Theoretical and Applied Genetics 43, 162–166 (1973)
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B Chromosome Selection in Rye[1]

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Summary. As a consequence of selection the distribution and frequency of *B* chromosomes varies among survivors of rye seedlings planted in different environments. The mean *B* frequency per plant decreased under conditions of "high" as compared with "low" density of planting. Differences in weather and soil type between two sites also caused a significant shift in the distribution and frequency of *B* chromosomes.

1. Introduction

It is characteristic of *B* chromosomes that their frequency varies between populations within species. There are good reasons for assuming the variation to be adaptive, and related to the differing environments in which the populations thrive. Surveys in *Festuca* (Bosemark, 1956), *Phleum* (Bosemark, 1967), *Centaurea* (Frost, 1958), *Dactylis* (Zohary and Ashkenazi, 1958) and *Myrmeleotettrix* (Hewitt and John, 1967), indicate that the *B* frequency is influenced by climate and soil type. The fact that *B* chromosomes are rare or absent in the intensively cultivated ryes of Northern Europe whereas they are common in "primitive" ryes from Iran, Korea and Japan (Müntzing, 1957; Kishikawa, 1965; Moss, 1966) has given rise to the suggestion that population density may also influence the frequency of *B*'s.

The following work was an attempt to confirm directly by experiment a shift in *B* frequency in response to selection under varying environmental conditions.

2. Material and Methods

a. Material

The rye carrying *B*'s was descended from a cross between *Secale cereale* and *S. vavilovii* (see Jones and Rees, 1967, 1968). Propagation by natural outcrossing over a number of generations produced a stock of plants with from 0 to 6 *B* chromosomes. From this stock random samples of seeds were germinated in trays and the seedling transplanted after three weeks.

b. The Environments

Sixteen populations were planted. They comprised two replicates, each of fifty seedlings, at each of two *sites* at two *densities* at two different *seasons*.

The sites were Penglais, 200 feet above sea level, and Syfrydrin at 1100 feet. Table 1 gives typical summer temperatures and rainfall at the two locations. Apart from the climatic differences the soil at Penglais is well drained, well limed and fertile whereas at Syfrydrin the soil is poorly drained, acid and of low fertility.

Seedlings were planted at two densities, 2 feet apart in rows with 2 feet between rows (Open populations) and 5–6 inches apart in rows with 5–6 inches between rows (Close populations).

Planting was in November for the Winter populations, in February for the Summer populations.

c. Classification

The *B* frequency of survivors was established at meiosis from anther squashes.

Table 1. *Weather at Syfydrin (1100′) and Penglais (200′). Data from April to September, 1967*

	Syfydrin	Penglais
Mean Monthly Maximum Temperature (°F)	57.2	68.5
Mean Monthly Minimum Temperature (°F)	45.8	38.8
Mean Soil Temperature at 4″ (°F)	51.9	59.2
Mean Monthly Rainfall (inches)	6.5	3.4

3. Results

a. Mortality

The number of survivors varies between populations (table 2). An analysis of variance, after angular transformation, showed a significantly greater mortality in winter than in summer populations ($P = < 0.001$). Rather surprisingly the mortality was greater at the lowland site, Penglais, than at Syfrydrin ($P = < 0.001$), the difference being significantly accentuated in winter ($P = < 0.001$). There was no significant variation due to spacing.

b. The Distribution of B Chromosomes

The distribution of *B*'s among the survivors is given in table 2 and represented by the histograms in fig. 1. The excess of plants with even as distinct from odd numbers of *B* chromosomes is a consequence of the non-Mendelian inheritance displayed by *B*'s in rye and many other species (see review by Battaglia, 1964).

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[1] We are grateful for the opportunity, in this commemorative issue, to pay tribute to Professor Rhoades as a scientist who has contributed massively to knowledge and who, on a more personal level, has inspired respect and affection among his many friends and acquaintances throughout the world.

Table 2. *The distribution of B chromosomes in experimental rye populations*
Population means (*B* frequency, variance etc.) are means of replicates

	Penglais					
	Close populations					
	Winter			Summer		
B class	rep. 1	rep. 2	total	rep. 1	rep. 2	total
0	5	8	13	11	17	28
1	2	0	2	3	2	5
2	2	4	6	12	9	21
3	1	1	2	1	0	1
4	2	0	2	4	2	6
5	0	0	0	9	0	0
6	0	1	1	0	0	0
Total	12	14	26	31	30	61
Mean *B* frequency			1.34			1.21
Mean variance			2.78			1.69
Mean per cent plants with *B* chromosomes			9.51			54
Mortality (angular values)			60			39

	Penglais					
	Open populations					
	Winter			Summer		
B class	rep. 1	rep. 2	total	rep. 1	rep. 2	total
0	2	4	6	8	15	23
1	1	1	2	1	1	2
2	2	8	9	17	8	25
3	2	0	2	2	2	4
4	4	2	6	5	4	9
5	1	1	2	1	0	1
6	0	2	2	0	0	0
Total	12	17	29	34	30	64
Mean *B* frequency			2.71			1.62
Mean variance			3.39			2.08
Mean per cent plants with *B* chromosomes			80			63
Mortality (angular values)			58			37

	Syfydrin					
	Close populations					
	Winter			Summer		
B class	rep. 1	rep. 2	total	rep. 1	rep. 2	total
0	15	16	31	17	17	34
1	5	3	8	3	1	4
2	6	8	14	10	13	23
3	1	2	3	1	0	1
4	0	4	4	2	4	6
5	0	0	0	1	0	1
6	0	0	0	0	0	0
Total	27	33	60	34	35	69
Mean *B* frequency			0.97			1.19
Mean variance			1.48			1.80
Mean per cent plants with *B* chromosomes			48			56
Mortality (angular values)			39			34

	Syfydrin					
	Open populations					
	Winter			Summer		
B class	rep. 1	rep. 2	total	rep. 1	rep. 2	total
0	12	16	28	19	12	31
1	3	4	7	2	2	4
2	13	11	24	9	9	18
3	3	4	7	4	2	6
4	8	4	12	3	3	16
5	0	0	0	0	1	1
6	0	0	0	0	0	0
Total	39	39	78	37	29	66
Mean *B* frequency			1.24			1.34
Mean variance			2.08			2.14
Mean per cent plants with *B* chromosomes			64			54
Mortality (angular values)			28			36

Initial planting, 50 seedlings per replicate

It is appropriate in the first place to ask whether there is, in general, a relationship between the distribution of *B*'s and the mortality within populations. In so far as the degree of mortality is an indication of stress there is the possibility that certain *B* classes are more resistant to stress conditions than others, and that a differential resistance is reflected by the distribution of *B* chromosomes among survivors.

Variances. A convenient measure of the distribution of plants with differing numbers of *B* chromosomes is the variance. In Fig. 2*a* the variance of the *B* frequency per plant is plotted against mortality in each of the eight populations. It is immediately apparent from the figure that the higher the mortality the higher the variance. An analysis of variance confirms that the regression is significant ($P = < 0.02$).

We must conclude that selection, under severe stress conditions, *increases* the variety of genotypes, in respect of *B* chromosome number. Assuming the selection to be of a stabilising or directional kind the results, on the face of it, are surprising. We normally expect the range of genotypes, and the variance, to be diminished. In this instance there is, however, a very good reason why we might have expected the variance should increase. It will be observed from figure 1 that the distributions of *B* chromosomes within the populations are distinctly skew with almost invariably a high peak of 0*B*. If the effect of selection is to cause a disproportionately high mortality among 0*B* plants it follows that the variance is likely to increase. Fig. 2*c* shows that the variance is

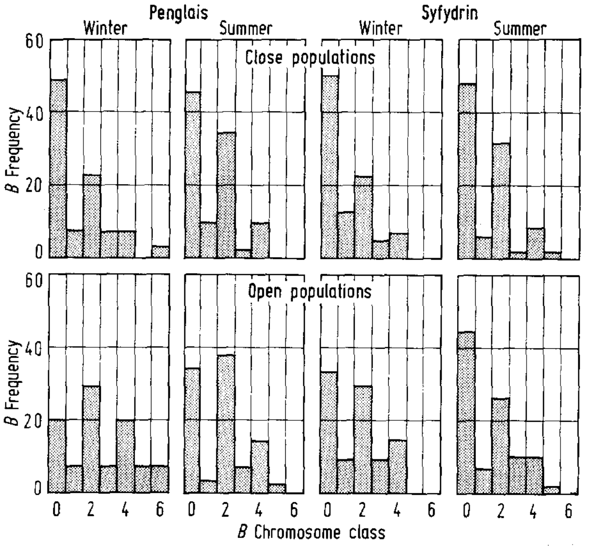

Fig. 1. The frequencies of *B* chromosomes among survivors of seedlings sown in Close and Open populations in winter and summer at Penglais and Syfydrin. The variation between replicates was not significant and the data are pooled in the histograms

indeed positively and highly correlated with the mean *B* frequency of the populations ($P = < 0.01$) and when we plot the mean *B* frequency against mortality (fig. 2*b*) we find a positive, albeit not significant, regression.

There is some indication, therefore, of a shift in the distribution of *B* chromosomes under conditions of stress as reflected by high mortality, such that the proportion of plants with the higher *B* frequencies among the survivors is increased. It needs to be emphasised, however, that the conditions which cause the greatest mortality are not necessarily those which have the greatest influence upon the *B* frequency distribution. A high mortality, after all, does not necessarily imply that there is discrimination between plants with different numbers of *B* chromosomes, as the following analysis of mean *B* frequencies amongst survivors shows.

Table 3. *An analysis of variance of the differences between populations in mean B frequencies per plant*

Item	*N*	Mean Square	Variance Ratio	*P*
Season	1	0.0099	—	
Spacing	1	0.1082	6.70	<0.05
Site	1	0.0970	6.01	<0.05
Season/Spacing	1	0.0230	—	
Season/Site	1	0.0469	—	
Spacing/Site	1	0.0325	—	
2nd Order	1	0.0090	—	
Error	8	0.0161	—	
Total	15			

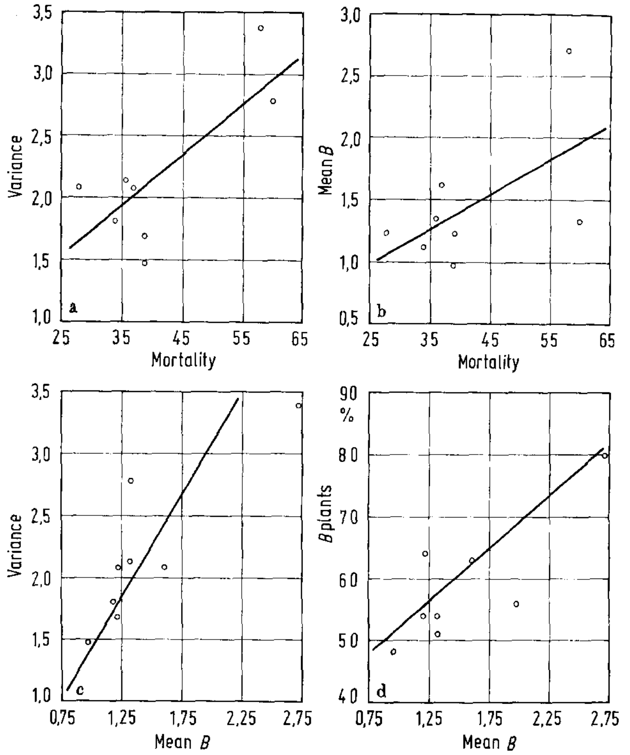

Fig. 2a. The variances in *B* frequency plotted against mortality (in angles) for each of the eight populations.
b. The mean *B* frequency plotted against mortality.
c. The variance plotted against the mean *B* frequency.
d. The proportion of plants carrying *B* chromosomes plotted against the mean *B* frequency

Means. An analysis of variance of differences in the mean number of *B* chromosomes per plant between populations is given in table 3. The analysis shows that the mean *B* frequency among survivors in Open populations (1.7) is significantly higher than in Close populations (1.2). Also, that the mean *B* frequency is higher at Penglais (1.7) than at Syfrydrin (1.2). The analysis clearly confirms that the survival of plants with different numbers of *B* chromosomes varies with the selection imposed by varying environmental conditions. The analysis confirms as well that the shift in *B* frequency is at least partly independent of the extent of mortality. For example the mean *B* frequency is significantly higher, but the mortality lower, in Open than in Close populations. In contrast, at Penglais as compared with Syfrydrin the high *B* frequency is associated with a higher mortality.

Table 2 shows that the variation in mean *B* frequency is caused mainly by alteration in the relative proportion of plants with and without *B* chromosomes. The proportion of 0*B* plants is significantly higher in Close than in Open populations. The proportion of 0*B* plants at Syfrydrin is also higher than at Penglais. The general relationship is illustrated in fig. 2*d*.

It is impossible to specify precisely which factors in the various environments at different sites are instrumental in shifting the mean *B* frequency by selection. The factors are confounded. The effects of weather, for example, are confounded with those of soil fertility and acidity. Even the interpretations of the shift in B frequency associated with the different spacing of plants is by no means unambiguous. On the face of it the relative increase of $0B$ plants in Close populations reflects their superiority in competing with B-carrying plants for limited nutrients or light. An alternative possibility, however, is that $0B$ seedlings are less tolerant of exposure when isolated in Open populations, more likely to survive in the comparatively sheltered conditions in Close populations. This second possibility is by no means unlikely. The 5″ spacing in Close populations is generous and, one would suppose, unlikely to stimulate severe competition for nutrients or light among seedlings.

4. Discussion

Our object was to demonstrate how the distribution of B chromosomes within populations may be altered by selection imposed by a variety of environmental conditions. The experimental results showed that within a single generation a substantial shift in B frequencies was readily achieved, by differential mortality of plants with and without B chromosomes. Much of the variation observed in the incidence of B chromosomes in natural populations is no doubt explained in much the same way, by the effects of selection pressures of various kinds and intensities.

While the results establish with some conviction the varying adaptive properties of B chromosomes in respect of survival in the face of different kinds of selection it would be unwise to conclude that the differences in the distribution and frequency of B chromosomes among natural populations were solely interpretable in these terms. It is now well established that B chromosomes regulate the distribution and frequency of chiasmata at meiosis (Hewitt and John, 1967; Jones and Rees, 1967; Ayonoadu and Rees, 1968). They must consequently influence, as Darlington envisaged (1956), the rate of release of genetic variability within the populations. The adaptive demands, in this respect, of the population as a whole may well be of overriding importance in comparison with the effects of B chromosomes on the differential survival of individual members of the population. Indeed the demands may well be in conflict, as would apply for example where a high recombination achieved by an increasing B frequency were, from the population standpoint, adaptive yet, from the standpoint of the individuals carrying B's, instrumental in severely reducing their prospects of survival. Conflicting demands of a comparable sort are, however, by no means uncommon ingredients of many genetic systems (Darlington and Mather, 1947).

The adaptive role of B chromosomes in relation to their regulatory role over recombination within populations is less amenable to experimental inquiry than is their influence upon the development and survival of individuals. The latter is well established by the present experiment although much needs to be clarified by way of details of their physiological effects.

It is fair to point out at this stage that not every one agrees with the interpretation of B chromosome variation in adaptive terms. Rhoades and Dempsey (1972) consider that B chromosomes are "parasitic" (see also Östergren, 1945), with effects invariably detrimental to fitness, maintained within populations by virtue of their non-Mendelian inheritance which fosters their accumulation within progenies. We dissent from this view on the following grounds. In the first place we consider it dangerous to conclude that because B chromosomes have palpably detrimental effects upon the phenotype they do not, albeit under special circumstances, confer benefit upon individuals or upon populations. After all many genes which confer unquestionably high fitness in certain environments have, equally unquestionably, severely detrimental effects. The sickle-cell gene in humans is one, extreme example. In the second place we would argue that the sole criterion for establishing *adaptive* change in genetic material, be it a gene or a chromosome, is whether the change is attributable directly to a consistent selection imposed upon it — however conjectural the basis of change, in physiological or genetical terms, may be.

On present evidence, admittedly, both points of view, both interpretations are tenable. If, on the other hand, it were convincingly demonstrated that the survival of B carrying individuals was distinctly superior to those without B's in the face of a specific selection pressure then an adaptive rather than a parasitic role would be irrefutable. Some of the evidence we have put forward, under *Variances* in Section 3, points in this direction.

As for the part played by the non-Mendelian mechanism by which the B's are transmitted, we have argued that it is an adaptive device fostering, above all, a preponderance of even numbers of B's among the progenies (Ayonoadu and Rees, 1971; Jones and Rees, 1969).

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Received September 11, 1972

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