REVIEW
OF
LITERATURE
# Review of Literature

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2.1 Introduction

The cultivation of plants was one of the greatest revolutionary accomplishments that presumably began in the Mesolithic or 'Middle stone age' from 12000 to 6000 BC, when man lived with spear, bow and fishing net. Since then the increasing needs urged man to search for better techniques to fulfill his needs. At present we live in 'space age', but even then agriculture faces many challenges world-wide due to interaction of several phenomenon, important being 'Population explosion'.

Agriculture in the advent of 'Green Revolution' was dominated by the efforts of increasing productivity, but it has now multiple objectives. The cropping system, the quality of crop production, the cost of crop production, pattern of efficiency of leaves for photosynthate production and increased use efficiency of nutrients occupy priority.

Oilseeds are essentially important crop of the tropical agriculture (Weiss, 1983) as they provide easily available and highly nutritious human and animal food. The industrial needs are also met with some of the oilseed crops. Oilseed Brassica accounts for approximately 10% of the total world oilseed production. In the Indian sub-continent, Brassica
juncturea is the dominant species grown due to high oil content in its seeds (Downey and Rimmer, 1993). The details of botany of the plant have been described in the section ‘Material and Methods’.

Mustard (Brassica juncea L.) has high mineral N requirement for good harvest. The roots are also able to increase their uptake rate capacity rapidly in order to compensate shoot N requirement, but only about 50% of the applied N fertilizer is recovered in the harvested seeds (Schjoerring et al., 1995). This implies that there exists inefficient N utilization and may cause potential risk of significant losses of the applied N to the environment. The efficiency with which the leaf N is mobilized to the seeds might be improved by increasing N assimilation capacity if the availability of photosynthate for reduction of nitrate is available to the plant. The plant with high photosynthate production may be an ideal ideotype for increased N assimilation and thereby with reduced N losses.

2.2 Strategies for crop improvement

There has always been increasing pressure to break yield plateau of crops by developing new cultivars that have high yields and at the same time improved quality. The sustained possibility of accomplishing the goal of breaking yield plateau is still far away. However, the strategic use of fertilizers and manures may help in assuring sustainability. Oilseed Brassica responds well to high nutrient status soils. Its N requirement is
greater (Weiss, 1983). Managing N nutrition is an important and an open avenue in crop management programme to improve the yield and minimize N losses. In addition, the management of leaf assimilation capacity may also help in increasing sink potential. As high N requirement and large number of leaves are feature of Brassica, the management of leaf number for efficacious incorporation of N and its conversion into photosynthate is another factor that needs to be looked into for research and a challenge before the scientists. Brassica relatively has large number of leaves at early stages of growth causing shading effect on leaves on the lower canopy. These lower leaves contribute less to plant productivity and they abscise at maturity when their C balance becomes negative. The retention of the critical leaf number and thus leaf area for a significant duration may increase photosynthetic biomass production and yield by maintaining the flow of assimilates to flowers and developing pods. Moreover, N encourages leaf development and maintaining photosynthesis over the crop growth period. Thus, an ideal situation with critical leaf number with greatest photosynthetic capacity and N assimilation and incorporation in mustard may be one aspect of crop improvement. Any suggestion for target metabolite may become worthy in improving C and N conservation in plants.

2.2.1 Source-sink system

Net photosynthetic rate is a pre-requisite for growth and
productivity. It is one of the most highly integrated and regulated metabolic processes required to maximize the use of available light and to optimize the use of limiting C and N resources. Photosynthate and N supply interact to control the development of leaves and the whole plant N acquisition, which provide the dominant basis for sink strength (Paul and Foyer, 2001). Therefore, alteration of photosynthetic rate may result in an increase in demand for N assimilation. Among several factors influencing photosynthetic activity, irradiance is of prime importance which affects plant growth and developmental responses. Irradiance environment during plant development phase affects its elongation rate and photosynthetic capacity of leaves (Allard et al., 1991). The distribution of available light over a maximum portion of the leaf area is necessary for high efficiency of photosynthetic apparatus. Accumulation of carbohydrates in leaves during photosynthesis can be enhanced by several other means; by manipulating photosynthesis source, translocation of photosynthate and photosynthate sinks (Herold, 1980; Neales and Incoll, 1968). The hormonal, nutritional or other interactions may follow in sink manipulation as plant hormones are involved in the regulation of photosynthetic rate and source-sink balance (Sweet and Wareing, 1966; Treharne and Stoddart, 1968; Wareing et al., 1968). Carbohydrate accumulation in leaves leads to N release, which can be used for growth processes. The mechanism that optimizes the whole
plant C to N balance may become important strategy in improving carbon and N acquisition. The physiological state that regulates photosynthesis and coordinate the plant C:N balance determines photosynthetic capacity. It has been reported that increased assimilation demand on a source leaf resulted in an increase in CO$_2$ fixation rate and a decrease in leaf starch concentration. It is possible therefore that at different stages of growth with changing sink demands, there may be significant shifts in carbon flow through leaf. The storage of photosynthate in the leaf and sink provides an important control in relation to partitioning of carbon in plants. Since source activity drives sink metabolism, photosynthetic control must also be responsive to the needs of the whole plant and, optimal use of C and N resources (Thorne and Koller, 1974; Paul and Foyer, 2001). The plants with higher sink:source ratio had higher photosynthetic and net assimilatory rates, increased translocation from photoassimilatory to sink organs and increased source and sink activities (Rogers et al., 1995; Mei and Yun, 1999). A sink is generally supplied with photosynthate from a nearby source and as growth proceeds new sources develop and the photosynthetic rate of older leaves declines (Rawson and Hofstra, 1969; Wardlaw, 1990). The source-sink interaction is often clouded by the possibility that changes in demand may influence photosynthesis not only directly, but indirectly through factors other than accumulation of
photosynthate, possibly hormonal changes. Artificially induced changes in the demand for photosynthate can influence the rate of photosynthesis (King et al., 1967; Neales and Incoll, 1968). Carbon partitioning in plants can be influenced by a range of factors, including hormonal and nutritional status. Leaf photosynthesis is generally the main source of carbon for growth and storage of plant. However, other chlorophyll containing organs such as stems, inflorescence and fruits can contribute significantly to the overall supply of photosynthate and thus influence the pattern of C partitioning. There are number of reports where the export of carbon from leaves has been positively correlated with the photosynthesis. Ho (1976, 1978) demonstrated a strong positive relation between photosynthesis and C export in tomato. Similar correlations between photosynthesis and the export of C have been shown for a range of plant species including cotton (Hendrix and Huber, 1986), sugar beet (Servaites et al., 1989) and sorghum and ryegrass (Wardlaw, 1990). Fader and Koller (1983) studied the relationship between C assimilation, partitioning and export in leaves of soybean and reported that rate of accumulation of leaf dry matter and rate of export increased as CO2 assimilation rate increased. Bélanger et al. (1994) studied the effect of N fertilization on carbon balance in Festuca arundinacea and reported that the effect of N fertilization on shoot growth is due to changes in C partitioning resulting in faster leaf area development and greater light
interception. Rate of senescence and leaf N remobilization was related to the activity of C fixation enzymes. These enzymes, representing a large proportion of leaf protein, tended to decline in relation to N loss (Crafts-Brandner et al., 1983).

Carbon metabolism is inextricably linked to N metabolism and any effect of a change in C abundance influences N metabolism and vice-versa (Noctor and Foyer, 2000; Lewis et al., 2000). Carbon assimilation of crop depends on the crop N through leaf area development (Gastal and Lemaire, 2002). The plants with higher source-sink ratio had higher photosynthetic rate and net assimilation rate. Modifications in source-sink relationships are considered as prominent factors in N reserve accumulation (Bouchart et al., 1998).

The diversity of function and the control of partitioning of dry matter to different plant organs is the platform on which crop yield is based and many agricultural plants improved yields have been associated, not with an increase in total production, but a greater partitioning of the available C to the organs being harvested. Arakawa et al. (1999) reported that grain filling of the barley plants deprived of leaf blades was superior to that of deep shaded plants. Kim et al. (1991) reported that defoliation induces changes in source-sink relationships for N and regrowing shoots exerted stronger sink behaviour in defoliated alfalfa plants. Khan et al. (2002a) studying the performance of mustard
(Brassica juncea) after defoliation reported that removal of upper leaves (sources) caused decline in seed yield, indicating that upper leaves contribute more towards seed yield (sink).

2.2.1.1 Defoliation

The removal of leaves, partial or complete is described as defoliation. Defoliation is an age old practice in many parts of the world. In northern India, mustard plants are defoliated for vegetables and or fattening lambs. The practice although beneficial to the plant has been in use without knowing its consequences on morphophysiological characteristics of plants. Responses of plants to defoliation are of considerable economic importance (McNaughton, 1979a, b). By reducing transpiration surface, defoliation also may conserve soil water stores, sustaining plant growth over a longer period. Klubertanz et al. (1996) reported that defoliation significantly increased soil-moisture percentage, regrowth of leaves, delayed senescence and compensatory regrowth. Respiration rate as measured in dark was higher in defoliated plants that in the control, which suggested that partial defoliation causes an increase in the photosynthetic rate even in leaves which have completed their growth (Wareing et al., 1968).

Plants have a light requirement for flowering since they need photosynthetic product to grow and develop. Photoperiodic induction occurs in the leaves and flowering stimulus moves out from the leaves to
the meristem where flowers are to be initiated. Specific factors, why they occur and their significance to breeders and farmers/growers are still being determining. One of these factors is shading, which affects overall performance of the plant (Weiss, 1983). Shading often occurs in dense crop canopies, causing maximum photosynthetic rate of new leaves to be reduced. Leaves developed in shade are usually longer, thinner, and lower in specific weight than those developed at high irradiance. Shade-grown leaves have lower stomatal density, but guard cell lengths are similar to those found in sun-grown leaves (Björkman, 1981). It has long been known that plants which occupy shaded habitats are incapable of high photosynthetic rates. Shaded plants have lower contents of soluble proteins and considerably lower ratios of soluble protein to chlorophyll (Björkman, 1981). Crookston et al. (1975) observed 70% decreases in the activities of glycolate oxidase, malate dehydrogenase and carboxylase in shaded bean plants. Paul and Driscoll (1997) reported that shaded leaves decline the Rubisco content that accompanies N deficiency.

Shading can reduce the number of flowers and pods produced by reducing the C assimilates, depending upon the duration and reduce pod size and number of seeds per pod (Tayo and Morgan, 1979). Field shading has been reported to alter the radiation environment, decrease assimilation, and reduce grain yield. Shading in winter wheat affected
tiller mortality, spike morphology, kernel weights and ultimately grain yield. The net assimilation rate has been shown to decrease with age of the plant. The decrease is caused by the shading of lower leaves by the upper leaves. In addition, there is an increasing proportion of respiring to photosynthetic tissue and the respiration rate is related to the rate of photosynthesis (Milthorpe and Moorby, 1979). Shaded lower leaves contain less N than the upper leaves. Furthermore, the proportion of cell wall constituents (cellulose, lignin) increases in stem tissues during aging and the protein concentration simultaneously decreases when compared to that of leaf blades (Lemaire et al., 1992).

For any crop the net productivity depends primarily on proportion of the light intercepted by the green organs and efficiency of photosynthetic conversion of intercepted light into biomass. In *Brassica*, these factors have special relevance as the leaves produced are large in number, broader in size and oblong shaped, and cause overshadowing effect. It has been reported that large number of leaves can affect the interception of photosynthetically active radiation (Ballare *et al.*, 1989; Grewal and Kolar, 1990; Krishnamoorthy, 1993; Kruger *et al.*, 1998). The shaded and unproductive leaves in *Brassica* become senescent and abscise prematurely. The rate of tissue senescence declines markedly if photosynthetic tissues are maintained in the light by preventing shading. This could be achieved by adopting strategies that lead to rapid loss of
lower leaves in the canopy at early growth stages. Thus once the physiological cost to the plant of maintaining these dying leaves are removed, the assimilate balance may be improved. Leaves make a substantial contribution to the seed yield up to flowering, after this other plant parts have the ability to compensate for the leaf removal by increasing their photosynthetic rate (Frayman et al., 1973; Clarke, 1978). During vegetative growth, roots, stems and leaves are competitive sinks for assimilate. The proportions of assimilate partitioned to these three organs can influence plant growth and productivity. Gautier et al. (1999) reported that competition for light reduces light interception by the plant and also changes the spectral composition of light. Such a change in light quality results in photomorphogenetic responses of the plant mediated through different photoreceptors and photosynthetic pigments. Partial defoliation not only increases the relative demand for photosynthates on the remaining leaves but also increases the photosynthetic efficiency by reducing the competition between leaves for mineral nutrients and possibly for specific hormonal factors (Wareing et al., 1968). Increased light intensity upon remaining photosynthetic tissues after defoliation results in an immediate increase in photosynthetic rate per unit of remaining leaf (Jameson, 1963; Robsen, 1973). Hunter et al. (1995) reported that partial defoliation in Vitis vinifera reduced canopy density leading to
increased light penetration, photosynthetic activity and yield. Increasing light intensity enhanced tillering and leaf production during plant growth, and increased the content of water-soluble carbohydrates in *Festuca pratensis* (Havstad, 1996). Leaves utilizing sufficient sunlight are commonly thicker, leathery and contain more densely packed cells, thus become dark-green and fully expanded (Ludlow and Wilson, 1971; Alderfer and Eagles, 1976; Caemmerer and Farquhar, 1984). This can lead to a higher assimilation rate per unit area in the leaves produced after defoliation. Ourry *et al.* (1996) reported that new source-sink relationships are established between organs remained after defoliation. The investment of assimilate into greater leaf area development results in greater light interception.

2.2.1.1.1 Defoliation and compensatory growth

Defoliation affects morphological and physiological characteristics of plants, including emergence of new leaves with modified assimilatory capacity. These changes have been described as compensatory growth (Ericsson *et al*., 1980; McNaughton, 1983; Foggo, 1996; Bruening and Egli, 1999; Collin *et al*., 2000). The regrowth following defoliation affects biomass production and C reserve remobilization. Growth of defoliated plants is influenced by nutritional status of plants (Ourry *et al*., 1988; Hamilton *et al*., 1998; Skinner *et al*., 1999; Thornton *et al*., 1994), time of defoliation (Ericsson *et al*., 1980)
and genotype (Nugent and Wagner, 1995). Stockhoff (1994) proposed a theoretical hypothesis that foliar losses are balanced by increased irradiance of the leaves remained after defoliation and that N allocation pattern of plants should depend on the severity of defoliation and whether the defoliation is done on the top or bottom canopy. Jarvis and Macduff (1989) reported that response of plants to defoliation has important implications for survival in natural ecosystems as well as for the efficient utilization of fertilizer N in the productive agriculture. It has been shown that rates of leaf appearance and stolon branching are closely related to air and soil temperature (Davies and Jones, 1992) and light intensity (Davies and Evans, 1990). Defoliation upto 40-50% of the leaves increased the rates of leaf emergence and the development of young leaves to maturity (Marriott and Haystead, 1990). An increase in leaf number and leaf area was reported in defoliated Sanguisooba minor (Douglas et al., 1994). Alados et al. (1997) reported an enlargement of the stem, increase in leaf and flower number, greater vegetative growth and inflorescence length in Anthylis cytisoides after clipping. Growth of frequently or periodically defoliated white clover was significantly enhanced upto 30-45% in plants grown under ambient CO₂ concentrations, however, forage regrowth of several grass species was affected little or reduced at elevated CO₂ (Hunt et al., 1995; Sæbø and Mortensen, 1995; Wilsey, 1996). Cresswell et al. (2001) reported that
*Brassica napus* showed the plasticity in floral dimensions. Saitoh *et al.* (2001) reported that removal of leaves enhanced flowering and this increase compensated for either source or sink restriction. Wallace *et al.* (1985) reported compensatory growth to moderate levels of clipping in African graminoids.

In defoliated white clover, increase in stolon elongation rate, leaf area, root mass, leaf number and stolon number, but total non-structural carbohydrates decreased with the decreased supply of phosphorus. However, the loss was restored by increasing phosphorus supply (Singh and Sale, 1996a, b). Ho *et al.* (1987) reported that head removal in sunflower plants delayed the rate of development of leaf senescence and illustrated the variability in different parameters associated with leaf senescence processes. Defoliation increased the release of soluble and organic compounds from roots and increased cumulative rhizodeposition. It was suggested that defoliation remobilized root carbohydrate for the initiation of shoot regeneration. It also affected crude protein, dry matter, total non-structural carbohydrates (Spitaleri *et al.*, 1994; Paterson and Sim, 2000). Schnyder and Visser (1999) reported that in defoliated ryegrass rapid regrowth was associated with the transient defoliation of water soluble carbohydrates and dilution of structural biomass and C:N ratio in growth substrate was re-established. Walker *et al.* (1999) reported that cut of *Sorghum plumosum* plant
moderately doubled their root volume after treatment. Ourry et al. (1989) reported the decrease in nitrate in roots of defoliated ryegrass, however, the lower carbohydrate concentrations compensated for the accumulation of nitrate. Bocaud and Bigot (1989) proposed that the fluctuations in nitrate reductase were related to the capacity for C assimilation and the nitrate availability in ryegrass. Defoliated plants retained a high capacity for absorption of nitrate and were unable to assimilate this nitrate, thus its net uptake decreased (Jarvis and Macduff, 1989).

Some crop plants such as most grasses have essentially no stem growth during vegetative development and favour partitioning to leaves and roots. Young developing leaves need imported assimilate to provide the energy and C skeletons for growth and development until they produce enough assimilate to handle their own requirements. Adaptation to defoliation in many grass species involves a capacity for remobilization of N compounds stored in perennial tissues such as roots or stubble allowing N to be supplied to the growing zones despite the reduced N uptake by roots that usually occurred as a response to defoliation (Volenc et al., 1996). The relative contribution of remobilization and root uptake in supplying N to new leaves after defoliation depends on grass species (Thornton et al., 1993). Moreover, the N status of the plant at the time of cutting is an important factor for
mineral N-uptake down regulation and the subsequent dynamics of N remobilization (Macduff et al., 1989; Louahlia et al., 1999). It is well established that organic reserves contribute to regrowth of defoliated plants (Ourry et al., 1994). Repeated defoliation decreased CO₂-induced growth enhancement under nutrient-limited conditions. However, when nutrients were abundant, positive CO₂-induced growth enhancements were maintained after defoliation. This indicated the importance of soil nutrients in sustaining CO₂-induced growth responses when subjected to defoliation (Hunt et al., 1995; Hebeisen et al., 1997; Morgan et al., 2001). About 40 to 60% of the total N in roots and crown is mobilized to meet the N demand of the shoots during early regrowth. Amino-N is the most readily available form of N (Lefevre et al., 1991; Hendershot and Volenec, 1993) and protein N the largest storage form (Ourry et al., 1989; Kim et al., 1991). Mobilization of N reserves from stubble and roots play a major role during early regrowth of grass plants. Grass plants subjected to defoliation can use either nutrients taken up by the roots or those remobilized from other tissues for regrowth of lamina (Thornton et al., 1993). Plants have two available sources of N for growth of young tissues: the external supply and organic reserves from older vegetative tissues (Lefevre et al., 1991). For a wide range of crop species, organic reserves and more particularly carbohydrates contribute to regrowth of new leaves following defoliation. Rapid degradation
followed by synthesis of carbohydrates such as polyfructan in ryegrass (Gonzalez et al., 1989) or starch and sucrose in alfalfa (Habben and Volenec, 1991; Kim et al., 1993) occurs in roots and crown during post defoliation regrowth.

The enhanced plant growth is often accompanied by shifts in biomass partitioning with increased partitioning of biomass to below ground organs (Bazzaz, 1990; Rogers et al., 1994). Heuvelink and Marcelis (1996) reported that increased assimilate supply in sweet petter and tomato increased dry weight of individual leaves. Defoliation leads to an increase in NO₃⁻⁻N content in young stems of defoliated soybean plant (Mei et al., 2002). Lötscher and Hay (1996) reported that defoliation in clover altered source-sink relationships and increased lateral transport to far side branches. Goulas et al. (2002) reported that the mobilization of N reserves from storage tissues of regrowing clover was closely linked to the pattern of differentiation of newly developed organs. The remobilization of N can be increased by increased N-fertilization in alfalfa defoliated plants (Skinner et al., 1999). Grasses tolerate defoliation through preferential allocation of assimilate, and remobilization of C and N storage compounds, from leaf blades, crowns and roots to support recovery of photosynthetic capacity (Johasson, 1993).

Age of a plant strongly influences the plant response to shoot
removal (Todorovic et al., 1999). Defoliation at vegetative stage enhanced leaf production and greater relative growth rate of tillers (Becker et al., 1997a, b), while as defoliation at anthesis reduced leaf area, plant dry mass and grain yield (Ockerby et al., 2001). Defoliation resulted in proportional partitioning of assimilates in leaves and stem and increased partitioning to non-structural dry matter (Pammenter and Allison, 2002). Defoliation of lower leaves promoted apical bud growth and initiation of flowering (Yeh and Chiang, 2001; Khan et al., 2002a).

2.2.1.1.2 Defoliation and photosynthetic capacity

Growth following defoliation depends first of all on the development of photosynthetic surface (Richards, 1993). Partial defoliation has rejuvenating effects on the remaining leaves, restoring their photosynthetic capacity to near the values of newly formed leaves (Warieng et al., 1968; Hodgkinson, 1974). An increase in CO$_2$ assimilation rate and changes in the light regime for the growth in a CO$_2$ enriched atmosphere cause parallel changes in RuBP carboxylase activity and the capacity for RuBP regeneration (Caemmerer and Farquhar, 1984). Partial defoliation leads to increased photosynthetic rates by increasing the supply of endogenous cytokinins to the remaining leaves, which in turn leads to increased enzyme synthesis, including carboxylating enzymes. This increased rate of photosynthesis seen after partial defoliation has been interpreted for photosynthesis on
the remaining leaves (Wareing et al., 1968). Becker et al. (1997a) reported that grasses rapidly re-establish photosynthetic capacity after defoliation. Photosynthetic rate in oilseed plant *Oenothera biennis* was enhanced after defoliation (Morrison and Reekie, 1995). Syvertsen (1994) also reported an increase in photosynthesis and stomatal conductance in citrus seedlings after partial defoliation.

Partial defoliation increased leaf net photosynthetic rate in wheat. (Wang et al., 1997). Donaghy and Fulkerson (1997) reported that most of the leaf regrowth in defoliated ryegrass was due to plant water soluble reserves and remainder due to photosynthesis. Belsky and Hill (1997) reported decrease in alkaloid production in *Festuca arundinacea* which may be due to photosynthetic rate to generate new leaves. Defoliation enhanced compensatory photosynthesis and stomatal conductance in *Festuca idahoensis* (Doescher et al., 1997). Anten and Ackerly (2001) reported that defoliation significantly increased the light available to the remaining leaves and light saturated photosynthesis per unit leaf area. This was due to an improved light penetration in the canopy in *Chamaedorea elegans*. Defoliation in maize increased the light penetration, thereby increased grain yield (Emam and Seghatoleslami, 1999). Kruger et al. (1998) reported that defoliating *Populus tremuloides* increased light penetration in the crop canopy. Clipping leads to increase in photosynthesis in *Panicum maximum* (Páez
and Gonzalez, 1995). An increase in PAR was reported in peanut by Jones et al. (1982). Ryle et al. (1985) reported that recovery of N₂ fixation in clover was related to the re-establishment and increase in the photosynthetic capacity.

2.2.1.1.3 Defoliation and enzyme activities

Photosynthetic rates are limited not only by the physical resistance to C dioxide diffusion but also by the levels of carboxylating enzymes in the leaf. Partial defoliation leads to increase in the carboxylating enzymes and thereby increased photosynthetic rates (Wareing et al., 1968). The rise in leaf protein content after defoliation indicates that the increased carboxylating activity is a result of increased enzyme synthesis, which may be a result of reduced competition between leaves for mineral nutrients or metabolites supplied by the roots (Wareing et al., 1968). Caemmerer and Farquhar (1984) reported an increase in the CO₂ assimilation rate following the removal of shaded leaves. Partial defoliation leads to increased levels of RuBP carboxylase and PEP carboxylase and to the parallel increase in the photosynthetic rate suggesting that there could not have been saturating levels of these enzymes present in the leaves of the control plants (Wareing et al., 1968). Partial defoliation caused an increase in CO₂ assimilation rate and a parallel change in RuBP carboxylase activity and capacity for RuBP regeneration in Phaseolus vulgaris (Caemmerer and Farquhar,
Hua and Rui (1998) reported that defoliation increased the activities of RuBP carboxylase and sucrose phosphate synthase in the flag leaf of rice. However, Gana et al. (1998) reported the decrease in amylase activity in roots of defoliated alfalfa plants. Roover et al. (1999) reported the decrease in fructan metabolizing enzyme activities in *Cichorium intybus* immediately after defoliation, however, at later stages the enzyme activities increased. Li et al. (1998) working with alfalfa applied with phosphorus fertilizer reported that defoliation increased endo-amylase activity in roots. Yamamoto et al. (1996) reported an increase in sucrose, glucose, fructose together with amylase activity in the taproot of alfalfa following defoliation.

Hartwig and Trommler (2001) reported an increase in the concentration of aspargine, glutamine and aspartate in white clover lupin following defoliation. Bound proteins in chicory roots were hydrolysed to provide extra free amino acids after defoliation. These amino acids were used for the growth of new foliage (Neefs et al., 2002). Culvenor and Simpson (1991) reported the increase in amino acid-N indicating the breakdown of soluble protein in excess in defoliated clover. Handershot and Volenec (1993) reported the increase in the concentration of aminoacids like leucine, isoleucine, tyrosine and phenylanaline in the tap roots of defoliated alfalfa. Gordon and Kessler (1990) reported that activities of invertase, sucrose synthase, glucose
pyrophosphorylase, aspartate aminotransferase, glutamine synthetase, phosphoenol pyruvate carboxylase and malate dehydrogenase increased at the later stages of regrowth and emergence of new leaves following defoliation.

Crafts-Brandner et al. (1983) reported an increase in the concentration of sugar by 42% in roots, enhanced nitrate assimilation (NRA and accumulation of reduced-N), uptake, transport and reduction of nitrate in soybean after the removal of vegetative shoot apex. The significant increase in total plant nitrate reductase activity was highly correlated with shoot regrowth. Boucaud and Bigot (1989) reported an increase in glutamine synthetase activity in regrowing tissues of ryegrass.

Khan (2002) studying the effects of defoliation on mustard reported an increase in the activities of carbonic anhydrase and RuBP carboxylase. Hartwig et al. (1994) reported an increase in the nitrogenase activity in nodules of defoliated white clover.

2.2.1.1.4 Defoliation and plant hormones

The morphological and physiological changes following defoliation are presumed to have brought about by signals produced by plant hormones. Therefore, the renewed growth of a terminal bud after removal of mature leaves may be associated with the changes in the plant hormones. Experiments aimed at studying changes in plant
hormones have less frequently been reported. Sporadic reports on the hormonal changes associated with the defoliation are available in the literature. Qi and Yan (2000) reported accumulation of abscisic acid in cotton leaves following defoliation. Earlier work conducted in the author's laboratory by N. A. Khan and associates showed that auxin and ethylene level changes accompanied with the defoliation in mustard (Khan et al., 2002a, Khan, 2003).

2.2.1.1.5 Defoliation and crop yield

Yield of a grain crop is a function of the production of assimilate by photosynthesis, translocation of assimilate to reproductive sinks and its utilization by the developing sinks to produce the storage materials, that give the seed its economic value. The ability of the seed to utilize assimilate is an important part of the yield production process. It has been reported that the assimilate requirement of an individual seed plays an important role in determining total seed output because the total assimilate requirement of all the seeds on the plant must be in balance with the available assimilate supply. Significantly higher seed productivity on the removal of lower leaves of Brassica juncea has been reported (Raut and Ali, 1986; Khan and Ahsan, 2000; Khan et al., 2002a, b). However, defoliation at flowering reduced the grain dry matter in maize hybrids (Sangoi et al., 2002). Martinez et al. (2001) reported that removal of first three leaves enhanced yield in tomato.
2.2.2 N assimilation

On a global scale terrestrial plants assimilate 1.4 gigatons of N annually, approximately 90-95% of the total in form of mineral N and remaining from symbiotic N fixation (Paul and Clark, 1988). Since N fixation by living organisms (except for some symbiotic N2 fixers) is generally quite limited, therefore, N is added to soils for most cropping systems to achieve high yield. One of the most important features in achieving crop productivity in the last half century has been the increased use of N fertilizer. Close relations are commonly found between crop yields and annual N application rates (Sinclair and Horie, 1989). N uptake of the field crops is highly variable within a single year, between the sites and between crops, even when N supplies from both the soil and additional fertilizer inputs are plentiful (Gastal and Lemaire, 2002).

The evaluation of crop N requirements and the analysis of yield components in relation to N supply have been mostly directed towards the general objective of satisfying crop N demand (Greenwood et al., 1986). A more functional approach linking the plant productivity with N supply was developed with the advancement of plant ecology. This approach was concentrated towards a search for adaptive strategies of N input which could conserve natural environments (Lambers and Poorter, 1992). Research conducted in the last one and half decade has allowed
the development of a functional approach for crops based on the ecophysiology of N uptake, N distribution and growth (Lemaire, 2001). In situations with a generous N supply, the variability in the dynamics of N accumulation in crops, under different climatic conditions and for different species has greater importance reduced when crop N content (amount of crop N per unit ground area) is related to crop biomass (Greenwood et al., 1986). Understanding the processes that govern N fluxes, particularly N uptake and distribution in crops is of major importance with respect to both environmental concerns and the quality of crop products (Gastal and Lemaire, 2002). This can be looked into as plant N consists of two pools: a metabolic pool corresponding to N storage structure and the other as metabolic functions. Crop respond favourably to nutrient N with regard to growth, development and yield (Marschner, 1995) as nutrients form the building blocks for the amino acids, proteins, nucleic acids and other cellular constituents necessary for the plant development (Fageria et al., 1991; Salisbury and Ross, 1992). N application enhances the soil moisture and increases water-use efficiency during the vegetative period through larger leaf area without affecting water-use during different levels of the stored soil moisture (Vyas et al., 1995; Zaman and Chaudhari, 1998; Dodd, 2001). Madakadze et al. (1999) reported that plant N concentration increases with the increase in the N fertilizer. The exogenous supply of N
increases the levels of protein and mRNA for PEPC (Sugiharto and Sugiyama, 1992). Increasing N levels in general bring about a significant increase in $^{14}$C assimilation, RuBP carboxylase, PEP carboxylase activities and dry mass production (Sharma and Sirohi, 1987; Khan, 1996; Khan et al., 1996). N supply alters the rates of cell division and cell expansion in growing leaves (Gastal and Lemaire, 2002). In grasses, N supply greatly stimulates cell production rate, and the final cell length is affected (Mac Adam et al., 1989; Gastal and Nelson, 1994; Fricke et al., 1997). In dicots, early studies showed that the impact of N supply on leaf growth was mostly due to an increase in cell growth rate, because a larger final cell size was observed and also because N supply increased leaf water potential (Radin and Parker, 1979; Radin and Ackerson, 1981; Radin et al., 1982).

2.2.2.1 N mineralization

It is generally assumed that N fertility of soil in natural agro-ecosystem reaches a maximum equilibrium level under specific environmental conditions where organic matter inputs equals loss (Tate, 1992). However, the intervention of mass in agro-ecosystems changed this equilibrium through effects of cultivation, which accelerates the oxidation of soil organic matter at or near the surface. This results in loss of potentially mineralizable N fraction of organic matter that serves as reservoir of N available to crops. Mineralization of organic N (native
or added organic N sources) is an important process in the N nutrition of wetland crops. The mineralization of organic N takes place in a three step reaction i.e. aminization, ammonification and nitrification. Aminization involves the breakdown of proteins in neutral and alkaline environments by bacteria, fungi and actinomycetes, one of the final stages of decomposition of proteins and release of amines and amino acids. The amines and amino acids so released are further utilized by still other groups of heterotrophs including both aerobic and anaerobic micro-organisms with the release of ammonical compounds, a process termed as ammonification.

Nitrification is referred to as biological oxidation of ammonium to nitrate. The nitrification process is generally controlled by ammonium availability (Guenzi et al., 1978; Robertson, 1982), soil pH and temperature (Francis, 1982; Gilmour, 1984). The use of nitrification inhibitors did not arrest the process completely. This resulted in a preponderance of ammonium over nitrate in the soil, which affected the persistence of applied N in the soil as well as plant N metabolism and N nutrition (Sharawart, 1996).

2.2.2.2 N immobilization

Immobilization is the reverse of mineralization and occurs when large quantities of low N crop residues such as cereal crop straw is decomposed in the soil. The high amount of carbohydrates in such
residues causes pollution of soil micro flora to build up quickly. As new cells are formed, N and other essential elements are used to build up protoplasm. Almost invariably this leads to a decrease in the levels of inorganic N for crops.

Nitrate is the dominant form of mineral N available to higher plants. The assimilation of nitrate by plants requires uptake, reduction and conversion of nitrate to ammonia and the incorporation of ammonia to organic compounds (Migge and Becker, 1996; Sivasankar and Oaks, 1996). Nitrate is first reduced to nitrate by the enzyme nitrate reductase and the nitrite is further reduced to ammonia in a reaction catalyzed by nitrite reductase. Ammonia formed is then converted to amino acids through the combined activities of glutamine synthetase and glutamate synthase (Miflin and Lea, 1976; 1980). The form of N ion supplied to roots also influences the absorption and transport of other nutrients (Pilbeam and Kirkby, 1992). Subsequently nitrogenous organic compounds such as amino acids are utilized through primary metabolic pathways for various aspects of the life cycle of plants. The uptake of ammonium and nitrate by plants is controlled metabolically. A specific active uptake system has been established for nitrate (Ansari and Bowling, 1972; Hewitt, 1975; Rao and Rains, 1976; Doddema et al., 1978; Doddema and Telkamp, 1979). In the case of ammonium, a concentration-dependent multi phase uptake pattern has also been
established, indicating the existence of an active uptake mechanism (Fried et al., 1965; Joseph et al., 1975).

The supply of nitrate to the roots is facilitated by diffusion and mass flow along with the water taken up. It has been ascertained in numerous investigations that nitrate as opposed to ammonium nutrition can lead to increased uptake of cations, while the anion uptake is diminished. Generally, it can be expected that pure ammonium nutrition is more favourable in species whose capacity for ammonium assimilation is greater than the capacity for nitrate reduction. Better growth with nitrate than with ammonium has been observed within numerous species (Gigon and Rorison, 1972; Chaillou et al., 1986). N uptake and translocation from organic N reserves of roots and stubble to new foliage were both enhanced during regrowth of ryegrass (Ourry et al., 1988).

2.2.2.3 Effects of N deficiency on plants

The supply of N in a plant available form is one of the main factors controlling plant productivity in agricultural ecosystems. Higher plants have, therefore, evolved a variety of strategies to increase the effectiveness by which N is retained and utilized for growth and development, following its acquisition from the environment by root uptake or N\_2 fixation. If less N is available in the soil than is required by the crop, N absorption is limited and the crop experiences N deficiency
(Ourry et al., 2001, Jeuffroy et al., 2002; Khan et al., 2002c). N deficiency is mainly characterized by poor growth rate. The plants remain small, the stems have a spindle appearance, the leaves are small and the older leaves often fall prematurely. Root growth is affected and in particular branching is restricted (Mengel and Kirkby, 1987). Plants suffering from N deficiency mature earlier, and the vegetative growth stage is shortened. N deficiency not only affects cell number, but also cell size in plants (Marschner, 1995). Deficiency of N affects leaf size through both cell production and cell expansion. It alters source-sink relations, strengthens root growth compared with leaf growth and reduces growth of whole plant and dry matter accumulation, N metabolism and photosynthesis are impaired, plant nitrate, free amino acids and protein decrease under N deficiency. Deficiency of N decreased rate of photosynthetic rate per unit leaf area (Van der Werf et al., 1993). It has been reported that N deficiency reduced leaf area duration, leaf area index, aerial dry matter, crop growth rate, intercepted PAR and water use efficiency (Novoa and Loomis, 1981; Lemcoff and Loomis, 1986; Sinclair and Horie, 1989; Uhart and Andre, 1995a, b; Mae, 1997; Dodd, 2001).

Researches have shown that N supply promotes growth of plants by way of better cell division and their elongation. In the following pages efforts will made to emphasize the role of N in growth and
photosynthetic characteristics, nutrient uptake, yield and quality characteristics in oilseed crops, particularly in mustards.

2.2.2.4 N and growth characteristics

Increase in N level from 0 to 80 kg N/ha significantly increased growth characteristics in Indian mustard (Sharma et al., 1994; Khan et al., 1990, 2001, 2002c). Application of N showed significant positive effect on mean plant height of *Brassica napus* and *Brassica campestris* (Al-Jaloud et al., 1996). The height of *Brassica juncea* increased significantly with increasing N from 0 to 90 kg N/ha at every growth stage (Tomar et al., 1996; Khanpara et al., 1993). The essential role of N in leaf growth has long been recognized. N fertilization increased leaf area and plant biomass. Leaf expansion rate is very responsive to N supply both under controlled and field conditions. Leaf growth is particularly responsive to large amounts of N in *Brassica* crops. N fertilizer application increased leaf area of *Brassica napus*. Increased allocation of dry matter to shoot was reflected in increased rates of leaf expansion and elongation in plants supplied with N. It is clear that if N supply rate to the crop for new leaf growth is restricted, the amount of leaf area produced is proportionately restricted (Larcher, 1995; Marschner, 1995; Dodd, 2001; Khan, 1996; Khan et al., 1996; 2000; 2002c). Increased levels of N show increased leaf area index progressively. High leaf area index indicates high mobilizable protein at
beginning of reproductive stage, which helps the crop to put forth higher production. N application to *Brassica juncea* significantly increased leaf area index and was considerably higher at all stages of growth at 100kg N/ha than 50kg N/ha (Grewal and Kolar, 1990). Khan and Agarwal (1988) reported that leaf area index increased with increasing N rates in the range of 0-80kg N/ha in *Brassica juncea*. Leaf area index increased with the increase in N levels, however there was no significant increase after 40kg N/ha in groundnut (Patra *et al*., 1995). Perumal (1999) also reported that leaf area index increased significantly with increasing N levels in rain-fed grown cotton. Pradhan *et al*., (1994) and Dey *et al*. (1989) also reported similar results for leaf area index in response to N. N application increased crop growth rate of castor (Bheemiah *et al*., 1998). Pradhan *et al*. (1994) also reported an increase in crop growth rate by N application. Increasing levels of N from 0-60kg N/ha increased crop growth rate of barley genotypes under moisture scarce conditions (Awasthi and Surajbhan, 1994). Patra *et al*. (1995) also reported that crop growth rate increased with the increase in N levels, however, there was no significant increase after 40kg N/ha in groundnut. The crop fertilized with 80kg N/ha showed higher crop growth rate over 40kg N/ha due to potential rate of N in metabolic activities and on vegetative growth of sunflower plants (Sarkar *et al*., 1999). Khan and Agarwal (1988) also reported that crop growth rate increased with
increase in N rates in *Brassica juncea* but did not increase further with 120kg N/ha. N application showed progressively higher relative growth rate than each respective level of N upto 45-60 days but at later stages the increase was inconsistent and even decreased in certain cases with increase in N levels in sunflower. Increasing levels of N upto 80kg N/ha increased net assimilation rate mainly due to increase in crop growth rate and relative growth rate in sunflower (Sarkar *et al.*, 1999).

Dry mass increase with increasing N doses has been reported (Cajuste *et al.*, 1996; Polly *et al.*, 1999). N application increased biomass production favourably from early stage and was significantly higher with 80kg N/ha at advanced stages of growth due to vigorous vegetative growth in sunflower (Sarkar *et al.*, 1999). Dry matter production in groundnut increased at all growth stages with increase in N levels, however, beyond 40kg N/ha no significant increase took place (Patra *et al.*, 1995). Sawan *et al.* (1998) reported that seedling fresh and dry masses increased with N rate (161kg N/ha) in cotton plants. Increase in N rates increased dry matter production under water scarce conditions (Vyas *et al.*, 1995). Khan and Agarwal (1988) reported that dry matter accumulation per plant increased with increasing N rates in the range of 0 to 80kg N/ha in mustard. However, it did not increase further with 120kg N/ha. Application of 60kg N/ha significantly increased dry matter in *Brassica campestris* genotypes (Satyavam *et al.*, 1999).
N at the rate of 90kg/ha produced maximum fresh weight and dry weight at vegetative as well as reproductive stages. N-fertilized plants of mustard produced appreciably more dry matter throughout the growing season than unfertilized plants (Singh and Saran, 1987).

2.2.2.5 N and photosynthetic characteristics

The effects of the form and concentration of nutrient N on photosynthetic carbon dioxide assimilation may arise from the influence of N source on photosynthetic enzymes, photorespiration, stomatal conductance or other aspects of photosynthetic metabolism. The amount of leaf N and Rubisco per unit leaf area is affected by N supply. Greater N supply generally results in increased N and Rubisco per unit leaf area in the developing leaves. CO₂ assimilation is generally higher at higher N concentration, as the N invested in the enzymes of the photosynthetic carbon reduction cycle and in the thylakoid protein constitutes the majority of leaf N. Leaves with a higher content of N utilize high photon flux densities more effectively for photosynthesis than those with a low N content (Lawlor, 2001). Increasing N from 0 to 50 kg/ha and 50 to 100kg N/ha helped the crop canopy of *Brassica juncea* L. to trap more radiation for photosynthesis (Grewal and Kolar, 1990; Grewal *et al.*, 1993). They also reported that interception of PAR by the crop canopy of *Brassica napus* improved significantly with the increase in N rates from 0 to 100kg/ha. It is well known that plants vary in the sensitivity of
the photosynthetic apparatus radiation of different wavelengths within the canopy. Mean sunlight irradiance on leaf surface diminishes as an exponential function of leaf area index (Saeki, 1963; Charles-Edwards, 1982). Changes in radiation quality also occur largely due to the spectral properties of leaf pigments leading to reduction in the red-far red ratio as light penetrates the canopy (Holmes, 1981; Ballare et al., 1989; Guimet et al., 1989).

2.2.2.6 N and nutrient uptake

The type and concentration of N in growth media extend a considerable influence not only on the growth and mineral composition of the crop plants, but also affect the relative uptake of cations and anions (Kurvitis and Kirkby, 1980; Gashaw and Mugwira, 1981; Kirkby, 1981; Lovatt, 1986; Jeschke et al., 1992). Increasing levels of N increased the uptake of N regularly irrespective of growth stage in linseed (Singh and Mishra, 1994). Application of 60kg N/ha significantly increased N uptake by seed, whereas uptake of N by stalk as well as total N increased linearly up to 90kg N/ha of N applied to *Brassica campestris* genotypes (Satyavam et al., 1999; Dubey and Khan, 1993; Patil and Bhargava, 1987; Kumar et al., 1989). The influence of N supply nutrient uptake in *Brassica juncea* has also been reported. Voluminous literature is available in this context. To quote few that has been reported from the author's laboratory include (Samiullah et al.,
1990; Khan et al., 1990; 2000, 2002c)

2.2.2.7 N and yield characteristics

Yield is determined by canopy photosynthesis during crop growth, and photosynthetic capacity is closely related to leaf N content. During sink development N is translocated from vegetative plant material to the sink. N is an important factor which influences the yield. The yield increases with an increase in N supply to a limited extent, irrespective of the forms of N (Larcher, 1995; Marschner, 1995). N application increased mean pod number per plant in *Brassica napus* under drought conditions (Asare and Scarisbrick, 1995). The number of pods per plant in Indian mustard increased by N application significantly upto 80kg N/ha under rainfed conditions (Thakuria and Gogoi, 1996). Increase in the number of siliqua per plant with increasing levels of N up to 60kg/ha in *Brassica juncea* has also been reported by Khanpara et al. (1993), Reddy and Sinha (1988), Rathore and Manohar (1989), while Tomar et al. (1996) and Dubey et al. (1993) reported the increase up to 90kg N/ha. Grewal and Kolar (1990) reported that number of pods per plant in *Brassica juncea* L. increased significantly with the increase in N from 0 to 100 kg/ha. Post-flowering application of urea solution significantly influenced the pods per plant of groundnut (Patra et al., 1995).

Seeds per siliqua in *Brassica juncea* significantly increased due to increment in level of N from 0 to 90kg/ha (Tomar et al., 1990), while
Khanpara et al. (1993) reported the increase in seeds per siliqua with increasing levels up to 60kg N/ha in Indian mustard. Increase in seeds per siliqua with an increase in application of N fertilizer has also been reported in *Brassica juncea* by Reddy and Sinha (1988), Rathore and Manohar (1989) and Dubey et al. (1993). The number of seeds per pod of *Brassica juncea* increased significantly with the increase in N from 0 to 100 kg/ha (Grewal and Kolar, 1990; Khan et al., 1990). Thakuria and Gogoi (1996) reported an increase in seed number under rainfed conditions in Indian mustard. Seed weight of combined seed samples of *Brassica napus* was increased by N application (Asare and Scarisbrick, 1995). 1000-seed weight in *Brassica juncea* increased with increasing levels of applied N upto 60kg/ha (Khanpara et al., 1993). Patra et al. (1995) reported that 1000-seed kernel-weight was significantly and positively increased by post-flowering application of urea solution to groundnut. Tomar et al. (1996) reported that 1000-seed weight was significantly increased due to increment in the level of N from 0 to 90kg/ha in *Brassica juncea*. Seed weight in *Brassica juncea* increased significantly with an increase in N level from 0 to 50kg/ha but decreased with the further increase in N from 50 to 100kg/ha (Grewal and Kolar, 1990). Thakuria and Gogoi (1996) also reported significant increase in 1000-seed weight in Indian mustard under rainfed conditions. Increase in 1000-seed weight in Indian mustard under rainfed conditions with the
increase in N up to 60 kg/ha has also been reported by Singh and Kumar (1996). Reddy (1983) reported that higher fertilizer rate increased seed yield in linseed. Application of 80kg N/ha gave significantly higher seed yield in sunflower over 0kg N/ha application (Sarkar et al., 1999). An increase in the seed yield of sunflower has also been reported by Zaman and Chaudhary (1989). An increase in the seed yield of *Brassica juncea* with the increase in applied N has been reported by Reddy and Sinha (1988), Rathore and Manohar (1989), Grewal and Kolar (1990), Chaudhary et al. (1992), Prasad and Shukla (1993), Tomar et al. (1992), Khan et al. (1990; 2000), Khanpara et al. (1993), Sharma (1992), Ghosh et al. (1995), Singh and Kumar (1996), Thakuria and Gogoi (1996), while the same effect on *Brassica napus* has been reported by Gendy and Marquard (1989), Grewal et al. (1993) and Asare and Scarisbrick (1995). Application of N showed significant positive effect on seed yield of *Brassica napus* and *Brassica campestris* under irrigated conditions (Al-Jaloud et al., 1996). Bheemaiah et al. (1998) also reported increase in seed yield of castor with increased N. An application of 40kg N/ha significantly increased harvest index in rainfed mustard but was reduced at 60kg N/ha (Ghosh et al., 1995).

### 2.2.2.8 N and quality characteristics

In oilseed crops N supply affects quality characteristics. Patra et al. (1995) reported that with the increase in N supply the quantity of
soluble proteins increased in groundnut. Nitrogen levels significantly affected the protein content with the increase in the dose of N up to 90kg/ha in *Brassica juncea*. As the N supply increased the formation of protein also increased (Dubey *et al.*, 1994). Asare and Scarisbrick (1995) also reported relationship between applied N and seed protein in *Brassica juncea* However, Gendy and Marquard (1989) reported that protein contents of *Brassica napus* seeds increased with the increase in N supply. Application of N showed significantly positive effect on mean protein content of *Brassica napus* cv. Canola and *Brassica campestris* cv. Rapeseed under irrigated conditions (Al-Jaloud *et al.*, 1996). Increase in protein content in rapeseed mustard with increasing rate of N applied has also been reported by Patil and Bhargava (1987) and Satayavam *et al.* (1999).

### 2.2.3 Plant hormones

Phytohormones play an important role in integrating many aspects of development and responses to environment (Ciardi and Klee, 2001). Regulation of hormonally controlled events can occur at the level of biosynthesis, catabolism, perception and signal transduction (Trewavas, 1983; Bradford and Trewavas, 1994; Nakatsuka *et al.*, 1998). Little work has been done on the hormonal changes associated with defoliation. Since defoliation and nitrogen application are likely to affect ethylene concentration or vice-versa, an attempt has been made to
focus on ethylene and its rate-limiting enzyme, 1-aminocyclopropane carboxylic acid synthase. Ethylene is gaseous phytohormones involved in a diverse assay of cellular, developmental and stress-related processes in plants. It is the simplest olefin with molecular formula \( H_2C=CH_2 \) and exists in the gaseous state under normal physiological conditions. Its effects on various physiological processes at different stages of plant growth, development, senescence, abscission and fruit ripening have been well documented (Abeles et al., 1992; Pua and Chi, 1993; McKeon et al., 1995; Khan, 2004). Ethylene is known to exert its effects at least in part by altering gene expression. Effects on both transcriptional and post-transcriptional processes have been identified. Depending on the plant material and state of development, promoting or inhibiting effects of ethylene on internode growth have been observed (Sisler and Yang, 1984). Physiological conditions like water stress or drought also promote the ethylene synthesis in plants (Tudela and Primo-Millo, 1992; Bergner and Teichmann, 1993; Michelozzi et al., 1995).

2.2.3.1 Biosynthesis of ethylene

The biosynthetic pathway of ethylene has been well established (Yang and Hoffman, 1984; Kende, 1993; Moeder et al., 2002). Ethylene is formed from methionine (Met) through S-adenosylmethionine (AdoMet) and the cyclic non-protein amino acid, 1-aminocyclopropane-1-carboxylci acid (ACC) by the action of ACC synthase and the
conversion of ACC to ethylene is carried out by ACC oxidase. In
addition to ACC, ACC synthase produces 5-methylthioadenosine, which
is utilized for the synthesis of new methionine via a modified
methionine cycle. Considerable progress has been made in the genetic
and molecular dissection of the ethylene-response pathway. Expansion
of leaves by suppressing cell enlargement rather than cell division,
increase in photosynthesis and biomass production in different plants
(Kieber \textit{et al.}, 1993; Rodrigues-Pousada \textit{et al.}, 1993; Lee and Reid,
1997; Hussain \textit{et al.}, 1999; Khan \textit{et al.}, 2000; 2002a, b; 2003) has been
reported. Ethylene enhances growth indirectly by increasing the activity
of endogenous gibberellin (Raskin and Kende, 1984). Young leaves
generally produce ethylene at higher rates than older leaves (Burg, 1968;
McAfee and Morgan, 1971; Morgan and Durham, 1980). Ethylene has
been reported to enhance glutamine synthetase activity, the enzyme that
supplies the cells with the amino acids needed for protein synthesis via
the pathway involving glutamine synthase (Pujade-Renaud \textit{et al.}, 1994).

Ethylene biosynthesis may be regulated by the activity of ACC
synthase (Kende and Boller, 1981) by the net transport of ACC from its
site of synthesis in the cytoplasm (Guy and Kende, 1984a, b) to its
probable site of conversion into ethylene in the vacuole (Guy and
Kende, 1984a, b) and/or compartments of the cell (Yang and Hoffman,
1984). In addition to ACC synthase activity, there also appears to be
other regulation point in the conversion of ACC to ethylene, high tissue
ACC levels control the rate of ethylene formation (Kende and Boller,
product ACC at the beginning of ethylene biosynthesis has been
demonstrated in every tissue studied (Boller et al., 1979; Jones and
Kende, 1979; Yu and Yang, 1979) suggesting that the synthesis or
activation of ACC synthase regulates ethylene biosynthesis. ACC
synthase, ACC accumulation and ethylene formation are strongly
inhibited by aminoethoxyvinylglycine (Konze and Kwiatkowski, 1981).
ACC is transported in the vascular system of the plants and is present in
relatively low amounts, however, exposure to some types of stress can
increase ACC and ethylene synthesis (Bradford and Yang, 1980a, b;
Hoffman et al., 1983a, b). ACC synthesis increases in flooded roots
from where it is transported in the xylem to the shoots and causes an
increase in ethylene production in leaves and petioles, which then
exhibit a number of changes in growth and development. These changes
may constitute physiologically active messages that modify shoot
physiology and development (Jackson and Campbell, 1978). Kende and
Boller (1981) reported an increase in the rate of ethylene synthesis, the
level of ACC and the activity of ACC synthase activity in wounded
tomato fruits. Ligero et al. (1986), Zaat et al. (1989), Ligero et al.
(1991) reported that root infection by Rhizobium increased the ethylene
evolution rate markedly leading to changes in root development, however, treatment with aminoethoxyvinylglycine at the time of inoculation significantly inhibited ethylene biosynthesis and stimulated nodule formation in alfalfa (Peters and Crist-Estes, 1989). Increase in ACC levels in organs distal to leaves prompted the proposal that ACC is a mode of inter organ transport of an ethylene signal (Finlayson et al., 1991). Inter organ transport of ACC was also shown by several authors (Bradford et al., 1982; Amrhein et al., 1981; Reid et al., 1984; Fuhrer and Fuhrer-Fries, 1985; Mor et al., 1985; Nichols and Frost, 1985; Guiragossian and Koning, 1989; Woltering, 1990; Tudela and Primo-Millo, 1992; Esle et al., 1995).

ACC occurs both in free form and as a conjugate with malonic acid, 1-malonyl aminocyclopropane-1-carboxylic acid in several plant tissues (Hoffman et al., 1982). ACC accumulates concomitantly with a rapid burst in ethylene production in the early stages of plant response to stress (Yu and Yang, 1980; Konze and Kwiatkowski, 1981). ACC is controlled among other factors by ACC synthase and ACC oxidase activities (Amrhein et al., 1981; Hoffman et al., 1982; Kende, 1993). ACC can also be conjugated to L-(malonylamino) cyclopropanone 1-carboxylic acid (Van Loon and Fontaine, 1984; Fuhrer and Fuhrer-Fries, 1985; Jiao et al., 1986; 1987; Bouzayan et al., 1988; 1989; Martínez-Reina et al., 1996) or L-Y-L-glutamylamino, cyclopropane-1-carboxylic
acid (Martin et al., 1995; Martinez-Reina et al., 1996).

2.3 Conclusion

It is known that mustard is an important crop of tropical and subtropical regions of the world characterized by the production of large amount of biomass due to supra-optimal leaf area indices. Its biomass production and productivity respond favourably to N inputs. Large volume of data is available in the literature showing positive effects of N on growth and productivity of the crop. Since the crop is used for green tissue and seeds, N is applied indiscriminately in an effort to enhance the desired characteristics. With the advancement in knowledge it has become clear that one can not afford to large amounts of N inputs for productivity gain because N may put serious economic and ecological concerns. The option seems to reduce the N inputs but this may adversely affect productivity of the crop. The option left is to manage the crop to have efficient leaf area indices for maximal production of photosynthates and efficient utilization of soil-applied N. As discussed in the previous pages that defoliation brings about increase in morphological, physiological and yield characteristics in various plants, including mustard, the present thesis reports an effort of management of nitrogen utilization through removal of 50% leaves on the lower axis of plant, which are below photosynthetic light compensation point. There contribution as photosynthates accumulation
exceeds the use of nutrients and water for their sustenance at later stages of life cycle. It is added that this study involving assay of biomolecules may lead to the identification of some signal metabolites, which may be targeted to have desired plant ideotype.