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GENETIC ANALYSIS OF HEXAPLOID WHEAT, *TRITICUM AESTIVUM* USING INTERVARIETAL CHROMOSOME SUBSTITUTION LINES – PROTEIN CONTENT AND GRAIN WEIGHT

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SUMMARY

The 21 intervarietal chromosome substitution lines of the cultivar Hope in Chinese Spring were used to analyse the genetic differences between the two cultivars Hope and Chinese Spring in grain protein content and grain weight.

Only one chromosome of 'Hope, 5D', significantly influenced grain protein content of 'Chinese Spring'. Its influence was of only minor effect and was to decrease protein content expression of 'Chinese Spring'. It has been postulated that the genetic control of protein content, in this instance, is most likely due to many genes each of small effect.

Five chromosomes of 'Hope' influenced the 1000 grain weight value of normal 'Chinese Spring', all increasing its expression. Chromosomes 1A, 4A and 5B were of major effect and 3A and 6A of comparatively minor effect. A minimal estimate of five genes determines the difference in grain size between these cultivars. The possible evolutionary significance of the contribution of the A genome of bread wheat to grain size determination is discussed. On the basis of certain findings of this study, proposals are made for breeding for increased grain size in hexaploid wheat.

INTRODUCTION

Intervarietal chromosome substitution lines of bread wheat afford wide scope for the study of the genetics of both physical and biochemical characteristics of the wheat grain. Knowledge gained from such studies could assist wheat breeders in producing yield improvement through increased grain size or number, or baking, or nutritive quality, improvement through genetic changes in certain biochemical attributes of the grain.

The two characters examined in this study, protein content and 1000-grain weight, have each been subjects of conventional genetical analysis, but, for which, no conclusive information on its genetic control has been obtained.

Protein content. Most of the studies of the genetics of grain protein content in wheat have indicated polygenic control (CLARK & HOOKER, 1926; AAMODT & TORRIE, 1935; SWEN, 1940; WORZELLA, 1942). Other studies (HAUNOLD, 1960; HALLORAN, 1975b) have indicated the likelihood of protein content being under the control of only a few

major genes and an undetermined number of modifiers. Dominance of low protein content has been reported (CLARK & QUISENBERRY, 1929; CLARK et al., 1928) and by other workers partial dominance (DAVIS et al., 1961; JOHNSON et al., 1973; HALLORAN, 1975a). Using intervarietal chromosome substitution lines of the cultivar Thatcher in Chinese Spring, KUSPIRA & UNRAU (1957) located five chromosomes of 'Hope', each of which increased grain protein content of normal 'Chinese Spring'. Studies by MORRIS et al. (1973), using monosomic analysis of the cultivar Atlas 66, revealed a contribution by chromosomes 5A, 5B and 5D to high protein content. In the same study the contribution of chromosome 5D to high protein content was confirmed from examination of the substitution lines of these three chromosomes of 'Atlas 66' in 'Chinese Spring'.

Grain weight. Grain weight as an inherited character in bread wheat has not been extensively studied but investigations indicate a detectable heritable component. Its inheritance has been reported to be monogenic (WORZELLA, 1942), trigenic (JASNOWSKI, 1935) and polygenic (WORZELLA & CUTLER, 1949). Grain weight analyses using intervarietal chromosome substitution lines in 'Chinese Spring' have located seven chromosomes but not all the same, in each of the cultivars Hope, Thatcher and Timstein which significantly influenced its expression (KUSPIRA & UNRAU, 1957). The influence of each chromosome was considered to be of minor, rather than of major, effect.

MATERIAL AND METHODS

Grain samples for the present study were obtained from a field trial consisting of the 21 chromosome substitution lines of 'Hope' and 'Chinese Spring' and the two cultivars Hope and Chinese Spring, which was of a randomized block layout of four replicates per line. The lines were hand-sown in rows at a 35 cm spacing and at a seed rate equal to 68 kg/ha.

Grain protein determinations were made using the Biuret Method (HALLORAN & MOSS, 1956) and the results expressed on a 13.5% moisture basis. Grain weight data were based on 1000-grain weight determinations, for which grain was counted on a vibration-feed electronic grain counter.

RESULTS

Analyses of variance of grain protein content and grain weight of the 21 substitution lines and the two cultivars Chinese Spring and Hope were carried out and the significance of the difference calculated of each character for each line from normal 'Chinese Spring'.

Protein content. The two cultivars Chinese Spring and Hope differed significantly ($P < 0.01$) in grain protein content. The difference in mean protein content of 1.8%, though not large, would have enabled significant differences in protein content within this range to be established because of the very low standard error between replicates. Only one chromosome of 'Hope', namely 5D, significantly influenced grain

Table 1. Grain protein content of the varieties Chinese Spring and Hope and the 21 Chinese Spring-Hope chromosome substitution lines.

Chromosome substitution line	Grain protein (%)	Difference from Chinese Spring
Chinese Spring-Hope – 1A	12.76	+0.13
Chinese Spring-Hope – 2A	12.99	+0.36
Chinese Spring-Hope – 3A	12.17	−0.46
Chinese Spring Hope – 4A	12.42	−0.21
Chinese Spring Hope – 5A	12.51	−0.12
Chinese Spring-Hope – 6A	12.13	−0.50
Chinese Spring-Hope – 7A	12.09	−0.54
Chinese Spring-Hope – 1B	12.62	−0.01
Chinese Spring-Hope – 2B	12.30	−0.33
Chinese Spring-Hope – 3B	12.85	+0.22
Chinese Spring-Hope – 4B	12.35	−0.28
Chinese Spring-Hope – 5B	12.70	+0.07
Chinese Spring-Hope – 6B	13.09	+0.46
Chinese Spring-Hope – 7B	12.57	−0.06
Chinese Spring-Hope – 1D	12.26	−0.37
Chinese Spring-Hope – 2D	12.75	+0.12
Chinese Spring-Hope – 3D	12.72	+0.09
Chinese Spring-Hope – 4D	12.58	−0.05
Chinese Spring-Hope – 5D	11.90	−0.73*
Chinese Spring-Hope – 6D	12.64	+0.01
Chinese Spring-Hope – 7D	13.11	+0.48
Chinese Spring	12.63	
Hope	14.43	1.80*

* Significant at the 5% level.
** Significant at the 1% level.
References to chromosomes 2A and 2B are according to the terminology of CHAPMAN & RILEY (1966).

protein content of 'Chinese Spring' but its effect was to reduce protein content of normal 'Chinese Spring' (12.6%) rather than increase it in the direction of 'Hope' (14.4%) (Table 1).

Grain weight. Grain weight differences between 'Chinese Spring' and 'Hope' were significant ($P < 0.01$) and a difference of 2.79 g per 1000 grains was considered to be a reasonably wide differential for a study of this nature. Six chromosomes of 'Hope' significantly influenced grain size of 'Chinese Spring', all in the direction of increased size (Table 2).

DISCUSSION

Protein content. The chromosomes of 'Hope' in 'Chinese Spring' do not produce a clear picture of the possible genetic control of the difference in this character between these two cultivars. Chromosome 5D of 'Hope' is the only chromosome which significantly influences protein content of normal 'Chinese Spring'. This chromosome has

Table 2. 1000-Grain weight of the varieties Chinese Spring and Hope and the 21 Chinese Spring-Hope chromosome substitution lines.

Chromosome substitution line	1000-grain weight (g)	Difference from Chinese Spring
Chinese Spring-Hope – 1A	25.54	+3.89**
Chinese Spring-Hope – 2A +	23.28	+1.63
Chinese Spring-Hope – 3A	24.20	+2,55*
Chinese Spring-Hope – 4A	26.78	+5.13**
Chinese Spring-Hope – 5A	22.70	+1.05
Chinese Spring-Hope – 6A	23.82	+2.17*
Chinese Spring-Hope – 7A	22.29	+0.64
Chinese Spring-Hope – 1B	21.20	−0.45
Chinese Spring-Hope – 2B	22.63	+0.98
Chinese Spring-Hope – 3B	22.39	+0.74
Chinese Spring-Hope – 4B	21.56	−0.09
Chinese Spring-Hope – 5B	25.07	+3.42**
Chinese Spring-Hope – 6B	21.01	−0.64
Chinese Spring-Hope – 7B	20.21	−1.44
Chinese Spring-Hope – 1D	23.72	+1.97
Chinese Spring-Hope – 2D	21.48	−0.17
Chinese Spring-Hope – 3D	21.76	+0.11
Chinese Spring-Hope – 4D	21.44	−0.21
Chinese Spring-Hope – 5D	23.00	+1.35
Chinese Spring-Hope – 6D	21.43	−0.22
Chinese Spring-Hope – 7D	22.80	+1.15
Chinese Spring	21.65	
Hope	24.44	+2.79**

*Significant at the 5% level.
**Significant at the 1% level.

previously been found to influence the expression of grain protein content (KUSPIRA & UNRAU, 1957; MORRIS et al., 1973). In the present study, the action of 'Hope' 5D is to depress grain protein content of 'Chinese Spring' and could be regarded as of only minor genetic status. The absence of a significant influence of any of the other 'Hope' chromosomes on grain protein content of 'Chinese Spring' is possibly due to a masking, or dilution, effect on grain protein content caused by yield differences between the critical substitution lines and normal 'Chinese Spring'. Unfortunately, owing to the occurrence of some grain shedding in the trial, satisfactory yield data were not obtainable and it was therefore not possible to investigate this possibility. However the general level for grain protein content shown by the substitution lines and the cultivars Chinese Spring and Hope in this trial, and the non-limiting soil nitrogen conditions during its growth, indicate that the interaction of grain yield with protein level for each line would most likely have been of little significance.

Another possible reason for this behaviour is that the difference between 'Chinese Spring' and 'Hope' in grain protein content is conditioned by the action of a number of genes each of small effect rather than by a small number of major genes. Previous observations on grain protein content using the chromosome substitution lines of

'Thatcher' in 'Chinese Spring' (KUSPIRA & UNRAU, 1957) revealed the presence of five chromosomes of 'Thatcher', each of minor effect, which significantly influenced protein content of 'Chinese Spring'. The data of the present experiment were also analysed to reveal possible significant genome and/or homoeologous group effects on protein content but each was non-significant.

Grain weight. Genes on five chromosomes of the cultivar Hope appear to determine the difference in grain weight between 'Chinese Spring' and 'Hope'. The effect of each chromosome is to increase grain weight of normal Chinese Spring. Assuming that the influence of each chromosome is due to the action of a single gene, a minimal estimate of five genes is therefore made as determining this difference. If the comparative influences of these chromosomes can quite arbitrarily be regarded as of major genetic status for those effective at the 1% level of significance and of minor effect for those at the 5% level, it can be postulated that three major genes and two minor genes are involved. The major genes would be situated on chromosomes 1A, 4A and 5B and the minor genes on chromosomes 3A and 6A. Previous cytogenetic studies of grain weight (KUSPIRA & UNRAU, 1957) showed the presence of a gene, or genes, on chromosomes 4A of 'Hope', 5B of 'Thatcher' and 'Timstein', and 6A of 'Hope' and 'Timstein' which increased grain weight of normal 'Chinese Spring'.

Although grain weight in wheat has not been much studied as a topic of inheritance, or breeding, the present results indicate that breeding and selection for increased weight could be a worthwhile pursuit. A comparatively simple genetic control of grain weight with the possibility of a small number of genes of major effect has been revealed, indicating that rapid and substantial improvements in this character might be expected in breeding. However, in practice, owing to the possible occurrence of physiological compensation amongst the component characters of yield in wheat, heritable differences may be somewhat masked.

A knowledge of the chromosome location of the genes influencing the expression of grain weight and of the relative magnitude of their influences may make possible the use of intervarietal chromosome substitution as a breeding technique for this character. Four of the five chromosomes of the cultivar Hope, which influence grain weight of 'Chinese Spring' are in the A genome which may be of evolutionary significance. Two of the chromosomes, 1A and 4A, are of major influence and two chromosomes, 3A and 6A are of minor influence. The 'concentration' of genes for this character in the A genome may reflect the influence of the *Triticum monococcum* progenitor on the determination of grain weight in cultivated wheat. *Triticum monococcum* was most likely originally cultivated as a grain producer in the early history of wheat's domestication. Selection, both conscious and unconscious, by early agriculturalists for increased productivity most likely was in the direction of increased grain size. It may be postulated that the combination of wild *Triticum monococcum* with a grass-like, and hence small-grained, B genome donor(s) to give tetraploid *Triticum*, provided a genetic combination(s) which gave greater potential, both initially and subsequently, for increased grain size. The increase in grain size shown by present day forms of wild and domesticated tetraploid wheat above that of both wild and cultivated forms of *Triticum monococcum*, represents a major advance in the evolution of grain size in wheat. The interaction of genes within the B genome with

those of the A genome for the expression of grain size was therefore most likely of major significance in this evolutionary step. It is possible that the gene, or genes, for grain size (weight) on chromosome 5B, as revealed in this study, may have been of significance in this change. The evolutionary development of hexaploid wheat does not appear to have resulted in an increase in grain size, but is perhaps even regressive from that exhibited by tetraploid *Triticum*, on the basis of comparisons of presently available tetraploid and hexaploid forms. Differences in grain size in wheat, of the order of magnitude being discussed, will be very strongly correlated with differences in grain weight. In comparison with the large grain size of some of the tetraploid forms of *Triticum* e.g. *T. dicoccoides*, *T. polonicum*, the upper limit of grain size variation in the hexaploids appears to be significantly lower than in the tetraploids. In this context it is of interest that in the present study, none of the D genome chromosomes exhibited any significant influence on the expression of this character in 'Chinese Spring'. However, it is considered wise to extend this form of study to more wheat genotypes to possibly establish a more generalized pattern of grain weight determination in hexaploid wheat.

It could be postulated that an optimal level of gene dosage for large grain size in wheat was achieved at the tetraploid level of its evolution. One consideration in breeding for increased yield in situations where grain size is considered to limit further yield improvement, is that of possibly altering the dosages in hexaploid wheat of genes influencing grain size. This could be approached, either through the use of irradiation techniques or the use of the nullisomic-5B condition, the latter to bring about homoeologous recombination within wheat (RILEY, 1965). The possible consequence of either approach might be the production of duplication-deficiency situations involving genes determining grain size and, hence the possibility of providing more scope for selecting for increased grain size at the hexaploid level. The possibility exists also with the use of the nullisomic 5B method in hybrids between large-grained tetraploid wheats with hexaploids, of selecting for possible duplication of A or B genome 'large grain genes' in the D genome as increased grain size in hexaploid offspring. The possibility of simple genetic control of grain weight (size) as few major genes, as indicated in this study, gives feasibility to the use of these methods for increasing grain size of hexaploid wheat.

The genetic analysis of the two characters of this study, particularly that of grain weight, indicates the potential role of chromosome substitution lines in providing a fuller understanding of the genetics of physical and biochemical characteristics of the wheat grain. However this form of study will be a greater impact when substitution lines are made between a genetically wider range of wheats and embracing genotypes known to differ significantly for particular biochemical and physical grain characteristics.

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