Receptacle cavity diameter and drupelet height contributed less to fruit strength, as determined by path analysis within the single genotype 'Meeker', than was evident in our previous study of 10 genotypes (Robbins and Sjulín, 1989). In 'Meeker', both characters were correlated to fruit weight, but not fruit strength (Table 2). Receptacle cavity diameter did provide a large contribution to fruit strength through paths other than those through fruit weight (path coefficient = 0.322) (Fig. 2). However, the relationship of cavity diameter to fruit weight decreased the total path coefficient (path coefficients through fruit weight to fruit strength = -0.144). Drupelet height showed little variation over the fruit weights (cv = 0.09, Table 1), and the total path coefficient to fruit strength was small.

Fruit strength decreased as drupelet diameter increased in 'Meeker', as indicated by the negative correlation to fruit strength (Table 2) and the negative total of path coefficients (Fig. 2).

The negative path coefficient for fruit weight and the significant quadratic component in the regression of fruit weight on fruit strength indicate an optimal fruit weight for 'Meeker' fruit that results in maximum fruit strength. The relationships of fruit morphological characteristics to fruit strength found here are probably unique to 'Meeker' red raspberry. However, our previous study, which used primarily large, firm cultivars (Robbins and Sjulín, 1989), and this study identified three morphological characteristics that contribute to fruit strength, whether through fruit weight (as in the previous study)

or through a direct contribution to fruit strength. These characteristics are drupelet number, individual pit weight, and receptacle cavity depth.

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Tomato Leaf Development and Distribution as Influenced by Leaf Removal and Decapitation

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Abstract. The influence of leaf removal and decapitation (removal of apical bud and top two nodes) of determinate tomato (*Lycopersicon esculentum* Mill cv. Mountain Pride) plants on canopy development was investigated. Leaf removal and decapitation influenced subsequent leaf development and distribution, and early fruiting of greenhouse-grown tomato plants. 'Removal of young axillary leaves increased the size of main (true) leaves in the middle and upper nodes, increased the number of nodes, and increased the number of early fruit produced. Removal of main leaves reduced axillary leaf development at nodes 5 and 9. Decapitation increased axillary leaf development in the middle and upper nodes and delayed early fruit production. These results suggest that cultural practices of tomatoes that remove leaves or apical buds to influence fruiting also affect canopy leaf development and distribution.

The canopy of mature tomato plants typically consists of leaves initiated from the apical meristem (main or "true" leaves) and axillary meristems (axillary leaves or "suckers"). The initiation of main leaves in tomato is influenced by temperature (Paul, 1984a, 1984b), light (Hussey, 1963a), and other environmental factors (Tucker, 1975).

Axillary leaf initiation and growth in tomato is precocious (Tucker, 1977), and the factors involved in axillary shoot outgrowth are not well understood. Removal of the apical bud (Tucker, 1977) and leaf removal or loss can increase budbreak and shoot formation (Aung and Byrne, 1978; Aung and Kelly, 1966).

The relative amount of axillary leaves to main leaves of mature tomato plants appears to exert an influence on fruit production. A large number of axillary leaves present on the plant during the vegetative growth phase often delays initiation of the reproductive phase. In addition, the resulting fruit are smaller than those produced from tomato plants that had many of their axillary leaves removed (Aung and Kelly, 1966; Leopold and Lam, 1960; Watts, 1937). Pruning, or the removal of, selected axillary leaves of tomato plants is a common commercial practice in many areas of the United States to increase early fruiting. Increasing the rela-

tive amount of axillary leaves on a tomato plant by removing the apical bud (decapitation) and releasing the plant from apical dominance has been reported to delay fruiting but increase the number of fruit (Brown et al., 1971). Limited information is available, however, on the effect of leaf removal and decapitation on subsequent leaf canopy development.

The objective of this research was to determine the influence of leaf removal and decapitation of tomato on subsequent leaf development and distribution.

Five-week-old transplants of the determinate tomato cultivar Mountain Pride were placed in 3.8-liter plastic pots (one plant per pot) containing a commercial potting mixture (Fafard Soilless Peat Mix No. 3; Anderson, S.C.). After growing for 5 weeks in the pots (≈15 nodes per plant), experimental treatments were initiated. These consisted of either a) all axillary leaves removed, b) main (true) leaves removed when the axillary leaves at the corresponding nodes exceeded 2.5 cm in length, or c) top two nodes and apical bud removed (decapitation). Plants in a control treatment had no leaves removed and were not decapitated. Leaves were removed at weekly intervals as needed and decapitation was done only once, at the initiation of experimental treatments. Treatments were arranged in a randomized complete-block design with four replicates and four plants per replicate. This study was conducted during winter (Nov. to Feb.) in a glasshouse (minimum 18C) with no supplemental lighting. Fertilizer and pesticides were applied as needed for optimum plant growth.

Four weeks after initiation of treatments, the plants were harvested for determination of canopy and early fruiting characteristics. Leaf area of main leaves and axillary leaves at each node was measured with a LI-COR Model 3100 Area Meter (LI-COR, Lincoln, Neb.). The number of fruit was counted and fresh weight of the fruit determined. Dry weight of leaves and stems was determined after complete drying at 106C. Results were

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Fig. 1 Nodal leaf area distribution of tomato as affected by leaf removal and decapitation. Leaf nodes were numbered from the cotyledon upward.

Table 1. Leaf removal and decapitation effects on tomato development.^a

Treatment	Leaf area (cm ²)			Dry wt (g)
	Total	Main	Axillary	
Axillary leaves removed	3440 b	3410 a	24.2 C	28.3 b
Main leaves removed	3020 b	1060 d	1950 b	26.2 b
Decapitated	4800 a	1910 c	2890 a	42.4 a
Control	4700 a	2570 b	2130 b	40.3 a

^aResults are per plant. Mean separation within columns by LSD, $P = 0.01$.

Table 2. Leaf removal and decapitation effects on early fruiting of tomato.

Treatment	Fruit per plant ^a	
	No.	Wt (g)
Main leaves removed	1.5 b	26 b
Axillary leaves removed	3.3 a	78 a
Decapitated	0.7 c	21 b
Control	2.3 b	29 b

^aMean separation within columns by LSD, $P = 0.05$.

statistically tested by analysis of variance; LSD values were calculated for use in pairwise multiple comparison of treatment means (Carmer and Walker, 1982).

Main leaf removal reduced the total plant leaf area by 36% and did not stimulate additional overall axillary leaf area development, as compared to controls (Table 1). Removal of axillary leaves reduced the total leaf area of the plant by 27%, but stimulated an increase in the size of the main leaves by 33%, relative to controls. All axillary leaves were at an immature stage of development when removed, with leaf lengths generally <15 mm. Decapitation effectively released tomato from apical dominance (correlative inhibition) and increased the development of

axillary leaves by 35% and correspondingly suppressed the development of main leaves by 27%. Decapitation had no effect on total leaf area per plant. Leaf removal treatments decreased the amount of plant biomass (top weight).

Tomato plants partition a greater amount of leaf area to the center nodes than to the older, lower nodes or the younger, upper nodes (Fig. 1). This leaf partitioning pattern gives tomato its characteristic bushy appearance. Removal of either axillary leaves or main leaves reduced the amount of leaf area in nodes 4 to 9. Removal of axillary leaves increased the leaf area partitioned to nodes 13 to 15, as compared to controls. Decapitation increased the leaf area in the center nodes (7 to 9) and reduced the total number of nodes.

The relationship of main leaf area to axillary leaf area at each node is presented in Fig. 2. Control plants (Fig. 2A) had a gradual increase in main leaf area from the bottom nodes until reaching a maximum size at node 9. There was a gradual decrease in main leaf area from node 9 to the top of the plant. Similar, but not as gradual, trends were observed with the nodal distribution of axillary leaves, but the maximum axillary leaf size was at node 7. Removal of axillary leaves

(Fig. 2B) generally increased the number of nodes and slightly stimulated main leaf development at most nodes. Removal of main leaves (Fig. 2C) reduced axillary leaf development in nodes 5 and 9.

Decapitation (Fig. 2D) stimulated axillary leaf growth, predominantly in nodes 7 to 10. Decapitation reduced the area of the main leaves at the older nodes, but the majority of the decrease in recorded total main leaf area of the plant from decapitation (Table 1) appears to be due to the reduction in the number of nodes.

Removal of main leaves had no effect on early fruiting, relative to control plants (Table 2). Removal of axillary leaves increased the number and weight of early fruit produced, and decapitation decreased the number of early fruit produced.

Leaf occurrence and distribution in a tomato plant canopy is important in plant growth. Leaves typically function in photoassimilate production during photosynthesis (Wolk et al., 1983), as receptors for perceiving photomorphogenic stimuli (Decoteau et al., 1988), and provide shading for young developing fruit to prevent physiological injury due to excessive heat accumulation (Adegoye and Jolliffe, 1983). The ability of plants to modify leaf development and distribution in response to environmental, biological, and mechanical stimuli appears to be an important mechanism for plants to optimally position and distribute leaves for survival.

Previous reports (Aung and Kelly, 1966; Hussey, 1963b; Watts, 1937) have documented the effect of leaf removal on production of new leaves, but most of these reports have been unclear as to whether ax-

Fig. 2. Main and axillary nodal leaf area distribution of tomato as affected by leaf removal and decapitation. Leaf nodes were numbered from the cotyledon upward.

illary or main leaves were removed. Aung and Kelly (1966) observed an increase in the size of relatively mature leaves when tomato plants had been partially defoliated of immature leaves. These observations are similar to the results in the present study when axillary leaves were removed. Watts (1937), in a much earlier study, also reported that the remaining leaves on tomato plants that had been pruned grew larger, were darker green, and thicker than leaves on nonpruned plants.

Removal of mature leaves of tomato has been reported (Aung and Kelly, 1966) to stimulate the growth of remaining leaves. Removal of mature leaves may be comparable to the main leaf removal treatment in the present study. We observed no increase in axillary leaf development following main leaf removal. Possible explanations for no increase in axillary leaf development following main leaf removal may be the few nodes from which main leaves were removed and the relatively late removal of these leaves. Generally, only main leaves in nodes 3 to 8 of the plant were removed, because these were often the only nodes in which the corre-

spending axillary leaves of one or more plants in this treatment were >25 mm long (our criterion for main leaf removal) at any time during the experiment. This criterion for main leaf removal was often only exceeded in these nodes 1 to 3 weeks after initiation of experimental treatments. The experiment was terminated 4 weeks after initiation of treatments because bottom leaves of selected plants at this time had begun to senesce and leaf areas were measured before any leaves had abscised. Future research concerned primarily with the influence of removal of main leaves on ensuing canopy development should investigate the effect of a longer interval from main leaf removal to plant harvest or removal of main leaves when axillary leaves at corresponding nodes are < 25 mm long, the criterion used in the present experiment.

Leaf removal tended to decrease the percentage of leaf area at the lower, older nodes and increase the percentage of leaf area at the upper, younger nodes. Leaves in the younger nodes of tomato are greater sinks for nutrients and photosynthates than leaves from the bottom nodes (Aung, 1976; Aung and Kelly, 1966). When all axillary leaves

were removed, main leaves at most of the individual nodes tended to increase. This result supports the suggestion of Aung and Kelly (1966) that the tomato can compensate for loss of leaves and maintain an equilibrium in the plant canopy by increasing the development of remaining leaves.

Several studies have documented the effect of decapitation on axillary bud outgrowth in tomato (Catalano and Hill, 1969; Tucker, 1977) and other crops (Rubenstein and Nagao, 1976). In many cases, the increase in axillary leaf growth is often at the expense of increased or continued main leaf growth (Tucker, 1977), as in the present experiment, and/or stem and root growth (Aung and Kelly, 1966; Tucker, 1977). Decapitation increased the total leaf area in the middle and upper nodes of the plant primarily because of increases in the number of axillary leaves.

Removal of leaves from a tomato plant canopy had been shown previously to affect flowering and fruiting. Leopold and Lam (1960) and Aung and Kelly (1966) reported that the date of first bloom of tomato was earlier when young expanding leaves were

removed. The stimulation of flowering, following removal of young leaves, may result from the release of an inhibitory factor originating from the young developing leaves (Leopold and Lam, 1960) and/or a greater supply of assimilates made available as a consequence of the removal of these leaves (Aung and Kelly, 1966). Our results suggest that the amount of axillary leaves present on the plant before fruiting exhibits the greatest influence on early fruiting and that early fruiting was inversely proportional to the relative amount of axillary leaves. Plants from the main leaf removal treatment and control treatment had different main and total leaf areas, but had similar axillary leaf areas and responded similarly in number of early fruit produced. Early fruiting was increased by removing the axillary leaves. The delay in fruiting following decapitation has been reported by others (Brown et al., 1971) and is probably a consequence of increased axillary shoot growth.

Cultural practices for tomato that remove leaves or apical buds to influence yields also affect the leaf development and distribution of main and axillary leaves. A better understanding of the consequences of leaf removal and decapitation on resulting leaf development should assist in the development of improved practices and/or cultivars for tomato.

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Regeneration of *Lachenalia* Species from Leaf Explants

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Additional index words. bulb, *Lachenalia*, tissue culture, physiological stage, explant orientation, explant size, and wounding

Abstract. The physiological stage of donor plants determined to a great extent the morphogenic potential of *Lachensalia* (Jacq.) hybrid leaves, but the optimal stage for various cultivars was different. Contact of the bud-forming adaxial epidermal cells with the medium did not significantly stimulate *in vitro* bud formation on *Lachenalia* leaf explants, but resulted in the formation of callus from the buds of certain hybrids. Wounding on either the adaxial or the abaxial side of leaves had a stimulating effect on certain hybrids, but others did not respond significantly. A reduction in the length of explants from 10 to 3.3 mm resulted in an increase in the total number of buds formed by a specific amount of explant tissue (width of explant = 15 mm).

Lachenalia, a genus of the Hyacinthaceae, is a seasonal bulb endemic to southern Africa and is currently being developed for use as a pot plant. The mass propagation of *Lach-*

enalia hybrids by means of tissue culture was first reported by Nel (1983). The first step in this process was the production of adventitious buds from adaxial epidermal cells of leaf tissue (Van Rensburg and Van Staden, 1988) to obtain first-generation shoots. These shoots could be subdivided repeatedly until the required number of shoots was obtained (Nel, 1983). The effects of the physiological stage of the donor plant and the orientation, wounding, and size of the explant on the initiation of first-generation buds from *Lachenalia* leaf tissue are discussed here.

Lachenalia cultivars and hybrids were used. Bulbs were planted in autumn in equal parts of loam, sand, and compost. Plants were cultivated in a commercial greenhouse with average minimum of 5C and average maximum of 21C. The daylength followed the natural seasonal pattern in the Southern Hemisphere. Plants were watered twice weekly and received no additional nutrients. The culture medium consisted of the inorganic salts of Murashige and Skoog (1962), 5% sucrose, 1 mg-liter⁻¹ each of benzylamino purine (BA) and naphthaleneacetic acid (NAA), 100 mg inositol/liter, and 0.7% agar. The pH was adjusted to 5.7 before autoclaving. Leaves were surface-sterilized by soaking them in 1% NaOCl for 30 min, followed by rinsing in sterile water. Cultures were kept at 23C and a photoperiod of 12 hr. Except where stated otherwise, donor plants in full bloom were used. Surface-sterilized leaves were cut into explant squares and these were cultured horizontally, with the abaxial surface on the medium. The size of explants was 15 x 10 mm, except where stated otherwise. Each experiment was done with five to eight leaves of each hybrid and with four to six replicates per leaf, depending on the size of the leaf. Buds formed directly from leaf tissue, and, 4 weeks after growth had started, the number of buds formed per explant was determined. Except in the experiment on the physiological stage of the donor plant, where tissue was cultured in 19 x 125-mm test tubes containing 10 ml of medium, explants were cultured in compart-

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