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***Research Article***

# THE ANEUPLOID SWITCH: EXTRA-CHROMOSOMAL EFFECT ON ANTIOXIDANT DEFENSE THROUGH TRISOMIC SHIFT IN *LATHYRUS SATIVUS* L.

***Dibyendu Talukdar**
*Department of Botany, R.P.M. college, University of Calcutta, Uttarpara, 712 258, West Bengal, India*
**Author for Correspondence*

## ABSTRACT
The shifting of 'critical chromosome' type from one trisomic to another resulted in development of seven different primary trisomics (tr) in *Lathyrus sativus* L. The switching over to aneuploidy triggered a massive dosage imbalance, as screened by specific activities of five prominent antioxidant defense enzymes in unstressed control and 150 mM NaCl treatment. This imbalance was manifested in three different directions-extra dosage on activities of superoxide dismutase (tr III), ascorbate peroxidase (tr V), dehydroascorbate reductase (tr II), glutathione reductase (tr IV), inverse dosage on catalase (tr VII) and disomic level of all five enzymes in tr I and tr VI. The dosage-effect had magnified in tetrasomics (tetra) and combined in double trisomics. The tr/tetra II, IV, V and their double trisomics exhibited better tolerance to NaCl-induced stress than disomic and other aneuploid types. The results revealed profound effect of extra-chromosomal dosage on vital cellular processes in plants.

***Key Words:*** *Aneuploidy, Antioxidant Enzymes, Trisomic Shift, and Lathyrus Sativus L.*

## INTRODUCTION
Aneuploidy refers to unbalanced gains and/or losses of individual chromosomes, or parts of chromosomes, from the normal diploid set. The gaining of chromosome/s results in trisomy (tr), tetrasomy (tetra) or in even higher aneuploid levels. Plants have traditionally provided unique systems for studying aneuploidy and resemble mammals in aneuploid-induced diverse genomic and epigenetic changes (Papp *et al*., 1996; Huettel *et al*., 2008). Moreover, the chromosome numbers in plants can be easily manipulated to allow systematic analyses of the consequences of chromosome numerical aberrations at different ploidy levels (Huettel *et al*., 2008).

Since the classic discovery of twelve trisomics in *Datura stramonium* by Blakeslee and his co-workers in the 1920's, trisomics are being used as excellent cytogenetic stocks in plants genome mapping (Sybenga 1996). Although poor growth has been generally considered as an obvious outcome of trisomy due to meiotic instability induced by an additional chromosome, reverse phenomenon like vigorous growth was not uncommon in trisomic population (Khush *et al*., 1984; Singh and Prasad 2000; Talukdar and Biswas 2007). These observations can be explained by gene balance hypothesis, where dosage imbalances of gene encoding regulatory molecules on different chromosomes disturb their stoichiometry within multi-protein complexes and disrupt cellular processes (Birchler and Veitia 2007). The functional aspects of this dosage effect can be better explained by the phenomenon of 'trisomic shifts' where a trisomic individual with a particular 'critical chromosome' (for which it is trisomic) may produce trisomic with different 'critical chromosome' upon selfing. The sequential appearance of progeny trisomics showing distinct phenotypic identities from its mother plants underlines the significance of shifting of aneuploid switch from one type of trisomy to another, giving rise to a complete set of primary trisomics in a species (Talukdar and Biswas 2007).

The 'biochemical basis of aneuploid syndrome' was studied in higher eukaryotes based on the principle that varying the dosage of a gene would produce a directly proportional amount of gene product (Birchler and Newton 1981; Birchler and Veitia 2007) As the effect of extra dosage may vary from chromosome to chromosome in a given organism, it can primarily be assessed on those cellular events which give simple but vital inputs for growth and development (Veitia 2004). Plants antioxidant defense is one such cellular

event, which relies on coordinated operation of several enzymes within ascorbate-glutathione cycle and outside it (Noctor and Foyer 1998), and is highly efficient in stress perception (Foyer and Noctor 2005). As aneuploidy is known to exert greater influence on phenotype than polyploidy, the present study was carried out on three different aneuploid types, primary trisomics, tetrasomics and double trisomics isolated and characterized in grass pea (*Lathyrus sativus* L.). Grown worldwide as a hardy legume crop showing tolerance to different biotic and abiotic stresses (Vaz Patto *et al.*, 2006; Biswas 2007, Talukdar 2011f) *Lathyrus sativus* L. (grass pea) has been used as an excellent material in diverse aspects of biological research (Kenicer *et al*., 2005; Brunet *et al*., 2008). In recent times, a robust stocks of diploid mutant lines showing desirable traits have been characterized for mutation genetic studies (Talukdar 2009a, c, 2011b, e; Talukdar and Biswas 2005, 2006) and breeding (Talukdar 2009b). A good number of cytological tester stocks including reciprocal translocations (Talukdar 2010a, 2011d), and different aneuploids like trisomics, tetrasomics and double trisomics have also been developed in grass pea and utilized in gene mapping (Talukdar 2009d). The crop reportedly shows high antioxidant properties (Pastor-Cavada *et al*., 2009) and activities of different antioxidant enzymes have been elucidated in NaCl-tolerant lines and in lead-induced stress conditions (Brunet *et al*., 2008; Talukdar 2011c). Although effect of polyploid genome was studied in different plant systems under stress (Xiong *et al*., 2006; Meratan *et al*., 2008; Van Laere *et al*., 2011), virtually nothing is known about the implication of aneuploid genome on antioxidant defense activities of plants. The main objective of the present work was, therefore, to investigate the effect of trisomy on specific activities of five prominent antioxidant defense enzymes (superoxide dismutase-SOD, ascorbate peroxidase-APX, dehydroascorbate reductase-DHAR, glutathione reductase-GR and catalase-CAT) in grass pea in control and NaCl-treated conditions. The dosage sensitive interactions originating from trisomy for a particular chromosome was verified in respective tetrasomic type and also in double trisomics.

## MATERIALS AND METHODS

### *Plant materials*

The experimental material comprised of disomic (2n=2x=14) variety 'BioR-231', seven different types of primary trisomics (2n+1; 2n=15) and tetrasomics (2n+2; 2n=16) and 21 different double trisomics (2n+1+1; 2n=16) in grass pea (*Lathyrus sativus* L.). The first trisomic (tr I) originated through 350Gy gamma ray treated variety 'BioR-231', and it produced tr II, III and IV in the next generations (2000-2004). Rest three appeared from selfing of tr III in the next two generations of study (2004-2006). In self-pollinated progenies of these seven trisomics, apart from trisomics and disomics, seven tetrasomic plants were also identified during the periods. Although sterility increased as an obvious consequence of aneuploidy, both trisomics and tetrasomics are self-fertile, and seven trisomics as well as seven tetrasomics can be easily separated from each other and also from disomic plants by distinctive phenotype even at the early seedling stage (Talukdar 2008; Talukdar and Biswas 2007, 2008) Double trisomics were obtained from crosses between seven trisomic parents in different combinations and showed combinations of phenotypes of two trisomic parents (Talukdar 2009c).

### *Imposition of NaCl treatment*

Fresh seeds of seven trisomics, seven tetrasomics, 21 different double trisomic plants and its disomic mother variety 'BioR-231' (used as disomic control) were surface sterilized by 10% (v/v) sodium hypochlorite for 3 min and allowed to germinate in the dark at 25 °C in four separate sets (disomics, trisomics, tetrasomics and double trisomics) with six replications for each parent. Germinated seedlings were immediately transferred to twelve inches earthen pots containing a mixture of soil, vermiculite and farm yard manure (1:1:1). Seedlings were thinned to one per pot (two pots replication$^{-1}$) and watered evenly for uniform growth until 7 d after first emergence. The pots were kept under control condition (temperature day 27 °C, night 20 °C, humidity of 70%, 200µmol m$^{-2}$ sec$^{-1}$ and a14h photoperiod), and only particular plant type (based on their characteristic phenotype) were maintained in respective set. Salt treatment was commenced on 15 d old seedlings in each set by watering the plants with equal daily

increments of NaCl-supplemented distilled water over three days to a final concentration of 150 mM. This was applied thrice a week for 2-weeks of continuous treatment. Dry weights of the shoots were obtained after drying the samples at 60 °C for 72 h. Plant type tolerant to NaCl-induced stress was ascertained by visual scoring of leaf injury level as proposed (Talukdar 2011a) for grass pea (0-no injury, 1-mild injury with leaflet tip and margin turn brownish yellow, 2-moderate injury with 50% of total leaflet portions turn whitish yellow, 3-severe injury where 80% of total leaflet becomes whitish yellow, and 4-extreme injury, leaflets crinkled and finally, fell off) and shoot dry weight. The unstressed condition of aneuploids was designated as aneuploid control (AC).

***Measurement of antioxidant enzyme activities and hydrogen peroxide content***

The mature fully expanded leaves (grown on primary branches) were collected from 30-d-old control and NaCl-treated plants from each set for biochemical studies. A pool of samples from twelve plants for each plant type was collected, and six independent experiments were performed. All operations were performed at 0-4 °C, except mentioned otherwise. Leaf samples (1g) were homogenized in an extraction medium containing 50 mM K-phosphate buffer pH 7.8, 0.1 mM EDTA, 2mM cysteine, 1% w/v PVP and 0.2% v/v Triton X-100. SOD (EC 1.15.1.1) activity was determined by the nitro-blue tetrazolium photochemical assay method (Beyer and Fridovich 1987). The reaction mixture (3ml) contains 50 mM phosphate buffer (pH 7.8), 13 mM methionine, 75 μM NBT, 0.1 mM EDTA, 2μM riboflavin and 0.1 ml of enzyme extract. One unit of SOD was defined as the amount of protein causing a 50% NBT photoreduction. For the APX (EC1.11.1.11), 20 mM ascorbate was added to the extraction buffer. The extracts were filtered through two layers of cheesecloth, and the homogenate was centrifuged at 14000 *g* for 20 min, at 4 °C. The supernatant fraction was filtered through a column containing 1 mL of Sephadex G-50 equilibrated with the same buffer used in homogenization. The hydrogen peroxide-dependent oxidation of ascorbate was followed by a decrease in the absorbance at 290 nm with extinction constant 2.8 $mM^{-1}$ $cm^{-1}$following the method of Nakano and Asada (1981). DHAR (EC 1.8.5.1) were extracted with 50mM K- phosphate buffer (pH 7.8), 1% PVP-10, 0.2mM EDTA and 10 mM β-mercaptoethanol, and its activity was assayed following ascorbate formation at 265 nm ($\varepsilon$ = 14.1 $mM^{-1}$ $cm^{-1}$) for 3 min (Nakano and Asada 1981). GR (EC 1.6.4.2) was extracted with the same medium as for DHAR but without β-mercaptoethanol and with 0.1% Triton X-100, and its activity was measured by monitoring glutathione-dependent oxidation of NADPH at 340 nm ($\varepsilon$ = 6.22 $mM^{-1}$ $cm^{-1}$) for 3 min (Dalton *et al*., 1986). CAT (EC 1.11.1.6) was extracted in 50 mM K-phosphate buffer (pH 7.0) and 0.5% PVP-10, and its activity was assayed by measuring the reduction of $H_2O_2$ at 240 nm ($\varepsilon$ = 39.4 $M^{-1}$ $cm^{-1}$) for 1 min (Aebi 1984). Hydrogen peroxide ($H_2O_2$) content of leaves was measured following the methodology as described by Cheeseman (2006).

***Statistical methods***

The results are presented as mean ± standard errors (s.e.m) of six replicates (n=12). Statistical significance (at $p<0.05$, alpha level) between mean of disomic control (DC) and those of aneuploids was estimated by *t-test* using 'Microsoft Excel data analysis, 2007 tool pack ANALYS32.XLL'.

## RESULTS

***Antioxidant enzyme activities in trisomics, tetrasomics and double trisomic plants***

Activities of five enzymes showed considerable changes in five different trisomics, otherwise they were as per disomic levels (Table 1). Compared to disomic control (DC), SOD activity increased significantly ($p<0.05$) both in tr III and tetra III plants under un-stressed (AC) condition. Its activity showed a 2-fold increase over AC in 150 mM NaCl-treated tr III plants, but remained unchanged in treated tetra III plants (Table 1). APX level had increased over DC plants by approximately 2.2-fold in tr V and by around 2.5-fold in tetra V over tr V. Likewise, measurable DHAR activity was found enhanced about 1.5-fold in tr II, and was further increased around 2-fold in tetra II over AC (tr II). GR specific activity had increased over DC approximately 2.5-fold in tr IV and by same magnitude in tetra IV over AC (Table 1). Marginal changes in activities of APX, DHAR and GR were, however, noticed in NaCl-treated trisomic and

tetrasomic plants from their respective AC values. Compared to DC plants, CAT level exhibited significant (3-fold) decrease in tr VII and nearly, 2-fold further reduction in tetra VII. No further reduction of CAT level, however, was noticed in these two aneuploids under NaCl treatment. Disomic levels (DC) of all five enzymes were maintained in tr I, tetra I, tr VI and tetra VI plants under unstressed condition (Table1), while tetra I and tetra VI died five days after commencement of salt treatment.

Higher enzyme activities were observed in double trisomics obtained from inter-crosses involving tr II, III, IV and V in different combinations. Tables 2 and 3 provided performances of 21 double trisomics, exhibiting important outcomes. Co-high expression of APX-GR, APX-DHAR, APX-CAT, DHAR-GR, DHAR-CAT and GR-CAT was observed in double trisomic plants derived from tr V × tr IV, tr V × tr II, tr V × tr VII, tr II × tr IV, tr II × tr VII and tr IV × tr VII, respectively, and there were no significant ($p<0.05$) changes in their activities under NaCl treatment (Tables 2 and 3). Likewise, in double trisomics involving tr III as one of the parents with tr II, IV and V, SOD level over-expressed with DHAR, GR and APX, respectively. Under salt stress, SOD increased over AC level, while activity levels of other enzymes remained unaffected in these three double trisomic types (Table 2). Interestingly, CAT level was at disomic level in all double trisomics, where tr VII was involved as one of the partners (Tables 2 and 3). Double trisomics derived from separate crosses between tr I or tr VI and tr II, tr IV and tr V exhibited over-activity of DHAR, GR and APX, respectively. Marginal variations of the activity levels were observed upon imposition of salt treatment. All the enzymes, however, showed activity, close to disomic parents, in double trisomic of tr I- tr VI, and it remained unperturbed in salt treatment.

***Leaf $H_2O_2$, leaf injury levels and shoot dry weight in aneuploids***

Under unstressed control condition, $H_2O_2$ level increased significantly in leaves of tr III and tetra III, whereas this level reduced substantially in trisomics and tetrasomic types (tr/tetra) II, IV and V in relation to disomic parent (Table 1). Marginal variation in $H_2O_2$ content from disomic control was observed in tr/tetra VII (Table 1) and in tr /tetra I and tr/tetra VI. After imposition of NaCl treatment, $H_2O_2$ level increased 2.4-fold in disomic parent, 1.7-fold in tr III, 2.4-fold in tetra III and nearly 3.5-fold in tr VII from their respective controls (Table 1). By contrast, no increase in $H_2O_2$ content was measured in leaves of salt-treated tr/tetra II, IV and V plants over their control values (Table 1). Visible leaf injury level was the highest (level 4) in NaCl-treated tr/tetra III and tetra VII, and it was closely followed by disomic parent (Table 1). Not any type of injury was visible in tr/tetra II, IV and in V under salt treatment. Compared to disomic control, shoot dry weight was found decreased in tr III and VII, and it was further decreased in their respective tetrasomic progenies. A 3-5-fold reduction from disomic control value of biomass production was recorded in these four aneuploid types under NaCl-treatment (Table 1). Shoot dry weight was normal in tr/tetra II, but was significantly ($p<0.05$) higher in tr IV, tetra IV, tr V and tetra V than disomic control, even under NaCl-treatment (Table 1). Marginal changes for these three traits were, however, observed in tr/tetra types I and VI in relation to disomic parent.

Double trisomics containing tr II, IV and V as parents in different combinations exhibited considerably lower $H_2O_2$ level and higher shoot dry weight than disomic control (Tables 2 and 3). No leaf injury mark was observed in these plants under NaCl treatment. This performance was closely followed by double trisomics obtained from crosses between tr I or tr VI and tr II, tr IV and tr V and then, by double trisomics of tr III-trIV/V/II and tr III-tr VII under control and NaCl-treated conditions (Tables 2 and 3).

## DISCUSSION

The seven different primary trisomics (tr) with distinctive phenotypes in grass pea (*Lathyrus sativus* L.) have arisen due to involvement of seven different primary chromosomes as extra (Talukdar and Biswas 2007, 2008). The shifting of 'critical chromosome' type resulted in origin of these seven types sequentially in population. Subsequently, this led to development of seven different tetrasomics (tetra), also (Talukdar 2008). The extra dosage effect due to trisomy and its magnification in tetrasomy have been manifested by poor and weak growth in tr/tetra I, III, VI and VII, but by quite normal and even vigorous growth in tr/tetra II, IV and V in relation to their disomic parents (Talukdar and Biswas 2007; Talukdar

2008). In order to understand the reasons primarily responsible for better fitness of certain aneuploid types than the others within a same organism, present investigation was carried out on three different types of aneuploids- trisomy, tetrasomy and double trisomy, taking trisomics as the basis stock of aneuploidy and disomics as their mother control. Tetrasomics were used to reveal the amplification of trisomic dosage for specific chromosomes, whereas 21 different types of double trisomics were utilized to study the combined dosage effect of the two trisomic crossing partners on antioxidant defense enzymes. Plant antioxidant defense systems being a basic cellular process for growth and development may be highly responsive to genome reorganization mediated via chromosome numerical aberrations in different magnitudes (Grant and Owens 1998; Makarevitch 2008). The present experimental protocol revealed a unique effect of aneuploid genome on activities of five different antioxidant enzymes, $H_2O_2$ accumulation and shoot biomass production in *L. sativus* L. under control and 150mM NaCl treatment for 15 d considering leaf injury level as an additional parameter for ascertaining salt stress. As suggested by *t*-test, there was a significant increase in activities of four enzymes (SOD, APX, DHAR and GR) in four different trisomics (tr III, V, II and IV, respectively), which further increased in respective tetrasomic types with duplication of 'critical chromosome'. This ascertained the direct dosage-effect of extra chromosomes in these aneuploids. On the other hand, significantly ($p<0.05$) decreased CAT level in tr VII and tetra VII indicated an inverse relationship between the chromosomal dosage and the amount of enzyme activity. Presumably, dosage effect of CAT gene is cancelled via an inverse effect produced by another part of the triplicated chromosome in tr VII, as explained in other plant aneuploids (Birchler and Veitia 2007). Interestingly, except SOD, no increase in activities of other four enzymes was recorded in the present aneuploids after imposition of salt treatment. SOD constitutes first line of defense against reactive oxygen species (ROS), but it converts one ROS (free radical) to another ROS (hydrogen peroxide or $H_2O_2$) during dismutation (Alscher *et al*., 2002). As a cellular oxidant, $H_2O_2$ is known to accelerate membrane lipid peroxidation and deactivation of thiol containing enzymes (Mittler 2002; Becana *et al*., 2010; Talukdar 2011c,g). Significantly, higher level of SOD was found associated with over-accumulation of $H_2O_2$, increase in leaf injury level and decrease in shoot dry weight in salt-treated tr III and tetra III. This strongly favored the idea that both tr III and tetra III experienced severe oxidative stress due to NaCl treatment, and APX and CAT at their disomic levels were unable to catalyze excess $H_2O_2$ generated by extra dosage of SOD in these two aneuploids. Similarly, decreased CAT level could not be compensated by disomic level of APX activity in tr/tetra VII, leading to over-accumulation of $H_2O_2$ and concomitant rise of injury level in their leaves. Interestingly, a completely reverse situation was found when elevated SOD activity (tr III) was augmented with high APX level (tr V) in double trisomics of tr III-tr V. This plant type showed normal level of $H_2O_2$, high shoot dry weight and no mark of leaf injury, indicating its tolerance to NaCl-induced stress. Functional interplay in the form of compensation among antioxidant defense enzymes particularly during $H_2O_2$-scavenging has recently been revealed in an ascorbate-deficient semi-dwarf mutant of *Lathyrus sativus* L. (Talukdar 2011g).

With at least seven isozymes, APX is the most prolific $H_2O_2$-scavenging enzyme in plants, and its expression regulates the availability of substrates for DHAR and GR activities in ascorbate-glutathione cycle (Asada 2006; Ishikawa and Shigeoka 2008). DHAR and GR play pivotal role in recycling of ascorbate and glutathione in their reduced forms, respectively, to enable them to function as efficient redox buffers in numerous cellular processes in plants (Foyer and Noctor 2011) as also reported in grass pea (Talukdar 2011g). The over-activity of APX, DHAR and GR, thus, reinforced antioxidant defense in chromosomally unbalanced tr/tetra V, II and IV plants, respectively, and also in their double trisomic types, ensuring their good growth even under high salt concentration. Quite surprisingly, CAT level increased and reached disomic level in double trisomics of tr V- tr VII, enabling this aneuploid type to scavenge $H_2O_2$ more efficiently than one of its parent, tr VII. This might be responsible for better tolerance of this double trisomic to NaCl-induced stress, as evidenced by absence of leaf injury level and normal shoot dry weight. Like APX, the involvement of DHAR and GR in triplicated dosage with high SOD level as well as with low CAT activity led the double trisomics, obtained from tr II × tr III or tr VII

**Table 1. Activities of SOD [unit $mg^{-1}$ (protein)], APX, DHAR, GR and CAT [nmol $mg^{-1}$ (protein)], $H_2O_2$ content (µmol $g^{-1}$ fresh weight), injury levels (0-4) in leaves and dry weight (DW, mg $plant^{-1}$) of shoot in disomic variety 'BioR-231' and its aneuploid types under control (C, 0mM NaCl) and 150 mM NaCl treatment in grass pea (*Lathyrus sativus* L.). Data are ± s.e.m of six independent experiments (n=12). Performances of tetra I and VI were studied only at control, as both died five days after imposition of NaCl treatment. * Significantly (*t-test*) different from disomic control at $p<0.05$.**

| Genotypes | SOD | APX | DHAR | GR | CAT | $H_2O_2$ | Injury levels | Shoot dry weight |
|---|---|---|---|---|---|---|---|---|
| Disomic (C) | 110 ± 0.52 | 137 ±1.5 | 11.5 ± 0.3 | 30.3 ± 1.5 | 60.8 ± 1.1 | 3.69 ± 0.1 | 0 | 32.6 ± 0.61 |
| Disomic(NaCl) | 113 ± 0.55 | 140 ±1.5 | 10.9 ±1.0 | 31.0 ± 1.3 | 57.5 ± 1.0 | 8.89 ± 0.4* | 3 | 12.2 ±0.10* |
| tr I (C) | 109 ± 1.1 | 137 ±1.0 | 11.7 ± 0.3 | 31.0 ± 1.9 | 60.2 ± 2.0 | 3.61 ± 0.7 | 0 | 31.8 ± 0.20 |
| tr I (NaCl) | 111 ± 1.1 | 138 ±1.9 | 11.5 ± 1.0 | 29.5 ± 1.7 | 59.9 ± 1.4 | 8.68 ± 0.8 | 3 | 12.3 ±0.11* |
| tetra I (C) | 109 ± 2.1 | 135 ±1.6 | 11.4 ± 1.5 | 30.0 ± 1.7 | 61.1 ± 2.1 | 3.73 ± 0.1 | 0 | 33.0 ± 0.21 |
| tr II (C) | 107 ± 1.0 | 138 ±1.9 | 17.7 ± 0.3* | 31.0 ± 1.9 | 61.0 ± 2.8 | 1.31 ± 0.7* | 0 | 37.8 ± 0.18 |
| tr II (NaCl) | 112 ± 1.3 | 136 ±1.0 | 16.5 ± 0.9* | 33.5 ± 2.0 | 61.8 ± 2.8 | 1.38 ± 0.6* | 0 | 35.3 ± 0.19 |
| Tetra II (C) | 108 ± 2.0 | 135 ±1.2 | 35.4 ± 0.6* | 33.0 ± 2.0 | 59.7 ± 2.8 | 1.33 ± 0.4* | 0 | 33.3 ± 0.17 |
| tetra II (NaCl) | 109 ± 1.8 | 135 ±1.5 | 34.3 ± 1.0* | 33.8 ± 2.2 | 62.2 ± 3.2 | 1.35 ± 0.8* | 0 | 31.7 ± 0.14 |
| tr III (C ) | 219±0.43* | 133 ±1.1 | 11.5 ± 0.6 | 29.7 ± 3.3 | 57.5 ± 2.5 | 6.93 ± 0.1* | 1 | 25.7 ± 0.19 |
| tr III (NaCl) | 439 ± 1.5* | 129 ±1.0 | 11.0 ± 0.2 | 31.3 ± 2.0 | 60.2 ± 3.0 | 12.2 ± 0.9* | 4 | 11.7 ± 0.10* |
| tetra III (C ) | 265 ± 1.1* | 133 ±1.3 | 11.9 ± 0.9 | 30.3 ± 2.0 | 58.0 ± 2.3 | 7.07 ± 0.4* | 1 | 20.3 ± 0.23* |
| tetra III(NaCl) | 526 ± 1.1* | 139 ±1.0 | 11.1 ± 0.5 | 33.3 ± 2.8 | 62.8 ± 3.5 | 16.8 ± 0.2* | 4 | 6.95 ± 0.28* |
| tr IV (C ) | 112 ± 0.9 | 132 ±1.1 | 11.7 ± 0.8 | 75.9 ± 0.7* | 58.8 ± 3.3 | 1.18 ± 0.1* | 0 | 44.1 ± 0.79* |
| tr IV (NaCl) | 117 ± 1.1 | 130 ±1.0 | 11.8 ± 1.1 | 76.2 ± 0.8* | 61.1 ± 3.9 | 1.20 ± 0.1* | 0 | 38.7 ± 0.31 |
| tetra IV (C ) | 108 ± 1.0 | 131 ±1.3 | 11.0 ± 0.7 | 189.9±1.8* | 60.8 ± 4.1 | 1.13 ± 0.1* | 0 | 40.6 ± 0.91* |
| tetra IV(NaCl) | 113 ± 1.3 | 138 ±1.8 | 12.5 ± 0.3 | 190.0±2.5* | 62.4 ± 3.7 | 1.20 ± 0.1* | 0 | 39.5 ± 0.33* |
| tr V (C) | 112 ± 1.2 | 300 ±2.7* | 10.9 ± 0.4 | 31.0 ± 2.0 | 57.4 ± 2.7 | 1.10 ± 0.1* | 0 | 43.8 ± 0.45* |
| tr V (NaCl) | 115 ± 1.4 | 297 ± 2.8* | 11.0 ± 1.2 | 32.3 ± 1.8 | 60.3 ± 2.8 | 1.17 ± 0.2* | 0 | 41.8 ± 0.39* |
| tetra V (C) | 112 ± 1.0 | 751 ± 3.5* | 10.8 ± 0.9 | 29.8 ± 1.9 | 57.7 ± 1.8 | 1.14 ± 0.1* | 0 | 38.6 ±0.53* |
| tetra V(NaCl) | 115 ± 1.7 | 739 ±3.3* | 12.2 ± 1.3 | 35.3 ± 2.0 | 59.8 ± 2.4 | 1.13 ± 0.1* | 0 | 38.3 ±0.48* |
| tr VI (C ) | 110 ± 3.3 | 133 ±1.1 | 11.5 ± 0.6 | 29.7 ± 3.3 | 59.5 ± 2.7 | 3.67 ± 1.7 | 0 | 35.7 ± 0.22 |
| tr VI (NaCl) | 109 ± 5.0 | 139 ±1.0 | 11.7 ± 0.7 | 31.5 ± 2.2 | 61.2 ± 2.8 | 8.70 ± 1.9 | 3 | 13.0 ±0.17* |
| tetra VI (C ) | 115 ±1.8 | 135 ±1.7 | 11.9 ± 1.3 | 30.0 ± 2.1 | 62.1 ± 2.3 | 3.68 ± 1.5 | 0 | 30.0 ± 0.26 |
| tr VII (C) | 111 ± 1.3 | 129 ± 0.8 | 10.3 ± 0.7 | 29.3 ± 1.8 | 20.3± 1.2* | 3.69 ± 0.3 | 0 | 28.8 ± 0.04 |
| tr VII (NaCl) | 108 ± 1.3 | 136 ±1.1 | 10.8 ± 1.0 | 30.3 ± 2.2 | 22.1± 1.2* | 10.3 ± 0.8* | 2 | 20.5 ±0.05* |
| tetra VII (C) | 115 ± 1.7 | 141 ±1.9 | 10.7 ± 1.9 | 30.7 ± 2.0 | 10.2± 0.4* | 3.83 ± 0.5 | 0 | 18.7 ±0.02* |
| tetra VII(NaCl) | 110 ± 1.2 | 144 ±1.7 | 12.0 ± 0.7 | 33.3 ± 2.5 | 10.9± 0.7* | 13.5 ± 1.5* | 4 | 9.09 ±0.07* |

**Table 2. Activities of SOD [unit $mg^{-1}$ (protein)], APX, DHAR, GR and CAT [nmol $mg^{-1}$ (protein)], $H_2O_2$ content (µmol $g^{-1}$ fresh weight), injury levels (0-4) in leaves and dry weight (DW, mg $plant^{-1}$) of shoot in disomic plants and different double trisomic types under control (C, 0mM NaCl) and 150 mM NaCl treatment in grass pea (*Lathyrus sativus* L.). Data are mean ± s.e.m of six independent experiments (n=12). * Significant (*t-test*) from disomic control at $p<0.05$.**

| Genotypes | SOD | APX | DHAR | GR | CAT | $H_2O_2$ | Injury levels | Shoot dry weight |
|---|---|---|---|---|---|---|---|---|
| Disomic (C) | 110 ± 1.2 | 137 ±1.3 | 11.3 ± 0.9 | 30.3 ± 2.9 | 60.8 ± 6.2 | 3.69 ± 0.3 | 0 | 32.6 ± 0.19 |
| Disomic(NaCl) | 113 ± 1.5 | 140 ±1.5 | 10.9 ±1.0 | 31.0 ± 2.3 | 57.5 ± 6.0 | 8.89 ± 0.4* | 3 | 12.2 ±0.10* |
| tr I-tr II (C) | 107 ± 1.3 | 140 ± 1.7 | 16.4 ±1.2* | 29.8 ± 2.2 | 60.2 ± 3.9 | 2.91 ±0.7* | 0 | 37.9 ±0.17* |
| tr I-tr II (NaCl) | 111 ± 1.3 | 139 ± 1.6 | 16.9 ±1.2* | 30.8 ± 2.8 | 62.0 ± 4.1 | 3.00 ±0.7* | 0 | 32.1 ± 0.14 |
| tr I-tr III (C) | 170 ± 1.7* | 134 ±1.2 | 11.0 ± 1.1 | 31.8 ± 3.0 | 61.0 ± 5.8 | 3.76 ± 0.6 | 0 | 31.4 ± 0.18 |
| trI-tr III (NaCl) | 297 ± 1.7* | 130 ±0.8 | 10.7 ± 1.0 | 30.1 ± 2.3 | 59.3 ± 5.3 | 4.36± 0.4* | 2 | 23.5 ±0.11* |
| tr I-tr IV(C) | 109 ± 1.3 | 135 ± 1.7 | 11.5 ±1.1 | 70.7 ±3.0* | 61.0 ± 5.6 | 2.72 ±0.6* | 0 | 38.2 ±0.18* |
| tr I-tr IV(NaCl) | 113 ± 1.2 | 140 ± 1.3 | 11.9 ± 1.5 | 73.2 ±3.5* | 59.1 ± 6.2 | 2.95 ±0.6* | 0 | 35.2 ± 0.16 |
| tr I-tr V(C) | 108 ± 3.3 | 288 ± 2.9* | 12.2 ± 1.0 | 30.6 ± 2.9 | 58.7 ± 5.7 | 2.45 ±0.3 | 0 | 41.6 ±0.16* |
| trI-trV (NaCl) | 109 ± 2.8 | 293 ± 3.6* | 11.9 ± 0.7 | 29.7 ± 4.3 | 59.7 ± 5.9 | 3.01 ±0.7* | 0 | 37.7 ±0.13* |
| tr I-trVI(C) | 109 ± 2.3 | 133 ±1.4 | 11.5 ± 0.6 | 30.7 ± 1.9 | 60.6 ± 5.7 | 3.67 ± 0.5 | 0 | 33.7 ± 0.19 |
| tr I-trVI (NaCl) | 111 ± 1.4 | 136 ±2.2 | 11.1 ± 0.8 | 29.9 ± 2.6 | 60.5 ± 5.6 | 7.77 ±2.9* | 3 | 20.5 ±0.23* |
| tr I-trVII (C) | 114 ±1.6 | 138 ±1.1 | 11.6 ± 0.4 | 31.2 ± 2.6 | 61.3 ±4.7 | 3.60 ±1.1 | 0 | 32.3 ±0.17 |
| trI-trVII(NaCl) | 115 ± 1.7 | 135 ±1.2 | 11.0 ± 0.7 | 29.8 ± 2.3 | 60.3 ±4.4 | 3.72 ±1.4 | 0 | 31.6 ±0.21 |
| tr II-tr III (C) | 167 ±1.3* | 134 ±1.1 | 15.9 ±1.2* | 31.0 ± 1.9 | 59.2 ± 4.5 | 3.77 ± 0.7 | 0 | 40.1 ±0.11* |
| tr II-trIII(NaCl) | 319 ±5.0* | 136 ±2.1 | 16.6 ± 1.3* | 29.0 ± 2.1 | 58.5 ± 5.5 | 3.81 ± 1.1 | 0 | 37.8 ± 0.17 |
| tr II-tr IV (C) | 109 ±1.3 | 139 ±0.1 | 17.1±0.7* | 69.5 ±3.0* | 59.1 ± 5.0 | 1.60 ±1.1* | 0 | 45.9 ±0.19* |
| tr II-tr IV (NaCl) | 114 ± 1.6 | 139 ±0.1 | 17.8±1.1* | 70.7 ±4.0* | 60.1 ± 5.0 | 1.60 ±1.1* | 0 | 42.2 ±0.37* |
| tr II-tr V (C) | 117 ±1.7 | 298±1.2* | 16.7±0.6* | 32.8 ± 2.2 | 61.4 ± 5.2 | 1.18 ±0.9* | 0 | 47.5 ±0.10* |
| tr II-trV (NaCl) | 119 ± 1.8 | 294±1.5* | 16.1±0.3* | 31.5 ± 2.5 | 60.1 ± 5.1 | 1.20 ±1.1* | 0 | 43.9 ±0.23* |
| tr II-tr VI(C) | 113 ± 2.0 | 136 ±1.1 | 16.7±0.9* | 30.8 ± 4.4 | 60.4 ± 5.0 | 3.01 ±0.9* | 0 | 40.5 ±0.18* |
| trII-trVI (NaCl) | 110 ± 1.8 | 133 ±1.5 | 15.9±0.5* | 31.0 ± 4.7 | 61.1 ± 5.3 | 3.37 ± 1.2 | 0 | 33.8 ± 0.14 |
| trII-trVII (C) | 111 ± 1.3 | 130 ±1.2 | 16.8±1.0* | 29.2 ± 2.8 | 60.1 ± 6.6 | 3.20 ± 1.0 | 0 | 30.7 ± 0.18 |
| trII-trVII(NaCl) | 115 ± 1.1 | 137 ±1.8 | 16.3±1.6* | 30.3 ± 3.1 | 61.6 ± 6.0 | 3.71 ± 1.4 | 0 | 29.9 ± 0.20 |
| tr III-tr IV(C) | 162 ±1.4* | 136 ±1.6 | 11.5 ±0.9 | 75.5 ±3.1* | 61.0 ± 6.0 | 3.30 ± 0.6 | 0 | 45.2 ±0.05* |
| trIII-trIV(NaCl) | 320 ± 7.2* | 138 ±1.9 | 12.3 ± 1.4 | 73.0 ±3.7* | 58.1 ± 6.0 | 3.29 ± 0.8 | 0 | 43.1 ±0.09* |
| tr III-tr V(C) | 175 ± 4.1* | 303±3.3* | 14.3 ± 1.1 | 30.7 ± 2.3 | 57.7 ± 6.5 | 3.15 ± 0.3 | 0 | 41.6 ±0.10* |
| trIII-trV (NaCl) | 339 ±6.9* | 299±3.1* | 12.0 ± 0.3 | 29.9 ± 4.0 | 58.3 ± 5.6 | 3.33 ± 0.7 | 0 | 38.7 ±0.10* |
| tr III-tr VI (C) | 171 ± 1.8* | 134 ± 1.1 | 11.1 ± 0.3 | 29.2 ± 2.0 | 61.0 ± 5.3 | 3.72 ± 0.3 | 0 | 31.8 ± 0.20 |
| tr III-tr VI (NaCl) | 301 ± 3.5* | 130 ± 1.8 | 10.9 ± 0.5 | 30.2 ± 2.2 | 60.8 ± 4.8 | 3.99 ±0.8* | 2 | 27.1 ± 0.16 |
| tr III-trVII(C) | 209 ±6.3* | 131 ±1.2 | 11.5 ± 0.1 | 31.6 ± 2.0 | 59.2 ± 6.0 | 4.02 ±0.9* | 1 | 23.7 ±0.18* |
| trIII-trVII (NaCl) | 365 ±1.5* | 133 ±2.0 | 11.1 ± 0.5 | 29.5 ± 2.2 | 58.5 ± 5.6 | 4.17 ±1.8* | 1 | 20.5 ±0.17* |

**Table 3. Activities of SOD [unit $mg^{-1}$ (protein)], APX, DHAR, GR and CAT [nmol $mg^{-1}$ (protein)], $H_2O_2$ content (µmol $g^{-1}$ fresh weight), injury levels (0-4) in leaves and dry weight (DW, mg $plant^{-1}$) of shoot in disomic control and different double trisomic types under control (C, 0mM NaCl) and 150 mM NaCl treatment in grass pea (*Lathyrus sativus* L.). Data are mean ± s.e.m of six independent experiments (n=12). * Significant (*t-test*) from disomic control at $p<0.05$.**

| Genotypes | SOD | APX | DHAR | GR | CAT | $H_2O_2$ | Injury levels | Shoot dry weight |
|---|---|---|---|---|---|---|---|---|
| Disomic (C) | 110 ± 1.2 | 137 ±1.3 | 11.3 ± 0.9 | 30.3 ± 2.9 | 60.8 ± 6.2 | 3.69 ± 0.3 | 0 | 32.6 ± 0.19 |
| Disomic(NaCl) | 113 ± 1.5 | 140 ±1.5 | 10.9 ±1.0 | 31.0 ± 2.3 | 57.5 ± 6.0 | 8.89 ± 0.4* | 3 | 12.2 ±0.10* |
| trIV-trV (C ) | 109 ± 1.1 | 300±6.1* | 11.0 ± 0.7 | 79.1±1.6* | 60.0 ± 8.0 | 1.93 ±0.9* | 0 | 41.4 ±0.28* |
| trIV-trV (NaCl) | 108 ± 0.8 | 296±5.8* | 11.7 ± 0.3 | 77.7±1.3* | 60.5 ± 6.7 | 2.02 ±0.4* | 0 | 40.6 ±0.22* |
| trIV-trVI (C) | 111 ± 1.3 | 137 ±1.7 | 12.2 ± 0.2 | 80.0±1.5* | 60.8 ± 6.7 | 2.59 ±0.3* | 0 | 39.3 ±0.20* |
| trIV-trVI (NaCl) | 110 ± 1.2 | 136 ±2.1 | 11.6 ± 0.7 | 79.7±1.8* | 59.5 ± 5.4 | 2.63 ±0.3* | 0 | 33.3 ± 0.22 |
| trIV-trVII(C) | 111 ± 1.0 | 137 ±1.3 | 12.0 ± 0.2 | 80.0±1.5* | 60.4 ± 6.7 | 3.19 ±0.4 | 0 | 35.5 ±0.17 |
| trIV-trVII (NaCl) | 107 ± 1.3 | 134 ±1.8 | 11.5 ± 0.5 | 80.4±1.4* | 59.8 ± 6.3 | 3.39 ±0.4 | 0 | 34.8 ±0.22 |
| tr V-tr VI (C) | 109 ± 1.5 | 267±4.9* | 11.5 ± 1.2 | 30.0 ± 2.2 | 60.0 ± 5.7 | 2.53 ± 0.3 | 0 | 40.9 ±0.19* |
| tr V-tr VI (NaCl) | 111 ± 1.0 | 255±5.0* | 11.0 ± 1.0 | 30.4 ± 2.7 | 60.9 ± 6.1 | 2.77 ±0.7* | 0 | 37.9 ±0.23* |
| trV-trVII(C) | 112 ± 1.2 | 291 ±4.2* | 11.5 ± 0.7 | 29.2 ± 2.2 | 57.9 ± 6.1 | 2.56 ±0.2* | 0 | 43.3 ±0.11* |
| trV-trVII (NaCl) | 110 ± 1.1 | 229 ±4.0* | 12.1 ± 0.8 | 30.4 ± 2.6 | 61.9 ± 6.0 | 2.88 ±0.9* | 0 | 41.8 ±0.16* |
| trVI-trVII(C) | 116 ± 2.7 | 141 ± 1.2 | 11.3 ± 0.5 | 30.2 ± 2.1 | 60.9 ± 5.8 | 3.22 ±0.5* | 0 | 37.3 ±0.23* |
| trVI-trVII (NaCl) | 121 ± 3.1 | 135 ± 1.6 | 11.0 ± 0.2 | 33.2 ± 2.1 | 56.9 ± 4.6 | 3.53 ±0.6 | 0 | 32.1 ±0.28 |

and tr IV × tr III or tr VII, to maintain their normal biomass production and to overcome NaCl-induced oxidative stress, quite efficiently over their respective trisomic parents (tr III and tr VII). The differences in extra-chromosome types between tetrasomics and double trisomics have been manifested magnificently by amplification of trisomic dosage of all five enzymes in five different tetrasomics, but by co-expression of enzyme activity at trisomic dosage in double trisomics. Furthermore, the increase or decrease of a particular enzyme activity in a specific trisomic and its progeny tetrasomic type (like SOD in tr III and tetra III) and the same trisomic dosage of that enzyme in the double trisomic, where that specific trisomic was involved as one of the parents, suggested unmodified nature of 'critical chromosome' type in self and inter-crossed progenies of a particular trisomic. As none of the enzymes over-expressed, performances of tr I and tr VI were very similar to disomic parent, exhibiting leaf injury level 3, over-accumulation of $H_2O_2$ and concomitant decrease in shoot dry weight as the marks of sensitivity to salt stress. Similar performances were manifested in double trisomics originating from crosses between tr I and tr VI. Certainly, disomic level of enzyme activity was not enough to counter the effect of NaCl-induced oxidative stress, and although trisomic and double trisomic plants countered it to some extent, tetrasomics could not nullify its effect, resulting in death of tetra I and tetra VI after five days of NaCl treatment.

Aneuploidy is generally viewed as developmentally detrimental due to perturbations of metabolism (aneuploid syndromes) by altered relationships of enzymes, but it may also be important in normal

contexts (Huettel *et al*., 2008). The derivation of additional six trisomics with altered enzyme activities from starting material of a single trisomic type (tr I) in the present study indicated shifting of 'critical chromosome' type from one trisomic to another, resulting in trichotomy of extra-chromosomal dosage: increased dosage (tr/tetra II, III, IV and V), disomic level (tr/tetra I and VI) and inverse effect (tr/tetra VII). It is also noteworthy, that, activities of other enzymes were maintained at the disomic levels when a particular enzyme over-represented in a specific trisomic type. All these indicated presence of a kind of dosage adjustment, the plants carried out to keep its cellular process functional in the background of chromosomally unbalanced aneuploids (Birchler and Veitia 2007). The aneuploid fitness was manifested by tolerance of three trisomics (tr II, IV and V) to salt stress, far better than the disomic and the other four trisomics. Increased capacity of aneuploid neuron in animal to perform diverse neural functions in normal brain can be taken as a glaring example of this fitness (Kingsbury *et al*., 2006). The balance of this dosage effect has been maintained in the present trisomics, and was not found disturbed even at higher aneuploid levels. Absence of chromosome structural variants in the present aneuploids may be one of the possible reasons behind this stability, as has recently been elucidated in grass pea karyotype (Talukdar 2010b) and in tobacco and *Arabidopsis* trisomic lines (Papp *et al*., 1996; Huettel *et al*., 2008).

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