

Influence of *wp* on Pod Characteristics and Agronomic Traits of Soybean Lines

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Introduction

Homozygous recessive *wp* alleles produce pink flower color in soybean when in the presence of the non-allelic gene *W1*[\[Soybase\]](#) by modifying the expression of purple pigmentation ([Stephens and Nickell, 1992](#)). [Stephens et al. \(1993\)](#) found no differences between pink and near-isogenic purple-flowered soybean lines for the agronomic traits yield, maturity, height, lodging, and seed quality. Pink flower soybeans differ from magenta flowered soybeans, which have the genotype *W1_wmwm*[\[Soybase\]](#). Magenta flower color lines were associated with a 3% reduction in yield, attributed to a lower photosynthetic rate and earlier leaf senescence compared with purple-flowered Harosoy[\[GRIN\]](#) ([Buzzell et al., 1977](#)).

[Stephens et al. \(1993\)](#) observed that two-seeded pods were more prevalent in pink flowered lines, while purple-flowered lines produced proportionally more three-seeded pods. However, seeds per pod or pods per plant were not counted to determine the possible effect of *wp* upon pod characteristics. In petunia and maize, it was determined that flavonols are required in the pollen grain to initiate pollen tube growth and ensure successful fertilization ([Taylor, 1995](#)). The most diverse group of flavonol compounds is the anthocyanins, which generate pigmentation in floral tissues. In soybean, the *wp* locus is thought to modify anthocyanin production to generate pink flowers instead of purple flowers, however it is unknown if there is a relationship between anthocyanin modification and seeds per pod, or pods per plant.

Other studies have found a relationship between leaflet shape and seeds per pod ([Bernard and Weiss, 1973](#)). The recessive gene *ln*[\[Soybase\]](#) is responsible for both narrow leaflet shape and a predominance of four-seeded pods. Another gene for leaflet shape, *lo*[\[Soybase\]](#), is associated with few-seeded pods ([Domingo, 1945](#)).

In the literature, there are no reports relating flower color with seeds per pod or loculi per pod. The objective of this study was to describe the influence of *w_p* upon pod characteristics and agronomic traits when crossed into a different genetic background.

Materials and Methods

The materials in this study were F5-derived lines from the cross LN89-5322-2 (*W1W1wpwp*) ([Stephens et al., 1993](#)) x 'Burlison'[GRIN] (*w1w1WpWp*) ([Nickell et al., 1990](#)), or its reciprocal. F2-derived families were generated based upon flower color with no selection pressure for agronomic characteristics. In the summer of 1994, individual plants from seven F2:5 families were selected at the University of Illinois Crop Sciences Research and Education Center, Urbana-Champaign IL. These families represent four possible combinations of flower color from this cross. Two families segregated pink/white (*W1w1wpwp*)(LNPk90-107-2-36 and LNPk90-114-1-15), two segregated purple/pink (*W1W1Wpwp*)(LNPk90-107-1-33 and LNPk90-107-1-18), one segregated purple/white (*W1w1WpWp*)(LNPk90-107-1-12), and two segregated purple/pink/white (*W1w1Wpwp*)(LNPk90-107-3-6 and LNPk90-1-27) for flower color ([Table 1](#)). Both pink/white families and one purple/pink family also segregated for pubescence color. From each family approximately 120 plants were tagged by flower color, and the total number of seeds and loculi of each pod were counted for each plant. One hundred plants were selected from each of the seven families, based on total seeds produced, for single progeny line testing in 1995. An equal number of plants with each flower color were selected from each family and each plant represents a replication of the effect a particular genotype may have upon agronomic traits.

Progeny rows were planted 3 June, 1995 at the University of Illinois Crop Sciences Research and Education Center, Urbana-Champaign IL, and were blocked by family in the field. Each block included the parental lines and Kenwood[GRIN] ([Cianzio et al., 1990](#)) so that each of the seven blocks contained a total of 115 entries. The cultivar Chapman[GRIN] ([McBlain et al., 1991](#)) was planted in every other row to serve as a common border. A common border allowed an additional estimate of soil fertility variation across the field and equalized the border effect of neighboring plots. Each plot consisted of one row, 2.3 m long, with 76 cm between row spacing, planted at 40 seeds per row.

Nine agronomic traits were recorded during and after the growing season, including:

1. yield (t ha⁻¹, adjusted for 130 g kg⁻¹ moisture)
2. plant height (cm) at harvest
3. maturity (date when at least 95% of the plants were physiologically mature)
4. seed weight (cg), based on weight of 100 seeds

5. seed quality, based on the amount of wrinkled and discolored seed (on a scale of 1 = good to 5 = poor)
6. seed protein (g kg⁻¹)
7. seed oil (g kg⁻¹)
8. loculi per pod
9. seeds per pod

Protein and oil concentrations (g kg⁻¹) of a clean 25 g sample were determined with near-infrared reflectance ([Rinne et al., 1975](#)) at the [National Center for Agricultural Utilization Research](#), Peoria, IL. Mean values for loculi per pod and seeds per pod were estimated by sampling four plants from selected lines ([Table 2](#)). These selected lines were homogenous for flower color and were selected from four families that represented each of the flower-color segregation types ([Table 2](#)). Lines were harvested 25 September, 2 October, and 4 October, 1995.

To account for spatial variability in the field, a modified nearest neighbor analysis was used ([Scharf and Alley, 1993](#)). The field was divided into grids consisting of 18 units of approximately the same area. Each unit was five or six plots deep and 16-18 rows wide. Two rows of Chapman were randomly selected from each grid unit from which to record the nine agronomic traits. From those two Chapman rows, a unit mean was calculated for yield, seed weight, seed protein, and seed oil. The overall Chapman mean (averaged across the entire experimental area) was divided by the unit mean to calculate a trait adjustment factor for each grid unit. Trait values for each line (including the standards) were multiplied by the appropriate factor to produce a new value adjusted for field position.

Statistical comparisons were made among flower color types within each family for each of the recorded agronomic traits. Student *t*-tests with alpha = 0.05 were used to compare means of purple, pink, and white flower color types. Correlation analysis was performed among the recorded agronomic traits to determine the influence of flower color on these relationships. Although correlation coefficients were calculated among all traits, the emphasis was to determine any relationships between yield and protein, oil and protein, and loculi per pod and seed weight. A correlation coefficient was calculated to find the relationship between single plant data from 1994 and progeny line data from 1995. The CORR procedure in SAS was used to calculate Pearson correlation coefficients for each flower color within a family ([SAS Institute, 1988](#)).

Results and Discussion

Overall, *W1W1* lines did not significantly differ from *w1w1* lines for yield, seed protein and seed weight ([Tables 1, 2](#)). Three families were heterogeneous for the *W1* locus and homogeneous for the *Wp* locus. Within one of those families (LNPk90-114-1-15), seed weight and protein of *W1W1* lines was higher than *w1w1* lines. No differences were identified between *W1W1* and *w1w1* lines in the

other two families. The results suggest that in this cross, the *W1* locus does not influence the measured agronomic traits.

In contrast, differences in agronomic traits were evident when *W1W1wpwp* (pink flower) lines were compared with *W1W1WpWp* (purple flower) lines. The data shows *wpwp* appears to be associated with reduced seed yield, fewer loculi per pod, fewer seeds per pod, and higher seed protein concentration compared to *WpWp* lines ([Tables 1, 2](#)). Within four families (LNPk90-107-1-33, LNPk90-107-1-18, LNPk90-107-3-6 and LNPk90-107-1-27), *WpWp* lines averaged higher yield than *wpwp* lines, with an average yield advantage of 11% ([Table 1](#)). These data differ from [Stephens et al. \(1993\)](#), who found no significant yield difference between pink- and purple-flowered F5:6 plant rows. In addition, pink-flowered material in this study did not exhibit earlier leaf senescence than purple-flowered lines from the same family. These data differ from magenta flowered lines (*W1_wmwm*), in which the reduction in seed yield was attributed to lower photosynthetic rate and earlier leaf senescence.

Yield differences in this study may be attributed to a reduction in seeds per pod associated with *wp* ([Table 2](#)). A comparison of purple- and pink-flowered lines within two different families (LNPk90-107-1-33 and LNPk90-107-3-6) in 1995 revealed that *WpWp* lines averaged 20% more loculi per pod and 24% more seeds per pod than *wpwp* lines. However, mean values for *wpwp* progeny lines were significantly higher than mean values of the pink-flowered parent, LN89-5322-2, in three of four families ([Table 2](#)).

The influence of *wp* on seeds per pod and loculi per pod appeared even when pink flower color phenotype was not expressed. White-flowered lines in the purple/pink/white family (LNPk90-107-3-6) include *Wp* and *wpwp*, however, purple and pink pigmentation will not be generated in the presence of *w1w1*. Mean values for loculi per pod and seeds per pod of white-flowered lines were between the values of purple- and pink-flowered lines ([Table 2](#)). White flowered lines were not always intermediate of purple and pink for yield, seed protein, and seed weight ([Table 1](#)). Similar results were observed in the single plant material counted in 1994. The data collected supports the observation of [Stephens et al. \(1993\)](#) in that pink-flowered lines produced more two-seeded pods while purple-flowered lines produced more three-seeded pods.

The results suggest that *wp* may influence seed protein concentration. Lines containing *wpwp* averaged 1.4% higher seed protein concentration than *WpWp* lines ([Table 1](#)). These data support the results of [Stephens et al. \(1993\)](#), who found that pink-flowered rows averaged 4% higher seed protein than purple-flowered rows.

[Stephens et al. \(1993\)](#) also reported that pink-flowered lines averaged 22% higher seed weight when compared with purple-flowered lines. Our analysis produced mixed results ([Tables 1, 2](#)). Within four families (LNPk90-107-1-33,

LNPK90-107-1-18, LNPK90-107-3-6, and LNPK90-107-1-27), direct comparisons between *WpWp* lines and *wpwp* lines were possible. Within two of those families (LNPK90-107-3-6, and LNPK90-107-1-27), *wpwp* lines averaged 10% higher seed weight. In the other two families the seed weight difference was not significant.

The correlation analysis suggested that flower color does not influence relationships among the agronomic traits that were studied ([Tables 3, 4](#)). Interestingly, no strong negative relationship was found between seed protein and seed yield, and an inconsistent relationship between seed protein and seed oil concentration ([Tables 3, 4](#)). Low variation in protein and oil values could produce low correlation coefficients. Seed protein and oil concentrations are typically highly negatively correlated, and seed protein concentration is usually negatively correlated with seed yield ([Leffel and Rhodes, 1993](#)). The correlation between progeny line data from 1995 and single plant data from 1994 was inconsistent, possibly the result of environmental differences between years.

In the populations examined, soybean lines containing *wpwp* averaged lower yield, fewer loculi per pod, fewer seeds per pod, and higher seed protein concentration than *WpWp* lines. Lower seed yield for pink flowered lines may be the result of a reduction in seeds per pod and loculi per pod. The association of *wp* and yield, seed size, protein, loculi per pod, and seeds per pod is likely the result of linkage or pleiotropy. If linkage is involved, then within a segregating population there should be evidence of recombination, given that the population contains enough individuals. The absence of such evidence would suggest pleiotropy or very tight linkage. No *wpwp* lines exceeded the mean of the *WpWp* lines for loculi per pod or seeds per pod, and no *WpWp* lines fell below the *wpwp* mean for loculi per pod or seeds per pod. Within a family, *wpwp* lines that are high-yielding or have low protein or seed size compared with other family members have been identified. In addition, *WpWp* lines have been identified which have higher protein or larger seed size compared with other *WpWp* lines within a family. These lines possibly represent recombinations between *wp* and seed size or protein genes. The data suggest that a plant breeder could develop a high-yielding, high-protein *wpwp* line through crossing and selection.

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Table 1. Means of three agronomic traits of F_{5:6} soybean lines selected from seven families of the cross LN89-5322-2[†] x Burlison[‡]. Seed weights in 1994 are means of single F₅ plants.

Family	Flower Color	Genotype	Yield t ha ⁻¹	Protein g kg ⁻¹	Seed Weight	
					1994	1995
					cg	
LNPk90-107-2-36	Pk	<i>W1W1wpwp</i>	2.50b¶	441a	18.8a	17.2a
	W	<i>w1w1wpwp</i>	2.62b	439a	19.2a	16.6ab
Burlison	W	<i>w1w1WpWp</i>	3.04a	438a		16.2b
LN89-5322-2	Pk	<i>W1W1wpwp</i>	2.63ab	425b		18.4a
LNPk90-114-1-15	Pk	<i>W1W1wpwp</i>	3.04a	438a	17.7a	14.7b
	W	<i>w1w1wpwp</i>	2.98a	433bc	17.3a	14.2c
Burlison	W	<i>w1w1WpWp</i>	3.22a	437ab		15.2b
LN89-5322-2	Pk	<i>W1W1wpwp</i>	2.91a	428c		16.6a
LNPk90-107-	P	<i>W1W1WpWp</i>	2.64b	433b	16.5a	14.9b

1-12	W	<i>w1w1WpWp</i>	2.64b	436b	16.5a	14.7b
Burlison	W	<i>w1w1WpWp</i>	3.00a	446a		15.4b
LN89-5322-2	Pk	<i>W1W1wpwp</i>	3.01a	435b		17.8a
LNPk90-107-1-33	P	<i>W1W1WpWp</i>	3.27a	419c	18.2a	15.7b
	Pk	<i>W1W1wpwp</i>	2.91b	426ab	18.1a	15.8ab
Burlison	W	<i>w1w1WpWp</i>	2.81b	431a		16.6ab
LN89-5322-2	Pk	<i>W1W1wpwp</i>	2.92ab	421abc		17.4a
LNPk90-107-1-18	P	<i>W1W1WpWp</i>	2.84a	437b	17.7a	15.3b
	Pk	<i>W1W1wpwp</i>	2.67b	442a	17.8a	14.9b
Burlison	W	<i>w1w1WpWp</i>	2.73ab	431b		15.2b
LN89-5322-2	Pk	<i>W1W1wpwp</i>	2.59ab	431b		17.3a
LNPk90-107-3-6	P	<i>W1W1WpWp</i>	2.91ab	419c	19.8a	17.6c
	W	<i>w1w1Wp_ and w1w1wpwp</i>	3.04a	422c	20.3a	18.6b
	Pk	<i>W1W1wpwp</i>	2.58c	427b	20.2a	19.4a
Burlison	W	<i>w1w1WpWp</i>	2.66abc	437a		14.9d
LN89-5322-2	Pk	<i>W1W1wpwp</i>	2.75abc	426bc		17.5bc
LNPk90-107-1-27	P	<i>W1W1WpWp</i>	3.10ab	417b	18.5a	15.4c
	W	<i>w1w1Wp_ and w1w1wpwp</i>	2.91b	410c	18.4a	15.4c
	Pk	<i>W1W1wpwp</i>	2.64c	421b	18.6a	17.0ab
Burlison	W	<i>w1w1WpWp</i>	3.31a	436a		15.8bc
LN89-5322-2	Pk	<i>W1W1wpwp</i>	3.06b	433a		17.7a

† [Stephens et al., 1993.](#)

‡ [Nickell et al., 1990.](#)

§ Flower color: Pk = pink, W = white, and P = purple.

¶ Means within a column of a family followed by the same letter are not significantly different

(*t*-test at *P* = 0.05).

Table 2. Mean loculi per pod and seeds per pod of single F₅ soybean plants (1994) and F₆ progeny rows (1995) from four families of the cross LN89-5322-2[†] x Burlison[‡].

Family	Flower color [§]	Genotype	Loculi	Seeds
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				quality	weight			plant ⁻¹	pod ⁻¹		
WpWp	Yield		-0.014	0.285	-0.116	0.110	0.079	0.114	- 0.568	0.201	0.226
	Maturity	0.173		0.461	0.075	0.074	0.046	- 0.278	0.270	-0.252	-0.233
	Height	0.626	0.397		-0.007	-0.205	-0.177	- 0.351	- 0.115	0.177	0.129
	Seed quality	0.043	0.017	0.198		0.384	0.263	- 0.026	- 0.053	-0.221	-0.235
	Seed weight	-0.158	-0.260	-0.262	0.410		0.276	0.072	- 0.044	-0.557	-0.476
	Protein	-0.061	-0.226	-0.275	0.128	0.266		- 0.212	0.082	-0.046	-0.170
	Oil	-0.146	-0.041	-0.076	-0.337	-0.142	-0.435		- 0.207	0.022	0.207
	Pods plant⁻¹	0.256	0.421	0.456	0.210	-0.281	-0.259	- 0.067		-0.133	-0.133
	Loculi pod⁻¹	-0.080	0.194	-0.031	-0.082	-0.189	-0.171	0.237	0.059		0.875
	Seeds pod⁻¹	-0.033	0.251	0.130	0.183	-0.239	-0.196	- 0.107	0.385	0.587	

† LNPk90-107-1-33 is the family that segregates only at the *wp* locus with *W1W1* generating purple (*W1W1WpWp*) and pink (*W1W1wpwp*) phenotypes (genotypes).

Table 4. Correlation coefficients among agronomic traits and pod characteristics of F_{5:6} *wpwp* and *WpWp* lines selected from LNPk90-107-3-6†; (top is among *wpwp* lines and bottom is among *WpWp* lines).

		<i>wpwp</i>									
		Yield	Maturity	Height	Seed		Protein	Oil	Pods plant ⁻¹	Loculi pod ⁻¹	Seeds pod ⁻¹
					quality	weight					
WpWp	Yield		0.417	0.538	0.212	- 0.028	-0.121	- 0.243	- 0.223	0.095	0.285

Maturity	0.29 9		0.815	0.635	- 0.165	-0.566	- 0.38 5	0.45 2	- 0.001	0.169
Height	0.26 2	0.775		0.482	- 0.259	-0.530	- 0.31 0	0.27 2	0.072	0.206
Seed quality	0.08 9	0.269	0.180		0.114	-0.421	- 0.05 9	0.25 0	- 0.131	- 0.077
Seed weight	- 0.13 8	-0.477	- 0.569	0.267		0.168	0.32 8	- 0.19 8	- 0.496	- 0.585
Protein	- 0.37 0	-0.121	0.129	- 0.154	- 0.079		- 0.02 2	- 0.19 8	- 0.013	- 0.191
Oil	- 0.28 0	-0.354	- 0.302	- 0.133	0.309	-0.210		- 0.23 5	- 0.179	- 0.249
Pods plant⁻¹	0.24 7	0.426	0.395	0.134	- 0.417	-0.178	- 0.14 2		- 0.011	0.019
Loculi pod⁻¹	0.36 5	0.124	0.007	- 0.156	- 0.322	-0.257	0.14 2	0.17 9		0.642
Seeds pod⁻¹	0.22 3	0.167	0.176	- 0.136	- 0.455	-0.116	- 0.24 6	0.32 2	0.723	

† LNPk90-107-3-6 is the family that segregates at both *wp* and *W1* loci generating purple (*W1W1WpWp*), white (*w1w1WpWp* and *w1w1wpwp*) and pink (*W1W1wpwp*) phenotypes(genotypes).