigation strategies. It includes a brief review of the root-to-shoot chemical signalling mechanisms involved in the stomatal control by PRD. Finally the details of the PRD trial at Mazowe Citrus Estate are discussed.

4.2 Vegetative growth and fruit development in citrus trees: literature review

4.2.1 Flowering

Citrus trees belong to the C_3 group of plants with photosynthetic rates lower than those of C_4 plants (e.g. most cereals like maize, millet and sorghum). Even among the C_3 group, citrus trees are in the low activity range being considerably lower than annual crop plants and lower still compared with deciduous fruit trees, e.g. apple (*Malus Domestica*) and grape (*Vitis vinifera* L.) (Spiegel-Roy and Goldschmidt, 1996). A typical growth cycle of the citrus fruit in northern Zimbabwe is shown in Table 4.1. Maximum shoot initiation occurs during late winter and spring with only sporadic growth occurring during summer and autumn (December and May). The shoots produced in spring (Fig 4.1) are the most important as these form the sites on which flowers develop. The spring period generally stretches from August to early October in Zimbabwe.

Table 4.1 *Typical growth cycle of citrus fruit at Mazowe Citrus Estate in northern Zimbabwe*

	Spring		Summer						Autumn		Winter		
	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
Bud-break (Spring flush)													
End of shoot elongation													
First flower opening													
Flowering													
Fruit-let drop (fruitset)													
Fruit growth			CELL DIVISION		CELL EXPANSION				MATURATION				
Summer flush													
Autumn flush													

A summary of the climatic conditions corresponding to each growth stage in a typical year at Mazowe Citrus Estate is shown in Table 5.3. Generally, most flowering shoots are produced on woody twigs of the previous year's spring flush, but they may also be borne on younger summer flush twigs or older twigs (Spiegel-Roy and Goldschmidt, 1996; Hutton, 2000). The newly formed shoots arise from lateral resting buds (Guardiola, 1997). Three types of shoots can be distinguished as illustrated in Fig 4.1, namely the vegetative, leafy inflorescent and the leafless inflorescent (regenerative) shoots. Citrus flowers develop on the leafy and leafless inflorescent shoots and none on the vegetative shoots although more fruitset occurs on the

leafy inflorescences than the leafless inflorescences. The primary role of the vegetative shoots is to ensure canopy growth to assist the trees to build up their carbohydrate reserves. These vegetative shoots are the dominant type of shoots produced in the summer and autumn flushes.

The process of flower development begins at bud break (i.e. when the shoots emerge). Whether this process occurs or not depends, to a large extent on correlative effects at shoot level. For example, when there is apical dominance, the development of the lateral flower buds is suppressed by a hormone called auxin produced by the terminal buds. But when growth of the terminal bud is slowed down (or stopped) then the lateral buds bearing flowers can develop. According to Guardiolla (1997), the extent of spring flowering is determined by three parameters which are not independent, namely 1) the number and age of the buds on the tree (as explained above), 2) the extent of bud break and 3) flower induction and development. Generally, induction is defined as the triggering of the flowering process by environmental factors resulting in a change in the pattern of development of the buds which become committed to flower (Guardiolla, 1997).

Two environmental stimuli play a major role in the induction of flowering in citrus trees. Chilling temperatures under the cooler subtropical climates (Lenz, 1969) and drought stress imposed for a period of several weeks under tropical conditions (Cassin *et al*., 1969) are the two main factors used for inducing flowering in citrus. Work by Southwick and Davenport (1986) showed that the two stimuli (drought stress and cold) operate independently and that they are separate flower inducing signals. Thus either of them can be used by growers to enhance flowering depending on the prevailing climatic conditions. Growers in northern Zimbabwe, for example, withhold water for several weeks in the winter season (May to July) to encourage intense flowering in spring. A common feature of these two stimuli is that they both cause dormancy of the terminal buds, which limits the production of auxins and thus promoting flowering by the lateral buds. Dormancy of the citrus buds is very weak and is imposed by the influence of other organs (paradormancy) and the intensity of flowering increases with the duration of the cold or water stress.

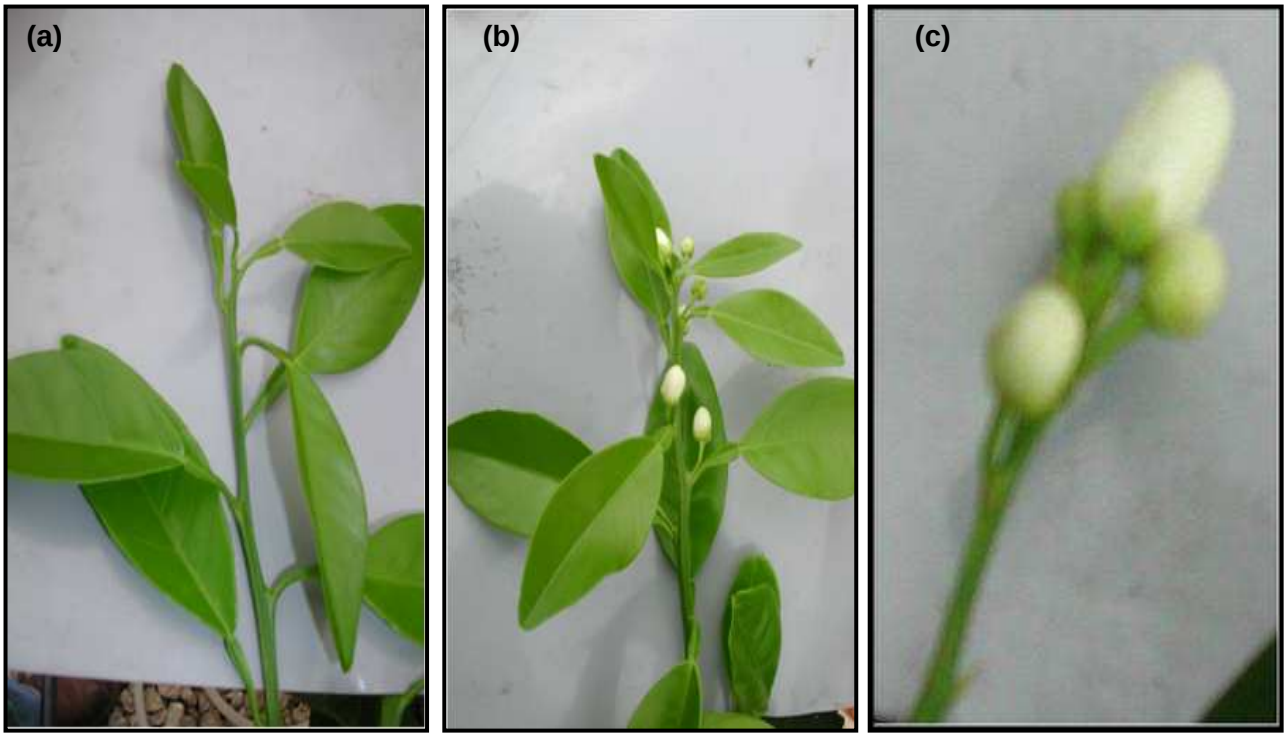

Fig 4.1 *Three types of shoots on a Navel orange tree. a) Vegetative shoot, b) Leafy inflorescence shoot and c) Leafless inflorescence shoots.*

4.2.2 Fruit development and maturation

Bain (1958) divided the development of citrus fruit into three major stages, namely stage I (cell division), stage II (cell expansion) and stage III (fruit maturation) as shown in Table 4.1. In reality these stages are not clearly distinguishable but they overlap considerably. The final crop load on the trees is dependent on both the flowering intensity and the severity of flower and fruit abscission during stages I and II. This stage I is assumed to commence at fruitset and extends from early October to early December in northern Zimbabwe. The final cell number of the fruit is determined at this stage and under ideal growth conditions, the final fruit size is to some extent also determined at this stage since fruit size depends on the number of cells in the fruit. The intensity of flowering is also thought to affect the final fruit size with high flower intensities leading to smaller sized flowers and ultimately smaller fruits (Guardiolla, 1997).

Fruitset is defined as the process through which the flower ovary adheres to the tree and becomes fruit (Davies and Albrigo, 1994). Normally citrus trees produce more flowers than the number that actually sets and produces harvestable fruits (0.1 – 3 % of the total). Though some researchers argue that fruit-let abscission, which occurs from mid November to mid December for Navel orange trees in Zimbabwe is a normal physiological mechanism to

regulate crop load, severe fruit-let drop can occur due to drought stress, heat stress and poor nutrition e.g. nitrogen deficiency thus negatively affecting the yield. Application of the deficit irrigation strategies during the fruit set period is thus not recommended as this can lead to substantial yield losses (Goldhammer and Salinas, 2000). In most cases, proper timing of the application of the deficit irrigation strategies is crucial to achieve desirable effects on fruit production.

The increase in fruit size during stage I is mainly due to the growth of the peel consisting mainly of cell division but there is already an element of cell expansion (stage II). The cell expansion phase (stage II) extends from December until April or early May in northern Zimbabwe depending on the cultivar. Fruit volume increases rapidly during the first three months of stage II and this period is important in the determination of the final fruit size. In fact, differences in fruit size at harvest reflect differences in cell division, while year to year variation in fruit growth rate is directly related to crop load (alternate bearing) and is mainly evident during the later part of stage II and stage III (maturation).

When the crop load in a given year is very high, the tree commits a substantial amount of its carbohydrate reserves to sustain the high yield and this usually leads to a smaller sized fruit. Excessive crop load in some years is thought to trigger alternate bearing due to fluctuations in the carbohydrate reserves from year to year with an excessive drain on the reserves occurring during the on-year (high yield year). Fruit growth continues during stage III with the growth rate depending on the availability of soil water, nutrients as well as the prevailing climatic conditions. A typical growth curve of a citrus fruit follows a sigmoid curve.

4.2.3 Fruit structure

Citrus fruit is composed of two major morphologically distinct regions namely the pericarp (also called the peel or the rind) and the endocarp which is the edible portion of the fruit (also called the pulp). A further distinction is also made within the peel. The external coloured portion is the epicarp mostly known as the flavedo whereas the internal white layer of the peel is the mesocarp (also known as the albedo). A detailed schematic diagram of the citrus fruit is shown in Fig 4.2.

During the early stages of fruit development, the flavedo is a dark green, photosynthetically active tissue with a relatively small number of stomata, approximately 20 – 40 mm^{-2} (Davis and Albrigo, 1994). Thus, some transpiration in fact occurs through the fruit as well. As the fruit approaches maturity, the chlorophyll is gradually lost and the chloroplasts are transformed into carotenoid-rich chromoplasts. During the early stages of fruit growth, when peel development

dominates, the albedo may occupy 60 – 90 % of the fruit volume. Later when pulp growth takes over, the albedo becomes thinner and the portion of the albedo declines (Spiegel-Roy and Goldschmidt, 1996). In the Navel cultivar of oranges, a small fruit is present at the stylar end of the main fruit although still enclosed in the peel. This fruit-let can reach a diameter of between 2 – 3 cm.

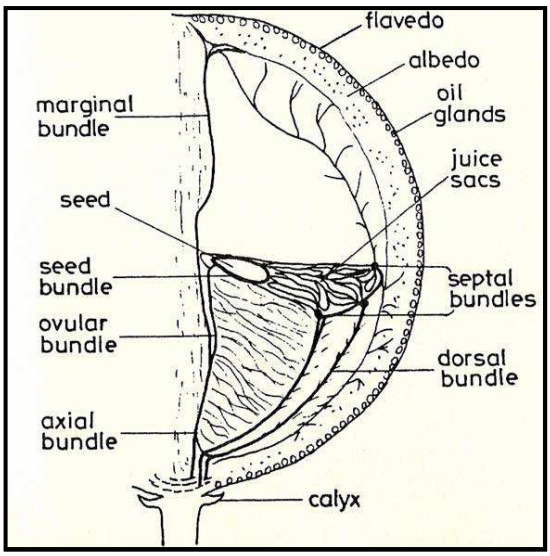

Fig 4.2 *Schematic diagram showing the structure of a mature orange fruit including its vascular system (after Spiegel-Roy and Goldschmidt, 1996).*

4.2.4 Effect of climatic factors on fruit development and quality

Temperature plays a crucial role in the world distribution of citrus given the high susceptibility to frost by both the citrus fruit and the trees themselves. In addition, the vegetative growth of citrus trees which determines the cropping potential of each tree and the growth rate of the individual fruit strongly depends on the ambient temperature. Little growth occurs in all citrus organs below a base temperature of 13 ℃. Given the relatively warm conditions in northern Zimbabwe, citrus fruit especially the Navel oranges mature earlier than fruit from elsewhere in the cooler parts of Southern Africa and, thus, they fetch competitive prices on the export market (Dupont, personal communication). In addition, the fruit from the warmer climates are generally larger in size than those from the cooler regions.

Climate affects the external quality of citrus fruit as well. For instance, peel colour is a major problem in the tropics since warm temperatures interfere with the loss of chlorophyll as well as the build up of carotenoids (red, orange and yellow pigments). When temperature is as low as 15 ℃, chlorophyll is degraded and carotenoids are synthesized. Increasing temperatures above 15 ℃ reduces carotenoid synthesis, but chlor ophyll degradation is increased until 28 ℃.

The best effect occurs in orange fruit exposed to a combination of cool day-air temperatures, cold–night-air temperatures and cool soil temperatures. Warm night-air temperatures (25 – 30 ℃) have a stronger effect than warm day-air tem peratures in producing re-green fruit. Consequently, orange fruit in the tropics do not acquire their attractive colour and they remain greenish. Combinations of high temperature and humidity result in tender, rapidly senescing fruit which has a low storage potential and is highly susceptible to peel blemishes (Davies and Albrigo, 1994).

The internal quality of the citrus fruit is also influenced by the prevailing climatic conditions. Fruit developing in the hot tropical climates tend to have a high total soluble solid content (TSS) which is a major requirement for the processing industry. In addition, these fruits are low in titratable acidity (TA) resulting in a poor edible quality. The soluble solids are mainly sugars, while the tritratable acids are brought about by the decomposition of citric acid which is the principal organic acid of citrus juice. The ratio of the TSS:TA is a widely used measure of the internal quality of citrus fruit (Goldhamer and Salinas, 2000; Hutton, 2000). Generally fruit with a high TSS:TA ratio are preferred for factory processing, while a low ratio is desirable for the fresh fruit market.

4.3 Response of fruit trees to soil drying

Severe drought stress on the one hand significantly limits canopy development by suppressing the vegetative growth which is essential for generating the flowering sites (Bacon, 2004). On the other hand, moderate drought stress often favours reproductive development rather than the vegetative growth in most fruit trees, including citrus trees (Chalmers *et al*., 1981; Hutton, 2000). This is a direct result of a changed resource allocation presumably due to the influence of endogenous chemical signals such as the abscisic acid (ABA). Bacon (2004) reported that fruit and seed development is accelerated in some species of fruit trees when drought stress is perceived, and chemical signals are again believed to be involved. Thus manipulation of the soil water environment with irrigation management can maximise biological activity and be used to improve economic return. A brief discussion of the role of the chemical signals in controlling plant response to soil drying which is the basis of the partial rootzone drying (PRD) irrigation technique is given below.

4.3.1 Chemical signalling

Plant roots can sense the availability of resources (e.g. water and nutrients) in the soil. This information is transmitted to the shoots by chemical signals (e.g. the ABA) so that appropriate control measures can be taken. For example, when the soil around the roots is drying the ABA

signals, generated in the roots in this case, are transported to the leaves via the xylem vessels to the guard cells. The presence of high levels of ABA in the leaves is known to be strongly correlated with stomatal closure (Wilkinson *et al*., 1998; Davies *et al*., 2002; Mingo and Davies, 2001; Bacon, 2004; Augé and Moore, 2002). In fact, the concentration of ABA signals in the leaves can be used as a proxy measure of the extent of soil drying. The ABA controls the stomatal aperture through the adjustment of the guard cell osmotic potential involving the active transport of K^+ and Cl^- ions across the guard cell plasma membranes as described by Assmann and Shimazaki (1999).

The fact that chemical signals play an important role in the control of water use and growth of fruit trees was convincingly demonstrated on potted apple trees (*Malus domestica*) planted with a split roots system by Gowing *et al*. (1990). The trees were planted with their root systems growing in two separate containers. They observed that by imposing severe drought stress on part of the root system by withholding water, while keeping the other pot near field capacity, both the stomatal conductance and the leaf growth rate declined. Leaf growth rate was only 50 % of that in the well-watered plants after three weeks of partial soil drying. However, after the excision of the roots in the dry soil, both the leaf growth rate and the stomatal conductance recovered to the same levels as the well-watered plants. This demonstrated the existence of a certain mode of signalling between the whole tree and the roots in the drying soil.

The abscisic acid (ABA) is arguably the most important stress response hormone involved in the control of water use by plants in drying soil (Wilkinson *et al*., 1998). This hormone is produced in the roots usually to maintain their growth rate so that they can continue to access water when subjected to soil drying. But it can also be produced elsewhere within the plant e.g. in the leaves of stressed plants. ABA produced in the leaves is transported to the roots via the phloem vessels and back up to the leaves via the xylem vessels (Davies *et al*., 2002). In this way, the ABA signals can be circulated through the different plant organs. This circulation of ABA is important since the roots are known to produce this hormone in large quantities such that if the large doses were to reach the leaves then the stomata will be in a permanent state of closure leading the death of the tree (Wilkinson *et al*., 1998; Davies *et al*., 2001). Thus only a small proportion of the hormone is filtered and reaches the stomata, while the rest circulates through the plant. The filtration process allows more ABA to reach the leaves with increasing levels of drought stress in the rootzone. The exact mechanism of the filtration process is still not fully understood. In addition to causing stomatal closure under drought stress, increased levels of the ABA in the leaves have also been observed to reduce the vegetative growth and, thus, minimising the transpiring leaf surface area (Davies *et al*., 2001; Mingo and Davies,

2001; Bacon, 2004). Recent experimental evidence (Christmann *et al*., 2005) suggests that instead of the ABA being generated in the roots in some plant species, it is in fact produced in the shoots when the roots are subjected to drought stress. But few studies exist to support this view.

Soil drying has been reported to raise the pH of the xylem sap such that there is often a good correlation between the soil water status and the xylem sap pH (Wilkinson *et al*., 1998; Mingo and Davies, 2001). For well-watered plants the sap pH is often acidic being approximately 6.0 and this rises to around 7.0 during the early stages of drought stress. The changes in the sap pH are thought to arise from the modified uptake and transport of inorganic ions by the roots in drying soil (Davies *et al*., 2001). For instance, nitrate deficiencies switch the activity of the enzyme nitrate reductase from the shoots to the roots giving rise to greater concentrations of the products of N reduction in the xylem, which are thought to alkanise the sap (Davies *et al*., 2001).

Slovik *et al*. (1995) provided evidence that ABA penetration to and uptake by the xylem vessels in the roots is maximised when the root sap pH is increased. Thus variations in the sap pH can also be used as another measure of soil drying. Other hormones which also have some control on the stomatal aperture include the xylem cytokinin concentration. Cytokinin transport to shoots will be disrupted by both soil drying and a modification in nutrient availability (Blackman and Davies, 1985; Davies *et al*., 2000). Cytokinins are important in the regulation of shoot growth and functioning. A schematic diagram of the chemical signalling network in a typical plant is shown in Fig 4.3.

Most importantly, however, chemical signals seem to respond faster to drought stress developing in the rootzone than the hydraulic signals e.g. changes in bulk water potential (Wilkinson and Davies, 2001). ABA synthesis in and transport from the roots can occur before the decreasing water content of the soil causes any measurable change in the water status of the leaves. Manipulation of the soil water status is therefore a potential tool for the orchard manager who wishes to exploit these long-distance root to shoot chemical signalling responses and this is best illustrated by techniques such as the PRD which will be discussed in detail in the next section.

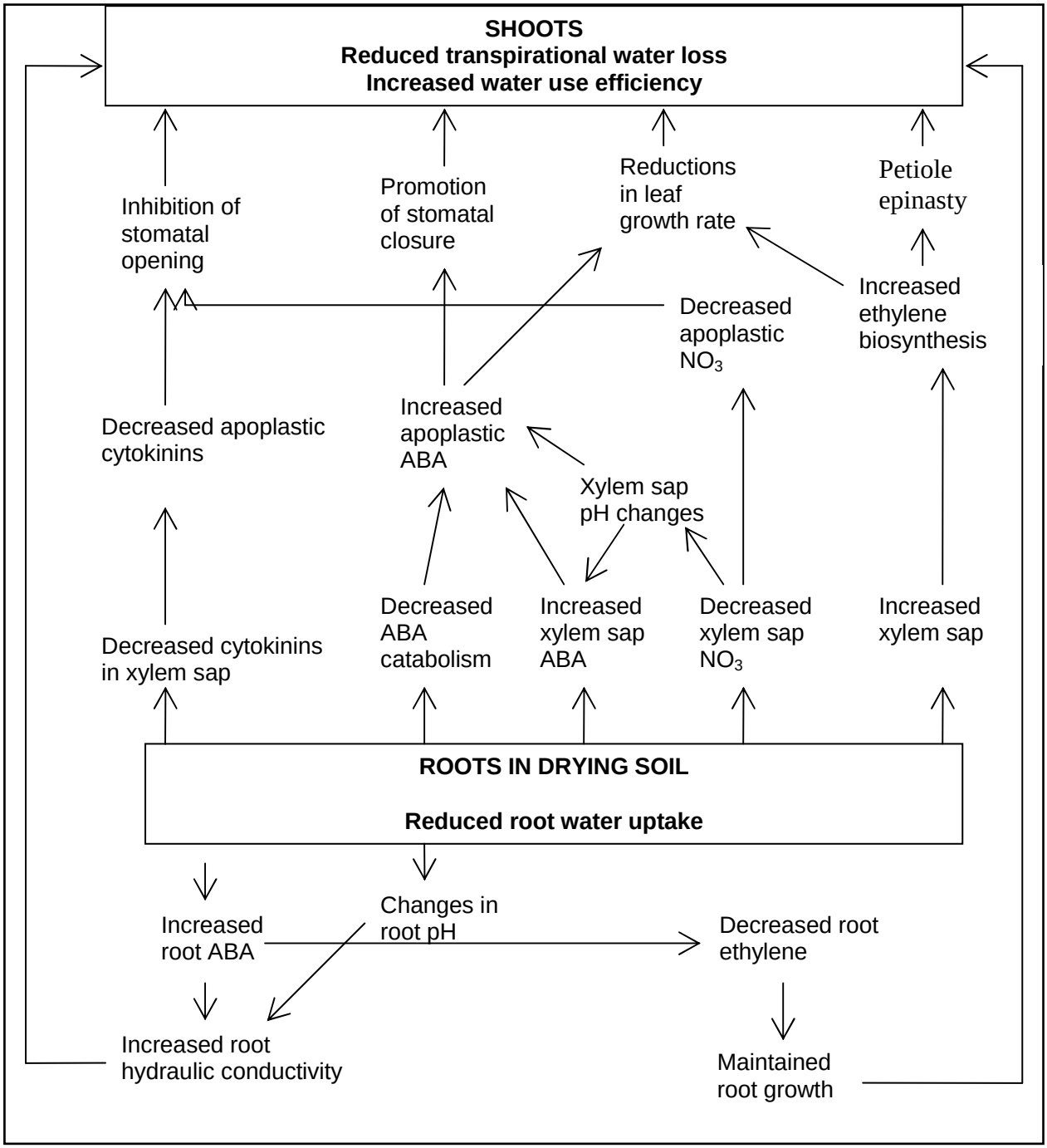

Fig 4.3 *Schematic diagram of the proposed signalling networks in a model plant experiencing a soil water deficit (adapted from Bacon, 2004).*

4.3.2 Regulated deficit irrigation and partial rootzone drying

Given the non-linear correlation between the decrease in water loss that is achieved and the decrease in CO_2 uptake as the stomata close when plants are subjected to soil drying, it is possible that water use efficiency can be improved by imposing a partial drought stress in the

rootzone. Water loss is restricted by stomatal closure sooner and to a greater extent than the reduction in CO_2 uptake. According to Bacon (2004), this non-linear relationship arises from the differences in the magnitude of the gradients of the two fluxes between the substomatal cavities and the outside of the leaf. The water vapour gradient is up to 100 times greater than the CO_2 gradient. Thus by imposing a controlled level of drought stress in the rootzone, it is possible that the stomatal aperture can reach an optimal size characterised by minimal transpirational losses and high (or unchanged) CO_2 assimilation rates. Irrigation techniques such as the regulated deficit irrigation (RDI) (Chalmers *et al*., 1981) and PRD are designed on the premise that improvement of water use efficiency can be achieved by manipulating the size of the stomatal aperture to maximise carbon gain at the expense of water loss as already explained above. This is in addition to the influence exerted by partial water stress to resource allocation which favours reproductive growth at the expense of vegetative growth.

4.3.2.1 Regulated deficit irrigation (RDI)

The regulated deficit irrigation (RDI) strategy is a technique in which water is either withheld or reduced during specific periods of fruit growth. A certain level of drought stress is maintained in the rootzone and the primary objective of its use in tree crops is to control the canopy size and to limit the applied water. Usually a fraction of the crop evapotranspiration (ET_c) is replaced during each irrigation rather than applying the full irrigation (100 % ET_c replacement). Successful implementation of the RDI strategy depends on a precise knowledge of the phenology of vegetative and reproductive development of the fruit tree under investigation. For example, periods when vegetative growth is normally high and fruit growth is low are ideal for the application of RDI since excess vegetative vigour can be curtailed by the water deficits and hopefully shift the resource allocation in favour of fruit development. On the other hand, application of the RDI during the sensitive periods e.g. flowering and fruitset is not advisable and thus much research has focused on the appropriate timing of the application of this strategy e.g. on citrus (Goldhammer and Salinas, 2000).

Recent work indicates that RDI can also improve certain horticulturally important aspects of various tree crops. For instance Goldhamer and Viveros (2000) showed that early season deficit irrigation can increase fruiting density in almond trees. Teviotdale *et al*. (2001) reported that midseason RDI can significantly lower the incidences of almond hull rot. The ability to maintain precise levels of drought stress in the rootzone is essential to achieve the desired results with RDI (Jones, 2004). Water deficits usually result in smaller fruit size at harvest, while excess water application will reverse the benefits of the RDI strategy namely to maintain fruit growth rate, while using less water and to improve some aspects of fruit quality. Application of the RDI method to mature Navel orange trees by Goldhamer and Salinas (2000)

in California showed that treatments that imposed water deficits early in the season resulted in slower fruit growth rates which then improved after the re-introduction of full irrigation such that fruit size at harvest was not affected. But severe midseason drought stress reduced the average fruit size at harvest.

However, the maintenance of the appropriate degree of water deficit is often difficult in practice and this poses a challenge for the successful implementation of the RDI strategy, especially in commercial orchards in developing countries where monitoring techniques for the soil and atmosphere environments are not well developed. In addition, the fact that reduced water application levels are only employed during short periods in the entire fruit growth cycle imply that overall water savings may not be significant at the end of each fruit growing season. For these reasons, techniques that lead to both water savings and good fruit yield and quality e.g. the partial rootzone drying (as reported for other crops) maybe better alternatives. But more work still need to be done to establish whether these benefits can indeed be obtained when PRD is applied to citrus trees.

4.3.2.2 Partial rootzone drying (PRD)

The idea of the partial rootzone drying (PRD) irrigation technique came from the split root experiment by Gowing *et al*. (1990) as described in section 4.2.1 above. The potential agricultural use of this split root drying technique was first realised by Loveys (1991) who suggested that it might be possible to use the technique as a method for controlling vegetative growth in crops where excess vegetative vigour was a disadvantage. Grape vines (*Vitis vinifera* L.) growing in South Australia generally produce excess foliage which has to be pruned away at some expense (Mingo and Davies, 2001). This crop has been used to show the positive effects of PRD.

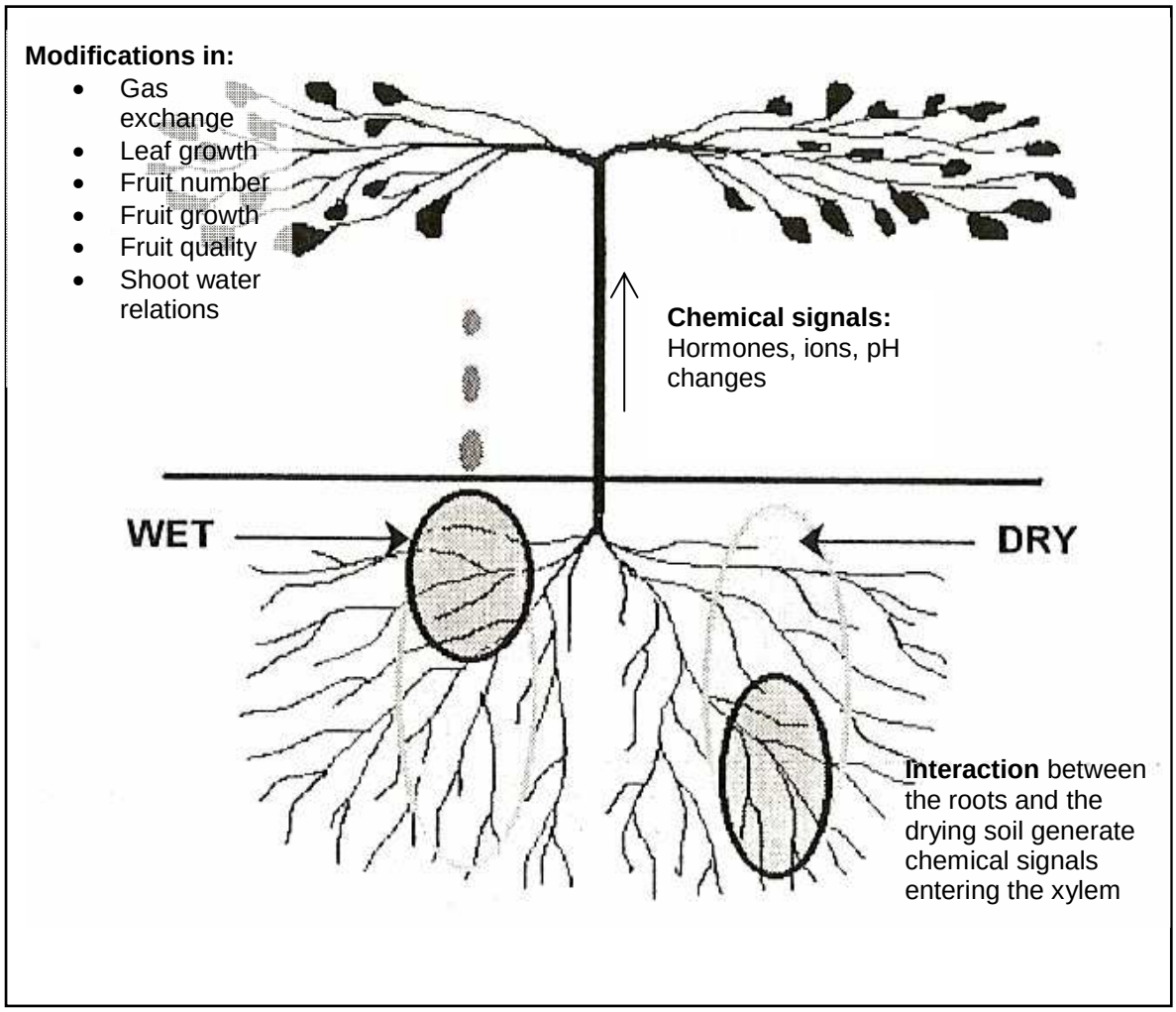

Fig 4.4 *Schematic diagram showing how roots might interact with drying soil to generate chemical signals in the xylem in a typical partial rootzone drying setting.*

Implementation of the PRD requires a split root system (e.g. an irrigation line down each side of the tree row) that vertically divides the root system. At a given moment, part of the root system of the plant is subjected to drying soil, while the other part is irrigated. In addition, the successful application of the PRD also relies on regular switching of the dry and the irrigated side at intervals between 10 - 21 days depending on the crop. A schematic diagram of the partial rootzone drying set-up is shown in Fig 4.4.

It is believed that an influx of chemical signals, e.g. the abscisic acid (ABA), into the guard cells occurs as a result of the partial soil drying as already explained above. This leads to a partial closure of the stomatal aperture. Transpirational water losses are thus reduced and a minimal or no reduction in CO_2 assimilation is expected since a greater reduction in transpiration rates than in CO_2 uptake occurs as the stomata close. Consequently a small or

no loss in yield is expected as well. Switching of the wet and dry sides of the rootzone is required for two reasons. Firstly, continuous drying of part of the root system results in a compensation in growth and functioning by the roots on the wet side (Mingo and Davies, 2001; Eissenstat *et al*., 2006). The roots in the dry soil remain alive, but inactive. They are sustained by the roots in the irrigated soil and they become a sink for assimilates leading to competition with the above ground parts of the tree. Secondly and most importantly, there is a gradual reduction with time in the xylem concentrations of the chemical signals produced by the roots in contact with the drying soil. Thus the ability to control the stomatal aperture is diminished. Because water is always available on the irrigated part of the rootzone to meet the water requirements of the plant, the water status of the tree is expected to remain unchanged. In summary, the hydraulic characteristics of the PRD effect are reflected by a reduction in stomatal conductance, while the plant water potential is maintained. Most importantly, the tree is not under drought stress.

The partial rootzone drying irrigation technique has been shown to reduce the need for pruning (Dry *et al*., 1996) due to a reduced vegetative vigor. As a result, extra photo-assimilates are partitioned to the fruit and wounding problems associated with the mechanical removal of the branches are reduced. In addition, opening up of the canopy increases light penetration to the fruit which increases the color e.g. of grape fruit and increases the content of compounds associated with flavor and aroma. Most importantly also, half the amount of water applied to control plants can be added to trees under PRD without yield reductions in the case of vines. Interesting results of the application of PRD on cotton showed that the crops were ready for harvest three weeks earlier than the control treatment (Mingo and Davies, 2001).

Apart from the work by Hutton (2000) in the cool sub-tropical climates, very few studies on the potential utility of the PRD irrigation strategy on citrus trees growing in the warm arid and semi-arid tropics have been done. Given the fact that the primary goal of the deficit irrigation strategies is to reduce irrigation levels by imposing controlled levels of drought stress thus reducing transpiration rates, the application of these strategies on low transpiring fruit trees should be thoroughly investigated before adoption for commercial use. Navel orange trees are typical low transpiring species which tend to maintain low stomatal apertures under natural climatic conditions as already explained in the earlier chapters of this thesis. Does the PRD strategy work on such low transpiring plants? For instance, a PRD experiment using bell peppers, a species where the fruit are apparently well connected to the vegetative plant, has shown that this species is not suited to the PRD irrigation technique (Mingo and Davies, 2001). It is suspected that the good hydraulic connectivity between the vegetative components of the plant and the fruit results in the chemical signals due to partial soil drying limiting fruit growth,

in the same way as it influences the vegetative growth. Thus not all crops are suited to the PRD irrigation strategy and detailed investigations are needed on a crop-specific basis to make informed decisions.

4.4 Materials and methods

4.4.1 Experimental site

Trials to investigate the potential application of the deficit irrigation strategies to the low transpiring Navel orange trees [*Citrus sinensis* (L.) Osbeck] under drip irrigation were set up in a 2 hectare commercial orchard at Mazowe Citrus Estate (MCE: block U5A), in northern Zimbabwe. Details of the location of the experimental site are given in section 2.2.1. Plant material comprised the Navel orange trees [*Citrus sinensis* (L.) Osbeck] budded on Troyer citrange rootstock [*Citrus sinensis* x *Poncirus trifoliata* Raf.] and the orchard was established in 2001. The trees were planted in rows with a north-south orientation. Tree spacing was approximately 2.75 m in each row and with an inter-row spacing of approximately 6 m. The trees were planted on ridges approximately 10 – 15 cm high to facilitate the drainage of excess water from the rootzone especially during the rainy season.

The soil, uniformly in excess of 1 m depth, belonged to the Banket 5E.2 series (Local classification), being dark red in color and with a high clay percentage. A detailed description of the soil characteristics is given in Table 1.1. All the trees in this orchard were surface drip irrigated using standard 15 mm polypropylene dripper lines (Netafim^{R}) with pressure compensated button emitters delivering water at a rate of 2.3 L/h. The emitters were spaced at 0.75 m along the drip line.

According to the local citrus growers' irrigation practice, all the trees in this orchard were watered using a single drip line running close to the main stem of the trees. During the 2004/05 season, when the trees were relatively young (four years old), they were subjected to a fixed irrigation cycle lasting for three hours each day. Harvesting from these trees was done for the first time during the 2004/05 season. This irrigation cycle was changed in the 2005/06 season as the trees grew bigger. A daily irrigation schedule with the duration of each irrigation event being dependent on the growth stage of the fruit as shown in Table 4.2 was introduced. Longer irrigation durations were implemented during the crucial growth stages, namely the flowering and fruitset phases, while shorter durations were used at maturation to improve the internal quality of the fruit. During summer, irrigation was applied to supplement rainfall (after fruitset). Visual observations of the trees' water status were used to decide on how much water to apply.

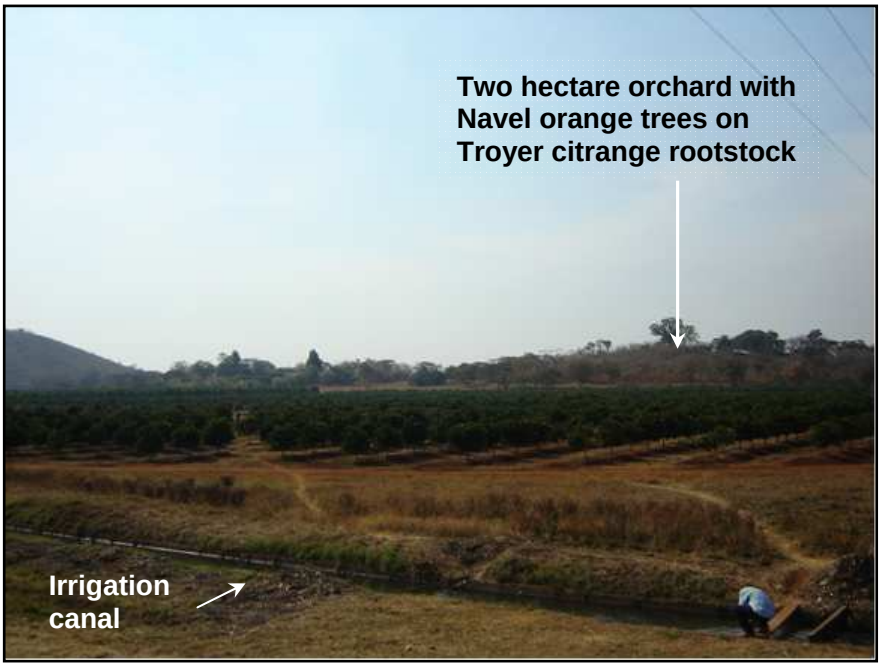

Fig 4.5 *A general view of the experimental orchard (Block U5A) with Navel orange trees budded on Troyer citrange rootstock at Mazowe Citrus Estate, Zimbabwe. Water conveyed in canals from the Mazowe dam, about 5 km from this orchard is first pumped from the canals into a control pump house and filtered before being distributed into the orchards.*

Table 4.2 *Typical irrigation schedule for the five-year-old Navel orange trees at Mazowe Citrus Estate, Zimbabwe during the 2005/06 season.*

Month	Duration of irrigation (h)	Fruit growth stage
June – July	4 - 6	Before spring flush
August – December	6 - 7	Flowering/fruitset
January - March	-	Fruit growth/cell expansion
April - May	~ 2	Maturation

4.4.2 Irrigation regimes

Three irrigation treatments were established in September 2004 and two more were added in late August 2005 as will be described below. Each treatment comprised a single row with ten trees selected such that the outermost rows were excluded to eliminate edge effects. The treatments were not replicated due to the limitation in the number of trees available for the

experiments. However, with ten trees, individual tree effects were eliminated by sampling from as many trees as possible.

The effect of the different irrigation treatments were evaluated against the current irrigation practice by the local citrus growers and this treatment shall be called the commercial control (or the control), henceforth. The irrigation depth for this single line treatment can be calculated by considering a hypothetical area of one hectare of the orchard with simplified dimensions of 100 m x 100 m. Given the fact that the rate of emission of water by the drippers is 2.3 L/h and if we consider an irrigation event lasting for say, three hours, then the total volume of water V_w applied per hectare in liters is

$$V_w = 3x2.3xn \tag{4.1}$$

where n is the total number of emitters per hectare.

$$n = \frac{100}{0.75} x \frac{100}{6} \tag{4.2}$$

The fraction of the orchard that is irrigated, can be estimated by considering the region between four emitters in neighboring tree rows as illustrated in Fig 4.6. The wetted region around each emitter is approximately elliptical extending for approximately 1.0 m along the major axis of the ellipse at right angles to the drip line and 0.375 m along the minor axis parallel to the drip line.

The wetted fraction of the soil = $\frac{\pi x0.375x1.0}{6x0.75} \approx 0.30$ (4.3)

Hence, the irrigation depth = $\frac{V_w}{10000x0.30} = \frac{15333}{3000} \approx 5.1$ mm.

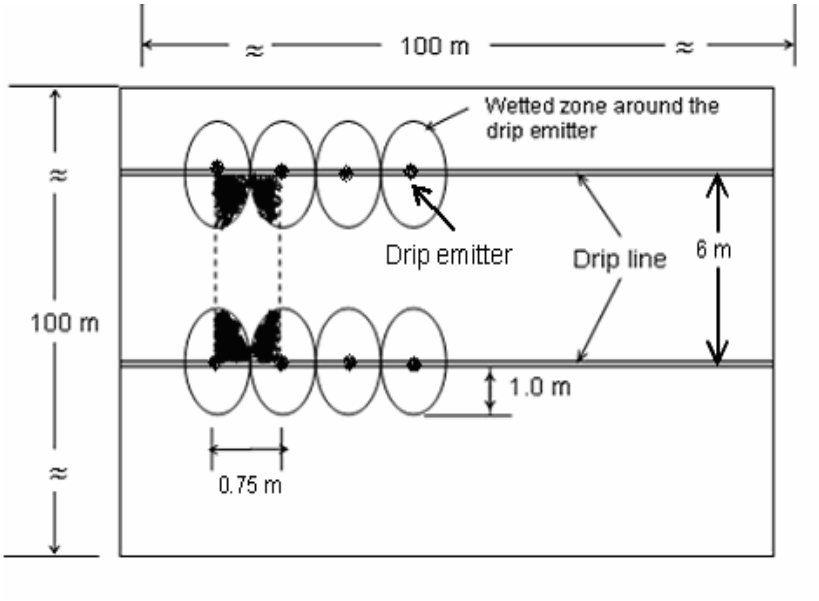

Fig 4.6 *Geometry of the wetted zone between the drip lines and between the emitters at MCE for the calculation of the irrigation depth. The wetted zone follows an elliptical shape extending for approximately 1.0 m along the major axis and approximately 0.375 m along the minor axis.*

A typical set-up of the control treatment is shown in Fig 4.7a. Irrigation by this single drip line was assumed to replace 100 % of the crop evapotranspiration (ET) on the irrigated side. The second treatment was the partial rootzone drying treatment also replacing 100 % of ET (PRD100) (Fig 4.7b). This comprised two drip lines, one either side of the tree row. Irrigation was done using one line at a time but with the wet and dry zones alternated every ten days. The same volume of water was delivered in this treatment as in the control treatment. The drip lines were spaced at a distance of approximately 1.1 m from the tree line in the PRD100 treatment. The third treatment was the well-watered treatment comprising two drip lines oriented in the same way as the PRD100 treatment. Both drip lines were used during each irrigation event such that the amount of water applied was twice that in the control and the PRD100 treatments. These three treatments were established in August 2004.

Two additional treatments, namely the regulated deficit irrigation treatment (RDI50) (Fig 4.7c) and another PRD treatment (PRD50; Fig 4.7d) both supplying 50 % of the control treatment were established in September 2005. Alternate emitters along the drip lines were blocked using a plastic tape and a UV treated plastic shield. Irrigation was via only one line in the RDI50 treatment, while double lines spaced at 1.1 m either side of the tree line were used for the PRD50 treatment. Irrigation was done using one drip line in the PRD50 treatment, but also switched every ten days. In this trial, both the PRD and the regulated deficit irrigation regimes were applied throughout the year.

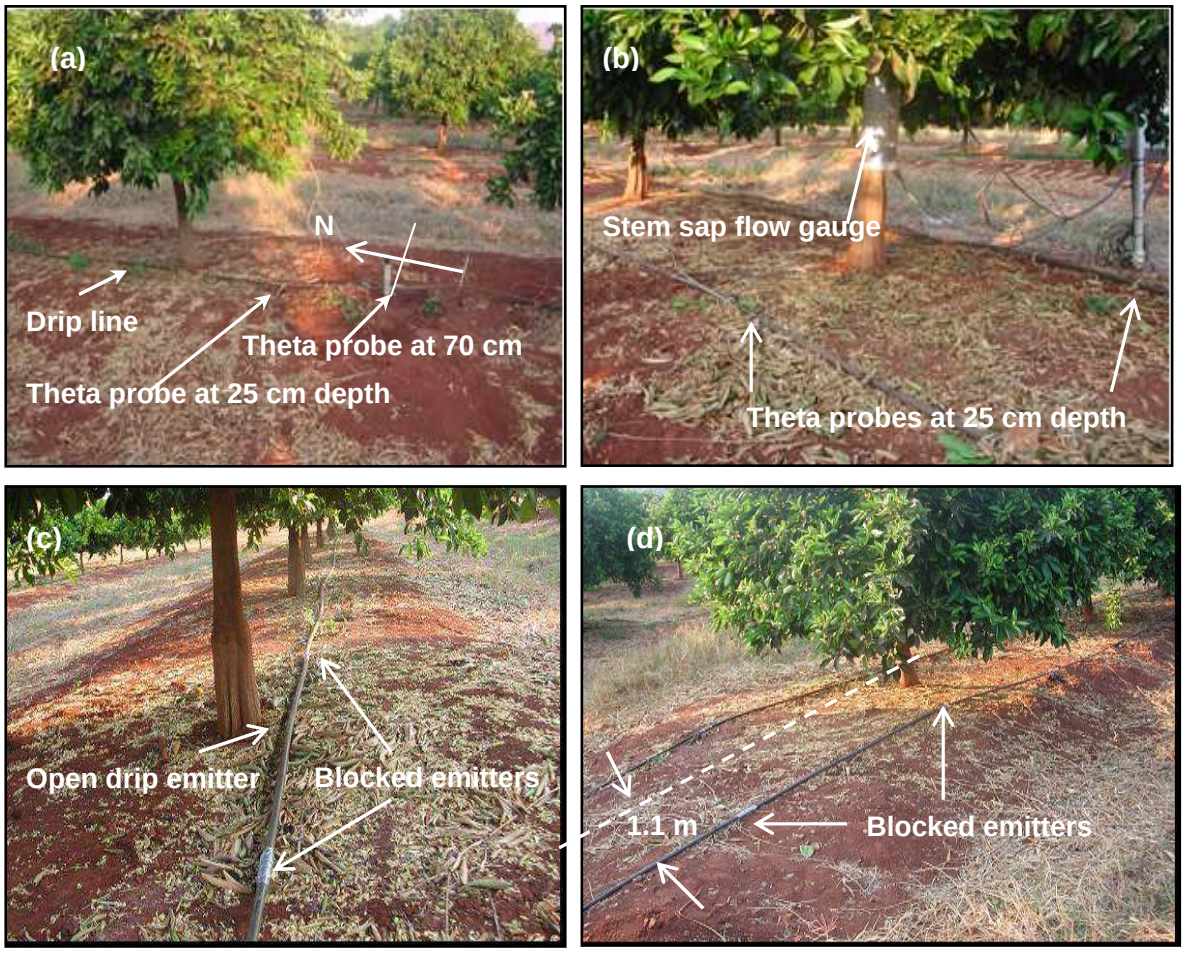

Fig 4.7 *Irrigation treatments established at Mazowe Citrus Estate (MCE), Zimbabwe.*

(a) The control treatment (100 % ET replacement) using one drip line next to the row of trees. This is the current irrigation practice at MCE;

(b) The partial rootzone drying treatment at 100 % ET replacement (PRD100). Irrigation is done using one drip line at a time and switched at 10 day intervals;

(c) The regulated deficit irrigation treatment with 50 % ET replacement (RDI50). Alternate emitters along the drip line were blocked to ensure that 50 % of the control treatment is applied, and

(d) The partial rootzone drying treatment at 50 % ET replacement (PRD50). Irrigation is done using one drip line at a time but switched at 10 day intervals.

4.4.3 Soil measurements

Before installing the devices to monitor the volumetric soil water content in the different treatments, the distribution of the root system for the Navel orange trees had to be established. This was important given the fact that unlike in most citrus orchards, the trees investigated in this study were planted on ridges. Four trenches each approximately 1.0 m deep were dug on randomly selected sites in the orchard, but at locations where we expected to find the roots

(next to drip emitters) as shown in Fig 4.8. This was done before the different irrigation treatments had been introduced in August 2004. An 80 mm x 150 mm (diameter x depth) root auger (Eijkelkamp, Agrisearch Equipment, The Netherlands) was used to collect disturbed soil samples containing the roots at 15, 25, 35, 45, 55 and 65 cm depth. The measurements were replicated three times at each depth at the position corresponding to the drip emitter (Fig 4.8). The approach by Barry and Castle (2004b) was used to study the density distribution of the roots. According to this approach, the soil samples were screened to recover fibrous roots with a diameter less than 2 mm and were oven dried for 48 hours at 70 ℃ and then weighed. Fibrous root density was expressed as milligrams of root dry mass per cubic centimeter of the soil and a typical profile is shown in Fig 4.9.

To establish the effect of the different soil water regimes on root development, additional soil samples were collected in October 2006 from the five irrigation treatments. The measurements were replicated with two pits per treatment being sampled and three soil samples were collected using the auger at each depth namely 10, 20, 30 and 40 cm were most roots were found. The results of the effect of the soil water regimes on root development are reported in section 4.4.

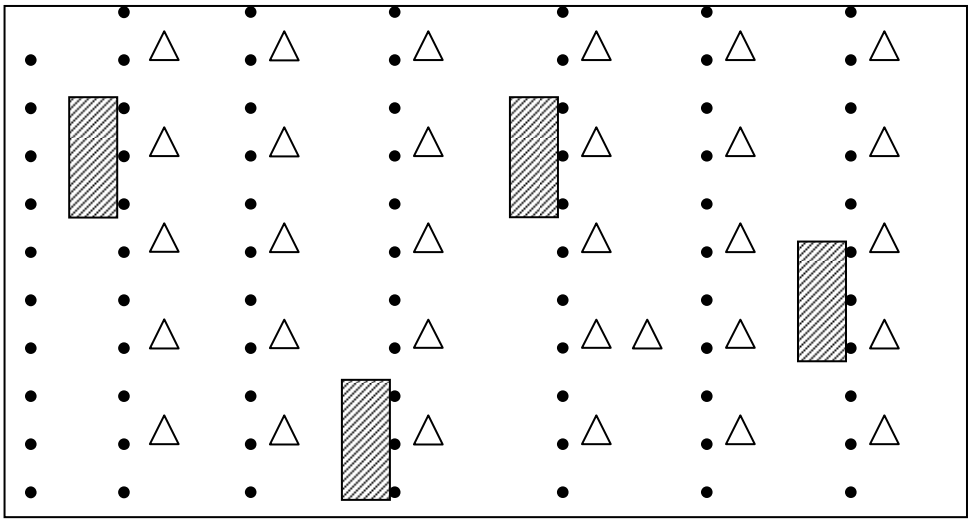

Fig 4.8 *Positions within the net plot where root sampling was done (Hashed rectangles). Open triangles represent the trees (2.75 m apart) while closed circles show the positions of the drip emitters (0.75 m apart).*

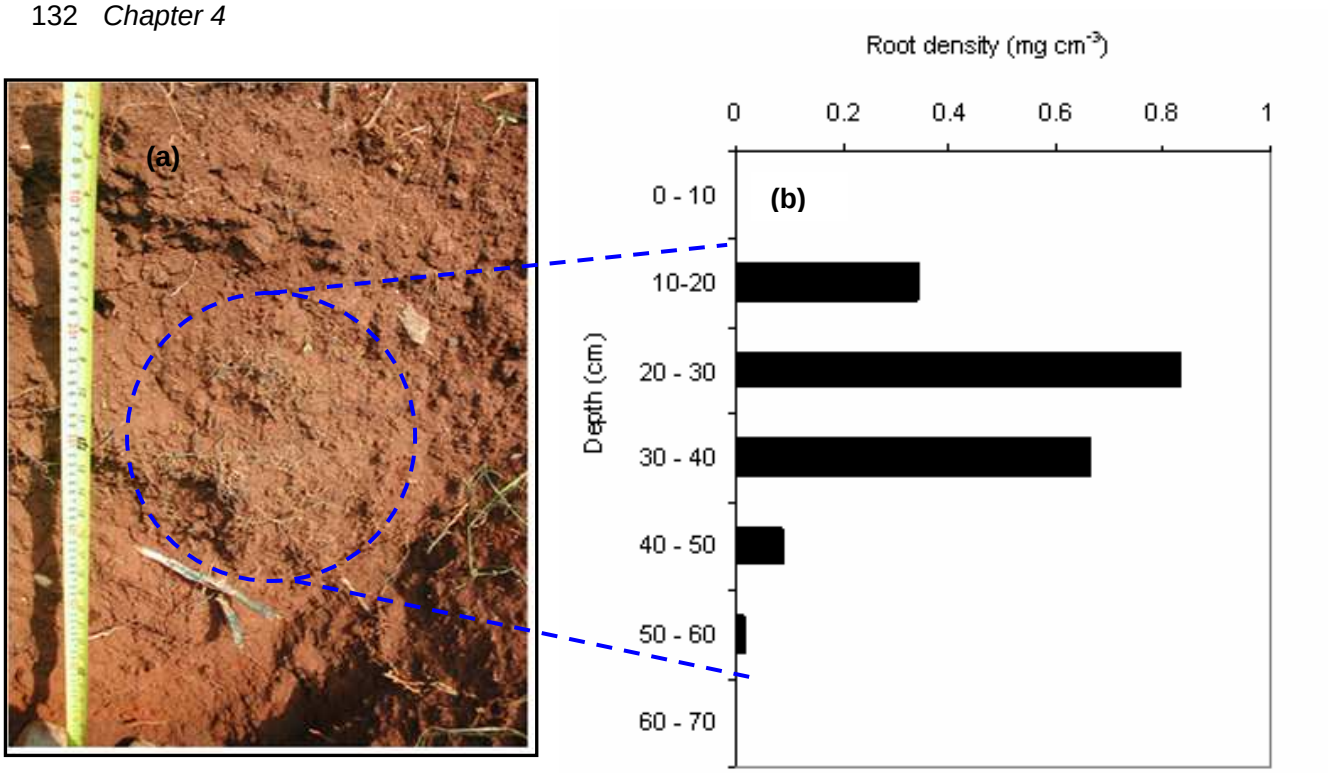

Fig 4.9 *(a) Region of active soil water uptake by the fibrous roots of the orange trees grown on ridges at Mazowe Citrus Estate, Zimbabwe;*
(b) Distribution of the root density of the Troyer citrange rootstock growing in the clayey loam soils on ridges.

The fibrous, feeder roots, responsible for water uptake were found in the depth range 15 to 55 cm with the highest density occurring between 20 and 40 cm. No fibrous roots were found in the top 10 cm on all the four sites sampled, while thick anchor roots which are mainly responsible for the support of the trees were predominant at depths beyond 60 cm.

Consequently, the volumetric soil water content was monitored in the rootzone (25 cm depth) and beyond (70 cm depth) in the control treatment using theta probes (Delta-T Devices, Cambridge, UK) as shown in Fig 4.7a. Two additional probes were installed in the rootzone, one on either line of the PRD100 as shown in Fig 4.7b. The soil water content could not be continuously monitored in the other treatments because only four probes were available. The theta probes were installed close to the drip emitters (within 10 cm radius of each emitter). Undisturbed soil samples were collected on selected days in all the treatments for the gravimetric determination of the soil water content. In the gravimetric method, three undisturbed soil samples were collected in the root zone of the trees (~ 25 cm depth) next to the drip emitters using standard moisture cans. The soil samples were stored in air-tight plastic bags and transported to the laboratory. The fresh mass of the soil samples was measured before drying the samples in the oven at 105 ℃ for at least 24 hours. The dry mass of the

samples was then measured and the volumetric water content calculated to establish the treatment effects on the soil water regimes.

4.4.4 Physiological measurements

The orchard microclimate was monitored using the automatic weather station as described in Section 2.2. Sap flow was measured at stem and branch level of one model tree in three treatments, namely the well-watered, the PRD100 and the control treatments as explained in detail in Section 5.2.

Although the roots to shoot chemical signaling processes described above play a central role in the operation of the PRD strategy, only the hydraulic signals were investigated to establish whether PRD effects occur in Navel orange trees or not. The stomatal conductance and leaf water potential were measured at hourly intervals throughout or during parts of the following days: 5 February 2005, 14 May 2006 and 1 June 2006. Leaf water potential was measured using a thermocouple pyschrometer located in the pump house approximately 100 m away from the orchard. One model tree was selected in each treatment for the assessment of the effect of the irrigation regimes on the plant water relations. Mature and fully expanded leaves which were well exposed to the solar radiation were selected for the measurements of both the leaf water potential and the stomatal conductance in the different treatments.

The thermocouple psychrometer comprised four standard C-52 sample chambers (Wescor Inc, Logan, UT, USA) connected to a microvoltmeter (HR-33T, Wescor, Inc, USA) as described in Chapter 2. Chambers were kept at a constant temperature inside a white datalogger enclosure box which was well insulated and kept inside the pump house. The stomatal conductance was measured using the AP4 porometer (Delta-T Devices, Cambridge, UK) on three tagged, mature and fully exposed leaves per treatment. Hourly measurements were necessary for two reasons. Firstly the cyclic oscillations in the water relations of the Navel orange trees already described in earlier chapters required more frequent measurements than the few readings at noon that are often taken with other plants (e.g. Chalmers *et al*., 2004; Bravdo *et al*., 2004). In addition, hourly readings corresponded to approximately twice the period of the oscillations for the Navel orange trees in the orchard (Fig 2.11b). Thus comparison of the treatment effects on the water relations of the trees was possible when the oscillations were presumably at the same stage. Lastly, in the case of the leaf water potential measurements, the fact that only four C-52 sample chambers were available, only four of the five treatments could be sampled allowing an equilibration period of about 50 min.

Water status measurements on 5 February 2005 were only done for three treatments namely the well-watered, the control and the PRD100 treatments, because the PRD50 and the RDI50 treatments had not yet been established. On 14 May and 1 June 2006, the leaf water potential measurements were taken in the well-watered, control, PRD50 and RDI50 treatments, respectively, while the stomatal conductance was measured in the PRD100 treatment as well.

4.4.5 Yield and fruit quality measurements

During the 2004/05 fruit growing season, fruit growth rate was monitored on two trees in the control, well-watered and the PRD100 treatments. Ten tagged fruits per tree with an equal number of fruit on the eastern and western side of the canopy were monitored at weekly intervals using hand-held vernier calipers. Two mutually perpendicular measurements were taken along the equator of each tagged fruit and an average value of the diameter calculated. The same number of fruit (10 per tree) were also tagged on two trees in each of the three treatments in mid October to monitor fruit abscission. The number of tagged fruit remaining on the trees by late December, after the major fruit drop period, was counted. During the 2005/06 season, fruit growth rate was monitored on one fruit in each of the five treatments using the DEX100 dendrometers (Dynamax Houston, USA) connected to the CR23X datalogger (Fig 4.10) (Campbell Sci. Ltd, Shepshed, UK). However, the tendency of the dendrometers to slip off the fruit during storms or on windy days led to inconsistent results of growth measurement using this technique.

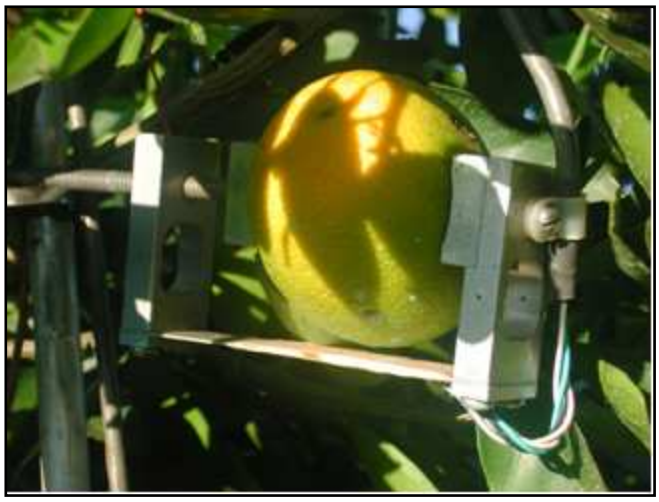

Fig 4.10 *The DEX100 dendrometer (Dynamax, Houston, USA) monitoring the growth rate of a fruit of a five-year-old Navel orange tree in the Mazowe Citrus Estate, Zimbabwe.*

Harvesting was done over three growing seasons, namely 24 May 2005, 25 May 2006 and 26 May 2007. Three trees with similar canopy dimensions per treatment were selected for yield analysis at the end of each growing season. Total mass of all the fruit was established by picking and weighing all the fruit and the average fruit mass per tree calculated. In addition, the total number of mature and immature green fruit with a diameter >50 mm was counted in each treatment to establish the effects of secondary flowering after the onset of the rainy season (October to April in northern Zimbabwe) only during the 2005/06 growing season. Ten fruits of similar diameter were selected for internal quality analysis. These were fully exposed fruit picked from the south-west part of the canopy (Barry and Castle, 2004b) of the model trees. Total soluble solids (TSS), total acidity (TA) and the average juice content of the fruit were determined by specialists in the fruit processing factory of the Mazowe Citrus Estate.

4.5 Results and discussions

4.5.1 Soil water regimes

The typical evolution of the soil water content in the control treatment from 1 – 18 November 2004 and the PRD100 treatment from 16 October to 5 November 2004 at Mazowe Citrus Estate are shown in Fig 4.11. This period corresponded to the fruitset period in the annual growth cycle of the Navel orange trees. Theta probe readings for the commercial control treatment are shown in Fig 4.11a, while Fig 4.11b shows the readings of the probes in the PRD100 treatment.

During days when each irrigation event lasted for at most three hours, the soil water content stayed close to field capacity (44 % v/v) in the rootzone. Minimal drainage and leaching of nutrients is presumed to have occurred since all the water appeared to stay within the active rootzone. In fact, the daily fluctuations in the soil water content in the rootzone were within the allowed depletion level for citrus of 33 % of the total available water (TAW). Given the fact that this period coincided with the end of the dry season in northern Zimbabwe, the soil water content at 70 cm depth was close to the permanent wilting point (~ 30 % v/v) at most times. But, on longer irrigation durations (e.g. on DOY 306; 309; 310 and 320 in Fig 4.11a) a rise in the soil water content was observed beyond the rootzone indicating excess water application. Instrument failure due to persistent power cuts resulted in discontinuous soil water data in the control treatment (Fig 4.11a) which was much further from the backup power source than the other treatments.

The ten day partial soil drying cycle due to the PRD strategy resulted in soil water content above the permanent wilting point, but was substantially lower than the allowed soil water

depletion level on the dry side as shown in Fig 4.11b. Thus significant levels of drought stress were induced on the dry side of the rootzone. Gravimetric measurements of the soil water content in the root zone in all the five treatments revealed that generally the average soil water content was much lower in the RDI50 and the PRD50 treatments than in the other treatments as expected.

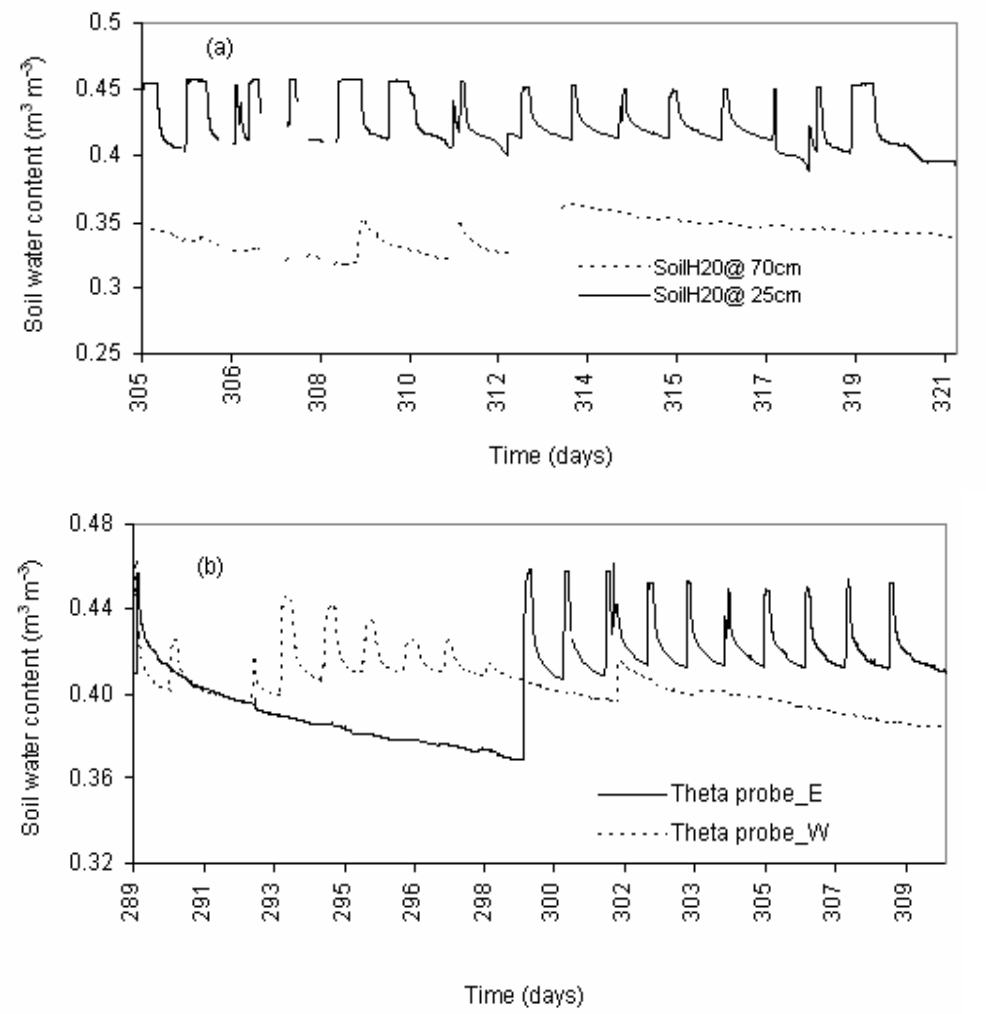

Fig 4.11 (a**)** *Typical course of the soil water content in the rootzone of the control treatment. The continuous line shows the output from the theta probe at 25 cm depth, while the dotted line is the reading from the theta probe beyond the rootzone at 70 cm depth. (b) The soil water regime in the rootzone of the PRD treatments being measured by two theta probes (25 cm depth), one to the east of the tree row (Theta probe_E) and the other to the west (Theta probe_W).*

4.5.2 Physiological responses to the irrigation regimes

4.5.2.1 Plant water status

Continuous measurements of the stomatal conductance (Fig 4.12a) and the leaf water potential (Fig 4.12b) on 5 February 2005 revealed that the differences in these two variables for the three treatments established in 2004 were not significantly large. Consequently, the PRD effects on the hydraulic characteristics of the trees, namely a reduction in the stomatal conductance and the maintenance of the leaf water potential, were not detected. This could be due to the fact that this experiment was conducted during a dry spell in the middle of the rainy season. Thus it is possible that the treatment effects on the water relations of the trees were not yet fully established.

A further experiment was conducted on 14 May 2006 (Figs 4.12c and d) after the rainy season to establish whether the PRD hydraulic signals could be detected on the low transpiring Navel orange trees. The stomatal conductance of selected leaves were measured at hourly intervals in all the five treatments, while the leaf water potential was monitored only on four treatments namely the control, PRD50, RDI50 and the well-watered treatment due to a limitation in the number of thermocouple psychrometer sample chambers available. It is apparent in Fig 4.12c that the leaves in the well-watered treatment had the highest stomatal conductance followed by those in the control treatment, PRD100, PRD50 and lastly the RDI50 treatment.

The leaf water potential of the well-watered treatment in Fig 4.12d was higher (less negative) than for all the other treatments throughout the campaign. Despite the fact that the stomatal conductance of the PRD50 treatment was much lower than that of the control treatment, the leaf water potential of the PRD50 treatment was comparable to that of the well-watered treatment reaching a minimum of approximately -2.50 MPa. The leaf water potential of the control and the RDI50 treatments remained consistently lower, reaching approximately -4.00 to -4.50 MPa suggesting that these trees were in fact under drought stress. But, the fact that the stomatal conductance of the PRD50 treatment was much lower, while the leaf water status was maintained reveals that PRD effects indeed do occur in Navel orange trees despite their already relatively low stomatal conductance under optimal environmental conditions. These observations were confirmed by a further experimental campaign conducted on 1 June 2006 as shown in Fig 4.12e and Fig 4.12f. However, more observations of the leaf water potential could not be done on this day due to technical problems with the C-52 sample chambers for the thermocouple psychrometer.

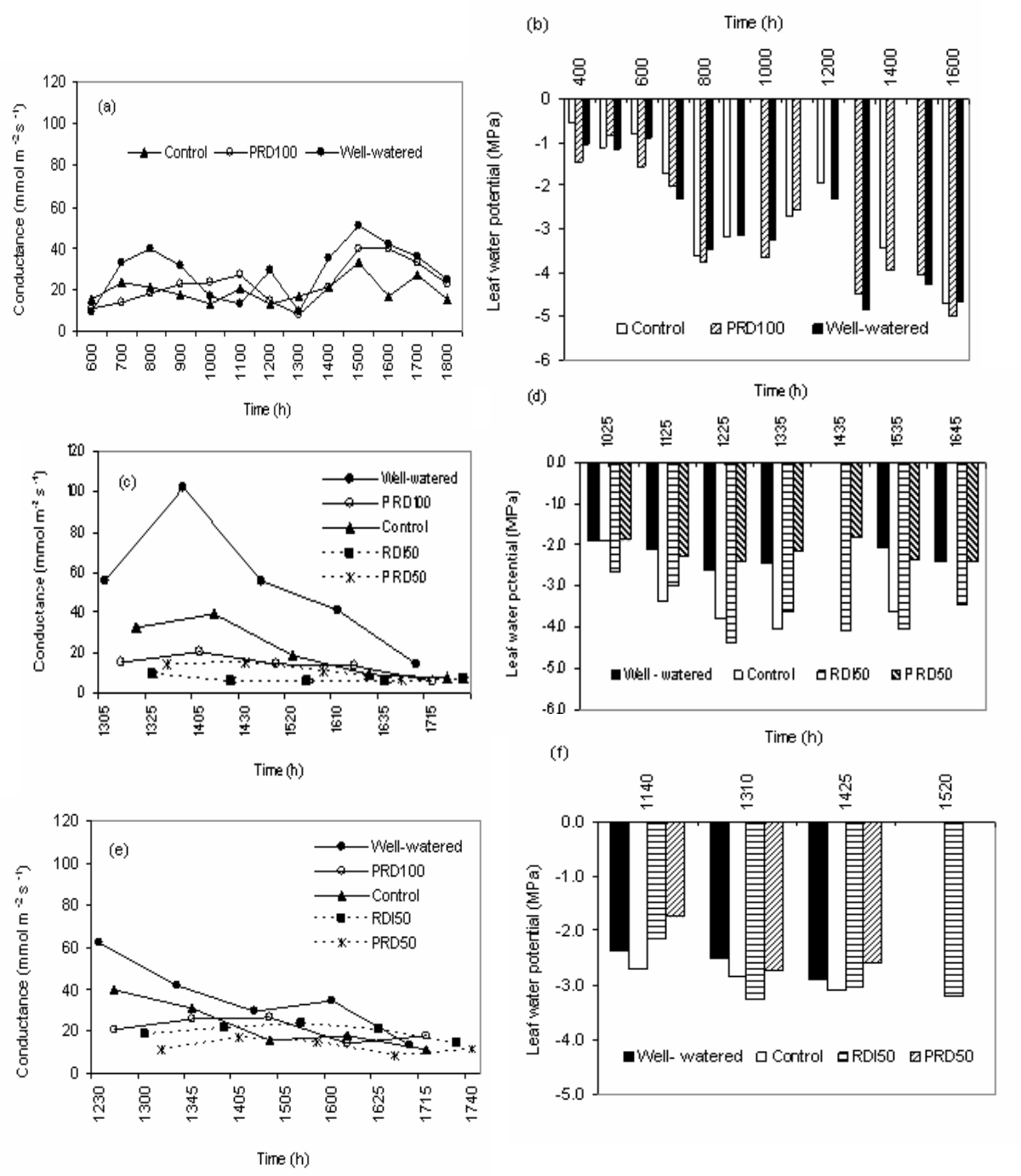

Fig 4.12 *Measurement of the plant water status to detect the PRD effects on Navel orange trees. a) Hourly measurements of the stomatal conductance in three treatments namely the control, PRD100 and the well-watered treatment during the rainy season on 5 February 2005; b) The diurnal pattern of the leaf water potential on 5 February 2005. Differences in the stomatal conductance within the treatments were small and no PRD effects were detected. c) The course of the stomatal conductance in five treatments namely the control, PRD100, PRD50, RDI50 and the well-watered treatment on 14 May 2006; d) Leaf water potential of four treatments namely the control, PRD50, RDI50 and the well-watered on 14 May 2006. PRD effects, namely, a reduction in stomatal conductance, while the leaf*

water potential was maintained is observed. e) Course of the stomatal conductance on 1 June 2006 in the five irrigation treatments; and f) The corresponding course of the leaf water potential on 1 June 2006 confirming the occurrence of PRD effects in the Navel orange trees at Mazowe Citrus Estate.

The high stomatal conductance coupled with the low leaf water potential in the control treatment indeed confirmed the theory of the partial rootzone drying strategy in which switching of the wet and dry sides of the root zone is essential to maintain the root sensitivity to soil drying and thus to sustain the efflux of root sourced chemical signals (e.g. ABA) to the leaves which control the size of the stomatal aperture. This is made more apparent by the fact that the PRD100 treatment which received the same irrigation amount as the control treatment (100 % ETc replacement) had a lower stomatal conductance. In addition, the observation that the trees on the single line control treatment where somewhat under drought stress poses some important questions on the suitability of this single fixed line treatment as the local standard irrigation practice for citrus. This possibility of drought stress existing on trees under the control treatment is further revealed in the yield statistics as will be detailed in subsequent sections of this chapter.

4.5.2.2 Sap flow

Given the fact that the plant water status measurements were taken on only three days during the two growing seasons, independent evidence that the reduced stomatal conductance due to PRD occurred for long durations was provided by sap flow measurements first on potted trees in the laboratory and then on mature trees in the orchard. For the potted tree experiments, stem sap flow rates were compared for a tree whose root zone was well-watered and for another tree with a partially stressed root zone as described in detail in Section 1.3.6. Although the leaf area was not measured for the potted trees, the crown sizes were similar. Plotting the daily total stem sap flow against the daily total solar radiation incident on the crowns of the two model trees revealed that there was a greater restriction in the sap flow rates for the partially stressed tree than the well-watered one. This is clearly illustrated in Fig 4.13. The reduction in the daily sap flow total was largest on cloudless days due to stronger stomatal control arising not only from the cyclic opening and closure of the stomata but presumably also from the influence of the root sourced drought stress signals.

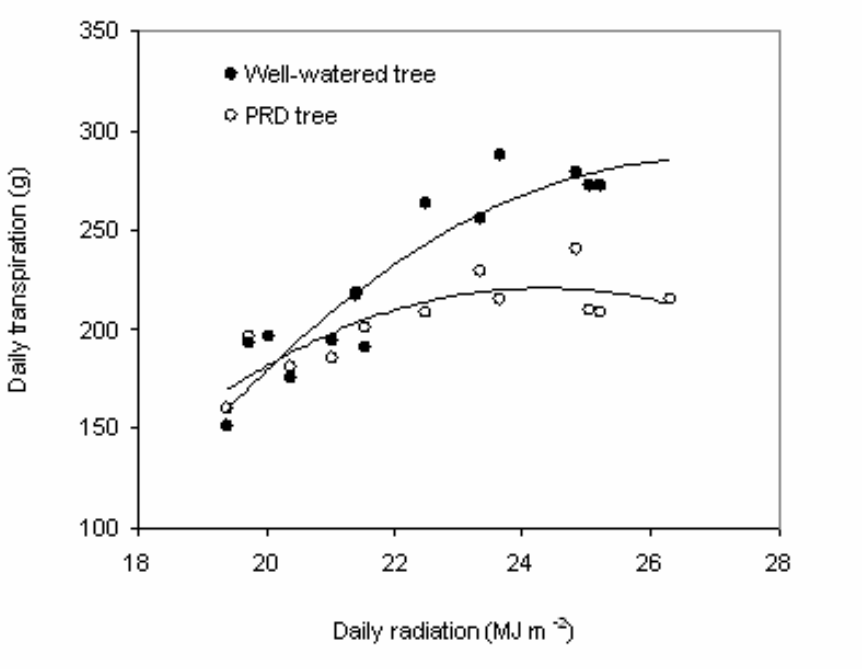

Fig 4.13 *Effect of the partial drought stress on the daily total transpiration of potted Navel orange trees. Closed circles show the effect of the daily total solar radiation on the daily total transpiration of the well-watered tree, while open circles show the effect of the partial drought stress on the daily total transpiration of the young potted tree. The extent of stomatal closure is clearly more pronounced for the partially stressed tree than the well-watered tree.*

In the orchard at Mazowe Citrus Estate branch sap flow rates normalized with the transpiring leaf area at the end of each branch were compared in only three treatments namely the control, PRD100 and the well-watered treatment due to the limitation in the number of sap flow sensors available. A typical installation of the branch sap flow sensor on a mature tree in the orchard at Mazowe Citrus Estate is shown in Fig 2.7. Branch sap flow sensors were installed, one per model tree in each of the three treatments on fully exposed branches on the southwestern part of the canopy of the tree. The SGA9 heat balance sap flow gauges (Dynamax Houston, USA) were used on the control and the well-watered treatments, while the SGB19 heat balance sap flow gauge (Dynamax Houston, USA) was used to monitor sap flow in the PRD100 treatment.

The total leaf area at the end of each branch was determined using a destructive method proposed by Medhurst and Beadle (2002). According to this approach, all the leaves at the end of the branch were removed. The leaf area of a subset of 15 randomly selected leaves was measured accurately for each treatment using the leaf area meter (Delta-T Devices,

Cambridge, UK) connected to a computer. The leaves were then dried at 80 ℃ for forty eight hours to determine their dry mass. A parameter, the specific leaf area, which is defined as the ratio of the total leaf area to the dry mass of the leaves, was then derived. Assuming that this parameter remained constant for all the leaves in a given treatment irrespective of age, all the leaves were then dried as described above to determine the total dry mass of leaves from each branch. Multiplying the total dry mass of the leaves with the specific leaf area for each treatment gave an estimate of the total leaf area for each branch. Typical results are presented in Table 4.3.

Table 4.3 *Estimates of the branch leaf area in three irrigation treatments, namely the control, the PRD100 and the well-watered treatments on which the sap flow sensors were connected.*

Treatment	Leaf area of the subset of 15 leaves (cm^2)	Total dry mass of the 15 leaves (g)	Specific leaf area (cm^2/g)	Total dry mass of the branch leaves (g)	Leaf area of the branch (cm^2)
Control	204.0	4.4	46.4	80.0	3712
PRD100	222.6	4.6	48.3	336.4	16248
Well-watered	196.0	4.2	46.7	99.1	4628

Typical results of the evolution of the daily total sap flow expressed per unit of leaf area in the three treatments mentioned above are presented in Fig 4.14b for a period of 17 days from 13 to 29 May 2006 while the course of the climatic driving variables for sap flow over this period are shown in Fig 4.14a. The PRD100 treatment generally gave lower sap flow per unit leaf area, while the trees in the well-watered treatment gave the highest sap flow rates per unit of leaf area. Thus it can be concluded that the PRD effects on the tree water relations were sustained throughout the dry periods of the fruit growing season.

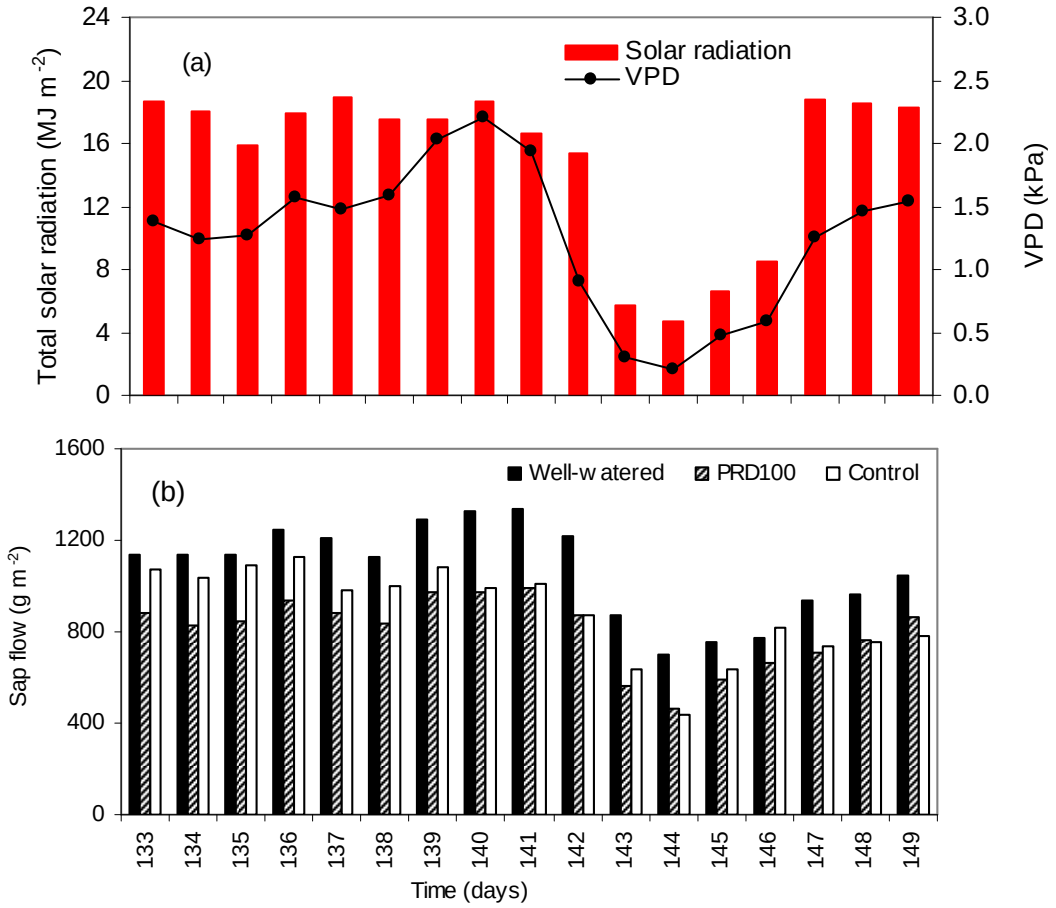

Fig 4.14 *(a) Variation of the daily total solar radiation (bars) and the mean daytime vapor pressure deficit of the air for the period 13 to 29 May 2006 (DOY 133 to 149).*

(b) *Effect of the irrigation treatments on the daily total branch sap flow normalized with leaf area of the respective branches for the period 13 to 29 May 2006 (DOY 133 to 149) at Mazowe Citrus Estate. Branch sap flow measurements were made on only three treatments due to a limitation in the number of sensors available.*

4.5.3 Effect of the irrigation regimes on root development

Whether or not the differences in the sap flow rates were somewhat related to the development of the roots was investigated in October 2006 as detailed above. Root density expressed as the ratio of the dry mass of roots (with diameters less than 2 mm) per unit dry mass of the soil was found to be almost twice as much in the well-watered treatment than in the other four treatments as shown in Fig 4.15a. In the well-watered treatment, most of the roots were found at shallow depths in the range 20 – 30 cm and no feeder roots existed at 10 cm and 40 cm depths, respectively. Only thick anchor roots were found beyond 40 cm. In both

the partial rootzone drying treatments (i.e. PRD100 and PRD50) the roots were spread over a larger depth than in the well-watered treatment with the highest root density occurring at approximately 30 cm depth (Fig 4.15b and 4.15e). Average diameter of the feeder roots tended to be much thinner under the partial rootzone drying treatments compared with those under the well-watered treatment. Higher density of roots occurred at larger depths (~ 30 - 40 cm) in the control and the RDI50 treatments (Fig 4.15c and Fig 4.15d).

The shallow and relatively thicker root system for trees in the well-watered treatment is a direct result of the abundance of water in this treatment. The trees do not need to extend their root system deeper to search for water as is the case in the other treatments and thus they are able to support higher transpiration rates as shown in Fig 4.14. The occurrence of deep thin roots was also reported by Bacon (2004), an adaptation presumably to commit limited carbohydrate supply to extension growth and allow plants to explore deeper water reserves.

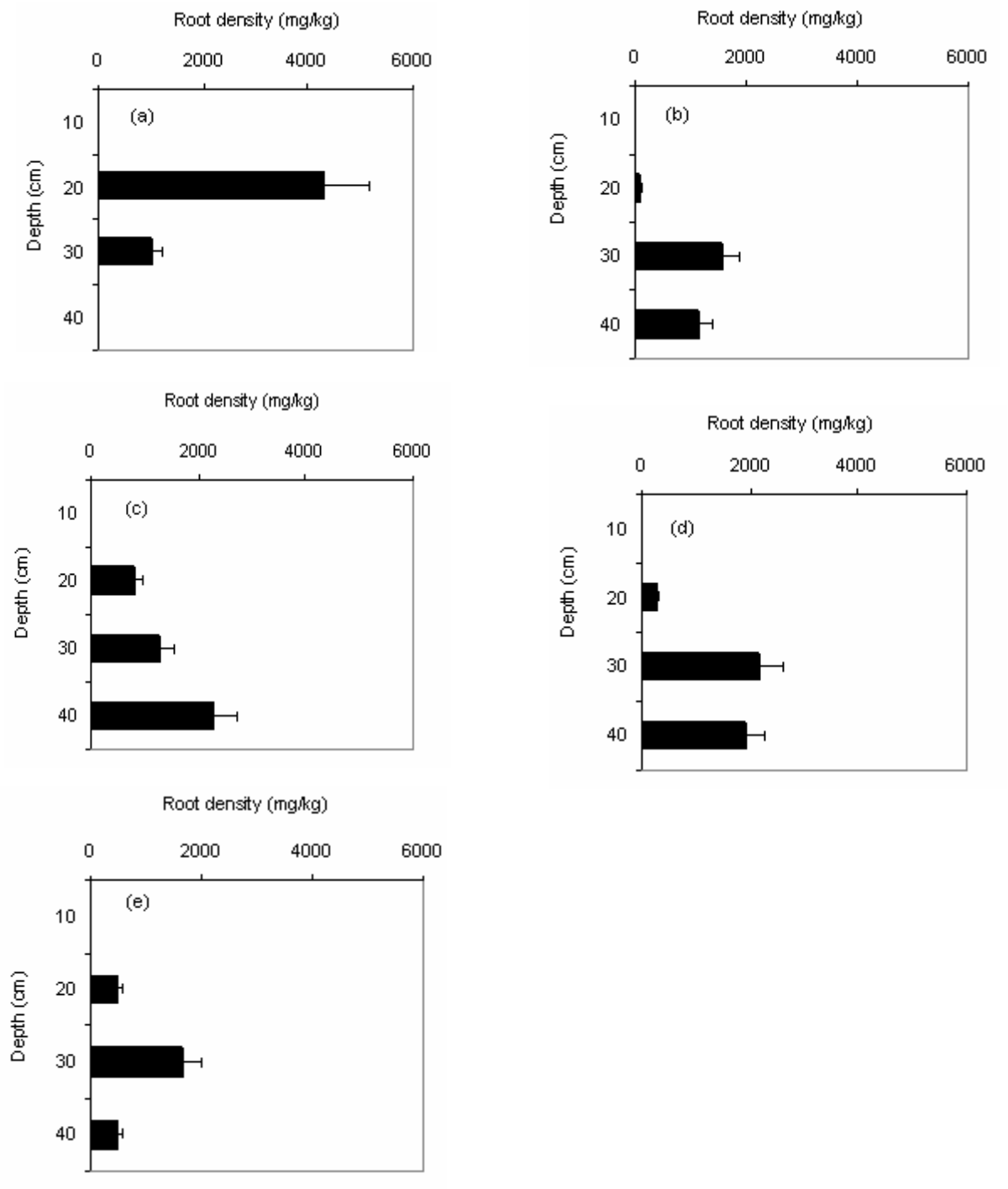

Fig 4.15 *Effect of the soil water regimes on root development in the citrus grove at Mazowe Citrus Estate. Root density distribution in the well-watered treatment (a), PRD100 treatment (b), the control treatment (c), the RDI50 treatment (d) and the PRD50 treatment (e). Each bar is an average of two readings per depth from two pits per treatment. Error margins of 20 % were included for the root density at each depth.*

Contrary to the observations by other researchers, notably Mingo and Davies (2001) that the partial root zone drying strategy promotes the development of a larger root density, this did not appear to be the case for the Navel orange trees. Rather, the PRD strategy appeared to affect more the distribution of the roots in the soil rather than the root density per se with more roots occurring at a larger depth than for the well-watered treatment. The finer and deeper root system under PRD probably developed to enhance water uptake by the dry side of the rootzone during the drying phase of the PRD cycle. Similar findings were obtained by Dry *et al*. (2001) and De la Hera *et al*. (2006) both working on grape vines (*Vitis vinifera* L.). The fact that the roots in the control treatment tended to be more concentrated at larger depths confirms the need to enhance water uptake suggesting that water supply was somewhat inadequate.

4.5.4 Effect of irrigation treatments on yield variables

4.5.4.1 Fruit abscission and growth rate

The causes of fruit drop in these trials were somewhat not distinctly clear although water stress seemed to have a significant effect. For example in the 2004/05 season much less fruit drop occurred in the well-watered treatment than the control and the PRD100 treatments (Fig 4.16). This trend can be attributed to the influence of the different quantities of water applied in each treatment. The same effect was observed in 2005/06 with the control, RDI50 and PRD50 having large fruit drops. High incidences of fruit drop were not always followed by a severe yield decline e.g. the well-watered, RDI50 and PRD50 treatments in 2006, suggesting that crop load somewhat affected yield drop since these treatments generally gave high yields in that year (Table 4.4). High rates of fruit drop are sometimes related to the self regulatory mechanism by the tree to control the crop load if there is an excess of fruits than it can support.

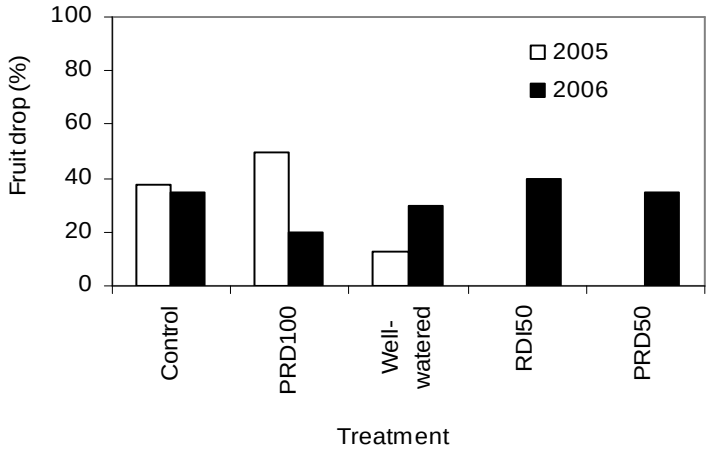

Fig 4.16 *Effect of the irrigation treatments on fruit abscission during two seasons at Mazowe Citrus Estate. No measurements were taken in the RDI50 and PRD50 treatments since these had not been set up.*

Weekly measurements of fruit size using the hand-held vernier calipers on ten fruits per treatment from 31 October 2004 to 24 February 2005 are shown in Fig 4.17 for the control, PRD100 and the well-watered treatments, respectively. The slope of the growth curve gives the growth rate of the fruit. Fruit growth rate in the PRD100 treatment was not significantly different from that in the well-watered treatment throughout the measurement period. This trend can be explained by the PRD effects on tree water relations which plays an important role in governing fruit attributes (Albrigo, 1977). Under PRD, the trees were not under water stress and plant water status was generally maintained (i.e. similar to that of the well-watered treatment as shown in Fig 4.12). This fact is further illustrated by the results of the final average mass of individual fruit over three growing seasons in Fig 4.18. Fruit under PRD treatments generally had larger sizes than the other treatments probably due to the combination of high water status of the trees and low crop load.

Although the fruit growth rate in the control treatment was initially similar to that in the other two treatments in 2004/05, it began to slow down during the tenth week after 31 October 2004 (Fig 4.17). This reduction in the growth rate was most probably a result of the heavy crop load in the control treatment during the 2004/05 season (Table 4.4). Trees in the control treatment had a larger number of fruit but of smaller size than the other two treatments. The high crop load presumably resulted in increased competition for assimilates between the individual fruit and thus causing a reduction in the mean size of the fruit.

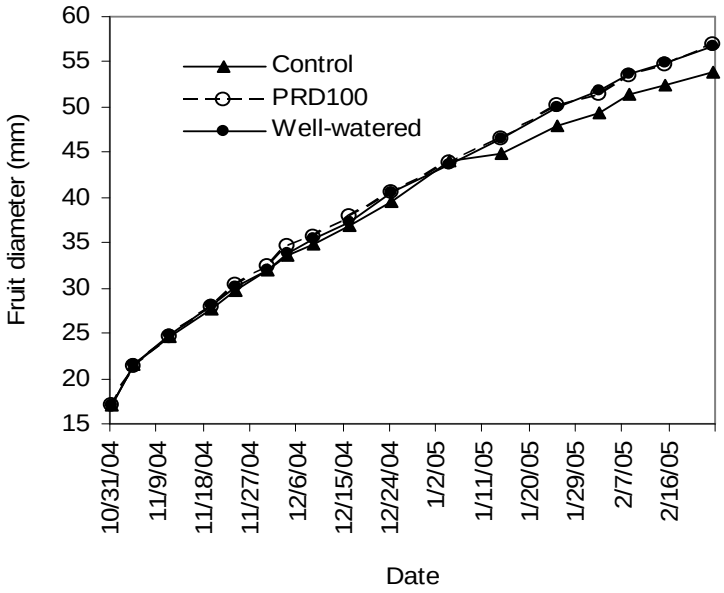

Fig 4.17 *Effect of the different soil water regimes on weekly fruit growth rate during the 2004/05 season. Closed triangles show the mean fruit diameter in the control treatment, while the closed circles show the trend in the well-watered treatment and the open circles show the fruit size in the PRD100 treatment.*

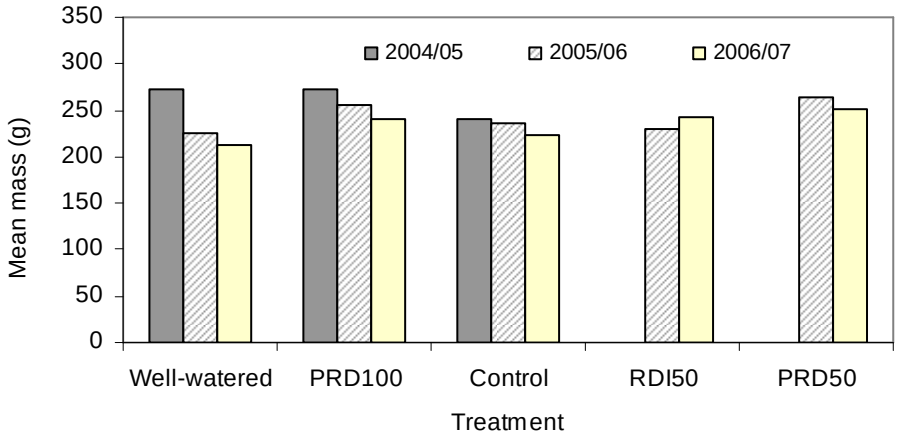

Fig 4.18 *Treatment effects on average mass of individual fruits over three growing seasons at Mazowe Citrus Estate.*

Fruit size distribution in the canopy of individual trees was influenced by the location of the fruit as shown in Fig 4.19a. Bigger sized fruit were found predominantly on the western side of the canopy and on the outer layers in all the treatments. This was probably because the western side of the canopy remained warm for a longer period than the eastern side although representative canopy temperature measurements were not taken. Warm temperatures encourage rapid fruit development than cooler conditions (Davies and Albrigo, 1994; Spiegel-Roy and Goldschmidt, 1996). The soil water regimes indirectly affected the final fruit size through its effects on crop load and presumably tree water status. The typical fruit size distribution at harvest in 2006 is shown in Fig 4.19b.

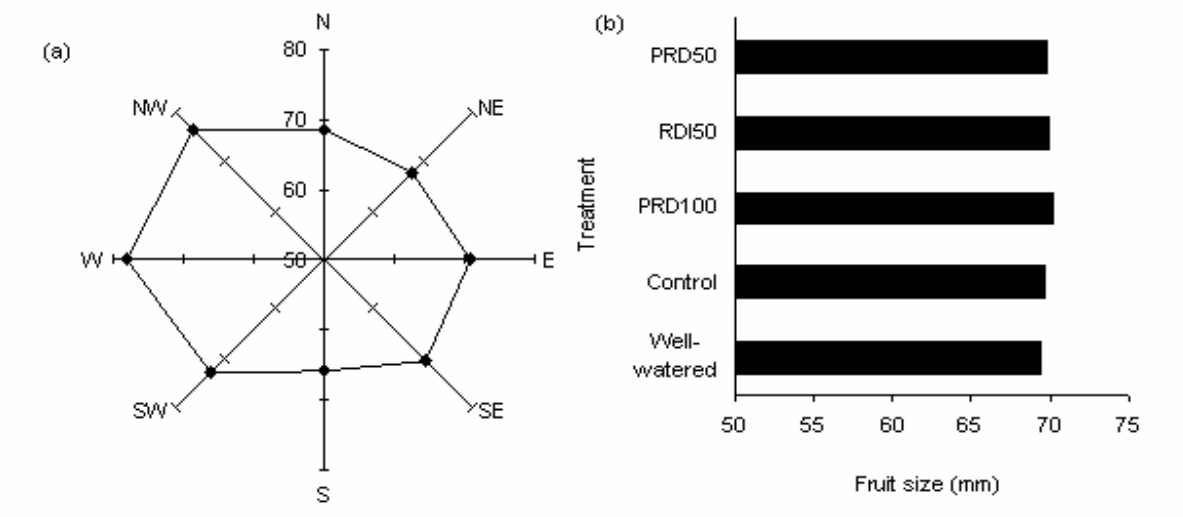

Fig 4.19 *(a) Fruit size distribution (in mm) at harvest as affected by location in the canopy of mature Navel orange trees at Mazowe Citrus Estate. Larger sized fruit were prevalent on the western side of the canopy in all the treatments. (b) Fruit size distribution of the fruit whose internal quality was sampled at harvest in 2006.*

4.5.4.2 Yield and fruit quality

During the 2004/05 season the PRD100 treatment gave a slightly lower average yield per tree than the single drip line control treatment and the well-watered treatment as shown in Table 4.4. Yield drops under PRD have also been observed, e.g. on hot pepper (Dorji *et al*., 2005), common beans (*Phaseolus vulgaris* L.) (Wakrim *et al*., 2005) and in olive trees (*Olea europaea*) (Wahbi *et al*., 2005). According to the approach by Caspari *et al*. (2004), crop load can be defined as the ratio of the number of fruit carried by a unit area of the stem. However, the number of fruit at harvest in 2005 was not counted and thus the crop load was only calculated for 2006 and 2007. A reduction in the average yield per tree of up to 18 % compared with that in 2004/05 occurred in the PRD100 treatment during the second year of the trial (2005/06 growing season). But an even larger decline of more than 30 % occurred in the control treatment, while a yield increase of approximately 10 % occurred in the well-watered treatment. The average fruit size was consistently larger in the PRD treatments in all the three years shown in Table 4.4. The reduced fruit size in the well-watered treatment can be attributed to the high crop load in this treatment and the fruit size can potentially be improved by thinning if desired.

The low and fluctuating yields between the years in the control, PRD and RDI treatments compared to the well-watered treatment have two or more possible causes. Firstly, it appears that levels of fruitset were generally low in these treatments probably due to water stress during this critical period. However, the source of the water stress is not certain given the high irrigation levels at Mazowe. The limited root system actively taking part in water and nutrient uptake at any given time in these single drip line treatments probably led to transient water deficits during the fruitset period which also coincided with the period of the highest atmospheric evaporative demand at Mazowe. This possibility is reinforced by the low rates of water up take (sap flow) by the Navel orange trees as demonstrated by Dzikiti *et al* (2007). It is highly probable that the trees under the well-watered treatment developed an extensive root system either side of the tree which supplied sufficient quantities of water and nutrients to ensure good fruitset. However, detailed measurements of plant water status were not taken during this period to verify this theory. Based on this theory, it appears that applying too much water to a limited soil volume did not significantly reduce water stress.

The second possible cause of the yield fluctuations between years in treatments with single drip lines is the phenomenon of alternate bearing which appeared to be more pronounced in these treatments. High yield in one year was followed by a low yield in the next year (Table 4.4). It is worthwhile to revisit the question of the need for an appropriate standard irrigation system, i.e. whether to use a single or double drip lines under the semi-arid conditions experienced in Zimbabwe. Based on this data it seems the well-watered treatment is most appropriate at least during the fruitset period if yields are to be maximized. Application of the deficit irrigation strategies including the current practice by the growers (single drip line with daily irrigations) at fruitset invariably leads to lower yields for citrus trees than can potentially be achieved.

Interestingly also, unexpectedly high average yields were found in the RDI50 and the PRD50 treatments in both 2006 and 2007, respectively. During 2006 both treatments in fact gave more fruit than in the control and the PRD100 treatments and the yields were comparable in 2007. This observation brings into question the long irrigation durations implemented by the local growers given the fact that these two treatments only used 50 % of the water compared to the control treatment. It is probable that high yields can still be achieved using 50 % less water than the current irrigation levels. However, the long-term effects of the reduced application levels is uncertain. For example, if indeed alternate bearing effects are more severe on trees receiving less water and fewer nutrients, then it will be difficult to obtain consistently high yields under the reduced application rates.

Table 4.4 *Effects of the irrigation regimes on yield, mean fruit weight, fruit number and crop load (number of fruit per cm^2 of trunk cross-sectional area) of the Navel orange trees at Mazowe Citrus Estate over three growing seasons (2004/05, 2005/06 and 2006/07). The average number of fruit per tree was not determined in 2005.*

Treatment	Fruit mass (g)			Fruit no.			Yield (kg/tree)			Crop load (no. of fruit cm $^{-2}$)		
	05	06	07	05	06	07	05	06	07	05	06	07
Control	239.7[a]	236.2[a]	223.4[a]	_	137	217	52.0	28.8	46.8	_	0.77	1.22
PRD100	272.2[b]	256.0[b]	241.4[b]	_	183	242	41.9	34.2	48.1	_	1.01	1.34
Well-watered	271.8[b]	226.2[a]	212.0[a]	_	243	279	47.4	52.0	55.1	_	1.36	1.56
RDI50	_	229.6[a]	242.6[b]	_	221	227	_	44.5	45.7	_	1.28	1.31
PRD50	_	264.0[b]	251.2[b]	_	209	214	_	42.3	49.2	_	1.19	1.22

Values within each year followed by different letters are significantly different from the control at ($P \leq 0.05$)

Another feature of the crop yield in 2006 is that the trees under the RDI50 treatment produced a large proportion of immature out-of-season fruit with diameters larger than 50 mm leading to fruit with two distinct age groups being carried on these trees. This phenomenon is clearly illustrated in Fig 4.20. Approximately 23 % of the total fruit in the RDI50 treatment were the out-of-season crop compared to less than 4 % in the PRD50 treatment which received the same volume of water but switched between two sides of the root zone. The immature fruit were not included in the yield data shown in Table 4.4. The off-season fruits were a result of a massive wave of secondary flowering which occurred after the onset of the rainy season in early October 2006 suggesting that water supply through irrigation was probably not adequate to support flowering by all the reproductive sites on the trees. But strangely, this same phenomenon was not observed in the 2006/07 growing season.

Fig 4.20 *(a) Composition of the fruit in the canopy of a tree in the PRD50 treatment a week before harvest at Mazowe Citrus Estate. (b) Canopy of the RDI50 treatment one week before harvest showing fruit with two distinct age groups.*

The influence of the different irrigation regimes on the internal quality of the Navel orange fruit is shown in Table 4.5. The percentage juice content of the individual fruit in the different treatment was comparable in all the three years although year to year variations occurred within each treatment. The year to year variations in the juice yield of the individual fruits also led to variations in the overall juice yield by the trees as shown in Table 4.5. The average juice yield per tree was calculated as the product of the average fruit yield per tree with the mean juice content per fruit assuming that the juice content of the fruit remained constant. The internal quality of the fruit expressed as the ratio of the total soluble solids (TSS) to the titratable acids (TA) appeared not to be significantly different between treatments. High levels of water application in the well – watered treatment did not reduce the internal quality of the fruit due to the dilution effect of the water as expected. As with the juice yield, year to year variations in the internal quality were also apparent.

Table 4.5 *Effect of the irrigation regimes on fruit quality attributes including the average juice yield per tree. Internal quality attributes are derived from ten fruit of the same size obtained from the exposed parts of the south-western quadrant of the canopy for each treatment. The fruit mass given in this table is for ten fruits*.

Treatment	Juice (%)			Acid (%)			TSS (%)			TSS:TA Ratio			Juice yield (kg/tree)		
	05	06	07	05	06	07	05	06	07	05	06	07	05	06	07
Control	49[a]	47[a]	46[a]	0.78	0.73	0.76	9.7[a]	9.0[a]	9.8[a]	12.4[a]	12.3[a]	12.9[a]	25.5	13.5	21.5
PRD100	49[a]	45[a]	46[a]	0.84	0.75	0.81	9.6[a]	9.0[a]	9.6[a]	11.4[a]	12.0[a]	11.9[a]	20.7	15.4	22.1
Well-watered	48[a]	51[a]	45[a]	0.81	0.71	0.79	9.2[a]	9.2[a]	10.3	11.4[a]	13.0[a]	13.1[a]	22.6	26.5	24.8
RDI50	_	48[a]	51[a]	_	0.78	0.64	_	9.2[a]	9.2[a]	_	11.8[a]	14.8[a]	_	21.4	23.3
PRD50	_	44[a]	47[a]	_	0.77	0.71	_	9.2[a]	9.0[a]	_	11.9[a]	12.7[a]	_	19.5	23.1

Values within each year followed by different letters are significantly different from the control at ($P \leq 0.05$)

4.6 Conclusions

The results presented in this chapter reveal that despite the relatively low stomatal conductance of the Navel orange trees under optimal conditions, PRD effects were detected in these trees. These occurred in the form of a further reduction in the mean size of the stomatal aperture, while the plant water status was maintained. Further evidence of the occurrence of the reduction in transpiration rates due to the PRD strategy was provided by sap flow measurements which showed consistently lower flow rates in the PRD treatments than in the control and the well-watered treatments both with potted trees and under field conditions.

Given the fact that the stomatal aperture is the pathway for the exchange of both the CO_2 and water vapor between the plant and the environment, a further reduction in stomatal conductance due to the PRD treatment on the Navel orange trees appeared to cause yield reductions in all the three growing seasons, namely 2004/05, 2005/06 and 2006/07 when compared with the well – watered treatment but not with the local growers' irrigation practice. Both the PRD100 and PRD50 treatments gave marginally higher yields than the current growers' practice. The lower yields under control, PRD, and the RDI treatments compared with the well – watered treatment was attributed to low levels of fruitset in these treatments and to some extent to the effects of alternate bearing. One way to resolve this will be to adopt the well-watered treatment, but with the emitters producing much less water per unit time than the ones currently in use. This will encourage the development of an extensive root system and probably enhance fruitset. The second possibility will be to apply the deficit irrigation strategies

only outside the critical periods e.g. the flowering and fruitset phase. While the yield reductions under the PRD treatments was undesirable, it is important to establish the relationship between the yield produced by the trees against the amount of water lost through transpiration to establish whether this technique is potentially cost-effective and this is the subject of the next chapter.

The different irrigation regimes did not appear to have a significant effect on the internal quality of the citrus fruit (TSS:TA ratio). Fruit size was influenced more by crop load which itself was controlled by the soil water regimes. Consistently large fruits were obtained under the PRD strategy in all the three growing seasons probably due to the effect of tree water relations on size.

Chapter 5 Water use efficiency of young Navel orange trees [*Citrus sinensis* (L.) Osbeck] in Zimbabwe

5.1 Introduction

This chapter seeks to quantify and to compare the water use efficiency by drip irrigated Bahianinha navel orange trees watered using the local growers' practice and with the deficit irrigation techniques discussed in the previous chapter. Information on the water use efficiency under the different irrigation methods will assist the citrus growers to decide on the best strategies that give more fruit and less water. Such irrigation methods are crucial especially in the Mazowe catchment of northern Zimbabwe where the competition for water has increased significantly in recent years.

The stomata are the main pathway for the diffusion of CO_2 into the plant and the loss of water from the plant. Irrigation techniques that seek to improve water use efficiency are designed to optimize the stomatal aperture so that the carbon gain by the plant outweighs water losses. The term 'water use efficiency' has been devised to describe this tradeoff of water for carbon. In various areas of plant science, water use efficiency is defined in different ways depending on the scale of the investigation (Jones, 1992; Weber *et al*., 2006). For example, at leaf level, the instantaneous water use efficiency can be defined as the ratio of the CO_2 assimilation to the transpiration rate (Davies *et al*., 2002; Bacon, 2004). But this parameter changes with changing environmental conditions. For agronomic use, where events at whole plant community level are of interest, it is more common to describe the water use efficiency as the ratio between the seasonal integrals of biomass production (or the harvested yield) and the total seasonal evapotranspiration or transpiration (De la Hera *et al*., 2006).

In some cases, the total water applied including rainfall can also be used as a measure of the seasonal water consumption in computing the water use efficiency (Shahnazari *et al*., 2007; Kang *et al*., 1998). But the closest causal relationships between carbon gain and water loss are between biomass production and crop transpiration since the use of the total

evapotranspiration can be biased by soil evaporation (Bacon, 2004). This is particularly the case in fruit tree orchards where the inter-row spacings are wide. The total biomass of interest to fruit tree growers is the yield of fruits and this can easily be obtained by weighing the fruits at harvest. But the total seasonal transpiration is more difficult to quantify given the fact that there are currently no direct methods of measuring it from all trees in an orchard which is several hectares in size. Often a few representative trees are selected and instrumented with transpiration monitoring devices, e.g. sap flow sensors and gas exchange chambers (Dragoni *et al*., 2005; Rana *et al*., 2005). Transpiration measurements at leaf level using porometers are also common (Verhoef, 1997). The measurements are then scaled up from individual tree to whole orchard level making certain assumptions in the process. A temporal up scaling is also required to derive the seasonal total transpiration, since most of the measurements are taken on a daily time scale or less (Samson, 2001; Wouters, 2004). In addition, the transpiration data is often discontinuous due to instrument failure or other practical considerations.

In this study, two different sap flow measurement techniques, namely the stem heat balance and the thermal dissipation probes, were used to quantify the water use by individual orange trees in a five-year-old orchard at Mazowe Citrus Estate, Zimbabwe. Spatial up scaling of the sap flow from single tree to plantation level was done using estimates of the leaf area index of the orchard. The total transpiring leaf area was estimated from allometric relations between the stem size and the transpiring leaf area. Temporal up scaling was achieved through empirical relationships obtained by correlating daily orchard-level transpiration rates with climatic variables. In addition, site-specific coefficients for use in irrigation decision making, e.g. the crop coefficients and the pan coefficients, were derived for the Mazowe trial site.

5.2 Quantification of water use by fruit trees

5.2.1 Devices for monitoring transpiration rates

The most common bio-sensors used for monitoring the transpiration rates of fruit trees are the sap flow sensors (Wullschleger *et al*., 1998). In reality, these sensors measure the sap flow rate and not the transpiration rate since these two quantities are not necessarily equal due to the buffering effects of plant capacitance which introduces a time lag between them. But when the sap flow measurements are integrated over a sufficiently long time (e.g. one day or longer) we can reasonably assume that the sap flow rate equals the transpiration rate since the capacitance effects are negligible on this time scale.

The approach of using sap flow sensors offers several advantages which include the direct measurement of the water stream inside the plant (or smaller sections of the water pathway), potentially high number of replicates, continuous and long-term monitoring, no disruption of the plant's canopy or root environment among others (Dragoni *et al*., 2005). Three general types of sensors are currently available, namely the heat balance, heat dissipation and heat pulse (Sakuratani, 1981; Granier, 1987; Steinberg *et al*., 1989; Allen and Smith, 1996; Zhang *et al*., 1997). All of them rely on the thermal transport properties of the water flow through the stem to estimate the sap flow rate.

However, these methods are still subject of uncertainty because of the assumptions used to convert measured parameters to mass flow which are difficult to prove (Shackel *et al*., 1992; Grime and Sinclair, 1999). Anatomical analysis of the test plant stem may be needed in order to obtain estimates of mass flow. This may be difficult and/or highly undesirable considering the economic value of the fruit trees. The uncertainties due to the technical difficulties or the assumptions made may lead to significant errors in sap flow estimates (Allen and Grime, 1995; Allen and Smith, 1996; Grime and Sinclair, 1999). Gas exchange chambers used with the infra-red gas analyzers connected to dataloggers have been used recently to estimate the transpiration rates of mature field-grown fruit trees (Dragoni *et al*., 2005). This method relies on few verifiable assumptions and therefore is less prone to errors than the sap flow gauges. The technical details and the specific advantages and disadvantages of each of the above mentioned techniques will be discussed in detail in the next section.

5.2.1.1 Heat balance sap flow sensors

The principles of operation of these devices have already been explained in Section 1.2 of this thesis. The main advantage of the heat balance sap flow sensors is that the method can be used to measure sap flow on both woody and herbaceous stems (Smith and Allen, 1996) and the response time of smaller gauges is fairly fast being less than 1 min (Grime and Sinclair, 1999).

The major disadvantage of the heat balance sap flow gauge is that there is a considerable uncertainty on the assumption of steady-state conditions on which it is based (Baker and van Bavel, 1987; Shackel *et al*., 1992; Dugas *et al*., 1993; Dauzat *et al*., 2001). These conditions are rarely truly achieved under field conditions and so there is a need for extra insulation both of the gauge and parts of the stem being measured. The right size of gauge is needed for a given stem for good thermal contact. Too much power input can raise the stem temperature and damage the tissue in contact with the gauge and ultimately the whole tree can be killed. This is highly undesirable for the high value trees such as the commercial fruit trees. An

accurate determination of the sap flow using the heat balance technique depends on the accurate determination of the radial sheath conductance (K_{sh}) in equation 1.5.

While the K_{sh} value varies with stem cross sectional area and thus with gauge size, ideally this parameter should be worked out each day for accurate flow measurements at short intervals. Since it is possible that some sap flow occurs at or before predawn mainly driven by the vapor pressure deficit of the air (VPD) or the internal water deficit of the plant (Dzikiti *et al*., 2007), other more reliable methods to ensure that sap flow is truly zero when the K_{sh} factor is worked out exist. These involve bringing the canopy of the plant to saturation (100 % relative humidity). For small trees, this can be done by enclosing the canopy with a plastic bag so that all the transpired water stays around the canopy. After a certain period, transpiration will be zero when the VPD of the air is zero after equilibration. The same state of saturation can also be achieved by spraying the canopy with a fine jet of water until the whole canopy is wet.

5.2.1.2 Thermal dissipation probes (Granier probes)

While the heat balance sap flow sensors have the advantage that they take absolute measurements of sap flow requiring no calibration, these sensors tend to be more complex and expensive when applied to larger stem sizes (> 50 mm). The average stem sizes for the trees at the trial site at Mazowe Citrus Estates was generally larger than 60 mm and thus the heat balance sap flow rates could not be used for monitoring the stem sap flow rate. Thermal dissipation probes, also known as Granier probes (Granier, 1987), which are more suitable for measurements of sap flow on larger stem sizes were used. A typical diagrams of the thermal dissipation probe is shown in Fig 5.1. A constant heat source is also needed as in the case of the heat balance sap flow sensors.

The thermal dissipation probe comprises a pair of needles inserted in tight-fitting holes approximately 4 cm apart and arranged in a vertical line as illustrated in Fig 5.1b. Commercial TDPs are typically 10 – 100 mm long, while their diameters range from 1.2 mm to 1.65 mm. The upper needle is fitted with a heater to raise its temperature above that of the lower reference needle. Inside the two sets of needles are T-type thermocouples (copper-constantan) configured to produce a differential voltage output proportional to the temperature difference (dT) between the needles.

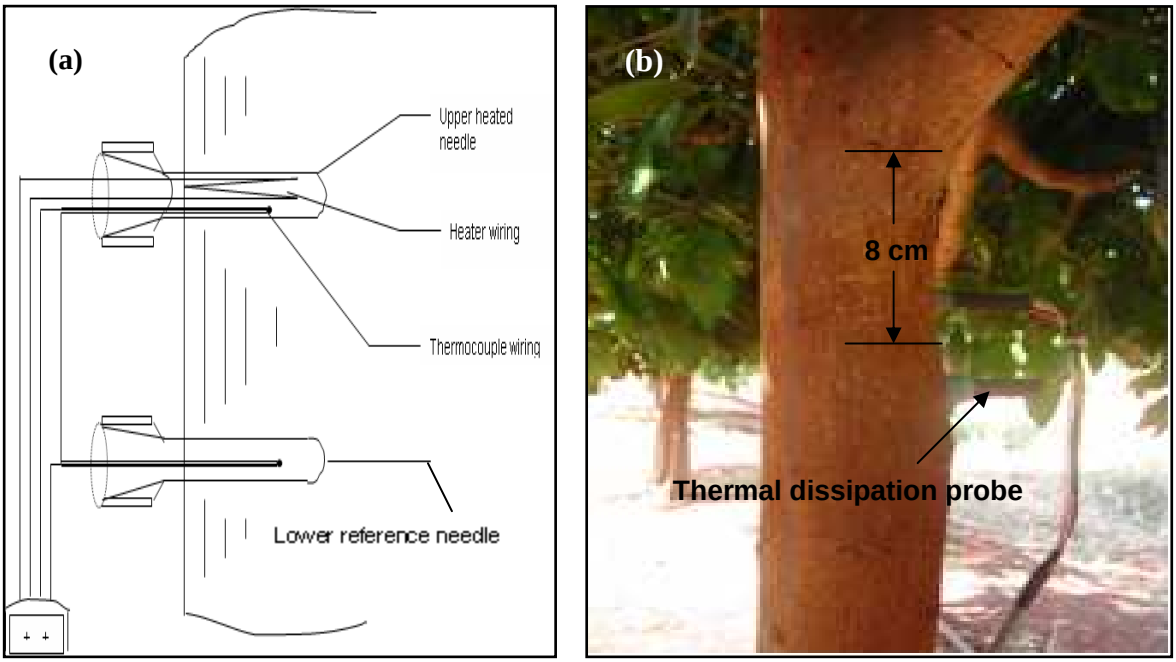

Fig 5.1 *(a) Diagram of the thermal dissipation probe (TDP) showing the technical details of the sensor. (b) A TDP installed on the stem of a citrus tree at Mazowe Citrus Estate, Zimbabwe.*

The probe measures the sapwood heat dissipation which increases with sap flow and the resultant cooling of the heat source as the apparent thermal conductance of sapwood increases with sap velocity. When the sap flow velocity is zero or minimal, the temperature difference approaches the maximum value, (dT_m). Thus the variations in the temperature differences can be calibrated and used as a measure of the sap velocity. Granier (1987) defined a dimensionless flow index 'K' as:

$$K = \frac{(dT_m - dT)}{dT} \qquad (5.1)$$

As dT tends to dT_m, then K tends to zero. The sap velocity (V, cm s^{-1}) averaged over the whole length of the needle is related to the variable K according to the empirical equation by Granier (1987) as:

$$V = 0.0119K^{1.231} \qquad (5.2)$$

To convert the sap velocity into the mass sap flow rate (F, g h^{-1}), then an estimate of the conducting sapwood area (A_s) is required so that:

$$F = 3600 A_s V \quad (5.3)$$

The advantages of using the TDP are that firstly, these require continuous heating and thus continuous sap flow measurements can be obtained. Secondly, the exact distance between the needles of the probe is not crucial as long as they are in a vertical line. The TDP is relatively cheap and easy to use and can be used on large stem diameters. Their major disadvantage is the need for an accurate estimate of the conducting sapwood area where the sensor is installed. This task is quite difficult for certain tree species (e.g. citrus trees) where the differences between the compartments of the stem cross-section are not readily distinguishable visually. In addition, injection of dyes into the stem of these trees using conventional techniques such as drilling holes in the stem does not yield desirable results since the dye is simply not taken up (James *et al*., 2003; Sano *et al*., 2005). This is probably a result of the rapid development of embolisms within the transpiration stream which inhibit the uptake of the dye. The dye can only be taken up if the injection is done under water (Sano *et al*., 2005) and this is difficult for trees growing in the field. Secondly, the sap velocity varies radially with distance across the stem (Granier, 1987; James *et al*., 2003). Thus what is measured by the TDP is the average sap velocity integrated over the whole length of the needles and this introduces some errors. A number of probes inserted at different depths are needed on bigger trees (Allen and Smith, 1996) to minimize this problem.

5.2.1.3 Heat pulse method

Heat pulse sap flow devices comprise pairs of identical probes fitted with thermistors to measure the temperature at each probe installation. The probes are inserted into the xylem vessels at unequal distances above and below the heater with the upstream probe being closer to the heater than the downstream probe as illustrated in Fig 5.2. When a pulse of heat of 1 - 2 s duration is released, the temperature gets higher at the closer upstream sensor than at the downstream sensor because of conduction. But the heat carried by the moving sap quickly warms the downstream sensor. After a time t_e (~ 60 s) the temperature of the two sensors is equal again. It has been demonstrated by Marshall (1958) that measuring the temperature changes produced by a heat pulse at distances X_u (m) upstream and X_d (m) downstream from the heater, the velocity of the heat propagation (V, m s $^{-1}$) is given by the equation:

$$V = \left(\frac{X_d - X_u}{2t_e} \right) \quad (5.4)$$

For datalogging purposes, a simple electronic wheatstone bridge circuit is needed to detect the null temperature difference (voltage) as a function of time and a precise timer to measure t_e which is the time between the imposition of the heat pulse and when the bridge is balanced.

Calculation of V from equation 5.4 based on the idealized theory of heat transport must be corrected for alterations in the heat flow patterns due to the wounding of the stem tissue during the installation of the probes and the physical presence of the probes themselves (Edwards and Warwick, 1984; Allen and Smith, 1996). Thus the corrected heat pulse velocity V_c (in m s^{-1}) is given by the equation

$$V_c = a + bV + cV^2 \qquad (5.5)$$

where V is the uncorrected heat pulse velocity calculated from equation 5.4 and a, b and c are the correction coefficients proposed by Swanson and Whitfield (1981), variable as functions of wound size.

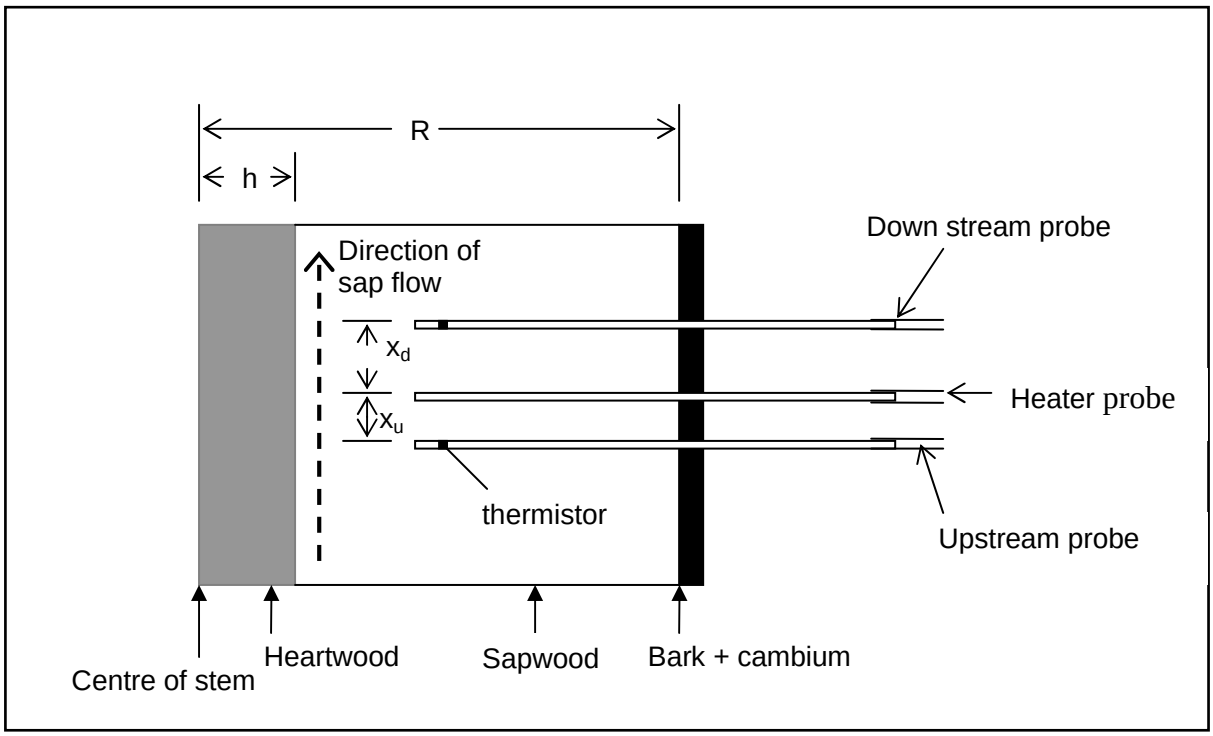

Fig 5.2 *Configuration of a single set of the heat pulse probes inserted radially into a stem of radius R at the cambium and h at the heartwood boundary (Smith and Allen, 1996).*

The advantage of the heat pulse technique is that for species that can be considered to be thermally homogeneous, the method can be used to measure the sap flow rate without calibration (Smith and Allen, 1996 ; Zreik *et al*., 2000; Giorio and Giorio, 2003; Kang *et al*., 2003).

The disadvantages are that the probes have to be installed at precisely known distances and with minimal wounding of the stem tissue. Quantifying the wound size is problematic as this depends not only on the size of drill bits used, but also on the thermal homogeneity of the stem tissue. Tissue thermal characteristics vary between species (Green and Clothier, 1988) and thus the method needs calibration when used on different species. The method can only be used on woody stems (Wouters, 2004). A waiting period is required between readings unlike the other two techniques discussed above and thus measurements are not continuous.

5.2.1.4 Whole-tree gas exchange technique

A typical whole-canopy gas exchange measurement system is shown in Fig 5.3. The gas exchange chambers are commonly made from infrared transparent material to avoid a build up of heat inside the chamber. An infrared gas analyzer is used to measure the gas exchange inside the chambers with the air pumped to the chambers at a flow rate allowing a residence time of approximately 1 min (Dragoni *et al*., 2005). A typical equation for the whole tree transpiration (E, mmol s^{-1}) is given by

$$E = \frac{U_e \Delta H_2O}{P_r - (\Delta H_2O + X_e)} \tag{5.6}$$

where P_r is the current atmospheric pressure (mbar), X_e the water moisture partial pressure measured using the gas analyzer at the inlet (mbar), ΔH_2O is the difference in the water moisture partial pressure between the outlet and the inlet (mbar), and U_e is the molar flow at inlet (mmol s^{-1}).

The major advantage of this technique is that it is based on a set of verifiable assumptions (Dragoni *et al*., 2005) and it measures the actual transpiration rate as opposed to the sap flow rate in the above mentioned methods. One key assumption is that the difference in moisture content between the outlet and the inlet to the chamber is solely due to transpiration. This presents problems in that the accumulation of water, though undesirable, can occur, (e.g. due to rain and condensation) and its subsequent evaporation causes errors in the transpiration measurements.

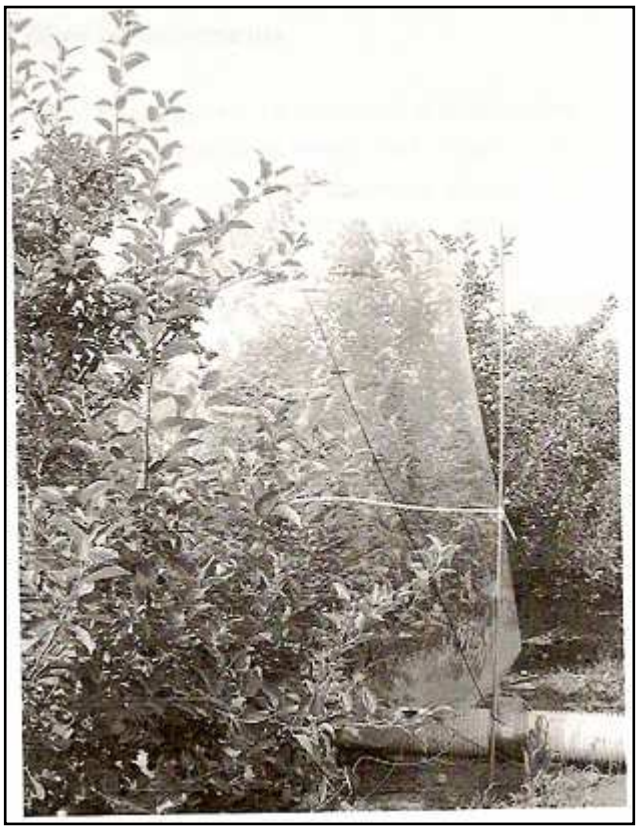

Fig 5.3 *Whole-canopy gas exchange system in apple trees (adapted from Dragoni et al., 2005).*

Constant visual inspection and the fitting of heater jackets around the tubings is needed to eliminate condensation. Many replications are not possible due to the high cost of the equipment involved. Some data has to be filtered off (e.g. during the switching of valves from one chamber to another) to eliminate the effects of voltage surges during the switching period and thus the measurements are not continuous. Another important disadvantage of this technique is that the chamber modifies the microclimate around the tree. This makes it difficult to get measurements of transpiration representative of all the trees in the orchard.

While the techniques mentioned above are largely restricted for research purposes only, the concept of crop evapotranspiration is more popular with fruit tree growers (Li *et al*., 2002; O'Connell and Goodwin, 2004). Under orchard conditions, evapotranspiration is estimated in different ways including the use of climate data (Intrigliolo and Castel, 2004) and the pan evaporation methods (Allen *et al*., 1998; Rana *et al*., 2005).

5.2.2 Estimation of evapotranspiration in fruit tree orchards

The term evapotranspiration (ET) is a combination of two processes, namely; evaporation wherein water is lost from the soil surface or from water bodies and transpiration where water mainly escapes from the plant through stomatal pores in the leaves. In both cases, water is converted into a gaseous state or vapor and this process needs energy. This energy is provided by the solar radiation and to a lesser extent by the ambient temperature (Allen *et al*., 1998). The driving force to remove the water vapor from the evaporating or transpiring surface is the difference between the vapor pressure at the surface and that of the surrounding air. The water vapor molecules removed from the surface in question accumulate in the air above and thus, they reduce the humidity gradient. Wind plays an important role by blowing these water vapor molecules away and thus maintaining the humidity gradient. Hence, radiation, air temperature, air humidity and wind terms are crucial factors when assessing evapotranspiration.

5.2.2.1 Factors affecting evapotranspiration

According to Allen *et al.* (1998), evapotranspiration, usually expressed as the depth of water lost (mm) in unit time, is affected by weather variables, crop factors, management and environmental conditions as summarized in Fig 5.4.

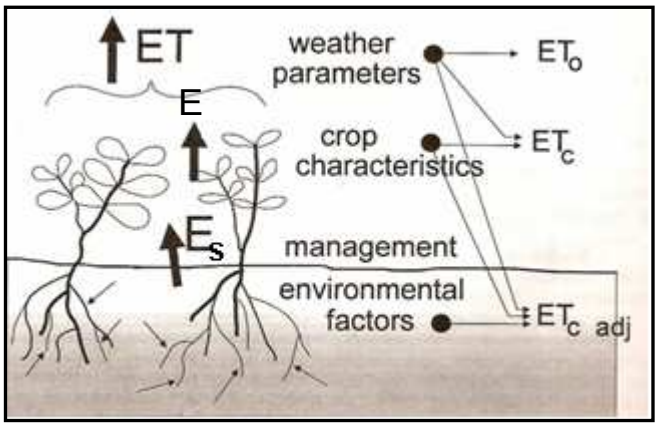

Fig 5.4 *Factors affecting evapotranspiration (adapted from Allen et al., 1998). ET is the evapotranspiration, ET_o the reference crop evapotranspiration, ET_c the crop evapotranspiration under standard conditions, E the transpiration rate, E_s evaporation from the soil and ET_{cadj}, the evapotranspiration under non-standard conditions.*

Weather variables

Weather variables of importance in the determination of evapotranspiration include the incoming radiation, air temperature and humidity and wind speed. These variables combined give the evaporating power of the atmosphere, expressed by the reference crop evapotranspiration (ET_o). By definition ET_o represents the evapotranspiration from a reference surface, namely a hypothetical short grass of height 0.12 m, with a fixed surface resistance of 70 s m^{-1}, an albedo of 0.23 and the grass is not short of water. The reference evapotranspiration is computed only from the weather variables and the Penman-Monteith equation discussed in Section 5.2.2.2 is the generally accepted method (Allen *et al*., 1998).

Crop factors

In commercial orchards, crop type, variety and development stage are factors that play a role in the observed evapotranspiration. Some fruit trees, e.g. apple (*Malus domestica*) are deciduous and thus the extent of vegetation cover changes significantly throughout the year, while smaller variations occur in evergreen species, e.g. citrus. Differences in resistance to transpiration, extents of ground cover and rooting depths occur between different varieties of fruit trees.

Management and environmental factors

Poor management factors, e.g. soil salinity, inadequate irrigation levels, limited application of fertilizers and poor pests and disease management limit the growth of the trees and, hence, the size of the transpiring canopy area. Reduction in growth is also achieved due to environmental factors, e.g. poor soil fertility and the presence of hard and impermeable soil media which restrict root development with a net reduction in the evapotranspiration levels. The type of irrigation method is also known to affect the rate of evapotranspiration with surface irrigation techniques, e.g. the flood and basin type of irrigation leading to higher soil evaporation rates than the drip method, where a relatively small soil surface is watered. Consequently, a distinction is made between evapotranspiration from different cropped areas based on the management practices. Crop evapotranspiration (ET_c) generally refers to the evaporating demand from crops that are grown in large fields under optimum soil water, management and environmental conditions and is related to ET_o via a crop factor K_c such that

$$ET_c = K_c ET_o \tag{5.7}$$

The value of K_c varies throughout the growing season due to the changing characteristics of the trees, e.g. changes in the size of the transpiring area and also for the manipulation of the

internal quality of the fruit (Castle, 1995). Typical crop factors for citrus trees are given in Table 5.1.

Table 5.1 *Crop coefficients of citrus trees for three developmental stages (after Wouters, 2004).*

Stage of development	**Crop coefficient, K_c**
Initiation	0.50 – 0.70
Reproductive	0.45 – 0.65
Maturation	0.55 – 0.70

5.2.2.2 Penman-Monteith equation

The FAO Penman-Monteith method is recommended as the sole method for determining reference evapotranspiration (Allen *et al*., 1998). The method requires radiation, air temperature, air humidity and wind speed as input data. It is a weighted combination of the energy balance and the aerodynamic methods of estimating evapotranspiration (Monteith and Unsworth, 1992) represented as:

$$\lambda ET = \frac{\Delta(R_{net} - G) + \rho_a c_p \dfrac{(e_s - e_a)}{r_a}}{\Delta + \gamma\left(1 + \dfrac{r_s}{r_a}\right)} \qquad (5.8)$$

where R_{net} is the net radiation (W m^{-2}), G is the soil heat flux (W m^{-2}), $(e_s - e_a)$ the vapor pressure deficit of the air (kPa), ρ_a is the mean air density at constant pressure (kg m^{-3}), c_p is the specific heat of the air at constant pressure (J kg^{-1} K^{-1}), Δ the slope of the saturation vapor pressure and temperature relationship (kPa K^{-1}), λ is the latent heat of vaporization (J kg^{-1}), γ is the psychrometric constant (kPa ℃ $^{-1}$) and r_s and r_a are the bulk surface and aerodynamic resistances (s m^{-1}), schematically represented in Fig 5.5.

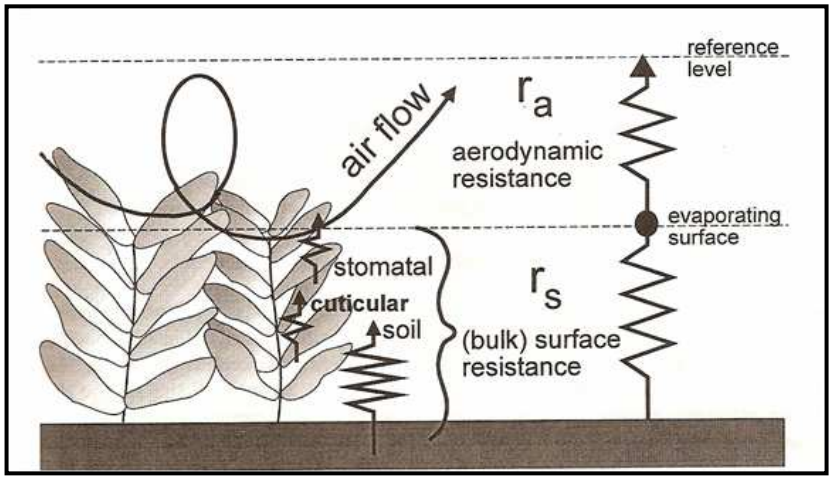

Fig 5.5 *Representation of the bulk surface and the aerodynamic resistances to water vapor transfer (adapted from Allen et al., 1998)*

Assuming neutral stability conditions over the trees with the air temperature, atmospheric pressure and wind velocity distributions following nearly adiabatic conditions (no heat exchange), r_a (s m $^{-1}$) can be calculated from the crop characteristics and wind speed data as follows:

$$r_a = \frac{\ln\left[\frac{z_m - d}{z_{om}}\right]\ln\left[\frac{z_h - d}{z_{oh}}\right]}{k^2 u_z} \qquad (5.9)$$

where z_m is the height of the wind speed measurement (m), z_h the height of the humidity measurement (m), d is the zero plane displacement height (m), z_{om} is the roughness length governing momentum transfer (m), z_{oh} is the roughness length governing the transfer of heat and vapor (m), k is the von Karman constant [0.41] and u_z is the wind speed at height z (m s $^{-1}$). The zero plane displacement and the roughness length can be derived from the plant height and architecture as explained in Monteith and Unsworth (1992).

In situations where the vegetation fully covers the ground such that evaporation from the soil is zero, the bulk surface resistance, r_s (s m^{-1}) can be estimated by

$$r_s = \frac{r_l}{LAI} \qquad (5.10)$$

where r_l is the stomatal resistance of well-illuminated leaves (s m^{-1}) and LAI is the leaf area index of the sunlit leaves (m^2 of leaf area m^{-2} of soil surface).

Assuming a standard height of 2 m for wind speed measurement over the reference crop of height 0.12 m, the Penman-Monteith equation takes the form

$$ET_o = \frac{0.408\Delta(R_{net} - G) + \gamma \frac{900}{T_a + 273} u_2 (e_s - e_a)}{\Delta + \gamma(1 + 0.34u_2)} \qquad (5.11)$$

where ET_o is the reference evapotranspiration (mm day^{-1}), R_{net}, is the net radiation (MJ m^{-2} day^{-1}), G the soil heat flux (MJ m^{-2} day^{-1}), T_a the mean daily air temperature at 2 m height (℃), u_2 the wind speed at 2 m height (m s^{-1}), e_s the saturation vapor pressure at air temperature (kPa), e_a the actual vapor pressure of the air (kPa), Δ the slope of the saturation vapor pressure and temperature relationship (kPa °C^{-1}) and γ is the psychrometric constant (kPa ℃$^{-1}$). Using this equation ET_o can be calculated from readily available climate data.

5.2.2.3 Class – A evaporation pan

Evaporation pans give an integrated effect of all the weather variables on water loss from an open water body measured as a change in the depth of water over a specific period (usually expressed in mm day^{-1}). In the absence of rainfall or leakages, changes in the depth of water are assumed to be due to evaporation (de Laat, 1996; Allen *et al*., 1998). Evaporation pans exist in different forms although the Class-A type (shown in Fig 5.6) is the more widely used one. Despite their inaccuracies in estimating evapotranspiration as will be explained below, these devices are still extensively used for irrigation management in fruit tree orchards. For example, irrigation scheduling in the citrus orchards in Florida (USA) and the apple orchards at Kibbutz Ortal in Israel (Li *et al*., 2002) are largely based on the pan methods.

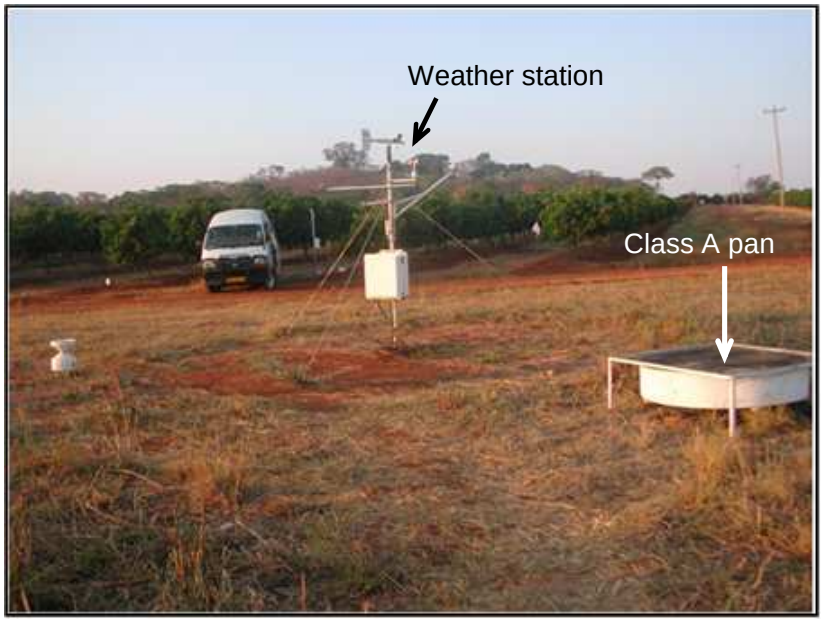

Fig 5.6 *Climatological station showing a Class-A evaporation pan installed adjacent to the experimental orchard at Mazowe Citrus Estate, Zimbabwe.*

Ease of operation and interpretation of readings and the relatively low cost are the major advantages of using the pan for irrigation management. Sources of error include the differences in the energy balance of the pan and that of the trees given the differences in the reflectance to solar radiation between the water surface and the trees. In addition, energy can be lost or gained through the sides of the pan, while the significant storage of heat by the pan ensures that water loss can continue to occur after sunset, while transpiration will have ceased. Generally, evaporation pans require rigorous local calibration and careful siting. An empirical correction factor called the pan coefficient, "K_p" is needed to estimate ET_o such that

$$ET_o = K_p E_{pan} \qquad (5.12)$$

where E_{pan} is the evaporation from the Class-A pan. The pan coefficient varies with site, e.g. the size and state of the upwind buffer zone (fetch). The FAO recommends the use of pan data for periods longer than 10 days. A typical value of the pan coefficient will be calculated for the experimental orchard at Mazowe Citrus Estate in Section 5.4.5.

5.3 Materials and methods

The experimental site was the five-year-old orchard with navel orange trees [*Citrus sinensis* (L.) Osbeck] grafted on troyer citrange rootstock [*Citrus sinensis* x *Poncirus trifoliata* L. Raf] at Mazowe Citrus Estates, Zimbabwe. Results for the 2005/06 season (September 2005 to August 2006) are reported in only three irrigation regimes, namely the control, well - watered and PRD100 treatments as described in Chapter 4. Transpiration measurements were only taken in these treatments since there were not enough sensors for the other treatments. Most work published in literature involves the comparison of the well - watered and control treatments with reduced water application in the partial rootzone drying treatments. However, in this study, a partial root zone drying treatment applying the same irrigation levels as the control treatment is investigated. In this way, the true partial root zone drying effects on the hydraulic signals can be unraveled without the influence of the variations in the irrigation levels. The PRD100 treatment will be called the PRD only, henceforth.

Climatic data were recorded using the automatic weather station located outside the orchard as described in Chapter 4, while the sap flow rate was measured on one model tree in each of the above three treatments at the branch and stem level, respectively. The selected model trees were of similar physical size and located away from the edges of the orchard to minimize edge effects. Branch level sap flow data was needed to check the accuracy of the stem sap flow measurements. Stem sap flow rates were measured using 30 mm thermal dissipation probes (Delta-T, Devices, Cambridge, UK) installed at approximately 8 cm below the first branch (Fig 5.1b) to avoid the complex wood anatomy near the branch points and at the bud union. An accurate estimate of the conducting sap wood area on the stem was thus required and the uncertainties in determining this parameter are large as already discussed above.

The SGA9 heat balance sap flow gauges (Dynamax Inc. Houston, USA) were installed on the branches of the model trees in the well - watered and the control treatments, respectively, while the SGB19 sap flow gauge (Dynamax Inc. Houston, USA) was installed on the tree in the PRD treatment. Well exposed branches located on the western part of the canopies were selected for the installation of the branch sap flow sensors (Cifre *et al*., 2005) as shown in Fig 5.7. Sap flow measurements in each treatment could not be replicated due to the shortage of sensors. However, to quantify the errors involved in the branch sap flow measurements, porometer measurements of transpiration were used to check the sap flow data and frequent calibrations were done to minimize the temperature effects on porometer readings.

Fig 5.7 *Sap flow gauges measuring the stem and the branch sap flow rates on a typical model tree at Mazowe Citrus Estates, Zimbabwe.*

Measurements of the stomatal conductance were made on 14 May 2006 using the AP4 porometer (Delta-T Devices, Cambridge, UK) from midday until sunset in all three treatments. Two mature, fully expanded and fully exposed leaves were measured on branches fitted with sap flow gauges to verify the sap flow measurements and the transpiring leaf area estimates. Lastly, the leaf area index (LAI), which is a measure of the ratio between the transpiring leaf to the ground areas was measured in the middle of the growing season on 20 March 2006 between 1145 and 1400 h (Local time: GMT + 2 h) on a typical clear day. Measurements were taken using the sunscan Ceptometer (Delta-T Devices, Cambridge, UK). This data was needed for up scaling the sap flow rates expressed per unit leaf area from single tree level to whole orchard level. The spatial distribution of the leaf area index was ascertained by randomly sampling approximately twenty trees of all age groups found in the whole orchard. In addition to the leaf area index, the corresponding stem diameter eight centimeters below the first branch was also measured using a hand-held vernier caliper. For the purposes of up

scaling, the trees were put into three diameter classes, namely; small (< 30 mm), medium (30 – 70 mm) and large (> 70 mm) which constituted approximately 5 %, 85 % and 10 % of all the sampled trees. Assuming that these proportions are representative of the age distribution of the trees in the entire orchard, an average value of the leaf area index for each class was worked out. The overall leaf area index of the orchard was derived as the weighted average of all the diameter classes with the proportion of each diameter class being the weighting functions. Typical values are shown in Table 5.2.

Table 5.2 *Mean values of the leaf area index (LAI) in three tree diameter classes in a 2 ha orchard at Mazowe Citrus Estate, Zimbabwe.*

Diameter class (mm)	Frequency (%)	LAI
< 30	5	1.2
30 - 70	85	4.7
> 70	10	5.4
Overall	**100**	**4.60**

Whole orchard transpiration rates are of more importance to the growers than the single tree level measurements. Thus, scaling up the transpiration measurements is a crucial step.

5.3.1 Upscaling from single tree to orchard level

5.3.1.1 Leaf area index as the scaling factor

In this study, the measurement of the branch sap flow rate normalized with the transpiring leaf area at the end of the branch are first checked at leaf level using the AP4 porometer. Expressing the sap flow rate per unit leaf area removes the variations due to differences in the size of the transpiring leaf areas since sap flow sensors of different sizes were used. In this way, the effect of the different irrigation regimes on the transpiration rates can be compared. The branch leaf area was obtained by stripping all the leaves from each branch after the experiment and a leaf area meter (Delta –T Devices, Cambridge, UK) connected to a computer was used (Medhurst and Beadle, 2002). For example, for trees under a particular irrigation treatment ‘i', and with the leaf area index in diameter class ‘j’ as defined above, the total transpiration rate by all the trees subjected to that treatment (E_{FL} , m^3 m^{-2} soil $time^{-1}$ or 10^3 mm $time^{-1}$) can be expressed as:

$$E_{FL} = \sum_{j} F_{LA}(i)LAI(j) \qquad (5.13)$$

where $F_{LA}(i)$ is the transpiration rate measured at leaf level (m^3 m^{-2} leaf $time^{-1}$) for treatment 'i' and LAI(j) is the leaf area index (m^2 leaf m^{-2} soil) for trees in diameter class 'j'. Spatial up scaling can also be done from leaf level to whole orchard level using the scheme shown in Fig 5.8, although this was not done due to lack of reliable data.

5.3.1.2 Stem diameter and sap wood area as scaling factors

In addition to the LAI, other quantities, e.g. the stem diameter (Rana *et al*., 2005) and the conducting sapwood area (Hutton and Hi, 1995; Samson, 2001; Medhurst and Beadle, 2002) can also be used for scaling up transpiration from single tree to plantation level. Given the practical difficulties to quantify the total transpiring leaf area, allometric relationships between different plant organs, e.g. the stem/branch diameter and the total leaf area can be developed (Medhurst and Beadle, 2002; Rana *et al*., 2005). Based on a detailed knowledge of the statistical distribution of the stem diameters at certain reference locations on the trees, the total transpiring leaf area of the plantation can be estimated.

A typical relationship between the stem diameter, 8 cm below the first branch point, and the transpiring leaf area for young navel orange trees [*Citrus sinensis* (L.) Osbeck] is shown in Fig 5.9. With special permission from the collaborating grower, all the leaves in seven young in-fill trees were stripped and their total leaf area measured. The corresponding stem diameters were also recorded using hand-held calipers. The parabolic relationship, described by a power function (Causton, 1985) between the stem diameter and the leaf area for the navel orange trees agreed with the observations by Rana *et al*. (2005) working with Clementine orange trees [*Citrus reticulata*, Blanco]. The major disadvantage of this approach is that such allometric relationships apply only to the range of diameters for which they are developed. Extrapolation to trees with different dimensions may introduce large errors (Samson, 2001). In addition, the functional form of the relationship may change when different parts of the tree are considered. Wouters (2004) working at the same trial site at Mazowe Citrus Estate estimated the total leaf area for a four-year Navel orange tree with a mean diameter of approximately 67.5 mm to be approximately 27 m^2. This additional point was also plotted in Fig 5.9 to ensure that the relationship could be valid for a wider diameter range.

Given the fact that the amount of leaf area supported by a given tree is a function of resource availability, especially water and nutrients, it is widely believed that the conducting sapwood area, which is the pathway in which water and nutrients are transported from the soil

to the canopy through the xylem vessels, is a more representative measure of the leaf area (Medhurst and Beadle, 2002) than the stem area. However, the uncertainties associated with estimating the proportion occupied by the sapwood area are large. The most common technique of distinguishing the sapwood area from the heartwood is by determining the xylem water content (Samson, 2001). The profile of the water content determined from cores collected from different locations on the stem section can then be used to estimate the extent of the sapwood since the sapwood generally contains more water than the heartwood. But this approach does not always yield consistent results as the relationships can be reversed in some cases (Samson, 2001).

Colored dye can also be injected into the trunk of the tree so that the water conducting pathway (sapwood) is clearly marked. This approach has limitations especially when applied to trees of commercial value such as citrus trees where there is a high risk of contamination of the fruit by the dye. In addition, the dye may simply not be taken up due to the rapid development of embolisms in the xylem vessels when holes are drilled in the trunk (Sano *et al*., 2005). As in the case of the stem diameter, the sapwood area - leaf area relationship depends on the plant organs considered. For example, it is known that the proportion of the stem area occupied by the sapwood tends to increase as we approach the upper parts of the trees, e.g. the branches (Medhurst and Beadle, 2002; Franks, 2004). Thus, the allometric relationships, e.g. developed for the stem cannot be generalized for the other organs.

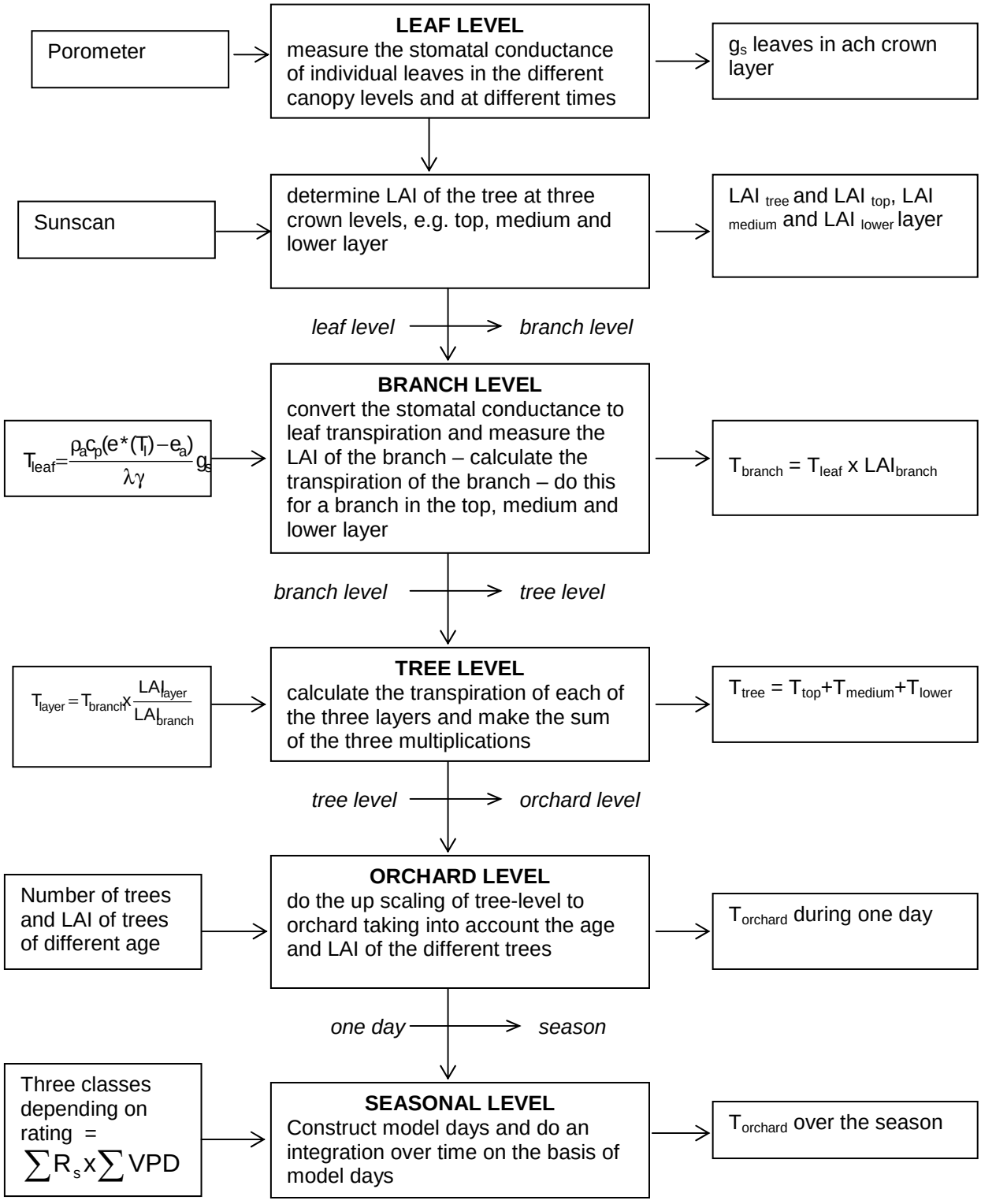

Fig 5.8 *Probable spatial and temporal up scaling criteria for transpiration rates from leaf level to orchard level and from one day to whole season (Wouters, 2004).*

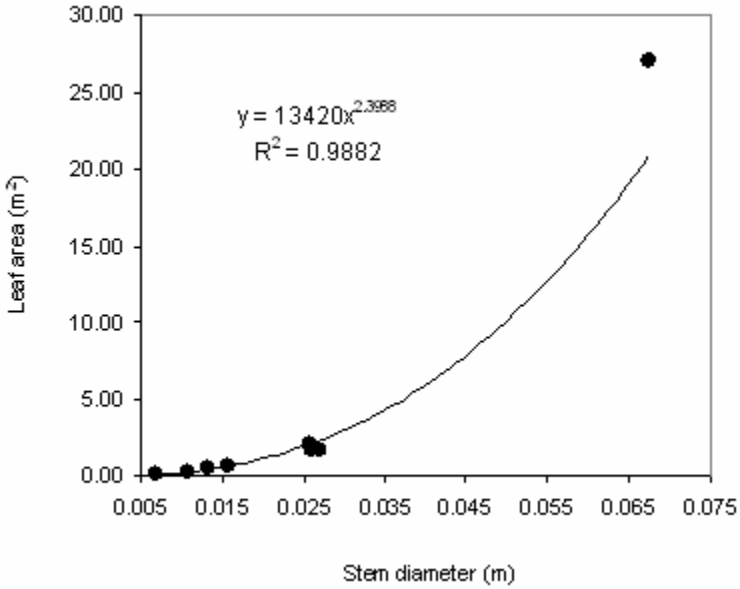

Fig 5.9 *Relationship between the total leaf area and the stem diameter below the first branch point for the young navel orange trees growing on ridges at Mazowe Citrus Estate, Zimbabwe. Larger bearing trees could not be used but an additional data point (0.0675; 27), which is an estimate of the total leaf area of a larger unprunned, bearing tree by Wouters (2004) working in the same orchard, is included.*

Notwithstanding the above weaknesses, the conducting sapwood area of the navel orange trees was estimated by injecting a dye (methylene blue) in the stem just above the bud union and on the rootstock on six potted trees since mature, bearing trees in the orchards could not be used for the reasons stated above. The stem was cut under the methyl blue dye using a sharp chisel as illustrated in Fig 5.10 to minimize the effects of embolisms on the uptake of the dye. Fresh stem discs, collected at 8 cm below the first branch point were cut after a day and estimates of the proportion of the conducting sapwood area were made using a traveling microscope. A typical relationship between the stem cross sectional area and the conducting sapwood area is shown in Fig 5.11.

Since the TDP was used for measuring the sap flux density at stem level, multiplying the sap flux density with the sapwood area of the specific tree in a given irrigation treatment yields the sap flow rate of that individual tree. Scaling the sap flux densities of the model trees in each treatment to transpiration by the whole plantation if all trees were subjected to that irrigation treatment can be done by multiplying the sap flux density with the total sapwood area of the plantation.

Fig 5.10 *Experimental set-up to determine the conducting sapwood area on potted navel orange trees. Deep cuts were made using a chisel under the methyl blue to minimize embolisms.*

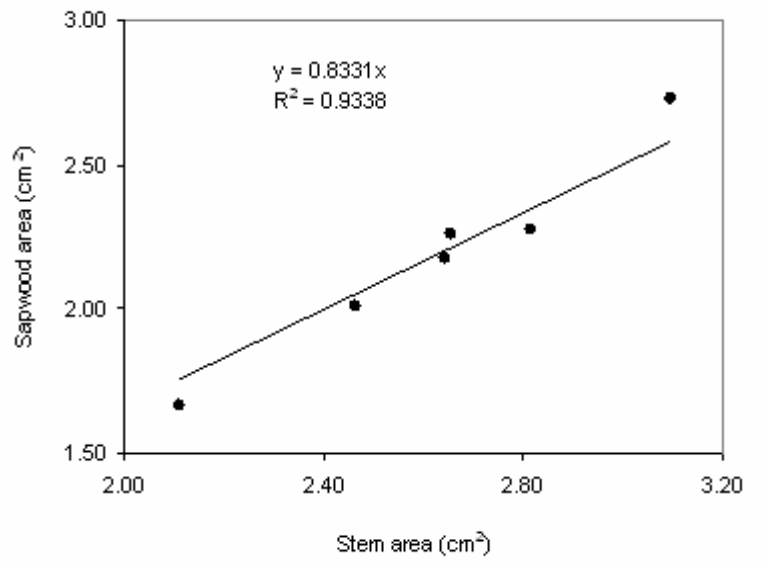

Fig 5.11 *The linear relationship between the conducting sapwood area and the stem cross sectional area in young potted navel orange trees showing that approximately 83 % of the stem area comprised the conducting sapwood.*

Since the sapwood area of larger trees could not be determined for the reasons already stated, we assumed that the relationship in Fig 5.11 is valid for all stem sizes, but this inevitably introduced significant errors. The total transpiration of the plantation subjected to a particular irrigation treatment E_{FS}, ($m^3\ m^{-2}$ soil $time^{-1}$ or 10^3 mm $time^{-1}$), can be estimated from

$$E_{FS} = \sum_i J_s(i).SAI \qquad (5.14)$$

where $J_s(i)$ is the sap flux density for the model tree in diameter class i ($m^3\ m^{-2}$ sapwood $time^{-1}$) and SAI is the sapwood area index (m^2 sapwood m^{-2} soil) assumed to be constant for the whole plantation and is given by

$$SAI = BAxRSA \qquad (5.15)$$

where BA is the basal area (m^2 stem m^{-2} soil) and RSA is the relative sapwood area of the navel orange trees (m^2 sapwood m^{-2} stem). Based on the diameter classification in Table 5.2, the basal area for the orchard was estimated to be approximately 2.27 m^2 of stem area per hectare of the orchard. However, this technique yielded unsatisfactory results probably due to the difficulty in ascertaining the proportion of the orchard covered by the plants and by the bare ground. Hence, detailed results will not be presented.

5.3.2 Time integration from one day to seasonal level

Prolonged use of the sap flow sensors on bearing orange trees was not feasible due partly to the possible physiological damage that could occur to the trees due to the heat and also because of sensor malfunctioning. Another factor peculiar to the Mazowe Citrus Estate trial site that affected data collection during the 2005/06 growing season was the high frequency of power failures experienced country - wide which could last for more than a day in some cases. This affected the sap flow measurements to a larger extent than the climatic data because the sap flow sensors generally require more energy and could not be sustained from the back up source for long periods. Thus, it was not possible to get a continuous data set of both the stem and the branch sap flow measurements throughout the season although the climatic data was uninterrupted.

However, to estimate the seasonal transpiration rates such a continuous dataset is needed. Earlier work by Dzikiti *et al.* (2006) showed a close correlation between the transpiration rates and key climatic driving variables for sap flow, e.g. the solar radiation and the vapor pressure deficit of the air for the navel orange trees. To take into account the

discontinuous nature of the sap flow data, climate data, which was continuous for the whole year (September 2005 to August 2006), was used in up scaling the daily plantation level transpiration rates to seasonal level. To minimize the number of equations, it was ideal to combine these two driving climatic variables for sap flow. The best way to combine these was to calculate the product of the daily total solar radiation ($\sum R_s$) and the daily sum of the VPD of the air ($\sum VPD$) (Wouters, 2004). This ensured that the influence of both climatic factors was taken into account. This product was then correlated with the daily transpiration rates by the orchard under the influence of each irrigation treatment and equations relating the climatic variables to the transpiration rates were derived. Thus, given the climatic data for each day of the season, it was possible to estimate the corresponding transpiration rate for the orchard.

5.4 Results and discussion

5.4.1 Climatology of the trial site in the 2005/06 growing season

Warm temperatures with an average of around 20 °C characterized the entire fruit growing season (September 2005 – May 2006) with a peak of approximately 36.4 ℃ reached during fruitset in October and a minimum for the growing season of around 0.8 ℃ reached during flowering in early September as shown in Table 5.3. The lowest temperature for the whole year was approximately -2.6 ℃ reached during August 2006. Excessively high temperatures and dry conditions during fruitset are undesirable as they lead to severe flower and fruitlet abscission which adversely affects the final yield. The average daily potential evapotranspiration reached its maximum in October with a daily average of approximately 5.9 mm per day.

The prevailing winds during the rainy season (October to March) were generally from the north and north-east directions (Fig 5.12) presumably due to the influence of the Inter-Tropical Convergence Zone (ITCZ). The ITCZ is a low pressure region of converging air masses. It tends to drift southwards of the equator during summer in Southern Africa and northwards during summer in the northern hemisphere. The convergence of the air along this belt of low pressure leads to uplifting of the air masses causing cloud formation and thus bringing rain. After the rainy season, from April onwards, the wind direction at the trial site tended to be predominantly westerly to north westerly. This was probably due to the influence of the high pressure cell characterized by descending winds which usually settles over Botswana to the west of Zimbabwe. The prevalence of this system is associated with dry conditions over Zimbabwe since the descending winds do not encourage cloud formation and this trend persists throughout the bulk of the dry season.

Based on the prevailing wind direction scheme shown in Fig 5.12, it is not surprising that the 2005/06 growing season was an exceptionally wet season during which 968 mm of rainfall were damped at the trial site at Mazowe Citrus Estate. This figure was higher than the long-term average rainfall for the area which is approximately 700 mm (Climate Handbook of Zimbabwe). The distribution of the rainfall is clearly illustrated in Fig 5.13 with over 50 % of the seasonal total being received during the months of December and January.

Table 5.3 *The annual variation of the key climatic variables at the trial site at Mazowe Citrus Estate, Zimbabwe during 2005/06. The data is calculated from 5 min mean values collected from the weather station located out side the orchard.*

Year	Month	Solar radiation (MJ m^{-2})	T_{max} (℃)	T_{mean} (℃)	T_{min} (℃)	RH (%)	ET_o (mm day^{-1})	Rainfall (mm)
	Sept	655.4	32.6	16.9	0.8	55.5	5.3	0.2
2005	Oct	757.2	36.4	21.9	6.4	42.2	5.9	1.4
	Nov	665.0	35.8	22.3	6.4	65.0	5.1	100.8
	Dec	591.6	32.2	21.0	13.0	85.5	4.3	250.2
	Jan	621.3	30.4	21.2	15.7	88.9	5.2	324.4
	Feb	560.0	29.8	21.3	13.1	87.6	5.0	155.6
	Mar	601.1	28.7	20.5	11.3	84.9	4.4	133.8
2006	Apr	606.1	29.7	19.0	8.2	78.6	4.5	1.8
	May	503.4	29.6	15.5	4.2	76.9	3.7	8.4
	Jun	445.6	29.0	13.0	-0.7	73.1	3.3	3.2
	Jul	492.5	27.9	12.5	-0.5	67.6	3.6	1.0
	Aug	604.7	30.6	14.7	-2.6	60.9	1.0	0.0

It must also be remarked that severe hail damage occurred during the initial stages of cell expansion in mid December, thus significantly affecting the export potential of the fruit. Figure 5.20 shows a hail damaged fruit whose picture was taken just before harvest in May 2006. As a consequence, the bulk of the fruit harvested in the 2005/06 season was crashed into juice as it was not suitable for export for the fresh fruit market.

The seasonal total evapotranspiration (September – May) assuming a constant crop coefficient of 0.7 for citrus was 921 mm. While rainfall alone could have sustained the crop for the season, the distribution of the rainfall was highly uneven as already explained above. In addition, the citrus fruit at Mazowe are most sensitive to drought stress during September to

December which corresponds to the flowering and fruitset phases. Thus irrigation remained a crucial component of the production system. According to the minutes of the meeting between Mazowe Citrus Estate and the Zimbabwe National Water Authority (ZINWA), an organization responsible for allocating water in Zimbabwe, of 24 April 2006 approximately 8.0 megaliters of water are needed to irrigate a hectare of citrus each year. This corresponds to a depth of 800 mm of irrigation with the balance being supplemented by rainfall. The annual total evapotranspiration on the other hand was 1169 mm.

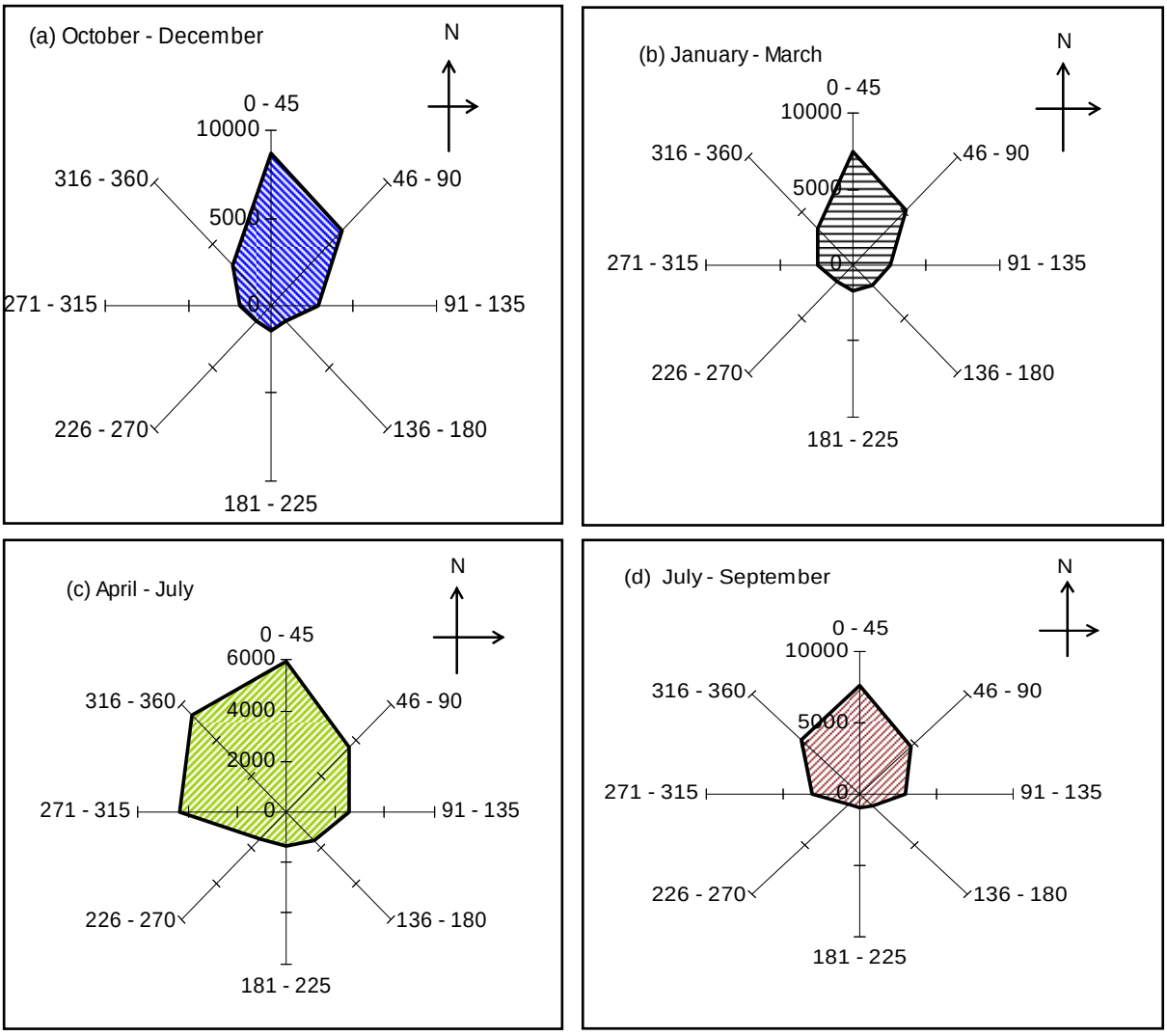

Fig 5.12 *Prevailing wind direction at Mazowe Citrus Estate, Zimbabwe during different periods in the year. Winds were generally northerly during the summer tending to be westerly during the dry periods. Wind direction in degrees are marked at the end of the axes, while the length of each axis indicates the total time that the wind is blowing from that particular direction.*

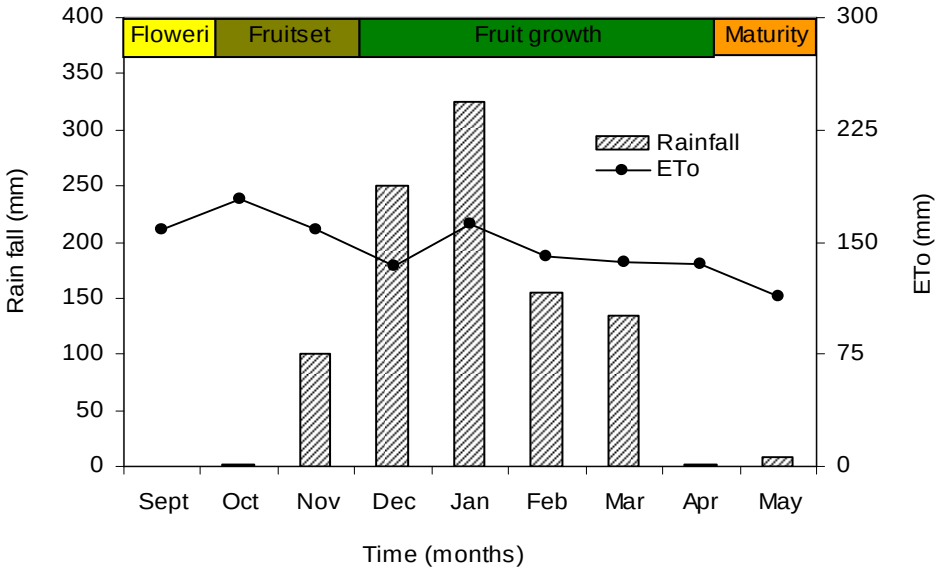

Fig 5.13 *Distribution of the rainfall and the potential evapotranspiration during the 2005/06 fruit growing season at the trial site at Mazowe Citrus Estate, Zimbabwe. Over 50 % of the seasonal total rainfall was received in two months (fruitset- fruit growth phase).*

Fig 5.14 *Navel orange fruit damaged by hail during the early stages of growth in December 2005 at Mazowe Citrus Estate, Zimbabwe. Because cell division is completed during fruitset the blemishes increased in size as cell expansion occurred (fruit growth) to form large scars on the peel of the fruit. The resulting fruit is not suitable for export because of the blemishes.*

5.4.2 Effect of the irrigation treatment on daily transpiration rates

Typical illustrations of the sap flow signals as affected by the climatic variables under field conditions at Mazowe Citrus Estate over a period of ten days during the rainy season are shown in Fig 5.15. For example, from 15 – 18 December 2005 (DOY 349 - 351) rainfall occurred around midday and this is clearly evident from the course of both the branch and the stem sap flow (Fig 5.15b and 5.21c). As expected when the canopy of the orange trees was drenched with water droplets, the branch sap flow ceased completely, while the stem sap flow continued at low rates driven by the internal water deficit in the plant (Dzikiti *et al*., 2007). On typical clear days, the sap flow followed cyclic oscillations as illustrated in Fig 2.11b but these oscillations were not readily clear under partly cloudy conditions.

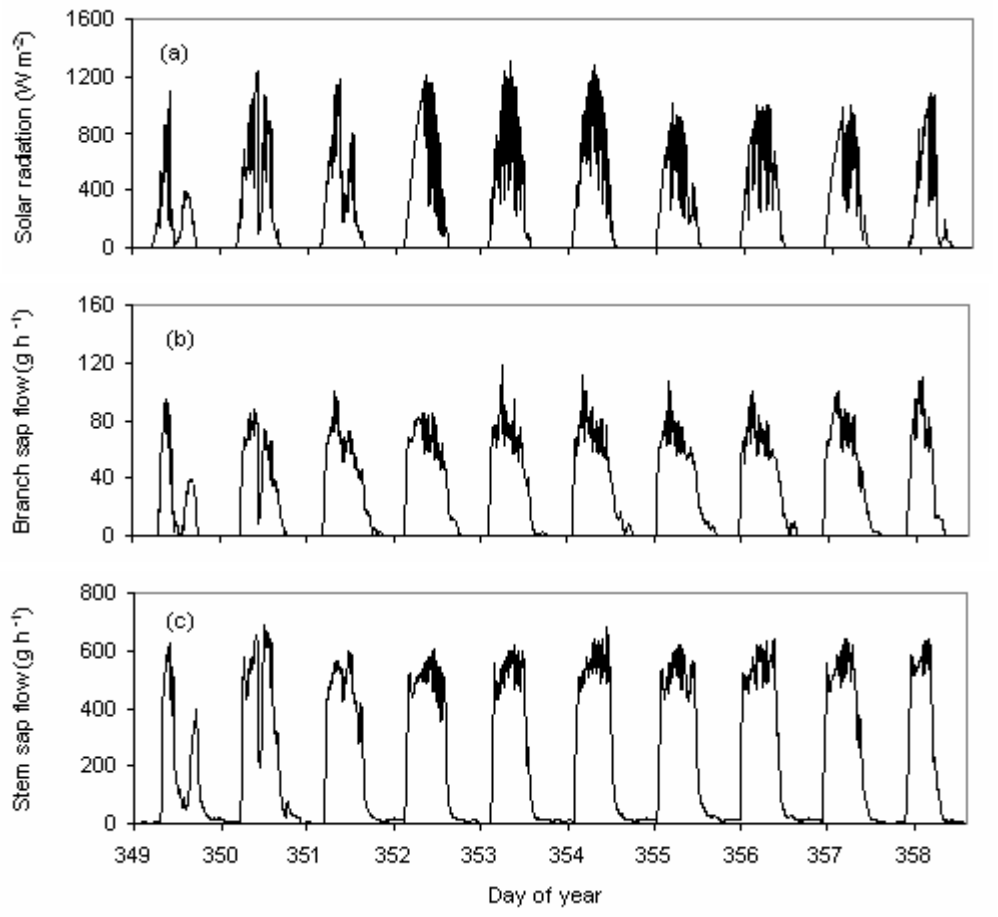

Fig 5.15 *Typical variations in the course of the solar radiation (a) the branch sap flow (b) and the stem sap flow (c) over a period of ten days from 15 – 25 December 2005 corresponding to Julian day of year [DOY 349 – 358] under field conditions at Mazowe Citrus Estate, Zimbabwe. Note the differences in the vertical scales for the branch and the stem sap flow measurements.*

The fact that the different irrigation regimes imposed on the Navel orange trees had a significant effect on the diurnal course of sap flow and, hence, of the transpiration rate is apparent in Fig 5.16. Data is presented for the October - November period when the atmospheric evaporative demand was highest and the effects of rainfall on the soil water regimes was minimal. Despite the gaps in the sap flow data due to frequent power failures, it is evident that sap flow rates responded to the different irrigation regimes with trees under the well - watered and the control treatments having higher transpiration rates per unit leaf area than in the PRD treatment. Sap flow rates were on average greater than 100 g m^{-2} h^{-1} in the well - watered and the control treatments during the daytime, while a lower rate occurred in the partial rootzone drying treatment.

It is easy to appreciate why the transpiration rates were high in the well - watered treatment. According to Kang *et al.* (2002), when the rootzone of a plant has plenty of water, the stomata open to the so-called “luxury state” leading to high transpiration rates. It is highly probable that the stomata in the well - watered treatment opened to larger extents than in the PRD treatment thus leading to higher rates of water loss. The same argument, however, cannot be used to explain the high sap flow rates under the control treatment which received the same quantity of water as the PRD treatment.

It appears from these results that switching the irrigation between the single lines for navel orange trees potentially cuts down on the transpirational losses. Similar observations have been made elsewhere on other crops, e.g. maize (Kang *et al*., 2002) and hot pepper (Dorji *et al*., 2005). In these two cases, the reduction in the transpiration rate in the partial rootzone drying treatment is attributed to the influence of the chemical signals generated in the drying soil by active roots. In the control treatment where the irrigated sides were not switched, the roots on the dry side were most probably dormant and not capable of generating the chemical signals needed to control the stomatal aperture (Loveys *et al*., 2000; Davies *et al*., 2001; Kang *et al*., 2002). The roots on the permanently dry side remain alive but inactive in terms of water and nutrient uptake (Eissenstat *et al*., 2006**)**. They essentially become sinks for assimilates as their survival depends on other roots elsewhere within the plant. It is possible that the high sap flow rates under the control treatment were a result of the lack of the chemical control of the stomatal aperture which happens during partial rootzone drying as described in Chapter 4.

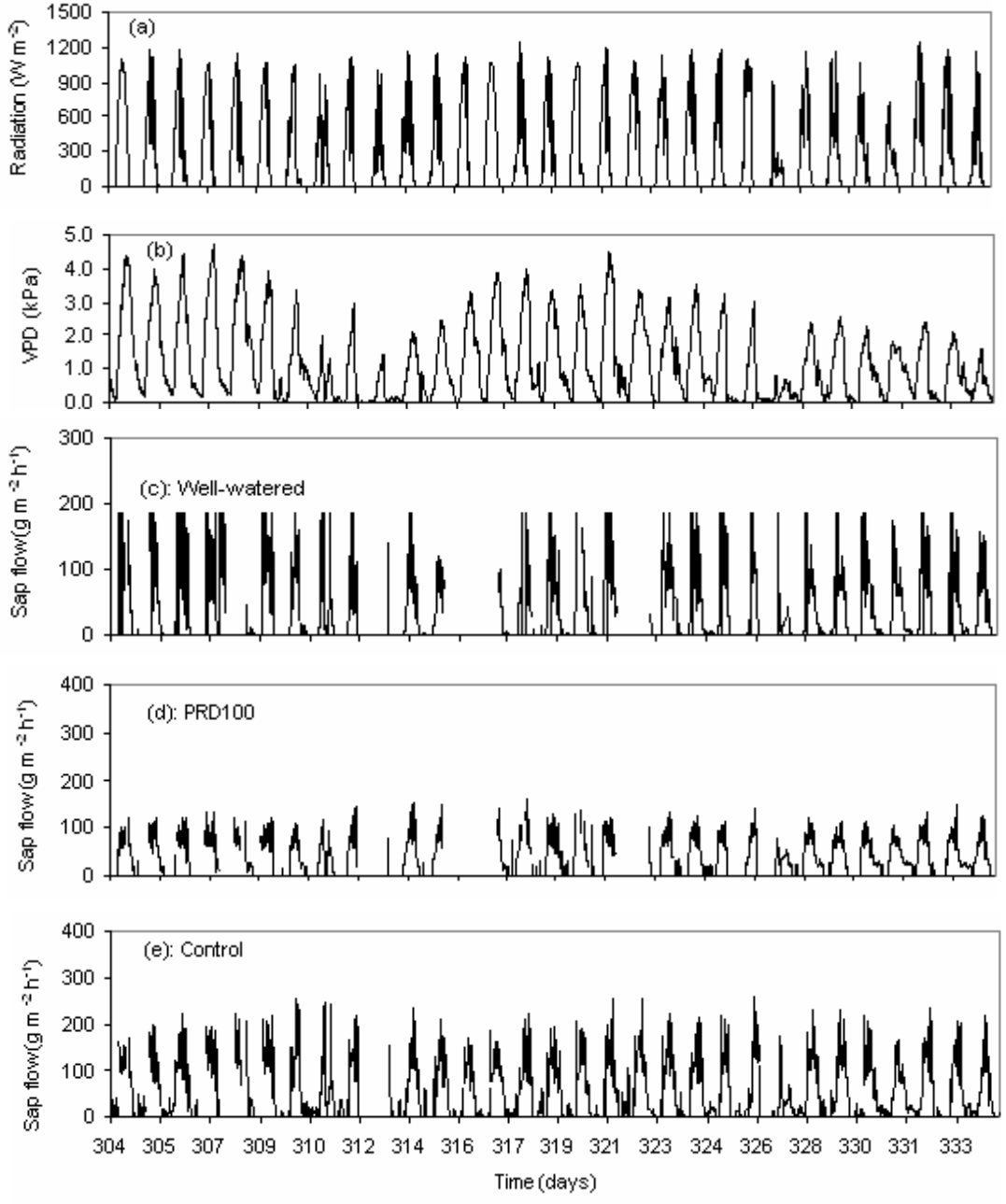

Fig 5.16 *Typical course of the climatic variables, namely the solar radiation (a), Vapor pressure deficit (VPD) (b) and the sap flow rate per unit leaf area in the well - watered treatment (c), the partial root zone drying (PRD) (d) and the control treatment (e) during the dry period in October - November 2005. Gaps in the sap flow data indicate incidences of power failure. Climate data with sensors requiring little power were not affected.*

Given the uncertainties in both the sap flow and the leaf area measurements, an independent check of these measurements was needed. Transpiration rates calculated from the stomatal

resistance measured using the AP4 porometer as described above (Fig 5.8) and the leaf surface temperature and typical results are shown in Fig 5.17.

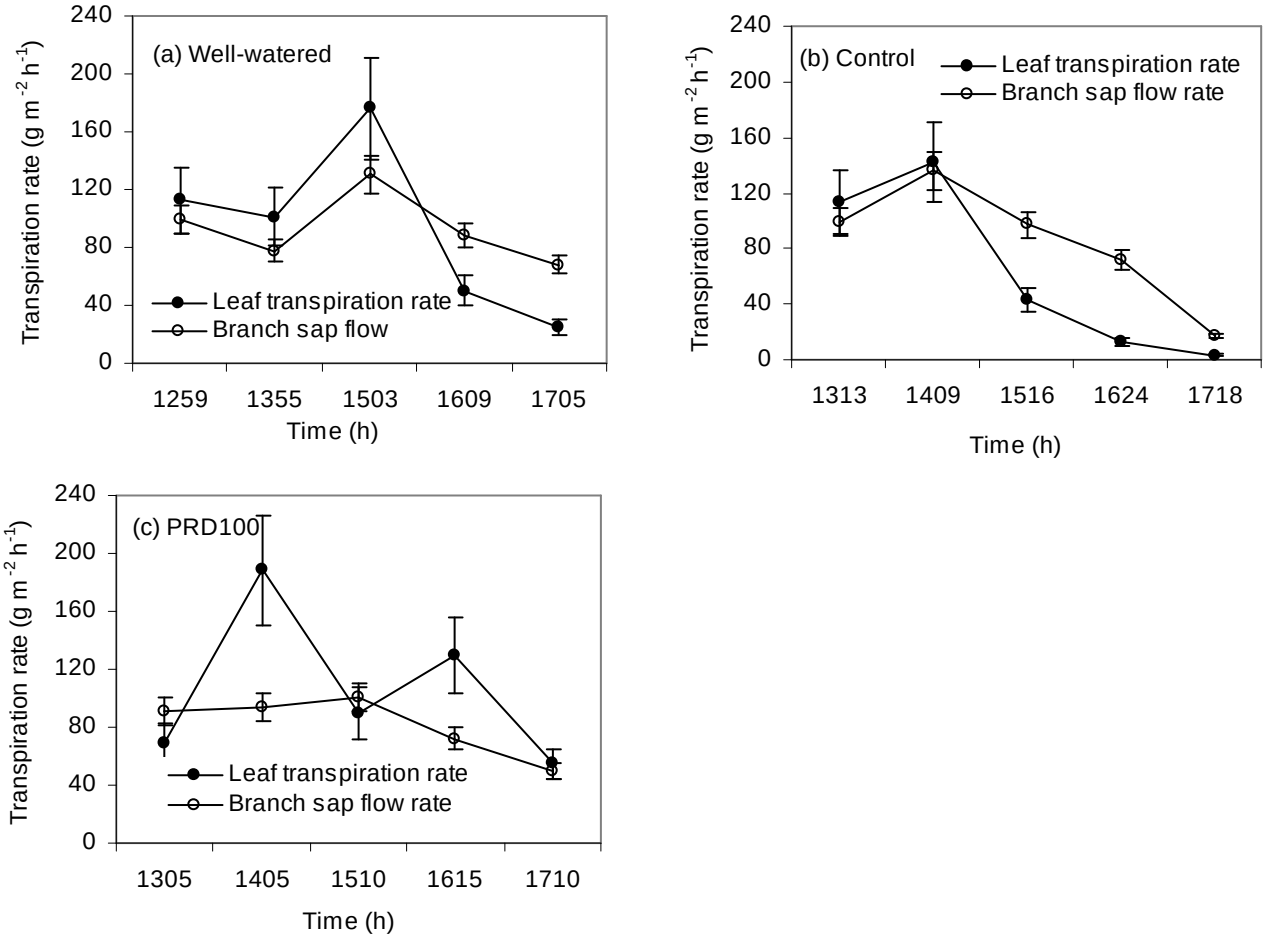

Fig 5.17 *Comparison of leaf level transpiration rates with the branch sap flow rate expressed per unit leaf area in three irrigation treatments, namely the well - watered (a), control (b) and the partial rootzone drying (PRD) (c) treatment. Errors of 10 % were assumed for the sap flow measurements, 15% for the leaf area measurements and an even larger error margin of 20 % for the transpiration. Error bars show the combined effects of these errors on the physical quantities presented in the diagrams.*

The leaf-level transpiration rates (transpiration per unit area) measured on leaves from branches on which the gauges were installed were somewhat similar to the branch sap flow rate expressed per unit of leaf area. Significant discrepancies occurred however, probably due to the large variability in the stomatal resistance and the surface temperature of the leaves since it was only practical to sample a few leaves at a time. This variability was most pronounced for the PRD100 treatment because the sap flow measurements were taken on a

larger branch (19 mm) compared to the smaller branches for the control and well – watered treatments (each approximately 9 mm). Nevertheless a somewhat reasonable agreement between the porometer and sap flow measurements was obtained. Indeed some confidence can be put in the up scaling results, albeit with appreciable error margins. In addition, the capacitance between the branches and the leaves ensured that in the short-term, the sap flow rate was not equal to the transpiration rates.

5.4.3 Whole orchard water use from branch level sap flow

For the purposes of irrigation management, growers are more interested in the quantity of water used by the whole orchard at various time scales, e.g. daily, monthly and seasonal time steps. This goal was achieved by scaling up the branch and stem sap flow measurements from individual tree to orchard level as described above. In this section, up scaling from branch to orchard level is discussed and assumptions are made in the process. Firstly, we assumed that the transpiration rate by a unit area of the leaf surface was the same for all the trees subjected to a particular irrigation regime. Secondly, we assumed that evaporation from the soil was negligible and the whole orchard water loss was due to transpiration only. This assumption was particularly reasonable during the dry season given the fact the trees were under drip irrigation (Andreu *et al*., 1997; Allen *et al.,* 1998; de Souza *et al*., 2005).

Using equation 5.13 and the leaf area index adjusted for variations in tree size in Table 5.2, the transpiration depth under a given treatment could be calculated. Figure 5.24 shows a typical comparison of the daily total transpiration by the orchard when subjected to a particular irrigation treatment. The potential evapotranspiration rate was calculated using the Penman-Monteith equation (equation 5.11). There were only 15 days with continuous sap flow data from 31 October until 29 November 2005 [DOY: 306 – 333] as shown in Fig 5.18. For these days, the daily potential evapotranspiration rate reached a minimum of less than 2.0 mm on a completely overcast day (26 November) and a maximum of 6.6 mm. The minimum transpiration rate was approximately 1.4 mm for all the three treatments except the PRD which had a marginally higher rate, while peak transpiration reached 5.5 mm in the well - watered, 4.7 mm in the control and 3.9 mm in the PRD treatment, respectively.

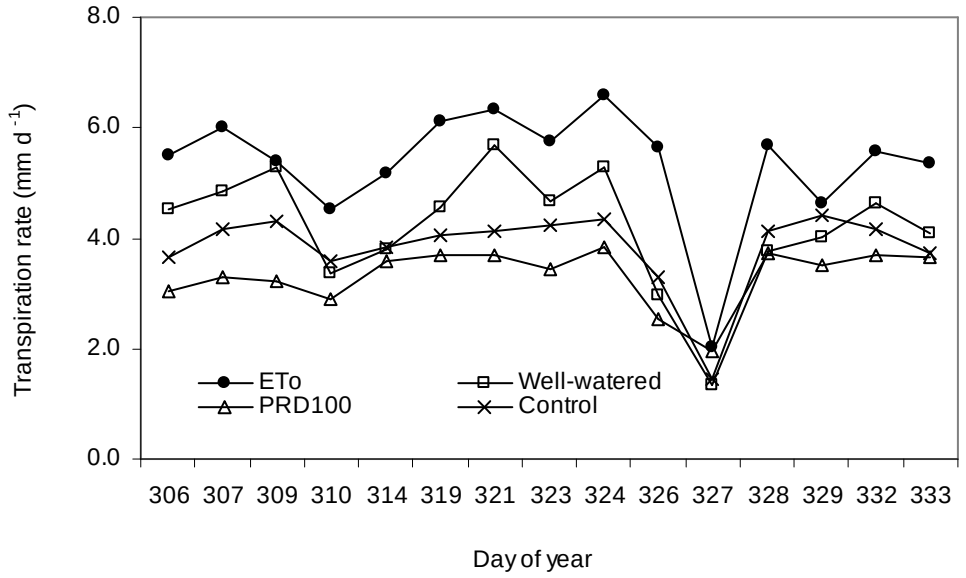

Fig 5.18 *Comparison of the potential evapotranspiration with the daily transpiration rates in the well - watered treatment (open squares), PRD treatment (open triangles) and the control treatment (crosses) in October - November 2005. Complete branch sap flow data was available only for the days shown due to sustained mains power failures experienced at the trial site.*

To derive the monthly transpiration rates throughout the growing season, temporal up scaling of the daily transpiration rates was done using the sap flow data for the period October to November 2005. Typical results for the relationship between the transpiration rate in each irrigation treatment and the product of the daily total solar radiation ($\sum R_s$) and the sum of the vapor pressure deficit of the air is shown in Fig 5.19. Power functions gave the best fit for the data as indicated by the coefficient of determination. According to the Dynamax user manual, the error margins for the branch sap flow measurements can be considered to be approximately 10 % while that of the LAI is significantly higher, typically 15 %. The errors in the up scaled transpiration rate in Fig 5.19 was then approximately 18 % as shown by the error bars.

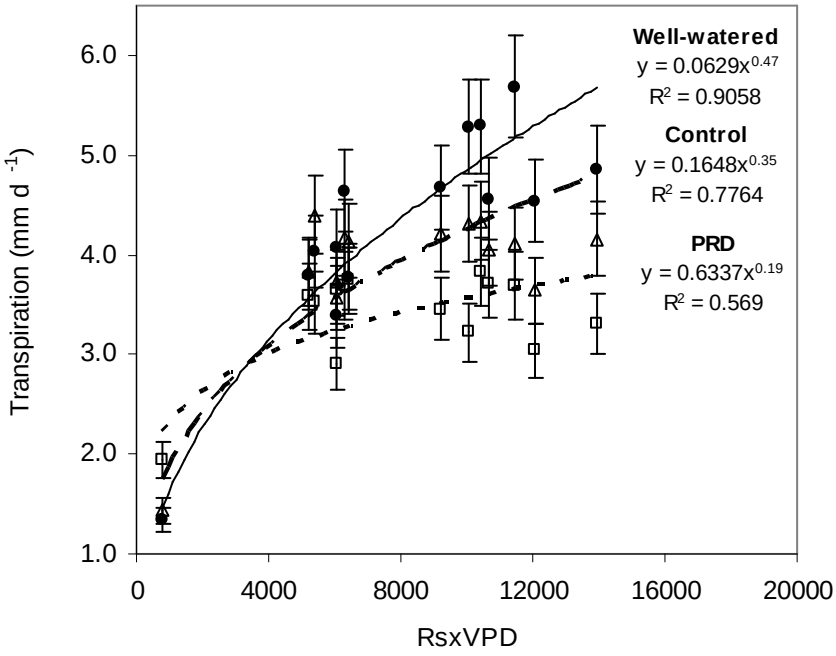

Fig 5.19 *Relationship between the product of the daily total solar radiation* ($\sum R_s$) *and the daily vapor pressure deficit (*VPD) *sum (*$\sum VPD$*) with the up scaled transpiration rate from branch sap flow measurements under each irrigation treatment.*

The product of the combined daily totals of solar radiation and the VPD is a proxy measure of the atmospheric evaporative demand. It is clear from Fig 5.19 that a higher correlation existed between the transpiration rates by the trees under the well - watered treatment and the atmospheric evaporative demand with a high coefficient of determination (R^2 = 0.907) than those under the control (R^2 = 0.778) and the PRD treatment (R^2 = 0.572). These differences reflect the variations in the levels of stomatal control of transpiration. At higher atmospheric evaporative demands, trees under the partial root zone drying treatment exercised a tighter control of their stomatal apertures than those in the other two treatments. As a consequence, the fact that the monthly total transpiration rates under PRD were lower than those under the control and the well - watered treatments during periods of high atmospheric evaporative demand is not surprising as shown in Fig 5.20. This was despite the fact that the control and the partial rootzone drying treatment received the same irrigation levels. This result agrees with the observations by Kang *et al*. (2003) working with irrigated pear (*Pyrus communis* L.) orchards and De la Hera *et al*. (2006) working with grape vines (*Vitis vinifera* L.). In the case of the orange trees at Mazowe, the monthly transpiration rate peaked during October and the lowest rates were found during the rainy period from

December 2005 to February 2006. Predominantly cloudy conditions and low radiation intensities during winter also led to low transpiration rates in June 2006.

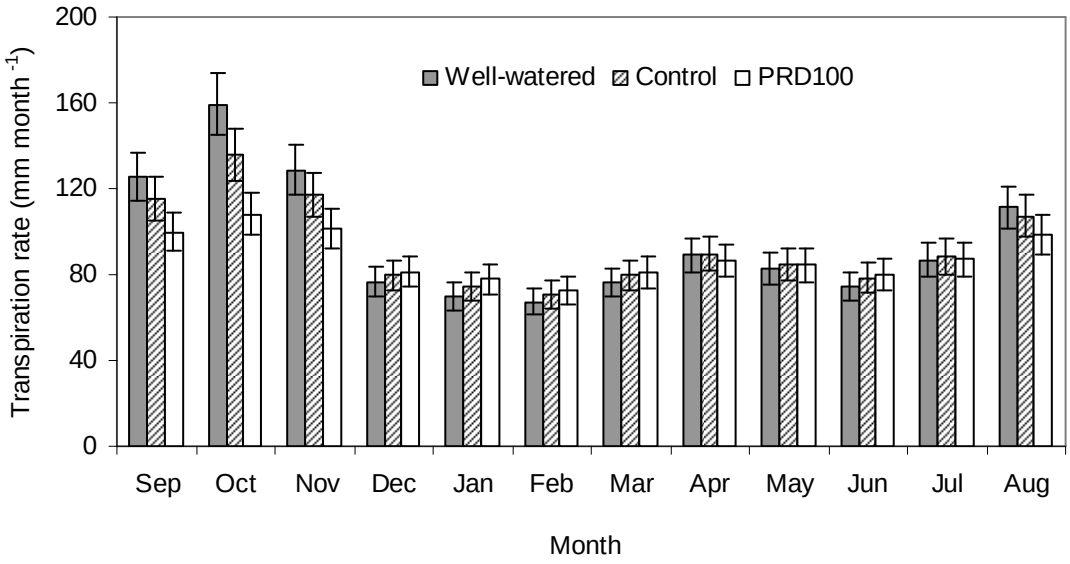

Fig 5.20 *Monthly total transpiration rates for the well - watered treatment (grey rectangles), the control treatment (checked rectangles) and the partial rootzone drying (PRD) treatment (open rectangles) during the 2005 – 2006 growing season.*

The seasonal total transpiration (September 2005 – May 2006) translated to approximately 8.75 Ml/ha for the well - watered, 8.46 Ml/ha in the control and 7.93 Ml/ha in the PRD treatment. The annual transpiration totals (September 2005 to August 2006) were 11.5 Ml/ha for the well - watered, 11.2 Ml/ha for the control and 10.6 Ml/ha for the PRD treatment. The monthly transpiration rates were comparable during the rainy period and also in winter when the atmospheric evaporative demand was generally low. Considering both the irrigation and the rainfall inputs, the total annual water applied was, respectively, 25.7 Ml/ha in the well - watered and 17.7 Ml/ha in the control and the PRD treatments. The application rates were calculated based on the total rainfall received, 968 mm, which was equivalent to 9.68 Ml/ha and the irrigation level (8.0 Ml/ha) using the local growers' irrigation practice comprising a single drip line. Thus the irrigation applied with double lines in the well - watered treatment was twice that in the other two treatments which used single lines.

Typical values of the water use efficiency, considered as the ratio of the total fruit yield to the total seasonal transpiration are shown in Table 5.4, being 3.54, 2.03 and 2.57 grams of fruit per liter of water transpired under the well - watered, control and PRD treatments. The

high water use efficiency in the well - watered treatment was most likely a result of the high fruitset percentage in this treatment which also led to high average yields per tree as shown in Table 5.4. Sampling procedures for the yield were discussed in Chapter 4. It is possible that the stomata opened to larger extents in the well - watered treatment than in the PRD and the control treatment resulting in greater CO_2 assimilation and consequently higher yields. The water use efficiency was higher under PRD than the control treatment practiced by the local growers. Whether the PRD strategy increases yield in fruit trees compared to the conventional methods, e.g. the single line control remains a subject of controversy (De la Hera *et al*., 2006). Some authors have suggested that partial rootzone drying is more successful on soil types that allow for high infiltration rates and deep root zones such as sandy loams (Kriedemann and Goodwin, 2003). In the case of the Mazowe Citrus Estate, the soils were clayey loam with the trees planted on ridges to facilitate drainage. Thus, it is likely that the partial rootzone drying had a significant effect on the hydraulic signals generated by the orange trees.

When the water use efficiency is considered as the ratio of the fruit yield to the total annual water application (rainfall + irrigation) per hectare, we get 1.20, 0.93 and 1.15 grams of fruit per liter of water applied in the well - watered, control and the PRD treatments. These values are significantly lower than those of other irrigated fruit trees. For example, De la Hera *et al*. (2006) working with wine grapes (*Vitis vinifera* L.) obtained water use efficiencies between 4.2 and 5.5 grams per liter of water applied under the single drip line control treatment and between 4.9 to 5.9 grams per liter of water applied under PRD. The well - watered treatment gave a better result than the single drip line treatments with the partial rootzone drying treatment also giving a favorable result compared with the control treatment (current practice by the local growers) at least for the 2005/06 season.

Table 5.4 *Water use efficiency obtained from the scaled up branch sap flow in the different irrigation treatments during the 2005/06 growing season. All trees (1191) in the 2 ha orchard are assumed to have the same yield.*

Treatment	Total water received (Ml/ha)	Total seasonal transpiration (±0.30 Ml/ha)	Average yield (± 0.1 kg/tree)	Total yield per hectare (kg)	Water use efficiency (± 0.30 g L^{-1})
Well - watered	25.7	8.75	52.0	30966.0	3.54
PRD	17.7	7.93	34.2	20366.0	2.57
Control	17.7	8.46	28.8	17150.4	2.03

5.4.4 Whole orchard water use from stem level sap flow

The second possibility to quantify the transpiration rates by the entire orchard is by using stem sap flow measurements using thermal dissipation probes, TDPs (Fig 5.1). The advantage of this approach is that the signal is an integral of transpiration by all the leaves in the canopy. If the total transpiring leaf area is known, then a potentially more reliable measure of the sap flow per unit leaf area can be obtained in the different irrigation treatments. However, as already mentioned above, estimation of the conducting sap wood area is a source of large uncertainty in the sap flow measurements by TDPs.

Typical values of the stem diameter and estimates of the size of the conducting sap wood area assuming that 83 % of the stem area was sapwood are shown in Table 5.5. Using the equation relating the stem area to the total transpiring leaf area derived in Fig 5.9, the total leaf area of each model tree was estimated and results are also presented in Table 5.5.

Table 5.5 *Estimates of the leaf area of the model trees on which the thermal dissipation probes (TDP) were installed obtained using measurements of the mean stem diameter.*

Treatment	Mean stem diameter (x 10^{-3} m)	Sap wood area (cm^2)	Whole-tree leaf area (m^2)
Well- watered	71.4	33.4	24.0
PRD	67.6	29.5	20.7
Control	68.3	30.5	21.6

Using the approach described in section 5.3.1.2 above, the total stem sap flow rates were normalized with the whole-tree leaf area for the three treatments and the transpiration depth by the whole orchard was obtained using the leaf area index in Table 5.2. Results of the transpiration rates by the whole orchard under a particular treatment as measured by the TDPs are shown in Fig 5.21 for the period October – November 2005. Very low rates of water use were obtained although similar treatment effects as for branch sap flow measurements were observed. Trees under the partial rootzone drying treatment gave lower transpiration rates than those under the well - watered and the control treatments.

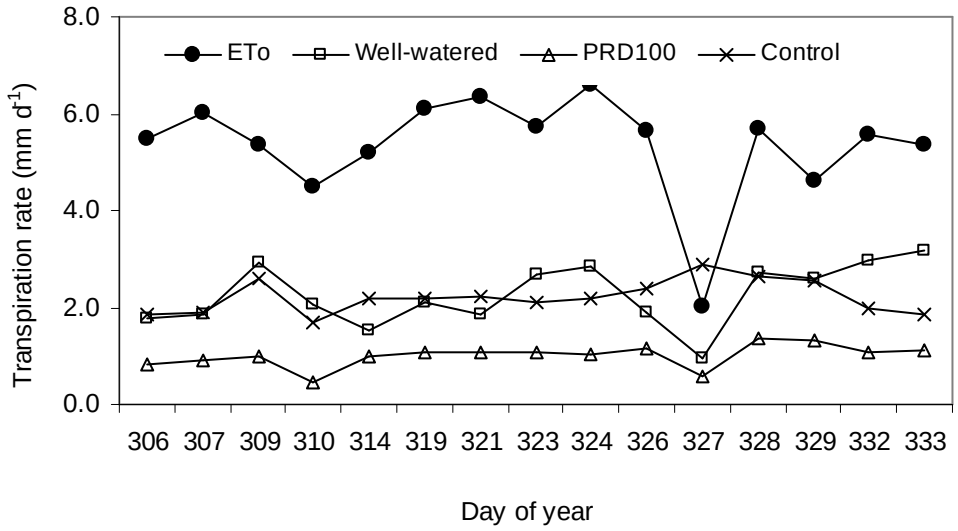

Fig 5.21 *Comparison of the potential evapotranspiration with the daily transpiration rates in the well - watered treatment (open squares), partial root zone drying (PRD) treatment (open triangles) and the control treatment (crosses) in October - November 2005 estimated from the stem sap flow measurements using TDPs.*

As a consequence, the monthly and seasonal transpiration totals as estimated from the measurements of sap flow rates using the thermal dissipation probes were very low as shown in Fig 5.22. Reasons for these somewhat low measurements include firstly a possible over-estimation of the whole-tree leaf area leading to a low ratio of the sap flow rate to the leaf area. However, this is less likely given the physical size of the trees which had a base area in the range 2.0 to 3.0 m and the height from the base of the canopy to the highest point in the range 2.0 to 2.5 m for trees in the majority diameter class (Table 5.2). The second possibility is that the TDPs simply underestimated the sap flow rates because the low sap flow rates were observed even when the whole stem diameter was assumed to be conducting. This possibility could not be independently verified but it is highly likely e.g. due to air gaps created in the drilled holes during sensor installation. In addition, sap flow rates under the PRD treatment were consistently much lower than the other two treatments for the TDP measurements than in the case of the heat balance sap flow sensors in Fig 5.20.

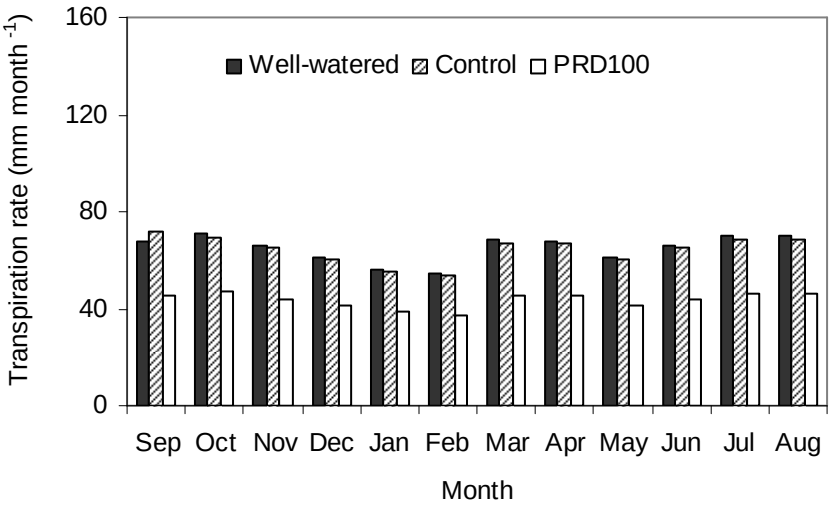

Fig 5.22 *Monthly total transpiration rates for the well - watered treatment (grey rectangles), partial root zone drying (PRD) treatment (checked rectangles) and the control treatment (open rectangles) during the 2005 – 2006 growing season as estimated from the thermal dissipation probes (TDPs) installed on the stem.*

5.4.5 Evapotranspiration estimates from the Class-A pan

Data for the measurements of the sap flow or transpiration rates is not always readily available to fruit tree growers. Rather the growers depend on meteorological data or evaporation pans to estimate the water requirements of their trees (Li *et al*., 2002; Rana *et al*., 2005). Correctional factors, e.g. crop coefficients (K_c), are needed to convert, for example, the potential evapotranspiration rate into the crop evapotranspiration as described in Section 5.1. Where evaporation pans are used, e.g. at Mazowe Citrus Estate, a pan coefficient (K_p) is needed to convert the pan evaporation into the potential evapotranspiration. Both factors, however, need local calibration as they are affected by various factors, e.g. the local climatic conditions, crop type and the phenological stage of the crop (Allen *et al*., 1998). Such information is currently not available for citrus trees at Mazowe Citrus Estate among other cropping enterprises in Zimbabwe.

Using the estimates of the monthly transpiration rates and ET_o in Section 5.4.3 above, typical variations in the crop coefficient for the Navel orange trees at Mazowe Citrus Estate are shown in Table 5.6. By so doing, evaporation from the soil is assumed to be negligible, which is an acceptable assumption for drip irrigated fruit trees (Naor and Cohen, 2002; Rana *et al*., 2005). These values agree with the figures provided by Wouters (2004) in Table 5.1 and were calculated using equation 5.7. While there were two up scaling procedures for transpiration

from single tree to orchard level as explained above, only the branch sap flow based method was used to derive the crop coefficients since it gave most reliable results.

If the trees are subjected to the well – watered treatment, then K_c can be as large as 0.9 during the flowering and fruitset phases, declining to around 0.45 during the cell expansion (fruit growth) phase. At maturity, a K_c value of 0.65 can be used (lower than the 0.7 calculated in Table 5.6) since lower irrigation rates are needed to improve the internal quality of the fruit before harvest. Typical K_c values of 0.8, 0.5 and 0.65 can be used for the three fruit growth phases (flowering/fruitset, growth and maturity) in the control, while lower values of 0.75, 0.50 and 0.65 may be appropriate in the PRD treatments. A slightly higher value of K_c than that estimated in Table 5.6 for the PRD may be required to ensure minimal flower and fruit-let abscission during flowering/fruitset. These figures agree with the ones derived for Navel orange trees by Consoli *et al*., 2006.

Table 5.6 *Evapotranspiration (ETo) and crop coefficients data for Navel orange trees at Mazowe Citrus Estate, Zimbabwe during the 2005/06 fruit growing season calculated for the different irrigation regimes (well - watered , partial rootzone drying and control).*

	ET_o	Crop coefficients (K_c)			Phenological stage
Month	(mm month^{-1})	Well - watered	PRD	Control	
Sep	157.7	0.80	0.63	0.73	Flowering
Oct	178.7	0.89	0.61	0.76	Fruitset
Nov	157.9	0.81	0.64	0.74	
Dec	134.6	0.57	0.60	0.59	Fruit growth
Jan	161.6	0.43	0.48	0.46	
Feb	140.0	0.48	0.52	0.50	
Mar	136.7	0.56	0.59	0.58	
Apr	135.5	0.66	0.64	0.66	Maturity
May	124.2	0.73	0.74	0.74	
Jun	98.3	0.76	0.81	0.80	
Jul	112.8	0.77	0.77	0.78	
Aug	141.5	0.79	0.70	0.76	

Currently, a Class-A evaporation pan is being used at Mazowe Citrus Estate for irrigation management. A pan coefficient of unity is then applied to estimate the irrigation need. Figure 5.29 shows that indeed the pan coefficient is close to 1.0 given by the slope of the graph of ET_o against the pan readings.

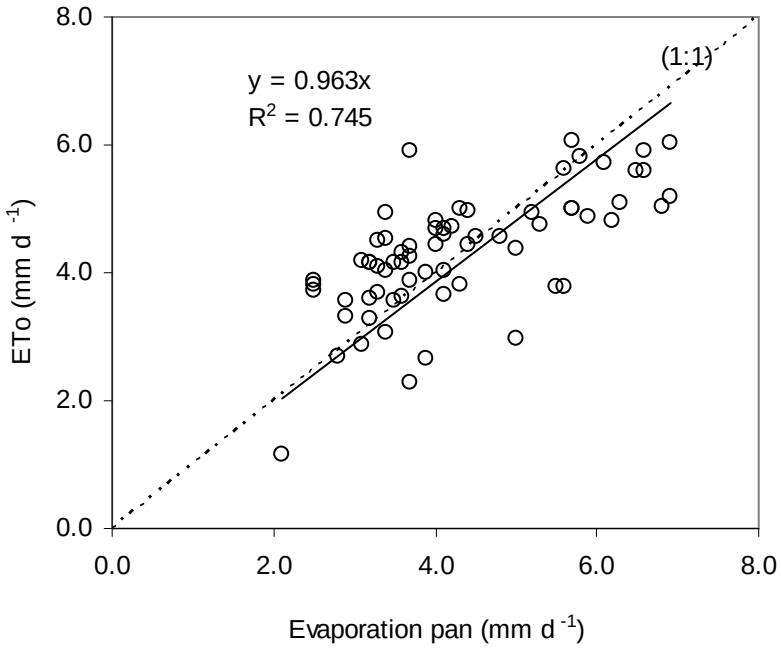

Fig 5.23 *Estimation of the pan coefficient (K_p) for the class-A evaporation pan measurements at Mazowe Citrus Estate. The data used was collected during the period June to October 2006, but spurious pan evaporation readings were filtered.*

5.5 Conclusions

When compared with the well - watered treatment between 2005 and 2006, it appears that the partial rootzone drying strategy led to lower yields although the yield difference was small when compared with the control treatment. Yield reduction under partial rootzone drying irrigation has also been observed on other crops, e.g. beans (Wakrim *et al*., 2005; Wahbi *et al*., 2005), although other studies showed yield increases, e.g. on grape vines (De la Hera *et al*., 2006), albeit with some controversy. A common feature between some varieties of citrus, e.g. the Navel orange trees and beans is that these plants maintain low stomatal apertures as a result of the phenomenon of stomatal cycling described elsewhere in this study (Cowan,

1977). Consequently, it is probable that further reductions in the stomatal apertures lead to reduced CO_2 assimilation causing reduced yields.

Despite the reduced yield, it is apparent that significant water savings can be obtained under partial rootzone drying of the citrus trees. Two different up scaling methods were used to derive transpiration at orchard level from single tree sap flow measurements, namely using the branch sap flow and the stem sap flow measurements respectively. Branch sap flow measurements using the heat balance sap flow sensors were more reliable compared to the stem sap flow measurements using TDPs. Relatively high water use efficiency, expressed as the ratio of fruit yield to the total seasonal transpirational loss was obtained under the PRD strategy than under the current growers' practice.

Annual transpirational losses can potentially be reduced by as much 1.0 Ml per hectare if the partial rootzone drying strategy is implemented leading to substantial water savings. It should also be noted that the differences in water use are most pronounced during the warm period (August – December) and less so during the rainy and winter periods. Coincidentally, this period corresponds to the flowering/fruitset periods when water availability is most crucial and it appears that applying PRD at this time leads to increased flower/fruitlet abscission. Proper timing of the application of the PRD strategy appears to be an important factor which the grower needs to consider is he aims to maximize yields. Water use efficiency was greatest under the well - watered treatment implying that the high water application rates directly translated to more fruit. As already stated earlier this is most probably a result of higher fruitset in this treatment than the single drip line treatments. Proper timing of the application of both the PRD and the well - watered treatments based on the physiological development of the fruit can potentially enhance water savings and produce more fruit.

Chapter 6 Future perspectives on stomatal oscillations and citrus irrigation in Zimbabwe

Potential alternative water saving irrigation strategies for citrus production in Zimbabwe are investigated in this thesis. Detailed information on the water relations of Navel orange trees [*Citrus sinensis* (L.) Osbeck] subjected to different irrigation regimes was obtained from experiments with young potted trees in the laboratory (Part A of the thesis). The results from the potted orange trees were then scaled up to plantation level wherein experiments with mature, bearing trees in a commercial orchard at Mazowe Citrus Estate were conducted (Part B of the thesis). Conclusions from these two parts of the thesis (Parts A and B) are presented in this section. Lastly, recommendations on ways to maximize citrus yields in northern Zimbabwe using less water and also for future work based on the experimental results are discussed.

6.1 PART A: Stomatal Oscillations in orange trees

Experiments with the young potted Navel orange trees [*Citrus sinensis* (L.) Osbeck] revealed that the tree water status followed oscillations due to the cyclic opening and closure of the stomata regardless of the environmental conditions. This led to low diurnal sap flow rates implying that the Navel orange trees are generally low transpiring species. The low transpiration rates led to high leaf surface temperatures, which exceeded the air temperature by up to 10 ℃ on clear days due to reduced evapora tive cooling.

Despite the low transpiration rates, further reductions in transpirational losses were observed when the young potted trees were subjected to uniform soil drying. Controlled stressing of the rootzone is practiced in the regulated deficit irrigation strategy (RDI) leading to improvements in fruit quality (Goldhammer and Salinas, 2000) and a reduction in vegetative growth (Chalmers *et al*., 1981). Reduced transpirational losses were also observed when alternating partial drought stress was applied to the rootzone (PRD) in the split root experiments with the potted orange trees. Most importantly, no significant decline in stem growth rate occurred when the young potted trees were subjected to PRD despite a reduction in the transpirational water losses. This suggested that the PRD strategy had the potential to improve water use efficiency of the Navel orange trees but field trials were needed to confirm this result.

The occurrence of the stomatal oscillations in Navel orange trees resulted in the bulk leaf water potential fluctuating by as much 2.0 to 2.5 MPa on typical clear days. The representativity of point measurements of the leaf water status taken during the day-time to determine irrigation need (e.g. Jifon and Syvertsen, 2003) is thus questionable. Given the fact that the tendency to oscillate gradually dissipated after sunset, predawn leaf/xylem water potential is probably a better measure of the water status of the Navel orange trees than day-time values. In addition, the water relations of citrus trees are important not only in establishing the irrigation need but also in determining the fruit quality (Castle, 1995). Stomatal oscillations are a dominant feature of the water status of the Navel orange trees. Thus, detailed investigations were done to gain insights into the phenomenon of stomatal cycling. The approach adopted was to investigate the role of the water transport dynamics in the roots, stem and branches of the trees. These were then related to events at leaf level, e.g. changes in the leaf water status and the stomatal conductance.

While the stomatal oscillations are commonly associated with the biochemical exchange of ions at leaf-level (Upadhyaya *et al*., 1988; Yang *et al*., 2003), it was demonstrated in this study that whole-tree water balance played an important role in triggering stomatal oscillations. The oscillations appeared to be somewhat related to fluctuations in the hydraulic resistance of the whole tree. It is not clear, however, why the hydraulic resistance of the trees changed throughout the day, but cavitation formation in some part of the transpiration stream and its rapid reversal are possible causes (Buckley, 2005) although definite evidence is still lacking. The essence of this observation is that events beyond the leaf-level appear to be important in triggering the stomatal movements.

The fact that the efficiency of water supply to the evaporating sites in the leaves was a crucial factor in the generation of the stomatal oscillations was further demonstrated when the oscillations from the Navel orange trees budded on different rootstocks were investigated. More pronounced oscillations occurred on rootstocks which had greater water uptake difficulties (the troyer citrange) than the rough lemon rootstock which is more efficient in water uptake. In addition, the hydraulic resistances of the orange trees predicted using a simple water balance model were significantly higher than those for trees which do not show this phenomenon. The largest source of this high resistance is suspected to be in the roots given a very large time lag in water transport between the roots and the stem of the young orange trees (>35 min) (Dzikiti *et al*., 2006). An additional high resistance or large capacitance, but probably smaller than in the roots, appeared to reside downstream of the branch also as shown by a high time lag in water transport between the branch and the leaves (~ 20 min).

6.2 PART B: Irrigation strategies of orange trees at Mazowe Citrus Estate, Zimbabwe

In the commercial orchard at Mazowe Citrus Estate, the performance of the irrigation practice by the local growers (control henceforth) was compared with the partial rootzone drying (PRD), the regulated deficit (RDI) and a well-watered treatment. One partial rootzone drying treatment applied the same levels of irrigation as the control (PRD100) and the other 50 % of the control (PRD50) but with the wet and dry sides switched every ten days. The RDI treatment also applied 50 % irrigation compared to the control while the well-watered applied 200 % of the control with double drip lines.

Despite the already low stomatal apertures, PRD effects were detected in Navel orange trees, namely; a reduction in the stomatal conductance (and hence in transpiration rates) while the plant water status was maintained. Average yield per tree was marginally larger in the control treatment during the first season of the trials (2004/05) compared to the well-watered and the PRD100 treatments although the yield differences were not significant. The PRD50 and the RDI50 treatments were introduced during the second season (2005/06). During 2005/06, average yield per tree was significantly larger in the well-watered treatment than the other treatments with the control treatment giving the lowest mean yield. The low yield in the control treatment could be attributed to the effects of alternate bearing due to a high crop load in the previous season (2004/05). Fruit size was affected more by crop load than by the irrigation regimes although the juice content of individual fruit under PRD was marginally lower in 2005/06.

Another interesting feature of the trials during the 2005/06 season is that treatments that used 50 % less water (i.e. PRD50 and RDI50) gave a higher yield than the control. We strongly suspect general excess irrigation application. Despite the small yield reduction, the water use efficiency for trees under PRD was higher than that for trees under the current irrigation practice by the local growers (the control). Thus, at least compared with the current practice, the partial rootzone drying technique seems to yield more fruit per drop of water transpired. However, a consistently high average yield per tree occurred under the well-watered treatment primarily due to a high fruitset under this treatment. Although more water was applied in this well-watered treatment, this translated directly to more fruit such that the water use efficiency was also high.

Up scaling of transpiration rates from single tree to plantation level based on stem sap flow measurements using the thermal dissipation probes (TDP) led to unrealistically low

transpiration rates. This either reflected that the probes somewhat underestimated the sap flow rates or that the error margins in the estimation of the sap wood area index were large.

6.3 Recommendations on the best irrigation strategy and future work

To better understand the water relations of the Navel orange trees and their implications on fruit yield, the phenomenon of stomatal oscillations has to fully explained. To gain a good understanding of its physical origin future research needs to focus on investigating:

- the possibility of cavitation formation and its rapid reversal during the daytime, to understand the cause of the varying hydraulic resistance;
- leaf-level water balance seeking a direct relationship with the stomatal movements. The source of the probable high resistance to water transport downstream of the branch (or a high capacitance) is also uncertain and needs to be identified.

More fruit at Mazowe Citrus Estate can be obtained using less water if a combination of the well-watered treatment and the partial rootzone drying strategies are adopted with the following adjustments to the current practice:

1) A second drip line be introduced but with emitters producing less water per hour than the current rating of 2.3 liters per hour. Emitters with low ratings will ensure that less water is used than if the current ones are maintained. Double lines will promote the development of an extensive root system capable of meeting the atmospheric evaporative demand during the hot and dry periods of the growing season (September – November) which coincidentally correspond to the flowering and fruitset phases. A limited root system coupled with the water uptake difficulties by the orange trees seem to lead to drought stress during the above mentioned growth phases.

2) The double lines be operated concurrently (as in the well-watered treatment) during the flowering and fruitset phases to minimize flower and fruit let abscission due to drought stress. The growers can then revert to the partial rootzone drying strategy for the rest of the season after the fruitset phase to reduce the transpirational losses.

3) As shown in Chapter 1 of this thesis, dendrometers (or linear variable displacement transducers, LVDTs) or indeed sap flow sensors can potentially be used for the precision irrigation scheduling of citrus trees.

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Summary

Horticultural crops (e.g. citrus), play an important role to the economies of developing countries such as Zimbabwe. The sustainable production of citrus depends on the availability of adequate water throughout the year since citrus is an evergreen crop. The increasing competition for water between citrus growers, other crop growers, recreation, industrial and domestic users means that less water is becoming available for irrigating large citrus plantations, such as the Mazowe Citrus Estate in northern Zimbabwe. The problem of water shortage is worsened by the effects of global climate change which has led to an increased frequency and severity of droughts in Sub-Saharan Africa in recent years (Makarau and Jury, 1997). Sustainable production of citrus, thus, requires not only the efficient management of the limited water resources, but also the development of new irrigation strategies which lead to improved water use efficiency. A typical irrigation strategy with the potential for improving the water use efficiency in tree crops is the partial rootzone drying (PRD) strategy (Dry *et al*., 1996).

The primary goal of this PhD is to explore methods of improving water use efficiency in citrus plantations in northern Zimbabwe. Particularly, the potential application of bio-sensors for irrigation management in citrus plantations, e.g. the sap flow sensors, dendrometers (diameter variations) and the infrared thermometers (leaf-air temperature difference) was investigated. Much progress has been made on the use of these plant-based irrigation scheduling tools in the protected cropping industry (e.g. in greenhouses) but rarely in plantations (Jones, 2004). Information is also sparse on the response of citrus trees to the PRD irrigation strategy and this technique is also evaluated in the present study. The approach adopted involved two experimental phases, the first being a laboratory based approach, wherein the response of young potted orange trees, planted with a split root system to environmental variables, including manipulations of the soil water regimes, was quantified. The commonly grown cultivar of orange trees in Zimbabwe, the Navel cultivar [*Citrus sinensis* (L.) Osbeck] of the Baianinha selection was investigated. These trees were budded on two rootstocks, namely the Rough lemon [*Citrus jambhiri* (Lush.)] and the Troyer citrange [*Citrus sinensis* x *Poncirus trifoliata* L. Raf]. Results with the potted trees were then up scaled to field conditions at Mazowe Citrus Estates in the second phase of the experimental campaign. The potential utility of the PRD irrigation strategy in improving the water use efficiency of citrus trees in northern Zimbabwe was evaluated. Carefully calibrated sensors were used to monitor

the soil, plant and atmospheric variables both in the laboratory and in the field at Mazowe Citrus Estate.

Proper interpretation and use of the plant-based signals for water resource management requires a good understanding of the plant water relations of the specific crop. Thus, a substantial proportion of the thesis is devoted to understanding the plant water relations of the Navel orange trees. Measurements on the potted Navel orange trees revealed that the sap flow, stem diameter, leaf surface temperature and the leaf water potential all followed cyclic oscillations with a period ranging from 35-75 min depending on the rootstock. These oscillations were unquestionably a result of the periodic opening and closure of the stomata under clear sky conditions and with optimal soil water conditions. This phenomenon of stomatal oscillations, though first discovered many decades ago (Cowan, 1977), still remains not yet fully explained. However, it is a common phenomenon occurring in more than 35 different plant species and many of them being crops of high commercial value e.g. some cultivars of beans, sunflower, cotton and citrus. In addition, point measurements of some aspect of the plant water status e.g. the leaf water potential has been used to make irrigation decisions e.g. on Navel orange trees (Jifon and Syvertsen, 2002), but with potentially large error margins given the large range of possible values that this variable can take under optimal environmental conditions.

The hypothesis that stomatal oscillations are mainly triggered by changes in plant water status, rather than by biochemical reactions in the leaves, is significantly advanced in this thesis. In addition, contrary to the widely held notion that changes in plant water status at leaf level are largely responsible for the generation of stomatal oscillations (Upadhyaya *et al*., 1981; Wang *et al*., 2001), we provide evidence that events elsewhere in the transpiration stream and distal to the leaves also play an important role in triggering stomatal oscillations. This was achieved by simultaneously tracking the water transport from the roots, stem and branches of the orange trees using sap flow sensors. Measurements of the stomatal conductance, to complement the sap flow measurements, were made on selected days. Parts of the transpiration stream where resistance to water transport was particularly high were isolated by cross-correlation of the water flow variables to quantify the time lags in water transport. The largest time lags resided downstream of the branch and up stream of the stem.

More importantly also, the resistance to water transport varied throughout the day, implying that the efficiency of water transport to the leaves also changed round the day. This led to transient internal water deficits, which appeared to control the stomatal aperture mediated by changes in the bulk leaf water potential. The cause of this short-term variation in

the plant resistance is not well known although cavitation formation and its rapid reversal is a possible cause (Buckley, 2005; Marenco *et al*., 2006). The fact that the efficiency of water transport to the leaves played an important role in triggering the stomatal oscillations was further illustrated by comparing the characteristics of the stomatal oscillations for Navel orange trees budded on two rootstocks with contrasting water uptake capabilities, namely the Rough lemon and the Troyer citrange. A dynamic water transport model was developed and used to derive typical hydraulic constants (plant resistance and capacitance) of the transpiration stream of the Navel orange trees budded on these two rootstocks.

Experiments with the young potted Navel orange trees also revealed that the sap flow and stem diameter variation measurements were sensitive to variations in the soil water regimes and thus, they could potentially be used in the irrigation scheduling of these trees. Use of the leaf surface temperature was complicated by the leaf-rolling tendency of the orange trees under water stress making the effect of the water stress on the leaf surface temperature less clear. In addition, partially stressing the root zone of the potted orange trees (PRD) caused significant reductions in sap flow rates while stem growth rates were maintained. Up scaling these laboratory results to field conditions at Mazowe Citrus Estate confirmed that the transpiration rates of the Navel orange trees were indeed reduced under partial root zone drying (PRD) compared with the current growers' irrigation practice and with a well-watered treatment. Seasonal transpirational water savings of up to 1 Ml per hectare could potentially be achieved under partial root zone drying compared with the well-watered treatment and approximately 0.5 Ml per hectare compared with the current irrigation practice by the growers at Mazowe Citrus Estate. However, small yield reductions also occurred under partial rootzone drying when compared with the well-watered treatment mainly due to the high fruitset under the well-watered treatment. No significant differences in the yield occurred when the partial rootzone drying treatment was compared with the current growers' irrigation practice implying that water use efficiency is increased under PRD. To maximize the water use efficiency at Mazowe Citrus Estate, Zimbabwe, it appears that a combination of the well-watered treatment and the partial root zone drying is needed but applied at different times. For instance, the well-watered approach could be adopted during flowering and fruitset to maximize fruitset (or to minimize fruit drop) and then switching to the partial rootzone drying for the rest of the fruit growing season (to minimize transpirational losses).

Samenvatting

Tuinbouwgewassen (bijv. citrus) spelen een belangrijke rol voor de economie van ontwikkelingslanden zoals Zimbabwe. Duurzame citrusproductie is echter sterk afhankelijk van de beschikbaarheid aan voldoende water gedurende het volledige jaar omdat citrus een immer groene plant is. Door de toenemende competitie voor water tussen citrusverbouwers enerzijds en andere gewasverbouwers, recreationele, industriële en huishoudelijke gebruikers anderzijds is er steeds minder water beschikbaar om grote citrusplantages te irrigeren, zoals de Mazowe Citrus Estate in het noorden van Zimbabwe. Het probleem van watertekort wordt verder nog versterkt door de effecten gerelateerd aan de globale klimaatsverandering, wat in de laatste jaren tot meer frequente en ernstigere droogtes heeft geleid in Afrika ten zuiden van de Sahara (Makarau & Jury, 1997). Duurzame productie van citrus vereist dus niet enkel een efficiënter beheer van de natuurlijke grondstof water, maar ook de ontwikkeling van nieuwe irrigatiestrategieën die kunnen leiden tot een verbeterde efficiëntie van het watergebruik. Een typische irrigatiestrategie met de mogelijkheid om de efficiëntie van het watergebruik in boomgewassen te verbeteren is de strategie van partiële uitdroging van de wortelzone (Partial Rootzone Drying of PRD) (Dry *et al*., 1996).

De hoofddoelstelling van deze thesis is om methoden te onderzoeken die toelaten om de efficiëntie van het watergebruik te verbeteren in citrusplantages in het noorden van Zimbabwe. Zo werd het gebruik van bio-sensoren, zoals sapstroomsensoren, dendrometers (diameter variaties) en infraroodthermometers (blad-luchttemperatuursverschil), voor irrigatiedoeleinden en management in citrusplantages onderzocht. Een grote vooruitgang in het gebruik van deze plantgebaseerde irrigatiecontrolemiddelen werd reeds geboekt in de beschermde gewasindustrie (bijv. in kassen), maar het gebruik ervan in plantages is eerder zeldzaam (Jones, 2004). Informatie over de respons van citrusbomen op de PRD irrigatiestrategie is eveneens beperkt en werd daarom ook geëvalueerd in deze studie. De gekozen benadering omvat twee experimentele fasen. In een eerste fase werd in laboratoriumomstandigheden de respons van jonge sinaasappelbomen in pot, geplant met een gesplitst wortelsysteem, op omgevingsvariabelen, inclusief manipulaties van het bodemwaterregime, gekwantificeerd. De algemeen gebruikte cultivar van sinaasappelbomen in Zimbabwe, namelijk de Navel cultivar [*Citrus sinensis* (L.) Osbeck] van de Baianinha selectie, werd onderzocht. Bomen geënt op twee verschillende onderstammen, namelijk de Rough lemon [*Citrus jambhiri* (Lush.)] en de Troyer citrange [*Citrus sinensis* x *Poncirus*

trifoliata L. Raf] werden gebruikt. De resultaten van de bomen in pot werden vervolgens opgeschaald en geverifieerd in veldomstandigheden in de Mazowe Citrus Estate in de tweede fase van de experimentele meetcampagne. De bruikbaarheid van de PRD irrigatiestrategie ter verbetering van de efficiëntie van het watergebruik van citrusbomen in het noorden van Zimbabwe werd geëvalueerd. Gekalibreerde sensoren werden gebruikt om bodem, plant en atmosferische variabelen te meten, en dit zowel in laboratorium- als in veldomstandigheden.

Optimale interpretatie en gebruik van plantgebaseerde signalen voor een beter management van de natuurlijke grondstof water vereist een goed begrip van de plant-water relaties van het specifieke gewas. Daarom werd een groot deel van deze thesis gewijd aan het beter begrijpen van de plant-water relaties van de Navel sinaasappelbomen. Metingen op Navel sinaasappelbomen in pot toonden aan dat de sapstroom, de stamdiameter, de bladtemperatuur en de bladwaterpotentiaal cyclische oscillaties vertoonden met een periode variërend tussen 35-75 min, afhankelijk van de gebruikte onderstam. Deze oscillaties bleken het resultaat te zijn van het cyclisch openen en sluiten van de stomata onder helderde hemel en optimale bodemwatercondities. Hoewel het fenomeen van stomatale oscillaties reeds tientallen jaren terug ontdekt werd (Cowan, 1977), is het mechanisme nog steeds niet volledig opgehelderd. Nochtans is het een algemeen optredend fenomeen dat vastgesteld werd in meer dan 35 verschillende plantensoorten, waarvan verschillende soorten gewassen zijn met een hoge commerciële waarde, zoals bijv. sommige cultivars van boon, zonnebloem, katoen en citrus. Merk hierbij ook op dat in het verleden puntmetingen van de bladwaterpotentiaal werden gebruikt om irrigatiebeslissingen te nemen, bijv. voor Navel sinaasappelbomen (Jifon & Syvertsen, 2002), maar dat een dergelijke irrigatiestrategie hoogst waarschijnlijk aan een grote foutmarge is onderworpen, gegeven de brede range van mogelijke waarden die deze variabele kan aannemen onder optimale omgevingcondities.

De hypothese dat stomatale oscillaties hoofdzakelijk veroorzaakt worden door veranderingen in de waterstatus van de plant, eerder dan door biochemische reacties in de bladeren, werd naar voor geschoven in deze thesis. Bovendien werd, in tegenstelling tot het algemeen aanvaarde idee dat veranderingen in de bladwaterstatus verantwoordelijk zijn voor de stomatale oscillaties (Upadhyaya *et al*., 1981; Wang *et al*., 2001), het bewijs geleverd dat gebeurtenissen ergens anders in de transpiratiestroom en stroomafwaarts van de bladeren ook een belangrijke rol kunnen spelen in het veroorzaken van stomatale oscillaties. Dit kwam tot uiting door tegelijkertijd het watertransport te meten met sapstroomsensoren in de wortels, de stam en de takken van de sinaasappelbomen. Bijkomend werden metingen van de stomatale geleidbaarheid uitgevoerd op geselecteerde dagen. Delen van de transpiratiestroom waar de hydraulische weerstand tegen watertransport hoog bleek te zijn,

werden geïsoleerd via een crosscorrelatie analyse van de variabelen gerelateerd aan de waterstroming om zo de tijdsvertragingen in watertransport te kwantificeren. De grootste tijdsvertragingen werden stroomafwaarts van de tak en stroomopwaarts van de stam gevonden.

Het is ook belangrijk om op te merken dat de weerstand tegen watertransport varieerde gedurende de dag, en dus ook de efficiëntie van het watertransport naar de bladeren. Dit veroorzaakte korte termijn veranderingen in het intern waterdeficit wat de stomatale opening leek te regelen in combinatie met veranderingen in de bladwaterpotentiaal. De oorzaak van deze korte termijn variaties in de hydraulische weerstand van de plant is nog steeds niet opgehelderd, hoewel cavitatie en het snel herstel hiervan als mogelijke oorzaak naar voor wordt geschoven (Buckley, 2005; Marenco *et al*., 2006). Het feit dat de efficiëntie van het watertransport naar de bladeren een belangrijke rol speelt in het teweegbrengen van stomatale oscillaties werd verder geïllustreerd door de karakteristieken van de stomatale oscillaties te vergelijken tussen Navel sinaasappelbomen, geënt op twee onderstammen (Rough lemon en Troyer citrange) met een verschillende wateropnamecapaciteit. Een dynamisch watertransportmodel werd ontwikkeld en gebruikt om de typische hydraulische constanten (namelijk de hydraulische plantweerstand en capaciteit) van de Navel sinaasappelbomen geënt op deze twee onderstammen te achterhalen.

De experimenten met de jonge Navel sinaasappelbomen in pot toonden ook aan dat metingen van de sapstroom en de stam-diametervariatie gevoelig zijn aan veranderingen in het bodemwaterregime. Aldus werd besloten dat deze sensoren kunnen aangewend worden voor irrigatiedoeleinden van deze bomen. Het gebruik van de bladtemperatuur werd echter bemoeilijkt door de neiging tot bladrolling van sinaasappelbomen onder waterstress, waardoor het effect van waterstress op de bladtemperatuur minder duidelijk werd. Het gedeeltelijk stresseren van de wortelzone van de sinaasappelbomen in pot (PRD) veroorzaakte echter een significante dalingen in de sapstroom, terwijl de groeisnelheid van de stam behouden bleef. Opschaling van de laboratoriumresultaten naar veldomstandigheden in de Mazowe Citrus Estate bevestigde dat de transpiratiesnelheid van de Navel sinaasappelbomen inderdaad kon gereduceerd worden door het toepassen van de PRD strategie in vergelijking met enerzijds de huidige irrigatiepraktijk van de tuinbouwers en anderzijds een goedbewaterde behandeling. Een seizoenale waterbesparing door een verminderd transpiratieverlies van 1 Ml per hectare werd gerealiseerd met de PRD strategie vergeleken met de goedbewaterde behandeling en een besparing van ongeveer 0.5 Ml per hectare vergeleken met de huidige irrigatiepraktijk van de tuinbouwers van de Mazowe Citrus Estate. Geringe opbrengstverliezen werden vastgesteld wanneer de PRD strategie werd

vergeleken met de goedbewaterde behandeling, wat kon toegeschreven worden aan de hogere vruchtzetting tijdens de goedbewaterde behandeling. Er konden echter geen significante verschillen in opbrengst worden vastgesteld wanneer de PRD behandeling werd vergeleken met de huidige irrigatiepraktijk van de tuinbouwers. Dit betekent dat de efficiëntie van het watergebruik was toegenomen door toepassing van de PRD strategie. Om de efficiëntie van het watergebruik te maximaliseren in de Mazowe Citrus Estate, Zimbabwe, blijkt een combinatie van de goedbewaterde behandeling en de PRD strategie noodzakelijk, toegepast op verschillende tijdstippen. Zo zou bijvoorbeeld de goedbewaterde benadering kunnen toegepast worden gedurende de bloei en vruchtzetting van de sinaasappelbomen om zo de vruchtzetting te maximaliseren (of om vruchtval te minimaliseren) en daarna zou kunnen overgeschakeld worden op de PRD strategie voor de rest van het groeiseizoen van de vrucht om transpiratieverliezen te minimaliseren.

Curriculum vitae

Sebinasi DZIKITI

7502 Harare North, Hatcliffe, Harare

+263-912-429146 and +263-4-303211 ext 1417

sdzikiti@science.uz.ac.zw

Nationality	: Zimbabwean
Date and place of birth	: 24 September 1972, Bulawayo, Zimbabwe
Marital status	: Married to Moleen Zunza
Children	: Munashe and Zvikomborero

PROFESSIONAL EXPERIENCE

2003 – 2007 **Lecturer, Physics Department, University of Zimbabwe**

2001 – 2002 **Teaching assistant, Physics Department, University of Zimbabwe**

2000 – 2001 **Research assistant, Agricultural Meteorology Group, Physics Department, University of Zimbabwe**

1997 – 2000 **School teacher (Mt Selinda High School, Chipinge, Zimbabwe) (Gateway Secondary School, Harare, Zimbabwe)**

EDUCATION

1998 – 1999 **MSc Agricultural Meteorology**
Department of Physics University of Zimbabwe

Thesis: Energy budget of a Class-A- pan: measurements and modeling.

1994 – 1996 **BSc (Honors) Physics**
University of Zimbabwe
Upper Second Class (2.1)

Dissertation: Modeling the radiation microclimate of crops grown under shade

1988 – 1993 **High School**: St Columbus High School (Bulawayo, Zimbabwe)

ADDITIONAL TRAINING

August 2002 Training on eco-physiological sensors and datalogging, Ghent University, Belgium

September 2003 Further training on eco-physiological sensors and data handling, Ghent University, Belgium.

July 2004 Training on gas exchange measurements, Biogeosciences Division, Max Planck Institute for Chemistry, Germany.

INTERNATIONAL PUBLICATIONS

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Dzikiti S. Response of young potted orange trees to soil drying. Seminar presentation to the Biogeosciences Division, Max Planck Institute for Chemistry, Mainz, Germany (July 2004) and the Crop Science Society of Zimbabwe (September 2004).

POSTER PRESENTATIONS

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ASSOCIATION MEMBERSHIP

Includes the following:

1. International Society for Agricultural Meteorology (INSAM);
2. International Society for Horticultural Sciences (ISHS)
3. Citrus Research International
4. European Geosciences Union

OTHER ACTIVITIES

1. Reviewer for Agriculture and Forest Meteorology Journal.