

# VEGETATIVE PHASE CHANGE IN SWEET CORN POPULATIONS: GENETICS AND RELATIONSHIP WITH AGRONOMIC TRAITS<sup>1</sup> (VEGETATIVE PHASE CHANGE IN OPEN-POLLINATED SWEET CORN)

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**ABSTRACT** - Vegetative development in maize can be divided into juvenile and adult phases, each with distinct anatomy and physiology. Transition from juvenile to adult vegetative growth may have some adaptive value since adult leaves have increased photosynthetic rates, xeromorphism, and resistance to certain insects and diseases. Variation in the timing of this transition (i.e., the node(s) at which phase change occurs) may be associated with agronomic performance. Our objectives were to investigate the genetics of the timing of vegetative phase change and the relationship between phase-specific developmental and agronomically important traits in a diallel among open-pollinated sweet corn cultivars. Significant variability existed for most developmental traits evaluated in this study. Environmental effects were significant for some traits, whereas genotype x environment interaction (G x E) was significant only for number of leaves above the ear. General combining ability was significant and specific combining ability was not significant for most phase-specific developmental traits. Last leaf with juvenile wax and first leaf with adult wax were positively correlated. Ear leaf and total leaf number were not correlated with other phase-specific developmental traits. Flowering time was negatively correlated with first leaf with adult wax but was not correlated with last leaf with juvenile wax or last node with adventitious roots, indicating that some aspects of vegetative phase change are not associated with the transition to reproductive growth. Yield was not associated with any developmental trait in this study. First leaf with adult wax and last leaf with juvenile wax may be useful in selection indices, since they were not influenced by the environment, had no G x E interaction in this study, and have been associated with insect and disease resistance in previous studies.

**KEY WORDS:** *Zea mays* L.; Development; Combining ability.

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## INTRODUCTION

Vegetative development in maize can be divided into juvenile (basal) and adult (distal) phases, each with distinct morphology and physiology (POETHIG, 1990). Juvenile leaves typically are short and narrow, lack bulliform cells and trichomes, have a thin cuticle, and are covered with an epicuticular waxy bloom. This juvenile, epicuticular wax is readily visible due to its grayish appearance and ability to cause water to bead upon wetting (AVATO *et al.*, 1987; BIANCHI and MARCHESI, 1960). Juvenile nodes produce adventitious roots, and axillary buds develop into tillers. Adult leaves are longer and wider than juvenile leaves, have bulliform cells, three types of trichomes (macrohairs, bicellular, and prickle), a thick cuticle, and lack the epicuticular wax of juvenile leaves. Instead, a cuticular wax is visible, which gives adult leaves a glossy appearance and increased wettability compared to juvenile leaves (AVATO *et al.*, 1987; BIANCHI and MARCHESI, 1960). Adult nodes do not produce adventitious roots. Axillary buds at adult nodes either develop into ear shoots or are suppressed. Morphological traits associated with each phase can be used as markers to determine the developmental timing of vegetative phase change (i.e., the node number at which juvenile traits no longer occur and/or adult traits are initiated).

Heterochrony is variation in the timing of development, which is best evidenced by the dissociation of developmental phases that are independently regulated (LORD and HILL, 1987; RAFF and KAUFMAN, 1983). The existence of heterochronic mutants (*Corngrass1* (*Cg1*), *glossy15* (*gl15*), *Teopod1* (*Ip1*), *Teopod2* (*Ip2*)), which alter the timing of vegetative but not reproductive development, suggests that heterochrony has a strong genetic basis in maize (EVANS *et al.*, 1994; GALINAT, 1953; MOOSE and SISCO, 1994; POETHIG, 1988). They also provide strong evidence that, rather than being a prerequisite for flowering, vegetative phase change is regulated

independently from reproductive phase change (POETHIG, 1990).

Studies of heterochronic mutants indicate that vegetative phase change is not a rapid switch from juvenile to adult-vegetative phase, but rather a transition involving independently regulated, overlapping developmental programs (POETHIG, 1988, 1990). Adult-vegetative traits are initiated before juvenile traits are fully repressed, creating a transition zone in which organs have characteristics of both phases. For example, adult and juvenile wax sectors are clearly evident in transition leaves in most backgrounds. The length of this transition zone depends on the duration of the juvenile-vegetative phase and the node at which adult-vegetative traits are initiated. The transition normally occurs between leaves five and eight, although earlier and later, and shorter and longer, transition zones have been observed (POETHIG, 1990; POETHIG and PASSAS, 1993).

Independent regulation of vegetative and reproductive phases suggests that heterochrony may have some adaptive value, per se, in maize as has been proposed for other plant species (LORD and HILL, 1987). Adult leaves have increased photosynthetic activity (THIAGARAJAH *et al.*, 1981), xeromorphism (ESAU, 1977), and resistance to certain insects and diseases relative to juvenile leaves (ABEDON and TRACY, 1996; BERGVINSON, 1993; HEADRICK and PATAKY, 1987; HOOKER, 1985; LEONARD and THOMPSON, 1976). Consequently, alterations in the timing of vegetative phase change may be a source of variability for agronomic performance. Vegetative phase change has been investigated with regard to disease and insect resistance, but not other agronomic traits. ABEDON and TRACY (1995, 1996) found that resistance to common rust (*Puccinia sorghi* Schw.) and European corn borer (*Ostrinia nubilalis* Hubn.) is associated with length of the juvenile-vegetative phase. PASSAS and POETHIG (1995) found that accelerated transition to an adult epidermis in leaves of *gl15* mutants resulted in increased resistance to European corn borer relative to wild-type siblings.

Use of developmental markers of vegetative phase change in breeding programs would depend on their heritability, type of gene action, and relationship with agronomic traits. If an association between specific developmental phases and agronomic performance is determined, selection for morphological markers associated with vegetative phases may be useful in selection indices or to indirectly select for agronomic traits with low heritability. Selection for vegetative traits would not affect flowering time given the independent regulation of vegetative and reproductive phase change. Our objectives

were to investigate variability in the timing of vegetative phase change, its genetics, and the relationship between vegetative phase change and agronomically important traits in a diallel among open-pollinated sweet corn cultivars.

## MATERIALS AND METHODS

Six open-pollinated (OP) sweet corn cultivars were used as parents in a diallel cross (method II of GRIFFING, 1956) made in 1993. 'Country Gentleman', 'Golden Bantam', 'Lindsay Meyer Blue' and 'Stowell's Evergreen' were from a collection maintained at the College of Agricultural and Life Sciences, University of Wisconsin-Madison. 'Howling Mob' (SS IA DR G) was acquired from the Seed Saver collection (ADELMANN *et al.*, 1993), and 'Pease Crosby' (PI 255983) from the North Central Regional Plant Introduction Center, Ames, Iowa. These cultivars were chosen because of their historical importance and contribution to modern sweet corn cultivars (GRIBDES *et al.*, 1995; REVILLA and TRACY, 1995a, b; TRACY, 1994).

The 15 hybrids and six parents were planted on 16 May 1994 and 8 June 1994 at the West Madison Agricultural Research Station, Madison, WI in a Plano silt loam (fine-silty, mixed, mesic Typic Argiudolls). These planting dates are within the range used by sweet corn producers in Wisconsin but represent widely varying growing conditions. Early plantings in the Midwest normally provide more favorable conditions for sweet corn production relative to late plantings, which typically are exposed to more environmental stress, including infestation by common rust and Maize Dwarf Mosaic Virus (MDMV), and cooler late season growing conditions. The experimental design was a randomized complete block with three replications per planting date. Four-row plots were overplanted with 30 seeds per row and thinned to a final density of approximately 44 500 plants ha<sup>-1</sup> for each planting date. The first planting date had rows 3.5 m long with a final stand of 15 plants per row while the second planting date had rows 4.1 m long with a final stand of 17 plants per row. Rows were 76 cm apart for both planting dates. All data were taken on the center two rows of each four-row plot.

Several phase-specific developmental traits were used to determine the timing of vegetative phase change. Because the juvenile and adult-vegetative phases are independently regulated, traits associated with each vegetative phase were scored separately. The duration of the juvenile phase was determined visually based on the last leaf with juvenile (epicuticular) wax, number of tillers, and last node with adventitious roots. The initiation of adult-vegetative growth was determined as the first leaf in which adult (cuticular) wax was visible. Because *Cg1*, and the Teopod mutants have increased leaf number below the uppermost ear (relative to wild-type) due to an elongated juvenile-vegetative phase (GALINSAT, 1953; POETHIG, 1988), we also scored total leaf number, ear leaf number, and number of leaves above the uppermost ear in order to determine if variation in the timing of vegetative phase change in these populations affects leaf number. Additional traits evaluated included the number of leaves below the uppermost ear with adult wax visible over the entire blade, and the percentage of leaves in the transition zone (i.e., having sectors of juvenile and adult wax).

The following agronomic traits were recorded and analyzed for a previously reported study of heterotic patterns among open-pollinated sweet corn cultivars (REVILLA and TRACY, 1996): days to 50% anthesis, days to 50% silking, prolificacy, plant height meas-

TABLE 1 - Mean squares from the analysis of variance of phase-specific developmental traits for 15 hybrids from a diallel among six open-pollinated sweet corn cultivars over two planting dates.

Source	df	Mean Square								
		Last juvenile wax <sup>a</sup>	Tiller number	Last adv. roots	First adult wax	Ear leaf number	Number leaves above ear	Total leaf Number	Adult wax below ear	Percent transition leaves
Planting Date	1	— <sup>b</sup>	10.9 <sup>c</sup>	12.5 <sup>oo</sup>	—	15.2 <sup>*</sup>	—	18.3 <sup>oo</sup>	15.1 <sup>oo</sup>	—
Hybrid	14	1.7 <sup>oo</sup>	—	0.3 <sup>oo</sup>	0.5 <sup>oo</sup>	4.3 <sup>oo</sup>	0.6 <sup>oo</sup>	7.1 <sup>oo</sup>	7.7 <sup>*</sup>	46.4 <sup>oo</sup>
GCA	5	3.9 <sup>oo</sup>	—	0.7 <sup>oo</sup>	1.2 <sup>oo</sup>	11.8 <sup>oo</sup>	1.5 <sup>oo</sup>	19.5 <sup>oo</sup>	20.3 <sup>*</sup>	96.2 <sup>oo</sup>
SCA	9	—	—	—	—	—	—	—	—	18.7 <sup>*</sup>
Hybrid x Pl. Date	14	—	—	—	—	—	0.14 <sup>c</sup>	—	—	—
Error	29	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.3	5.8

<sup>a</sup> Last juvenile wax = last leaf with juvenile wax; Last adv. roots = last node with adventitious roots; First adult wax = first leaf with adult wax visible; Adult wax below ear = number of leaves below the uppermost ear with adult wax visible over the entire blade; Percent transition leaves = percentage of leaves in the transition zone.

<sup>b</sup> —, <sup>c</sup> \*, <sup>oo</sup> non-significance, significant at 0.05 and 0.01 probability levels, respectively.

TABLE 2 - Means of phase-specific developmental traits for six parents, per se, and 15 hybrids over three replications and two planting dates.

Genotype	Last juvenile wax <sup>a</sup>	Last adv. roots	First adult wax	Ear leaf number	Number leaves above ear	Total leaf number	Adult wax below ear	Percent trans. leaves
<i>Parents, per se</i>								
Country Gentleman	7.8	6.0	5.1	11.1	7.2	18.2	3.3	15.2
Golden Bantam	9.6	6.2	6.3	9.3	5.8	15.1	-0.3	21.3
Howling Mob	8.2	6.3	6.0	9.8	6.2	16.1	1.6	13.6
Lindsey Meyer Blue	8.9	6.7	6.4	10.4	6.5	16.9	1.5	14.9
Pease Crosby	9.7	6.0	6.2	7.9	5.7	13.6	-1.8	25.1
Stowell's Evergreen	9.8	6.6	6.3	12.2	6.4	18.6	2.4	18.5
<i>Hybrids<sup>b</sup></i>								
CGxGB	8.9	6.0	5.7	10.4	6.6	17.0	1.5	19.4
CGxHM	7.9	5.8	5.5	10.7	6.7	17.4	2.8	14.1
CGxLM	8.5	6.2	5.7	10.9	6.9	17.8	2.4	15.8
CGxPC	9.3	6.0	6.1	10.0	6.6	16.7	0.7	19.5
CGxSE	8.7	6.2	6.1	11.8	6.9	18.6	3.1	14.1
GBxHM	8.7	6.1	6.0	9.6	5.9	15.6	1.0	17.5
GBxLM	9.1	6.5	6.5	10.1	6.3	16.4	1.0	16.0
GBxPC	9.8	6.2	6.3	8.9	6.0	14.9	-0.9	23.6
GBxSE	9.2	6.5	6.1	10.8	6.2	16.9	1.6	18.1
HMxLM	8.6	6.4	6.2	9.9	6.6	16.4	1.2	15.0
HMxPC	8.2	6.1	6.1	9.0	6.0	15.1	0.9	14.0
HMxSE	8.6	6.4	5.9	11.0	6.4	17.4	2.4	15.1
LMxPC	9.6	6.2	6.5	9.1	6.2	15.4	-0.5	20.1
LMxSE	9.0	6.6	6.2	11.3	6.6	17.9	2.3	15.8
PCxSE	9.5	6.1	6.3	10.0	6.2	16.2	0.5	19.5
LSD, 5%	0.8	0.3	0.5	0.4	0.3	0.5	0.7	2.8

<sup>a</sup> Last juvenile wax = last leaf with juvenile wax; Last adv. roots = last node with adventitious roots; First adult wax = first leaf with adult wax visible; Adult wax below ear = number of leaves below the uppermost ear with adult wax visible over the entire blade; Percent trans. leaves = percentage of leaves in the transition zone.

<sup>b</sup> CG = Country Gentleman; GB = Golden Bantam; HM = Howling Mob; LM = Lindsey Meyer Blue; PC = Pease Crosby; SE = Stowell's Evergreen.

TABLE 3 - Pearson correlation coefficients (n=21) between agronomic and phase-specific developmental traits in a diallel among six open-pollinated sweet corn cultivars.

Genotype	Last juvenile wax <sup>a</sup>	Last adv. roots	First adult wax	Ear leaf number	Number leaves above ear	Total leaf number	Adult wax below ear	Percent trans. leaves
<i>Phase-specific developmental</i>								
Last adv. roots	— <sup>b</sup>							
First adult wax	0.75 <sup>c</sup>	0.53						
Ear leaf number	—	—						
N. leaves above ear	-0.53	—	-0.61	0.72				
Total leaf number	—	—	—	0.98	0.84			
Adult wax below ear	-0.66	—	-0.59	0.90	0.80	0.92		
Percent trans. leaves	0.82	—	—	-0.56	-0.58	-0.60	-0.80	
<i>Agronomic</i>								
Anthesis date	—	—	-0.60	0.81	0.73	0.84	0.77	—
Silking date	—	—	-0.60	0.75	0.69	0.78	0.71	—
Prolificacy	—	0.52	0.44	—	—	—	—	—
Plant height	—	—	—	0.78	0.44	0.74	0.65	—
Ear height	—	—	-0.44	0.88	0.56	0.84	0.78	—
Ear length	—	—	—	—	—	—	—	—
Ear diameter	—	—	-0.46	0.45	0.46	0.48	0.50	—
Row number	—	-0.48	-0.60	—	0.48	—	—	—
Yield	—	—	—	—	—	—	—	—

<sup>a</sup> Last juvenile wax= last leaf with juvenile wax; Last adv. roots= last node with adventitious roots; First adult wax= first leaf with adult wax visible; Adult wax below ear= number of leaves below the uppermost ear with adult wax visible over the entire blade; Percent trans. leaves= percentage of leaves in the transition zone.

<sup>b</sup>— non-significant at  $p < 0.05$ .

<sup>c</sup> Coefficients with absolute value over 0.43, 0.55, and 0.67 are significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

ured at the collar of the flag leaf (cm), ear height measured at the collar of the leaf subtending the uppermost ear (cm), ear length (cm), ear diameter (cm), kernel row number, and kernel yield at 15% moisture ( $Mg\ ha^{-1}$ ).

Analyses of variance (ANOVA) including parents and hybrids were performed for each of the nine phase-specific developmental traits combined across planting dates. ANOVA was also performed for hybrids so that combining ability effects could be determined. Cultivar effects were considered fixed and other effects random. Pearson correlation coefficients were determined after pooling data over blocks and planting dates ( $n = 21$ ). SAS was used for combined analysis of variance and correlation analysis (SAS, 1989). Combining abilities were computed using the program 'Diallel analysis and simulation' (BURROW and COORS, 1994).

## RESULTS AND DISCUSSION

Planting date effects were significant for all phase-specific developmental traits except first leaf with adult wax, last leaf with juvenile wax, number of leaves above the ear, and percentage transition leaves while hybrid effects were significant for all traits except tiller number (Table 1). All traits had non-significant genotype x environment (G x E) interaction ex-

cept number of leaves above the ear. Planting dates resulted in substantially different environments and in a related study on agronomic traits in the same diallel, significant G x E effects for about half the traits (days to 50% anthesis and silking, prolificacy, and yield) were observed (REVILLA and TRACY, 1996). These results suggest that last leaf with juvenile wax, first leaf with adult wax, and percentage transition leaves are highly heritable. When analyzed together, parent and hybrid effects were significant for all traits except tiller number (data not shown).

Last leaf with juvenile wax ranged from 7.8 for Country Gentleman to 9.7 for Pease Crosby and 9.8 for Stowell's Evergreen while first leaf with adult wax ranged from 5.1 for Country Gentleman to between 6.0 and 6.4 for the other parents (Table 2). These data indicate that Country Gentleman had an accelerated vegetative phase change relative to the latter two genotypes. Yet, Country Gentleman and Stowell's Evergreen had the most leaves (approximately 18.5) and were late-flowering, while Pease Crosby had the fewest leaves (13.6) and was early-flowering (REVILLA and TRACY, 1996). Leaves with adult wax visible over

the entire blade occurred below the uppermost ear for all parents except Golden Bantam and Pease Crosby, and most hybrids (Table 2). Pease Crosby had nearly two leaves with juvenile wax above the uppermost ear node. Together, these results indicate that vegetative phase change and reproductive development are coordinated differently in the varying genetic backgrounds evaluated in this study.

Adventitious roots occurred up to the sixth or seventh node and tillers were present in almost every plant (Table 2). Because tiller number did not vary among genotypes but other phase-specific developmental traits did vary, tiller number is not a reliable indicator of the timing of vegetative phase change in these populations and hybrids. The percentage transition leaves ranged from 13.6 for Howling Mob to 25.1 for Pease Crosby. Hybrid values were generally close to the midpoint of parent values for all phase-specific developmental traits.

General combining ability (GCA) was highly significant for every trait with significant variability while specific combining ability (SCA) was significant only for the percentage transition leaves. This indicates that intrapopulation recurrent selection schemes should be effective in altering these developmental traits.

First leaf with adult wax was positively correlated with last leaf with juvenile wax and last node with adventitious roots, indicating that the timing of the end of the juvenile-vegetative phase and initiation of the adult-vegetative phase were associated in this study (Table 3). Last leaf with juvenile wax was positively correlated with percentage transition leaves while first leaf with adult wax was not. Since last leaf with juvenile wax was not correlated with total number of leaves (a component of percentage transition leaves), these data suggest that the length of the transition zone between vegetative phases is dependent more on the timing of the juvenile than the adult-vegetative phase, even though the latter two developmental events are associated.

REVILLA and TRACY (1996) reported significant parent and hybrid effects for all agronomic traits except prolificacy and ear length. Planting date effects occurred for about half the traits (days to 50% anthesis and silking, prolificacy, and yield), due to changes in both order and magnitude.

Last leaf with juvenile wax and percent transition leaves were not correlated with any agronomic traits (Table 3). First leaf with adult wax was positively correlated with prolificacy and negatively correlated with days to 50% anthesis and silking, ear height, ear diameter, and row number. Last node with adventitious roots

was positively correlated with prolificacy and negatively correlated with row number. Ear leaf number, number of leaves above the ear, total leaf number, and number of leaves below the uppermost ear with adult wax visible over the entire blade were positively correlated with each other, days to 50% anthesis and silking, ear and plant height, and ear diameter, and negatively correlated with percentage transition leaves. Unlike studies involving heterochronic mutants, no correlation between ear leaf or total leaf number and most phase-specific developmental traits was observed, indicating that number of leaves is not a reliable marker of vegetative phase change in these populations.

Although some phase-specific developmental traits were correlated with several agronomic traits, none were significantly correlated with yield. Therefore, selecting for changes in phase-specific developmental traits should not affect yield in these populations and hybrids. Two developmental traits, first leaf with adult wax and last leaf with juvenile wax, were not affected by the environment and displayed no G x E interaction. These two traits may be the best indicators of vegetative phase change (relative to other traits evaluated in this study) and may be useful when selecting for associated insect and disease resistances. Their use in breeding programs deserves further investigation. Due to high GCA and low SCA values, per se selection should be effective in altering these traits. Since sweet corn represents a relatively narrow genetic base with in maize (REVILLA and TRACY, 1995a,b) further investigation of the relationship between the timing of vegetative phase change and agronomic traits in other maize backgrounds would be useful. These studies are currently in progress.

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