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# Studies on Induced Mutants with Reference to Species Relationships in Some Tetraploid *Triticums**

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**Summary.** A mutational analysis of five tetraploid species of *Triticum* was carried out to study different types of systematic mutants. Rare systematic mutants viz., free-threshing mutants and the timopheevioid mutant of *T. dicoccum*, *polonicum*-type mutants of *T. durum*, *turgidum*-type mutants of *T. carthlicum* and *durum*-type mutants of *T. turgidum* and *polonicum*, which occurred with consistently high frequencies, are discussed in relation to the phylogenetical interrelationships of these species. The study supports Mac Key's (1966) proposal that all these species would be best grouped as sub-species of *Triticum turgidum*.

## Introduction

The various species of *Triticum* were originally given their specific rank on morphological criteria. The genetic studies performed since the investigations of Schulz (1913), Sakamura (1918) and Sax (1918) have not supported the species boundaries within each chromosome number level. Conclusions on the species relationship have been drawn mostly from hybridization studies (Mac Key, 1966). While hybridization experiments have given many interesting results, the problem can be approached in greater detail by mutational analysis. Mac Key (1954 and 1959) and Swaminathan (1963 and 1966) reported valuable results in this direction from their mutational studies in hexaploid species of *Triticum*, but our knowledge of the types of systematic mutants that can be induced in tetraploid *Triticum* species is still fragmentary. In the present study, varieties of *Triticum durum*, *T. dicoccum*, *T. turgidum*, *T. polonicum* and *T. carthlicum* were treated with gamma rays and chemical mutagens and the $M_2$ generations were critically studied. It was anticipated that such data would be helpful in examining Mac Key's (1966) proposal, formulated on the basis of hybridization studies, that all these species should be grouped as sub-species of *T. turgidum*.

## Material and Methods

1. The various tetraploid species of *Triticum* ($2n = 4x = 28$) used in the present study are listed in Table 1 and their salient features described.

2. The various mutagens used are listed in Table 2. (i) *Gamma rays*: Dry dormant seeds with 10–12 per cent moisture content were irradiated with gamma rays of the required dose. (ii) *E. M. S.*: Dry dormant seeds were soaked for 5 hours in distilled water and later transferred to (a) buffered EMS solution of pH 7 and (b) aqueous EMS solution, for 12 hours at 30 °C with intermittent shaking. A buffer solution of citric acid – disodium hydrogen phosphate was used. Immediately after treatment, the seeds were washed thoroughly in water and sown. (iii) *NMU* and (iv) *NG*: Dry dormant seeds were soaked for 5 hours in distilled water and transferred to NMU and NG solutions of the required concentrations for 12 hours at 30 °C, with intermittent shaking. After treatment the seeds were thoroughly washed and sown. (iv) *Combined treatments with gamma rays and chemicals*: Dry dormant seeds were irradiated with gamma rays and then given chemical treatments.

After observing germination and seedling growth under different mutagenic treatments at varying doses and concentrations, it was found that 40 KR dose of Gamma rays, EMS pH 7,04%, EMS aqueous 0,2%, NMU aqueous 0,015%, and NG aqueous 0,02% induced similar biological effects as far as germination and seedling growth were concerned, in all the above species (Prasad, 1968). Hence, these treatments were used, so as to have a basis for comparison.

The treated seeds were sown in a well prepared field and special care was taken to raise the $M_1$ plants. Each $M_1$ plant was bagged immediately after ear emergence, to avoid out-crossing, and was harvested and threshed separately. Seeds collected from the $M_1$ plants were sown in observation rows in the following season to raise the $M_2$ generation. Morphological variations in growth habit, leaf size, shape and position, plant height, and ear mutations were recorded. The mutation frequency in the $M_2$ generation was calculated as follows: (i) percentage of $M_2$ families (the progeny of a single $M_1$ plant was regarded as one $M_2$ family) segregating for mutations and (ii) number of mutant plants per 100 $M_2$ plants.

All the mutants were harvested separately, and tested for their cytological and breeding behaviour in the following season.

## Results

### *Observations in $M_2$ generation*

Table 3 shows the number of $M_2$ families and plants showing some frequent viable mutations in various mutagenic treatments of *T. durum*. It can be seen that a large number of families consistently segregated in all the treatments for mutants with long narrow glumes and *polonicum*-type mutants. Of the different

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Table 1. *Tetraploid species of Triticum* ($2n = 4x = 28$) *used in the study*

| S. No. | Material | Source | Salient features |
|---|---|---|---|
| 1. | *Triticum durum* desf. var. NP 404 | Indian Agricultural Research Institute | Spring habit, early, medium tall, ear bearded, stiff rachis, free threshing, glumes beaked, keel curved and prominent from tip to base, grains amber. |
| 2. | *T. dicoccum* Sehubl. var. NP 202 | Indian Agricultural Research Institute | Spring habit, early medium, tall, coleoptile pink, ear bearded, rachis fragile, hard threshing, glumes medium long, tough, beakless, grains flinty or semiflinty 7–9 mm long with a tuft at the stylar end. |
| 3. | *T. polonicum* L. var. Polish | Institute of Plant Industry, Leningrad, USSR | Spring habit, tall, late, ear lax and bearded, glumes very long, empty, keeled with an apical beak, free threshing, grains long and soft. |
| 4. | *T. turgidum* L. var. *Lusitanium* | Institute of Plant Industry, Leningrad USSR | Spring habit, late, tall, broad leaves, ear bearded, square in section, rachis tough, spikelets as long as broad, glumes short and broad, firm, free threshing, grains amber. |
| 5. | *T. carthlicum* var. Stramenium | —do— | Spring habit, matures later than *T. turgidum*, ear bearded, narrow, lax rachis, tough, but thin glumes very loose and easily shedding, keel very weak, outer glumes prominently awned, free threshing, seeds small, dark dirty brown and shrivelled. |

treatments, NMU and $\gamma$ + NMU showed a higher frequency of such families. Other types of mutants which occurred in several families, in various treatments, were mutants with partial outer-glume awning, compactoid and sphaerococcoid types. Mutants showing full outer glume awning and speltoid mutants also occurred in quite a few treatments, but not in all. The vavilovoid mutant occurred in only 3 families with the NMU treatment and one family with the $\gamma$ + NMU treatment.

In the case of *T. dicoccum* more families segregated for different degrees of outer glume beaking and for mutants with the *araraticum* type of glume (Table 4). It was interesting that rare systematic mutants viz., compact free threshing (resembles compactoid of *T. carthlicum*) and the *timopheevi* type of mutants, each occurred in one family from NMU treatment. The other types, such as compactoid, sphaerococcoid and vavilovoid mutants, were not observed.

In the case of *T. polonicum*, the data given in Table 5 show that mutants with dense ears and tight glumes, open panicles and long chain open panicles appeared in several families in all the treatments. Sphaerococcoid and vavilovoid mutants were not observed, although accordion type, compactoid and speltoid mutants occurred in a few families in most of the treatments.

The $M_2$ data for *T. turgidum* (Table 6) showed that a number of families consistently segregated for lax ear types, mutants with prominent beak on outer glumes and *durum* type mutants, in all the treatments. The lax ear mutants and mutants with prominent outer glume beak showed a phenotypic tendency towards *durum* types. Another mutant which occurred in several families was the compactoid type. Sphaerococcoid and speltoid mutants occurred in only a few families of the $r$ + NMU, NMU and EMS buffer treatments.

In the $M_2$ generation of *T. carthlicum* (Table 7), mutants with dense ears, dense ears and reduced awns and the *turgidum* type of mutants occurred in a consistently large number of families in all the treatments. Compactoid mutants also occurred in several families in all the treatments.

Table 2. *Mutagens used in the study*

| Mutagen | Source and Chemical formula | Nature of action |
|---|---|---|
| i) Gamma rays | From a 2000 curie $CO^{60}$ Gamma Cell at the Genetics Division of I. A. R. I. for irradiation of dry seeds. | Gamma irradiation |
| ii) Ethylmethane-sulfonate (EMS) | Eastman Kodak Chemicals, U. S. A. $C_2H_5\,OSO_2\,CH_3$ | Chemical mutagen Alkylating agent |
| iii) N-Nitroso-N-methyl Urea (NMU) | K and K Laboratories U. S. A. $CH_3N(NO)$ $CONH_2$ | Chemical mutagen Alkylating agent |
| iv) N-methyl-N-nitro-N-nitroso-guanidine (NG) | K and K Laboratories<br>NH<br>‖<br>$CH_3N$ C $NHNO_2$<br>\|<br>NO | Chemical mutagen. Acts through alkylation, found to be highly mutagenic in microorganisms probably due to its structure. |

Table 3. $M_2$ *of Triticum durum var. NP 404*

| Treatment | Number of | | Types of mutants scored | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Compactoid | | Sphaerococcoid | | Speltoid | | Vavilovoid | | Fully awned glumes | | Long narrow glumes | | Polonicum type | |
| | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants |
| Control | 200 | 16891 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| γ-rays 40 KR | 99 | 4531 | — | — | — | — | 1 | 4 | — | | — | — | 6 | 13 | 4 | 4 |
| EMS pH7 0.4% | 142 | 8647 | 6 | 8 | 4 | 5 | 2 | 3 | — | — | 3 | 9 | 8 | 12 | 9 | 14 |
| EMS Aq 0.2% | 109 | 5038 | 4 | 4 | 6 | 6 | 4 | 6 | — | — | — | — | 3 | 7 | 3 | 6 |
| NMU Aq 0.015% | 127 | 5912 | 6 | 10 | 7 | 9 | 6 | 13 | 3 | 4 | 8 | 28 | 6 | 7 | 12 | 21 |
| γ-rays 25 KR + EMS pH 7 0.2% | 2374 | 2374 | 1 | 1 | 3 | 4 | 3 | 5 | — | — | 5 | 14 | 1 | 3 | 6 | 9 |
| γ-rays 25 KR + NMU Aq 0.01% | 69 | 1736 | 3 | 6 | 6 | 13 | — | — | 1 | 2 | 1 | 16 | 8 | 13 | 11 | 19 |
| NG Aq 0.02% | 92 | 3147 | — | — | — | — | — | — | — | — | — | — | 2 | 2 | — | — |

Table 4. $M_2$ *of T. dicoccum var. NP 202*

| Treatments | Number of | | Types of mutants scored | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Free threshing compact ears | | Completely beaked outer glumes | | Slightly beaked outer glumes | | Long ears with prominent beak | | Araraticum type glumes | | Timopheevi type | |
| | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants | $M_2$ families | $M_2$ plants |
| Control | 200 | 14572 | — | — | — | — | — | — | — | — | — | — | — | — |
| γ-rays 40 KR | 117 | 5323 | — | — | 4 | 10 | 3 | 6 | 5 | — | 3 | 3 | — | — |
| EMS pH 7 0.4% | 136 | 3468 | — | — | 8 | 17 | 9 | 12 | 6 | — | 7 | 9 | — | |
| EMS Aq 0.2% | 106 | 3021 | — | — | 7 | 15 | 2 | 2 | 2 | 2 | 11 | 14 | — | — |
| NMU Aq 0.015% | 104 | 3087 | 1 | 1 | 12 | 23 | 15 | 24 | 9 | 10 | 9 | 19 | 1 | 7 |
| γ-rays 25 KR + EMS pH7 0.2% | 108 | 2998 | — | — | 5 | 14 | 2 | 2 | 1 | 1 | 3 | 5 | — | |
| γ-rays 25 KR + NMU Aq 0.01% | 93 | 2843 | — | — | 3 | 9 | 8 | 10 | 11 | 24 | 10 | 27 | — | — |
| NG Aq 0.02% | 121 | 4692 | — | — | — | — | 2 | 4 | — | — | — | — | — | — |

Table 5. $M_2$ *of T. polonicum*

| Treatment | No. of $M_2$ families | No. of $M_2$ plants | Compactoid $M_2$ families | Compactoid $M_2$ plants | Speltoid $M_2$ families | Speltoid $M_2$ plants | Open panicle $M_2$ families | Open panicle $M_2$ plants | Long chain open panicle $M_2$ families | Long chain open panicle $M_2$ plants | Durum types $M_2$ families | Durum types $M_2$ plants | Accordion $M_2$ families | Accordion $M_2$ plants | Reduced ears $M_2$ families | Reduced ears $M_2$ plants |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Control | 200 | 14305 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| γ-rays 40 KR | 105 | 5117 | 1 | 2 | 1 | 4 | 2 | 2 | 1 | 2 | 1 | 1 | — | — | — | — |
| EMS pH 7 0.4% | 137 | 6458 | — | — | 2 | 4 | 8 | 11 | 4 | 9 | 6 | 6 | 1 | 3 | 2 | 2 |
| EMS Aq 0.2% | 93 | 3417 | 1 | 3 | 1 | 2 | 2 | 2 | 6 | 6 | 3 | 6 | — | — | — | — |
| NMU 0.015% | 97 | 2913 | 4 | 9 | — | — | 4 | 9 | 8 | 14 | 9 | 10 | 6 | 12 | 3 | 10 |
| γ-rays 40 KR + EMS pH 7 2% | 92 | 2764 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 5 | — | — |
| γ-rays 40 KR + NMU Aq 0.01% | 87 | 2566 | 3 | 3 | 1 | 2 | 12 | 17 | 4 | 21 | 6 | 8 | 4 | 4 | 2 | 2 |
| NG Aq 0.02% | 118 | 4853 | — | — | — | — | 1 | 1 | 1 | 1 | 1 | 1 | — | — | — | — |

Table 6. $M_2$ *of T. turgidum*

| Treatment | No. of $M_2$ families | No. of $M_2$ plants | Compactoid $M_2$ families | Compactoid $M_2$ plants | Sphaerococcoid $M_2$ families | Sphaerococcoid $M_2$ plants | Speltoid $M_2$ families | Speltoid $M_2$ plants | Lax ears $M_2$ families | Lax ears $M_2$ plants | Prominently beaked glumes $M_2$ families | Prominently beaked glumes $M_2$ plants | durum types $M_2$ families | durum types $M_2$ plants | Dense short ears $M_2$ families | Dense short ears $M_2$ plants |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Control | 200 | 15361 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| γ-rays 40 KR | 108 | 6117 | 2 | 4 | — | — | — | — | 2 | 5 | 8 | 13 | 2 | 4 | 1 | 2 |
| EMS pH 7 0.4% | 106 | 6312 | 3 | 7 | 1 | 2 | 1 | 4 | 3 | 6 | 10 | 17 | 8 | 12 | 2 | 4 |
| EMS Aq 0.2% | 96 | 2865 | 1 | 2 | — | — | — | — | 4 | 7 | 7 | 14 | 3 | 5 | — | — |
| NMU Aq 0.015% | 93 | 2918 | 2 | 3 | 1 | 2 | 2 | 3 | 8 | 11 | 9 | 12 | 6 | 18 | 3 | 5 |
| γ-rays 25 KR + EMS pH7 0.2% | 68 | 2463 | 2 | 2 | — | — | | ... | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 2 |
| γ-rays 25 KR + NMU Aq 0.01% | 82 | 2367 | 1 | 2 | 1 | 1 | — | — | 1 | 3 | 4 | 15 | 1 | 3 | — | — |
| NG Aq 0.02% | 97 | 3544 | — | — | — | — | — | — | 1 | 1 | — | — | — | — | — | — |

Table 7. *$M_2$ of T. carthlicum*

| Treatment | No. of $M_2$ families | No. of $M_2$ plants | Compactoid $M_2$ families | Compactoid $M_2$ plants | Speltoid $M_2$ families | Speltoid $M_2$ plants | Vavilovoid $M_2$ families | Vavilovoid $M_2$ plants | Dense ears $M_2$ families | Dense ears $M_2$ plants | Turgidum type $M_2$ families | Turgidum type $M_2$ plants | Hard threshing prominent keels $M_2$ families | Hard threshing prominent keels $M_2$ plants | Dense ears with reduced outer glume awns $M_2$ families | Dense ears with reduced outer glume awns $M_2$ plants |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Control | 200 | 13848 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| $\gamma$-rays 40 KR | 113 | 5613 | 1 | 1 | 1 | 1 | — | — | 4 | 6 | 1 | 3 | — | — | 2 | 3 |
| EMS pH7 0.4% | 126 | 8025 | 3 | 5 | — | — | 1 | 3 | 12 | 19 | 6 | 9 | 1 | 2 | 8 | 11 |
| EMS Aq 0.2% | 103 | 5156 | 4 | 7 | 1 | 4 | — | — | 8 | 9 | 4 | 7 | — | — | 5 | 9 |
| NMU Aq 0.015% | 109 | 3978 | 3 | 9 | 1 | 2 | 2 | 4 | 18 | 23 | 4 | 11 | — | — | 4 | 16 |
| $\gamma$-rays 25 KR + EMS pH7 0.2% | 96 | 2014 | 2 | 2 | — | — | — | — | 4 | 8 | 3 | 5 | — | — | 4 | 4 |
| $\gamma$-rays 25 KR + NMU Aq 0.01 | 93 | 2116 | 6 | 11 | — | — | 2 | 3 | 6 | 8 | 2 | 2 | — | — | 9 | 24 |
| NG Aq 0.02% | 98 | 4307 | — | — | — | — | — | — | 3 | 7 | — | — | — | — | — | — |

Families with vavilovoids and speltoids were relatively few. Sphaerococcoids were not observed. Dense ear mutants and mutants with dense ears and reduced outer glume awns tended towards the *turgidum* type of ear morphology. It was observed that with an increase in the density of the ear, there was a progressive reduction in the length of the awns in the outer-glumes. A hard threshing ear type with prominent keels, isolated from EMS buffer treatment of *T. carthlicum*, resembled *T. dicoccum*.

It is evident from Tables 3, 4, 5, 6 and 7 that each species had several families segregating for one or two mutants in which the characters affected are key systematic ones. Such mutants occurred in many families in the NMU and $\gamma$ + NMU treatments. Rare mutants, which probably are being recorded for the first time, viz., the free threshing and *timopheevi*-type of mutants of *T. dicoccum*, occurred only in the NMU treatment. It can be seen that mutations affecting ear characters were rare in *T. dicoccum* compared with other species.

### *Description of some mutants*

Some rare mutants and certain mutants of phylogenetic importance are described below:

a. *Compact-free-threshing mutant of T. dicoccum*: Only one mutant occurred in the $M_2$ progeny of the primary tillers of NMU treatment. The mutant was shorter than the control and flowered a few days later. The ear resembled the compactoid mutant of *T. carthlicum*. The outer glumes were completely awned and the spikelets were free threshing. The seeds were typical of the *dicoccum* type (Prasad, 1968).

b. *Durum-type mutants*: *Durum*-type mutants were isolated from the $M_2$ progenies of *T. turgidum* and *T. polonicum*. In key characters like glume shape and length and beak length, the mutants were very much nearer to *T. durum*. The *durum*-type mutants of *T. turgidum* showed a relatively lax disposition of the spikelets on the ear, slightly longer glumes and beak, unlike the parent. The *durum*-type mutants of *T. polonicum* had denser ears, markedly shorter glumes and longer beak than the control. There was a marked reduction in the size and shape of the ear as a whole (Prasad, 1968). The frequency of *durum*-type mutants and mutants with a phenotypic tendency towards *durum* type was far greater in the $M_2$ generation of *T. turgidum* than in that of *T. polonicum* (see Tables 5 and 6). These mutants were free threshing.

c. *Polonicum-type mutants*: These occurred at a very high frequency in the $M_2$ generation of *T. durum*. The ears of the mutants tended more towards *T. polonicum*, with larger and narrow glumes, and with the spikelets disposed rather laxly on the rachis. The overall length of the ear was also enhanced compared with the control. The seeds were longer and slightly narrower than *T. durum* seeds and tended towards the *polonicum* types of grain morphology (Prasad, 1968).

d. *Turgidum-type mutants*: The $M_2$ generation of *T. carthlicum* segregated for *turgidum*-type mutants. The mutants were characterized by a dense, shorter ear with very much reduced outer-glume awning, tending towards the *turgidum* type of ear morphology (Prasad, 1968). With the increase in ear density, there was a progressive reduction in outer-glume awning. The seeds of *turgidum*-type mutants were relatively well-filled, bold and light brown in colour, unlike the seeds of *T. carthlicum*, which were shrivelled small, and dirty dark brown in colour.

Table 8. *Length of glume and beak in systematic mutants and parents*

| Species/Mutant | Glume length in cms. | | Mean length of the beak in cms. |
|---|---|---|---|
| | Mean | Range | |
| *T. durum* var. NP 404 | 1.00 | 0.95 – 1.10 | 0.22 |
| *T. polonicum* | 2.62 | 2.00 – 3.20 | 0.15 |
| *T. turgidum* | 1.00 | 0.95 – 1.05 | 0.20 |
| *T. carthlicum* | 1.00 | 0.95 – 1.05 | 4.00 |
| *T. dicoccum* var. NP 202 | 1.00 | 0.95 – 1.05 | 0.05 |
| *durum* type of mutants from: | | | |
| i) *T. polonicum* | 1.35 | 1.20 – 1.50 | 0.23 |
| ii) *T. turgidum* | 1.10 | 0.95 – 1.20 | 0.22 |
| *turgidum* type of mutants from: | | | |
| *T. carthlicum* | 1.00 | 0.90 – 1.05 | 0.25 |
| *polonicum* types from *T. durum* var. NP 404 | 2.20 | 1.70 – 2.40 | 0.17 |
| Free threshing compact ear mutant of *T. dicoccum* var. NP 202 | 1.00 | 0.93 – 1.05 | 3.75 |

e. *Pyramidale-type mutants*: The $M_2$ generation of *T. turgidum* produced mutants simulating *T. pyramidale* (dense, short ear column of Table 6). The ear was very rectangular, denser and shorter, tending towards *T. pyramidale* (Prasad, 1968).

f. *Timopheevi-type mutant of T. dicoccum*: A $M_1$ primary tiller progeny row of NMU treatment in *T. dicoccum* segregated for plants with a late and spreading habit. The leaves of the plants were narrower and densely hairy. The variation in the leaf hair length was from 1.4 mm to 1.8 mm and strikingly similar to that of *T. timopheevi*. The ears were hairy and almost like *T. timopheevi* ears in glume and beak pattern. Seeds of the mutant were much smaller than the seeds of the parent, and showed the tuft at the stylar end of the seed which is characteristic of *T. dicoccum* var. NP 202 (Prasad, 1968).

It can be seen from Table 8 that all these systematic mutants tend towards the respective species in glume-length and beak length.

All the above mutants showed normal meiotic behaviour and bred true to type, whereas the intermediate types segregated indicating their heterozygosity in the $M_2$ generation.

## Discussion

### *Genetic control of free-threshing character*

Mac Key (1954 and 1966), using the results from backcross experiments involving a speltoid and *T. carthlicum*, suggested that the direct control of free-threshing nature (Q factor) is based on a polygenic system scattered over almost the whole germplasm and does not constitute a simple homomeric series. On the other hand, Swaminathan (1966) studied (1) the range of speltoid mutations observed in all the free-threshing sub-species, (2) the dosage effect of Q in the sub-species *spelta* and *macha*, (3) the behaviour of *vavilovii* and (4) the free-threshing forms found in crosses between different strains of *spelta*, *macha* and *spelta*, and suggested that Q exists at different strengths in various free and hard-threshing species of *Triticum*. He suggests that free-threshing forms like *T. carthlicum* have arisen from wild emmers like *T. dicoccoides* by a tandem repeat of the Q 1 locus to Q 3 condition on the 5th chromosome of the A genome. This is supported by the findings of Muramatsu (1963), who showed the dosage effect of the *spelta* gene Q of the hexaploid, and by Kuckuck (1959) from crosses involving *T. macha* and *T. spelta*.

Many authors have shown that Q is a complex locus with dosage effect so it is very difficult to understand the polygenic mechanism proposed by Mac Key (1966). The recovery of a free-threshing mutant resembling Compactoid of *T. carthlicum* from the $M_2$ generation of *T. dicoccum* in the present investigation shows that a rare mutation of the Q locus from a hard-threshing to free-threshing condition, probably involving a repeat, is possible.

### *Origin of timopheevi — araraticum complex*

*T. timopheevi* Zhuk., a member of the emmer group of wheat, is endemic in Transcaucasia. It has been effectively isolated from the other *Triticum* species through interspecific hybrid sterility. Lilienfeld and Kihara (1934) concluded that one of the genomes of *T. timopheevi* is fairly homologous with the A genome, but the remaining one is considerably differentiated from A and B. It was designated as the G genome. Kostoff (1936, 1937) found a certain degree of homology between B and G and proposed the symbol $\beta$ to indicate partial differentiation from the B genome. Sachs (1953) found that the hybrids between *T. timopheevi* and *T. dicoccoides* var. *nudiglumis* showed a regular meiosis, but associated sterility which was attributed to the common origin of the B and G genomes followed by differentiation due to cryptic structural changes. Wagenaar (1961) observed normal meiosis and good fertility in a number of hybrid combinations between *timopheevi* and tetraploid *Triticum* species, and concluded that the genomic constitution of *T. timopheevi* is AB but it carries genes for irregular meiosis, with the implied differential asynaptic or desynaptic effect restricted to the B genomes.

The recovery of the *timopheevi* type of mutant from the $M_2$ generation following NMU treatment of *T. dicoccum* in the present study indicates that the so-called G or $\beta$ genome of *T. timopheevi* is nothing but a mutated B genome of *T. dicoccum*, involving the mutation of a "gene block" or a complex locus of that genome. This mutation appears to affect a whole range of characters, from plant habit, leaf hairiness, ear size and shape, to meiotic behaviour in hybrid combinations with other species of *Triticum*. The present finding supports the observations of Sachs (1953) and Wagenaar (1961), that *Triticum timopheevi* is not unrelated to *T. dicoccoides* and other emmers. It also appears that the "gene block" or the complex locus of B genome in question mutates very rarely in nature, but that a powerful alkylating agent such as nitrosomethyl urea can bring about this drastic mutation giving rise to the asynaptic genetic system observed in the present study. Mutants simulating the glume and beak pattern of *T. araraticum* were also recovered in the $M_2$ generation following different mutagenic treatments of *T. dicoccum*. It appears probable that, in nature, species such as *T. timopheevi* and *T. araraticum* might have originated from wild emmers such as *T. diccocoides* (which is close to *T. dicoccum*). Mutations in the B genome appear to have erected or imposed strong isolation barriers between them and other species of *Triticum*.

*Differentiation of turgidum-durum-polonicum complex*

Examination of the $M_2$ generation of *T. durum* revealed that the mutants which occurred most frequently in all the treatments and particularly in the NMU and $\gamma$ + NMU treatments, were those tending towards *T. polonicum*, with long narrow glumes and longer ear. The occurrence of such mutants was consistent. Similarly, the $M_2$ generation of *T. turgidum* showed a consistently higher frequency of *durum* types than others in all the treatments, and the *pyramidale* type mutants less frequently. The $M_2$ generation of *T. polonicum* also gave *durum*-type mutations, with reduced glume length, dense, shorter ears with beak on outer glumes. However, the frequency of *durum* type mutants was far greater in the $M_2$ of *T. turgidum* (see Table 6 and 5). No *polonicum*-type mutants were observed in the $M_2$ generation of *T. turgidum*; they were confined to the $M_2$ generation of *T. durum*. Similarly no *turgidum*-type mutations were observed in the $M_2$ generation of *T. polonicum*, but a few mutants with dense ears tending to *turgidum* ear morphology were observed in very low frequency in the $M_2$ of *T. durum*.

All this suggests that *T. turgidum* and *T. polonicum* are independently more closely related to *T. durum* than to each other. The high occurrence of *durum*-type mutants in the $M_2$ generation of *Triticum turgidum* suggests that *T. turgidum* may have given rise to *T. durum* and its close relative *T. pyramidale* by simple mutations, or that these three are a closely related group. The recovery of a very high frequency of *polonicum*-type mutants from *T. durum* also suggests that *T. polonicum* might have arisen from *T. durum*; the frequency of *durum*-type mutants in the $M_2$ of *T. polonicum* was lower than the frequency of *polonicum*-type mutants from *T. durum* or of the *durum*-type mutants from *T. turgidum*. Mac Key (1966) also feels that *Triticum turgidum*, *T. durum* and *T. polonicum* are closely related.

It was also interesting to come across a consistently high frequency of *turgidum*-type mutants and mutants with dense ears tending towards *T. turgidum* in the $M_2$ generation following all the treatments of *T. carthlicum*. These mutants showed a marked decrease in the outer glume awn to a long beak with an increase in the density of the ear. The glume shape and other key characters tended more towards *T. turgidum*. This indicates that *T. turgidum* may have originated from *T. carthlicum* by the mutation of gene(s) affecting ear density and beak length.

It appears that the free-threshing character may have arisen by a rare macromutation at the Q locus of 5A chromosome in the oldest wild emmer species, such as *T. dicoccoides* (which is closely related and nearly identical to *T. dicoccum*), and resulted in types like *T. carthlicum*, as shown by the present study. Mac Key (1966) proposed that *T. dicoccoides* and *T. dicoccum* might be closely related to *T. carthlicum* (the hard-threshing strong-keeled ear mutant of *T. carthlicum* resembles *T. dicoccum* in ear morphology). On the other hand, a rare mutation of a complex locus or "gene block" in the B genome of *T. dicoccoides* might have resulted in forms like *T. timopheevi* and *T. araraticum* with the asynaptic genetic system which has imposed a strong isolation barrier. By simple mutations *T. carthlicum* might have given rise to *T. turgidum*, from which *T. durum* might have originated by mutations. *T. polonicum* seems to be the youngest of the tetraploid *Triticum* complex and might have arisen from *T. durum* by mutation of the 'P' gene affecting glume length and ear laxity. *Turgidum*, *pyramidale* and *durum* have their distinctive characteristics based on a series of minor genes.

This "species-cluster" has an evolutionary theme or core characters (Zohary, 1965, Zohary and Feldman, 1962) in the form of the free-threshing gene (Q — locus) and asynaptic gene complex, which are subject to little mutability or variation, buffered by many peripheral characters, such as glume shape and size, beak or awn length, density or laxity of ear and growth habit, which are mutable at higher frequencies. A change in the core characters, as shown by a mutation to the free-threshing form being accompanied by other changes such as outer glume awning and changes in glume shape and size etc., and also mutation to the timopheevoid condition, is accompanied by a change in the constellation of characters. The *durum*-type mutants from *T. turgidum* and *polonicum*, and *turgidum*-types from *T. carthlicum* seem to represent peripheral or buffer characters which mutate very rapidly, unlike the core characters which determine the basic "species characters" whose unrestricted mutation or recombination might throw the population off balance and off the adaptive peak, as proposed by Zohary (Zohary and Feldman, 1962, Zohary, 1965).

In general, it appears from the mutational analysis that the dividing lines between species at the tetraploid level are not very distinct. The study shows that only a few gene mutations, such as mutations at the 'Q' locus and in the asynaptic gene system of the B-genome, are able to give a more clear-cut picture of morphological discontinuity. As a marked discontinuity does not seem to exist, it seems reasonable to refer to all the above tetraploid species of *Triticum* as sub-species, as in Mac Key's (1966) system of nomenclature for the genus *Triticum* L. These species follow Vavilov's (1922) law of homologous series, as a similar and homologous type of variation has been observed in the $M_2$ generations of all the species.

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