Effects of Irradiance on Relative Growth Rates, Net Assimilation Rates, and Leaf Area Partitioning in Cotton and Three Associated Weeds

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ABSTRACT

Cotton (Gossypium hirsutum L. var. 'Stoneville 213'), velvetleaf (Abutilon theophrasti Medic.), redroot pigweed (Amaranthus retroflexus L.), and hemp sesbania (Sesbania exaltata [Raf.] Cory) were grown in a controlled environment room at 31/25 C day/night temperature and three irradiances: 90, 320, and 750 peintsteins meter⁻² second⁻¹. From total dry weights and leaf areas determined at intervals during the first exponential phase of growth, we used mathematical growth analysis techniques to calculate net assimilation rates (NAR), relative growth rates (Rw), relative leaf area expansion rates (Rw), leaf area partition coefficients (LAP), and leaf area ratios (LAR). In all four species, Rw, Rw, and NAR decreased with decreasing growth irradiance, while LAP and LAR increased. Within each species, Rw was positively correlated with NAR but negatively correlated with LAP and LAR. In comparisons among the four species within each growth irradiance, Rw was positively correlated with LAP. We discuss the relationship between LAP and LAR and show that LAP = (Rw/Rw) (LAR).

The growth rate of a plant depends on the amount of leaf area present and the rate of dry matter increase per unit of leaf area or the NAR.¹ Mathematical growth analysis provides a means of assessing the relative importance of leaf area and NAR in accounting for differences in growth rates among species or among plants of the same species grown under different environmental conditions. Early work in this area showed the importance of differences in the "efficiency index" or Rw (rate of dry matter production per unit of dry matter present) in accounting for different absolute amounts of growth (1). West et al. (6) showed that Rw was the product of NAR and LAP (amount of leaf area per total amount of dry weight). Various workers since have attempted to analyze the components of Rw and thus to assess the relative importance of LAP and NAR in accounting for differences in growth. Watson (4, 5) concluded that differences in leaf area production were more important than differences in NAR in determining growth. More recently Thornley and Hurd (3) concluded that when tomato was grown under various combinations of irradiance, day length, and CO₂ concentration, differences in Rw could best be accounted for by differences in NAR. On the other hand, Potter and Jones (2), in comparing Rw of nine species of weeds and crop plants grown in three different temperature regimes, reported that differences in Rw were not well correlated with differences in NAR. They described a new growth function LAP ("partitioning of daily weight gain into new leaf area") and showed that Rw was closely correlated with LAP.

The conflicting results of these various studies indicate that the relative importance of NAR and leaf area in determining growth rate is still an open question. They also suggest that the relative importance of NAR and leaf area may differ depending on the particular environmental factors (e.g., temperature, irradiance, CO₂ concentration) and genetic factors responsible for observed differences in relative growth rates.

As part of a continuing investigation of the comparative ecophysiology of crop plants and associated weeds, we examined the components of Rw in cotton and three weeds grown under different irradiance conditions. We also reexamined the term LAP (2) and attempted to clarify its relationship with LAP.

MATERIALS AND METHODS

Plant Material. Cotton (Gossypium hirsutum L. var. 'Stoneville 213'), velvetleaf (Abutilon theophrasti Medic.), redroot pigweed (Amaranthus retroflexus L.), and hemp sesbania (Sesbania exaltata [Raf.] Cory) were grown in a 1:1(v/v) mixture of Bosket sandy loam and sand in a controlled environment room at a 31/25 C day/night temperature, 80% RH, and a 15-hr photoperiod. The plants were started in small cups (volume 200 ml), selected for uniformity, and transplanted to 10-cm pots 2 weeks after emergence. There was no evidence of the plants becoming rootbound during the course of the experiments. The soil was watered daily to field capacity with Hoagland solution. Lighting was provided by a mixture of fluorescent and incandescent lamps supplying a maximum irradiance of 750 µE m⁻² sec⁻¹ at plant height. Screening provided two additional irradiances of 90 and 320 µE m⁻² sec⁻¹. The plants were widely spaced so that no interplant shading occurred. The arrangement of the plants in the chamber was changed twice weekly to eliminate any effects of uneven lighting.

Harvest Procedures. Five plants of each species from the three irradiance treatments were harvested at intervals of 1 week or less during the first 30 to 40 days after emergence. Leaf areas to the nearest mm² were determined with a Lambda model LI3050A leaf area meter. Total plant weights were determined after drying at 65 C for 3 days.

Growth Analysis Procedures. We used the formulas described by Potter and Jones (2) to calculate the various growth analysis functions. Since these formulas are valid only during exponential growth, we first plotted the natural logarithms of dry weight and leaf area versus time to determine the duration of the first exponential phase of growth in each species at each irradiance. Then, using only the harvest data from the first exponential phase, we fitted exponential equations of the form y = ae⁻bx to the leaf areas

¹ Abbreviations: W: dry weight; A: leaf area; t: time; Rw: relative growth rate ((I/W)(dW/dt)); Rw: relative leaf area expansion rate ((I/A)(dA/dt)); NAR: net assimilation rate ((I/A)(dA/dt)); LAR: leaf area ratio (A/W); LAP: leaf area partition coefficients (A/LA) (dL/A/dt).
and dry weights. The equation $W = W_0e^{t}$ describes total weight (W) at any given time in days (t) after emergence as a function of the weight ($W_0$) at $t = 0$, and $R_w = \frac{1}{W_0} \frac{dW}{dt} = g g^{-1} d^{-1}$. Similarly, the equation $A = A_0e^{t}$ describes leaf area as a function of t, the leaf area ($A_0$) at $t = 0$, and $R_a = \frac{1}{A_0} \frac{dA}{dt} = \text{dm}^2 \text{dm}^{-2} \text{day}^{-1}$. The values for $R_w$ and $R_a$ are constant during exponential growth. Following the reasoning of Potter and Jones (2) we calculated the values of NAR, LAP, and LAR at the midpoint of the first exponential phase:

$$\text{NAR} = \frac{R_w W_0 e^{t/2}}{A_0 e^{t/2}} \quad \text{LAP} = \frac{R_a A_0 e^{t/2}}{R_w e^{t/2}} \quad \text{LAR} = \frac{A_0 e^{t/2}}{W_0 e^{t/2}}$$

(Correlation Analyses). After plotting the various combinations of the growth analysis functions on coordinate paper, we tested the observed relationships between $R_w$ and $R_a$, NAR, LAP, and LAR using correlation analysis.

RESULTS

Growth Equations. The equations relating dry weight and leaf area to time after emergence during the first exponential phase of growth are described in Table I. The correlation coefficients for $\ln W$ and $\ln A$ versus t were all at least 0.98, indicating a satisfactory fit of the exponential equations to the data.

The duration of the first exponential phase tended to decrease with increased light intensity (and increased plant size). It is likely that greater intraplant shading in the larger plants was responsible for the shorter duration of the exponential phase in these plants. The leaf arrangement and more open canopies of hemp sesbania lessened intraplant shading in this species and allowed exponential growth to continue for a longer period even at the highest growth irradiance.

In all four species, $R_w$ and $R_a$ decreased with decreasing growth irradiance. At each of the three growth irradiances the $R_w$ values were ranked as follows: pigweed $>\,$velvetleaf $>\,$sesbania $>\,$cotton. At the high and medium growth irradiances $R_w$ values were ranked the same as $R_a$. However, at the lowest growth irradiance the ranking of $R_w$ was slightly different: pigweed $>\,$velvetleaf $>\,$cotton $>\,$sesbania. The ranking of LAP was the same as the ranking of $R_a$, both within each species and within each growth irradiance.

Correlation Analyses. We recognize that several of the growth analysis parameters may be positively or negatively related to each other by definition. However, the existence of such relationships does not indicate a statistically significant linear correlation. Therefore, we calculated correlation coefficients to define clearly the relationships among the various parameters.

Within each species, $R_w$ was significantly negatively correlated with LAP (Fig. 1 and Table II). From Figure 2, it is evident that $R_w$ increased as NAR increased with growth irradiance, although the relationship was not linear. We found $R_w$ to be significantly positively correlated with $\ln \text{NAR}$, within each species (Table II).

To examine further the correlations of $R_w$ with LAP or NAR within each species, we normalized the values as a per cent of the maximum within that particular species. Thus, NAR and $R_w$ became 100% at 750 $\mu$E m$^{-2}$ sec$^{-1}$ and LAP became 100% at 90 $\mu$E m$^{-2}$ sec$^{-1}$ for all four species. When the normalized values were subjected to correlation analysis we again found a significant negative correlation between $R_w$ and LAP and a significant positive correlation between $R_a$ and NAR (Figs. 3 and Table II).

In comparisons of the four species within each growth irradiance (Table II), we found significant positive correlations between $R_w$ and LAP at all three irradiances. However, $R_w$ was significantly correlated with NAR only at the medium irradiance. The correlation between $R_w$ and $R_a$ for all combinations of

<table>
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<tr>
<th>Plant</th>
<th>Growth irradiance (wEm$^{-2}$sec$^{-1}$)</th>
<th>Duration of exponential phase (days)</th>
<th>$W_0$</th>
<th>$R_w$</th>
<th>$r_w$</th>
<th>$A_0$</th>
<th>$R_a$</th>
<th>$r_a$</th>
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<td>320</td>
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<td></td>
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<td>0.999</td>
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<td>0.0105</td>
<td>0.284</td>
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<tr>
<td></td>
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<td>0.174</td>
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<td>0.0116</td>
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Fig. 1. Relationship between relative growth rate ($R_w = [1/W] \frac{dW}{dt}$) and leaf area partition coefficient ($LAP = [dA/dt]/[dW/dt]$) for pigweed (O), velvetleaf (■), hemp sesbania (□), and cotton (□) grown at 90 (L), 320 (M), and 750 (H) $\mu$E m$^{-2}$ sec$^{-1}$. 

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Table II. Linear correlation (model: \(Y = mx + b\)) of relative growth rate \(R_w\) with:
- leaf area partition coefficient \(\text{LAP}\); leaf area ratio \(\text{LAR}\); net assimilation rate \(\text{NAR}\); and relative leaf area expansion rate \(R_w\). All abbreviations are CT = cotton; VL = velvetleaf; PW = pigweed; HS = hemp sesbania; * = significant at 0.05 level; ns = not significant. The numbers 750, 320, and 90 designate the growth irradiance in \(\mu\text{E m}^{-2}\text{sec}^{-1}\).

<table>
<thead>
<tr>
<th>(R_w)</th>
<th>(\text{LAP})</th>
<th>(\text{LAR})</th>
<th>(\text{NAR})</th>
<th>(\text{LAP})</th>
<th>(\text{LAR})</th>
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<td>-1.000*</td>
<td>-0.976</td>
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<td>-1.000*</td>
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</tr>
<tr>
<td>90</td>
<td>-0.998*</td>
<td>-0.820*ns</td>
<td>-0.968*</td>
<td>-0.820*ns</td>
<td>-0.968*</td>
<td>-0.820*ns</td>
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</tbody>
</table>

![Figure 2](image2.png)  
**FIG. 2.** Relationship between relative growth rate \(R_w = [1/W] \text{ dW/dt}\) and net assimilation rate \(\text{NAR} = [1/A] \text{ dA/dt}\) for pigweed (○), velvetleaf (●), hemp sesbania (■), and cotton (■) grown at 90 (L), 320 (M), and 750 (H) \(\mu\text{E m}^{-2}\text{sec}^{-1}\). Species and growth irradiance was significantly positive (Table II). Furthermore, when we calculated the regression of \(R_w\) on \(R_w\), we obtained a regression coefficient of 1.043 which indicated that on the average, the values of \(R_w\) and \(R_w\) were similar. As will be shown later, when \(R_w = R_w\), \(\text{LAP} = \text{LAR}\). We examined the relationship between \(\text{LAP}\) and \(\text{LAR}\) and found the correlation coefficient for \(\text{LAP}\) and \(\text{LAR}\) to be 0.949. When we calculated the regression of \(\text{LAP}\) on \(\text{LAR}\) we obtained a regression coefficient of 1.193. The similarity and correlation between \(\text{LAP}\) and \(\text{LAR}\) resulted in \(R_w\) being about as well correlated with \(\text{LAP}\) as with \(\text{LAR}\) (Table II).

**DISCUSSION**

**Relationship between \(R_w\) and \(\text{LAP}\) or \(\text{NAR}\).** Our results show that when plants grown at different irradiances at the same temperature are compared, \(R_w\) is better correlated with \(\text{NAR}\) than with \(\text{LAP}\). We interpret this to mean the instantaneous ratio in the rates of change with time of leaf area and total weight. Potter and Jones (2) further indicated that “\(\text{LAP} = \text{LAR}\) is the daily change in \(\text{LAR}\).” However, we submit that \(\text{LAP}\) is not equal to the rate of change of \(\text{LAR}\) with time \(\text{LAR}'\), since \(\text{LAP} = \frac{A}{W}\) and

\[
\frac{\text{dA/dt}}{\text{dW/dt}} = \frac{\text{LAP}}{\text{NAR}}\tag{2}
\]

![Figure 3](image3.png)  
**FIG. 3.** Relationship between relative growth rate \(R_w = [1/W] \text{ dW/dt}\) normalized as per cent of maximum within each species and leaf area partition coefficient \(\text{LAP} = [1/A] \text{ dA/dt}\) normalized as per cent of maximum within each species for pigweed (○), velvetleaf (●), hemp sesbania (■), and cotton (■) grown at 90 (L), 320 (M), and 750 (H) \(\mu\text{E m}^{-2}\text{sec}^{-1}\). with \(\text{LAP}\) or \(\text{LAR}\). This is true because low irradiance depresses \(R_w\) and \(\text{NAR}\) but causes a simultaneous increase in \(\text{LAP}\) and \(\text{LAR}\).

The positive correlation we found between \(R_w\) and \(\text{NAR}\) should be considered in conjunction with the report of Potter and Jones (2). In their study where temperature was varied and irradiance was held constant, they found that temperature influenced \(\text{LAP}\) and \(\text{LAR}\) more than \(\text{NAR}\) with the result that \(R_w\) was better correlated with \(\text{LAP}\) than with \(\text{NAR}\). In our study where irradiance was varied and temperature held constant, \(\text{NAR}\) varied more with irradiance than did \(\text{LAP}\), \(\text{LAR}\), or \(R_w\). Therefore, the irradiance effects on \(R_w\) were better correlated with \(\text{NAR}\) than with \(\text{LAP}\) or \(\text{LAR}\). Our results and those of Potter and Jones (2) demonstrate the contrasting effects of variations in temperature and irradiance on the growth analysis parameters. Our results support the importance of \(\text{LAP}\) demonstrated by Potter and Jones (2) because the different \(R_w\) values among species within a single irradiance treatment were highly positively correlated with \(\text{LAP}\).
IRRADIANCE AND GROWTH ANALYSIS

LAR' = \frac{d(LAR)}{dt} = \frac{d(A)}{dt} - \frac{d(W)}{dt} \tag{3}

In fact,
\frac{d(A)}{dt} = \frac{\lambda dW}{\partial t} - \lambda \frac{dW}{\partial t} \tag{4}

Thus, if
W = W_0 e^{B_0 t} and A = A_0 e^{B_0 t} \tag{5}

then
LAR' = \frac{d(LAR)}{dt} = \frac{(W_0 e^{B_0 t}) (R_a e^{B_0 t}) - (A_0 e^{B_0 t}) (R_a e^{B_0 t}) - (R_a - R_w) (A_0 e^{B_0 t})}{(W_0 e^{B_0 t})^2} \tag{6}

or simply \((R_a - R_w)\) (LAR). This last expression describes the rate of change of LAR with time during exponential growth and is clearly not equal to LAP as defined. Furthermore, LAP can be shown to be equal to \((R_a/R_w)\) (LAR) as follows: If LAP =
\frac{d(A)}{dt} = R_a A_0 e^{B_0 t} and \frac{d(W)}{dt} = R_a W_0 e^{B_0 t} \tag{7}

is the instantaneous LAR at time \(t\), then LAP is simply \((R_a/R_w)\) \times (LAR). Since \(R_a\) is often very nearly equal to \(R_w\) (cf. our data and those of Potter and Jones [2]), \(R_a/R_w\) approaches unity and LAP approaches LAR. In fact, if \(A\) and \(W\) are increasing exponentially and \(R_a = R_w\), then LAR' = 0, LAP = LAR, and LAR = \(A_0\)/\(W_0\). This close relationship between LAP and LAR is demonstrated by the high correlations we observed between \(R_a\) and \(R_w\) and LAP and LAR. The value of LAP as a growth analysis function is that it takes into account differences in \(R_a\) and \(R_w\) when they do occur. Thus, \(R_a\) is better correlated with LAP than with LAR when \(R_a\) is not similar to \(R_w\), e.g. our data for hemp sesbania. Future work should include investigations of the behavior of LAP, LAR, and LAR' throughout the complete growth period, extending beyond the first exponential phase. This will require suitable mathematical functions describing growth from emergence to maturity.

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