ABSTRACT- Four papaya genotypes, two from the ‘Solo’ group (Sunrise Solo TJ and Improved Sunrise Solo line 72/12) and two from the ‘Formosa’ group (Tainung 02 and Know You 01) grown in ultisol under field conditions in Macaé, RJ, Brazil, were used in this study. Two different effective depths (ED) were determined in the area using a penetrometer with average soil moisture of 11.2%. The area with ED of 0.35 m with a maximum pressure of 4.12 MPa for penetration was defined as an area with restriction (WR) to root growth, while, the area with minimum ED of 0.60 m and a pressure lower than 2.30 MPa as an area with no restriction (NR). The net CO$_2$ assimilation rate ($A$), stomatal conductance ($g_s$), leaf temperature ($T_l$), intercellular partial pressure of CO$_2$ ($c_i$) and intrinsic water use efficiency (IWUE) were evaluated for three consecutive days after irrigation. Mechanical root restriction affected gas exchange of the four papaya genotypes. All genotypes grown in the WR area had lower $A$, $g_s$ and $c_i$ and higher $T_l$ than the same genotypes in the NR area. All genotypes grown in the WR area had high IWUE and Sunrise Solo TJ had the highest IWUE.

TERMS ADDITIONAL INDEX: Carica papaya L., photosynthesis, leaf temperature, stomatal conductance, intrinsic water use efficiency.
irrigação. A restrição do crescimento do sistema radicular afetou as trocas gasosas dos quatro genótipos de mamoeiro. Na área CR, todos os genótipos apresentaram valores reduzidos de $A$, $g$, e $c$, e elevados de $T_l$, em relação aos genótipos crescidos na área SR. Todos os genótipos crescidos na área CR apresentaram elevados valores de IWUE e o genótipo Sunrise Solo TJ foi o que apresentou o maior valor de IWUE.

TERMOS ADICIONAIS PARA INDEXAÇÃO: *Carica papaya* L., fotossíntese, temperatura da folha, condutância estomática, eficiência intrínseca no uso da água.

**INTRODUCTION**

Soil physical limitations to root growth may arise from several sources, including soil compaction resulting from harvesting of a previous crop (Misra and Gibbons, 1996). Compacted soil that limits root growth may be the result of a naturally dense layer or fragipans, or a result of the forces applied to the soil by implements or animals (Unger and Kaspar, 1994). In Brazil, the soils with a dense sub-surface are classified as oxisols and ultisols (Resende et al., 1988). These soils represent a significant area for potential agricultural production because of their close proximity to areas of intense agricultural use in the southeast and to areas with accentuated rainfall and intense demand for agriculture in the northeast.

Soil characteristics that prevent root penetration or reduce root elongation rates can reduce plant development and yields, by limiting availability of water and nutrients. The degree of reduction of water and nutrients depends, to a large extent, on the soil depth at which the restriction zone occurs (Unger and Kaspar, 1994). In peach seedlings, root restriction reduced plant dry weight, the number of root apices, leaf number, shoot initiation, root extension, dry weight and root length, leaf area and water uptake by 30-60% (Richards and Rowe, 1977). Root restriction also reduced chlorophyll concentration in spreading euonymus (*E. kiautschovica* Loes ‘Sieboldiana’ ) (Dubik et al., 1990) and alder seedlings (Tschaplinski and Blake, 1985).

The main consequence of the reduced root growth is a subsequent decrease of shoot growth (Liu and Latimer, 1995; Hsu et al., 1996; Young et al., 1997; Hee Choi et al., 1997), because a restricted root system will supply insufficient water (Hameed et al., 1987; Tschaplinski and Blake, 1988; Ran et al., 1992) and nutrients (Hanson et al., 1987; Dubik et al., 1990; Rieger and Marra, 1994) to the shoot. As a result of root restriction, shoot growth may also be limited by insufficient carbon supply, because more carbon may be required by roots for increased osmotic pressure (Greacen and Oh, 1972). Also, a reduction in the root “sink” as a result of root restriction can cause carbohydrates to accumulate in the leaves, resulting in a feedback inhibition of photosynthesis (Arp, 1991; Schaffer et al., 1996).

In a previous paper we examined the effects of root restriction on shoot growth (Yamanishi et al., 1998). In the present study we determine the effect of soil resistance to root penetration on gas-exchange of four papaya genotypes grown under field conditions.

**MATERIALS AND METHODS**

**Plant material and growth conditions**

Experiments were conducted at Macaé Experimental Station, Empresa de Pesquisa Agropecuária do Estado do Rio de Janeiro (PESAGRO-RIO/EEM, Macaé-Brazil, lat. 22°24’S, long. 41°42’W). Four papaya genotypes, two from the ‘Solo’ group (Sunrise Solo TJ and Improved Sunrise Solo line 72/12) and two from ‘Formosa’ group (Tainung 02 and Know-You 01) were grown in ultisol under field conditions at two distinct effective depths (*ED*) (thickness of the A horizon). The *ED* was determined using a penetrometer SC-60, cone/axe standard American Society Agricultural Engineers, solid angle cone with 60°, base area 129.0 mm² and 9.5 mm diameter of the axis (Soilcontrol, Santo Amaro, São Paulo, Brazil). The average soil
moisture during the measurements was 11.2 ± 2.50%. Area with 34.5 cm ED and maximum pressure of 4.12 MPa for penetration was defined as an area with restriction (WR) to root growth, while, the area with minimum ED of 60.0 cm with pressure lower than 2.30 MPa as an area with no restriction (NR) (Unger and Kaspar, 1994). The soil textural class, bulk density, particle density, porosity and macroporosity of the soil were classified according to EMBRAPA (1997).

The experimental area was fertilized and the pH adjusted according to Marin et al., (1993). Throughout the experiment the plants were subjected to periodic sprinkle irrigation to keep the soil moisture close to field capacity.

**Determination of the physiological characteristics**

The net CO$_2$ assimilation rate ($A$), stomatal conductance ($g_s$), leaf temperature ($T_l$) and intercellular partial pressure of CO$_2$ ($c_i$) were evaluated on 28, 29 and of 30 March [150 days after transplanting (DAT)], respectively as the first, second and third day after irrigation, in leaves grown in full sunlight using a portable photosynthesis system (LI-6200; LI-COR Inc., Lincoln, NE, USA) on four trees in each treatment. Plants were transplanted 45 days after seed germination. Data was collect from 9:00 to 11:00 h using the seventh leaf from the apex. Intrinsic water use efficiency ($IWUE$) was calculated as the slope of the linear portion of the regression line of $A$ vs. $g_s$ for each genotype in each of the two treatments (Martin et al., 1994; Pimentel et al., 1999). Soil moisture was determined in the first, second and third days after irrigation by a gravimetric method (Bernardo, 1995).

**Data analysis**

Results were statistically analyzed according to genotype and soil mechanical resistance as a randomized design, each with four replications. Analysis of variance was determined using Statistica (Statsoft, Inc., Tulsa, OK, USA). Duncan’s Multiple Range Test (p 0.05) was used to determine difference among means. Significant differences in $IWUE$ between WR and NR of each genotype were determined by testing for homogeneity of slopes (“T”-test) (Minitab, Inc., State College, PA, USA).

**RESULTS AND DISCUSSION**

Significant difference in ED among NR and WR areas was found using a penetrometer. The NR area had a deeper ED, >0.60m (<2.30 MPa), compared with ≤ 0.35m (maximum of 4.12 MPa) in the WR one. Roots of several species are highly sensitive to the resistance imposed by physical characteristics of the soil, and plant growth is inhibited or completely stopped when resistance to the penetration exceeded 2.5 MPa (Unger and Kaspar, 1994). Soil macroporosity in B horizon was lower than A horizon indicating the presence of a physical alteration in the B horizon (Table 1). When soil is submitted to this type of physical alteration, the macroporosity decreases and roots cannot penetrate the small pores (Wiersum, 1957). In this case, the rate of root growth is reduced to extremely low levels or ceases (Marschner, 1995). In addition, the NR area presented a deeper A horizon without compaction zone which provided better conditions for root growth compared to a thinner A horizon with compaction zone that restricted the root growth in WR area (Camposstrini et al., 1997). This may explain the reduced root growth in plants grown in WR area (Camposstrini et al., 1997).

All genotypes grown in the WR area had lower $A$, $g_s$, than genotypes in the NR area (Tables 2 to 4). Masle and Passioura (1987) and Lipiec et al., (1996) observed significant reductions of $g_s$ in plants grown in soil with high mechanical impedance. If the stomatal movements affect the partial pressure of CO$_2$ at the sites of carboxylation and the rate of transpiration (Farquhar and Sharkey, 1982), the correlation between $A$ and $g_s$ (Figure 1) can be explained as a function of the high concentration of CO$_2$ in the sites of carboxylation when $g_s$ increases (Farquhar and Sharkey, 1982, Krieg and Hutmacher, 1986, Mansfield et al., 1990, Lawlor, 1993, Martin et al.,
1994). This correlation is verified when no other factor limits the light reactions and biochemistry.

The reduced values of $A$ in the WR area cannot be justified by the reduced stomatal density, because the abaxial stomatal density was the same in all plants (data not shown).

**TABLE 1 -** Textural class, bulk density, particle density, porosity and macroporosity of the soil in Macaé/RJ/Brazil

| Horizon  | $B_d$ (g cm$^{-3}$) | $P_d$ (g cm$^{-3}$) | Porosity (%) | Macroporosity ($\times 0.1$ atm) |
|----------|---------------------|---------------------|--------------|-------------------------------|
| A$^\text{v}$ (sandy-loam) | 1.74 | 2.60 | 33.1 | 13.3 |
| B$^\text{v}$ (clay) | 1.64 | 2.61 | 37.2 | 7.9 |

$B_d$ = Bulk Density, $P_d$ = Particle Density, Macroporosity $\times 0.1$ atm, (sandy-loam, 58% coarse, 15% fine sandy, 15% silt and 20% clay)$^\text{w}$, (clay, 25% coarse, 19% fine sandy, 08% silt and 48% clay)$^\text{y}$.

In conditions of physical impedance of the soil to the root system, several studies mentioned an increase in the concentration of abscisic acid (ABA) in the exudate of the xylem (Tardieu et al., 1991, Hartung et al., 1994, Liu and Latimer, 1995). Probably, the reduced stomatal conductance observed in leaves of WR plants is probably due to the increase in the levels of ABA produced by the roots and transported to the shoot by the transpiration process by xylem sap. Further studies are required to give more insight to ABA function in stomatal conductance in papaya plants. On the other hand, Hameed et al., (1987) proposed that, under conditions of root system restriction, plants are subjected to water stress when cultivated in a nutrient solution. These authors explained that the stress induction was caused by a high hydraulic resistance in the roots, which reduced the absorption and the translocation of water to the shoot.

Plants water deficits generally occur as a result of either soil water or atmospheric water deficit or both (Flore and Lakso, 1988). Although the atmospheric component is important in all plants (Schulze, 1986), it is particularly important in fruit trees such as papaya (El-Sharkawy et al., 1985). This is due to the very low hydraulic conductivity of root systems that causes a pronounced effect of transpiration on water potentials in the top of the tree (Jones et al., 1985). Consequently, the regulation of leaf water status by atmospheric conditions is relatively more important in fruit trees than in other crops, specially annuals, that have much higher root conductivities (Flore and Lakso, 1988). This means that leaf water status of fruit crops is strongly dependent on the evaporative demand of the atmosphere. The leaf water status will vary much more diurnally than in many annuals, and leaf water stresses may occur under high evaporative demands even though soil water is adequate. Consequently, stomatal response to humidity is particularly important in fruit crops (Flore and Lakso, 1988). For this reason atmospheric factors that regulate leaf water...
status and photosynthesis should be considered as well as those that regulate soil water deficits when evaluating fruit tree physiology (Flore and Lakso, 1988). If plants grown under conditions of root system restriction had a high hydraulic resistance in the roots (Hameed et al., 1987), the papaya genotypes grown in the WR area seemed to have experienced a high leaf water stress due to a high vapour pressure deficit (summer) at measuring time than genotypes in the NR area. This condition may have contributed to a significant decrease in stomatal opening followed by reduced \( A \) values of papaya leaves in WR area (Table 2 to 4). Possibly, the mechanical root restriction increased the effects of atmospheric components in plants grown in WR area.

Although it also showed a considerable reduction in gas exchange rates, the Know-You genotype was the least affected by root restriction (Tables 2 to 4). It presented the highest values of \( A \) and \( g_\text{s} \) in the WR area in the three consecutive days that the plants were not irrigated. This genotype had the greatest leaf area of the four genotypes in the WR area (Yamanishi et al., 1998). Notwithstanding the greatest evaporative surface area, it was able to extract enough water from the soil to maintain a high stomatal conductance than the other genotypes in the WR area. Future research on this genotype should be conducted in order to study the effects of the root mechanical restriction in relation to stomatal conductance and root hydraulic conductance.

**TABLE 2** - Net CO\(_2\) assimilation rate (\( A \)), stomatal conductance (\( g_\text{s} \)), intercellular partial pressure CO\(_2\) (\( c_i \)) and leaf temperature (\( T_l \)) of four papaya (Carica papaya L.) genotypes as influenced by root zone restriction in Macaé/RJ/Brazil. Determined in the first day after the irrigation.

| Genotypes        | \( A \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) | \( g_\text{s} \) (\( \text{mol m}^{-2} \text{s}^{-1} \)) | \( c_i \) (\( \mu \text{L L}^{-1} \)) | \( T_l \) (°C) |
|------------------|---------------------------------|---------------------------------|---------------------------------|-------------|
|                  | NR\(^x\) | WR\(^y\) | NR | WR | NR | WR | NR | WR |
| Sunrise Solo TJ  | 24.2 Aab\(^z\) | 14.3 Bb | 0.155 Ab | 0.031 Bb | 262.6 Aa | 232.3 Ba | 36.5 Bb | 40.0 Aa |
| Sunrise Solo 72/12 | 20.8 Ac | 13.8 Bb | 0.093 Ab | 0.039 Bb | 251.3 Ab | 230.9 Aa | 37.8 Ba | 39.2 Aa |
| Tainung 02       | 25.8 Aa | 12.7 Bb | 0.292 Aa | 0.036 Bb | 261.7 Aa | 245.9 Ba | 36.6 Ab | 37.8 Ab |
| Know -You 01     | 23.3 Ab | 16.8 Ba | 0.131 Ab | 0.067 Ba | 259.7 Aab | 253.0 Aa | 36.7 Bb | 38.1 Ab |

\(^z\) Determined at hundred fifty days after transplant, first day after irrigation; Photosynthetic photon flux 2141.0 ± 298.0 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Data collected at 9:00-11:00 AM. Air Temperature 38.08 ± 0.9°C. CO\(_2\) concentration into chamber 331.50 ± 9.46 µL L\(^{-1}\). Partial pressure of water vapour into chamber 3.57 ± 0.207 kPa; Soil moisture on volume basis 11.01 ± 1.72 %, [Field Capacity=11.00%]; \(^y\) NR= Area with no restriction to root growth; \(^x\) WR= Area with restriction of the growth root system; \(^w\) The columns and lines, average followed by the same small or capital letters for each analyzed characteristic did not differ at level of 5% (\( p \leq 0.05 \)) of probability using the Duncan's Multiple Range Test.
TABLE 3 - Net CO\textsubscript{2} assimilation rate (A), stomatal conductance (g\textsubscript{s}), intercellular partial pressure CO\textsubscript{2} (c\textsubscript{i}) and leaf temperature (T\textsubscript{l}) of four papaya (Carica papaya L.) genotypes as influenced by root zone restriction in Macaé/RJ/Brazil. Determined in the second day after the irrigation.

| Genotypes          | A\textsuperscript{z} (µmol m\textsuperscript{-2} s\textsuperscript{-1}) | g\textsubscript{s} (mol m\textsuperscript{-2} s\textsuperscript{-1}) | c\textsubscript{i} (µL L\textsuperscript{-1}) | T\textsubscript{l} (°C) |
|--------------------|-----------------|-----------------|------------------|--------|
|                     | NR\textsuperscript{y} | WR\textsuperscript{x} | NR | WR | NR | WR | NR | WR |
| Sunrise Solo TJ     | 21.3 Aa\textsuperscript{w} | 14.0 Bb | 0.123 Ac | 0.034 Ba | 278.0 Aa | 252.5Bc | 37.1Aab | 37.3 Ab |
| Sunrise Solo 72/12  | 20.2 Aa | 11.2 Bc | 0.223Aab | 0.037 Ba | 273.9 A | 267.3Ab | 37.7 Ba | 39.0 Aa |
| Tainung 02          | 22.0 Aa | 15.0 Bab | 0.181 Abc | 0.062 Ba | 274.0 B | 295.0Aa | 36.7 Ab | 34.5 Bc |
| Know-You 01         | 22.6 Aa | 16.6 Ba | 0.249 Aa | 0.081 Ba | 268.0 Aa | 276.0Ab | 36.7 Ab | 37.0 Ab |

\textsuperscript{z} Determined 150 days after transplanting, on the second day after irrigation; Quantum flux of photons 2084.0 ± 71.20 µmol m\textsuperscript{-2} s\textsuperscript{-1}. Data collected at 9:00-11:00 AM. Air Temperature 37.0 ± 1.46°C. CO\textsubscript{2} concentration in chamber 345.79 ± 18.60 µL L\textsuperscript{-1}. Partial pressure of water vapour into chamber 3.50 ± 0.266 kPa; Soil moisture on volume basis 10.00 ± 1.15 %. [Field Capacity=11.00%]; \textsuperscript{y} NR= Area with no restriction to root growth; \textsuperscript{x} WR= Area with restriction of the root growth; \textsuperscript{w} Averages followed by the same small letters in the columns or capital letters in the rows (for each characteristic) did not differ at the probability level of 5% (p < 0.05) using Duncan's Multiple Range Test.

TABLE 4 - Net CO\textsubscript{2} assimilation rate (A), stomatal conductance (g\textsubscript{s}), intercellular partial pressure CO\textsubscript{2} (c\textsubscript{i}) and leaf temperature (T\textsubscript{l}) of four papaya (Carica papaya L.) genotypes as influenced by root zone restriction in Macaé/RJ/Brazil. Determined in the third day after the irrigation.

| Genotypes          | A\textsuperscript{z} (µmol m\textsuperscript{-2} s\textsuperscript{-1}) | g\textsubscript{s} (mol m\textsuperscript{-2} s\textsuperscript{-1}) | c\textsubscript{i} (µL L\textsuperscript{-1}) | T\textsubscript{l} (°C) |
|--------------------|-----------------|-----------------|------------------|--------|
|                     | NR\textsuperscript{y} | WR\textsuperscript{x} | NR | WR | NR | WR | NR | WR |
| Sunrise Solo TJ     | 17.1 Aa\textsuperscript{w} | 10.0 Bb | 0.110 Ab | 0.021 Ba | 282.1 Ac | 261.4 Bb | 36.7 Ba | 38.1 Aa |
| Sunrise Solo 72/12  | 22.0 Aa | 11.5 Bb | 0.226 Aa | 0.052 Ba | 296.7 Ab | 271.3 Bab | 35.3 Bb | 36.5 Ad |
| Tainung 02          | 22.2 Aa | 12.3 Bab | 0.131 Ab | 0.029 Ba | 309.4 Aa | 276.8 B | 36.8 Ba | 37.6 Ab |
| Know-You 01         | 21.8 Aa | 15.2 Ba | 0.210 Aa | 0.062 Ba | 293.2 A | 282.8 Aa | 35.7 Bab | 37.8 Aab |

\textsuperscript{z} Determined 150 days after transplanting, on third day after irrigation; Quantum flux of photons 1650.60 ± 160.90 µmol m\textsuperscript{-2} s\textsuperscript{-1}. Data collected at 9:00-11:00 AM. Air Temperature 36.90 ± 0.8°C. CO\textsubscript{2} concentration in chamber 360.00 ± 11.70 µL L\textsuperscript{-1}. Partial pressure of water vapour into chamber 3.59 ± 0.11 kPa; Soil moisture on volume basis 9.36 ± 1.73 %. [Field Capacity=11.00%]; \textsuperscript{y} NR= Area with no restriction to root growth; \textsuperscript{x} WR= Area with restriction of root growth; \textsuperscript{w} Average followed by the same small letters in columns or capital letters in the rows (for each characteristic) did not differ at the probability level of 5% (p < 0.05) using Duncan's Multiple Range Test.
The reduction in the $g_s$, verified in the leaves of all genotypes in the WR area may have contributed to increase the $T_l$ except for Tainung 02 on the second day after irrigation. As $T_l$ is related to $E$ (Nobel, 1991), plants grown in the WR area showed reduced $g_s$, and as a result of the limited $E$ increased $T_l$ (Tables 2 to 4).

The high concentration of CO$_2$ in the intercellular space ($c_i$), for all genotypes grown at NR area, during the three days after irrigation (Tables 2 to 4), was caused by high $g_s$ values in the NR area, since $c_i$ is directly proportional to the stomatal conductance and inversely proportional to $A$ ($c_i=C_a - A/g_s$), for constant values of the concentration CO$_2$ in the bulk air ($C_a$) (Mansfield et al., 1990, Field et al., 1990, Long and Hällgren, 1993, Farquhar and Sharkey, 1982). The contrasting results for the genotypes Tainung 02 and Know-You 01 on the second day after the irrigation were due to the high values of the CO$_2$ concentration in the bulk air at the measurement time of the two genotypes. However, these genotypes grown in the NR area had larger rates of $A$ that contributed to reduced concentration of CO$_2$ in the leaf intercellular air spaces. These elevated $A$ values for genotypes grown in the NR area were not sufficient to reduce the $c_i$. The high $c_i$ of Tainung 02 and Know-You 01 was caused by the high stomatal conductance.

The values of the IWUE in all genotypes were higher in the WR area than in the NR area (Table 5). These elevated values can be explained by the much larger reductions in $g_s$ than in $A$ in plants grown in the WR area. This fact may explain the high IWUE in Sunrise Solo TJ, since this genotype presented the smallest $g_s$ values in this area. This adjustment in the $g_s$, reducing the values of $A$ is a possible mechanism that facilitates the acclimatization of the plant exposed to a limiting factor. This acclimatization allow plants to continue incorporating carbon to the biomass, avoiding the excessive loss of water. Possibly, the genotype Sunrise Solo TJ presents a high efficiency in the stomatal adjustment compared to other genotypes.

| TABLE 5 - Intrinsic water use efficiency (IWUE) of four papaya (Carica papaya L.) genotypes as influenced by root zone restriction in Macaé/RJ/Brazil |
| Genotypes     | IWUE* (µmol mol$^{-1}$) | NR$^y$ | WR$^x$ |
|---------------|-------------------------|--------|--------|
| Sunrise Solo TJ | 70.6 Ba$^w$               | 398.4 Aa |
| Sunrise Solo 72/12 | 44.4 Ba                 | 259.4 Ab |
| Tainung 02   | 66.9 Ba                 | 271.6 Ab |
| Know-You 01  | 39.5 Ba                 | 167.9 Ac |

$^z$ Determined using data $A$ and $g_s$ collected in the first, second and third days after irrigation; $^y$ NR= Area with no restriction to root growth; $^x$ WR= Area with restriction of root growth; $^w$ Average followed by the same small letters in columns or capital letters in the rows did not differ at the probability level of 5% (p<0.05) using the Duncan's Multiple Range Test.

Root system restriction, imposed by soil, impaired some physiological characteristics of the four papaya genotypes studied. All genotypes presented higher values of IWUE in plants grown in WR area where Sunrise Solo TJ showed the highest IWUE. Further investigations are required to understand if the stomata closure in papaya plants growing in soil with mechanical impedance is due to a hormonal effect or reduced leaf water potential caused by high vapour pressure deficit and/or high hydraulic resistance in the roots.

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