

Cotton Leaf Photosynthesis and Age Relationship is Influenced by Leaf Position

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ABSTRACT

Photosynthesis rate per unit leaf area and leaf longevity are significant components of field cotton performance. The objective of this study was to determine the relationship between photosynthesis rate and age for leaves located at different positions in canopy. Cotton cultivars 'Sri Sumrong 60' was sowed weekly from June to September 1995 and on May 30, 1996 at Kasetsart University's Suwan experiment station. Net photosynthesis rates at light saturation (P_{max}) were measured using open system portable photosynthesis system equipped with LED lamp. The relationship between P_{max} and main stem leaf age, without regard to nodal position, was influenced by plant age. Furthermore, relationships between P_{max} and leaf age appeared to be similar for main stem leaves on nodes 3-10. For leaves on nodes 12-15, P_{max} declined at slower rate than for nodes 3-15. The main difference of P_{max} -age relationships of sympodial and monopodial from main stem leaves seemed to be the proportion of leaves that had P_{max} less than the average for main stem leaf at the same leaf age. At specific leaf age, P_{max} tended to decline with increase sympodial position. In addition, P_{max} of monopodial leaves had very large variation, and were less responsive to leaf age than for main stem leaves. Analysis of P_{max} -node position for specific age revealed that for main stem leaves at lower node P_{max} peaked earlier and longevity was shorter than leaves at higher nodes. Differences in P_{max} -age relationships for leaves at various main stem, sympodia, and monopodial position were thought to result from leaf acclimation to limiting available PPF resources.

Key words: cotton, photosynthesis, position, and leaf age

INTRODUCTION

Photosynthesis is a significant determinant of cotton production and yield (Guinn *et al.*, 1976). According to simulation studies using GOSSYM model, and increase of cotton photosynthesis rate by 15% could result in a 50% yield increase, provided nitrogen and water were adequate (Landivar *et al.*, 1983). Genetic differences in

photosynthesis rates between okra and normal leaf cotton were illustrated by Pettigrew *et al.* (1993). Moreover, Pettigrew and Meredith (1994) proposed that some cotton breeder selected for greater photosynthesis while breeding for higher yield. Although in some crops, such as soybean (Ford *et al.*, 1983) tall fescue (Nelson *et al.*, 1975) and sugarcane (Irvine, 1975), photosynthesis rates were not positively related to yield, study in pima cotton

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showed that genetic advances of cultivated lines with higher yield were closely associated with increasing single leaf photosynthesis rate and stomatal conductance especially in the morning (Cornish *et al.*, 1991). In addition, modification of photosynthesis and leaf age relationship, as stated by Wullschleger and Oosterhuis (1990), specifically leaf longevity and photosynthesis rate, had potential to substantially increase net carbon production by individual leaf and thus increase potential for cotton yield.

Constable and Rawson (1980) found that relationships between net photosynthesis rate measured at saturating light (P_{max}) and leaf age were essentially similar for main stem leaves at node 5, 7, 9 and sympodial leaf at node 9. They stated that the performance of leaves was tied to their age after unfolding, regardless of position on the plant or along the branches. Although it is indisputable that after leaf initiation P_{max} increase with age, reach the peak, subsequently decline and eventually die, more study is still needed to illustrate the P_{max} -leaf age relationships in detail for leaves from different nodal, sympodial and monopodial positions in canopy, especially in tropical conditions such as Thailand where large number of productive nodes are typical characteristic for cotton.

The objective of this study was to investigate the influence of position on relationship between leaf age and leaf net photosynthesis rate, measured at saturating light for field grown cotton in tropical condition.

MATERIAL AND METHOD

First experiment

Cotton cultivar 'Sri Sumrong 60' was grown in 1.0x0.1 m² spacing at Suwan experiment station (latitude 14.7, longitude 101.24), Kasetsart University, Thailand. Fifteen plots, each consisted of 5 five-meter rows were sowed weekly started

from June 5, 1995. Date of initiation, defined as leaf first unfolded, for all leaves on 20 plants per plot was recorded. Photosynthesis data collections were from September to December 1995. Average daily total solar radiation, monitored with a model 200 SB pyranometer (Li-Cor, Inc., Lincoln, NE), during this experiment was 17.5 MJ m⁻² day⁻¹ with the highest and lowest radiation days having 25.5 MJ m⁻² day⁻¹ and 6.6 MJ m⁻² day⁻¹, respectively. Air temperatures averaged 26°C, with high temperature sometimes reaching 36°C.

Second experiment

Cotton cultivars Sri Sumrong 60 was sowed in 1.25x0.40 m² spacing at Suwan experiment station on May 30 1996. Photosynthesis data collections were from July to September 1996.

Photosynthesis measurement

Net photosynthesis rates at light saturation (P_{max}) were measured using open system portable photosynthesis system model 6400 (Li-Cor, Lincoln, NE) equipped with optional LED lamp providing 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPF. Air flow to the chamber was adjusted to give approximately 50% humidity. The effort was made to maintain leaf temperature at $28 \pm 1^\circ\text{C}$ for most leaves with the exception of very young and very old leaves whose temperatures were close to ambient and very difficult to manipulate. Data was taken when photosynthesis rates were steady. To eliminate difference in environmental factors during growing season prior to the measurement, P_{max} was determined on the same day for the study on the effect of plant age on P_{max} .

Mathematical equation: $Y = a + bX[\exp(cX)]$ (Constable and Rawson, 1980) was fitted to P_{max} -age relationships using procedure non linear regression, Statistical Analysis System (SAS Institute, NC).

RESULTS

Effect of plant age on P_{\max} -age relationship

The relationships between P_{\max} and main stem leaf age, without regard to nodal position, were influenced by plant age (Figure 1). First, P_{\max} for leaves from 92 DAP plants peaked at an average of $35 \mu\text{mol m}^{-2}\text{s}^{-1}$ compared to $30 \mu\text{mol m}^{-2}\text{s}^{-1}$ for 64 DAP plants. Second, peak P_{\max} for leaves from 92 DAP plants remained unchanged for almost 15 days before declining when leaves were over 30 day old while for 64 DAP plants P_{\max} declined rapidly after peaking at approximately 15-18 day old.

P_{\max} -age relationship for main stem leaf

From data collected over 2 months period on several weekly sowing plots, it was illustrated that relationships between P_{\max} and leaf age appeared to be similar for main stem leaves on nodes 3-10 (Figure 2). During the first 10 days after unfolding, P_{\max} increased rapidly and peaked at

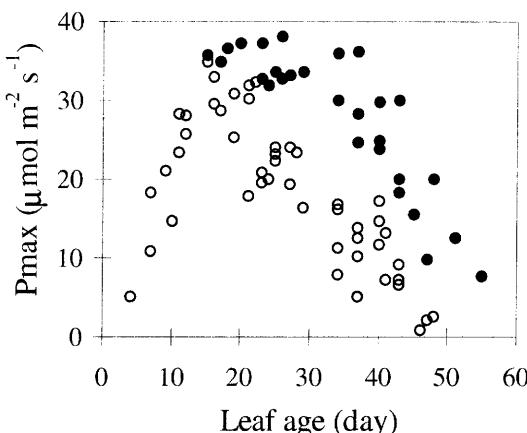


Figure 1 P_{\max} of main stem leaves as functions of leaf ages for two cotton fields at 64 DAP (open circle) and 92 DAP (closed circle). P_{\max} was measured on the same day.

12-15 days, approximating $30 \mu\text{mol m}^{-2}\text{s}^{-1}$. Extrapolation of data indicated that P_{\max} was close to zero on the day of unfolding. A few days (3-5 days) after peaking, P_{\max} started to linearly decline and, at approximately 40-45 days, appeared to be approximately at 20% ($6 \mu\text{mol m}^{-2}\text{s}^{-1}$) of P_{\max} at the peak.

For main stem leaves on nodes 12-15, P_{\max} also increased rapidly during early leaf development

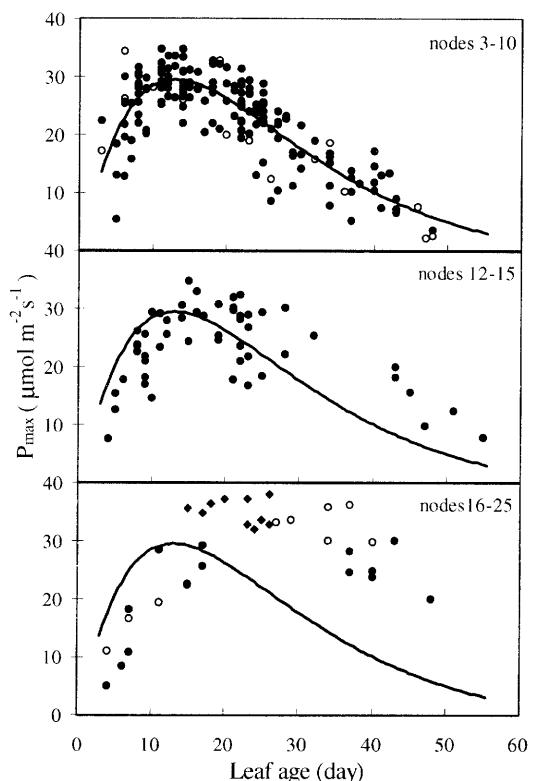


Figure 2 P_{\max} - age relationships for three main stems nodal position groups. Line was fitted to observed P_{\max} for nodes 3-10 and was displayed in all there nodal position groups to facilitate comparison. For nodes 3-10, open circle represented node 4. For node 16-25, closed circle represented node 16-17, open circle represented nodes 18-19, and diamond represented node 20-25.

and, at 10-15 days, reached the peak at approximately $30 \mu\text{mol m}^{-2}\text{s}^{-1}$ and then declined linearly after peaking. The rate of decline, however, was slower than that of leaves on nodes 3-10. Extrapolation indicated that 20% of P_{\max} at the peak was expected to be reached at more than 60 days.

For main stem leaves on nodes 16-25, peak of P_{\max} at $35 \mu\text{mol m}^{-2}\text{s}^{-1}$ was reached within 18 days and P_{\max} remained unchanged for more than 15 days. After 35 days, P_{\max} began to decline at significantly slower rate than for nodes 3-10 and for nodes 12-15. At 40-45 days, P_{\max} still remained approximately $20-30 \mu\text{mol m}^{-2}\text{s}^{-1}$ compared to just $15-20 \mu\text{mol m}^{-2}\text{s}^{-1}$ for nodes 13-15 and less than $10 \mu\text{mol m}^{-2}\text{s}^{-1}$ for nodes 3-10.

Projected leaf duration was approximately at 50-55 days for leaves on nodes 3-10, and at more than 60 days for leaves on nodes 12-15. Although

not enough information was available for exact prediction, it was evident that leaf duration for nodes 16-25 should be greater than 60 days.

P_{\max} -age relationship for sympodial leaf

P_{\max} -age relationship for leaves on the first horizontal sympodial position (P1) on nodes 11-15 was not significant difference from main stem leaves (Figure 3). For most of P2 leaves, P_{\max} tended to be $2-5 \mu\text{mol m}^{-2}\text{s}^{-1}$ less than main stem leaves. For P3 leaves, however, P_{\max} was significantly less (up to $12 \mu\text{mol m}^{-2}\text{s}^{-1}$) than those of main stem leaves for all age range examined. In addition, P_{\max} of P3 leaves was less responsive to leaf age than main stem, P1 or P2 leaves. These differences in P_{\max} -age relationship between leaves on main stem and on the first three horizontal sympodial positions (P1, P2, and P3) for nodes 6-10 and 16-20 were also observed (data not shown).

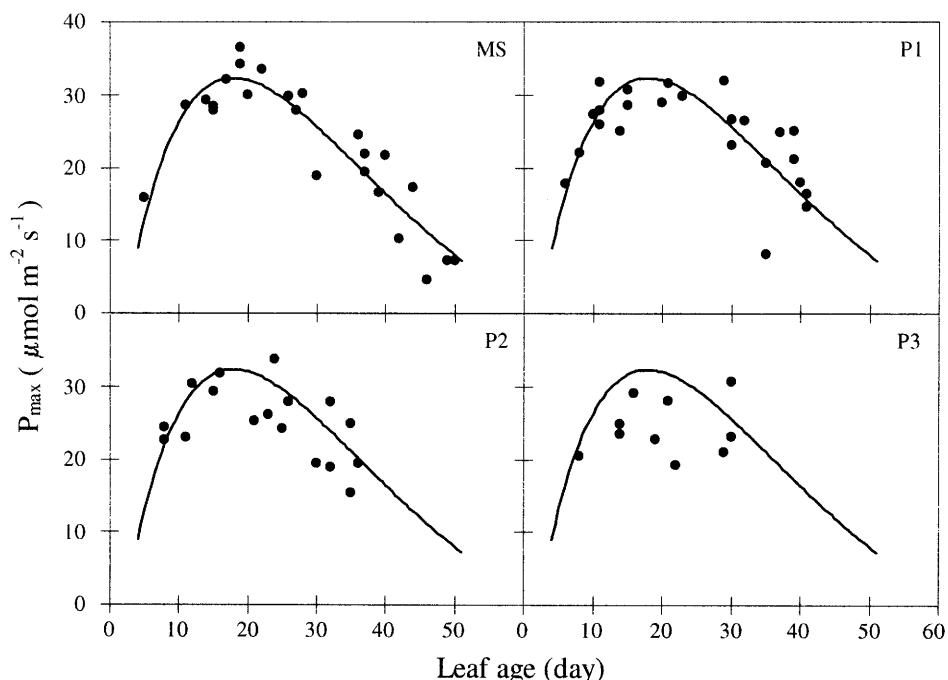


Figure 3 P_{\max} - age relationships of main stem and sympodial leaves on nodes 11-15. Line was fitted to main stem P_{\max} data and displayed for all sympodial position P1 to P3.

P_{\max} -age relationship for monopodial leaf

Leaves on monopodial (vegetative) branches were characterized as being either on main stem (VBMS) or on fruiting branch (VBFB) positions. For monopodial branches initiated from main stem nodes 5 and 6 (Figure 4), P_{\max} of VBMS leaves peaked approximately 16-20 days and linearly declined in similarity to the relationship observed for main stem leaves on nodes 3-10. P_{\max} of large percentage of leaves on VBFB at nodes 5 and 6 were lower than those for VBMS leaves and were characterized with great variation for range of leaf age.

For monopodial branches initiated from main stem nodes 3 and 4, P_{\max} of VBMS leaves tended to peak at 15 to 25 days and began to decline thereafter. P_{\max} at peaking ($28 \mu\text{mol m}^{-2}\text{s}^{-1}$) was

less than that of nodes 5 and 6 ($30 \mu\text{mol m}^{-2}\text{s}^{-1}$). For VBFB leaves, P_{\max} was significantly less than the average for VBMS on node 5 and 6. Moreover, P_{\max} was less responsive to leaf age and the upper limit of P_{\max} -age relationship tended to show the same response to leaf age as observed in P_{\max} -age relationship for main stem leaf. Furthermore, P_{\max} of VBFB leaves had very large variation, ranging from the low of $10 \mu\text{mol m}^{-2}\text{s}^{-1}$ to the high of approximately $30 \mu\text{mol m}^{-2}\text{s}^{-1}$ between 15-20 days, which was the normal peaking time for leaves at main stem positions.

It was remarkable that the main difference of P_{\max} -age relationships of sympodial and monopodial leaves from that of main stem leaves seemed to be the substantial proportion of sympodial and monopodial leaves that had P_{\max} less than the

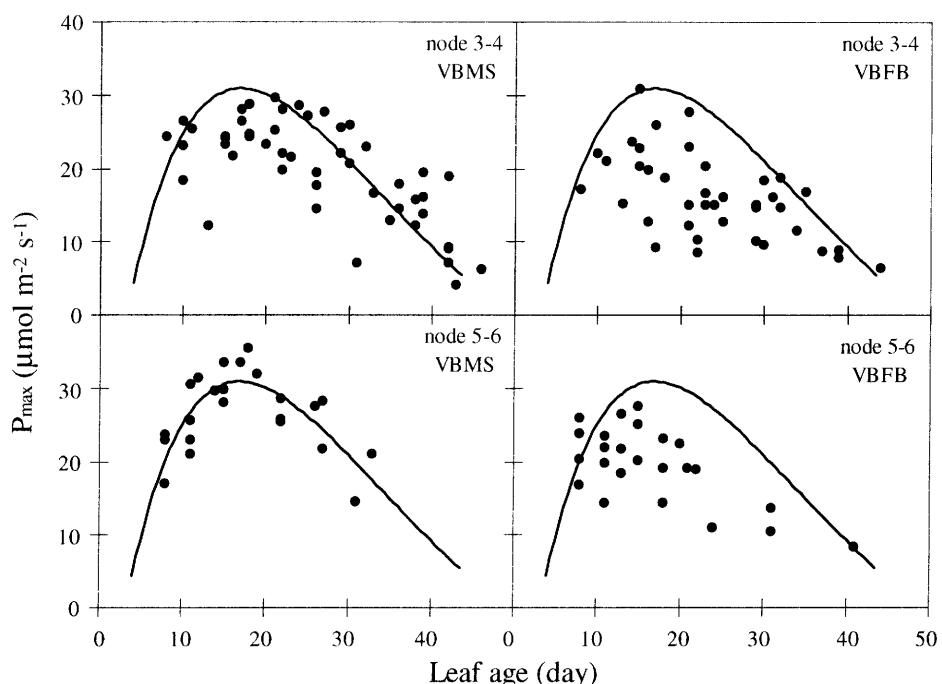


Figure 4 P_{\max} -age relationships of monopodial leaves on nodes 3-4, and 5-6. Leaves were characterized as being either on monopodial branches (VBMS) or on fruiting branches on monopodial branches (VBFB). Line was fitted to P_{\max} data of node 3-4 VBMS leaves and displayed for all leaf groups.

average for main stem leaf at the same leaf age.

P_{max}-nodal position relationship

Relationships between P_{max} and node position of main stem leaves (Figure 5) for different leaf age clearly illustrated the influence of leaf position on P_{max}-age relationship. For 7 day-old leaves, P_{max} was negatively correlated with nodal

position with large variation among leaves from different nodes. That the variation was among the greatest observed for all age could resulted from fast leaf growth and development and high rate of increase in P_{max} during this period. For 14 day-old leaves, P_{max} ranged from 18 to 28 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and P_{max} of leaves on lower nodes tended to be greater than those on higher nodes. Next, for 21 day-old

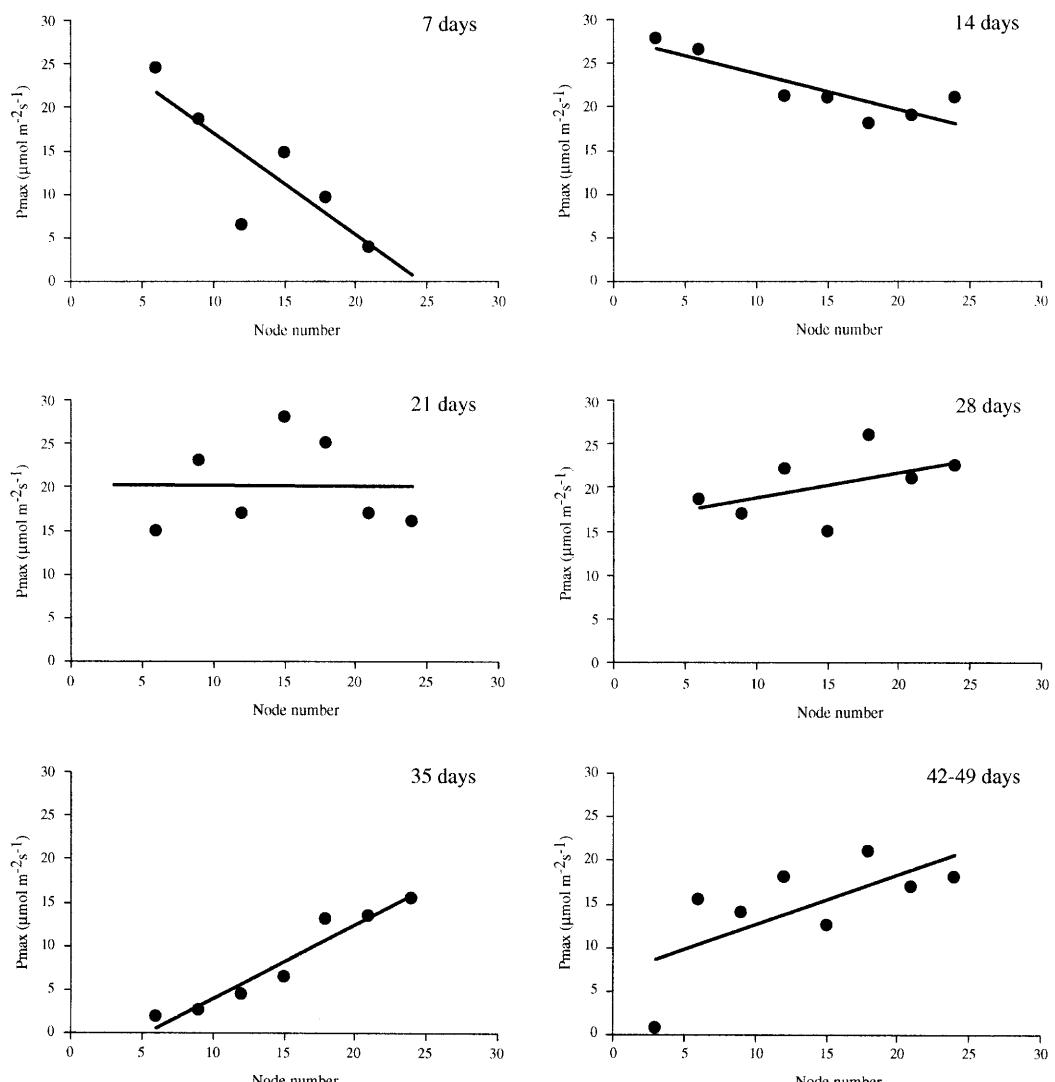


Figure 5 P_{max} - nodal position relationships for main stem leaves at different ages.

leaves, P_{max} averaged approximately $21 \mu\text{mol m}^{-2}\text{s}^{-1}$ with substantial variation.

For 28 day-old leaves, P_{max} ranged from $0 \mu\text{mol m}^{-2}\text{s}^{-1}$ at node 3 to approximately $19 \mu\text{mol m}^{-2}\text{s}^{-1}$ at nodes 18 to 24. For 35 day-old leaves, P_{max} of node 3 was negative as the leaf was nearly shed and P_{max} linearly increased with nodal positions from 6 to 24. For age 42 to 49 day-old, a substantial number of leaves have been shed especially for lower nodes (3 to 15). P_{max} of the remaining leaves on nodes 18 and 21 varied from $2 \mu\text{mol m}^{-2}\text{s}^{-1}$ to $20 \mu\text{mol m}^{-2}\text{s}^{-1}$.

It is worth noting that the data set used to illustrate the P_{max} -nodal position relationship was extracted from photosynthetic light response curve study, which is not presented here. The same relationship between P_{max} and nodal positions of main stem leaves for different leaf age classes was also observed in data set illustrated in Figure 2.

DISCUSSION

P_{max} -age relationship

Relationships between P_{max} -age in this study were similar to the ones from Constable and Rawson (1980) with some exceptions. The similarities included the initial rapid increase of P_{max} before reaching a peak at 12-15 days after leaf unfolding and the linear decline in P_{max} after peaking. Furthermore, main stem leaves from lower nodal positions (nodes 3-10 in this study; nodes 5, 7, and 9 in Constable and Rawson, 1980) appeared to have the same P_{max} -age relationship. In contrary, variations in P_{max} -age relationships were found between main stem leaves from nodes 3-10, 12-15, and 16-25, between leaves on main stem and horizontal sympodial positions on nodes 11-15, and between leaves on monopodial position. Furthermore, longevity of leaves in this study was less than 68 days, which was observed in Constable and Rawson (1980) study. On the other hand,

longevity of leaves on higher nodal positions tended to be greater than for lower nodal positions and this was consistent with Wullschleger and Oosterhuis (1990b) study.

Differences in P_{max} caused by leaf positions and plant ages were clearly demonstrated by the comparison of P_{max} measured on the same day from plots that were sown on different date. Furthermore, the relationships of P_{max} -nodal position (Figure 5) for particular leaf age also implied P_{max} -plant age relationship because leaves on later nodes initiated later when the plant was older. It was evident that, depending on leaf age, P_{max} could be either positively or negatively correlated to plant age (or nodal position). For 35 day-old leaves, P_{max} -plant age had positive correlation while for 7 and 14 day-old leaves P_{max} -plant age had negative correlation. Moreover, for 21 day-old leaves, no correlation was evident. The result was in contrast with Peng and Krieg (1991) study that, in an experiment that followed P_{max} from 65 to 115 DAP, illustrated the decrease of P_{max} for 20 day-old leaves as cotton plant aged.

Synchronization of P_{max} with fruit form development

Several investigators have indicated that photosynthesis rate is seldom synchronized with assimilate utilization by boll growth (Constable and Rawson 1980; Wullschleger and Oosterhuis, 1990b). Subtending leaf photosynthesis rate peaks approximately at anthesis and then decline throughout boll-filling period. Net photosynthesis rate, when measured under unaltered incident irradiance and undisturbed canopy, decreased by 50% during maximum dry-weight accumulation by the boll (Wullschleger and Oosterhuis, 1990a). The results from this experiment also supported the absent of synchronization of P_{max} and boll growth since photosynthesis peaked at approximately anthesis period.

Our suggestion is that reproductive sinks do not entirely regulate changes in photosynthesis rate. Being an indeterminate plant, cotton has a large number of alternative sinks, both vegetative and reproductive, in existence essentially during entire growing season. Present study confirms results by several investigators that P_{max} (expressed on leaf area basis) is positive right after unfolding and increase rapidly as the leaf itself is rapidly expanding. This indicates that the node unit (including stem of branch, buds, petiole, square, and leaf) itself is the important sink. Moreover, development of successive new node unit further along sympodial of monopodial positions, which usually starts only in 5-10 days after present leaf initiation, also requires large amount of assimilate supply. Thus, if there is a sink regulation of photosynthesis rate, there could be several responsible sinks. Finally, the proportion of regulation by alternative sinks may be high in our experimental conditions where fruit abscission was rather high compared to those observed in USA or Australia.

Regulation of P_{max} by available PPF resource

Leaf growth and development are plastic in response to environment (Loomis and Connor, 1992). Photosynthesis is strongly influenced by available environmental resources, especially light and CO_2 (Salisbury and Ross, 1992). Leaf acclimation to changes in the radiation environment has been shown by several researchers in many crops (Loomis and Connor, 1992). Difference in light quantity, such as shading, has been known to cause variations in leaf physiological and morphological characteristics including specific leaf mass (SLM or specific leaf weight, SLW; Loomis and Connor, 1992), chlorophyll content, and photosynthesis rate (Salisbury and Ross, 1992). Moreover, different light quality (FR/R ratio) from soil surface colors has been shown to affect cotton

leaf morphology and photosynthesis rate (Bauer and Kasperbauer, 1994).

In cotton canopy, light environment differs greatly both qualitatively and quantitatively. Sassenrath-Cole (1995) showed that the decrease in PPF at lower portion of canopy was particularly striking as leaves below mid-height in the canopy received very low PPF. In contrast, leaves near the top of the canopy received PPF levels that were near full sun.

The following explanations for variations in P_{max} of leaves on different positions are presented based on the reasoning that leaf photosynthesis acclimates to available PPF resource in canopy during leaf growth and development. Initiating at the top of canopy, main stem leaf, for a long period of time, would not be substantially shaded and, thus, P_{max} increase rapidly during early ontogeny and reach the peak level. P_{max} decreases as the leaf acclimate to the reduction of available PPF. Duration of P_{max} at peaking for leaves at nodes 16-25, which were located at top of canopy and received relatively less shading, tended to be greater than those at low nodal positions.

Furthermore, leaves on sympodial position P1 initiated when there were only a few small leaves above to provide shading. P2 leaves may be partially shaded during early development period. P3 usually initiated later and substantially shaded compared to main stem, P1, and P2 leaves. For example (Figure 3), at node 11, main stem leaf was initiated without any leaf above, P1 leaf had only one main stem leaf on node 12 which was only 5 day-old and P2 initiated below four other leaves, which ranged from 2 to 10 day-old and averaged only 5.6 day, while P3 leaf initiated under the shading of 11 other leaves, which ranged from 3 to 18 day-old. Therefor, P_{max} -age relationships for main stem and P1 leaves were similar while both relationships were substantially different from P3.

VB leaves generally developed under shade

inside the canopy so their P_{max} were less than sun leaves. Very large variation in P_{max} for VB leaves probably resulted from the large variation of PPF resource in the canopy.

Finally, the explanation of influence of positions on P_{max} -age relationships of cotton leaves based on available PPF resource reasoning would imply that after anthesis, subtending leaf is not senescing as suggested by Wullschleger and Oosterhuis (1990) but rather acclimates itself to changing environment.

CONCLUSION

Position influences relationship between P_{max} and age of cotton leaf. Main stem leaf on nodes 3-10 had similar relationships between P_{max} and leaf age. For leaves on higher nodes, P_{max} declined at slower rate than for nodes 3-10. The main difference of P_{max} -age relationships of sympodial and monopodial from main stem leaves seemed to be the proportion of leaves that had P_{max} less than the average for main stem leaf at the same leaf age. At specific leaf age, P_{max} tended to decline with increase sympodial position. In addition, P_{max} of monopodial leaves had very large variation, and were less responsive to leaf age than for main stem leaves. Analysis of P_{max} -node position for specific age revealed that for main stem leaves at lower nodes P_{max} peaked earlier and longevity was shorter than leaves at higher nodes. P_{max} was not synchronized with boll growth as P_{max} of sympodial leaves peaked at approximately anthesis. Differences in P_{max} -age relationships for leaves at various main stem, sympodia, and monopodial position were thought to result from leaf acclimation to limiting available PPF resource. Additional research focused on correlation between P_{max} and PPF resource in cotton canopy is necessary for better understanding of leaf position influence on P_{max} -age relationship.

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LITERATURE CITED

Bauer, P.J. and M.J. Kasperbaure. 1994. Leaf morphology and photosynthesis of cotton seedlings as influenced by spectral balance of light reflected from the soil surface, pp.1339-1340. *In Proc. Beltwide Cotton Prod. Res. Conf.* Natl. Cotton Council, Memphis, TN.

Constable, G.A. and H.M. Rawson. 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency. *Aust. J. Plant Physiol.* 7:89-100.

Constable, G.A. and H.M. Rawson. 1980. Carbon production and utilization in cotton: Inferences from a carbon budget. *Aust. J. Plant Physiol.* 7:539-553.

Cornish, K., J.W. Radin, E.L. Turcotte, Z. Lu, and E. Zeiger. 1991. Enhance photosynthesis and stomatal conductance of pima cotton (*Gossypium barbadense L.*) Bred for increased yield. *Plant Physiol.* 97:484-489.

Ford, D.M., R. Shibles, and D.E. Green. 1983. Growth and yield of soybean lines selected for divergent leaf photosynthetic ability. *Crop Sci.* 23:517-520.

Guinn, G., J.D. Hesketh, J.E. Fry, J.R. Mauney, and J.W. Radin. 1976. Evidence that photosynthesis limits yield of cotton, pp.60-61. *In Proc. Beltwide Cotton Prod. Res. Conf.*, Las Vegas, NV. 5-7 Jan. 1976. Natl. Cotton Council, Memphis, Tennessee.

Irvine, J.E. 1975. Relations of photosynthetic rates

and leaf and canopy characters to sugarcane yield. *Crop Sci.* 15:671-676.

Landivar, J.A., D.N. Baker, and J.N. Jenkins. 1983. Application of Gossym to genetic feasibility studies: II. Analysis of increasing photosynthesis, specific leaf weight and longevity of leaves in cotton. *Crop Sci.* 23:504-510.

Loomis, R.S. and D.J. Connor. 1992. *Cropecology: Productivity and Management in Agricultural systems*. Cambridge University Press. New York. 538 p.

Nelson, C.J., K.H. Asay, and G.L. Horst. 1975. Relationship of leaf photosynthesis to forage yield of tall fescue. *Crop Sci.* 15:476-478.

Peng, S. and D.R. Krieg. 1991. Single leaf and canopy Photosynthesis response to plant age in cotton. *Agron. J.* 83:704-708.

Pettigrew, W.T., J.J. Heitholt, and K.C. Vaughn. 1993. Gas exchange differences and comparative anatomy among cotton leaf-type isolines. *Crop Sci.* 33:1295-1299.

Pettigrew, W.T. and W.R. Meredith, Jr. 1994. Leaf gas exchange parameters vary among cotton genotypes. *Crop Sci.* 34:700-705.

Salisbury, F.B. and C.W. Ross. 1992. *Plant Physiology*. 3rd ed. Wadsworth Publishing Company, California. 540 p.

Sassenrath-Cole, G.F. 1995. Dependence of canopy light distribution on leaf and canopy structure for two cotton (*Gossypium*) species. *Agric. For. Meteorol.* 77:55-72.

SAS Institute Inc. 1987. *SAS User's guide: Statistics*. 1987. ed. SAS Institute, Inc., Cary, NC.

Wullschleger, S.D. and D.M. Oosterhuis. 1990a. Photosynthetic carbon production and use by developing cotton leaves and bolls. *Crop Sci.* 30:1259-1264.

Wullschleger, S.D. and D.M. Oosterhuis. 1990b. Photosynthesis of individual field-grown cotton leaves during ontogeny. *Photosyn. Res.* 23:163-170.