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Source Limitation by Defoliation and Its Effect on Dry Matter Production and Yield of Cucumber

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Abstract. **Source–sink ratios were modified in cucumber (*Cucumis sativus* L.) by defoliation and defruiting to investigate the role of assimilate supply and demand in regulating fruit growth. Plants of the cultivar Calypso were subjected to 0%, 25%, 50%, and 75% defoliation levels. Each level was applied by three different methods of defoliation involving removal of whole or half leaves or a combination of the two. Plants in the 0% defoliation treatment (control) were divided into two groups: defruited and pollinated. Defoliation treatments were begun at fruit set and maintained throughout growth. Defoliation of the plants significantly decreased total plant weight and the fresh and dry weight of the fruits relative to the fruited control. An increase in the level of defoliation caused an increase in accumulation of dry weight in the leaves and a decrease in the dry weight of the fruits. Defoliation of 50% or 75% was followed by an increase in carbon exchange rates determined 7 days after defoliation. Vegetative controls had equal plant dry weight but only half as much fresh weight as the fruited controls. Carbon exchange rate was significantly reduced in defruited compared to fruited plants 16 days after defoliation.**

Dry matter production in crop plants depends on the amount of photosynthetic surface that they display and on the rate of carbon dioxide fixation (photosynthesis per unit of leaf area). Most of the variation in yield of agricultural crops is related to differences in the rate of increase in leaf area rather than to differences in net assimilation rate (19). Leaf area per fruit has been found to be a limiting factor for fruit growth in the grapefruit (*Citrus paradisi* MacF.) (4).

When source–sink ratios of whole plants were lowered experimentally, net photosynthetic and net assimilation rates of the remaining leaves increased in tomato (*Lycopersicon esculentum* Mill.) (16), beans (*Phaseolus vulgaris* L.) (1), soybeans [*Glycine max* (L.) Merr.] (12), and other crops (15). These results suggest that assimilate accumulation is operating below its maximum potential. In tomato, 25% or 50% defoliation resulted in yield reduction, whereas only the 80% defoliation treatment decreased yield if plants were defoliated at first or full bloom (21). Yield restriction resulted from a reduction in either flower numbers or fruit set. Other researchers found that defoliation of tomato plants during the reproductive stage limited yield in proportion to the level of defoliation (2).

Flower removal on cucumber showed that a short delay in fruit set was beneficial for total dry-weight production and number of fruits produced per plant (14). These results suggest that actual photosynthetic leaf area in the cucumber plant might be limiting at the normal fruit development stage. Photosynthetic leaf area is a limiting factor in fruit-yielding ability of cucumber (13). The objective of this research was to investigate the effect of decreasing source size on cucumber fruit growth.

Seeds of 'Calypso' were planted in 50-mm peat pots. Plants were transplanted to 250-mm diameter pots 19 days after seeding. The potting medium used was a mix of 1 sand : 1 soil : 1 peat. Finely ground dolomitic limestone was added at 833 $g \cdot m^{-3}$ of medium to adjust the pH to 5.8. A 10N–4P–8K fertilizer at 142 $g \cdot m^{-3}$ was mixed into the medium. The plants received three 0.5-liter fertilizations containing 2 $g \cdot liter^{-1}$ 10N–4P–8K. Aldicarb at 0.3 g per pot was applied about 2 weeks after transplanting. Dinocap at 1.3 g in 4 liters of water was applied at early flowering.

The plants for the experiment were seeded 19 Oct. and harvested 21 Dec. 1983 (63 days later). The following characteristics were measured: leaf area, stem length, and fresh and dry weight of leaves, stems, and fruits.

Hand-pollination of the flowers was started 35 days after seeding and continued until all plants had one pistillate flower fertilized. Flowers were pollinated daily for 17 days. Extra plants were grown originally to assure that enough flowers for at least one replication would open on any one day. A replication consisted of plants having flowers that were pollinated on the same day. The experiment consisted of six defoliation treatments, one fruited control, and one vegetative control (pistillate flowers removed) arranged in a completely randomized design.

Table 1. Fresh and dry weight of leaves, stems, and fruits in response to defoliation of 'Calypso' cucumber grown in a greenhouse.

Defoliation (%)	Type of defoliation[z]	Leaf area (m^2)	Weight per plant (g)			
			Leaves	Stems	Fruits	Total
				Fresh		
0	Vegetative control	0.41	85	108	0	193
0	Fruited control	0.29	57	54	278	389
25	Half	0.22	54	52	205	306
25	Whole	0.22	55	51	228	333
50	Half	0.16	50	51	205	311
50	Whole	0.19	56	58	177	292
75	Half and whole	0.16	57	65	65	187
75	Whole	0.12	50	57	54	161
LSD (5%)		0.03	9	9	44	55
CV (%)		9	11	10	20	14
				Dry		
0	Vegetative control		12.2	9.0	0.0	20.9
0	Fruited control		5.5	2.9	12.5	21.0
25	Half		5.2	2.6	9.7	17.5
25	Whole		5.8	2.7	10.1	18.6
50	Half		5.5	2.6	7.6	15.7
50	Whole		6.3	3.3	7.3	16.9
75	Half & whole		6.2	3.5	2.6	12.3
75	Whole		6.1	3.0	2.0	11.1
LSD (5%)			1.5	0.5	2.1	3.4
CV (%)			15	10	22	14

[z]Defoliation was performed by cutting away half of the leaf along the midrib, by removing whole leaves, or by a combination of removing half and whole leaves.

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Table 2. Effect of several levels of defoliation and method of defoliation on carbon exchange rate (CER) in leaves and on fruit size for 'Calypso' cucumbers grown in a greenhouse.

Defoliation (%)	Type of defoliation[z]	CER ($mg \cdot dm^{-2} \cdot hr^{-1}$ of CO_2)				Fruit size (cm^3)	
		5 Dec.	7 Dec.	16 Dec.	Mean	7 Dec.	16 Dec.
0	Vegetative control	33	45	28	35	---	---
0	Fruited control	38	40	36	40	139	364
25	Half	38	44	33	38	123	276
25	Whole	40	44	34	40	115	298
50	Half	36	51	40	42	85	245
50	Whole	33	55	38	42	68	234
75	Half and whole	40	48	35	41	11	24
75	Whole	38	44	38	40	8	22
LSD (5%)		7	7	5	5	34	48
CV (%)		12	9	7	7	34	18

[z]Defoliation was performed 4 days after fruit set and twice subsequently by cutting away half the leaf along the midrib, by removing whole leaves, or by a combination of removing half and whole leaves.

The treatments were 0%, 25%, 50%, and 75% defoliation levels; these were accomplished by removal of entire leaves, leaf halves (cutting off one-half of the leaf lamina along the midrib), or a combination of both. The treatments were applied 4 days after pollination had been completed. Additional defoliations were made 8 and 17 days after the initial defoliation (14 to 16 and 16 to 19 leaf stages, respectively).

Plants were maintained as single stems by removing all of the new lateral shoots. Only one fruit was allowed to grow on each plant, and the position of the fruit was at the sixth and seventh node. At the time the defoliation treatments were made, single-plant samples from each treatment were harvested and leaf area determined with an electronic leaf area meter (LICOR LI 3100, Lincoln, Neb.).

Carbon exchange rate (CER) was measured three times: 5 days after the first defoliation and 1 day before each of the two additional defoliations. CER was determined by means of an infrared gas analyzer (ANARAD AR-500 R, Santa Barbara, Calif.). A flow of ambient air of 1 $liter \cdot min^{-1}$ was pumped through a 20-liter glass container for mixing before being used as the source of incoming air. CER was estimated as the difference in CO_2 concentration between the intake and the exhaust air by use of the following formula:

$$CER\ (mg \cdot cm^{-2} \cdot h^{-1}\ of\ CO_2) = 0.1092\ (ppm\ CO_2) \times air\ flow\ (liter \cdot min^{-1})/leaf\ area\ (cm^2)$$

The sample chamber was a 10-cm^3 cuvette that was clamped onto intact leaves positioned on the plant two nodes above and two nodes below the fruit for the first measurement, two nodes above and four nodes above the fruit for the second measurement, and six nodes above the fruit for the third measurement. Length and diameter of the fruits were measured after each CER measurement, and fruit volume calculated assuming that fruits were cylinder shaped.

Twenty-five percent to 75% defoliation of the plants significantly decreased total (leaf + stem + fruit) and fruit fresh and dry weight per plant (Table 1); fresh and dry weight of fruits in the 25% defoliation treatment when whole leaves were removed were an exception. Simple linear regression indicated that (g fruit fresh weight per plant) = 294 − 2.82 (% defoliation) with a good fit to the data ($r^2 = 0.88$).

When plants were 75% defoliated by combined removal of both half and whole leaves there was a significant increase in fresh and dry weight of stems. The plants without fruits produced the same total dry weight but only about half as much total fresh weight as the control with fruits. Dry weight of leaves and stems of vegetative plants was twice as high in the vegetative plants as in the fruited control plants. Leaf areas measured at final harvest were slightly higher in defoliation percentages compared to the control because leaf area increased after the last defoliation. The vegetative control produced more leaves, stems, and total dry weight than the fruited control. Otherwise there were few differences in these characteristics among the various defoliation treatments.

CER of the plants was highest across all treatments for the 7 Dec. determination, which was 6 days after pollination and 2 days after defoliation. Fruits were growing actively before and on 7 Dec, but CER also peaked on that date in the defruited plants (Table 2). CER in the 50% defoliation treatments was higher than in the fruited control treatments for the determinations of 7 Dec. The CER values for this second determination were higher from the 75% defoliation with half and whole leaves removed. Data from the first determination showed no apparent trend, probably because fruits had not started active growth or had not recovered from the shock of defoliation. The third determination (16 Dec., 15 days after pollination) showed a general decrease in CER for all treatments, probably as a result of leaf senescence and less active fruit growth. CER values were high for the vegetative control at the second determination but dropped sharply at the third one and to levels that were lower than those of plants from any of the fruited plants.

Fruit yield and total fresh- and dry-weight production per plant were limited nearly in proportion to percentage of defoliation (Table 1). The fact that even a 25% reduction in leaf area caused a significant restriction in yield of fruit suggests that the growth of fruits (size of sink) in the cucumber plant is limited by the amount of leaf area (size of source). Assimilate supply from source leaves has been found to limit yield in mung bean (*Phaseolus mungo* L.) (3) and tomato (2, 20), with the restriction in fruit yield being proportional to the level of defoliation.

Our data also indicated that as plants were defoliated, accumulation of dry matter in the leaves did not change (Table 1). Others (1, 9, 17, 18, 21) have found that partial defoliation of plants stimulated the photosynthetic rates of the remaining leaves. There is evidence that net photosynthetic rate is controlled by the level of assimilate (mainly starch) in the leaves by a feedback control mechanism (5, 6, 10). Perhaps damaged leaves have lower net photosynthetic rates than undamaged leaves.

Our data suggest that as the level of defoliation is increased, dry-weight accumulation (possibly as starch) acts as a feedback mechanism to inhibit CO_2 assimilation. The rate of photosynthesis in a leaf may be regulated by the demand for photosynthetic products in other tissue (5, 11, 17). The inhibitory effect of defoliation on fruit growth might impose a self regulatory mechanism by decreasing the demand for assimilates from a sink.

Photosynthetic rates averaged 12.5% lower in vegetative plants than in the control plants, but leaf area in the former was 42% larger; consequently, total dry weights were similar. A combination of the mechanisms mentioned before could also be inhibiting CO_2 assimilation under these conditions. Leaf senescence has been reversed by defoliation (7, 8) and might have been accelerated by the absence of fruit on the vegetative control in this experiment.

The effect of sink size on CER cannot be explained from the defoliation experiment because it was confounded with defoliation effects. Our studies on the effect of fruit size on plant growth indicate that fruit growth affects mostly dry matter partitioning but not net photosynthetic production per plant. Vegetative sinks were capable of replacing reproductive sinks in their role for assimilate demand (Ramirez et al., unpublished data).

In summary, all of the leaves on the plants of 'Calypso' pickling cucumber grown in the greenhouse are necessary for maximum fruit yield. Removal of whole or parts of leaves resulted in restricted fruit production per plant. Leaf removal also induced the plant to compensate for the loss by producing extra leaves.

Thus, increase in fruit yield might be achieved in cucumber by developing cultivars with greater leaf area and by preventing defoliation by diseases and insects.

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