Relation of CO₂ Compensation Concentration to Apparent Photosynthesis in Maize

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Abstract. Significant differences in CO₂ compensation concentration measured in the field among varieties of the species Zea mays L., are reported for the first time. CO₂ compensation concentrations were significantly (P ≤ 0.01) and negatively correlated with apparent photosynthesis at 300 μl CO₂/liter air. The Michaelis constant (as defined) for a leaf was significantly (P ≤ 0.01) and positively correlated with apparent photosynthesis among varieties. While the first correlation is similar to behavior of CO₂ compensation among species of different photosynthetic efficiency, the latter correlation is the converse of the behavior of Km among species.

The CO₂ compensation concentration (hereafter, [CO₂]c) of an illuminated leaf sealed in a closed chamber reflects an equilibrium between photosynthesis and respiration. In many species the [CO₂]c increases with temperature (3, 9), water stress (14, 15), and O₂ concentration (23), but decreases with irradiance (2, 8). The [CO₂]c is high (50-100 μl CO₂/l air) for species with inefficient photosynthesis and high photorespiration, and low (<10 μl CO₂/l air) for species with efficient photosynthesis and negligible photorespiration (4, 16, 25, 26). Maize belongs to this latter group (14, 16), and has a [CO₂]c independent of O₂ concentration (15, 20).

Recent models demonstrate that the magnitude of the [CO₂]c depends upon the diffusive resistance of the leaf to CO₂, the efficiency of CO₂ fixation in the chloroplasts, and the respiration rate of the leaf (1, 21, 24).

A second, lesser used, method exists for predicting the photosynthetic efficiency of leaves. The Michaelis constant (Km) of a leaf has been postulated (7) as “the external CO₂ concentration which enables the leaf, at saturating light intensity, to fix CO₂ at half the maximal velocity”. The Km depends upon the affinity of the carboxylating enzymes for CO₂, the diffusive resistance of the leaf, and the rate of respiration. Thus Zelitch (27), whose convention we adopt, designates the Km for a leaf as an “overall Michaelis constant”. Goldworthy (7) and Zelitch (27) found that the Km for photosynthesis of maize was only 10 to 15% lower than tobacco when photorespiration of tobacco was suppressed by low O₂. Since maize is superior to tobacco in photosynthesis in normal air, the Km values of these 2 species may differ by 60% (at a low irradiance) because of differences in respiration (27).

We recently reported differences in apparent photosynthesis (AP) at 300 μl CO₂/l air and saturating irradiance among leaves of several maize varieties (10). In this communication we report experiments in which we tested for differences in [CO₂]c, Michaelis constants, and the relation of these parameters to AP in 15 varieties of maize.

Materials and Methods

These experiments were conducted on the Central Experiment Station, College of Agriculture, University of the Philippines, near Los Banos, Laguna, between November 1965 and June 1966. This was the dry season of a tropical monsoon climate. The characteristics of the experimental site, the experimental material, and the methods of planting and crop culture have been described (10). Plants were well watered throughout growth and measurement.

Measurements were made on plants growing in the field during the ear-filling stage of development 2 weeks following pollination. The fifth or sixth leaf from the top of the plant was chosen for testing. One of these leaves was often attached to the same node as the developing fruit (ear). All leaves were fully expanded for 3 weeks before measurements were begun. Differences in leaf age among varieties were small. Measurements were made continuously throughout the day, but no time-of-day effects on observations were noted.

All AP and [CO₂]c measurements were made by infrared analysis of air surrounding attached leaves in an acrylic plastic, recirculating leaf chamber which closely mimics a corn leaf. Repro-
ducible conditions of leaf temperature (32 ± 2°) and air velocity (4 m sec⁻¹) were maintained in all experiments. The chamber and its accessories were mobile to permit ready access to the plants.

The irradiance reaching the leaf from a portable, incandescent source was 1.10 cal cm⁻² min⁻¹ (502-697 nm), as determined with an Epply Model 15 Spectral Radiometer equipped with standard Schott filters. This irradiance was determined to be saturating by comparison with full sunlight. The irradiance below 502 nm was negligible.

The [CO₂]e was measured by converting the leaf chamber into a closed system, lowering the CO₂ concentration to 100 μL CO₂/l air, and allowing the leaf to deplete CO₂ until an equilibrium between photosynthesis and respiration was reached. Subsequently the response of AP to CO₂ concentration was measured by adjusting the flux of CO₂-enriched air into the chamber until equilibria were established at 85 (for only 40% of the measurements), 150, 250, and 300 ± 3 μL CO₂/l air. AP (mg CO₂ dm⁻² hr⁻¹) at the various CO₂ levels was computed from flow, concentration, and leaf area measurements.

Mean AP and [CO₂]e values were obtained from measurements on a single leaf of 10 plants. The Km for each variety was estimated by linear regression from a double reciprocal plot of the rectangular hyperbola (11):

\[ AP = \frac{P_{\text{max}} ([CO₂]_a - [CO₂]_c)}{Km + ([CO₂]_a - [CO₂]_c)} \]

where AP = mean apparent photosynthesis (mg CO₂ dm⁻² hr⁻¹) for a variety, P_max = estimated maximum rate of photosynthesis at saturating irradiance and CO₂, and ([CO₂]_a - [CO₂]_c) = difference between the ambient CO₂ concentration ([CO₂]_a) and the mean CO₂ compensation concentration for a variety. Since this function passes through [CO₂]_a, all estimates of Km are made with (CO₂)_e as the reference. Thus Km = ([CO₂]_a - [CO₂]_e) when AP = P_max/2 at (CO₂)_a. The coefficients of determination for fitting the hyperbolic model were 0.92 ≤ r² ≤ 0.99 for the 15 varieties.

**Results**

The response of AP to ambient CO₂ concentration is shown in Fig. 1 and 2. The 7 varieties shown exemplify the marked differences in AP among the 15 varieties in this study. The following characteristics of these curves are noteworthy. Between 85 and 300 μL CO₂/l air significant varietal differences in AP are apparent; these differences are greatest at the highest CO₂ concentration. In addition, Fig. 2 shows that a hybrid was superior in AP compared with its inbred parents. The curvilinear response of AP of maize to ambient CO₂ shows that successive increments of CO₂ are not equally effective in enhancing AP.

The mean varietal [CO₂]e, mean varietal AP at 300 μL CO₂/l air, and estimated Km values for the 15 varieties are listed in Table I. More than half of
Table I. CO₂ Compensation Concentrations, Rates of Apparent and Estimated Maximum Photosynthesis, and Overall Michaelis Constants for 15 Maize Varieties

<table>
<thead>
<tr>
<th>Variety</th>
<th>[CO₂]₁₀⁻⁶ CO₂/air</th>
<th>AP²</th>
<th>Pₘₐₓ³</th>
<th>Kₘ₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cuba 9</td>
<td>9 ± 1 a</td>
<td>64 ± 4</td>
<td>122</td>
<td>299</td>
</tr>
<tr>
<td>Ganga III</td>
<td>10 ± 1 a</td>
<td>68 ± 4</td>
<td>147</td>
<td>329</td>
</tr>
<tr>
<td>W22XNY821</td>
<td>11 ± 1 a</td>
<td>75 ± 2</td>
<td>162</td>
<td>324</td>
</tr>
<tr>
<td>CM109</td>
<td>12 ± 1 ab</td>
<td>77 ± 4</td>
<td>194</td>
<td>420</td>
</tr>
<tr>
<td>Amarillo de Cuba</td>
<td>12 ± 2 ab</td>
<td>70 ± 5</td>
<td>182</td>
<td>446</td>
</tr>
<tr>
<td>Pa 83</td>
<td>13 ± 1 ab</td>
<td>85 ± 3</td>
<td>215</td>
<td>437</td>
</tr>
<tr>
<td>Llera III</td>
<td>13 ± 1 ab</td>
<td>74 ± 3</td>
<td>255</td>
<td>694</td>
</tr>
<tr>
<td>Eto Blanco</td>
<td>15 ± 2 ab</td>
<td>74 ± 2</td>
<td>220</td>
<td>541</td>
</tr>
<tr>
<td>CM110</td>
<td>16 ± 0.5 bc</td>
<td>63 ± 2</td>
<td>178</td>
<td>505</td>
</tr>
<tr>
<td>L316XL317</td>
<td>16 ± 1 bc</td>
<td>52 ± 5</td>
<td>100</td>
<td>268</td>
</tr>
<tr>
<td>A619</td>
<td>20 ± 2 cd</td>
<td>67 ± 4</td>
<td>139</td>
<td>295</td>
</tr>
<tr>
<td>NY821</td>
<td>20 ± 1 cd</td>
<td>63 ± 2</td>
<td>143</td>
<td>355</td>
</tr>
<tr>
<td>A632</td>
<td>23 ± 1 de</td>
<td>50 ± 2</td>
<td>97</td>
<td>213</td>
</tr>
<tr>
<td>W19</td>
<td>23 ± 2 de</td>
<td>28 ± 2</td>
<td>41</td>
<td>127</td>
</tr>
<tr>
<td>W22</td>
<td>25 ± 2 e</td>
<td>45 ± 3</td>
<td>95</td>
<td>293</td>
</tr>
</tbody>
</table>

¹ Mean CO₂ compensation concentration of 10 plants ± standard error. Means sharing the same letter are not significantly different at the 5% level (Duncan's Multiple Range Test).

The dissimilar parameters of the hyperbolae for these 2 species predict that the CO₂ response functions for corn and tobacco will converge when the CO₂ is increased, and at low irradiance they do (27).
The great dissimilarity between the CO₂ responses of these 2 species has been attributed largely to photorespiration of tobacco, since the $K_m$ values for these species are nearly equal in the absence of photorespiration (7, 27).

In contrast to the negative correlation between $K_m$ and AP in normal air in tobacco and maize, within maize there is a positive correlation between these 2 parameters (Fig. 4). This positive correlation arises because among maize varieties the CO₂ responses tend to diverge at elevated CO₂ concentrations (Fig. 1 and 2), rather than converge as for maize and tobacco. Since appreciable photorespiration has not been observed in maize (6, 17, 25), the reasons for differences in photosynthesis among maize varieties are less obvious than the difference in photosynthesis between species such as tobacco and maize. Other factors which influence $K_m$, such as dark respiration and internal resistances to CO₂ diffusion, have not been extensively studied within a species such as maize. The reasons for a positive correlation between $K_m$ and AP will remain obscure until the theoretical basis of a leaf $K_m$ is explained. Nevertheless the correlation between $K_m$ and AP may have predictive value for comparison of varieties, as similar correlations have proved useful in comparisons of species (24).

The correlation (Fig. 3) of the [CO₂]e with photosynthetic rate among varieties is not inconsistent with the hypothesis (1, 21, 24) that [CO₂]e represents some kind of balance between photosynthesis and respiration. Furthermore, these results show that a low (less than 10 μl CO₂/l air) [CO₂]e does not necessarily occur in maize growing under field conditions. Systematic leaks of CO₂ into the closed system would have caused the [CO₂]e to be inversely related to the area of leaf in the chamber. However, the correlation between leaf area and [CO₂]e was insignificant. Our results do not suggest whether dark respiration, diffusive resistances, or a combination of the 2 factors causes positive [CO₂]e. Although previous results (6, 12, 19) suggested that light inhibits dark respiration in several plant species, this inhibition may be as unimportant for maize as it is for Scenedesmus (13).

The high [CO₂]e that we observed contrast markedly with observations of Forrester, Krotkov, and Nelson (6). This apparent disagreement may be due to several circumstances. Plants used by Forrester et al. were only 2 weeks old and grown in a controlled environment, while ours were grown in the field and had flowered. In our investigation, the plants were grown and measured in a tropical temperature regime of 30 to 34°C, 5 to 9 degrees warmer than used by Forrester et al. Differences between the 2 contrasting investigations in stage of plant development and method of plant culture raise questions which are not easily answered. However, our results support Meidner's (14) observation that field-grown maize at temperatures above 30°C can have [CO₂]e above zero. Clearly our results are different from the phenomenon Poskuta (20) observed which caused positive [CO₂]e in young maize plants.

This is the first report of significant differences in [CO₂]e among varieties within a species. Differences in [CO₂]e were not found among genetic lines of Triticum aestivum or Hordeum vulgare (18) but [CO₂]e as different as 10 and 50 μl CO₂/l air were found among species of the same genera (5, 22) and among related subgenera (18).

**Literature Cited**