Review of Literature
2. REVIEW OF LITERATURE

2.1 Molecular diversity in chilli

Chilli is an important spice and commercial crop of the world, in which not much molecular work has been done to find out the genetic relationships among and within the cultivated genotypes. The level of variation among domesticated chilli is lower than that among bell peppers and that the variation among large fruited peppers was limited compared with that among the domesticated pungent peppers. (Mcleod et al., 1983; Pickersgill 1988; Loaiza-Figueroa et al., 1989; Prince et al., 1992; Lefebvre et al., 1993; Rodriguez et al., 1999; Ryzhova and Kochieva 2004 and Ince et al. 2009).

RAPD technique provides an unlimited number of markers, it was successfully applied to characterize germplasm lines developed through inter specific hybridization in cotton (Williams et al., 1990). RAPD markers have been used for the estimation of genetic similarities and cultivar analysis for introgressed genes through amplified genomic reasons. The reproducibility of random amplified polymorphic DNA phenotypes by using different concentrations of reaction systems has been reviewed by Weeden et al. (1992). Although, template DNA of high purity was found to be crucial for reproducible results, the concentration of the template could be varied 10 fold without seriously affecting RAPD pattern. They concluded that the RAPD technique or modification of it should be very useful for genetic mapping, gene tagging and varietal identification.

Wang et al. (1997) subjected diverse pepper accessions to RAPD analysis and divided them into four groups indicating that RAPD markers could be effectively and reliably used for the classification of Capsicum spp. RAPD markers have been used for detection of polymorphism and assessment of level of genetic variation within populations of chilli (Wang et al., 1997). Capsicum germplasm was subjected to RAPD analysis and sufficient degree of polymorphism was detected to differentiate among the species.
Capsicum annuum, C. chinense and C. pubescence were more closely related to one another than Capsicum bacatum (Kang et al., 1997). Studies have also been conducted using more than one kind of markers. Paran et al. (1998) employed both RAPD and AFLP markers to study the variation in Capsicum annuum. The percentage of polymorphic markers was lower for AFLP than for RAPD markers. They also revealed that RAPD primers are more efficient in their ability to detect polymorphism in pepper. A comparative evaluation of RFLP and RAPD revealed that, 17 per cent of clones used singly were sufficient for the differentiation of these varieties (Prince et al., 1995).

Pawar (2000) attempted to study the genetic diversity among and within the three native cultivars of chilli viz., Byadgi dabbi, Byadgi kaddi and Sankeshwar both at morphological and molecular level. The molecular polymorphism assessed employing the RAPD analysis using five random decamer primers generated 187 RAPD loci of which 97 were polymorphic. The level of polymorphism generated was 48.5 per cent and highest number of polymorphic bands was recorded by the primer OPJ-10.

Yadwad et al. (2008) observed maximum diversity between Sankeshwar local and Byadgi dabbi varieties followed by LCA-312 and Byadgi dabbi and least diversity was noticed between VN-2 and Sankeshwar. Intra and inter varietal molecular polymorphism was studied using 5 primers of which the primer OPJ-01 amplified highest number of polymorphic bands with an average 9.12 bands per cultivar followed by OPJ-10 (8.00).

Vani et al. (2007) attempted to study the genetic diversity and observed maximum diversity between the accession IC-14 and IC-31 followed by Pusa Jwala and VN-2 and high similarity was observed between Byadgi dabbi and G-4. Forty-two genotypes representing all the fourteen clusters were selected to assess the molecular diversity using twenty primers of which the primer OPJ-01 amplified the highest number of polymorphic bands with an average nine bands per cultivars followed by OPJ-10 (8.00).

Dhanya et al. (2008) used fifteen RAPD primers for identification of plant based adulterants in chilli powder.
Ince et al. (2010) estimated genetic relationship among 24 accessions belonging to 11 species of Capsicum. Seven primers were used to amplify DNA of each accession. The DNA of each accession was amplified in replicates and found to produce the same banding patterns. Their results confirmed that the RAPD-PCR approach is useful in assessing genetic diversity and in identification of promising genotypes which could be effectively used in breeding programme.

2.2 Genetic variability, heritability and genetic advance

2.2.1 Genetic variability

Plant breeding is referred to as an art and science of modifying the genetic pattern of plants in order to enhance their economic use and requires detailed study on genetic variability which is a pre-requisite for initiating appropriate breeding procedures for crop improvement. The determination of genetic variability and its partitioning into various components like genotypic, phenotypic and environmental variability is necessary to have an insight into genetic nature of yield and its components which enables the breeder to adopt a suitable breeding program.

Charles and Smith (1939), Powers (1942) and Powers et al. (1950) partitioned genetic variance from total variances using the estimate of environmental variance in non-segregating population. The heritable variation was further divided into additive and non-additive components and later fraction, included dominance and inter allelic interaction (Fischer et al., 1932, Panse 1940, Lush 1945, Mather, 1949 and Falconer, 1981). Nelson–Ehle (1909) and East (1916) reported that partitioning of the phenotypic variance into its genetic and non-genetic components is very important to understand the amount of variability in a germplasm. Yule (1906) proposed that, continuous quantitative variation could result from a large number of genes, each having a small effect on the character measured. Basavaraj (1997) reported that, both GCV and PCV were low for days taken for flowering, Sreelathakumary and Rajamony (2002) and Verma et al. (2004) noticed lower GCV and PCV values. Pitchaimurthy and Pappaih (1992) reported that earliness is highly sensitive to environmental factors. High phenotypic and genotypic variability was observed in the form of GCA, PCV and variance for number of branches (Ibrahim et al., 2001). However, low variation was
also observed for number of branches by Shaik (2002), Nandadevi and Hosmani (2003). They opined that, selection for yield should be based on number of secondary branches.

High GCV and PCV values were observed for number of fruits per plant and fruit diameter by Sreelathakumary and Rajamony (2002) and Verma et al. (2004). Low variability was also observed for fruit number by Ghai and Thakur (1987) and for fruit diameter by Pandey and Dobhal (1994). High GCV and PCV were observed for fruit length by Sreelathakumary and Rajamony (2002). Low variability for fruit length was reported by Basavaraj (1997). Significantly high variation was also observed for number of seeds per fruit (Warade et al., 1996). However, Thangarajan and Muthukrishnan (1991) observed low variation for seed weight and seed number. Acharya et al. (1992) suggested that improvement in capsicum should be made based on the selection for fruits per plant, yield per plant, fruit diameter, fruit length and seeds per fruit. Similarly, Verma et al. (2004) confirmed the statement for most of the characters.

Chatterjee (2006) reported higher PCV and GCV for number of fruits plant, seed weight, number of seeds per fruit indicating the higher magnitude of variability for these traits and consequently more scope for their improvement through selection. Plant height, spread and fruit diameter exhibited moderate PCV and GCV estimates suggesting the possible role of environment in influencing these characters. Similar results were reported by other workers also (Wasule et al. 2004, Mishra et al. 2001). Days to 50% flowering and days to maturity recorded low PCV and GCV suggesting limited variability indicating need to generate more variability for wider spectrum of selection (Chatterjee, 2006).

Surya Kumari et al. (2010) reported higher phenotypic and genotypic coefficient of variation for plant height and plant spread, while fruit diameter exhibited moderate PCV and GCV estimates suggesting the possible role of environment in expression of these characters.

Sharma et al. (2010) reported significant differences among the 94 genotypes for fruit yield per plant, average fruit weight, and number of fruits per plant and took less number of days to 50% flowering. The phenotypic coefficient of variation and
genotypic coefficient of variation were high for fruit yield per plant indicating that these traits had wide genetic variability and would respond better to selection.

2.2.2 Heritability

In crop improvement, the genetic component of variation is important as only this component is transmitted to the next generation. According to Hanson et al. (1956), heritability in broad sense is the ratio of genotypic variance to total variance in non-segregating population. Thus, heritability denotes the proportion of phenotypic variance that is due to genotype which is heritable.

Heritability is known to differ to some extent depending on the populations handled. The estimates of heritability serve as a useful guide to the breeder. The breeder is able to appreciate the proportion of variation that is due to genotypic effect in case of broad sense heritability and due to additive effects in narrow sense heritability. Selection for this trait would be fairly easy as there would be close correspondence between genotype and phenotype due to a relatively smaller contribution of environment to the phenotype. But, for a character of low heritability selection may be considerably difficult or virtually impractical due to the masking effect of environment on the genotypic effect (Singh, 1991). High heritability was reported for plant height, days to 50 per cent flowering, number of primary branches per plant, number of fruits per plant, fruit length, fruit diameter, stalk length, dry fruit weight, and number of seeds per fruit. However, contradicting reports were available for all the above characters where moderate to low heritability was also reported.

High magnitude of heritability was noticed for days to 50% flowering (Sreelathakumary and Rajamony, 2002). The high heritability values in broad sense are also helpful in selection if coupled with high phenotypic performance. The reports of Sharma and Roy (1995) revealed high heritability for number of primary branches per plants. Whereas, Nandi (1993) observed low heritability for flowering characters. Moderate heritability was observed by Basavaraj (1997) for number of branches in chilli. Number of fruits per plant is the most important yield attributing character in capsicum. High heritability was reported for number of branches per plant indicating predominance of additive gene action which is amenable to improvement through selection and exploiting the additive variance (Verma et al., 2004). High heritability
estimates for fruit weight was observed by Sreelathakumary and Rajamony (2002) but, Rani and Singh (1996) reported that fruit weight was moderately heritable. Fruit size, in terms of length and width was reported to have high heritability (Sreelathakumary and Rajamony, 2002, Verma et al., 2004), Whereas Munshi and Behera (2000) observed low heritability for fruit length and width. Number of seeds per fruit showed high heritability estimates as reported by Basavaraj (1997). However, Bhagyalakshmi et al. (1990) noticed moderate heritability estimates for the same characters.

Heritability of number of branches and fruit number were found to be high (Korla and Rastogi, 1977) which was supported by the observations of Natarajan et al. (1993).

Surya Kumari et al. 2010), reported higher phenotypic and genotypic coefficient of variation (PCV and GCV) and heritability coupled with high genetic advance was observed for number of fruits plant, fresh fruit yield plant, seed weight, number of seeds fruit indicating the higher magnitude of variability for these traits and consequently more scope for their improvement through selection. Plant height, plant spread and fruit diameter exhibited moderate PCV and GCV estimates suggesting the possible role of environment in expression of these characters.

2.2.3 Genetic advance

Genetic advance is the improvement in the performance of selected lines over the base or original population. High genetic advance gives a substantial scope for selection to improve the yield and its attributing characters. A high heritability is not always accompanied by high genetic advance (Panse, 1957). Genetic advance is the measure of improvement that can be achieved by practicing selection in a population. Since, the estimates of heritability gives the indication of the amount of progress expected from the selection, they are most meaningful when accompanied by estimates of genetic advance. Genetic advance is affected by factors like intensity of selection, heritability and phenotypic variance. High genetic advance coupled with high heritability is an indication of more additive gene action (Panse, 1957). Reports on high genetic advance were available for all the characters studied except days to 50 per cent flowering and fruit colour which was moderate to low. High genetic advance was reported for fruit length, fruit diameter, number of fruits per plant by Verma.
High genetic advance was observed for days to 50 per cent flowering (Meshram, 1983) and number of branches (Ado and Samarawira, 1988). However, low genetic advance for number of branches per plant was observed by Sharma and Roy (1995) and for days to flower by Kataria et al. (1997). On the contrary low GA was recorded for days to 50 per cent flowering by Verma et al. (2004).

Sreelathakumary and Rajamony (2002) reported high estimates of heritability and genetic advance for fruit length and genetic advance for fruit length and number of fruits per plant. These characters could be effectively improved through selection. This could be treated as an indication of additive gene action and the consequent high expected genetic gain for selection from these characters. The fruit characters like size, length and width has been reported to have high genetic advance. Premsingh et al. (1976) reported high genetic advance for fruit size, Verma et al. (2004) for fruit length, Shah et al. (1986) for fruit width.

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Sharma et al. (2010), reported high heritability and high genetic advance for average fruit weight, fruit yield per plant and fruit diameter indicating the role of additive gene action for the inheritance of these traits.
Berhanu Yadeta et al. (2011) estimated the nature and magnitude of variability among twenty chilli genotypes. They reported significant genotypic variability for all the traits studied. In general PCV was higher than that of GCV. Genetic advance that could be expected from selecting the superior 5% of the genotypes as percent of mean varied from 6.2 % for days to maturity to 143.22% for fruit weight. They demonstrated the existence of adequate genetic variability, high degree of genetic determination and genetic advance among chilli genotypes for majority of the traits.

2.3 Inheritance studies

Chilli plants have often been studied for their agricultural value, the inheritance of certain morphological and pigmentation traits have not been well established (Lippert et al., 1966). Because of the interest in transferring useful genes from wild-type chilli into widely grown cultivars, it is desirable to have genetic information on important pigmentation and morphological traits.

Inheritance of various characters has been studied by many workers. Qualitative characters have been given more stress when compared to quantitative characters. Inheritances of characters studied are pigmentation in node, internodes, leaf, flower colour, anthers, stigma and fruits, nature of calyx, fruits position, stem branching, clustering of fruits, (Table 1).

Chilli plant offers an interesting material for genetic investigations as the variations in the several morphological as well as physiological characters are enormous, whose inheritance pattern is observed to be simple in some genotypes while in others, reported to be complex with an involvement of interacting genes of varying actions (Halsted (1909), (1918) and Dale (1928, 1930), Ikeno (1928), Deshpande (1933), Hagiwara and Oomura (1947), Ohta and Chuong (1975). Selection of Capsicum accessions had produced new breeding lines and cultivars with a diverse array of fruit and foliage pigmentation (Stommel and Griesbacc 1993, 2004, 2005).

2.3.1 Flowering

Capsicum annuum L., the most widely grown chilli species on a world basis, sets single flower at each node, whereas C. chinense Jacq., a popular species grown in
Table 1: Different Characters, Genes, F2 Segregation ratio and References

<table>
<thead>
<tr>
<th>Character</th>
<th>Gene (s)</th>
<th>F2 Segregation ratio</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant colour</td>
<td>'al', 'al', 'p1', 'p2', 'C1', 'R1', 'R2', 'C', 'R'</td>
<td>3:1</td>
<td>Deshpande (1939); Odland (1960); Hari Singh et al. (1992); Endo (1953); Ramanujam et al. (1965).</td>
</tr>
<tr>
<td>Flower colour</td>
<td>'C1', 'R1', 'R2', 'C', 'R'</td>
<td>3:1</td>
<td>Ikeno (1913); Hagiwara and Oomura (1947); Khan and Munir (1954)</td>
</tr>
<tr>
<td>Fruit Orientation</td>
<td>'cl', 'ci', Up1, up2</td>
<td>3:1</td>
<td>Shaw and Khan (1928); Deshpande (1933); Hagiwara and Oomura (1947); Ohta and Chuong (1975); Gopal krishnan et al. (1989).</td>
</tr>
<tr>
<td>Unripe fruit colour</td>
<td>'F', 'A', 'R1', 'R2', 'im'</td>
<td>9:6:1</td>
<td>Hagiwara and Oomura (1947) and Hagiwara et al. (1959)</td>
</tr>
<tr>
<td>Ripe fruit colour</td>
<td>'y' and 'y-', 'y-' 'y-', Yc and yc</td>
<td>3:1</td>
<td>Webber (1911); Ramanujam et al. (1965); Barrios and Mosokar (1972)</td>
</tr>
<tr>
<td>Fruiting habit</td>
<td>'fa', Ct, dt</td>
<td>13:3</td>
<td>Webber (1911): Shaw and Khan (1928); Khan and Munir (1954); Kormas and Kormos (1960); Ghafar et al. (1970); Kormas and Kormos (1960); Ohta and Chuong (1975)</td>
</tr>
<tr>
<td>Fruit tip</td>
<td>Ft</td>
<td>1:2:1</td>
<td>Ikeno (1913); Lippert and Smith (1965); Barrios and Mosokar (1972); Ohta and Chuong (1975); Mc Cammon and Honna (1984).</td>
</tr>
<tr>
<td>White petals, purple or blue anthers and nodes, and colourless filaments and styles.</td>
<td>al + al, As + Moa</td>
<td>1:2:1</td>
<td>Lippert and Smith (1965); Deshpande (1939); Odland (1960) (Odland 1960) (Deshpande 1939)</td>
</tr>
</tbody>
</table>
Latin America sets two or three flowers at each node. The character of two or three flowers set at each node was defined as the multiple-flower trait. Multiple flowers may be potentially useful to increase yield and enhance uniform maturity which may make mechanical harvesting feasible (Shuh and Fontenot, 1990)

Subramanya (1983) reported a possible gene introgression for the multiple-flower trait from *C. Chinense* into *C. annuum*. He suggested that three major dominant genes may control double flowers at each node, and that additional genes may be involved in the expression of more than two flowers at each node. Greenleaf (1986) reported that seven additive genes determine the multiple flowering in *C. chinense*.

Regarding anthocyanin pigmentation, several major genes (Lippert and Smith, 1965) are responsible for localizing the pigments in various organs like internode, leaves, part of the flower, and an immature fruits. Minor genes may explain the variation in the intensity of pigmentation.

### 2.3.2 Flower colour

The usual or "normal" condition in *C. annuum* (Lippert et al., 1966) is white petals, purple or blue anthers and nodes, and colourless filaments and styles. Such phenotypic expression is controlled by the gene *al*+, whereas recessive *al* prevents purple anthocyanin in any portion of the plant. An incompletely dominant gene *A* produces purple colour in foliage, petals, filaments, and styles in the *al*+ genotype (Deshpande 1939, Odland 1960). *As*+ (originally *W*) is reported to produce purple filaments and styles in *al*+ types in the absence of *A*, but does not intensify the purple colour of *A* (Odland 1960). *Mo* intensified purple colourations of *AA* types, this gene being ineffective alone (Deshpande, 1939). The segregation for flower colour was 3 purple to 1 white in some crosses (Ikeno, 1913, Hagiwara and Oomura, 1947), and 15 purple to 1 white in another cross (Hagiwara and Oomura, 1947). Genetic control of flower colour was postulated as due to three factors, *C, R1, and R2*, with *C* and *R* genes complementary, and the *R* genes equally effective or polymeric in the presence of *C*. Purple style *As* was independently inherited as dominant to white *As*+, but purple styles were produced in the *CR1* or *CR2* genotypes irrespective of *As* or *As*+ (Hagiwara and Oomura, 1947). In another study of flower colour (Khan and Munir, 1954) the *F2* ratio of 9 purple to 7 white blossoms was observed, indicating action of two
complementary genes which apparently also control filament and style colour. A trigenic \( F_2 \) ratio of 57 Purple to 7 white was obtained for filament and style colour, suggesting interaction of the two complementary genes with a third apparently independent and completely dominant gene for filament and style colour. Yellow anther colour is controlled by the anthocyanin-less gene, \( al \), but a brown anther colour, with single gene inheritance recessive to blue, was also described (Murthy and Murthy, 1962). No crosses were reported between yellow and brown anther mutants to determine if these were controlled by separate genes, or were modified phenotypic expressions of the same mutant in different genetic backgrounds. Khan and Munir (1954) indicated genetic distinction between purple and blue anthers and postulated the following ideographic genotypes for anther colour: \( AAbb \) or \( AAbb \): Purple, \( aaBB \): blue and \( aabb \): yellow.

The segregation for flower colour was 3 Purple: 1 White in some crosses and 15 Purple: 1 White in another cross (Ikeno, 1913 and Hagiwara and Oomura, 1947). Genetic control of flower colour was postulated as due to three factors \( (C_1, R_1 \text{ and } R_2) \) with \( C \) and \( R \) genes being complementary. Action of two complementary genes \( A \) and \( B \) has been observed in controlling blossom colour, with an \( F_2 \) ratio of 9 pink: 7 white. Absence of either or both genes may result in white petals (Khan and Munir, 1954). Monogenic flower colour with \( F_2 \) ratio of 3 pigmented: 1 non-pigmented has been observed (Ramanujam et al. 1965). Inheritance of petal, anther and filaments have also been studied (Odland, 1960 and Murthy and Murthy, 1962), homozygous recessive for petal colour have yellow anthers white petals and white filaments and style. Dominant \( S \) changes the yellow anthers to purple anthers, \( W \) changes the white filament and style to purple.

### 2.3.3 Fruit characters

#### 2.3.3.1 Fruit orientation

The gene \( up \) for upright or erect pedicel is recessive to its allele \( up^+ \) for pendent or drooping pedicel (Shaw and Khan, 1928; Deshpande, 1933; Miller and Fineman, 1937; Singh and Roy, 1945; Hagiwara and Oomaru, 1947). Earlier reports on this character indicated the heterozygotes to be intermediate, \( i.e. \), more or less horizontal in fruit orientation (Halsted, 1909; Webber, 1911; Ikeno, 1913). Classification of
segregants is complicated in many crosses by intra plant variability and by apparent changes in dominance with pod maturity or with season (Ikeno, 1928; Deshpande, 1933). Heterozygous plants may exhibit pods in different stages of maturity with upright, intermediate, or pendent fruits. Classification of plants for these phenotypes is best accomplished by readings throughout the fruiting period (Ikeno, 1928). Kaiser (1935) presented evidence that the single gene inheritance of fruit orientation operated through the genetic determination of a specific geotropic growth response. Ikeno's (1928) investigation showed that there was dominance of "erect" position in the F1 in summer, while in the autumn the "Pendent" position was dominate. He contributed the change of dominance to the difference in temperatures in the two seasons. The gene 'up' represents upright or erect pedicel (Shaw and Khan, 1928; Deshpande, 1933; Hagiwara and Oomura, 1947 and Ohta and Chuong, 1975). The dominance of pendant nature found to be governed by single factor (Murthy and Murthy 1962; Ohta and Chuong, 1975). However, earlier reports indicated that the heterozygote to be intermediate i.e. more or less horizontal in fruit orientation (Halsted, 1909; Webber, 1911 and Ikeno, 1913).

Bal and Singh (1995) observed pendent fruit type in F1, except the earlier fruits which were intermediate, indicating the dominance of pendent fruiting type in F2 they showed goodness of 3:1 ratio suggested monohybrid segregation. Kaiser (1935) and Sayed and Bagvandas (1980) reported similar results.

Dealing with the same character Webber (1911) obtained contrasting results in two different crosses. In one the "Pendent" position and in the other the 'erect' was dominate. This indicates that the "fruit-position" in one of his two crosses was genetically different from that in the other or in the light of Ikeno's results this difference in the behaviour of "fruit-position" in the two crosses may be the outcome of environmental influence. He also reported that their variability in the F1 of one of the crosses for this character which he attributed to impurity in one of the parents.

2.3.3.2 Fruit shape

Crosses of oblate by elongate fruit shapes gave a tri-modal F distribution as measured by length, width, shape indexes indicating the segregation of a major gene (Kaiser, 1935; Khambanonda, 1948; 1950; Peterson, 1959; Dempsey, 1960). The gene
O for oblate fruit shape was inherited as completely dominant in crosses with elongate fruit having a shape index of approximately 2.0 (Peterson 1959), however, where elongate types in the crosses approached a shape index of 4.0, segregation was less distinct (Khambanonda, 1950). Intermediate classes in later progenies suggested either an incomplete dominance for the oblate gene (Khambanonda, 1950) or the influence of additional genes operating in control of fruit length (Peterson, 1959). Dale (1928) concluded from crosses involving parents with mean fruit length of 23 and 157 cms, the fruit length inheritance is based on multiple genes with proportionate rather than additive effects.

### 2.3.3.3 Fruit Apex

The gene $Pt$ for pointed fruit is incompletely dominant to its allele for blunt fruit apex (Deshpande, 1933; Schmidt, 1935). Difficulty of classification, reversal of dominance in crosses, and poor fit to expected ratios have been reported (Webber, 1911, Miller and Fineman, 1937). Webber (1911) got conflicting results with the fruit apex, pointed or blunt. In one of his crosses, he found $F_1$ to be intermediate for this character and in $F_2$ he got a 1 pointed: 2 intermediate: 1 blunt ratio, while in another cross the "pointed" condition was dominant.

### 2.3.3.4 Base and Calyx Condition

The fruit base may be either bulging or non-bulging, with the gene $fb$ designating the non-bulging character (Deshpande, 1933; Miller and Fineman, 1937, Odland, 1948). The gene $ce$ conditions a non-enclosing calyx as opposed to the enclosing type (Deshpande, 1933). Linkage has been reported between the two genes, $fb$ and $ce$, with crossovers variously determined at three per cent (Deshpande 1933), 4.7 per cent (Miller and Fineman, 1937), and 18 per cent (Khan and Munir, 1954). However, it has been suggested that perhaps these two characters are morphologically interdependent upon one another rather than the genes being linked.

Jeswani et al. (1956) studied inheritance of deciduous nature of calyx of unripe fruit colour in chilli. They reported that deciduous nature of calyx is governed by single dominant gene.
2.3.3.5 Immature fruit Colour

Colour of unripe fruits varies from dark purple or nearly black through shades of green and yellow to ivory or sulfury white. Gene $A$ controls purple fruit colour as dominant to green ($A^+$. Various shades of purple are evident (Deshpande, 1933), but the distinction between purple and non-purple is clear and non-integrating (Peterson, 1959). Crosses of purple x ivory indicated two incompletely dominant genes, $A \sim A^+$ separating purple and green and $G \sim \sim G^+$ distinguishing green and ivory. Nine phenotypic classes were reported in the F$_2$ population with varying shades from purple through green to ivory (Murthy and Murthy, 1962). The gene for purple immature fruit colour, designated by symbol $F$ (Hagiwara and Oomura, 1947; Hanagata, and Takano, 1959), functions generally the same as $A$ except expression is apparently possible only in combination with $R_1$ or $R_2$ genes for purple flower colour. The gene $im$ (originally $i$) has been proposed for an intermediate maturity colour of purple in originally non-purple unripe fruit as found in the Japanese variety 'Goshiki' (Hagiwara et al., 1959). Green and yellow immature fruit colours were reported to segregate into 3:1 F$_2$ ratios (Webber, 1911, Schmidt, 1935). Within the green types, however, a series of dominant factors appear to be responsible for chlorophyll intensity in unripe fruit, with both cumulative and duplicative mechanisms of gene action proposed. Under the suggested cumulative mechanism, the presence of any one factor pair, designated $sw^{t_1}$, $sw^{t_2}$, $sw^{t_3}$, $sw^{t_4}$ . . . $sw^+$, produces lettuce green or yellowish-green pod colour, two factor pairs produce cedar green, and the very dark green colour appears due to four pairs. Ivory or sulfury white pods result from the absence of all such chlorophyll factors (Odland and Porter, 1938, Odland 1948, Peterson, 1959). The symbols $IV_1$ $IV_2$ have also been proposed for this colour inheritance (Hagiwara et al., 1959). The duplicate gene system was proposed (Jeswani et al., 1956) to account for 15:1 F$_2$ ratios from the cross cedar green x lettuce green. Four pairs of duplicate genes would produce cedar green colour, two pairs, the lettuce green colour, whereas the absence of all dominant pairs would result in sulfury white. The many true breeding lines of varying shades of unripe fruit colours available in Capsicum may be explained by either type of genetic mechanism (cumulative or duplicate).
2.3.3.6 Unripe fruit colour

Colour of unripe fruits varies from dark purple to almost black through shades of green and yellow to ivory/sulphury white (Deshpande, 1933), but distinction between purple and non-purple is clear and non-integrating (Peterson, 1959).

Crosses of purple with ivory indicated two incompletely dominant genes, A for purple and G for green. Nine phenotypic classes were reported with varying shades from purple through green to ivory (Murthy, 1962). The gene for immature fruit colour designated by symbol F, (Hagiwara and Oomura, 1947) and Hagiwara et al., 1959), Functions generally the same as 'A' except expression is possible only in combinations with R₁ and R₂ genes for purple flower colour. The gene 'im' has been proposed for an intermediate fruit colour (Hagiwara et al., 1959). Green and yellow immature fruit colours segregate into 3:1 F₂ ratio (Webber, 1911; Ramanujam et al., 1965). Ivory white pod result from the absence of chlorophyll factors (Odland and Porter, 1938 and Peterson, 1959). The duplicate gene system was proposed (Jeswani, et al., 1956) to account for 15:1 F₂ ratio from the cross between cedar green with lettuce green. It is concluded that purple or green fruit colour is dominated over yellow or ivory white and is controlled by one or two major genes with some modifiers (Barrios and Mosokar, 1972).

2.3.3.7 Ripe fruit colour

Ripe fruit colour yellow 'Y' is recessive to red 'Y⁺' (Webber, 1911; Shaw and Khan, 1928; Khan and Munir, 1954; Kormos, 1957 and Gafar et al., 1970). Various colour shades from red to ivory indicated the action of three gene pairs Y and Y⁺, C₁ and C₁⁺ and C₂ and C₂⁺ (Kormos and Kormos, 1960). Red and yellow mature fruit colour, is controlled by two complementary genes (Y and C), having new class of salmon red (Yc) and Orange (yC) as recombinants (Ohta and Chuong, 1975). Yellow mature fruit colour, combinations of C₁, C₂, Cl, y, and their alleles provide range of mature colours (Deshpande, 1933; Smith, 1948; 1950; Kormos and Kormos, 1960; Kormos, 1962).
As regards the inheritance of colour of ripe fruits the results of all previous workers, suggested dominance of red colour over orange on a 3:1 basis:1 blunt ratio of the many ripe colour available in Capsicum fruits, yellow y, was early reported as recessive to red, y+ (Webber, 1911; Atkins and Sherrard, 1915 and Shaw and Khan, 1928), and was substantiated by later investigations (Smith, 1950; Khan and Munir, 1954, Kormos, 1957).

Kormos (1957) determined by chromatographic analysis that levels of eight pigments in the red-fruited Fi progeny of a cross of Red x Yellow types exactly matched the pigment content of the red-fruited parent. Similarly, pigments in the red and yellow F2 segregants matched the respective parental types, suggesting total pigments to be controlled by the same factor. More extensive studies with various colour shades from red to ivory indicated the action of three gene pairs, y and y+, q and ql and q and co+ (Kormos and Kormos, 1960). The factors q1 and q2 reduced colours of y+ and y by inhibition of the Beta carotene system, with q1 causing approximately 1/10 reduction in red pigments. With ca present, red pigments occurred only in traces. Colour development under these three gene-pair system was postulated as follows:

\[ y^+_q \text{ red, } y^+_q \text{ salmon red, } y^+_c \text{ pink, } yq^- \text{ orange, } yq \text{ lemon yellow and } yc^2 \]

ivory/white.

2.3.3.8 Fruit Orientation

Classification of segregants was complicated in many crosses by intra-plant variability and by apparent changes in dominance with pod maturity or with season (Ikeno, 1928; Deshpande, 1933).

2.3.3.9 Fruiting habit

Productions of four to eight flowers and fruits in clusters have been described in chilli varieties (Deshpande, 1944, Murthy and Murthy, 1962; Ohta and Chuong, 1975). The clustering habit of fruit bearing is controlled by a single recessive gene now designated as 'fa' far fasciculate (Ikeno, 1913; Barrios and Mosokar, 1972 Bergh and Lippert et al., 1975). Shifriss and Hakim (1977) reported that pre-bifurcation shooting is controlled by relatively few genes with different action, and modified by environment conditions.
Murthy and Murthy (1962), Meshram (1983) and Thomas and Peter (1986) observed all solitary in F1 generation indicating dominance of solitary fruiting over cluster. In F2 population they reported 3 solitary, 1 cluster bearing habit. However Tanskley and Oliver (1984) reported dominance of cluster bearing, while McCammon and Honma (1984) reported 9:3:4 ratios. They suggested that the umbrella phenotype was controlled by three major recessive genes, ‘ct’ and ‘dt’ determining plant habit and ‘fa’ determining fruit bearing habit.

2.3.4 Plant characters

2.3.4.1 Habit

Several investigations of the inheritance of growth habit in Capsicum annuum L have been reported. Deshpande (1944) conducted an analysis of the inheritance of bushy habit. The bunchy character was shown to be recessive and was later termed fasciculate (Lippert et al. 1966).

Kormas and Kormas (1957) crossed a fasciculate type of pepper with various non-fasciculate types and recovered F2 progeny exhibiting completely determinate growth. In these plants, the main axis stopped growing early in the season and produced a cluster of fruits, after which no lateral shoots developed. This character was found to be recessive.

A compact or bunchy mutant plant type, characterized by shortened internodes, reduced lateral and terminal branching, and production of 4-8 flowers and fruits in clusters, was described in chilli varieties ‘I P 46A’ and ‘Huntaka’ from India and Japan (Anonymous 1940, Desphande 1944, Murthy and Murthy 1959, 1962b). This character had been determined earlier by Ikeno (1913) in C. fasciculatum (C. annuum) as controlled by a single recessive gene, now designated ‘a’ for fasciculate (Bergh, and Lippert, 1975). Variations of this dwarfed fasciculate habit, referred to as determinate, are reported in Hungary with main and axillary branches terminating in clustered inflorescences, and with some plants completely void of lateral shoots. Inheritance was not determined (Kormos, 1957). Webber (1911) crossed two medium-sized varieties, 'Golden Dawn' which had few, coarse, horizontal branches, and 'Red
Chilli having many, fine, erect branches, and obtained F₂ segregants both giant and dwarf in comparison to the parents. The progeny distributed nearly equally between the two parental types within each of the three branch conditions.

2.3.4.2 Plant Colour

Purple leaves and stems as well as other plant parts are due to incompletely dominant gene A (Deshpande, 1939; Odland 1960), with MoA intensifying purple colour in AA genotypes (Deshpande, 1939). Purple node of the normal plant type is conditioned by al§ whereas al (anthocyanin-less) prevents purple colouration in any portion of the plant (Deshpande, 1939; Odland 1960)

A pair of dominant complementary genes 'P₁' and 'P₂' controlled purple leaves while a third gene 'Y' caused variegation of leaf colour which was affected by some modifiers (Endo, 1953). Foliage colour ratio 55 green: 9 purple in F₂ generation has been observed (Ramanujam et al., 1965) indicating the action of two complementary genes and an inhibitory factor, whose presence makes the leaf lamina to remain green. The stem colour in seedling stage of chilli was controlled by 3 pairs of genes. The purple stem colour was dominant over green (Habib and Mensinkai, 1971, Ghai et al., 1972). The colour of the leaves was controlled by two genes, one gene exhibited incomplete dominance 'fr' pigmentation and the second expressed it only when it is homozygous dominant condition (Hari Singh, et al., 1992).

Several types of chlorophyll deficiencies or variegations have been observed. The gene vg⁻ (variegated mottled) produces a uniform yellow to light green mottle on foliage. The locus contains two additional alleles: the dominant vg⁺ for normal green foliage and a recessive dwarfed type vg⁻ termed variegated Virescent in which cotyledons and first true leaves, as well as all subsequent new growth, are initially yellow, becoming nearly normal green with maturity (Lippert and Smith, 1965). Recessive bv (bushy variegated, originally Cook's "mutant2") produces small, excessively branched plants with creamy-white and green mottled leaves (Cook, 1962; Lippert et al., 1966). Marbled m, has distinct zones of white, light green, and normal green on true leaves and immature fruits (Lippert and Smith, 1965).
Hereditary changes in *C. annuum* have been made with respect to leaf colour, pedicel direction and ripe fruits colour. The changes were at genie level and were in both the directions from dominant (Vijayakumar, 1979).

### 2.4 Linkage Relationships

Linkage in Capsicum has been reported by Deshpande (1933). Linkage of three loci was observed by Peterson (1959). These consists of genes A (purple immature fruits colour), O (round versus elongate fruit shape) and G₁ (green versus yellow immature fruit colour). The linear order and map distance of genes was as follows: A --- 6.5 ---- O --- 18.8 ---- G₁. Weak linkage between colour of plant and ripe fruit colour was observed by Deshpande (1933).

Comprehensive studies of linkage relationships between available characters in *Capsicum* have not been undertaken. Linkage of A, O, and swL (Peterson, 1959) represents the only definite association of three genes on a single chromosome. From combined information on linkage it can be assumed tentatively that *C. pi, sp*, and short fruit length may represent a linkage series. Carrying the assumption further, if one of the factors (three factors calculated) for fruit length by Deshpande (1933) is comparable to the O gene, it is possible that these six genes are located on the same chromosome. Ramanujam *et al.* (1965) reported that there was no linkage between the loci governing immature fruit colour and ripe fruit colour.

### 2.5 Comparative studies of resistant and susceptible chilli genotypes

The knowledge of the relationships between the plant and the insects is essential in devising efficient methods of pest management in crop plants without disturbing the environment balance. Out of many insect plant relations, host plant resistance is of great importance. This kind of interaction is useful in agricultural development because existence and exploitation of such interaction could be made of in increasing the production of crops for the use of mankind. Exploitation of host plant resistance could be a very meaningful practical answer to socio-environment and economic concerns posed by chemical control measures which are increasing endlessly. The present study is an attempt to understand the mechanism of host plant resistance in chilli genotypes. A good number of scientists in the field of entomology, physiology and plant breeders
are engaged in the study of host plant resistance. Mubarak (2002) reported that the AR-75, VN-2 were resistant to mites, while Byadgi kaddi and dabbi as susceptible. Yadawad et al. (2008) also showed that VN-2 and S-32 were resistant, and Byadgi kaddi and dabbi as susceptible.

2.5.1 Screening of chilli for thrips and mites

Musalwadi selection was found to be promising based on population density, incidence and intensity of attack (Borah, 1987). Under natural field conditions, Rajput et al. (1988) screened 23 chilli genotypes against thrips and mites but none were found to be resistant. A replicated greenhouse study was conducted by Fery and Schalk (1991) to confirm the availability of resistance to western flower thrips in pepper germplasm and found that there was considerable amount of variability with pepper germplasm. They concluded that the resistance to western flower thrips in pepper appears to be due to antibiosis or antixenosis mechanisms. Varadharajan and Veeravel (1996) carried out field trials to screen the possible sources of resistance in chilli accessions to thrips S. dorsalis. Out of 58 accessions screened two (Pant C-1 and G-5) were found resistant and five moderately resistantly, 40 moderately susceptible, 13 susceptible and 8 highly susceptible. Lingeri et al. (1998) evaluatyed eleven chilli genotypes for resistance of P. latus and S. dorsalis. The genotypes viz, GPC-77, GPC-80,KDSC-3-27 and Jwala were selected as most resistant based on the population density, incidence and intensity of attack, whereas KDSC-510-10,G-3 and Byadgi as most susceptible and further found that GPC-80 as least susceptible to both the pests followed by GPC-77.

Singh and Singh (1998) studied the response of promising chilli cultivars to thrips and found that thrips population in these varieties ranged from 0.81 to 4.82 per plant with significant variation with the lowest population ranging from 0.81 to 0.82 per plant. Lowest population was significantly lesser than rest of the varieties. Assessment of loss caused by P. latus (Banks) on chilli was studied by Sudharma and Nair (1999). They reported significant yield reduction in potted chilli plants, when P.latus population was 24, 50 and 100 mites per plant.
Reddy et al. (2000) screened 33 genotypes of chilli for leaf curl caused by *S. dorsatis* and *P. latus*. The selection 1-12 recorded highest yield (30.59 tonnes/ha) while lowest incidence was recorded in selection 4-1 (13.88 and 17.22 percent at 90 and 120 days after planting respectively). Selection 7-11-3-1 exhibited the highest tolerance to leaf curl.

Mallapur (2000) screened 62 chilli genotypes against *S. dorsalis* and *P. indicus* and found 13 genotypes with lower percentage of leaf curl of which two viz., KDSL-6 and KDSC-210-3 gave very high yields. Based on infestation of yellow mite, injury grade and damage index the cultivars were classified as resistant, susceptible and highly susceptible. 21 accessions of chilli were studied for the incidence of thrips and mites (Rajaram and Ramamurthy, 2001) of which accession 45 recorded least population of thrips. Phule Sai (GCH-8) selected from advanced generations of pant C-1 x Kamandalow under rainfed conditions, was found to be promising in terms of both yield and quality (Jadhav et al., 2000). Phule sai, in multilocation trails in India yielded more than S-32, Byadgi and high yielding standard NP-46A and was found to be moderately resistant to thrips.

2.5.2 Mechanism of resistance for thrips and mites

Plant tissues are largely made up of water, cellulose and lignin, thus providing a potential source of water and nutrients. Fresh leaves are made up of 90 per cent water, one to three per cent of proteins and rest is made up of carbohydrates (Hukinson and Huges, 1982). Thus, to acquire the required quantities of energy, nitrogen and proteins, the insects must consume proportionately large quantities of plant material for each unit of insect growth. At the same time, plants develop a number of defence mechanisms that resist the damage caused by the insect feeding. Some of the research work conducted with respect to mechanism of host plant resistance is reviewed here.

2.5.3 Role of morphological characters in host-plant resistance

Some of the structural differences in plant varieties have been reported to be concerned with insect pest resistance. However, in the field of host-plant resistance, the role of morphological and anatomical characters of the plant is not given much importance and hence the literature in this respect is very scanty. The presence or
absence of shelter for insects has sometimes been of importance in resistance (Jones et al. 1934). It has been shown that a small angle of contact of leaves between which those insects prefer to live contributed towards an increase in the thrips population of the varieties with such leaves, revealing susceptibility of the host-plant.

2.5.4 Role of leaf pubescence in host plant resistance

A phytophagous insect faces purely mechanical problem such as gaining a firm attachment on the plant surface and penetrating the hard tissue. The problem of obtaining secured anchorage on the smooth surface of plant organ exposed to wind and rain presents formidable difficulties (Edwards and Wratten, 1987). A smooth cuticle which was hard in nature was resistant to sucking pests.

Tidke and Sane (1962) observed that thickness of leaf lamina was a major factor for resistance than the number of hair on veins or lamina. Hunter et al. (1965) reported the pubescent varieties were found to be tolerant to boll weevil and pink boll worm (Smith et al., 1975) as the trichome interlock the bracts and protect the buds.

Trichomes are unicellular or multicellular out growths from the epidermis of leaves, shoot and root (Uphof and Hummel, 1962) and occur in diverse form and structure. Some plants such as tomato have several types of morphological and chemically distinct trichomes or hair (Beckman et al., 1972)

2.5.4.1 Stem

Howe (1948) established the factors responsible for resistance to squash borer in cucurbits. It was reported that resistant strains provided insufficient food of poor quality and larval growth and development was decreased because the resistant varieties had smaller stem containing only comparatively small amount of parenchyma and a high proportion of tough lignified vascular bundles. Chiang and Norris (1983) conducted a study on morphological and physiological parameters for soyabean resistance to Agromyzid bean flies and observed that susceptible varieties had largest leaf area, lower moisture content and larger stem diameter than the resistant genotypes.
Moore (1984) reported that silica content of the plant is important in protecting against *Diptem* stem borer in Italian rye grass *Loliom mullifolium* and further, he suggested that the level of silica in the stubble was inversely related to the degree of infestation by stem borer. Talekar *et al.* (1988) revealed highly resistant strains had smaller diameter stems. Based on the characters studied they suggested that combination of several characters had contributed for *Agromyzid* resistance in mungbean. The knowledge of such host-plant relations could be utilized in implementing the host-plant resistance breeding programme. However, not much work has been done on these aspects in respect to chilli crop which is subjected to a number of insect pests which cause severe crop damage resulting in yield losses. Since chemical control is posing the problem of pest resistance, pest escalation and pollution, host-plant resistance offers good scope for keeping the pest at lower levels if not totally controlled.

2.6 Histological studies in male sterile and male fertile VN2 lines

Formation of defective reproductive organs, specially the male ones, is not uncommon in nature. The selective damage to male reproductive organs suggests that they require very precise growth conditions. Even slight alteration in external and internal environment might cause male sterility. Influence of environmental factors on pollen development has been well documented by several researchers. Rice anthers, especially at meiosis, are very sensitive to low temperature and become male sterile (Nishiyama, 1984). Similar range of temperature, in combination with water deficit, is deleterious for anther development in wheat (Saini and Sharma., 1978). Studies by Koonjul *et al.* (2005) have shown that water deficit alone, during male meiosis, is enough to induce male sterility in wheat.

Male-sterile pepper (*Capsicum annuum* L) is a useful germplasm for heterosis breeding. However, the process of male gamete development and the sterility mechanism is unclear. Economic $F_1$ seed production using male sterility will help to increase the area under $F_1$ hybrids by farmers in turn increasing the productivity and production to meet the internal and export demand.
The realization of importance of male sterility in plant breeding program has paved way to the development of techniques to generate male sterility in crop plants. Gametocides either suppresses the stamen development, or inhibits the anther dehiscence or cause alteration in the size and shape of stamens. One drawback of using chemicals that induce male sterility is that they also cause some degree of female sterility, which is not desirable.

Genetic engineering is a more dependable technique for the production of male sterile plants. This technique is based on the imitation of mechanism of male sterility as it occurs in in vivo conditions (Goetz et al. 2001). Therefore, it is not only essential to understand the successive developmental steps of anther, but also to know causative factors that disturb the normal development of anther and lead to male sterility. In this regard, a careful comparative investigation of cytological, anatomical and physiological aspects of developing anthers of male sterile and male fertile lines is very important to understand the mechanism of male sterility. The understanding of the indispensable role of tapetum in pollen development has lead to the techniques that cause selective destruction of the tapetum. Tapetal ablation techniques, using chimeric ribonuclease genes, have successfully yielded male sterile lines in tobacco and oil seed rape (Mariani et al., 1992). Recently, male sterility has been induced in tobacco through metabolic engineering of the carbohydrate supply (Goetz et al., 2001).

Apart from their agronomic importance in hybrid seed production, functional female (pistillate) plants have some selective advantages. For some species, there is sound evidence that female plants produce more seeds than hermaphrodites. According to Hanson and Bentolila (2004), it is probably because of more, saved by the suppression of male organs. In those species where anther development halts at a very early developmental stage, maximum seeds are produced because these species save considerable output of resources. In other species where disruption occurs late in development of anther, after considerable energy has been already utilized, no increase in seed set has been detected (Hanson and Bentolila, 2004). Thus, the genes that confer male sterility may somehow confer a survival advantage to the individuals.
Plenty of histological descriptions of male sterility are available (Laser and Lersten, 1972; Frankel and Galun, 1977; Kaul, 1988; Hegde and Isaacs, 1992). These descriptive studies provide the information on structural aberrations of sterile anthers. Few histochemical studies performed on sterile anthers have provided combined information on structural details as well as chemical composition of male cells/tissues (Katti et al., 1994). The picture that has emerged from these studies is, anther tapetum and the reproductive cells are the chief casualties of male sterility.

Since the process of male sterility operates through specific anther tissues, and at specific developmental stage, it is very important to trace the changes in biochemical composition of these tissues during their development. Assessment of altered biochemical changes of tapetum and reproductive cells is possible by comparing them with fertile anther which serves as a control. Employing histochemical techniques, it is possible to study in situ localization of important components of cells/tissues.

Male sterility in pepper (Capsicum annuum L.) was reported for the first time by Martin and Crawford (1951) and the first cytoplasmic male sterile (CMS) plants were described by Peterson (1958). Since then, nuclear and nuclear-cytoplasmic male sterile genotypes in chilli have been obtained by mutagenic induction (Daskalov, 1968) or by interspecific hybridization (Yazava et al., 2001). Much information has been published concerning the nature, inheritance and stability of pepper male sterility, and the possibility to include sterile forms in breeding programs and sterile lines in hybrid seed production (Daskalov, 1968; Pathak et al., 1983; Patel et al., 2001; Yazava et al., 2002; Kumar et al., 2003) and Krouleva and Daskalov (1978) concluded that there were no essential differences in the moment and mechanisms of degeneration and lethality of the meiocytes between nuclear male sterile and CMS plants. Novak (1971) and Kumar et al. (2001) reported irregular meiosis, especially at the second cytological particularities in Nuclear and Nuclear-Cytoplasmic Male Sterile Pepper Line 263 in CMS individuals. Abnormal function of the tapetum in both types of male sterility and a sterilizing effect in the CMS plants was found by Novak (1971), Horner and Rogers (1974) and Krouleva and Daskalov (1978).
Tadahiko and Yukihiro (1981) reported that, the development of archesporial cells and tapeta, meiosis of pollen mother cells and formation of pollen tetrads progressed normally. However, pollen tetrads, which were somewhat larger than those normal plants, did not release microspores, and gradually collapsed and disappeared. Just before anthesis, the anther loculi became empty and nothing was detected except for dead remains of collapsed tissues.

Nikolova (2010) studied meiosis in the pollen mother cells (PMCs) of nuclear and nuclear-cytoplasmic male sterile (CMS) pepper lines No.1647 \textit{ms8ms8} and No.K587 \textit{Srfrf} to establish the causes of male sterility. The microspore degeneration started either after the tetrad stage, as the callose was not dissolved and the microspores were not released from the spore tetrads, or in some cases at various phases of the microgametogenesis. The chromosome rearrangements and chromosome breakage leading to those aberrations could damage the genetic system responsible for the regular initiation, running and termination of late meiotic stages, especially the termination of TII and initiation of cytokinesis in \textit{ms8ms8} plants, and loss of callose dissolving in the CMS plants.

Krouleva and Daskalov (1978) made the conclusion that there is no essential difference in the moment or mechanisms of degeneration and perishing of the meiocytes. This is in contradiction to Nikolova’s results. Novak (1971), Homer and Rogers (1974) and Krouleva and Daskalov (1978) found abnormal function of the tapetum in nuclear and nuclear-cytoplasmic male sterile lines and a sterilizing effect in the CMS forms of \textit{Capsicum}. According to Papini et al. (1999) in two angiosperms (\textit{Tillandsia albida} Mez. and \textit{Lobivia rauschii} Zecher.) tapetum degeneration appears to be a type of programmed cell death events, influencing the development of the microspores. Most likely the chromosome breakage and chromosome rearrangements might also initiate some disorders, as early tapetum degeneration or irregular and significant tapetal growth, that produce the PMCs lethality and male sterility. According to Dong et al. (2007), mitochondrial gene (orf456) generally is sterilizing factor in cytoplasmic male sterility in chili pepper.
Singh and Hadley (1961) in their study on male sterile and fertile lines of sorghum reported that the tapetal cells of the male sterile anthers showed a weakly staining property and a higher frequency of endomitosis and these tapetal cells persisted even after the abortion. They concluded that the tapetal cells were deficient in some substances which brought about the failure of the tapetal cells to degenerate which in turn caused the failure in the supply of nutrition vital for the development of microspores into viable pollen grains.

Chauhan and Singh (1966) observed the association between abnormal behaviour of the tapetum and pollen abortion in hexaploid wheat (Norin) having *Aegilops ovata* cytoplasm. They grouped the anthers of male sterile wheat into three types based on the behavior of the tapetum.

a) Primary degeneration of tapetum, which resulted in degeneration of the sporogenous tissue.

b) The tapetum remained intact and was accompanied by the increase in nuclear size even after the formation of microspore tetrads.

c) The third type resulted in the formation of a tapetal periplasmodium, when PMCs entered meiosis.

So, the intermingling of the contents of the Plasmodium with the PMCs caused the degeneration of PMCs. They concluded that male sterility in all the three types resulted from improper nourishment of the developing sporogenous cells as microspores due to abnormal behaviour of tapetum.

Choudhary and Das (1967) gave an account on the cytomorphological aspects of male sterility in *Brassica campestris*. In yellow sarson, the tapetum did not seem to function as a nutritive layer as it persisted beyond the prescribed time of breakdown. In brown sarson non-dehiscence of anthers due to the presence of large and irregular cells of anther wall in the form of a thick, compact layer led to the functional male sterility.
In a study by Choudhary *et al.* (1968) revealed that the deviation in the behaviour of the tapetum from its normal functioning as a nutritive layer caused the degeneration in wheat. But they reported the presence of functional male sterility in wheat in which the non-dehiscence of anthers was due to the presence of thick and hard anther walls resulting from deposition.

Based on histological studies in male sterile sorghum, Raj (1968) concluded that the degeneration of male gametes was not confined to any particular stage. It occurred right from the PMC stage to the first mitotic division of the microspores and no chromosomal abnormalities were noticed. The cytoplasm degenerated resulting in collapsed cells. The tapetum in normal fertile plants was parietal in position till the completion of microspores development, but in sterile plants, the tapetum was of periplasmodial type. In semi sterile hybrids, the tapetal cells enlarged radially with large vacuoles and enlarged nuclei. Such hypertrophied cells were either unilateral appearing towards one side or all round the sporocytes. In either case they concluded the entire anther cavity crushing the sporogenous tissue at the centre.

Nakashima and Hosokawa (1974) studied the histological features of genic male sterility in sunflower. Their abnormalities on fertile and male sterile plants revealed that in fertile anthers the tapetal cell walls were broken down after the microspore stage and the tapetal plasmodium extruded in to the locule to envelop the microspores, whereas in sterile anthers the tapetal cells remained intact and increased in size. Also the nuclei of the tapetal cells in fertile anthers were irregular in shape and peripherally disposed while in sterile anthers they were large spherical and positioned centrally.

In genetic male sterile lines of soybean, Albertson and Palmer (1979) observed that, after normal meiosis cytokinesis failed to occur resulting in coenocytic tetrads. They developed a typical pollen wall, which is further aborted.

The vacoulation and invasion of the tapetum after tetrad formation was the main cause for the pollen degeneration in CMS rye. This followed the formation of an unorganized mass of tapetum and the contents of the locule remained as a compressed layer over the endothecium of the anther (Scoles and Evans, 1979).
Gray Bosch and Palmer (1987) carried out analysis of a male sterile character in mutant soybeans cytological comparison demonstrated that both mutants displayed similar phenotypic effects. Due to abnormal behaviour of tapetum the sheath of the callose wall that surrounds both PMCs and young microspores failed to dissolve properly and microspores subsequently aborted.

Kajjidoni (1997) carried out a detailed comparative study on histological basis of male sterility in two genetic male sterile lines of *Gossypium arborium* L. (DS-5 and GAKA-7423) and their fertile counterpart lines. His investigation revealed that, the process of microsporogesis was normal with regular meiosis until the formation of microspores. Abnormality was noticed during further development of microspores at the time of pollen grain formation in both the GMS lines.