

Regulation of seed yield and agronomic characters by photoperiod sensitivity and growth habit genes in soybean

Elroy R. Cober · Malcolm J. Morrison

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Abstract Soybean genotypes are adapted to narrow bands of latitude due to photoperiod sensitivity. There are several photoperiod-sensitive loci (E1, E2, E3, E4, E5, E6, E7, E8). Determinate and indeterminate growth habits are controlled by a single locus. The objective of our research was to examine the effects of photoperiod sensitivity and growth habit alleles on seed yield and other agronomic characters using isogenic lines. Twenty ‘Harosoy’ isolines with 11 photoperiod-sensitive genotypes many with both indeterminate and determinate growth habits were grown in the field at Ottawa, ON, from 2003 to 2007. Maturity ranged from 97 to 127 days, and seed yield increased linearly with maturity until about 112 days when it plateaued. Determinate lines were always shorter than indeterminate lines of equivalent maturity. Seed yield was associated with plant height, maturity, seed sugar concentration, seed weight and lodging. Effects of alleles at individual loci, and additive and epistatic effects across multiple loci were examined. At a single locus, photoperiod-insensitive alleles produced isolines that matured 8–11 days earlier, yielded less, and had shorter plants with reduced lodging. In multiple loci analyses, additive effects explained most of the variation in agronomic characters since additive models with E1, E3, E4, E7 and Dt1 loci included compared well to additive plus epistatic models and genotype-based models. Variation in photoperiod sensitivity and growth habit alleles results in a range of maturity, with pleiotropic

effects on seed yield and agronomic characteristics, and play an important role in providing adaptation across latitudes.

Introduction

In soybean [*Glycine max* (L.) Merr.], eight loci with two alleles at each locus have been reported to control time to flowering and maturity: E1 and E2 (Bernard 1971); E3 (Buzzell 1971); E4 (Buzzell and Voldeng 1980); E5 (McBlain and Bernard 1987); E6 (Bonato and Vello 1999); E7 (Cober and Voldeng 2001b); and E8 (Cober et al. 2009). Alleles at these loci control time to flowering and maturity through their response, or lack of response, to photoperiod (Cober et al. 1996a, b; Cober and Voldeng 2001a) and should more accurately be referred to as photoperiod-sensitive loci (Cober et al. 1996a; Upadhyay et al. 1994). In the case of E3 and E4, the functional genes underlying these loci were found to code for phytochrome A (Liu et al. 2008; Watanabe et al. 2009).

Several photoperiod-sensitive genes have been identified in other crops which have pleiotropic effects on many agronomic traits beyond maturity. A single locus in bean (*Phaseolus vulgaris* L.) controlling photoperiod sensitivity also affected above-ground biomass, harvest index, seed yield and many other related traits (Wallace et al. 1993). In rice (*Oryza sativa* L.), a quantitative trait locus (QTL) was identified which controlled flowering time, yield and plant height with a flowering time related CCT (CO, CO-LIKE and TIMING OF CAB1) domain protein as the functional gene underlying the QTL (Xue et al. 2008).

A number of studies have examined the effects of alleles at soybean photoperiod-sensitive loci. Studies limited to E1, E2, and E3 were carried out in the field (Hartung et al.

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E. R. Cober (✉) · M. J. Morrison
Eastern Cereal and Oilseed Research Center,
Agriculture and Agri-Food Canada, 960 Carling Avenue,
Ottawa, ON K1A 0C6, Canada
e-mail: elroy.cober@agr.gc.ca

1981), in microplots (Wilcox et al. 1995) or in pots in polytunnels (Ellis et al. 2000). The analysis was extended to include E4 in the field (Curtis et al. 2000). These previous studies emphasized time to maturity and crop physiology processes such as crop growth rate, seed filling period, and radiation use efficiency.

Indeterminate and determinate growth habits are controlled by alleles at the Dt1 locus (Bernard 1972). Determinate lines are shorter compared to indeterminate lines both in the case of isolines (Bernard 1972; Curtis et al. 2000) and full sibs (Cober and Tanner 1995; Robinson and Wilcox 1998). Determinate lines, compared to isogenic indeterminate lines, are earlier maturing (Curtis et al. 2000). Agronomic comparisons of indeterminate and determinate lines have been inconclusive since some reports showed similar seed yield (Cober and Tanner 1995), while others found indeterminate lines to be higher yielding (Ablett et al. 1989; Robinson and Wilcox 1998), and Curtis et al. (2000) found a mixed response.

The objective of this work was to move beyond a genotype-based analysis to include a gene-based analysis and examine the individual, as well as additive, and

epistatic effects of alleles at multiple photoperiod sensitivity (E1, E3, E4, E7) and growth habit loci (Dt1) on seed yield and other agronomic characters by growing a series of Harosoy isolines in the field over five growing seasons.

Materials and methods

Isolines with a ‘Harosoy’ (Weiss and Stevenson 1955) background were used as treatments in this study (Table 1). L62-667 and L67-153 were described by Bernard et al. (1991). The remaining isolines were developed at the Eastern Cereal and Oilseed Research Center, Ottawa, ON, Canada. These 20 isolines vary for photoperiod sensitive/insensitive alleles at loci E1, E2, E3, E4, and E7 and for indeterminate/determinate growth habit alleles at the Dt1 locus. Additionally isolines varying for gray or tawny pubescence alleles at the T locus were developed to break linkages between photoperiod-sensitive alleles and pubescence color since the E1 and E7 loci are linked to the T locus (Cober and Voldeng 2001b) and some of these were

Table 1 Genotype and agronomic performance of Harosoy soybean isolines grown from 2003 to 2007 at Ottawa, ON

Isoline	Genotype ^a	Seed yield (kg ha ⁻¹)	Maturity (days)	Plant height (cm)	Lodging (1–5) ^b	Seed weight (g 100 ⁻¹)	Seed composition (g kg ⁻¹)		
							Protein	Oil	Sugars
Harosoy	e1e2E3E4E7Dt1t	2,782	127	110	3.6	19.3	420	199	121
L67-153	e1e2E3E4E7dt1t	2,747	121	65	1.3	19.4	422	200	119
OT94-41	e1e2E3e4E7Dt1t	2,912	120	104	3.8	18.6	409	208	120
L62-667	e1e2e3E4E7Dt1t	2,860	120	103	3.1	20.8	418	203	119
OT93-28	E1e2e3e4E7Dt1t	2,707	119	100	3.2	19.4	407	210	121
OT93-26	E1e2e3e4E7Dt1T	2,859	118	105	3.8	19.0	409	211	118
OT94-39	e1e2E3e4E7dt1t	2,742	116	61	1.2	20.0	410	208	120
OT94-51	E1e2e3e4E7dt1t	2,836	115	72	2.4	18.4	409	207	120
OT94-37	e1e2e3E4E7dt1t	2,585	115	53	0.9	20.3	414	206	118
OT94-49	E1e2e3e4E7dt1T	2,774	114	76	2.9	17.3	405	212	119
OT99-17	e1E2e3e4E7Dt1t	2,900	111	86	3.0	19.6	410	209	119
OT90-17	e1e2e3E4e7Dt1t	2,775	111	83	2.0	20.4	425	205	115
OT89-5	e1e2e3e4E7Dt1t	2,626	107	80	2.1	20.6	417	208	116
OT90-18	e1e2e3E4e7dt1t	2,301	104	52	1.1	18.5	423	205	114
OT94-47	e1e2e3e4e7Dt1t	2,183	104	75	2.1	19.3	414	211	115
OT94-45	e1e2e3e4E7dt1t	2,406	103	62	2.1	17.8	415	208	116
OT99-15	e1e2e3e4e7Dt1T	2,079	103	70	2.3	19.3	422	208	111
OT89-6	e1e2e3e4E7dt1t	1,560	100	40	1.0	17.9	435	197	112
OT02-18 ^c	e1e2e3e4e7Dt1t	1,451	97	58	2.0	17.5	424	208	111
OT94-43	e1e2e3e4e7dt1t	1,405	97	41	1.6	18.1	423	207	112
LSD 0.05		279	2	9	0.6	1.0	7	5	2

^a E alleles are photoperiod sensitive and result in later maturity, e alleles are photoperiod insensitive and result in earlier maturity, Dt1 is indeterminate growth habit, dt1 is determinate growth habit, T is tawny pubescence, and t is gray pubescence

^b Lodging scored from 1 (no lodging) to 5 (completely lodged)

^c OT02-18 also carries an additional introgressed photoperiod-insensitive allele identified as e8 (Cober et al. 2009)

included. There were 11 different photoperiod-sensitive genotypes in this study.

The isolines were grown in generalized lattice design trials with three replications at Ottawa, ON, from 2003 to 2007. Since the 20 isolines common over 5 years were a subset of larger annual trials, the combined trials were analysed as randomized complete blocks. Trials were planted between 20th and 30th of May (21 May 2003, 20 May 2004, 25 May 2005, 30 May 2006, and 23 May 2007). The seeding rate was 500,000 seeds per ha⁻¹ in four rows of plots spaced 0.4 m apart and 5 m long. Weed control was achieved with post-emergence application of recommended herbicides. Days to maturity, plant height and lodging were recorded for each plot. All four rows in each plot were combine-harvested, and seed yield was reported at 130 g kg⁻¹ moisture. Seed weight was determined for 100 seeds from each plot. Seed composition (protein, oil, and soluble sugars) was determined by near-infra red transmission (Infratech 1241 Grain Analyser, Foss North America, Inc., Brampton, ON, Canada) for each plot.

A combined ANOVA was carried out for the 5 years using the mixed model procedure of SAS (SAS, Cary, NC, USA). Years, replications within year, and isolate by year were considered random effects while isolate was considered a fixed effect. The LSD ($P = 0.05$) was calculated for isolate mean separation. The correlation procedure of SAS was used to determine correlations and associated probabilities, between agronomic traits among isolines. A genotype by trait biplot created using GGE biplot (Yan 2001) was used to visualize the relationships between the genotypes and all agronomic traits in addition to pair-wise comparisons of traits using correlation analyses. GGE biplot was used to calculate the proportion of genotype to genotype-plus-genotype-by-year-interaction effects using variance components.

An analysis was done on a gene basis for each of the five factors (E1, E3, E4, E7, and Dt1 loci) with two levels possible for each factor (dominant or recessive alleles). Least square means (and LSD $P = 0.05$), for agronomic characters, were calculated for each of the two alternative alleles at each locus using PROC GLM of SAS. Factorial genetic analyses were also carried out on models including only additive main effects, as well as additive plus all possible interloci, epistatic, interactions both with and without environmental effects (year and replicate within year) included. Model fit was reported using the coefficient of determination (R^2) value.

Results

The 20 isolines covered a wide range of adaptation with time to maturity ranging from 97 to 127 days. Five-year

mean seed yield varied from 1,405 to 2,912 kg ha⁻¹ (Table 1). Seed yield showed a linear relationship with maturity over the range of approximately 97–112 days with a yield plateau at about 2,800 kg ha⁻¹ (Fig. 1a). Differences in growth habit were primarily seen in comparisons of plant height and maturity where indeterminate lines were taller and showed a significant linear relationship with maturity while the plant height–maturity relationship was not as pronounced in shorter determinate plants (Fig. 1b). Clear distinctions were also seen in plotting seed yield versus plant height where equivalent yielding determinate lines were always shorter than the indeterminate lines (Fig. 2). Distinctions between indeterminate and determinate lines were not seen in plotting seed weight versus

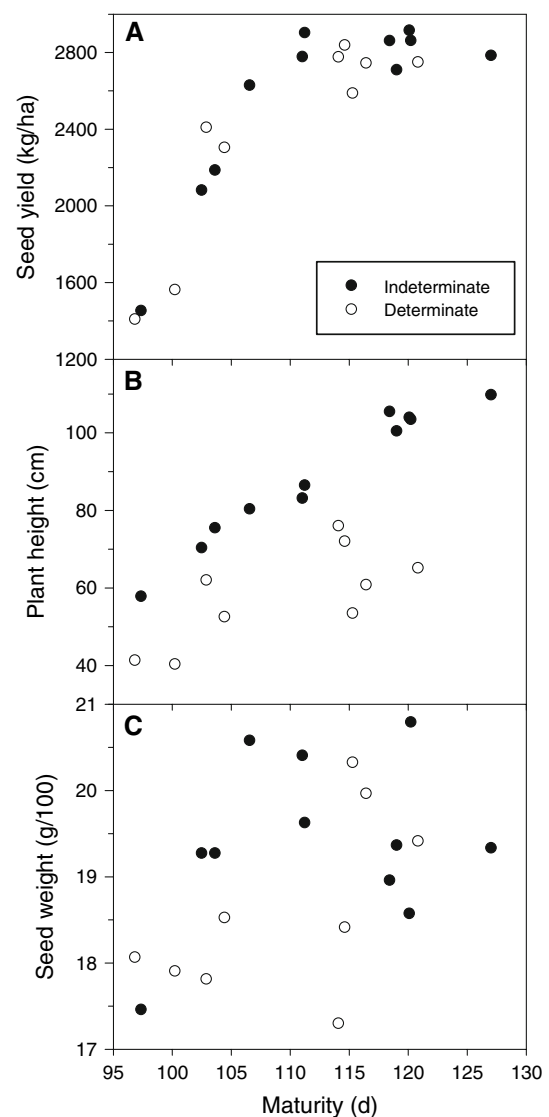


Fig. 1 Relationship between **a** mean seed yield, **b** mean plant height and **c** mean seed weight with mean maturity of Harosoy soybean photoperiod-sensitive isolines with indeterminate and determinate growth habits grown from 2003 to 2007 at Ottawa, ON

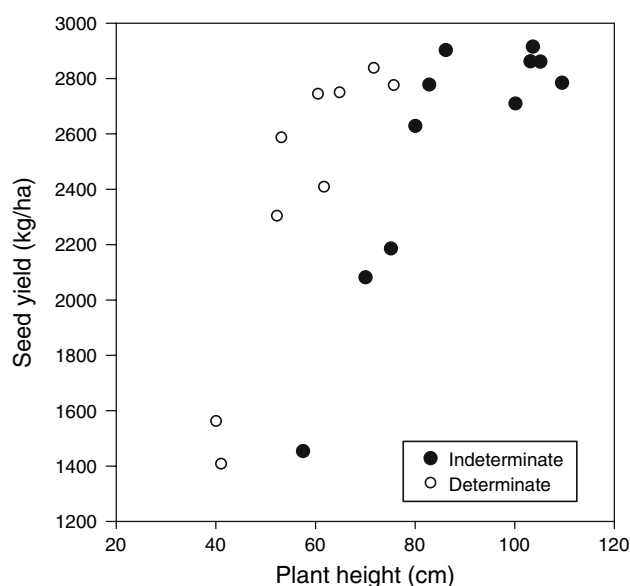


Fig. 2 The association between seed yield and plant height in Harosoy soybean photoperiod-sensitive isolines grown from 2003 to 2007 at Ottawa, ON

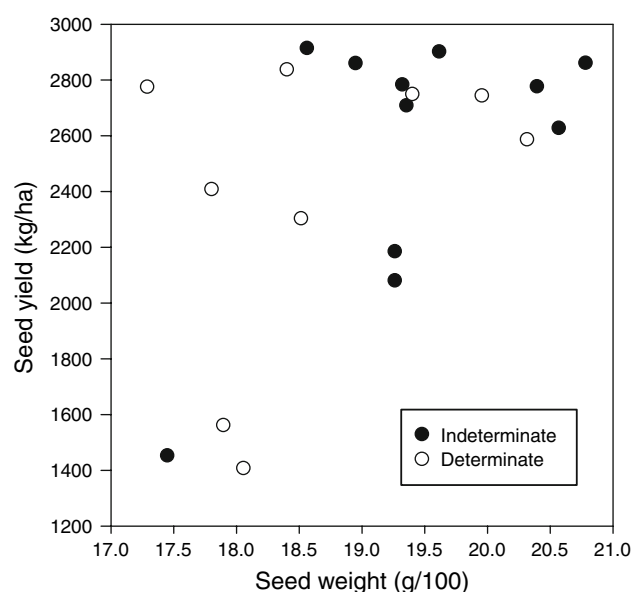


Fig. 3 Seed yield and seed weight of Harosoy soybean photoperiod sensitivity isolines grown from 2003 to 2007 at Ottawa, ON

maturity (Fig. 1c) or seed yield versus seed weight (Fig. 3). There was some association between seed yield and seed weight ($r = 0.57$, $P < 0.001$) but high yields were possible throughout a range of seed sizes.

Mean results over the 5 years were reported although the ANOVA showed significant year \times isolate effect ($P < 0.001$) for every trait as were the year and isolate effects (Table 2). A GGE biplot year-isolate biplot was generated for each trait in an attempt to visualize the interactions. Three patterns were apparent (data not shown). Year 2003 had lower yield for the early maturing isolines. All isolines in 2003 were later than other years. Lodging ratings were greater in 2006 than the other years. A single genotype (OT89-6) had higher protein and lower sugar and oil concentration when the other isolines had the reverse. No pattern was apparent for seed weight. The proportion of genotype to genotype-plus-genotype-by-year-interaction effects was high for seed yield, maturity, plant height, and lodging (Table 2). Since the mean value calculated across 5 years accounted for many possible combinations of weather, it resulted in a useful value for presentation compared to the alternative many isolate-year values.

A GGE biplot-derived genotype-trait biplot (Fig. 4) was used to visualize the relationships between traits and isolines. Seed yield was positively correlated with plant height, maturity, and seed sugars, and negatively correlated with seed weight and lodging. Seed yield was independent of seed oil and negatively correlated with seed protein.

An examination of the effects of alleles at individual loci showed recessive, photoperiod-insensitive alleles resulted in 8–11 days earlier maturity compared to the

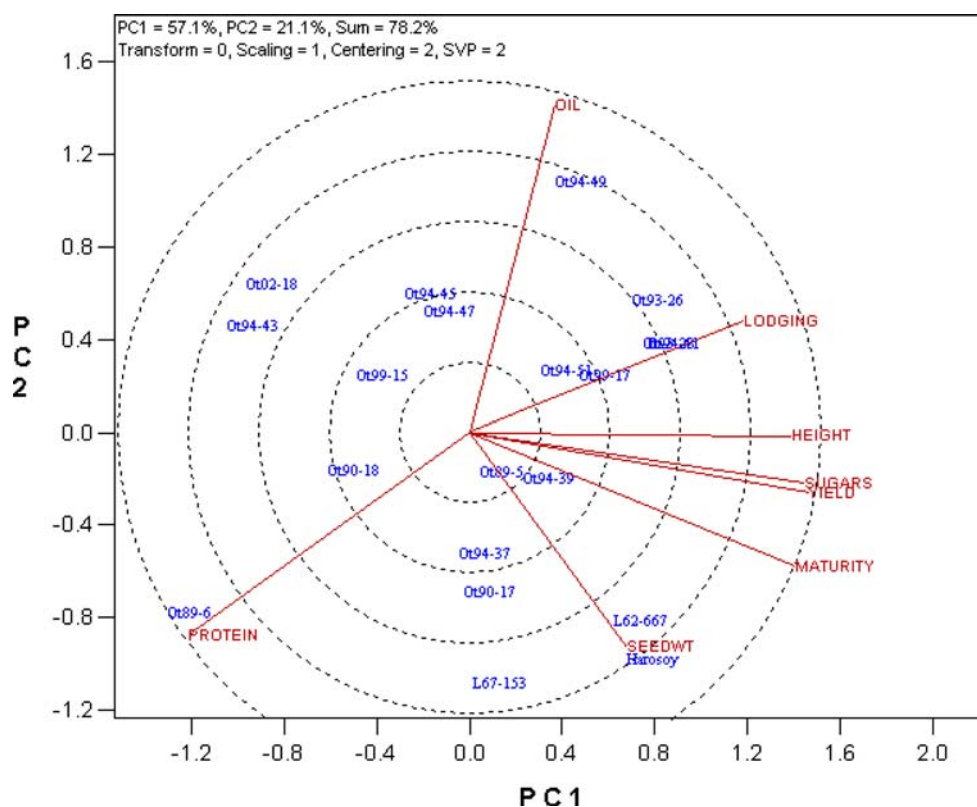
dominant, photoperiod-sensitive alleles at the four E loci (Table 3). Co-incident with early maturity was lower seed yield (ranging from 278 to 536 kg ha⁻¹ less yield), reduced plant height (12–19 cm shorter) and reduced lodging. While seed size differences were significantly different for alleles at three of the four E loci, the differences were not consistent with E4E4 and E7E7 alleles having larger seed than e4e4 or e7e7 while E1E1 alleles had smaller seed than e1e1 (Table 3). Early maturity was coincident with higher seed protein and reduced seed sugar content (Table 3).

Determinate alleles resulted in 5 days earlier maturity, about 200 kg ha⁻¹ lower seed yield, and larger seeds compared to indeterminate alleles. Isolines with indeterminate alleles resulted in plants that were 32 cm taller and lodged more than isolines with determinate alleles. Seed composition was not consistently affected by alleles at the Dt1 locus (Table 3).

Coefficients of determination (R^2) were used to determine the fit of genetic models (Table 4). Simple genetic models, including only one photoperiod-sensitive locus, did not fit the data well although the models for each E locus were significant for maturity (R^2 of 0.03–0.12) and seed yield (R^2 of 0.07–0.3). The growth habit locus (Dt1) was significant for plant height ($R^2 = 0.31$) and lodging ($R^2 = 0.2$). On comparing multiple loci, additive, gene-based models to the entry-based models for seed yield, the additive models fit well (explaining 65 and 85% of the variability of the entry-based models without and with environmental effects, respectively). The models with additive and epistatic (inter-loci interactions) effects fit somewhat better than the additive-only models (85 and 94%

Table 2 Mean squares and significance values derived from ANOVA and the proportion of genotype to genotype plus year interaction variance components for agronomic and seed composition characters from soybean isolines grown from 2003 to 2007 at Ottawa, ON

Isoline	DF	Seed yield	Maturity	Plant height	Lodging	Seed weight	Seed composition		
							Protein	Oil	Sugars
Year	4	23095153***	1796***	11934***	39.6***	303***	64.8***	20.6***	108***
Rep (year)	10	155716*	3	154	0.2	3***	3.6***	0.7***	0.1*
Genotype	19	3641265***	1160***	6916***	13.1***	16***	8.6***	2.4**	1.6***
Year \times genotype	76	341119***	20***	352***	1.6***	4***	1.9***	1.1***	0.2***
G/(G + GY)		0.67	0.92	0.79	0.60	0.35	0.42	0.18	0.53

* $P = 0.05$; ** $P = 0.01$; *** $P = 0.001$ **Fig. 4** A genotype-trait biplot of Harosoy soybean photoperiod-sensitive isolines grown from 2003 to 2007 at Ottawa, ON. Axes show the first two principle components

of the entry-based model without and with environmental effects, respectively). For time to maturity, the additive models fit very well (96 and 97% of the entry-based model without and with environmental effects, respectively) with only a very slight improvement with epistatic effects included (97 and 98% of the entry-based model without and with environmental effects, respectively).

Discussion

The 20 Harosoy isolines with a 30-day range in maturity provided a way to visualize optimum maturity for maximum seed yield at this location. Seed yield was maintained

at the level of the recurrent parent, Harosoy, while maturity decreased from 127 to 112 days in isolines with introgressed photoperiod-insensitive alleles. In this genetic background, 112 days maturity resulted in optimum seed yield with minimized maturity requirements.

Determinate isolines maturing equivalent to indeterminate lines were always shorter than indeterminate lines (Fig 1b). This is common in comparisons of determinate and indeterminate isolines (Bernard 1972; Curtis et al. 2000), and determinate and indeterminate full sibs (Cober and Tanner 1995; Robinson and Wilcox 1998). Since comparisons of determinate and indeterminate lines are often confounded because determinate lines are earlier maturing compared to isogenic indeterminate lines (Curtis

Table 3 Least square means of agronomic characters for alternate alleles at E1, E3, E4, E7 and Dt1 loci from Harosoy soybean isolines grown from 2003 to 2007 at Ottawa, ON, derived from an additive model which included all five loci

Alleles	No. of isolines	Seed yield (kg ha ⁻¹)	Maturity (days)	Plant height (cm)	Lodging (1–5) ^a	Seed weight (g 100 ⁻¹)	Seed composition (g kg ⁻¹)		
							Protein	Oil	Sugars
e1	4	2,510	112	73	2.2	19.0	419	206	116
E1	16	2,804	123	92	3.0	18.4	409	208	120
LSD 0.05		127	1	4	0.2	0.4	3	2	1
e3	4	2,518	112	77	2.4	18.9	416	207	116
E3	16	2,796	122	89	2.8	18.6	412	206	119
LSD 0.05		127	1	4	0.2	0.4	3	2	1
e4	6	2,389	113	77	2.6	18.2	413	209	117
E4	14	2,925	122	89	2.6	19.3	416	205	119
LSD 0.05		111	1	3	0.2	0.4	3	2	1
e7	6	2,442	113	77	2.3	18.4	416	208	116
E7	14	2,872	121	89	2.8	19.1	412	206	120
LSD 0.05		111	1	3	0.2	0.4	3	2	1
dt1	9	2,556	115	67	2.0	18.2	415	206	117
Dt1	11	2,758	120	99	3.2	19.3	414	207	118
LSD 0.05		102	1	3	0.2	0.3	2	2	1

^a Lodging scored from 1 (no lodging) to 5 (completely lodged)

Table 4 R^2 values of models including single or multiple loci for photoperiod sensitivity and growth habit for agronomic and seed composition characters from Harosoy soybean isolines grown from 2003 to 2007 at Ottawa, ON

Model	Seed yield	Maturity	Plant height	Lodging	Seed weight	Seed composition		
						Protein	Oil	Sugars
Single locus								
E1	0.04	0.07	0.06	0.08	ns	0.09	0.04	ns
E3	0.03	0.24	0.03	ns	ns	ns	0.02	ns
E4	0.03	0.12	ns	0.02	0.03	0.03	0.07	ns
E7	0.12	0.30	0.08	0.04	ns	0.05	ns	0.03
Dt1	ns	0.02	0.31	0.20	0.02	ns	ns	ns
All loci								
Additive	0.22	0.67	0.53	0.34	0.08	0.13	0.10	0.05
Additive and environment ^a	0.68	0.90	0.75	0.62	0.69	0.56	0.45	0.93
Additive and interactions	0.29	0.68	0.56	0.41	0.13	0.18	0.13	0.05
Additive, interactions and environment ^a	0.75	0.91	0.78	0.68	0.74	0.61	0.49	0.94
Entry basis	0.34	0.70	0.59	0.44	0.15	0.24	0.18	0.06
Entry and environment ^a	0.80	0.93	0.80	0.72	0.76	0.66	0.52	0.94

ns Not significant

^a Environment effects were year and replicate within year

et al. 2000), we used a large group of determinate and indeterminate isolines with a range of maturity to allow visualization of differences between the two growth habits. Figure 1a shows similar seed yield for the two growth habits throughout a range of maturity dates similar to

comparisons between full sibs (Cober and Tanner 1995; Robinson and Wilcox 1998). Equivalent yields were produced by determinate and indeterminate lines although the determinate lines were shorter (Fig. 2) similar to previous reports (Cober and Tanner 1995) but in contrast to other

work where indeterminate lines were higher yielding (Ablett et al. 1989; Robinson and Wilcox 1998).

Seed yield was positively associated with plant height as seen in both the two-factor (Fig. 2; $r = 0.55$, $P < 0.0001$) and multiple-factor GGE biplot analyses (Fig. 4) similar to other reports (Ablett et al. 1989; Mansur et al. 1996). Seed size is one important component of seed yield (Borrás et al. 2004) and while there was an association between seed yield and seed size ($r = 0.57$, $P < 0.001$) in these isolines, high yields were possible throughout a range of seed sizes (Fig. 3).

Genetic analysis on a single locus basis for four loci demonstrated significant effects for maturity and seed yield where photoperiod-sensitive alleles were responsible for later maturity and higher yield similar to previous work of this type (Curtis et al. 2000; Ellis et al. 2000; Wilcox et al. 1995). To our knowledge there are no reports of a factorial type analysis where multiple loci with additive and epistatic effects were used to estimate seed yield, maturity and other agronomic characteristics since analyses in the literature tend to use entry-based approaches. We found a gene-based analysis of agronomic characteristics fit the data only slightly less well compared to an entry-based analysis. This is similar to previous work modeling flowering time in soybean isolines where a gene-based model compared well to an entry-based model (Stewart et al. 2003). An additive model for the E loci fit the agronomic data well although there was a small improvement when additive and epistatic (inter-genic interactions) effects were added to the model. We found that the photoperiod-sensitive genes in our work produced pleiotrophic effects beyond maturity, including seed yield, plant height, lodging, seed weight and seed composition. Wallace et al. (1993) also found that a single photoperiod-sensitive locus in bean also had affected many agronomic traits beyond duration to maturity. As well, a photoperiod gene in rice (*O. sativa* L.) coding for a CCT (CO, CO-LIKE and TIMING OF CAB1) domain protein affected heading date as well as a number of agronomic characteristics (Xue et al. 2008). Advances have been made in the identification of the functional genes underlying two of the soybean loci studied in this work. The E3 locus has been associated with phytochrome A3 (Watanabe et al. 2009) and the E4 locus has been associated with phytochrome A2 (Liu et al. 2008). Therefore, in soybean, genes for red:far-red light-quality-sensing proteins are implicated in the control of maturity and a range of agronomic characteristics.

In summary, a series of photoperiod-sensitive genes, with two of these identified as phytochrome A, resulted in isolines with a wide range of maturity times and seed yields. In comparisons of indeterminate and determinate lines, equivalent yielding determinate lines were always shorter than indeterminate lines. Within isolines varying

for alleles at E loci, not only was maturity affected but there were pleiotrophic effects on seed yield, plant height, lodging, seed weight, and seed composition. Variation in alleles at the E and Dt1 loci play an important role in providing a range of adaptation for soybean as well as affecting productivity.

References

- Ablett GR, Beversdorf WD, Dirks VA (1989) Performance and stability of indeterminate and determinate soybean in short-season environments. *Crop Sci* 29:1428–1433
- Bernard RL (1971) Two major genes for time of flowering and maturity in soybeans. *Crop Sci* 11:242–244
- Bernard RL (1972) Two genes affecting stem termination in soybeans. *Crop Sci* 12:235–239
- Bernard RL, Nelson RL, Cremeens CR (1991) USDA soybean genetic collection: Isoline collection. *Soyb Genet Newsl* 18:27–57
- Bonato ER, Vello NA (1999) E6, a dominant gene conditioning early flowering and maturity in soybeans. *Genet Mol Biol* 22:229–232
- Borrás L, Slafer GA, Otegui ME (2004) Seed dry weight response to source-sink manipulations in wheat, maize and soybean: a quantitative reappraisal. *Field Crops Res* 86:131–146
- Buzzell RI (1971) Inheritance of a soybean flowering response to fluorescent-daylength conditions. *Can J Genet Cytol* 13:703–707
- Buzzell RI, Voldeng HD (1980) Inheritance of insensitivity to long daylength. *Soyb Genet Newsl* 7:26–29
- Cober ER, Tanner JW (1995) Performance of related indeterminate and tall determinate soybean lines in short-season areas. *Crop Sci* 35:361–364
- Cober ER, Voldeng HD (2001a) Low R:FR light quality delays flowering of E7E7 soybean lines. *Crop Sci* 41:1823–1826
- Cober ER, Voldeng HD (2001b) A new soybean maturity and photoperiod-sensitivity locus linked to E1 and T. *Crop Sci* 41:698–701
- Cober ER, Tanner JW, Voldeng HD (1996a) Genetic control of photoperiod response in early-maturing, near-isogenic soybean lines. *Crop Sci* 36:601–605
- Cober ER, Tanner JW, Voldeng HD (1996b) Soybean photoperiod-sensitivity loci respond differentially to light quality. *Crop Sci* 36:606–610
- Cober ER, Molnar SJ, Charette M, Voldeng HD (2009) A new locus for early maturity in soybean. *Crop Sci* 50. doi:10.2135/cropsci2009.04.0174
- Curtis DF, Tanner JW, Luzzi BM, Hume DJ (2000) Agronomic and phenological differences of soybean isolines differing in maturity and growth habit. *Crop Sci* 40:1624–1629
- Ellis RH, Asumadu H, Qi A, Summerfield RJ (2000) Effects of photoperiod and maturity genes on plant growth, partitioning, radiation use efficiency, and yield in soybean [*Glycine max* (L.) Merrill] ‘Clark’. *Ann Bot* 85:335–343
- Hartung RC, Specht JE, Williams JH (1981) Modification of soybean plant architecture by genes for stem growth habit and maturity. *Crop Sci* 21:51–56
- Liu B, Kanazawa A, Matsumura H, Takahashi R, Harada K, Abe J (2008) Genetic redundancy in soybean photoreponses associated with duplication of the phytochrome A gene. *Genetics* 180:995–1007
- Mansur LM, Orf JH, Chase K, Jarvik T, Cregan PB, Lark KG (1996) Genetic mapping of agronomic traits using recombinant inbred lines of soybean. *Crop Sci* 36:1327–1336

- McBlain BA, Bernard RL (1987) A new gene affecting the time of flowering and maturity in soybeans. *J Hered* 78:160–162
- Robinson SL, Wilcox JR (1998) Comparison of determinate and indeterminate soybean near-isolines and their response to row spacing and planting date. *Crop Sci* 38:1554–1557
- Stewart DW, Cober ER, Bernard RL (2003) Modeling genetic effects on the photothermal response of soybean phenological development. *Agron J* 95:65–70
- Upadhyay AP, Ellis RH, Summerfield RJ, Roberts EH, Qi A (1994) Characterization of photothermal flowering responses in maturity isolines of soybean [*Glycine max* (L.) Merrill] cv. Clark. *Ann Bot* 74:87–96
- Wallace DH, Yourstone KS, Masaya PN, Zobel RW (1993) Photoperiod gene control over partitioning between reproductive and vegetative growth. *Theor Appl Genet* 86:6–16
- Watanabe S, Hideshima R, Xia Z, Tsubokura Y, Sato S, Nakamoto Y, Yamanaka N, Takahashi R, Ishimoto M, Anai T, Tabata S, Harada K (2009) Map-based cloning of the gene associated with soybean maturity locus E3. *Genetics*. doi:[10.1534/genetics.108.098772](https://doi.org/10.1534/genetics.108.098772)
- Weiss MG, Stevenson TM (1955) Registration of soybean varieties, V. *Agron J* 47:541–543
- Wilcox JA, Wiebold WJ, Niblack TL, Kephart KD (1995) Growth and development of soybean isolines that differ for maturity. *Agron J* 87:932–935
- Xue W, Xing Y, Weng X, Zhao Y, Tang W, Wang L, Zhou H, Yu S, Xu C, Li X, Zhang Q (2008) Natural variation in *Ghd7* is an important regulator of heading date and yield potential in rice. *Nat Genet* 40:761–767
- Yan W (2001) GGE biplot—a windows application for graphical analysis of multienvironment trial data and other types of two-way data. *Agron J* 93:1111–1118