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SEED GROWTH RATE, GROWTH DURATION, AND YIELD IN SOYBEAN

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GUFFY R. D., HESKETH J. D., NELSON R. L. and BERNARD R. L. *Seed growth rate, growth duration, and yield in soybean.* BIOTRONICS **20**, 19–30, 1991. Seed growth rate and duration of growth were studied for different soybean [*Glycine max* (L.) Merr.] cultivars and isolines differing in maturity and stem termination behavior under field conditions. Various methods for estimating rate and duration were compared, and such estimates were compared with yield, along with mature seed weight, seed number, and days from planting to maturity. Three estimates of seed filling period were all highly correlated with each other, but the final seed weight, divided by its growth rate during the linear phase of dry matter accumulation, or the 'effective filling period', correlated best with yield. Two estimates of seed growth rate were also highly correlated with each other but not with yield. Alleles that delayed maturity did not generally increase the seed filling period, and, in some cases, caused slight reductions. None of the genes studied affected seed growth rate or final seed size.

Key words : *Glycine max* (L.) Merr. ; soybean ; flowering genes ; maturity genes; yield components; physiological genetics.

INTRODUCTION

More information is needed about genetic variation in seed yield components, such as mature seed mass, number of seeds per plant or ground area, growth rates and growth duration. When comparing differences among these factors among plant strains, effects of differences in maturity and stem termination behavior need to be separated out, if the data are to be used to study independent differences in seed yield components. The numbers and dry weights of mature seeds are easy to measure and tend to be inversely related (*2*). The seed filling period (*SFP*, see Table 1 for definitions), or the duration of dry matter accumulation in seeds, varies greatly among soybean (*Glycine max* (L.) Merr.) strains in the USDA germplasm collection (*7, 27*) and has been associated with increased yield (*4, 11, 13, 19, 30*) and final seed weight (*7*). Modern cultivars tend to have a longer *SFP* than older ones (*11, 19*), and the *SFP* can be changed

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by selection (*29*).

Seed growth rate (*SGR*), or the accumulation of seed dry matter per unit time, also varies among strains (*7, 17*) and has been positively correlated with final seed weight (*7*), but rarely with yield, because of an inverse correlation with seed numver (*28*). Both *SFP* and *SGR* are affected by temperature (*8, 14*) moisture stress (*20*), the source/sink ratio (*5*) and photoperiod (*10, 15, 21, 26, 33*).

Reproductive phenological events, or R-stages (for definitions, see Table 1), have been used for estimating both *SFP* and *SGR*. There are numerous studies of effects of photoperiod and temperature, or date-of-planting, on such events for strains differing in time to maturity (*25*). Others (*1, 18, 34*) have studied the effects of maturity (E_1/e_1, E_2/e_2, and E_3/e_3 and stem termination (Dt_1/dt_1) allelles on the timing of various R-stages for different latitudes, climates, dates-of-planting, and imposed photoperiods and temperatures. *SFP* and *SGR* vary among different combinations of maturity or stem termination allelles in plants exposed to different photoperiods and temperatures. Our objectives in this study were a) to determine the effect of maturity and stem termination alleles on the rate and duration of seed growth, b) to compare methods for estimating rate and duration of seed growth, and c) to examine general relationships between seed growth, maturity and yield. At the same time we attempted to evaluate further the feasibility of selecting strains with large differences in rate and duration of seed growth from the USDA germplasm collection, with emphasis on accessions selected from a preliminary survey of 1435 strains from Maturity Groups II–IV (soybean strains have been grouped for earliness to maturity at different latitudes, with 10 classes, Groups 00, 0 and I–VIII, used for commercial cultivars in the U.S.A.) adapted to the Urbana latitude (40°) (*24*).

MATERIALS AND METHODS

Soybean stains were planted 26 May 18 May in 1983 and 1984, respectively, at the Urbana Illinois Agronomy South Farm in a Flanagan silt loam (fine, montmorillonitic, mesic Aquic Argiudoll). The Various entries were planted at 26 to 33 seeds per m in single row plots three m long and 0.76 m apart, arranged in a randomized complete blook with three replications. There was an additional restriction on plot randomization in that strains with similar maturity times were planted together. Irrigation was provided as needed.

Table 1 defines reproductive growth stages or phenological events used in this report, with relevant sources. Successive events can be used to estimate duration. Successive dry weights were measured to determine rates during the linear phase of dry matter accumulation. The linear phase began at approximately R5 and the maximum dry weight (physiological maturity) occurred when pods turned yellow (approximately R7). In both years 10 plants of each entry were scored three times weekly to deterimine the date when five or more plants had attained full flower (R2), beginning seed fill (R5), and physiological maturity (R7). The plants in the test sample were uniformly

Table 1. Terms and definitions used to describe plant reproductive development, and the rate and duration of seed development in soybean.

Whole plant reproductive growth stages	
Stage	Description
R1 (*27*)*	One open flower at any node on the main stem.
R2 (*9*)	Open flower at one of the two uppermost nodes on the main stem with a fully developed leaf.
R4 (*9*)	Pod 20 mm long at one of the 4 uppermost nodes on the mainstem with a fully developed leaf.
R5 (*9*)	Seed 3 mm long in a pod at one of the four uppermost nodes on the main stem with a fully developed leaf.
R7 (*9*)	One normal pod on the main stem that has reached its mature pod color.
R8 (*9*)	95% of pods have reached the mature pod color.
BS	Seed 3 mm long in a pod anywhere on the mainstem.
Seed development	
Term	Description
Beginning seed fill (*BSF*) (*27*)	The time at which the seed begins to accumulate dry matter at the maximum linear rate. Approximately R5.
Physiological maturity (*PM*) (*32*)	Point of maximum dry matter accumulation in the seed(s): on an individual seed (yellow pod) or whole plant (R7) basis.
Final seed size (*FSS*) (*3*)	The dry weight of a mature seed.
Seed growth rate (*SGR*) (*3*)	The rate of dry matter accumulation in a seed during its linear phase of growth.
Effective filling period (*EFP*) (*3*)	*FSS* divided by *SGR*.
Seed filling period (*SFP*) (*27*)	The time for *BSF* to pod yellowing.
Effective seed growth rate (*ESGR*)	*FSS* divided by the *SFP*.

* Literature source, see references

spaced.

In 1983, 71 strains, comprised of 13 modern U.S.A. cultivars, 17 older U.S.A. cultivars, 21 foreign cultivars from the USDA Soybean Germplasm Collection at Urbana and 20 near isogenic, backcross derived lines (isolines), were tested. Introductions were selected from a preliminary survey of flowering dates (R1), maturity dates (R8), the weights of 100 seeds, and yields in 1435 cultivars from Maturity Groups II through IV (*24*). Unpublished data collected in this preliminary survey included beginning of seed fill (*BS*) for lines in Maturity Groups II–III. *BS* occurred when a fully developed pod contained a three mm seed anywhere on the stem. Using BS to R8 in Maturity Groups II and III and R1 to R8 in Maturity Group IV, strains with long and short filling periods were selected. These estimates of seed filling periods and measurements of 100 seed weights were used to estimate seed growth rates. Selected lines exhibited wide variations in both seed growth rate and duration, as estimated by these methods.

A smaller number of USA cultivars, [Corsoy, (Maturity Group II), Amcor (II), Harosoy (II), Calland (III) and Clark (IV)], and foreign introductions (273.483D, 347.539A, 407.795A, 404.166, 416.773, Bansei (Ames), 424.255B, 416.822, 416.989, and 427.107C), were selected for large differences in seed growth rate and duration for further study in 1984. A set of isolines differing in maturity (E_1/e_1, E_2/e_2, and E_3/e_3, capital letters associated with dominance and lateness to maturity) and stem termination (Dt_1/dt_1, indeterminate/determinate) alleles was also studied. These entries [Maturity Group I-$e_1e_2e_3$: L71-920 (C, Clark backcross isoline; Dt_1), L73-1543 (H, Harosoy backcross isoline, Dt_1; Maturity Group II-$e_1e_2E_3$: Harosoy (H, Dt_1), L63-3117 (C, Dt_1), L65-778 (C, dt_1); Maturity Group III-$e_1E_2e_3$; L63-2404 (C, Dt_1), Maturity Group IV-$e_1E_2E_3$: Clark (C, Dt_1), L72-1737 (C, dt_1), L63-3016 (C, dt_1), L74-21 (H, Dt_1), L69-4755 (C, Dt_1, y_9 or yellow-green chlorophyll deficient); Maturity Group IV-V-$e_1E_2E_3$: L74-441 (C, Dt_1), -$E_1e_2e_3$: L80-5918 (C, Dt_1), L71-802 (H, Dt_1), -$E_1e_2E_3$: L66-432 (C, Dt_1), L67-2324 (H, dt_1); Maturity Group V-$E_1E_2E_3$: L65-3366 (C, Dt_1), L66-546 (C, dt_1)] were planted in plots 4 rows wide and 6 m long, with 0.76 m between rows.

Approximately 80 pods per plot were marked at the beginning of seed fill (when the pod was fully expanded and the seed was approximately three mm long) by placing a dot of paint on the pod tip. No more than three pods per plant were marked. A 20 pod sample was harvested twice during the linear phase of seed dry matter accumulation to estimate the seed growth rate (*SGR*). The remaining pods were harvested after maturity to determine the final seed size (*FSS*). The effective filling period (Table 1) was estimated from *FSS/SGR*.

In 1984, 10 to 15 pods at the beginning seed stage (*BS*), were tagged on 10 consecutive plants at least 0.3 m from the end of a bordered row (this is modified somewhat from the method used by Reicosky *et al.* (*27*), as given in Table 1). These pods, tagged between R4 and R5, were located on nodes near the middle of the main stem and were the first or second to develop on the plant. These pods were monitored three times weekly near maturity for the change from green to yellow, an indicator of physiological maturity (see Table 1). The time from tagging to yellowing was taken to be the seed filling period (*SFP*). Final seed size (*FSS*) was measured at maturity, and an effective seed growth rate (*ESGR*) was estimated from *FSS/SFP*.

At harvest, plants from four meters of row from the center of the two unsampled border rows were threshed for yield. The harvested beans were weighed and subsampled for moisture content.

RESULTS AND DISCUSSION

Cultivars

In the 1983 test, large differences were found in the time from reproductive stages R5 to R7, the final seed size (*FSS*), the seed growth rate during the linear phase of dry matter accumulation (*SGR*) and the effective filling period (*EFP*), or *FSS/SGR* (see Table 1 for definitions), Table 2. The correlations among the 1983 measurements and the estimates from the preliminary studies of the duration of seed fill and the seed growth rate were large and highly significant among

Table 2. The rate and duration of seed fill and seed size of cultivars in 1983.

Maturity Group (MG)	Days from R5 to R7	Effective filling period	Seed growth rate	Final seed size
	(days)		(mg seed^{-1} day^{-1})	(mg seed^{-1})
MG II				
Mean	32.9	25.9	6.0	154.8
Range	26.0–40.0	19.2–30.7	4.4–9.5	88.4–213.5
CV	5.8	10.8	11.0	9.8
LSD 0.05	3.1	4.7	1.1	25.3
n	18	17	17	17
MG III				
Mean	33.1	27.6	5.5	147.7
Range	24.7–45.3	21.4–35.9	2.8–7.4	64.4–183.9
CV	4.2	20.5	16.3	7.9
LSD 0.05	2.3	9.5	1.5	19.5
n	17	15	15	15
MG IV				
Mean	33.6	23.3	5.7	133.3
Range	25.3–45.7	14.7–31.4	3.4–7.8	49.8–206.2
CV	6.1	15.2	13.8	6.0
LSD 0.05	3.4	5.9	1.3	13.7
n	18	11	11	11

Table 3. Comparisons among methods for estimating seed growth duration and rate, 1983 studies.

Maturity group (MG)	Correlated measurement	Direct measurement	Correlation
MG II, III	BS to R8	R5 to R7	0.49, $P<0.05$
MG II, III	BS to R8	*EFP*	0.65, $P<0.05$
MG IV	R1 to R8	R5 to R7	0.42, $P=0.5$
MG IV	R1 to R8	*EFP*	0.39, $P=0.75$
MG II, III	*FSS* / (BS – R8)	*SGR*	0.91, $P<0.001$
MG IV	*FSS* / (R1 – R8)	*SGR*	0.67, $P=0.1$

Group II and III strains, but not among the later maturing Group IV strains (Table 3).

All the U.S.A. cultivars had long seed filling periods, compared to most of the introduced strains (data not shown). Introductions with filling periods longer than USA cultivars have been reported for Maturity Group IV (*7*), but not for other Maturity Groups (*22, 27*). These introductions had a wider range of both *FSS* (50 to 208 vs. 134 to 213 mg seed^{-1}) and *SGR* (2.9 to 9.5 vs. 4.9 to 7.1 mg seed^{-1} d^{-1}) values than U.S.A. cultivars.

In the 1984 studies, strain differences ($P<0.01$) were found among each of three estimates of the seed filling period (R5 to R7, *EFP* and *SFP*) and among two estimates for the rate of seed fill (*SGR* and *ESGR* or *FSS/SFP*) (Table 4). The different estimates for the seed filling period and seed filling rate were well correlated (Table 5). *FSS* and measurements of the seed filling rate can vary

Table 4. Measurements of the rate and duration of seed growth and seed size among domestic and foreign cultivars in 1984.

	Days from R5 to R7	*EFP** (days)	*SFP**	*SGR** (mg seed^{-1} day^{-1})	*ESGR**	*FSS** (mg)	Yield (g m^{-2})
Mean	36.1	26.2	33.5	6.2	4.8	163.6	179.9
Range	27.7–44.0	19.4–31.0	25.9–37.7	4.3–9.0	2.9–7.2	92.6–234.8	115.4–286.1
CV	5.8	10.8	5.2	10.2	6.8	7.1	11.5
LSD 0.05	3.5	4.7	2.9	1.1	0.5	20.3	38.1

* *EFP* = Effective filling period, *SFP* = Seed filling period, *SGR* = Seed growth rate, *ESGR* = Effective seed growth rate, *FSS* = Final seed size from pods tagged for *SGR*. See Table1.

with the timing of pod set and position on the plant (*12*). The two estimates of seed filling rate, *SGR* and *ESGR*, were highly correlated. *ESGR* values were smaller because of the longer estimate for *SFP* (Table 5). Both *SGR* and *ESGR* were correlated with independent measurements of *FSS*, as seen earlier (*6*). Each estimate of the duration of seed fill correlated well with *FSS*, as reported earlier (*7*). However, Smith *et al.* (*31*) have demonstrated that *FSS* is not always related to duration of seed fill. Estimates of *EFP* and *SGR* or *SFP* and *ESGR* are not independent of each other (Table 1) and cannot be validly correlated.

Between years, cultivar mean *EFP* ($r=0.56$, $P<0.05$), R5 to R7 ($r=0.80$, $P<0.001$) and *SGR* ($r=0.91$, $P<0.001$) values correlated well, as reported earlier (*27*) from similar comparisons. R5 to R7 in days correlated well with the same period in degree days, base 10℃, in 1983 ($r=0.76$, $P<0.001$) and 1984 ($r=0.79$, $P<0.001$), as reported earlier (*7*) for similar measurements of the filling period. In comparisons of R5 to R7 vs. planting to R7, only the 1984 degree day values

Table 5. Correlation coefficients (levels of significance) among measurements of rate and duration of seed fill, based on means of domestic and foreign cultivars in 1984.

	*SFP**	Days from R5 to R7	Seed size I	Seed size II	*SGR**	*ESGR**
EFP	0.80 (0.001)	0.62 (0.02)		0.88 (0.001)		0.40 (0.16)
SFP		0.88 (0.001)	0.75 (0.002)		0.52 (0.06)	
R5 to R7			0.80 (0.001)	0.81 (0.001)	0.62 (0.02)	0.63 (0.02)
R7						
FSS I				0.98 (0.001)		0.92 (0.001)
FSS II					0.88 (0.001)	
SGR						0.88 (0.001)

* *SFP* = Seed filling period, *SGR* = Seed growth rate, *ESGR* = Effective seed growth rate. *FSS* I and II refer to final seed size from populations of pods for *SGR* and *SFP* measurements, respectively.
Correlations not independent for Seed size I + II comparisons.

correlated ($r=-0.81$, $P<0.01$); day comparisons did not correlate. *EFP* ($r=0.72$, $P<0.005$) and *SFP* ($r=0.54$, $P<0.05$) were both highly correlated with yield, Table 6; whereas the time from R5 to R7 was not. While this suggests that *EFP* and *SFP* based upon seed measurements seem to be the preferred parameters to be measured in any selection effort, the plant-based reproductive stages are effective and more practical for screening large populations, as demonstrated earlier (*29, 30*).

Seed number per unit area was significantly correlated with yield ($r=-0.54$, $P<0.05$) but not to various estimates or filling duration (Table 6). *FSS* and *SGR* were negatively correlated with seed number per unit area.

Isolines

The effects of the alleles at the three *E* loci and Dt_1 alleles on time between

Table 6. Correlation coefficients (levels of significance) between measurements of seed growth, yield and seed number per unit area, based on cultivar means.

	Yield ($g\ m^{-2}$)	Seed number (seed m^{-2})
EFP (days)	0.72 (0.004)	0.06 (0.85)
SFP (days)	0.54 (0.03)	−0.24 (0.40)
R5 to R7 (days)	0.41 (0.14)	−0.39 (0.17)
Seed number (seed m^{-2})	0.54 (0.05)	—
FSS (mg)	0.25 (0.38)	−0.67 (0.009)
SGR (mg day^{-1})	−0.05 (0.85)	−0.79 (0.001)

growth stages are summarized in Table 7. These results confirm earlier findings (*1, 19, 34*). *The* Dt_1 allele for determinate stem termination in three combinations of maturity alleles decreased the number of days to R5 by 11.9. The time from R5 to R7 was increased by nearly the same amount. The time to flowering and maturity was not significantly changed by a substitution at the Dt_1 locus, nor was *EFP*, *SGR* and *FSS*. The only parameter not related to time to R5, *SFP*, was significantly changed. The effect of Dt_1 on days to R5 is probably due to the abrupt termination of main stem node development and the pattern of more uniform pod set characteristic of determinate cultivars. For determinate isolines, the pods at the 4 uppermost nodes on the main stem are among the first to to develop on the plant. By contrast, indeterminate isolines begin setting pods at lower nodes while the main stem is still growing. These results confirm earlier reports (*21*) that comparisons between determinate and indeterminate cultivars for the period R5 to R7 may not reflect any real differences in the duration of the development of individual seeds.

The substitution of the dominant allele for each of the maturity genes

Table 7. Changes in days to reproductive growth stages R2, R5, R7, days from R2 to R5 and R5 to R7, duration of the seed filling period (*EFP, SFP*), *SGR* and *FSS* due to *DT* and *E* alleles in 1983–1984.

	R2	R5	R7	R2–R5 (days)	R5–R7	*EFP*	*SEP*	*SGR* (mg day^{-1})	*FSS* (mg)
Clark (e_1 E_2 E_3)									
Years									
('83 vs. '84)	−4.4**[a]	−3.4**	−5.8**	0.8	−3.8**	−2.1*	—	0.4*	−9.2*
E_1 vs. e_1 (E1)	16.3**	17.8**	14.5**	−1.2	−2.4**	−0.8	−2.0**	−0.3	−11.6
E_2 vs. e_2 (E2)	10.9**	11.9**	13.6*	2.0*	−1.6*	−0.7	−1.1	−0.4	−7.7
E_3 vs. e_3 (E3)	3.4	5.8*	4.0*	2.3*	−1.8*	−2.8	−0.2	0.3	−7.0
E1 × E2	3.5**	0.3	1.9	−3.3	1.6*	—	−2.3**	−0.4	—
E1 × E3	1.3	−2.0	−1.2	−3.4*	0.9	2.1	−0.5	−0.5	3.3
E2 × E3	−0.6	−0.8	−0.7	−0.3	0.1	1.9	3.6**	−0.4	0.5
Dt_1 vs. dt_1	2.6	11.9**	0.9	9.2**	−12.1**	−3.6	−8.5**	1.3	22.4
Harosoy (e_1 e_2 E_3)									
Years									
('83 vs. '84)	−3.3*	−5.0**	−10.4**	−1.8	−5.5**	0.3	—	−1.0	−37.5**
E_1 vs. e_1	18.1**	23.8**	19.6**	5.7**	−4.1	−3.0	−4.2**	0.7	−11.8
E_2 vs. e_2	7.2*	18.5**	13.2**	11.3**	−5.3	1.9	0.4	0.1	13.8
E_3 vs. e_3	4.0*	4.8*	6.3**	0.9	1.5	−1.3	−2.3*	0.9	7.4
Combined									
Clark vs. Harosoy (B)	−0.6	0.8	1.4	1.3	0.3	−1.5	−0.3	0.4	4.2
B × E1	−1.3	−4.4**	−4.3**	−3.0**	0.1	−1.3	−2.1**	0.2	3.2
B × E2	−3.8	−4.2*	−1.7	−0.4	2.5**	0.2	0.5	−0.2	−7.1
B × E3	−0.1	2.0	0.6	2.2**	−1.4	−2.6	−1.3*	0.8*	−1.7

*, ** Significant at $P=0.05$ and 0.01 respectively.

[a] Single degree of freedom contrasts used to estimate and test genetic effects.

studied delayed R2 and R7, but as previously reported (*1*), the magnitude of the effects differed (Table 7). The large changes in R2 and R7 were not found in the estimates of the seed filling period. None of the differences in *EFP* were significant in either the Harosoy or Clark background. The only significant differences in *SFP* were small reductions that occurred with the E_1 allele in both backgrounds and the E_3 allele in Harosoy. Number of days from R5 to R7 were not significantly changed in the Harosoy background whereas small changes (mostly negative) were noted in the Clark background. Changes in maturity did not have any significant effect on *SGR* or *FSS* in either background. Some (*7, 27*) have reported that cultivars with long seed filling periods were associated with late maturity but others (*23, 29*) have not found such an association. These results indicate that these maturity alleles are not responsible for a positive association between long filling periods and late maturity.

Number of days from R5 to R7 was correlated with degree days between the

same events in 1983 ($r = 0.71$, $P < 0.01$) and 1984 ($r = 0.68$, $P < 0.025$) for the indeterminate (dt_1) isolines. Correlations for other comparisons, such as discussed above for cultivars, were not significant. Although late maturing isolines were exposed to lower temperatures during seed fill, the duration in days was not affected. Temperature has been shown to decrease seed growth rate (*8*) and the timing of growth stages for constant photoperiods (*14*) ; the way temperature and daylength were changing in our field studies may have induced faster growth rates. Short days enhance seed growth rates and shorten the duration (*26, 33*), but short days also reduce the *E/e* allele affects on maturity and associated effects on seed growth rates and duration as well (*18*).

Yield, seed number, and seed size were increased by the presence of the Dt_1 allele in Clark. Yield and seed number were decreased by the E_1 allele in the study (Table 8). Yield differences across all isolines were correlated with the number of seed per unit ground area ($r=0.9$, $P<0.05$) but not seed size ($r=0.31$). Yields decreased with days to R7, Fig. 1, with seed numbers decreasing at approximately R7=120 days, Fig. 2.

Table 8. Increases in yield, seed number per unit area and seed size due to *Dt* and *E* alleles for isolines in 1984.

	yield ($g\ m^{-2}$)	seed number (seed m^{-2})	seed size (mg)
Clark			
E_1 vs. e_1 (E1)	−40.1**	−264.6*	4.6
E_2 vs. e_2 (E2)	−18.4	−59.9	−3.6
E_3 vs. e_3 (E3)	−12.4	−58.0	−3.1
E1 × E2	—	—	—
E1 × E3	0.9	52.8	−13.1
E2 × E3	−56.8	−439.6	19.3
Dt_1 vs. dt_1	84.1**	340.6**	28.6**
Harosoy			
E_1 vs. e_1	−88.4**	−506.4*	5.0
E_2 vs. e_2	−12.4	93.3	−21.3
E_3 vs. e_3	−48.5	−244.9	−0.6
Combined			
Clark vs. Harosoy (B)	8.7	77.9	−5.6
B × E1	25.7	106.0	2.1
B × E2	−9.7	−34.0	1.0
B × E3	20.0	142.9	−4.0

*, ** Significant at $P=0.05$ and 0.01 respectively

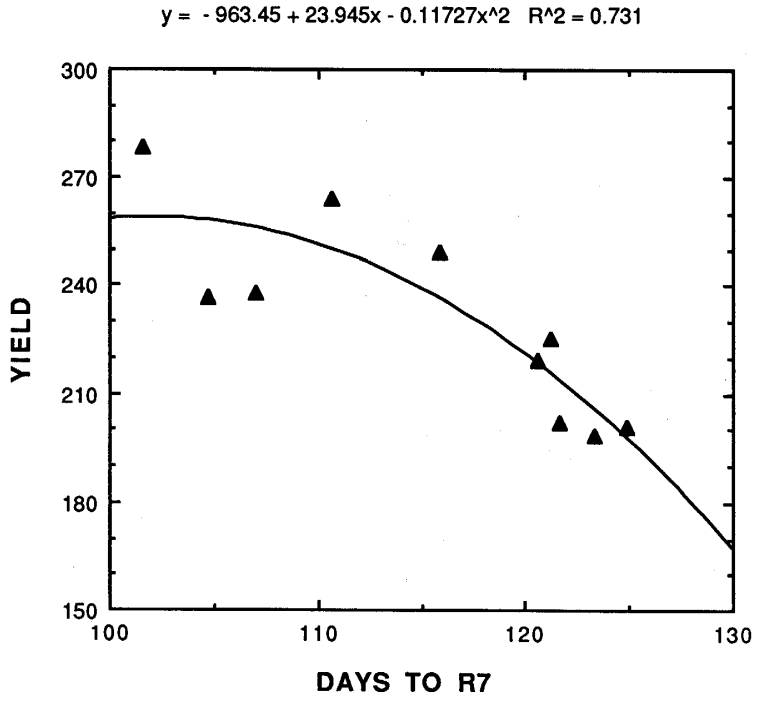

Fig. 1. Seed yield vs. the number of days from planting to maturity (R7) for the indeterminate isolines in 1984.

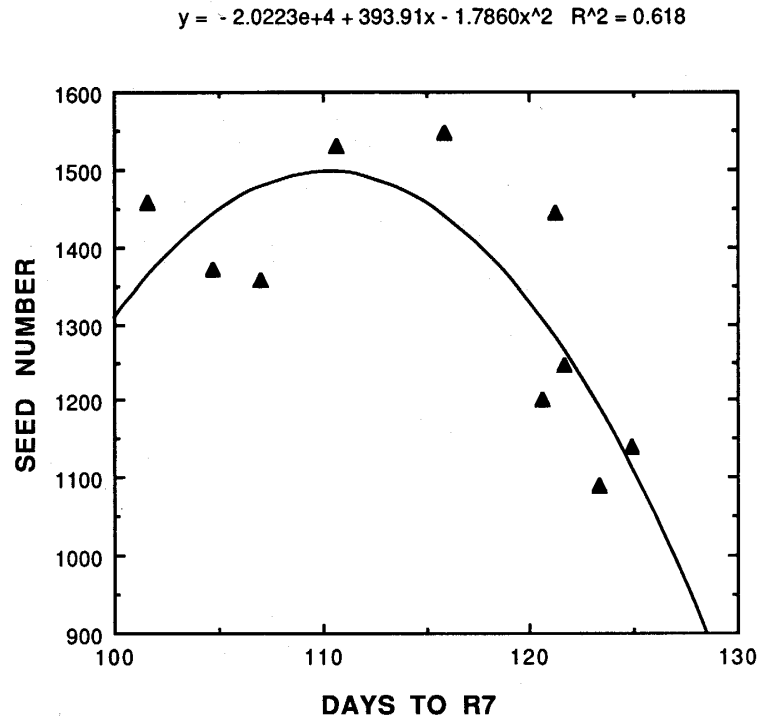

Fig. 2. Seed number per unit ground area vs. the number of days from planting to maturity for the indeterminate isolines in 1984.

GENERAL CONCLUSIONS

The simplist way to select for seed yield is to weigh seeds at maturity. However, methods available for measuring growth stages, duration of seed growth and seed growth rates can provide additional information about the process of seed dry matter accumulation. The results demonstrate that several methods can effectively estimate the length of the seed filling period and confirm the positive relationship between this duration and yield. The rate of seed fill can also be estimated. Large variations in rate were found but no association between this parameter and yield was found. Large changes in the timing of flowering and maturity can be achieved with known maturity genes but duration of the seed filling period and seed growth rate are minimally affected.

The changing daylengths and temperatures make the quantification of separate effects ambiguous, but selection at the field level, unless modified by artifical lights, is done under these same conditions. Controlled enviroment studies are needed to quantify some of these effects and to develop better associated selection and prediction (*16*) tools. The use of genetic engineering technology may well depend upon more detailed studies of the genetics of these enviromental responses, and it seems urgent that this information become available soon if research funds are to be used efficiently for such a purpose.

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