CHAPTER 2: REVIEW OF LITERATURE

2.1 Review on Floristics of Indian Grasses

About 4,22,000 flowering plant species have been reported from world (Govaerts 2001), including 15,000 species from India. In general, first floristic survey of India was made by J.D. Hooker (1872-1897) and subsequently, Santapau (1958) and Hajra et al. (1995) also endowed with significant details on the subject. Firstly, the floristics of the India was studied from time to time by botanists at state level as for Uttarakhand (Gupta 1968; Raizada & Saxena 1978; Gaur 1999), Jammu & Kashmir (Kachroo et al. 1977; Dhar & Kachroo 1983; Naqshi & Aman 2001; Dar et al. 2002, 2010; Singh et al. 2002 and Khuroo et al. 2007) and Himachal Pradesh (Chowdhery & Wadhwa 1984). Further for district Himachal Pradesh, the exploration was extended to district level, Shimla (Collett 1921), Lahaul-Spiti (Aswal & Mehrotra 1994), Kullu (Dhaliwal & Sharma 1999), Chamba (Singh & Sharma 2006) and Sirmaur (Kaur & Sharma 2004). Phenomenon of cytomixis reported in some grasses by Church (1929), Brown and Emery (1958), Kamru (1960), Clausen (1961) and Sheidai et al. (2011).

2.2 Review on Cytology of grasses from Outside India:

Regarding cytological aspect, the study and analysis of chromosome numbers as well as utilization of this data has always remained a useful systematic tool for over the last century. The present information on chromosome numbers of grasses is available from various Chromosome Numbers Atlases by Darlington and Wylie (1955), Fedorov (1974), Kumar and Subramaniam (1986), Khatoon and Ali (1993); Chromosome Number Indexes by Ornduff (1966, 1967), Moore (1967-1974), Goldblatt (1975-1985), Goldblatt and Johnson (1986-2003), IAPT/ IOPB Chromosome data 1-14 by Marhold (2006-2012) and SOCGI as published in Journal of Cytology and Genetics and Internet (vide internet site: http://www.tropicos.org/Project/IPCN) as well as research papers published in recent Journals.
The examination of literature brings to light that first attempt to count chromosome numbers in the flowering plants was made by a German cytologist Strasburger in 1882, in Orchids (cf. Fedorov 1969). The first report on cytological work of grasses was reported in *Saccharum spontaneum* (c.f. Fedorov 1969) from Japan while on wild grasses, the cytological studies have been made by Evans (1926) for a few species of *Lolium* and *Festuca*. From India, the first efforts to report chromosome count in wild grasses were made by Dutt and Subba Rao (1933) for Sugarcane.


2.3 Review on Cytology of Indian Grasses:

Maximum work on the cytology of grasses is from temperate Himalayas covering Western, Central and Eastern parts. Mehra and his team at Panjab University, Chandigarh studied the cytology of large number of grasses from different parts of Himalayas (Mehra et al. 1968; Mehra & Sunder 1970; Mehra & Singh 1971; Mehra & Remanandan 1973a, b; Khosla & Sharma 1973; Mehra & Sharma 1975a, b, c, d, e; Sharma & Sharma 1979; Mehra 1982). Some of the interesting points of these studies are discussed in the following paragraphs.

Mehra et al. (1968) contains information on meiotic studies of 145 species belonging to 68 genera of grasses from North Western parts of India. Thirty five species and two genera have been worked out for the first time, besides new chromosome counts for 20 other species and intraspecific chromosome races in 15 species. Base number and phylogeny of family is discussed with x=6 as the original base number for the family, from which x=5 is derived through aneuploidy, which further gave rise to x=10 through polyploidy. Other base numbers (x=7, 8, 9) derived through aneuploidy from x=10. The role of polyploidy and aneuploidy was also evaluated.

Mehra and Sunder (1970) reported the meiosis in 63 species of 23 genera of sub-family Pooidae from Kashmir Himalayas. Of these, 25 species have been worked out for the first time, besides new cytotypes in many more species. Morphological comparison is made in intraspecific cytotypes reported in many species.

Khosla and Singh (1971) worked out meiosis of 28 species of tribe Andropogoneae of Punjab plains which includes one species worked out for the first time, besides new reports for 6 more species. Further, they suggested x=5 to be basic number for the tribe.
Mehra and Remanandan (1973a) studied 28 species falling in 16 genera of Pooideae from Kumaon Hills (Nainital) and Kashmir Himalayas. Studies cover 5 species worked out for the first time, besides varied chromosome reports for two species. Intraspecific polyploid races reported in *Avena fatua* (n=7, 14), *Bromus japonica* (n=7, 21), *Dactylis glomerata* (n=7, 14), *Festuca undata* (n=14, 21) and *Poa bulbosa* (n=21, 28). All the three species of *Alopecurus* and *Avena fatua* show multivalent formation due to reciprocal translocations.

Mehra and Remanandan (1973b) studied the cytology of 28 species of subfamily Pooideae from Western Himalayas, which includes first chromosome report for three species i.e. *Chrysopogon echinulatus* (n=10), *Erianthus versicolor* (n=10) and *Pennisetum lanatum* (n=9), new chromosome reports for six species, besides intraspecific cytological races in many more species.

Mehra and Sharma (1975a) covers meiotic studies on 44 taxa belonging to 35 species and 18 genera of tribes Agrostideae, Aveneae, Brachypodieae, Bromeeae, Festueae, Phalarideae and Triticeae from Eastern Himalayas. This includes 10 species worked out for the first time, besides new chromosome reports for two other species. Base numbers and phylogenetic relationship of different tribes are discussed.

Mehra and Sharma (1975b) presents cytological studies on 6 species belonging to 3 genera of Bamboos from Darjeeling in Eastern Himalayas, five of which (*Arundinaria aristata* n=24, *A. japonica* n=24, *A. pantliigii* n=24, *A. racemosa* n=24 and *Dendrocalamus hamiltonii* n=35) had been worked out for the first time and suggested x=12 as the base number for this group.

Mehra and Sharma (1975c) made meiotic studies on 35 species of 16 genera of tribe Paniceae reported from Darjeeling and Nainital hills of Eastern Himalayas, which includes 2 species (*Panicum khasianum*, 2n=18 & *Setaria berbisiana*, 2n=36) worked out for the first time and varied reports for two other species. Intraspecific cytotypes found in 6 species. Further suggested x=9 as the primary base number for the tribe Paniceae.

Mehra and Sharma (1975d) studied meiosis in 44 species of 21 genera of tribe Andropogoneae from East Himalayas (Darjeeling, Nainital hills), which includes
first reports for two genera and 13 species, besides varied chromosome reports for 6 species. Further intraspecific polyploid cytotypes reported in five species were compared morphologically. Suggested x=5 as the primary base number for the tribe Andropogoneae.

Mehra and Sharma (1975e) studied the meiotic course of 21 species belonging to 14 genera of the tribes Arundinelleae, Eragrostieae, Isachneae, Chlorideae, Sporoboleae, Meliceae, Stipeae, Arundineae and Garnotieae from Darjeeling and Nanital. It includes first chromosome reports for 10 species and varied chromosome reports for 4 other species. Further, they discussed the base numbers for the different genera and tribes.

Mehra and Sharma (1977) reported meiosis in 26 species, from Kashmir which includes 5 species (Duthiea bromoides n=14, Helictotrichon virescens n=14, Oryzopsis lateralis n=12, Poa araratica n=7 and P. koelzii n=14) worked out for the first time, besides varied chromosome numbers for 4 other species. B-chromosomes reported in two species belonging to genus Duthiea.

Sharma and Sharma (1979) presents meiotic studies on 49 taxa and 39 species, from North Indian plains and Himalayas, which includes one species worked out for the first time, besides varied numbers in 8 other species. Different meiotic abnormalities reported in some taxa.

Besides, some of the papers deal with the details of some genera or species of grasses (Khosla & Sharma 1973; Mehra & Kalia 1975; Sharma & Kaur 1980; Mehra & Chaudhary 1981; Sharma & Salam 1984; Sharma & Kumar 1985; Kalia & Mehra 1989).

Khosla and Sharma (1973) studied cytology of 11 species of Setaria from North Indian plains and Western, and Eastern Himalayas, which included varied chromosome reports for two species and one species worked out for the first time at world level. Further, discussed the inter-relationship among different species along with base number and ploidy levels.
Mehra and Kalia (1975) studied the detailed meiosis and mitosis of some populations of *Saccharum benghalense* and reported B-chromosomes in it.

Mehra and Chaudhary (1981) studied male meiosis in 8 species of *Paspalum* from Eastern Himalayas with desynapsis reported in four species, *P. conjugatum* (2n=40), *P. dilatatum* (2n=60), *P. longifolium* (2n=40) and *P. orbiculare* (2n=60), leading to unreduced gametes and are suspected to be apomictic in nature.

Sharma and Salam (1984) studied biosystematics of *Dactyloctenium aegyptium* complex from Punjab plains by taking into consideration leaf characters and chromosome numbers.

Sharma and Kaur (1980), and Sharma and Kumar (1985) have published the chromosome numbers of some grasses in IOPB chromosomal reports.

Kalia and Mehra (1989) studied comparative morphology and karyotype of three cytotypes (2n=20, 40, 60) of *Saccharum benghalense*.

On the basis of cytological observations on large number of grasses, Mehra (1982) and Sharma (1979, 1985) made some generalizations on the phylogenetic tendencies operative in Himalayan and North Indian grasses.

Sharma (1979), on the basis of cumulative cytological data coupled with some anatomical and physiological characters, considered x=6 to be the ancestral for the family Poaceae. From this, he proposed two main lines of evolution, together a few smaller lines. First, Bambusoid line represented by tribes Olyreae, Parianeae, Streptochaeteae, Streptogyneae, Anomochloaeae, Bambuseae, Phareae, Oryzeae, Phaenospermeae and Stipeae possessing small to medium sized chromosomes based mostly on x=12, which is secondarily derived from original base number x=6 and has C-3 photosynthetic system. The second main line, represented by tribes, Andropogoneae, Maydeae, Paniceae, Arundinellaeae, Aleurpodeae, Perotideae, Eragrostaeae, Chlorideae, Sporoboleae, Pappophoreae and Zoysieae with x=5, derived from x=6 by elimination of chromosomes and giving more stable secondary base number x=10, from which other base numbers were derived. These have better
photosynthetic system C-4. Further, he has discussed the origin of different tribes within these two lines.

Mehra (1982) reviewed the cytological picture of Indian grasses, on the basis of chromosomal studies on 270 species covering 110 genera, which includes 73 newly worked out species, 50 new cytotypes, intraspecific races in 44 species. On the basis of cumulative data on chromosome number, morphology, anatomy, karyomorphology proposed the various evolutionary lines operative in the different tribes which are similar to proposed earlier by them (Mehra et al. 1968; Sharma 1979).

Sharma (1985) on the basis of cytological data of 697 taxa from Himalayas reviewed the frequency of polyploidy in Himalayan grasses. He reported 63.41% polyploidy in the family, with a relatively higher value in Eastern Himalayas (68.61%), followed by Central Himalayas (59.74%), Western Himalayas (56%) and the least in Kashmir Hills of Western Himalayas (48.30%). Thus, suggesting that the incidence of polyploidy in Himalayan grasses, decreases with increasing latitude together with change from sub-tropical to sub-temperate and temperate climates.

From Kashmir Himalayas, major contributions to the cytological studies were made by Koul and Gohil (1987, 1988, 1989a, b, 1990a, b, 1991a).

Besides Mehra and co-workers, another active group working on the cytology of North Indian grasses is at Punjabi University, Patiala lead by Bir and co-workers (Bir & Sahni 1985, 1987, 1988; Bir & Singh 1988; Bir et al. 1987a, 1988).

Bir and Sahni (1985) reported the cytology of 22 species on population basis from Punjab plains with new chromosome counts in 10 species and a lot of variability in chromosome number and meiotic behaviour.

Bir et al. (1987a) worked out cytology of 33 species from Punjab plains with new chromosome counts for 7 species. 71.43% species show polyploidy with maximum frequency of tetraploidy. Further, they discussed the chromosome data of these genera at world level.

Bir and Sahni (1987 b) on the basis of chromosomal information on 112 species of grasses from Punjab plains, discussed the morphological and genetical
variabilities in the family and pointed out the role of various cytogenetical phenomenon such as polyploidy (68.5%), aneuploidy, hybridisation, apomixis, multivalent, etc. in intraspecific variability in the species.

Bir and Sahni (1988) reported meiotic studies on 12 species of *Eragrostis* from Punjab plains. They reported the intraspecific polyploid cytotypes in 8 species, i.e. *E. atrovirens* (2x, 4x, 6x), *E. ciliaris* (2x, 4x), *E. diarrhena* (2x, 4x, 6x), *E. pilosa* (2x, 4x), *E. tenella* (2x, 4x) and *E. tremula* (2x, 4x) with 69.5% polyploidy. Base numbers for the genus are suggested as x=9 and 10.

Bir and Singh (1988), reported the meiotic studies on 25 species of grasses from Gurdaspur district of Punjab and reported two new cytotypes with 72% polyploidy in the studied taxa.

Bir *et al.* (1987 b, 1988) studied cytology of five species of *Sporobolus* from Punjab plains with intraspecific cytotypes in two species. *S. diander* and *S. marginatus*, and stressed the need for taxonomic revisions of the genus.

Presently, another active team of cytological workers at Punjabi University, Patiala is of Gupta and Kumari (Gupta *et al.* 2008a; Akshita *et al.* 2010, 2011; Kaur *et al.* 2010a, b; 2011a, b, c) which have made significant contributions to the cytology of grasses of Haryana and Shiwalik hills and Western Himalayas.

Akshita *et al.* (2010) worked out the frequencies of polyploidy in annual and perennial grasses from Haryana and reported the higher frequencies in perennials. Akshita *et al.* (2011) analyzed cytomorphology of different populations of *Cynodon dactylon* from Haryana and Shiwalik hills and reported three cytotypes, n=8, 9 and 18. Meiosis in both diploid cytotypes is normal, whereas it is highly abnormal in tetraploid cytotype and this cytotype is more robust as compared to diploid ones.

Kaur *et al.* (2010a) reported the phenomenon of cytomixis in different populations of *Polypogon fugax* from Kangra district (H.P.). The species was found to have many more meiotic abnormalities like laggards, chromatin stickiness, inter-bivalents connections, reduced pollen fertility, etc.
Kaur et al. (2010 b) made detailed population analysis on Poa annua from North Indian plains. They reported variable number of B-chromosomes in some of the populations. Kaur et al. (2011a, b) reported the new chromosomal numbers in 15 species of grasses from Kangra district, which includes first chromosome count at world level for 6 species, varied chromosome counts for Eleusine indica (n=14) and high frequency of B-chromosomes in Poa annua. Further, the Indian populations of four other grass species were worked out for the first time.

Kaur et al. (2011c) carried out population based cytomorphological studies on 38 accessions belonging to 6 species of genus Setaria from different parts of India. New reports are reported in two species, S. barbata and S. megaphylla from India along with reporting of meiotic abnormalities and low pollen fertility in S. barbata and S. palmifolia.

From South India, the major work on the cytology of Indian grasses is made by Christopher and his Co-workers (Christopher 1971, 1978; Christopher & Abraham 1971, 1974, 1976; Christopher & Raj 1986; Christopher & Jacob 1990; Christopher et al. 1996) at University of Kerala, Trivandrum, who have studied the meiosis in large number of species from different tribes and has reported the cytology of many new species, besides pointing out the various evolutionary tendencies in different tribes.

Christopher (1971) reported asynaptic behaviour in two species of Paspalum (P. commersonii & P. conjugatum) and suggested these to be apomictic, as in spite of abnormal meiotic course, there is normal seed setting.

Christopher and Abraham (1971) studied cytology, covering meiosis and mitosis, of 24 species representing 16 genera from South India, which includes 14 species worked out for the first time. Chromosome size is small (1-2.5µm). Further, they discussed the phylogenetic position of subfamilies Bambusoideae, Oryzoideae, Arundinoideae and Festucoideae. Bambuseae, Oryzeae and Arundinea having high polyploidy series on x=12 are closely related. Festuceae and Aveneae which are morphologically similar have large sized chromosomes based on x=7.

Christopher and Abraham (1974) reported cytology of 29 species, covering 15 genera of tribes Eragrostiaceae, Chlorideae, Pappophoreae and Zoysieae of sub family
Eragrosoideae from South India. This includes first chromosome reports for 14 species and identified the base numbers; x=5, 6, 9, 10 and 12.

Christopher and Abraham (1976) reported the cytology of 57 species representing 21 genera of tribe Paniceae from South India which includes the first reports for 20 species. Further, it covers karyotyping of 29 species with size range of 1-1.4 µm. Most common base number is x=9, other being x=7, 8 and 10. They reported intraspecific polyploids in three species and asynaptic behaviour in two species of *Paspalum*. They considered that the evolution in three tribes is accompanied by change in base numbers and polyploidy, and represent the same evolutionary line.

Christopher (1978) reported the cytology of 48 species belonging to 30 genera representing the tribe Andropogoneae and Maydeae, which include new reports for many species. The species are based on x=5, 7, 8, 9 of which x=5 is proposed to be basic, with x=10 derived through polyploidy and others derived secondarily from x=10. Three tribes Paniceae, Andropogoneae and Maydeae considered to be derived from same ancestral stock.

Christopher and Raj (1986) made meiotic and karyological studies on 15 species of *Cymbopogon* from different parts of South India. Chromosome numbers reported with 2n=20, 30, 60 based on x=10. Four species have B-chromosomes. Most of the species show intraspecific polyploid races with mostly normal meiotic course. Chromosomes are small sized (1-3.5 µm). Further, suggested the genetic relationship and origin from common ancestral stock.

Christopher and Jacob (1990) studied the karyotype and meiotic course in hexaploid (2n=30) cytotype of *Coix lacryma-jobi* which is new chromosome report for the species.

Christopher *et al.* (1996) made detailed cytomorphological studies of *Coix gigantea* (2n=12) from South India.

From Central India, there are few reports on the cytology of grasses (Gill *et al.* 1980; Chauhan *et al.* 1998).
Gill et al. (1980) made meiotic studies in 21 species of grasses from Pachmarhi hills in Central India, which includes new chromosome report for *Ischaemum duthiei* (n=10) and varied reports for another four species. Further, 10-12 B-chromosomes were reported in *Capillepedium assimile*. Among these species, 71.4% show polyploid cytotypes.


Malik and Tripathi (1969) studied the meiosis in 2 varieties of *Echinochloa* species. Malik and Tripathi (1972) reported the meiotic course in tetraploid and pentaploid races of *Paspalum longifolium*. Malik and Grover (1972) reported high polyploid race of *Echinochloa frumantacea* (2n=90) from Udaipur.

Additionally, there are some other reports on the cytology of some grasses from Uttar Pradesh by Srivastava (1979a, b, 1980), Srivastava and Purnima (1990), and Gupta and Srivastava (1969, 1970, 1972, 1974).

Various other workers who made their contribution towards the cytology of grasses from different areas of India are Saxena and Gupta (1969) from Dehra Dun Sharma et al. (1978) from Orissa and Swami (1963) from Andhra Pradesh.

Besides some other, cytologists studied different tribes of the family Poaceae such as Paniceae (Nath et al. 1970), Eragrostieae (Bhattacharyya 1973), Bambuseae, Festuceae (Ghorai & Sharma 1980, 1981a, b), Agrostideae, Festuceae and Paniceae of Kashmir (Koul & Gohil 1991). In addition, Jauhar and Joshi (1969), pointed out that, x=9, is common in tribe Paniceae and x=10, in tribe Andropogoneae. Further, suggested that evolution of species in these two, tribes is accompanied by alteration in basic chromosome numbers.

Some other workers worked on individual genera such as Verma and Sobti (1985a, b) discussed the meiotic behaviour and their effect on cytological,
morphological and biochemical parameters in some species of *Cymbopogon* and their hybrids.

Singh and Gupta (1977) studied the meiosis of 18 species of *Setaria* collected from different parts of globe, including 6 species from India. This included, 3 species worked out for the first time at world level and 2 other with new chromosome counts and further analysed the chiasma distribution and various meiotic abnormalities in few species. Meiotic abnormalities in the form of multivalents, univalents, laggards, asynapsis, etc. were recorded in 3 species. Further, stressed role of dysploidy and polyploidy in evolution of genus.

Murthy and Basavaiah (1990) analysed the karyotype of 4 species of *Urochloa* i.e. *U. mosambicensis* (2n=28), *U. pullulans* (2n=28), *U. trichopus* (2n=28), *U. oligotricha* (2n=36) and *U. panicoides var. panicoides* (2n=48). The chromosomes are reported to be mostly small sized (0.76-1.90 µm) and metacentric type.

Basavaiah and Murthy (1987) reported the phenomenon of cytomixis in three different varieties of *U. panicoides*. The frequency of cytomixis was reported to be more during summer and it decreases with advancement of meiosis. Besides, cytomictic channels, hypo- and hyper-ploid cells were recorded in about 6% PMCs. This was explained due to unbalanced genetic makeup in response to environmental factors.

Basavaiah and Murthy (2001) studied the meiosis in two apomictic species of *Urochloa* (*U. oligotricha*, n=18 & *U. trichopus*, n=14) and reported the presence of 1-3 quadrivalents along with other meiotic abnormalities and considered these to be segmental polyploids.


Sisodia (1971), studied meiosis in 4 species of *Urochloa* with the presence of 1-2 quadrivalents in *U. moschambicensis* and 2-4 quadrivalents in *U. setigera.*
Further, meiotic course is abnormal with the presence of laggards, bridges and abnormal microsporogenesis.

Reddy and Rao (1975) studied chromosomal association at pachytene in artificially induced interchanged heterozygote of *Sorghum bicolor* and pointed out that translocations are induced at random in this species.

Levan (1987) reported chromosomal unstability in lemon grass *C. flexuosus*.

Swaminathan and Nath (1965) suggested two new chromosome numbers in the genus *Pennisetum*. Sujatha et al. (1989) studied the detailed meiotic course in 12 species of *Pennisetum* obtained from ICRISAT and on the basis of their meiotic behaviour and frequency of multivalents pointed out the nature of genomes in the polyploids. Further, reported 3 different base numbers (x=7, 8, 9) for the genus.


Malik and Thomas (1966) studied the meiosis of intergeneric hybrids of *Lolium multiflorum* (2n=14) and *Festuca arundinacea* (2n=70), and its amphidiploids (2n=84). On the basis of chromosomal pairing in hybrids and karyomorphology genomic relationship were drawn.

On the basis of hybrids produced, Malik and Thomas (1966) reported chromosomal polymorphism in indigenous and exotic populations of *Festuca arundinacea*. Malik and Mary (1971) studied induced mutations in *Lolium multiflorum* and *L. temulentum*. Besides them, Mini *et al.* (1991) made karyomorphological and phylogenetic studies in *Hygroryza aristata*.

### 2.4 Systematics and Phylogeny:

#### 2.4.1 Role of chromosomes in Systematics:

Avdulov (1931) was the first to recognise the role of chromosomes in grass taxonomy. On the basis of karyotype studies in 232 species taking chromosome number and chromosome size divided into 3 different groups: first with x=9, 10 with small chromosome size and the second with x=12 and small chromosomes and third group with x=7 and large chromosomes. Further, suggested that the phylogenetic evolution is from high basic chromosome number and small sized chromosomes to low basic number and large chromosome numbers.

Stebbins (1956) on the basis of morphological and chromosome characters, pointed out four evolutionary lines: Panicoid and Eragrostoid-Chloridoid lines with x=9, 10 in the tropics showing reduction in number of florets and specialised leaf anatomy; Festucoideae (=Pooideae) in the temperate area with x=7 and having large sized chromosomes; Bambuseae in moist tropical forests with x=12. Three other small lines are Arundinoid (x=6), Orzoid (x=12) and Stipoid (x=6), besides some other groups with 1-2 genera were also recognised.

Carnahan and Hill (1961) proposed that grasses fall into two major groups. First group of tropical and subtropical species with small chromosomes having x=10 or its derivatives such as x=9 and 12; second group species with temperate distribution having small sized chromosomes based on x=7.
McWilliam (1964) considered that the different basic chromosome number reflects different taxonomic grouping in the family. This is in consonance with the most of the recent classifications based on various molecular characters also with morphological and anatomical characters. For example the classification of Clayton and Renvoize (1986) into six subfamilies has specific base numbers: Bambusoideae (x=12), Centothecoideae (x=12), Pooideae (x=7), Arundinoideae (x=6, 7, 13), Chloridoieae (x=9, 10), and Panicoideae (x=9, 10). Similar diversification in base number is evident in 12 subfamilies recognised by Grass Phylogeny workers group (2001). The two subfamilies Chloridoideae and Panicoideae with the same base numbers n=9, 10 for most of the genera show some similarities in many other morphological and biochemical characters also (Roodt & Spies 2003).

Goldblatt (1980) considered x=9 or higher number to be paleopolyploid which has been secondarily diploidized by chromosomal rearrangements (Leitch & Bennett 1997) or genetic changes (Feldman et al. 1997).

Stebbins (1956) proposed common ancestry for Chloridoideae and Panicoideae. Tateoka (1957), and Clayton and Renvoize (1986) proposed the ancestors of Chloridoideae and Panicoideae to be Arundinoid with x=6, which through paleopolyploidy and consequent reduction gave rise to x=9. The same is supported by many molecular studies (Barker et al. 1995, 1999; Hilu et al. 1999; Hilu & Allice 2001). Similarly the paleopolyploid origin of x=10 from x=5 in Andropogoneae is supported by many molecular studies (Roodt & Spies 2003).

2.4.2 Predictive Phylogenetics:

Stebbins (1956) in his phylogenetic plan did not form a phylogenetic tree but rather a view of a canopy with an unknown ancestral taxon in the centre with various grass lineages placed in distances that correspond to their degree of specialization.

Tateoka (1957) pointed out the importance of various features with more emphasis on cytology and leaf anatomy along with morphological and geographical distribution to present his taxonomic and phylogenetic schemes.

Tzvelev (1976) depicted the relationship in a circular form with subfamily placement reflecting relative close affinities and tribe positions within those
subfamilies placed at a relative distance from a central ancestral group. Further pointed out all tribes and subfamilies cannot be derived from a single existing tribe.

Clayton and Renvoize (1986) stressed the importance of evolution of photosynthetic pathways and their associated anatomical and ecological features for subfamilies relationship.

2.4.3 Phenetic Studies:

Clifford et al. (1969) recorded 50 characters for 92 grass genera and analysed the data set with MULTCLAS and MULTBET for cluster analysis and GOWER for principal coordinate analysis and reported two major clusters one representing Pooid and Bambusoid grasss and other Andropogonoid grasses.

Similarly, Watson et al. (1985) made another numerical analysis with 720 genera and 85 morphological and microscopic characters reported two cluster groups.


2.4.4 Analytical Phylogenetics:

Kellogg and Campbell (1987) studied 390 genera using 23 to 33 morphological and anatomical characters and pointed out monophyly of Pooideae, Bambusoideae and Panicoideae and polyphyly of Arundinoideae.

Hilu (2007) has reviewed the progress in systematics of grasses moving from an initial intuitive classification and phylogenetics to one incorporating analytical phenetic approach and culminating in current stage of analytic phylogeny. He further cautioned about hasty interpretation, conclusions and commented that the pattern of chromosome evolution in the family has been inconsistently depicted by various authors due to the immense variability in basic chromosome numbers, prominence of polyploidy and subsequently lack of a well substantial phylogeny.

On the basis of cumulative chromosomal data and the studies on phylogenetic relationship by various workers, Hilu (2004) proposed a phylogenetic and chromosomal evolution for grasses and tribes of family Poaceae. He commented
that there are many contrasting views regarding the phylogeny of family due to wide range of basic chromosome number (x=2-18), prevalence of polyploidy (80%) and frequent hybridisation. Pointed out the origin of Poaceae from Restionaceae ancestor with x=9. Further pointed out the origin of higher (x=10, 11, 12) and lower basic numbers (x=5, 6, 7, 8) through aneuploid increase or reduction. He refutes the secondary polyploidy hypothesis but supports the reduction hypothesis for chromosomal evolution in Poaceae.

De Wet (1954) and Stebbins (1956) considered subfamily Arundinoideae to be nearest living representative of ancestral grass line. According to Clayton (1974), Arundinoideae evolved into two directions, namely Chloridoideae and Panicoideae, which has been supported by many workers (Roodt & Spies 2003) with x=5 giving rise to x=10 and 9. However, on the basis of molecular markers (ndhF sequence), Barker et al. (1995, 1999), Hilu et al. (1999), Spangler et al. (1999) and many other proposed x=5, representing reduction in Andropogonaeae and not the basic chromosome number. Hilu and Alice (2001) proposed that x=9 and 10 are present in taxa with primitive morphological characters such as spicate inflorescence, reduction in fertile florets and flower-nerved lemmas.

Döring et al. (2007) on the basis of matK chloroplast sequence data of 100 species representing 48 genera of tribes Avenaeae/ Poeae complex, data was evaluated using maximum parsimony and Bayesian methods. On the basis of number of synapomorphies from morphological and molecular data, Lygeium and Nardus, are lumped under Nardeae, whereas Brachypodium is supported as separate tribe Brachypodieae.

Levy and Feldman (2002) has reviewed the impact of polyploidy on grass genome evolution. They have pointed out that polyploidy is an evolutionary successful path chosen by most of the grasses right from their formation to the present. On the basis of review on molecular studies coupled with the Bioinformatics pointed out the origin of wheat (Feldman 2001), maize (Gaut & Doebley 1997) and rice (Goff et al. 2002) through allopolyploidy, segmental allopolyploidy or paleopolyploidy, respectively. Polyploidy provides plasticity and enables creativity through inter-genomic reshuffling of chromosomal segments and genes, which is not
possible in diploid background. Further pointed out that polyploid species seem pre-adapted to chromosome doubling and stability linked to reproducible elimination of DNA sequences.

Genome analysis of so called diploid species like *Arabidopsis* and rice with small genomes are found to be paleopolyploids. Thus, many species considered to be diploid on the basis of genetic and cytological behaviour must be ancient polyploid with extensive diploidization.

Several reviews on polyploidy in plants and their impact on speciation, genome structure and gene repression are available (Soltis & Soltis 2000; Wendel 2000).

2.5 Polyploids:

Polyploidy is not only widespread in the grasses but it is also an ongoing process as depicted by natural hybridization and polyploidy levels for the creation of new invasive species in *Spartina* (Levy & Feldman 2002). Soltis *et al.* (2009) has reviewed the role of polyploidy in Angiosperm diversification including Poaceae on the basis of recent molecular data including genome analysis. They found lot of genome duplication in so called diploid species. Wendel and Doyle (2005), and Adam and Wendel (2005) discussed the role of polyploidy in evolution of plants.

2.6 Molecular markers:

Now, there is a major shift towards the use of molecular data for constructing the phylogeny of the family. Some of the important workers in this direction are: Hilu and Alice (2001) on matK sequence, Hsiao *et al.* (1999) on nuclear ribosomal DNA (ITS), plastid gene rpoC2 by Barker *et al.* (1999), ndhF sequence data by Clark *et al.* (1995), rp116 intron sequence data by Zhang (2000), nuclear gene Phytochrome by Mathew *et al.* (2000), Kellogg and Campbell (1987), and Soreng and Davis (1998) on the basis of representative data of large number of species from 72 different genera and tribes combined morphological, anatomical, chromosomal, biochemical and molecular data of 364 chloroplast restriction sites to analyse the phylogenetic relationship with in the family and found some to be monophyletic and others as

Duvall et al. (2001) on the basis of grass specific insert sequence of plastid locus rpoC2 of 57 species studied the molecular phylogeny of Paniceae and proposed it to be paraphyletic with Andropogoneae.