

Ecophysiology of papaya: a review

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Papaya (*Carica papaya* L.) is a principal horticultural crop of tropical and subtropical regions. Knowledge of how papaya responds to environmental factors provides a scientific basis for the development of management strategies to optimize fruit yield and quality. A better understanding of genotypic responses to specific environmental factors will contribute to efficient agricultural zoning and papaya breeding programs. The objective of this review is to present current research knowledge related to the effect of environmental factors and their interaction with the photosynthetic process and whole-plant physiology. This review demonstrates that environmental factors such as light, wind, soil chemical and physical characteristics, temperature, soil water, relative humidity, and biotic factors such as mycorrhizal fungi and genotype profoundly affect the productivity and physiology of papaya. An understanding of the environmental factors and their interaction with physiological processes is extremely important for economically sustainable production in the nursery or in the field. With improved, science-based management, growers will optimize photosynthetic carbon assimilation and increase papaya fruit productivity and quality.

Key words: *Carica papaya*, environmental factors, photosynthesis, water relations, water-use efficiency

Ecofisiologia do mamoeiro: uma revisão: O mamoeiro (*Carica papaya* L.) é uma das principais culturas das regiões tropicais e subtropicais. O conhecimento das respostas dessa cultura aos fatores do ambiente pode fornecer bases científicas para traçarem-se estratégias de manejo que possam otimizar a produção e a qualidade dos frutos. Um melhor entendimento das respostas dos genótipos aos fatores específicos do ambiente poderá contribuir para um eficiente zoneamento agrícola e para futuros programas de melhoramento da espécie. Objetivou-se apresentar o estado-da-arte do conhecimento relacionado aos efeitos e à interação dos fatores ambientes sobre o processo fotossintético e a fisiologia da planta inteira. Nesta revisão, demonstra-se que os fatores do ambiente, como luz, vento, característica físicas e químicas do solo, temperatura, água no solo, umidade relativa, além de fatores bióticos, como fungos micorrízicos e o genótipo, podem afetar intensamente a produtividade e a fisiologia do mamoeiro. Uma compreensão da ação dos fatores do ambiente e suas interações com o processo fisiológico dessa espécie são de grande importância para a sustentabilidade econômica da produção do mamoeiro, em condições de viveiro e de campo. A partir de um manejo da cultura baseado em resultados científicos, será possível otimizar a assimilação fotossintética do carbono e elevar a qualidade e produção de frutos do mamoeiro.

Palavras-chave: *Carica papaya*, eficiência do uso da água, fatores ambientes, fotossíntese, relações hídricas

INTRODUCTION

Papaya (*Carica papaya* L.) is herbaceous, but its stature is not that of a typical herbaceous plant. Papaya plants may reach heights of 9 m, and are thus described as giant herbs (Malo and Campbell, 1986). The plants have a rapid growth rate, are usually short-lived, but can

produce fruit for more than 20 years (Malo and Campbell, 1986). The center of diversification of papaya was in the lowlands of Central America and southern Mexico, possibly the West Indies (Caribbean) (Crane, 2005). Though the exact area of origin is unknown, the papaya is believed to be native to tropical America, perhaps in

southern Mexico and neighboring Central America (Morton, 1987). Commercial papaya cultivation is restricted to tropical and subtropical areas due to chilling damage at temperatures above freezing (Yadava et al., 1990). Understanding the interaction of papaya with environmental factors such as light, wind, temperature, relative humidity, soil water, and soil physical and biological characteristics, is necessary to maximize yield and quality limiting effects of these factors on the photosynthetic process. Knowledge of how papaya responds to these environmental factors provides a scientific basis for the development of management strategies to optimize fruit yield and quality (Schaffer and Andersen, 1994). A better understanding of genotypic responses to the environmental factors will contribute to efficient agricultural zoning and genetic breeding programs for papaya. The objective of this review is to present the current research knowledge related to the effect of environmental factors and their interaction with the photosynthesis process and whole plant physiology in papaya.

ECOPHYSIOLOGY OF PAPAYA

Environmental factors affecting photosynthesis: Papaya is classified as a plant with C_3 metabolism (Imai et al., 1982; Marler et al., 1994; Campostrini, 1997; Marler and Mickelbart, 1998; Jeyakumar et al., 2007) with characteristic C_3 leaf anatomy. The absence of margin cell formation in the vascular bundles of papaya leaves (Buisson and Lee, 1993) is a characteristic associated with C_3 metabolism. Maximum net carbon assimilation (A) rates of 25 to 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ are achieved at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photo flux density (PPFD) (Marler and Mickelbart, 1998; Campostrini and Yamanishi, 2001; Reis, 2007). While photorespiration in C_3 plants can decrease the net efficiency of carbon assimilation by 25 to 30% (Lawlor, 1993), papaya can maintain high A rates under well-watered and PPFD saturating conditions suggesting minimal photorespiration losses and adaptation to high light intensities. Cultivar also influences maximum A rates, as noted by Campostrini et al. (2001) who found maximum A rates of 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for cv. 'Baixinho de Santa Amália' and 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for cvs. 'Sunrise Solo 72/12', 'Sunrise Solo TJ' and 'Know-You'. While high A rates are possible in papaya, environmental factors often limit

A . The PPFD response of papaya may also decline with PPFD above saturating levels. Jeyakumar et al. (2007) demonstrated that in field-cultivated papaya, PPFD light saturation was 1250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with $A = 12 \mu\text{mol m}^{-2} \text{s}^{-1}$ but at PPFD levels above 1250 $\mu\text{mol m}^{-2} \text{s}^{-1}$, A rates fell sharply to values of 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The decrease in A that begins at light saturation is due, in part, to the decrease in stomatal conductance (g_s) through the direct action of radiant energy on leaf heating. Chronic photoinhibition also decreases A rates at light levels above saturation, in this case through damage and replacement of the D1 protein in the reaction center of PSII by excess PPFD (Critchley, 1998). Sink strength will also limit A rates in papaya (Campostrini and Yamanishi, 2001).

The photosynthetic response of papaya is strongly linked to environmental conditions through stomatal behavior. Clemente and Marler (1996) measured the interaction of A and g_s in 'Red Lady' papaya leaves in response to sudden changes in PPFD. When the PPFD decreased sharply from 2000 to 320 $\mu\text{mol m}^{-2} \text{s}^{-1}$, A decreased from 20 to 9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in only 20 s while g_s decreased from 385 to 340 $\text{mmol m}^{-2} \text{s}^{-1}$ in about 200 s demonstrating a non-stomatal response to short-term variation in PPFD. Rapid stomatal response is important in tropical regions due to the intermittent clouds that create high fluctuations in the PPFD during the day. The intermittent clear skies and cloud cover of tropical regions impose severe stress on plants as leaves adapt to large changes in radiant energy. Clemente and Marler (1996) demonstrated that papaya leaves react to these transitions with a tracking response by stomata in which g_s declined in response to a rapid reduction in irradiance. Tracking of g_s was not of the same speed or magnitude as that of A , but it did limit water loss quickly under simulated cloud cover. This tracking response provided an increase in water-use efficiency (WUE) during periods of low irradiance. The WUE returned to maximum almost immediately after the return to full sunlight. The rapid response of g_s would allow papaya plants to maximize WUE throughout the day. A consequence of maximizing WUE by minimizing water loss during episodes of low irradiance is that carbon gain is not maximized. Papaya plants under a mild water stress maintained higher g_s during simulated cloud cover than plants under more severe water stress resulting in greater carbon gain.

Midday depression of photosynthesis (MDP) has been observed in papaya (Reis, 2003, 2007). The MDP occurs because the increasing PPFD on the leaf surfaces raises leaf and air temperature resulting in a greater leaf-to-air vapor pressure deficit ($VPD_{leaf-air}$) and g_s decreases with increasing $VPD_{leaf-air}$. In many cases MDP is an evolutionary strategy to cope with environmental stress (Xu and Shen, 1997). Midday stomatal closure and down-regulation of photochemical efficiency are effective ways to avoid excessive water loss and photodamage to the photosynthetic apparatus under strong sunlight and dry conditions (Xu and Shen, 1997). For example, Marler and Mickelbart (1998) reported that 'Red Lady' papaya had decreased g_s under clear sky conditions as midday approached but the quantum efficiency of open photosystem II centers (estimated via the variable-to-maximum chlorophyll fluorescence ratio, F_v/F_m) was above 0.75 and comparable to less harmful conditions. While MDP as a regulatory process is advantageous for the survival of plants under stressful conditions, it occurs at the expense of effective use of light energy and plant productivity. It is estimated that midday depression may decrease overall crop productivity by 35-50% or more (Xu and Shen, 1997).

Reis (2007) found papaya MDP during the summer, which was primarily attributable to stomatal response to high $VPD_{leaf-air}$; in contrast he did not observe MDP during winter conditions when $VPD_{leaf-air}$ values were low. According to Reis (2007) canopy microspray irrigation prevented MDP and increased g_s and transpiration at midday in the summer by reducing the leaf temperature and the $VPD_{leaf-air}$. Canopy irrigation increased fruits per plant by maintaining A rates at midday similar to A rates at 0800 h ($A = 20 \mu\text{mol m}^{-2} \text{s}^{-1}$). Allan and Jager (1978) also used intermittent spray irrigation of papaya canopies to reduce high temperature stress by evaporative leaf cooling and improved plant growth. Similarly, Reis and Campostrini (2005) demonstrated that microspray irrigation above the canopy of 'Golden' papaya at midday on summer days with clear skies reduced $VPD_{leaf-air}$, increased g_s and transpiration and, ultimately, increased A .

The $VPD_{leaf-air}$ may be a fundamental factor for agricultural zoning of papaya cultivation because it will determine the regions with the greatest productive capacity. Several studies (El-Sharkawy et al., 1985; Marler and Mickelbart, 1998; Reis, 2003; Machado Filho et al.,

2006) have shown that even with high soil water availability, a high $VPD_{leaf-air}$ contributes significantly to the reduction of g_s and, consequently, to reduction in A . In papaya plants cultivated in the field, Reis (2003) reported a high and negative relationship between $VPD_{leaf-air}$ and g_s . He found that on days with clear skies and high soil water availability, $VPD_{leaf-air}$ values between 6 and 7 kPa corresponded to A rates approaching zero. A similar relationship between $VPD_{leaf-air}$ and g_s was obtained by El-Sharkawy et al. (1985). According to El-Sharkawy et al. (1985), papaya was extremely responsive to $VPD_{leaf-air}$ and in environments with a 3.5 to 4.5 kPa $VPD_{leaf-air}$, the A rates were nearly halved as compared with plants grown in environments with $VPD_{leaf-air}$ of 1.0 to 1.5 kPa. In the Savanna region of Bahia State, northeastern Brazil, the VPD_{air} in November and December is ca. 1.25 kPa at 1500 h, but ca. 2.6 kPa at 1500 h. in July and September (dry season). These seasonal environmental conditions caused stomata closure in two papaya genotypes ('Tainung' and 'Sunrise Solo') resulting in reduced A rates (Machado Filho et al., 2006).

There is genetic variation in papaya response to $VPD_{leaf-air}$. For example, Torres-Netto (2005) found that the 'Golden' genotype, which has a low leaf chlorophyll content compared to other cultivars ('JS12', 'Tainung', 'Solo7212' and 'Hybrid UENF/Caliman 01') with dark green leaves, had greater g_s and transpiration at midday on cloudless days in the greenhouse. The pale green coloring of the 'Golden' leaf may substantially increase reflection of light and reduce leaf temperature, thus allowing increases in g_s . Chlorophyll ($a+b$) contents from 10 to 50 $\mu\text{g cm}^{-2}$ increased papaya leaf absorptance from 50 to 88% (Lin and Ehleringer, 1982a). An understanding of the mechanisms controlling gas exchange is important in developing papaya genotypes adapted to specific regions.

Papaya has optimal growth and development at air temperatures between 21 and 33°C (Knight, 1980), or, according to Lassoudiere (1968), between 22 and 26°C. Allan and Jager (1978) reported that A increased when air temperature rose from 16 to 30°C, and then A decreased linearly at temperatures above 30°C, the value at 41°C being half that at 30°C. Air temperature acts indirectly on papaya via increases $VPD_{leaf-air}$. As stated earlier, the $VPD_{leaf-air}$ is a major environmental control factor of g_s . For example: when air temperature increased from 20° to 40°C

for 'Sunrise Solo' growing in Linhares, southeastern Brazil, the $VPD_{leaf\ air}$ increased from 2 to 6 kPa and A decreased from 20 to 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Torres-Netto, 2000).

Due to its origin in tropical environments, papaya is classified as a species sensitive to low temperatures (Ogden et al., 1981). The quantum efficiency of open photosystem II centers (F_v/F_m) was 0.42 in the winter (6/17°C, minimum/maximum temperatures) and 0.72 in the summer (18/26°C) minimum/maximum temperatures) demonstrating that low temperatures likely reduced PSII activity (Smille et al., 1979). Papaya fruits become insipid when they ripen in periods when the temperature is at a sub-optimal level (Wolfe and Lynch, 1940) and temperatures below 20°C result in other problems such as carpelloidly, gender changes, reduced pollen viability, and low-sugar content of fruits (Galán-Saúco and Rodríguez-Pastor, 2007).

Wind action (2.78 to 4.30 m s^{-1}) reduced plant height and decreased leaf and stem dry matter, but not root dry matter, in some papaya cultivars; these changes were accompanied by a reduction in A rates and increase in dark respiration rates (Clemente and Marler, 2001). Decreases in A could be associated with wind effects on decreasing g_s (and consequently transpiration). From the above, it may be proposed that where strong wind is frequent, windbreaks should be recommended to improve crop performance.

Actual and potential A rates are positively correlated with chlorophyll content and transient chlorophyll fluorescence (Strasser and Strasser, 1995; Force et al., 2003; Castro, 2005). Chlorophyll pigments are particularly sensitive to oxidative attack and photodamage, whereas carotenoids function naturally as antioxidants and in quenching photoinduced excitations. Changes in chlorophyll-to-carotenoid ratios are therefore potentially sensitive indicators of oxidative damage (Hendry and Price, 1993). The loss of these pigments may also be considered as an indicator of water deficiency (Hendry and Price, 1993) and senescence (Lin and Ehleringer, 1982b; Torres-Netto et al., 2002, 2005; Castro, 2005). Castro (2005) found that F_v/F_m and the physiological state of the photosynthetic apparatus (F_o/F_m) in PSII were unrelated to chlorophyll content for 'Golden' and 'Sunrise Solo' when chlorophyll content was adequate but there was a correlation at reduced chlorophyll levels. This lack of correlation suggests that degradation of PSII

in these genotypes occurs after the degradation of a specific number of chlorophyll molecules (<556 $\mu\text{mol m}^{-2}$ for 'Sunrise Solo' and <604 $\mu\text{mol m}^{-2}$ for 'Golden'). Apparently, the genotype 'Sunrise Solo' was more sensitive to PSII damage at reduced chlorophyll levels. Decreased chlorophyll concentration in papaya leaves of 'Golden' and 'Sunrise Solo' reduced the effective antenna size, maximal trapping rate of PSII, concentration of active reaction centers, and electron transport in a PSII cross-section (Castro, 2005).

Single-leaf measurements of photosynthesis in papaya are useful in comparing experimental treatments and provide information that cannot be obtained by other biological indicators of plant productivity such as dry matter (Perez Pena and Tarara, 2004). However, leaf-level photosynthesis measurements can provide incomplete and potentially misleading information if extrapolated to quantify photosynthesis or infer differences in crop productivity at the whole-plant level (Quereix et al., 2001). Unlike single-leaf photosynthesis measurements, whole-canopy measurements provide an integrated value of net carbon fixation and transpiration and integrate the response of the entire canopy (Poni et al., 1997). T.M. Ferraz (unpublished results) measured whole-canopy A rates of 19 $\text{g CO}_2 \text{ m}^{-2} \text{ leaf area day}^{-1}$ (67 $\text{g CO}_2 \text{ plant}^{-1} \text{ day}^{-1}$) and transpiration rates of 2.46 $\text{L H}_2\text{O m}^{-2} \text{ leaf area day}^{-1}$ (8.6 $\text{L H}_2\text{O plant}^{-1} \text{ day}^{-1}$) under commercial field conditions. There was a high correlation between single-leaf and whole-canopy photosynthesis measurements, possibly due to the angles and distribution of papaya leaves that optimized canopy structure allowing more light to reach lower leaves. In contrast, instantaneous transpiration single leaf measurements overestimated whole-canopy transpiration by more than 50%. Water-use efficiency was about 154 g of water use for every gram CO_2 assimilated by photosynthesis (T.M. Ferraz, unpublished results).

The source-sink balance is critical for papaya fruit set, development, and sugar accumulation. In general, each mature leaf can provide photoassimilate for about three fruits (Zhou et al., 2000). The photosynthetic capacity also influences papaya fruit quality (Salazar, 1978). Defoliation by *ca.* 75% significantly reduced new flower production and fruit set, decreased ripe fruit total soluble solids (TSS), whereas 50% defoliation did not reduce new fruit set or ripe fruit TSS. Continual removal of old leaves

reduced new fruit set, fruit weight, and TSS (Zhou et al., 2000). Fruit thinning increased new fruit set and ripe fruit TSS.

Light quality effects on papaya anatomy, physiology and photosynthesis: Papaya adapts to light quantity and quality. Buisson and Lee (1993) compared plants cultivated in high (full) sunlight (HL) to those either cultivated with light reduction (60%) using greenhouse plastics that did not alter the spectral quality (neutral shade, NS) or cultivated under altered spectral quality of the light [modified by reducing the red-to-far red radiation ratio (R:FR = 0.26)] without reducing the PPFD by using an experimental spray paint designed to reduce R:FR to ratios under forest canopies (Lee, 1998) (filtered shade, FS). Compared to HL-grown plants, the plants cultivated in the NS and FS environments had reduced leaf thickness, petiole length, specific leaf weight and stomata density with increased chlorophyll content, and degree of air space. Papaya grown in the FS environment had reduced leaf lobules, and longer internode length compared to the other treatments. Plants grown under HL produced the thickest stems compared to FS and NS treatments, whereas FS-grown plants were the tallest, followed by HL- and NS-grown individuals. Buisson and Lee (1993) reported that the reduced (0.26) R:FR ratio of foliage shade presumably altered the phytochrome equilibrium and consequently the morphology and anatomy of papaya leaves.

Reis et al. (2005) also demonstrated that the photosynthetic apparatus of papaya may adapt to changes in light intensity and quality. 'Baixinho de Santa Amália' papaya cultivated in the summer and winter in the greenhouse (ca. 30% sun light interception), compared to plants grown in full sunlight, had higher A and greater g_s at midday, which was attributable to reductions in the $VPD_{\text{leaf-air}}$ under greenhouse conditions. Similarly, Galán-Saúco and Rodríguez-Pastor (2007) found that in the Canary Islands, where papaya is often grown in greenhouses, growth and flowering habits benefited from the climatic modifications of the greenhouse. These authors also noted that, in addition to improved yields, both in quantity and quality, and reduced water consumption, there was the additional benefit of Papaya Ringspot Virus (PRV) exclusion, which may facilitate

profitable greenhouse production in subtropical areas. Thus, we propose that greenhouse papaya cultivation may be an alternative production system because papaya can adjust to as much as 30% reduction in PPFD.

Soil water availability effects on papaya physiology and productivity: Papaya exhibits both stomatal and non-stomatal response to soil water deficits and the source of the response signals are both hydraulic and non-hydraulic in nature. Marler et al. (1994) proposed that it is highly unlikely that stomata of drought-stressed papaya plants closed due to hydraulic signals from leaf dehydration since leaf relative water content (RWC) and pre-dawn xylem potential (Ψ_{pd}) were unrelated to g_s at mild and moderate soil water deficits. They proposed that other non-hydraulic plant signals are controlling stomatal behavior. Marler et al. (1994) also suggested that delaying dehydration appears to be the adaptation that papaya uses in response to drought, even though osmotic adjustment was not demonstrated. However, Mahouachi et al. (2006) found that osmotic adjustment is a contributing factor in drought adaptation in 'Baixinho de Santa Amália' papaya. In any case, Marler et al. (1994) and Torres-Netto (2005) demonstrated that there is genetic variability in papaya cultivar response to soil water deficits providing clues to the mechanisms of drought adaptation. In some cultivars there was no alteration in the leaf RWC and Ψ_{pd} whereas in others these characteristics were affected by water stress. In 'Golden' and 'Hybrid UENF/Caliman 01' grown under moderate and severe water deficits, leaf RWC, Ψ_{pd} , osmotic potential, SPAD chlorophyll content and g_s all were reduced (Torres-Netto, 2005) regardless of the studied cultivars. In addition to the stomatal effects, moderate and severe water stress reduced the photochemical quenching values (q_p) and F_v/F_m while increasing non-photochemical quenching (q_N). 'Golden' had the largest reduction in F_v/F_m , although water stress effects on q_p and q_N were similar for both 'Golden' and 'Hybrid UENF/Caliman 01' cultivars. Torres-Netto (2005) also found that, irrespective of cultivars, the epoxidation state increased mainly under severe stress whereas the specific leaf weight was remarkably reduced in moderate and severe stress. In any case, the 'hybrid' cultivar had greater reductions in canopy and root dry matter than 'Golden' in

response to water deficit treatments. In contrast to the results of Torres-Netto (2005), Marler and Mickelbart (1998) observed in field-grown papaya that A was halved in 'Red Lady' with no reduction in F_v/F_m under drought stress, suggesting tolerance of PSII to drought events.

Non-stomatal effects of soil water deficits are demonstrated when a stressed plant is re-watered but fails to return to the pre-stressed physiological state. Upon withholding watering for 'Golden' cv. for 5 d, A rates were reduced by both stomatal and non-stomatal effects (Reis et al., 2004). After re-watering g_s , but not A , returned to pre-stress levels; probably A was limited by biochemical and photochemical damage affecting chlorophylls. Campostrini et al. (2004) demonstrated that under severe water deficit, the energy absorbed in the pigment antenna was greater than the electron transport resulting in increased energy dissipation and a smaller quantity of energy used in the photochemistry. Water stress damaged the PSII chemical efficiency and this damage could be measured on the first day after suspending irrigation. Lawlor and Cornic (2002) demonstrated that severe water stress ($RWC < 75\%$) would damage the photochemical and biochemical system and such damage may be associated with ribulose-1,5-bisphosphate regeneration that would decrease ATP synthesis. This damage may chronically reduce the photosynthetic process and delay or even prevent complete re-establishment of photosynthesis after re-irrigation. In contrast, in 'Baixinho de Santa Amália', despite A having been progressively decreased over the course of the dehydrating cycle, reaching 73% of the control after 40 d of water deficit, it fully resumed upon re-hydration (Mahouachi et al., 2007), even though the stress caused leaf drop that began to occur 7 d upon suspending irrigation. Non-hydraulic signals such as abscisic acid (ABA) and jasmonic acid (JA), but not indole-3-acetic acid, differed in their accumulation patterns under stress. Whereas ABA continuously increased in leaves and roots during the whole period of stress, JA initially increased and then decreased in both organs. Mahouachi et al. (2007) proposed the involvement of ABA as an accumulative, non-hydraulic hormonal signal that could be involved in the induction of several physiological responses in papaya under progressive water stress such as the reduction in gas exchange parameters and leaf abscission.

Irrigation management of papaya to increase water-use efficiency: Manipulating wetting patterns of the papaya root zone is a technique to increase WUE. Partial Rootzone Drying (PRD) is a technique in which a portion of the root system is dried while the remaining roots are kept well watered (Loveys et al., 2004). In PRD, ABA and other chemical signals produced in the drying roots will presumably reduce g_s and leaf growth (Gowing et al., 1990) while increasing WUE. In Brazil, Gomes et al. (2005a,b) demonstrated that, compared to well-watered controls, PRD increased papaya WUE in 'Golden' and 'UENF/Caliman 01' via reduction in g_s , but without affecting the dark-adapted activity of PSII reaction centers, SPAD readings, A rates or growth characteristics. The expected ABA accumulation under PRD conditions was not measured in 'Golden' but was demonstrated in 'UENF/Caliman 01'. In 'Golden', the interaction between the $VPD_{\text{leaf-air}}$ (2 to 3 kPa) and the PRD treatment might have caused earlier stomata closure at lower leaf ABA levels compared to 'UENF/Caliman 01' (Gomes et al., 2007).

Subsurface irrigation is another technology that may increase WUE in papaya production. Subsurface drip irrigation led to significantly higher fruit yield (121.4 compared to 110.6 t ha⁻¹) and higher WUE (40.6 compared to 37.2 kg ha⁻¹ mm⁻¹) at the 20% and 120% replenishment rates than surface drip irrigation (Srinivas, 1996). These studies demonstrate that the papaya root system will adapt to alternative wetting patterns of PRD and subsurface irrigation to increase WUE.

A direct measurement of sap flow through the papaya trunk would insure efficient water management in commercial orchards and provides a useful methodology to measure papaya response to environmental stress. Reis et al. (2006) determined the relationship between sap flow through the trunk and temperature gradients in the trunk using probes inserted in the papaya plant stem (Granier method). These authors constructed an instrument that maintained a stable water flux through 0.30 m stem section with a constant pressure, simulating the xylem sap flow through the stem. A sap flow rate of 0.6 L h⁻¹ m⁻² corresponded to A rates of 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and there was a significant relationship ($R^2 = 0.76$, $P < 0.05$) between A rates and xylem flow in field-grown papaya. There are, however, limitations to the use of the water flow equipment in papaya. Reis (2007) measured a

significant relationship ($R^2 = 0.68$) between potential evapotranspiration, ET_0 (mm h^{-1}), $VPD_{\text{leaf-air}}$ (kPa), irradiance (W m^{-2}) and sap flow ($\text{L h}^{-1} \text{m}^{-2}$ leaf area) in the summer, but in the winter no relationship could be established. The lack of winter season correlation is due to a 'lag phase' between environmental demand for water and papaya supply capacity. In the winter there was water loss through the canopy early in the morning with no water movement from the trunk region where the probes were inserted. Thus, there was a water demand from the atmosphere without an effect on the sap flow probes. Conversely, at sunset, when there was no demand from the atmosphere, water passage was observed through the probe and this movement was to supply the water deficit in the papaya canopy (leaves, petioles and fruits).

Environmental effects on gender determination: Papaya is a polygamous species with three basic plant types: Male (staminate), female (pistillate) and bisexual (hermaphrodite) plants (Crane, 2005). The female plant has putatively more vigorous growth than the hermaphrodite. Air temperature can influence papaya plant gender expression (Marler et al., 1994) because there is a tendency to produce male flowers at high temperatures (Malo and Campbell, 1986). However, little is known about the effect of supra-optimal temperature on gender expression in papaya. Chutteang et al. (2007) demonstrated that under optimal conditions for photosynthesis, female plants, compared to hermaphrodite individuals, had increased chlorophyll content, electron transport in PSII, and g_s . If physiological characteristics can identify plant gender, simple physiological measurements could identify plant gender in the vegetative stage (Chutteang et al., 2007).

Soil compaction and root restriction effects on papaya physiology: In commercial papaya plantations, the use of heavy equipment on wet soils results in soil compaction (Hakansson et al., 1988). In addition, naturally dense soil layers or fragipans, common in tropical and subtropical soils that represent a significant area for potential papaya production, may ultimately impede root growth (Unger and Kaspar, 1994). Soil compaction will reduce gas exchange, chlorophyll content, F_v/F_m , and growth (Campostrini et al., 1998; Yamanishi et al., 1998; Campostrini e Yamanishi, 2001). In studies (Yamanishi et

al., 1998; Campostrini and Yamanishi, 2001) evaluating cultivar adaptation to soil compaction and root restriction, all cultivars had reduced total leaf number, average leaf area, length of leaf central vein, total leaf area, trunk diameter and tree height compared to non-restricted plants. Campostrini et al. (1998) concluded that rooting volume restriction induced senescence as a general physiological response.

Soil chemical effects on papaya productivity: Papaya is considered a species sensitive to low oxygen availability in the soil (hypoxia), which is commonly caused by waterlogging (Ogden et al., 1981; Malo and Campbell, 1986). Reduced oxygen can occur as a result of tropical storms that saturate the soil for several days, flood irrigation, as well as micro-irrigation practices that create microenvironments of reduced soil oxygen. A completely flooded soil can cause death to papaya plants in 2 d (Wolf and Lynch, 1940; Khondaker and Ozawa, 2007) or 3 to 4 d (Samson, 1980). Under hypoxic conditions, simulated by alterations in the oxygen concentration in a hydroponic system, Marler et al. (1994) showed that compared to the control ($6.54 \text{ mg O}_2 \text{ L}^{-1}$), g_s decreased shortly after 1 d of treatment with low and moderate oxygen levels (0.63 and $3.62 \text{ mg O}_2 \text{ L}^{-1}$, respectively). The stomata closed completely 3 d after treatment with low O_2 . The plants subjected to a moderately reduced O_2 availability responded with complete stomatal closure on the ninth day. The control treatment did not show stomatal closure. Khondaker and Ozawa (2007) constructed chambers that controlled soil gas composition at ambient (20%), 18% and 11% oxygen; under soil oxygen at and below 18%, A , chlorophyll content, large and small roots, and shoot dry matter were all decreased. According to Schaffer et al. (1992), even in species considered tolerant, reduction in gas exchange is common during hypoxia conditions, although they promptly resume growth and gas exchange after the stress is removed. Papaya, considered sensitive to hypoxia, responds with accentuated senescence (chlorotic leaves), leaf fall and does not recover after hypoxic conditions are removed (Marler et al., 1994). These studies indicate that papaya is sensitive to small reductions in soil oxygen content and it is likely that micro-irrigation saturation of a small portion of the soil is having some negative effects. Consequently, a well-drained soil is essential for high productivity.

Papaya grows well on a range of well-drained soils. Soil pH is generally not a limiting factor. Seedling germination was unaffected by pH from 3.0 to 9.0 (Marler, 2007) and seedling growth was not affected by pH from 4.0 to 9.0 (Marler, 1998) but nevertheless papaya generally grows best in near neutral soils with pH in the range 6 to 7 due to the interaction of soil pH with nutrient availability.

Papaya seed germination is inhibited by very low levels of salinity (Kottenmeier et al., 1983), yet seedling growth can be stimulated by 1/10 seawater salinity levels (8 mS cm^{-1}) when compared to a Hoagland's nutrient solution control. Maas (1993), however, classified papaya production as moderately sensitive with salinity effects at 3 mS cm^{-1} . Wu and Dodge (2005) found that papaya was moderately tolerant to saline over-head irrigation with symptoms appearing on less than 10% of leaves when plants were irrigated with water containing $200 \text{ mg Na}^+ \text{ L}^{-1}$ and $400 \text{ mg Cl}^- \text{ L}^{-1}$ (approximately 1 mS cm^{-1}). Papaya was also moderately tolerant of soil electrical conductivity greater than 2 and less than 4 mS cm^{-1} . Similarly Elder et al. (2000) found that moderately saline water (1.4 to 4 mS cm^{-1}) applied in trickle or under-tree mini-sprinkler irrigation had no adverse affect on productivity but when overhead applied, there was leaf damage and reduced growth.

Mycorrhizal fungi effects on papaya productivity: The beneficial effects of arbuscular mycorrhizal (AM) fungi in the plant kingdom and agricultural cropping systems are well documented, and include increased P, water, and nutrient uptake as well as improved pest resistance (Harley and Smith, 1983; Bethlenfalvay and Linderman, 1992). Arbuscular mycorrhizal fungi colonize papaya under natural conditions. Papaya appears to be very dependent on AM since plants in sterilized soil, as compared to inoculated, showed poor growth and particularly P uptake (Habte, 2000). However, natural inoculation of AM is not always sufficient for maximal growth of papaya. For example, Mamatha et al. (2002) demonstrated that field-planted, 1.5-year-old plants (var. 'Solo') had increased fruit yield when inoculated with *Glomus mosseae* and *G. caledonium* with or without the addition of *Bacillus coagulans* which increases AM colonization. Cover crops and pastures of Bahiagrass (*Paspalum notatum*) and millet (*Pennisetum glaucum*) promote AM infection of papaya (Cruz et al., 2003). The

species of AM used affects plant productivity. Effective species include: *G. mosseae*, *G. claroideum* and *G. fasciculatum*. A survey of 67 soil and papaya samples the north of Espírito Santo and Bahia States, Brazil, demonstrated a range of colonization ranging from 6% to 83% (Trindade et al., 2006). Colonization rates and spore density were positively correlated with soil organic matter and coarse sand fractions and negatively correlated with fine sand. All Glomerales families were represented and the most common species were *G. etunicatum*, *Paraglomus occultum*, *Acaulospora scrobiculata* and *Gigaspora sp.*

The mycorrhizal network is a key to improving the acquisition of nutrients and water in papaya production. Management factors that increase colonization of effective fungi can be expected to improve nutrient and water-use efficiencies. Cruz et al. (2000) grew 'Solo' papaya in pots with or without AM for three months, then conducted a water stress study. During a 20-d water stress treatment, leaf water potential of all plants decreased (more negative), but to a greater extent in non-AM than in AM treatments, suggesting larger internal water deficit in the former. Soil ethylene levels and ACC activity were reduced by AM under these water deficit conditions, further supporting a reduced water stress severity in AM-treated plants. Such a reduction occurred despite an increase in above-ground mass and leaf area and was due largely to a significant increase in root mass in the AM treatment that was more effective in water uptake than the non-AM treatment.

CONCLUSIONS

Environmental factors profoundly affect the photosynthetic processes in papaya and an understanding of the environmental factors and their interaction with physiological processes is extremely important for economically sustainable production in the nursery or in the field. With improved, science-based management, growers will optimize photosynthetic carbon assimilation and increase papaya fruit productivity and quality. The challenge for papaya production will be to increase high quality fruit production in marginal sites where the abiotic environment is limiting. Supra-optimal temperatures and water deficits are the most likely environmental factors

limiting production. Science-based management can meet the water demands of the plant in a more efficient manner through improved irrigation technology. Plant temperature can be reduced through overhead cooling systems or reflectant materials. These cultural techniques only serve to moderate the environment for the existing genetic base of papaya. Considerable genetic variation exists in present-day papaya genotypes. Maximum *A* rates, PS II sensitivity to light and temperature, stomatal response to VPD and wind action, chlorophyll content and dry matter partitioning to fruit are key ecophysiological parameters under some degree of genetic control. The rapid expansion of genetic knowledge relating gene expression with physiological response, functional genomics, will provide papaya breeders with information to develop productive phenotypes adapted to the tropical and subtropical climatic variation.

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