1. Introduction
The increasing demand for food products in the world requires greater productivity of cultivated crops. Wide hybridization is a first and critical step to introduce alien variation, and prior to the transfer of desirable traits from the wild into the cultivated species. Wide hybridization between cultivated species and their wild relatives in interspecific or intergeneric combinations is an important tool in the breeding of cereal crops for transferring agronomically important characters and cytogenetic studies on these plants. Many wild species of Poaceae are known to possess agronomically beneficial genes such as pathogen resistance, salt- and alkaline-tolerance, wide adaptation, cold hardiness, high protein and lysine content and drought tolerance.

The cultivated barley (*Hordeum vulgare* L.) is predominantly self pollinating, (Saghai-Maroof *et al.*, 1984) whereas *H. bulbosum* is self-incompatible. The genus *Hordeum* belongs to the tribe Triticeae, family Poaceae consists of over 30 species and distributed in a wide climatic conditions (Bothmer, 1992). The basic chromosome number is 7, few species exist as tetraploids and hexaploids in addition to the diploid cytotypes. Barley ranks fourth among cereals after wheat, maize, and rice.

Reciprocal crosses between diploids of *H. vulgare* and *H. bulbosum* result in *vulgare* haploids (Kasha and Kao, 1970; Lange, 1971) upon embryo rescue, through selective elimination of *bulbosum* chromosomes (Subrahmanyam and Kasha, 1973a). Morphological characteristics of the derivatives and chromosome numbers in the resulting embryo further indicate absence of maternal effects on this unique process (Subrahmanyam and Kasha, 1973b). This is akin to mammalian somatic cell hybrids (Handmaker, 1973). The elimination is always of *bulbosum* chromosomes producing haploids of *H. vulgare* (unidirectional). So far neither loss of *vulgare* genome nor recovery of *bulbosum* haploids are reported in the extensively studied *vulgare*-bulbosum cross combination. Diploid crosses results 99% monohaploids and remaining 1% *vulgare*-bulbosum hybrids, whereas crosses be *ween* diploid *vulgare* and tetraploid *bulbosum*.
result in 99% of triploid hybrids suggesting that 1 *vulgare* to 1 *bulbosum* genome leads to elimination, whereas 1 *vulgare* to 2 *bulbosum* genomes results in triploid hybrids.

Furthermore, increasing the number of *bulbosum* genomes increases the stability and development of the endosperm as depicted in the following order: BBBBV > BBBBVV, BBV > VVBB > VVB (Subrahmanyam and Kasha, 1973a). Further it was shown using trisomics that *H. vulgare* chromosomes 2 and 3 carry at least three factors which control elimination (Ho and Kasha, 1975).

Production of haploids only from *H. arizonicum* by diploid *bulbosum*, hybrids and haploids from *arizonicum* by tetraploid *bulbosum*, and similarly haploids from *lechleri* by diploid *bulbosum*, and only hybrids (2n=35) or near hybrid chromosome numbers in embryos from *lechleri* by tetraploid *bulbosum* crosses, strongly suggest that a balance between the ratio of the parental genomes in each hybrid determines whether predominantly haploid or hybrid progeny are produced (Subrahmanyam, 1977, 1980). For example, a ratio of 3 *arizonicum* (*arz*) genomes to 1 *bulbosum* (*blb*) genome leads to the elimination of *bulbosum* genome and subsequent formation of *arizonicum* haploids, whereas the 3*arz* : 1 *blb* genomic ratio results in some hybrids. Similarly a ratio of 3 *lechleri* (*Ich*) : 1 *blb* genomes gives haploids of *lechleri*, while the 3 *Ich* : 2 *blb* results in embryos with hybrid chromosome number. It is well documented in *vulgare*-*bulbosum* crosses (Subrahmanyam and Kasha, 1973a), and other interspecific cross combinations in *Hordeum* (Subrahmanyam, 1977, 1978, 1979, 1980; Bothmer et al., 1983), that stable hybrids are obtained by increasing *bulbosum* genomes. The formation of haploids from *arizonicum* by diploid *vulgare* crosses and the absence of chromosome instability in embryonic cells from the *arizonicum* by tetraploid *vulgare* cross also indicates that a genome balance effect may be operative in elimination or retention of *vulgare* chromosomes upon hybridization with *arizonicum*. It is thus likely that crosses of tetraploid *vulgare* by *lechleri* (6x) result in stable hybrids unless physiological disturbances, such as dormancy etc., interfere with the germination of hybrid embryos (Subrahmanyam,
Occasionally haploid *vulgare* sectors arise from triploid hybrids *via* sectorial elimination (delayed elimination). Genotypic variation among *vulgare* and *bulbosum* accessions influences elimination/stability. Several studies indicated that some combinations of parental accessions produce haploids/hybrids though the frequency may vary (*Fukuyama* and *Takahashi*, 1975) and some of the diploid *bulbosum* accessions on hybridization with a range of *vulgare* genotypes give up to 70% hybrids (*Simpson et al.*, 1980).

General features of chromosome elimination in interspecific hybrids of barley are degraded type of chromatin (*Subrahmanyam and Kasha*, 1973a; *Lange*, 1971), acentric fragments, loss of whole genome, chromosomes or part thereof (Subrahmanyam and Kasha, 1973a; Subrahmanyam and *Bothmer*, 1987; *Bothmer* and Linde-Laursen, 1989; Bennett, 1995). The *in vivo* pattern of elimination could be mimicked *in vitro*, by incubating root-tips with restriction endonucleases (Subrahmanyam *et al.*, 1976). The rate of chromosome elimination is known to be influenced by the temperature at which the hybrids are raised (Humphrey, 1978). Elimination can occur in the first zygotic division itself or prolonged for few days. Nevertheless the frequency of cells with haploid (*gametic*) chromosome complement reaches ~95% by day 11 (Subrahmanyam and *Kasha*, 1973a; Bennett *et al.*, 1976).

Preferential elimination of *vulgare* chromosomes occurs in an order (7, 6, 5, 4, 3, 2, 1) in crosses of *H. vulgare* (*Tuleen 346*) with *H. marinum* (*Finch*, 1983). However, in *vulgare-bulbosum* hybrids chromosome elimination is random and progressive. Different cells in the VB hybrid embryo and different tillers of the same plant exhibited variation in chromosome number (*Subrahmanyam and Kasha*, 1973a). Progeny from the crosses between *H. lechleri* and *H. vulgare* exhibit variation in morphology and chromosome number (*Subrahmanyam*, 1980). Increasing the *vulgare* genomes from 1
to 2 in crosses with *H. lechleri* led to the loss of 3 to 6 chromosomes of *lechleri* parent (Linde-Laursen and Bothmer, 1988). It was shown in *lechleri-vulgare* combination that chromosome 7 is lost first while the order of other chromosomes was more or less random (Linde-Laursen and Bothmer, 1988). In somatic cell hybrids, ordered elimination of human chromosomes was reported (Norum and Migeon, 1974).

Selective chromosome elimination is widespread in *Hordeum* interspecific crosses and occurs in over 30 combinations with either *vulgare* and/or *bulbosum* resulting in haploidy (Subrahmanyam and Bothmer, 1987). A hierarchy of species dominance in chromosome elimination among interspecific cross combinations of barley is evident (Subrahmanyam, 1982). Species eliminating one *vulgare* genome exhibit elimination of up to 2 *bulbosum* genomes.

<table>
<thead>
<tr>
<th>Hierachy of chromosome elimination in <em>Hordeum</em> interspecific hybrids*</th>
<th>Group I</th>
<th>Group II</th>
<th>Group III</th>
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<tbody>
<tr>
<td><em>vulgare</em> (4x)</td>
<td><em>bulbosum</em> (4x)</td>
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<td>(2x)</td>
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*arizonicum* (6x) > *vulgare* (2x) > *bulbosum* (2x)

*lechleri* (6x) > *procerum* (6x)

*parodii* (6x)

*jubatum* (4x) > *brachyantherum* (4x) > *bulbosum* (2x)

*brevisubulatum* (4x)

*depressum* (4x)

*vulgare* (2x) > *chilense* (2x)

*flexuosum* (2x)

*The* dominant species or group of species is placed on the left of the species whose chromosomes are eliminated. More efficient species within the group is placed on the top.
In *H. marinum* X *vulgare* cross, elimination of *vulgare* genome from endosperm and elimination of *marinum* genome from embryo occur alternatively where double dose of *marinum* genome (from secondary nucleus) in combination with single dose of *vulgare* genome result in the elimination of *vulgare* genome whereas in the embryo 1 *vulgare* to 1 *marinum* genome leads to the elimination of *marinum* genome from this combination (Finch, 1983). Hybridization of tetraploid *marinum* with diploid *vulgare* produced dihaploids of *marinum* (Jorgensen and Bothmer, 1988). Further studies have shown that crosses of *H. marinum* ssp. *marinum* H515 (2x) with *vulgare* (2x) result in haploids of *vulgare*, while *H. marinum* ssp *gussonianum* H588 (2x) with *vulgare* result in haploids of *marinum*, indicating that the direction of elimination is determined by the species/line used. In this combination only haploids of either species were reported. This indicates reversible elimination/stability resides on the genotypic make up of the species used.

Ten combinations of intergeneric hybridizations with *Hordeum* as one of the parental species resulting in elimination have been reported. These include combinations with *Triticum aestivum* var. Chinese spring (Miller and Chapman, 1976), *Secale cereale* (Fedak, 1977), *Dasypyrum villosum* (Fedak, 1983), *Aegilops crassa* (Shigenobu and Sakamoto, 1977), *Psathyrostachys fragilis* (Bothmer *et al.*, 1984), *Zea mays* (Laurie and Bennett, 1988a), *Taeniatherum caput-medusae* (Frederickson, 1989), *Elymus pseuodanutans* (Lu and Bothmer, 1990).

In other intergeneric crosses *Secale cereale* X *Zea mays* (Zenkteler and Nitscche, 1984), *Triticum aestivum* var Chinese spring X *Avena sterilis* (Zenkteler and Nitscche, 1984), *Thynopyrum elongatum* X *Agropyron mongolicus* (Wang, 1987), *Triticum aestivum* var Chinese spring X *Zea mays* (Laurie and Bennett, 1988b; Chen *et al.*, 1991), *Triticum aestivum* var Chinese spring X *Sorghum bicolor* (Laurie and Bennett, 1988c), *Triticum aestivum* var Chinese spring X *Pennisetum glaucum* (Laurie, 1989,
Ahmad and Comeau, 1990), *Elymus shandogenesis* X *Triticum aestivum* var Chinese spring (Lu and Bothmer, 1990) and *Avena saliva* X *Zea mays* (Rines and Dahleen, 1990) chromosome elimination leading to haploidy were reported.

Elimination might have evolved as a defense mechanism that carried from prokaryotes and utilized for speciation and serving as potential barrier for silencing against deleterious sequences as a system of defense/protection mechanism (Bestor, 1990; Doerfler, 1991).

Nucleolar organiser (NO) regions which are associated with secondary constrictions of specific chromosomes, named SAT chromosomes (Heitz, 1931), have been shown to be the sites of 18S, 5.8S and 28S, and 18S, 5.8S, 2S, 26S ribosomal RNA (rRNA) cistrons in *Drosophila* (Ritossa and Speigelman, 1965), *Xenopus* (Wallace and Birnsteil, 1966), maize (Phillips et al., 1971, 1974; Givens and Phillips, 1976; Liang et al., 1977; Ramirez and Sinclair, 1975; Doerschug, 1976), wheat (Flavell and O'Dell, 1976) and a variety of mammals (Miller et al., 1976 a, b). The multiplicity of r RNA cistrons and the broad variation in the degree of multiplicity have been demonstrated in many organisms (see Subrahmanyam and Azad, 1978 a).

Navashin (1934) described that the SAT chromosomes of two different species brought together by hybridization suffered striking alterations in their individuality and mainly the secondary constriction formation was suppressed in the SAT chromosome from one of the two parental species. The affected chromosome was always from the same parental species in a given cross. This phenomenon was termed as differential amphiplasty (Navashin, 1934). Such differential amphiplasty was reported in *Hordeum* interspecific hybrids (Kasha and Sadasivaiah, 1971; Lange, 1971; Lange and Jochemsen, 1976). Furthermore, a strong correlation exists between the selective chromosomal elimination and the selective suppression of secondary constriction formation in *Hordeum*
interspecific hybrids (Subrahmanyam and Kasha, 1973 a, b; Lange and Jochemsen, 1976) as in mammalian somatic cell hybrids (Croce, 1976; Croce et al., 1977; Miller et al, 1976 a, b). A comparison of the number of SAT (secondary constriction) chromosomes in the metaphase cells and the maximum number of nucleoli in interphase cells in barley interspecific hybrids revealed that the chromosomes capable of organizing nucleoli were not always reflected through secondary constriction formation (Jessop and Subrahmanyam, 1984). The presence of a higher number of nucleoli than the number of SAT chromosomes seen and the presence of expected number of rRNA cistrons led Subrahmanyam and Azad, (1978b) to suggest that the suppression of secondary constriction formation in interspecific hybrids represents a complete or partial repression of rRNA genes on chromosomes contributed by one of the two parents. Detection of human rRNA in human-mouse somatic cell hybrids destined to lose mouse chromosomes and mouse rRNA in similar hybrids destined to lose human chromosomes (Croce et al, 1977) are consistent with the proposal that the suppression of secondary constriction formation is not due to the selective loss of rDNA from its site and perhaps represents a part of an overall phenomenon of selective silencing of DNA (Sager and Kitchin, 1975).

Genes coding for the 18S, 5.8S and 25S rRNAs are organized in tandem arrays of repeating units in enormous amounts in higher plants. The number of units per haploid genome varies from 570 in Arabidopsis thaliana to over 32,000 copies in Hyacinthus orientalis (Ingle et al, 1975; Timmis et al., 1972; Pruitt and Meyerowitz, 1986). There is also distinct variation within the same species (Birnstein et al., 1971; Flavell and Smith, 1974; Cullis, 1975, 1976; Cullis and Davies, 1974; Hotta and Micseche, 1974; Phillips, 1978; Shaw et al, 1993; Linde-laursen, 1984; Subrahmanyam and Azad, 1978a, b).

The number of arrays of rDNA repeats per genome is usually small, e.g., in
barley where chromosomes 6 and 7 carry these two loci (Subrahmanyam and Azad, 1978a; Appels et al., 1980). The length of the rDNA repeats varies between species from 7 Kb in soybean (Varsanyi-Breiner et al., 1979) to over 12 Kb in wheat (Appels et al., 1980). This length variation is due to different amounts of intergenic subrepeats as shown in wheat (Gerlach and Bedbrook, 1979; Appels et al., 1980), barley (Gerlach and Bedbrook, 1979; Saghai-Maroof et al., 1984), Allium (Garrido et al., 1994), cucumber (Zentgraf et al., 1990) and Vicia faba (Yakura and Tanifuji, 1983; Rogers et al., 1986; Rogers and Bendich, 1987). In spite of the variation for rDNA repeat lengths within species, and even within a plant at individual loci, there is considerable homogeneity for the number of subrepeats of intergenic DNA (Appels et al., 1980; Appels and Dvorak, 1982).

Investigations on the location of different restriction sites in cereal rDNA repeats (Gerlach and Bedbrook, 1979; Appels et al., 1980) and the rDNA spacer length polymorphism (Saghai-Maroof et al., 1984) revealed two rDNA repeat lengths at the two rDNA loci Rrn1 and Rrn2. The rDNA repeat length in wheat is 9.5 Kb whereas barley carry 9.9 Kb and 9 Kb repeats (Gerlach and Bedbrook 1979) at two different NOR loci (Subrahmanyam et al., 1994) while H. bulbosum genome has a single SAT chromosome with a rDNA repeat length of ~8.5 Kb (Molnar et al., 1989).

Duplication of the Nucleolar Organizer Region (NOR) in maize results in a larger pachytene nucleolus and a double copy number of rRNA genes (Phillips et al., 1971), while the monosomic for the nucleolar organizer (chromosome 6) contains half the number of rRNA genes. In barley, NOR6 contains 1,600 copies and NOR 7 carries 2,600 copies (Subrahmanyam and Azad, 1978a), yet chromosome 6 organizes a larger nucleolus than chromosome 7. This fact suggests that the size of the nucleolus is related to the proportion of total active rRNA genes rather than the absolute number of rRNA genes (Subrahmanyam and Azad, 1978a). The conclusion is supported by the findings
in wheat (Flavell and O’Dell, 1979). Thus, most of the rRNA genes are inactive and they are condensed as heterochromatin (Ramirez and Sinclair, 1975; Givens and Phillips, 1976; Doerschug, 1976; Phillips, 1978).

The active NOR loci in wheat have a higher proportion of rRNA genes with unmethylated cytosine residues in comparison with less active or inactive loci. The proportion of genes with methylated cytosine residues at CCGG sites also increases as the total rDNA increases (Flavell et al., 1988). Specific cytosine methylation of subrepeat is correlated with transcriptional repression of the repeat (Flavell et al., 1993; Sardana et al., 1993; Jupe and Zimmer 1993; Thompson and Flavell 1988).

The total number of rRNA genes in barley is known to be influenced by the increased dosage of chromosomes, not only NOR 6 and NOR 7 but also other chromosomes (1,2,4,5) not known to carry any NOR (Subrahmanyam and Azad, 1978a). Subsequently, it was shown that these chromosomes (1,2,4 and 5) carry minor rDNA loci (Peaderson and Linde-Laursen, 1994). In wheat, deleting or duplicating any one of 14 out of the 17 chromosomes with no rDNA loci brings about alteration in the number of nucleoli formed (Longwell and Svihla, 1960; Flavell and O’Dell, 1979). In barley, when both NOR6 and NOR 7 are brought on to the same chromosome through translocation, the activity of NOR 7 is reduced (Anastassova-Kristeva et al., 1980). However, in maize the translocation of NOR to other chromosomes does not prevent its activity (Ramirez and Sinclair, 1975; Givens and Phillips, 1976; Doerschug, 1976; Phillips, 1978).

Size of the nucleolus is correlated with the degree of the NOR expression (Flavell and O’Dell, 1979; Reeder, 1985; Subrahmanyam and Azad, 1978a,b) which is reflected in the size of the secondary constriction. Each NOR has the ability to organize a nucleolus. Despite having less number of rRNA genes, NOR6 organizes a bigger nucleolus than NOR7 in barley. In wheat 1B constitutes 30% whereas 6B constitutes
60% of rDNA, yet 1B organizes a larger nucleolus (Flavell et al., 1988). Introduction of *Aegilops umbellulata* chromosome bearing NOR (1U) suppresses wheat NORs and 1U organizes a bigger nucleolus. Substitution / deletion of NOR bearing chromosomes in wheat with non-NOR chromosomes increased the volume of other nucleoli indicating compensation for the deletion (Sardana et al., 1993). It was shown that NOR of 1U has more number of 130 bp subrepeats in its rDNA repeat units. In wheat line Cheyenne 6B organizes a larger nucleolus and the rDNA repeats of 6B contain more number of 130bp subrepeats (enhancer-like) in the repeat (Appels and Dvorak 1980; Sardana et al., 1993).

Attempts to introduce alien genetic variation into cultivated species, led to the designing and deployment of refined techniques for the production of addition lines of barley in wheat background (Islam et al., 1981; Islam and Shepherd, 1990; Koba et al., 1991). Rye addition lines in wheat, maize addition lines in oat (Rines et al. 1995; Riera-Lizaraju et al. 1996)) were produced. These are invaluable tools in assigning markers/genes onto individual chromosomes, studying interaction of genes and construction of high density chromosome specific linkage maps (Klienhofs et al., 1995). Barley addition lines are produced following hybridization between wheat and barley. The amphidiploid on crossing with wheat produces 49 chromosome plants. Such hybrids are pollinated with *H. bulbosum*. During the embryo development, elimination of *bulbosum* chromosomes occurs and on embryo rescue, progeny with 21 wheat chromosomes and 1 chromosome of barley could be obtained. Doubling the chromosome numbers results in disomic barley addition lines in wheat background. These addition lines are useful to delineate locus-specific changes particularly at the two *Rrn* loci in barley.

Variations in the relative amounts of the two (9.9 and 9 Kb) rDNA repeats were utilized to detect the role of the chromosomal segment in differential amplification and methylation of rDNA repeats in barley (Subrahmanyan et al, 1994). It was dem-
onstrated that the relative position of the segment “12 to 16” of chromosome 6 in barley determines differential amplification of the two rDNA repeats while the duplication of the same segment controls methylation and the overall rDNA content (Subrahmanyam et al., 1994).

Scope of the Present Investigation

Crosses between diploids of *H. vulgare* and *H. bulbosum* results in haploids of *vulgare* upon embryo rescue via selective elimination of *bulbosum* chromosomes. Genetic factors on *vulgare* chromosomes 2 and 3 control elimination process while stability factors present on the *bulbosum* genome plays an opposite role in overcoming elimination leading to stability. Parental genomic ratio in the hybrid cell determines commencement of elimination or stability in a given combination although "escapes" at a low frequency are known. Elimination is widespread in *Hordeum* interspecific and intergeneric crosses and a hierarchy of species dominance in selective chromosome elimination is correlated with the suppression of secondary constriction formation (nucleolus organization) at the NOR of the genome which would have otherwise been eliminated at an appropriate genomic ratio in a given combination. Thus it is often considered that these could be different aspects of an overall process of selective silencing of DNA. Though the factors involved in the elimination were known, details of the mechanism(s) involved in this process are yet to be elucidated.

Several hypotheses were put forward regarding the mechanism of chromosome elimination: (1) Mitotic rhythm/cell cycle timings (Lange, 1971), (2) Spindle abnormalities/centromere inactivation (Bennett et al., 1976; Finch and Bennett, 1983; Bennett, 1995), (3) Genome position - peripheral / central (Laurie and Bennett 1989; Anamthawat-Jonsson et al. 1993; Bennett, 1995) and (4) Restriction- modification system (Davies, 1974).
Mitotic rhythms/cell cycle timings - It has been proposed that differing cell cycle timings could lead to elimination of the late replicating genome. In *vulgare* and *bulbosum*, the DNA content and the cell cycle timings are more or less similar, and hence the possibility of mitotic rhythms playing any possible role is ruled out.

The proposed spindle abnormalities and centromere inactivation processes cannot account for the presence of acentric fragments and degraded type of chromatin among the cells of the tissues in which elimination commenced. Moreover, the centromeres of eliminated genome and parents did not show any discernible differences in experiment to test this hypothesis (Noda and Shiraishi, 1990).

It has been proposed that peripheral genome in the hybrid is predisposed to elimination (Laurie and Bennett, 1989; Anamthawat-Jonsson *et al.*, 1993; Bennett, 1995), based on the observations in *vulgare-bulbosum* hybrids the *vulgare* genome is located centrally and the *bulbosum* genome being peripheral. However, in *P. fragilis* × *H. vulgare* and *H. lechleri* × *H. vulgare* combinations the genomes that are centrally located are eliminated (Bothmer *et al.*, 1984; Linde-Laursen and Bothmer, 1988; Linde-Laursen and Jensen, 1991) which is contrary to the proposal of Laurie and Bennett, (1989) and Anamthawat-Jonsson *et al*, (1993).

Davies (1974) proposed that loss of genome in *Hordeum* interspecific hybrids may have a mechanism similar to the prokaryotic restriction modification system (Boyer *et al.*, 1973). Modification plays an important role in countering such restriction was known in phages (Arber, 1974; Bickle and Kruger, 1993). Further it was shown that treatment of *bulbosum* and *vulgare* root-tip cells with bacterial restriction endonucleases resulted in chromosome degradation (Subrahmanyam *et al*, 1976) which is similar to the occasionally observed degradation of chromosomes in *vulgare-bulbosum* hybrid cells (Subrahmanyam and Kasha, 1973a). The product of *H. vulgare* chromosomes 2 and 3 causes the loss of the chromosomes of *H. bulbosum* (Ho and Kasha, 1975). There
are recognition sites which allow a distinction to be made between them. To protect the
*H. vulgare* genome from degradation of its own chromosomes it must either lack those
sites which are susceptible to breakage or it has the capacity to modify such sites. The
survival of the triploid hybrids which have two doses of *H. bulbosum* chromosomes
could be related to the presence of two copies of this genetic information. Alternati-
vely, the exceptional VB or VVBB hybrids may be due to a modification of the
*bulbosum* as well as of the *vulgare* chromosomes i.e the sites on the bulbosum chromo-
somes are altered such that they are protected.

Since hierarchy of selective chromosome elimination and selective nucleolar
organizer suppression are correlated, these can be viewed as part of an overall selective
silencing mechanism (Sager and Kitchin, 1975). Structural organization and locus-
specific modifications can be monitored effectively using rDNA probe. The present
investigation was undertaken to identify the nature and extent of changes at rDNA loci
in barley *interspecific* hybrid(s) / derivatives, addition lines and segmental aneu-
loids.