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Genetic changes in plant growth and their associations with chromosomes from *Gossypium barbadense* L. in *G. hirsutum* L

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Abstract Cotton (*Gossypium* spp.) plant growth is an important time-specific agronomic character that supports the development of squares, flowers, boll retention, and yield. With the use of a mixed linear model approach, we investigated 14 cotton chromosome substitution (CS-B) lines and their chromosome-specific F_2 hybrids for genetic changes in plant growth that was measured during the primary flowering time under two environments. The changes in additive and dominance variances for plant height and number of mainstem nodes are reported, showing that additive effects for these two traits were a key genetic component after initial flowering occurred in the field. Time-specific genetic variance components were also detected where phenotypic values observed at time t were conditioned on the events occurring at time $t - 1$, demonstrating new genetic variations arising at several time intervals during plant growth. Results also revealed that plant height and number of nodes shared some common influence due to additive effects during plant development. With the comparative analyzes, chromosomes associated with the genetic changes in plant growth were detected. Therefore, these results should add new understanding of the genetics underlying these time-specific traits.

Keywords Cotton · Plant height · Developmental genetics · Chromosome substitution line · Chromosome association

Abbreviations

CS-B	Chromosome or chromosome arm substituted from *Gossypium barbadense* into *G. hirsutum*
AD	Additive-dominance genetic model

Introduction

Cotton (*Gossypium* spp.) is one of the most important long-season cultivated crops in the world. Cotton yield is determined by number of mature bolls that are developed from squares and flowers during the growing season. The flowering period that contributes most to the final yield production generally covers the first four to six weeks of flowering in most of the Southern USA cotton growing areas (Heitholt and Meredith 1998; Biles and Cothren 2001; Bednarz and Nichols 2005). Thus, as a foundation for reproduction, appropriate plant development, and growth during this flowering period should have an important impact on flowering rate and boll retention and ultimately on cotton yield. Therefore, it is important to investigate genetic behavior of plant growth in upland cotton (*G. hirsutum* L.). The results from such an investigation should add to new understanding of plant growth during the primary flowering period and provide information on how to make yield improvement and field management decisions.

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It is well-known that many developmental traits are quantitative traits, which are usually affected by many genetic and environmental factors and their interactions. A series of developmental quantitative genetic models have been proposed to deal with complex morphological traits. According to the theory of developmental genetics, genes are expressed selectively at different growth stages. Genetic changes in developmental traits are the results of the actions and interactions of developmental genes with other genes that act differentially during growth and interaction with the growth environment (Atchley 1984, 1987; Atchley and Hall 1991; Cowley and Atchley 1992; Atchley et al. 1994). Therefore, detecting genetic changes in time-specific traits during a growing season is important. Many reports have demonstrated that gene expressions are time-dependent at various developmental stages. They included flowering and fruiting rates in cotton (Zhu 1995; Chen et al. 1999, 2000; Ye and Zhu 2001a, b, c; McCarty et al. 2006), plant growth in tomato (Peat and Whittington 1965) and in maize (Wu 1987), plant height and tiller number in rice (Xu and Shen 1991; Yan et al. 1998a, b), and body weight and tail length in mice (Atchley and Zhu 1997). One of the complications of many approaches for developmental traits is that it is often difficult to elucidate time-specific genetic effects. The conditional model (Zhu 1995; Wu et al. 2006b) is a new procedure that offers a way to detect new expressions of genetic effects which are independent of the influence of cumulative genetic effects from previous time periods. New genetic variations can be detected by the conditional models before cumulative genetic variations are normally detected by the traditional (unconditional) models for some developmental characters (Zhu 1995; Yan et al. 1998a, b).

Many of the above genetic studies were whole-genome based, revealing genetic changes accumulated from all genetic effects. Chromosome substitution (CS) lines have been extensively used to associate genetic effects with specific chromosomes in wheat (Zemetra et al. 1986; Al-Quadhy et al. 1988; Zemetra and Morris 1988; Berke et al. 1992; Korzun et al. 1997), cotton (Kohel et al. 1970; Ma and Kohel 1983; Ren et al. 2002; Saha et al. 2004, 2006; Jenkins et al. 2006; McCarty et al. 2006; Wu et al. 2006a), rice (Kubo et al. 1999, 2002; Wan et al. 2004, 2005; Wang et al. 2006), and mice (Nadeau et al. 2000; Singer et al. 2004). However, there are no reports available regarding genetic analysis of time-specific traits in cotton and their genetic associations with chromosomes. With the cotton CS-B lines, it is feasible to examine which chromosomes are associated with plant growth in a developmental fashion.

In this paper, plant height and number of mainstem nodes at different times after initial flowering were measured for 14 cotton chromosome substitution lines (CS-B), TM-1 (recurrent parent), line 3–79 (donor parent), and their F_2 hybrids with TM-1. The AD genetic models were applied to explore the genetic behavior of cotton plant growth during the primary flowering period that covers early July to the middle of August in 2002 and 2003 at Mississippi State, MS. The main purpose of this study was to identify the genetic changes in plant growth and their associations with chromosomes with the use of the MINQUE approach and the conditional model. The results should provide an insight into plant growth related to particular chromosomes in the TM-1 genetic background.

Materials and methods

Materials and experiments

Fourteen near-isogenic BC_5S_2 chromosome substitution lines containing different pairs of 3–79 (*G. barbadense* L.) chromosomes or segments, namely, CS-B lines, were used as male parents and crossed to the recurrent parent, TM-1 (*G. hirsutum*) to develop chromosome-specific F_2 hybrids. These CS-B lines are listed with a number specific to the introgressed chromosome or chromosome arm of the alien species as follows: CS-B02, CS-B04, CS-B06, CS-B07, CS-B16, CS-B17, CS-B18, CSB-25, CS-B5sh (sh = short arm), CS-B14sh, CS-B15sh, CS-B22sh, CS-B22Lo (Lo = long arm), and CS-B26Lo (Stelly et al. 2005). TM-1 is an inbred line derived from the commercial cultivar Deltapine-14 (Kohel et al. 1970). These crosses were made at Mississippi State in the summer of 2000. F_1 plants were grown at a winter nursery in Tecoman, Mexico to produce F_2 hybrid seeds.

The 14 chromosome-specific F_2 hybrids, the F_2 hybrid between TM-1 and 3–79, all CS-B lines except CS-B26Lo (due to seed shortage), TM-1, and 3–79 were grown in field plots at Mississippi State University with a randomized complete block design in 2002 and 2003 each with four replications. Plant dates were 12 May and 28 May for 2002 and 2003, respectively. Standard cultural practises were followed in the growing season both years (treated as environments). Plant height (PH) and number of mainstem nodes (ND) were measured weekly for 6 times following initial flowering which occurred approximately 6 weeks to 2 months after field planting. The beginning date for measurements in 2002 and 2003 was 2 July and 8 July, respectively. Ten and five normally growing plants were chosen at random in each plot and measured for plant height and number of nodes in 2002 and 2003, respectively. Mean values from each plot were used for our data analysis.

Genetic model and statistical methods

An additive-dominance (AD) with G × E interaction genetic model was used for data analysis (Zhu 1994;

Wu et al. 1995; Tang et al. 1996; Jenkins et al. 2006; Saha et al. 2006). The phenotypic mean measured at time t for parent i at environment h can be expressed as follows,

$$y_{hiik(P)(t)} = \mu_{(t)} + E_{h(t)} + 2A_{i(t)} + D_{ii(t)} + 2AE_{hi(t)} + DE_{hii(t)} + B_{k(h)(t)} + e_{hiik(t)}. \quad (1)$$

The genetic model for a F_2 hybrid at time t between parents i and j at environment h is expressed as follows,

$$\begin{aligned} y_{hijk}(F_2)(t) = {} & \mu_{(t)} + E_{h(t)} + (A_{i(t)} + A_{j(t)}) \\ & + (0.25D_{ii(t)} + 0.25D_{jj(t)} + 0.5D_{ij(t)}) \\ & + (AE_{hi(t)} + AE_{hj(t)}) + (0.25DE_{hii(t)} \\ & + 0.25DE_{hjj(t)} + 0.5DE_{hij(t)}) \\ & + B_{k(h)(t)} + e_{hijk(t)} \end{aligned} \quad (2)$$

where $\mu_{(t)}$ = population mean at time t, $E_{h(t)}$ = environmental effect at time t, $A_{i(t)}$ or $A_{j(t)}$ is an individual additive effect at time t, $D_{ii(t)}$, $D_{jj(t)}$, or $D_{ij(t)}$ is an individual dominance effect at time t, $AE_{hi(t)}$ or $AE_{hj(t)}$ is an individual additive-by-environment interaction effect at time t, $DE_{hii(t)}$, $DE_{hjj(t)}$, or $DE_{hij(t)}$ is an individual dominance-by-environment interaction effect at time t, $B_{k(h)(t)}$ is an individual block effect at time t, and $e_{hijk(t)}$ is an individual residual at time t.

Both unconditional and conditional genetic effects and variance components including additive, dominance, additive × environment, dominance × environment, and residual were analyzed by a mixed linear model approach (Zhu 1993, 1995; Wu et al. 2006b). The genetic effects at time t conditional on the genetic effects at time $(t-1)$ will imply the new effects of genes that are independent to the genetic effects at time $(t-1)$. The changes of conditional genetic variation can be used to measure the epigenetic effects of the genetic components on the dynamic variability of developmental behaviors (Atchley and Zhu 1997). Resampling (the jackknifing) method was applied to calculate the standard error (SE) for each parameter by removal of each block within each environment (Miller 1974). There were 4 replicates in each of 2 years thus the degrees of freedom were 7. An approximate t-test was used to detect the significance of each parameter and 95% confidence intervals were used to test the significant differences between parameters. All data analyzes were conducted using self-written programs in C^{++} (Wu et al. 2003, 2006b).

Results

Phenotypic means for two traits at 6 weeks

On average, mean plant height increased from 36 to 102 cm from measurement day 1 to measurement day 36 after initial flowering (Table 1). The mean number of nodes showed an increase from 9.9 to 17.6 during this time period. There were greater changes in plant height in the first two time periods (15 cm from day 1 to day 8 and 18 cm from day 8 to day 15, respectively) and tended to be smaller at later time intervals (8 cm from day 29 to day 36). This was probably due to flowering and boll load from the early stage having an impact on plant growth as estimated by number of mainstem nodes during this flowering period.

Variance components

The variance components for two plant traits at the six times after initial flowering were estimated and are presented in Table 2.

Number of nodes

Significant additive variance for number of nodes was detected at the six data collection times after initial flowering (Table 2), indicating that additive effects were an important genetic contributor to this trait. The additive variance for number of nodes at the first three data collection times was similar (0.19, 0.17, and 0.19) but it peaked at day 22 (0.39) and remained above 0.20 at day 29 and day 36. Significant dominance variance for number of nodes was detected at days 8 and 15. Significant additive × environment variance was detected for day 1 and 15. Dominance × environment variance was detected at all six times except at day 15. Residual effects made large contributions to the phenotypic variance in number of nodes at all six dates.

Plant height

Both additive variance and additive × environment variance for plant height were significantly detected at all six collection times after initial flowering occurred in the field (Table 2). The additive variance at the first three dates (day 1, 8, and 15) was small and reached a higher value at day

Table 1 Mean plant height (PH) and number of nodes (ND) with their standard errors at six different developmental stages after initial flowering over two years

	Day 1	Day 8	Day 15	Day 22	Day 29	Day 36
ND	9.90 ± 0.09	11.62 ± 0.08	13.63 ± 0.10	14.51 ± 0.11	17.00 ± 0.12	17.58 ± 0.12
PH (cm)	35.94 ± 0.62	51.39 ± 0.79	68.67 ± 0.90	82.17 ± 1.07	93.63 ± 0.99	102.20 ± 1.05

Table 2 Variance components (SE) for number of nodes and plant height at different growing stages

	Day 1	Day 8	Day 15	Day 22	Day 29	Day 36
Number of nodes						
V_A	0.189 ± 0.022	0.173 ± 0.023	0.191 ± 0.029	0.389 ± 0.031	0.218 ± 0.028	0.277 ± 0.047
V_D	0.000 ± 0.000	0.139 ± 0.045	0.152 ± 0.059	0.000 ± 0.000	0.019 ± 0.016	0.087 ± 0.054
V_{AE}	0.031 ± 0.014	0.000 ± 0.000	0.282 ± 0.045	0.048 ± 0.024	0.024 ± 0.017	0.051 ± 0.045
V_{DE}	0.157 ± 0.058	0.864 ± 0.096	0.006 ± 0.006	0.162 ± 0.078	0.439 ± 0.149	0.529 ± 0.176
V_e	0.856 ± 0.035	1.181 ± 0.055	1.159 ± 0.047	1.252 ± 0.047	1.262 ± 0.061	1.724 ± 0.049
Plant height						
V_A	6.88 ± 1.24	10.26 ± 2.00	6.97 ± 2.44	21.31 ± 2.98	26.47 ± 2.56	25.49 ± 3.45
V_D	0.78 ± 0.66	3.09 ± 1.40	20.88 ± 6.50	6.88 ± 2.64	2.31 ± 1.76	8.01 ± 4.18
V_{AE}	7.42 ± 1.72	7.99 ± 2.31	19.65 ± 3.70	8.89 ± 2.48	7.30 ± 1.73	12.91 ± 3.81
V_{DE}	2.92 ± 2.92	5.40 ± 3.95	2.99 ± 2.38	3.12 ± 3.12	1.76 ± 1.26	14.23 ± 7.28
V_e	56.98 ± 3.17	86.84 ± 5.05	86.61 ± 4.00	88.08 ± 2.70	85.08 ± 2.88	86.97 ± 2.38

22 and thereafter remained stable. The additive × environment variance peaked at day 15 and then decreased at days 22 and 29. Significant dominance variance was detected for plant height at day 8, 15, and 22 and peaked at day 15. No significant dominance × environment variance was detected at any time after initial flowering. As with number of nodes, residual effects made large contributions to the phenotypic variance (Table 2).

In summary, the patterns of additive and dominance variances including their G × E components for these two traits differed, suggesting the patterns of gene expressions for these traits were different during this flowering period. The additive variances for these traits were significant at all six data collection times after initial flowering. In addition, with a few exceptions, it appeared that additive effects played a more important role than dominance effects during this flowering period. Residual effects accounted for a large contribution to the phenotypic variances at all six times, ranging from 50 to 80%, indicating these cotton plant height traits are affected by many uncontrolled and/or unpredictable environmental factors.

Conditional variance components

The classic AD genetic model measures the cumulative genetic effects at each of six developmental stages for these two time-specific traits. The variance components described in the previous section were also analyzed by the conditional approach (Zhu 1995; Wu et al. 2006b) with the same AD genetic model (McCarty et al. 2006; Saha et al. 2006) where the phenotypic values at time t were conditioned by the events at time $t - 1$ (i.e. day 8/day 1). Such results would provide a perspective on genetic variability of the ontogenetic component to quantitative genetic variability and insight into temporal patterns of gene expression. Table 3 gives the conditional variance components for number of mainstem nodes and plant height where the genetic effects are conditioned on gene expression of the traits one week before.

Number of nodes

No conditional additive variance was detected at day 8 conditional on day 1 (simplified as at day 8 and this principle applied throughout this paper). It was detected at day 15, peaked at day 22, followed by a decline at day 29 with an increase at day 36 (Table 3). The results suggested new effects of gene expression occurred following day 8 that gave rise to new additive variance. Conditional dominance variance peaked at day 8 and sharply decreased to be insignificant after day 8, indicating that the new dominance effects were only expressed between day 1 and day 8. Significant conditional additive × environment variance was detected at day 15 and day 29. Significant conditional dominance × environment variance was detected at day 8, day 22, and day 36 (Table 3).

Plant height

Significant conditional additive variance for plant height was detected at days 15, 22, and 36 and the value peaked at day 22, indicating new additive effects occurring in these three time intervals (Table 3). Significant conditional dominance variance was detected at days 8, 15, 29, and 36, implying that strong new dominance effects were expressed between day 8 to day 15, and between day 29 to day 36. Conditional additive × environment variance was detected at day 8 and peaked at day 29. No significant conditional dominance × environment variance was detected at any developmental stages.

The above results showed that not only the patterns of different conditional variance components were different

Table 3 Conditional variance components for two time-specific traits at different growing stages

	Day 8/Day 1	Day 15/Day 8	Day 22/Day 15	Day 29/Day 22	Day 36/Day 29
Number of nodes					
V_A	0.000 ± 0.000	0.043 ± 0.017	0.179 ± 0.021	0.071 ± 0.024	0.156 ± 0.034
V_D	0.219 ± 0.055	0.061 ± 0.045	0.000 ± 0.000	0.025 ± 0.014	0.026 ± 0.024
V_{AE}	0.000 ± 0.000	0.236 ± 0.041	0.000 ± 0.000	0.055 ± 0.020	0.030 ± 0.030
V_{DE}	0.474 ± 0.082	0.024 ± 0.024	0.461 ± 0.090	0.213 ± 0.121	0.215 ± 0.084
V_e	0.971 ± 0.031	1.059 ± 0.037	0.919 ± 0.024	1.262 ± 0.067	1.653 ± 0.031
Plant height					
V_A	0.19 ± 0.13	1.93 ± 0.76	3.15 ± 0.72	0.38 ± 0.30	2.57 ± 0.98
V_D	4.70 ± 0.73	5.67 ± 1.76	0.45 ± 0.30	2.76 ± 1.21	5.48 ± 2.30
V_{AE}	4.29 ± 0.56	1.91 ± 0.59	4.52 ± 1.11	9.90 ± 0.89	3.93 ± 1.57
V_{DE}	0.00 ± 0.00	0.00 ± 0.00	0.28 ± 0.28	0.00 ± 0.00	0.26 ± 0.26
V_e	19.84 ± 0.62	26.34 ± 0.45	40.25 ± 0.78	42.70 ± 1.24	49.68 ± 0.86

for each time-specific trait, but also the patterns of a conditional variance component varied greatly among different developmental traits.

Dynamics of additive effects for two plant height traits

The individual genetic effects contributed to the genetic variance components are predictable since these genetic effects were treated as random. Examining these individual genetic effects may facilitate an understanding of the ontogenetic behavior of the genetic components in the various genotypes (inbred lines) and clarify whether the expression of new genes as suggested above occurs in all inbred lines. With a few exceptions, it appeared that the additive effects were more important than the other genetic effects for the two traits at different developmental stages after initial flowering. Due to many results generated by in this study, we only report specific results in Figs. 1 and 2 for unconditional and conditional additive effects, respectively. The results in Figs. 1 and 2 clearly reveal that the patterns of individual unconditional additive effects and those of individual conditional additive effects varied greatly among substituted chromosomes or chromosome arms.

Number of nodes

CS-B16 and CS-B14sh had significant negative additive effects for number of nodes for all six dates whereas CS-B26Lo and 3–79 had significant positive additive effects at all six times (Fig. 1). TM-1 had significant additive effects for number of nodes at all six dates but the pattern was not consistent. For example, it had negative additive effects at days 1, 8, 22, and 36 while positive at days 15 and 29. CS-B16 and CS-B14sh had lower additive effects for number of nodes compared to TM-1 at all six dates while CS-B26Lo had greater additive effects than TM-1 at all six developmental stages, suggesting that chromosome 16 and chromosome arm 14sh of 3–79 in TM-1 background were associated with reduced number of nodes while chromosome arm 26Lo of 3–79 in TM-1 background was associated with increased number of nodes.

Plant height

CS-B14sh had significant negative additive effects for plant height at all dates whereas CS-B26Lo and 3–79 had significant positive additive effects (Fig. 1). CS-B16 had significant negative additive effects at all 6 dates except day 22 while TM-1 had significant positive additive effects at all 6 dates except day 1. With one or two exceptions, CS-B16 and CS-B14sh had lower additive effects for plant height compared to TM-1 while CS-B26Lo had greater additive effects, suggesting that chromosome 16 and chromosome arm 14sh of 3–79 in TM-1 background were associated with shorter plants while chromosome arm 26Lo of 3–79 in TM-1 background was associated with increased plant height.

Compared to the time-specific additive effects (Fig. 1), we observed that chromosome 16 and chromosome arm 14sh were associated with reduced chromosome additive effects for both plant height and number of nodes at all six times while chromosome arm 26Lo was associated with increased chromosome additive effects for both plant height and number of nodes at all six developmental stages. This indicated that the change in plant height was related to the change in number of nodes.

Conditional additive effects

No significant conditional additive effects for number of nodes at day 8 were detected when this trait at day 8 was

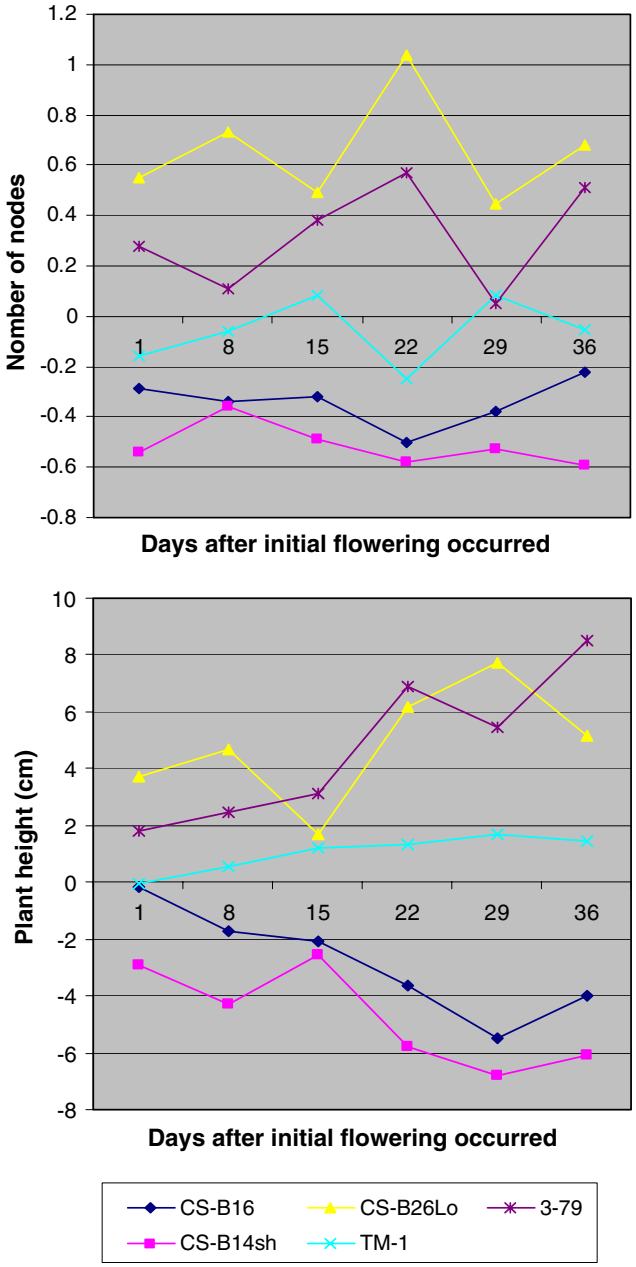

Fig. 1 Additive effects for number of nodes and plant height at different days after initial flowering

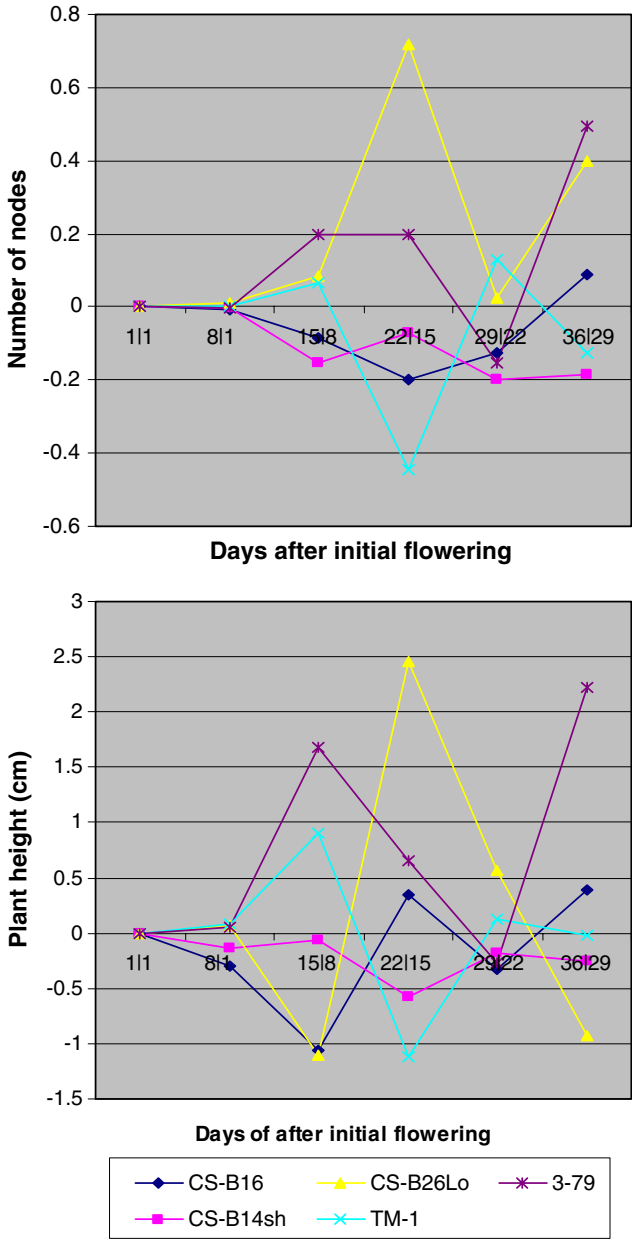

Fig. 2 Conditional additive effects for number of nodes and plant height at different days after initial flowering

conditioned on the event at day 1 (Fig. 2), indicating that no new additive effects were being expressed between day 1 and day 8. After 8 days of initial flowering, many significant conditional (new) additive effects were observed weekly. For example, 13 out of 16 parents had significant conditional additive effects for number of nodes at day 15 and 14 parents had significant conditional additive effects at day 22. No significant conditional additive effects for plant height were detected at day 8 or day 29, whereas many parents had significant conditional additive effects at days 15, 22, and 36 (Fig. 2).

The results showed that some CS-B lines had conditional additive effects that deviated significantly from TM-1, suggesting new additive effects occurring in a specific time period being associated with chromosomes or chromosome arms of 3–79 in TM-1 background. For example, the new additive effects for number of nodes for CS-B14sh between day 8–15, day 22–29, and day 29–36 were significantly lower than those for TM-1 while the new additive effects for CS-B26Lo between day 15–22 and day 29–36 were significantly greater than those for TM-1. The results revealed that chromosome arm 14sh was negatively associated with new additive effects for number of nodes

that were expressed in several time periods while chromosome arm 26Lo was positively associated with new additive effects that were expressed at different time periods after initial flowering.

The changes in additive effects for number of nodes between different developmental stages were reflected by the occurrences of the new additive effects during these time periods. For example, a negative new additive effect on plant height for CS-B26Lo that occurred between day 8 and day 15 (Fig. 2) resulted in a decreased additive effect from day 8 to day 15 (Fig. 1). Then a new positive additive effect occurred the following week (Fig. 2) that caused a significant increase in additive effect from day 15 to day 22 (Fig. 1).

Discussion

A trait like plant height is composed of number of nodes and internode length whose patterns of growth and morphogenesis and underlying controlling genetic factors may differ considerably at different stages in its development (Atchley and Hall 1991; Atchley and Zhu 1997). The change and morphogenesis of different characters may occur at different times (Riska and Archley 1985). For example, in mammals growth of the nervous system begins much earlier than other tissues. Furthermore, the impact of various genetic effects may have significant yet very different effects on progeny growth. Similarly, plant height and number of mainstem nodes are two important characters related to plant growth. Investigation of genetic changes in these two characters helps our understanding of cotton plant growth during the primary flowering time period.

One of the advantages of using chromosome substitution lines in quantitative genetics study is that each of these lines has uniform genetic background with only one chromosome or chromosome segment different compared to its recurrent parent and any pair of lines have two chromosomes different from each other (Saha et al. 2004, 2006). Thus, these chromosome substitution lines can be used to dissect the genetic factors associated with specific chromosomes. Our previous studies regarding these CS-B lines revealed several chromosome associations with traits of importance (Saha et al. 2004, 2006; Jenkins et al. 2006; McCarty et al. 2006). For example, CS-B25 was associated with longer and stronger fibers and lower micronaire, CS-B16 and CS-B18 with decreased yields; and CS-B5sh with higher flowering production in a developmental fashion during the primary flowering time period. Ren et al. (2002) identified quantitative trait loci (QTLs) contributing to boll weight, lint percentage, fiber length, and fiber elongation were located on chromosome 16 using 178 families from its cross with TM-1. Therefore, it is also a unique procedure to use these cotton CS-B lines to discover the genetic changes associated with specific chromosomes in plant growth even without the support of DNA markers.

Based on the genetic analysis for number of nodes and plant height at six different times after initial flowering where the phenotypic data at time t were not conditioned on the events at time $(t-1)$, we discovered that each of these two developmental traits had different patterns for different variance components. For example, additive variance component was significant for the two traits at all six times while significant dominance variance was detected only occasionally (Table 2). The conditional analysis given the phenotypic values at time t conditional on time $(t-1)$ revealed that new genetic variations like new additive and dominance variances were detected at different time periods after initial flowering. For example, a large new additive variation in number of nodes was observed between 15–22 and 29–36 days after initial flowering; new additive variance in plant height were found 8 and 15 days, 15 and 22 days, and 29 and 36 days after initial flowering. Our results are in agreement with the demand of carbohydrates produced in cotton leaves during photosynthesis needed for vegetative growth and fruiting structure (Mauney 1986). After two weeks of flowering in the field, the bolls retained on fruiting nodes 5–10 have priority for the demand of carbohydrate produced by the plant, thus it will slow the vegetative growth rate. As we observed in Table 1 this study, the growth rate for both plant height and number of node decreased from days 15 to day 22. This was reflected by the significant increase in both unconditional and conditional additive variance for these two traits (Tables 2, 3). It was also confirmed by the unconditional additive effects for days 15 and 22 and the conditional additive effects at day 22 given day 15. Therefore, the results obtained in this study demonstrated the genetic complexity for a time-specific trait, as claimed by many articles (Peat and Whittington 1965; Wu 1987; Xu and Shen 1991; Zhu 1993 Zhu 1995; Atchley and Zhu 1997; Yan et al. 1998a, b; Chen et al. 1999, 2000; Ye and Zhu 2001a, b, c; McCarty et al. 2006).

Based on the predicted additive effects for these two time-specific traits, we uncovered that CS-B16 and CS-B14sh consistently had lower additive effects for plant height compared to TM-1, while CS-B26Lo consistently had greater additive effects for plant height (Fig. 1). The results implied that chromosome 16 and chromosome arm 14sh of 3–79 in the TM-1 background were associated with shorter plants while chromosome arm 26Lo of 3–79 in the TM-1 background was associated with taller plants. CS-B16 and CS-B14sh had lower additive effects for number of nodes than TM-1 while CS-B26Lo had greater additive effects. Thus, it implied that chromosome 16 and chromosome arm 14sh of 3–79 in TM-1 background had

the time-specific additive effects associated with reduced plant height are mainly due to these chromosomes being associated with reduced additive effects for number of nodes. On the other hand, chromosome arm 26Lo in TM-1 was associated with greater additive effects for plant height because this chromosome arm was also associated with increased additive effects for number of mainstem nodes. These results along with our additive correlation analysis between time-specific traits (data not shown) implied strong evidences that plant height and number of nodes shared several additive genetic effects on common chromosomes. Atchley and Zhu (1997) also reported that body weight and tail length in mice shared some common genetic effects at early ages.

Conditional genetic effects for a time-specific trait at time t conditional on time $(t - 1)$ are independent of the (unconditional) genetic effects at time $(t - 1)$. Thus, the conditional genetic effects are equivalent to the new genetic effects expressed between time $(t - 1)$ and t (Zhu 1995; Atchley and Zhu 1997; Yan et al. 1998a, b). Between day 1 and day 8, no new additive effects for plant height were expressed, while additive variance for this trait at both early dates was significant. Thus additive variance for plant height at day 8 was mainly contributed by the additive effects already expressed by day 1. The results were confirmed by a high additive correlation of this trait between these two dates (data not shown). Even though chromosome arm 14sh showed a reduced plant height, a negative new additive effect only between days 15 and 22 was detected, while chromosome arm 26Lo maintained improved additive effects on plant height at six times except at day 15; however, a negative new additive effect was expressed between days 8 and 15, a new positive additive effect was expressed between days 15 and 22, then a new negative additive effect was expressed between days 29 and 36. The conditional analysis also gave a good explanation that a significant decrease in additive effects on plant height for CS-B26Lo was observed from days 8 to 15, then a significant increase from days 15 to 22, followed by a significant decrease from days 29 to 36. The additive effects obtained in this study not only demonstrated a high agreement between the conditional and unconditional effects, but also implied the complexity of gene actions at different developmental stages.

An important aspect of many developmental genetic models is that the underlying genetic control of a complex trait may change significantly during ontogeny (Atchley 1984, 1987; Atchley et al. 1994). Considerable experimental evidence from quantitative genetic analyzes in different organisms has shown that genetic variations and/or covariations including additive, dominance, and maternal genetic effects, exhibited a dynamic behavior during growth. Another important aspect in developmental genetics is heritable epigenetic effects (Atchley and Hall 1991; Cowley and Atchley 1992; Atchley et al. 1994). Epigenetic effects occur because of the regulatory, interactive, sequential, and hierarchical nature of development (Atchley and Zhu 1997). For example, one component may induce activities in other components or genes and alter the target or eventual phenotype in a unidirectional or "cause and effect" fashion. Thus, one trait (i.e. plant height in this study) in early development may have a significant genetic impact on itself or other traits later in development (Atchley and Zhu 1997). Our additional correlation analyzes demonstrated that each trait at early developmental stages had a considerable genetic impact on itself at later stages in terms of additive effects (data not shown). In addition, both component traits, number of nodes and internode length, at early stages exhibited indirect significant genetic impact on plant height at later stages. It was very visible that plant height had significant additive correlations with number of nodes at six different developmental times after initial flowering, indicating plant height shared some common influences with number of nodes during cotton plant growth. It was also observed that plant height at day 29 had higher additive correlation with number of nodes at days 1, 8, 15, and 22 (0.75, 0.78, 0.80, and 0.77) respectively, than plant height at day 36 with itself at day 29 (0.73), indicating that gene expression responsible for number of nodes at early developmental stages could play a very important role on plant height at later growing stages, and provides evidence of epigenetic effects in ontogeny, as stated by other scientists.

With the help of DNA markers screened in a mapping population, precisely mapping quantitative trait loci responsible for genetic variation of developmental traits on specific linkage groups or chromosomes would be possible. QTL for number of tillers and plant height in rice at different times were identified (Yan et al. 1998a, b). Cheverud et al. (1996) provided information on age-specific patterns of gene expression in QTLs influencing body growth in mice. Chromosome segment substitution lines developed from a CS line and its recurrent parent, provide a more uniform genetic background compared to the recurrent parent and have been used extensively to dissect QTLs contributing to traits of interest in wheat (Berke et al. 1992; Korzun et al. 1997), rice (Wan et al. 2004, 2005; Wang et al. 2006), cotton (Ren et al. 2002), and mice (Nadeau et al. 2000; Singer et al. 2004). Thus, it will be an interesting investigation to develop cotton chromosome segment substitution lines using CS-B14sh and CS-B26Lo and to precisely identify specific chromosome segments related to cotton plant growth. Such an issue remains to be further investigated in the future.

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