DOI: 10.1007/s11099-016-0223-9 PHOTOSYNTHETICA 55 (2): 301-307, 2017

Evolution characteristics related to photosynthesis, growth and yield in some old and new cotton cultivars

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Abstract

Changes in photosynthetic attributes related to genetic improvement of cotton yield were studied in seven Chinese cotton cultivars widely grown in Xinjiang during the past 30 years. Our results showed that a chlorophyll (Chl) content and net photosynthetic rate (P_N) of the 1980s cultivar was the highest among all after 60 days from planting (DAP). However, after 75 DAP, the Chl content, P_N, and actual photochemical efficiency of PSII of the old cultivars declined gradually, whereas those of the new cultivars remained relatively high. Compared to the old cultivars, leaves of the new cultivars endured a longer period and their senescence was slower, shoot and boll dry mass was higher, but the root to shoot ratio was lower. The lint yield of the 2000s cultivars was 14.7 and 21.4% higher than that of 1990s and 1980s cultivars, respectively. The high yield of the new cultivars was attributed to a greater number of bolls per unit of area with high lint percentage. We suggested that the improved photosynthetic capacity and the increased ability to deliver photosynthates to reproductive sites during the peak boll-setting stage to boll-opening stage were the key physiological basis in the evolution process of cotton cultivars from 1980s to 2000s for the cotton yield improvement within a short growing period.

Additional key words: chlorophyll content; dry matter partitioning; fluorescence quenching; gas exchange.

Introduction

Cotton is widely grown in semiarid and arid zones of the world. Cotton growth and yield are impacted by both plant genetic factors and environmental factors, such as weather conditions, water availability, and soil conditions (Saranga *et al.* 2001, Liu *et al.* 2013). Most of the increases in the cotton yield over the past years could be attributed to genetic improvement (Meredith 2000, Aguado *et al.* 2008). Researchers and producers are concerned that the genetic potential for yield and fiber quality is already exhausted (Mackay *et al.* 2011, Kilby *et al.* 2013). Landivar *et al.* (2010) believed that the improvements in some physiological traits had played an important role in the past yield increases, although they had not been consciously selected for. In future, knowledge of genetic and physiological processes that underlie such an increase could provide avenues for future crop yield improvements (Richards 2006, Lightfoot *et al.* 2013), but these processes are not well understood.

Increase in the yield of cotton cultivars, which has resulted from increased dry matter accumulation during the blooming and boll-setting stage and which has probably occurred due to an increase in the harvest index, has largely stagnated (Bange and Milroy 2004, Du *et al.* 2009). More than 90% of cotton biomass is derived from photosynthetic products. There is substantial evidence that newer cultivars exhibited higher photosynthetic rates than the older ones under environmental stresses (Leidi *et al.* 1999, Meloni *et al.* 2003). It was suggested that increase in cotton yield might be at least partly accounted for by higher photosynthetic rates (Cornish *et al.* 1991, Pettigrew and Meredith 1997, Hu *et al.* 2012). An increase in photosynthesis of modern cultivars should ultimately provide more assimilates for both vegetative and reproductive organs. It is empirically known that under

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Received 17 November 2015, *accepted* 16 March 2016, *published as online-first* 6 April 2016.
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Abbreviations: C_i – intercellular CO_2 concentration; DM – dry mass; g_s – stomatal conductance; F_v/F_m – maximal efficiency photochemistry of PSII; LA – leaf area; P_N – net photosynthetic rate; DAP – days after planting; Φ_{PSII} – actual photochemical efficiency of PSII.
Acknowledgements: This study was financially supported by the Research Fund for the Doctoral Program of The Xinjiang Production and Construction Corps (2014BB009), the National Natural Science Foundation of China (Grant No. 31460325 and U1203283), and the Pairing Program of Shihezi University with Eminent Scholar in Elite University (SDJDZ201510).

optimal environmental conditions, the new cotton cultivars can produce more dry matter because they remain photosynthetically active during flowering to boll-opening stages and the delayed leaf senescence is an improved characteristic in the new cotton cultivars (Richards 2006, Pettigrew and Gerik 2007, Tao *et al.* 2013).

The Xinjiang Uyghur Autonomous Region is located in arid lands, northwest China. The growing period of cotton in northern Xinjiang is usually 40–90 d shorter than that in other parts of China (Wang *et al.* 2004) as well as in USA (Jost and Cothren 2000). It is mainly due to a rapid decrease of air temperature during late August and early September. Hence, the yield of cotton is usually low in old cultivars released before 1990 (Zhu *et al.* 1991). However, recently some cotton cultivars with comparatively high yield ability have been developed for growing in this area and the yield has been much improved (Constable and Bange 2015). Several researchers have elucidated the connection between photosynthesis and yield of cotton grown in other areas of China and in the world (Pettigrew and Gerik 2007, Chen *et al.* 2013). However, no data were available to reveal physiological mechanisms and lead to the differences in photosynthesis between the new and old cotton cultivars in northern Xinjiang with a short growing period. Therefore, the objectives of our research were to: (*1*) characterize changes of photosynthetic traits in cotton cultivars widely grown in northern Xinjiang during the last 30 years in different eras, and (*2*) analyze the physiological mechanisms, which result in differences in photosynthetic traits and yield in newer and older cultivars.

Materials and methods

Experimental site: The experiment was carried out at a research station at Shihezi University, Xinjiang, in northwestern China (45º19′N, 74º56′E) from April to October in 2013. Cotton was grown in polyvinyl chloride (PVC) tubes, 30 cm in diameter and 120 cm in height. The bottom of the tube was covered with a wire mesh fine enough to hold the soil while allowing the water to pass through. Clay loam soil taken from the station field was passed through a 2 mm sieve and packed in the PVC tubes with 0.1 m to 1.2 m increments. Characteristics of the soil were as follows: pH 7.5, bulk density of 1.4 g m^{-3}, field capacity of 24.7%, 12.5 g(organic matter) kg^{-1}, 1.4 g(total N) kg^{-1}, 16.8 mg(available P) kg^{-1}, and 187 mg(available P) kg^{-1}. N was applied as urea at 6 g per pot before planting and 14 g per pot after plant emergence. P was applied as KH_2PO_4 at 28 g per pot before planting. The pot was drip irrigated and maintained well-watered throughout the whole season. Four seeds were sown on 20 April in rows 10 cm apart and 20 cm apart from the other tubes. Then, the top of the pot was covered with a polyethylene film in order to reduce evaporation. Each pot received 4 L of water to promote germination and seedling establishment. All schemes used good-quality water (EC was 0.33 dS m^{-1}) in the drip-irrigation system. Pest and weed control was carried out according to the local standard practice.

Experimental details: The experiment consisted of a randomized complete blocks design. Fourteen tubes for each treatment were buried vertically in the field. Seven early-maturing cotton cultivars were used in this experiment. Xinluzao1 was the most widely grown cultivar during the 1980s after its initial release; Xinluzao6, 7 and 10 were the most widely grown cultivars during the 1990s; Xinluzao13, 24 and 33 were widely grown in Xinjiang of China during the 2000s till now. All cultivars have similar dates of flowering at 62 d after planting, but days to physiological maturity varied among these cultivars. The physiological maturity of the older cultivars was slightly earlier (5–7 d) as compared to the newer ones.

At 60, 75, 90, 105, 120, and 135 days after planting (DAP), the chlorophyll (Chl) content, gas exchange, and Chl fluorescence measurements were taken on the fourth fully expanded leaves on the main stem from the top of plant for each cultivar. After the measurement of photosynthesis at 75 DAP and 135 DAP, the tubes were used for the root and shoot dry mass (DM) studies.

Gas exchange and Chl fluorescence measurements: For each cultivar, four individual leaves from each pot were sampled and labeled. The net photosynthetic rate (P_N), the stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of each leaf were measured with a *LI-6400* photosynthesis system (*LI-COR Inc.*, NE, USA) under light intensity of 1,800 μmol(photon) m^{-2} s^{-1} between 10:00 and 12:00 h. During the measurements, the air relative humidity was about 80%, the leaf temperature ranged from 31–33°C, and the ambient CO_2 concentration was 340 μmol mol^{-1}.

Chl fluorescence was measured using a portable saturation pulse fluorometer *PAM-2100* equipped with a *2030-B* leaf clip holder (*Walz*, Effeltrich, Germany). Maximal (F_m) and ground (F_0) fluorescence yields of dark-adapted leaves were measured at predawn. F_0 was obtained with a measuring light of 0.5 μmol(photon) m^{-2} s^{-1} at a frequency of 0.6 kHz, while the F_m was measured with a 0.8 s saturating pulse at >8,000 μmol(photon) m^{-2} s^{-1}. The maximum photochemical efficiency of PSII (F_v/F_m) was calculated, where F_v is the variable fluorescence ($F_v = F_m - F_0$). During the diurnal time courses, F_s (fluorescence of the light-adapted leaf) and F_m' (the maximum light-adapted fluorescence) were measured. F_s was obtained by setting the measuring light to a frequency of 20 kHz; F_m' was measured with a 0.8-s saturating pulse at >8,000 μmol(photon) m^{-2} s^{-1}. Actual photochemical efficiency of PSII (Φ_{PSII}) was calculated as $(F_m' - F_s)/F_m'$ (Genty *et al.* 1989).

Chl content: After the measurement of gas exchange and Chl fluorescence, Chl contents of leaves was determined in discs from four leaves removed by a calibrated metallic borer (4 mm in diameter). Discs of leaves were extracted in 80% (v/v) acetone for 24 h at room temperature in the dark. The absorbance of extracts was measured with a spectrophotometer (*UV-2401*, *Shimadzu Corporation*, Japan), and the Chl content was calculated according to Lichtenthaler (1987).

Leaf area, dry matter and yield: Three tubes from each cultivar were dug from the ground, laid down horizontally on the soil surface, and opened at each sampling date. Roots were separated from soil and other residues by gentle washing under a flow of swirling water. The aboveground biomass was cut off at ground level and then separated into leaves, stems, branches, flowers, and bolls. Leaf area (LA) was measured with a *LI-3100* leaf area meter (*LI-COR Inc.*, NE, USA). Samples were oven-dried at 80 °C until a constant mass was obtained. Seed cotton was harvested by hand and weighed. The number of bolls harvested from each plant was counted and the mean boll mass was taken. Seed cotton was ginned and lint percentage was determined.

Statistical analysis: Analysis of variance (*ANOVA*) was performed with *SPSS version 11.5* software. Differences between treatments were considered significant at $P<0.05$ according to least significant difference (*LSD*) tests. The figures were plotted using *SigmaPlot version 10.0* software. The data are presented as the mean ± standard error (SE).

Results

Chl content: The Chl content increased sharply from the first blooming stage (60 DAP) and peaked at a peak of the blooming stage (75 DAP) (Fig. 1). After reaching the peak, the Chl content sharply declined. The Chl content of the 1980s cultivars (Xinluzao1) was the highest among all cultivars before 60 DAP. After 75 DAP, the Chl content showed generally similar patterns of a decline in the 1980s and 1990s cultivars (the average values of Xinluzao6, Xinluzao7, and Xinluzao10); however, the Chl content of the 2000s cultivars (the average values of Xinluzao13, Xinluzao24, and Xinluzao33) was the greatest at a given time after planting.

Gas exchange: P_N values of the 1980s cultivars were higher than that of all other cultivars at 60 DAP (Fig. 2*A*). The parameter showed generally similar patterns of a decline in the 1980s and 1990s cultivars as Chl content did. P_N of the 2000s cultivars, however, decreased slowly from 75 DAP until 105 TAP, after which the parameter decreased more rapidly, but still remained higher than that in the 1980s and 1990s cultivars.

The g_s showed a decreasing trend along with a developmental stage in different cultivars (Fig. 2*B*). g_s of the 1980s cultivars were the highest among all cultivars during the first blooming stage to peak boll-setting stage (120 DAP). However, after 120 DAP, this parameter did not show any significant difference. C_i rose sharply from 60 DAP (Fig. 2*C*). The parameter showed generally similar patterns of an increase in the 1980s and 1990s cultivars. C_i of the 2000s cultivars was the lowest among all cultivars.

Chl fluorescence: The F_v/F_m of all cultivars remained at a value of 0.85 until 60 DAP and then slowly decreased (Fig. 3*A*). There was no significant difference in the F_v/F_m between all cultivars. The Φ_{PSII} showed a decreasing trend along with the process of growth in different cultivars (Fig. 3*B*). No difference was found in Φ_{PSII} between all cotton cultivars at 60 DAP (Fig. 3*B*). Φ_{PSII} of the 2000s cultivars declined from 75 DAP similarly as the Chl content, but with a relatively lower rate. Φ_{PSII} of the 2000s cultivars were the highest among all cultivars after 90 DAP.

Dry matter production: A high value of LA was recorded for 1980s and 1990s cultivars at 75 DAP, but the LA later declined by 180 and 76.5%, respectively, whereas that of the 2000s cultivars only declined by 35.8% (Table 1). The 2000s cultivars produced higher shoot DM and root DM at 75 and 135 DAP, although there was no significant difference between the 1990s and 2000s cultivars.

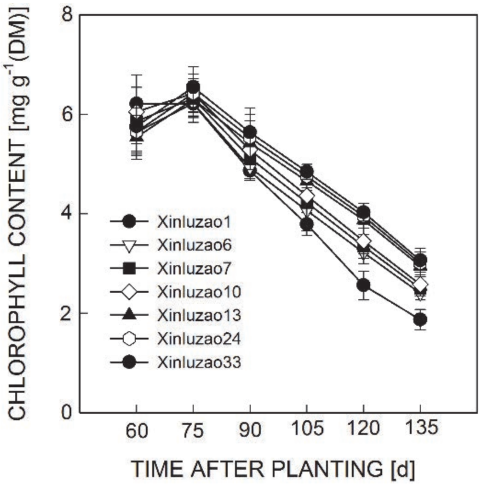

Fig. 1. Chlorophyll content in leaves of cotton cultivars released in different years with time after planting. Data represent the mean ± SE ($n = 4$).

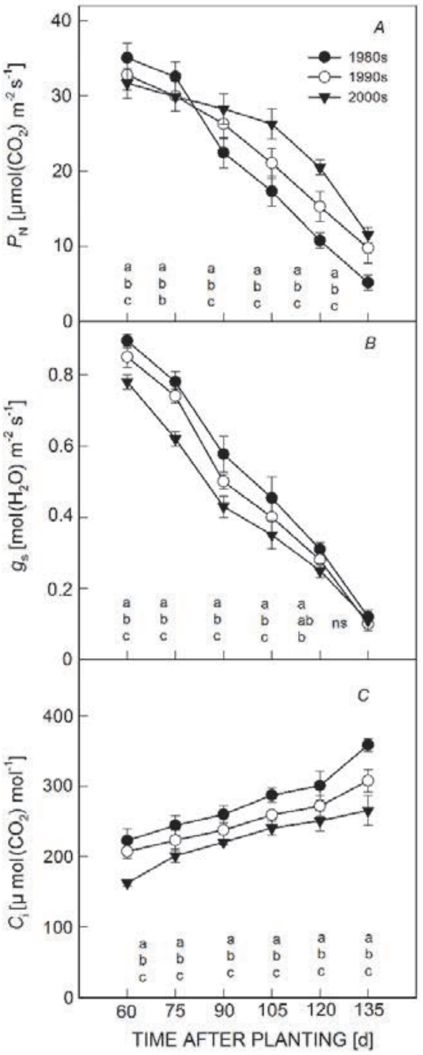

Fig. 2. (*A*) Net photosynthetic rate (P_N), (*B*) stomatal conductance (g_s), and (*C*) intercellular CO$_2$ concentration (C_i) in leaves of cotton cultivars released in different years with time after planting. Data represent the mean ± SE (*n* = 4, 12, and 12 in 1980s, 1990s, and 2000s, respectively). *Different lowercase letters* indicate significant ($P<0.05$) differences between the treatments. NS – no significant difference.

The boll mass of 1980s cultivars was the highest among all cultivars at 75 DAP, but at 135 DAP, boll mass of the 2000s cultivars became the highest among all cultivars. The root:shoot ratio showed a decreasing trend during the process of growth. There was significant difference in the root:shoot ratio between all cultivars. The root:shoot ratio of the 2000s cultivars was 21 and 12% lower than those of the 1990s and 1980s cultivars, respectively.

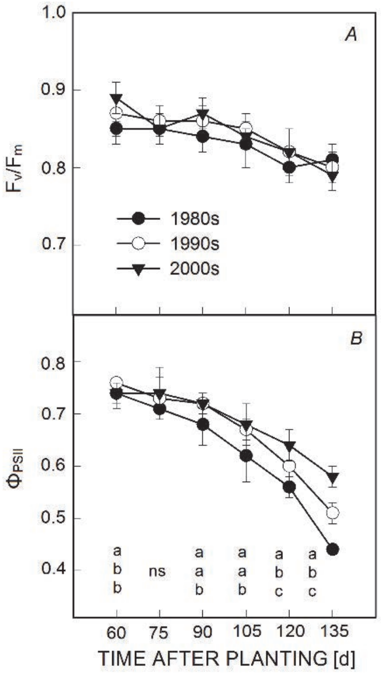

Fig. 3. (*A*) Maximal efficiency of PSII photochemistry (F_v/F_m) and (*B*) actual photochemical efficiency (Φ_{PSII}) in leaves of cotton cultivars released in different years with time after planting. Data represent the mean ± SE (*n* = 4, 12, and 12 in 1980s, 1990s, and 2000s, respectively). *Different lowercase letters* indicate significant ($P<0.05$) differences between the treatments. NS – no significant difference.

Table 1. Leaf area, dry mass, and root:shoot ratio of cotton cultivars released in different years with days after planting. Data represent the mean ± SE (*n* = 3, 9, and 9 in 1980s, 1990s, and 2000s, respectively). Means with *the same letter* for each column are not significantly different (*LSD* test; $P<0.05$).

Time after planting [d]	Cultivars	Leaf area [cm^2 per plant]	Shoot dry mass [g per plant]	Boll dry mass [g per plant]	Root dry mass [g per plant]	Root:shoot
75	1980s	1,880^{a} ± 85	41.5^{c} ± 2.8	18.6^{a} ± 0.9	11.5^{b} ± 0.7	0.28^{a}
	1990s	1,500^{b} ± 75	49.9^{b} ± 3.6	15.1^{b} ± 0.8	12.1^{ab} ± 0.6	0.25^{b}
	2000s	1,330^{c} ± 68	58.0^{a} ± 3.2	13.4^{c} ± 1.1	13.1^{a} ± 0.7	0.22^{c}
135	1980s	670^{b} ± 50	94.5^{c} ± 8.7	42.3^{c} ± 2.1	17.5^{c} ± 0.8	0.19^{a}
	1990s	850^{ab} ± 46	110.0^{b} ± 9.2	50.4^{b} ± 3.2	18.7^{b} ± 0.9	0.17^{b}
	2000s	980^{a} ± 20	131.8^{a} ± 10.1	61.1^{a} ± 2.9	19.8^{a} ± 0.7	0.15^{c}

Table 2. Yield and yield components of cotton cultivars released in different years. Data represent the mean ± SE (n = 3, 9, and 9 in 1980s, 1990s, and 2000s, respectively). Means with *the same letter* for each column are not significantly different (*LSD* test; $P<0.05$).

Cultivars	Seed yield [kg m^{-2}]	Lint yield [kg m^{-2}]	Lint percentage [%]	Boll number [per plant]	Boll mass [g]
1980s	$387^c \pm 16$	$154^c \pm 11$	$39.7^c \pm 0.7$	$4.7^c \pm 0.2$	$4.8^a \pm 0.2$
1990s	$413^b \pm 21$	$170^b \pm 14$	$41.1^b \pm 1.1$	$5.3^b \pm 0.3$	$4.6^a \pm 0.3$
2000s	$454^a \pm 17$	$196^a \pm 12$	$43.2^a \pm 0.8$	$7.0^a \pm 0.4$	$4.4^a \pm 0.3$

Yield and yield components: The seed yield and lint yield of the 2000s cultivars were 9.2 and 14.7% and 13.2 and 21.4% higher than those of 1990s and 1980s cultivars, respectively (Table 2). The number of bolls and lint percentage were significantly greater than those in the old cultivars, probably due to yield variance among different cultivars. In terms of yield components, no difference was found in boll mass per plant between all cotton cultivars.

Discussion

The process of photosynthesis is pivotal to the production of food and fiber as it provides raw materials for all plant products. Therefore, high photosynthetic activity during the growing stage has always been considered a desirable characteristic. Photosynthetic area, rate, and duration during the bloom and boll-setting stage of cotton are important factors that determine dry matter accumulation in cotton (Du *et al.* 2009, Landivar *et al.* 2010). During crop breeding improvement, physiologists focused on improving crop photosynthesis (Furbank *et al.* 2015).

Our results revealed that P_N of the new cultivars was not always higher than that of the old ones. At 60 DAP, P_N of the 1980s cultivars was the highest among all cotton cultivars (Fig. 2*A*), which was associated with their highest Chl content. After 75 DAP, P_N of the old cultivars declined gradually whereas the new cultivars remained relatively constant. A decrease in photosynthetic capacity is the most striking event during leaf senescence (Liu *et al.* 2015). A prominent feature of the senescence process is the dismantling and the remobilization of chloroplasts (Crafts-Brandner *et al.* 1990). Čatský and Šesták (1997) reported that the decrease in photosynthesis in senescing leaves is always associated with the decrease in Chl contents and enzyme activities. Here in our study, the Chl content of the old cultivars decreased more rapidly than that of the new cultivars (Fig. 1). It indicated their higher senescence rate. The reduction in P_N of the old cultivars after 75 DAP was associated with a decrease in the Chl content.

Stomatal and nonstomatal factors, particularly g_s, mainly influence P_N (Pettigrew and Gerik 2007). In the present study, g_s of different cotton cultivars gradually decreased at different stages (Fig. 2*B*), whereas the values of C_i continuously increased (Fig. 2*C*). The increasing rates of C_i of the old cultivars were higher than that of new cultivars. Hence, P_N reduction and differences in cotton cultivars at different growth stages were not due to decrease in g_s. This finding might be related to different energy capture capacities and photochemical efficiencies of cotton cultivars at different growth stages (Pascal *et al.* 2005).

Previous research on changes in chloroplast electron transport during foliar ontogeny and senescence have shown that rates of chloroplast electron transport in isolated thylakoids, expressed on a Chl basis, generally follow similar patterns of rise and decline as photosynthesis in the whole leaves (Jenkins and Woolhouse 1981, Ding *et al.* 2005). The efficiency and stability of PSII have been widely monitored through the measurement of F_v/F_m in dark-adapted leaves (Maxwell and Johnson 2000). For monitoring the efficiency of photochemical processes in PSII in light-adapted state, Φ_{PSII} is usually used (Maxwell and Johnson 2000). The results in the present study showed that the F_v/F_m of all cotton cultivars remained relatively constant at different growth stages (Fig. 3*A*) and it was always maintained at 0.8 or greater. It indicates that there was no difference in efficiency and stability of PSII between cultivars bred in different years. However, a downregulation of Φ_{PSII} of the old cultivars was observed from 75 DAP (Fig. 3*B*), which might be a regulatory mechanism how to lower CO_2 assimilation capacity in order to avoid photodamage to the photosynthetic apparatus under excess light conditions (Demmig-Adams and Adams 1992). At the same time, the photochemical efficiency of the new cultivars, however, remained constant after 90 DAP.

The dynamics of photosynthate production and reproductive demand may also have significant impact on the yield of different genotypes (Bange and Milroy 2004). The shoot and root DM of the 2000s cultivars was the highest among all cultivars at 75 and 135 DAP (Table 1). Yang *et al* (2001) reported that from an evolutionary point the yield potential of soybeans increased with increases in root DM. However, the root:shoot ratio of the 1980s and 1990s cultivars were higher than that of the 2000s cultivars, but boll mass in the 2000s cultivars were the highest among all cultivars at 135 DAP. Furthermore, the LA of 2000s cultivars decreased at a slower rate than that of 1980s and 1990s cultivars, thereby maintaining a longer functional period. It indicated that photosynthetic capacity was synchronously improved with the photosynthetic area of leaves during evolutionary succession of early-maturing cotton cultivars, which gave priority to an increase of the available photosynthates to aboveground reproductive organs.

Wells and Meredith (1984) reported that modern cultivars had a small boll size and higher lint percentage (above 35%) than the cultivars used in the past. The mean boll mass obtained in this study was much lower than that in California and in other similar areas of China (Wang *et al.* 2004). The cultivars used in this study have been released in the recent past and seem to have been bred for the small boll size and high lint percentage similar to those in the other countries (Meredith and Wells 1989, Bassett and Kebby 1996). The seed yield and lint yield of the 2000 cultivars followed the similar patterns of increase as the number of bolls (Table 2), suggesting that the high yield in this experiment occurred due to the large number of bolls with high lint percentage in spite of the small boll size.

Conclusion: The 2000s cultivars could increase photosynthetic rate and photosynthetic area of leaves after peak blooming stage in comparison with 1980s and 1990s cultivars. The values of chlorophyll content and Φ_{PSII} were also improved. The new cultivars also gave priority to an increase the availability of photosynthates to aboveground reproductive organs. The new cotton cultivars produced the higher lint yield compared to the old ones which was due to the greater number of bolls with high lint percentage. In summary, the synchronous improvement of photosynthetic capacity and increasing the photosynthate distribution to reproductive organs of leaves during evolutionary succession of early-maturing cotton varieties were the main reason for continuous increase in the cotton yield.

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