VARIATION AND APOMIXIS IN *HETEROPOGON CONTORTUS*, GRAMINEAE

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SUMMARY

An extensive assessment of the patterns of variation found in the polymorphic species *Heteropogon contortus* (L.) Beauv. ex Roem. and Schult. has indicated that the variation in frequency and distribution of the tubercle-based bristles of the pedicellate spikelets, upon which Hackel's subspecific classification is based, is not meaningful.

Two scales of variation are recognised:

A primary scale of variation which accounts for a general pattern of morphology associated with broad geographic distribution. This pattern is closely correlated with a polyploid series.

A secondary scale of variation concerns patterns of phenologic variation within geographic regions and this seems largely associated with environmental variations. Apomixis is suggested as an important process in developing and maintaining the pattern of variation within this scale.

It is considered that occasional reversion to sexuality is responsible for generating the variability which is observed in populations of *H. contortus*. It is suggested that only occasional sexual forms need arise, which, by establishing in new niches during times of abnormal environmental change or migration of the species into new areas, would generate great arrays of new biotypes, both apomictic and sexual. So the cycle would continue until a new equilibrium established itself.

INTRODUCTION

The grass *Heteropogon contortus* (L.) Beauv. ex Roem. and Schult. of the Andropogoneae is widely distributed throughout the drier tropics and subtropics of the world. As such it covers a multitude of climatic and edaphic variations and hence it is not unexpected that considerable intraspecific variation has been recorded.

Past considerations of intraspecific variation have been limited to morphological variation which, though considerable (Häckel,

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1889) and subject to much systematic scrutiny, appears not to be related in any meaningful way to ecological or phytogeographic factors. However, more recently a new dimension has been added by Tothill (1966) drawing attention to the vast reservoir of phenological variation in populations of the Australian subtropics and (Tothill, unpublished) Africa.

This paper attempts to reconcile the existence of great variability in *H. contortus* with the apparent block to the generation of variability which the reproductive system of obligate, aposporous apomixis (Emery and Brown, 1958) suggests.

1. VARIABILITY IN "HETEROPOGON CONTORTUS"

a) *Morphological*

Much of the early taxonomic literature dealing with *H. contortus* (Häckel, 1889; Domin, 1915; Burns *et. al.*, 1925; Blatter and McCann, 1934); draws attention to the polymorphic nature of the species. However, both Hooker (1897) and Stapf (1934) consider the variation to be too inconstant for meaningful discrimination. Brown and Emery (1958) consider the species to consist of a relatively uniform series of populations, but this is perhaps the result of the limited amount of material available to them.

Hackel's (1889) subspecific classification into two varieties and five sub-varieties is based primarily on the number and position of the tubercle-based bristles or hairs on the outer glumes of the pedicellate (male) spikelets of the inflorescence. That the variation in bristle number appears not to be related to any environmental or geographic pattern is apparent in Table 1, in which the character is scored from the collections of the U.S. National Herbarium of the Royal Botanic Garden, Kew, and the Botanic Museum, Berlin. The exclusive occurrence of glabrous forms in Italy is the only exception and might be explained on the basis of it being an atypical extraterritorial distribution in which the species is not truly indigenous. It is noteworthy also from this table that the morphological variation seems to cut across the different ploidy levels outlined in Table 2.

Thus is may be assumed that the variation in glume hairiness either predates polyploidy or has arisen independently on numerous occasions since polyploidy became manifest. If this latter has been the case is has appeared in spite of the limitations imposed by apomixis. since polyploidy presumably occurred subsequent to apomixis.

In contrast to the morphological variability associated with inflorescence hairiness, there is an overall pattern of morphological variation which is difficult to define and is expressed more strongly

TABLE 1

The degree of hairiness of the outer glume of the pedicellate spikelet in *Heteropogon contortus* and its geographic distribution.

	Frequency of various degrees of hairiness of the pedicellate spikelet				
Geographic origin	Glabrous	Slightly hispid	Hispid	Very hispid	Total Nº
Australia	12	12	15	9	48
Oceanía					
Hawaii	3	5	3	2	13
Fiji			1	7	8
Tonga				2	2
New Caledonia	2	3	2		7
New Guinea		2	2		4
Hong Kong			1		1
Marianas Is.		1	10	5	16
Laccadive Is.			1		1
Asia					
India	3	1	11	5	20
Ceylon	1		1		2
Indonesia	1	2	2	5	10
China	12	4	10	4	30
Siam				1	1
Burma			1		1
Assam		1			1
Malaya			1		1
Africa					
Congo			3	3	6
Tanzania				3	3
Uganda			2	1	3
Kenya	1		1	1	3
Malawi				2	2
Liberia				1	1
Madagascar			1		1
South Africa	6	1	1	1	9
America					
Mexico		11	9	3	23
Venezuela		1	2		3
Columbia		1			1
Bolivia		1	5		6
Peru			5		5
Ecuador	1	1	2		4
Guyana		1	2		3
Brazil	3	3	1	1	8
Paraguay	5	2	1		8
Argentina		1	2	2	5
Mediterranean					
Italy	17				17.

TABLE 2

The geographic distribution of ploidy level in *Heteropogon contortus*

Geographic origin.	2n	4n	6n	8n
Australia		4‡, 9		
Oceanía				
Hawaii		9		
Asia				
India	1*	4, 5, 8, 9	4, 5	
Indonesia		8		
Africa				
Congo		8		
Tanzania		4		
Kenya		8	9	
Madagascar		4, 8		
Rhodesia		2‡	9	
South Africa			6; 9	
América				
Texas			3, 7, 8, 9	7
México			7, 8	

* 1. Darlington and Janaki Ammal, 1946; 2. Moffett and Hurcombe, 1949; 3. Brown, 1951; 4. Celarier and Harlan, 1953; 5. Mehra, 1954; 6. de Wet and Anderson, 1956; 7. Gould, 1956; 8. Emery and Brown, 1957; 9. Tothill, unpublished.

† Aneuploid forms 2n = 44.

in living than in herbarium material. Table 3 is an attempt to summarize the variation between collections of *H. contortus* from an extensive geographical range when they were grown under cultivation in a uniform grass garden at Lawes in south-east Queensland. The defining criteria used in this table are not adequate to differentiate morphological forms in all cases so that a "general type" designation is also given. Where populations are mixtures of two general types two designations are shown.

From Table 3 it is obvious there is a fairly well defined pattern of variation which is geographically determined, cutting across the apparently random morphological variation associated with hairiness of the inflorescence or the more specific variation associated with flowering behaviour which is discussed later. It is suggested that

TABLE 3

General morphology of a geographic range of *Heteropogon contortus* collections

Geographic origin	Leaf width	Leaf distribution	Culm robustness	Inflorescence disposition	General type	Nº of. Accessions
Australia tropical	broad	B + C *	coarse	A †	I	> 20
sub-tropical	medium to broad	B + C	medium to coarse	A	I, II	> 20
Oceanía						
Hawaii	broad	B + C	coarse	A	I	2
Fiji	broad	B + C	coarse	A	I	1
New Caledonia	broad	B + C	coarse	A	I	1
Philippines	broad	B + C	coarse	A	I	1
New Guinea	broad	B + C	coarse	A	I	1
Hong Kong	broad	B > C	coarse	A	I	1
Asia						
India	medium	B > C	medium	B	III	3
Ceylon	medium	B > C	fine	B	III	3
Africa						
West	broad	B + C	coarse	A	I	5
East	medium to broad	B + C	medium to coarse	A, B	II, IV	10
Central	medium	B > C	fine	B	IV	5
South	meduim to fine	B > C	fine	B	IV, V	17
America						
Sth U.S.A.	broad	B + C	coarse	A	VI	5
Mexico	broad	B + C	coarse	A	VI	5

* B = Basal
C = Cauline

† A Inflorescence in or only slightly above the foliage.
B Inflorescence borne above the foliage.

this pattern be called the Primary Scale of Variability. Polyploidy has undoubtedly played an important part in stimulating adaptive radiation through greater phenotype plasticity, hence the general relationship which exists between ploidy level and geographic distribution outlined in Table 2. As a natural consequence of this geographic spread, differing patterns of selection pressure would favour morphological divergences which could eventually become characteristic of a particular migrating line. These geographic types perhaps approximate Turesson's (1953) agamospecies.

b) *Phenological*

Tothill (1966) has shown great variation in flowering behaviour in *H. contortus* and has associated this with differing patterns of rainfall distribution for a given region. The actual control of the phenological response of individual lines appeared largely to reside in day length responsiveness. In the regions of reliable rainfall distribution in tropical Australia the populations were genetically more uniform in their flowering behaviour than in subtropical regions, where both the rainfall distribution and flowering time varied considerably. Thus there was both inter —and intro— population variability. More recently a similar though more extensive pattern of variation has been shown for Africa (Tothill, unpublished).

This type of variability is obviously of adaptive significance, and, as such, resembles ecotypic fragmentation of sexual species. According to Heslop-Harrison (1961) this type of ădaptation requires a high level of recombination, such as sexuality provides, but which could also be ensured by a "partial apomixis" system such as that suggested by Clausen (1954). According to Evans (1964) such a system provides "sufficient reproducibility to perpetuate successful gene combinations, and sufficient variability to adapt to changing environments". Thus the biotypes which make up the population are analogous to Turesson's (1943) agamotypes.

The variability associated with phenological variation has been termed the secondary scale of variability. It is unrelated to the primary scale discussed previously, although it forms an undefined. component of the variation in that scale.

It is within the framework of this secondary scale that apomixis plays an important role. Tothill (1966) has suggested that in a fluctuating environment, apomixis, by ensuring the exact replication of individual genotypes, imparts the greatest reproductive efficiency on the most adapted biotypes at any one time. Perenniality ensures that these types are not lost from the system during periods when they are less well adapted than others.

In a population of extreme biotype variability, e.g. in south east Queensland, the system must be almost self-perpetuating without further generation of new biotypes. Only in the case of a new environmental departures or in the migration of the species into new ecological or geographic niches may it be necessary for new variation to be generated by recombination or mutation. Bisset (1962) has described a recent and continuing spread of *H. contortus* and it could well be in this context that new biotypes are finding niches for adaptation.

Table 4 outlines how this type of variation is related to the local distribution of the species.

TABLE 4

Geographic distribution of flowering characteristics for *Heteropogon contortus* as determined by their behaviour in a uniform grass garden at Lawes, Queensland (27.5°S latitude).

Geographic origin.		Early*	Mid Season	Late	Accessions No. of
Australia	tropical			X	> 20
	sub-tropical	X	X	X	> 20
Oceanía	Hawaii			X	2
	Fiji			X	1
	New Caledonia			X	1
	Philippines			X	1
	New Guinea			X	1
	Hong Kong			X	1
Asia	India	X	X		3
	Ceylon			X	3
Africa	West			X	5
	East			X	10
	Central		X	X	5
	South	X	X	X	17
América	Sth U.S.A.		X		5
	México		X	X	5

* These criteria are based on whether the types flower early, midway or late in the wet season.

It is evident that there is some geographic basis for the extent of phenologic variability, since the subtropical populations for both Australia and Africa are highly variable while tropical population tend to be uniform. Thus, if the centre of origin of the species is in southern Asia, as suggested by Emery and Brown (1958), then these southern subtropical populations must have arisen from material which had passed through a tropical bottleneck in the course of migration where, presumably, much of the potential variabiliy was not expressed, since it was not selectively advantageous. It is thus reasonable to assume that the extreme variability of these peripheral, subtropical populations has been generated *in situ*.

2. THE ROLE OF APOMIXIS IN THE EVOLUTION OF VARIATION IN "H. CONTORTUS"

Heslop-Harrison (1964), in reviewing the matter of ecological adaptation in apomictic complexes, comments that "obligate apomixis, by suspending entirely the capacity for recombination, must, like obligate inbreeding, presage ultimate extinction once the circumstances for which a lineage is adapted cease to be available". Emery and Brown (1958) have classified *H. contortus* as an obligate apomict. Yet, as with other apomictic species, this species has achieved considerable ecological success, presumably by genecological differentiation. This requires the generation of much variability. Thus, Heslop-Harrison (1961) has pointed out two aspects of the flexibility of the genetic system possessed by amphimictic apomictic groups. In the first instance partial apomixis may generate variability at the whole genome level, or as Clausen suggest, through large chromosome blocks. Such a situation may exist where occasional crosses take place between apomictic and sexual types. In this case the boundaries between biotypes are abrupt. In the second instance where continuous ecological adaptation has resulted from a similar continuous quantitative reaction to the habitat, a polygenic situation almost certainly exists, and this requires a high level of recombination.

There are a number of ways in which variability may be generated, but by far the most effective means is by recombination through sexuality.

RETENTION OF SEXUALITY

Sexual recombination may arise from certain populations harbouring sexual forms. In this respect Harlan (1963) has described for Bothriochloininae in Western India the occurrence of locally distributed sexual diploids. Janaki Ammal (Darlington and Janaki Ammal, 1964) has reported a diploid (2n = 20) form of *H. contortus* from India. This does not necessarily mean all such diploides are sexual but Gustafsson (1947) suggests that most diploid plants, in a species which is usually both apomictic and polyploid, are likely to be sexual. However, Knox (personal communication) indicates that apomictic diploids can occasionally arise from apomictic tetraploids through the parthenogenetic development of reduced eggcells. These forms are then strictly monoploids and have been observed by him in *Dichanthium annulatum*. However, sexual diploids can only influence the population if their capacity for recombination can be transmitted into the other levels of ploidy e.g. through aneuploidy or autopolyploidy.

Reversion to sexuality

Brown (1958) and Brown and Emery (1958), in investigating the tribes Andropogoneae and Paniceae for apomixis, found most species that were apomictic to be incompletely or facultatively so. Furthermore, almost without exception were they aposporous and perennial. Heslop-Harrison (1961) does not regard apospory as being a very serious modification of normal sexual development and suggest that the potential for competition between haploid and diploid embryo sacs allows for environmental control. This suggestion is manifest in the report by Knox and Heslop-Harrison (1963) of facultative apomixis being under environmental control in *Dichanthium aristatum*. Brooks (1958) has also studied the developmental embryology of apomixis and sexuality in *Bothriochloa* and *Dichanthium*, and while she recognises that *Bothriochloa* tends more strongly to obligate apomixis than does *Dichanthium*, she draws attention to the potential for sexuality and the possibility for environmental or cultural control.

Bashaw (1962) has reported the occurrence of a sexual form of buffel grass (*Cenchrus ciliaris*) which is tetraploid (2n = 36) in an otherwise apomictic population of this grass. In investigating the genetics of apomixis in *C. ciliaris*, he suggests that the trait is recessive and probably involves more than one gene locus. However the inconclusiveness of much of the genetic work suggests a more complex genetic situation than this.

Whatever the origin of sexuality in *H. contortus* the presence of sexual types in a population leads to recombination and reconstitution of apomictic lines. Unlike the outcome of self-fertilization, which tends to result in increasing homozygosity, the heterogeneity which apomixis preserves, when brought into combination with other heterogeneous lines, releases a vast array of variability, such as has been suggested by Clausen (1954) for partially apomictic *Poa* species.

Since apomixis is likely to be genetically recessive, only one infrequent occurrence of a sexual plant would have a very lasting effect on the population as most of the progeny of an apomict sexual cross would be sexual, and so the process would be repeated. Under normal conditions these deviant types would be strongly selected against because of the lack of suitable niches for their establishment. However, where the enviroment is undergoing change, some new types could become established. With a new normal set of environmental conditions prevailing, selective advantage would again be accorded the apomictic types which replicate themselves exactly.

Mutation

Mutation must undeniably add a certain amount of variation to an otherwise non-variable situation. This is particularly conceivable with respect to morphological traits which are of no apparent selective consequence e.g. inflorescence hairiness. Thus it is possible that much of the morphological variation outlined in Table 1 is the result of mutation. Subsequently these mutant forms are proliferated exactly by apomixis and form islands of the same type in the population; a situation quite frequently observed in *H. contortus* populations in Queensland.

On the other hand the effects of mutation on plant function are likely to be less obvious since the full expression of a plant process, such as flowering, is likely to be controlled by a number of gene loci and also linked responses. Mutation alone contributes to variation in such a system at a very slow rate and could not account for the range of phenotypic variation found in *H. contortus*.

AUTOSEGREGATION

While Haskell (1959) and Gustafsson (1947) have indicated the possible role of autosegregation in producing variation in apomictic plants, this only applies to diplosporous apomixis where chromosomal rearrangement can occur through partial meiosis and the subsequent formation of a restitution nucleus. This does not apply to aposporous apomixis where meiosis is entirely avoided.

POLYPLOIDY

The evolutionary advantages a species can enjoy through utilizing polyploidy as a means of adaptive radiation have been discussed at length by Stebbins (1950) and also by Darlington (1956). Polyplaidy itself does not increase variability but the plasticity of the genotype, so that it becomes more widely adapted than the ancestral forms of a lower ploidy level.

There is an important interaction between amphimixis, apomixis and polyploidy. Apomixis overcomes the sterility barrier which usually prevents the successful proliferation of sterile hybrids and of aneuploid forms resulting from e.g. a sexual diploid crossing with an apomictic tetraploid. Some useful variation could be introduced by this means. However, the selective advantages of polyploidy and aneuploidy must be low or else higher euploid and aneuploid levels might be expected in many regions. In this respect, aneuploid forms have been reported from Australia and Africa (Moffet and Hurcombe 1949, and Celarier and Harlan 1953) though they are apparently not common.

CONCLUSION

The discussion has attempted to outline the different types and scales of variation in *H. contortus* and to place this in relation to the environment and the potential for adaptation by the plant. This has been useful because it has shown clearly that the most obvious variation in morphology, which concerns the hairiness of te inflorescence, is apparently of no adaptive significance. This character appears to be randomly distributed across the other patterns and scales of variation. It also provides no meaningful criterion for the subspecific classification of the species as atempted by Häckel (1889).

Two important levels of variation have been delimited. The first or primary level of variation concerns that associated with the geographic distribution of the species. There is a complex set of morphological characteristics wihch define these groups in broad geographic or continental categories. It is likely that polyploidy has played an important role in defining this scale through allowing adaptive radiation of the species into new geographic regions. Apomixis has tended to bring about a measure of stability to these populations subsequently.

The secondary scale of variability follows from the primary scale. It concerns the variability within geographic regions and is largely the result of phenological responses to environmental variables. Depending on the nature of these variables, so this scale is expressed to a greater or lesser extent. Thus the variation does bear some relation to geographic factors, but only so far as this concerns climatic variability.

Apomixis plays an important role in maintaining this scale of variation, firstly in preserving and proliferating successful gene combinations and secondly, by its circumvention, in allowing infrequent recombinations and consequent release of variability. Such continuous ecological adaptation, as is evident in some subtropical populations of *H. contortus*, can oly be achieved by a very high level of recombination.

Variation generated by plant species which are regarded as obligate apomicts is difficult to conceive unless all facets of the plants' behaviour are carefully considered. It has often been stated that apomixis provides a blind alley to further evolution and adaptation by the extreme limitations imposed on the generation of variation. However, a very clear distinction must be made between natural and cultivated populations, and perennial and annual plants.

Natural populations of an apomictic species are seldon uniform but exhibit varying degrees of variability depending on the nature of the environment (e.g. *H. contortus*). Variant types which may arise are difficult to detect because of the existing variation in the population, but there is potential for their occurrence since these populations are usually extensive and large numbers of plants are involved. Also it is likely that the environment fluctuates quite significantly. Deviant types are easily seen in cultivated populations, however, but the numbers of plants involved are generally much smaller and the environment brought under some measure of control. The longevity of the plant is of considerable significance for, in natural populations, apomictic lines which are not adapted to a particular sequence of seasons can survive in the population until suitable conditions return, whereas annual forms would not. However, the perenniality of the plants reduces the rate of natural regeneration in a population and this would reduce still further the chances of deviant forms appearing in cultivated populations. It is noteworthy that Brown and Emery (1958) record almost no annual grasses in the Andropogoneae and Paniceae as being apomictic.

The various ways by which an apomictic plant may generate variability have already been discussed. With respect to *H. contortus* it seems most likely that occasional reversion to sexuality has been the main vehicle. Evidence supporting this suggestion may lie in part in the observation that the greatest phenological variability exists in the regions of peripheral distribution while those closer to the suggested (Emery and Brown, 1958) area of origin are less inherently variable. Since the variation within the species increases centrifugally it is reasonable to suggest it has arisen *in situ*. This type of functional variation is complex and its inheritance is unlikely to be simple. This, associated with continuous ecological adaptation over the range of the environment, requires great variation generated from a high level of sexual recombination. The finding of aneuploid forms in at least two areas also provides some evidence of sexuality having appeared at some time.

In order to achieve the variation that has been observed. it is not necessary to postulate a continual and regular reversion to sexuality. The occasional occurrence of a sexual plant which, if it became established, would result in a considerable number of sexual offspring being produced and a very large array of variability being expressed, since the combining biotypes are highly heterozygous. If the environment is undergoing changes some of the biotypes coud become established, the sexual ones giving rise to more variation and more sexual types. Once the selection pressure on new variability no longer exists, as with the stabilizing of the environment, then new types will no longer be favoured and the sexual types would be eliminated.

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