

# Relationships Among Rate of Leaf Area Development, Photosynthetic Rate, and Rate of Dry Matter Production Among American Cultivated Cottons and Other Species<sup>1</sup>

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APPLICATIONS of photosynthetic and growth characteristics of crop plants to plant breeding methods have been suggested by Watson (10), Milthorpe (6), Donald (1), and especially by Stoy (9) in a review paper on plant physiological aspects of breeding for yield. Milthorpe stressed the importance of rate of leaf area development as a factor affecting growth rate and minimized the importance of leaf photosynthetic rate. Stoy (9) and Murata (7) have suggested that leaf photosynthetic rate can be very important in determining growth rates. In the experiments reported here these factors were studied using the analytical techniques described by other workers (1, 6, 7, 8, 9, 10) in an effort to characterize and assess their relative importance in contributing to rapid growth of crop plants.

## MATERIALS AND METHODS

Two groups of species were studied. The first group consisted of sunflower and cotton and the second group consisted of corn and other grasses (scientific names and varieties of species are listed in Tables 1 and 2). Plants in the former group had leaf net photosynthetic rates (P) of 35 to 50 mg. CO<sub>2</sub> dm.<sup>-2</sup>hr.<sup>-1</sup>; whereas the latter group had P of 45 to 65 mg. CO<sub>2</sub> dm.<sup>-2</sup>hr.<sup>-1</sup>.

A chamber which could be quickly clamped onto a leaf was built of plexiglass with a replaceable top of plastic film. Outside air of approximately 300 ppm CO<sub>2</sub> by volume was drawn from a chamber, 5' X 5' X 8', to ensure a constant CO<sub>2</sub> concentration. This air was cooled before passing through the leaf chamber, 9" X 7½" X 3½", to maintain leaf temperatures at about 35° C. A fan was mounted inside the leaf chamber to provide uniform air CO<sub>2</sub> concentration around an entire cotton leaf. Air exchange rates of 40 to 50 liters per minute were used. The chamber was mounted on a tripod; this system made it possible to measure P of 9 different leaves in 1 hour. The leaves were oriented into the sun to ensure incident light intensities greater than 8000 foot-candles. A Beckman infrared CO<sub>2</sub> analyzer and recorders were enclosed in a small house trailer where constant temperature was maintained with a refrigeration unit. Details of the equations of calculating P and a description of the laboratory technique have been described elsewhere (2, 4).

The seedlings for plants used in the determination of P during the month of June were grown in the greenhouse in early April.

Later these seedlings were transplanted to large pots which were placed outdoors for a final period of growth. The plants were taken to the laboratory for measurement of P. Seedlings were also transplanted to the field.

The simple dry matter accumulation rate per unit of land area (dW/dt) is useful in describing growth rate, but in the study of its components as to why it varies it must be separated into leaf area (A) and photosynthetic rate. Net assimilation rate of dry matter (N.A.R.) was used as an estimate of P (as dry weight of individual plants per unit leaf area per unit time or mg. CH<sub>2</sub>O dm.<sup>-2</sup>day<sup>-1</sup>). On a whole plant, N.A.R. represents an average estimate of P for all leaves, some of which are shaded and, therefore, not photosynthesizing at the maximum rate. P is defined above as photosynthetic rate in intense light or close to full sunlight. N.A.R. values are also less than measured P because of uncontrollable factors of the environment such as cloudiness and low temperatures.

The relationship between dW/dt and its components N.A.R. and A are defined in the following equation (10):

$$dW/dt = N.A.R. (A) \quad [1]$$

where W = dry weight, t = time, and A = leaf area. During early growth (8),

$$\log_e W \cong k_1 t, \quad [2]$$

and

$$\log_e A \cong k_2 t. \quad [3]$$

Therefore, from equations [1] and [2], and since  $d \log_e x = dx/x$ ,  $N.A.R. \cong W k_1 / A$ . [4]

In later growth, the relation between  $\log_e W$  and t became curvilinear. Slopes of such curves were determined, where

$$\text{slope} = d(\log_e W)/dt = 2.3 d(\log_{10} W)/dt = (1/W) 2.3 dW/dt, \quad [5]$$

and, from [1] and [5],

$$N.A.R. = (2.3 W/A) d(\log_{10} W)/dt \quad [6]$$

N.A.R. values determined during May and June for cotton plants are shown in Table 1; whereas N.A.R. values determined during July for cottons and other species are shown in Table 2. Leaf area determinations per plant (not per unit soil area) were discontinued when leaves of plants of *G. hirsutum* and *G. barbadense* were beginning to shade one another among plants or at stages of growth before competition for light among plants had begun. Competition for light had begun long before this in sunflower and the efficient grasses. The dry weight and leaf area measurements were made in standard field plantings, whereas photosynthetic rates were determined with spaced plants. Skies were clear during June, but there was some cloudiness during July.

## DISCUSSION OF RESULTS

Mean P ( $\bar{P}$ ) of 2 leaves for potted plants and cotyledons in June and  $\bar{P}$  of 3 leaves for field plants in July and August are listed in Table 1. No consistent differences in

<sup>1</sup> Journal paper No. 926 of the Arizona Agricultural Experiment Station, Tucson. This study was aided in part by a research grant No. GB-2273 from the National Science Foundation to J. Hesketh. Received for publication Sept. 29, 1964. The data of this paper were presented at the ASA meetings, November 17, 1964.

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P among varieties and  $F_1$  crosses of *G. barbadense* and *G. hirsutum* are apparent. However, P was less for the variety Sea Island Virescent of *G. barbadense*, which might be expected since leaves of this plant are very low in chlorophyll.  $\bar{P}$  of  $45 \pm 7$  and  $40 \pm 4$  mg.  $\text{CO}_2$  dm. $^{-2}$ hr. $^{-1}$  were measured for leaves of a normal tetraploid and a polyhaploid plant, respectively, of *G. barbadense* ( $2n = 4x = 52$ ) (individual leaves and leaf area per plant of the polyhaploid were much smaller than the tetraploid).

For the observations in the first 5 columns in Table 1, variability in P was large, the average standard error being  $\pm 5$ ,  $\pm 6$ ,  $\pm 12$ , and  $\pm 5$  mg.  $\text{CO}_2$  dm. $^{-2}$ hr. $^{-1}$ . Observations of column 4 with error of  $\pm 12$  mg.  $\text{CO}_2$  dm. $^{-2}$ hr. $^{-1}$  were obtained soon after the soil began to dry out from a series of summer rains.

Small differences in P were difficult to measure under optimum, natural conditions. P is a function of many variable (2, 3, 4). Even though temperature, light, air movement around the leaf, and  $\text{CO}_2$  were controlled in the present experiments, it is evident that there were other important factors which were not controlled, such as stomatal opening.

There were differences among mean N.A.R. ( $\bar{N.A.R.}$ ) (Table 1), but variability due to sampling was large. There was no clear cut relation between  $\bar{N.A.R.}$  and W at the end of the experiment. There was a very good relation between the final A and W and also  $k_2$  and W, except for the variety Dwarf A. The initial slopes of the curves of  $\log_e A$  as a function of time are reported in Table 1 as  $k_2$ ; Dwarf A had a leaf area greater than the  $F_1$   $\Delta P \times PS-2$  even at 4 weeks (Figure 1) but the rate of leaf area development slowed down very rapidly after this, as evidenced by the final A (Table 1). One can conclude that major differences in vigor of growth, or W over time, are associated with differences in rate of leaf area development. Also, hybrid vigor of one example of interspecific  $F_1$  plants,  $\Delta P \times PS-2$ , was associated with differences in  $k_2$  or rate of leaf area development (Figure 1). Shibles and MacDonald (8) have shown that differences in vigor of two varieties of *Lotus corniculatus* L. were associated with differences in  $k_2$  and not photosynthetic rate; hence, a similar finding associated with hybrid vigor in cotton was not unexpected.

PS-2 and  $\Delta P$  had similar  $\bar{P}$ ,  $k_2$ , W, and A (Table 1); however, in the general experimental area, the yield of cotton of  $\Delta P$  is nearly double that in PS-2. Apparently this difference in yield is caused by differences in flowering and setting of bolls, because the two species are very similar in productivity of dry matter at onset of flowering, this being the stage of growth when W and A of Table 1 were measured. This difference in yield indicates the existence of many very important factors controlling yield other than P and  $k_2$ . In the hybrid, however, increased  $k_2$  does contribute to vigor of growth, and late in the experiment these plants attained a specific A and W more than a week earlier than the parents,  $\Delta P$  and PS-2 (Figure 1). In other words, this earliness in the development of photosynthetic area of the hybrid plant can extend the effective growing season by more than a week, or the hybrid is in the field with a full set of leaves one week before its parents. Apparently this increase in growing season is reflected in an increase in the yield of cotton.

Among spaced plants, White and Richmond (11) attributed heterosis of yield of cotton hybrids to greater weight of vegetative parts of single plants. To achieve the greater

Table 1. Leaf photosynthetic rates, net assimilation rates, and leaf area development rates of American cottons.

Variety	$\bar{P}$ spring	$\bar{P}$ cotyledons	$\bar{P}$ Exp. 1 Jul 11	$\bar{P}$ Exp. 2 Aug 10	$\bar{P}$ Exp. 3 Aug 17	$\bar{N.A.R.}$ † mg/ dm <sup>2</sup> day	W, g/pl.	A, dm <sup>2</sup> /pl.	$k_2$ †
*Deltapine Smoothleaf ( $\Delta P$ )	39 ± 18	40 ± 9	50 ± 5	39 ± 11	44 ± 3	141 ± 27	21.5	14.3	0.094
*Acala-44(A-44)	47 ± 8	39 ± 2	52 ± 5	43 ± 18	43 ± 6	147 ± 8	18.7	10.9	0.105
Pima S-2(PS-2)	44 ± 1	--	--	45 ± 10	41 ± 6	121 ± 16	20.3	14.1	0.106
$\Delta P \times PS-2$	42 ± 3	35 ± 1	--	45 ± 10	43 ± 4	140 ± 18	68.5	56.3	0.120
* $\Delta P \times A-44$	45 ± 6	--	57 ± 2	53 ± 21	44 ± 6	134 ± 14	24.6	14.5	0.111
Pima S-1	37 ± 6	37 ± 1	--	--	--	119 ± 14	--	--	--
Pima CB-58	47 ± 6	42 ± 5	53 ± 5	--	--	100 ± 16	13.6	9.7	0.110
*Del Cerro	44 ± 13	--	--	46 ± 2	--	--	--	--	--
*Red Dwarf	33 ± 6	50 ± 10	--	37 ± 2	--	--	--	--	--
Dwarf A	39 ± 1	38 ± 9	--	44 ± 2	--	97 ± 9	12.2	9.8	0.143
*Lankart (L)	48 ± 4	43 ± 12	54 ± 7	--	--	--	--	--	--
Pima 32	35 ± 3	40 ± 3	--	--	--	--	--	--	--
( $\Delta P \times L$ ) $\times$ PS-2	45 ± 10	--	--	46 ± 16	--	--	--	--	--
Sea Island	44 ± 3	--	40 ± 2	--	--	--	--	--	--

\* *Gossypium hirsutum* L., all others *Gossypium barbadense* L. and  $F_1$  species hybrids.  
†  $\log_e \text{dm}^2/\text{day}$  per plant.  $k_2$  is an estimate of the initial slope of graphical plots of  $\log_e A$  as a function of time, see Figure 1. ‡ Maximum daily temperature 33 to 42°C., minimum daily temperature 19.5 to 25.5°C. § Standard Error. W and A here were determined at 9 weeks.

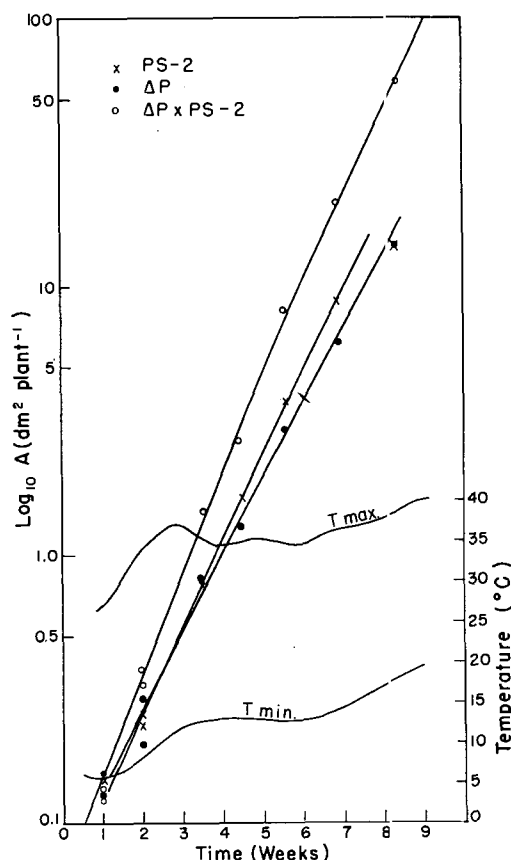


Figure 1. Logarithm to the base 10 of leaf area as a function of time for 2 species and their  $F_1$  hybrid. Smooth lines  $T_{max}$  and  $T_{min}$  are drawn through daily maximum and minimum temperatures. N.A.R. of Table 1 were calculated from the leaf area and dry matter data obtained between 3 and 9 weeks.

size such plants probably had a greater  $k_2$  value than the parents, such as the hybrid  $PS-2 \times \Delta P$  in our experiments. However, in closed stands, rapid development of photosynthetic area and resultant extension of the growing season would contribute to increased yields; whereas increases in vegetation or final size of the plant might contribute little or nothing. Some simplification of the standard dry-

Table 2. Net assimilation rate and other growth characteristics of cotton and other species during July.

Species	P*	N. A. R.	W	A	k <sub>2</sub>
<i>Helianthus annuus</i> L. var. Manchurian Grey Striped	40	214 ± 22	294	144	0.288
<i>Zea mays</i> L. var. Funks F 711 A	60	143 ± 25	114	80	0.220
<i>G. barbadense</i> var. PS-2	45	124 ± 12	28	28	0.149
<i>G. hirsutum</i> var. ΔP	45	137 ± 6	25	24	0.133
<i>Pennisetum glaucum</i> L. var. Starr	60	140 ± 20	102	83	0.282
<i>Sorghum vulgare</i> L. var. Hegari	60	137 ± 19	109	85	0.230

\* The "generalized" P values in mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> were taken from Table 1 and previous papers. N. A. R. is the mean of 4 or more consecutive determinations of A and W over the growth period of 9 weeks and is expressed as mg dry matter per dm<sup>2</sup> of leaf area per day. W is given as g dry matter per plant. A is given as dm<sup>2</sup> of area per plant. k<sub>2</sub> is given as the rate of change of log dm<sup>2</sup> per day per plant. W and A here were measured at the end of the experiment (9 weeks).

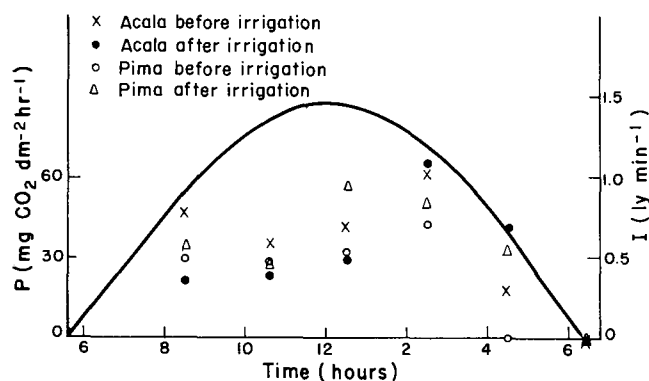


Figure 2. Photosynthesis (P) estimated from Equation [10], using data of Hawkins, 1927. Solid line is an idealized indication of light energy on clear days.

matter and leaf area sampling techniques (10) employed in our studies may offer great potential in selecting for early development of leaf area associated with early flowering but not with increased vegetation.

Sunflower had a much greater  $dW/dt$  than cotton, which can be attributed to the larger  $k_2$  and the larger N.A.R. This fact shows the importance of factors other than P, for here P was the same (Table 2). The differences in W become very great with time because of the logarithmic nature of growth (see equations [2] and [3]).

The present data support Milthorpe's emphasis on rate of leaf area development as the most important variable in determining growth rate. Recently, Jarvis and Jarvis (5) have compiled N.A.R. values among species with a range of 14 to 217 mg. dm<sup>-2</sup> day<sup>-1</sup>. *Amaranthus* sp., corn, and sunflower had the maximum N.A.R., cool weather crops had intermediate values, and tree species had the lowest values. These N.A.R. values are closely associated with a parallel range in measured P values. Hence, among species, N.A.R. and P are very important in determining  $dW/dt$ . Milthorpe considered only the cool weather species of intermediate N.A.R.

## THEORETICAL DISCUSSION

From definition of  $dW/dt$  [1]

$$\text{N.A.R.} = dW/dt(1/A). \quad [7]$$

N.A.R. can be separated into photosynthetic rate and other complex factors:

$$\text{N.A.R.} = bP t' (30/44) - RW/A. \quad [8]$$

Equation [8] is adapted from Murata (7); b is a characteristic of light interception of A or the "light receiving coefficient"; t' is the hours of effective daylight or photosynthetic rate for a horizontal leaf for a clear day divided

by P (such t' are obtained from photosynthetic-light response data of a single leaf and light data over a day such as in Figure 2); 30/44 is an approximate conversion factor from CO<sub>2</sub> to dry matter (CH<sub>2</sub>O); and RW is the respiration rate of non-photosynthetic tissue for 24 hours and photosynthetic tissue for the dark hours. b is difficult to define and represents a complex composite effect made up of the following leaf characteristics: angle of orientation, position on the plant, fraction of the total leaf area per plant or soil surface, reflectivity, transmissivity, shape, size, and age. Since P is measured for leaves in intense light, b also contains errors in estimating t'. One must consider these factors when interpreting leaf chamber P values under standard conditions in relation to individual leaves in a crop surface. It should be pointed out that rate of dry matter production,  $dW/dt$ , can be a linear function of P, providing  $bt'A$  remains constant. For cotton, a difference in P of 5 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> would change  $dW/dt$  10% providing  $bt'A$  remains constant. Since it was not possible to determine a difference in P of 5 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> because of the large standard error, it cannot be concluded from  $\bar{P}$  of Table 1 that photosynthetic rate is not an important factor affecting N.A.R. Small differences in P should be greatly magnified over time because of the exponential nature of growth.

As A approaches 0, b should approach 1 for horizontal leaves, or b should approach  $\cos \theta$  for leaves at an angle  $\theta$  from an imaginary line normal to the sun. For this reason, N.A.R. values were determined for young plants. With t' of 10 hours for a cotton leaf where  $P = 45$  mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> (for a corn leaf, t' = 9 hours, for a light-saturated leaf where  $P = 20$  mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>, t' = 11 hours), and ignoring R, a N.A.R. of 100 mg. dm<sup>-2</sup> day<sup>-1</sup> is equal to P of 15 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>. From N.A.R. of Table 1, P of 21 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> are approached. W/A is usually between 0.5 and 1.0 g. W dm<sup>-2</sup>. If a respiration rate of 2 mg. CO<sub>2</sub> per g. dry weight per 24 hours is assumed, a P of 23.4 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> would be required. P estimated from N.A.R. will always be less than measured P, because of shading among leaves and reduction of incident light due to leaf angle. Such differences between estimated P and the measured P are attributed in Equation [8] to the factor b or the "light receiving coefficient."

N.A.R. values were determined for standard cotton varieties and other species in July (Table 2). Here, P as high as 33 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> can be estimated for leaves of sunflower, *H. annuus*. N.A.R. is not associated with P among the 2 groups of species mentioned in Methods and Materials where P differs by 10 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>; in fact, sunflower had a greater N.A.R. than the grasses. Cotton and sunflower have horizontal leaves; whereas the grasses have leaves at a large angle to the horizontal. The lower N.A.R. of the grasses can be attributed to leaf angle or small b.

Warren-Wilson (personal communication) has determined an N.A.R. of 260 mg. dm<sup>-2</sup> day<sup>-1</sup> for sunflower, from which one can calculate an estimated P greater than 40 mg. CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>. From N.A.R. among species compiled by Jarvis and Jarvis (5) and measured P from our own studies, b as we calculate it with t' = 10 is generally 0.5, including that of corn and *Amaranthus* sp. For species of low P which are "light saturated" in low light, b should be larger than that for species of high P which are not as often "light saturated" in nature. In any case,

N.A.R. values are reported for which measured P must be greater than 30 mg. CO<sub>2</sub> dm.<sup>-2</sup>hr.<sup>-1</sup>.

A large N.A.R. and large b from which a rapid P can be estimated is not necessarily associated with maximum dW/dt or productivity. The relationships between dW/dt and N.A.R., b, A and  $\Theta$  are discussed in great detail elsewhere (1, 6, 7, 9, 10); here we were mainly interested in P estimated from N.A.R. that are greater than the standard 20 mg. CO<sub>2</sub> dm.<sup>-2</sup>hr.<sup>-1</sup>.

Estimated P from N.A.R. values of Tables 1 and 2 are generally low, probably because of low temperatures affecting cotton in May and cloudy weather in July, and angle of leaves, particularly in the grasses. Many measurements of W of individual cotton leaves over two-hour periods over the day have been reported by Hawkins (3). Here, R is eliminated as a factor (see equation [8]). Such data need to be corrected for translocation of photosynthate out of the leaf. Translocation can be estimated by:

$$dB/dt = K(W - W_0) \quad [9]$$

where W<sub>0</sub> is the leaf weight early in the morning and dB/dt the rate of translocation of photosynthate. K can be estimated from actual dB/dt data later in the day when light and P are low and W - W<sub>0</sub> is large. P can then be estimated from:

$$P = \frac{[dW/dt + K(W - W_0)] 44/30}{10} \quad [10]$$

P calculated from [10] are presented in Figure 2. Such P are well within the range of measured P in Table 1. K was between 0.18 (Pima) and 0.25 (Acala) per hour. W - W<sub>0</sub> reached as high as 108 mg. dry weight dm.<sup>-2</sup> around 3:00 p.m., W<sub>0</sub> being 440 to 500 mg. dm.<sup>-2</sup>.

With such close agreement between the techniques of dry matter sampling and photosynthetic CO<sub>2</sub> exchange, it seems likely that dW/dt and W(t) can be accurately broken down into the components b, P, t', k<sub>2</sub>, W/A, k<sub>1</sub>, and R of Equations [3], [4], [7], and [8]. Very significant differences in these variables exist among species as illustrated by the significant differences in W (Tables 1 and 2).

Rapid rate of development of photosynthetic area and rapid dW/dt or N.A.R. are characters which should be associated with the rapid development of maximum amounts of the economically usable parts of the plant. With rapid growth rates of species such as sunflower as an upper limit, the plant breeder can potentially make great improvements in rate of growth and subsequent yield of many other crops; however, the components of this growth rate must first be thoroughly understood.

## SUMMARY

Differences in net photosynthetic rates (P) of leaves of many cotton varieties and several hybrids were not detectable using the leaf chamber techniques. Variability of P within any one plant was great. Net assimilation rate (N.A.R.) of dry matter did not differ greatly among these same plants. Differences in rate of leaf area (A) development were measurable and were associated with differences in rates of dry matter production among cottons and between cottons and other species. P of 30 to 40 mg. CO<sub>2</sub> dm.<sup>-2</sup>hr.<sup>-1</sup> could be estimated from N.A.R. values of *H. annuus*; P of 40 mg. CO<sub>2</sub> dm.<sup>-2</sup>hr.<sup>-1</sup> could be estimated from dry weight measurements with individual leaves of cotton. It seems likely that once further refinements in measurement of P, N.A.R., and A are attained, major differences in growth rates among different plants within and between species can be accounted for; thereby providing new knowledge for development of criteria for selection of higher yielding plants.

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