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Genetic control of vegetative growth index in oats (*Avena* spp.) *

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Summary. Vegetative growth index of cereals is defined as the mean quantity of vegetative tissue produced per unit land area per day. Thus, increasing vegetative growth index is a route by which biomass yield can be increased. The proportion of biomass that is translocated to grain is defined as harvest index. In midwestern USA, where harvest index of oats is optimum at ca. 45% and growth duration is restricted to 100–110 days by high temperature, diseases, and drought, breeding for higher vegetative growth index has been proposed as a way to increase grain yield potential for new cultivars.

Twelve matings involving *Avena sterilis*-derived lines and *A. sativa* cultivars were used to study vegetative growth index. F_2-derived lines from these matings were evalutated for vegetative growth index in microplots in field experiments in three environments with four replicates per environment. Vegetative growth index was found to be a quantitatively inherited trait. Heritability values for this trait averaged 54% when the unit of measurement was a microplot. Additive genetic control for vegetative growth index was indicated in seven matings, but in the remaining five, nonadditive gene action was involved in the inheritance patterns. High vegetative growth index segregates were produced more frequently from matings among unrelated parents than from matings of related ones.

Key words: *Avena sterilis* – Oats-Grain yield – Harvest index

Introduction

Typically, yield of cereal grains is expressed in terms of grain production, whereas biological yield (biomass) generally is ignored. Although biomass is a primary factor in determining grain production per unit land, grain yield is given primary consideration because it provides economic return. Biomass is a product of vegetative growth index (expressed in daily dry matter production per unit area) and growth duration. The ratio of grain yield to biomass is harvest index, so the product of biomass and harvest index equals grain yield. The role of harvest index in improving grain yield of cereal crops has been noted by many researchers (Donald 1962; Nass 1973; Rosielle and Frey 1975a, b; Sims 1963; Singh and Stoskopf 1971; Syme 1972; Vogel et al. 1963). A high harvest index, however, does not insure a high grain yield if biomass is low. In spring oats (*Avena sativa* L.), biomass production often is low because the species has a short growth duration, and low biomass limits grain yield.

Increasing biomass by lengthening growth duration for oats is not a suitable alternative for midwestern USA because high temperatures, diseases, and drought often cause severe stresses on this crop in mid- to late summer. Biomass, however, can be increased by producing a higher vegetative growth index. Takeda and Frey (1976) found that vegetative growth index and harvest index accounted for >90% of the variation in grain yield among oat lines from *A. sativa* × *A. sterilis* and *A. sativa* × *A. sativa* matings, and of these two traits, vegetative growth index had the greatest impact on grain yield.

Because vegetative growth index is a trait by which grain yield of oats may be increased in the temperate zone, we have studied its inheritance. Knowledge about the genetic control of vegetative growth index should aid breeders to genetically manipulate this trait in developing higher-yielding cultivars.

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Materials and methods

F_2-derived lines from 12 parental combinations (matings) involving six oat cultivars and five experimental lines were used in this study (Table 1). Parents were of two types with respect to origin: (a) lines containing introgressed *A. sterilis* germplasm (referred to as *A. sterilis*-derived lines) and (b) *A. sativa* cultivars adapted to midwestern USA. Five matings consisted of *A. sterilis*-derived lines backcrossed to their *A. sativa* recurrent parents, three were *A. sterilis*-derived lines mated with unrelated *A. sativa* cultivars, and four consisted of matings among *A. sterilis*-derived lines. Parental cultivars were CI 8044, 'Clintford' (CI 7463), 'Grundy' (CI 8445), 'Dal' (CI 9159), 'Noble' (CI 9194), and 'Otter' (CI 8304). The experimental lines used as parents were derived from backcrosses involving CI 8044, Clintford, or Grundy as the recurrent parent and *A. sterilis* collections as the donors. The five experimental lines were higher in grain yield than their respective recurrent parents (Frey 1982). Y286-53 came from Grundy*4/CI 9170; CI 9268 and CI 9273 came from Clintford*5/B443. CI 9271 was selected from Clintford*5/B444, and CI 9277 was from CI 8044*6/B443. B443 and B444 are *A. sterilis* accessions from Israel, and the "yield" gene in CI 9170 was derived from the *A. sterilis* accession CI 8079 (Frey 1972; Frey and Browning 1971).

One F_1 seed from each of the 12 matings, obtained in fall, 1975, was grown to produce F_2 seeds. F_2 seeds were space planted in the field at the Agronomy Research Center near Ames, Iowa in 1976. When mature, F_2 plants were harvested and threshed individually. Four F_3 spaced-plants from each F_2 were grown in 1977, and equal quantities of seeds from the four F_3 plants were mixed to form an F_2-derived line.

Evaluation experiments, three per mating, were conducted, two in 1978 and one in 1980, in randomized-block designs with four replicates each. For each mating, two experiments, one in 1978 and one in 1980, were sown on a productive Clarion (fine loamy, mixed, mesic typic hapladoll)-Webster (fine loamy, mixed, mesic typic haplaquoll) soil at the Agronomy Field Research Center near Ames, Iowa, and the third experiment was sown in 1978 at Nashua, Iowa, on Kenyon (fine loamy, mixed, mesic typic hapladoll) soil. The experiments used for a mating contained from 30 to 100 F_2-derived lines, depending upon the mating, plus the parents, each entered several times. The same lines were used in all experiments to evaluate a mating. A plot was a hill sown with 30 seeds, and plots were spaced 30 cm apart in perpendicular directions. Experiments were hand-weeded, and a fungicide, Dithane (active ingredients Zn-Mn ethylene bis dithiocarbanate), was sprayed onto the plants at weekly intervals between anthesis and maturity to control foliar fungal diseases.

Six traits were recorded from each plot. Days to heading was recorded as days after sowing when 50% of the panicles were fully emerged. When mature, the plants in a plot were harvested at ground level, dried, and weighed to obtain biomass yield, and subsequently, the bundle of plants was threshed, and grain yield was recorded. Vegetative yield was computed as biomass – grain yield, and harvest index was calculated as (grain yield/biomass) × 100. Vegetative growth index was calculated as vegetative yield/heading date (Takeda and Frey 1976).

Data for an entry from the three environments were averaged for statistical analyses and presentation. All data were subjected to analyses of variance, and genotypic, genotype × environment, and error variances were computed by equating expected variance components to the appropriate mean squares. Broad sense heritability values (on an environment basis) were computed by using the formula:

$$\text{Heritability} = V_g/(V_g + V_{ge}/m + V_e/rm)$$

where V_g, V_{ge}, and V_e are the genotypic, genotype × environment, and error variances, respectively, and r is the number of replications and m the number of environments.

An F_2-derived line was considered to have a positive transgressive vegetative growth index when its value was 1.96 times the standard error above the high parent mean. This definition for a transgressive segregate is conservative, but it does take into account the fact that both the parental and line means are subject to errors of estimation.

Results

Means for the plant-vigor traits, grain yield, vegetative yield, biomass, and vegetative growth index of the *A. sterilis*-derived parents were significantly greater than comparable means for the *A. sativa* cultivars (Table 2).

Table 1. Parentages for the 12 oat matings, mating type, and numbers of F_2-derived lines and parent samples tested for each mating

Mating	Parents		Mating type	No. of entries tested	
	Female	Male		F_2-derived lines	Parental lines
D237	CI 9273	Clintford	Backcross	17	23
D238	CI 9273	Grundy	Backcross	18	12
D239	CI 9277	CI 8044	Backcross	82	18
D241	CI 9271	Clintford	Backcross	33	27
D242	Y286-53	Grundy	Backcross	82	18
D245	CI 9273	CI 9271	Both *A. sterilis* derived	41	19
D246	CI 9277	CI 9271	Both *A. sterilis* derived	29	11
D248	CI 9268	CI 9277	Both *A. sterilis* derived	82	18
D249	CI 9273	CI 9277	Both *A. sterilis* derived	82	18
D250	Dal	CI 9268	Unrelated	48	22
D251	Noble	CI 9268	Unrelated	82	18
D252	Otter	CI 9268	Unrelated	82	18

Table 2. Means for several traits measured on the *A. sterilis*-derived lines and *A. sativa* cultivars used in the 12 oat matings

Trait	*A. sativa* cultivars	*A. sterilis*-derived lines
Grain yield (q/ha)	34.5[a]	36.6
Harvest index (%)	40.0	39.2
Vegetative yield (q/ha)	50.7[a]	55.4
Biomass (q/ha)	84.5[a]	91.8
Vegetative growth index (q/ha/da)	0.77[a]	0.84
Heading date (date after sowing)	66	67

[a] Indicates means for *A. sativa* cultivars are significantly different from mean of *A. sterilis*-derived lines at the 1% level

Table 3. Parental and midparent values and minimum, maximum, mean vegetative growth indexes and genotypic variances for F_2-derived lines from 12 oat matings

Mating	Parental values			F_2-derived values			Genotypic variance[b]
	P_1	P_2	MP	Mean	Min.	Max.	
D237	0.90	0.79	0.84	0.86	0.78	1.07	0.0023
D238	0.90	0.74	0.83	0.79[a]	0.71	0.93	0.0017
D239	0.83	0.68	0.75	0.74	0.58	0.92	0.0044
D241	0.85	0.79	0.82	0.79[a]	0.65	0.91	0.0018
D242	0.77	0.74	0.75	0.76	0.61	0.87	0.0016
D245	0.90	0.85	0.87	0.81[a]	0.67	1.00	0.0033
D246	0.83	0.85	0.84	0.85	0.62	0.96	0.0023
D248	0.84	0.85	0.84	0.78[a]	0.65	0.98	0.0024
D249	0.90	0.83	0.86	0.86	0.57	1.08	0.0036
D250	0.86	0.84	0.85	0.86	0.64	1.02	0.0049
D251	0.79	0.84	0.81	0.83[a]	0.63	1.05	0.0046
D252	0.74	0.84	0.79	0.78	0.51	1.05	0.0048

[a] Indicates F_2-derived line means and MP values that are significantly different at the 1% level

[b] All genotypic variances were significantly different from zero at the 1% level

The superiority was ca 10% for each trait. Means for harvest index and heading date were not significantly different for the two parental groups.

Midparent values and means of vegetative growth indexes for F_2-derived lines are presented in Table 3. Mating means for vegetative growth index were not significantly different from their respective midparent values in seven matings, a behavior typical of additive gene action whether for one or several loci. Five matings had F_2 means significantly different from their corresponding midparent values, which signals a departure from additivity. Significant inferiority of F_2-derived line means occurred in two backcrosses and two matings involving two *A. sterilis*-derived lines as parents. The fifth incidence of significantly different F_2 and midparent values occurred in an unrelated mating where the F_2 mean was comparable with the high-parent value.

Populations of segregates from all 12 matings contained significant genotypic variation (Table 3). Intuitively, genotypic variances should have been smallest for backcrosses and matings among *A. sterilis*-derived lines and greatest for unrelated matings. And in general, genotypic variances were as anticipated. The exception was D239, a backcross, which had a variance (0.0044) comparable to those of unrelated matings. The mean genotypic variance for unrelated matings was 0.0048, whereas for matings with related parents, the mean was 0.0026, a value about half the size of that for matings among unrelated parents. These means suggest that unrelated matings provided more diverse populations of segregates for selection for vegetative growth index than would matings among related parents.

Matings that produced segregates with vegetative growth indexes ≥ 1.0 were D237, D245, D249, D250, D251, and D252 (Table 3). These six matings produced segregates with vegetative growth indexes significantly above the high parent. Also, they had either CI 9268 or CI 9273 as a parent, and both of these parental lines were descendents of the same mating, Clintford × B443.

From a plant breeding perspective, the worth of a mating can also be assessed by the number of positive transgressive segregates that it produces for vegetative growth index. The three matings among unrelated parents produced an average of six positive transgressive segregates for vegetative growth index (Table 4). From all matings, 41 positive transgressive segregates were identified. Eleven of these, however, occurred in one backcross, D242. This was an abnormal case, because the other four backcrosses, D237, D238, D239, and D241, had only 0 or 1 positive transgressive segre-

Table 4. Number of positive transgressive segregates and heritability of vegetative growth index from 12 oat matings

Mating	Parents		No. positve transgressive segregates	Heritability percentage
	Female	Male		
D237	CI 9273	Clintford	1	50
D238	CI 9273	Grundy	0	52
D239	CI 9277	CI 8044	1	66
D241	CI 9271	Clintford	0	45
D242	Y286-53	Grundy	11	44
D245	CI 9273	CI 9271	1	66
D246	CI 9277	CI 9271	2	35
D248	CI 9268	CI 9277	2	57
D249	CI 9273	CI 9277	5	51
D250	Dal	CI 9268	7	64
D251	Noble	CI 9268	9	58
D252	Otter	CI 9268	2	63
Mean			3	54

gate. The aberrant reaction of D242 probably is an unreal phenomenon due to the low standard error of the line mean and to the low value for the high parent. This mating holds no promise for selection of high vegetative growth index lines. The matings among *A. sterilis*-derived lines produced from one to five positive transgressive segregates with an average of 2.5. Thus, with the exception of D242, the numbers of positive transgressive segregates for the different types of matings were according to expectation, i.e., mean numbers for five backcrosses, four matings between *A. sterilis*-derived lines, and three matings among unrelated parents were 0.5, 2.5, and 6.0, respectively.

Heritability values for vegetative growth index ranged from 35 for D246 to 66 for D239 and D245 (Table 4), with the mean heritability for all matings being 54%. For unrelated matings, mean heritability was 62, whereas the mean for related matings was 52%.

Discussion

Vegetative growth index, if responsive to selection, should have a great impact on increasing grain yield. Helsel (1980) and Johnson et al. (1982) predicted and verified that genetic gains for grain yield can be made using vegetative growth index as an indirect selection criterion. In fact, Johnson et al. (1982) found that indirect selection via vegetative growth index gave greater grain yield than did direct selection for grain yield itself.

Takeda et al. (1979) showed that matings among *A. sativa* lines and cultivars did not release much genetic variation for this trait. Of the more than 20 parents representing adapted, semi-exotic, and exotic strains of *A. sativa* that they used, only matings in which 'Tippecanoe' was a parent gave consistently positive transgressive segregates for vegetative growth index. On the other hand, Takeda and Frey (1976, 1977) found a very high rate of positive transgressive segregates for this trait from interspecific matings of *A. sativa* × *A. sterilis*. As many as 20% of the progenies in BC_0 and BC_1 and 12% in the BC_4 were positive transgressive segregates for vegetative growth index when the interspecific hybrids were backcrossed to *A. sativa*. Introgression of *A. sterilis* germplasm into an *A. sativa* genetic background increased vegetative growth index while maintaining the genetic balance necessary to produce genotypes with good grain yield and acceptable agronomic traits.

The type of gene action involved in the inheritance of vegetative growth index varied among matings. Additive gene action predominated in seven while nonadditve gene action was found in the other five. Perhaps, partial dominance of low vegetative growth index was the source of nonadditive gene action in four of these matings. Takeda and Frey (1976) found a high degree of positive nonadditive gene action involved in the expression of this trait in interspecific matings, and Takeda et al. (1979) reported similar results in some intraspecific matings.

Heritability of vegetative growth index tends to be moderate. Our heritability was 54%, and intraspecific oat matings studied by Takeda et al. (1979) gave a comparable value when calculated on an environment basis. Heritability averaged about 40% for interspecific oat matings, however, in a study by Takeda and Frey (1976). Progress from selection for vegetative growth index with a heritability of 50% should be quite good.

The 41 positive transgressive segregates found for vegetative growth index is a small percentage of the total number of F_2-derived lines evaluated, but this was not an unexpected result considering our conservative definition for positively transgressive segregates. Note that 11 positive transgressive segregates were identified for mating D242 (Table 4), a backcross mating with insignificant variation for vegetative growth index among the P_1, P_2, MP and F_2-derived line means (0.77, 0.74, 0.75 and 0.76, respectively). The maximum F_2-derived line value produced from among 82 offspring was an 0.87 the lowest F_2 maximum of all 12 matings. Although the 11 positive transgressive segregates make this mating appear noteworthy, there is little promise for selection in this mating (e.g. $V_g = 0.0016$) compared to the others. The high number of positive transgressive segregates is a byproduct of the low standard error and a low high parent value. Another mating worth discussion is D250 which produced 7 positive transgressive segregates even though P_1, P_2, MP and F_2 means were close (0.86, 0.84, 0.85 and 0.86, respectively). The range of F_2-derived line values (0.64 to 1.02) is consistent with the genotypic variance (0.0049) and would be a mating worth exploiting. The release of this variation from parents with similar means is likely due to complimentary gene action. Because the two parents are unrelated, it is reasonable to assume that the genes for vegetative growth index in the two parents differ. Recall also that an *A. sterilis* derived line, CI 9268, is present in all 3 unrelated matings which average 6 positive transgressive segregates. This indicates that CI 9268 is a valuable parent for vegetative growth index. For matings D250 and D252, high positive transgressive segregates were the notable result of this lineage while in D251 positive heterosis (nonadditive gene action) for vegetative growth index was also apparent. Takeda et al. (1979) found a similar specificity for certain parents: For example, Tippecanoe was the only cultivar that consistently gave positive transgressive segregates for vegetative growth index in intraspecific matings. The general superiority of unrelated matings for heritability, genotypic variance, and positive transgressive segregates likely resulted because (a) one parent contained a small quantity of productive germplasm from *A. sterilis* and (b) the other parent was an *A. sativa* cultivar that was unrelated to the *A. sterilis*-derived line. CI 9268 was derived from a mating in which Clintford was the recurrent parent, and *A. sativa* cultivars in the unrelated matings were Dal, Noble, and Otter, all having pedigrees quite diverse from Clintford.

In oats, vegetative growth and reproductive growth occur in separate time periods: pre- and post-anthesis, respectively. Vegetative growth index quantifies the rate of vegetative tissue development prior to anthesis, and vegetative tissue of plants is the photosynthate source which determines the quantity of grain produced per unit land. Vegetative yield can be increased by lengthening the period of vegetative growth or by increasing vegetative growth index. In Iowa, growth duration for oats is restricted because late summer heat, drought, and disease restrict photosynthesis and thus grain filling. Harvest index for the midwestern USA is optimal at 45% for maximizing grain yield, so this trait is not amenable to genetic manipulation for increasing grain yield. As suggested by Takeda and Frey (1976, 1977), this leaves vegetative growth index as the only component by which to improve genetic potential for grain yield in oats for midwestern USA.

Plant breeding programs attempting to capitalize on increasing vegetative growth index to improve grain yielding capacity of oats would differ depending on whether the goals were short term or long term. In a program with short-term goals, single and perhaps double cross matings among cultivars and lines of diverse origin but all of which had desired genotypes for heading date and harvest index, should provide appropriate populations within which to practice early generation or pedigree selection for vegetative growth index. A breeding program with long-term goals should also make use of parent lines from diverse origin, but less attention would need to be paid to the parental heading dates and harvest indexes. After appropriate intermatings had been made among hybrid plants for several generations, the intermated population could be used to initiate a recurrent selection program for vegetative growth index. A suggested selection criterion would be a restricted selection index in which complete weight is given to vegetative growth index and heading date and harvest index are restricted to 65 days and 45%, respectively (Rosielle and Frey 1975 a).

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