Inhibition of photosynthesis by flowering in mango (*Mangifera indica* L.). A study by gas exchange methods

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**Abstract**

A regular (cv. Thothapuri) and an irregular (cv. Langra) bearing cultivar of mango were selected to study the gas exchange parameters such as photosynthesis, stomatal conductance and internal carbon dioxide concentrations in flowering and non-flowering branches. Photosynthetic rates at different carbon dioxide concentrations were also recorded in both the branches to calculate the carboxylation efficiency by generating CO$_2$ response curves. Photosynthetic rate and stomatal conductance were higher in non-flowering branches as compared to the flowering ones, in both cultivars. The reduction in photosynthetic rate was not due to variation in the water status of the leaves, since relative water content (RWC) of the leaves in both types of branches was not significantly different. Hence, the reduction in photosynthetic rate could be mainly due to the reduction in carboxylation efficiency. Such a reduction in carboxylation efficiency could be due to the presence of inhibitors in the leaves of flowering branches. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** *Mangifera indica*; Regular and irregular flowering; Carboxylation efficiency; Carbon dioxide response curves; Carbon dioxide compensation point; Photosynthetic rate; Carbon dioxide saturation point
1. Introduction

Irregular bearing is a major problem of commercial importance in some fruit trees, affecting the productivity of mango orchards to a great extent. Even though a lot of research has been done in this area, conclusive evidence is not yet available to pinpoint the physiological basis of this phenomenon. Much of the work done so far in this area is on the role of hormones in flowering (Pandey, 1988). However, information on the relationship of leaf gas exchange parameters with growth, flowering and fruit development in mango are scarce. Hence, in the present investigation, we have made an attempt to study the variations of leaf gas exchange parameters in flowering and non-flowering branches of regular (cv. Thothapuri) and irregular (cv. Langra) bearing mango cultivars. Gas exchange parameters of a leaf are the indicators of biochemical processes taking place in the mesophyll cells (Caemmerer and Farquhar, 1981). Carbon dioxide response curves are often used to estimate the carboxylation efficiency and factors limiting the process of photosynthesis (Sharkey et al., 1986). These curves are also used to calculate the CO$_2$ compensation as well as saturation points of a leaf. Using these curves we tried to find out the relationships between the leaf metabolic activities and flowering in regular and irregular bearing mango trees.

2. Materials and methods

The experiment was conducted in 14-year-old regular (cv. Thothapuri) and irregular (cv. Langra) bearing mango (*Mangifera indica* L.) cultivars, at Hessaraghatta farm of the Indian Institute of Horticultural Research, Bangalore, situated at 13°58' N and 78°E and at an altitude of 890 M MSL, during the year 1995–1996. Three trees each were selected from both the cultivars. Selected trees of irregular bearer were in the ‘Off’ year of bearing during the previous year of experimentation. All the observations were recorded on 30 flowering and non-flowering branches with 10 branches per tree in each cultivar.

Carbon dioxide fixation was recorded in fully expanded leaves of eight-month-old branches using a portable photosynthesis system (LICOR model 6200) during December and January. Observations were recorded at different carbon dioxide concentrations which were generated by mixing varying quantities of respired and ambient air in different polythene bags. Carbon dioxide concentration was continuously checked by the Licor-6200 system by connecting polythene bags through the open system knob (Fig. 1). Once the required concentration was reached, the leaf was clamped in and allowed to become equilibrated with the given carbon dioxide concentration till the leaf chamber RH was stabilised. After stabilisation of the chamber RH, data on gas exchange were recorded by closing the system. Lower carbon dioxide concentrations were generated by passing the
ambient air through the soda lime tube (scrubber) connected to the system through the open system knob. Readings were recorded once the leaf was equilibrated to low CO₂, as explained earlier.

Carbon dioxide response curves were fitted to the data using a polynomial equation. Differential coefficient of the equation was taken as the carboxylation efficiency of the leaf (Caemmerer and Farquhar, 1981).

Relative water content of the leaf was also estimated using the following formula (Weatherley, 1970),

\[
\text{Relative water content (RWC)} = \left( \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \right) \times 100
\]

where FW is the fresh weight of leaf, DW the dry weight and TW the turgid weight.

3. Results and discussion

Net photosynthetic rates (Pₙ) were significantly lower in flowering branches as compared to the non-flowering ones in both cultivars. However, such a significant difference was not seen in stomatal conductance (gs) and mesophyll efficiency (Pₙ/Ci). Amongst cultivars, flowering branches of the regular bearer showed a significantly higher net photosynthetic rate, stomatal conductance and mesophyll
efficiency, whereas, in non-flowering branches the differences were narrower (Table 1). Carbon dioxide response curves were later generated in these two types of branches to understand the possible mesophyll factors responsible for the variation in photosynthetic rates.

Carbon dioxide response curves in flowering and non-flowering branches of both cultivars showed (Figs. 2 and 3) variations in initial slopes as well as in CO2 saturation points (Table 2). In the regular bearer, the carbon dioxide saturation point was higher (520 ppm internal CO2 concentration) for non-flowering branches when compared to flowering branches (440 ppm). Non-flowering branches also showed a higher saturated photosynthetic rate (23.5 and 44 μmol m⁻² s⁻¹ in flowering and non-flowering branches, respectively). The carboxylation efficiency was also significantly higher in non-flowering branches

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>Branches</th>
<th>( P_N ) (μmol m⁻² s⁻¹)</th>
<th>gs (mmol m⁻² s⁻¹)</th>
<th>Ci (ppm)</th>
<th>( P_N/Ci )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thothapuri</td>
<td>Flowering</td>
<td>6.41</td>
<td>80.71</td>
<td>209</td>
<td>0.034</td>
</tr>
<tr>
<td></td>
<td>Non-flowering</td>
<td>7.78</td>
<td>82.32</td>
<td>181</td>
<td>0.043</td>
</tr>
<tr>
<td>CD (p = 0.05)</td>
<td></td>
<td>0.892</td>
<td>NS</td>
<td>12.19</td>
<td>NS</td>
</tr>
<tr>
<td>Langra</td>
<td>Flowering</td>
<td>3.86</td>
<td>76.79</td>
<td>243</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>Non-flowering</td>
<td>7.02</td>
<td>83.68</td>
<td>219</td>
<td>0.028</td>
</tr>
<tr>
<td>CD (p = 0.05)</td>
<td></td>
<td>1.67</td>
<td>NS</td>
<td>23.37</td>
<td>NS</td>
</tr>
</tbody>
</table>

Fig. 2. Carbon dioxide response curves taken in the leaves of flowering (▽) \( (P_N = -7 + 0.123 Ci - 0.00012 Ci^2, R^2 = 0.93) \) and non-flowering (□) \( (P_N = -13.89 + 0.203 Ci - 0.00017 Ci^2, R^2 = 0.96) \) branches of cultivar Thothapuri (Regular bearer). Curves were generated by recording photosynthetic rates at different CO2 concentrations on a bright sunny morning.
(0.169 μmol m$^{-2}$ s$^{-1}$ ppm$^{-1}$) as compared to the flowering branches (0.099). However, the differences in the CO$_2$ compensation points were negligible between the branches (60 and 75 ppm in flowering and non-flowering branches, respectively). In the irregular bearer, the saturated photosynthetic rate, CO$_2$ saturation point and the carboxylation efficiency were significantly lower in flowering branches (11, 425 and 0.060, respectively) when compared to the non-flowering ones (44.50, 560 and 0.154, respectively). The difference in the CO$_2$ compensation point between the branches was not significant in this cultivar either. All the photosynthetic characteristics of flowering branches calculated using CO$_2$ response curves were significantly superior in the regular bearer. However, the differences between the non-flowering branches of the cultivars were negligible.

Table 2
Photosynthetic characteristics in flowering and non-flowering branches of cultivars Thothapuri and Langra

<table>
<thead>
<tr>
<th></th>
<th>Langra</th>
<th>Thothapuri</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flowering</td>
<td>Non-flowering</td>
</tr>
<tr>
<td>Saturated photosynthetic rate (P$_N$ sat)</td>
<td>11.00</td>
<td>44.50</td>
</tr>
<tr>
<td>CO$_2$ compensation point (ppm)</td>
<td>90.00</td>
<td>80.00</td>
</tr>
<tr>
<td>CO$_2$ saturation point (ppm)</td>
<td>425</td>
<td>560</td>
</tr>
<tr>
<td>Carboxylation efficiency</td>
<td>0.060</td>
<td>0.154</td>
</tr>
</tbody>
</table>

Fig. 3. Carbon dioxide response curves taken in the leaves of flowering ($P_N = -6.22 + 0.077$ Ci$ - 0.000086$ Ci$^2$, $R^2 = 0.94$) and non-flowering ($P_N = -13.17 + 0.182$ Ci$ - 0.00014$ Ci$^2$, $R^2 = 0.95$) branches of cultivar Langra (Irregular bearer).
Increased demand for photosynthates during the initiation and development of flowers (Monselise and Lenz, 1980) was reported to increase the rates of photosynthesis of supporting leaves of a branch in apples (Masarovicova and Novara, 1994). This was attributed to the increased sink demand by the developing panicles (Ferree and Palmer, 1992). However, our results show a reduction in the photosynthetic rates at ambient as well as saturated CO₂ concentrations in flowering branches of both regular and irregular bearers. Such a reduction is also reported in sweet cherry by Roper et al. (1988) and Rom and Ferree (1986). Even between the cultivars also the regular bearer showed higher saturated as well as ambient photosynthetic rates in flowering branches (Tables 1 and 2). Surprisingly such a cultivar difference was not seen in non-flowering branches.

Carbon dioxide response curves generally indicate the status of mesophyll activity which controls the photosynthetic rate of a leaf (Figs. 2 and 3). These are also often used to calculate the CO₂ compensation points, limitations to potential photosynthetic rates and CO₂ sensitivity of photosynthesis (Sharkey et al., 1986). The initial slope of the CO₂ response curve is a reflection of the carboxylation efficiency of the leaf (Brooks, 1986). The initial slope of CO₂ response curve of the flowering branch was much lower than that of the non-flowering branch in both cultivars indicating the lower carboxylation efficiency of flowering branches. In cv. Langra (Irregular bearer) the difference between the flowering and non-flowering branches was wider than in cv. Thothapuri.

The lower CO₂ saturation point of the flowering branches also shows that the mesophyll efficiency in fixing carbon dioxide was affected during the flowering process in mango varieties.

A reduction in net photosynthetic rate and carboxylation efficiency during flowering could be due to differences in the water status of the branches. Hence, to know the water status of the leaves, relative water content was estimated in both flowering and non-flowering branches.

Relative water content (RWC) did not show significant differences between flowering and non-flowering branches (Table 3). Therefore, the differences in saturated as well as ambient photosynthetic rates between the branches may not be due to water stress induced changes in stomatal conductance (gs). These observations thus suggest the possible involvement of factors controlling the mesophyll activity in reducing the $P_N(sat)$ values of flowering branches.

While reasons for such reductions in assimilation rates are unknown, it is possible that there are inhibitors affecting the carboxylation enzymes in the mesophyll cells. Accumulation of carbohydrates in flowering branches can also inhibit the carboxylating enzyme (Stitt and Quick, 1989). But the increased demand for carbohydrates during flowering on the other hand would have depleted the carbohydrate pool and consequently caused an increase in
photosynthesis. Therefore, it may not be entirely due to the accumulation of carbohydrates in flowering branches instead it could also be due to the accumulation of inhibitors. Abscisic acid may be one of the possible inhibitors responsible for the reduction in the carboxylation efficiency (Raschke and Fischer, 1987) during flowering, since it is reported to be accumulated during flowering (Jones et al., 1976; Bangerth et al., 1986 and Bower et al., 1990). Patil et al. (1992) also reported the increase in total phenol accumulation in mango during the flower bud differentiation stage. However, they did not find any variation in starch content during the different stages of differentiation (Patil et al., 1991).

Results suggest the possibility that certain carboxylation enzyme inhibitors are synthesised or accumulated in the leaves of a branch in response to environmentally induced signals. The greater reduction in carboxylation efficiency and photosynthetic rate of the flowering branches in the irregular bearer also indicates the need for a higher accumulation of inhibitors for flower induction when compared to the regular bearers. Therefore, two main reasons for the irregular flowering in a few mango cultivars are, the need for a higher accumulation of inhibitors which requires stronger environmental signals (low temperature and high water stress) and the wider branch to branch variations in physiological parameters (Shivashankara and Mathai, 1995) leading to the variations in metabolite levels in the branches.

Acknowledgements

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