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Floral Development, Flowering Patterns, and Growth Rate of Monoecious and Gynoecious Buffalo Gourd

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Abstract. **The effect of sex expression on floral development, floral distribution, plant form, and growth rate was observed in monoecious and gynoecious buffalo gourd (*Cucurbita foetidissima* HBK.). Monoecious plants exhibited vegetative, male floral, mixed floral, and secondary vegetative phases in progression. During potentially male and potentially mixed floral phases of gynoecious plants, staminate flowers developed normally until male buds reached 2 to 3 mm in length. Thereafter, stamens degenerated and the resulting stamenless buds aborted. Gynoecious phenotypes produced pistillate flowers at earlier nodes than did their monoecious counterparts and, on individuals selected for detailed study, gynoecious plants produced about four times as many pistillate flowers as did monoecious plants. However, sex expression did not affect female bud ontogeny. On monoecious individuals, pistillate buds reached anthesis in about half as many days as was required for development of staminate buds. Growth rates and the patterns of growth were similar in monecious and gynoecious plants.**

Diversity in sex expression within genera is more prevalent among cucurbits than in most plant families (14). The genus *Cucurbita*, however, was thought to be exclusively monoecious aside from exceptional individuals or lines of *C. moschata* Poir, and *C. pepo* L. (9, 13, 14). In contrast, feral buffalo gourd (*Cucurbita foetidissima* HBK.) populations often exhibit sexual dimorphism, producing both gynoecious and monoecious individuals (1, 4, 15). Domestication of this species, both as an oilseed and a root starch crop for arid/semiarid regions, has been underway since 1946. Within the last decade, several university and corporate research groups have intensified exploration of its agronomic potential and the suitability of its products for food and industrial uses. Domestication progress has been recently reviewed (2, 5, 6, 12).

Gynoecy in buffalo gourd is considered to be stable. The trait is presumed to be controlled by a single dominant gene maintained within the population in a heterozygous state (4, 11). Gynoecious segregates were described as developing stamenless floral structures at nodes potentially bearing male flowers (Fig. 1A) (1). These stamenless buds usually aborted early during their ontogeny and persisted on vines as dried remnants throughout the season. The relative size of stamenless buds at desiccation differed among gynoecious plants, but also varied at successive nodes on vines of an individual. In exceptional cases, these stamenless flowers reached anthesis (Fig. 1B) (1, 15).

The results presented herein were compiled from several studies elucidating the effects of sexual dimorphism on floral development, flowering patterns, plant form (growth patterns), and growth rate of buffalo gourd plants.

Materials and Methods

Duration of floral development. A field study to quantify floral development periods (elapsed time to anthesis) was initiated during late Aug.–early Sept. 1985 at the Univ. of Arizona. About 100 plants of heterogeneous genetic background in their first season of growth were used in the study. On monoecious plants, 50 staminate and 50 pistillate flower buds residing in the axils of first free-standing leaves adjacent to the meristematic region of developing vines were tagged and dated. Their subsequent development was observed daily and the number of days required to reach anthesis was recorded. In addition, development of 50 pistillate buds on gynoecious phenotypes was monitored in a similar manner.

Ontogeny of abortive male floral buds. Two-year-old plants were sampled in 1975 to examine early stages of male floral ontogeny in both phenotypes. Potentially male flower buds were collected from 10 consecutive nodes commencing with those extant in the axils of first free-standing leaves. Buds were prepared, sectioned, stained, and photographed using standard techniques (10).

Effect of sex expression on flowering patterns. Differences in flowering patterns between phenotypes were studied during the 1975 growing season. A segregating population of 301 F_1 progenies from 90 gynoecious (*Gg*) x monoecious (*gg*) crosses was examined during its second season of growth for differences in flowering habits and for variability in node number (the number of nodes from the plant crown to the first female flower). In addition, 10 random plants of each sex were chosen for detailed study. Each of these plants was trimmed to four main vines. [A perennially grown plant often develops several main axes that arise from separate initials at the crown of its fleshy storage root (3)]. Vines were monitored on five sampling dates throughout the season for floral expression at each node.

Effect of sex expression on plant form and growth rate. Selected second-season plants described previously also were monitored on the five sampling dates for total vine length, the rate of node differentiation, and the distribution of nodes on main vines and lateral shoots.

The effect of sex expression on the growth rate of individual vines in their first season of growth was studied in 1984 at the Marana Agricultural Center. Seventeen monoecious and 20 gyn-

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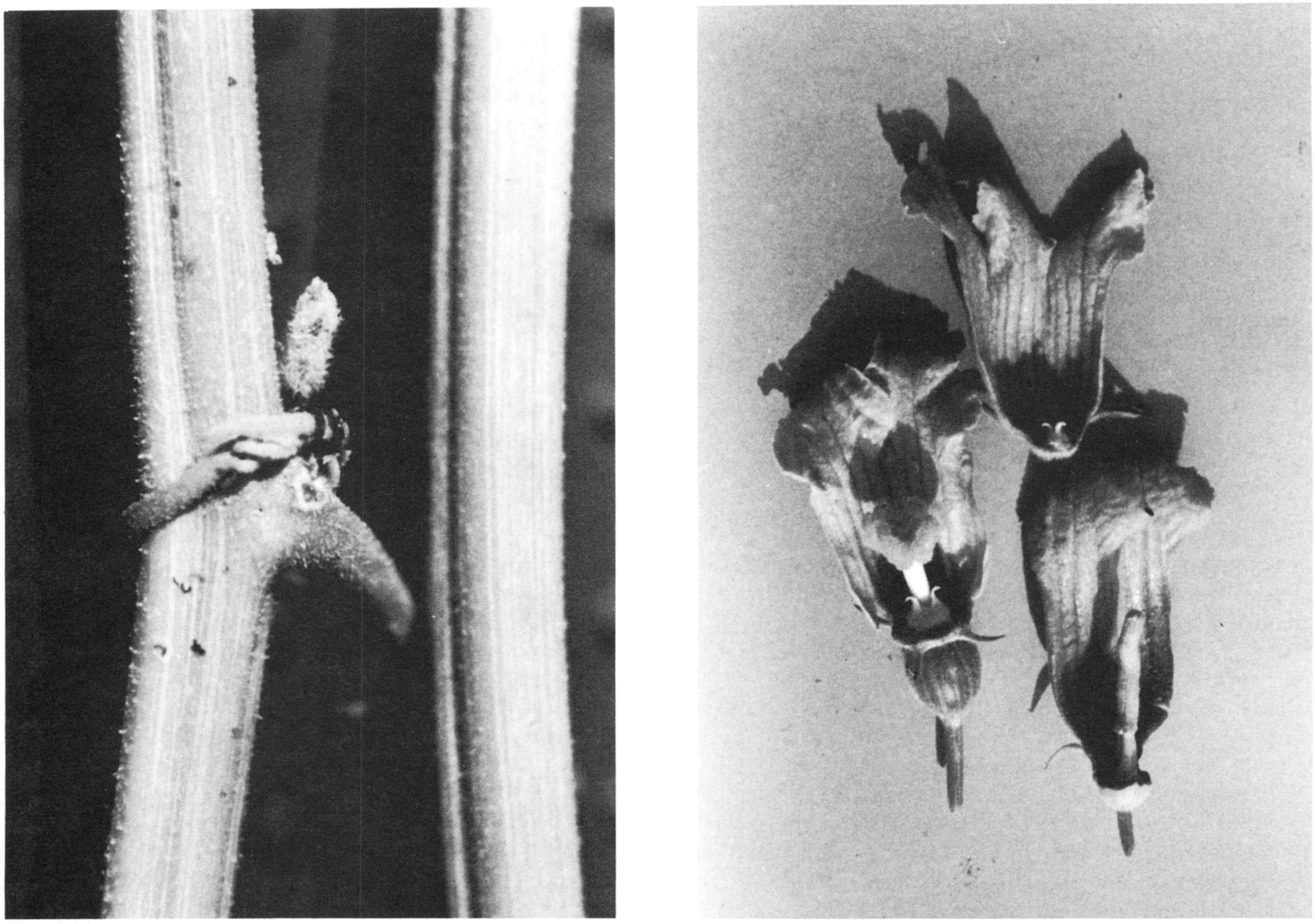

Fig. 1. Buffalo gourd flowers. (**A**) Abortive stamenless. (**B**) Staminate, pistillate, and stamenless at anthesis.

oecious plants were chosen from a population of Arizona Syn-1 [an advanced generation synthetic composed of germplasm from seven population hybrids and three open-pollinated lines (6)]. After 5 weeks of growth, main vines of each plant were measured and tagged at the internode nearest to the first free-standing leaf. The number of nodes and internode lengths of each axis were recorded for two consecutive periods, each ≈2 weeks in length.

Results and Discussion

Morphologically, staminate and pistillate flowers of buffalo gourd resembled those of other *Cucurbita* species (Fig. 1b). Plants predominantly bore diclinous (unisexual) flowers singly at nodes, although abberant individuals that developed nodes bearing multiple staminate or pistillate buds have been observed (8). Staminate flowers (≈85 mm in length) were composed of the following tissue groups. Perianths included adnate calyces (which were chlorophylous) and corollas (which were yellow to deep orange) with five coalescent sepals and five fused petals, respectively. Typically, five stamens were differentiated, but segregates exhibiting four to six structures were not uncommon. Anthers were coalescent. Pistillate flowers (≈95 mm in length) developed typical corollas and sepals; ovaries were inferior. Ovaries often contained three carpels, but individual plants have been identified that produced both tri- and tetracarpellate fruit. Placentation was axile and ovaries normally matured 200–300 seeds. Stigmas and styles were lobed. Flowers functioned from sunrise to mid-moring of a single day; cross-pollination was usually accomplished by bees of several feral or domestic species.

Duration of floral development. For controlled hybridization, it is often advantageous to predict the period of time necessary for floral bud maturation. The average period of time required for maturation of staminate buds on monoecious plants (19.5 ± 3.0 days) was almost twice as long as that for pistillate buds on the same phenotype (10.9 ± 1.0 days) (Fig. 2). Elapsed time to anthesis for pistillate buds on gynoecious individuals (9.7 ± 5 days) resembled that required for similar buds on monoecious plants. Range in maturation period was greatest in staminate flowers, as tagged individuals differed as much as 11 days in time to anthesis (8).

Ontogeny of abortive male floral buds. Photomicrographs failed to reveal evidence for morphological bisexuality in young staminate buds from monoecious plants (Fig. 3, lower) (15). These results reflected previous work of Pereira (7), which failed to uncover a morphological bisexual stage in developing staminate buds of 'Acorn' squash (*C. pepo*).

Stamen growth in functional male buds from monoecious plants was compared with staminate tissue in potentially abortive male buds isolated from gynoecious phenotypes (Table 1, Fig. 3). Stamen primordia development was evident in buds isolated from both phenotypes when they were <1 mm in length. The size of stamens remained comparable in both bud types until they reached 2 to 3 mm in length. At that developmental phase,

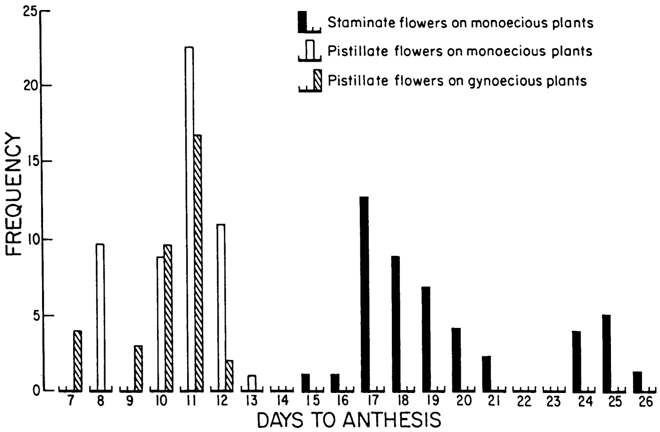

Fig. 2. Elapsed time to anthesis for floral buds in the axils of the first free-standing leaves on shoots of buffalo gourd plants in their first season of growth.

the staminodia in staminate buds from monoecious plants filled the urn-shaped receptacle, whereas their counterparts from gynoecious segregates had ceased to develop. Physiological mechanisms effecting staminate abortion in the latter case remain unknown. However, the induction of functional staminate flowers on aminoethoxyvinylglycine (AVG)-treated gynoecious plants indirectly suggested the natural occurence of high ethylene levels in the meristems of these individuals (11).

Effect of sex expression on flowering patterns. Sexual development in buffalo gourd has been reported to progress through marked flowering phases (4, 15). In the present study, monoecious plants were characterized by a sequence of vegetative, staminate, mixed (staminate and pistillate), and secondary vegetative phases. Gynoecious plants exhibited similar developmental phases, except that the potentially staminate and potentially mixed phases lacked functional male flowers. In some instances, individuals of either sex failed to produce female flowers during their first season of growth (1, 4, 15).

In the population studied, staminate flowering of second-season monoecious plants commenced after a relatively brief vegetative phase, whereas vegetative phases of first-season monoecious seedlings often encompass a substantial number of nodes (unpublished data). The onset of the mixed/potentially mixed phase (as quantified by node number) differed among individuals, but generally occurred at earlier nodes on gynoecious plants. A frequency distribution of node numbers characterizing main vines of 106 monoecious and 195 gynoecious segregates is displayed in Fig. 4. The mean node numbers were found to be 23.5 (CV = 32.4%) and 15.5 (CV = 34.3%), respectively. Means were statistically different ($P = 0.05$). In this perennially grown population (which resumed growth in late February–early March), the transition to the mixed/potentially mixed phase most frequently occurred in May.

Selected plants were monitored throughout the season for floral development at each node of both main vines and lateral shoots (Table 2). On the earliest sampling date, developing pistillate flowers were present at very few nodes. Thereafter, the average number of nodes bearing pistillate flowers increased in both phenotypes. Gynoecious plants bore a greater proportion of their seasonal total of pistillate flowers by mid-season (15 July) than did monoecious plants. However, regardless of sex expression, individuals differentiated few pistillate flowers during the period between 11 Aug. and 10 Sept., when plant were presumbly entering the second vegetative phase. In contrast, pistillate flower differentiation of plants in their first growing season (planted in May) is greatest from mid-August to mid-September (unpublished data). By the last sampling date, gynoecious individuals had produced nearly four times as many female buds as their monoecious counterparts. Pistillate flowers were more prevalent on lateral shoots than on main vines (15).

In monoecious phenotypes, nodes bearing staminate buds were

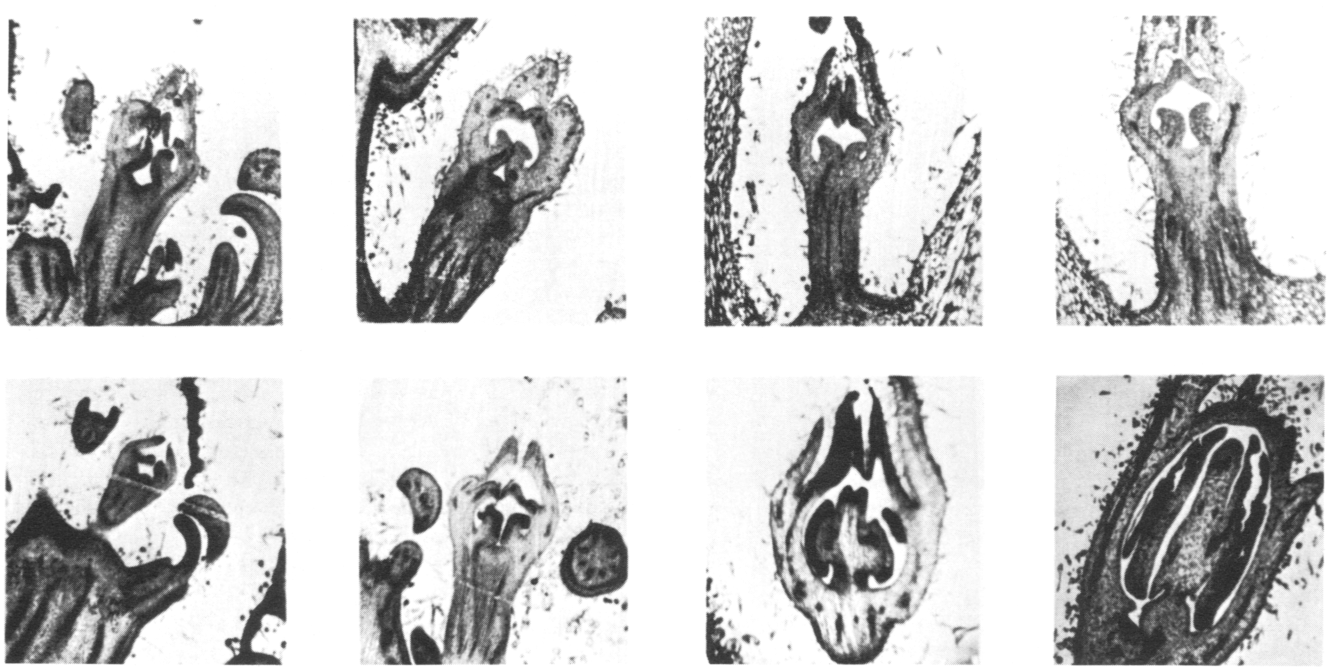

Fig. 3. Staminate development in buffalo gourd flower buds. (**upper**) Isolated from gynoecious plants. (**lower**) Isolated from monoecious plants.

Table 1. Organ dimensions in longitudinal sections of staminate floral buds isolated from comparable nodes of monoecious and gynoecious plants.

Flower bud length (mm)	Gynoecious Stamen length (mm)	Gynoecious Stamen width (mm)	Monoecious Stamen length (mm)	Monoecious Stamen width (mm)
0.76	- - -[z]	- - -	0.08	0.08
1.36	0.23	0.23	- - -	- - -
1.52	0.15	0.23	0.61	0.53
1.67	0.27	0.30	- - -	- - -
2.27	0.23	0.38	0.30	0.23
3.79	ds[y]	ds	0.61	0.53
5.30	ds	ds	1.52	0.53
9.09	ds	ds	4.55	1.66

[z] Buds of comparable size not available.
[y] ds = buds of comparable size exhibited degenerate staminate structures.

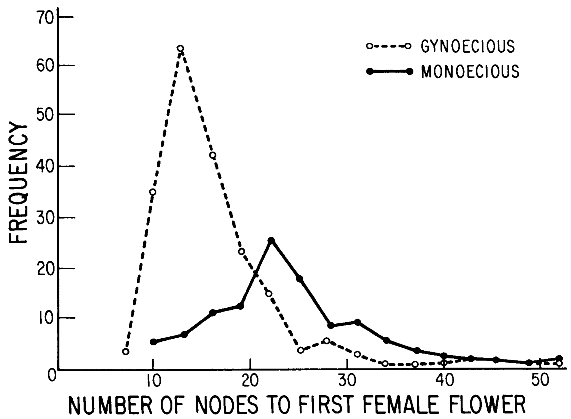

Fig. 4. Frequency of node numbers (number of nodes from plant crown to first pistillate flower) in a hybrid population of gynoecious (n = 195) and monoecious (n = 106) buffalo gourd plants in their second season of growth.

differentiated throughout the season. However, the greatest increase in staminate flowering occurred between 17 June and 15 July. On the last sampling date, the sex ratio (staminate : pistillate flowers) was ≈14:1.

As flowering declined, vegetative growth continued, especially in monoecious plants (Table 2). A substantial portion of the vegetative nodes developed throughout the season were differentiated during the period 11 Aug.–10 Sept. (32% and 21% of vegetative nodes on monoecious and gynoecious plants, respectively).

Effect of sex expression on plant form and growth rate. Characteristic growth patterns of selected second-season gynoecious and monoecious plants are shown in Table 3. During early sampling periods (e.g., 17 June), gynoecious plants developed more extensive vine growth and exhibited a more highly branched form than monoecious plants. Nevertheless, variability in growth patterns among individuals within groups was substantial. Therefore, visual comparison of growth patterns was of little use in distinguishing between phenotypes, and subsequent attempts to predict the sex expression of seedlings or perennially grown plants prior to the onset of flowering have failed.

By the end of the season, the influence of sex expression on plant form was apparently slight as indicated by the similarity in values between groups for growth parameters monitored. In both phenotypes, vine growth was greatest between the 17 June and 11 Aug. sampling periods, and the predominant portion of this increased vine matter could be attributable to lateral shoot development. The accumulation of nodes on main vines occurred at almost identical rates on both phenotypes.

In addition, the effect of sex expression on growth rates of individual vines was examined using plants in their first season of growth. At experiment initiation (23 June), the main vines of young monoecious and gynoecious plants exhibited similar mean lengths (85.5 and 77.6 cm, respectively; not statistically different, $P = 0.05$). Monoecious plants were forming well-developed male floral buds, whereas nodes of gynoecious phenotypes held either stamenless buds or were vegetative. During the course of the experiment (23 June–23 July), plants of both phenotypes entered their mixed/potentially mixed flowering phases.

The average main vine of monoecious plants grew 3.54 m and proliferated 27.5 nodes; their gynoecious counterparts averaged 3.50 m and 26.3 nodes (Table 4). Differences between means were not statistically significant ($P = 0.05$) for either growth parameter on either sampling date. However, the number of nodes differentiated per day was significantly reduced and mean internode lengths significantly increased during the

Table 2. Floral differentiation at nodes on 10 monoecious and 10 gynoecious plants on five sampling dates in their second season of growth[z].

Sampling date	Gynoecious: Nodes bearing pistillate buds, No. cumulative to date	Gynoecious: Nodes bearing pistillate buds, Proportion of season total (%)	Gynoecious: Nodes bearing abortive staminate buds and veg. nodes[y], No. cumulative to date	Gynoecious: Nodes bearing abortive staminate buds and veg. nodes[y], Proportion of season total (%)	Monoecious: Nodes bearing pistillate buds, No. cumulative to date	Monoecious: Nodes bearing pistillate buds, Proportion of season total (%)	Monoecious: Nodes bearing staminate buds, No. cumulative to date	Monoecious: Nodes bearing staminate buds, Proportion of season total (%)	Monoecious: Vegetative nodes, No. cumulative to date	Monoecious: Vegetative nodes, Proportion of season total (%)
26 May	2	2	53	4	1	3	28	6	19	2
17 June	52	40	250	20	7	21	160	34	35	4
15 July	111	85	609	49	20	60	368	78	237	30
11 Aug.	127	97	980	79	32	97	450	96	541	68
10 Sept.	131	100	1244	100	33	100	471	100	792	100

[z] Plants trimmed to four main vines with subsidiary lateral shoots.
[y] Stamenless buds were fragile and subject to mechanical damage or abscission. Visual separation of the two node classes was unreliable.

Table 3. Shoot growth and distribution of nodes on 10 monoecious and 10 gynoecious plants on five sampling dates in their second season of growth[z].

Sampling period	Gynoecious: Shoot growth: Cumulative to date (cm)	Gynoecious: Shoot growth: Proportion of season total (%)	Gynoecious: Nodes: No. cumulative to date	Gynoecious: Nodes: Proportion of season total (%)	Gynoecious: Nodes: Ratio of nodes on main vines : lateral shoots	Monoecious: Shoot growth: Cumulative to date (cm)	Monoecious: Shoot growth: Proportion of season total (%)	Monoecious: Nodes: No. cumulative to date	Monoecious: Nodes: Proportion of season total (%)	Monoecious: Nodes: Ratio of nodes on main vines : lateral shoots
26 May	360	4	55	4	53:2	273	4	48	4	46:2
17 June	1973	25	302	22	109:193	1176	15	202	16	93:109
15 July	4592	57	720	52	151:569	3561	46	625	48	156:469
11 Aug.	6682	83	1107	80	188:919	6650	85	1023	79	194:829
10 Sept.	8016	100	1375	100	206:1169	7782	100	1296	100	207:1089

[z] Plants trimmed to four main vines with subsidiary lateral shoots.

Table 4. Mean growth rate of 17 monoecious and 20 gynoecious plants in two growth periods during their first season of growth[z].

Growth period	Gynoecious: No. nodes/day	Gynoecious: Internode length (cm)	Monoecious: No. nodes/day	Monoecious: Internode length (cm)
23 June – 7 July	0.9	12.0	1.0	12.5
8 July – 23 Aug.	0.8	14.4	0.9	13.2

[z] Effect of sex expression on parameter means was nonsignificant whereas growth periods had a significant effect on parameter values (5% level) as determined by analysis of variance.

second growth period (indicated from analysis of variance). Physiological and/or environmental factors responsible for differences in growth rate between periods remain unidentified.

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