Senescence in Parental and F₁ Plants of a *shrunk2* Sweet Corn

V.M. Russo

United States Department of Agriculture, Agricultural Research Service, South Central Agricultural Research Laboratory, POB 159, Lane, OK 74555

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Abstract. Senescence occurs at the cellular and tissue levels. It is under genetic and environmental control and factors affecting initiation and speed of development of senescence can be passed from parental to F₁ plants. This study was conducted in the greenhouse and field to determine how senescence patterns in F₁ plants of a *shrunk2* sweet corn (*Zea mays* L.) hybrid compared to those of parental inbreds. Greenhouse grown plants were left intact and field grown hybrids and parental inbreds had one or both reproductive organs removed or were left intact. Senescence patterns in stalk internodes were similar in greenhouse and field grown F₁ and inbred plants. Senescence patterns in shank internodes in greenhouse grown plants were different from those of field grown plants. Senescence ratings in stalks increased as developmental stage advanced. Expression of stalk senescence in internodes below the node bearing ears appears to be suppressed by hybrid vigor. In field tests, destruction of the tassel before expansion (decapitation) appears to suppress senescence in internodes above I7, with this effect somewhat dependent on plant developmental stage.

As plants develop they pass from periods of high metabolic activity to periods of reduced metabolic activity. This latter stage is representative of senescence. Senescence is a process that is initiated before the terminal stage of plant morphogenesis. BeMiller et al. (1976) defined senescence as a phase of genetic expression and subject to control mechanisms operating on the transfer of information through the transcription and translation processes, or which may be caused by an accumulation of errors in RNA and in the synthesis of RNA and proteins.

As corn (*Zea mays*) plants senesce, cells in stalk and shank internodes and cobs lose water and fill with gas (BeMiller et al., 1969). These cells appear white and fluffy when the tissue is cut, and the amount of senescent cells can be measured (Pappelis and Williams, 1966). Initiation and progression of senescence in corn occurs in conjunction with or following anthesis (Pappelis and Katsantos, 1969). Cell death may be associated with mineral nutrition. However, Russo (1995a) found that there was no direct relationship between residual minerals at fresh market harvest and stalk internode senescence at that stage. This does not rule out the possibility that concentrations of minerals in tissues at earlier stages of plant development may affect the senescence process.

Russo and Pappelis (1994) determined that, in sweet corn, senescence in stalk internodes 1) can be rated in the same manner as field corn (Pappelis and Williams, 1966), 2) is different among cultivars, and 3) varies as the plant ages. In some field corn cultivars, Pappelis and Katsantos (1969) found that removing ears at formation slowed the onset of senescence. Detasseling may also affect development of senescence without affecting yield (Wilhelm et al., 1995).

Senescence can lead to lessened stalk resilience and internal strength because of reduced cellular integrity. Senescent sweet corn stalk tissues can be colonized by fungi, which leads to significant losses to seed producers (Foley, 1962). Hybrid seed from these plants could harbor symptomless infection (Headrick and Pataky, 1989)

and suffer reduced germination and stand establishment.

Hybrid seed carry the genetic information controlling senescence contributed by one or both parents. A better understanding of how senescence is controlled could lead to maintaining tissues in a more juvenile stage so that plant vigor could be continued through seed harvest. Greenhouse and field experiments were designed to determine whether development of senescence patterns in F₁ progeny were similar to one or both parents. Field experiments also examined the effects that removal of ear shoots and/or tassels had on senescence patterns.

Material and Methods

Seed were supplied by Illinois Foundation Seed (Champaign, Ill.). Male (lot no. 562159) and female (lot no. 592089R) inbreds of 'Illini Gold', a *shrunk2* (*sh2*) hybrid, were sown in 26-cm-diameter pots containing 11.5 liters of potting soil (Redi-Earth 3CF, Grace Sierra, Milpitas, Calif.). Controlled cross-pollination was used to produce F₁ hybrid seed.

Greenhouse experiments. Seeds of male and female inbreds and F₁ plants were sown in the planting medium in pots of the size described previously. Plants were thinned to one per pot. Vegetative and reproductive development of the corn plant was based on the system of Ritchie and Hanway (1982). Vegetative stages were based on the number of the leaves on the plant from emergence (VE, no leaves) to tassel emergence (VT). Reproductive stages were designated from 50% silking (R1) to physiological maturity (R6). Nodes were numbered from one (N1 to N15) and the internode above each node was given the same numerical designation (I1 to I15).

Pots were arranged in a randomized complete block with three replications. Three plants per replication of each inbred and 11 F₁ plants per replication were harvested at midwhorl (V9), VT and R1, fresh-market (20 days postanthesis), and seed harvest (50 days postanthesis) stages. Although inbred plants are not normally harvested at fresh market, they were rated at that stage to compare to F₁ plants. Also, F₁ plants were carried through seed harvest, although this is also not a normal practice.

At each stage, stalks of all plants were split longitudinally past the last ear bearing node. Although ears could be formed at N8 to N10, most of the primary ears generally occur at I10. Senescence

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Table 1. Stalk internode senescence ratings^z in greenhouse grown parental and F₁ plants.^y

Treatment	Internode (I)					Avg
	6	7	8	9	10	
Stage (S)						
Tassel (VT)	0.2 b ^x	0.6 b	1.3 c	1.3 c	1.1 b	0.9 c
Silk (R1)	0.3 b	0.9 b	2.4 b	3.3 b	3.7 a	2.1 b
Fresh market	0.4 b	1.1 b	2.9 b	3.8 a	3.9 a	2.4 b
Seed harvest	2.1 a	3.0 a	3.6 a	3.9 a	3.9 a	3.3 a
Genetic material (G)						
Male parent	0.9 a	1.8 a	3.0 a	3.4 a	3.2 a	2.5 a
F ₁	0.6 b	1.3 b	2.1 b	2.6 b	2.8 b	1.9 b
Female parent	0.7 b	1.1 b	2.5 b	3.2 a	3.5 a	2.2 a
Interaction						
S × G	**	*	NS	NS	NS	*

^zRatings are from 0 to 6 (after Pappelis and Williams, 1966).^yAll internode ratings at mid-whorl (V9) were 0.0; for male and female N = 9 and for F₁ N = 33 at each sampling time.^xValues in a column followed by the same letter are not significantly different (Duncan's multiple range test, $P \leq 0.05$).NS,*,** Nonsignificant or significant at $P = 0.05$ or 0.01 , respectively.

ratings were based on the areas of spongy, dry tissue, which appeared white and fluffy in longitudinal sections. These areas were rated as follows: 0, no senescent tissue in the internode or node; 0.5, 1% to 12%; 2, 12% to 25%; 3, 50% to 75%; 4, >75%; 5, white tissue in internodes linked by white tissue in nodes; and 6, like 5 but no green color in rind (after Pappelis and Williams, 1966). Using the rating scale, the amount of senescence in N6 to N10 and I6 to I10 was determined.

At fresh-market and seed harvest, all nodes and internodes in shanks were rated in the manner described previously. Shank internodes were counted beginning with the internode proximal to the stalk. To rate senescence in cobs, they were split longitudinally and the amount of tissue exhibiting senescence, measured from the end proximal to the shank to the tip, determined the rating.

Field experiments. The soil was a Bernow fine-loamy, siliceous, thermic Glossic Paleudalf, at Lane, Okla., fertilized according to soil test recommendations. Inbred seeds, from the same seed lots as before, and F₁ hybrid seeds were sown in single rows in beds on 0.9-m centers on 11 Apr. 1994 with 0.23 m between plants, giving a density of about 47,000 plants/ha. Plots were 5 m long and

two beds wide. Water to supplement rainfall was supplied by overhead irrigation. The experimental design was a randomized complete block with four replications. Treatment rows were surrounded by guard rows.

Male, female, and F₁ plants 1) were detasseled, 2) had the initial and subtending ears removed (deared), 3) were detasseled and deared, 4) had the top of the shoot (top two leaves) removed before tassel emergence and the tassel initials mechanically destroyed (decapitated), or 5) were left intact. Two of the male, female, and F₁ plants from each replication were chosen at random at developmental stages from V9 to seed harvest. Although inbred plants are not normally harvested at fresh market, they were rated at that stage to compare to F₁ plants. Also, F₁ plants were carried through seed harvest, although this is also not a normal field practice. Fresh-market and seed harvests were based on development of intact plants and were 20 and 50 days postanthesis, respectively. Senescence in all stalks and shanks and cobs of intact plants was rated as described previously.

Data in greenhouse and field experiments were analyzed with the general linear models procedures in SAS (SAS, Cary, N.C.).

Results

Stalk internodes

Greenhouse experiments. Plant developmental stage and the genotype source (male, female, F₁) affected senescence ratings in stalk internodes (Table 1). Senescence ratings for I6 to I8 were greatest at seed harvest, and for I9, I10, and the average of I6 to I10 were lowest at VT. Senescence ratings of the F₁ in I6 to I8 were more like the female parent. In I9, I10, and the average of I6 to I10 in F₁ plants, senescence ratings were significantly lower than either parent.

The interaction of developmental stage × genetic material affected senescence in I6, I7, and the average of I6 to I10 (Table 2). At VT, the senescence rating of the average of I6 to I10 in the F₁ plants was significantly less than the male and female parents. As plants aged, there was either no difference between genotypes or male plants had significantly higher senescence ratings than F₁ plants.

Field experiments. Plant developmental stage, the genotype, and type of neutering affected senescence ratings in stalk internodes (Table 3). In all internodes, senescence ratings increased as plants aged from VT to seed harvest. Senescence ratings of the F₁

Table 2. Stalk senescence ratings as affected by significant interactions for specific internodes in greenhouse grown plants.

Developmental stage	Genetic material	Internode (I) ^z		
		6	7	Avg (6–10)
Tassel (VT)	Male ^y	0.13 ^{NS}	0.69 ^{NS}	1.01 [*]
	F ₁	0.19	0.44	0.30
	Female	0.25 ^{NS}	0.63 ^{NS}	1.36 ^{**}
Silk (R1)	Male	0.60 ^{NS}	1.13 ^{NS}	2.30 ^{NS}
	F ₁	0.63	1.06	1.91
	Female	0.31 ^{NS}	0.38 ^{NS}	2.09 ^{NS}
Fresh market	Male	0.56 ^{NS}	1.25 ^{NS}	2.69 [*]
	F ₁	0.19	0.63	2.05
	Female	0.50 ^{NS}	1.38 ^{NS}	2.50 ^{NS}
Seed harvest	Male	3.00 ^{**}	4.00 ^{**}	3.83 [*]
	F ₁	1.38	2.94	3.19
	Female	1.81 ^{NS}	2.13 ^{NS}	2.88 ^{NS}

^zRange of ratings is 0 to 6 after Pappelis and Williams (1966).^yValues for the F₁ plants in the interaction are compared to the male or female parent.NS,*,** Nonsignificant or significant at $P = 0.05$ or 0.01 , respectively.

Table 3. Stalk internode senescence ratings^y in intact, detasseled, deearred, deearred and detasseled, and decapitated female and male parental, and F₁ field grown plants.^z

Treatment	Internode (I)					
	6	7	8	9	10	Avg
Stage (S)						
Tassel (VT)	0.2 c ^x	0.6 d	1.3 d	1.4 d	1.2 d	0.9 d
Silk (R1)	0.3 bc	1.0 c	2.2 c	2.8 c	2.9 c	1.8 c
Fresh market	0.5 b	1.4 b	2.7 b	3.5 b	3.6 b	2.3 b
Seed harvest	1.8 a	2.7 a	3.6 a	3.8 a	3.9 a	3.0 a
Genetic material (G)						
Male	0.9 a	1.8 a	2.8 a	3.2 a	3.0 a	2.3 a
F ₁	0.6 b	1.3 b	2.1 b	2.4 b	2.5 b	1.8 c
Female	0.6 b	1.1 b	2.3 b	3.0 a	3.1 a	2.0 b
Treatment (T)						
Intact	0.8 a	1.4 ab	2.5 ab	3.1 ab	3.1 ab	2.2 a
Detassel	0.6 a	1.6 a	2.8 a	3.3 a	3.2 a	2.2 a
Dear	0.8 a	1.4 ab	2.5 ab	2.9 bc	2.9 bc	2.1 ab
Detassel–deear	0.7 a	1.2 b	2.3 b	2.8 c	2.7 c	1.9 b
Decapitate	0.6 a	1.3 ab	2.0 c	2.2 d	2.3 d	1.6 c
Interaction						
S × G	**	**	*	**	**	**
S × T	NS	NS	NS	**	NS	*
T × G	NS	NS	NS	NS	NS	NS
S × T × G	NS	NS	NS	NS	NS	NS

^zAll internode ratings at mid-whorl (V9) were 0.0; N = 8 at each sampling time.

^yRatings are from 0 to 6 (after Pappelis and Williams, 1966).

^xValues in a column followed by the same letter are not significantly different (Duncan's multiple range test, $P \leq 0.05$).

NS, *, ** Nonsignificant or significant at $P = 0.05$ or 0.01 , respectively.

Table 4. Stalk senescence ratings as affected by significant interactions in field grown plants.

Developmental stage	Genetic material	Internode (I) ^z					
		6	7	8	9	10	Avg
Tassel (VT)	Male ^y	0.35 ^{NS}	0.84*	1.78**	1.94**	1.55**	1.27**
	F ₁	0.23	0.40	0.75	0.40	0.20	0.39
	Female	0.10 ^{NS}	0.37 ^{NS}	1.33*	2.01**	2.02**	1.16**
Silk (R1)	Male	0.25 ^{NS}	1.36*	2.40 ^{NS}	3.16**	3.00*	2.01**
	F ₁	0.45	0.89	1.96	2.38	2.57	1.64
	Female	0.25 ^{NS}	0.61 ^{NS}	2.22 ^{NS}	2.81*	2.98 ^{NS}	1.76 ^{NS}
Fresh market	Male	0.65*	1.75 ^{NS}	3.10**	3.75**	3.69 ^{NS}	2.55**
	F ₁	0.33	1.54	2.29	3.06	3.40	2.04
	Female	0.60 ^{NS}	1.14 ^{NS}	2.79*	3.71**	3.83 ^{NS}	2.47**
Seed harvest	Male	2.33**	3.41*	4.01 ^{NS}	3.89 ^{NS}	3.93 ^{NS}	3.31 ^{NS}
	F ₁	1.73	2.87	3.59	3.96	3.85	3.14
	Female	1.29*	1.78**	3.09 ^{NS}	3.59 ^{NS}	3.83 ^{NS}	2.67**
Neutering treatment							
Silk (R1)	Intact				3.29 ^y		2.10
	Detassel				3.46 ^{NS}		2.22 ^{NS}
	Dear				2.85*		1.93 ^{NS}
	Detassel–deear				2.63 ^{NS}		1.63 ^{NS}
	Decapitate				1.65**		1.13**
Fresh market	Intact				3.58		2.26
	Detassel				1.65**		1.13*
	Dear				3.79**		2.41*
	Detassel–deear				3.88 ^{NS}		2.68 ^{NS}
	Decapitate				3.44 ^{NS}		2.39 ^{NS}

^zRange of ratings is 0 to 6 after Pappelis and Williams (1966).

^yValues for the F₁ plants in the interaction are compared to the male or female parent.

NS, *, ** Nonsignificant or significant at $P = 0.05$ or 0.01 , respectively; least squares means.

Table 5. Shank internode and cob senescence ratings^z in greenhouse and field grown parental and F₁ plants at fresh market and seed harvest.^y

Treatment	Greenhouse					Field				
	Internode (I)				Cob	Internode (I)				Cob
	1	2	3	4		1	2	3	4	
Genetic material										
Male parent	1.8 b ^x	2.2 a	2.1 a	1.8 a	3.2 b	1.3 b ^y	1.4 b	1.9 ab	1.9 a	3.5 b
F ₁	1.3 b	1.6 a	1.9 a	1.8 a	3.4 b	2.7 a	2.7 a	2.8 a	1.8 a	3.9 a
Female parent	3.5 a	2.5 a	2.5 a	2.2 a	4.0 a	1.5 a	1.7 b	1.3 b	1.7 a	3.4 b
Stage										
Fresh market	1.4 b	1.4 b	1.7 b	1.5 b	3.4 b	1.5 b	1.7 a	1.8 a	1.3 b	3.5 a
Seed harvest	3.7 a	3.8 a	3.8 a	3.4 a	4.0 a	2.2 a	2.2 a	2.3 a	2.3 a	3.7 a

^zRatings are from 0 to 6 (after Pappelis and Williams, 1966).

^yFor greenhouse plants male and female N = 9 and for F₁ N = 33, and for field plants N = 8 at each sampling time;

^xValues in a column followed by the same letter are not significantly different, Duncan's multiple range test ($P \leq 0.05$); there were no significant interactions.

in I6 to I8 were more like the female parent, and in I9, I10, and average of I6 to I10 were less than both parents. The lowest senescence ratings for I8 to I10 and the average of I6 to I10 were in decapitated plants.

Senescence rating was affected by the interaction of developmental stage $\times$ genetic material in I6 to I10 and the averages of I6 to I10 (Table 4). As internodes were higher on the stalk and as developmental stage advanced through fresh market, senescence ratings of F₁ plants were equal to both parents, less than both parents, or less than the male and equal to the female parent. At seed harvest, the senescence rating of the male parent and the F₁ were greater than the female in I6 and I7, and for the average of I6 to I10 male and F₁ plants were similar and greater than the female parent.

The developmental stage $\times$ neutering treatment interaction affected internode senescence ratings of I9 and the average of I6 to I10 (Table 4). At R1 in I9 and the average of I6 to I10, decapitated plants had the lowest senescence ratings. At fresh market, these internodes in detasseled plants had the lowest senescence ratings.

Shank and cob senescence

Greenhouse experiment. Senescence ratings in some shank internodes and cobs were affected by genetic material and developmental stage (Table 5). Senescence ratings in the first shank internode in F₁ plants were like those of the male parent and equal to both parents for all other internodes. Cob senescence rating was the same for male and F₁ plants and increased from fresh market to seed harvest.

Field experiment. Senescence in some shank internodes was affected by the genetic material and developmental stage, while cob senescence was only affected by genotype (Table 5). Senescence ratings in the shanks of F₁ plants in the 1) first internode were more like the female parent, 2) second internode were greater than both parents, 3) third internode were closer to the male parent, and 4) fourth internode were equal to both parents. Between fresh-market and seed harvest, senescence ratings for the first and fourth shank internodes increased and for the second and third internodes were the same. At fresh-market and seed harvest, cob senescence rating were greater than for both parents. Cob senescence ratings of the F₁ plants were greater than both parents.

Discussion

Senescence in stalk internodes of greenhouse and field grown parental plants generally progressed in the same manner. That is,

senescence rating increased as plants aged from V9 to seed harvest. Also, the pith tissue in internodes lower on the stalk (I6 to I7) progressed to full senescence at a slower rate than those that would be below ear bearing nodes (I9 to I10).

The period between VT and R1 appears to be important in the onset of stalk internode senescence. This response has been noted previously (Russo, 1995b). By R1 internodes below nodes giving rise to the primary ear had higher senescence ratings than those lower on the stalk. It may be that once the tassel is produced there is a rapid redistribution of resources to support the formation of fruit. There also appears to be genetic control of senescence since F₁ plants exhibited senescence ratings that were lower than one or both parents. For this cultivar, hybrid vigor appears to suppress the onset of senescence in internodes below the ear bearing nodes. It is likely because of this that once plants become established in the field the problems of stalk rots and lodging are minimized through fresh-market harvest. Cobs were almost completely senescent at fresh market, but <50% of the tissues in shank internodes were senescent.

Colonization of shank tissue from infected stalks could be retarded if cells in shanks are in a juvenile state and contain fungal inhibiting glucosides (BeMiller and Pappelis, 1965). This would also reduce risk of kernel infection in fresh market ears. Colonization of kernels can still occur with infection by airborne fungal spores through silks, or damage of ears by insects.

For inbreds, where the aim is to produce seed, cobs were almost completely senescent and shank internodes were >50% senescent, which would make them susceptible to infection and colonization by fungi. This combination of factors could contribute to infection of kernels, with or without obvious signs (Kedera et al., 1992), which may lead to reduced vigor in F₁ seed (Wann, 1980).

Selfing parental material will likely cause stalks of parental plants to exhibit higher senescence ratings and therefore continue to contribute to the problems associated with reduced tissue integrity. In field grown plants, removing the tassel before emergence (decapitation) significantly reduced senescence overall, while detasseling after emergence reduced senescence at the important fresh-market harvest developmental stages in internodes below ear bearing nodes. This may be due to the prevention of formation of growth regulating substances associated with male anthesis.

Genetic opportunities may exist to improve *sh2* inbreds and F₁ plants by selecting for maintenance of the juvenile condition. The destruction of the tassel before emergence may slow the onset of senescence, which may be a beneficial aspect of typical seed production practices.

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