Ecophysiology of papaya
*(Carica papaya L)*

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Papaya (*Carica papaya* L.) is a principal horticultural crop of tropical and subtropical regions (Campostrini et al, 2010).

Papayas are produced in about 60 countries, with the bulk of production occurring in developing economies!

**Faostat 2015:**
- **Area harvested** in the world: 441,042 ha
- **Brazil:** 31,989 ha (7.3%)

Asia is the largest papaya-producing continent, providing 55.5% of the total production, followed by South America (23.0%) and Africa (13.2%)

**Production** in the world: 12,420,584 tonnes
- **Brazil:** 1,582,638 ton (13%)
Papaya (*Carica papaya* L.) is a principal horticultural crop of tropical and subtropical regions.

**Faostat 2015:**

**Yield** in the world: **28,161 kg ha\(^{-1}\)**  
**Brazil:** **43,333 kg ha\(^{-1}\)** (**65%** higher!)

World-wide production of papaya has been increasing approximately **372,000** tonnes year\(^{-1}\) (FAOSTAT, 2015)  
Brazil has been increasing **20.290** tonnes per year!!
Gaining in popularity worldwide, papaya is now ranked third with 11.22 Mt, or 15.36 percent of the total tropical fruit production, behind mango with 38.6 Mt (52.86%) and pineapple with 19.41 Mt (26.58%) 

Total tropical fruit production:

Mango – 52.86%

Pineapple – 26.58%

**Papaya – 15.36%** (Evans e Ballen, 2012)

**Papaya in Europe:**

- Tropical fruits are grown in very limited countries in Europe due to the climatic constraints

- However, some of them are grown due to a favorable climate on the Mediterranean coast and Atlantic Islands for local consumption (Voth, 2000)

- Papaya is cultivated under protected cultivation in subtropical country such as the Canary Islands (Spain) (Galan Sauco et al. 2008).

- However, global climate changing should cause an increase in air temperature, and will be expected that cultivation of papaya will be expanded in the subtropical regions in Europe and Asia
Region of Production

Production - Exportation

- Rio Grande do Norte: 10% - 29%
- Bahia: 45% - 14%
- Espírito Santo: 37% - 55%
Brazilian Exportation Company

**Espírito Santo state**
- Caliman
- Frutasolo
- Frutamel
- Interfruit
- UGBP
- Marin papaya

**Bahia state**
- Frutas Belo

**Rio Grande do Norte state (Formosa group) (Semi-arid)(400 mm per year)**
- WG Fruticultura
- Agrícola Famosa
Production cost

<table>
<thead>
<tr>
<th>Cultivation</th>
<th>Valor - Euro</th>
</tr>
</thead>
<tbody>
<tr>
<td>month 1</td>
<td>755.2</td>
</tr>
<tr>
<td>month 2</td>
<td>278.6</td>
</tr>
<tr>
<td>month 3</td>
<td>314.1</td>
</tr>
<tr>
<td>month 4</td>
<td>234.5</td>
</tr>
<tr>
<td>month 5</td>
<td>228.6</td>
</tr>
<tr>
<td>month 6</td>
<td>298.8</td>
</tr>
<tr>
<td>month 7</td>
<td>221.3</td>
</tr>
<tr>
<td>month 8</td>
<td>238.6</td>
</tr>
<tr>
<td>TOTAL</td>
<td>2,570.5</td>
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<table>
<thead>
<tr>
<th>Starting</th>
<th>ud</th>
<th>Valores - euro</th>
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<tbody>
<tr>
<td>Production</td>
<td>Euro ha⁻¹</td>
<td>5,133.0</td>
</tr>
<tr>
<td>Total</td>
<td>Euro ha⁻¹</td>
<td>7,704.3</td>
</tr>
<tr>
<td>Yield</td>
<td>T ha⁻¹</td>
<td>68.58</td>
</tr>
<tr>
<td>Production cost</td>
<td>Euro kg⁻¹</td>
<td>0.11</td>
</tr>
<tr>
<td>Price average</td>
<td>Euro kg</td>
<td>0.13</td>
</tr>
<tr>
<td>Profitability</td>
<td>%</td>
<td>15.31%</td>
</tr>
</tbody>
</table>
## Consumo de água (litros/planta/dia) nas condições do norte do ES – Caliman (2003 a 2010)

<table>
<thead>
<tr>
<th>Idade da planta - dias</th>
<th>dez/fev</th>
<th>mar/abr</th>
<th>maio/jun</th>
<th>jul/set</th>
<th>Consumo de água - l</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>inicio</td>
<td>fim</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>30</td>
<td>6.00</td>
<td>5.00</td>
<td>3.00</td>
<td>549.00</td>
<td>610.00</td>
</tr>
<tr>
<td>30</td>
<td>60</td>
<td>10.00</td>
<td>8.00</td>
<td>5.00</td>
<td>915.00</td>
<td>976.00</td>
</tr>
<tr>
<td>60</td>
<td>90</td>
<td>12.00</td>
<td>9.00</td>
<td>6.00</td>
<td>1.096.00</td>
<td>1.096.00</td>
</tr>
<tr>
<td>90</td>
<td>120</td>
<td>15.00</td>
<td>13.00</td>
<td>8.00</td>
<td>1.372.50</td>
<td>1.586.00</td>
</tr>
<tr>
<td>120</td>
<td>360</td>
<td>16.00</td>
<td>14.00</td>
<td>10.00</td>
<td>1.464.00</td>
<td>1.708.00</td>
</tr>
<tr>
<td>360</td>
<td>720</td>
<td>16.00</td>
<td>14.00</td>
<td>10.00</td>
<td>1.494.00</td>
<td>1.708.00</td>
</tr>
</tbody>
</table>

### Chuveiro
- Chuva – mm: 1.200.00
- L/m²: 6.480.00
- Espacemento: 3.5 x 15
- Produção – kg/planta: 51.35

### Microaspersão
- Chuva – mm: 1.200.00
- L/m²: 6.480.00
- Espacemento: 3.5 x 15
- Produção – kg/planta: 51.35

### Gotejamento
- Chuva – mm: 1.200.00
- L/m²: 6.480.00
- Espacemento: 3.5 x 15
- Produção – kg/planta: 51.35

**Nota:** Os consumos de água são apresentados em litros por planta por dia, com intervalos de dezembro a setembro. As produções são calculadas em kg por planta e incluem o aumento de % de 11.83%.
Papaya plant

- Semi-woody (an intermediate position between herbs and trees)
- Latex-producing
- Usually single-stemmed
- Reproductive precocity (3-4 months)

- High photosynthetic rates \((\approx 26 \, \mu\text{mol m}^{-2} \, \text{s}^{-1} \text{ - field condition in } 2000 \, \mu\text{mol m}^{-2} \, \text{s}^{-1} \, \text{PAR})\)
  - café: 8-9 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}
  - milho: 40-50 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}
  - feijão: 12 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}
  - arroz: 13 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}
  - cana de açúcar: 40-50 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}
  - banana: 12 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}
  - abacaxi: 7 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}

- Fast growth
- Production of many seeds
  ‘Solo’ group: \textbf{270 seeds per fruit (5g)}
  ‘Formosa’ group: \textbf{350 seeds per fruit (17g)}

- Low construction cost of hollow stems

- Continuous fruit production (indeterminate growth)
Chapter 2
Biology of the Papaya Plant

Víctor M. Jiménez, Eric Mora-Newcomer, and Marco V. Gutiérrez-Soto

Papaya plant
Papaya plant
Chapter 2
Biology of the Papaya Plant

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Papaya plant
Fig. 2.6 Papaya fruits according to sex type. (a) Fruit of a hermaphroditic plant. (b) Fruit from a female plant. (c) Misshapen fruit from a hermaphroditic plant due to carpel lody
Fig. 2.5 Female sterility and carpellody of papaya. (a–d) Gradual reduction in pistil size due to female sterility of flowers and approximate phenotype of the corresponding fruit. (a) Normal elongata flower with five carpels. (b, c). Reduced ovary due to loss of carpels as a result of partial female sterility. (d) Completely female sterile flower. (e, f) Increasing levels of carpellody and approximate phenotype of corresponding fruit. (e) Normal elongata flower. (f–g) Fusion to the ovary and partial transformation to carpels and of one (f) and two (g) stamens, leading to misshapen fruits. (h) Complete transformation of the five antepetalous whorl of stamens into carpels, leading to the “pentadria” type of flower, with a rounded ovary (and fruit) and almost free petals.
Root development of ‘Red Lady’ papaya plants grown on a hillside

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Shape of the root system influences the nutrient and water uptake capabilities of a plant. Therefore, knowledge of the root distribution of papaya plants is useful for determining suitable placement of cultural inputs such as fertilizer or sensors for monitoring soil moisture depletion. Substrate aeration is highly controlling of papaya plant physiology and growth (Marler et al., 1994). Thus, we hypothesized that lateral roots on the uphill side of papaya plants growing on a hillside would ascend into the more favorably aerated surface soil, rather than maintain a 90° inclination angle or cease growing altogether. In non-saturated soil conditions negatively gravitropic roots ensure root proliferation in the better aerated soil surface (Jackson, 1985).
Root ⇒ 70 a 75% in 30cm ⇒ 1 year old ≈ 3.5 m
Figure 2. Scaled root map of a ‘Red Lady’ papaya plant 17 weeks after transplanting to a hillside with a 62% slope. The heavy line indicates the hillside surface. The vertical arrow indicates plant location. The arrows below the hillside surface indicate 15-cm depth increments which are parallel to the surface. The vertical line indicates position of the taproot system. The horizontal line depicts the horizontal plane positioned at the stem base.
Table 2. Root characteristics of ‘Red Lady’ papaya plants growing on a hillside with a 60% to 70% slope following 17 weeks of growth. Root concentration data were obtained from trench profiles, and root length and mass data were obtained from excavations (n = 4).

<table>
<thead>
<tr>
<th>Root characteristic</th>
<th>Zone</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Downhill</td>
<td>Uphill</td>
</tr>
<tr>
<td>Root concentration</td>
<td>435</td>
<td>262</td>
</tr>
<tr>
<td>(&lt; 1 mm, roots per m²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Root concentration</td>
<td>508</td>
<td>312</td>
</tr>
<tr>
<td>(total, roots per m²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length (cm)</td>
<td>9287</td>
<td>3737</td>
</tr>
<tr>
<td>Dry mass (g)</td>
<td>25.96</td>
<td>11.92</td>
</tr>
</tbody>
</table>

²Significance of F values.
³Significance according to t test.

Figure 1. Depth distribution of ‘Red Lady’ papaya plant roots seven weeks (Experiment 1, n = 3, □) or 17 weeks (Experiment 2, n = 4, □) after transplanting to a 60% to 70% sloped hillside. Symbols and lateral bars indicate mean ± standard error.

Table 1. Root characteristics of ‘Red Lady’ papaya plants growing on a hillside with a 60% to 70% slope following 7 weeks of growth. Root number data were obtained from trench profiles (n = 3). Root length and mass data were obtained from excavations (n = 4).

<table>
<thead>
<tr>
<th>Root characteristic</th>
<th>Zone</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Downhill</td>
<td>Uphill</td>
</tr>
<tr>
<td>Root number (&lt;1 mm)</td>
<td>61</td>
<td>26</td>
</tr>
<tr>
<td>Root number (total)</td>
<td>65</td>
<td>29</td>
</tr>
<tr>
<td>Length (cm)</td>
<td>1038</td>
<td>811</td>
</tr>
<tr>
<td>Dry mass (g)</td>
<td>2.53</td>
<td>1.44</td>
</tr>
</tbody>
</table>

²Significance of F values.
³Significance according to t test.
Leaves arranged in a spiral pattern

> light interception
> Number of sun leaves
Leaf

- Plant produce large palmate leaves (~0.6 m²)
- Five to nine pinnate lobes of various widths (40-60 cm)
- Leaf epidermis and the **palisade parenchyma** are composed of a single cell layer, while **spongy mesophyll** consists of four to six layers of tissue
Stomata

- Papaya leaves are hypostomatics

- Stomatal density of sunlight leaves is 400 to 800 stomata mm$^{-2}$
Stem (trunk)

- The single stem provides structural support
- Stem diameters of adult plants vary from 10 to 30 cm at base to 5 - 10 cm at the crown.
Stem (trunk)

- C. papaya exhibits a very unusual functional anatomy
- Stem density is only 0.13 g cm$^3$
- Carica papaya L. does not contain wood, according to the botanical definition of wood as lignified secondary xylem

- Despite its parenchymatous secondary xylem, these plants are able to grow up to 10 m high, and each plant can produce 50 fruits with 0.5kg each fruit (25kg) (‘Solo’ group) and 25 fruits with 1.5kg each fruit (45kg) (‘Formosa’).

This is surprising, as wooden structural elements are the ubiquitous strategy for supporting height growth and high fruit weight in papaya plants!

Proposed possible alternative principles to explain the compensation for lack of wood in C. papaya are **turgor pressure of the parenchyma**, **lignified phloem fibres in the bark**, or **a combination of the two**
Fig. 1. Detail of papaya stem’s cross section (A) and fibres after removal of parenchyma in longitudinal view (B)
Each plant with 20cm diameter!!
‘Solo’ group can support 25kg
“Formosa’ group can support 45kg

The construction of fibers and high-pressure matrix parenchyma is unique in tree-like plants, and guarantees adequate flexural rigidity with a minimum fibre content!!
Turgor pressure was between 0.82 and 1.25 MPa, indicating that turgor is essential for flexural rigidity of the entire stem!!!! Kempe et al (2014)

A car tire is typically inflated to about 0.2 MPa. The water pressure in home plumbing is typically 0.2-0.3 MPa.
Stem (trunk)

The lower internodes are compact and wider and seem to mechanically support the entire weight of the plant (Morton 1987).
Stem (trunk)

-The lower internodes are compact and wider and seem to mechanically support the entire weight of the plant (Morton 1987).

-The xylem is poorly lignified and aids in storage of water and starch (Fisher 1980).

-The xylem is composed of wide vessels that can be seen with the naked eye, imbibed in non-lignified parenchyma tissues and rays.
Single-leaf photosynthesis

Stomata

-Papaya leaves are hypostomatics

-stomatal density of sunlight leaves is \(400 \text{ to } 800\text{ stomata mm}^{-2}\)
Single-leaf photosynthesis

Papaya is classified as a plant with C3 metabolism (Imai et al., 1982; Marler et al., 1994; Campostrini, 1997; Marler and Mickelbart, 1998; Jeyakumar et al., 2007). The absence of margin cell formation in the vascular bundles of papaya leaves (Buisson and Lee, 1993) is a characteristic associated with C3 metabolism.
Single-leaf photosynthesis

The average $^{13}C$ value of C4 plants is $-14\%$.

C3 plants is $-23$ to $-36\%$.

Campostrini, 1997

Torres-Netto 2005
Maximum net carbon assimilation (A) rates of 25 to 30 μmol m⁻² s⁻¹ are achieved at 2000 μmol m⁻² s⁻¹ photosynthetic photon flux (PPF) in soil field capacity (Marler and Mickelbart, 1998; Campostrini and Yamanishi, 2001; Reis, 2007)
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 75% significantly reduced new flower production and fruit set, decreased ripe fruit total soluble solids (TSS)

50% defoliation did not reduce new fruit set or ripe fruit TSS (Zhou et al, 2000)
In general: (Brazil)

**Solo group**: < leaf area  
**High yield:**  
95 t ha\(^{-1}\)  
95 fruits  1 leaf support 4 fruits  
24 leaves  
**Average yield:**  
61 t ha\(^{-1}\)  
62 fruits  1 leaf support 3 fruits  
19 leaves

**Formosa group**: > leaf area  
**High yield:**  
150 t ha\(^{-1}\)  
73 fruits  1 leaf support 3 fruits  
25 leaves  
**Average yield:**  
85 t ha\(^{-1}\)  
42 fruits  1 leaf support 2 fruits  
21 leaves
Increase net photosynthetic rate \((A)\) is very important to high papaya production.

While high \(A\) rates are possible in papaya, environmental factors as PPF (light), water (soil and air), soil compaction, wind, VPD, temperature, soil oxygen, often limit \(A\).

1) **Light (PPF)**

Sun leaf

![Graph showing the relationship between PPF and net photosynthetic rate (A)](image)

\[
\psi_{\text{soil}} = -20 \text{ kPa} \\
\psi_{\text{soil}} = -68 \text{ kPa}
\]
With rapid reductions in irradiance, photosynthesis declines due to rapid biochemical adjustments. With the return to high irradiance, and in the absence of any stomatal limitation, photosynthesis quickly increase.
Light compensation point in papaya single leaf. Field condition
60 μmol m\(^{-2}\) s\(^{-1}\)

Dark respiration
1.75 to 2.5 μmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)
The PPF response of papaya may also decline with PPF above saturating levels.
The decrease in A that begins at light saturation is due, in part, to the decrease in stomatal conductance (gs) through the direct action of radiant energy on leaf heating (stomatal limitation).
Net carbon assimilation (μmol m\(^{-2}\) s\(^{-1}\))

Leaf-to-air vapor pressure differences (kPa)

Stomatal conductance (mol m\(^{-2}\) s\(^{-1}\))

11:00 to 14:00 hours
High light (2200 µmol m\(^{-2}\) s\(^{-1}\))
High leaf temperature (40ºC)
High VPD (≈ 6 kPa)
Low g\(_s\) (0.20 mol m\(^{-2}\) s\(^{-1}\))
Low A (5 µmol m\(^{-2}\) s\(^{-1}\))

Midday depression of photosynthesis can reduce yield

The photosynthetic response of papaya is strongly linked to environmental conditions through stomatal behavior.
Papaya leaves showed paraheliotropic movement associated with reduced leaf turgor (Reis 2008).

Paraheliotropic movement can be translated into decreased radiation load per unit leaf area which, in turn, could prevent the photoinhibition.
Irradiance can control stomatal conductance and can reduce photosynthesis

**Papaya stomata are able to track rapid changes in irradiance**! (Clemente and Marler, 1996)

Most plants experience continuous fluctuations in light under natural conditions rather than long periods of uniform irradiance!!

Even individuals of pioneer and other species growing in open habitats experience high and low light periods in the order of several minutes each due to broken cumulus cloud cover (Knapp and Smith, 1990).
The graph shows the variation of VPD air (kPa) and PAR (μmol m⁻² s⁻¹) with the hour of the day. The VPD air and PAR levels rise significantly during the day, particularly from 08:00 to 10:00 and then again from 14:00 onwards. The PAR level is higher in the external air compared to the PAR level, indicating a possible difference in light intensity or availability.

Figure 1: Light Diffraction Through Clouds

- White light is scattered in all directions.
- Some light penetrates to cloud base.
Fig. 1. Response of net CO$_2$ assimilation (A, ■), stomatal conductance (g$_s$, ▲),...
1600 μmol m^{-2} s^{-1} - 250 μmol m^{-2} s^{-1} durante 2.5 min - 1600 μmol m^{-2} s^{-1}
Leaf age and light intensity affect gas exchange parameters and photosynthesis within the developing canopy of field net-house-grown papaya trees

Ren-Huang Wang a,b, Jer-Chia Chang c, Kuo-Tao Li b, Tzong-Shyan Lin b, Loong-Sheng Chang b,c

*Fig. 2. Effects of leaf age on leaf position (A), leaf area (B) and total chlorophyll concentration (C) of the tagged leaves in 'Taihong No. 2' papaya in 2009–2010 cropping season. Bars indicate standard errors of the mean (n = 8).*
Leaf age and light intensity affect gas exchange parameters and photosynthesis within the developing canopy of field net-house-grown papaya trees.

Ren-Huang Wang, Jer-Chia Chang, Kuo-Tan Li, Tzong-Shyan Lin, Loong-Sheng Chang.

Fig. 1. Changes in PPFD, % of value at top of canopy, on the tagged leaves in 'Tainung No. 2' papaya in 2009-2010 cropping season. Bars indicate standard errors of the mean (n = 8).
Fig. 6. Effects of leaf positions on the maximum net CO₂ assimilation \( (A_{\text{CO}_2}) \) of the leaves in 'Tainung No. 2' papaya in 2009-2010 cropping season. Bars indicate standard errors of the mean \((n = 5)\).
3.6m x 1.5m = 5.4m² field condition in Brazil  
Almeria greenhouse: 3.0m x 1.6m = 4.8 m²
The papaya photosynthetic capacity can be linked to non stomatal limitation in soil field capacity condition.

As example:
- Nitrogen leaf concentration

15 g kg\(^{-1}\)DM

35 g kg\(^{-1}\)DM

18 g kg\(^{-1}\)DM

37 g kg\(^{-1}\)DM

Fig. 2 Relationship between chlorophyll concentration (\(a+b\)) (\(\mu\)mol m\(^{-2}\)) and leaf \(N_{\text{org}}\) (g kg\(^{-1}\) DW) in ‘Solo’ and ‘Golden’ papaya plants cultivated in greenhouse conditions. The \(R^2\) indicated significant correlation at the 0.1 % level.
Figure 4. The relation between the organic nitrogen content and the PCM reading, in Sunrise Solo and Golden papaya plants, cultivated in a greenhouse. The open circles with reduced PCM readings (<30) refer to the senescent 6th–7th leaves.
Fig. 4 Relationship between chlorophyll concentration (a + b) (µmol m\(^{-2}\)) and SPAD values in ‘Solo’ and ‘Golden’ papaya plants cultivated in greenhouse conditions. R\(^2\) indicate significant correlation at the 0.1% level.

Fig. 6 Relationship between total maximum quantum efficiency (F\(_\text{v}/F\text{m}\)) and SPAD values in ‘Solo’ and ‘Golden’ papaya plants cultivated in greenhouse conditions. R\(^2\) indicate significant correlation at 0.1% level.
Portable chlorophyll meter (PCM-502) values are related to total chlorophyll concentration and photosynthetic capacity in papaya (*Carica papaya* L.).

Fernanda Assunção De Castro • Eliemar Campostrioli • Alena Torres Netto • Mara De Menezes De Assis Gomes • Tiago Massi Ferraz • David Michael Glenn

**Fig. 3** Relationship between net photosynthetic rate (A) (μmol m⁻² s⁻¹) and chlorophyll concentration (a + b) (μmol m⁻²) in ‘Solo’ and ‘Golden’ papaya plants cultivated in greenhouse conditions. R² indicate significant correlation at the 0.1 % level.
Individual light sensors, available individually or as a set of 3 or 6 sensors, allow you to measure site-specific aspects of light. The hand-held sensors feature cosine correction, built-in mounting brackets for stationary measurements. These sensors are frequently used when measuring across a greenhouse.  

3415FX  Field Scout External Light Sensor Meter  
3668I  Quantum Light Sensor  
3668I3  Quantum Light 3 Sensor Bar  
3668I6  Quantum Light 6 Sensor Bar  
3676I  UV Light Sensor  
3670I  Silicon Pyranometer Sensor
g CO₂ m⁻² h⁻¹ to μmol m⁻² s⁻¹
conversion factor is 6.30

The crop was irrigated with a drip/fertigation system providing supplemental irrigation of 10 L per plant per day (winter) and 16 L per plant per day (summer)

Summer: (clear sky, during 4 days)
PPF_max: 2400 μmol m⁻² s⁻¹
T_max: 38ºC
VPD_max: 4 kPa

Winter: (clear sky during 4 days)
PPF_max: 1400 μmol m⁻² s⁻¹
T_max: 33ºC
VPD_max: 3.5 kPa
Under the environmental conditions evaluated:

(4 sunny days)

**Winter:**
- Maximum vapor pressure deficit ($\text{VPD}_{\text{air}}$) = 3.5 kPa
- Air maximum temperature of $33^\circ\text{C}$
- Maximum PPF: $1400 \ \mu\text{mol m}^{-2} \ \text{s}^{-1}$

**Summer**
- Maximum $\text{VPD}_{\text{air}}$ = 4.0 kPa
- Air maximum temperature of $38^\circ\text{C}$
- Maximum PPF: $2400 \ \mu\text{mol m}^{-2} \ \text{s}^{-1}$

Each chamber had a volume of $3.4 \text{ m}^3$

Leaf area each plant
5 months old
Winter: $3.5 \text{ m}^2$
Summer: $4 \text{ m}^2$
\( T_{\text{air inside ballon}} - T_{\text{air outside}} \, ^\circ C \)
Luz

![Graph showing leaf temperature (°C) over time for winter and summer.](image1)

- **Leaf Temperature (°C)**
- **Time (08:00 - 17:00)**
- **Winter**
- **Summer**

![Leaf temperature measurement](image2)

![Irrigation system](image3)
Air temperature

Optimal temperature:

21 a 33ºC (Knight, 1980)
22 A 26ºC (Lassoudiere, 1968)
30ºC (Allan, 1978)

Allan and Jager (1978) reported that A increased when air temperature rose from 16 to 30ºC, and then A decreased linearly at temperatures above 30ºC, the value at 41ºC being half that at 30ºC.

However, air temperature acts indirectly on papaya photosynthesis via increases in leaf-to-air VPD! (stomatal limitation)

When air temperature increased from 20º to 40ºC for 'Sunrise Solo' papaya growing in Linhares, southeastern Brazil, the VPD_{leaf,air} increased from 2 to 6 kPa and A decreased from 20 to 5 μmol m⁻² s⁻¹ (Torres-Netto, 2000)
**Air temperature**

High air temperature and low Relative Humidity increase $V_{PD_{air}}$

$$V_{PD_{air}} = 0,61137 \times \exp \left(17,502 \times \frac{T^{\circ}}{240,97 + T^{\circ}} \right) \times (1,0 - (UR\% / 100))$$

Threshold VPD values to papaya:

- $V_{PD_{air}} = < 1kPa \ (e_{sair} - e_{air})$
- $V_{PD_{leaf-air}} = < 2kPa \ (e_{sleaf} - e_{air})$

High $V_{PD_{air}}$ and $V_{PD_{leaf-air}}$ reduce $g_{s}$

$V_{PD_{leaf-air}}$
In addition, air temperature acts directly on papaya leaves photosynthesis via increases in leaf temperature (non stomatal limitation)

Nonstomatal limitation:
- **inhibition of Rubisco**, 
- heat stress results in a loss of the oxygen evolving complex activity ([Enami et al., 1994; Yamane et al., 1998]),
- dissociation of the peripheral antenna complex of PSII from its core complex ([Gounaris et al., 1984; Srivastava et al., 1997])
- inhibition of electron transfer from primary/secondary electron-accepting plastoquinone of PSII at the acceptor side ([Bukhov et al., 1990; Cao and Govindjee, 1990]),

High temperature increases the membrane fluidity and electron transport is blocked!! Than $F_o$ increase
Fig. 1. Determination of the critical temperature ($T_c$, the temperature at which basic fluorescence $F_0$ increased sharply when leaf was exposed to high temperature treatment at about 1 °C min$^{-3}$ graduation in darkness) as the intersection point of two regression lines extrapolated from the slow and the fast rising portions of the temperature-dependent $F_0$ response.

Carica papaya is heat tolerant!
Fig. 1. Changes in chlorophyll fluorescence in leaves of three plants heated continuously at a rate of 1°C per minute. The temperature values (t₁ to t₅) used to compare the fluorescence-heating curves for different plants are shown on the curve for *P. glacialis* (see also text).
The crop was irrigated with a drip/fertigation system providing supplemental irrigation of 10 L (winter) and 16 L per plant per day (summer).

$WUE_{\text{winter}} = \frac{77}{15} = 5 \text{gCO}_2 \text{ kg H}_2\text{O}^{-1}$

$WUE_{\text{summer}} = \frac{50}{10} = 5 \text{gCO}_2 \text{ kg H}_2\text{O}^{-1}$
Reduced whole-canopy photosynthesis and transpiration in papaya in the summer were due to high leaf temperatures ($T_{\text{max}}=43.9^\circ\text{C}$) (due high radiation and high air temperature) and high $\text{VPD}_{\text{air}}$ (4.0kPa) that caused stomatal closure.

However, high temperature did not affect photochemical efficiency ($F_v/F_m$) when assessed by chlorophyll fluorescence ($F_v/F_m$).


The water use of field-grown papaya plants during four days:

Summer:
**2.5 L H₂O m⁻² leaf area day⁻¹ plant⁻¹**

Winter:
**4.2 L H₂O m⁻² leaf area day⁻¹ plant⁻¹**

Papaya (summer and winter):
- **2 µmol CO₂ mmol H₂O⁻¹**
- **4.8 g CO₂ kg H₂O⁻¹**
- **0.208 L H₂O g CO₂⁻¹**
- **0.0020 mol CO₂ mol H₂O⁻¹**
- **496 mol H₂O⁻¹ mol CO₂**

C3:
- **2.48 µmol CO₂ mmol H₂O⁻¹**
- **6.1 g CO₂ kg H₂O⁻¹**
- **0.164 to 0.5 L H₂O g CO₂⁻¹**
- **0.0025 mol CO₂ mol H₂O⁻¹**
- **400 mol H₂O⁻¹ mol CO₂**

C4:
- **2 to 5 g CO₂ kg H₂O⁻¹**
What strategies to reduce negative effects of high PPF on photosynthesis in summer

**Particle film**
What is a ‘Particle Film’?

- A microscopic layer of mineral particles
- allows water and carbon dioxide to pass through the film

Source:
Dr. David Michael Glenn USDA, ARS, West Virginia, USA
Stomates are not blocked

After initial application

After 24 hours
Reflective surfaces are common plant adaptation

- Plants “use” pubescence and cuticular waxes to reduce environmental stresses and reduce disease and insect damage

- Particle film technology builds on this strategy of a reflective plant surface that repels insects
Licania tomentosa
3% kaolin

Source:
Dr. David Michael Glenn USDA, ARS, West Virginia, USA

12% kaolin
Source:
Dr. David Michael Glenn USDA, ARS, West Virginia, USA
Infrared image of apple trees

- Untreated control 26.0°C
- Surround treated 24.4°C

Temperature (°C)

- Surround WP
- Control
- Air temperature

Hour

900 1100 1300 1500 1700 1900