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# LEAF AREA DEVELOPMENT IN MAIZE AND SOYBEAN PLANTS*

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CAO J., HESKETH J. D., ZUR B. and REID J. F. *Leaf area development in maize and soybean plants*. BIOTRONICS **17**, 9–15, 1988. Leaf area emergence data for individual maize (*Zea mays* L.) leaves and expansion data for soybean [*Glycine max* (L.) Merr.] leaves were fitted with Gompertz, logistic and Richards functions. The latter function, with the most parameters (four), worked best. Leaf area expansion or emergence duration and rates were derived from the Richards function parameters and were compared among nodal positions of each leaf for the two crop species. Duration of leaf expansion was independent of node position in soybean but not for the emergence of new leaf area in maize, where it increased with node position up to the last three nodes. As a consequence leaf area development rates were not as closely related to final leaf area in maize as in soybean. This information forms a base for predicting leaf area development in plant canopies.

**Key words:** *Glycine max* (L.) Merr.; *Zea mays* L.; soybean; maize; leaf growth.

## INTRODUCTION

The quantification of environmental, nutritional and genetic effects on leaf expansion, or the emergence of newly expanded leaf area in the case of grasses, is important for understanding and predicting the effects of these same factors on crop growth and yield (cf. *6*). The development of credible plant models depends upon an aggressive research effort dedicated to such an objective.

Once a leaf is initiated, expansion rate and duration control the maximum area attained. Logistic (*2*, *8*, *9*) and Gompertz (*1*, *3*, *10*) functions have been used for many years to compare leaf area expansion or emergence rate and duration; thus

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far duration has been found to be independent of the leaf position on the mainstem. The Richards function, derived relatively recently (*12*, *13*), has been used to study effects of temperature and species (*4*, *5*, *7*) on maximum area per leaf, expansion rate, expansion duration, and a growth curve shape factor. The group at Urbana and Haifa and other collaborators have been interested in predicting canopy LAI from heat sum models for the initiation and expansion or emergence or individual leaves in maize, soybean and associated weed species. We describe here preliminary results suggesting fundamental differences between expansion duration in a $C_3$ legume and the emergence of newly expanded leaf area in a $C_4$ grass.

## MATERIALS AND METHODS

### *Experiment I*

The soybean [*Glycine max* (L.) Merr.] cultivar 'Williams' was grown as single plants in 4 liter plastic pots filled with a mixture (2: 1 by volume) of a commercial potting mix ('Jiffy Mix' made up of shredded spaghnum peat moss and horticultural grade vermiculite) and a Flannigan silt loam soil (Aquic Argiudoll). At the beginning of the experiment, six seeds were sowed in each pot placed in a growth chamber with a 28/25°C 16-h/8-h day/night temperature regime. After the third trifoliolate appeared, each pot was thinned to one plant. Temperatures were kept constant throughout the experiment within$\pm 1$°C. The chamber was lit with a $2.5 \times 1.35$ m$^2$ bank of fluorescent lamps (General Electric fluorescent Deluxe cool white lamps) which provided a light intensity of 350 $\mu$mol m$^{-2}$ s$^{-1}$ PAR (approximately 1/5 maximum values in the field on a clear day at noon). The humidity was set at 80% RH. Lengths and maximum widths were measured in mm for each expanding leaflet. Leaf areas of central leaflets of the soybean trifoliolates were used for analysis in this paper. Leaflet area was estimated from [($A \times$length$\times$width)+($B\times$length)+($C\times$width)], where $A$, $B$ and $C$ were 0.736, $-1.831$ and 2.581, respectively. The constants were derived from area measurements on a number of leaflets using the Li-Cor model 3000 (LI-COR, Inc.) leaf area meter. Four plants were measured to give the mean values used in our analysis.

### *Experiment II*

The maize (*Zea mays* L.) cultivar 'Pioneer 3377' was planted five seeds to a pot in 20 liter plastic containers filled with the same mix described above in Experiment I. Plants were thinned to three per pot at the 7-leaf tip stage and one per pot at the 15-leaf tip stage. Plants were grown in a $2.5\times 1.35\times 3$ m$^3$ chamber with a mobile light bank the same as in Experiment I which could be raised as the crop grew to the silking stage. The light flux at the top of the crop was 400 $\mu$mol m$^{-2}$ s$^{-1}$ PAR. The temperature regime used was a 30/24°C 16-h/8-h day/night period. Air humidity was maintained at 70–80% RH during the light period and 95% RH during the dark period. The mean temperature as determined from recorded values throughout the experiment was 27°C. Leaf areas were calculated from the product of (leaf length$\times$the maximum width$\times$0.73). Mean values were determined for each leaf position on 6 plants. This is the same data set used by Zur *et al.* (*14*) in an associated paper.

*The Gompertz function*

The Gompertz function used in this study was:

$$a = A \exp\left[-b \exp\left(-ct\right)\right] \quad (1)$$

where $a$ is the leaf area at time $t$ and $A$, $b$ and $c$ are fitted constants. $A$ is the final leaf area attained, the constant $b$ has little biological meaning, and $c$ is the rate constant. The point of inflection occurs at $a/A = 0.5$. The linear form of the Gompertz function, which was used in the estimation of parameters $b$ and $c$ by linear regression, is:

$$\ln\left[\ln\left(A/a\right)\right] = \ln\left(b\right) - ct. \quad (2)$$

*The logistic function*

The logistic function used in this study was:

$$a = A/\left[1 + \exp\left[-\left(\lambda + kt\right)\right]\right] \quad (3)$$

where $a$ is the leaf area at time $t$ and $A$, $\lambda$, and $k$ are fitted constants. $A$ is the maximum leaf area attained, $\lambda$ determines the position of the curve on the time axis, and $k$ is a rate constant. The logistic function has a symmetrically placed point of inflection at $(a/A) = 0.5$.

*The Richards function*

The form of the Richards' function used was:

$$a = A/\left[1 + \exp\left[-\left(\lambda + kt\right)/\theta\right]\right]^{\theta} \quad (4)$$

where $a$ is the leaf area at time $t$ and $A$, $k$, $\lambda$, and $\theta$ are fitted parameters (*7*). The coefficient $A$ represents the maximum area attained for each leaf. The coefficient $\lambda$ is an integration constant determined by the choice of zero time. The coefficient $k$ is essentially a rate constant that takes on significance when associated with the coefficient $\theta$. The coefficient $\theta$ determines the shape of the growth curve. When $\theta = 1.0$, the function reduces to the logistic equation discussed above. When $\theta$ approaches infinity, the function approaches the Gompertz equation discussed above. The weighted mean absolute growth rate '$E$' becomes:

$$E = (Ak)/[2(2\theta + 1)] \quad (5)$$

and the duration for growth '$\zeta$' becomes:

$$\zeta = k/[2(2\theta + 1)] \quad (6)$$

For a detailed discussion on the physiological significance of coefficients $E$ and $\zeta$ see Dennett *et al.* (*7*).

*Analytical procedure*

In order to obtain values for the coefficients in the above functions, least square equations were set up and solved by iteration with an optimization computer program. The residual mean square roots were calculated and used for comparisons of goodness of fit of the various functions to the data set. The Gompertz function coefficients were also estimated using the linear regression method and substituting the maximum area per leaf measured, or the mature value, for the $A$ coefficient.

## RESULTS AND DISCUSSION

Residual mean square roots were used as an indication of how well Gompertz, logistic, and Richards functions fitted the leaf area data for maize and soybean; leaf position mean values are given in Table 1. The Richards' function, with its four coefficients (vs. 3 coefficients in the other two functions), fitted the data best. The Gompertz function did not fit the data for maize leaves 9–15 as well as the logistic function did. Also the optimal estimation method used for the Gompertz fit did better than the regression method, but the optimization method did over-predict the actual maximum area per leaf by 2% (509 vs. 499 $cm^2$, see the footnote, Table 1), as reported earlier by Baker *et al.* (*3*) for another data set. Using the optimization method, Gompertz $b$ values for corn were 5.5 for leaves 4–12 and 4 for leaves 13–17; $c$ values for associated leaves were 0.51 for 4–7, 0.38 for 8–10, 0.32 for 11–13 and 0.26 for 14–18.

Leaf area vs. time is shown for successive individual leaves for soybean and maize, Fig. 1. The weighted mean absolute growth rate from Eq. (5), the duration of the growing period from Eq. (6), the maximum area per leaf attained, and the growth curve shape $\lambda$ factor are shown in Fig. 2. The biggest difference between maize and soybean was the effect of leaf position on expansion duration, as we measured it. The duration for expansion was relative constant in soybean but that for the emergence of new leaf area from the whorl of expanding leaves at the apex of the maize shoot increased with leaf position, up to leaf 15. Since final area is the integral of the expansion rate and duration, the constant duration values among leaf positions resulted in a close fit between final area and expansion rate in soybean, as reported earlier (*11*).

The rate of emerging newly expanded area in maize was not as closely related

Table 1. Goodness of fit of three growth functions to maize and soybean leaf expansion or emergence data

| | Residual mean square roots ($cm^2$) | | |
|---|---|---|---|
| | Function: Gompertz* | Logistic | Richards |
| Soybean, leaves 3–14 | 2.73 | 1.35 | 0.89 |
| Maize, leaves 3–18 | 9.61 | 9.55 | 6.97 |
| leaves 9–15 | 11.85 | 14.5 | 9.64 |
| Maize, linear regression, leaves 3–18 | 10.92 | | |

* Optimization method used except where linear regression method is indicated. The mean actual maximum area per leaf achieved was 499 $cm^2$; the optimization method predicted 509 $cm^2$.

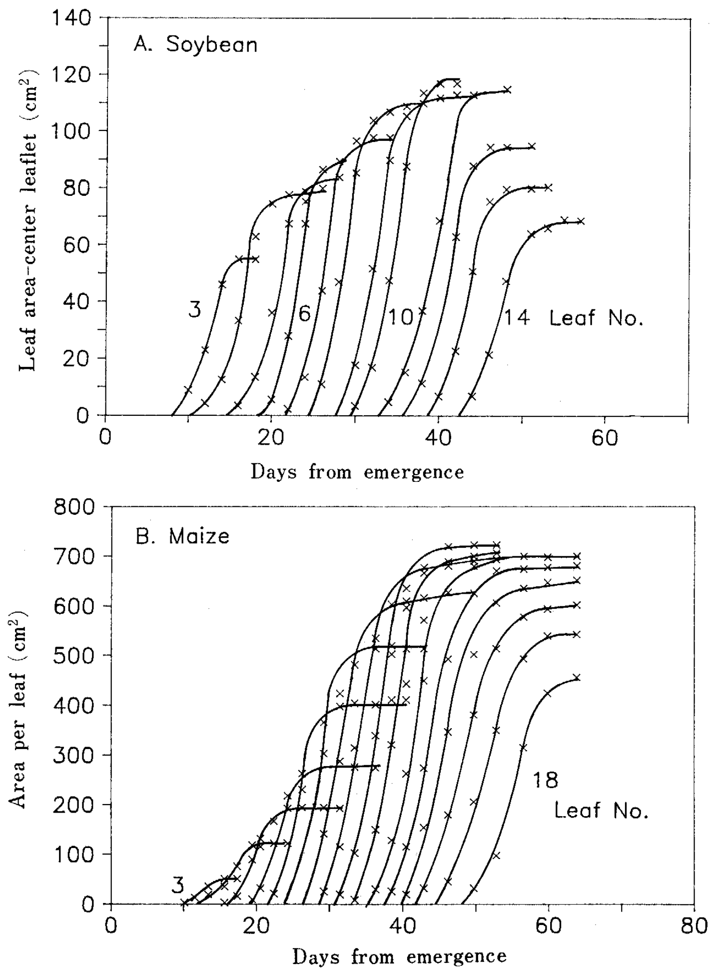


Fig. 1. (a) The mean leaflet area for the center leaflet of a soybean trifoliolate at each mainstem node position on 5 plants vs. time from emergence. For the approximate trifoliolate area, multiply by three. (b) The mean exposed leaf area at each mainstem node on 6 corn plants.

to final area, because of changes in emergence duration with leaf position. The Richards shape coefficient varied considerably but seemed to be larger for maize leaves 9–15. Such values for soybean were close to one; when it equals one the Richards function collapses to the logistic function. As pointed out above, when the shape parameter $\lambda$ approaches infinity, the Richards function collapses to the Gompertz function. In general, maize leaves had larger shape parameter values for leaves 9–15, and as shown in Table 1, the Gompertz function did fit the areas of such leaves better than the logistic function. In a similar comparison, the logistic equation fitted the soybean data better than the Gompertz, because the Richards shape parameter $\lambda$ was close to one. Therefore the behavior of the Richards' shape parameter explains some of the species differences in how well the logistic and Gompertz functions fitted the area data.

We may not need the detail that such an analysis provides to predict crop LAI

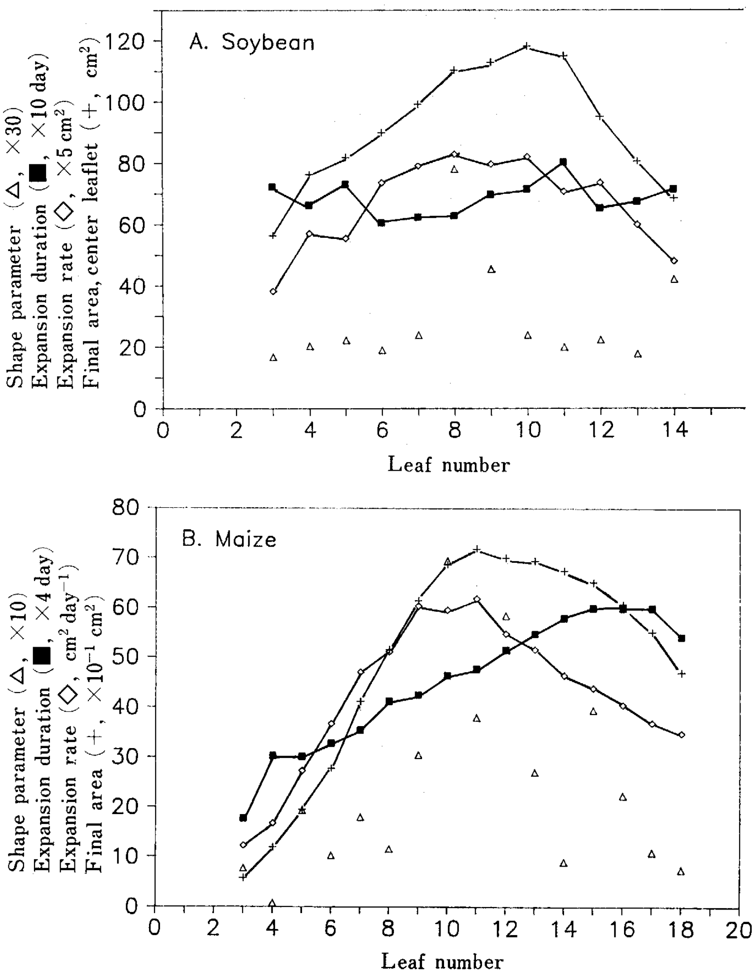


Fig. 2. Shape parameters, final areas, expansion or emergence rate, and expansion or emergence duration, as derived from analyses of the data shown in Fig. 1, using the Richards function and associated equations given in the text.

within the desired error limits; however, we do need further studies based upon all these functions to provide background information for developing credible logic for LAI models. A considerable proportion of the resources committed to any modeling effort might well be used on needed research or data analysis and synthesis; credible models can only summarize what is available in the existing scientific literature. We do have a model for predicting corn LAI based upon the above and similar research.

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