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## **Correlation Between Meiotic Behaviour and Species Reproductive Performance and Ecological Spread: A Case Study of Eight Nigerian *Solanum* L. Species**

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### **ABSTRACT**

The unstable genomes among the diploid *Solanum* species viz: *Solanum macrocarpon*, *S. aethiopicum*, *S. gilo*, *S. anguivi* and the varieties of *S. melongena* are indicative of progressive evolutionary changes. The high occurrence of chromosome bridges, clumps unequal anaphase chromosomes and faulty cytokinesis led to the production of poor quality pollen. However, bivalents were regular in *S. torvum*, *S. erianthum* and the tetraploid *S. scabrum* while their mitotic chromosomes were small-sized and symmetrical. The diploids with unstable genomes were cosmopolitan and found in the four ecological zones while the regular and normal diploids were limited in their distribution to the savanna, arid and semi arid. However, the tetraploid *S. scabrum* was restricted to the rainforest of Southern Nigeria. The colchicine induced tetraploid and its intermediate aneuploids suggest the likely origin of the natural polyploids. Consequently, the impact of genome changes was revealed in the evolution of different adaptive features and species ability to occupy new environment.

**Key words:** Meiosis, aneuploid, polyploidy, chromosome, *Solanum*, diploidization

### **INTRODUCTION**

Meiosis is a complex but regulated cellular event that ensures continuity of life. Constant genomic changes through specific gene interactions (Kumar and Bennetzen, 1999; Bennetzen, 2002) and the synthesis of new cellular components (Kimura *et al.*, 1999) such as required for the new adaptive complexes are essential for species survival in constantly changing environment (Cai and Xu, 2007). The production of viable gametes for next generation of individual species is predicated on normal and harmonious meiosis (Pagliarini, 2000) and dependent on nuclear content, cytoplasmic inclusions and including lots of abiotic factors (Porch and Jahn, 2001; Erickson and Markhart, 2002). The emergence of novel characters is a consequence of several cytogenetic interplay that regulates gene expression pattern (Liu and Wendel, 2003; Levy and Feldman, 2004) and capable of producing new genotypes within a population (Oyelana and Ogunwenmo, 2009a).

The production of gametes with inherent numerical or structural chromosome variations have been well documented (Bretagnolle and Thompson, 1995; Page and Hawley, 2003; Kato and

Palmer, 2003) and the expanded genomes in the emerging polyploids are maintained on a somewhat different cytogenetic processes (Bennetzen and Kellog, 1997; Xu and Joppa, 2000) to ensure stability. These several meiotic processes including methylation and epistasis (Doyle *et al.*, 2008; Leitch and Leitch, 2008) and loss of sequences of DNA (Raina *et al.*, 1994; Eilam *et al.*, 2009) subsequently ensure the production of balanced gametes. This is a critical step in polyploid speciation (Rieseberg and Willis, 2007; Rezaei *et al.*, 2010) and the basis for the functionality of polyploid genomes (Carroll, 2000; Chen, 2007) and their colonization and success in new environment (Soltis *et al.*, 2003; Brochmann *et al.*, 2004).

The population analyses of *Solanum* spp. in Nigeria including similar tropical environment reveal a mix population of cytotypes viz.: diploids ( $2n = 24$ ) (Oyelana and Ugborogho, 1997; Oyelana, 1997), triploids ( $2n = 36$ ) (Bir and Neelam, 1984; Okoli, 1988), group of aneuploid numbers (Omidiji, 1983; Govindarajan and Vijayakumar, 1986) and tetraploids ( $2n = 48$ ) (Ceschmedjiev, 1976; Oyelana, 2005) growing in close proximity and constantly exchanging genes. This gives credence to a constantly expanding genome for members of this genus (Ugborogho and Oyelana, 1999; Oyelana, 2005) and the ease by which polyploids are formed following hybridization.

A number of polyploid hybrids including triploids (Gavrilenko *et al.*, 1999), Colchicine induced tetraploids (Oyelana and Ogunwenmo, 2005), pentaploids (Oyelana and Ogunwenmo, 2009b) and hexaploids (Oyelana *et al.*, 2009) were successfully generated and were able to compete favourably alongside the natural populations of diploids and tetraploids. Hijmans *et al.* (2007) reported similar mixed population of diploids, triploids tetraploids and pentaploids in Central and South America. The genus *Solanum* is diversified morphologically and are mostly shrubs to small trees, annual and rarely perennial (Omidiji, 1983; Gbile, 1985). The different species express variation and rare overlaps in growth habit and distribution (Lester and Seck, 2004) across the four ecological zones in Nigeria in spite of similar and closely related genomes (Okoli, 1988; Oyelana, 2005). Some species are habitat specific and inhabit the mountain zones, particularly the highlands of Mambilla, Obudu Vogel peak and Jos Plateau across the Nigerian savanna and arid belt while others are Lowland species (Heine, 1963; D'Arcy, 1979). The continuous morphological variations, near similar genomes, overlaps in cytological features (Gbile, 1985; Edmonds, 1986; Knapp, 1991) and emergence of new cytotypes (polyploids) could be attributed to the extensive hybridization and breeding programmes involving a number of past intra and interspecific crosses (Marfil *et al.*, 2006; Oyelana and Ugborogho, 2008) aimed at improving species productivity and agronomic qualities.

The significance of meiosis in providing the platform for the synthesis of both morphological and physiological features essential for species adaptation in new environment through a set of intrinsic network of gene regulatory mechanism is the focus of this review. Consequently, the distribution pattern of eight *Solanum* species involving ten taxa of different genomic constitution Table 1 is analysed to establish any correlation (s) between meiotic behaviour and the performance or productivity of the different species across the four different ecological zones in Nigeria.

## **MEIOTIC BEHAVIOUR AND STRUCTURAL CHANGES IN THE SPECIES' CHROMOSOMES**

The diploid and tetraploid chromosome numbers of  $2n = 24, 48$  (Omidiji, 1983; Okoli, 1988; Oyelana and Ugborogho, 1997; Oyelana, 2005) revealed 12 and 24 bivalents, respectively for the diploid and Tetraploid species. However, the variants:  $n = 10, 13, 18$  and  $22$  (Ceschmedjiev, 1976; Labadie, 1976; Oyelana and Ugborogho, 1997) and  $2n = 20, 22, 26$  and  $28$  (Gill, 1975; Crompton and Bassett, 1976; Leslie, 1978; Bir *et al.*, 1978; Oyelana, 2005) constitute the

Table 1 : Species cytological traits and ecological distribution

Group	Species	Ploidy	Meiotic behaviour	Somatic chromosomes	Ecological distribution	Remarks
1	<i>S. erianthum</i> ; <i>S. torvum</i>	Diploid 2n = 24	Regular meiosis and stable genomes. Regular pollen and Species highly fertile	Chromosomes small-sized, metacentric and symmetrical in shape	Savanna, Arid and semi-arid zones	Small trees to shrubs. Generally regarded as weeds
2	<i>S. macrocarpon</i> , <i>S. aethiopicum</i> , <i>S. anguini</i> , <i>S. gilo</i> , <i>S. melongena</i> var. <i>Golden</i> and var. <i>Melongena</i>	Diploid, 2n = 24 including 2n = 20, 22 and 26 Cytotypes	Irregular meiosis: multivalents, chromosome clumps, unequal anaphase chromosomes, chromosome bridges. Unstable genomes. Regular to irregular pollen and sp. fairly fertile	Large chromosomes and asymmetrically shaped. Combination of metacentric, submetacentric and subtelocentric chromosomes.	Cosmopolitan (broad-based and found in all identified zones); wide spread in savanna, arid, semi arid and rainforest zones.	Domesticated. shrubs and cultivated as fruit and leafy vegetables
3	<i>S. scabrum</i> subsp. <i>scabrum</i> and subsp. <i>erectum</i>	Tetraploid 2n = 48	Regular meiosis and stable genomes. Regular pollen. Species very fertile	Chromosomes small-sized, symmetrical and mostly metacentric.	Rainforest zone	Herbs and medicinal

Adapted from Oyelana and Ugborogho (1997)

aneuploid cytotypes particularly among the diploid populations of *Solanum macrocarpon*, *S. gilo*, *S. aethiopicum*, *S. anguivi* and the varieties of *S. melongena*. The few triploids including *S. nigrum* (Vasudevan, 1975) and hexaploid in *S. erianthum* (Crompton and Bassett, 1976; Leslie, 1978) have been reported. Meiosis was normal with regular bivalents in *S. erianthum*, *S. torvum* and the two sub species *S. scabrum*. Their somatic chromosomes length were found as small-sized (1.29-1.88 $\mu$ m), symmetrical and mostly metacentric to submetacentric. The homomorphic pairs revealed 6 long and 6 short and all 24 short chromosomes, respectively for the two diploids (*S. erianthum* and *S. torvum*) and the tetraploid (*S. scabrum*) (Oyelana, 2005).

The deviation from the basic chromosome number and the existence of aneuploid in *S. macrocarpon*, *S. gilo*, *S. anguivi*, *S. aethiopicum* and *S. melongena* suggest extensive meiotic irregularities. The unstable genomes and the high occurrence of diads and triads may have generated the 2n gametes reported for some members of this group (Oyelana and Ugborogho, 1997; Oyelana, 2005). Lagging and unequal anaphase chromosomes as commonly observed in *S. aethiopicum* and the varieties of *S. melongena* may have been responsible for the production of diads and triads through faulty cytokinesis in these species.

Rezaei *et al.* (2010) attributed the production of polyads in wheat to this phenomenon. Lyrene *et al.* (2003) explained that the occurrence of unreduced gametes from faulty cytokinesis may constitute a major mechanism for the emergence and wide spread of polyploids. Chromosome breaks and shift in centromeric positions may have produced the large (2.33-3.52 $\mu$ m) and asymmetrically shaped chromosomes in *S. melongena*, *S. macrocarpon*, *S. anguivi* and *S. gilo* (Oyelana, 2005). Genome arrangement involving relocation of chromosome segments equally gave rise to asymmetrical chromosomes in *Hepatica nobilis* var. *pubescens* (Weiss-Schneeweiss *et al.*, 2007).

Evidently, the pachytene chromosomes revealed inversion loops in *S. aethiopicum*, *S. melongena* 'Melongena', *S. anguivi* and *S. macrocarpon*. A few x-shaped chromosomes in *S. aethiopicum* and *S. melongena* 'Golden' suggests possible chromosome inversion and segment duplication in these diploid species as mentioned by Oyelana and Ugborogho (1997). Consequently, the emergence of subtelocentric chromosomes in this second group of diploid species (Oyelana, 2005) appears a recent development and suggesting that the metacentric chromosomes are primitive features in members of this genus as observed in the first and third groups of species.

This feature (Karyotype) has severally been used to assess phylogenetic relationships between Angiosperm species (Pandit and Badu, 1993; Pringle and Murray, 1991). The presence of isolated chromosomes may further explain the inclusion of foreign gene through past hybridization efforts (Oyelana and Ugborogho, 1997) and the source of genomic instability in members of this second group of diploids.

## MEIOSIS, SPECIES REPRODUCTIVE SUCCESS AND VIGOUR

Excessive multivalents and chromosome clumps are known to generate illegitimate meiotic recombination (Cai and Xu, 2007) thereby counteract genome expansion and produce unequal cross-over (Wicker *et al.*, 2003; Ma *et al.*, 2004). These two major processes may have constituted the major force 'downplaying' the potentials inherent in most diploid *Solanum* species. The hybrids (2n = 24) from *S. gilo* × *S. aethiopicum* (Ugborogho and Oyelana, 1999) had no fruits while the hexaploid hybrid (2n = 72) of *S. melongena* 'Golden' (2n = 24) × *S. scabrum* sub species *scabrum* (2n = 48) was morphological similar to the male parent and without any special agronomic feature of economic values (Oyelana *et al.*, 2009). Also the inherent chromosome mutations (Ugborogho and Oyelana, 1999) existing in the genomes of both or either parent species may have downplayed the potential of an expanded genome in this hexaploid hybrid.

The increasing number of polyploids in *S. tuberosum* was linked to the occurrence of 2n gametes resulting from faulty asynapsis and desynapsis (Ramanna, 1983), abnormal spindle orientation at the second division (Veilleux *et al.*, 1982) and abnormal cytokinesis (Mok and Peloquin, 1975). The presence of a modulating mechanism worked through these genomic changes and significantly lowered pollen viability to 8 and 49.7%, respectively in the F<sub>1</sub> diploid hybrid and its backcross from *S. gilo* × *S. aethiopicum* compared to the 83.8 and 90% in both male and female parents. The 71 and 97.4% pollen viability in the male and female parents *S. melongena* 'Golden' × *S. scabrum* sub species *scabrum* was reduced to 38.2% in the hexaploid hybrid and these two hybrids produced intermediate values for most of the morphological features (Ugborogho and Oyelana, 1999; Oyelana *et al.*, 2009).

Meiotic abnormalities and consequent low meiotic indexes (few dividing cells) were equally observed in *Adesmia ciliate* (Tedesco *et al.*, 2002) and adduced for the low pollen fertility. Equally the low percentage of pollen fertility in certain hybrids (Bione *et al.*, 2000) was attributed to meiotic abnormalities.

Chromosome arm rearrangement was adduced for the reduction of fertility in hybrids involving interspecific crosses among certain taxa of the genus *Draba* (Skrede *et al.*, 2008). A possible large dosage of recessive alleles from cross-over of genes and exchange of chromosome segments between homologous pairs may have contributed to the reduction in fertility in this second group of diploids. The high rate of multivalents and chromosome clumps in these diploid species equally help confirm the extent of homogeneity of genomes in this group of species.

The low pollen fertility in two of the thirteen species of *Leucaena* (Boff and Schifini-Wittmann, 2002) was attributed to the degree of multivalent chromosomes and chromosome stickiness. Jiang *et al.* (2011) demonstrated that in *Epimedium acuminatum*, *E. pubescens*, *E. chlorandrum*, *E. davidii* and *E. ecalcaratum* with 11, 8.6, 31.6, 38.3 and 3.3% meiotic abnormalities revealed a corresponding 82, 87, 80, 76.6 and 90% pollen fertility.

The occurrence of diads and triads has been linked to poor quality pollen in *Solanum* species and the subsequent small sized fruits and low number of seeds in fruits (Oyelana and Ogunwenmo, 2009a,b). Mendes-Bonato *et al.* (2001) and Caetano-Pereira and Pagliarini (2001) linked the occurrence of sterile pollen to the formation of diads, triads and polyads and which often manifests in reduction of the number of seeds in fruits (Stone *et al.*, 1995).

The reduction in the sizes of most morphological features including number and dimension of leaves in the tetraploid *S. scabrum* shows an unexpected departure from the predicted additive effects of genome doubling. An epigenetic modulating mechanism may have helped restored a diploid-like behaviour and appearance in this tetraploid. Soltis *et al.* (2007) observed a number of natural autopolyploids which were typically morphologically similar to their diploid progenitors. However, this natural autotetraploids (the two sub species of *S. scabrum*) were resistant to the larvae of *Papilio polyxenes* (*Lepidoptera*) and adults of *Toxoptera graminum* (*Homoptera*) (Oyelana, 1997). This special feature offered them a competitive advantage over their diploid relatives found growing in the rainforest where these insects were prevalent and according to Felber (1991) and Schranz and Osborn (2004), higher tolerance of stress and diseases allow polyploid plants to occupy new ecological niche and expand their geographical range.

## MEIOSIS AND SPECIES GENOME UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

Meiotic behaviour and estimate of pollen fertility help assess species potentials for reproductive success, genetic variability, biodiversity and survival in new environment

(Boff and Schifini-Wittmann, 2002). The genomic instability in the second group of diploid species and their ability to be wide spread across the four eco-geographical zones of Nigeria over and above the other diploid and Tetraploid species (with much stable genomes but somewhat restricted distribution) may highlight the adaptability of genome in a new environment.

The whole process of meiosis is under some form of genetic and environmental control as explained by Porch and Jahn (2001), Sun *et al.* (2004) and Bajpai and Singh (2006). The temperature range of the typical savanna and semi arid zones may have impacted the processes of meiosis and gametogenesis in this second group of diploid species and which led to the production of the different aneuploid cytotypes. The unstable genome and irregular meiosis equally reflect in high number of asymmetrical chromosomes in these species They are less fertile and the number of hybrids produced from crosses involving these species was rarely fertile.

However, the first group of diploid species had smaller and symmetrically shaped chromosomes, highly fertile and readily produce viable hybrids. Fuzinato *et al.* (2008) highlights the impact of high temperature and reduction in microspore development and they linked this to low pollen viability. According to Dafni and Firmag (2000) and Palma-Silva *et al.* (2008), the quantity and quality of pollen do not only ensure reproductive success but equally reflect the impact of environment on the process of gametogenesis and the success of any breeding programme.

The preponderance of (2n) gametes in the members belonging to the second group of diploids was attributed to meiotic abnormalities and faulty cytokinesis (Oyelana and Ugborogho, 1997). These two meiotic processes have been closely associated to the impact of the environment (Brochmann *et al.*, 2004; Parisod *et al.*, 2010) and were equally confirmed to trigger the production of (2n) gametes and subsequent development of polyploids.

The relative improvement in pollen viability, increase number of seeds and bigger fruits in the backcross progeny from *S. gilo* × *S. aethiopicum* (Ugborogho and Oyelana, 1999) and the vigorous growth and bigger fruits in the pentaploid hybrid from the cross involving *S. macrocarpon* and its colchicine induced mutant (Oyelana and Ogunwenmo, 2005) help confirm the presence of a mechanism for genome repairs in these species This equally affirms that the inherent chromosomal abnormalities in this group are transient (environmental) and not as a result of permanent mutations.

### **IMPAIRED MEIOSIS, INCREASED ANEUPLOIDY AND HIGHER POLYPLOIDY**

The members of the second group of diploids have under gone intense breeding and selection process for decades (Omidiji, 1983; Oyelana, 1997). They are majorly introduced plants which later became domesticated as these species constitute both the fruit and leafy vegetables among the different tribes in Nigeria and across the West Africa subregion (Gbile, 1985; Oyelana, 1997). The stress of adapting to new environment may have contributed to the observed genomic changes in members of this group. The first group of diploid and the tetraploid are more of natural species, less cultivated and grow in the wild. According to Parisod *et al.* (2010), the rate of autopolyploid formation increases with increasing environmental stress. Hence, the production of unreduced gametes through which polyploids are frequently formed is stimulated by environmental factors such as temperature, water and nutrient stress (Ramsey and Schemske, 1998).

The subsequent evolution of tetraploid genome in *S. scabrum* could be attributed to doubling of chromosome number via faulty cytokinesis and fusion of 2n gametes following crosses involving two distantly related diploid species Increased aneuploidy is equally an established phenomenon of evolutionary significance in this group. The preponderant of aneuploid cytotypes in

the second group of diploids may continue to generate other higher levels of ploidies (Mehra, 1976; Aminuddin *et al.*, 1985; Oyelana, 2005) as described in some reports. This is may be a driven force in the evolution of higher ploidy in this group of species.

Oyelana and Ogunwenmo (2005) successfully induced an autotetraploid mutant ( $2n = 48$ ) from a diploid genome ( $2n = 24$ ) and other aneuploid intermediates using different concentrations of colchicine. The regular bivalents and the small-sized chromosomes in the colchicine induced autotetraploid may help confirm *S. scabrun* as natural autotetraploid. *Biscutella laevigata* (an autotetraploid) showed successive downsizing of its genome (Konig and Mullner, 2005) while Rivero-Guerro (2008) established a corresponding decrease in chromosome length for most autopolyploids.

A number of triploids (Omidiji, 1983) and pentaploids (Sangowawa, 1986; Okoli, 1988) hybrids have been reported for the genus and were claimed to have arisen through the production of  $2n$  gametes. Oyelana and Ogunwenmo (2009b) produced a pentaploid hybrid ( $2n = 60$ ) by crossing an aneuploid mutant with its natural relative ( $2n = 24$ ). The hybrid was vigorous, stout and highly fertile.

## CONCLUSION

The haploid number viz: 10, 13 and 18 confirmed the preponderance of the aneuploid series with  $2n = 20, 22, 26$  and  $28$  and the tetraploid *S. scabrum* ( $2n = 24$ ) as earlier reported. The seemingly low meiotic index in the colchicine induced mutants and the high meiotic irregularities helped trace the source of low pollen fertility in *S. melongena*, *S. macrocarpon*, *S. anguivi* and *S. aethiopicum* and the reason for poor hybrids from crosses involving members of this group. However, the viable and vigorous hexaploid hybrid ( $2n = 72$ ) from *S. melongena* × *S. scabrum* supports the evidence of the presence of genomic repair mechanism operating to restore normal meiosis and cytokinesis in some member species and subsequently the possibility for an expanded genome through successful hybridization. The diploid species with unstable genomes were broad-based (cosmopolitan) in distribution across the four ecological zones in Nigeria, the tetraploid *S. scabrum* was restricted to the rainforest zone while *S. erianthum* was predominant in the savanna and arid ecological zones.

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