Selection for Delayed Leaf Senescence in Sugarbeet

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ABSTRACT

Sugarbeet growth is characterized by the continuous dying of old leaves and initiation of new leaves. If the photosynthetic activity of leaves can be extended, fewer leaves may be needed and more photosynthate can be translocated to the root for sucrose production. Two cycles of divergent selection for early and late senescence of the first leaf were conducted in a very heterogeneous population. Significant genetic changes in each direction were obtained for the green leaf duration of the first leaf. Populations produced from the two cycles of divergent selection were evaluated for their effects on canopy in replicated multi-harvest field trials. The early senescing populations had significantly more and smaller leaves than the late senescing populations but equal total leaf area. Root and canopy dry matter were not affected by selecting for extended leaf duration, but selection for reduced leaf duration reduced root dry matter and total dry matter accumulation.

Additional Key Words: *Beta vulgaris* L., canopy, leaf size, leaf number.

Duration of growth of the harvestable component of a crop has been reported as one of the physiological determinants of crop yield. Forage yield of *Stylosanthes humilis* H.B.K. increased approximately linearly with the length of the vegetative growth phases (Fisher et al., 1980). The seed yield of soybean *(Glycine max* (L.) Merr.) (Jones and Laing, 1978) and mungbean *(Phaseolus aureus* Roxb.) (Muchow and Charles-Edwards, 1982) increased linearly with the duration of their reproductive growth phases. Gebeyehou et al. (1982) reported that longer duration of the vegetative period had positive effects on grain yield. Increased yields in oat *(Avena* sp.) and cotton *(Gossypium* sp.) have been positively correlated with increased leaf life spans (Helsel and Frey, 1978; Wullschleger and Oostehuis, 1990). The grain yields of contrasting wheat cultivars also were a function of the duration of the period of grain filling (Austin et al., 1980).

In sugarbeet *(Beta vulgaris* L.), the economic product (sucrose) is a component of vegetative root growth. During the growth phase of sugarbeet, leaf initiation is indeterminate, i.e., new leaves are initiated continually and old leaves are dying continually (Lee and Schmehl, 1988). New leaf production and growth rate can be enhanced by high nitrogen (N); however, this increased leaf production channels photosynthate into leaf production while concurrently decreasing the sucrose stored in the root (Lee and Schmehl, 1988). Loomis and Nevins (1963) found N level to have little or no effect on leaf senescence.

Snyder and Carlson (1978) found that the taproot to leaf weight ratio (TLWR) in sugarbeet was genetically controlled and could be altered by appropriate selection procedures. Snyder (1985) later reported that selections for high TLWR (the partitioning of relatively more photosynthate to the root versus the top) significantly increased sucrose yield in sugarbeet hybrids. If the photosynthetic activity of leaves could be extended, fewer leaves might be needed and more photosynthate could be translocated to the root. The partitioning of photosynthate within the root has received much attention, due to a negative relationship between root yield and root sucrose percentage (Doney, 1984; Doney, 1988). However, any increase of photosynthate to the root should result in increased sucrose yield because sucrose yield is the product of root yield and sucrose concentration.

Doney (1979) reported that genetic differences in growth and partitioning characteristics in young plants remain throughout the growing season. Preliminary studies (unpublished) indicate that significant genetic variation exists for green leaf duration of the first true leaf. This study was initiated to investigate the feasibility of genetically altering sugarbeet green leaf duration and to determine the effect of change in green leaf duration on leaf canopy in the field.

METHODS AND MATERIALS

Selection and testing of selected progeny were carried out under uniform growth chamber conditions of continuous light at 300 μmol m^{-2} s^{-1} and a constant temperature of 26°C. Seed was planted in 40 mm x 125 mm cones filled with Sunshine mix #1 (Fisons Horticulture, Inc., Missisauga, Ontario). All plants were watered three times per wk with 20 ml of nutrient solution [Peters General Purpose 20-10-20 (W. R. Grace and Co., Fogelsville, PA) at a N concentration of 470 mg kg^{-1}). Each test consisted of only plants that emerged within 24 hr after the first plants began emerging.

Selection was conducted in the highly heterogeneous WC5 population. This population was developed by intercrossing 160 lines of *Beta vulgaris* L. from the NC-7 *Beta* collection (mixture of sugar, fodder, garden and leaf types) and advancing this intercross through five cycles of unselected open-pollination to allow random recombination to occur. In the first cycle of divergent selection (390 plants), 10 plants whose first true leaf senesced (the first appearance of necrosis at the leaf margin of yellowed leaves) prior to 24 d post-planting were intercrossed to produce population V763E. Twenty plants whose first true leaf senesced after 32 d post-planting were intercrossed to produce population V762L.

Progeny of the two resulting populations (V763E and V762L) were tested under identical growth chamber conditions to determine if selection pressure had altered the green leaf duration of the first leaf before proceeding with the second selection cycle.

The second cycle of selection was performed on 250 plants from each first cycle population (V763E and V762L) and planted in a completely randomized design (CRD). The number of days from planting to senescence of the first leaf was determined for each plant. Twenty-six plants from population V763E whose first leaf senesced prior to 24 d post-planting (one SD unit below the mean) were selected and intercrossed to produce population W250E-E. Sixty plants from population V762L whose first leaf senesced after 32 d post-planting (one SD unit above the mean) were selected and intercrossed to produce population W249L-L.

The four populations derived from the two cycles of divergent selection and the parent population were evaluated in the growth chamber. Eighty plants of each entry were arranged in a CRD. Number of days from planting to senescence of the first true leaf was recorded for each plant. Duncan's Multiple Range Test was used to test differences among population means.

The parent population (WC5) and the four selection populations (V763E, V763L, W250E-E, and W249L-L) were planted in a split plot field trial at the Fargo experimental farm (soil type = fine frigid, montmorillonitic Vertic Haplaquoll) in 1991. This field trial was replicated six times in a completely randomized block design split into six harvest dates (June 12, July 3 and 24, August 14, and September 4 and 25). Plots were two rows with 55 cm between rows and 3.7 m length. Seedlings were thinned at the four- to six-leaf stage to approximately 30 cm between plants.

Green leaf blade area, green leaf number, senescent leaf number, root number, root fresh and dry weights, and canopy fresh and dry weights were measured for each harvest. Tops were removed by trimming just below the oldest visible leaf scars. Roots were washed free of soil before weighing. Green leaf blade area was determined from a random sample of leaves from each plot. Leaf area was measured with a model AAC-400 (Hayashi Denkoh Co., Ltd., Japan) area meter.

Heavy precipitation in late June 1991 prevented the second harvest on July 3, 1991. Split plot analysis of variance was performed over all other harvest dates for senescent leaf number, root number, root fresh and dry matter, canopy fresh and dry matter, and total dry matter production plot^{-1}. Split plot analysis of variance was performed for the last three harvests after the canopy completely covered the ground for leaf number, leaf area leaf^{-1}, and total leaf area plot^{-1}.

RESULTS AND DISCUSSION

The first cycle of divergent selection showed a significant 2-day difference in the senescence of the first leaf between the early senescing population (V763E) and the late senescing population (V762L) (Table 1, preliminary test). The range in days to senescence was about the same for each first cycle selection even though a significant shift in means was observed (Fig. 1).

Two cycles of divergent selection resulted in successive shifts in both directions (Table 1, combined test). The first leaf of the late senescing selection from the second cycle senesced 3.9 days later than the parent population, whereas the first leaf of the early senescing selection from the second cycle senesced 3.2 days earlier than the parent (Table 1, combined test). The cumulative distribution of the progeny from the selected populations shows the shifts of each population away from the parent for each of two successive cycles of divergent selection (Fig. 2).

Realized heritability for late senescence of the first leaf was 1.94 ± 0.13 days later for each cycle of selection. Realized heritability for early senescence of the first leaf was 1.54 ± 0.18 days earlier for each cycle of selection.

Table 1. Mean senescence of the first true leaf for two cycles of divergent selection and the parent population.

	Days from planting to senescence	
Entry	Preliminary test[†]	Combined test
W249L-L		32.4a[‡]
V762L	29.3a	30.8b
Parent (WC5)		28.5c
V763E	27.3b	27.1c
W250E-E		25.3d

[†] Tested prior to initiation of the second selection cycle.

[‡] Means followed by the same letter are not significantly different based on Duncan's Multiple Range Test at $P = 0.05$.

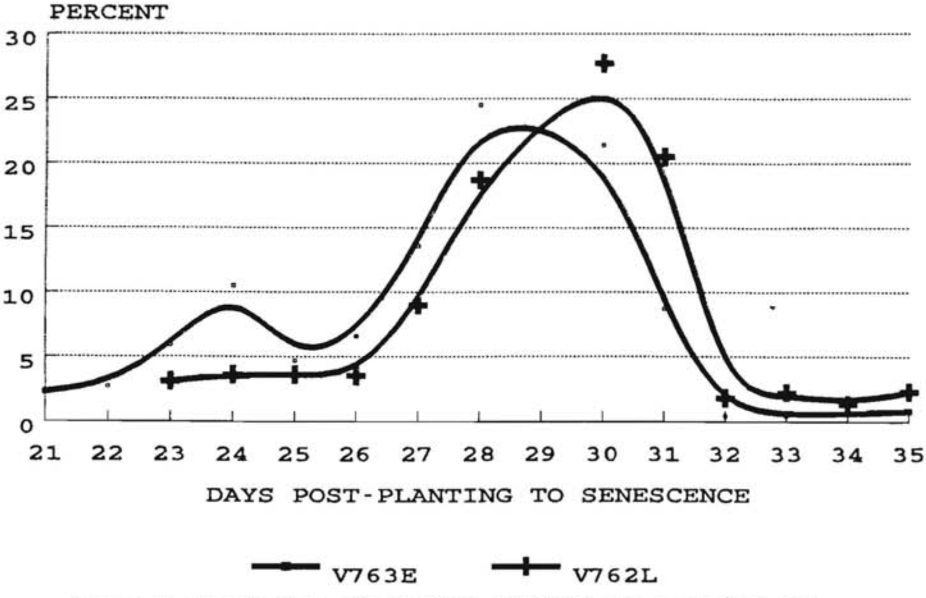

Figure 1. Distribution of selections V763E (early senescing) and V762L (late senescing) for leaf senescence (days from planting to senescence) of the first true leaf.

In the 1991 field trial (Table 2), senescent leaf number per plant for population V763E tended to be higher than the WC5 parent population, whereas population W250E-E tended not to differ from WC5. Populations V762L and W249L-L had fewer senescent leaves

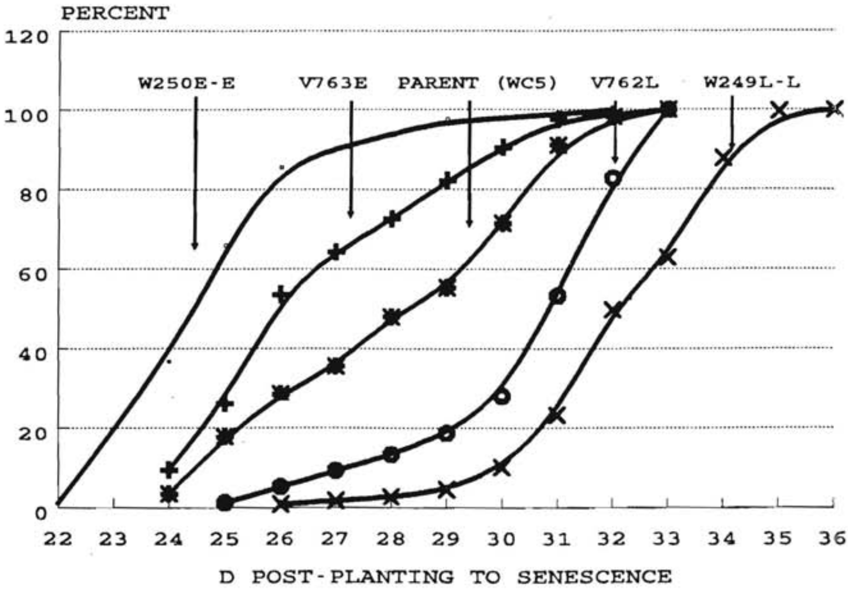

Figure 2. Distribution (cumulative) of the progeny from two cycles of divergent selection and the parent population (WC5) of senescence of the first true leaf.

Table 2. Mean number of senescent leaves per plant for each population at the June 12, July 24, August 14, September 4, and September 25 harvests. Fargo, ND, 1991.

	Harvest date				
Population	June 12	July 24	Aug 14	Sept 4	Sept 25
W249L-L	2.15c[†]	3.73d	5.71c	12.17c	19.82c
V762L	2.35bc	4.00d	6.26c	14.95b	22.85c
Parent (WC5)	2.65abc	4.64bc	7.19b	16.64ab	27.46b
W763E	2.76ab	4.97a	8.33a	17.97a	32.75a
W250E-E	2.68abc	4.84ab	7.84a	16.91ab	29.78ab

[†] Within columns, means followed by the same letter are not significantly different by Duncan's Multiple Range Test at $P = 0.05$.

than WC5 but did not differ from each other except at the September 4 harvest. This trend for senescent leaf number per plant was apparent at each harvest date (Table 2). At the last harvest on September 25, the late senescing populations W249L-L and V762L produced significantly fewer senescent leaves, and the early senescing population V763E produced significantly more senescent leaves than the parent population.

Canopy leaf number and leaf size also were affected by divergent selection for green leaf duration of the first leaf. The early senescing populations produced more and smaller leaves than the late senescing populations (Table 3). The increased number of leaves was offset by smaller leaf size and resulted in no difference in total leaf area.

Recurrent mass selection on population WC5 for extended green leaf duration did not affect root and canopy dry matter accumulation, but selection for decreased leaf duration had a detrimental effect on root dry matter accumulation (Table 4). Differences in total dry matter

Table 3. Mean leaf number, leaf size and total canopy leaf area for the parent and early and late senescing populations.

Population	Leaf number	Leaf size	Total leaf area
	plot^{-1}	cm^2 leaf^{-1}	cm^2 plot^{-1}
Parent (WC5)	1000b[†]	177b	194,975a
Early senescing (E+EE)	1231a	168b	206,601a
Late senescing (L+LL)	1064b	204a	217,184a

[†] Within columns, means followed by the same letter are not significantly different by Duncan's Multiple Range Test at $P = 0.05$.

Table 4. Mean root, canopy and total plant dry matter summed over harvest dates. Fargo, ND, 1991.

	Dry matter (g plot^{-1})		
Population	Root	Canopy	Total
W249L-L	1182.61a[†]	900.07a	2082.68a
V762L	1117.64a	993.85a	2111.49a
Parent (WC5)	1206.36a	812.40a	2018.76a
V763E	958.93b	817.22a	1776.15b
W250E-E	829.13c	850.84a	1679.97b

[†] Within columns, means followed by the same letter are not significantly different by Duncan's Multiple Range Test at $P = 0.05$.

can be attributed to differences in root dry matter. Reduced root dry matter observed in the early senescing selections may be a result of inbreeding depression, since the first selection cycle consisted of a relatively small number of plants. There was, however, observable variation in all selection populations. The distribution of senescence of the first leaf in these populations (Figs. 1 and 2) also suggests that considerable variation remained.

Another explanation of the reduced root dry matter of the early senescing selections may be that selection favored annual type beets. A very low frequency of annual type beets was present in the original population. Even though all bolting plants were discarded when they were observed, the early senescing selections had a higher frequency of annuals than the parent population, suggesting that early senescence favored annualism. Diverse heterogeneous populations that do not carry annual type genes are the subject of current studies.

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