SEASONAL PATTERNS OF VEGETATIVE GROWTH AND PHOTOSYNTHESIS IN MANGO (*Mangifera indica* L.) TREES

by

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DECLARATION

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

Signed: _____   Date: _____
                     Khathutshelo Oswald Neluheni

DEDICATION

In the memory of my beloved parents, Johannes and Sarah, who regretfully did not live to see this work, which in no small part resulted from their gift of many years of love to me. To both of them: Thanks and I love you.

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ABSTRACT

Shoot growth and leaf photosynthesis of 6-7 year-old, field-grown mango (*Mangifera indica* L. cv 'Kent') trees subjected to the following irrigation regimes were monitored during the season of 2002/2003: Co, control ($\pm$95% of field capacity, FC); DI-1 and DI-2, continuous deficit irrigation (±79% and ±69% of FC, respectively); RDI, regulated deficit irrigation (like Co except that irrigation water was withheld for 2 weeks in Dec 2002/Jan 2003 during the final stage of fruit growth); and Co-F, farm control, full irrigation when soil moisture was lower than -10 KPa). During the post-harvest flushes in 2002 and 2003, Co-F shoots showed 56% more shoot volume and dry mass than Co indicating that a large amount of irrigated water was used for such vigorous growth. There were no significant differences in the number of flowering canes between all irrigation treatments during the flowering flush in 2002. However, the pattern of decreasing numbers of flushing terminals and shoot numbers was concurrent with decreasing amounts of irrigation water applied (Co-F>Co>RDI>DI-1>DI-2). The results indicated that part of the irrigation water applied to Co-F was used for vigorous vegetative growth; while in the DI-2 treatment severe shoot growth reduction seemed to seriously hinder productivity.

Midday leaf assimilations in well-irrigated 'Kent' mango trees in the field during winter and spring amounted to (4.5 $\pm$ 0.6 and 5.9 $\pm$ 0.3 µmol CO_2 m^{-2} s^{-1}, respectively) and were lower than in autumn and summer (6.4 $\pm$ 1.8 and 11.1 $\pm$ 0.8 µmol CO_2 m^{-2} s^{-1}, respectively). Differences in mean photosynthetic (Pn) rates between the three field-grown and well-irrigated cultivars, 'Kent', 'Keitt' and 'Heidi', were not significant except for January and April 2003. Young leaves (<25 DABB, days after bud break) photosynthesized only to a small extent in winter and summer at midday (0.2 $\pm$ 0.9 and 0.4 $\pm$ 0.3 µmol CO_2 m^{-2} s^{-1}, respectively). However, high Pn rates at midday were reached in leaves aged 90-180 DABB in summer (10.3 $\pm$ 2.0 µmol CO_2 m^{-2} s^{-1}) and maintained at leaves that were older than 365 DABB (10.4 $\pm$ 0.7 µmol CO_2 m^{-2} s^{-1}), while those in winter were lower for both leaf age groups (3.2 $\pm$ 0.6 and 3.5 $\pm$ 0.8 µmol CO_2 m^{-2} s^{-1}, respectively). In field-grown 'Kent' mango trees, water deficit reduced significantly the photosynthetic capacity in the irrigation treatment DI-2

across the entire year, especially during late spring and early summer, in comparison to the Co-F treatment, while differences between the treatments Co, DI-1, and RDI were negligible (in the range of 7.0-7.3 µmol CO_2 m^{-2} s^{-1}) across the entire year. Generally, the Co-F treatment maintained slightly higher photosynthetic rates (7.9 $\pm$ 3.2 µmol CO_2 m^{-2} s^{-1}) over the entire year than the other treatments showing that they received more water. Nevertheless, DI-2 maintained reasonable rates (6.5 $\pm$ 1.7 µmol CO_2 m^{-2} s^{-1}), even though they were severely stressed indicating that those trees apparently adapted to low water regimes by increasing their water use efficiency.

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1   General Introduction

Mango (*Mangifera indica* L.) is native to India as well as South East Asia (Smith, 1979; Crane and Campbell, 1994). Mango is mostly grown in the subtropical and tropical lowlands. These growing areas are characterized by very hot summers and mild winters. In South Africa water is a scarce resource because rainfall is highly variable, unstable and poorly distributed (Scotney and van der Merwe, 1995). The area around Hoedspruit, where the study was conducted, is relatively hot and suitable for mango and citrus production as well as annuals such as sweet corn. Despite the fact that mango is slightly drought tolerant (Schaffer et al., 1994; de Villiers, 1998) irrigation is a must in this area in order to obtain profitable yields with this crop. Furthermore, the sandy nature of the soil in this area may indicate that the soil has poor water and nutrient holding capacity. Poor water holding capacity of such soil raise the need for irrigation scheduling in order to supply sufficient water for tree growth, while the poor nutrient holding capacity may suggest the reduction of unnecessary irrigation to avoid leaching of nutrients to deeper soil horizons and into the groundwater.

Water for agriculture is characterized as high volume and of low value. Many countries are under pressure to reduce water used for irrigation, since water resources are allocated to other uses, such as industries and municipalities, and increasing competition for such limited resources takes place (Scotney and van der Merwe, 1995; Chartzoulakis, 1997). Furthermore, changes of water laws by the South African government have put fruit production and profit at stake because farmers are paying for water regardless of the source, e.g. boreholes or dams. Water supply may therefore not be enough to fully satisfy crop water requirements and it is necessary to find more efficient ways to irrigate this crop (Girona et al., 1994). As a result it is important to use irrigation scheduling in the form of deficit irrigation (DI) in order to reduce applications of irrigation water while optimizing yield. Irrigation scheduling is the technique to apply water timely and accurately to the crop and is the key to conserving water and improving irrigation performance and sustainability of irrigated agriculture (Mhlauli, 2000). Fischer (1995) and Behboudian and Mills

(1997) defined deficit irrigation as applying less water (regulated deficit irrigation) to the plant than the prevailing evaporative demand at selected stages during the growing season. Regulated deficit irrigation (RDI) may offer an approach to saving water in some fruit trees with little or no negative impacts on yield and revenue (Torrecillas et al., 2000). RDI has been successfully used in suppression of excessive vegetative growth and sometimes increased yield in peaches (Tatura, 2003) and pears (Mitchell et al., 1989). Despite being slightly drought tolerant, mango is, however, thought to be more sensitive to poor water management (Cull, 1991). Severe water deficits may affect the present growth and yield as well as future growth of the plant (Pavel and de Villiers, 2000). In tropical areas where the temperatures are not too low, slight water deficits in winter before flowering may promote mango flowering by increasing the total amount of floral stimulus produced by the canopy (Smith, 1979; Cull, 1991; de Villiers, 1998). Water deficits before flowering decreases vegetative flushing, thereby increasing the proportion of mature to immature leaves in the canopy. Mature leaves produce the floral stimulus whereas immature leaves are rich sources of floral inhibitors (Schaffer et al., 1994). This phenomenon stimulates the post-harvest vegetative flush during the autumn months and concurrently influences flower formation in spring (de Villiers, 1998).

The vegetative growth of the plant is significantly dependent on the moisture levels in the soil as such water deficits could reduce excessive growth. Reduction of excessive vegetative growth may be beneficial to farmers because it might reduce some of the costs involved in production. With reduced irrigation, pruning weights and water used for irrigation might be greatly reduced and at the same time tree canopies would be opened (Kilili et al., 1996). The openness of the canopy could lead to maximum penetration of radiation to the inner side of the canopy (Flore and Lakso, 1989) as well as the ease of spraying agro-chemicals. The former is of great importance, since it improves photosynthesis that determines the plant growth and yield and it also helps in fruit ripening.

Photosynthesis, the process of synthesizing carbohydrates responsible for growth and its maintenance, is highly influenced by various environmental factors such as temperature, water deficit, salt stress and light (Zulfugarov, 2001). Among these factors, effects of water deficits on photosynthesis have been studied extensively

(Chartzoulakis et al., 2002; Pretorius and Wand, 2003). Water deficit affects the plant assimilation by altering the metabolic activity of the plant, either inhibiting a single metabolic sequence or enzyme reaction, causing a disruption of the whole system or by changing the balance between parts of the system (Lawlor, 1979). The disruption of photosynthesis may lead to a reduction of dry matter produced. However, many authors question the reported relationship between net assimilation rates and yield (Kramer and Kozlowski, 1979). Plant reactions to reduced photosynthesis may be different depending on climatic conditions, cultivars and soil properties. Carbohydrates and energy are produced through photosynthesis. The produced carbohydrates are then stored as starch, while others are transported to other plant parts. Apart from fruits, vegetative growth is one of the major carbon sinks (Pretorius and Wand, 2003). For this reason, excessive vegetative growth can result from highly photosynthetically active trees under optimum conditions.

It is imperative to consider how water manipulates plant parts controlling carbohydrate formation and use (Cull, 1991). It is also important to understand the phenological growth stages under specific climatic conditions. This will make it possible to identify growth stages that are appropriate for implementation of regulated deficit irrigation (RDI) strategies (Chalmers et al., 1984; Cull, 1991). Therefore, the general objectives of the study were to evaluate the response of vegetative growth and photosynthesis to different irrigation regimes with the goal to optimize yield.

2 Literature Review

The most important goal in any orchard is productivity. The productivity of a tree depends on interaction and balance between numerous factors including, vegetative root growth and shoot growth, flowering as well as fruiting. The majority of production is formed from carbohydrate; therefore it is the tree's photosynthetic capacity that dominates production control (Du Preez, 1997). It is well established that crop productivity is determined by many factors (Clipson, 1994a). These productivity-determining factors are environmental processes acting on the plant population within the crop, or are the components of the internal physiological processes of the plant species, particularly the fixation of carbon from atmospheric CO_2 into organic compounds by photosynthesis in the green tissues of the plant. Several plant (endogenous) factors, such as cultivars, and environmental factors, such as water stress, may determine the rate at which the plant fixes carbon and subsequent crop growth as well as final yields of that crop (Kramer and Kozlowski, 1979; Clipson, 1994a). Furthermore, quantification of crop photosynthetic responses, carbon allocation patterns and source-sink relationships contribute to understanding plant growth and yield potential (Fernandez and Pritts, 1994).

2.1 Vegetative Growth

2.1.1 General background

Vegetative growth is regarded as the most important plant trait leading to carbohydrate production and subsequent plant growth. Shoots, including trunk, branches, and growth of new flushes provide structural support and storage of tree reserves; while leaves are critical for their role in utilizing sunlight to produce carbohydrates. These carbohydrates are the energy source for tree growth and therefore it is important to understand the effect of any management input on shoot

and root growth, since roots absorb nutrients and water (Du Preez, 1997). The production of photosynthates takes place through the process of photosynthesis. The disruption of photosynthesis might ultimately affect the distribution of carbohydrates thereby altering sink-source relationships in the plant. Like any other plant component and process, vegetative growth is sensitive to any form of stress as in extreme temperatures, high light intensities and water deficit. The latter seems to hold more attention of researchers, since its optimal management may not only enhance sufficient vegetative growth but also save water and improve fruit quality (Cull, 1991). Such results have been achieved by applying optimum amount of water during critical plant growth stages, thus through the regulated deficit irrigation (RDI) technique (Besset et al., 2001).

Phenological cycles of trees vary with different plant species and their respective climatic conditions. In deciduous fruit trees, leaves last for one season, while those of evergreens last for about four years (Kramer and Kozlowski, 1979). However, deciduous fruit trees have higher photosynthetic rates than evergreen ones in order to compensate for the shorter life span (Whiley et al., 1999). In evergreens, leaf senescence occurs throughout the year in any season (Y.L. Grossman, 2003: personal communication). There are some notable differences even within each group, for instance mango leaves may hang for more than three years, while avocado leaves can grow rapidly and last for less than one year on the tree (Schaffer et al., 1994). Compared to mango trees the physiology of avocado trees more closely resembles that of a woody deciduous species. In comparison to avocado, mango leaves are very sclerophyllous with a high investment of carbon during growth (Whiley et al., 1999). Cashew, belonging to the same family as mango, has comparatively shorter life span (one year) (Schaper and Chacko, 1993). Such information on growth cycles may allow a better understanding of when to manipulate plant growth through reduced irrigation.

2.1.2 Vegetative growth forms

Trees such as peach and mulberry have indeterminate growth habits that have lateral flower buds and a terminal that remains vegetative. Some woody species, such as apple and pear, form terminal mixed buds with both leaf and flower primordial usually on short shoots, which do not grow until next spring. The resultant growth is a sympodial pattern of branches because growth begins from lateral buds not the mixed terminal bud (Harris, 1992). Buds and node initials of all deciduous trees and some evergreens are formed in the terminal (preformed shoot initials). This makes it possible to have one flush only once a year as in deciduous trees; in contrast, favourable conditions may induce vegetative bud formation in evergreens anytime. Under favourable conditions the internodes of both deciduous and evergreens may be elongated (Kozlowski and Kramer, 1979).

Most fruit trees have a rounded shaped canopy (Harris, 1992), resulting from a decurrent growth form, where the terminal shoot loses apical dominance and is overtaken by lateral shoots as in mangoes (Cull, 1991). Strong apical dominance of current growth usually leads to a weak apical control of subsequent growth and *vice versa*. Therefore, vigorous shoots exhibit less apical dominance than those of low vigour. Species with terminal flowers or inflorescence normally exhibit decurrent form of growth since the following year's growth will come from lateral buds. More than one bud will usually break; thus speeding the process that leads to round headedness. Competition between two or more shoots results in co-dominant stems and reduces growth of each, leading to a more compact canopy (Harris, 1992).

2.1.3 Water deficit and vegetative growth

For a tree to develop and produce appreciable amount of vegetative growth that is sufficient for further tree growth and maintenance, no environmental and plant factors should be limiting. Excessive vegetative growth is, however, unnecessary in fruit production because it competes with fruits for photosynthates (Kilili et al., 1996). Horticulturists have developed different ways of managing the vegetative vigour,

such as pruning, dwarfing rootstocks, plant growth regulators and deficit irrigation (DI). The latter has been widely researched particularly with deciduous crops (Chalmers et al., 1984, Mitchell et al., 1989, Mills et al., 1996, Besset et al., 2001). Water is said to be the most limiting factor in fruit production due to its scarcity and subsequent distribution to non-agricultural uses (Scotney and van der Merwe, 1995). Optimising the amount of irrigation water could lower costs of production (Mpelasoka et al., 2001) and also decrease nutrients and pesticides leaching into the ground water (Scotney and van der Merwe, 1995; Mills et al., 1996; Chartzoulakis, 1997).

According to de Villiers (2001), water supply in South Africa is limited and addition of water through irrigation during summer months ensures successful production of crops in general and mango in particular. Successful crop production is not only influenced by environmental factors but also by the genetic composition of the cultivar (Kramer and Kozlowski, 1979). Actual yield, tree growth and development are mediated by several endogenous factors, including previous fruit load, pre-and post-harvest vegetative growth, flowering, maturity of terminal shoots, nutritional status and carbon to nitrogen ratios (Westwood, 1988; Cull, 1991). These plant factors are both directly and indirectly influenced by environmental factors such as light, temperature, vapour pressure deficit (VPD), and water availability, and will be affected more severely with sudden changes in these environmental factors leading to a possible decline in tree growth. This is particularly true with respect to water deficit, since no crop would grow without water.

Water optimisation through regulated deficit irrigation (RDI) offers the possibility to increase yield, while excessive vegetative growth might be suppressed, as it was found in apples, pears (Kilili et al., 1996) and peaches (Besset et al., 2001), thereby reducing pruning costs (Mills et al., 1996). RDI is especially useful when one needs to manipulate certain phenological stages of the tree. Periods may be identified, where the tree is able to tolerate water stress without affecting productivity and irrigation could be reduced. When fruit shows little growth during stage II of fruit development then less water is likely to be needed (Du Preez, 1997). When reducing excessive vegetative growth, correct amount and timing of irrigation withdrawal or reduction is vital, otherwise fruit quality and return bloom may be compromised. Marsal et al. (2002) failed in their experiments to reduce the vegetative growth of

pears but managed to improve fruit quality due to their implementation of reduced irrigation during fruit maturity when vegetative growth had ceased. In temperate climates, water deficits that are applied early in the season may successfully control excessive vegetative growth without negatively affecting fruit growth, yield and bearing capacity (Chalmers et al., 1981; Mitchell et al., 1989; Caspari et al., 1997; Tatura, 2003). Water deficits applied during flowering, pollination and fertilisation or early fruit developmental stages may lead to premature abortion of fruits and seeds as well as fruit drop (Walker and Nel, 1995), since water use is high during these stages (Du Preez, 1997). Sufficient water is necessary during these stages for optimum development, whereas excessive water could result in poor quality of fruit. Late season withdrawal of irrigation improved apple quality in terms of intensified skin colour, increased total soluble solids (TSS), and flesh firmness without reducing fruit weight, yields and return bloom (Kilili et al., 1996; Behboudian and Mills, 1997). Early season withdrawal of irrigation, however, caused reduction in the fruit size (Kilili et al., 1996). In contrast, Besset et al. (2001) indicated that reduction of water supply during the early stages of peach fruit growth until the end of shoot growth only slightly affected final fruit size, number or yield. According to Du Preez (1997), immediately after harvest when there is little growth activity, water would not be as critical, however this might not be the case with mango plants since there is a post-harvest flush that is important for bearing fruit.

Besset et al. (2001) reported that shoot length, shoot diameter, flower bud numbers, young shoot length, young shoot numbers and leaf numbers of 'Big Top' peaches did not differ under different irrigation regimes. However, their trials were conducted on plants grown in 50 L nursery pots implying that the pot size could have suppressed root growth even in well-watered plants. By contrast, in it was reported that after six months of water deficit, trunk diameter of potted (50 L) 'Fuerte' and 'Hass' avocado trees was reduced by 34 and 39%, respectively (Chartzoulakis et al., 2002), and the difference could be explained by higher sensitivity of young (2 years old) avocado to water deficits as compared to peaches (6 years old). Chartzoulakis et al. (2002) further indicated that moderate water deficits significantly reduced total plant leaf area by 57 and 69% and the total plant dry weight by 63 and 80% for 'Fuerte' and 'Hass', respectively. Their period of drying plant material could have been too short (24 hrs at 105°C), since it is imperative to dry until equilibrium is reached.

2.1.3.1   Influence of deficit irrigation on trunk growth

Trunk diameter measurements are regarded as the simplest measurements that can accurately reflect tree size and growth, and such growth is positively related to yield (Westwood, 1988). Expansive growth appears to be the plant process most sensitive to water deficits for fruit trees, thus trunk growth could be a very sensitive stress indicator to changes in plant water status (Moriana and Fereres, 2002). Irrigation effects on increases of trunk cross sectional area (TCA) in mango was noticed during the second season of water deficit stress (de Villiers, 2001) indicating that mango trees take some time before effects of water deficit can be seen. Such increase in water stress effects with time was also found in asparagus (Drost and Wilcox, 1997) where the number of bud and shoot vigour was reduced during the second stress season. During summer, growth reduction of TCA appeared to be pronounced especially in reduced irrigation treatments owing the decline to the higher sensitivity of those reduced irrigation regimes to high temperatures and water deficit in contrast to the controls. The trunk relative growth rate was found to be constant over the season but only decreased during the winter months. It was indicated that during that period no active growth was really taking place associated with cold temperatures (de Villiers, 2001).

In pears, trunk growth rate was significantly reduced in trees irrigated with 30% (T130) more water compared to the control (100% of FC) and 70% (T70) of control trees probably due to over-irrigation, however the effects were successfully reversed when RDI was introduced into the treatment (Marsal et al., 2002). The highest accumulation of TCA in the T70 treatment showed that fruit trees could still grow appreciably despite mild water stress. The initial reduction in TCA in the control (100% FC) might have been due to the deleterious effects of over-irrigation because of anaerobic conditions in the soil (Marsal et al., 2002). In addition, Ruiz-Sanchez et al. (2000) showed that irrigating with smaller amounts of water frequently promoted hardening in young apricot trees. When those plants were subjected to severe water deficits, they showed higher tolerance hence higher water use efficiency in comparison to the control. In another trial, Girona et al. (1993) reported that peach trunk growth over the study period was significantly lower in the RDI treatment than in the well-irrigated (control) treatment.

2.1.3.2   Shoot growth and water deficits

Shoot growth consists of stem lengthening and expansion depending on the age of the shoot. For example, young shoots (2-4 weeks) are mainly characterized by stem extension, while older ones, when extension is ceased display cambial growth and therefore stem thickening (Kramer and Kozlowski, 1979). Like trunk growth, shoot growth is said to be a very sensitive water deficit indicator. Nevertheless, tree height was not found to be significantly different between the control, RDI and the reduced irrigation treatments in mango (de Villiers, 2001). Shoot growth, however, appeared to be significantly affected by different irrigation regimes during the November/December 2000 flush. Thus, those treatments with deficit irrigation had smaller and thinner shoots as compared to those that were well-irrigated (de Villiers, 2001).

Sritharan and Lenz (1988) found that shoot growth in 'Golden Delicious' apple responded proportionally to different irrigation treatments. At a water supply of 50% FC, longitudinal shoot growth was reduced by 55%, while at a water supply of 25% FC the growth reduction was about 79%, with both water regimes being compared to the control treatment (100% FC) (Sritharan and Lenz, 1988). These results emphasize the sensitivity of shoot extension to severe stress induced by water deficit (Harris, 1992). Chartzoulakis et al. (1993) also reported significant reductions in kiwi shoot growth under mild water deficits. By contrast, no adverse effects of deficit irrigation regimes on shoot growth were reported in 'Fino' lemon trees (Domingo et al., 1996).

According to Besset et al. (2001), number of vegetative shoots and flower buds in 'Big-Top' peach trees were not significantly reduced by deficit irrigation when compared to standard irrigation. Interestingly, the highest number of flowers per shoot length was obtained at the 25% FC treatment. The number of reproductive organs was, however, few due to little vegetative growth (terminals) resulting from reduced irrigation. Sritharan and Lenz (1988) indicated that in apples, stressed plants had more short shoots with terminal flower buds. Those shoots of the deficit irrigation treatment consisted of strong inflorescences with more flowers in lateral shoots than those in fully watered plants. Inflorescences appeared to be in better fruit set

positions and that could compensate for the lower number of inflorescences that resulted from reduced irrigation (Sritharan and Lenz, 1988).

2.1.3.3   Effects of water deficit on leaves

During severe water deficit stress, plant leaves develop adaptive and tolerance mechanisms. During water stress plants undergo modifications of leaf area leading to decreases in light interception by decreased leaf area, abscission of leaves, leaf folding, rolling or reorientation or other changes in growth (Flore and Lakso, 1989; Walker and Nel, 1995). In water stressed apricot trees, when midday leaf water potential was about -3.5 MPa, leaf insertion angle was reduced from 90 to 30°. Leaf water potential appeared not to be regarded as a good plant water stress indicator; nevertheless leaf angular changes emphasised the view that epinastic movements in apricot trees are dependent on plant water status (Ruiz-Sanchez et al., 2000). Changes in leaf orientation allowed lower incidence of solar radiation through reduction of leaf area, and consequently a reduction in water loss and leaf heating. In mangoes, leaves may have increased pubescence or additional wax deposits to reduce decreasing radiation load (Walker and Nel, 1995).

According to Behboudian and Mills (1997) many trees respond to water by reducing leaf area expansion hence the sensitivity of cell growth. Sritharan and Lenz (1988) reported that the leaf area in 'Golden Delicious' apple trees was reduced by 80% at the end of a three-year period of continuous water deficit. In response or adaptation to water deficits pear trees reduced leaf area expansion hence the total leaf area was reduced (Behboudian and Mills, 1997). Similar adaptive mechanisms to stress induced by water deficit were observed in olives (Nuzzo et al., 1997) and kiwis (Chartzoulakis et al., 1993). Under water deficits there is reduction in average leaf size hence the reduction in relative leaf area expansion (Behboudian and Mills, 1997). In addition, the leaf initiation rate in kiwi fruit reportedly remained low and constant in reduced irrigation treatments throughout the experimental period (Chartzoulakis et al., 1993). Research in 'Fino' lemon trees showed that at the end of the trials, leaf chlorosis and tree defoliation were evident in trees where water supply

was low, however the symptoms disappeared when the soil profiled was filled up to 100% field capacity (Domingo et al., 1996). Water stress may also induce changes in leaf morphological characteristics. In avocado, water stressed trees had smaller leaves and a lower specific leaf weight (Chartzoulakis et al., 2002).

2.1.4 Plant growth analysis

Quantifying plant growth is an essential step in developing cultural practices that increase yield in crop plants (Fernandez and Pritts, 1994). Vegetative growth can be expressed in different ways when analyzing plant growth over a certain period. Usually dry weights or net photosynthetic rates are used (Kramer and Kozlowski, 1991). Pavel and DeJong (1993b) indicated that in peach the best way might be to express fruit growth through relative growth rates (RGR). Relative growth rates of a plant are defined as the increase in dry matter over a time period in relation to the dry matter at the beginning of the time period (Clipson, 1994a; Morse, 1997). Relative growth rates, unlike absolute growth rates (AGR) are said to be reliable growth parameters because they take the original size, weight etc. of the plant organ and time into consideration (Kramer and Kozlowski, 1979; Clipson, 1994a). The RGR concept was initiated by Blackman in 1919 who compared plant production to the compound interest law used to calculate bank interests (Clipson, 1994a).

Chartzoulakis et al. (1993) emphasized the sensitivity of dry weight as a growth parameter under reduced irrigation regimes. Total dry weight of kiwi fruits was reduced by 60-65% under severe water deficits. Shoot dry weight (stem and leaves) was 35 and 25% of the control (100% FC) in water regimes of 65 and 40% of FC, respectively (Chartzoulakis et al., 1993). Nuzzo et al. (1997) also found that non-irrigated olive trees showed only 30% less total dry weight as compared to irrigated plants. The less severe reduction in dry weight under no irrigation showed that olives are apparently drought tolerant (Giorio et al., 1999).

2.1.5 Sink-source relationships

Vegetativeness is the ultimate visual plant character that commonly has a major controlling influence on tree carbohydrate status or sink-source relationships (Cull, 1991). Vegetative growth, particularly shoot growth (leaves and stems), produce and store photosynthates while simultaneously competing with other sinks for utilization of some of the carbohydrates for growth and maintenance. It is, however, interpreted that during flowering vegetative dormancy in mango allows a threshold of carbohydrate accumulation and growth regulator level to be reached, thus stimulating flowering. It also allows sufficient carbohydrates to be carried forward into the fruit developmental stages. It has been shown that the growing area could also affect source-sink relationships. In mango and avocados lower photosynthesis of container-grown than field-grown plants might be due to a carbon sink limitation, thus causing the supply of photoassimilates to exceed the demand as a result of root restriction in containers (end product of inhibition of photosynthesis) (Whiley et al., 1999). Increased starch contents in both crops growing in containers were higher (130 to 230 %) in container-grown trees compared to field-grown ones. An increase in starch, accompanied by a reduction in maximum photosynthesis, was concluded to be due to feedback inhibition.

Morse (1997) studied growth in bananas and found that the source-sink relationships throughout the crop cycle must be considered, since the complex interaction between carbon fixation, carbohydrate assimilation and carbohydrate allocation affects the growth pattern. Leaf growth and canopy development influence photosynthesis by production of photosynthesizing tissues (Clipson, 1994a) and interception of light indicating an interrelationship between growth and photosynthesis (Fernandez et al., 1997). Drost and Wilcox-Lee (1997) emphasised the dependency of yield on photosynthates highlighting that more yields could be realised if there is increased vegetative growth under sufficient irrigation. Pavel and DeJong (1993b) found that trees with lower crop loads had increased fruit dry weights compared to unthinned trees in three peach cultivars. Pavel and DeJong (1993b) suggested that there was a competition for assimilates between fruits in trees with high crop loads similar to what was reported in other crops (Hetherington, 1997). Mango fruits and inflorescence have a high-energy requirement due to the comparatively large investment in

reproductive versus vegetative tissues, and developing fruits draw both current season assimilates and reserve carbohydrates in woody tissues. Heavy cropping in mango can deplete stored reserves and results in poor yields the following season (biennial bearing) (Hetherington, 1997).

2.2 Photosynthesis

2.2.1 Definition and background

Harris (1992) defined photosynthesis as the transformation of carbon dioxide from air and water, primarily from soil, into simple carbohydrates and oxygen in the presence of light. These simple carbohydrates are quickly converted into more complex carbohydrates and other organic substances. Photosynthesis primarily occurs in the leaves though some takes place in the fruits and young stems, contributing significantly to photosynthesis in deciduous plants during winter (Kramer and Kozlowski, 1979; Harris, 1992).

Photosynthesis is regulated by the interaction of different internal and external factors, and plant growth is dependent upon photosynthesis (Harris, 1992). Internal factors favouring photosynthesis include young mature leaves with large spongy mesophyll space, numerous, large and responsive stomata, high chlorophyll content, adequate turgor and availability of carbohydrates. Stomatal aperture may have the most significant control of photosynthesis. The resistance to carbon dioxide entrance due to stomata size is a major limitation to photosynthesis. The two bean-shaped guard cells that form the stomata opening increase in sugar in the presence of light, resulting in an increase in turgor due to water flow to lower higher solute concentration (Hastie, 2002) and therefore stomata open. A localized water deficit (happening often on hot afternoons in summer) or insufficient light results in closure of stomata.

A leaf is generally known as the major organ responsible for photosynthesis, where carbohydrates are produced. However, fruits could also achieve assimilation rate of around 1% of total leaf photosynthesis (Schaffer et al., 1994), though chlorophyll fluorescence measurements proved that mango fruits might exceed that threshold (Hetherington, 1997). Fruits were capable of photosynthesizing hence their exposure to light would change CO_2 evolution in comparison to evolution from fruits in the dark (Pavel and DeJong, 1993a). However, fruits photosynthesize well under low or moderate sunlight since higher photosynthetic photon flux density (PPFD) may cause photoinhibition (Hetherington, 1997).

Most leaves of broad-leaved fruit trees have a thin broad blade and slender petiole. The cross section of leaf blade reveals the upper and lower epidermis covered with a waxy cuticle to reduce water loss e.g. in mango (Kramer and Kozlowski, 1979). The small openings (stomata) on the lower surface are responsible for water loss and gaseous exchange control. The mesophyll of the leaf is composed of the palisade and spongy parenchyma (Chartzoulakis et al., 2002). Parenchyma cells, particularly the palisade below the epidermis, contain the chlorophyll being responsible for photosynthesis in the granules called chloroplasts. Water, minerals, organic compounds are conducted by xylem and phloem cells found in leaves (Harris, 1992).

2.2.2 Effect of radiation on photosynthesis and yield

Many external factors including water, carbon dioxide, temperature, minerals (Kramer and Kozlowski, 1979) and light may influence the chlorophyll level and the rate of photosynthesis. Leaves exposed to sun are smaller, thicker and have more spongy mesophyll cells than do shade leaves. Most hardwoods have their sun leaves reaching the light saturation point (where photosynthesis will no longer increase with increasing light intensities) at 20-40 % of full sunlight (Harris, 1992). Leaves of conifers reach saturation points at light intensities of up to 40-80 % of full sunlight (Kramer and Kozlowski, 1979). Light intensity and photosynthetic rate of sun leaves are about 15 and 3.5 times, respectively, as much as those of shade (interior) leaves of mature apple trees (Kramer and Kozlowski, 1979; Flore and Lakso, 1989). Plants

growing in full sun usually defoliate when subjected to low light intensities (Harris, 1992).

During the course of the growing season a finite amount of photosynthetically active radiation (PAR) is incident upon a unit of ground area (e.g. a hectare) and therefore available to the growing crop. The amount of PAR that is incident on a particular site varies due to changes in day lengths and seasonality (Kramer and Kozlowski, 1979; Clipson, 1994b). Under South African conditions in subtropical regions, maximal incidence occurs during summer months and is markedly affected by latitude. The total amount of radiation is a function of irradiance and duration. Clouds and dust determines how much light is absorbed and reflected on its way to the surface (Clipson, 1994b).

Leaf canopy consists of several leaf layers; and the incident (incoming) radiation for the second layer will be the radiation that is transmitted through the upper layer. The incident PAR is reduced at each layer and CO_2 assimilation is also reduced in lower layers. However, efficiency of light use in terms of CO_2 assimilated per unit of incident light energy absorbed rises at the lower light intensities. Leaves of C_3 plants become light saturated at PAR values of 250 J^{-2} s^{-1}. As this value is approached, the use of absorbed light in terms of CO_2 assimilation becomes inefficient. If the light intensity increases the modest assimilation rate will increase because more light would penetrate the lower layers. However, the first layer would have lower light efficiencies than the others would (Clipson, 1994b). Net CO_2 assimilation rate increased and internal carbon dioxide decreased asymptotically in response to increasing PAR in field-grown avocado and mango trees (Whiley et al., 1999).

There is a linear relationship between biomass production (through photosynthesis) and PAR. Physiologists concluded that photochemical efficiency is constant through a growing season and that when canopy development is complete crop photosynthesis is independent of temperature over the range of 10-25°C. This suggests that solar radiation is the most important factor determining crop yield, assuming that water and nutrients are not limiting (Clipson, 1994b).

The amount of PAR absorbed depends largely on the architecture of the canopy and the presence of that canopy at the right times to maximize the availability of solar radiation. The complex arrangement of leaves also determines absorbed or intercepted radiation. Leaf area index (LAI) should therefore be kept above a critical level because the higher the leaf area the higher the PAR intercepted until saturation. Tree canopies with LAI above critical level result in wastage of water and reduce maximal profitability. The relationship between biomass production and incident PAR is dependent on the morphology of the leaves, especially the angle at which they are held relative to the ground and the incident light (Clipson, 1994b).

During the day, light can reach compensation point, a low light intensity at which there is no net CO_2 assimilation. Therefore, photosynthesis (Pn) is equal to respiration meaning that the rate of CO_2 assimilation is equal to the rate of air released. When the radiation incidence increases further, a light saturation point is reached. This happens when an increase in photosynthesis associated with increased irradiance end, eventually Pn reaches maximum photosynthesis while light continues to increase and therefore leaf photosynthesis is said to be saturated (Leach, 1994). In mango, for non cold-stressed, field-grown trees the light saturation point for Pn was 1284 µmol CO_2 m^{-2} s^{-1} compared to 1180 µmol CO_2 m^{-2} s^{-1} for cold-stressed, field-grown trees and 563 µmol CO_2 m^{-2} s^{-1} for container-grown trees. The light compensation point for field-grown mango was 29 and 66 µmol CO_2 m^{-2} s^{-1} for cold-stressed and non cold-stressed mango trees, respectively. This implied that photosynthetic capacities and light sensitivity of plant leaves could be reduced due to chill-induced photoinhibition (Pongsomboon et al., 1992). On the other hand, smaller pot size in containerised mango was possibly the cause of reduced photosynthesis due to carbon-sink limitation resulting from root restriction in containers. Avocados responded in their light compensation and saturation points in magnitudes similar to those of mango. In container-grown mango and avocado trees, light compensation and saturation points were reduced by about 50% in comparison to field-grown trees (Whiley et al., 1999). Similar trends were shown in the tree carbon fixation capacities.

2.2.3 Diurnal variations of photosynthesis

In fruit trees diurnal variations of photosynthesis can be higher than that of annuals, since the leaf water status of fruit crops is strongly dependent upon evaporative demand (Flore and Lakso, 1989). Environmental and plant factors determine the diurnal trend of photosynthesis. Photosynthetic rates are usually low early in the morning of any bright, clear, warm day under field conditions (Kramer and Kozlowski, 1979), while no specific pattern exists in laboratory or in the field with less than optimum environmental conditions over the day (Flore and Lakso, 1989). The lower assimilation rate in the morning may be attributed to low light intensities and temperatures despite a high leaf moisture content (turgid cells) and high carbon dioxide concentration in the intercellular spaces of leaves. As light intensity increases and air warms up, stomata open and net photosynthesis begins to rise rapidly and may reach maximum before noon. As soon as the maximum is reached there is a decrease in photosynthetic rates at midday hence high photosynthetically active radiation and temperatures that are conducive to stomatal closure (Kramer and Kozlowski, 1979). This midday decline in photosynthesis is often linked to increased vapour pressure deficit (Yoon and Richter, 1991) resulting from high transpiration in the leaves (Gimenez et al., 1997). However, Flore and Lakso (1989) pointed out that the midday decrease in photosynthesis might be controlled internally, since the same pattern may occur when environmental factors around the leaf are held constant.

Yoon and Richter (1991) reported that stomatal conductance was high in the morning and abruptly decreased at midday until sunset while vapour pressure deficit (VPD) remained high and constant. The stomatal response to VPD was attributed to epidermal water stress resulting from cuticular water loss from an epidermis in poor hydraulic contact with the mesophyll. The depressed stomatal conductance at midday gives evidence to the coupling of stomatal conductance and photosynthesis since photosynthesis also decreased (Ruiz-Sanchez et al., 2000). Although stomatal conductance gradually decreased in pear, as opposed to an abrupt one in apple, the diurnal patterns were similar. Flore and Lakso (1989) attributed the midday depression to the decreased stomatal conductance associated with minimum xylem water potential and also to the build-up of photoassimilates as a non-stomatal mechanism. Temperature, VPD, and hormonal changes may affect stomata.

After midday, photosynthesis increases again in the late afternoon and then decreases resulting from declining light intensities and temperatures during late afternoon and early evening. The late afternoon peak is associated with the fact that turgor may be regained and then stomata reopen after midday depression (Kramer and Kozlowski, 1979). In contrast, Yoon and Richter (1991) indicated that stomatal conductance values remained low after midday in apple and sweet cherry leaves. Diurnal pattern is, however, not fixed and depends on day-to-day variation of environmental and internal plant factors. External factors include light; temperature and VPD (Yoon and Richter, 1991), water availability, CO_2 content of the air and the interaction amongst them. Internal control of CO_2 is variously attributed to water stress, leaf water potential, stomatal closure, excessive respiration, accumulation of photosynthetic end products and photooxidation of enzymes. There is often a shift in importance of these factors controlling CO_2 absorption as has been explained above (Kramer and Kozlowski, 1979).

Generally the diurnal pattern of photosynthesis is positively correlated to light intensity with the exception of the midday decreases. The daily photosynthesis may be different on cloudy and sunny days. Under fully exposed conditions on cloudy days, the photosynthetic rate reaches the maximum about noon and then decreases or remains more or less constant for an hour or two and finally drops. In contrast, on bright sunny days, photosynthesis normally rises rapidly and then reaches a peak between 9:00 and 12:00 h, then decreases until about 14:00 h, where it reaches a second but much lower peak followed by a final decrease (Kramer and Kozlowski, 1979).

2.2.4   Seasonal trends of photosynthesis

There are fluctuations in seasonal patterns of photosynthesis due to variations in environmental conditions. The changes are more gradual in gymnosperms than in deciduous angiosperms. During spring when night frosts are less frequent the photosynthetic capacity of gymnosperms increases and diminishes gradually in

autumn. Photosynthetic rates are high in deciduous fruit trees in spring when trees re-foliate, are maintained throughout summer and decline to zero as leaves senesce and abscise (Kramer and Kozlowski, 1979). Whiley et al. (1999) observed that photosynthetic processes were normally functioning in autumn for mango hence the major post-harvest flushes. However during winter, lower photosynthetic rates are likely to be achieved in contrast to summer mainly due to low temperatures in mango (Pongsomboon et al., 1992) and apple (Pretorius and Wand, 2003). However in avocados and mangos, reduced photosynthesis in winter could also have been due to feedback inhibition since the canopy of both fruit species is relatively quiescent during winter (Whiley et al., 1999). The resultant reduction in sink strength promotes an increase in starch concentration in leaves (Whiley et al., 1999) and the latter would inhibit photosynthesis. Generally, daily photosynthesis of a tree increases after bud break, becomes positive around bloom and rises until full canopy development, reaching maximum near mid-summer. Photosynthesis remains fairly constant, and then decreases gradually as day length and temperature decrease until leaf senescence at the end of the season.

The early growth in deciduous perennials during springtime, unlike annuals, does not have to depend on current season's photosynthesis but on stored reserves (Flore and Lakso, 1989). The pattern might be influenced by cropping, differences in season and light exposure. Flore and Lakso (1989) indicated that sour cherry displayed different patterns in two different years and that the difference was attributed to crop load and different spring conditions. Photosynthesis was highest during periods of maximum vegetative growth or during the period of final fruit swell (Flore and Lakso, 1989). There was a strong positive relationship between photosynthesis and leaf emergence rate when growth was rapid in spring but not under cooler conditions which caused a moderate leaf emergence rate. Furthermore, photosynthetic rate and total daily rate of peach tree photosynthesis were closely related to changes in carbon requirements caused by changes in the stage of fruit growth and by fruit removal at harvest (Flore and Lakso, 1989). Fruits might regulate carbohydrates allocation (Pretorius and Wand, 2003).

Seasonal photosynthetic capacity increases with increasing leaf area during flushing, but shading reduces photosynthesis. Species with fully preformed shoots in the

winter bud achieve maximum leaf area early in the season, whereas heterophyllous and recurrently flushing species continue to add foliage over the season, either gradually or in flushes. In gymnosperms, photosynthetic capacity also increases as foliage is added, and it is maintained until autumn in comparison at a higher level than that of angiosperms (Kramer and Kozlowski, 1979). During summer, developing young plum leaves did not exhibit significantly different stomatal conductance rates as compared to apple and pears (Yoon and Richter, 1991) since they were still developing. In areas with warm winters, photosynthesis in evergreen gymnosperms may occur throughout the year (Kramer and Kozlowski, 1979).

In a study conducted with 'McIntosh' apple under American conditions, leaf development was rapid from about the middle of May until the middle of June; afterwards leaves were added slowly (Kramer and Kozlowski, 1979). Leaves began to fall in mid-October and about 90% had been shed by the middle of November but photosynthesis was still taking place. During May, respiration was higher than photosynthesis due to high metabolic activities when leaves and flowers developed. After full bloom photosynthesis was higher than respiration and the highest rate was recorded in June. However, higher total photosynthesis was recorded three months following June hence optimal leaf area. Photosynthesis gradually decreased during November, and this was attributed to a decline in light intensities, decrease in photoperiod and leaf area since many leaves were abscising. The few leaves left on the tree, however, were efficiently photosynthesizing during the short periods of high light intensity and therefore proportional correlation between light and photosynthesis was shown (Kramer and Kozlowski, 1979). Most fruit trees have considerable photosynthesis during mild winters. However, photosynthesis becomes negligible for weeks during cold winters and the assimilation rate can decline to 0 $\mu molCO_2$ m^{-2} s^{-1}. During a dry year, net gain photosynthesis constitutes one fourth of total annual photosynthesis (Kramer and Kozlowski, 1979).

2.2.5 Genetic or cultivar variations in photosynthesis

In plants, differences in photosynthetic capacity among genetic materials may be due to anatomical and/or biochemical differences as well as stomatal characteristics. For instance, diploid plants of currant had higher photosynthesis rates compared to tetraploids. The diploids contained about 45% more stomata per unit leaf area and slightly lower chlorophyll content than tetraploids, therefore, the differences in photosynthesis was attributed primarily to a greater resistance of leaf mesophyll CO_2 in tetraploids (Kramer and Kozlowski, 1979). Behboudian and Singh (2001) reported that stomatal conductance and photosynthesis of grapevine cultivars were more sensitive to water stress in 'Granache' of Mediterranean origin than in 'Syrah' of Mesic origin. Furthermore chlorophyll fluorescence data showed higher sensitivity of the 'Granache' cultivar to water deficits than did 'Syrah'. Few consistent differences in Pn rate were observed in several fruit species between rootstocks or cultivars within a species (Flore and Lakso, 1989). Differences in photosynthetic rates were found in potted cherry trees, but the differences were reportedly due to differences in vigour or growth pattern and not inherent differences in leaf photosynthetic potential (Flore and Lakso, 1989). In two blueberry genotypes, differences in temperature responses accounted for the difference in photosynthesis with highbush blueberry being relatively intolerant to higher temperatures and *V. darrowi* being tolerant to temperatures four to five degrees higher (Kramer and Kozlowski, 1979).

2.2.6 Leaf age

Shoot growth of mango and avocado is synchronized in major flushes forming a composite canopy with varying leaf ages and photosynthetic efficiency (Whiley and Schaffer, 1994). Changes in photosynthetic rates with leaf age are associated with anatomical and physiological alterations (Kramer and Kozlowski, 1979). Generally, photosynthesis increases with leaf age, peaks before full expansion, and then remains steady for a period of time before declining with leaf ageing. The rate of decline may be inhibited by presence of fruit and by decapitation or debudding (Flore and Lakso, 1989). Increases in leaf expansion are related to development of internal

leaf structure and stomata, synthesis of chlorophyll, decrease in diffusion resistance, increase in the rate of photosynthetic phosphorylation, increase in protein synthesis, increase in RuBP carboxylase activity, and an abrupt decrease in mitochondrial respiration (Kramer and Kozlowski, 1979). Developing young leaves of plum were more sensitive to environmental conditions than mature ones and therefore their photosynthetic rates were low (Yoon and Richter, 1991). Apple leaves took six weeks from leaf emergence to have morphologically mature stomata though they started functioning earlier than that (Flore and Lakso, 1989). Maximum photosynthesis was reached during the earliest stages of leaf development, coinciding with the period of greatest leaf expansion and chlorophyll synthesis (Flore and Lakso, 1989). In avocado, new leaves attained a positive photosynthesis approximately 17 days after emergence and maximum photosynthetic rates were observed approximately 50 days after emergence corresponding to the time when the leaf colour had developed to dark green (Liu et al., 1999). The maximum photosynthesis during leaf expansion could be explained by the decrease in leaf resistance, transpiration rate, CO_2 compensation point and mesophyll resistance, while carboxylation efficiency increased.

Apple leaves may maintain high photosynthetic rates for up to four months provided they are well exposed to light (Flore and Lakso, 1989), but in subtropical fruit trees such as mango high photosynthetic rates may be maintained for longer than a year (Y.L. Grossman, 2003: personal communication). The lack of consistent pattern of leaf aging, the strong effects of source-sink balance and cultural practices on late-season photosynthesis raises questions as to whether apple leaves in fact have genetically programmed aging. This can partly be reflected by adaptation of apple to a wide range of seasons (Flore and Lakso, 1989).

It was found that sour cherry leaf photosynthesis increased 4-5 times between 25-80% of full expansion and remained stable for four weeks and then decreased gradually (Flore and Lakso, 1989). Under normal conditions, citrus leaves may remain on the tree for up to three years before abscission occurs; therefore leaf age and development can have a considerable effect on net gas exchange of individual leaves (Kramer and Kozlowski, 1979). There was no increase in leaf length after the first months, but cuticle thickness and leaf age continued to increase over a period of

12 months from leaf emergence. Stomatal conductance increased with leaf age and then levelled off. Mesophyll conductance peaked at 30 days and then levelled off, even though the leaf continued to thicken. Photosynthesis peaked at the same time as mesophyll conductance then gradually declined. Water use efficiency followed the photosynthesis curve rather than that of stomatal conductance. The limitation to photosynthesis in older leaves did not seem to be determined by stomatal conductance (Flore and Lakso, 1989). Fernandez and Pritts (1994) indicated that as leaves aged in raspberry, the chloroplast begins to break down and consequently, electron transport ceased. Generally, the gradual decrease in photosynthesis after leaf expansion is completed is correlated with increase in diffusion resistance, decrease in synthetic activity of the phosphorylation system of the chloroplast, in protein, RNA and DNA, and in RuBP carboxylase activity. Furthermore, relatively high levels of photorespiration develop and a considerable decrease in mitochondrial respiration occurs (Kramer and Kozlowski, 1979).

2.2.7 Water deficits and photosynthesis

Photosynthesis and plant water relations are closely associated with environmental conditions and directly affect plant growth and productivity (Whiley and Schaffer, 1997). Water is essential in the plant for photosynthesis and also for turgidity in plants. Any soil moisture deficits or excess will result in the closure of stomata, wilting of leaves (reducing the transpiring surface exposed to sun) and protoplasm dehydration, and all these processes lower leaf assimilation. Inadequate water supply also leads to formation of small leaves (Chartzoulakis et al., 2002) that usually abscise early (Harris, 1992).

Drought is known to limit plant productivity in many regions of the world. Water deficit may change biological and physiological processes ranging from photosynthesis to protein synthesis and salt accumulation (Boyer, 1976; Townley-Smith and Hurd, 1979). Both soil and atmospheric water deficits are crucial in plant photosynthesis but the former is particularly important in fruit trees. This is due to the very low hydraulic conductivity of their root systems causing pronounced effects of transpiration on

water potentials in the top of the tree (Flore and Lakso, 1989). Low water potentials lead to loss of turgor in leaves and ultimately to the inhibition of photosynthesis due to stomatal closure (Flore and Lakso, 1989). Fruit trees with deep root systems might counteract the development of water stress compared to plants with root systems exploring the topsoil only (Flore and Lakso, 1989). A slow commencement of stress may allow such adaptations as (1) active osmotic adjustment for turgor maintenance in leaves and/or roots, (2) modifications of leaf area and therefore light interception by decreased leaf area production, abscission of leaves, leaf folding, rolling or reorientation or other changes in growth, or (3) root growth or increase in hydraulic conductivity for maintenance of water status (Flore and Lakso, 1989). The extent to which photosynthetic capacity of a plant is maintained during periods of water deficit and ability to recover rapidly may play a role in plant adaptation to the drought environment. In order to maintain photosynthesis, plants have physiological processes to maintain the tissue for stomata opening to some extent, even under water deficit stress (Chartzoulakis et al., 2002).

The first inhibitory effects of water deficits on photosynthesis were observed by a researcher known as Kreusler in 1885 (Boyer, 1976). It was indicated that photosynthesis was linearly related to stem water potential and that stomatal adjustments might be involved in photosynthetic responses to water deficits. In contrast, Flore and Lakso (1989) reported photosynthesis to be rather dependent on turgor than total water potential. The link between stomatal adjustment and photosynthesis may explain why photosynthesis and respiration appear to function interdependently (Boyer, 1976).

Generally, it appears that soil water deficits may also induce non-stomatal effects on photosynthesis reduction. Effects of soil moisture stress on potted apple trees were shown to include reductions in both stomatal and non-stomatal components of photosynthesis. The non-stomatal components include the C_i (internal carbon dioxide) and mesophyll conductance that may be affected simultaneously with gaseous exchange (Flore and Lakso, 1989). In water stressed greenhouse tomato plants, higher reductions of stomatal conductance than of mesophyll conductance was observed (Xu et al., 1994) emphasizing the stomatal control of plant water use efficiency. Ruiz-Sanchez et al. (2000) found, during preconditioning stress, that

young apricot trees that were heavily stressed had significantly lower photosynthetic rate, compared to the fully irrigated treatment, suggesting a limitation in carbon assimilation during water stress. The reduced photosynthesis was attributed to lower stomatal conductance since the two were positively correlated (r= 0.87). This is contrast to other findings where non-stomatal limitations such as mesophyll play a role in photosynthesis limitation (Chartzoulakis et al., 2002).

The mechanism of stomatal response to soil water status might be hormonal or nutritional and it might be a direct or indirect effect. Soil water deficits have been reported to influence cytokinin levels in the xylem, providing a possible signal from the roots to the shoots (Flore and Lakso, 1989). Abscisic acid (ABA) is known to accumulate with increasing water deficit and may play a role, although in the split root study leaf ABA did not change (Flore and Lakso, 1989). Interactions of ABA with cytokinins and auxins on stomatal conductance may suggest that a balance between these hormones may regulate stomata aperture. Although it is not clear how soil water deficits affect photosynthesis, there are physical and chemical transductions of stress to the top of the plant that are important (Flore and Lakso, 1989)

Trees previously subjected to water deficits may maintain photosynthesis more than irrigated trees during times of drought. Photosynthetic rates of apricot trees daily irrigated to 25% of field capacity were lowered by 55% compared to control (100% FC) control while 75% reduction in Pn was observed in the rest of water deficit stressed treatments (Ruiz-Sanchez et al., 2000). Such trees previously exposed to drought showed increased water use efficiency. However, five days after re-watering all water deficits stressed treatments had the same photosynthetic rate as the control. Recovery of photosynthesis, especially in severely stressed trees, is attributed to high stomatal conductance resulting from remaining active younger leaves since most of the old leaves were defoliated (Ruiz-Sanchez et al., 2000).

Leaf water status of fruit crops is strongly dependent on the evaporative demand of the atmosphere. This implies that leaf water status of fruit crops may vary much more diurnally than in many annuals and leaf water deficits may occur under high evaporative demands even though soil moisture is adequate. Normally on a light saturated day there is a negative correlation between VPD and photosynthesis.

Consequently, stomatal response to humidity is particularly important in fruit crops (Flore and Lakso, 1989). Flore and Lakso (1989) indicated that in most species stomata respond directly to air humidity independent of the mesophyll and there may be feedback responses of stomata in which transpiration is stabilized at high vapour pressure deficits as well as feed-forward responses in which transpiration declines at high vapour pressure deficits. Furthermore, the cuticle is thought to be involved in stomatal responses and the non-stomatal component of photosynthesis also responds to humidity in a manner similar to that of stomata. Effects of relative humidity on photosynthesis may be attributed to cell volume or hormonal changes (Whiley and Schaffer, 1994).

Generally, significant effects of water deficits on photosynthetic efficiency of a plant are mainly visible on severely stressed plants. Such effects are influenced firstly by environmental factors, such as light, wind speed, temperature, humidity and also vapour pressure deficit, and secondly by plant factors, such as cultivar variation, tree canopy and architecture as well as morphology and biochemistry of the leaves.

3 Responses of Vegetative Growth to Different Irrigation Regimes

3.1 Introduction

Responses of vegetative growth of plants to irrigation have not received much attention in South African irrigation experiments except for those crops where the vegetative parts were harvested (van Zyl and Bredell, 1995). However, the response of vegetative growth to water regimes have been well documented in many temperate fruit trees such as olive (Moriana and Fereres, 2002), pear (Mitchell et al., 1989), peach (Chalmers et al., 1984; Besset et al., 2001) and apricot (Ruiz-Sanchez et al., 2000), though little has been done for subtropical fruit such as mango (de Villiers, 2001).

Responses to water deficit of perennials (fruit trees) are much slower than in annuals due to the perennial's ability to explore deeper soil profiles for water. The response of subtropical fruit trees to water deficit may be different to that of deciduous fruit trees due to their phenological cycles. Subtropical trees, mango included, are evergreen and their leaves can remain on the tree for more than two years. In contrast, deciduous fruit trees only have leaves for about 6-9 months in a year. Mango tree growth is characterized by episodic flushes during which leaves in older flushes are replaced (Schaffer et al., 1994). On the other hand deciduous trees only flush once a year (mostly in spring) from preformed buds. Furthermore, flowering comes before or at the same time with shoot growth in deciduous trees, and developing leaves grow faster because they are the source of carbon for the fruitlets. Nevertheless, deciduous fruit tress store large amounts of carbohydrates in order to maintain the developing flowers and shoots in spring. In contrast, mango trees flower in early spring, and leaves from older flushes leaves provide photosynthates for developing fruitlets as well as vegetative growth (Kramer and Kozlowski, 1979).

It is important to understand the phenological cycle of mangoes and study the impact of water deficits at the different stages of the cycle and their relevant impact on

vegetative growth, flowering and fruit developmental stages (Cull, 1991) in order to identify critical periods of the cycle. Less critical growth stages may be able to cope with water deficits without affecting productivity and hence irrigation scheduling (Besset et al., 2001), while at other stages irrigation must be applied to maintain plant growth. Reduced irrigation may suppress vegetative growth and enhance flowering (Cull, 1991). In tropical and subtropical regions with cool winter temperatures, moderate water deficit stress prior to flowering may induce flowering in mango trees (Cull, 1991; Whiley and Schaffer, 1997). According to Schaffer et al. (1994), drought prevented vegetative flushing, thereby increasing the proportion of mature to immature leaves in the canopy. Mature leaves produce floral stimuli, whereas immature leaves are rich sources of floral inhibitors. However, water use at flowering and early fruit development is high, and late water deficits could be expected to be detrimental to productivity (Cull, 1991).

Environmental conditions outside the range for optimum growth may impose stress that results in physiological changes that reduce growth or cause permanent damage to mango trees. Water deficits may limit the overall growth of the tree leading to adverse effects on yield. However, proper irrigation scheduling (application of the right amount of water at the right time) through implementation of regulated deficit irrigation (RDI) strategies allowed sufficient reduction of excessive vegetative growth, particularly shoot growth, without affecting fruit growth of peach (Chalmers et al. 1981); pear (Mitchell et al., 1989); and apricot (Torrecillas et al., 2000). Reduction of vegetative growth would simultaneously result in saving of pruning costs and water, therefore reducing the farming operational costs. In addition, it has been widely reported that the RDI technique may enhance fruit quality and colour (Kilili et al, 2000). Although water deficits could be used to control excessive vegetative growth (Chalmers et al., 1981), excessive or lengthened drought conditions may negatively affect yield hence reduction in vegetative growth. Excessive water deficits were reported to reduce bud development and shoot growth in asparagus (Drost and Wilcox-Lee, 1997) because water deficit affected cell growth (division and expansion) (Borchert, 1994), a very sensitive indicator of water deficit stress (van Zyl and Bredell, 1995). Chartzoulakis et al. (1993) reported a significant reduction in kiwi shoot growth under mild water deficits. In contrast, no adverse effects of deficit irrigation regimes on shoot growth occurred in 'Fino' lemon trees (Domingo et al.,

1996). Different tree crops that were used could explain the differences. Besset et al. (2001) found that vegetative shoots and flower buds numbers of 'Big-Top' peach trees were not significantly reduced by deficit irrigation when compared to standard irrigation. Water deficit stress reduced leaf area in apples (Sritharan and Lenz, 1988) and anatomical characteristics of avocado leaves (Chartzoulakis et al., 2002). Chlorenchyma cells of leaves in stressed avocado trees were denser than those of well-irrigated trees, therefore intercellular air spaces were decreased leading to reduced gaseous exchange (Chartzoulakis et al., 2002).

The objectives of this research were to evaluate effects of reduced irrigation regimes on a) shoot development and growth and b) vegetative growth during the flushes after harvest (vegetative shoots) and flowering (vegetative shoots, mixed and floral canes) of mango trees. This knowledge would enable the grower to optimize irrigation scheduling and to manage vigorous vegetative growth.

3.2 Materials and Methods

3.2.1 Location of the experimental site and description

The study was conducted on a 1 ha commercial, 6-7 year-old mango orchard located at the Westfalia Mango Estate, Moriah (Hans Merensky Holdings) in Hoedspruit, South Africa (latitude: 24° S, longitude: 34° E), during the 2002/2003 season. The mango trees (cv Kent grown on 'Sabre' rootstock) were planted at a density of 1.5 x 6 m. Apart from irrigation, all other cultural farm practices, such as pruning, fertilization, and pest management, were conducted according to commercial farm practices.

3.2.2 Irrigation treatments

Five irrigation treatments (10-12 trees x 4 replicates, randomised block design over 10 rows) were applied:

Co: Control (95±3% of field capacity, FC)

DI-1:   Continuous deficit irrigation (when 30 mm was extracted the profile was filled up to 89 mm, ±20 mm below FC, ±79% of FC)

DI-2:   Continuous deficit irrigation (when 40 mm was extracted the profile was filled up to 83 mm, ±30 mm below FC, ±69% of FC)

RDI: Regulated deficit irrigation (like Co except that irrigation water was withheld for 2 weeks in December 2002/January 2003 during the final stage of fruit growth)

Co-F: Farm Control, full irrigation according to daily tensiometer readings; trees were irrigated once per day when soil moisture was lower than -10 KPa

All five treatments were subjected to a period of irrigation water reductions before flowering. From June until the middle of July 2002, the treatments Co, DI-1, DI-2, and RDI, were irrigated to $73 \pm 6\%$ of FC followed by 2 weeks of full irrigation ($98 \pm 6\%$ of FC). The farm control (Co-F) was irrigated when soil moisture reached values lower than -20 KPa from June 2002 until the third week in July 2002.

Until August 2002, the four irrigation treatments (Co, DI-1, DI-2 and RDI) were irrigated with a drip system (4 L hr^{-1} emitters at a distance of 30 cm on both sides of each tree). The farm control (Co-F) was irrigated also with a single line drip system but with one 8 L hr^{-1} emitter situated at the tree trunk. In August 2002, the drip irrigation system was replaced with a microjet system (1 emitter between two trees within the row at a distance of 0.75 m from each tree trunk) across the entire orchard providing irrigation water at a flow rate of 6.0 ± 2.4 mm h^{-1}. Irrigation scheduling was conducted according to daily soil moisture determinations at depth intervals of 10 cm (0-90 cm depth) using a hydroprobe (CPN 503, Campbell Pacific Nuclear Corp., CA, USA) in the four irrigation treatments (Co, DI-1, DI-2, and RDI), while the farm (Co-F) used tensiometers at depths of 30 and 60 cm. Neutron probe access tubes were inserted to a depth of 1 m at about 20 cm from the tree in each replicate of the

various irrigation treatments. Field capacity (FC, 103 mm up to a depth of 90 cm) was determined in the field as described by Vanassche and Laker (1989).

3.2.3 Analysis of shoot growth and development

After harvest and during the post-harvest flush in May/June 2002, 8 terminals per tree (4 terminals with one shoot and 4 terminals with 2-4 shoots) were selected and tagged on 8 'Kent' mango trees of each treatment. Shoot growth (stem length and diameter) was monitored twice per week until shoot extension had ceased (33 days after bud break), and number of leaves per shoot was then counted. Internode volumes were calculated by dividing shoot volumes by half the number of leaves, since mango trees develop two leaves per node. Twenty-five shoot samples were randomly collected from a separate set of trees on the same days when measurements were taken. Stem length and stem diameters were measured using a measuring tape and digital calliper (Mitutoyo Digimatic, Japan), respectively. Stems without the leaves were dried in an oven at 55⁰C until dry weight had reached equilibrium. Dry weight of the shoots was then determined using a balance (PC 4400, Mettler AG, Zurich, Switzerland). Measurements of stem diameter and length were used to calculate shoot volume according to the following equation as described by Westwood (1988), assuming that stems were cylindrical in shape:

$$\text{Volume (cm}^3) = r^2 \, \pi \, h$$

whereby r = radius, d = diameter, h = length, and r = d/2. Dry weight of the tagged shoots was estimated via regression analysis by using the values of stem volume and dry weight of the sampled shoots.

Shoot relative growth rates were calculated using the following formula as described by Clipson (1994a):

$$\text{RGR} = (\text{Ln } W_2 - \text{Ln } W_1)/ (t_2 - t_1)$$

whereby W_2 and W_2 are the biomass weights at times, t_1 and t_2.

In June 2002 and May 2003 after the post-harvest flushes when extension growth of shoots had ceased, numbers of terminals that had flushed and of new shoots of each data tree (10-12 trees x 4 replicates of each irrigation treatment) were counted. In August 2002, the number of floral canes, mixed canes (floral canes with leaves), and vegetative shoots were counted (2 x 5-6 trees per treatment).

3.2.4 Photosynthetically active radiation measurements

Photosynthetically active radiation (PAR) was measured below the canopy at midday in monthly intervals from October 2002 until March 2003 using a ceptometer (Model PAR-80, Decagon Devices, Pullman, WA, USA). Readings were taken just above the soil surface covering a rectangular area with a width of 1.5 m (from one micro-sprayer to another within the row) and a length of 1.8 m perpendicular to the row on both sides of the tree row. A control treatment was introduced by measuring in an open space where there was full sun. Each recorded value was an average of 20 readings. The reason for measuring PAR at full sun was to calculate the % PAR intercepted by the tree canopy using the following equations:

$$\text{Percentage PAR transmitted} = \frac{\text{amount of below canopy PAR}}{\text{full sun PAR}} \times 100\% \qquad (1)$$

$$\text{Percentage PAR intercepted} = 100\% - \text{Percentage PAR transmitted} \qquad (2)$$

3.2.5 Statistical analysis of data

Data were analysed using analysis of variance (ANOVA) with one or two factors (irrigation treatment, year, shoot/cane type). Means were compared using the Tukey and Tukey-Kramer tests for equal and unequal sample sizes, respectively, between treatments at a significance level of 5%.

3.3 Results and Discussion

3.3.1 Shoot growth and development during the post-harvest flush

The genetic composition of a mango cultivar is the primary determinant of its yield potential. However, actual yield, tree growth and development are mediated by several endogenous factors including previous fruit load, post-harvest vegetative growth, pre-flowering maturity of terminal shoots, production and mobilization of carbohydrates, plant growth regulators and carbon to nitrogen ratios (Schaffer et al., 1994; Whiley and Schaffer, 1997). More of the variation in shoot dry mass was accounted for by shoot volume (r^2=0.95) than by shoot extension (r^2=0.86) in young shoots (Fig. 3.1). In older shoots (1-1.5 years old), differences between using shoot extension (r^2=0.51) and shoot volume (r^2=0.92) for dry mass estimations became even more pronounced (Fig. 3.2). The poor regression ($r^2 = 0.50$) between the shoot dry mass and shoot extension in older shoots indicated that the shoots were no longer increasing in length but increasing in girth. Growth of older shoots is characterised primarily by secondary growth (cambium), while in young shoots mainly primary growth (shoot extension at apical meristems) occurs (Kramer and Kozlowski, 1979).
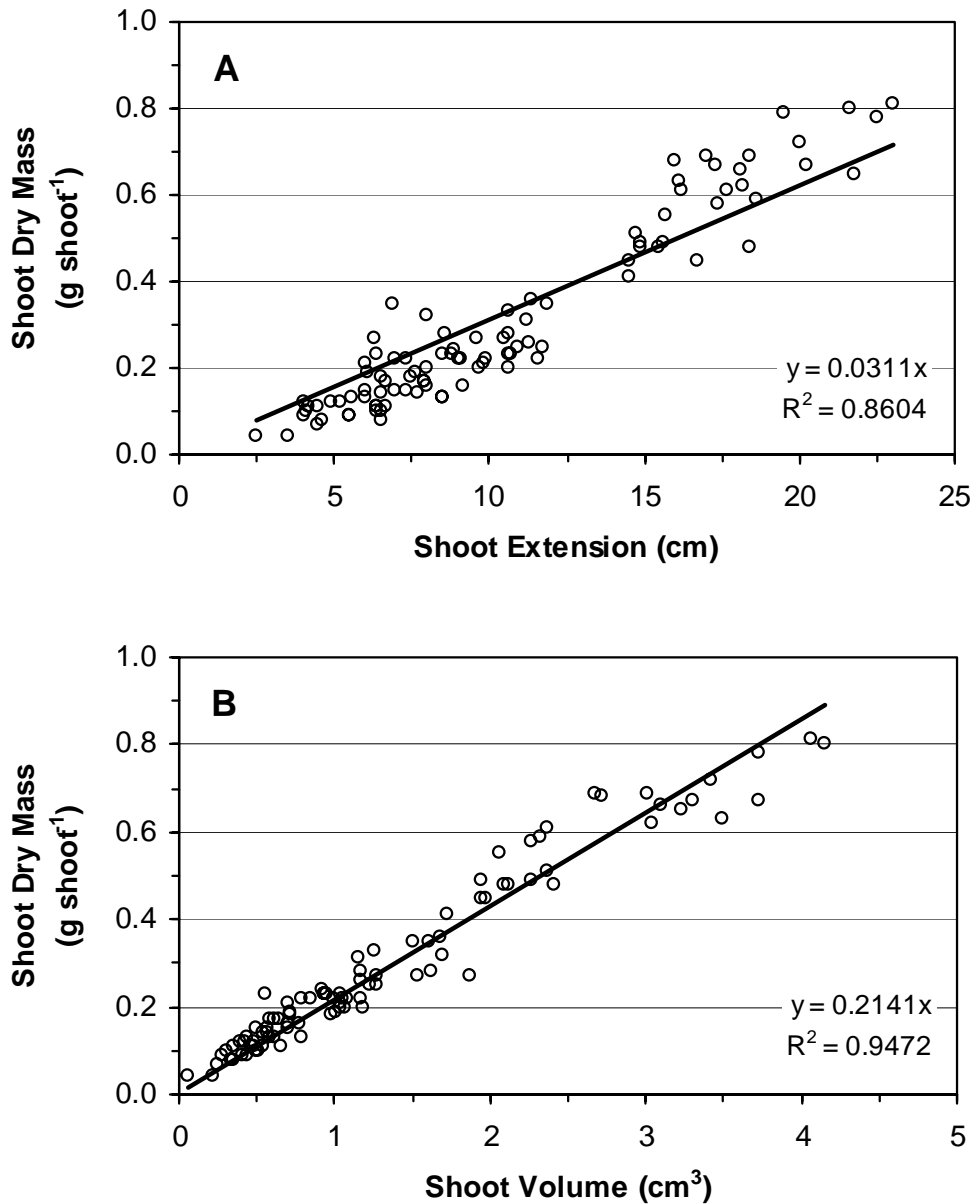
Fig. 3.1 Relationship between shoot dry mass estimations from shoot extension (A) and shoot volume (B) in 2-5 week old shoots of well-irrigated, 6-7 year old 'Kent' mango trees during the post-harvest flush in May/June (n=94-96).
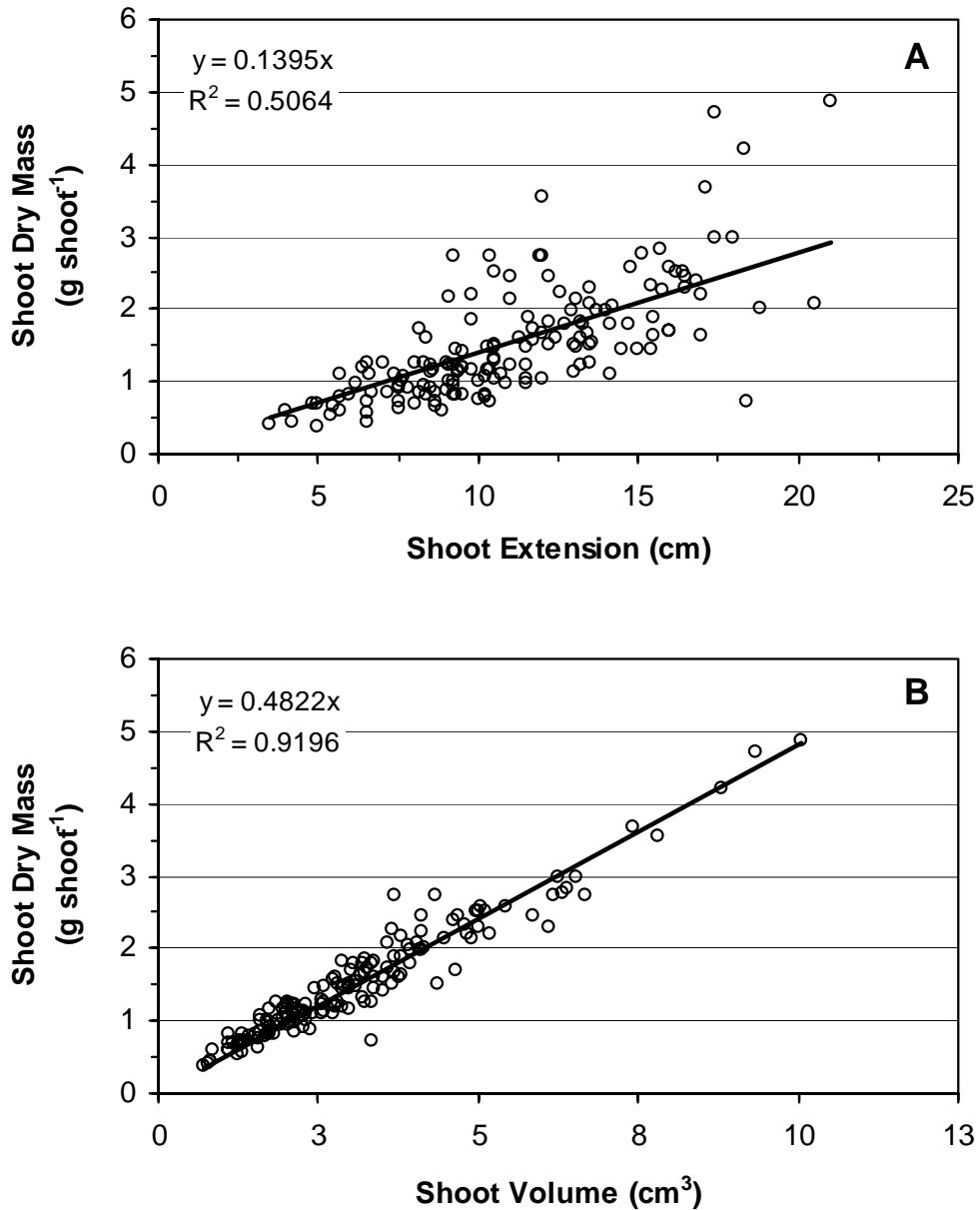
Fig. 3.2   Relationship between shoot dry mass estimations from shoot extension (A) and shoot volume (B) in 1-1.5 year old shoots of well-irrigated, 6-7 year old 'Kent' mango trees during the post-harvest flush in May/June 2002 (n=157).

Stem growth was affected by irrigation treatments as shown by stem volume and estimated stem dry mass over the measurement period (15-33 DABB) (Fig. 3.3). The farm control (Co-F) displayed significantly higher accumulations of stem volume and dry mass in comparison to the other treatments throughout the measurement period. Differences between the other four treatments (Co, DI-1, DI-2, and RDI) were minor and not significant. Shoots of the Co treatment reached a mean shoot volume of 0.55 $\pm$ 0.2 cm^3 and mean dry mass of 0.12 $\pm$ 0.05 g in comparison to Co-F (shoot volume: 1.23 $\pm$ 0.5 cm^3; shoot dry mass: 0.26 $\pm$ 0.11 g). These results implied that Co trees had 56% less shoot volume and dry mass, respectively, when compared to Co-F trees indicating that Co-F trees used a large part of their high irrigation water applications (E.W. Pavel, 2004: personal communication) in vegetative growth.
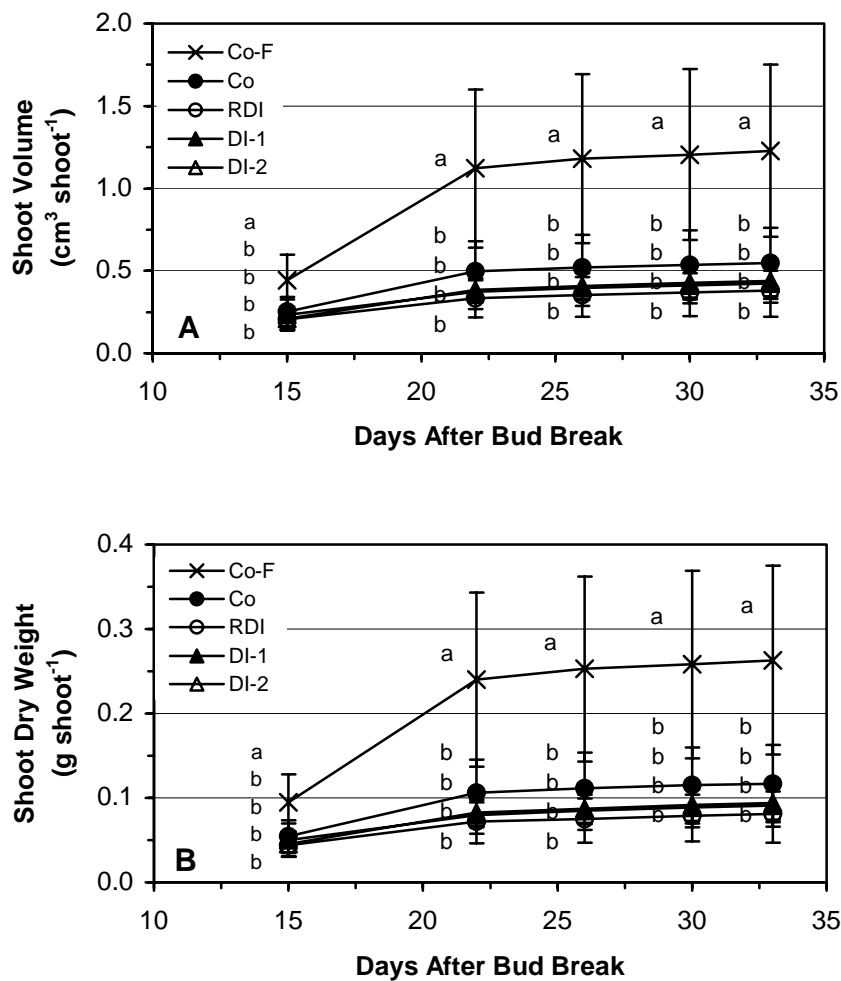
Fig. 3.3   Accumulation of calculated shoot volume (A) and estimated shoot dry mass (B) in 6-7 year old 'Kent' mango trees exposed to different irrigation treatments (Co: 95±3% of field capacity, FC; DI-1: deficit irrigation, ±79% of FC; DI-2: ±69% of FC; RDI: regulated deficit irrigation, like Co except for water withholding for two weeks at the end of Dec 2002/beginning of Jan 2003; Co-F: farm control, ±-10 KPa) from day 15-33 after bud break (DABB) in May/June 2002 (post-harvest flush) (mean ± SD of 6-8 replicate shoot samples; different letters in descending order according to values indicate significant differences between irrigation treatments at each sampling date at P=0.05).

Bud break, shoot growth and flowering of trees involves cell expansion, known to be sensitive to water deficit (Borchert, 1994; van Zyl and Bredell, 1995). As a result any water reduction may reduce vegetative growth, and that was evident in this study (Fig. 3.3). Shoot growth increased rapidly until day 22 after bud break (DABB) and then started to level off. Leopold and Kriedemann (1975) reported that shoot growth followed a sigmoid growth pattern. However, the initial growth stage was not displayed in our results because of a late start in taking measurements.

Relative growth rates of developing shoots declined rapidly between 22 and 26 DABB exhibiting an exponential curve (Fig. 3.4). Thereafter, relative growth rates of mango shoots decreased only slightly and followed an asymptotic course indicating that the shoots seemed to cease their elongation.
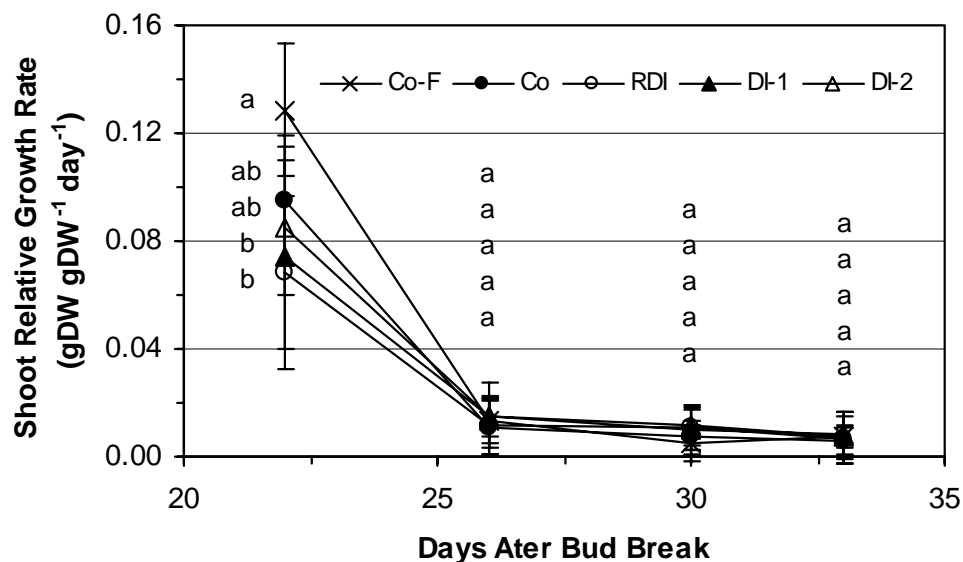

Fig. 3.4   Relative growth rates of shoot dry weight in 6-7 year old 'Kent' mango trees exposed to different irrigation treatments from day 22-35 DABB in May/June 2002 (post-harvest flush) (mean SD of 6-8 replicate shoot samples; different letters in descending order according to values indicate significant differences between irrigation treatments at each sampling date at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Shoot relative growth rates were significantly different between irrigation treatments on day 22 after bud break thereafter differences between treatments were minor and not significant since growth started to cease (Fig 3.4). Shoot relative growth rates of

the three irrigation treatments Co-F, Co, and DI-2 were not significantly different from each other on day 22 after bud break, although shoot relative growth rates in Co-F trees were the highest across all treatments indicating that lower irrigation water applications in the four treatments (Co, RDI, DI-1 and DI-2) reduced vegetative growth in comparison to Co-F. RDI and DI-1 exhibited significantly lower shoot relative growth rates compared to Co-F but were not significantly different from the other two former treatments (Co and DI-2). Our data indicated that shoot growth could be manipulated by the amount of irrigation water applied.

Although trees of the Co-F treatment exhibited more vegetative growth (shoots) than Co and the other irrigation treatments (Fig. 3.3), mean leaf number per shoot was not significantly different to that of Co but higher than the reduced irrigation treatments (RDI, DI-1, DI-2) (Fig. 3.5A). The larger amounts of water supplied to Co-F resulted, however, in a higher production of wood as shown by internode volume (Fig. 3.5B). Internode volume indicated that there was vigorous vegetative growth with 97% more shoot growth in Co-F compared to Co, while shoot growth of DI-1 was reduced by 17%, DI-2 by 14%, and RDI by 26% when compared to Co (Fig. 3.5 B).

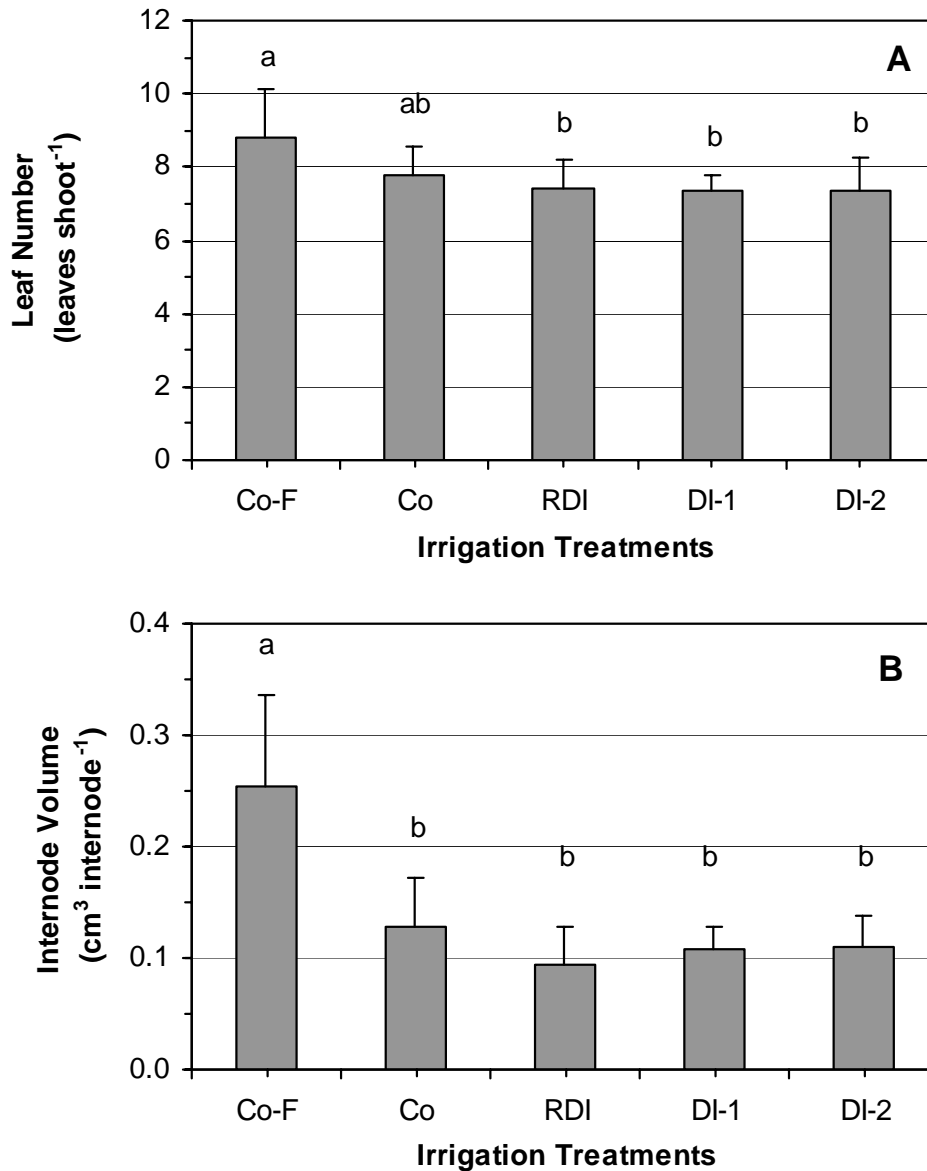**Fig. 3.5**   Effects of different irrigation treatments on number of leaves per shoot (A) and internode volume (B) at 33 DABB during the post-harvest flush (May/June 2002) in 6-7 year old 'Kent' mango trees (mean SD of 6-8 replicate shoot samples; different letters depict significant differences between irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

3.3.2 Effect of irrigation regime on shoot production during the post-harvest flush

Numbers of flushing terminals (Fig. 3.6A) and shoots per tree were not significantly influenced by irrigation treatment during the post-harvest flush in 2002, but the contrary was observed in 2003. In the treatments Co, RDI, DI-1, and DI-2 numbers of flushing terminals and shoots per tree increased in 2002 and declined in 2003 with decreasing amounts of irrigation water applied indicating that low irrigation water applications induced alternate bearing. In the treatments DI-1 and DI-2 with the lowest irrigation water applications among all treatments alternate bearing became most pronounced. In contrast, there was little effect of irrigation water supply on number of flushing terminals and shoots per tree in the Co-F treatment during both years indicating that water was not limiting. Studies in peach showed that RDI actually stabilised alternate bearing (Mitchell et al., 1989). However, alternate bearing was observed in the RDI treatment in mango (Fig. 3.6) over both years and might indicate that the irrigation scheduling of this treatment was not fully optimized.
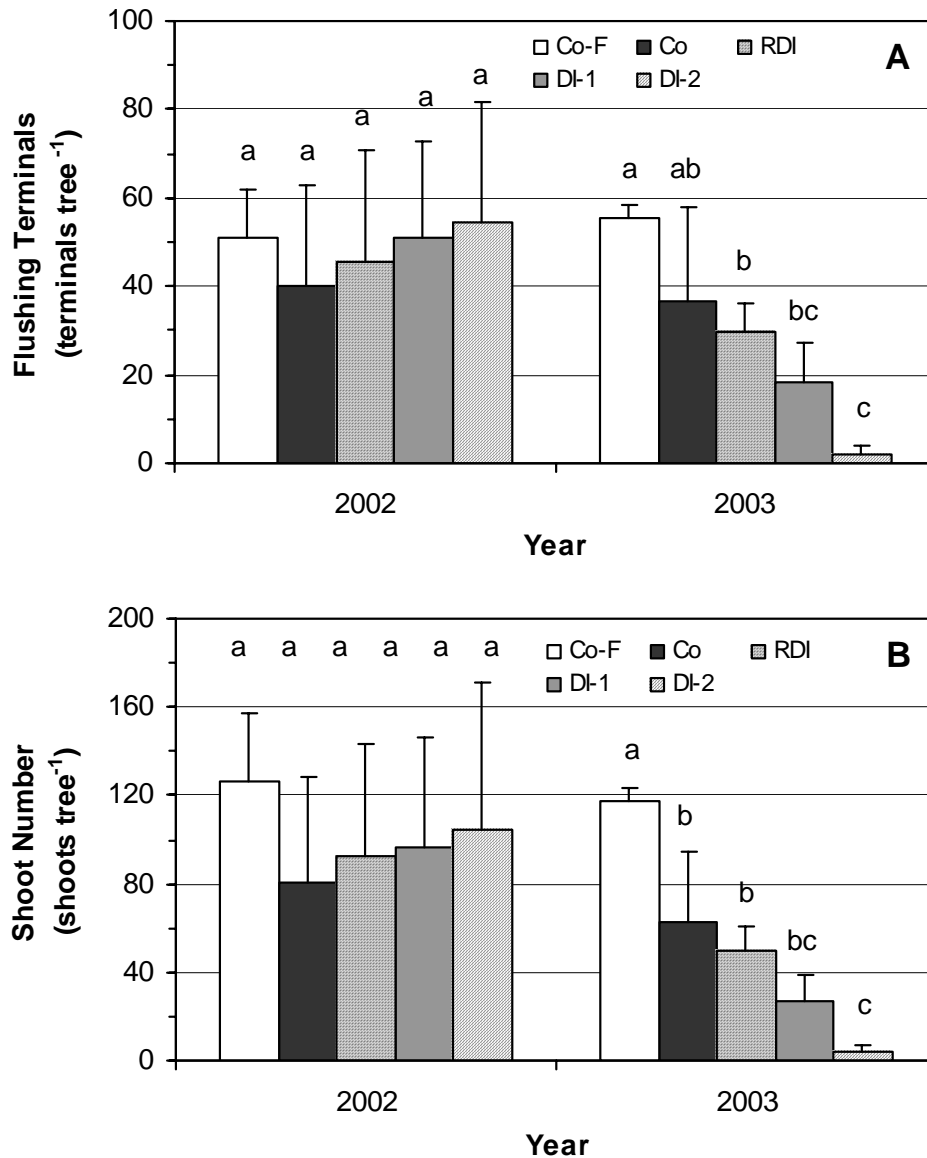
Fig. 3.6 Mean numbers of flushing terminals per tree (A) and shoots per tree (B) during the post-harvest flushes (May/June 2002 and 2003) in 6-7 year old 'Kent' mango trees exposed to different irrigation treatments (mean ± SD of 4 replicate tree samples; different letters depict significant differences between irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Interactions between irrigation regimes and years were significant regarding number of flushing terminals but were not significant in terms of shoot number per tree (Table 3.1). Significantly lower numbers of flushing terminals and total shoots per tree in 2003 compared to 2002 showed alternate bearing characteristic for mangoes (Cull, 1991), whereby 2002 represented an on-year and 2003 an off-year (Table 3.1).

Across both years, differences in number of flushing terminals between the various irrigation regimes were not significant.

Table 3.1 Effect of irrigation regime and year on mean number of flushing terminals and shoots per tree in 6-7 year old 'Kent' mango trees during the post-harvest flushes in May/June of 2002 and 2003 (irrigation treatment: n=8; year: n=20; different letters depict significant differences between irrigation treatments and year at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Factor	Number of Flushing Terminals (terminals tree^{-1})		Shoot Number (shoots tree^{-1})	
Irrigation Treatments				
Co-F	53 ± 8	a	122 ± 21	a
Co	38 ± 20	a	72 ± 39	ab
RDI	37 ± 19	a	71 ± 41	ab
DI-1	35 ± 24	a	62 ± 50	b
DI-2	28 ± 33	a	54 ± 69	b
Years				
2002	48 ± 21	a	100 ± 48	a
2003	28 ± 21	b	52 ± 42	b

Shoot numbers per tree in the treatments Co-F, Co and RDI were not significantly affected by irrigation regime across both years (Table 3.1). However, shoot number per tree was significantly reduced in the treatments DI-1 and DI-2 in contrast to the farm control (Co-F) over both years but was not significantly different from the irrigation treatments Co and RDI. Such severe reductions in shoot growth as observed in the irrigation treatment DI-2 might threaten future growth and fruit production as suggested by Parker and Marini (1994) in deficit irrigated fruit trees, because unavailability of sufficient vegetative shoots might limit flowering and bearing capacity of trees. Similarly, Sritharan and Lenz (1988) found in apples that

the number of reproductive organs was reduced due to little vegetative growth that resulted from deficit irrigation practices. On the other hand, those deficit-irrigated apple trees adapted to low soil moisture regimes at field capacities of 25% in contrast to well-irrigated trees by reducing their transpiration surface through an 80% reduction in shoots and leaves indicating that they increased their water use efficiency (Sritharan and Lenz, 1988).

The larger number of shoots per tree than flushing terminals (Fig. 3.6, Table 3.1) indicated the production of multiple shoots per terminal that was especially pronounced in Co-F in both years (Fig. 3.7). The significantly highest number of shoots was recorded in flushes with 4-10 shoots per terminal (40% across both years) in Co-F in contrast to the other treatments, while the relative number of one shoot per terminal tended to be lower in Co-F (Table 3.2). Part of the high volumes of irrigation water applied to Co-F (E.W. Pavel, 2004: personal communication) was apparently used in vegetative (shoot) growth indicating vigorous vegetative growth. Development of multiple shoots per terminal (>4 shoots) is not very desirable, since those shoots might not be strong enough to bear and support fruit because of a relatively small storage volume of carbohydrates. Shoots with small stem volumes store and supply less carbohydrate to their sinks than shoots with larger stem volumes (Lauri et al., 1996). In contrast to Co-F, the irrigation treatments Co, RDI, DI-1, and DI-2 produced a higher percentage of their shoots in flushes of 1 and 2-3 shoots per terminal in both years except for DI-2 in 2003 (Fig. 3.7, Table 3.2). Across both years shoot production in DI-2 was the lowest among all treatments indicating that irrigation water reductions were too severe and might lead to declining tree productivity.

Fig. 3.7 Relative shoot number per tree according to production of single and multiple shoots (2-3 and 4-10) per terminal during the post-harvest flushes in May/June of 2002 (A) and 2003 (B) in 6-7 year old 'Kent' mango trees exposed to different irrigation treatments (mean ± SD of 4 replicate tree samples; different letters depict significant differences between irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Interactions between irrigation treatments and year were significant in the group of 1 and 2-3 shoots per terminal but not when 4 or more shoots were produced per terminal (Table 3.2).

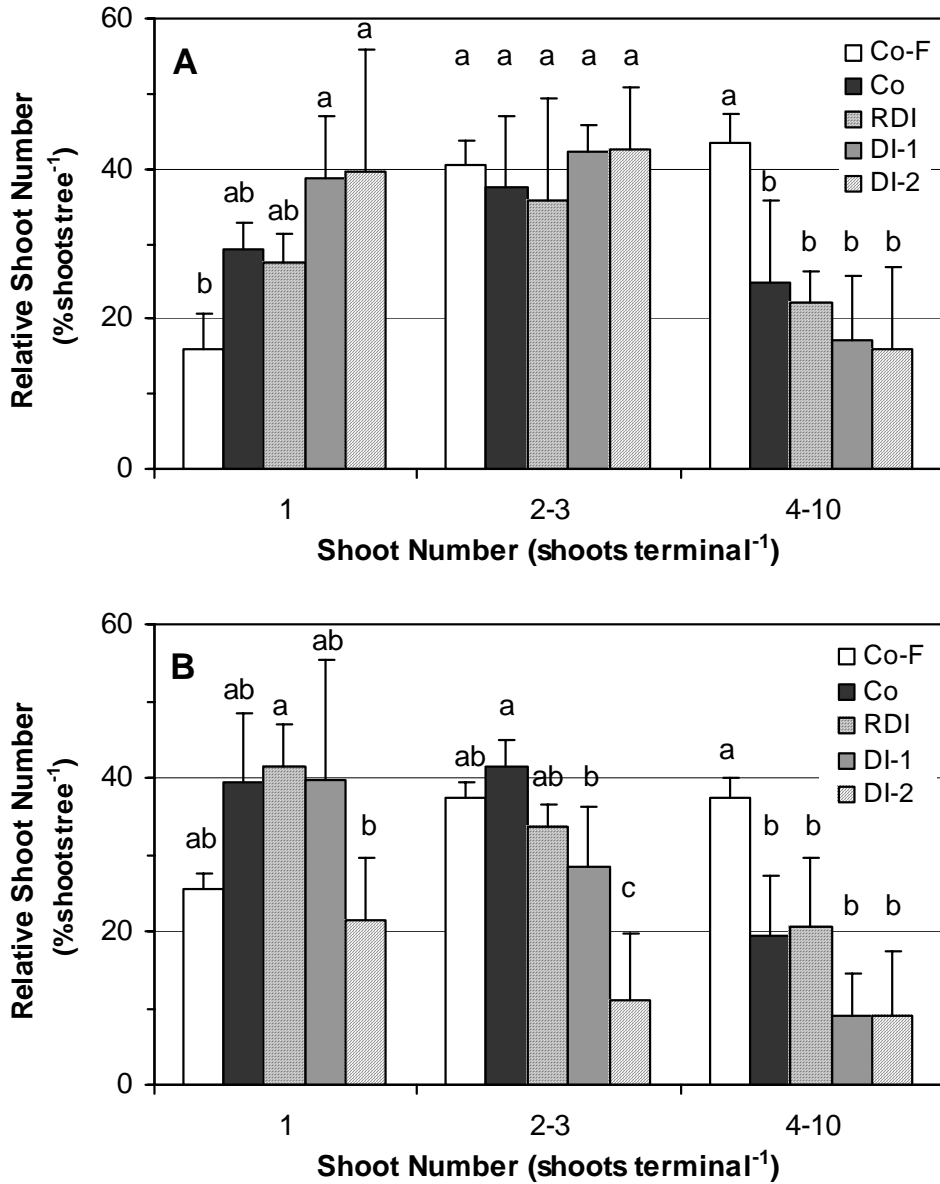**Table 3.2** Effect of irrigation regime and year on the relative shoot number per tree according to production of single and multiple shoots (2-3 and 4-10) per terminal in 6-7 year old 'Kent' mango trees during the post-harvest flushes in May/June of 2002 and 2003 (irrigation treatment: n=8; year: n=20; different letters depict significant differences between irrigation treatments and year at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Factor	Relative Shoot Number (%shoots^{-1} tree^{-1})					
	Shoot Number (shoots terminal^{-1})					
	1		**2-3**		**4-10**	
Irrigation Treatments						
Co-F	21 ± 6	b	39 ± 3	a	40 ± 5	a
Co	34 ± 8	a	39 ± 7	a	22 ± 9	b
RDI	35 ± 9	a	35 ± 9	a	21 ± 6	bc
DI-1	39 ± 12	a	35 ± 9	a	13 ± 8	bc
DI-2	31 ± 15	ab	27 ± 19	b	13 ± 10	c
Years						
2002	30 ± 40	a	40 ± 8	a	25 ± 13	a
2003	34 ± 30	a	30 ± 12	b	19 ± 12	b

Production of vigorous and a large number of shoots (Table 3.1, Fig. 3.5) as observed in trees of the farm control increased the density of the canopy, since significantly more light was intercepted in Co-F (86%) compared to the other irrigation treatments (Fig. 3.8). Trees with highly dense canopies resulted in wastage of water and reduced maximal profitability (Clipson, 1994b). Whiley and Schaffer (1997) indicated that the quantity of light intercepted by a tree canopy is the primary environmental factor affecting photosynthesis. Dense canopies might also lead self-shading of leaves leading to reductions in canopy photosynthesis and therefore negatively affecting fruit set and quality (Kramer and Kozlowsky, 1979). In contrast, shaded navel orange fruit developed better external colour than sun-exposed fruit (Syvertsen et al., 2003). Differences in light interception between Co (65%) and the

other three treatments RDI, DI-1, and DI-2 (54-55%) were significant. Concurrent with low numbers of shoots per tree, canopies in the treatments RDI, DI-1 and DI-2 were the least dense and, therefore, the lowest amount of light was intercepted in those trees in contrast to both controls. Olive trees exposed to increasing water deficits might intercept less radiation compared to well-irrigated trees because of a smaller and less dense canopy (Moriana and Fereres, 2002). Moriana and Fereres (2002) suggested that deficit-irrigated trees might experience a decline in the potential fruit number in the following season.
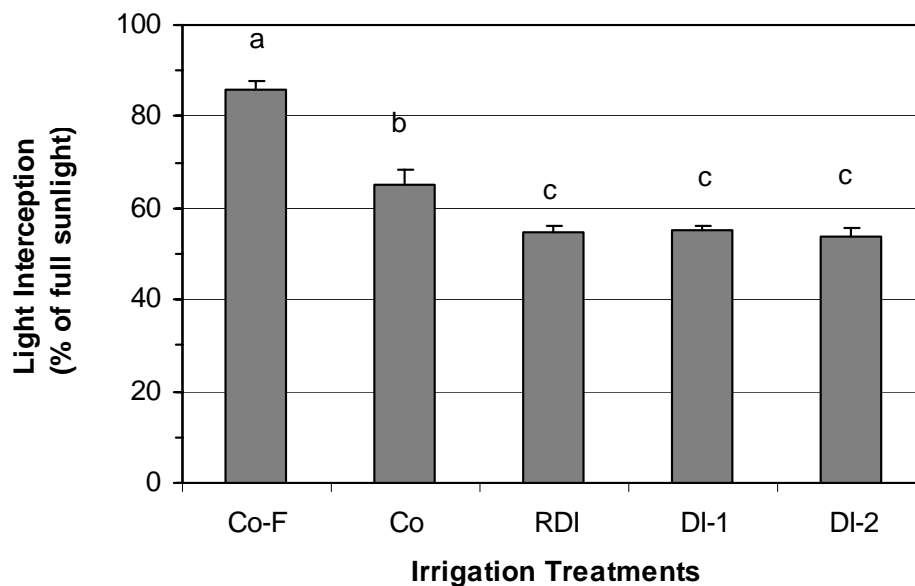

Fig. 3.8   Mean light interception per tree in the different irrigation treatments during October 2002 until March 2003 (each bar represents the mean ± SE of 4 replicate tree samples; different letters depict significant differences at P=0.05; for details of irrigation treatments see legend Fig. 3.3).

Apart from increased pruning weights (Behboudian and Mills, 1997), dense canopies also limit management practices like spraying of agro-chemicals because they do not effectively penetrate the canopy. Pruning weights might be reduced through deficit irrigation as indicated by Nuzzo et al. (1997) in kiwi, Mitchell et al. (1989) in pear and by Behboudian and Mills (1997) in several other fruit crops.

3.3.3 Effect of irrigation regime on production of shoots and floral canes during the flowering flush

During the flowering flush in August 2002, there were no significant differences between irrigation treatments with respect to number of flushing terminals (Fig. 3.9A) and shoot number (Fig. 3.9B). However, the pattern of decreasing numbers of flushing terminals and shoot numbers concurrent with decreasing amounts of irrigation water applied (CO-F>Co>RDI>DI-1>DI-2) were similar to that of the post-harvest flush in the following year (2003, Fig. 3.6). Results indicated that the season of 2002/2003 was an off-year in mangoes following an on-year the previous season (2001/2002). Competition between young citrus leaves and flowers for limited supplies of photosynthates determined growth, flowering and yield (Syvertsen et al., 2003). Shoot growth during the flowering flush in 2002 might have been inhibited because of competition for a limited supply of photosynthates between shoots and floral canes.

The significantly larger number of flushing terminals producing floral canes as well as the number of floral canes per tree in contrast to those of shoots and mixed canes indicated that floral canes appeared to be the dominant sinks during the flowering flush (Fig. 3.9, Table 3.3). In floral canes, irrigation regime significantly affected the production of terminals and number of floral canes while it had no influence on mixed canes (Fig. 3.9). Declining applications of irrigation water led to reductions in the number of flushing terminals and floral canes. Interactions between irrigation treatments and shoot/cane type were not significant (Table 3.3). The treatment DI-2 exhibited the highest reductions among all treatments (Table 3.3, Fig. 3.9) indicating that with this irrigation treatment, declining yields can be expected, although the most water was saved in this treatment. Similar to our results, Drost and Wilcox-Lee (1997) observed that deficit irrigation reduced the total shoot production in asparagus plants thus affecting crop productivity.
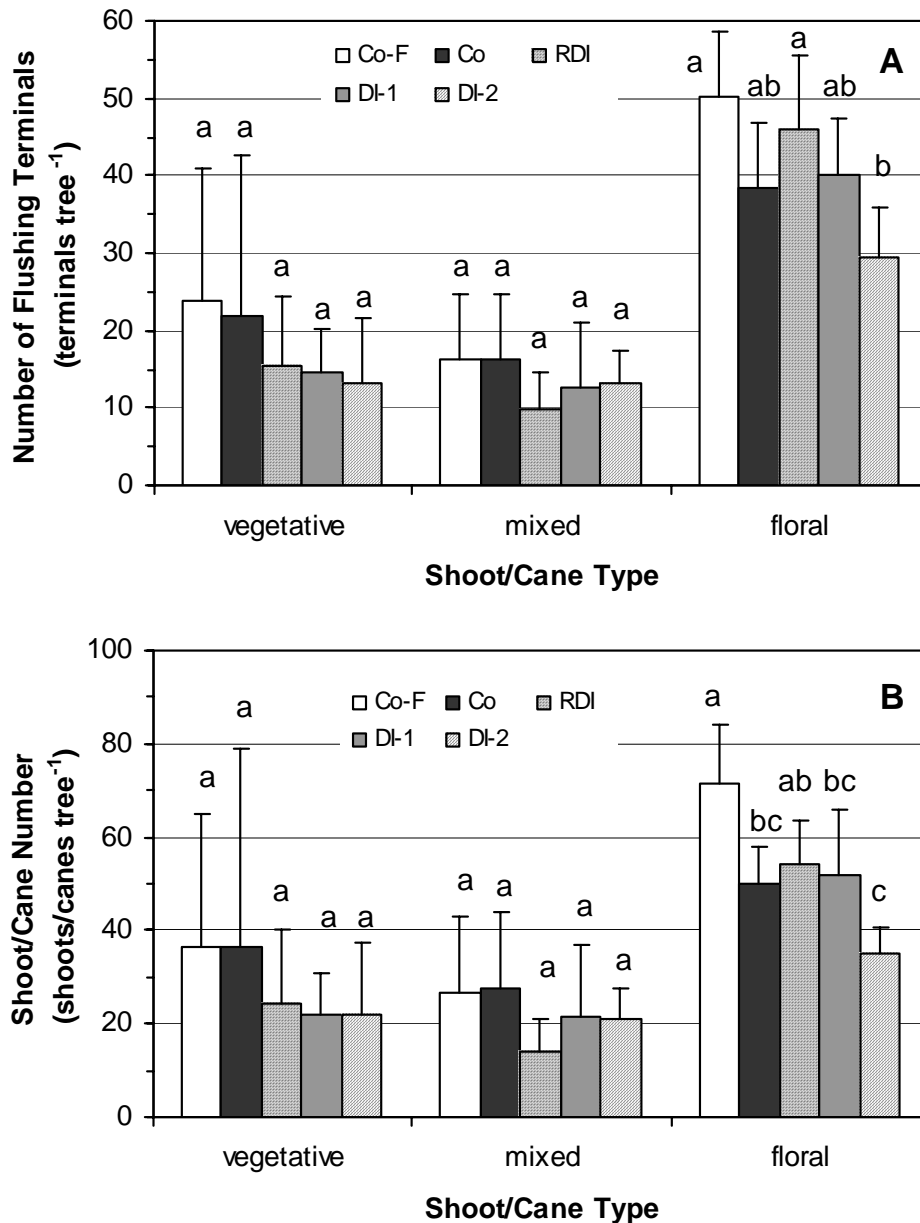
Fig. 3.9 Mean number of flushing terminals per tree (A) and shoots/canes per tree (B) according to shoot/cane type during the flowering flush (August 2003) in 6-7 year old 'Kent' mango trees in response to different irrigation treatments (mean ± SD of 5-6 replicate tree samples; different letters depict significant differences between irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Visual observations during the pre-flowering period of water deficits showed that in less irrigated treatments (Co, DI-1, DI-2, RDI) new vegetative shoots were dying or losing leaves while vegetative shoots were growing well in Co-F. Some of those shoots that survived and defoliated later developed into flowering shoots. This is in

agreement with reports by Lauri et al. (1996) who found that reproductive apex was produced through gradual modification of the vegetative apex. Similarly, Smith (1979) reported that water deficits prior to flowering might result in large inflorescences with leaves reduced to small bracts. Transition to flowering is associated with a reduction in size of some vegetative traits, e.g. the presence of bracts instead of leaves in the inflorescence (Lauri et al., 1996). The opposite would be expected after rain or prolonged irrigation, as was found in Co-F, where the flowering flush consisted of full-sized leaves with occasionally small auxiliary flower panicles (mixed flush) (Smith, 1979). Lauri et al. (1996) concluded that there was an antagonistic relationship between vegetative growth and flowering in mango and therefore all factors that reduced vegetative growth would promote flowering. Schaffer et al. (1994) observed that drought prior to mango flowering prevents vegetative flushing thereby increasing the proportion of mature to immature leaves in the canopy. Mature leaves produced floral stimuli, whereas immature mango leaves were rich sources of floral inhibitors (Schaffer et al., 1994). Cull (1991) suggested that vegetative dormancy allowed a threshold of carbohydrate accumulation and growth regulator level to be reached, therefore stimulating flowering.

Table 3.3 Effect of irrigation regime and shoot/cane type on mean number of flushing terminals and shoots per tree in 6-7 year old 'Kent' mango trees during the flowering flush in August 2002 (irrigation treatment: n=15-18; shoot/cane type: n=29; different letters depict significant differences between irrigation treatments and year at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Factor	Number of Flushing Terminals		Shoot/Cane Number	
	(terminals tree^{-1})		(shoots/canes tree^{-1})	
Irrigation Treatments				
Co-F	30 ± 19	a	45 ± 27	a
Co	25 ± 16	ab	38 ± 27	ab
RDI	24 ± 18	ab	31 ± 20	ab
DI-1	22 ± 15	ab	32 ± 19	ab
DI-2	19 ± 10	b	26 ± 12	b
Shoot/Cane Type				
vegetative	18 ± 21	b	28 ± 48	b
mixed	13 ± 21	b	22 ± 21	b
floral	40 ± 21	a	48 ± 42	a

Declining pattern of relative shoot number per tree (according to production of single and multiple shoots per terminal) in response to reductions of irrigation application during flowering (Fig. 3.10) showed in some aspects similarities to that of the post-harvest flush in 2003 (Fig. 3.7). However in contrast to the post-harvest flush in 2003 and to the other treatments, Co-F produced relatively more shoots in the classes of 1 and 2-3 shoots per terminal. Effect of reduced irrigation was most pronounced in the treatment DI-2 (Fig. 3.10). Although little vegetative growth is beneficial during flowering, this significant reduction of shoots in DI-2 indicated that the magnitude of water deficit the trees were exposed to was too severe and resulted also in a significant reduction of mixed and floral cane production in most cases (Fig. 3.11, Table 3.4).
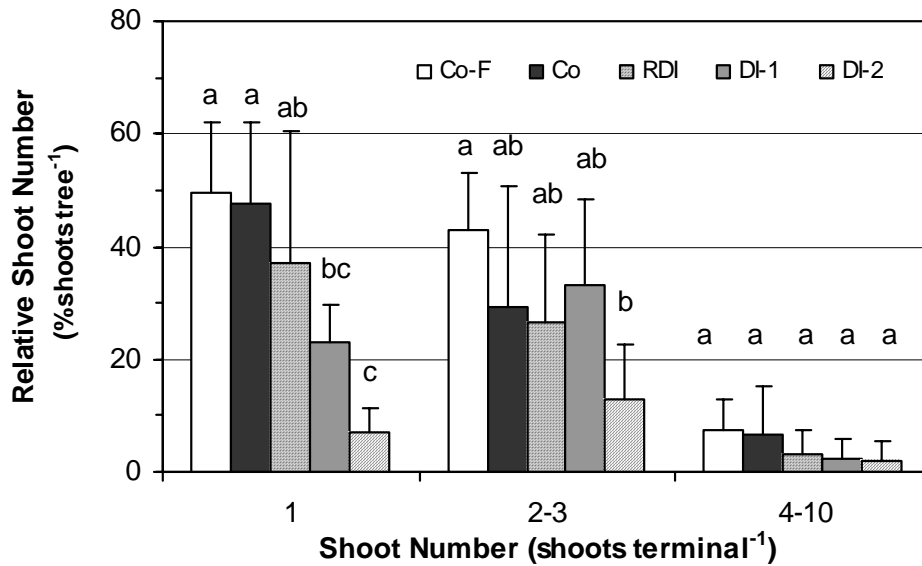
Fig. 3.10 Relative shoot number per tree according to production of single and multiple shoots (2-3 and 4-10) per terminal during the flowering flush in August 2003 in 6-7 year old 'Kent' mango trees exposed to different irrigation treatments (mean ± SD of 5-6 replicate tree samples; different letters depict significant differences between irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Relative number of mixed canes in the three cane classes responded to reductions of irrigation water applications in a manner similar to that observed in shoots (Fig. 3.11A, 3.10). The same pattern was observed in floral canes when multiple shoots per terminal were produced (Fig. 3.11B). Except for DI-2 there were no significant differences between irrigation treatments in terminals consisting of one floral cane (Fig. 3.11B, Table 3.4). The low relative number of canes in DI-2 indicated that those trees were severely stressed by water deficit to an extent that productivity was reduced in comparison to the other treatments (E.W. Pavel, 2004: personal communication).
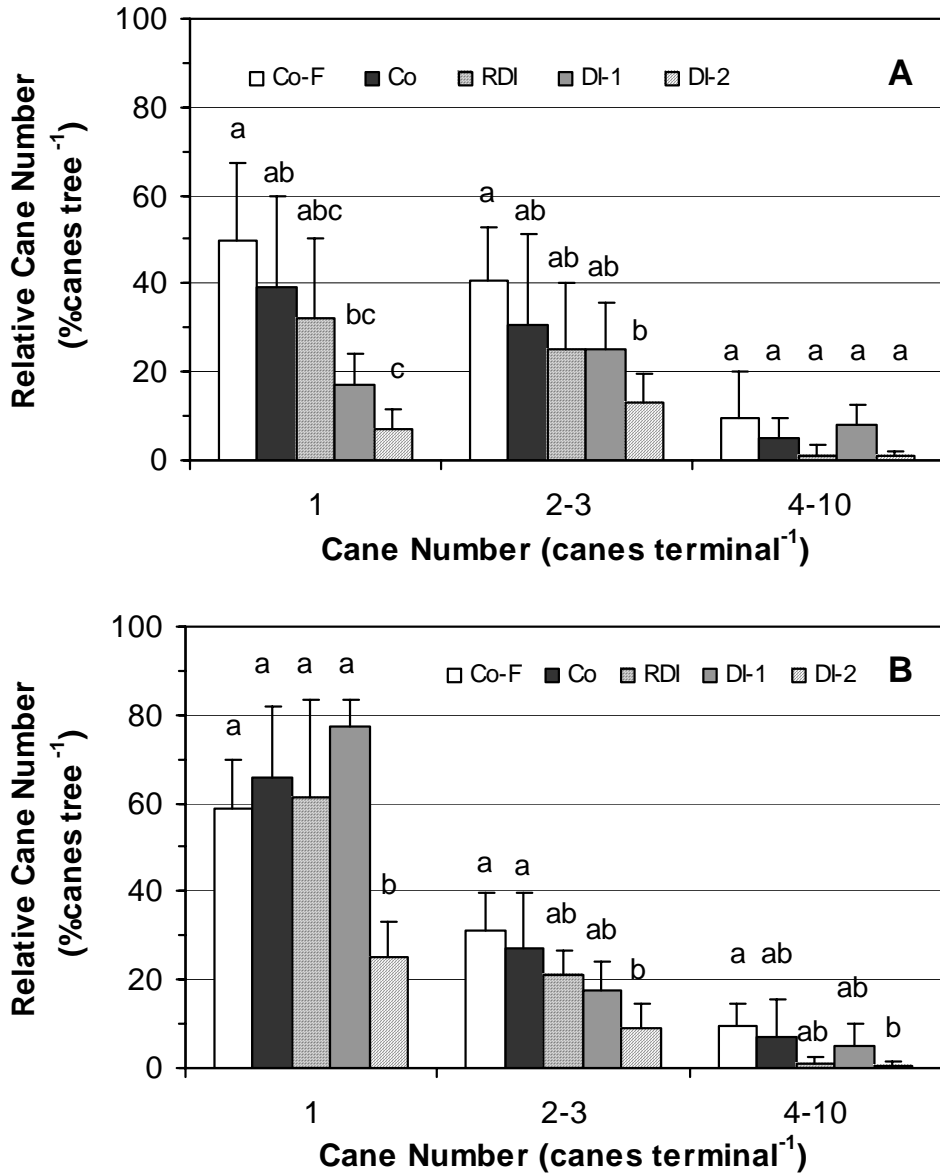
Fig. 3.11 Relative cane number per tree according to the production of single and multiple canes (2-3 and 4-10) per terminal during the flowering flush in August 2003 in 6-7 year old 'Kent' mango trees exposed to different irrigation treatments (mean ± SD of 5-6 replicate tree samples; different letters depict significant differences between irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Table 3.4 Effect of irrigation regime and shoot/cane type on the relative number of canes/shoot per tree in 6-7 year old 'Kent' mango trees during the flowering flush in August 2003 (irrigation treatment: n=15-18; shoot/cane type: n=29; different letters depict significant differences between irrigation treatments and year at P=0.05; for details about irrigation treatments see legend Fig. 3.3).

Factor	Relative Shoot/Cane Number ($\%$shoots/canes tree^{-1})					
	Shoot/Cane Number (shoots/canes terminal^{-1})					
	1		2-3		4-10	
Irrigation Treatments						
Co-F	53 ± 13	a	38 ± 11	a	9 ± 7	a
Co	51 ± 20	a	29 ± 18	ab	6 ± 7	ab
RDI	43 ± 24	a	24 ± 12	b	2 ± 3	bc
DI-1	39 ± 29	a	25 ± 12	b	5 ± 5	abc
DI-2	13 ± 10	b	12 ± 7	c	1 ± 2	c
Shoot/Cane Type						
vegetative	33 ± 21	b	26 ± 17	a	4 ± 6	a
mixed	28 ± 21	b	28 ± 16	a	5 ± 6	a
floral	58 ± 22	a	21 ± 11	a	5 ± 6	a

Interactions between irrigation treatment and shoot/cane type were only significant when one shoot per terminal was produced (Table 3.4). Irrigation reductions generally reduced shoot/cane productions across all three shoot/cane number classes. Differences between vegetative shoots, mixed and floral canes were only significant when produced as single shoots.

3.4 Conclusion

Our results indicated that vegetative growth could be manipulated with irrigation. This was evident in the irrigation treatment Co-F, which appeared to be over-irrigated leading to vigorous vegetative growth. On the other hand, the treatment DI-2 showed that deficit irrigation was too severe reducing drastically vegetative growth and production of floral canes and, therefore, resulting in declined tree crop productivity. The other three treatments, Co, RDI, and DI-1, appeared to be in the middle of the two extremes in terms of vegetative growth. The vigorous growth in Co-F resulted in a dense canopy and therefore spray coverage might prove to be insufficient. In addition, such a dense canopy may lead to self-shading compromising fruit quality, and in high costs of pruning and irrigation water, therefore, reducing crop productivity.

It is recommended that for further studies, growth of flushes should be monitored over the entire year so that one would know whether through over-irrigation or deficit irrigation there are more flushes per year than usual or not. It would also be vital to verify if the summer flush in mango affects fruit growth hence sink-source relationships. Furthermore, it is important to investigate if multiple production of floral canes per terminal would produce smaller fruit and more fruit than production of single, double or triple floral canes per terminal. Starch determination in shoots would also help to provide information on shoot growth sensitivity to different irrigation regimes. Through measuring pruning weights it will be possible to determine and quantify to what extent over-irrigation will induce excessive vegetative growth.

4 Seasonal Characterisation of Photosynthetic Capacity in Mango Trees under Well-irrigated and Reduced Irrigation Conditions

4.1 Introduction

It is well known that photosynthetic systems in higher plants are most sensitive to high temperature, water and salt stress. The effects of water deficits on photosynthesis in plants have been in the spotlight of plant physiologists for many years, and conflicting results have been reported depending on the plant material and the experimental procedures used for investigations. In response to a water deficit, a decrease in net CO_2 assimilation rate is generally observed. This effect can however result from different processes, such as an inhibition of electron transport activity or a limitation in the metabolic activity (Zulfugarov, 2001). The capacity of plants, particularly fruit trees, to photosynthesize during or following stress induced by water deficit is an important indicator of drought resistance (Townley-Smith and Hurd, 1979). Townley-Smith and Hurd (1979) further indicated that almost all biochemical and physiological processes in plants are relevant components of yield, e.g. net assimilation rate (Lawlor, 1979; Townley-Smith and Hurd, 1979). Therefore, factors that affect photosynthesis, even by diverting it from one metabolic pathway to another, may influence yield of tree crops.

Water deficit and heat stress may affect plant assimilation by altering metabolic activity: either inhibiting a single metabolic sequence or enzyme reaction (preventing by feedback control the proper functioning of the whole system) or changing the balance between parts of the system. Water deficit is an important factor that may lead to reduction of agricultural production and crop quality across the world (Lawlor, 1979). According to Boyer (1976) research has shown enough evidence that stomatal aperture is involved in the inhibition of photosynthesis by water stress. However, little is known about the other physiological mechanisms involved and the agricultural importance of photosynthetic inhibition by water deficits.

Photosynthetic responses to water deficits have been well documented in deciduous tree crops, such as peach (Besset et al., 2001), apple (Pretorius and Wand, 2003), apricot (Ruiz-Sanchez et al., 2000), and olive (Moriana and Fereres, 2002). However, less has been done on subtropical fruits such as mangoes (de Villiers, 2001) and avocados (Chartzoulakis et al., 2002). Reduced photosynthetic rates were reported in peach under light and severe water deficits (Besset et al., 2001), though the trials were conducted in potted plants. The reduction of photosynthesis was partly attributed to stomatal closure (Moriana and Fereres, 2002) and non-stomatal factors such as mesophyll resistance (Flore and Lakso, 1989; Chartzoulakis et al., 2002). In mango (cv Kent), mean photosynthesis was higher in summer than in winter highlighting the seasonal differences, and the deficit irrigation treatment (DI-2) had significantly lower photosynthetic rates during summer in comparison to the other treatments (de Villiers, 2001). The author further indicated that such low Pn values could have resulted from the effect of leaf age and the phenological stages that some branches were in, or the effect the irrigation treatment had on the tree.

High water deficits and low temperatures may reduce photosynthesis (Smith, 1979), and subsequent photosynthetic reduction may provide inhibitors that reduce alternate bearing in mango trees (Shivashankara and Mathai, 2000) since it is a problem in commercial mango production. In winter, photosynthesis was found to recover faster after midday depression while in summer the midday depression continued much later into the afternoon (de Villiers, 2001). Under optimum temperatures (around 30°C), photosynthesis in potted mango trees (cv. Nam Dok Mai) increased between 08:00 and 10:00 h, and then it started to decline during the rest of the day (Pongsomboon et al., 1992). The reduction in photosynthesis was attributed to various factors including decreased stomatal conductance (g_s) during the day. Stomatal conductance decreased with declining leaf water potentials, and stomatal regulation in mango significantly reduced the rate of development of internal water deficit compared to other species (Schaffer et al., 1994). Studies by Schaffer et al. (1994) in mango and Girona et al. (1993) in peach showed that the function of stomatal conductance could be to reduce excessive water loss when evaporative demand is higher than water supply.

The objectives of these investigations were therefore a) to study seasonal and diurnal patterns of photosynthesis in different cultivars and of different leaf ages in well-irrigated mango trees, and b) to evaluate photosynthetic responses of mango trees to water deficit induced by various irrigation regimes in 6-7 year-old mango trees and 1 year-old potted trees under field conditions.

4.2 Materials and Methods

Details about the study site, orchard, and cultural management practices, are as described in section 3.2.1.

4.2.1   Photosynthetic measurements

Leaf photosynthesis was measured on the abaxial surface of 4-5 attached, mature, and fully exposed leaves using a portable, open infrared gas analyzer (IRGA) system (Ciras-1, PP Systems, UK). Climatic data, such as ambient air temperatures, solar radiation, relative humidity, windspeed, and rainfall, were monitored at a weather station located within 5 km of the study site. Daily evaporative demand was calculated using a modified Penman-Monteith equation (Allen et al., 1998).

4.2.2   Photosynthetic capacity of well-irrigated mango trees

Leaf photosynthesis was measured in 2-hour intervals over the day. The data were collected from 6 trees in well-irrigated 'Kent' mango trees of the control (Co) treatment (see section 3.2.2. for irrigation treatments) over the season of 2002/2003.

For cultivar comparisons, 'Keitt' trees from a neighboring block were used in addition to 'Kent' and 'Heidi' trees of the experimental orchard. There was no difference in irrigation treatment between both blocks and all three cultivars were managed according to farm management practices (see section 3.2.2. for description of the farm control, Co-F). Water was assumed to be non-limiting. Measurements were conducted at midday (between 11:00-13:00 h) on 4-5 fully exposed and mature leaves on 4 trees of each cultivar.

Leaf photosynthesis with respect to leaf age was characterized on mango trees (cv. Kent) of the well-irrigated treatment (2-4 trees per treatment) during July 2002 as well as January and July 2003. Photosynthetic measurements for leaf age comparisons were taken at around 10:00 h in addition to diurnal curves in about 1.5 hour intervals at selected dates over the season. Generally, well-irrigated mango trees exhibited three distinct vegetative flushes during the season: the post-harvest flush (March to May), flowering flush (July to August), and summer flush (December to January). From each of the three vegetative flushes four leaf ages where distinguished and characterized according to the number of days after bud break (DABB):

- < 25 DABB- very delicate, young and chocolate/brown in colour;
- 30 to 60 DABB –young immature and light greenish in colour;
- 90 to 270 DABB- mature young and dark green in colour;
- > 365 DABB- mature old and leathery and dark green in colour.

4.2.3 Leaf photosynthesis in deficit-irrigated mango trees

One-year-old 'Sabre' mango seedlings grown in 5 L nursery plastic bags were exposed to two irrigation treatments (well-irrigated and non-irrigated) during June-July 2002 (winter). The growth media consisted of pine bark, sand, and red clay (5:4:1, v:v:v). Trees were placed in open ground near the orchard. Before the commencement of the experiment, all the trees of both treatments were fully irrigated. Thereafter, the well-irrigated trees were irrigated every day after the measurements, while the non-irrigated trees (deficit treatment) received no water during the course of the experiment. Water drainage was ensured by punched holes

at the bottom of the containers in order to prevent water-logging. Photosynthetic measurements were taken at midday on four trees per treatment.

A similar experiment was conducted in summer (February 2003) in 1 year-old, potted mango trees, but a recovery phase after the drying cycle was included in the studies. In addition to 'Sabre' seedlings, 'Kent' trees grafted on 1 year-old 'Sabre' rootstocks were incorporated. Trees of the deficit treatment (non-irrigated) were not irrigated from day 1-5 followed by a recovery phase of 4 days under full irrigation. Trees were irrigated 4-5 times per day until runoff during the recovery phase like the ones of the well-irrigated treatment. Photosynthetic measurements were conducted at midday throughout the trial. However during day 4-7, measurements were taken over the day in about 2 hour intervals to monitor diurnal changes in photosynthetic rates.

Photosynthesis of 6-7 year-old 'Kent' mango in response to various irrigation treatments (details about irrigation treatments have been described in section 3.2.2.) was measured throughout the season in the field. Photosynthetic measurements were conducted as described in section 4.2.1. on 4-8 mango trees (2-4 replicates of each irrigation treatment) at midday (between 11:00-13:00 h) from May 2002 until July 2003.

4.2.4 Statistical analysis of data

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

4.3 Results and Discussion

4.3.1 Photosynthetic characteristics of well-irrigated mango trees in the field

4.3.1.1 Seasonal and diurnal trends

Leaf photosynthesis (Pn) increased from December until March (4.7 ± 1.0 to 11.3 ± 0.9 µmol CO_2 m^{-2} s^{-1}) (Fig. 4.1) and was apparently associated with favourable environmental conditions, such as temperature (25.7 ± 1.0°C), solar radiation (17.0 ± 1.2 MJ m^2 s^{-1}), and low vapour pressure deficits (VPD, 1.2 ± 0.2 KPa). High rainfall (48.5 mm) and relative humidity (69 ± 9%) as well as relatively low evaporative demand (ETo, 5.4 ± 1.4 mm day^{-1}) in March 2003 might also have played a major role in promoting photosynthesis. Low assimilation rates (7.7 ± 1.5 µmol CO_2 m^{-2} s^{-1}) in April 2003 could have resulted from low solar radiation incidences (13.0 ± 2.9 MJ m^{-2} s^{-1}) on leaves primarily due to partly cloudy weather conditions. Photosynthetic rates reached the overall seasonal maximum (12.6 ± 1.9 µmol CO_2 m^{-2} s^{-1}) during May 2003, when winter was approaching indicating that relatively low temperatures (18.1 ± 1.8°C) and low solar radiation (11.6 ± 1.8 MJ m^{-2} s^{-1}) did not negatively affect photosynthesis. Low VPD (0.6 ± 0.3 KPa) might have favoured these high rates. Increased photosynthetic efficiency was reported in mangoes during autumn in autumn due to the post-harvest flush in mangoes since the developing flushes require carbohydrates to grow. (Whiley et al., 1999). These results are in contradiction to those reported in lychee during the same seasonal period where the net assimilation rate and stomatal conductance declined in response to low average noon temperatures of 20°C (Menzel and Simpson, 1994).

The high Pn rates in mango could be partly attributed to the altered sink-source relationship due to branch thinning in April 2003 (Fig. 4.1). Trees may have increased their photosynthetic capacity to compensate for the removed source. Partial defoliation of apple trees enhanced photosynthetic rates primarily due to acceleration of photosynthetic capacity (Zhou and Quebedeaux, 2003). Branch thinning apparently opened the canopy and therefore allowed more light penetration and consequently increased photosynthesis (Kozlowski and Kramer, 1979; Flore and Lakso, 1989; Lakso, 1994).

Relatively low photosynthetic rates in June and July 2002 might have been associated with water reductions during the pre-flowering period in addition to low temperatures during that time (16.7 ± 0.5°C) (Fig. 4.1). Mean temperatures below 15°C severely reduced CO_2 assimilation rate in young, potted mango trees (Pongsomboon et al., 1992). In addition, it was found with avocados and mangos that reduced photosynthesis in winter could also have been due to feedback inhibition since the canopy of avocado and mango trees is relatively quiescent during winter, the resultant reduction in sink strength promotes an increase in starch concentrations in leaves (Whiley et al., 1999). The higher starch concentrations in leaves would inhibit photosynthesis. It is also common knowledge that mango trees should be subjected to a water reduction period in winter in order to enhance flowering (Smith, 1979; Cull, 1991; Schaffer et al., 1994).
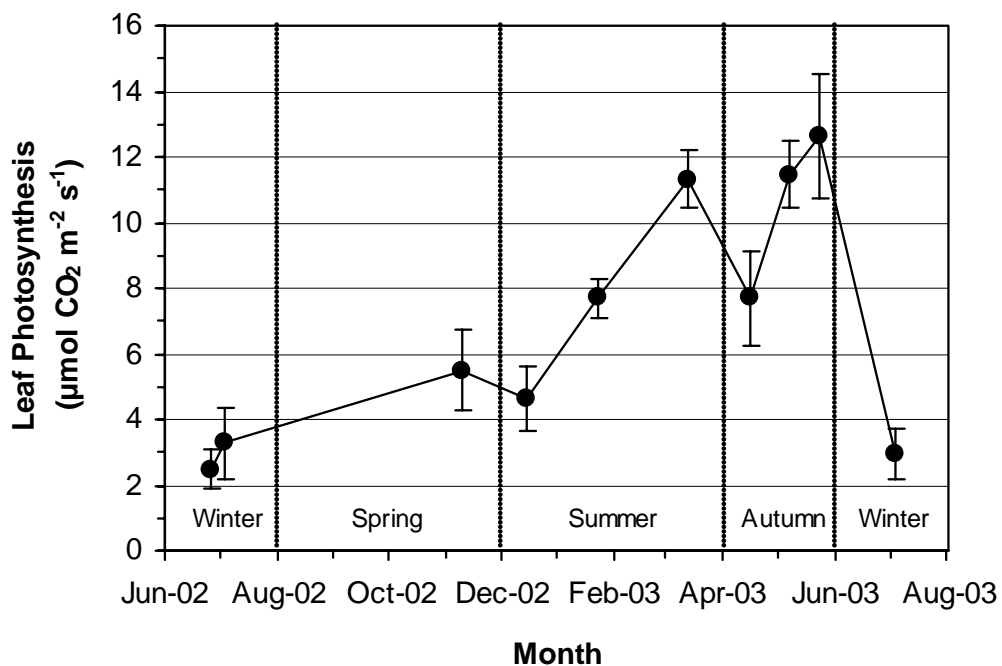

Fig. 4.1   Pattern of mean leaf photosynthesis of well irrigated 6-7 year-old 'Kent' mango trees at midday in the field during the season of 2002/2003 (each point represents the mean ± SD of 6 replicate leaf samples).

During August, net assimilation rates increased slightly with increasing temperatures and solar radiation as expected until December where there was a slight drop in Pn rates (Fig. 4.1). The slow increase in Pn rates could have been related to increasing

ETo (from 3.9 ± 0.8 to 5.9 ± 1.6 mm day^{-1}) during that period, while the sudden decline in December was probably due to cloudy skies. Optimal temperatures (25.7 ± 1.0°C) and high solar radiation (17.0 ± 1.2 MJ m^{-2} s^{-1}) from Dec 2002 until Mar 2003 might have accounted for the sharp increase in mean photosynthetic rates. Temperatures ranging from 24-30°C are considered to be optimal for mango (de Villiers, 2001) in the absence of water stress (Urban et al., 2003).

Generally, photosynthesis during winter and autumn was low during the early hours of the day and increased to its maximum during the late morning hours in 'Kent' mango trees (Fig. 4.2). After a midday depression during some seasons, Pn rates tended to increase during late afternoon before they declined towards sunset. Similar diurnal patterns of photosynthesis have been reported in apples (Flore and Lakso, 1989). Midday Pn rates were in winter around 2.8 ± 0.4 µmol CO_2 m^{-2} s^{-1} and in summer around 9.5 ± 0.6 µmol CO_2 m^{-2} s^{-1}. These values are contrary to those reported by de Villiers (2001) in 'Kent' mangoes (winter: 11 µmol CO_2 m^{-2} s^{-1}, summer: 6 µmol CO_2 m^{-2} s^{-1}). Generally, Pn rates in mango were lower than those of apples and olives under non-limiting conditions (Bongi and Palliotti, 1994; Lakso, 1994). Healthy sun-exposed leaves of apple might reach Pn rates of 15 µmol CO_2 m^{-2} s^{-1}. (Lakso, 1994) while those of olives 18 µmol CO_2 m^{-2} s^{-1} (Bongi and Palliotti, 1994). In comparison to avocado (23 µmol CO_2 m^{-2} s^{-1}) under field conditions (Whiley and Schaffer, 1994) Pn rates of mangoes were lower.
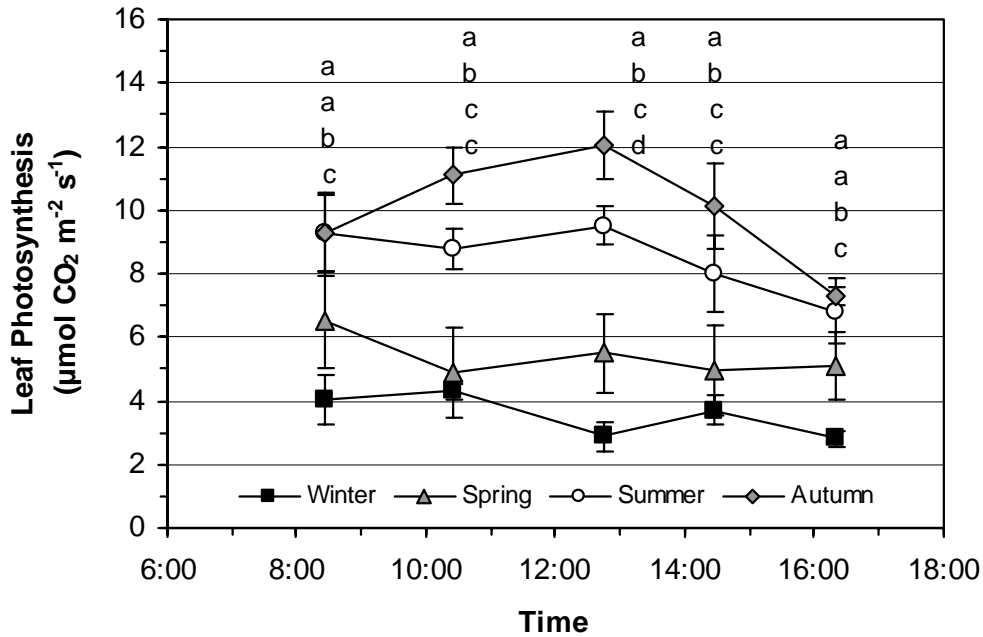
Fig. 4.2   Diurnal patterns of mean photosynthesis in well-irrigated 6-7 year-old 'Kent' mango trees under field conditions during the season of 2002/2003 (winter: Jun-Jul 2002, spring: Oct 2002, summer: Jan/Mar 2003, autumn: May 2003; each point represents the mean ± SD of 6 replicate leaf samples; different letters in descending order according to values depict significant differences between seasons at each measurement time at P=0.05).

Diurnal patterns of Pn rates were highest in autumn followed by those in summer, spring, and winter. Seasonal differences were also shown by the depression of photosynthesis at around 10:30 h during spring and summer, while in winter the midday decline took place at around 12:30 h (Fig. 4.2). No decrease in Pn rates was observed in autumn during midday in comparison to the other seasons. The difference of midday decline in the different seasons may have been associated with temperature and to a lesser extent to changes in radiation over the season. High midday Pn rates in autumn (12.0 ± 1.1 µmol CO_2 m^{-2} s^{-1}) might be attributed to low ETo (3.9 ± 0.3 mm day^{-1}) and high relative humidity ($72 \pm 0\%$), while the low values in spring (5.5 ± 1.3 µmol CO_2 m^{-2} s^{-1}) were apparently associated with higher ETo (4.9 ± 0.9 mm day^{-1}) and lower relative humidity ($62 \pm 2\%$).

Interactions of leaf photosynthesis between season and time of the day were significant (Table 4.1). Differences in Pn rates between seasons were significant.

Mean seasonal photosynthetic rates were highest in autumn, followed by those of summer, spring, and winter. Time of the day did not significantly affect mean Pn rates except for 16:30 h, when Pn rates where significantly lower than the others. Such low Pn rates could be explained by decreasing solar radiation as the day approached sunset.

Table 4.1 Effect of season and time of the day on mean leaf photosynthetic rates in well-irrigated 6-7 year-old 'Kent' mango trees during winter (Jun/Jul 2002), spring (Oct 2002), summer (Jan/Mar 2003), and autumn (May 2003) (season: n=30; time of the day: n=24; different letters depict significant differences between season and time of the day at P=0.05).

Factor	Leaf Photosynthetic Rate $(\mu mol\ CO_2\ m^{-2}\ s^{-1})$	
Season		
Winter	3.5 ± 0.8	d
Spring	5.4 ± 1.4	c
Summer	8.5 ± 1.3	b
Autumn	10.0 ± 1.9	a
Time of the Day		
08:30 h	7.3 ± 2.5	a
10:30 h	7.3 ± 3.0	a
12:45 h	7.5 ± 3.7	a
14:30 h	6.7 ± 2.8	a
16:15 h	5.5 ± 1.9	b

4.3.1.2   Cultivars

Under well-irrigated conditions, mean photosynthetic rates at midday did not differ significantly between the three mango cultivars, 'Heidi', 'Kent', and 'Keitt', over the season of 2002-2003 except for January and April 2003 (Table 4.2). Lower Pn rates of 'Heidi' were associated with low transpiration rates indicating a higher sensitivity of 'Heidi' to high temperatures (35.2 $\pm$ 1.0°C) compared to the other two cultivars in January 2003. 'Heidi' displayed reduced transpiration rates (3.7 $\pm$ 1.3 mmol H_2O m^{-2} s^{-1}) compared to those of 'Kent' (7.4 $\pm$ 2.2 mmol H_2O m^{-2} s^{-1}) and 'Keitt' (9.3 $\pm$ 0.8 mmol H_2O m^{-2} s^{-1}) showing that the stomata were more closed in 'Heidi' in comparison to the other two cultivars. Differences in Pn and transpiration rates between 'Heidi' and the other two cultivars ('Kent' and 'Keitt') could have been related to differences in their leaf anatomy. 'Hass' avocado had higher photosynthetic rates compared to those of 'Fuerte', and differences were attributed to anatomic arrangements of cells in the leaves (Chartzoulakis et al., 2002). 'Hass' exhibited a higher percentage of intercellular air space in the leaves than did 'Fuerte' (Chartzoulakis et al., 2002).

Capellini and Dettori (1992) emphasised that genotypic differences may influence stomata and chlorophyll content of leaves resulting in differences in assimilation rates. Genetic studies in 'Keitt' and 'Kent' mango cultivars showed that both were indirect progenies of 'Turpentine' mango and showed therefore genetically no significant differences in their DNA band (Adato et al., 1995). Consequently, leaf photosynthesis of both cultivars was not significantly different except for April 2003 (Table 4.2). However, no difference was expected between 'Kent' and 'Heidi' since the latter was developed from a 'Kent' seedling by the ARC-Institute for Tropical and Subtropical Crops, Nelspruit, South Africa (Human and Snyman, 1998).

Table 4.2 Seasonal differences in mean photosynthetic rates ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) at midday between the mango cultivars 'Heidi', 'Keitt', and 'Kent' under well-irrigated conditions during the season of 2002/2003 (each value represents the mean $\pm$ SD of 4 replicate leaf samples; different letters depict significant differences between cultivars at each measurement date at P=0.05).

Month	Leaf Photosynthetic Rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)					
	Cultivar					
	Heidi		**Kent**		**Keitt**	
Jun 02	9.9 ± 1.3	a	9.3 ± 2.1	a	9.3 ± 0.7	a
Jul 02	5.5 ± 1.1	a	3.6 ± 1.4	a	5.3 ± 1.3	a
Jan 03	6.2 ± 0.9	b	10.9 ± 2.6	a	9.7 ± 1.0	a
Mar 03	12.6 ± 1.2	a	12.0 ± 1.4	a	9.7 ± 2.0	a
Apr 03	5.6 ± 0.5	b	5.6 ± 1.3	b	10.9 ± 0.3	a
Jul 03	9.4 ± 1.8	a	8.6 ± 2.0	a	9.0 ± 1.0	a

In April 2003, 'Heidi' and 'Kent' had lower Pn rates in contrast to 'Keitt'. Partly cloudy skies experienced during the measurements may have played a role in Pn reduction. In addition, 'Keitt' a late-maturing cultivar could have been in its peak of post-harvest flush and, therefore, more photosynthates were needed leading to increasing Pn rates compared to the other two midseason cultivars. Flore and Lakso (1989) observed increasing Pn rates in several fruit species during shoot growth when the demand for photosynthates was high.

4.3.1.3   Leaf age

In fruit trees, the study of CO_2 gas exchange during leaf ontogeny is essential for a basic understanding of leaf physiology and tree productivity (Schaper and Chacko, 1993). More than four different shoot generations may co-exist in one branch in mango trees (Kramer and Kozlowski, 1979), thereby providing different leaf generations. Generally, mean leaf photosynthetic rates of well irrigated, 6-7 year-old 'Kent' mango tree were higher in summer than in winter except for the very young leaves (<25 DABB, days after bud break) (Fig 4.3, Table 4.4). Apparent seasonal differences of leaf photosynthetic rates in mango could have been primarily due to low temperatures in winter causing low CO_2 assimilation (Pongsomboon et al., 1992; Schaffer et al., 1994).

During winter, the midday depression in the photosynthetic rates in all diurnal curves was more pronounced at 13:30 h while that of summer was slightly visible in the 30-60 DABB leaves only. It was found that during winter trees recovered faster during the afternoon than in summer when midday depression continued much later into the afternoon (de Villiers, 2001). However, we found that very young (<25 DABB) and older leaves (>90 DABB) displayed no midday photosynthesis depression in summer as opposed to that of winter. The low winter midday assimilation rates may have been associated partially with photoinhibition. Schaffer et al. (1994) indicated that mango leaves were often exposed to conditions that favour photoinhibition in winter as a result of low temperatures interacting with high incident light levels. Photosynthesis was light saturated at 450-500 µmol CO_2 m^{-2} s^{-1} in potted 'Turpentine' mango (Schaffer et al., 1994). During this period it is expected that enhanced transpiration would exceed replacement of water to mango leaves resulting in increased moisture deficit (Pongsomboon et al., 1992).
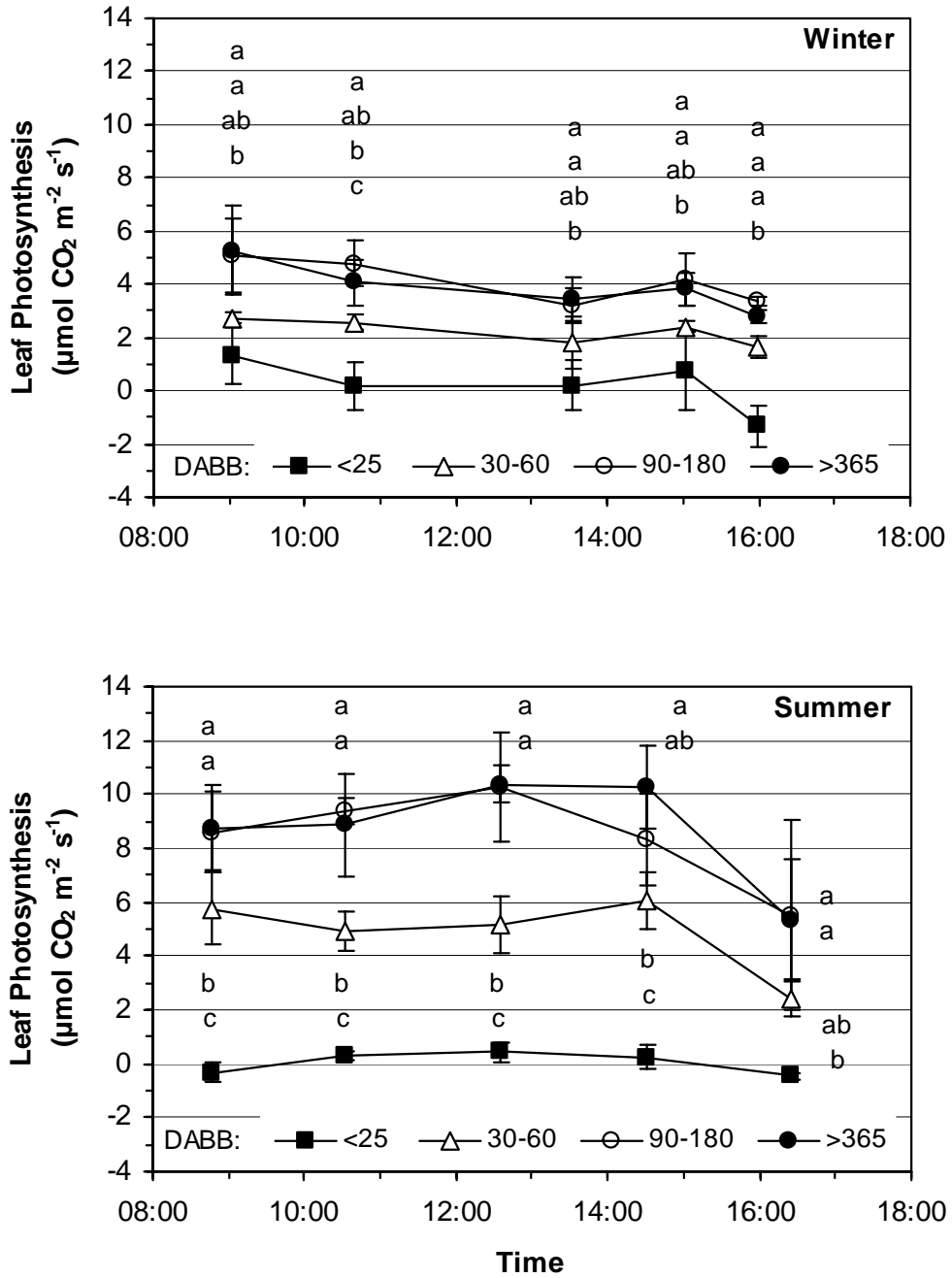
Fig. 4.3 Diurnal pattern of mean photosynthetic rates of different leaf ages in well irrigated 6-7 year-old 'Kent' mango trees during winter (Jun 2002/Jul 2003) and summer (Jan 2003) (each point represents ± SD of 2-6 replicate leaf samples; different letters in descending order according to values depict significant differences between leaf ages at each time of measurements at $P=0.05$).

In winter and summer, older leaves showed no significance difference throughout the day in photosynthesis (Fig. 4.3). However, mean photosynthetic rates of these two

leaf age groups were significantly higher than those of the younger leaves (30-60 DABB and <25 DABB) across both seasons (Table 4.3). Leaf assimilation of leaves aged 30-60 DABB represented an intermediate between the older (90-180 DABB and >365 DABB) and younger leaves (<25 DABB). Especially during summer, differences in photosynthetic rates between leaves aged 30-60 DABB and the older and younger leaf generations were significant in the morning, while differences between the leaf generations were less pronounced and not consistently significant in winter (Fig. 4.3).

The youngest leaf generation (<25 DABB) displayed mean photosynthetic rates lower than 1 $\mu molCO_2$ m^{-2} s^{-1} suggesting that these leaves were still sinks and respiration was higher than photosynthesis as reported by Flore and Lakso (1989) for several deciduous fruit tree species. This is in agreement with the results of Schaper and Chacko (1993), where Pn was close to zero in 2 week-old cashew leaves, since they have few and underdeveloped stomata (Liu et al., 1999). Furthermore, younger plant tissues typically have higher metabolic processes and their demand for photosynthates is higher than that of mature leaves (Kramer and Kozlowski, 1979). Dark respiration decreased rapidly during weeks 2-5 in young cashew leaves and then levelled off to a fairly constant value until the end of the measurements (Schaper and Chacko, 1993). Nooden (1980) indicated that as plant leaves grow they shift from being importers to exporters of photosynthates.

Photosynthesis increased significantly with increasing leaf age until the third leaf generation (90-180 DABB) (Table 4.3). Maximum photosynthetic rates were reached at 90-180 DABB when leaves were fully matured and thereafter remained constant. In cashew, a close family member of mango, leaves acquired their maximum Pn, stomatal conductance, and chlorophyll content at 50 days after leaf emergence (Schaper and Chacko, 1993), being very early compared to 90 DABB in mango (Fig 4.3). The relatively short period in the former crop was related to the shorter life span (1 year) of the leaves (Schaper and Chacko, 1993). Both older leaf generations (90-180 and >365 DABB) indifferently exhibited maximum Pn rates. The constant maximum net assimilation rate attained by leaves even older than 1 to 2 years showed that mango leaves remained photosynthetically active for a long time before their CO_2 assimilation rates declined concurrent with leaf senescence suggesting that they still represented sources of photosynthates (Schaffer et al., 1994). Lakso (1994)

indicated that apple leaves showed a similar pattern and such slow ageing was to enable adaptation to long growing seasons with high productivity. It was reported that photosynthetic rates in mature apple leaves declined slowly with age while maintaining relatively constant rates until harvest. This would be especially advantageous, since new apple leaf production usually stops in midsummer and productivity depends on existing leaves (Lakso, 1994). Contrasting results were found in cashew leaves, where maximum Pn was maintained from 50 to 196 DABB before it declined (Schaper and Chacko, 1993). In comparison to mango, many deciduous and subtropical/tropical fruit tree species showed an early decline in Pn after maximum assimilation has been reached. (Flore and Lakso, 1989; Schaper and Chacko, 1993; Lakso, 1994; Patakas et al., 1997; Whiley et al., 1999).

However, Flore and Lakso (1989) and Lakso (1994) indicated that deciduous trees had higher photosynthetic rates than those of tropical fruit trees, in order to compensate for the shorter life span (Whiley et al., 1999). Chartzoulakis et al. (2002) observed declining photosynthetic rates in mature avocado leaves and attributed the decrease to increasing stomatal and mesophyll resistance associated with ageing. Similarly, in grapes, maximum photosynthesis was reached at 35 days after unfolding and thereafter decreased gradually (Patakas et al., 1997). The lower ratio of mesophyll to stomatal resistance contributed to such high values and the gradual decrease was attributed to increasing mesophyll resistance with leaf age (Patakas et al., 1997). Schaper and Chacko (1993) and Schaffer et al. (1994) attributed the declined to decreasing chlorophyll content.

Interactions between season, leaf age, and time of the day were significant (Table 4.3). Across all leaf ages and both seasons, differences in diurnal photosynthetic rates were not significant except for late in the afternoon (16:15 h). The low Pn rates may have been attributed to decreasing PAR and temperature towards sunset.

Table 4.3 Effect of leaf age, season, and time of the day, on mean leaf photosynthetic rates in well-irrigated 6-7 year-old 'Kent' mango trees during winter (Jun 2002/Jul 2003) and summer (Jan 2003) (leaf age: n=20; season: n=40; time of the day: n=16; different letters depict significant differences between leaf age, season, and time of the day at P=0.05).

Factor	Leaf Photosynthetic Rate $(\mu mol\ CO_2\ m^{-2}\ s^{-1})$	
Season		
Winter	2.6 ± 1.8	b
Summer	5.5 ± 3.8	a
Leaf Age (DABB)		
> 25	0.1 ± 0.7	c
30-60	3.6 ± 1.7	b
90-180	6.3 ± 2.6	a
< 365	6.3 ± 2.9	a
Time of the Day		
09:00 h	4.7 ± 3.1	a
10:30 h	4.4 ± 3.3	a
13:00 h	4.4 ± 3.9	a
15:45 h	4.5 ± 3.4	a
16:15 h	2.4 ± 2.4	b

4.3.2 Photosynthetic responses of potted mango trees to water deficit

Water deficits have been shown to affect plant photosynthesis negatively (Townley-Smith and Hurd, 1979; Zulfugarov, 2001). However, reaction of plants to water deficit stress is influenced by various environmental factors such as light, VPD, and prevailing temperatures (Kramer and Kozlowski, 1979). During winter (Jun/Jul 2002), effects of water withdrawal on photosynthesis in 1 year-old, potted 'Sabre' mango

seedlings were significant after 9 days (Fig. 4.4). The onset of decreasing photosynthetic rates in response to water withdrawal took place most likely already at an earlier date between 5-9 days after the initiation of the drying cycle. Mean photosynthetic rates in the deficit irrigation treatment (non-irrigated) were lower than those of the well-irrigated treatment (irrigated), and some leaves started to respire indicating a severe water stress. Towards the end of the experiment (day 10-11) leaves of the non-irrigated seedlings showed some wilting signs and necrotic lesions although the latter ones may have been attributed also in part to sunburn, since the trees were exposed to sun during the entire period. Similar leaf degeneration characteristics at day 10 of water stress were observed in water stressed tomato leaves (leaf water potential = 0.7 MPa). Pn rates were reduced due to decreased chlorophyll content in the leaves (Kramer and Kozlowski, 1979; Schaper and Chacko, 1993). Very low photosynthetic rates (around 0 µmol CO_2 m^{-2} s^{-1}) of the deficit irrigation treatment indicated that leaves were severely dehydrated. The results suggested a strong reduction in the biochemical activity in the leaves as they dehydrated. In potted 'Tai so' (Mauritius) lychee trees photosynthesis fell to 18% of the value of watered plants at a leaf water potential of -3.2 MPa (Roe et al., 1995). Chartzoulakis et al. (2002) attributed the reduced CO_2 assimilation to the denser chlorenchyma (spongy) cells in non-irrigated 'Furte' leaves, thereby lowering the diffusion of CO_2, hence resulting in decreased amount of intracellular air spaces.

Visual observations in our experiment showed that some mango leaves were hanging vertically but upside down and had a papery texture. Water deficits apparently induced changes in the anatomy of avocado leaves (Chartzoulakis et al., 2002). Significant reductions in all histological components of the mesophyll as well as of the lamina thickness were observed in both 'Hass' and 'Fuerte' potted avocado trees (Chartzoulakis et al., 2002). Stems and petioles of the potted avocado trees showed some level of shrinkage due to loss of turgidity.

Non-irrigated 'Sabre' showed a quick decline in photosynthesis in response to water deficit in summer (Feb 2003) at day 2 after the onset of the drying cycle (Fig. 4.5) compared to day 4 in winter (Fig 4.4). The faster sensitivity of drought stressed trees could be attributed to higher evaporative demands in summer (6.4 $\pm$ 1.4 mm day^{-1}) in comparison to those in winter (3.4 $\pm$ 0.4 mm day^{-1}) leading, therefore, to more severe

water deficits in summer than in winter. During a period of water deficit, it is expected that enhanced transpiration would exceed the replacement of water to leaves resulting in an increased moisture deficits (Pongsomboon et al., 1992). In *Vitis vinifera* (grapes), the effect of VPD on stomatal closure appeared to be enhanced when plants were undergoing water stress (Behboudian and Singh, 2001).
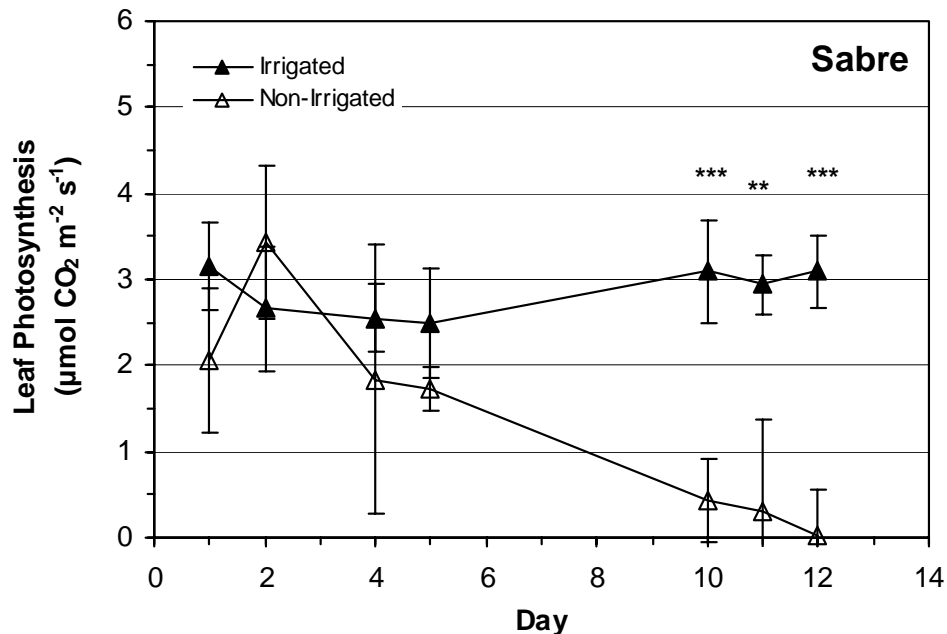

Fig. 4.4 Photosynthetic responses of non-irrigated 1 year-old, potted 'Sabre' mango seedlings to water deficit in comparison to irrigated ones at midday over an 11-day period during winter (Jun/Jul 2002) (each point represents mean ± SD of 4 replicate leaf samples, and asterisks depict significant differences between treatments at P=0.05).

During summer, water deficits significantly reduced net assimilation rate in both mango cultivars (Fig. 4.5). Net assimilation rates in non-irrigated 'Sabre' declined earlier than in 'Kent'; the decline taking place at day 2 in 'Sabre' and day 4 in 'Kent' after irrigation withdrawal. These results suggested that 'Kent' appeared to be more tolerant to water stress than 'Sabre'. However, 'Sabre' maintained generally slightly higher Pn rates than 'Kent' throughout the experiment.

In both cultivars, photosynthesis was severely reduced by water deficits during day 4 and 5 after the onset of the drying cycle (Fig. 4.5). Net assimilation rates were

significantly lower in non-irrigated 'Sabre' (2.5 ± 0.9 µmol CO_2 m^{-2} s^{-1}) and 'Kent' (1.4 ± 0.9 µmol CO_2 m^{-2} s^{-1}) than the well-irrigated treatments ('Sabre': 7.3 ± 1.2 µmol CO_2 m^{-2} s^{-1}, 'Kent': 5.6 ± 0.9 µmol CO_2 m^{-2} s^{-1}) during these two days. Non-irrigated 'Sabre' and 'Kent' leaves only photosynthesized 34 and 25%, respectively, of their respective irrigated treatment trees during day 4 and 5 of water withdrawal. Reductions in Pn rates of mangoes were similar to those reported for drought-stressed cucumber plants in greenhouse and field (37 and 27%, respectively, of photosynthesis) compared to well-watered plants (Janoudi et al., 1993). Similar results (27 and 35%, respectively) were reported for two avocado cultivars, 'Fuerte' and 'Hass' after 12 days of exposure to water deficit (Chartzoulakis et al., 2002).

Severe reductions of photosynthetic activity in mango trees were primarily effects of water deficit, since weather conditions (ETo: 6.0 ± 1.3 mm day^{-1}, temperature: 27.6 ± 1ºC, RH: 64 ± 7%, VPD: 1.4 ± 0.3 KPa, solar radiation: 15.0 ± 4 MJ m^{-2} day^{-1}) were favoring high carbon assimilation during day 4 and 5 in contrast to climatic conditions on day 1-3 (ETo: 6.6 ± 0.5 mm day^{-1}, temperature: 26.8 ± 1ºC, RH: 55 ± 2%, VPD: 1.6 ± 0.1 KPa, solar radiation: 20.4 ± 2 MJ m^{-2} day^{-1}). It has been shown that water deficits resulted in stomatal closure reducing photosynthesis (Janoudi et al., 1993; Pretorius and Wand, 2003). In cucumbers, VPD values in the range of 1.5-3.5 KPa associated with higher temperatures (34ºC) reduced CO_2 assimilation significantly in drought stressed plants, thus decreasing the water use efficiency (Janoudi et al., 1993). Similarly high VPD values of 3.7 KPa reduced photosynthesis in 'Braestar' apples at 30ºC (Pretorius and Wand, 2003). Photosynthetic inhibition may be caused by limitation of metabolic sequence (Zulfugarov, 2001), enzyme reaction (Lawlor, 1979), or electron transport (Townley-Smith and Hurd, 1979).

In some mango trees, leaves showed signs of wilting while some abscised. It has been widely established that water deficit in plants might result in accumulation of leaf abscisic acid (ABA) enhancing leaf drop (Fernandez et al., 1997). ABA was reported to reduce stomatal opening leading to reductions in Pn and transpiration, and consequently improving water use efficiency. Similarly, Yoon and Richter (1991) suggested that reductions in stomatal conductance were probably due to increased levels of ABA in leaves of sweet cherry.
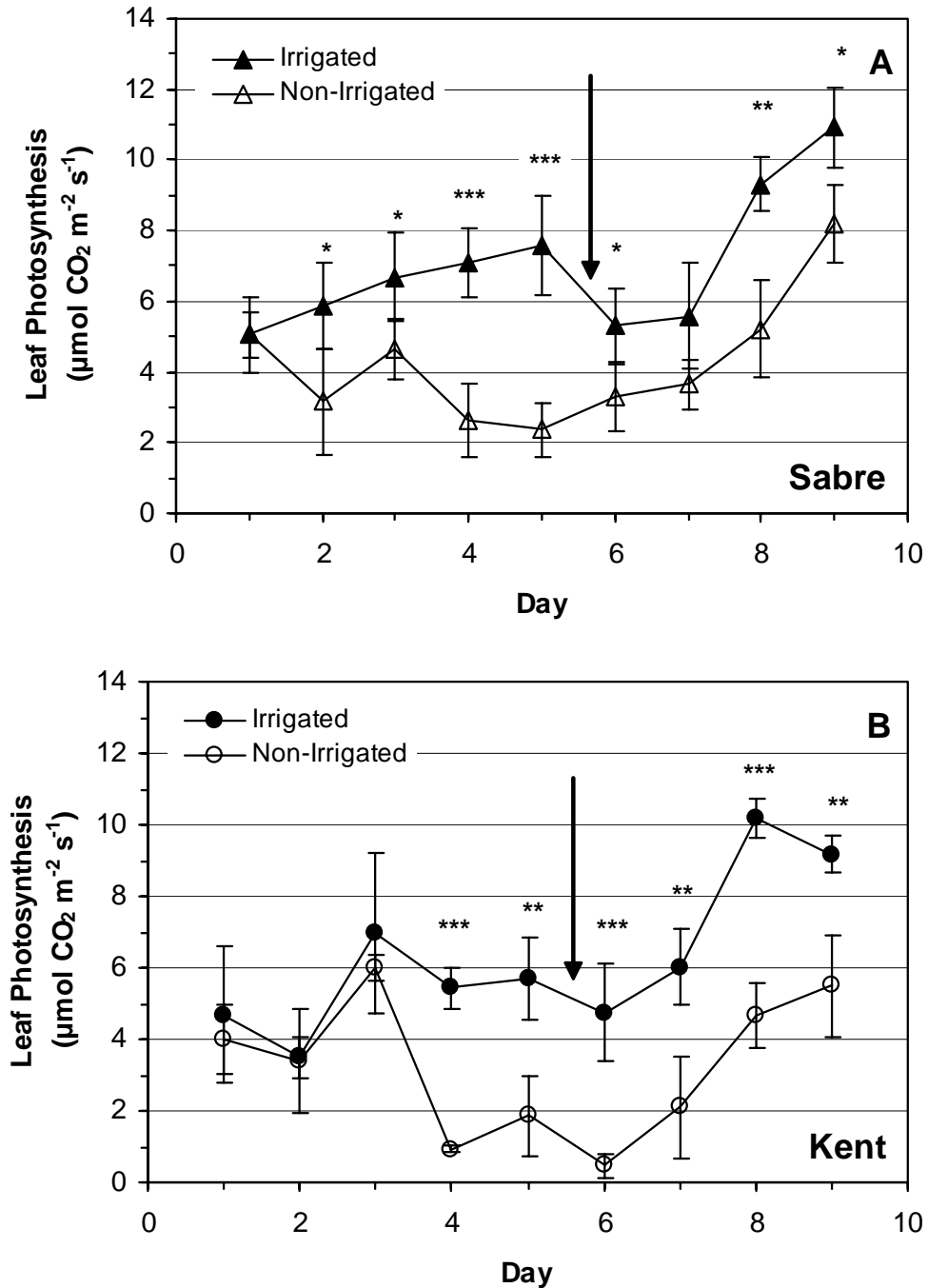
Fig. 4.5   Photosynthetic responses of non-irrigated, 1 year-old, potted 'Sabre' (A) and 'Kent' (B) trees to water deficit at midday in comparison to irrigated trees over a 10-day period during summer (Feb 2003) (each point represents mean ± SD of 4 replicate leaf samples, asterisks depict significant differences between treatments at P=0.05, and arrows indicate the date of re-irrigation in the deficit treatments (non-irrigated)).

Both stressed 'Sabre' and 'Kent' trees responded well to re-irrigation as shown by increasing Pn rates after re-irrigation. 'Sabre' was the earliest to recover on day 6 while 'Kent' started with the recovery a day later. However, recovery of both species was not completed within the 4 days studied, since Pn rates of well-irrigated trees were still significantly higher than those of non-irrigated ones, although Pn rates were generally higher on days 6-9 compared to the first days of the experiment concurrent with slightly decreasing evaporative demands (days 1-5: 6.3 ± 0.8 mm day^{-1}; days 6-9: 5.9 ± 1.0 mm day^{-1}). Lychees exposed to drought took up to 10 days after re-watering to achieve full recovery in photosynthesis (Roe et al., 1995). The slow recovery of lychee trees appeared to be related to the soil medium (clay) taking time to wet after a long drying cycle. Recoveries of mango and lychee took a longer time compared to cucumbers that recovered just 12 hours after re-irrigating (Janoudi et al., 1993). Janoudi et al. (1993) indicated that RuBP carboxylase activity recovered partially within one day after water stress was relieved suggesting that enzymatic activity might be regained very soon after dehydration.

Our results clearly showed the effects of water deficit on photosynthesis of potted mango trees. However, the results would not be completely applicable to the field trees, since the field grown trees might dry out more slowly because of a larger soil volume compared to potted trees. Reductions in gaseous exchange of potted mango trees took place after about 2-4 days of water withdrawal depending on cultivar. The small size of the pot and sandy nature of the growth media contributed to such rapid reduction in Pn rates by water deficits. According to Whiley et al. (1999) the lower Pn of container grown than field grown plants (mango and avocados) might be due to a carbon sink limitation (causing the photoassimilate supply to exceed the demand) as a result of root restriction in containers (end product inhibition of photosynthesis). Roe et al. (1995) suggested that pot experiments might mimic field trials, if young trees were to be exposed to intermittent drought periods.

Diurnal trends of potted mango trees on day 3 of water deficit showed that differences in photosynthetic rates between irrigated and non-irrigated 'Sabre' trees were significant over the day except for early in the morning (Fig. 4.6A). In 'Kent' trees, photosynthetic rates were only significantly different between treatments early in the morning and late in the afternoon (Fig. 4.6B).
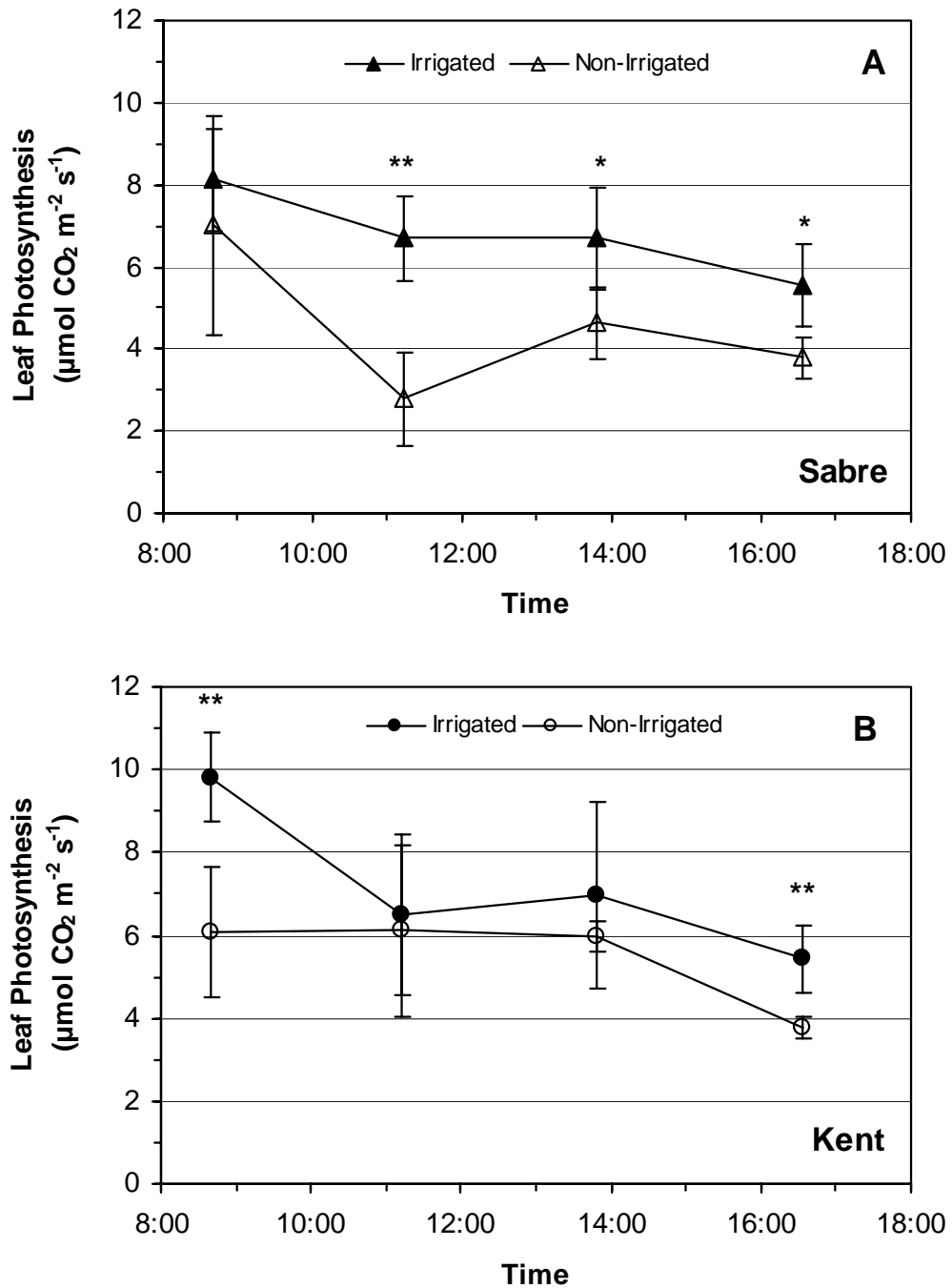
Fig. 4.6 Diurnal pattern of mean photosynthetic rates in irrigated and non-irrigated 1 year-old, potted 'Sabre' (A) and 'Kent' (B) mango trees on day 3 of the drying cycle in summer (Feb 2003) (each point represents mean ± SD of 4 replicate leaf samples; asterisks depict significant differences between treatments at P=0.05; ETo = 6.0 mm day^{-1}).

Severity of water stress induced by withholding of irrigation increased strongly from day 3 to day 5 as indicated by significantly lower Pn rates of non-irrigated trees compared to well-irrigated ones in both cultivars (Fig. 4.7), although evaporative demand was lower on day 5 than on day 3 (ETo: 5.1 and 6.0 mm day^{-1}, respectively). Roe et al. (1995) indicated that lower photosynthetic rates in potted lychee trees were attributed to stomatal closure in non-irrigated treatments. Such stomatal adjustment has been reported to increase water use efficiency (WUE) accompanied by a reduction of water loss in some plants (Clemente and Marler, 1996; Behboudian and Singh, 2001). In contrast, Pretorius and Wand (2003) concluded that decreased maximum photosynthesis in apples as a result of decreased stomatal conductance reduced the leaf WUE under optimum temperatures. Climatic conditions were favorable on day 5 for high photosynthetic rates (ETo: 5.1 mm day^{-1}; temperature: 27°C; RH: 68; VPD: 1.1 KPa) indicating that water deficit primarily caused reductions in photosynthesis of the non-irrigated mango trees.

Photosynthetic rates increased during the morning in 'Sabre' on day 5, while those of 'Kent' remained relatively constant (Fig. 4.7). Towards sunset Pn rates declined in both cultivars. Decreasing Pn rates towards sunset are common, since they are typical for the diurnal pattern of photosynthesis in woody trees (Flore and Lakso, 1989). This could be attributed to lack of photosynthetically active radiation and subsequent cooling experienced during the second half of the day. The cooling reaction allowed the night recovery of the water lost through transpiration during the day (Pongsomboon et al., 1992). However, Pongsomboon et al. (1992) found that stomatal conductance of 'Nam Dok Mai' potted mango trees recovered to near dawn levels by 18:00 h. Clemente and Marler (1996) suggested that the recovery of photosynthesis after stress might be slower than that of the stomata in papaya.
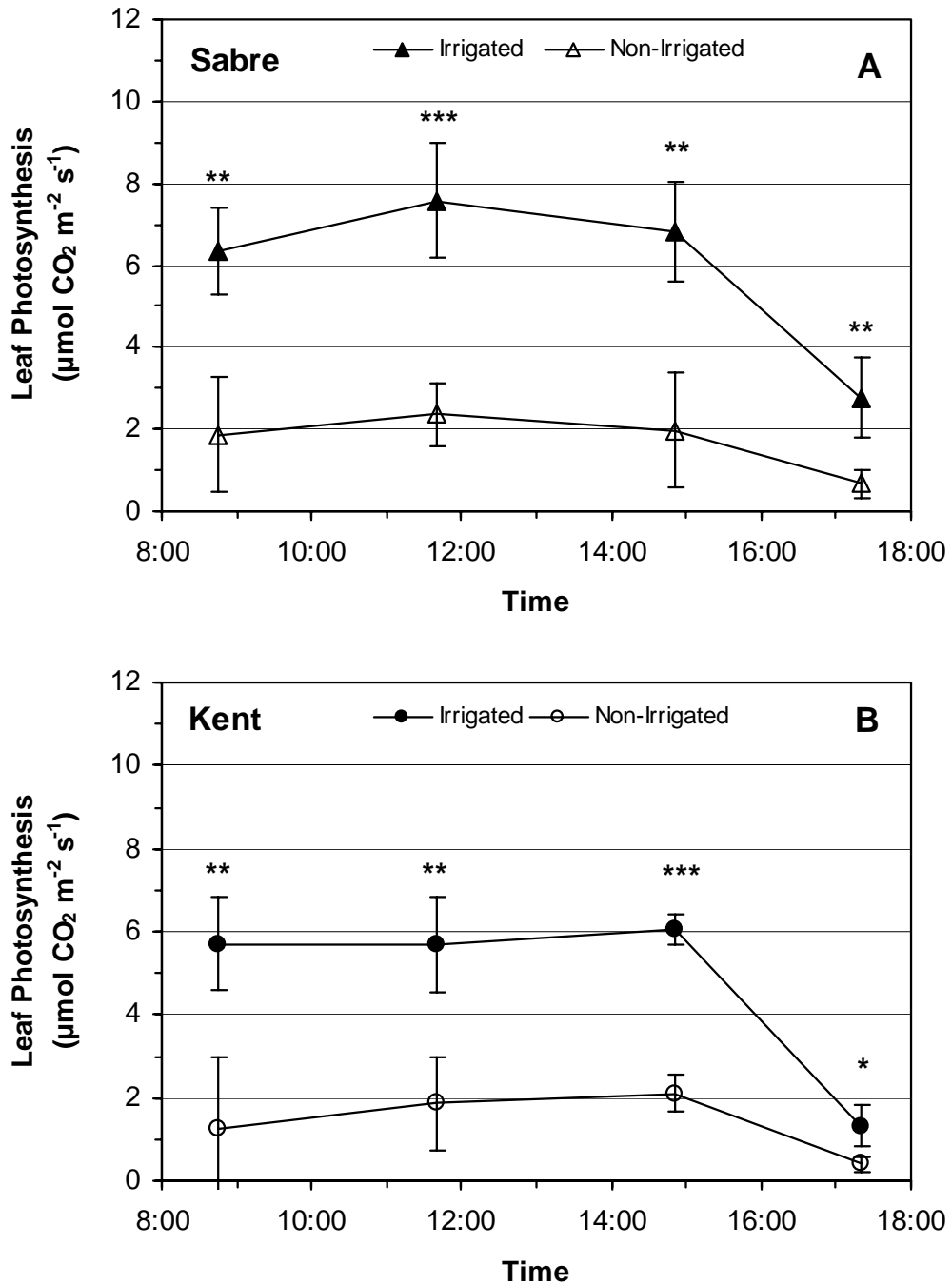
Fig. 4.7   Diurnal pattern of mean photosynthetic rates in irrigated and non-irrigated, 1 year-old, potted 'Sabre' (A) and 'Kent' (B) mango trees on day 5 of the drying cycle in summer (Feb 2003) (each point represents mean ± SD of 4 replicate leaf samples; asterisks depict significant differences between treatments at P=0.05; ETo = 5.1 mm day^{-1}).

4.3.3 Photosynthetic responses of mango trees to different irrigation regimes in the field

Responses to water deficits of plants grown under field conditions are different from that of plants cultivated in pots or under greenhouse structures, since environmental, soil and plant conditions vary. Contrasting results have been reported, and differences were explained with different climatic and soil conditions, different cultivars and techniques used for the studies. Mean photosynthetic rates were influenced by the various irrigation treatments over the season except for June and late July 2002 (Fig. 4.8). The lack of differences between the treatments in June 2002 (winter) was most likely associated with water reductions during the pre-flowering stage imposed on all treatments in order to induce flowering in growing areas where temperatures are not low enough (Smith, 1979; Cull, 1991). The deficit irrigation treatments, DI-1 and DI-2, photosynthesized at the same level as the well-irrigated treatments suggesting that these deficit-irrigated trees showed adaptation to water deficit stress. Preconditioning of plants to water deficit might have enabled them to tolerate subsequent water deficit stress better than trees not previously exposed to water deficits (Roe et al., 1995).

Stress adaptation was associated with less dense canopies, reduced leaf area and few vegetative flushes suggesting increased water use efficiency in comparison to the well-irrigated treatments. In contrast, trees of the standard farm treatment (Co-F) appeared to be less tolerant to water reductions, since the trees were acclimatized to higher moisture conditions. In addition, leaf reactions to water deficit were observed in Co-F trees, where the leaves changed their positional angles and rolled, showing higher sensitivity to water deficits. Water-stressed leaves normally change their positional angles, roll, curl, or display a V-shaped form in an attempt to reduce radiation load (Kramer, 1990; Walker and Nel, 1995; Schwabe and Lionakis, 1996). This way they limit the leaf area and subsequently the exposure of the stomata to sun leading to reduced leaf photosynthesis. Significantly higher photosynthetic rates of Co-F in June 2003 in comparison to the other treatments showed that Co-F was apparently not exposed to water reductions during the pre-flowering stage.

Mean photosynthetic rates of the farm control (Co-F) were not significantly different from those of the control (Co) except for June 2002 and 2003, although the farm applied 36% more water than it was applied to Co (E.W. Pavel, 2004: personal communication).
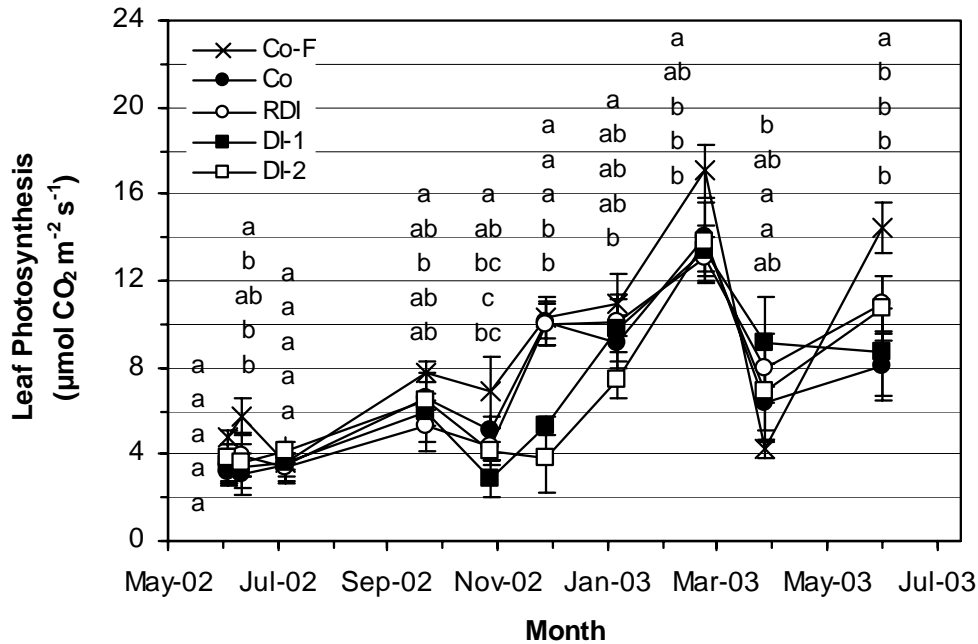

Fig. 4.8   Effect of different irrigation treatments (Co: 95 ± 3% of field capacity, FC; DI-1: deficit irrigation, ±79% of FC; DI-2: ±69% of FC; RDI: regulated deficit irrigation, like Co except for water reductions/withholding for two weeks at the end of Dec 2002/beginning of Jan 2003; Co-F: farm control, ±-10 KPa) on mean leaf photosynthesis of 6-7 year-old 'Kent' mango trees over the season 2002/2003 (each data point represents the mean ± SD of 4 replicate leaf samples; different letters in descending order according to the treatments Co-F, Co, RDI, DI-1, DI-2 depict significant differences between irrigation treatments at P=0.05).

During December 2002 (summer), photosynthesis was significantly reduced in the two deficit irrigation treatments (DI-1 and DI-2) in contrast to the other treatments indicating that photosynthesis was inhibited mainly by water supply in addition to environmental factors (Fig. 4.8). Low photosynthetic rates were associated with stomatal closure in avocado (Chartzoulakis et al, 2002) and olive (Giorio et al., 1999). Stomata closed in peach to reduce excessive water loss when evaporative demand was higher than water supply (Girona et al., 1993). An abrupt decrease in diurnal Pn

rates was observed in peach associated with increasing leaf temperatures (32-36°C), decreasing leaf water potential, and increasing VPD (Girona et al., 1993). Behboudian and Singh (2001) indicated that the effect of VPD on stomatal closure appeared to be more severe when plants were undergoing water deficit stress.

Field grown 'Kent' mango trees reached maximum leaf assimilation rate in March 2003 (late summer) in a manner similar to that observed in field grown olive (Giorio et al., 1999). Giorio et al. (1999) suggested that the decreased evaporative atmospheric demand that resulted from the decrease in air temperature, PAR and VPD contributed to the re-increase in leaf water status during this period. The farm control had significantly higher photosynthetic rates (17.1 $\pm$ 1.2 µmol CO_2 m^{-2} s^{-1}) than the irrigation treatments RDI, DI-1, and DI-2. The higher values in Co-F could have attributed to its higher tree water status favouring photosynthesis. The lack of differences between the other four treatments could have been an effect of apparent weather conditions relieving water stress. During April 2003, net assimilation rate of Co-F was the lowest (4.2 $\pm$ 0.5 µmol CO_2 m^{-2} s^{-1}) across all treatments. Increasing Pn rates during June could have resulted from branch thinning that was conducted in April. Thus the removal of shoots allowed better light penetration in contrast to the previous months, thereby promoting the light harvesting process especially in Co-F as indicated by the significantly high photosynthetic rates in comparison to the other four treatments.

When data of leaf photosynthesis in 'Kent' mango trees were confined according to season (winter, spring, summer, autumn), photosynthetic rates were significantly higher in summer than in autumn (Fig. 4.9, Table 4.4). Differences in Pn rates between spring and winter were not significant but both were significantly lower than autumn and summer across all irrigation regimes indicating the seasonal change in environmental conditions influencing photosynthesis. Low photosynthetic rates in winter seemed to be associated with low temperatures as observed by Pretorius and Wand (2003) in apple and with low photosynthetically active radiation in winter as suggested by Kramer and Kozlowski (1979) in trees.
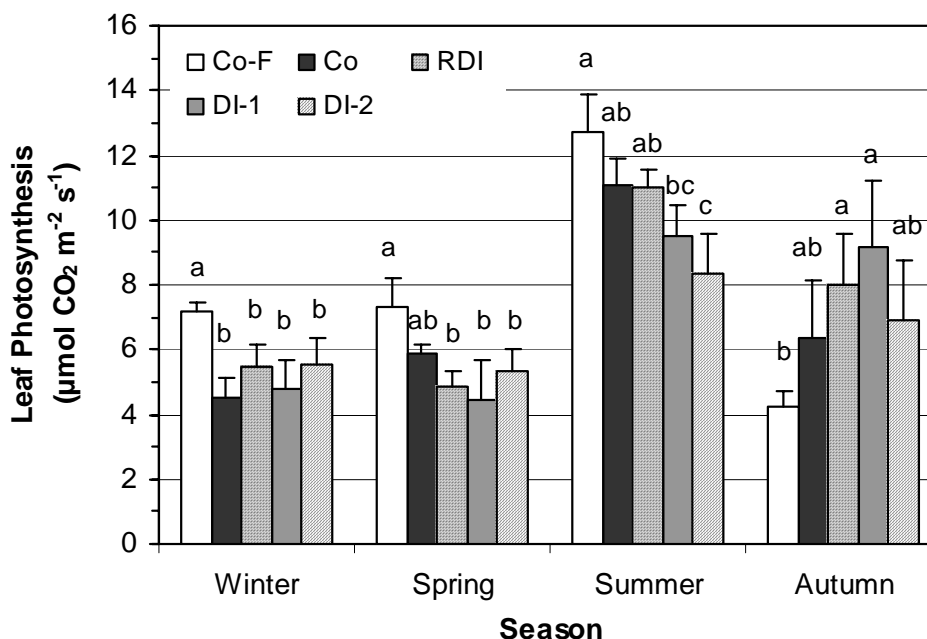
Fig. 4.9   Mean leaf photosynthesis of 6-7 year-old 'Kent' mango trees as affected by irrigation treatments during winter (Jun/Jul 2002/2003), spring (Oct/Nov 2002), summer (Dec 2002, Jan/Mar 2003), and autumn (Apr/May 2003) (each data point represents the mean $\pm$ SD of 4 replicate leaf samples; different letters depict significant differences between irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 4.8).

Interactions between season and irrigation treatments were significant (Table 4.4). The observed lack of significant differences in photosynthesis among the four irrigation treatments (Co, RDI, DI-1, and DI-2) throughout the season with the exception of summer might be due to the fact that deficit irrigation treatments were adapted to water deficit stress (Fig. 4.9, Table 4.4). The fact that photosynthesis of trees of the irrigation treatments DI-1, DI-2, and RDI appeared to be little affected by water deficit might indicate that these trees seemed to have been more water use efficient with respect to leaf assimilation than the control trees (Co) as has been observed in peach (Girona et al., 1993). Such response appears to be characteristic for plants that were preconditioned to water deficit stress or have been exposed to gradually increasing water stress over a fairly long period as reported in apricot by Ruiz-Sanchez et al. (2000). Considerable water savings were achieved because of higher water use efficiency of deficit irrigated trees, since they were adapted to lower irrigation regimes (E.W. Pavel, 2004: personal communication). Studies in peach indicated that 40% water savings were achieved in the RDI treatment (Girona et al.,

1993). In mango, about 26, 36, 62, and 75% water was saved in the irrigation treatments Co, RDI, DI-1, and DI-2, respectively, in comparison to the farm control (Co-F) (E.W. Pavel, 2004: personal communication). However, the treatment DI-2 appeared to be too severely stressed compared to the other treatments especially during summer (Fig. 4.9, Table 4.4) as shown by reduced vegetative growth (section 3.3.) concurrent with yield reduction (E.W. Pavel, 2004: personal communication).

Table 4.4 Effect of season and irrigation treatment on mean leaf photosynthetic rates in 6-7 year-old 'Kent' mango trees during the four seasons (winter: Jun/Jul 2002/2003; spring: Oct/Nov 2002; summer: Dec 2002, Jan/Mar 2003; autumn: Apr 2003 (season: n=20; irrigation treatment: n=16; different letters depict significant differences between season and irrigation treatments at P=0.05; for details about irrigation treatments see legend Fig. 4.8).

Factor	Leaf Photosynthetic Rate $(\mu mol\ CO_2\ m^{-2}\ s^{-1})$	
Season		
Winter	5.5 ± 1.1	c
Spring	5.6 ± 1.3	c
Summer	10.5 ± 1.8	a
Autumn	6.9 ± 2.2	b
Irrigation Treatment		
Co-F	7.9 ± 3.2	a
Co	7.0 ± 2.7	ab
RDI	7.3 ± 2.7	ab
DI-1	7.0 ± 2.7	ab
DI-2	6.5 ± 1.7	b

Several studies have been conducted to test the effectiveness of CO_2 assimilation rate as a water stress indicator (Girona et al., 1993; Marsal et al., 1997; Moriana and Fereres; 2002). According to Moriana and Fereres (2002), leaf photosynthesis might

not be a good indicator without other parameters such as stomatal conductance and stem water potential. When studying gas exchange in response to water stress, it has been shown in peach (Girona et al., 1993; Marsal et al., 1997) and olive (Moriana and Fereres, 2002) that photosynthesis responds more slowly to water deficits than stem water potential and stomatal conductance indicating that the parameter leaf assimilation rate was apparently not as efficient in detecting water deficits.

4.4 Conclusions

Our results showed the seasonal characterization of leaf assimilation in well-irrigated mango trees in the field. Information about diurnal curves and seasonal pattern of photosynthesis in the field is essential to optimize mango production, hence photosynthesis is related to the amount of dry matter produced and consequently to yield. The results will also provide important information for plant physiologists for further research. However, it would be more accurate in leaf age studies to tag the leaves and take measurements from the same leaves continuously. This way more reliable information can be achieved for as long as the leaves are not shaded.

Water deficits will without doubt reduce photosynthetic efficiency in mango trees, and plant productivity would be greatly hindered. Apart from measurements of photosynthesis, more advanced studies need to be conducted simultaneously in order to gain knowledge on physiological mechanisms involved in reduction of photosynthesis in mango trees by reduced irrigation. These would involve studies of all histological components of leaves, e.g. stomata, mesophyll, chloropyll and cells, as well as the biochemical reactions involved in response to water deficits. Although many farmers consider photosynthesis less important, it provides an indication of when production can be affected by water deficits. However, trees can have reduced photosynthesis and still attain reasonable yields due to increased water use

efficiency. Therefore, leaf photosynthesis, as a water deficit stress indicator would be more efficient if conducted with other plant water status indicators such as trunk growth, stem water potentials, etc. Simultaneous determination of fruit growth, yield, and quality would also be helpful to indicate if reduced photosynthesis in mango trees stressed by water deficit would consequently reduce yield.

5 Summary

During the 2002 post-harvest flush, shoot growth in young shoots (1 month old) was more prevalent through shoot extension whereas with older shoots (1- 1.5 years old) only diameter increase was visible, showing that older shoots displayed cambial growth. When irrigation treatments were compared in terms of vegetative growth, only the farm control (Co-F) showed significant growth, owing the vigorous growth to larger amounts of irrigation water applied. Shoots of the Co-F showed more than 50% shoot volume and dry mass than those of the control (Co) treatment indicating that a large amount of irrigated water was used for such vigorous growth. The other four irrigation treatments Co, DI-1 (continuously deficit irrigation 1), DI-2 (continuously deficit irrigation 2) and RDI (regulated deficit irrigation) did not differ significantly between each other in terms of vegetative growth.

At the end of the post-harvest flushes (June 2002 and May 2003) shoots were counted. During 2002 there were no significant differences in shoot number across all irrigation treatments, while the mean shoot number was higher in 2002 than that in 2003, indicating that 2003 was an off year in the biennial bearing cycle. During the second year, shoots of the continuously deficit irrigation treatments were severely reduced in number (only very few new shoots in the DI-2 treatment). The severe reduction of the post-harvest flush showed that after a long time of reduced irrigation, the physiological cycle of the mango tree could be manipulated. However, too severe reductions of irrigation water will be detrimental to future yield as observed in the treatment DI-2, since there were only few fruit bearing branches. The significantly higher number of shoots was recorded in flushes with 4-10 shoots per terminal (40% across both years) in Co-F in contrast to the other treatments, while the relative number of one shoot per terminal tended to be lower in Co-F. Furthermore, the larger number of new shoots per tree compared to the number of flushing terminals indicated that the production of multiple shoots per terminal was especially pronounced in this treatment across both years. The multiple shoots of one terminal might not be ideal for bearing not only due to their lack of physical support of the

fruits but also because of a lack of starch reserves attributed to their small stem volumes.

During the flowering flush in August 2002, vegetative and floral (mixed shoots included) shoots were counted and characterized according to number of canes/shoot per terminal. There were no significant differences between irrigation treatments with respect to number of flushing terminals and shoot number in the 2001/2002 season. However, the pattern of decreasing number of flushing terminals and shoot numbers concurrent with decreasing amounts of irrigation water applied (Co-F>Co>RDI>DI-1>DI-2) were similar to that of the post-harvest flush in the following year (2003). Results indicated that the 2002/2003 season was an off-year in mangoes following an on-year the previous season (2001/2002) in a biannual bearing cycle. Generally, the number of floral canes was up to 50% higher than that of vegetative shoots and mixed canes during the flowering flush.

Seasonal pattern of mango leaf photosynthesis revealed that in comparison to spring and summer net assimilation rate was highest during autumn and lowest in winter probably due to environmental conditions. Diurnal curves showed similar results as those of seasonal curves but there were differences in the shape of the curves in each season. For instance, during spring and winter midday depression of carbon assimilation rate was evident while photosynthesis increased to a maximum at 12:00 h during autumn and summer. Comparisons between cultivars showed that photosynthetic differences between 'Kent', 'Keitt' and 'Heidi' were inconsistent and less significant. With regard to leaf age comparison, young leaves (<25 days after bud break, DABB) appeared to have almost no photosynthetic activity since they were still sinks and not source of carbohydrates. Photosynthetic rate increased from leaves aged 30-60 DABB to those aged 90-180 DABB. There where no significant differences between leaves aged 90-180 DABB and those older than 365 DABB indicating that mango leaves might reach maximum photosynthesis when they are 1 year old and could maintain such rates for a longer period of time before leaves drop due to leaf senescence.

Water deficits affected negatively photosynthesis of potted and field-grown mango trees. Potted trees (1 year old) that were not irrigated yielded lower photosynthetic

rates than well-irrigated trees and the stress responses intensified with time taking approximately 4-5 days. When trees were re-irrigated after a period of water deficit, they did not reach the rates of well-irrigated trees even after a recovery period of 4 days. Effects of water deficit on leaf assimilation in field-grown trees were the very similar to those in potted plants. Among all irrigation treatments, trees of the Co-F treatment achieved the highest photosynthetic rates. Generally, photosynthetic rates were lower in potted trees compared to field-grown ones. Such reduced rates in 1-year-old trees were probably attributed to the small volume of growth media for roots due to the size of the pots.

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