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Genetic Studies of Phasic Development and their Application to Wheat Breeding

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Considering the pre-eminent status of wheat as a world crop, surprisingly little is known of the genetics and physiology of developmental processes. The position is in striking contrast with, say, rice and sorghum.

Bell and Kirby (1965) conclude that "very little use has been made by the plant breeder of physiological analysis to explain different growth responses encountered in breeding programmes". They further state—"all the major physiological differences are necessarily of a quantitative nature, there being no sharp qualitative difference between spring and winter varieties for example; nor can one draw definite lines of demarcation between early, midseason or late varieties". It is suggested that the latter does not represent the true position; rather does it merely reflect our deep ignorance of the subject.

This paper has been prepared with a view to illustrating a type of approach which, if pursued in a determined manner by groups of workers, could be very productive indeed in both its basic and applied aspects. Too often in the past research in this field has been incidental to other studies. The results have been both sketchy and fragmentary with almost no attempt at integration. There is little doubt that a systematic and co-ordinated study of a selected range of varietal material would very soon clarify the picture we currently have of the behaviour of wheat varieties under the wide range of environments under which the crop is grown. Most certainly more effective breeding programmes would follow.

In New South Wales there are two major climatic hazards facing the wheat crop—stem frosting in the early spring, followed a little later by severe periods of moisture stress during the post-flowering period. Such hazards may be partly met through the genetic control of development. Recent experience has provided a much clearer understanding of the processes leading to flowering and at the same time has added a greater degree of precision to breeding programmes. This has involved both low temperature vernalization and daylength studies.

So far local studies have led to the recognition of a relatively few major genes which condition responses to both photoperiod and cold temperature vernalization. Backcrossing procedures have been extensively used in the transference of these genes and has led to the production of a number of crossbred lines which are near-isogenic with certain commercial varieties. These genes have been found to exert their influence through controlling the time for ear initiation and ear emergence. At the same time it has been found that other associated features of growth and development such as ear size, tillering and plant height may be brought under partial control simultaneously with the floral induction process.

METHODS

Up to the present most of the work to be described has been undertaken in the greenhouse at appropriate times of the year. On some occasions care is necessary to avoid vernalizing temperatures (with respect to ripening ears as well as during the seedling stages). At other times short daylight periods are supplemented with additional artificial illumination.

In daylength studies it is preferable to select varieties which are non-responsive to vernalization. If winter varieties are involved they should first receive their full vernalization treatment. When vernalization responses are under study it is preferable to raise the plants under long days.

Plants are usually raised singly in four inch pots, measurements being taken on the main axis. Leaf number and spikelet number are recorded in this way but plant height and tillering are best measured on plants raised under fertile soil conditions in the field.

Now that controlled environment facilities have become available verification of current results will be sought under specified environments.

PHOTOPERIOD

It is only in recent years that there has developed an appreciation of the range of sensitivity to daylengths existent in the world's wheats. Most Australian varieties are relatively insensitive to short days and this enables them to initiate ears during the short days of winter and to flower relatively early in the spring. On the other hand many northern hemisphere varieties are quite sensitive to short days and are therefore too late in ear emergence under Australian conditions.

Major genes for day length sensitivity have been detected in the spring varieties Selkirk and Thatcher, one gene in the former and two in the latter (PUGSLEY 1965, 1966). For the time being these may be referred to as p_1p_1 and p_2p_2. A close association between time to ear emergence, leaf number and spikelet number has been noted. The degree of development of the basal spikelets of the ears of sensitive varieties like Thatcher depends upon the length of the daylight periods during the early stages of growth—long days result in full development while short days result in rather rudimentary development. Sometimes, as in the case of club wheats, ear shape can reflect variations in daylength.

Three American winter wheats—Blackhull, Early Blackhull, and Extra Early Blackhull appear to differ rather strikingly in their sensitivity to photoperiod. Data for days to ear emergence, leaf and spikelet numbers under long and short days (following upon a prior seven weeks vernalization period) are set out in TABLE 1.

TABLE 1. Comparison of Blackhull Type Wheat (Vernalized 7 weeks and transplanted to glass-house).

	Days to ear emergence	Leaf number	Spikelet number
Blackhull (short day)	116.5	13.0	23.5
Blackhull (long day)	40.5	7.5	11.0
Early Blackhull (short day)	59.0	9.5	15.0
Early Blackhull (long day)	38.5	7.0	10.0
Extra Early Blackhull (short day)	36.0	6.0	10.0
Extra Early Blackhull (long day)	35.5	6.0	8.0

Short day—natural day approx. 10.5-11.5 hours.
Long day—lengthened to 16 hours with incandescent lights.

Experience would suggest that where wheat crops grow and develop through winter-spring-summer, an environment of lengthening daylight periods, then the time of ear emergence is more generally controlled by daylength sensitive genes rather than through genes governing the vernalization response.

VERNALIZATION

Although the world's wheats are commonly classified as of either winter or spring habit there is certainly a range in responsiveness to cold temperature vernalization. Quite apart from the perplexing results from "autumnization" experiments (RAJKI 1967) there is a great deal yet to be learned about the growth and developmental processes of wheat in both the greenhouse and field as they are modified by vernalization treatments.

Locally, progress can be reported in the working out of procedures for such studies and some preliminary results have been obtained. For instance, one gene conditioning a positive response to vernalization has been detected in the spring wheat Insignia 49 (PUGSLEY 1963). Later studies, as yet unpublished, have embraced the varieties Winter Minflor, the three Blackhull wheats, and Elgin and Jones Fife. The first is of Australian origin (MACINDOE and WALKDEN-BROWN 1958) and the Blackhull wheats were described by ATKINS *et al.* (1962). Elgin and Jones Fife were selected for study following upon the work of TSUNEWAKI and JENKINS (1961) in establishing that their winter habit was governed by two recessive genes sg_1 and sg_2 on chromosomes 5D (XVIII) and 5A (IX). Both the latter varieties have a greater vernalization response than the Blackhulls which, in turn, have a greater response than Winter Minflor.

TSUNEWAKI and JENKINS (1961) have also recognised a third locus for growth habit on chromosome 2B (XIII), indicating the presence of a recessive winter allele in spring varieties such as Thatcher, Prelude and Red Bobs. This recessive allele was not detected in any winter varieties. As will be seen, this adds particular interest to local studies as well as to those of ANDERSON and MCGINNIS (1960), KNOTT (1959) and LEGRAND (1965) who each reported transgressive segregation of winter habit in crosses between spring wheats.

As a first step towards the integration of previously published studies, a detailed examination of the variety Winter Minflor has been made. Unpublished results reveal that the winter habit of this variety is dependent on the presence of two recessive complementary genes, either of which singly results in spring habit. Until such time as they can be related to Sg_1, Sg_2 and Sg_3 genes of TSUNEWAKI and JENKINS the two genes of Winter Minflor are designated v_1 and v_2. These two genes, together and separately, have been transferred to a common genetic background for further study (see next section). Alone, v_2v_2 delays ear initiation and ear emergence. Preliminary data suggests that, alone, v_1v_1 is without effect and for this reason it might well be that v_1v_1 is equivalent to sg_3sg_3. Supporting evidence for this view comes from the cross of Winter Minflor with Thatcher (known to carry sg_3sg_3) where a single gene difference was detected. At present it is not possible to comment on the relationship of v_2v_2 to the other genes sg_1sg_1 and sg_2sg_2 of TSUNEWAKI and JENKINS, although steps are being taken to determine this.

The close association of time to ear emergence, leaf number and spikelet number noted in populations segregating for sensitivity to daylength (PUGSLEY 1965) has also frequently been noted in cases of populations segregating for vernalization response. Delayed ear initiation is expressed as an increase in leaf number and spikelet number.

FIELD STUDIES

Having detected major genes governing developmental patterns it then remains to determine their likely impact when used in breeding programmes. To this end backcrossing techniques have led to the production of three lines, each near-isogenic with Triple Dirk—a variety only slightly sensitive to daylength and non-responsive to vernalization. Triple Dirk (A) is daylength sensitive, Triple Dirk (B) possesses spring habit and responds to vernalization, Triple Dirk (C) possesses winter habit.

In 1967 these lines were grown in the field at bi-monthly intervals with results summarized in TABLE 2.

For each sowing time Triple Dirk was earliest in ear-emergence, the other lines being delayed in an anticipated manner. While there was a wide range in ear emergence times for the autumn (March) and spring (Sept.) sowings, differences between the four lines were much reduced for the May and July sowings.

TABLE 2. Time of sowing trials—Near-Isogenic Lines of Triple Dirk.

Sowing Date	Near-Isogenic Line	Genotype	Days to ear initiation	Days to ear emergence	Date of ear emergence	Leaf number	Spikelet number
March 16	Triple Dirk	$P_1P_1V_1V_1V_2V_2$	25	79	June 3	9.0	19.0
,,	Triple Dirk (A)	$p_1p_1V_1V_1V_2V_2$	34	134	July 28	11.0	23.0
,,	Triple Dirk (B)	$P_1P_1V_1V_1v_2v_2$	50	122	July 16	12.0	17.7
,,	Triple Dirk (C)	$P_1P_1v_1v_1v_2v_2$	102	189	Sept 21	16.0	23.0
May 19	Triple Dirk	$P_1P_1V_1V_1V_2V_2$	57	138	Oct 4	9.8	21.6
,,	Triple Dirk (A)	$p_1p_1V_1V_1V_2V_2$	78	148	Oct 14	10.5	25.5
,,	Triple Dirk (B)	$P_1P_1V_1V_1v_2v_2$	78	141	Oct 7	11.0	20.7
,,	Triple Dirk (C)	$P_1P_1v_1v_1v_2v_2$	84	146	Oct 12	12.0	21.3
July 14	Triple Dirk	$P_1P_1V_1V_1V_2V_2$	48	99	Oct 21	9.0	20.0
,,	Triple Dirk (A)	$p_1p_1V_1V_1V_2V_2$	59	104	Oct 26	9.0	24.0
,,	Triple Dirk (B)	$P_1P_1V_1V_1v_2v_2$	59	102	Oct 24	9.0	21.0
,,	Triple Dirk (C)	$P_1P_1v_1v_1v_2v_2$	70	104	Oct 26	10.0	19.5
Sept 13	Triple Dirk	$P_1P_1V_1V_1V_2V_2$	28	61	Nov 13	9.0	17.0
,,	Triple Dirk (A)	$p_1p_1V_1V_1V_2V_2$	31	65	Nov 17	9.0	18.3
,,	Triple Dirk (B)	$P_1P_1V_1V_1v_2v_2$	42	73	Nov 25	11.0	19.0
,,	Triple Dirk (C)	$P_1P_1v_1v_1v_2v_2$	78*	137*	Jan 28	18.0	22.0

* irregular ear initiation and ear emergence.

Differences were noted in the post-flowering response to the cold temperatures of winter. Triple Dirk and Triple Dirk (B) were so severely frosted as to be almost fully sterile and as a result each produced a strong secondary growth of tillers in the spring. In contrast, only approximately half the ears of Triple Dirk (A) were frosted while Triple Dirk (C), being so much later, escaped frost damage completely. No secondary regrowth developed in the latter two lines.

In this experiment height differences between lines were small for all sowing dates although, as a rule, tallness is associated with lateness—particularly so for summer sowings.

During the current year all four lines are being grown under a selected range of environments throughout Australia in order to extend the information obtained from this one location in 1967.

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