



Responses of papaya seedlings (*Carica papaya* L.) to water stress and re-hydration: growth, photosynthesis and mineral nutrient imbalance

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Abstract

The effects of water stress and subsequent re-hydration on growth, leaf abscission, photosynthetic activity, leaf water potential and ion content were investigated in papaya seedlings (*Carica papaya* L.) cv. “Baixinho de Santa Amalia”. Water stress was imposed by suspending irrigation during 34 days. Thereafter, plants were regularly re-watered. Drought arrested plant growth, induced leaf abscission and drastically decreased photosynthetic rate. However, leaf water potential was hardly reduced. Water deficit also induced sodium, potassium and chloride accumulation in leaves and roots, and did not modify nitrogen levels in both organs. Re-hydration stimulated growth, promoted emergence of new leaves, reactivated photosynthetic machinery function and reduced ion content to control levels. The results indicated that the ability of papaya plants to improve drought tolerance is not mediated through the reduction of leaf abscission, the detention of growth or the decrease of net CO₂ assimilation. In contrast, the data suggested that under water stress conditions these plants appear to possess a certain capacity to increase ion content, which might contribute to osmotic adjustment.

Introduction

Papaya plants are considered to be relatively resistant to drought, although to achieve optimum growth or yield, sufficient water for irrigation is required (Kruger and Mostert, 1999). Several studies showed that leaf relative water content and xylem pressure potential were unaffected by drought and classified papayas as a species that responds to drought primarily via dehydration postponement (Marler et al., 1994). It has also been indicated that the osmotic adjustment and the maintenance of the root system water conductivity, characteristics of some plants which tolerate drought by postponing tissue dehydration, are also expressed in papaya under

water deficits (Stokes and Stokes, 2000). Nevertheless, papaya leaf gas exchange was reduced under drought conditions (Marler et al., 1994; Marler and Mickelbart, 1998). Furthermore, depletion of soil moisture reduced plant height, trunk diameter and the number of attached leaves per tree, and also retarded growth and development of papaya fruit (Masri et al., 1990).

In general, water stress reduces nutrient uptake by roots and transport from roots to shoots, due to restricted transpiration rates and membrane permeability (Erlandsson, 1975). However, it has been indicated that K inflow was not limited by soil water content in maize (Mackay and Barber, 1985), and plant nitrogen concentration increased with water stress in pearl millet (Payne et al., 1995). On the other hand, under drought conditions, maintenance of cell turgor in plants may be dependent upon osmotic adjustment which implies

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a net accumulation of solutes in order to maintain a favourable water potential gradient (Turner and Jones, 1980). K and Na are involved in the osmotic adjustment of leaf tissue to low external water potential (Osmond et al., 1980). These ions increased in shoots of *Atriplex* species under water stress (Martínez et al., 2003). In other experimental systems, hyperosmotic stress induced by mannitol treatment, resulted in a significant increase in the K and Cl uptake into leaf mesophyll cells of bean (*Vicia faba* L.) (Shabala et al., 2000).

In order to study the physiological characteristics determinant for water stress tolerance in papaya, its responses under these conditions were investigated. The effects of water deficiency and subsequent re-hydration on leaf gas exchange, leaf water potential, plant growth parameters, leaf abscission and specially on the capacity to accumulate inorganic solutes were studied.

Material and Methods

Plant material

The “Baixinho de Santa Amalia” cultivar of papaya (*Carica papaya* L.) used in this study is a mutant of Sunrise cv., belonging to “Solo” group and characterised by its dwarfism and precocious flowering. Papaya seedlings (25-cm long) were transplanted to large plastic pots (70 l) under glasshouse with controlled temperature (20–30 °C during the experimental period), 60–95% relative humidity and maximum photosynthetically active radiation (PAR): 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Before transplanting, pots were filled with sterilised substrate (2:3 clay loam soil and 1:3 organic material). In the aqueous extract, the soil contained 49, 7, 48 and 40 mg Kg^{-1} available N, K, Na and Cl, respectively. Exchangeable K and Na were 438 and 193 mg Kg^{-1} of soil, respectively. Seedlings were watered daily with a chemical solution to maintain plant nutrient requirements according to De Villiers (1999).

Treatments of water stress and growth measurements

One month after plant acclimation, water stress was imposed by suppressing irrigation until soil

moisture reached the lowest values and growth detention was apparent. Plants were subjected to drought during 34 days under glasshouse conditions. Thereafter, re-watering was applied in excess until soil moisture showed the same percentage than in regular irrigated plants. Control plants were irrigated normally to maintain optimum soil moisture. The experiment was replicated three times using 48 plants for each one (half of plants were well watered and the other half were water-stressed).

During both periods, stress and re-hydration, plant height, stem circumference and vegetative fresh weight were periodically determined. Root fresh weight was measured at the end of stress period and the end of the experimental period. Relative growth rate was calculated as the changes in stem dry weights (DW) between each period relative to the DW determined at the beginning of that period according to Hunt (1982). Samples of leaves, stems and roots were periodically harvested, frozen with liquid nitrogen, lyophilised and stored at -20 °C until analysis.

Soil moisture and leaf water potential

Soil moisture was determined regularly during the period of water stress and subsequent re-hydration. Moisture determinations were carried out using the Trime-FM Time Domain Reflectometry (TDR) equipment (Imko equipment, Germany) with two-rod connector probes that were 15 cm in length. The space between rods was 5 cm. Permanent TDR probes were vertically inserted within the pot substrate into the root-zone at a depth of 15 cm. The probes were placed at a distance of 10 cm with the pot edge and with the drips. The TDR method is based on the determination of the apparent dielectric constant (Ka) of soil that is related to moisture (Topp and Davies, 1985). This instrument determine finally the percentage of volumetric soil moisture content.

In papaya seedlings, leaf water potential was periodically determined during the periods of non irrigation and re-watering. The measurements were performed in the morning (8–10 a.m) with a pressure chamber model 3000, Soil Moisture Equipment, Santa Barbara, CA, (Scholander et al., 1965).

Photosynthesis

Photosynthetic rate was measured in papaya leaves during the period of water stress and subsequent re-hydration, using an LCpro portable photosynthesis system (LCpro, ADC Bioscientific LTD. UK) with a broad leaf chamber window area of 6.25 cm². Determinations were performed under an air flow rate of 200 $\mu\text{mol s}^{-1}$, at environmental humidity and CO₂. During measurements, radiation within the cuvette was supplemented with a 110 V lamp (LCpro, ADC). At the beginning of the study, measurements were carried out with increasing photosynthetic photon flux (PPF) from 50 to 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to estimate saturating values under these experimental conditions. Thereafter, all determinations were performed on fully expanded leaves, generally, the third leaf counting from the top, at 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is a saturating value in the system. Measurements were made during the morning (8–10 a.m) and temperature within the leaf chamber varied from 23 to 26 °C.

Ion analyses

Lyophilised leaf and root tissues of plants sampled during the period of water stress and after re-hydration were used to determine their ion content.

Nitrogen

Total nitrogen analysis was measured on samples of 0.5 g DW using selenium catalysis (Bremner, 1965). Plant tissues were calcined in a muffle oven for 3 h at 400 °C and nitrogen content was determined through colorimetric measurements with the ammonium salicylate complex at 660 nm.

Potassium and Sodium

Samples of 0.5 g DW were calcined in a muffle oven for 4 h approximately at 450 °C and then, ashes were extracted with chloride acid. Cation determination was carried out by atomic absorption spectrophotometry at 766.5 and 589 nm for K and Na, respectively.

Chloride

Total chloride content in leaf and root tissues was determined by AgNO₃ titration (Chapman and Pratt, 1961). Lyophilised samples (0.5 g

DW) were extracted in distilled water (50 ml), stirred during 10 min and centrifuged at low speed about 20 min. The supernatant was filtered by a Whatman paper N° 1. The titration was performed in 25 ml of filtrate with 0.05 N AgNO₃ using 5% K₂CrO₄ as an indicator.

Statistical analyses

Determinations were compared using the least significant difference (LSD) test ($P \leq 0.05$) and correlation between parameters were determined by linear regression analyses. Statistical analyses were performed using Systat 10 (SPSS inc, USA).

Results

Water status

To confirm the effectiveness of the water stress treatment imposed on papaya plants, leaf water potential and soil moisture were determined during the period of water deprivation and subsequent re-hydration. Leaf water potential in control and in water-stressed plants did not show large differences during the experimental period (−0.5 to −0.6 MPa and −0.7 to −0.8 MPa, respectively) (Figure 1). Re-hydration increased this

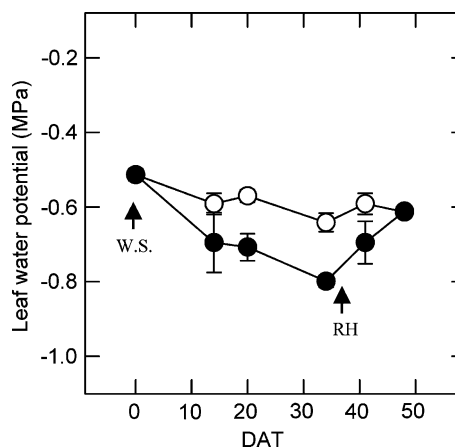


Figure 1. Leaf water potential in papaya seedlings. Treatments were: regular irrigated plants (○) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (●). Data are means \pm SE and each value was determined in at least three different plants with three replicates per treatment ($n \geq 9$). DAT = days after treatment. WS: Water Stress. RH: Re-hydration.

parameter, reaching the same values as control in few days. It should be noted that the reduction of papaya leaf water potential by water stress was not drastic in spite of the severity of stress imposed. Soil moisture was reduced progressively in non-watered soils and reached a minimum value (11%, 34 days after treatment (DAT)). In watered soils, moisture varied between 22% and 23% during the experiment. Re-irrigation applied 35 DAT induced rapid recovery of soil moisture (Figure 2).

Plant growth

Water stress did not affect plant height nor stem circumference during the first 14 days after water shortage (Table 1). This treatment reduced significantly growth parameters from the 20th day and reached a maximum reduction at the end of stress period (34 DAT). At this time, plant height and stem circumference were reduced about 9% and 8%, respectively in treated plants compared to control ones. On the contrary, re-hydration promoted plant growth but this was lower than in controls at the end of experiment (48 DAT). Relative growth rate was also determined during the period of water stress and subsequent re-watering (Figure 3). This parameter was reduced significantly from the 20th day after water deprivation and reached its minimum (86% reduction)

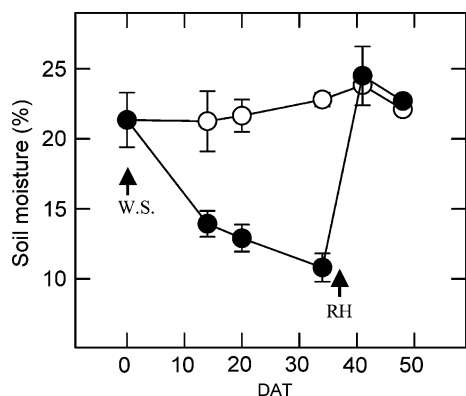


Figure 2. Moisture (%) in watered (○) and non-watered pot soils (●) of papaya seedlings. In non-watered soils, irrigation was suspended during 34 days and re-established thereafter until the end of experiment. Data are means \pm SE and each value was determined by three TDR probes with three replicates per treatment ($n \geq 9$) (one probe per pot). DAT=days after treatment. WS: Water Stress. RH: Re-hydration.

with respect to control at the last period of stress (20–34 DAT). Re-irrigation alleviated water stress effects and resulted in relative growth rate recovery. Hence, control and stressed plants showed alike values at the end of experimental period. Water shortage reduced root fresh weight about 44% (34th day), while re-hydration induced an increase of root biomass. This remained 34% lower than control two weeks after its application (Table 2).

Leaf number

In well-watered plants, leaf number did not show large changes during the experimental period (9–11 leaves per plant) (Figure 4). However, the non-irrigation treatment reduced leaf number progressively. Therefore, at the end of stress period (34 DAT), half of leaves per plant were dropped. Re-watering promoted the emergence of new leaves (about one leaf per week).

Photosynthetic rate

In well irrigated plants, photosynthetic rate (A) measured in fully expanded leaves, varied between 8.3 and 9.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the experimental period (Figure 5). Water stress altered CO_2 assimilation after a few days inducing a progressive decrease of photosynthetic rate that reached minimum values (2.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$) at the end of stress period. Re-watering stimulated gas exchange in stressed plants. Those plants showed control values 6 days after recovery.

Ion content

Nitrogen

Total foliar nitrogen content in well-irrigated plants did not show significant modifications during the first 34 days, but, it decreased thereafter at the end of the experimental period (4.8–4.4% of DW). Water stress treatment did not alter statistically the pattern of change of nitrogen levels (Figure 6a), although that absolute N levels were higher in water stressed plants. In well-watered roots, nitrogen showed a slight increase from the beginning until the end of the experiment (1.8–2.1% DW). Water shortage did not disturb significantly nitrogen levels, that showed the tendency of the control roots (Figure 6b).

Table 1. Plant height and stem circumference of papaya seedlings subjected to water stress and re-hydration. The treatment consisted of irrigation suppress during 34 days and re-watering establishment thereafter until 48 days (total experimental period). The data ($n \geq 9$) presented in each line followed by dissimilar letters differ significantly at ($P \leq 0.05$). *: $P \leq 0.01$. **: $P \leq 0.001$

Treatments	Plant height (cm)		Stem circumference (cm)	
	Control	Water stress	Control	Water stress
Water stress (Days)				
0	38.45 ± 0.67a	38.50 ± 0.56a	8.23 ± 0.09a	8.08 ± 0.15a
14	41.67 ± 0.80a	39.63 ± 0.58a	9.04 ± 0.10a	8.72 ± 0.13a
20	42.21 ± 1.06a	39.88 ± 0.60b	9.51 ± 0.11a	8.94 ± 0.15b*
34	43.83 ± 1.15a	40.13 ± 0.67b	9.79 ± 0.12a	8.98 ± 0.12b**
Rehydration (Days)				
41	46.13 ± 1.28a	41.20 ± 0.87b	10.10 ± 0.23a	8.98 ± 0.19b*
48	46.83 ± 1.86a	43.25 ± 1.75b	10.60 ± 0.32a	9.40 ± 0.35b

Potassium

In control plants, foliar level of potassium firstly increased from 2.1% to 2.4% DW (34 DAT) and then decreased again to 2.1% DW at the end of the experiment. In stressed plants, relative K content of leaves at 34 DAT was 10% higher than controls. After irrigation, the accumulation was reduced to the control values (Figure 7a). Root K levels were slightly higher than foliar ones (2.6–3.1% DW in control plants). The last day of the stress, K content was 12% higher in stressed roots than in controls. However, after stress release, their levels were similar (Figure 7b).

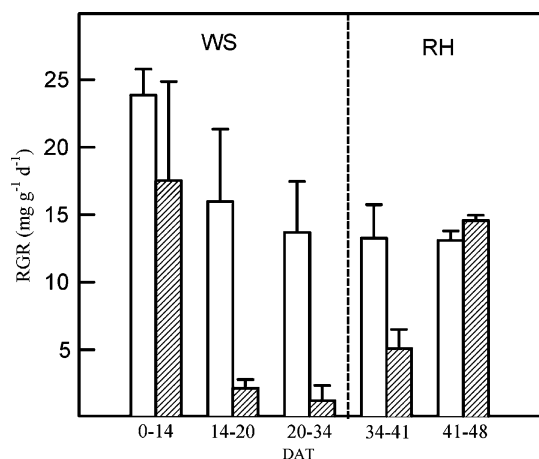


Figure 3. Relative growth rate using stem DW of papaya seedlings. Treatments were: regular irrigated plants (□) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (▨). Data are means ± SE and each value was determined in at least three different plants with three replicates per treatment ($n \geq 9$). DAT= days after treatment. WS: Water Stress. RH: Re-hydration.

Therefore, severe water stress seems to stimulate K accumulation in leaves and roots.

Sodium

Foliar Na content did not varied significantly during the period of experiment in irrigated plants (0.047–0.052% DW) (Figure 8a). In contrast, this element progressively accumulated from the 20th day of drought until the last day of water shortage (34 DAT). At this time, Na levels were 30% higher in stressed than in control plants. After stress release by irrigation, Na levels in leaves were reduced and values were similar to control plants. In roots, Na content varied from 0.6% to 1% DW during the experiment period, indicating that the accumulation of Na in roots was (12–19 fold) higher than in leaves. Water stress slightly increased Na levels in roots compared to control (Figure 8b). Hence, the data indicate that sodium accumulated in leaves of

Table 2. Root fresh weight of papaya seedlings subjected to water stress and re-hydration. The treatment consisted of irrigation suppress during 34 days and re-watering establishment thereafter until 48 days (total experimental period). The data ($n \geq 9$) presented in each line followed by dissimilar letters differ significantly at ($P \leq 0.05$)

Treatments	Root fresh weight (g)	
	Control	Water stress
Water stress (Days)		
34	181.9 ± 16.5a	101.4 ± 18.7b
Rehydration (Days)		
48	183.0 ± 23.5a	119.7 ± 8.70b

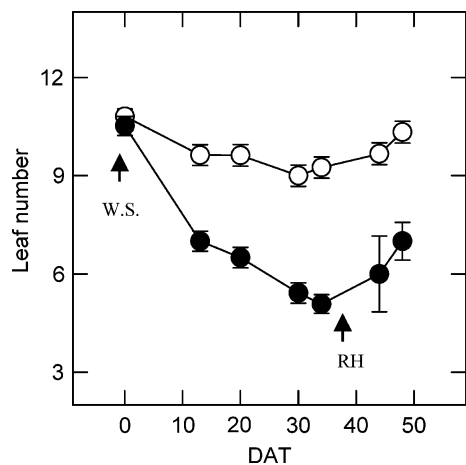


Figure 4. Number of remaining leaves in papaya seedlings. Treatments were: regular irrigated plants (○) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (●). Data are means \pm SE and each value was determined in at least three different plants with three replicates per treatment ($n \geq 9$). DAT=days after treatment. WS: Water Stress. RH: Re-hydration.

papaya plants subjected to drought. Re-irrigation reduced the Na content to control levels.

Chloride

Under normal irrigation, foliar chloride levels were constant during the experimental period (0.18–0.23% DW). Drought applied during 34 days induced an

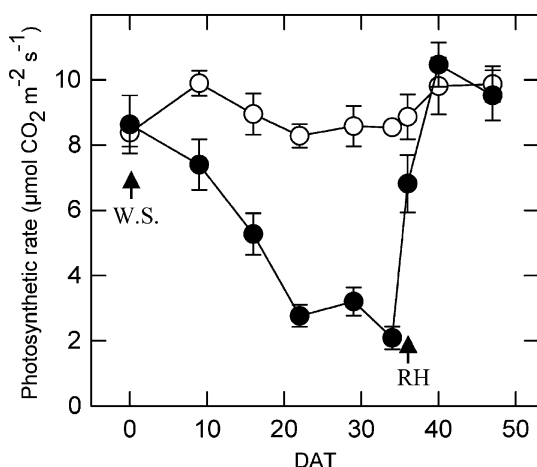


Figure 5. Photosynthetic rate (a) in fully expanded leaves in papaya seedlings. Treatments were: regular irrigated plants (○) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (●). Data are means \pm SE and each value was determined in at least three different plants with three replicates per treatment ($n \geq 9$). DAT=days after treatment. WS: Water Stress. RH: Re-hydration.

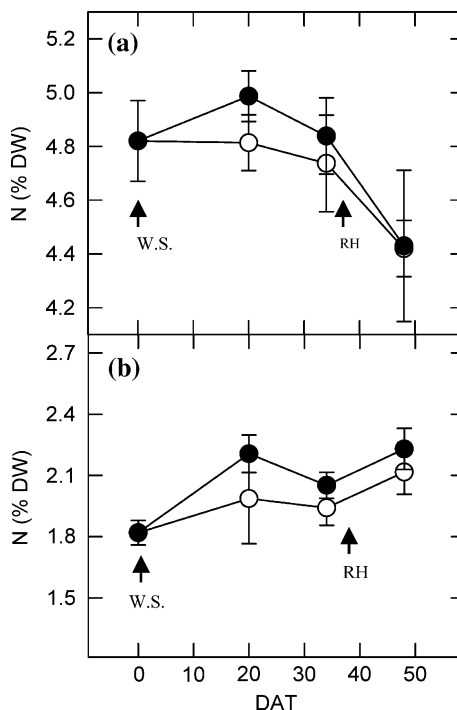


Figure 6. Total nitrogen content in leaf (a) and root (b) tissues in papaya seedlings. Treatments were: regular irrigated plants (○) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (●). Each value is the mean of at least three independent measurements \pm SE. DAT=days after treatment ($n \geq 3$). W.S.: Water Stress. RH: Re-hydration.

increase of this ion in leaves by about 28% compared to control (Figure 9a). On the contrary, stress release decreased chloride levels. In irrigated seedling roots, Cl decreased continuously and varied between 0.5% and 0.23% DW during the period of study (Figure 9b). However, in roots subjected to drought, Cl content was stable and higher than in controls. In contrast, release of water deficit reduced Cl accumulation to control values.

Correlations between soil moisture and photosynthesis, leaf abscission and foliar ion content

In papaya seedlings subjected to water stress during 34 days, progressive moisture depletion induced by drought intensity correlated positively with net photosynthetic rate ($r=0.96$, $P \leq 0.01$) (Table 3). Moreover, soil moisture reduction correlated highly with remained leaf number

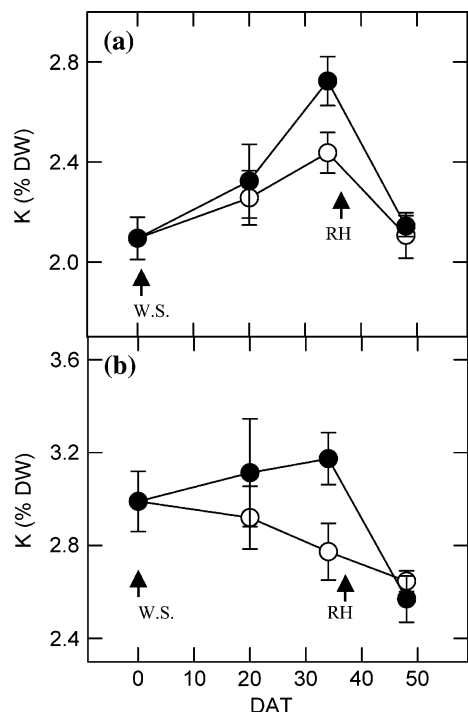


Figure 7. Potassium content in leaf (A) and root (B) tissues in papaya seedlings. Treatments were: regular irrigated plants (○) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (●). Each value is the mean of at least three independent measurements ($n \geq 3$) \pm SE. DAT=days after treatment. WS: Water Stress. RH: Re-hydration.

($r=0.99$, $P \leq 0.001$). On the other hand, soil moisture correlated negatively with foliar ion, such as, sodium ($r=-0.88$, $P \leq 0.05$), potassium ($r=-0.87$, $P \leq 0.05$) and chloride ($r=-0.86$, $P \leq 0.05$) (Table 3). No significant correlation were observed between soil moisture and these ions in root tissues (data not shown).

Discussion

The above results indicate that under water stress conditions papaya (*Carica papaya* L.) seedlings increased mineral solutes such as Na, K and Cl, especially after a long period of drought. The increase of these elements might be beneficial for papaya drought tolerance, since this process appears to contribute substantially to osmotic adjustment in plants. The increase of Na and K has been also reported to occur under water deficit on shoots of *Atriplex halimus* L., a halophyte

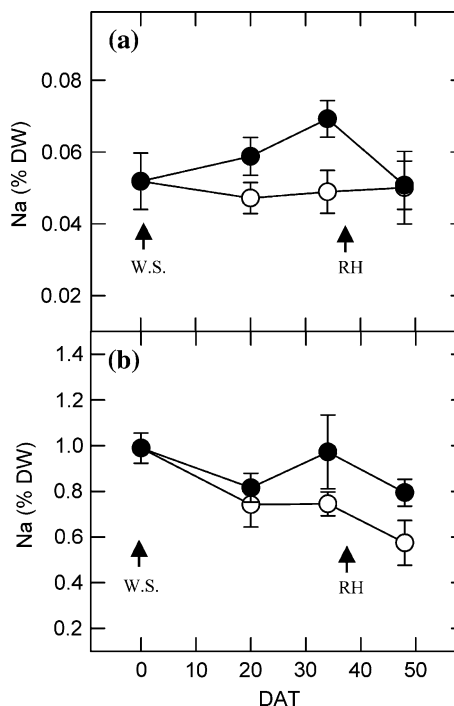


Figure 8. Sodium content in leaf (A) and root (B) tissues in papaya seedlings. Treatments were: regular irrigated plants (○) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (●). Each value is the mean of at least three independent measurements ($n \geq 3$) \pm SE. DAT=days after treatment. WS: Water Stress. RH: Re-hydration.

well adapted to extreme environmental conditions (Martínez et al., 2003). In these species, both Na and K are involved in the osmotic adjustment of leaf tissue to low external water potential (Osmond et al., 1980). In other experimental systems such as bean (*Vicia faba* L.), hyperosmotic stress induced by mannitol treatment, caused a significant increase in the K and Cl uptake into leaf mesophyll cells (Shabala et al., 2000), providing an adequate osmotic adjustment. Moreover, in *Arabidopsis* similar results, increase in K uptake into cultured cells in response to hyperosmotic treatment (Curti et al., 1993) and decrease on Cl efflux induced by mannitol (Teodoro et al., 1998), were showed. In the present investigation, the data indicated a high negative correlation between soil moisture and build up of Na, K and Cl (Table 3). The accumulation of these ions together with organic solutes glycine betaine, proline, sucrose, polyols, sugar alcohols and oligosaccharides during

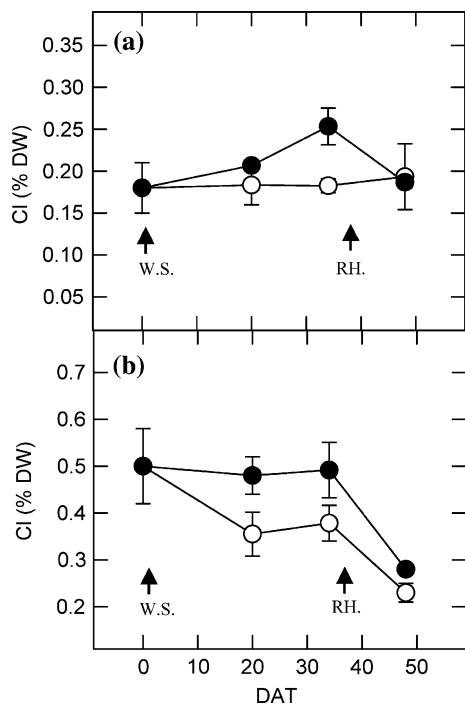


Figure 9. Chloride content in leaf (a) and root (b) tissues in papaya seedlings. Treatments were: regular irrigated plants (○) and non-irrigated plants during 34 days followed by re-watering until the end of experiment (●). Each value is the mean of at least three independent measurements ($n \geq 3$) \pm SE. DAT=days after treatment. WS: Water Stress. RH: Re-hydration.

Table 3. Correlation coefficients (r) between soil moisture (%) and photosynthetic rate, leaf number and leaf ion content (Na, K y Cl) in papaya seedlings subjected to water stress withholding irrigation during 34 days. $n \geq 9$. $P \leq 0.05$. *: $P \leq 0.01$. **: $P \leq 0.001$

Variable	r with soil moisture (%)
Photosynthetic rate	0.958*
Leaf number per plant	0.997**
Leaf ion content	
Na	-0.879
K	-0.862
Cl	-0.858

osmotic adjustment has been also indicated in other experiment systems (Bohnert et al., 1995; Hasegawa et al., 2000; Ramachandra Reddy, 2004; Shen et al., 1999; Tamuara et al., 2003). The organic solutes are osmolytes compatible with cellular processes and accumulate to high levels in the cytosol with increasing drought.

Although water shortage did not modify statistically nitrogen content in leaves and roots (Figure 6), data on leaf abscission (Figure 4) might suggest that the maintenance of nitrogen levels as control in the remained leaves despite the shortage of nitrogen and water supply could be the result of the partition of the available content of this element in the plant between the persisting organs after diminution of leaf number by abscission. Other studies showed that defoliation tended to increase nitrogen assimilation rates and nitrogen levels (Fujita et al., 1994).

The initial response to stress was the reduction of photosynthetic rate. This parameter correlated positively with low soil moisture (Table 3) from the 9th day of treatment imposition. At the end of stress period (34 DAT), photosynthetic rate was drastically reduced (76%). On the other hand, growth was also practically arrested and the remained leaves reached a minimum (50% reduction). In contrast, re-hydration recovered completely photosynthetic machinery function, stimulated growth and the emergence of new leaves. A dissimilar behaviour of net CO_2 assimilation compared to papaya was reported in citrus plants under drought and subsequent recovery (Arbona et al., 2005). In this report, re-watering did not fully recover photosynthetic rate in young citrus plants subjected to successive water stress and re-hydration cycles indicating that water stress injured leaf tissues. In papaya, it has been reported that net CO_2 assimilation was reduced on response to drought in seedlings (Marler et al., 1994) and under field conditions (Marler and Mickelbart, 1998). It is also been indicated, that at the reproductive stage, water stress reduced height and trunk diameter of papaya plants. Moreover, plants under stress had 50% fewer attached leaves per tree (Masri et al., 1990). In several species such as citrus, it is known that leaves did not abscise during water stress; however, abscission occurred after stress release by irrigation (Gómez-Cadenas et al., 1996; Tudela and Primo-Millo, 1992). Papaya did not show this characteristic behaviour, since leaf abscission took place during the period of water shortage.

An interesting result obtained in this work was the reduced variation of leaf water potential under a long stress period. This finding is supported by Marler et al. (1994) that showed that the leaf

relative water content and the xylem pressure potential were unaffected by drought in young plants of papaya. According to these studies, papaya is thought to be a specie that responds to drought via dehydration postponement.

In conclusion, papaya plants subjected to water stress showed a tendency to accumulate ions such as K^+ , Na^+ and Cl^- . The ion increases that were registered on per DW basis might apparently contribute for osmotic adjustment, enhancing water stress tolerance of these plants. The data also indicate that stress tolerance was not mediated through the reduction of leaf abscission, the detention of growth or decrease of net CO_2 assimilation. Re-irrigation induced plant morphological and physiological recovery without irreversible effects of water stress.

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