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THE SIGNIFICANCE OF POLYPLOIDY IN THE ORIGIN OF SPECIES AND SPECIES GROUPS.

by

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Summary

Polyploidy is an unique mechanism for the elaboration of altogether new taxonomic and physiologic patterns of species origin. The phenomenon is widespread under conditions of hermaphroditism, apomixis and ecological plasticity. Where the habitat requirements are rather stringent and narrow, as in the case of many gymnosperms and some woody angiosperms, changes in the physiological and developmental rythm often arising from polyploidy seem to be of negative selection value, thus rendering its incidence rather rare in such groups. The selection value of alterations in the nuclear-cytoplasm volume, cell surface-volume, chromosome volume and gene dosage largely determines the frequency of successful survival of polyploids. The fact that among numerous types of genome combinations, only a few pass through the sieve of natural and/or human selection emphasise the importance of developmental coherence as reflected in intra- and inter-cellular integration and qualitative and quantitative balance in the synthesis of gene products. The polyploids arising from sterile or partially sterile hybrid combinations have proved in many cases to be extremely valuable for domestication not so much because of the excellence of the original genotype, but because polyploidy conferred the wherewithal to withstand mutations of various types more readily. While micro-mutations have been dominant in the differentiation of taxons at the diploid level, macro- and systematic mutations could survive readily in polyploids and have served as an important source of new variation. Thus, many of the cultivated polyploid plants differ from their wild relatives in one or two key mutations. If the pivotal genome concept of Zohary and Feldman is generally operative, polyploidy is an ideal mechanism for striking a balance between stability and mutability. In addition, it provides scope for the exploitation of judicious combinations of disomic and polysomic genetic constitution and for the perpetuation of additive as well as dominant, epistatic and other forms of gene action.

The relative role of autoploidy in the evolution of polyploids needs re-examination, following the discovery of genetic control over multivalent formation. The significance of autoploidy in sustaining mutations for apomixis and in enabling the origin of triploid and aneuploid taxons in vegetatively propagated plants has been more apparent than its role in the evolution of new sexually propagated plants. Intra-varietal autoploidy has obviously limited advantages in a sexually propagated plant but in plants with excellent seed dispersal mechanisms chromosome races are more common and are indicative of the role that opportunities for finding new ecological niches could play in the perpetuation of such polyploids. Under the stress of disruptive selection, altogether new constellations of characters tend to get stabilised, resulting in the origin of new systematic categories.

Thus, polyploidy confers a means of achieving both abrupt and gradual speciation, a balance between adaptation and adaptability and new developmental rythms. An analysis of the needs of a specific habitat in terms of the dynamics of plant adaptation would help to identify broadly the regions where polyploids may thrive. In future plant collections, emphasis should be paid not only to the collection of the wild relatives of polyploid crop plants but also to the collection of the variation found in the genome donors of the present-day polyploids.

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I. Introduction

Giganticism is one of the primary distinguishing features of cultivated plants from the wild ones and polyploidy, being a good means of achieving this, has consequently been an important mechanism in the origin of domesticated plants. Numerous variations of the polyploid theme are now recognised and Lôve (1964) has proposed a classification based on the genetic and taxonomic characteristics of the diploid(s) involved in the origin of the polyploid. His "panautoploids" and "panalloploids" correspond to Stebbins' (1950) auto- and allo-polyploids, while his "hemialloploids" formed from F_1 hybrids which are partially fertile and "hemiautoploids" formed either through differentiation of the chromosome set of successful panautoploids (as could have happened in *Solanum tuberosum*, Swaminathan, 1954) or through chromosomes doubling in intra-specific hybrids (as might have happened in *Dactylis glomerata*) would cover the segmental-allopolyploid and auto-allopolyploid groups of Stebbins. All these categories provide in varying degrees opportunities for a synthesis of disomic and polysomic genetic constitution and thereby to an efficient exploitation of phenomena such as mutation, recombination and additive and heterotic interaction of genes. Abrupt and gradual speciation are both facilitated. The elaboration of an altogether new developmental and physiological rythm is rendered possible through changes in the surface-volume relationships of the cell. Thus, polyploidy is a potent mechanism for traversing the evolutionary scale with jumps of larger quanta in terms of time, a fact beautifully brought out by Haldane (1958) by changing Blake's (1792) verse to read "To create a little flower is the labour of ages, *except by allopolyploidy*" (portion underlined, added by Haldane).

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II. Nature of ceiling on the increase of chromosome number

From observations on the behaviour of experimentally induced polyploids there has often been a tendency to regard the octoploid level as about the ceiling for the multiplication of the basic number. Studies in lower plants, particularly ferns, have however revealed that polyploidy may be a recurrent theme in the origin and diversification of species. For example, in the family *Ophioglossaceae* of the order Fillicales, the species *Ophioglossum reticulatum* has a chromosome number $2n = 1260$ but exhibits functional diploidy in cytological behaviour (Abraham and Ninan, 1954). The basic number in the genus is regarded to be $x = 120$ and Stebbins (1966) regards the evolutionary pathway adopted by this genus as an example of the fact that successful polyploids can become adjusted or "dipoidized" over long periods of time, so that further elevation of the chromosome number by recurrent cycles of polyploidy then becomes possible. The situation in *Ophioglossaceae* thus suggests that given a sufficiently long span of time, accompanied by diploidization at successively higher chromosome levels, almost no limit exists to the upward trend of polyploid chromosome numbers. This will be particularly true if the plant has acquired an apomictic mode of reproduction, as has happened in *O. reticulatum*, which lends itself to propagation through root buds.

The ceiling on levels of chromosome duplication also seems to vary, depending upon whether a species is wild or domesticated. For example, in the genus *Solanum*, triploids are infrequent among the wild species, whereas in the cultivars the opposite is true (Marks, 1966).

III. Mechanisms of diploidization

(a) *Chromosome mechanisms* : The incidence of structural differences among the chromosomes of the component genomes, either present already prior to the origin of the polyploid or developed during the subsequent evolution, has long been considered as the causal factor for the diploid-like cytological behaviour of most naturally occurring polyploids (Giles and Randolph, 1951; Stebbins, 1950 and Gerstel, 1963). Darlington (1937) proposed that preferential pairing arising from differential affinity is responsible for the fairly regular bivalent formation occurring in polyploids like *Primula kewensis*, where the F_1 hybrids between *P. floribunda* and *P. verticillata* also exhibit bivalent formation. The orientation of quadrivalents so as to promote regular adjacent segregation, as found in *Dactylis glomerata* (Myers, 1943) and the occurrence of sub-terminal centromeres limiting chiasma formation to one arm as in *Medicago sativa* (Clement and Stanford, 1963) have been other mechanisms for reducing the chances of disjunctional abnormalities and multivalent formation respectively. Gerstel (1963) has suggested that in *Nicotiana tabacum* and *Gossypium hirsutum* the accumulation of structural differences during evolution may have taken place to a greater degree in one genome than in the other. He thus supported the view of Zohary and Feldman (1962) who observed that the members of at least one closely interrelated group of allopolyploid species in the genus *Aegilops* have one genome in common whereas the other genome or genomes vary from species to species or even within the species.

(b) *Genetic Mechanisms* : Sears and Okamoto (1958) and Riley and Chapman (1958) discovered that regularity in bivalent pairing is achieved in *Triticum aestivum* by one or more factors located in the long arm of chromosome 5B, which in some still unknown way prevents homoeologous pairing. Riley (1960) referred to this phenomenon as the "genetic enhancement of differential affinity." Many years prior to this discovery Muntzing and Prakken (1940) had already invoked genetic suppression of multivalent formation to explain regular bivalent pairing in polyploid *Phleum pratense*. Since the publication of the wheat findings, interest on understanding the genetic regulation of the formation of chiasmata and multivalents has grown and control over the time and rate of chromosome condensation has been found to be an important pathway in this phenomenon (Endrizzi, 1962; Upadhyaya and Swaminathan, 1967).

Seed fertility of autoploids can be subjected to improvement and even brought to the level of the diploid through selection, thus indicating that when raw polyploids undergo a period of evolution, their characteristics might undergo considerable alteration. This has been clearly demonstrated in the induced autotetraploids of *Brassica campestris* var. *toria* ($2n = 4x = 40$) where the seed fertility was raised from 2 to 3 seeds per siliqua in the C_2 generation to over 15 per siliqua in the C_{18} generation through the adoption of the mass pedigree system of selection (Rajan, 1955; Swaminathan and Sulbha, 1959).

IV. Polyploidy as a means of evolution through macro- or systematic mutations

It is now recognized that evolution has largely progressed through selection operating upon "blind" mutations and their recombination products, a process termed by Muller as "muddling through." It is also known that the frequency of mutations increases with a decrease in the magnitude of the change involved. The rigour of the somatic and gametic sieves, which determines the extent to which mutations survive and find phenotypic expression, is largely determined by the genetic architecture of the plant. The rigour is acute in a highly evolved diploid, while it is much less severe in a polyploid with either homoeologous relationships among the constituent genomesor a predominantly polysomic genotype. Zohary (1965), while discussing the characters of polyploid colonizer species in *Aegilops*, has postulated that a successful polyploid cluster may evolve from the operation of a dual system of differentiation. First, there should be a conservative gene complex in control of the evolutionary "theme" (designated the pivotal genome) and secondly, there should be genomes which have undergone modification through the accumulation of mutations and the operation of recombination. If the pivotal-cum-differentiated genome concept is generally operative, polyploidy would be an ideal mechanism for striking a balance between stability (immediate adaptation) and mutability (adaptability). In addition, it would offer scope for the exploitation of judicious combinations of disomic and polysomic genetic constitution and of additive as well as dominant, epistatic and other forms of gene action and interaction.

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The hemialloploids and hemiautoploids of Löve (1964) have proved in many cases to be extremely valuable for domestication not so much because of the excellence of the original genotype but because of polyploidy having provided the wherewithal for the expression and realisation of various types of mutations without any coincident lowering of the reproductive potential. Thus, new systematic categories have arisen through mutations (termed macro- or systemic-mutations by Goldschmidt, 1955) in genera like *Triticum* and *Avena*. Thus, sub-species *spelta*, *compactum* and *sphaerococcum* of *Triticum aestivum* differ from sub species *vulgare* only in the genes Q, C and S respectively. These loci seem to have arisen through tandem repeats (Swaminathan, 1963) and are good examples of the abrupt origin of species through mutations. Thus, polyploidy is not only by itself a potent mechanism for quantum jumps in evolution but is also an excellent substrate for the incidence and survival of systematic mutations of the type envisaged by Goldschmidt (1955).

A shift from one adaptive norm to another is usually needed for a major evolutionary advance (Simpson, 1953). Some of the systematic mutants in *Triticum* enable such a shift. For example, *T. sphaerococcum* which has been recorded only in North west Pakistan and Baluchistan is extremely drought-resistant, a characteristic which seems to account for its selective survival in the area. A population with a high potential for the creation, conservation and release of genetic variability has obviously a great future in rapidly changing and exacting environments. Since polyploidy confers these advantages, its frequent incidence among angiosperms becomes explicable.

The studies of Frankel (Frankel and Munday, 1962) on flower morphogenesis in *Triticum aestivum* have revealed that in polyploids loci which exhibit a detrimental effect in the absence of a regulatory gene, may survive due to "genetic inertia." Swaminathan (1963) suggested that such loci may have a positive function under normal conditions. Thanks to the development of a complete set of aneuploids in *T. aestivum* by Sears (1954), the various forms of gene expression and interaction are better understood in this hexaploid plant than in any other polyploid. These studies reveal that some loci like the free-threshing gene Q may have several regulatory functions. Thus, Q not only suppresses speltoidy but also the expression of various forms of flower abnormalities, vavilovoid expression and rachis brittleness. Linkage relationships are also highly complex in polyploids, particularly in autoploids and the consequences of inbreeding are different. Thus, polyploids have several unique genetic features (Fisher, 1947).

V. Genome and genetic coherence in relation to survival of polyploids

The poor vigour and survival value of most trisomics and tetrasomics of diploids suggest that the presence of one set of genes alone in a multiple condition has usually no advantage. What is important is the relative balance in gene products. Autoploids and hemiautoploids can, however, develop a balanced genotype, once the sterility problem has been overcome. In alloploids, not all genomecombinations are successful, as for example in *Triticum* where out of the numerous combinations possible at the hexaploid level, only that involving *Aegilops squarrosa* has had success. The importance of genome combinations capable of functioning in an integrated manner or possessing what Clausen and Hiesey (1960) have called "genetic coherence" for the stability and survival of polyploids is apparent for numerous studies on induced amphidiploids. In the genus *Oryza*, for example, Shastry (1966) has shown that desynapsis and failure of pairing occur in several F_1 hybrids and amphidiploids due to the non-synchronous time sequence of meiotic division phases and condensation. Besides difficulties in division, developmental imbalance could also arise due to the lack of coherence in gene action. A comparative analysis of the entire spectrum of growth and development in polyploids with successful and unsuccessful genomecombinations would help to identify the operational components of coherence.

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VI. The adaptive significance of polyploidy

For understanding the circumstances under which polyploidy confers an adaptive advantage on a species group, it may be worthwhile examining why polyploidy is rare in some groups of plants. A conspicuous instance of a general absence of polyploidy is in the gymnosperms (especially *Ginkgo* and coniferales). These occupy relatively stable mesophytic habitats where they form great forest belts. Polyploidy is also rare among the woody angiosperms of the temperate zone. These plants have long life, frequent vegetative vigour and small chromosomes, factors which have been regarded as favourable for the incidence of polyploidy. The basic chromosome number of many of these genera is often high, thus suggesting that they may be secondary polyploids. In any case, it is clear that polyploids in this group ought to have been at a selection disadvantage during their recent evolutionary history. Thus, where the habitat requirements are rather stringent and specific, as in the case of gymnosperms and woody angiosperms, changes in the physiological and developmental rythm often arising from polyploidy seem to be of negative selection value. Conversely, in changing and altogether new habitats, polyploids have been successful colonizers, as demonstrated by Hagerup (1932). Even reduced vegetative vigour resulting in early flowering could be an advantage when temperature conditions during seed development are likely to become either too high or too low.

Under conditions where there is either too much shade or too much sun at the time of the early seedling growth, a large seed size as may occur in polyploids, will be an advantage. Many chromosome races or cytotypes occur in species of grasses and in most cases the polyploids have been very successful. For example, Heteropogon contortus consists of a polyploid complex native to the tropics and sub-tropical regions of both the old world and the New, the North American forms consisting entirely of apomictic hexaploids (Emery and Brown, 1958).

Stebbins (1956) suggested that diploid plants which do not respond favourably to artificial chromosome doubling might have already acquired an optimum cell volume, with the result that any disturbance in this character has an adverse consequence. The importance of an optimum balance in the surface-volume relationship of the cell (Schwanitz, 1949) is also clear from the parallelism observed in many primary diploids between response to gibberellic acid application and colchicine-induced polyploidy (Swaminathan, Rana and Gupta, unpublished).

VII. Polyploidy, apomixis and taxonomy

Gustafsson (1946-47) explained many years ago how polyploidy promotes the survival of mutations for agamospermy. Intra-specific chromosome races are most frequent in apomictic grasses with an efficient seed dispersal mechanism. Besides promoting the occurrence of apomixis itself, polyploidy helps to generate variability in such plants through the less rigorous elimination of somatic mutations.

The problem of nomenclature is particularly difficult in the case of intra-specific chromosome races. The view that such chromosome races should all be given specific status was expressed by Löve (1951), while several others have felt that this will not be correct, particularly if a specific systematic key is difficult to evolve. In my view it would be better to apply the same genetic and systematic criteria as far as the fixation of status is concerned, for all plants, whether diploids or polyploids. Delimitation of the boundaries of recombination would help to define the confines of the species. When this criterion is employed apomicts alone will present a major problem in classification. Systematic and spatial isolation characteristics may have to be used to a greater extent in them than genetic criteria. Morphological differentiation usually accompanies chromosome number differences except in recently evolved polyploids.

VIII. Plant collections in relation to polyploidy and plant breeding

From the foregoing, it would be clear that polyploidy confers a means of achieving both abrupt and gradual speciation, a balance between adaptation and adaptability and new developmental rythms which enable the colonisation of diverse ecological niches. An analysis of the needs of a specific habitat in terms of the dynamics of plant adaptation would help to identify broadly the regions where polyploids may thrive. In plant collections, the isolation and accumulation of wild polyploid relatives by themselves will constitute only one aspect of the requirements of the plant breeder. Now that the diploid donors of many of the genomes of polyploid crop plants are fairly well understood, greater emphasis should be paid to the collection of the genotypes of the putative parents. This would help to resynthesise the polyploid crop plants using parents of a different genetic background. Hagberg and Åkerberg (1961) have summarized the value of this approach in the breeding of oilseed crops. While monosomic analysis of the location of genes for rust resistance in varieties of *Triticum aestivum* has shown that the D genome derived from *Aegilops squarrosa* seldom contains genes for resistance, the Japanese collections of *A. squarrosa* have revealed some strains with a high degree of resistance (Yamashita, 1959). With the growing application of fertilizers and intensity of farming all over the world, the importance of isolating altogether new genes for resistance to the principal diseases and pests hardly needs emphasis. The resynthesis of some of the existing polyploid plants using altogether new parental material may have an important impact in future plant breeding. This is particularly because of our growing understanding of the methods of manipulating gene recombination.

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