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Germplasm evaluation in genus *Carex* of family Cyperaceae

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Abstract- To prepare a database of germplasm diversity in the Indian sedges, cytological studies were initiated on population basis from Punjab plains and adjoining areas. About 2000 taxonomical species have been recorded for major genus *Carex* but the cytological picture is quite dismal at the world level with chromosome records for only 579 species and 14 out of about 148 Indian species. The chromosome number varies from 2n=12 to 2n=114 on worldwide basis. Polyploids, intraspecific and aneuploid cytotypes are very common. Data suggest the existence of x=6, 7, 8, 9, 10, 11, 13, 17 and 19. Chromosome numbers 2n=60 is most frequent which support x=6 as the primary base numbers for *Carex.* The genus is dominated by polyploids with 98.96% of the taxa being polyploid ranging from 4x-12x ploid level. The chromosome size of the genus is small which support the breakage of diffuse centric chromosomes to account for existence of high %age of chromosome number variations which are perpetuated through vegetative multiplication prevalent in the family.

Index Terms- Aneuploidy, Diffuse centric chromosome, Germplasm, Polyploidy, Sedge, Vegetative propagation.

I. Introduction

Family Cyperaceae to which belong the sedges is one of the largest and widely distributed families of the monocots represented throughout the world by about 4000 species (Santapau and Henry 1973). In India around 400 species of the family are found as dominant constituent of the marshy flora. Due to prevalence of chromosomal diversity, polyploidy and aneuploidy coupled with vegetative means of propagation, the family forms a very good object to understand the various evolutionary processes involved in speciation. Some of the genera like *Carex, Cyperus, Scirpus*,etc. show high polyploid and aneuploid series.

The importance of cytology as one of the parameters to solve the problems related to interrelationships and evolution of plant groups, their reproductive behaviour and their systematic disputes has been realized long ago. Sedges have also attracted good attention particularly from Japan, Europe and North America. As far as Indian sedges are concerned cytological studies have been done by Sharma and Bal (1956), Sanyal and Sharma (1972), Rath and Patnaik (1974, 1978), Mehra and Sachdeva (1975a,b; 1976) from Eastern India; Nijalingappa (1972, 1973, 1975, 1977), Nijalingappa and Leela Bai (1990), Nijalingappa *et al.* (1978), Tejavathi and Nijalingappa (1990), Subramanium (1988) from Southern India and Bir and Cheema (1994), Cheema (1991), Cheema *et al.* (1992a,b; 1993a,b), Bir *et al.* (1982; 1986; 1988a, b; 1990a,b; 1991; 1992a,b; 1993a,b; 1996), Cheema and Bir (1994a,b; 1995; 1996; 1997), Wujek *et al*. (1997), Kaur and Gupta (2008-2009), Cheema and Gupta (2011, 2012) from Punjab state of NW India.

There has been a considerable confusion about phylogenetic and systematic position of the family as well as delimitation of some genera within family. Frequently different members belonging to one genus are transferred to another. Hooker (1897) divided the family into four sections **Cypereae** including tribes Eucypereae, Scirpeae and Rhynchosporeae; **Hypolytreae**; **Sclerieae** and **Cariceae**. To assess the evolutionary patterns of sedges, in present communication an attempt has been made to elucidate the total chromosomal diversity in the *Carex* at India and world level based on chromosomal data available till date. Approximately 16% of described *Carex* species have been sampled (Roalson, 2008).

II. Collection of chromosomal data

All the available information on chromosome numbers of *Carex* has been documented and analysed from Darlington and Wylie (1955); Fedrov (1969); Index to Plant Chromosome Numbers (1970–2003)compiled by Goldblatt (1973-2003); IOPB chromosome number reports published in Taxon from 1965 onwards and Biological Abstacts from 1971 onwards; Roalson (2008) and other recent papers published in different journals and internet sites.

III. Chromosome numbers

Carex Linn. with an estimated 2000 species is the largest genus of the family Cyperaceae. In India, it is represented by 148 species of which 22 occur in South India (Clarke 1894 , Fischer 1931). On the basis of inflorescence morphology, Kükenthal (1909) divided this genus into four subgenera and reorganized 69 sections. In addition, *Carex* has remained a classic example of cytotaxonomic confusion (Heilborn 1939). A perusal of literature pertaining to the cytology of *Carex* revealed that a majority of the species investigated are from temperate zones and many tropical ones have remained either untouched or insufficiently examined. Considering the size of this genus, the cytological work done in India is very inadequate.

The variation of chromosome numbers within the genus and even within the species is quite common in Cyperaceae. At world level 249 species out of 579 and at India level 7 species out of 14 show either intraspecific or aneuploid cytotypes as reflected in Table 1. Further *Carex* is characterized by very high aneuploid chromosome numbers. These range from 2n=12 in

Carex ciliato-marginata, *C. siderosticta* Hance to 2n=114 in *C. cuspidata* Host, *C. hirta* Linn. and *C. pilosa* Scop. Thus like Poaceae, the *Carex* and in turn Cyperaceae represents a group of flowering plants with highly variable chromosome numbers.

From Fig.1, it is concluded that chromosome number in the genus ranges from 2n=12 to 2n=114 with 2n=60 (75 taxa) being the most frequent followed by 2n=56 (62 taxa), 2n=58 (60 taxa) and 2n=68 (58 taxa). The variation on the lower and higher side might have been due to phylogenetic decrease and increase in the chromosome numbers at diploid level.

IV. Diffuse centromere

Chromosomes in Cyperaceae are diffuse centric or holocentric or polycentric meaning that centromeric activity is distributed along the entire chromosome (Håkansson 1954). Heilborn (1928) noted that *Carex* chromosomes lack an obvious constriction, but it took more precise studies (Sharma and Bal 1956) to demonstrate that this was due to lack of a localized centromere. Holocentry had previously been identified in the chromosomes of the Juncaceae (De Castro 1950; La Cour 1952), the sister family to the Cyperaceae. In holocentric chromosomes, fragments that arise by breakages are retained during meiosis and inherited in Mendelian fashion (Faulkner 1972; Luceño 1993). Consequently, breakages may result in viable gametes with aneuploid numbers that can become stabilized through backcrossing or selfing. Holocentric chromosomes occur throughout the Cyperaceae and Juncaceae as well as in four other Angiosperm genera *Cuscuta* L. subgenus *Cuscuta* (Pazy and Plitmann 1994; Guerra and García 2004), *Drosera* L. (Sheikh *et al.* 1995), *Chionographis* Maxim. (Tanaka and Tanaka 1977), and *Myristica fragrans* Houtt. (Flach 1966). It has been suggested that non-localized centromeres, i.e. holocentric chromosome structure appears to be uniform across the Cyperaceae.

V. Post-reductional meiosis

Unlike most groups of organisms, the Cyperaceae undergo post-reductional meiosis. In pre-reductional meiosis, which is the more common type, homologous chromosomes segregate in the first round of meiosis, and sister chromatids segregate in the second. In post-reductional meiosis, this order is reversed (Battaglia and Boyes 1955). Post-reductional meiosis was first observed in *Carex* by Heilborn (1928) and demonstrated conclusively by Wahl (1940) whereas Tanaka (1941) had reported pre-reductional meiosis from the Cyperaceae. The order of meiosis has been confirmed, however, using molecular cytogenetic methods (Hoshino *et al.* 1999). Invariably associated with post-reductional meiosis in angiosperms is the absence of localized centromeres (Battaglia and Boyes 1955). Chromosomes in sedges and other organisms that undergo post-reductional meiosis are holocentric.

VI. Base numbers

A perusal of literature reveals that the basic number in Angiosperms vary from x=2 in *Haplopappus* of Compositae to x=44 in *Uncinia* of Cyperaceae. Stebbins (1950) considered x=10 or lower numbers as the base numbers of the primary origin and all the other numbers as secondary base numbers. It may be stressed here that adequate data pertaining to chromosome numbers is a foremost necessity for deducing base number of a genus.

As far as family Cyperaceae is concerned, a lot of confusion exists about the base numbers. According to Wulff (1939), x=5 is supposed to be the original base number of the whole family and it is also supported by Mehra and Sachdeva (1975b) where as Subramanium (1988) considered the existence of x=8 as the primary base number for the family. According to him x=8 should have given rise to other basic numbers x=9, 10, and 11 by means of aneuploidy. An analysis of various basic chromosome numbers on world-wide basis reveals that many genera show dibasic, tribasic or polybasic nature.

Various base numbers reported in the largest genus of the family, *Carex* are x=6, 7, 8, 9, 10, 11, 13, 17 and 19. The chromosome numbers recorded for this genus range between 2n=12 to 2n=114. The occurrence of this unusually wide range of chromosome numbers which are not in multiples of any common basic number led earlier workers to postulate different basic numbers. Heilborn (1924) inferred the base number of *Carex* to be 7 while Wahl (1940) suggested x=5, 6, 7 and 8. Supporting Heilborn, he believed that many of the species are derived by secondary polyploidy balancing at a number just below or just above the real euploid numbers from the species with a basic number 7 which is the most common. Löve *et al.* (1957) argues for a base number of x=5. Both Heilborn and Löve *et al.* however, believed that chromosome numbers were essentially invariant within species, and consequently they considered base numbers within the genus to be readily inferable from counts of individual species. A more recent study finds majority of the chromosome numbers as multiples of 6 (Roalson *et al*. 2007). Present analysis also support 6 as base number as reflected by chromosome maxima at 2n=60 (Fig. 1). According to Hipp *et al*. (2009) the concept of base numbers may not be useful in *Carex* because of the uncertainty in chromosome numbers due to intraspecific variation prevalent in the genus.

Large variation in basic numbers clearly reflect the role of aneuploidy and neopolyploidy in the origin of these numbers.

VII. Polyploidy

Sedges exhibit a wide range of chromosome numbers which is clear indication of the prevalence of polyploidy. On world-wide basis the overall polyploidy in Cyperaceae has been estimated to be 77% (Goldblatt 1980) and 94.7% (Bir *et al.* 1988a). As far as Indian sedges are concerned 89% of them are noticed to be by Bir *et al.* (1988a), 85.5% by Cheema (1991), 72.3% by Cheema and Bir (1997) and 90% at world level and 87.64% by Cheema and Gupta (2012).

In *Carex*, 98.96% at world level and 100% Indian species are found to be polyploidy (Table 1). Various levels of ploidy in the tribe are 2x, 4x, 5x, 6x, 7x, 8x, 9x, 10x, 11x and 12x with 10x being the most frequent. So it can be concluded that higher grades of polyploidy are very common in the genus.

Autopolyploidy and allopolyploidy

Polyploidy has been demonstrated in a few species in the genus (Tanaka, 1949), though it plays a much more important role in chromosome evolution in the rest of the family (Luceño *et al*. 1998; Vanzela *et al*. 2000; Yano et al. 2004; Yano and Hoshino 2005). Yano *et al.* (2013) has reported polyploidy as significant player in the chromosomal variations in *Siderostictae* section of *Carex*. According to Löve et al. 1957 the only case of polyploid speciation with invariant chromosome numbers in *Carex* is in section *Chlorostachyae* Tuck. Ex Meinsh. (=*Capillares* (Asch. and Graebn.) Rouy). However, this study, which suggests speciation associated with autopolyploid changes in chromosome number, is based on mitotic counts, and it is difficult to interpret type of ploidy in *Carex* except in species with the lowest numbers (Hipp *et al*. 2009).

Autopolyploidy is well documented in just three carices (Tanaka 1949) e.g. *Carex siderosticta* Hance. (2n=12, 24), *C. dolichostachya* Hayata subsp. *dolichostachya* (=*C. multifolia* Ohwi) (2n=30, 60, 64, 65, 66). As hypothesized by Heilborn (1924) and supported by most subsequent workers, allopolyploidy is rare if present at all in *Carex*. Only two taxa, *C. jacIkiana* Boott subsp. *parciflora* (Boott) Kük. (=*C. parciflora* Boott) and *C. roraimensis* Steyerm. have been proposed to have allotetraploid origin.

Infraspecific Polyploidy

Infraspecific cytotypes have been observed in about 20 species (table 1) e.g. *C. filicina* Nees (2n=14, 42), *C. flacca* Schreb. (2n=38, 76), *C. humilis* Leyss. (2n=36, 72), *C. insniae* Koidz. (2n=50, 60) etc. Infraspecific agmatoploidy or aneuploidy is widespread in *Carex* (Tanaka 1940a,b, 1948, 1949; Wahl 1940; Faulkner 1972; Whitkus 1981, 1988, 1991; Cayouette and Morisset 1985, 1986a, b; Luceño and Castroviejo 1991; Hoshino et al. 1994; Hoshino and Waterway 1994; Rothrock and Reznicek 1996, 1998; Naczi 1999). Some species exhibit variation within populations (Luceño and Castroviejo 1991) or even individual plants (Schmid 1982; Luceño 1994). The different euploid chromosome races within species all show regular meiosis and are indistinguishable from one another morphologically (Schmid 1982; Cayouette and Morisset 1986b; Whitkus 1988; Rothrock and Reznicek 1996, 1998), though some chromosome races exhibit disrupted meiosis (Cayouette and Morisset 1986b).

A few studies demonstrate apparent correlations between geography and infraspecific chromosomal variation. While the incidence of polyploidy across angiosperms increases with latitude (Grant 1981) there is not a general correlation between latitude and chromosome number in *Carex* (Hipp *et al*. 2009).

Aneuploidy

Cyperaceae is characterized by extensive aneuploid series as stated by Stebbins (1971). High aneuploid series of chromosome numbers found in the family are probably modified form of polyploidy through increase or decrease in chromosome number (Stebbins 1950). Chromosomal records for *Carex* indicate widely varying chromosome numbers for the genus with 249 cytotypes at world level and 7 Indian cytotypes with more than one base number or aneuploidy. H**å**kansson (1954), Jones (1978) and Sachdeva (1972) have suggested centric fission and fusion as one of the main factors responsible for aneuploidy in Cyperaceae with diffuse nature of centromere.

Chromosome number change in most angiosperms proceeds by duplication of chromosomes, but in *Carex* these are primarily by fission and fusion (Wahl 1940; Davies 1956; Hoshino 1981, Hipp *et al*. 2009). Malheiros-Gardé and Gardé (1950) coined the term agmatoploidy to describe chromosome number changes via fission in *Luzula* (Juncaceae). The term has subsequently been used to describe decreases due to fusion as well (Löve et al. 1957; Luceño 1994). Agmatoploidy contrasts with strict or quantitative aneuploidy, which refers to chromosome number changes due to duplication of single chromosomes. Heilborn (1924) held that although chromosome fission probably played a role in the origins of *Carex*, more recent chromosome number increases in the genus must be a consequence of chromosome duplications. Further, according to Rothrock and Reznicek (1998) the presence of only even-numbered haploid counts and tetravalents in most individuals counted suggests that chromosome number change in that species may be associated with chromosome duplication rather than or in addition to agmatoploid changes.

VIII. Conclusion

While there have been more than 4,000 chromosome counts in the family, these only represent approximately 16% of the species currently recognized in the Cyperaceae. Further, the maximum counts have been made in *Carex*, with few or no counts made in many genera. Assessment of the counts presented here is also complicated by questions of specimen identification accuracy and a lack of vouchers in some prominent studies of chromosome number variation in the family. Despite this, the patterns of chromosome number distributions within family suggests that while aneuploidy may dominate the overall pattern of chromosome number there is evidence for both aneuploid and polyploid chromosome number changes within the genera. From the above discussion it is clear that the chromosomal variations in number have played a major role in the speciation and genetic diversity in the *Carex*. Further to elucidate the relationships in this complex group, there is a need for integration of biosystematic, cytogenetic and genomic studies across the genus and to have more information from the modern tools of genetic markers at DNA level.

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Table 1 Data on total number of taxonomically and cytologically known species, level and frequency of polyploidy, frequency of different cytotypes and probable base number/ in genus *Carex* Linn. on World basis (+) and from India (++)

Genus	Total no of taxono-mically known species	No. of cytologically worked out species			%age of poly-ploidy	Levels of ploidy	Total number of cytotypes	Known chromosome number (2n) Fig. in parenthesis represent the no. of cytotypes	No. of species with intraspecific cytotypes at the same base number which is in parenthesis	No. of species with more than one base number or aneuploid cytotypes	Probable base numbers*
		Total	Diploid	Polyploid							
+	1500-2000	579	6	573	98.96	2x, 4x, 5x, 6x, 7x, 8x, 9x, 10x, 11x, 12x	1144	12(2),14(2), 16(2), 18(6), 20(2), 24(3), 25(1), 26(10), 28(3), 30(12), 32(14), 33(3), 34(19), 35(4), 36(20), 38(26), 39(3), 40(27), 41(1), 42(15), 43(1), 44(24), 46(20), 48(33), 50(35), 52(53), 54(49), 55(2), 56(62), 58(60), 60(75), 61(2), 62(43), 63(2), 64(46), 65(1), 66(42), 67(5), 68(58), 69(6), 70(52), 71(2), 72(37), 73(4), 74(45), 75(3), 76(48), 77(6), 78(30), 79(4), 80(41), 82(1), 84(32), 85(3), 86(10), 88(7), 90(5), 92(3), 94(1), 98(2), 100(1), 104(2), 105(1), 106(2), 108(1), 110(1), 112(4), 114(3)	2(6), 3(7,9,19), 4(8), 10(10), 1(13,17)	249	6, 7, 8**, 9**, **10**, **11**, **13**, **17, 19**
++	148	14	-	14	100.00	6x, 8x, 10x, 12x	19	42(2), 44(3), 46(3), 48(2), 52(1), 58(2), 60(2), 68(1), 74(1), 84(1), 104(1)	-	7	6, 7, 8, 9, 10, 13

*Base numbers in bold are more common

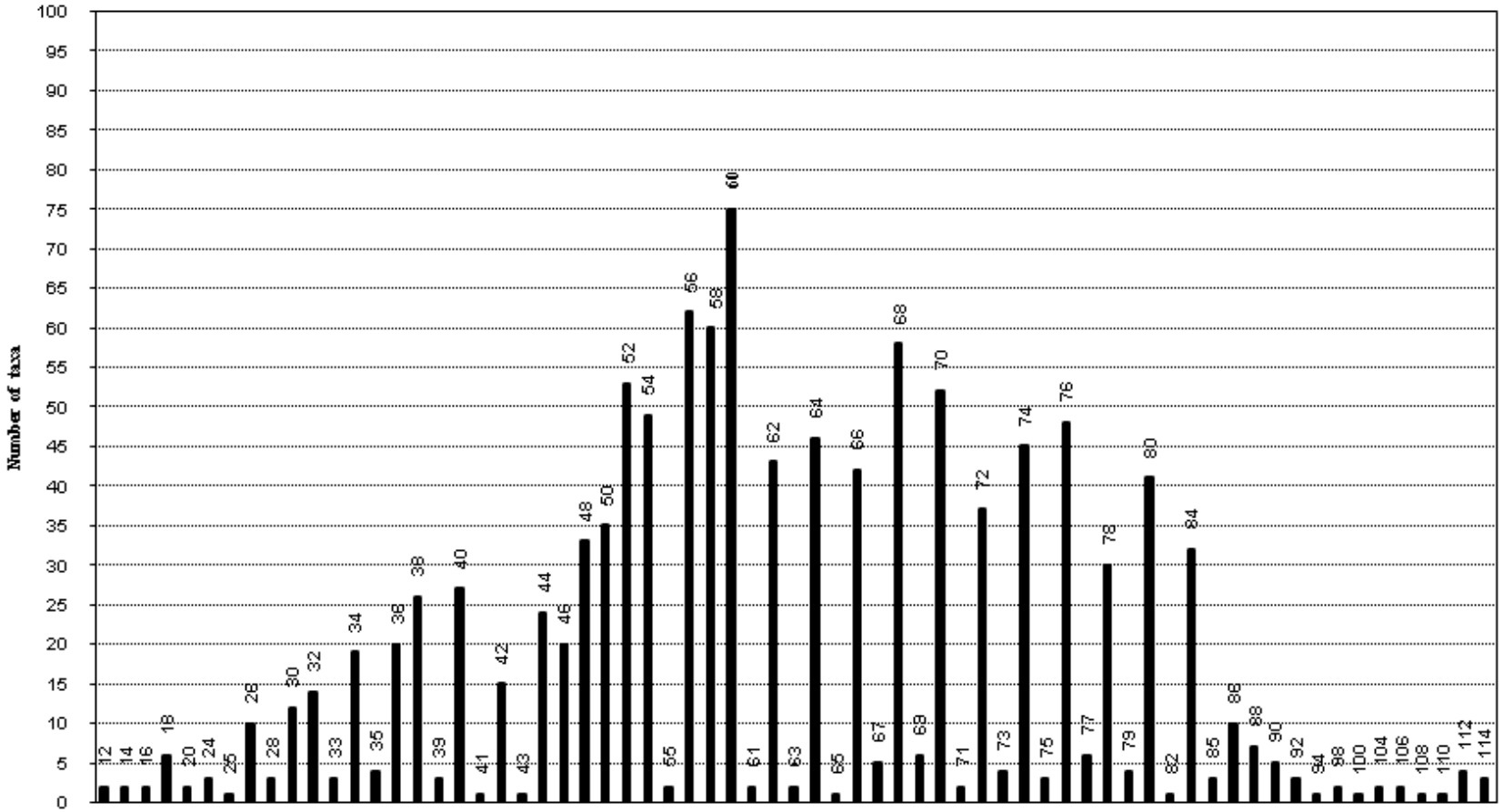

Fig.1 : Frequency of 2n chromosome numbers in *Carex*