

# INDUCED MUTATIONS IN RELATION TO PHYLOGENETIC ANALYSIS IN *TRITICUM*

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## INTRODUCTION

IT is well known now that spontaneously occurring mutations provide the raw material for natural selection to build upon and that through selection operating upon "blind" mutations microbes have evolved into men over millions of years. This process has been aptly termed by Muller (1960) as "mudding through". While the slow accumulation of small differences provides the basic mechanism for evolution of both intra- and inter-specific categories, the scrambling and repatterning of polarized sequences of chromosomal sections may occur occasionally in a single event and may lead, if viable, in one step to a major evolutionary deviation (Goldschmidt, 1955). Goldschmidt (1955) has designated such a change as "systemic mutation" and has cited several examples from both animals and plants in support of his view that such changes could have been important in macro-evolutionary divergence. Swaminathan (1961) has shown that in angiosperms polyploidy is a particularly potent mechanism for facilitating the viability of macro-mutations. Since it is now possible to induce a high frequency of mutations in most plants through the use of a wide array of physical and chemical mutagens, the study of induced mutations provides an additional source of information in reconstructing the phylogenetic history of plant species. The value of induced mutations in studies of this kind is enhanced by the identity of most of the experimentally induced mutations with those occurring spontaneously. The present paper provides data from a study of this kind carried out in the genus *Triticum*.

## CYTOGENETIC HISTORY OF *Triticum*

Members of the genus *Triticum* belong to a polyploid series with  $2n = 14, 28$  and  $42$ . The cytogenetic studies of Kihara and his co-workers (Kihara and Lilienfeld, 1949), McFadden and Sears (1946), Sarkar and Stebbins (1956), and Riley *et al.* (1958) have clearly established that the tetraploid ( $2n = 28$ ) and hexaploid ( $2n = 42$ ) species of *Triticum* arose respectively by chromosome doubling in hybrids between einkorn wheat ( $2n = 14$ ) and *Aegilops speltoides* ( $2n = 14$ ) and emmer wheat ( $2n = 28$ ) and *Aegilops squarrosa* ( $2n = 14$ ). Among

tetraploid *Triticum* species there are both free-threshing and non-free-threshing forms. McFadden and Sears (1946) synthesised the non-free-threshing hexaploid species, *T. spelta*, from the cross *T. dicocoides* × *A. squarrosa*, while Kihara and Lilienfeld (1949) obtained plants similar to the hexaploid free-threshing bread wheat, *T. aestivum*, from the cross *T. carthlicum* × *A. squarrosa*. Thus, the divergence existing at the tetraploid level with regard to the threshing character has also been transmitted to the hexaploids.

The hexaploid *Triticum* group comprises the following species (Plate I, Fig. 1).

- |                        |                                   |
|------------------------|-----------------------------------|
| 1. Free-threshing:     | <i>T. aestivum</i> L.             |
|                        | <i>T. sphaerococcum</i> Perc.     |
|                        | <i>T. compactum</i> Host.         |
|                        | <i>T. amplissifolium</i> Zhuk.    |
| 2. Non-free-threshing: | <i>T. spelta</i> L.               |
|                        | <i>T. macha</i> Dek. et Men.      |
|                        | <i>T. vavilovi</i> Jakub.         |
|                        | <i>T. zhukovskyi</i> Men. et. Er. |

Mac Key (1954 a) has shown that *T. aestivum* and *T. spelta* differ by one major gene *Q* situated on the long arm of chromosome 5 A (nomenclature of Sears, 1959 a). Sears (1947) and Unrau *et al.* (1950) found that *T. sphaerococcum* and *T. compactum* are each separated from *T. aestivum* by a single gene: *S* located on chromosome 3 D and C on 2 D respectively. Thus, the *sphaerococcum* and *compactum* types could have arisen only after the origin of the first hexaploid *Triticum*. *T. amplissifolium* is a little known Chinese wheat with compactoid ears of the inflatum type. Among the non-free-threshing species, *T. macha* has been considered by Kihara (1959) as the probable ancestral hexaploid species. Singh *et al.* (1957) found that *T. vavilovi* differs from *T. aestivum* only in 2 genes. *T. zhukovskyi* is also a little known species found only in Georgia in the U.S.S.R. It resembles the tetraploid *T. timopheevi* in phenotype and is believed to have been derived from it (Jakubziner, 1959). The available data thus show that the key characters separating most of the hexaploid *Triticum* species are governed by only 1 or 2 genes. Hence, Mac Key (1954 b) and Sears (1959 b) have suggested that all the hexaploid species should be regarded as subspecies of *T. aestivum* L. Since phenotypically, each of the subspecies possesses a whole constellation of morphological traits, systematists have had sufficient grounds for describing them as distinct species.

From a developmental standpoint, the origin of several distinctive characters from the effect of one gene would imply that the mutant action affects one of the early determinative processes. In this way, one primary action could have manifold consequences. If, however, the single unit of recombination is in fact a string of tightly linked genes,

the possibility is open to get the different phenotypic effects separated. From the view-point of the plant breeder, the latter situation would be more desirable as otherwise he cannot hope to separate the constellation of characters. Studies on induced mutations would facilitate an understanding of the prevailing situation, since owing to the low resolving power of genetic analysis in higher plants, conventional crossing procedures may not throw much light.

#### INDUCED MUTATIONS OF PHYLOGENETIC INTEREST IN HEXAPLOID *Triticum* SPECIES

All the hexaploid species were treated with several dosages of X-rays, gamma-rays, Fast Neutrons and Ethyl Methane Sulphonate (Swaminathan and Rao, 1960; Rao, 1962). Different types of mutations were found in the  $M_2$  and subsequent progenies. Those of phylogenetic interest alone are referred to in this paper. The ears of mutations in *T. aestivum* resembling the naturally occurring subspecies are given in Plate I, Fig. 2.

##### (a) *T. aestivum*

(i) *Speltoid mutations*.—A commonly occurring mutation is the "Speltoid" type in which the glumes get strongly keeled and threshing becomes difficult as in *T. spelta*. Associated with this change there may be others such as laxity of the ear, narrowness of leaves and lateness in maturity. Mac Key (1954 a) has shown that the speltoid mutation arises from the loss or inactivation of the free-threshing gene *Q*. This is the principal gene differentiating *T. spelta* and *T. aestivum*.

(ii) *Vavilovoid mutation*.—Mutations characterised by the elongation of rachillae as in *T. vavilovi* occur in speltoid types of *T. aestivum*. *Q* suppresses the expression of this character and it is hence that Singh *et al.* (1957) found a 2-gene segregation in crosses between *T. aestivum* and *T. vavilovi* (Rao and Swaminathan, 1963).

(iii) *Sphaerococcoid mutation*.—Mutations giving rise to rigid and bayonet-like flag leaf, inflated and hemispherical glumes and spherical grains occur rarely in irradiated material and more frequently in the progenies of plants treated with ethyl methane sulphonate. These mutants thus possess the key characteristics of *T. sphaerococcum*. When varieties of *T. aestivum* and *T. sphaerococcum* are crossed, segregates combining the spherical grains of the latter species with the plant characters of the former never occur (Singh, 1946). In mutation experiments, however, such phenotypes are found. Thus, the "S" locus seems to be a compound one with several recones and mutons.

(iv) *Compactoid mutation*.—Plants resembling *T. compactum* occur frequently in irradiated progenies. The strong keeling of glumes found in *T. compactum*, however, is absent in such mutants. Mac Key (1954 a) has shown that an overdose of *Q* gives rise to compactoid ears. The Chinese wheat *T. amplissifolium* appears to have arisen in this way.

(b) *T. sphaerococcum*

Mutations resembling *T. aestivum* frequently occur in this species following treatment with mutagens. The suggestion of Ellerton (1939) that *T. sphaerococcum* arose through a chromosome deletion in *T. aestivum* is thus rendered improbable. The constellation of characters associated with *T. sphaerococcum* is broken up in irradiated material thereby making available combinations of characters not usually found in nature.

(c) *T. compactum*

The *aestivum* mutation occurs commonly when this species is subjected to treatment with mutagens. The *C* locus can be either deleted or broken up through suitable treatments.

(d) *T. spelta*

It has not been possible to obtain a free-threshing mutation from *T. spelta* so far. Obviously, this mutation must be an extremely rare one and might have occurred only once at the tetraploid level in the phylogenetic history of the polyploid *Triticum* species. The speltoid suppressor factor *Q* has played a dominant role in the evolution of the widely cultivated *durum* and bread wheats. *Q* not only inhibits spelt-ing but also brittleness of rachis, a development of obvious importance in cultivated forms. It also inhibits various forms of spikelet sterility and vavilovoid expression.

(e) *T. vavilovi*

Forms resembling *T. spelta* can be obtained in this species through the loss of *v*, the factor responsible for the elongation of rachillae.

(f) *T. macha*

This species is basically a spelt type with a factor for ear compactness. When the gene for compactness is removed, spelta-like forms are produced. This species is a very old one having been found in the ancient remains in Colchis. It appears to have been derived from the tetraploid Georgian wheat *T. palaeocolchicum*.

#### DISCUSSION

The few mutations described in this paper make it obviously clear that mutation analysis will be rewarding from the phylogenetic angle. What have been described as distinct species by competent systematists in the genus *Triticum* are seen to have arisen through single step mutations. Such phylogenetically important mutants have been described in *Bromus* (Cuznac, 1939), *Zea-Euchlaena* hybrids (Langham, 1940), *Chlamydomonas* (Moewus, 1940), *Streptocarpus* (Oehlkers, 1940), *Marchantia* (Burgeff, 1943), ferns (Andersson-Kottö and Gairdner, 1936), maize (Singleton, 1951), *Pisum* (Rosen, 1944; Lamprecht, 1948),

*Linaria* (Schwanitz, 1955), *Secale* (Stutz, 1957) and *Antirrhinum* (Stubbe, 1959). In *Antirrhinum*, mutants having the key characters of the genera *Hemimeris*, *Mohavea*, *Ixianthes*, *Verbascum*, *Veronica*, *Lagotis* and *Wulfenia* have been isolated (Stubbe, 1959). Stubbe (1959) has also shown how through hybridization with other types such macromutants can easily acquire the necessary modifiers for normal vitality. Gustafsson (1954) and Wettstein (1954) have found that in the erectoides mutants of barley, a single mutant step leads to several pleiotropic effects. Goldschmidt (1955) has given examples of this kind in *Drosophila*. It thus seems that though the process of evolution through mutation is an extremely slow one, jumps of larger quanta in the evolutionary scale are occasionally possible. In polyploid plants, the buffering effect caused by the presence of duplications facilitates the survival of such large changes.

Maheshwari (1950) has elegantly shown how embryological research is many times useful in solving taxonomic puzzles. The availability of potent tools for inducing a high frequency and wide spectrum of mutations has opened up yet another path for reconstructing the phylogenetic history of the plants and animals with which we have the good fortune to live.

#### SUMMARY

Mutants resembling *T. spelta*, *T. vavilovi*, *T. compactum*, *T. sphaerococcum* and *T. amplissifolium* occur in progenies of *T. aestivum* treated with different doses of physical and chemical mutagens. Similar macromutants also occur in the other hexaploid species of *T. aestivum*. With a single-step mutation, a constellation of new characteristics may sometimes arise thereby giving scope for a systematist to designate the mutant as a new species. Induced mutation analysis provides information of value in understanding the nature of genetic change involved in species differentiation and in reconstructing the phylogenetic history of plant species.

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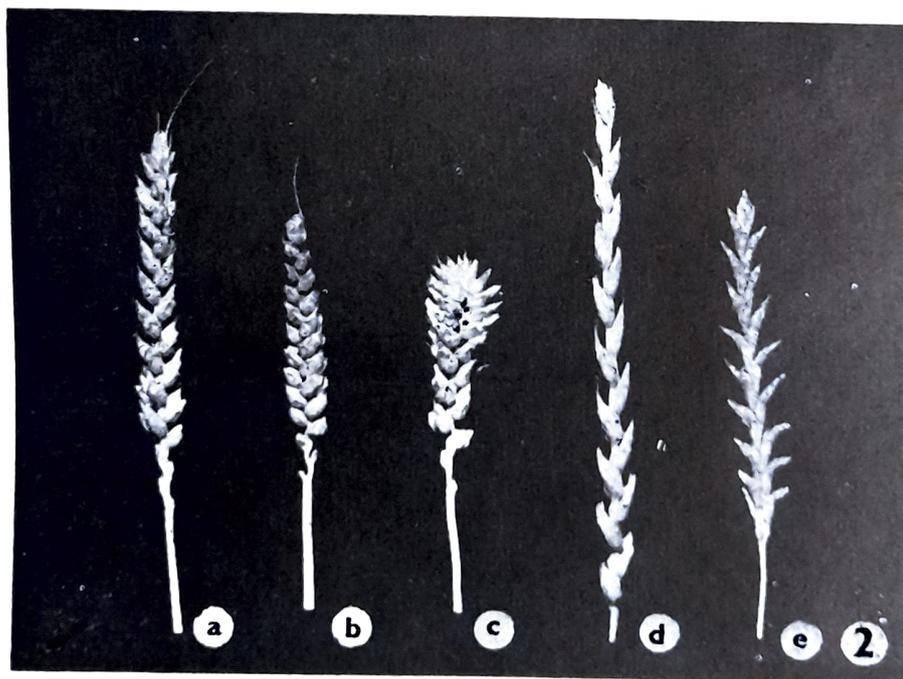
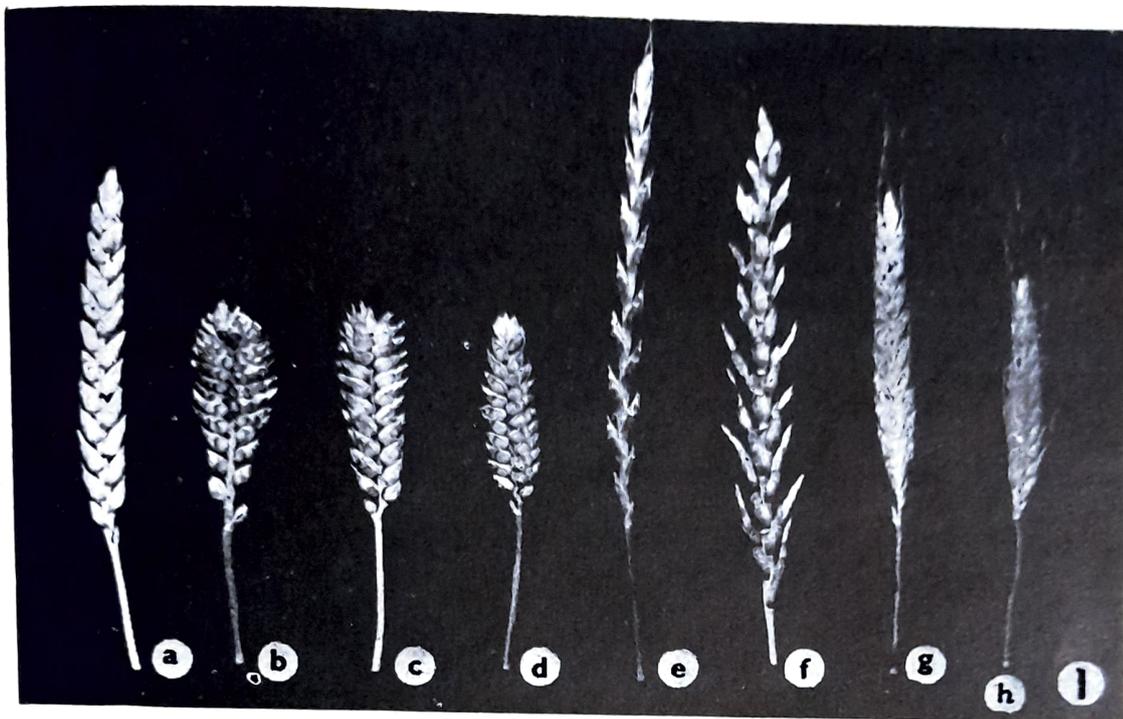
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## EXPLANATION OF PLATE I

- FIG. 1. Ears of hexaploid *Triticum* species. (a) *T. aestivum*. (b) *T. amplissifolium*. (c) *T. compactum*. (d) *T. sphaerococcum*. (e) *T. spelta*. (f) *T. vavilovi*. (g) *T. macha*. (h) *T. zhukovskyi*.
- FIG. 2. Ears of *T. aestivum* and some induced mutants. (a) *T. aestivum* var. N.P. 798, (b) to (c) Induced mutants in *T. aestivum*. (b) Sphaerococcoid mutant. (c) Compactoid mutant. (d) Speltoid mutant. (e) Vavilovoid mutant.



FIGS. 1-2

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