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Inter-specific differences in cotton for nutrient partitioning from subtending leaves to reproductive parts at various developmental stages: consequences for fruit growth and yield

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Abstract

A field study was carried out to unravel the inter-specific differences in cotton for the partitioning of N, P, K, S, Ca, Mg, Na and Cl from the subtending leaves to the reproductive parts of *Gossypium hirsutum*, *G. barbadense* and *G. arboreum* at various developmental stages. Results revealed significant differences among the species for the various parameters studied. Overall there was a greater fresh and dry matter yield of various reproductive parts and subtending leaves of *G. hirsutum* and *G. barbadense* than *G. arboreum*, although the leaf photosynthetic rate was similar. Age-dependent increase in leaf area/leaf mass ratio indicated a greater partitioning of earlier acquired assimilates to the growth of reproductive parts. Results indicated greater partitioning of N, P, S and Ca during later reproductive growth (from boll production to its opening) in *G. hirsutum* and *G. barbadense* but during earlier reproductive growth in *G. arboreum* (from bud up to flower formation) as was evident by decreased subtending leaf/reproductive parts ratio. It is concluded that better N, P, S and Ca partitioning ability of *G. hirsutum* and *G. barbadense* at the onset of boll development played a major role in the better yield and good quality fiber characteristics.

Additional key words: *Gossypium arboreum, G. barbadense, G. hirsutum,* mineral elements, testa.

Introduction

Partitioning of nutrients plays a crucial role particularly during reproductive growth. However, plant species may show considerable differences for their nutrient contents in various parts. The materials partitioned from the leaf to reproductive parts, in addition to containing major bulk of the organic compounds (sugars, proteins, organic acids, *etc.*) also contain nutrients, albeit in smaller amounts (Unruh and Silvertooth 1996b, Kavakli *et al.* 2000). These nutrients are incorporated as structural constituents of macromolecules, membrane components and/or act as cofactors in the seed/grain filling and many other physiological activities (McIntyre 2001, Taiz and Zeiger 2002). Acquisition of essential nutrients in optimum amounts by root followed by their transport and partitioning into various vegetative and reproductive parts play a pivotal role in dry matter and economic yield. This entails paramount importance during various phases of vegetative and reproductive growth particularly during bud formation (Booij *et al.* 1997, McIntyre 2001), fruit formation, its maturation and seed growth (Boquet *et al.* 1994, Unruh and Silvertooth 1996a, Velemis *et al.* 1999, Drake *et al.* 2002).

The partitioning pattern of leaf nutrients varies considerably during the course of plant development. The nutrient contents may increase (per unit basis) during early stages and decrease afterwards due to proportionately greater growth rate (Sorensen 2000, Egli and Bruening 2001). Deficiency of nutrients to critical concentrations causes reductions in leaf chlorophyll content and photosynthetic rate, and the growth of reproductive structures, and can therefore be used to predict changes in yield of different crops (Chapin and Wardlaw 1988, Velemis *et al.* 1999, Pettigrew 2000).

The nutrients accumulated in vegetative parts of plant are translocated to fruit and finally to seed through vascular tissues (Komor 2000, Turgeon 2000). It is often

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Abbreviations: B - bud; BL - leaf subtending bud; F - flower; FL - leaf subtending flower; MB - mature boll; MBL - leaf subtending mature boll; OPL - open boll with lint; OBLL - leaf subtenting open boll.

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argued that during reproductive stage fully expanded actively photosynthesizing leaf in close proximity to the reproductive parts is principally involved in the partitioning of assimilates possibly due to having direct connections with it (Wahid *et al.* 1997, Turgeon 2000, Offler *et al.* 2000). This implies that leaves at this stage act as active sources while the reproductive parts as active sinks (Hellman *et al.* 2000, Ruan *et al.* 2000). The partitioning of assimilates inclusive of nutrients determines the final productivity in terms of yield of grain, fruit, fibre, *etc.*, depending upon the plant species (Wullschlenger and Oosterhuis 1990, Unruh and Silvertooth 1996b, Heitholt and Meredith 1998, Bednarz *et al.* 2000).

Among the various cotton species, *Gossypium hirsutum* (upland cotton) and *G. barbadense* (pima cotton) have greater lint and seed yield potentials and good quality fibre characteristics than *G. arboreum* (short staple cotton) in different regions of the world. Improvement in cotton yield demands the understanding of various physiological mechanisms which are specifically conducive to reproductive growth. The nutrient distribution pattern is of greater importance and differences between low and high yielding plants are sometimes reflected from the changed nutrient patterns (Hocking and Mason 1993, Bednarz and Oosterhuis 1999). We postulate that plant species capable of exhibiting greater economic yield have tendency to better partition essential nutrients from leaves to growing reproductive parts. This study attempts to elucidate the inter-specific differences in cotton for the pattern and characteristic role of partitioning of nutrients from subtending leaves to the reproductive parts at various stages of their development and finally their implications for economic yield.

Materials and methods

Crop growth: Pre-basic category seeds of cotton species *Gossypium hirsutum* L. (cv. MNH-552), *G. barbadense* L. (cv. Giza) and *G. arboreum* L. (cv. FDH-170) were sown in loam soil field plots measuring 5 × 2 m (completely randomized design) with three replication in the third week of May of the year 2000. The row to row distance was 30 cm. Thinning was carried out 15 d after the emergence of seedlings in order to maintain 15 to 18 cm plant to plant distance. The plants were supplied with recommended rates of N, P and K fertilizers and were irrigated with canal water.

Plant sampling, growth and photosynthetic rate: The following reproductive parts with subtending leaves were sampled at various stages of development: bud (B), leaf subtending bud (BL), blossom flower (F), leaf subtending blossom flower (FL), mature boll (MB), leaf subtending mature boll (MBL), open boll with lint (OBL), leaf subtending open boll with lint (OBLL) and seed. As the cotton has indeterminate growth habit, the sampling for various parts was possible the same day. At least ten samples per replicate of all the parts were collected from middle branches. Sampling was done in the third week of September and first and third week of October. Each replicate represented the mean of samples taken at three times. Leaf area was determined of intact leaves by taking image on a graph paper and then estimating area per leaf. In all the parts fresh mass was determined immediately after sampling, while dry mass was taken after drying them at 70 °C for a week. Ratios of leaf area/ leaf mass (LA/LM) were computed for all the species.

The net photosynthetic rate (P_N) of leaves was measured using an open gas exchange system (*LCA-4, Analytical Development Co.*, Hoddesdon, UK) between 10:00 to 11:00, prior to sampling and leaf area determination. The set of conditions for this determination were: molar air flow per unit leaf area 344 mmol m^{-2} s^{-1}, atmospheric pressure 99.4 kPa, PAR on the leaf surface 1280 µmol m^{-2} s^{-1}, CO_2 concentration 357 µmol mol^{-1} and ambient temperature 30 to 35 °C.

Nutrient analysis: Nitric acid and perchloric acid (3:1) digested samples (at 280 °C for 2 - 3 h) of the above mentioned parts were determined for the content of P, K, SO_4-S, Ca, Mg and Na (Yoshida *et al.* 1976). Na and K were determined on flame-photometer (*Sherwood Model 410*, Cambridge, UK). Ca and Mg were measured using atomic absorption spectrophotometer (*Perkin Elmer Model 303*, New York, USA). Total N was measured by micro-Kjeldahl method, while total P was determined using Barten's reagent (Yoshida *et al.* 1976). The Cl was measured by Cl meter in the boiling water-extracted (for 55 - 60 min) and filtered samples. The SO_4-S was determined by using turbidometric method (Beaton *et al.* 1968).

Economic yield and staple characteristics: The seeds were saw-ginned after removal from the open boll. The seed and lint mass was taken per boll. The fiber characteristics were determined using High Volume Fiber Test System (*HVI 900*, *Zellwager*, Uster, Switzerland) for micronaire, strength, staple length and elongation.

Statistical analysis: The data were statistically analyzed using nested two-way analysis of variance among species and comparison among parts within a species. The comparison of means was carried out using Duncan's New Multiple Range test at 5 % level of probability.

Results

Growth and photosynthesis: All the species indicated a significant ($P < 0.01$) difference for fresh and dry mass of reproductive structures and the leaves subtending them, total leaf area, leaf area/leaf mass (LA/LM) ratio and leaf P_N (Table 1). Moreover, the differences among the parts within a species were also significant ($P < 0.01$) for these parameters. *G. hirsutum* and *G. barbadense* had much higher fresh and dry mass of all these structures than *G. arboreum* at various stages of their growth and development. Lowered fresh and dry matter yield of *G. arboreum* appeared to be an inherent character of this species, but the trend of variation in fresh and dry matter yield of different parts in the species was similar. *G. hirsutum* and *G. barbadense* had much higher leaf area and LA/LM at various stages than *G. arboreum*. The leaf P_N did not fall markedly in *G. hirsutum* and *G. barbadense*, but it was much reduced at later stages in *G. arboreum*.

Table 1. Some growth characteristics of various parts of three cotton species at various stages of their development. Means ± SE. Means sharing same letter differ non-significantly. Nested two-way analysis of variance (F-values significant at ** - $P < 0.01$).

Species	Parts	Fresh mass [g part^{-1}]	Dry mass [g part^{-1}]	Leaf area [cm^2 leaf^{-1}]	LA/LM [cm^2 g^{-1}]	P_N [μmol m^{-2} s^{-1}]
G. hirsutum	B	2.11 ± 0.20cd	0.61 ± 0.05d	-	-	-
	BL	2.65 ± 0.18cd	0.43 ± 0.08d	20.44 ± 2.64c	47.97 ± 7.32c	6.89 ± 0.23ab
	F	1.52 ± 0.08d	0.41 ± 0.03d	-	-	-
	FL	1.92 ± 0.18cd	0.46 ± 0.04d	34.73 ± 5.65bc	74.67 ± 7.45bc	7.59 ± 0.29a
	MB	13.71 ± 1.05a	2.88 ± 0.09a	-	-	-
	MBL	3.01 ± 0.40c	0.53 ± 0.07d	50.27 ± 3.75b	96.07 ± 6.26b	7.55 ± 0.30ab
	OBL	4.40 ± 0.36b	2.15 ± 0.15b	-		-
	OBLL	2.58 ± 0.21cd	0.41 ± 0.02d	69.48 ± 7.38a	169.46 ± 12.10a	5.51 ± 0.56b
	seed	2.30 ± 0.17cd	1.39 ± 0.08c	-	-	-
G. barbadense	B	2.10 ± 0.32cd	0.46 ± 0.04c	-	-	-
	BL	2.46 ± 0.27cd	0.49 ± 0.03c	21.77 ± 1.40c	44.43 ± 6.49b	6.41 ± 0.41ab
	F	1.35 ± 0.21d	0.26 ± 0.05d	-	-	-
	FL	2.74 ± 0.55c	0.50 ± 0.04c	33.86 ± 5.59bc	68.17 ± 10.39b	7.48 ± 0.10a
	MB	12.77 ± 0.34a	2.19 ± 0.20a	-	-	-
	MBL	2.43 ± 0.35cd	0.59 ± 0.06c	50.79 ± 4.19ab	87.89 ± 14.13b	7.22 ± 0.43ab
	OBL	5.63 ± 0.39b	2.08 ± 0.17a	-	-	-
	OBLL	2.08 ± 0.36cd	0.50 ± 0.08c	73.95 ± 7.06a	152.19 ± 18.69a	5.41 ± 0.87b
	seed	2.46 ± 0.20cd	1.48 ± 0.08b	-	-	-
G. arboreum	B	0.74 ± 0.06c	0.22 ± 0.03c	-	-	-
	BL	0.90 ± 0.06bc	0.30 ± 0.05c	11.29 ± 1.87a	41.18 ± 10.36a	6.42 ± 0.29ab
	F	0.39 ± 0.06c	0.16 ± 0.02c	-	-	-
	FL	0.55 ± 0.05c	0.35 ± 0.04c	14.51 ± 2.54a	51.68 ± 6.26a	7.32 ± 0.29a
	MB	5.72 ± 0.15a	1.54 ± 0.07b	-	-	-
	MBL	0.72 ± 0.05c	0.31 ± 0.02c	20.96 ± 2.09a	59.23 ± 9.03a	5.26 ± 0.34bc
	OBL	3.06 ± 0.05b	1.90 ± 0.06a	-	-	-
	OBLL	0.56 ± 0.05c	0.30 ± 0.04c	23.38 ± 3.91a	1.61 ± 14.40a	3.63 ± 0.27c
	seed	0.86 ± 0.08bc	0.76 ± 0.03b	-	-	
Source of variation	df			df		
Species	2	118.34**	41.64**	2 54.50**	11.35**	10.48**
Parts	24	76.94**	49.95**	9 17.49**	11.22**	8.26**

Mineral nutrient composition: The determinations carried out for the mineral nutrient content at various stages of development of reproductive parts and their subtending leaves indicated significant ($P < 0.05$) difference among species and different parts within a species (Table 2). The content of all the mineral nutrients were lower at bud development stage as compared to the subtending leaf which increased in the flower, boll, open boll and the seed of *G. hirsutum* and *G. barbadense*. However, *G. arboreum* indicated a differential accumulation of various nutrients (Table 2).

G. hirsutum and *G. barbadense* indicated a similar accumulation of N in the various parts but *G. arboreum* appreciably deviated from this trend. Both the former species were able to maintain greater N content in various reproductive parts and the seed. *G. arboreum* exhibited such a trend of N accumulation at initial stages of development, but behaved otherwise later on (Table 2). All the species indicated much reduced content of P in the bud which was markedly enhanced in the flower and

Table 2. Concentrations of nitrogen [%] and different mineral nutrients [mg g^{-1}(d.m.)] in the reproductive parts and their subtending leaves of three cotton species. Means ± SE. Means sharing same letter differ non-significantly. Nested two-way analysis of variance (F-values significant at ** - $P < 0.01$, * - $P < 0.05$; SV - source of variation).

Species	Parts	N	P	K	SO_4-S	Ca	Mg	Na	Cl
G. hirs.	B	3.03±0.21b	1.97±0.08d	14.69±1.12b	2.40±0.07de	15.78±2.14e	4.32±0.18f	2.43±0.22b	12.76±0.70b
	BL	3.10±0.11b	3.97±0.15ab	16.55±0.73a	4.40±0.26c	19.10±1.37d	12.23±0.45c	2.97±0.21b	14.16±1.39a
	F	2.08±0.07b	2.44±0.09cd	14.35±0.31bc	2.29±0.21de	16.86±0.38de	8.54±0.21d	2.50±0.10b	8.14±0.79e
	FL	2.85±0.13ab	3.48±0.15b	14.69±0.91b	4.93±0.15a	32.27±0.24a	12.42±0.28b	2.68±0.13b	14.70±0.81a
	MB	2.85±0.14b	3.38±0.09b	12.32±0.16d	3.12±0.09d	17.14±0.95de	9.37±0.91d	2.61±0.13b	8.43±0.42e
	MBL	3.36±0.06a	3.11±0.15bc	13.51±1.13bcd	3.75±0.60b	29.38±0.45b	14.36±1.51a	3.29±0.16b	12.27±0.21bc
	OBL	2.65±0.07b	4.77±0.26a	13.18±0.21cd	3.56±0.15b	17.31±0.28de	7.15±0.35e	2.32±0.10bc	9.87±0.83d
	OBLL	2.12±0.11b	3.48±0.17b	12.83±0.33cd	4.81±0.08bc	26.36±1.65c	13.54±0.81ab	5.54±0.23a	11.47±0.26c
	Seed	3.28±0.24a	2.13±0.07d	5.97±0.15e	1.80±0.06e	7.29±0.74f	2.84±0.09g	1.25±0.13d	1.90±0.21f
G. bar.	B	3.56±0.22ab	2.18±0.02d	13.36±0.26cde	2.47±0.15d	10.09±0.24c	6.27±0.37f	2.50±0.08b	10.80±0.15c
	BL	3.89±0.15a	4.02±0.17ab	13.87±0.26bcd	5.19±0.56bc	25.78±0.59a	10.34±0.39cd	3.04±0.06b	12.86±0.91b
	F	2.96±0.31bc	3.15±0.08bc	14.87±0.55b	4.39±0.40c	12.72±0.43b	8.15±0.18e	2.61±0.10b	8.94±0.82d
	FL	3.86±0.11a	3.25±0.09bc	16.81±0.46a	7.06±0.49a	26.06±0.98a	11.97±0.25b	4.11±0.06a	16.13±0.45a
	MB	2.61±0.17cd	2.86±0.11cd	12.12±0.40e	3.02±0.09d	11.40±0.89bc	11.40±0.25bc	2.79±0.11b	9.60±0.22cd
	MBL	2.96±0.13bc	2.99±0.20cd	14.45±0.30bc	6.09±0.36b	28.30±0.85a	18.24±0.33a	2.80±0.06b	12.20±1.06bc
	OBL	2.63±0.07cd	4.92±0.68a	12.84±0.32de	4.32±0.46c	10.02±0.49c	7.92±0.43e	2.68±0.14b	6.17±0.22e
	OBLL	2.18±0.15d	3.30±0.16bc	13.36±0.20cde	5.98±0.76b	27.04±1.29a	9.47±0.25d	4.62±0.08a	13.03±0.65b
	Seed	3.13±0.08bc	1.92±0.06d	6.50±0.15f	2.92±0.44d	6.62±0.26d	3.16±0.14g	1.07±0.08c	1.47±0.08f
G. arb.	B	2.72±0.04b	3.00±0.08c	12.16±0.33c	2.11±0.07d	8.09±0.15d	1.14±0.08e	2.97±0.06c	8.87±0.06c
	BL	3.02±0.07ab	5.97±0.18a	15.36±0.74a	8.91±0.53a	25.78±0.26ab	8.09±0.26c	3.11±0.05c	16.10±0.48a
	F	2.78±0.13ab	3.00±0.11c	9.29±0.54d	3.43±0.18c	8.72±1.01d	2.58±0.07d	2.32±0.21c	8.50±0.21c
	FL	3.19±0.09ab	4.39±0.16b	14.18±0.34a	6.52±0.07b	14.18±1.05c	12.88±0.91b	5.19±0.09a	17.30±0.51a
	MB	2.59±0.07b	4.16±0.19b	12.44±0.24bc	1.06±0.08e	8.40±0.54d	8.87±0.31c	4.29±0.15b	6.55±0.22d
	MBL	3.31±0.05a	9.31±0.82b	13.84±0.35b	7.33±0.70b	28.30±0.96a	15.28±0.76a	4.37±0.21b	12.70±0.71b
	OBL	1.73±0.07c	1.60±0.06d	9.12±0.22d	1.32±0.11de	9.81±1.08d	7.92±0.29c	4.80±0.45ab	6.17±0.24d
	OBLL	3.45±0.11a	4.92±0.21b	9.79±0.44d	7.32±0.20b	24.04±0.75b	12.51±0.07b	5.53±0.22a	13.03±0.52b
	Seed	1.62±0.08c	0.94±0.06d	5.60±0.32e	1.04±0.05e	3.62±0.05e	2.35±0.04d	2.11±0.06cd	1.47±0.04e
SV	df								
Species	2	9.46**	9.48**	54.24**	43.01**	97.61**	58.46**	51.84**	4.41*
Parts	24	11.04**	24.89**	57.06**	66.32**	95.68**	193.53**	23.80**	203.96**

Table 3. Ratio of mineral nutrients in the reproductive structures relative to their subtending leaves of three cotton species. Means ± SE. Means sharing same letter differ non-significantly. Nested two-way analysis of variance (F-values significant at ** - $P < 0.01$).

Species	Parts	N	P	K	SO_4-S	Ca	Mg	Na	Cl
G. hirs.	BL/B	1.03±0.09ab	2.09±0.42a	1.13±0.05a	1.91±0.31a	1.24±0.15b	2.84±0.10a	1.26±0.20b	1.19±0.03b
	FL/F	1.37±0.02a	1.44±0.09ab	1.02±0.03ab	2.20±0.29a	1.91±0.00a	1.44±0.08b	1.07±0.04b	1.81±0.07a
	MBL/MB	1.19±0.13ab	0.93±0.03b	1.05±0.04ab	1.23±0.19a	1.71±0.07a	1.54±0.08b	1.27±0.12b	1.46±0.00b
	OBLL/OBL	0.81±0.11b	0.73±0.01b	0.97±0.04b	1.35±0.00a	1.53±0.11ab	1.91±0.16b	2.52±0.12a	1.16±0.05b
G. bar.	BL/B	1.17±0.02a	1.86±0.19a	1.04±0.04b	2.16±0.40a	2.56±0.20ab	1.65±0.04a	1.22±0.02bc	1.19±0.03b
	FL/F	1.14±0.08a	1.03±0.07b	1.13±0.01ab	2.07±0.11a	2.60±0.12a	1.47±0.00a	1.58±0.04ab	1.60±0.21a
	MBL/MB	1.13±0.02a	1.11±0.09ab	1.20±0.06a	2.03±0.08a	1.60±0.01bc	0.96±0.04a	1.17±0.18c	1.27±0.06b
	OBLL/OBL	0.83±0.05a	0.67±0.01b	1.04±0.12b	1.40±0.12a	1.21±0.02c	1.21±0.10a	1.74±0.07a	1.38±0.08ab
G. arb.	BL/B	1.13±0.15b	2.36±0.39a	0.79±0.01c	3.99±0.11a	3.19±0.07a	5.47±0.48a	1.04±0.07b	1.82±0.08a
	FL/F	1.03±0.09b	1.59±0.15a	1.53±0.01a	2.78±0.18b	2.99±0.10ab	5.01±0.18a	1.83±0.03a	2.04±0.08ab
	MBL/MB	1.28±0.02ab	2.24±0.03a	1.07±0.00b	3.09±0.41ab	3.38±0.18a	1.71±0.02b	1.29±0.30b	1.96±0.19a
	OBLL/OBL	1.58±0.23a	1.72±0.22a	0.90±0.02c	3.18±0.15ab	2.76±0.05a	1.58±0.01b	1.17±0.12b	2.12±0.05b
SV	df								
Species	2	6.28**	12.45**	14.01**	32.49**	40.03**	184.99**	0.60ns	68.59**
Parts	24	7.58**	23.79**	5.67**	4.47**	9.10**	51.74**	9.91**	12.63**

the mature boll. Beyond this stage, there were differences ($P < 0.01$) among the species for this element. *G. arboreum* indicated a marked reduction in the content of P in the open boll with lint (OBL) and the seed. On the other hand, P-content in the OBL and seed was much greater in case of *G. hirsutum* followed by *G. barbadense*. Leaves subtending reproductive parts indicated decreasing N-content in *G. hirsutum* and *G. barbadense* but an increasing one in *G. arboreum*. However, all the species had no clear trend for P of leaves subtending the reproductive parts.

All the species and their parts displayed significant ($P < 0.01$) differences for the accumulation of K at various stages of development. The bud of all the species had slightly lower content of K than the subtending leaf, however these differences were more clearly evident at rest of the reproductive stages. However, seed of the species did not differ markedly for this nutrient. The K-contents of the species were more or less comparable in the reproductive parts. The seed of all the species had no great difference for this nutrient. *G. hirsutum* and *G. barbadense* maintained a comparable K-contents in the leaves, but *G. arboreum* indicated decreasing contents at later stages. The reproductive parts of all the species showed wide differences ($P < 0.01$) in the content of SO_4-S both for buds and subtending leaves, but this difference was considerably narrowed down at later stages in *G. hirsutum* and *G. barbadense* (Table 2). Consequently both these species had much higher content of this nutrient than *G. arboreum*. Surprisingly, SO_4-S content in the subtending leaves showed a slight increase in all the species.

All the species, reproductive parts and leaves subtending them displayed significant ($P < 0.01$) difference for Ca-content. Ca levels were much greater in the reproductive parts of *G. hirsutum* and *G. barbadense* than *G. arboreum*. Subtending leaves, however, did not indicate any clear trend (Table 2). More notably, seed-Ca was substantially higher in *G. hirsutum* and *G. barbadense*. Likewise, the concentration of Mg in all the species was much reduced in the reproductive parts compared with subtending leaves during early stages of development, but it accumulated greatly with the further growth of these parts. The seed of *G. barbadense* had greater accumulation of Mg followed by *G. hirsutum* and *G. arboreum*. The leaves subtending the reproductive parts of all the species had much higher Mg than reproductive parts themselves.

The levels of Na did not change much during the early growth of reproductive parts or the leaves subtending them. However, at later stages, the Na contents were much greater in the leaf subtending open boll with lint (OBLL) of *G. hirsutum* and *G. barbadense*, and OBL and OBLL of *G. arboreum* ($P < 0.01$). Seed of both the former species had much lower Na than the latter. Contrarily, the Cl content in the reproductive parts of all the species was higher during the bud stage but showed a decrease at the later development of rerpoductive parts. OBLL of all the species displayed much higher while the seed had much lower content of Cl in all the parts. Seed-Na was considerably higher in *G. arboreum* and seed-Cl was higher in *G. hirsutum* than rest of the species.

Subtending leaves/reproductive parts (SL/RP) nutrient accumulation ratio: All the species differed significantly ($P < 0.01$) in the ratio of subtending leaves to reproductive parts (SL/RP) for all the nutrients except Na, where no-significant ($P > 0.05$) difference was seen among the species. However, the parts within a species had significant ($P < 0.01$) difference for this ratio (Table 3). The SL/RP ratio indicated a variable trend of the partitioning of various nutrients being higher at one stage and lower at the other. In general, *G. hirsutum* and *G. barbadense* showed a decreasing SL/RP with the growth of reproductive parts for N, P and S, while reverse of it was noted in *G. arboreum*. In particular, OBLL/OBL was markedly lower for N, P, S, and Ca for *G. hirsutum* and *G. barbadense* but much higher for *G. arboreum*. All the species had a comparable SL/RP for K. This ratio was decreasing for Ca in *G. hirsutum*, did not change much in *G. barbadense* but increased in case of *G. arboreum*. However, SL/RP for Mg was increased in all the species. SL/RP showed no clear trend at initial stages, got an increase in OBLL/OBL of *G. hirsutum* and *G. barbadense* but reverse trend was noted in *G. arboreum*. Na was in decreasing order for *G. hirsutum* and *G. barbadense*, but no clear trend was evident for *G. arboreum*. Contrarily, SL/RP was generally lower for Cl in most cases for *G. hirsutum* and *G. barbadense* but was higher for *G. arboreum*.

Table 4. Lint and fiber characteristics of three cotton species. Means ± SE. Means sharing same letter differ non-significantly.

Species	Lint yield [g boll^{-1}]	Fibre micronaire	Fibre strength [g tex^{-1}]	Staple length [cm]	Staple elongation [mm]
G. hirsutum	0.87 ± 0.04a	4.80 ± 0.46c	21.10 ± 1.38a	2.74 ± 0.04b	11.91 ± 0.72a
G. barbadense	0.88 ± 0.03a	4.81 ± 0.28b	24.41 ± 1.47a	2.97 ± 0.06a	11.92 ± 1.17a
G. arboreum	0.59 ± 0.04b	6.79 ± 0.45a	15.89 ± 0.76b	1.88 ± 0.07c	13.82 ± 1.92a

Seed yield and staple characteristics: *G. hirsutum* and *G. barbadense* had a comparable lint yield per boll, but it was significantly lower for *G. arboreum* (Table 4). Fiber micronaire was significantly ($P < 0.05$) different for all the species being higher for *G. arboreum* and lower for the other species. However, staple strength was higher in case of *G. hirsutum* and *G. barbadense* but much lower for *G. arboreum*. *G. barbadense* had the greatest staple length followed by *G. hirsutum*. Staple elongation was comparable in *G. hirsutum* and *G. barbadense* but higher in *G. arboreum*, albeit no significant inter-specific difference.

Discussion

This study concerning the growth and mineral nutrient distribution indicated significant inter-specific difference in the fresh and dry matter yield of reproductive parts and leaves subtending them in three cotton species. *G. arboreum* indicated a much reduced fresh and dry mass of parts at various developmental stages and reduced leaf area and LA/LM ratio although the P_N rate was comparable (Table 1). This revealed that leaf P_N during late reproductive growth is not so crucial rather partitioning of earlier acquired assimilates is of greater significance for seed and lint growth of cotton (Tables 2, 4). This finding is supported by an increased LA/LM ratio, implicating a greater reduction in dry matter than leaf area (Table 1). This is a physiological maturity related phenomenon, when most of the leaf reserves are utilized for seed growth (Booij *et al.* 1997, Egli and Bruening 2001). At that time, nutrient partitioning and utilization tendency of any species especially during fruit growth is an important determinant of its productivity (Unruh and Silvertooth 1996a,b, Velemis *et al.* 1999).

Many reports witness the effect of induced nutrient deficiency on the vegetative and reproductive growth of various crop species (Tewolde and Fernandez 1997, Bednarz and Oosterhuis 1999), but those concerning the inter-specific variation during reproductive growth are few. There are reports of K and N deficiency on the photosynthate translocation from the source to the sink tissue, resulting in reduced lint yield and fiber quality in cotton (Pettigrew 2000) and grain yield in barley (Chapin and Wardlaw 1988). Unruh and Silvertooth (1996b) have suggested a specific N, P and K requirement to obtain optimum lint yield in cotton. In the present study, although the supply of soil nutrient was similar, but the species revealed great differences in the partitioning during reproductive development possibly due to the inherent capability of each species in doing so. *G. arboreum* seemed to be on a physiological disadvantage in this respect (Table 4). A comparison of parts revealed that partitioning of nutrients starting from mature boll and onward were the most important where both *G. hirsutum* and *G. barbadense* showed excessive partitioning of N, P, S and Ca (Table 2). This seems greatly advantageous because at this particular stage, the seed is at the onset of its maturity and lint formation from the testa is likely to initiate (Ruan *et al.* 2000).

Few reports highlight the rationale between nutrient and crop yield at various growth stages. Boquet *et al* (1994) found that increased N supply to a certain limit at later stages of cotton growth increased the harvestable boll per branch. During vegetative stage of wheat growth, the P levels were constant but decreased thereafter (Elliott *et al.* 1997). Likewise, bud of fruiting pistachio indicated greater demand for nutrient than non-fruiting ones (Vemmos 1999). Although there were low contents of all the nutrients in the seed, N, P and Ca were present in a relatively greater amounts followed by SO_4-S and K (Table 2). We believe that the success of *G. hirsutum* and *G. barbadense* to exhibit better yield and good quality fiber characteristics was due to the partitioning of leaf nutrients in greater amounts during late reproductive development. The partitioning of all the nutrients to the seed has implications in the lint growth during boll and seed maturity (Helenarum and Schaal 1996), and seedling growth during seed germination (Tyler and Zholen 1998).

To determine the tendency of each species to partition nutrients from the subtending leaves to respective reproductive structures, SL/RP ratio was derived. This ratio indicated a decreasing trend with the development of the reproductive parts, for all the nutrients except Mg, Ca and Cl in *G. hirsutum* and *G. barbadense* (Table 3). This suggested a shift of nutrient partitioning from subtending leaves to reproductive parts. Most likely any further requirement for photo-assimilates is partially met by green boll P_N although in lower amounts (Wahid *et al.* 1997). *G. hirsutum* and *G. barbadense* appear to have an advantage over *G. arboreum* for having bigger boll size providing greater surface area for P_N. All these factors appeared to constitutively contribute to both qualitatively and quantitatively better lint and staple characteristics of *G. hirsutum* and *G. barbadense*. These results are consistent with the findings that a greater reproductive growth of cotton was due to increased tendency to partition N and P to seed (Unruh and Silvertooth 1996a).

In conclusion, there are great inter-specific differences in cotton for the partitioning of nutrients especially from boll development to the seed and lint yield. Greater boll growth, seed and lint yield seem to be related to the enhanced capability of *G. hirsutum* and *G. barbadense* to utilize nutrients during boll formation and the growth of seed and lint.

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