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Light-saturated \( \text{CO}_2 \) assimilation rates of corn and velvetleaf in response to leaf nitrogen and development stage

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A relationship between crop productivity and nitrogen (N) supply is commonly used for fertilizer management schedules (Evans 1987). Because 50 to 80% of the N in plant leaves is found in photosynthetic proteins (Hikosaka and Terashima 1995; Makino and Osmond 1991; Sage and Pearcy 1987), a strong correlation between light-saturated \( \text{CO}_2 \) assimilation rate (\( C_A \), \( \mu \text{mol} \ \text{CO}_2 \ \text{m}^{-2} \ \text{s}^{-1} \)) and N content per unit leaf area (\( N_L \), g N m\(^{-2} \)) is commonly observed (Ampong-Nyarko and DeDatta 1993; Hilbert et al. 1991; Hunt et al. 1985; Marshall and Vos 1991; Muchow 1990; Sage and Pearcy 1987; Sage et al. 1990; Sinclair and Horie 1989). Increased leaf N concentration in response to N supply will, therefore, promote greater photosynthetic rates (Hasegawa and Horie 1996) and plant productivity. This relationship greatly benefits crop productivity, but also has strong implications regarding crop–weed competition relationships under conditions of limited N supply.

Sinclair and Horie (1989) reviewed a number of studies that showed a high correlation between \( C_A \) of crop leaves and their \( N_L \). They proposed that the relationship could be quantified using the equation:

\[
C_A = A_m(2/(1 + \exp(-a(N_L-b)))) - 1
\]

where \( A_m \) represents the asymptote of \( C_A \) at high \( N_L \), \( b \) represents the \( N_L \) below which \( C_A \) becomes negative, and \( a \) is a species-specific shape coefficient. Sinclair and Horie (1989) quantified this relationship for corn using data from Wong et al. (1985) and from their own experiment, in which \( C_A \) was measured on solution-culture or pot-grown corn during early developmental stages. Lindquist and Mortensen (1999) quantified the relationship between \( C_A \) and \( N_L \) for field-grown corn and velvetleaf during corn-grain fill and obtained a smaller estimate of \( A_m \) than that reported by Sinclair and Horie (1989).

Leaf N content typically declines during later stages of plant development (Lindquist and Mortensen 1999). Effects of this decline on \( C_A \) must be accounted for within our plant growth models to accurately predict dry matter production (Peng et al. 1995), leaf area development, and crop–weed competition. Hasegawa and Horie (1996) suggested that an ontogenetic decline in \( C_A \) occurs as a consequence of reduced \( N_L \) as well as factors such as the quantity and activation state of carboxylating enzymes, nonstructural carbohydrate concentration, and sensitivity of stomatal function. If the latter factors affect \( C_A \) independent of \( N_L \), then a decline in \( C_A \) at later development stages may be expected, regardless of \( N_L \). Therefore, the smaller estimate of corn \( A_m \) observed by Lindquist and Mortensen (1999) may be the result of these ontogenetic changes in the overall physiological efficiency within the leaves of these species. Hasegawa and Horie (1996) proposed a relationship similar to that found in Equation [1] but allowed \( A_m \) to vary with development stage (DVS) of the crop:

\[
A_m = A_{\text{max}} - c(DVS)
\]

where \( A_{\text{max}} \) is the absolute maximum observable \( C_A \) and \( c \) defines the rate at which \( A_m \) declines with development stage. The objectives of this research were to quantify field-grown corn and velvetleaf \( \text{CO}_2 \) assimilation rate under full-sun conditions as influenced by leaf N and stage of development.
Materials and Methods

Field experiments were conducted under rain-fed conditions in 1998 and 1999 at the University of Nebraska Agricultural Research and Development Center near Mead, NE. Soil at the site was a Sharpesburg silty clay loam (fine, smectitic, mesic, Typic Argiudoll) with 3.5% organic matter. The field was previously cropped with corn and disked in the spring followed by seedling preparation. The experiment was designed as a randomized complete block with four replications; treatments included four N application rates (0, 45, 90, and 180 kg N ha⁻¹) and corn (Pioneer 3448 and 33A14 in 1998 and 1999, respectively) or velvetleaf grown in monoculture or in mixture. Corn and velvetleaf were planted 0.76 m apart, with five plants m⁻² (65,790 plants ha⁻¹) and velvetleaf at 2 or 10 plants m⁻² row. Corn was seeded on May 11, 1998, and May 3, 1999, with a conventional planter. Velvetleaf seed was obtained from the University of Nebraska Agricultural Research and Development Center near Havelock, NE, the previous fall. Untreated seeds (100 times the desired density) were sown directly into all corn rows with a push planter immediately after planting the crop. Crop and weeds emerged simultaneously on May 17, 1998, and May 16, 1999. Each experimental unit was 5 by 13 m, and N was applied as NH₄NO₃ granules using a calibrated wheel-drive fertilizer spreader on May 13, 1998, and May 3, 1999. Velvetleaf treatment densities were established by hand thinning beginning on June 5, 1998, and May 25, 1999. Weeds other than velvetleaf were removed by hand as needed and by interrow cultivation on June 25, 1998, and June 15, 1999. Corn began anthesis on July 10, 1998, and July 19, 1999, and maturity was reached on September 8 in both years. The zero N treatments were approximately 3 d later in their development than all other treatments.

Instantaneous light-saturated leaf CO₂ assimilation rate (Cₐ) was measured on individual leaves of corn and velvetleaf under full-sun conditions (> 1800 μmol m⁻² s⁻¹) using a portable photosynthesis system² at least seven times in each year (36, 44, 50, 58, 63, 78, and 92 d after planting [DAP] on 1998 and 45, 53, 59, 65, 87, 103, 108, and 120 DAP in 1999). Because only 20 to 25 measurements of each species were possible at each sampling date, it was not possible to sample one leaf of each species from each subplot. Therefore, measurements were taken on randomly selected, recently fully expanded and fully illuminated leaves in as many treatments as possible within two blocks of the experiment at each sampling date. A 1.0-L chamber with restrictors to maintain constant leaf area was clamped across the entire width of a corn leaf approximately 20 cm from the leaf tip, where the midrib was not large enough to cause chamber leakage. For velvetleaf, the chamber was clamped across a portion of the leaf or the entire leaf, depending on leaf size. All measurements were taken between 10:00 A.M. and 2:00 P.M. central U.S. standard time. Following each measurement, the leaf was clipped to include approximately 30 cm of the distal portion of the corn leaf, or the entire velvetleaf lamina. Each leaf was measured for area, dried, weighed, and N concentration (μg N g⁻¹) was determined. Leaf Nₐ (μg N g⁻¹) was obtained from [N] and specific leaf area (cm² g⁻¹).

Daily weather data were obtained through the High Plains Climate Center from an automated weather station approximately 0.5 km from the experimental field (Table 1). Thermal units accumulated from emergence were calculated using a base temperature of 10°C for both species. Thermal units to anthesis and maturity were 583 and 1,419 in 1998, respectively, and 716 and 1,432 in 1999, respectively. Development stage at time of measurement was quantified using a dimensionless scale: 0 (emergence), 1.0 (corn anthesis or velvetleaf first flower), and 2.0 (corn physiological maturity or complete velvetleaf leaf dry down). Intermediate stages were determined from the number of thermal units accumulated between emergence and the sampling date (Lindquist and Mortensen 1999). The relationship between leaf appearance and thermal units accumulated from emergence is approximately linear during vegetative corn growth (Muchow and Carberry 1989). Therefore, vegetative growth stage can be inferred directly from DVS and thermal units to anthesis, when corn had an average of 19 leaves.

Analysis of variance (ANOVA) (PROC GLM³) was conducted to evaluate the effect of N rate and mixture treatment on Cₐ, Nₐ, and [N]. Because not all treatments could be measured at every sampling time, this analysis was conducted with all sampling dates pooled to provide sufficient degrees of freedom. Nonlinear regression analysis (PROC NLLIN³) was conducted to quantify the relationship between Cₐ and Nₐ and in relation to DVS. Measured Cₐ was regressed on Nₐ and DVS using Equations 1 and 2. Dummy variables were initially included in the model (Swinton et al. 1992) to evaluate whether parameter estimates varied between years. If the approximate 95% confidence interval of a parameter estimate included zero, the null hypothesis that the parameter did not differ from zero was accepted and the parameter was removed from the analysis.

Results and Discussion

Average daily air temperature and precipitation were close to the 30-yr norm during the growing season in both 1998 and 1999 (Table 1). Optimal temperature for corn CO₂ assimilation rate ranges between 28 and 40°C (de Wit et al. 1978). Mean temperatures during measurements were below 38°C for all but one sampling time in 1999 (July 29, DVS = 1.26), when mean temperature during sampling was 42°C. Therefore, measurements made at that sampling time were not used in the statistical analyses, but are plotted in Figure 1.

Year and treatment did not interact to affect mean corn and velvetleaf Cₐ, Nₐ, and [N] when pooled across all sam-

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**Table 1.** Average daily air temperature (degrees C) and precipitation (mm) in 1998 and 1999, and the 30-yr normal. Data were obtained from the High Plains Climate Center; the normals reported were for Ashland, NE.

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<table>
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<th>Month</th>
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FIGURE 1. Light-saturated CO₂ assimilation rate (Cₛ) in corn (Zea mays L.) and velvetleaf (Abutilon theophrasti) as a function of leaf nitrogen content (Nₗ) and development stage (DVS) in 1998 and 1999. Development stage at the time of sampling was identical between corn and velvetleaf in each year, using a dimensionless scale based on accumulated thermal units.

TABLE 2. Parameter estimates (± standard error), coefficient of determination (r²) values, residual mean square error (RMSE) values, and P values for the relationship between full-sun CO₂ assimilation (Cₛ, μmol CO₂ m⁻² s⁻¹) and leaf nitrogen (Nₗ, g N m⁻²) in corn and velvetleaf, as affected by development stage in 1998 and 1999.¹²

<table>
<thead>
<tr>
<th>Species</th>
<th>a (g⁻¹ m²)</th>
<th>b (g N m⁻²)</th>
<th>A_max (μmol CO₂ m⁻² s⁻¹)</th>
<th>c (μmol CO₂ m⁻² s⁻¹ DVS⁻¹)</th>
<th>r²</th>
<th>RMSE</th>
<th>n</th>
<th>P value</th>
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<tr>
<td>Corn</td>
<td>3.68 (0.67)</td>
<td>0.45 (0.09)</td>
<td>63.8 (1.19)</td>
<td>15.54 (0.96)</td>
<td>0.51</td>
<td>66.4</td>
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<td>Velvetleaf</td>
<td>1.45 (0.26)</td>
<td>NS</td>
<td>29.5 (1.43)</td>
<td>2.80 (0.82)</td>
<td>0.06</td>
<td>28.6</td>
<td>299</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

¹ The relationship was described by the equation Cₛ = Aₒ((2(1 + exp(−a(Nₗ−b)))))−1), where Aₒ = A_max − c (DVS). A_max represents the asymptote of Cₛ at high Nₗ. b represents the Nₗ below which Cₛ becomes negative, and a is a species-specific shape coefficient; A_max is the absolute maximum observable Cₛ, and c defines the rate at which Aₒ declines with development stage. NS indicates that the parameter did not differ from zero at the 95% confidence level.

² Data were pooled over years.
values reported by Louwerse et al. (1990), Muchow and Sinclair (1994), and Sinclair and Horie (1989), respectively. The maximum decreased at a rate of 15.5 \( \mu \text{mol CO}_2 \text{m}^{-2} \text{s}^{-1} \) per DVS, so that \( A_m \) at high \( N_L \) was estimated at 40.6 \( \mu \text{mol CO}_2 \text{m}^{-2} \text{s}^{-1} \) (DVS = 1.5), which was consistent with the value of 40.5 \( \pm 1.3 \mu \text{mol CO}_2 \text{m}^{-2} \text{s}^{-1} \) reported by Lindquist and Mortensen (1999). Estimates of parameters \( a \) and \( b \) of Equation 1 were within the range of those reported by Muchow and Sinclair (1994) and Sinclair and Horie (1989).

Corn \( N_L \) ranged from 0.6 to 2.8 g N m\(^{-2} \) (Figure 1), which contrasted greatly with the results reported by Sinclair and Horie (1989), in whose study \( N_L \) ranged between 0.25 and 1.0 g N m\(^{-2} \). Corn leaf \( [N] \) ranged between 0.02 and 0.05 g N g\(^{-1} \) biomass, which was consistent with whole-plant leaf \([N]\) reported by Lindquist and Mortensen (1999). The discrepancy between the \( N_L \) values reported here and those of Sinclair and Horie (1989) may have resulted if there were large differences in the quantity of \( N \) available for uptake in these studies or if the growth chamber-grown corn reported by Sinclair and Horie (1989) was sufficiently stressed to reduce capacity for \( N \) uptake. It is likely that the field soil in this study supplied greater quantities of \( N \) through mineralization than did the \( N \)-limited solution and sand culture reported by Sinclair and Horie (1989). However, corn also may be more efficient at \( N \) acquisition under field conditions than it is when roots are restricted in pots within a controlled-environment chamber. In either case, because corn \( N_L \) in this experiment was rarely less than 1.0 g N m\(^{-2} \), corn may restrict leaf growth in order to maintain constant \( N_L \) under conditions of limited soil \( N \) supply.

Velvetleaf \( C_A \) varied as a function of both \( N_L \) and DVS (Table 2, Figure 1). The estimate of velvetleaf \( A_{max} \) was 29.5 \( \mu \text{mol CO}_2 \text{m}^{-2} \text{s}^{-1} \) (Table 2), which was only slightly greater than the value of 24.6 \( \mu \text{mol CO}_2 \text{m}^{-2} \text{s}^{-1} \) reported by Louwerse et al. (1990), Muchow and Sinclair (1994), and Sinclair and Horie (1989).

The lack of leaf \( N \) in this experiment was rarely less than 1.0 g N m\(^{-2} \), corn may restrict leaf growth in order to maintain constant \( N_L \) under conditions of limited soil \( N \) supply. As with corn, velvetleaf \( N_L \) levels may be greater in velvetleaf than corn leaves because velvetleaf has greater leaf \([N]\) throughout the growing season (Lindquist and Mortensen 1999). Moreover, because corn produces all of its leaf area by anthesis, whereas velvetleaf continues leaf production throughout its life cycle, the effects of soil \( N \) supply on total leaf area production may be expected to be greater for velvetleaf than for corn.

Sources of Materials

1. John Deere Max Emerge planter, Deere and Co., Moline, IL.
2. Portable photosynthesis system, Model LI-6200, LI-COR, P. O. Box 4425, Lincoln, NE 68504.

Acknowledgments

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