

THE GENETIC ORGANISATION OF NATURAL POPULATIONS OF *LOLIUM PERENNE* L.

III. PRODUCTIVITY

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1. INTRODUCTION

EARLIER papers in this series (Hayward and Breese, 1966; Hayward, 1967) have described investigations into the genetic control of seed and seedling characters and inflorescence production in differentiated populations of persistent perennial ryegrass. Although the populations were phenotypically distinct, the results suggested that they had not undergone any great degree of chromosomal differentiation. Thus differences were controlled at the nuclear level by genes showing simple additive action. There was, however, considerable evidence of maternal effects and reciprocal differences which suggested differentiation at the extra-nuclear level. This was interpreted as being, perhaps, a consequence of extended periods of asexual propagation and a corresponding diminished importance of sexual reproduction. The present paper examines the genetic situation with regard to a succession of harvestable yield determinations taken over 18 months, and collates the evidence from all three papers.

2. MATERIAL AND METHODS

The productivity of 6000 individual plants of the diallel cross-families described by Hayward and Breese (1966) and Hayward (1967), was measured by a series of four harvests taken over 18 months. The first harvest measured growth during the first five months of establishment in the field, and took place in September 1963. The second cut followed six weeks later, and assessed autumn growth during the first year. The subsequent two harvests estimated growth in the second year under a conservation system, *i.e.* a conservation (hay) cut at the completion of inflorescence emergence and a recovery (aftermath) cut some 10 weeks later. Yields for the first cuts in both years were measured as the weight, in grammes, of fresh material; for the other cuts, yields were recorded as the weight of oven dried material (8 hours at 80° C.) from a random sample of five plants per plot. Only two of the four replicates were used in the final cut.

3. RESULTS

(i) *Seeding year production*

The mean yields of the establishment cut and autumn growth cut are shown in table 1, and are in the form amenable to the generalised analysis of variance of a diallel table (Hayman, 1954), the results of which are presented in table 2.

As the interactions of the main effects with blocks were homogeneous when compared by a Barlett's test ($\chi^2_{(3)} = 2.45$; $P = 0.3-0.2$; and $\chi^2_{(3)} = 3.9$; $P = 0.3-0.2$) the pooled error variance was used for examining the main items. For both these cuts the highly significant *a* item would indicate considerable additive variation over populations. In contrast, the *b* mean square measuring average dominance effects is only significant for the second cut.

TABLE 1
*Mean yield gm. per plant of establishment cut (fresh weight)
and autumn growth cut (dry weight)*

♀	♂	1	2	3	4	5	6	7	8	9	10
1	343	308	347	348	360	403	427	394	327	349	
	25	28	42	35	31	42	47	36	37	42	
2	360	495	377	351	245	478	451	396	329	434	
	29	31	49	29	24	37	30	38	30	33	
3	295	382	364	377	339	378	436	342	336	418	
	29	27	30	23	28	26	31	38	25	30	
4	390	352	423	432	376	390	396	466	398	354	
	31	34	40	38	40	24	30	36	33	33	
5	404	432	378	368	359	358	358	384	278	424	
	34	34	30	29	28	32	32	39	23	26	
6	321	279	387	363	353	374	357	322	275	318	
	33	32	39	28	30	32	28	30	22	24	
7	376	337	359	394	411	316	458	395	274	304	
	26	34	34	28	36	29	33	34	26	31	
8	345	393	366	312	266	317	420	417	350	401	
	30	28	34	28	27	37	43	30	29	36	
9	326	287	293	255	257	171	336	272	235	181	
	33	33	18	18	20	14	33	31	21	16	
10	433	474	421	431	443	427	470	444	420	435	
	41	39	30	41	36	35	39	20	34	30	

TABLE 2
Analysis of variance of establishment and autumn growth cuts

Item	N	Establishment cut (mean square)	Autumn growth cut (mean square)
<i>a</i>	9	68,709***	11,026***
<i>b</i>	45	5,366	2,450
<i>c</i>	9	37,067***	8,468**
<i>d</i>	36	8,704*	2,305
Blocks	3	187,496***	8,844
Error	297	4,829	1,640

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

The two remaining items, *c* measuring average maternal effects and *d* specific reciprocal interaction, are significant in each case revealing the participation of a maternal component in the control of these two characters. Moreover, in both analyses the mean squares measuring general combining ability or additivity are no greater than the average maternal component

and hence may be considered as a reflection of this latter component (Wearden, 1964). Similarly, since the *b* item in the second analysis is non-significant when tested against the corresponding *d* mean square, there is in neither case any real evidence of specific combining ability, or dominance/epistasis effects.

A further indication of the nature of the reciprocal effects can be obtained from application of the analysis developed by Durrant (1965) for the separation of reciprocal effects into α and β inheritance. The former has a constant effect on all the members of an array, whilst the latter leads to a change in dominance relationships due to different male and female gametic environments. A comparison of the *c* item of the main part of the analysis against the *d* mean square yields evidence on these points. For both cuts the *c* item is significant and hence α inheritance is mainly responsible for this effect.

The direction of the reciprocal effect, as obtained from the relationship of $\Sigma ap'$ (see Durrant, *loc. cit.*) is positive for both cuts (+197 for the establishment cut and +207 for the second cut). The mode of action does not however reinforce any basic genetic control, because the correlation of the *a'* values with the corresponding parental mean is non-significant ($r = 0.43$ for the first cut and 0.31 for the second). This is not unexpected, however, in view of the fact that the additive mean square is no greater than the reciprocal item (table 2). The correlation of the *a'* values over the two cuts is positive and significant ($r = 0.8$, $P = 0.01-0.001$), showing that the pattern of control is consistent at this stage of development. It is thus concluded that productivity at the establishment phase in these populations is very decidedly maternally controlled.

(ii) First harvest year production

The results of the total yield produced during the first harvest year measured over the hay and aftermath cut are presented in table 3, with the corresponding analysis of variance in table 4. With the exception of the

TABLE 3
Total yield produced during the first harvest year (mean per plant)

♀	♂ 1	2	3	4	5	6	7	8	9	10
1	113	114	120	110	102	118	125	116	106	130
2	105	118	117	91	78	129	117	112	88	122
3	101	115	128	120	105	113	138	109	103	130
4	122	122	121	125	119	110	115	135	113	100
5	102	122	118	100	98	93	105	106	57	105
6	109	85	97	107	99	114	96	95	85	97
7	139	106	116	122	109	109	137	113	91	89
8	106	108	110	92	92	102	119	110	80	108
9	94	91	84	74	89	54	100	96	49	68
10	128	131	118	123	112	120	122	123	130	122

b item the main effects are all highly significant when compared with the mean squares for the interaction of the main effects with cuts. The interaction items were themselves tested against the overall error mean square. Of these latter items only the additive \times cuts interaction is significant. As may be expected, the difference between the hay and aftermath cuts, making up this total production in the first harvest year, is highly significant.

Here again the most striking feature of the analysis is the importance of the reciprocal items. Unlike the previous two cuts, however, the additive mean square is still significant when tested against the average maternal mean square, thus revealing the presence of a relatively simple system of variation in addition to the reciprocal component. The average reciprocal mean square c for this total production is no greater than the specific mean square d . The reciprocal effects in this analysis would thus appear to consist of effects other than the straightforward α type of inheritance. This may be examined by application of the joint analysis for α and β inheritance (see Durrant, *loc. cit.*), the results of which are presented in table 5.

TABLE 4

Analysis of variance of total production during the first harvest year

Item	N	Sum of squares	Mean square
a	9	1,818,063	202,007***
b	45	415,592	9,235
c	9	393,716	43,746***
d	36	767,136	21,309***
Cuts	1	1,070,404	1,070,404***
$c \times a$	9	212,086	23,565
$c \times b$	45	280,709	6,238
$c \times c$	9	62,734	6,970
$c \times d$	36	138,519	3,848
Pooled error	600	3,555,488	5,925

*** = $P < 0.001$.

TABLE 5

Joint analysis of reciprocal differences

Item	N	Sum of squares	Mean square
Alpha plus Beta	17	5,502,383	323,669*
a'	8	1,920,846	240,102
b'	8	3,450,167	431,270*
b	1	87,695	87,695
Residual	28	3,784,439	135,158
Total	45	9,286,822	—
		Sum of products $\times 2$	
b'/a'	—	612,752	—
b'/b	—	-527,936	—

* = $P < 0.05-0.01$.

Whilst the joint item for α and β is significant, of its components only b' is significant, indicating that the reciprocal effect is mainly due to β inheritance. There would appear to be no overall β effect because \bar{b} is non-significant. The b' values range from -0.4 for population 6, to $+0.5$ for population 5. In crosses with parent 6, therefore, it is the male parent which is mainly responsible for the characteristics of the progeny, whilst for crosses involving population 5, it is the female parent which is operative. Populations 4, 6, 9 and 10 fall into the first group, *i.e.* exhibiting male

dominance, whilst the remaining 1, 2, 3, 5, 7 and 8 form the female dominant group.

(iii) *Seedling characters and adult plant productivity*

The relationship between seedling characters and the productivity as spaced plants in the field may be examined from two aspects. Firstly the direct developmental relationships between such characters, and secondly the pattern of genetic control over these two sets of characters.

A series of correlation coefficients was calculated on a family mean basis between selected seedling measurements and the three main productivity characters considered here (see table 6). Of the two seedling characters,

TABLE 6
Correlation of characters

	2	3	4	5	6	7
1	0.11	0.14	0.12	0.15	0.11	-0.20*
	2	0.60***	0.37***	0.62***	0.27**	-0.41***
		3	0.57***	0.82***	0.25**	-0.34**
			4	0.57***	-0.04	-0.26*
				5	0.28**	-0.33**
					6	-0.25*

1. Tiller number.
2. Length fifth leaf.
3. Establishment cut.
4. Autumn growth cut.
5. Total yield first harvest year.
6. Number of inflorescences per plant.
7. Date of inflorescence emergence.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

leaf length and tiller number, only the former is correlated with productivity in the field, being positive and significant for each production phase. Hence, for this series of populations, potentially high producing families may be identified at the seedling stage according to the length of the fifth leaf (see Cooper and Edwards, 1961). Similarly, the correlations between the three cuts are all positive and significant.

With regard to the three production phases measured here, one may consider the possibility of influence by other developmental processes. For instance, the yield at the establishment cut is positively correlated with the number of inflorescences produced during the preceeding summer months (see Hayward, 1967), whilst production during the main harvest year is negatively correlated with the date of inflorescence emergence for that year; *i.e.* the higher yielding plants are those which flower early in the season.

The influence of the date of flowering on the hay cut component of production in the first harvest year may be examined by an analysis of covariance as applied to the Hayman analysis (table 7). After correcting the mean squares for the regression, production at the hay cut is predominantly under the control of the maternal component, the additive *a* item being non-significant when tested against this *c* item. This latter item is significant against the specific reciprocal mean square *d*.

This would indicate that although a developmental relationship between characters may be apparent, it does not necessarily imply a common genetic control.

The changing pattern of genetic control during the growth and development of these populations may be assessed from the relative proportions of the various components of the Hayman analysis of variance as applied throughout this series of investigations. These proportions were calculated according to the expectations of the mean squares from a combined model of the maternal and reciprocal models as described by Cockerham (1963). This has been applied to the results from the time of germination (see Hayward and Breese, 1966) up to the first harvest year production data; a total span of approximately 28 months. The various components are presented in the form of a histogram in fig. 1.

TABLE 7

Analysis of variance and covariance for date of inflorescence emergence and hay production cut

Item	N	Ear emergence M.S.	Hay cut M.S.	Corrected hay cut M.S.
<i>a</i>	9	208***	80,395***	73,832***
<i>b</i>	45	11***	8,314*	3,654
<i>c</i>	9	23***	32,003***	39,754***
<i>d</i>	36	10***	13,095***	13,178***
<i>B</i>	3	2	36,923***	32,252***
Error	297	3	4,388	4,153

* = $P < 0.05$; *** = $P < 0.001$.

It can be seen that of the several genetic components, the additive effect is by far the most important during the early seedling phases. Later in development, *e.g.* at the time of transplanting into the field during the seeding year, the maternal and reciprocal controls begin to exert their influence. Indeed, for the number of inflorescences produced during the seeding year the only effect present is that attributable to the specific reciprocal component.

For the later phases of vegetative production during the same year, the major part of the variation may be accounted for by the average maternal component, whilst during the mature plant phases of the first harvest year production, the specific reciprocal effect is of overriding importance.

Whatever the precise nature of these reciprocal effects might be, it is quite clear from the pattern of influence that they cannot be attributed to gross characteristics of the seed, such as weight or size, which would show most markedly during the seedling phase. Nor is there evidence that they can be associated with differential self-fertilities among the normally highly self-sterile plants (see Hayward and Breese, 1966) during the process of crossing without emasculation. The evidence points again to the more subtle and permanent effects which would be expected from differences in the extra-nuclear portion of the female gamete (the plasmon).

4. DISCUSSION OF RESULTS

For all cuts taken during the seeding and first harvest year there are significant differences between the populations for production, whether measured as fresh or dry weight. Two salient points emerge from the genetic

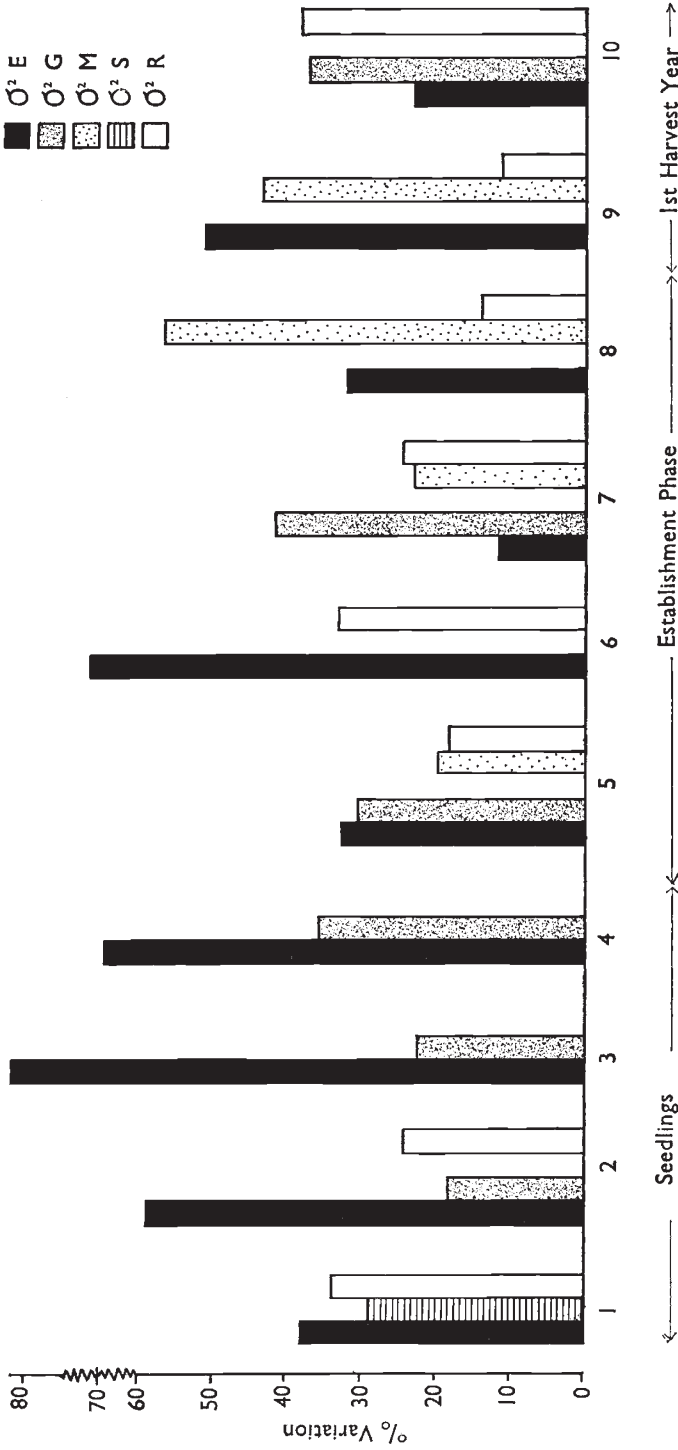


FIG. 1.—Components of variation during development from the seedling to the adult plant.

- 1. = Per cent. germination
- 2. = Leaf number
- 3. = Tiller number
- 4. = Length of 5th leaf
- 5. = Number plants flowering
- 6. = Number flowers produced
- 7. = Establishment cut
- 8. = Autumn cut
- 9. = Date inflorescence emergence
- 10. = Total production

analysis. First, only part of the heritable differences can be attributed to nuclear genes and these exhibit only simple additivity in action. The hybrids show no evidence of the dominance or epistasis patterns of the heterotic expression, or physiological imbalance, which classical studies with *Drosophila*, maize, and other sexually reproduced organisms lead us to expect in crosses between differentiated races or populations. Thus, although there appears to have been some selection at the nuclear level it has not involved re-organisation and co-adaptation of the nuclear genes in a way that we now understand to be necessary if the differences are to be preserved over sexual generations (Breese and Mather, 1960). Indeed the situation contrasts markedly with that reported by Breese (1960) for ryegrass material deliberately selected over seed generations, where differentiation was associated with relatively high levels of dominance, and bred varieties were distinguished by an accumulation of favourable dominant genes. On genetic grounds, therefore, it would appear that differentiation in the persistent ryegrass populations presently under study has been achieved in the absence of any high frequency of sexual reproduction. Comparable results have been provided by Fejer (1958) for genotypes originating from old permanent pastures in New Zealand. In this sense these ecotypes cannot be regarded as true Mendelian populations.

Secondly, a part, and often an important part, of the differences is matrilinear in inheritance. If we consider all phases in the development of the plant from the seedling to the mature stage, an interesting pattern of extra-nuclear control is presented (see fig. 1). At the seedling stage it is of small significance, but becomes increasingly important in the adult plant. The type of action also changes; thus in the establishment cuts there is a constant maternal effect, whilst in the subsequent year there is more evidence of an interaction between the plasmon and the nuclear complement. Even in these latter stages, however, if the effect of the date of inflorescence emergence as a contributory factor is removed by covariance analysis, then the remaining yield factors (which perhaps reflect more specifically such vegetative features as tiller number and size) are again seen to be predominantly under the control of a constant maternal plasmon effect. It would appear, therefore, that differentiation which may be ascribed to changes in the plasmon is most pronounced for the vegetative features of the adult plant, but for these as well as for the inflorescence features the importance of the plasmon/nucleus interactions cannot be discounted.

Population structure and reproductive biology

Throughout these investigations we have been concerned to relate genetic structure to ecological background in the belief that we may so achieve a better understanding of reproductive biology within the species. At this point it is opportune to recount genetic and ecological features and see how closely they relate one to another.

The ryegrass populations under investigation are distinguished by the fact that they derive from permanent pastures with no known history of deliberate reseeding and where management discouraged the formation of seed heads, or establishment from any seed which may occasionally be set. This is not to say that some seedling establishment did not take place with an unknown, but presumably low frequency. Nevertheless, survival must have depended largely on an ability for asexual rather than sexual repro-

duction. Under these conditions, as Langer (1956) has pointed out, the organisational unit of the grass plant is the individual tiller which, although itself having a life-span of but a few months, can generate new tillers asexually and thereby confer on the plant a virtually unlimited existence. By these means individual genotypes achieve the life form of the long-lived perennial with characteristic stability at the chromosome level (Darlington, 1956), but they only do so through the medium of a dynamic population of ephemeral tillers. It is against this general biological background that we have to consider the extent to which, and the means whereby, population differentiation is achieved.

That phenotypic differentiation had occurred was very evident in the experiments of Breese and Charles (1962). Indeed, the populations showed a remarkable distinctness for a number of quantitative characters some of which could be related to differing managements and edaphic factors. Although individuals within a population were comparatively uniform for certain characters, there was nothing to suggest that they were simply samples of one widespread clone as Harberd (1962) has found in some populations of *Festuca ovina*. More recently, selfing studies have lent support to the supposition that each individual had a unique genotype. Thus phenotypic uniformity does not bespeak genotypic similarity.

The crossing experiments, described in this series of papers, first and foremost aimed to determine to what extent nuclear differentiation in the chromosomal genes had accompanied phenotypic differentiation. In so far as phenotypic differences between populations were at all controlled by nuclear genes, the uncomplicated type of gene action did not indicate that the genes had been so integrated and organised as to suggest that differences had been selected over many sexual generations. Furthermore, seed and seedling studies indicated a general degradation of the sexual process and provided evidence of relaxed selection pressures for characters associated with the seedling phase. Thus genetical experimentation supports ecological observation in discounting sexual reproduction during differentiation.

We now have to consider the persistent ryegrass ecotype as being a collection of individuals which owe little to sexual intercompatibility or, indeed, to sexual efficiency for their immediate success. The unifying feature is apparently a common phenotypic expression which allows them to compete on equal terms with each other, and successfully against other sward constituents. How then is this situation achieved during the evolution of a sward? Part of the answer is supplied by field experiments carried out by Charles (1961, 1964). During the first 12 weeks after sowing with standard seed rates some 75 per cent. of all seedlings were eliminated from the sward, and after 9 months this figure rose to 90 per cent.; coincidentally the between plant variability is reduced. At this period, therefore, selection pressure is intense and the treatment imposed is critical in determining the predominant type of surviving plant. Management will continue to modify the genotypic constitution after this period, although elimination will be at a diminished rate. The frequency of elimination is difficult to estimate since each genotype is now represented by a clone of independent tiller units. It is clear from these experiments, however, that selection pressures can fairly quickly restrict the number of genotypes to those with similar phenotypic potential which are thereafter perpetuated by asexual propagation. It is equally clear that eventually selection must operate through

independent tiller units of each clone so that any variability between tillers must affect selective processes and could endow the genotype with a phenotypic plasticity. Thus in considering genotypic equilibria in swards and their stabilities, we not only have to consider selective forces but also any special phenotypic flexibility achieved through tiller variability during vegetative propagation.

To investigate this latter possibility, selection for high and low rates of tillering (asexual reproduction) was initiated within clones of *L. perenne*, the results of which have been reported by Breese *et al.* (1965). Response was obtained in some of the clones, particularly those which derived from persistent pastures; this was interpreted as being due to changes in the plasmon. Although this evidence needs support and clarification from further investigations, it is enough to suggest that certain genotypes of *L. perenne* do indeed have the capacity for adaptive change during asexual propagation through the medium of extra-nuclear cell components.

This leads us to consider, perhaps, the most salient features of the present experiments, namely the high degree of maternal control and reciprocal differences revealed by the analyses. If, as appears most likely, these must be referred to differences between the plasmons of populations, then we must assume that the plasmon has played a major role in the adaptation of the populations. Thus circumstantially, the evidence, taken as a whole, indicates that the plasmon can provide adaptive variability during asexual reproduction, and can lend a degree of permanence to adaptive change which operates not only over the vegetative life, but also over sexual reproduction.

5. THE ROLE OF EXTRA-NUCLEAR VARIABILITY IN POPULATION DIFFERENTIATION

The importance of the plasmon in controlling variation in micro-organisms is now well established and has been reviewed by Jinks (1964). Differentiation between races and between species, which is based at least in part on changes in the plasmon, is not uncommon in higher plants and has been reported in a number of genera. Oehlkers (1964) has shown that speciation in *Streptocarpus* has been accompanied by changes in the plasmon, while Michaelis (1964) found that *Epilobium hirsutum* was differentiated into a number of distinct plasmon types which could be associated with different geographical regions. The recognition of these plasmon differences is derived from a study of the developmental patterns observed between reciprocal F_1 's and back-crosses involving widely dispersed races or species. Specific combinations of nucleus and cytoplasm failed to develop normally, failure being manifested as gross physiological upsets which usually also involved sterility. As a consequence, the importance of these plasmon differences has often been interpreted, at least from the evolutionary point of view, solely in terms of the ability to produce more or less effective crossing barriers. Perhaps this is so because, in the study of such widely differentiated material, the effects of the cytoplasm can only be seen in terms of a massive imbalance in the presence of a foreign nucleus with a consequent failure in normal development. Certainly this emphasises that cell processes can be equally subjected to chromosomal and plasmon control. But it fails to tell us whether the plasmon is changed passively through the agency of a

continually modified nucleus, or whether it has itself a dynamic role in response to environmental change which is of an adaptive nature. If the latter, does it operate in partnership with a changing nucleus, or can it on occasion take over as the medium of responsive change?

In considering these points it is perhaps significant that in most genera, where plasmon differentiation has been reported, the plants can be propagated asexually by vegetative means as well as sexually by seed. This is true of *Epilobium* and *Streptocarpus*, while in the grasses, of course, the ability to regenerate vegetatively is the phenomenon which most fits them to their role as herbage plants. The somatic selection experiments of Breese *et al.*, referred to earlier, point to this prolonged period of vegetative propagation as being critical in determining the importance of the plasmon, as indeed it is in asexual fungi (Jinks, 1964). It was noteworthy that no response was obtained to selection within clones of the shorter-lived ryegrasses which are frequently perpetuated by seed. The results argue that during continual asexual reproduction when, barring infrequent mutation, chromosomal genes are constant, the control of adaptive response may be transferred from nuclear genes to plasmon constituents. However, it must be emphasised that responses to somatic selection were genotypically dependent, so that effective selection for plasmon differentiation initially involves selection of an appropriate nuclear constitution. This interdependence of nucleus and plasmon is further emphasised by the high frequency of nuclear/plasmon interactions in the crossing experiments at present under discussion; but here again, most significantly, the balance (interaction) of the nucleus as a whole with the plasmon is more important than the balance (interaction) of chromosomal genes within the nucleus, thus indicating the dominant role of the plasmon.

At this stage in our investigations the results from the somatic selection experiments are no more than an indication of how the type of plasmon differentiation we see in the interpopulation crosses could have arisen; we have yet to demonstrate that artificially induced differences can be perpetuated over sexual cycles. Nevertheless, the overall genetic picture justifies the conclusion that alternating cycles of asexual and sexual reproduction involve the plasmon in a dynamic role and force a special co-adaptation of nucleus and plasmon. Under such a reproductive system it is easy to conjecture that speciation will depend as much on plasmon differentiation as on nuclear differentiation.

6. SUMMARY

The present paper examines the results of an investigation of the genetic control of productivity in a diallel cross of ten persistent ryegrass populations from the Monmouthshire Moors area of South-East Wales. The analyses indicate that ecotypic differentiation involves not only the nuclear genetic constitution but also an extra-nuclear (plasmon) component. These results, together with those of the previous two papers in this series, are examined in relation to the reproductive biology of the species. They show that genetical principles and concepts, deriving from classical studies with laboratory organisms, have to be profoundly modified in considering species with alternative modes of reproduction. Although the plasmon appears to

assume an important role only in the more persistent populations, it nevertheless provides an added dimension in the control of heritable variation and must thereby confer considerable flexibility on the species at large. As discussed by Breese (1966), this phenomenon could well explain how the extreme adaptability of the *Lolium* genus has been achieved over a wide range of conditions without recourse to polyploidy, the erection of mating barriers, or indeed, to any extensive nuclear differentiation.

7. REFERENCES

- BREESE, E. L. 1960. The genetic assessment of breeding material. *Proc. VIII Int. Grassld Congr.*, 45-49.
- BREESE, E. L. 1966. Reproduction in ryegrass. Paper presented to conference on "Reproductive Biology and Taxonomy of Vascular Plants", B.S.B.I.
- BREESE, E. L., AND CHARLES, A. H. 1962. Population studies in ryegrass. *Rep. Welsh Pl. Breed. Stn.*, 1959, 30-34.
- BREESE, E. L., HAYWARD, M. D., AND THOMAS, A. C. 1965. Somatic selection in perennial ryegrass. *Heredity*, 20, 367-379.
- BREESE, E. L., AND MATHER, K. 1960. The organisation of polygenic activity within a chromosome in *Drosophila*. II. Viability. *Heredity*, 14, 375-401.
- CHARLES, A. H. 1961. Differential survival of cultivars of *Lolium*, *Dactylis* and *Phleum*. *J. Brit. Grassld Soc.*, 16, 69-75.
- CHARLES, A. H. 1964. Differential survival of plant types in swards. *J. Brit. Grassld Soc.*, 19, 198-204.
- COCKERHAM, C. C. 1961. Estimation of genetic variances. *Statistical Genetics and Plant Breeding*, pp. 53-94. Ed. W. D. Hanson and H. F. Robinson. N.A.S.N.R.C. Washington D.C., 1963.
- COOPER, J. P., AND EDWARDS, K. J. R. 1961. The genetic control of leaf development in *Lolium*. I. Assessment of genetic variation. *Heredity*, 16, 63-82.
- DARLINGTON, C. D. 1956. *Chromosome Botany*. George Allen and Unwin, London.
- DURRANT, A. 1965. Analysis of reciprocal differences in diallel crosses. *Heredity*, 20, 573-608.
- FEJER, S. O. 1958. Genetic and environmental components of the productivity of Perennial ryegrass (*Lolium perenne* L.). *N.Z. J. agric. Res.*, 1, 86-103.
- HARBERD, D. J. 1962. Some observations on natural clones in *Festuca ovina*. *New Phytol.*, 61, 85-100.
- HAYMAN, B. I. 1954. The analysis of variance of diallel tables. *Biometrics*, 10, 235-244.
- HAYWARD, M. D. 1967. The genetic organisation of natural populations of *Lolium perenne*. II. Inflorescence production. *Heredity*, 22, 105-116.
- HAYWARD, M. D., AND BREESE, E. L. 1966. The genetic organisation of natural populations of *Lolium perenne*. I. Seed and seedling characters. *Heredity*, 21, 287-304.
- JINKS, J. L. 1964. *Extra chromosomal inheritance*. Prentice-Hall, Inc., New Jersey. 176 pp.
- LANGER, R. H. M. 1956. Growth and nutrition of Timothy (*Phleum pratense*). (i) The life history of individual tillers. *Ann. appl. Biol.*, 44, 166-187.
- MICHAELIS, P. 1954. Cytoplasmic inheritance in *Epilobium* and its theoretical significance. *Advan. Genet.*, 6, 287-401.
- OEHLKERS, F. 1964. Cytoplasmic inheritance in the genus *Streptocarpus* Lindley. *Advan. Genet.*, 12, 329-370.
- WEARDEN, S. 1964. Alternative analyses of the diallel cross. *Heredity*, 19, 669-680.