

Improving cultivated oats (*Avena sativa* L.) with alleles for vegetative growth index from *A. sterilis* L. *

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Received November 2, 1983; Accepted February 8, 1984

Communicated by P. L. Pfahler

Summary. Ten *Avena sterilis* L. lines of Mediterranean origin were crossed with six *A. sativa* L. cultivars from the North Central USA. Additionally, six intervarietal crosses were made among the *A. sativa* cultivars. F₂-derived lines from each cross type (interspecific and intraspecific) were evaluated for transgressive segregation for grain yield and several vigor traits. Mean percentages of transgressive segregates one LSD_{0.05} above the high parent for vegetative growth index and biomass were 9.0% and 9.8%, respectively, from interspecific crosses, but only 4.5% and 2.9%, respectively, from intraspecific crosses. However, there were two and a half times more high transgressive segregates for grain yield from intra than from interspecific crosses. The maximum vegetative growth index among segregates from interspecific crosses was 0.2 q/day/ha greater than the highest segregate from intraspecific crosses. However, mean harvest index was reduced materially by the introgression of *A. sterilis* germplasm. Because there was no genetic association between vegetative growth index and harvest index, however, it should be possible to improve both harvest index and vegetative growth index and, thus, the grain yield of cultivated oats.

Key words: *Avena sterilis* – Biomass – Vegetative growth index – Transgressive segregation

Introduction

Transgressive segregation from interspecific hybrids can give rise to new plant characteristics (Stebbins 1977) or an abundance of extreme forms (Barbacki et al. 1976).

* Journal Paper No. J-11228 of the Iowa Agric. and Home Econ. Exp. Stn., Ames, IA 50011. Project 2447

Harlan (1976) and Stalker (1980) published reviews of research in which wide hybridization has produced derived lines adapted to stress environments, or with improved quality, pest resistance, or productivity.

Significant increases in total biomass have been attributed to the incorporation of germplasm from the wild relatives of sugarcane (*Saccharum officinarum*) (Panje 1972), tobacco (*Nicotiana tabacum*) (Wernsman et al. 1976), and sorghum (*Sorghum bicolor*) (Dangi and Paroda 1978) into each of these cultivated species, respectively. In one such case, a selection from a *S. roxbirghii* × *S. bicolor* cross outyielded a superior check by 24% for green fodder and 6% for dry matter (Dangi and Paroda 1978). Increases in grain yield have been reported for crosses between bread (*Triticum aestivum*) and durum (*T. durum*) wheats (Brezhnev 1977), maize (*Zea mays*) and teosinte (*Z. mexicana*) (Reeves 1950), and barley (*Hordeum vulgare*) and its weedy relative *H. spontaneum* (Vega and Frey 1980).

Lawrence and Frey (1975) demonstrated a large increase in grain yield with the introgression of *A. sterilis* germplasm into cultivated oats. The BC₁F₂ through BC₄F₂ of interspecific oat crosses contained the greatest proportion of segregates that combined transgressive grain yield with growth duration and harvest index similar to the *A. sativa* parents. Takeda and Frey (1976) found that improvement in grain yield from introgression of *A. sterilis* germplasm was due primarily to increased vegetative growth index.

For this study, additional *A. sterilis* accessions were evaluated to determine the magnitude of gain feasible, with regard to grain yield, biomass, and vegetative growth index, via interspecific crossing with cultivated oats. Additionally, comparisons are made between the proportion of transgressive segregated produced by interspecific and intraspecific crosses for each of these traits.

Materials and methods

Materials

Ten *A. sterilis* accessions were crossed with six *A. sativa* cultivars (Table 1) to form 60 hybrids according to the Design II

Table 1. Name, and origin for *A. sativa* cultivars and *A. sterilis* accessions used as parents

Parental line	Origin
<i>A. sativa</i>	
'Wright'	Wisconsin
'Nodaway 70'	Missouri
'Ogle'	Illinois
'Benson'	Minnesota
'C.I. 9170' ^a	Iowa
'Tippecanoe'	Indiana
<i>A. sterilis</i>	
P.I. 324785	Libya
P.I. 324748	Sicily
P.I. 411560	Ethiopia
P.I. 309033	Southern Israel
P.I. 318253	Northern Israel
P.I. 412645	Turkey
P.I. 411728	Iran
P.I. 411976	Iraq
P.I. 282731	Central Israel
P.I. 412364	Tunisia

^a 'C.I. 9170' is a near-isogenic, component line of 'Multiline E68', 'E69' and 'E70' cultivars

mating plan (Comstock and Robinson 1948). *A. sativa* cultivars were used as females. *A. sterilis* accessions were chosen one each from seven Mediterranean countries and three from Israel. To ensure that the *A. sterilis* accessions used as parents in our study originated from diverse sources of germplasm we selected *A. sterilis* lines that previously had been grouped into separate clusters based on similarity for 15 traits (Rezai 1977). One cross, 'Wright' × P.I. 411976, was lost. Also, six intraspecific crosses were made among five *A. sativa* cultivars (Table 2).

F₂ seeds from each cross were space planted in the field. Non-shattering F₂ plants were harvested and threshed individually, and the bulk seed from a plant was used to establish an F₂-derived line in the F₃. Approximately 40 F₂-derived lines per cross were obtained.

Field evaluation

The 2,658 F₂-derived lines in F₃ from the 65 crosses, plus the six *A. sativa* parents, each entered five times, were evaluated in a randomized complete-block design with two replicates at each of three locations. The *A. sterilis* parents, each entered five times, were grown in a separate block contiguous to each replicate to allow bagging of *A. sterilis* plots with translucent, high-density polyethylene mesh bags to catch shattered seed. A plot was a hill sown with 30 seeds, and plots were spaced

Table 2. Crosses among *A. sativa* cultivars

'Nodaway 70' × 'Ogle'
'Ogle' × 'Benson'
'Benson' × 'C.I. 9170'
'C.I. 9170' × 'Tippecanoe'
'Tippecanoe' × 'Nodaway 70'
'Tippecanoe' × 'Ogle'

30.5 cm apart in perpendicular directions. Two rows of hills were planted around each replicate to provide competition for peripheral plots. Plots were sown on 22 April, 19 April, and 24 April at the Agronomy Field Research Center near Ames, Iowa, the Northwest Research Center near Sutherland, Iowa, and the Northern Research Center near Kanawha, Iowa, respectively. The soil types at the Ames and Kanawha sites are loam soils of the Clarion-Webster association, whereas the soil type at the Sutherland site is a Galva-Sac silty clay loam. The preceding crop at all sites was soybeans. The fertilizer applications per ha were 51.5 kg N and 7 kg each of P and K at the Kanawha site; 16.8 kg N, 67.2 kg P, and 33.6 kg K at the Sutherland site; and 33.6 kg N and 51.5 kg each of P and K at the Ames site. An eradicant fungicide was applied to the plots 1 month before harvest to eliminate crown rust caused by *Puccinia coronata* Cda. *avena* Frazier and Led.

Six traits were measured or computed on a plot basis. Heading date was recorded (on the Ames plots only) as the number of days from planting until 50% of the panicles were completely emerged. When mature, plants in a plot were harvested at ground level, dried, and weighed to obtain biomass (g). Next, the bundle of culms was threshed, and grain yield (g) was obtained. Straw yield was calculated by subtracting grain yield from biomass. Harvest index was computed as the ratio of grain yield to biomass and expressed as a percentage. Vegetative growth index was calculated (on the Ames plots only) as straw weight divided by number of days to heading.

Statistical analysis

Phenotypic correlations were estimated on an intrapopulation basis from line means for pairs of traits.

Comparisons between inter and intraspecific crosses were made by defining extreme progeny types as transgressive (i.e., lines that exceeded their high parent or were lower than their low parent) or significantly transgressive (i.e., lines with mean values greater or lesser than one LSD_{0.05} above the high or low parent) segregates.

Results

Transgressive segregation

Generally, *A. sativa* cultivars released in the late 1970's and the 1980's ('Ogle' and 'Benson') yielded in excess of 40 q/ha of grain, whereas cultivars released in the mid 1970's and earlier ('Wright', 'Nodaway 70', 'C.I. 9170', and 'Tippecanoe') yielded from 27 to 39 q/ha (Table 3). A similar relationship occurred for biomass and vegetative growth index, also. *A. sterilis* accessions were less productive than *A. sativa* cultivars but their grain, biomass, and straw yields were quite high for unadapted oat genotypes. For example, the *A. sterilis* parents, P.I. 411560 and P.I. 412364, had grain and biomass yields comparable to those of 'Nodaway 70' and 'C.I. 9170', and greater than those of 'Tippecanoe' and 'Wright'.

In general, F₂-derived line means for biomass, grain yield, and harvest index showed that introgression of *A. sterilis* germplasm into the cultivated oat gene pool caused decreases in these three traits (Table 4). Mean

Table 3. Means of the *A. sativa* parents, and *A. sterilis* parents for grain yield, biomass, straw yield, heading date, harvest index, and vegetative growth index

	Year released	Grain yield q/ha	Biomass q/ha	Straw yield q/ha	Heading date days	Harvest index %	Vegetative growth index q/day/ha
<i>A. sativa</i> , parents							
'Wright'	1975	29.7	89.2	59.5	66.2	33.4	0.95
'Nodaway 70'	1970	38.4	99.9	61.6	61.4	39.2	1.10
'Ogle'	1980	49.8	126.2	76.3	66.0	40.4	1.36
'Benson'	1979	40.3	107.0	66.7	68.7	38.2	1.14
'C.I. 9170'	—	34.8	84.7	50.0	58.7	41.2	0.90
'Tippecanoe'	1965	26.8	72.8	46.0	61.2	37.9	0.71
<i>A. sterilis</i> , parents							
P.I. 324785	—	23.0	52.5	29.6	67.5	43.2	0.40
P.I. 324748	—	20.5	64.4	43.9	74.0	31.8	0.64
P.I. 411560	—	39.5	96.0	57.8	68.1	41.0	0.82
P.I. 309033	—	27.0	64.1	38.8	66.0	40.9	0.56
P.I. 318253	—	28.4	74.5	46.1	65.8	36.9	0.71
P.I. 412645	—	31.2	74.5	43.3	69.8	41.8	0.67
P.I. 411728	—	29.4	73.2	43.8	67.4	40.4	0.60
P.I. 411976	—	27.2	91.8	64.6	74.0	30.7	0.90
P.I. 282731	—	20.2	44.0	29.9	70.2	41.2	0.52
P.I. 412364	—	35.6	93.6	57.9	70.0	37.3	0.81

Table 4. Means and ranges of lines grouped as parents or F₂-derived lines from interspecific and intraspecific crosses for heading date, biomass, grain yield, harvest index, straw yield, and vegetative growth index

Traits		<i>A. sativa</i> parents	<i>A. sterilis</i> parents	F ₂ -derived lines from <i>A. sativa</i> × <i>A. sterilis</i>	F ₂ -derived lines from <i>A. sativa</i> × <i>A. sativa</i>
Heading date (days)	Mean	63.7	69.3	62.8	62.3
	Range	58.7 – 68.7	65.8 – 74.0	51.5 – 77.0	54.0 – 77.0
Biomass (q/ha)	Mean	96.6	72.9	89.1	102.4
	Range	72.8 – 126.2	44.0 – 96.0	12.0 – 149.2	49.0 – 156.2
Grain yield (q/ha)	Mean	36.6	28.2	27.6	39.1
	Range	26.8 – 49.8	20.2 – 39.5	1.8 – 52.2	4.0 – 59.0
Harvest index (%)	Mean	38.4	38.5	31.2	38.4
	Range	33.4 – 41.2	31.8 – 43.2	2.0 – 49.8	7.7 – 48.7
Straw yield (q/ha)	Mean	60.0	45.6	61.5	63.4
	Range	46.0 – 76.3	29.6 – 57.9	8.2 – 107.0	25.3 – 108.8
Vegetative growth index (q/day/ha)	Mean	1.03	0.67	1.05	1.15
	Range	0.71 – 1.36	0.52 – 0.90	0.19 – 2.04	0.44 – 1.84

grain yield for lines from interspecific crosses was only 70% of that for lines from intraspecific crosses. Biomass and harvest index means for lines from interspecific crosses were 87% and 81%, respectively, of the means for lines derived from intraspecific crosses. There was little difference between crossing types for mean heading date and straw yield.

Ranges of F₂-derived lines for most traits were greater for inter than for intraspecific crosses. Maxi-

imum values were similar for the two population types for all traits except vegetative growth index, however, lower minimum values occurred for lines derived from inter than from intraspecific crosses. Six interspecific crosses produced F₂-derived lines with a vegetative growth index equal to or greater than 1.84 q/day/ha, the maximum value observed for a segregate of intraspecific crosses. A vegetative growth index of 2.04 q/day/ha was found for one line derived from an inter-

Table 5. Percentages of transgressive F_2 -derived oat lines from interspecific and intraspecific crosses pooled by *A. sativa* parent for biomass, grain yield, and vegetative growth index

Parents	Low transgressive segregates			High transgressive segregates		
	Biomass	Grain yield	Vegetative growth index	Biomass	Grain yield	Vegetative growth index
Interspecific crosses						
'Wright'	22	57	6	41	14	63
'Nodaway 70'	15	38	5	35	19	44
'Ogle'	11	39	3	9	1	18
'Benson'	20	50	7	22	5	37
'C.I. 9170'	19	57	5	42	19	64
'Tippecanoe'	15	46	6	60	27	80
Mean	17	48	5	35	14	51
Intraspecific crosses						
'Nodaway 70'	35	36	26	13	8	24
'Ogle'	19	13	21	24	13	34
'Benson'	19	19	22	38	44	39
'C.I. 9170'	8	11	7	56	60	64
'Tippecanoe'	15	16	6	37	37	47
Mean	19	19	16	34	32	42

Table 6. Percentages of F_2 -derived lines with biomass, grain yield, or vegetative growth index mean values of one $LSD_{0.05}$ above the high parent mean or $LSD_{0.05}$ below the low parent mean for interspecific and intraspecific crosses pooled by *A. sativa* parent

Parents	1 $LSD_{0.05}$ below low parent			1 $LSD_{0.05}$ above high parent		
	Biomass	Grain yield	Vegetative growth index	Biomass	Grain yield	Vegetative growth index
Interspecific crosses						
'Wright'	1	25	0	9	2	12
'Nodaway 70'	2	15	0	9	3	4
'Ogle'	3	17	0	1	0	2
'Benson'	1	23	0	5	0	3
'C.I. 9170'	2	25	0	14	6	13
'Tippecanoe'	1	18	1	21	7	21
Mean	2	20	0	10	3	9
Intraspecific crosses						
'Nodaway 70'	6	16	1	0	0	1
'Ogle'	3	1	2	1	1	3
'Benson'	2	1	0	5	7	5
'C.I. 9170'	0	0	0	0	13	7
'Tippecanoe'	2	9	0	8	16	7
Mean	3	5	1	3	7	5

specific cross. This value is 0.2 q/day/ha greater than the highest line from an intraspecific cross.

Sixteen of the 59 interspecific oat crosses had vegetative growth index means significantly greater than the high parent. Thus, in general, introgression of genes from *A. sterilis* tended to cause the F_2 -derived lines to head earlier than the early parent, yield less

grain but more biomass and straw than the midparent, and have a harvest index lower than low parent values.

Percentages of F_2 -derived lines that were transgressive and significantly transgressive from inter and intraspecific crosses and pooled by *A. sativa* parents are presented in Tables 5 and 6, respectively. Mean percentages of low transgressive segregates for grain yield

Table 7. Percentages of F₂-derived lines with biomass, grain yield, and vegetative growth index above the high parent mean and one LSD_{0.05} above the high parent mean, pooled by parent for the 59 interspecific crosses

Parents	Above the high parent			One LSD _{0.05} above the high parent		
	Biomass	Grain yield	Vegetative growth index	Biomass	Grain yield	Vegetative growth index
<i>A. sterilis</i>						
P.I. 324785	15	3	28	2	1	4
P.I. 324748	32	20	40	10	7	8
P.I. 411560	56	20	57	16	2	8
P.I. 309033	15	4	36	3	0	6
P.I. 318253	29	7	53	5	0	6
P.I. 412645	48	23	64	16	6	12
P.I. 411728	44	20	54	14	5	11
P.I. 411976	46	34	54	14	6	2
P.I. 282731	32	13	52	11	4	11
P.I. 412364	36	7	62	7	0	16

were 48% for the interspecific and 19% for the intraspecific crosses, whereas the converse occurred for high transgressive segregates, i.e., 14% and 32% for inter and intraspecific crosses, respectively. Mean percentages of high and low transgressive segregates for biomass were similar for intra and interspecific crosses. However, there were 9% more high transgressive segregates for vegetative growth index from inter than from intraspecific crosses. The relationship between intra and interspecific crosses became more definitive for high and low segregates when the criterion was changed to that of one LSD_{0.05} above or below the high or low parents. There were twice as many significantly high segregates for vegetative growth index and more than three times as many for biomass from inter than from intraspecific crosses. The mean percentage of lines with grain yield significantly greater than the high parent was 2½ times larger for intra than for interspecific crosses, however. Thus, *A. sterilis* parents tend to be a good source of genes for high biomass and high vegetative growth index. All 10 *A. sterilis* lines were sources of alleles for high vegetative growth index as shown by the existence of high transgressive segregates derived from all parents from this species (Table 7). Further, the relatively large percentages of high transgressive segregates obtained for nearly all *A. sterilis* parents (28% for P.I. 324785 to 64% for P.I. 412645) suggest that alleles for increasing this trait occur generally in this species, whatever its origin.

Correlations

Phenotypic correlations among traits, pooled over crosses, are given in Table 8. Grain yield was positively and significantly correlated with all other traits except heading date. Grain yield and heading date were

negatively and significantly correlated in the interspecific crosses, and harvest index and heading date were negatively and significantly correlated in both inter and intraspecific crosses. Heading date and biomass showed no or low association, and heading date and straw yield showed low but significant positive association. These relationships indicate that lengthening the growing season would increase straw yield but decrease grain yield.

Table 8. Phenotypic correlations pooled over 59 interspecific oat crosses and six intraspecific oat crosses for all pairwise combinations between grain yield (GYD), biomass (BIO), straw yield (SYD), harvest index (HI), heading date (HD), and vegetative growth index (VGI)

Traits	F ₂ -derived lines from interspecific matings	F ₂ -derived lines from intraspecific matings
GYD-BIO	0.78**	0.87**
SYD	0.51**	0.69**
HI	0.66**	0.33**
HD	-0.36**	0.00
VGI	0.60**	0.60**
BIO-SYD	0.94**	0.95**
HI	0.05*	-0.18**
HD	-0.04	0.22**
VGI	0.95**	0.95**
SYD-HI	-0.29**	-0.46**
HD	0.13**	0.32**
VGI	0.96**	0.98**
HI-HD	-0.54**	-0.39**
VGI	-0.04	-0.34**
HD-VGI	-0.12**	0.15**

*, ** Significantly different from zero at the 5% and 1% levels of probability, respectively

The greater phenotypic correlation between grain yield and biomass than between grain yield and harvest index for intraspecific crosses is consistent with the results of Rosielle and Frey (1975). Thus, increasing biological yield would be a more efficient means of improving grain yield of lines derived from intraspecific cross than would increasing harvest index. Phenotypic correlations from interspecific matings for grain yield with biomass and grain yield with harvest index were 0.78 and 0.66, respectively, suggesting that improvements in either biomass or harvest index would make significant contributions to increasing grain yield in such crosses.

Discussion

The genetic improvement of grain yield of cereals has been accomplished largely by increasing harvest index (Donald 1962; Vogel et al. 1963; Nass 1973; Kulshrestha and Jain 1982). Kulshrestha and Jain (1982) evaluated Indian wheat cultivars representative of the last eight decades and found that increase in grain yield were attributable almost exclusively to increased harvest index, with biomass remaining nearly constant over the 80-year period. Austin et al. (1980) contend that a harvest index of 60% may be attainable in winter wheat; however, Takeda and Frey (1976) have shown that highest yields of oats occur at a harvest index of 45% for this crop grown in Iowa, USA. Actually, of course, grain yield of cereals is a function of three traits, harvest index, growth duration, and growth rate. Generally, however, crops with a long growth duration have high biomass production, and a crop with short growth duration must have a high growth rate to produce high biomass yields. Oats in Iowa is an example of a crop limited to a short growing season because this crop is predisposed to temperature stress and rust-disease infection in mid to late summer.

Donald and Hamblin (1976) have proposed that small grain breeders should use crosses involving one parent with high harvest index and another with high biomass production to obtain increases in grain yield. Other reports support the rationale that sizable improvements in grain yield will require greater photosynthate production (Moss and Musgrave 1971; Nasyrov 1978).

Takeda and Frey (1976) found that from 92 to 97% of the grain yield variation in progeny of *A. sativa* × *A. sterilis* crosses was accounted for by fluctuations in harvest index and vegetative growth index. These two traits were of about equal importance to variation in grain yield in the BC₀ generation, but in later backcross generations, vegetative growth index was 1.5 to 1.8 times more important than harvest index in determining the variation for grain yield.

Our interspecific oat crosses provided more extreme progenies for high transgressive vegetative growth index than did intraspecific crosses. Further, the maximum vegetative growth index for an interspecific-

derived line exceeded that of any intraspecific-derived line by 0.2 q/day/ha. Takeda and Frey (1976) estimated that an increase of 0.108 q/day/ha caused a 14% improvement in grain yield for a cultivar with an initial vegetative growth index of 0.71 q/day/ha. The introgression of genes for high vegetative growth index from *A. sterilis* into cultivated oats, therefore, should cause immediate improvement in biomass yield and ultimate improvement in grain yield. The positive association of vegetative growth index with other productivity traits and the negative association between vegetative growth index and heading date imply that the alleles for high vegetative growth index carried by *A. sterilis* lines can be used in a breeding program to increase grain yield. Further, the lack of association between vegetative growth index and harvest index suggests independent inheritance, which would permit improvement of both traits simultaneously. Mean harvest index for interspecific-derived lines was 31%, which is considerably less than the 40% to 45% characteristic of cultivars currently grown in the Central Corn Belt, USA. However, backcrossing progeny with high vegetative growth index from *A. sativa* × *A. sterilis* crosses to *A. sativa* should provide for recovery of the *A. sativa* harvest index necessary for increased grain yield. Takeda and Frey (1976) observed increases in harvest index with succeeding backcross generations, until the BC₄ generation, when it leveled off at 43% for progeny of interspecific oat crosses.

The highest segregate for grain yield from intraspecific crosses produced 59 q/ha, whereas the highest one from interspecific crosses produced 52 q/ha. For comparison, the highest-yielding *A. sativa* cultivar produced 50 q/ha. Therefore, for the short term, intervarietal crosses among *A. sativa* cultivars would be more lucrative than interspecific crosses for extracting high-yielding lines. The results of Rodgers (1982) and Lawrence and Frey (1975), however, indicate that for the long term, genes from *H. spontaneum* and *A. sterilis* would be useful for increasing yields of barley and oats, respectively, above present levels. They found that the percentage of transgressive segregates increases during early backcross generations, and probably, the proportion could be increased even further with selection within an early backcross generation (Dudley 1982). Oat lines isolated from advanced backcross generations yielded up to 30% more grain than their respective recurrent parents, due largely to increased vegetative growth index (Frey 1983).

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