TEST OF THE ADDITIVE-DOMINANCE MODEL OF GRAIN WEIGHT AND GRAIN UNIFORMITY OF OAT, *AVENA SATIVA* L, GENOTYPES

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ABSTRACT

An investigation of the genetic mechanisms controlling grain weights for the primary and secondary grains uniformity expressed in primary: secondary individual grain weight (P: S IGW) ratio and % tertiary grains produced was conducted using a backcross experiment'. Two oat, parental genotypes, I.L82-1657 (pistillate) and 10589 Cn (staminate) with different grain weight characteristics were hybridized to obtain 6 backcross generations viz. P_1, P_2, F_1, B_1, B_2 *and* F_2. *The scaling test indicated that overall average, primary and secondary individual grain weights and % tertiary grain weight produced failed to satisfy the additive - dominance model and digenic interactions were detected except for the secondary individual grain weight. Grain weight uniformity expressed as P:S IGW ratio satisfied the additive - dominance model and was highly heritable (h2 narrow sense >98%). However, additive gene effect was important in the control of all the grain weight variables except the primary: secondary grain yield ratio. Dominance effect was important only for the overall average grain weight and the proportion of tertiary grains produced. Attainment of uniformity of oat grains looks promising through genetically improving the P:S IGW ratio but is challenged by the presence of non-allelic interactions in the control of % tertiary grain weight.*

INTRODUCTION

Grain quality in oats (*Avena sativa L.*) is important in the oat processing industry. Crops producing large, uniform sized grains are the most desirable (Ganssman 1989). It is also recognized that seeds composed of large uniform grains will lead to high field germination and result in uniform establishment (Frey & Wiggans 1956). Grain size or mass also plays an important role in determining final grain yield because yield is a multiplicative product of individual grain weight (IGW's) and number of grains (Grafius 1956). Grain quality is usually expressed in terms of average grains weights and uniformity of grain size within a sample of oat grains. However, a sample of oat grains would be composed of a mixture of grains of different origins in which each spikelet namely primary, secondary and tertiary grains correspondingly decrease in IGW's. Such differences in grain within a panicle are the root cause of grain size variations in samples of oat even though they have the same genetic constitution. High quality of an oat grain sample will have low or no tertiary grains produced with large sized grains but little difference between individual weights of primary and secondary grains.

Genetic improvement for grain size uniformity in oat grain is important as a stable strategy to overcome grain size variations in oats. For a more reliable improvement strategy, the nature of gene action and inheritance controlling the trait should be known. Studies on inheritance and gene action on grain size uniformity in oats are limited. The present study investigated the types of gene action and inheritance behaviour of grain size and uniformity of oat grain using a backcross experiment involving two genotypes differing in origin and grain weight characteristics.

METHODS

Parental oat genotypes differing in average grain weights were hybridized at the glasshouse of the Welsh Plant Breeding Station (UK) during the summer of 1991. The two parents were 1L82-1657 (pistillate) and 10589 Cn (staminate). 1L82-1657 has characteristically large grains, high yielding, and exhibited early maturity; it was developed at Illinois USA 10589. Cn produced large number of small grains per panicle and exhibited later maturity; it was developed at the Welsh Plant Breeding Station (WPBS, UK). Mature hybrid seeds were harvested, labelled and stored in paper packets in a cold room (2°C, 15-20% RH) during the winter. F_1 hybrid seeds from the cross were grown in pots under halogen lights in a glasshouse during late August to produce the F_2 generations. The F_1 plants were selfed by emasculating flowers and pollinating with their own pollen. Seeds from these plants were harvested as they matured during October-December, 1991. These were labelled, dried and also stored in the cold room. F_1 seeds from the cross were used to produce pollen parents to hybridize the parents so as to obtain 2 backcross generations. F_1 seeds were sown on different dates to facilitate synchrony of flowering. At maturity, seeds of the parents (P_1, P_2), B_1, B_2, F_1 and F_2 generations were harvested, labelled and stored in packets in the cold room over winter.

Seed of parents, F1, F2, Bi and B2 generations were sown individually in 4 cm diameter peat pots on 6th April 1992 in the glasshouse. Some 25% excess of seed required was sown to provide sufficient numbers of established seedlings for transplanting. Using plastic labels each pot was labelled for the cross number of the seedlings and for its random number position generated by a computer programme (GENSTAT). Each of the 3 blocks contained a total of

90 seedlings individually randomized as follow: 10 plants/parent, 10 plants/F_1 hybrid, 15 plants/backcross generation, 30 plants/F2 generation. Thus, the whole experiment contained 270 plants individually randomized.

The boxes were taken outside on 11th April 1992 to harden off. On 15th April, when the seedlings were at the 1-2 leaf stage, they were transfered to the field and the pots containing the seedlings transplanted into cultivated and fertilized land which had previously been under-grass. Each block consisted of 1 strip of 18 rows with each row containing 5 plants giving a total of 90 plants/block. All the plants were surrounded by border plants at the appropriate spacing of 15 cm x 15 cm. Prior to panicle emergence, a bird proof net was erected in the experimental area and appropriate husbandry practices were done to ensure optimum fertility and control of pests. At harvest, 3 main panicles were cut from each plant, tied together and labelled. These were taken to the laboratory and stored in a cool and dry environment. The mainshoot panicle from each plant was selected for detailed measurements. The terminal spikelet from each whorl was detached and the grains separated into primary, secondary and where present, tertiary groups. Grains in the same groups were counted, put in small packets and later weighed using an electronic weighing machine. The rest of the grains on the panicle were threshed in bulk, counted and weighed.

The raw data was used to derive various grain weight variables viz. overall individual grain weight, primary and secondary individual grain weights, primary: secondary individual grain weight ratio and % tertiary grain weight.

The analyses of the backcross experiment were based on calculations following the procedures outlined by Mather and Jinks (1971). The generation means were used to estimate A, B and C components as follows:

$$A = 2B_1 - P_1 - F_1$$
$$B = 2B_2 - P_2 - F_1$$
$$C = 4F_2 - 2F_1 - P_1 - P_2$$

Variances of generation means were used to compute standard errors as follows:

$$VA = 4V_{B1} + V_{P1} + V_{F1}$$
$$VB = 4V_{B2} + V_{P2} + V_{F1}$$
$$VC = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2}$$

In each variable, P1 is the parent with a larger value while P2 represents the parent with a smaller value. The quantities A, B and C and their variances were used to test the adequacy of the additive-dominance model. The standard errors of the quantities A, B, C were obtained as the square root of the appropriate variances and these were used to test for the significance of each using an approximate c-test. Estimates of the mean of the parents M, the additive effect [d], dominance effect [h] and the digenic interactions were obtained. An estimate of the relative magnitude of the digenic interactions, namely (additive x additive), j (additive x dominance) and 1 (dominance x dominance) were made using generation means as shown below:

$$M = \tfrac{1}{2}P1 + \tfrac{1}{2}P2 + 4F2 - 2B1 - 2B2$$

$$[d] = \tfrac{1}{2}P1 - 1\tfrac{1}{2}P2$$

$$[h] = 6B1 + 6B2 - 8F2 - F1 - \tfrac{1}{2}P1 - \tfrac{1}{2}P2$$

$$[I] = 2B1 + 2B2 - 4F2$$

$$[j] = 2B1 - P1 - 2B2 - P2$$

$$[l] = P1 + P2 + 2F1 + 4F2 - 4B1 - 4B2$$

The standard errors of these estimates were obtained in the usual way where for examples,

$$V_{[d]} = \tfrac{1}{4}V_{P1} + \tfrac{1}{4}V_{P2} \text{ and } S[D] = \pm\sqrt{}V_{[D]} \text{ and } c = \frac{[d]}{S_{[d]}}$$

RESULTS AND DISCUSSION

Results of the scaling test and estimates of the components of the generation means for the grain variables are given in Tables 1 and 2 and show that additive gene effect was important in the control of all the oat grain variables studied. The dominance effect was however important for average terminal individual grain weight and % tertiary grain weight. For the average terminal individual grain weight, the dominance effect was negative while for the % tertiary grain weight, it was positive and significant. The apparent over dominance ([h] > [d]) obtained for terminal individual grain weight and % tertiary grain weight could be a consequence of dispersed genes and directional dominance or the observed epistasis which might have overestimated the dominance effects. The presence of epistasis as shown by the significant values of the quantities A, B and C were reflected in the duplicate dominance epistasis as expressed by the significant values and opposite signs of [h] (dominance) and [11 (dominance x dominance) components. Mean dominance as expressed by the deviation of the F, from the mid parent value was negative for average individual grain weight, primary and secondary individual grain weights, primary: secondary yield ratio and % tertiary grain weight. The distribution of the individual plants in the six generations of the backcrosses for the grain weight variables is given in Figures 1 and 2, together with the generation means and standard deviations based on untransformed data. The tendency for lower overall terminal grain weight to be dominant was evident in the means of the F1, F 2 and both backcross generations. As expected from the segregation, the FZ generation had the widest range (30-55 mg), but no plants in the FZ generation achieved overall individual grain weights as high as the heaviest grains in parent P, (1L82-1657). The sealing test for primary, secondary and primary: secondary individual grain weights are indicated in Table 1. For the primary individual grain weight, the data fail the A, B and C tests and for the secondary individual grain weight, the B test was also significant confirming the presence of non-allelic interactions for these characters but not for the primary: secondary individual grain weight ratio. In all of these 3 traits, viz. average terminal primary, secondary individual grain weight and primary: secondary individual grain weight ratio, the additive component [d] was significant but the dominance component [h] was not important. The present of nonallelic interaction was confirmed by significant dominance x dominance interaction [l] for the primary individual grain weight. While the digenic interactions were not detected for the secondary individual grain weight, possibly higher order interactions and or linkages might be controlling the expression of this trait. Such interactions might have overestimated the dominance effects [h] which were numerically higher (though not significant) than the additive effects [a] in these variables. Due to the presence of the non allelic interactions, no attempt was made to estimate further component of genetic variances and hence no estimates of heritability were made for the overall, primary, secondary individual grain weights and % tertiary grain weight. For the primary: secondary IGW ratio, only additivity was important and the narrow sense heritability was high, being over 98%.

Table 1: Scaling tests and estimates of the components of the generation means of the cross 182-1657 x 09562Cn for the individual grain weight variables ($\log_e$)

Item	VARIABLE			
	TERMINAL INDIVIDUAL GRAIN WEIGHTS			
Scaling test	Average	Primary(P)	Secondary(S)	P:S IGW Ratio
A	-0.114±0.0421**	-0.103±0.034***	-0.069±0.0470	-0.020±0.0155
B	-0.227±0.0400***	-0.100|0.0333**	-0.084±0.0414*	-0.009±0.0133
C	-0.213±0.0712**	-0.191±0.0580***	-0.129-+0.0758	-0.036±0.0276
Estimates m	3.866±0.0716***	4.018±0.0626***	3.620+-0.0838***	0.924±0.0202***
[d]	0.178±0.0140***	0.146±0.0109***	0.065±0.0130***	0.048±0.0199*
[h]	-0.636±0.1773***	-0.273±0.1548	-0.256±0.2073	0.002±0.0395
[I]	-0.128±0.0702	-0.012±0.0617	-0.024±0.0823	-
[j]	0.113±0.0521*	-0.003±0.0448	0.015±0.0586	-
[l]	0.469±0.1131***	0.215±0.0974	0.177±0.1295	-
Means P1	3.915±0.1135	4.151±0.0869	3.660±0.1069	0.975±0.0346
P_2	3.560±0.0993	3.860±0.0796	3.531±0.0904	0.877±0.0257
F_1	3.699±0.0986	3.960±0.0680	3.541±0.0853	0.931±0.0358
B_1	3.750±0.1036	4.004±0.0926	3.566±0.1300	0.943±0.0407
B_2	3.516±0.1001	3.860±0.0890	3.494±0.1131	0.899+n.0345
F_2	3.665±0.1268	3.935±0.1103	3.536±0.1483	0.919±0.0529
Mid-parent	3.738	4.006	3.660	0.926
Heterosis	-0.039	-0.046	-0.119	0.005
% Heterosis	-1.0	-1.1	-3.3	0.6
$\%h^2$(N)	-	-	-	98.3

Table 2: Scaling tests and estimates of the components of the generation means of the cross IL82-1657 x O9562Cn for the proportions of grain weight produced (loge)

ITEM	VARIABLE	
Scaling test	Primary: secondary yield ratio	% tertiary grain weight
A	-0.027±0.0453	0.425±0.39052
B	-0.018±0.0274	1.409±9,3755***
C	-0.024±0.0552	0.944±1.4282
Estimates m	0.925±0.0605***	0.250±0.6505
[d]	0.054±0.0593	0.875±0.1148***
[h]	-0.007±0.1020	3.444±1.6289*
[I]	-	0.890±0.6403
[j]	-	0.9840±0.4736*
[l]	-	-2.724±1.0599*
Means P1	0.983±0.1024	1.015±1.0029
P_2	0.876±0.0936	0.265±0.7224
F_1	0.923±0.0752	0.970±1.0457
B_1	0.939±0.1272	2.197±0.8668
B_2	0.891±0.0528	0.830±1.0457
F_2	0.921±0.0938	1.291±1.1320
Mid-parent	0.930	1.140
Heterosis	-0.006	-0.17
% Heterosis	-0.67	-14.9
%h^2(N)	0	-

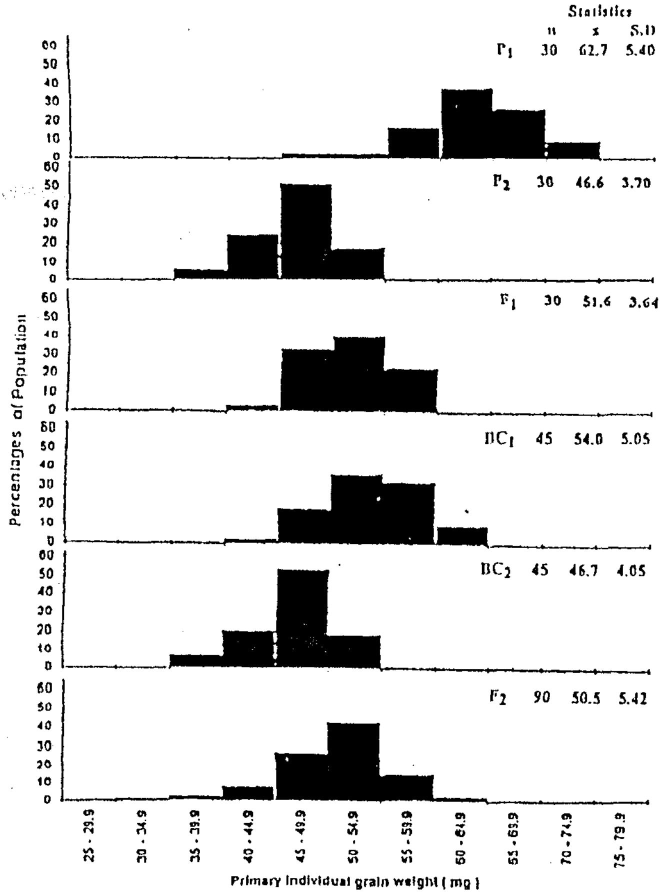

Fig 1a: Frequency distribution of terminal primary individual grain weight

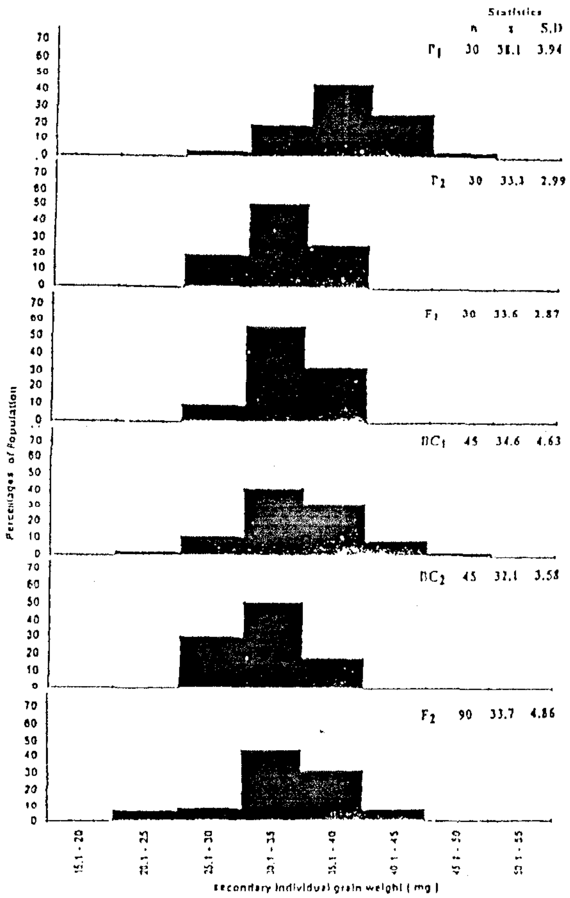

Fig 1b: Frequency distribution of terminal secondary grain weight

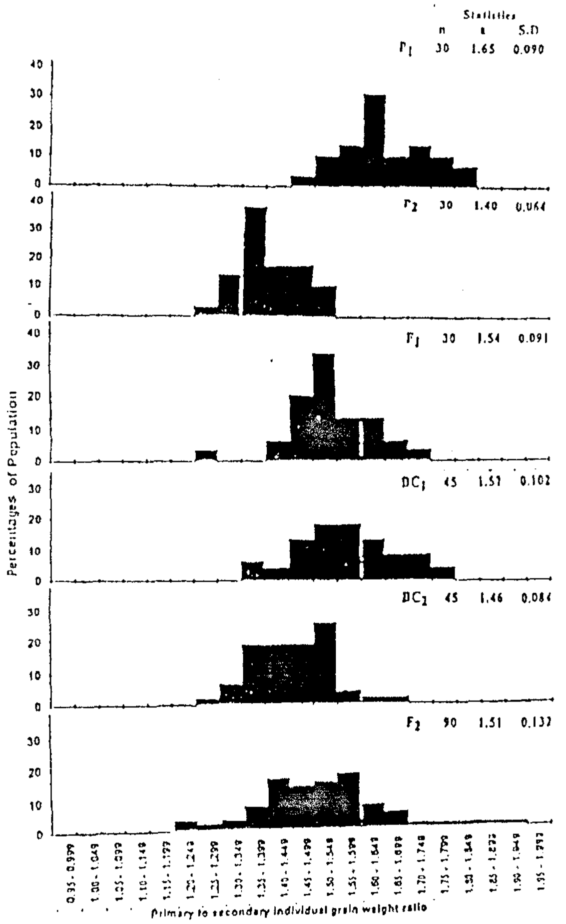

Fig. 1c: Frequency distribution of terminal primary: secondary IGW ratio

From an inspection of the means and distribution of the F1, F2 and backcross generations, it appears that there is a tendency for the smaller individual grain weights to be dominant in the analysis of the primary and secondary individual grain weights. However, the dominance effects though negative, were not significant. As with the overall terminal individual grain weight, the distribution of plants show that the cross is capable of producing FZ segregates as good as P2 (10589Cn) but not P, (IL82-1657). The % tertiary grain weight produced indicated significant non allelic interaction and dominance effect although additivity was also important. There were no significant differences between parents and means of the progency in any of the derived generations for the primary: secondary yield ratio and % tertiary grain weight produced (Fig. 2).

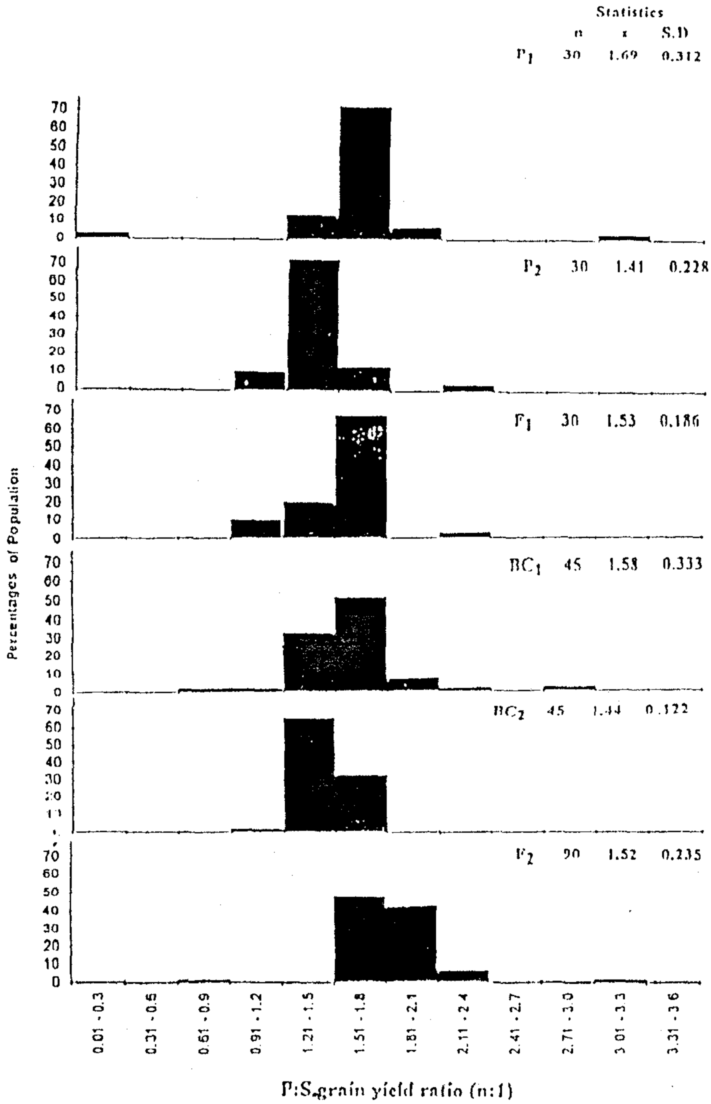

Fig. 2a: Frequency distribution of Primary: secondary yield ratio

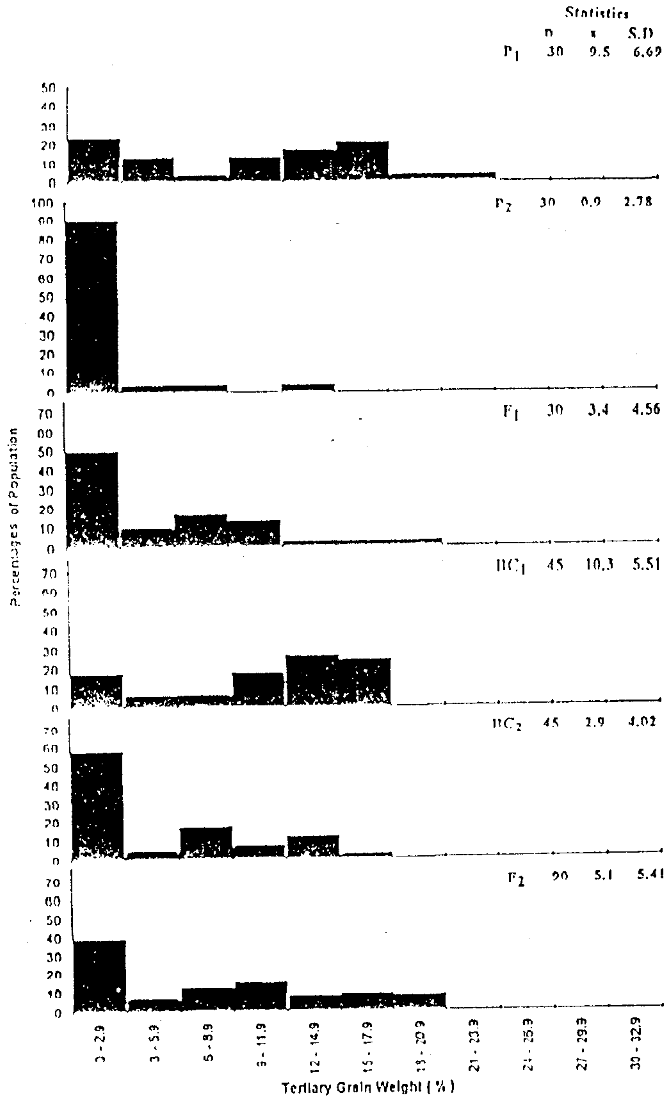

Fig. 2b: Frequency distribution of % tertiary grain weight of the backcross generations

In the present study, additive gene effects were detected for individual grain weight variables investigated while dominance was relatively not important except for the overall average individual grain weight. In the latter, dominance was significant and negative, suggesting a tendency for negative heterosis in the F I for average grain weight. For the primary, secondary individual grain weights and primary: secondary IGW ratio, there were no dominance effects in the F, generation. Thus, additivity is the main feature of the genetic system controlling inheritance of grain weight in oats. This is to be expected in a self fertilising species such as *Avena* in which the loci are homozygous and consequently the genetic system would not have undergone selection for fitness based on dominance effects. High heritability registered for the primary: secondary individual grain weight ratio suggests the easiness of improving grain size uniformity. Predomiance of additivity has also been reported in other populations of oats by Takeda and Frey (1980) for average thousand grain weight. In other studies, Tibelius and Klinck (1986) also observed the predominance of additive variance in the inheritance of primary: secondary individual grain weight ratio.

Appreciable amounts of non allelic interactions were detected for most of grain weights except primary: secondary IGW ratio and primary: secondary yield ratio. The [h] (dominance effect) and [11] (dominance x dominance interaction effect) components were significant with opposite signs and this according to Jinks and Jones (1958) suggested the presence of duplicate - dominance or recessive suppresser kind of epistasis for the average terminal and primary IGW's and % tertiary grain weight. Duplicate genes may be present as a result of the polyploid origin of oats. In an hexaploid like *A. sativa,* with three homologous genomes and diploid like meiosis, considerable non allelic interactions can be expected. Law *et al.* (1978) suggested that where [h] > [d] (e.g. % tertiary grain weight, average grain weight, primary and secondary individual grain weights), the presence of epistasis may overestimate the dominance effect. Thus, both dominance and epistatic effects were apparently responsible for the heterotic effects observed in the F, generation of the backcross for the grain weight variables. Few workers have reported non allelic interactions in other populations of oats, for example for the ratio of primary: secondary individual grain weight (Tibelius & Klinck 1986).

The large additive effects detected suggest that substantial progress can be made using standard selection schemes to develop improved pure line varieties for these traits. The presence of non-allelic interactions however, implies that expression of these traits will depend on presence of particular genes in the background. Of particular interest, is the situation concerning the ratio of the primary: secondary individual grain weight. The predominantly additivity and the absence of dominance effects indicate that it should be relatively easy to improve grain uniformity in this material by the conventional and modified breeding producers.

With respect to the % tertiary grain weight, it is evident that dominant alleles increase this variable and hence for practical purposes, it would be necessary to utilize recessive genes if expression of genotypes with low levels of tertiary grains are required. Tertiary grains are lighter and do not reach the optimum grain size required for industrial oat processing. Thus, breeding procedures which produce genotypes with low or no tertiary grains are desirable for more uniform grains. Plants which produce heavier secondary grains (and thus a lower P:S IGW ratio) offer the possibility of increased uniformity of grain.

Selection for improved ratio of P:S IGW by selecting for larger secondary grain would be the most promising tactic to employ in selecting for improved grain quality. Although no digenic interaction was detected in the control of this variable, higher order interactions and or linkage are possibly present due to failure of the scaling test to satisfy the simple model and thus selection of the best parents may not necessarily reflect production of best plants in subsequent generations. Digenic interactions were detected for overall average terminal grain weight, primary grain weight and the % tertiary grains produced. Thus it may be difficult (unpredictable) to obtain desired genotypes for these variables based on segregates from mating of the best parents. The only grain variable likely to yield desirable genotypes from mating of the best parents is grain uniformity, measured in terms of the primary: secondary IGW ratio. The scaling test adequately satisfied the additive-dominance model and the narrow sense heritability was exceptionally high (>98%) for the P:S IGW ratio. The challenge set, however, is that tertiary grain production lowers grain quality in terms of uniformity, but genetic improvement may be dodgy due to non allelic interactions. This leaves oat breeders with an option of selecting for genotypes which do not produce tertiary grains and then improve on the P:S IGW ratio through breeding. For the traits in which non allelic interactions are evident, modified breeding techniques involving progeny testing can be expected to improve the efficiency of the improvement programme. Dominance was important in the expression of overall average grain weight and % tertiary grain weight produced, however, the use of hybrids in the improvement of these variables will not be economically viable on a large scale in the predominantly selfing oat crop.

Improvement of grain uniformity in terms of primary: secondary individual grain weight ratio looks promising due to its high heritability and absence of non-allelic interactions. However, breeding for reduced levels of tertiary' grains may not be predictable due to presence of digenic interactions. Choice of genotypes with few or no tertiary grains and then improving the primary: secondary individual grain weight ratio through breeding seems to be the most rational approach. Further studies are suggested using crosses from other populations of oats to confirm consistency of the finding.

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