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Association of two measures of vegetative growth rate with other traits in inter and intraspecific matings of oats*

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Summary. F_2-derived oat lines from inter (*Avena sativa* L.×*A. sterilis* L.) and intraspecific (among *A. sativa* cultivars) matings were evaluated in the F_3, F_4, and F_5 generations for heading date, grain and straw yields, biomass, vegetative dry weight at anthesis, vegetative growth rates until anthesis (GRA) and until maturity (GRM), and harvest index. The associations of GRA and GRM with harvest index ranged from zero to slightly negative. The positive correlations of GRA and GRM with grain yield were stronger in inter than in intraspecific matings. Grain yield was positively associated with harvest index in both inter and intraspecific matings. The results suggest the use of *A. sterilis*×*A. sativa* matings to improve vegetative growth rate, grain yield, and, to a certain extent, harvest index simultaneously without affecting the growth duration of the crop.

Key words: *Avena sterilis* – Biomass – Vegetative growth rate at anthesis – Vegetative growth rate at maturity – Dry weight at anthesis

Introduction

It was shown by Takeda and Frey (1976) that grain yield of oats (*Avena sativa* L.), and cereals in general, is the product of growth rate, growth duration, and harvest index. More than 90% of variation for grain yield was due to variation in growth rate and harvest index as reported by Takeda and Frey (1976) and Takeda et al. (1979a), who worked with interspecific matings of oats and oat cultivars, respectively. Rosielle and Frey (1975) concluded that harvest index was an efficient criterion for indirect selection for grain yield of oats, especially when restrictions were placed on heading date and plant height. Helsel and Frey (1981) reported that grain yield was strongly correlated with vegetative development of oat plants.

In the midwestern USA, growth duration for oats is restricted to 100 to 110 days by high temperature and foliar diseases in late summer, and harvest index of improved cultivars has been optimized at approximately 45%. Thus, the remaining component of grain yield, growth rate, is the only one that can be manipulated to increase grain yield (Takeda and Frey 1976, 1977; Takeda et al. 1979a).

Growth rate during the first two-thirds of the oat growing season (i.e., until anthesis) determines the quantity of vegetative tissue available for photosynthesis and the maximum number of florets that will be differentiated and sustained (Helsel and Frey 1978; Frey et al. 1967). Both factors are critical for the production of high grain yield. Frey and his colleagues (Takeda and Frey 1976; Helsel and Frey 1981; Cox and Frey 1984a) previously have measured vegetative growth rate by dividing straw weight at maturity by days to heading. Wych et al. (1982) have reported that vegetative growth rate would be more accurately measured, however, if it was estimated from plant dry weight at anthesis.

In this study, we have measured the vegetative growth from samples taken either at anthesis or maturity and have estimated the interrelationships between these two measures of growth rate and other traits by using F_2-derived lines of interspecific (*A. sativa* and *A. sterilis*) and intraspecific matings of oats.

Materials and methods

Materials

The materials for this study were 2359 F_2-derived lines from *A. sativa*×*A. sterilis* matings and 299 F_2-derived lines from mat-

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ings among *A. sativa* cultivars, all evaluated in the F_3 (Cox and Frey 1984b). Smaller sets of these lines, 172 and 49 from the inter and intraspecific matings, respectively, were evaluated again in F_4 and F_5.

Field evaluation

The 2658 F_2-derived lines in F_3 from both inter and intraspecific matings were evaluated in a randomized complete-block design with two replicates at each of three locations in 1982. Sowing dates were 23 April, 19 April, and 24 April at the Agronomy Field Research Center near Ames, Iowa, the Northwest Research Center near Sutherland, Iowa, and the Clarion-Webster Research Center near Kanawha, Iowa, respectively. The soil type at the Ames and Kanawha sites was a loam of the Clarion-Webster association, whereas the soil type at the Sutherland site was a silty clay loam of the Galva-Sac association. The preceding crop at all sites was soybeans. Fertilizer applications per hectare were 51.5 kg N and 7 kg each of P_2O_5 and K_2O at Kanawha; 16.8 kg N, 67.2 kg P_2O_5, and 33.6 kg K_2O at Sutherland; and 33.6 kg N and 51.5 kg each of P_2O_5 and K_2O at Ames. A plot was a hill sown with 30 seeds, and plots were spaced 30.5 cm apart in perpendicular directions. Two rows of hills were planted around each replicate to provide competition for peripheral plots. All experiments were hand weeded, and Bayleton, an eradicant fungicide, was applied to the plants one month before harvest to eliminate fungal foliar diseases.

The 221 F_2-derived lines in F_4 and F_5 were evaluated in randomized block experiments in 1983 and 1984, respectively. The experiments, each with six replicates, were planted on 24 April 1983 and 20 April 1984 at the Agronomy Field Research Center near Ames, Iowa. The fertilizer application and experimental procedures in 1983 and 1984 were the same as used in the 1982 Ames experiment.

In 1982, six traits were measured or computed on a plot basis. Heading date (HD) was recorded as the number of days from planting until 50% of the panicles were completely emerged. When ripe, plants in a plot were harvested at ground level, dried, and weighed to obtain biomass (BWT). Next, the bundle of culms was threshed and grain yield (GYD) was obtained. Straw yield (SYD) was obtained by subtracting grain from biological yield, and harvest index (HI) was computed as the ratio of grain to biological yield and expressed as a percentage. Vegetative growth rate until maturity (GRM) was calculated as straw yield divided by number of days to heading. HD and GRM were measured or computed from the Ames site only.

In 1983 and 1984, two additional traits were measured or computed. Heading date, dry weight at anthesis (DWT) and vegetative growth rate until anthesis (GRA) were measured or computed upon plots in three of the six replicates. At anthesis, the plots in these three replicates were harvested at ground level, dried, and weighed to obtain DWT, and GRA was computed as DWT divided by days to heading. The remaining five traits were measured or computed as in 1982 upon plots in the remaining three replicates.

Statistical analysis

Phenotypic and partial correlations were computed on a line mean basis using standard formulas (Steel and Torrie 1980). Phenotypic correlations were computed among all pairs of traits on eight data sets: F_2-derived lines from inter and intraspecific matings evaluated in F_3, F_4, and F_5 and means across F_4 and F_5 for F_2-derived lines from inter and intraspecific matings. Partial correlations of GYD and HI with GRM and GRA when HD was held constant were estimated on all data sets except for F_2-derived lines in F_3.

Results

Means and ranges for eight traits recorded on F_2-derived lines from inter and intraspecific matings are presented in Tables 1 and 2, respectively. Variation among lines was significant for all traits. Generally, means for HD were similar in all three years of testing, whereas HI's were similar and low in 1982 and 1983 but higher in 1984. GYD and BWT ranged from lowest to highest in 1983 and 1984, respectively, whereas SYD's were similar in 1982 and 1984 but lower in 1983. GRM was highest in 1982 and lowest in 1983.

GRA was positively correlated with GRM, and five of the six correlations were significant (Tables 3 and 4). In most instances, both GRA and GRM were negatively associated with HI, but the correlations of HI with GRM tended to be larger than those of HI with GRA. This relationship suggests that there might be a slight difficulty in improving both HI and growth rate simultaneously.

Table 1. Means and ranges for eight traits measured on F_2-derived lines from interspecific matings of oats evaluated in the F_3, F_4, and F_5 in 1982, 1983, and 1984, respectively

Trait[a]	F_3 (1982)		F_4 (1983)		F_5 (1984)	
	Mean	Range	Mean	Range	Mean	Range
GRA	–	–	5.5	3.3– 7.8	7.3	4.4– 11.2
GRM	9.8	1.8– 19.0	7.2	4.4–10.2	8.8	5.3– 11.6
HI	31.2	2.0– 49.8	32.7	17.9–44.9	39.2	27.4– 48.4
GYD	25.7	1.7– 48.6	21.8	9.7–36.3	36.4	20.3– 58.7
HD	62.8	51.5– 77.0	63.0	58.0–69.0	64.2	59.0– 72.0
BWT	82.9	11.2–138.8	66.9	39.0–91.7	93.0	53.3–128.0
SYD	57.2	7.6– 99.5	45.1	27.0–64.5	56.6	33.0– 83.0
DWT	–	–	35.0	20.3–53.7	47.1	26.0– 80.3

[a] GRA and GRM are expressed in g/plot/10 days, HI in % , HD in days and the remaining traits in g/plot. See text for trait abbreviations

Table 2. Means and ranges for eight traits measured on F_2-derived lines from intraspecific matings of oats evaluated in the F_3, F_4, and F_5 in 1982, 1983, and 1984, respectively

Trait[a]	F_3 (1982)		F_4 (1983)		F_5 (1984)	
	Mean	Range	Mean	Range	Mean	Range
GRA	–	–	6.2	5.0– 7.5	7.0	5.2– 11.1
GRM	10.7	4.1– 17.1	7.5	5.5–10.3	8.8	7.2– 11.4
HI	38.4	7.7– 48.7	38.4	24.2–47.4	43.8	33.3– 48.7
GYD	36.4	3.7– 54.9	28.6	16.7–38.3	43.3	31.7– 54.7
HD	62.3	54.0– 77.0	62.0	58.7–67.0	62.9	59.7– 70.3
BWT	95.3	45.6–145.3	75.0	59.3–92.0	98.8	81.0–125.7
SYD	59.0	23.5–101.2	46.5	33.3–62.3	55.5	44.7– 76.3
DWT	–	–	38.3	30.3–46.7	44.4	32.3– 78.3

[a] GRA and GRM are expressed in g/plot/10 days, HI in % , HD in days and the remaining traits in g/plot. See text for trait abbreviations

Table 3. Phenotypic correlations among eight traits measured on F_2-derived lines from interspecific oat matings

Traits correlated		F_3	F_4	F_5	Mean of F_4 and F_5
GRA vs	GRM	–	0.30**	0.41**	0.42**
	HI	–	0.11	−0.24**	−0.06
	GYD	–	0.37**	0.30**	0.37**
	HD	–	0.23**	0.77**	0.70**
	BWT	–	0.42**	0.55**	0.59**
	SYD	–	0.33**	0.60**	0.59**
	DWT	–	0.97**	0.99**	0.98**
GRM vs	HI	−0.04	−0.38**	−0.32**	−0.29**
	GYD	0.60**	0.34**	0.57**	0.45**
	HD	−0.12**	0.19*	0.32**	0.34**
	BWT	0.95**	0.89**	0.91**	0.88**
	SYD	0.96**	0.97**	0.95**	0.95**
	DWT	–	0.32**	0.40**	0.42**
HI vs	GYD	0.66**	0.72**	0.55**	0.68**
	HD	−0.54**	−0.28**	−0.45**	−0.38**
	BWT	0.05*	0.02	−0.03	0.08
	SYD	−0.29**	0.43**	−0.42**	−0.38**
	DWT	–	0.03	−0.31**	−0.15*
GYD vs	HD	−0.36**	−0.02	0.10	0.08
	BWT	0.78**	0.70**	0.81**	0.77**
	SYD	0.51**	0.30**	0.51**	0.40**
	DWT	–	0.32**	0.25**	0.30**
HD vs	BWT	−0.04	0.30**	0.45**	0.47**
	SYD	0.13**	0.41**	0.60**	0.62**
	DWT	–	0.46**	0.86**	0.82**
BWT vs	SYD	0.94**	0.89**	0.92**	0.89**
	DWT	–	0.46**	0.54**	0.58**
SYD vs	DWT	–	0.40**	0.62**	0.62**

*, ** Significant at 5% and 1% levels of probability, respectively. See text for trait abbreviations

GRA was positively associated with GYD for F_2-derived lines from interspecific matings (r = 0.37** for the mean of F_4 and F_5) (Table 3), but it was unrelated with GYD of lines from intraspecific matings (Table 4). Positive correlations of GYD with GRM tended to be greater than those with GRA for the oat lines from interspecific matings. In intraspecific matings, correlations of GYD and GRM ranged from −0.20 to 0.60** across the three generations, but for the means of F_4 and F_5, r = −0.02.

The associations of GRA and GRM with HD generally were positive and significant; exceptions were negative correlations between GRM and HD for the F_3 of interspecific matings and between GRA and HD for the F_4 of intraspecific matings. GRA tended to be more strongly associated with HD than with GRM.

GRA and GRM were positively and strongly associated with DWT (r = 0.96 to 0.99) and SYD (r = 0.95 to 0.98), respectively. These high correlations were expected because DWT and SYD occur in the numerators of the equations used to compute GRA and GRM, respectively. Associations between DWT and SYD were positive, significant, and moderately high, suggesting that, in general, selection for vegetative yield of oat lines could be practiced at either anthesis or maturity. Note, however, that the correlations of DWT and SYD were higher in 1984 than in 1983, which supports the results of Wych et al. (1982), who showed an interaction of environment with retention of vegetative weight during grain filling. HI was positively and strongly associated with GYD, uncorrelated with BWT, and negatively correlated with all other traits. Its strong negative correlation with HD indicates that early lines tend to have high HI.

HD was not associated with GYD in either intra or interspecific matings, but it was correlated positively and significantly with all measures of vegetative yield. It should be possible to select for high GYD and early HD in both types of matings.

Because HD was positively correlated with GRA and GRM, uncorrelated with GYD, and negatively correlated with HI, we decided to determine whether the association among GRA, GRM, GYD, and HI would change if HD did not vary. Partial correlations comput-

Table 4. Phenotypic correlations among eight traits measured on F_2-derived lines from intraspecific oat matings

Traits correlated		F_3	F_4	F_5	Mean of F_4 and F_5
GRA vs	GRM	–	0.22	0.32*	0.35*
	HI	–	– 0.13	– 0.38**	– 0.36*
	GYD	–	– 0.02	0.09	0.00
	HD	–	– 0.06	0.83**	0.69**
	BWT	–	0.18	0.41**	0.42**
	SYD	–	0.20	0.53**	0.52**
	DWT	–	0.96**	0.99**	0.98**
GRM vs	HI	– 0.34**	– 0.76**	– 0.48**	– 0.69**
	GYD	0.60**	– 0.20	0.48**	– 0.02
	HD	– 0.15**	0.18	0.27	0.25
	BWT	0.95**	0.80**	0.89**	0.77**
	SYD	0.98**	0.98**	0.96**	0.96**
	DWT	–	– 0.27	0.32*	0.35*
HI vs	GYD	0.33**	0.76**	0.51**	0.71**
	HD	– 0.39**	– 0.32**	– 0.39**	– 0.35**
	BWT	– 0.18**	– 0.27	– 0.12	– 0.16
	SYD	– 0.46**	– 0.78**	– 0.55**	– 0.71**
	DWT	–	– 0.21	– 0.41**	– 0.39**
GYD vs	HD	0.00	– 0.08	0.09	0.00
	BWT	0.87**	0.40**	0.79**	0.58**
	SYD	0.69**	– 0.20	0.43**	– 0.02
	DWT	–	– 0.03	0.08	– 0.02
HD vs	BWT	0.22**	0.28*	0.43**	0.42**
	SYD	0.32**	0.36*	0.54**	0.52**
	DWT	–	0.20	0.89**	0.81**
BWT vs	SYD	0.95**	0.81**	0.90**	0.80**
	DWT	–	0.25	0.41**	0.44**
SYD vs	DWT	–	0.29*	0.55**	0.55**

*, ** Significant at 5% and 1% levels of probability, respectively. See text for trait abbreviations

Table 5. Partial correlations of GRA and GRM with HI and GYD with HD held constant within interspecific and intraspecific matings of oats

Mating type	Traits correlated				
	GYD vs		HI vs		GRA vs
	GRA	GRM	GRA	GRM	GRM
Interspecific					
F_4	0.38**	0.35**	0.19*	– 0.35**	0.27**
F_5	0.35**	0.57**	0.19*	– 0.21**	0.28**
Average	0.44**	0.45**	0.30**	– 0.19*	0.27**
Intraspecific					
F_4	– 0.02	– 0.19	– 0.16	– 0.75**	0.24
F_5	0.03	0.47**	– 0.10	– 0.42**	0.16
Average	– 0.01	– 0.02	– 0.17	– 0.66**	0.26

*, ** Indicates values significantly different from zero at the 5% and 1% levels, respectively

ed with HD held constant are given in Table 5. Partial correlations for GRA with GRM are positive, but generally, they are lower than the corresponding phenotypic correlations. Corresponding partial and phenotypic correlations between GRM and HI for the interspecific matings were similar in magnitude and sign, whereas for GRA and HI, the phenotypic correlations showed no association, but the partial ones showed significant positive associations. For the intraspecific matings the corresponding phenotypic and partial correlations for HI with GRA and GRM were similar. Correlations of GYD with GRA and GRM were affected little by holding HD constant.

Discussion

Gifford et al. (1984) have presented a summary that shows that most, if not all, of the genetic improvement in GYD of cereals accomplished via plant breeding has been due to increased HI. Little if any increase has occurred in total plant or biomass yield of cereals due to breeding. The current harvest index of approximately 50% for high-yielding cereal cultivars may not be the maximum attainable (Austin et al. 1980; Gifford et al. 1984), but it is probably about optimum to be compatible with high GYD.

Current high-yielding cultivars of oats have an HI of 45–50%; therefore, Takeda and Frey (1976) proposed that future genetic improvement of this crop for GYD would need to come via increased BWT. Biomass is the product of growth duration and growth rate. For oats grown in the midwestern USA, growth duration is limited to 100–110 days because of late summer stresses of high temperature and disease. This leaves growth rate as the only component by which biological and grain yields can be improved genetically.

As breeding programs are developed to increase vegetative growth rate of cereals, it will be necessary (a) to have significant genetic variability available for this trait, (b) to know its inheritance pattern and association with other traits, and (c) to have a rapid method for its measurement.

Takeda et al. (1979a) have shown that little genetic variability for vegetative growth rate exists in the *A. sativa* gene pool; however, Takeda and Frey (1976, 1977) and Cox and Frey (1984a) have demonstrated that a major source of alleles for improving this trait occurs in the progenitor of cultivated oats, *A. sterilis* (Coffman 1946). Similarly, Bramel-Cox et al. (1985) showed that a wild accession, *Pennisetum americanum* ssp. *monodii* carried alleles that increased the vegetative growth rate of cultivated pearl millet (*P. americanum* ssp. *americanum*).

In both inter and intraspecific matings of oats, vegetative growth rate has been shown to be quantitatively inherited (Takeda and Frey 1977; Cox and Frey 1984b). Both additive and nonadditive gene action are significant in its determination (Helsel and Frey 1983; Cox and Frey 1984b), and from 6 to 9 and 3 to 9 effective factor pairs are involved in the inheritance of vegetative growth rate in intra and interspecific matings, respectively (Takeda et al. 1979a; Takeda and Frey 1977). Heritability of vegetative growth rate of oats varies from 20 to 54% (Takeda and Frey 1977; Takeda et al. 1979a; Helsel and Frey 1983; Gupta et al. 1985).

We found that both measures of vegetative growth rate, GRA and GRM, were positively and significantly correlated with GYD in interspecific matings but not in intraspecific ones. These results corroborate the GYD-GRM associations obtained by other researchers, but generally they reported higher correlations than we found (Takeda et al. 1979a, b; Helsel and Frey 1981; Takeda and Frey 1977). GRM tends to be negatively correlated with HI; however, when HD was held constant via partial correlation analysis, the association between GRA and HI became significantly positive in interspecifiic matings. This suggests that GRA and HI could be used jointly to select for GYD via a restricted selection index with HD being the restricted trait (Rosielle and Frey 1975). Other researchers have reported correlations between HI and GRM to vary from zero to −0.4 (Takeda and Frey 1977; Takeda et al. 1979a, b; Helsel and Frey 1981). According to these results, it should be possible to breed oat cultivars with both high growth rate and high HI. In general, HD is nearly independent of vegetative growth rate. None of the associations reported between vegetative growth rate of oats and other agronomic traits would seem to prohibit breeding for high vegetative growth rate as a way to increase biological and grain yields.

Crop or vegetative growth rate usually is determined by making dry-weight measurements several times during the growth cycle and subsequently regressing dry-weight increase upon days from sowing (Frey et al. 1967). This is a destructive and laborious procedure that severely limits the number of genotypes that can be evaluated. To accommodate the need for breeders to evaluate hundreds, and even thousands, of entries for this trait, Takeda and Frey (1976) suggested that a crude measure of vegetative growth rate of oats could be obtained by dividing straw weight by days to heading. This involved making one extra measurement, (i.e., biological yield) on plots already grown for grain yield, and doing computer manipulations to calculate GRM. This method of measuring vegetative growth rate has been used extensively by Frey and his colleagues (Takeda and Frey 1976, 1977; Takeda et al. 1979a, b; Helsel and Frey 1981, 1983; Cox and Frey 1984a, b). Wych et al. (1982), however, suggested that measuring vegetative growth rate on the basis of dry weight at anthesis would be more accurate than GRM because (a) cereal cultivars vary as to whether their vegetative dry weights increase, decrease, or stay constant from anthesis to maturity and (b) environment influences the retention of vegetative dry weight from anthesis to maturity. Our results show that GYD is phenotypically correlated equally with GRA and GRM in interspecific matings and uncorrelated with either of them in intraspecific matings. Gupta et al. (1985), however, did show that the genotypic correlations of GYD with GRA and GRM were 0.46 and 0.26, respectively. The cost to measure GRA and GRM would be similar if plots were grown only to measure these traits. If plants are harvested at anthesis, HD, DWT, and GRA are the only traits that can be measured, but if harvested when ripe, additional traits (e.g., GYD, BWT, HI) can be evaluated with little extra cost. To grow separate sets of plots, one to measure GRA and a second to measure other traits at maturity, as we did in this study, adds greatly to the cost of experimentation. Bramel-Cox et al. (1984) correlated several measurements of vegetative growth rate of pearl millet, each calculated for a specific stage of development, with growth rate determined via the multiple sampling and regression method. They found that straw weight divided by anthesis date + 10 gave a satisfactory estimate of growth rate measured via regression. A similar study is needed for oats.

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