Substantial Leaf Shedding—A Consistent Phenomenon among High-yielding Sweetpotato Cultivars

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Abstract. Four high-yielding sweetpotato [*Ipomoea batatas* (L.) Lam.] cultivars displayed substantial leaf shedding, under typical field production conditions, that was not due to pathological or herbivory causes. Losses ranged from $\approx 45\%$ to 60% of the total leaves formed by the normal harvest date during 2 years. There was a strong positive correlation between leaf shedding and the number of vines ($r^2 = 0.80$) and nodes ($r^2 = 0.89$) per plant. Likewise, positive correlations were found between leaf shedding and total dry weight ($r^2 = 0.67$), root fresh weight ($r^2 = 0.65$), root dry weight ($r^2 = 0.60$), and vine dry weight ($r^2 = 0.68$). Distinct differences were found among cultivars in dry-matter allocation within the plant. 'Jewel' allocated a lower percentage of dry matter into vines and a higher percentage into storage roots. Estimated leaf dry matter losses due to leaf shedding ranged from 1.2 to 2.6 t·ha⁻¹. High leaf losses appear to be closely related to vigorous vine growth and subsequent shading of older leaves but did not have a negative impact on storage root yield in the cultivars tested.

The sweetpotato canopy differs substantially from most crops in that it has a vining growth habit. Of more than 300 vegetable crop species grown commercially around the world, only $\approx 12\%$ exhibit this trait. Like other nonclimbing vine crops, the sweetpotato develops a largely two-dimensional canopy, having rapid radial expansion rather than vertical growth (Kays, 1985). The rapid horizontal spread of the canopy maximizes the time in the growing season during which sunlight strikes the canopy rather than the soil surface.

When grown in a homogeneous population, vine growth does not terminate on reaching the shaded areas of neighboring plants (Somda and Kays, 1990). Rather, the petioles of newer leaves become progressively longer, placing new leaves above older leaves in the canopy. As a consequence, older leaves become situated in a progressively less favorable position in the canopy's light reception hierarchy. Analysis of the canopy architecture of the cultivar Jewel indicated that this growth pattern appears to be a significant factor contributing to shedding older leaves (Somda and Kays, 1990). A surprisingly large number of leaves (i.e., $\approx 60\%$) were lost from this cultivar by the end of the growing season due to nonherbivory and nonpathogenic causes.

Leaf shedding can be viewed as a beneficial phenomenon in that it removes organs that are no longer a benefit to the plant. Photosynthetic efficiency declines markedly with leaf age (Thomas and Stoddart, 1980); thus, new

leaves allow a higher photosynthetic efficiency per unit area of land. Though a significant portion ($\approx 37\%$) of the minerals and nutrients are recycled out of sweetpotato leaves before shedding, leaf loss is not without significant cost to the plant (Somda et al., 1991). An estimated 2.8 t of dry matter/ha is lost in this manner. Likewise, a progressively smaller leaf area relative to total plant weight is available to support a unit weight of plant material; hence, plant maintenance costs require an increasing percentage of photosynthate.

To ascertain the biological significance of the extensive leaf shedding in sweetpotato, we determined the extent of leaf shedding among several high-yielding cultivars grown in the United States. In addition, we analyzed the relationship between other characteristics directly or indirectly affecting yield and the extent of leaf shedding.

The experiments were conducted on the Univ. of Georgia horticulture farm, Watkinsville, in 1991 and 1992. The field, a Cecil sandy clay-loam, was plowed, disked, and formed into beds 30 cm high and 60 cm wide. 'Centennial', 'Jewel', 'Resisto', and 'Regal' plants were planted 10 June 1991 at a 30-cm within-row spacing and 96 cm between rows in three-row plots, 4.5 m long. A randomized complete block design with three replications was used. The cultivars were grown according to recommended sweetpotato production practices for Georgia (Barber et al., 1986). The field was monitored during the growing season to ensure that leaf losses were not due to insect or disease damage. The plants were harvested after ≈ 140 days of growth.

Five consecutive plants were harvested from the central row of each experimental plot. The vines for each plant were carefully untangled, the base of the plant severed at

ground level, and the entire plant and storage roots placed in a large plastic bag. The leaves, flowers and peduncles, vines, and storage roots were removed, counted, and weighed. In addition, total nodes were counted. Components (e.g., leaves and vines) for each plant were dried individually at 60°C, until reaching a constant weight, and weighed. The number of missing leaves (leaves shed) was calculated by subtracting total leaves from total nodes [one leaf forms at each node (Somda and Kays, 1990)]. Data were analyzed by analysis of variance (ANOVA) with means separated by Duncan's multiple range test. For characteristics lacking a normal distribution (e.g., flower count), a square root transformation was used. Linear regressions were run between various plant components and yield. A similar experiment was conducted the following year (1992), except only the characteristics associated with the main effects of interest were monitored (i.e., number of leaves, missing leaves, nodes, and storage roots; and the dry weight of storage roots, leaves, and vines). These attributes were analyzed by year and for cultivar $\times$ year interactions. The second year represented a good test of the effect of environment on leaf shedding, in that the weather during the growing season was atypical, being unseasonably cool and wet. Selected data for the second year are presented in the text.

Each of the four cultivars lost many leaves (Table 1). 'Jewel' and 'Regal' lost significantly more leaves than 'Centennial' or 'Resisto' (Table 1). No significant difference in the number of missing leaves was found between years, although the growing conditions differed considerably (data not shown). The percentage of leaf shedding was similar for individual cultivars between years. In 1991, leaf loss ranged from 48% to 63%, and in 1992, from 48% to 59%. This finding supports the contention that shading is a primary factor controlling leaf shedding in sweetpotato.

The percentage of leaves lost per plant (Table 2) did not coincide with numerical leaf losses (for which 'Regal' losses > 'Centennial' > 'Jewel' > 'Resisto'). The difference between number of leaves missing and percentage lost can be attributed in part to differences in leaf size. 'Centennial', which has the largest surface area per leaf, had significantly fewer leaves formed during the season (total nodes) and fewer leaves present at harvest but the second highest percentage of missing leaves. The percentage of missing leaves for 'Jewel' (52.8%) (Table 2) was similar to that reported previously for 'Jewel' [60%; Somda and Kays (1990)]. Variation among years and locations in the percentage of missing leaves within a cultivar is partly a function of the plant size, in that the percentage of missing leaves increases linearly ('Jewel') during the growing season (Somda and Kays, 1990). A declining leaf area index late in the season, reported in several studies (Bourke, 1984; Li and Yen, 1988), also could serve to increase the percentage of missing leaves.

By calculating mean leaf weight, number of missing leaves, and plant population density, we estimated the amount of dry matter

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Table 1. Number and total dry weight of individual canopy and yield components of four sweetpotato cultivars.

Cultivar	No. organs/plant						Dry wt (g)/plant for components				
	Leaves	Missing leaves	Vines	Nodes	Storage roots	Flowers	Leaves	Vines	Roots	Flowers	Total
Centennial	138 b [*]	176 b	12.7b.	314b	7.3 ab	0.4 c	65.6 a	70.9 be	343 a	0.02 c	480 a
Jewel	288 a	316a	18.3 a	604 a	6.3 b	0c	77.0 a	62.8 C	436 a	0 c	576 a
Regal	211 ab	366 a	18.9 a	578 a	9.4 a	59.7 b	65.4 a	117.7 a	351 a	5.15 b	539 a
Resisto	288 a	241 b	18.1 a	529 a	5.6 b	312.7 a	64.2 a	91.3 b	326 a	29.9 a	511 a

^{*}Mean separation within columns at $P \leq 0.05$ by Duncan's multiple range test.

Table 2. Percentage of total dry weight of individual components and dry weight ratios between components for four sweetpotato cultivars.

Cultivar	Missing leaves (%)	Total dry wt (%)				Dry wt ratio				Harvest index
		Leaves	Vines	Roots	Flowers	Top : root	Leaf: vine	Leaf : root	Vine : root	
Centennial	55.8 b [*]	13.3 a	14.8 b	71.8 a	>0.1 c	0.40 b	0.91 b	0.19 a	0.21 bc	72a
Jewel	52.8 be	13.4 a	10.9 c	75.8 a	>0.1 c	0.33 b	1.29 a	0.18 a	0.14 c	76a
Regal	63.3 a	12.1 a	21.8 a	65.1 b	>1.0 b	0.63 a	0.56 d	0.22 a	0.40 a	65 b
Resisto	48.0 C	12.6 a	17.9 b	63.7 b	>5.9 a	0.56 a	0.70 c	0.20 a	0.29 b	64 b

^{*}Mean separation within columns at $P \leq 0.05$ by Duncan's multiple range test.

lost from the plants via leaf shedding during the growing season. Assuming 37% of the dry matter was exported from leaves into the plant before leaf shedding [based on measurements for 'Jewel' (Somda et al., 1991)], the amount of dry matter lost from the cultivars ranged from 2.57 ('Regal') to 1.20 t-ha⁻¹ ('Resist').

Only 'Centennial' differed substantially in growth habit from the other cultivars. 'Centennial' had fewer leaves, vines, and nodes than the other cultivars (Table 1), although storage root count and dry weight were similar for 'Centennial' and the others; it also had fewer missing leaves than 'Jewel' or 'Regal'. Another notable difference among cultivars was the number of vines vs. the percentage of total dry weight allocated to vines. 'Jewel' had essentially the same vine numbers as 'Regal' and 'Resisto' (Table 1) but allocated a substantially lower percentage of dry matter into vines (Table 2). There was a significant year effect on the number of nodes and leaf and vine dry weights, characteristics that would be affected by growing season length or differences in total plant growth (data not shown). Likewise, vine dry weight was significantly affected by the cultivar $\times$ year interaction, but this effect was attributed largely to one cultivar. 'Resisto' had 'substantially higher vine dry matter and reduced storage root fresh and dry weights during the second year.

The number of flowers per plant (Table 1) differed significantly among cultivars. 'Resisto' had the most flowers, and 'Jewel' had none. The total dry weight allocated to flowers (e.g., 'Resisto', 30 g) underestimated the actual total, since by harvest (October), a significant portion of the flower parts had shed, leaving only the peduncles and fruit, when present. The results demonstrated wide genetic diversity in flowering in the sweetpotato gene pool. Flower count and dry weight negatively correlated with root yield.

We analyzed the dry-matter allocation between individual components of the cultivars (Table 2). 'Centennial' and 'Jewel' had lower

top: root and vine: root dry-weight ratios than the others, and 'Jewel' had the highest leaf : vine dry-weight ratio. Major economic yield increases for many crops have resulted from genetically altering photosynthate allocation within the plant. The greatest difference among cultivars in dry-matter allocation was the amount of dry matter partitioned into the vines. This ranged by a factor of about two (Table 2). Significant differences also were found in the top: root, leaf: root, and vine: root dry-weight ratios. 'Jewel' and 'Centennial' had a significantly greater percentage of dry weight allocated to the storage roots than 'Resisto' or 'Regal'. Harvest index, an indication of the relative distribution of photosynthate between the storage roots and the remainder of the plant, differed among cultivars, with those for 'Jewel' and 'Centennial' being significantly higher (Table 2).

Analysis of the relationship between the number of missing leaves and other canopy and yield components indicated no negative correlations. Consequently, leaf shedding did not appear to represent a serious detriment to productivity. Positive correlations were found between the number of missing leaves and the number of vines ($r^2 = 0.80$) or nodes ($r^2 = 0.89$); both were anticipated, since previous reports showed that greater top growth resulted in higher leaf losses (Somda and Kays, 1990). Positive correlations also were found between missing leaves and total plant dry weight ($r^2 = 0.67$), root fresh weight ($r^2 = 0.65$), root dry weight ($r^2 = 0.60$), and vine dry weight ($r^2 = 0.68$). To test the relationship further, total plant dry weight and root dry weight were regressed against the number of missing leaves for individual observations within cultivars. Significant linear relationships were found for both attributes in all cultivars, with the exception of root dry weight in 'Regal'. Varied regression coefficients within each cultivar indicated a genotype effect.

The absence of a strong correlation be-

tween missing leaves and economic yield, and the significant variation in dry-matter allocation patterns among the high-yielding cultivars, even though there were no significant differences in root yield, suggest that leaf shedding has no negative impact on yield. This conclusion might be strengthened if existing cultivars could be tested against several high-yielding lines that have little or no leaf shedding. However, in a quantitatively inherited trait, such as yield, it is uncommon to find a single plant morphological trait or partitioning characteristic that markedly affects yield once highly negative traits have been eliminated. Hence, selection for a sweetpotato idiosyncrasy with positive traits based in part on theoretical assumptions (e.g., significance of leaf angle or vine length) may represent a possible alternative or supplementary approach to standard correlation analysis in the selection of new cultivars with substantially higher root yields.

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