The Asian and Australasian Journal of Plant Science and Biotechnology ©2007 Global Science Books

The Source-Sink Relationship in Mustard

Nafees A. Khan[*] • Sarvajeet Singh • Rahat Nazar • Pervez M. Lone

Department of Botany, Aligarh Muslim University, Aligarh 202 002, India

Corresponding author: * **naf9@lycos.com**

ABSTRACT

Mustard is an important oilseed crop of the tropical and sub-tropical regions of the world. The languid production of oilseeds has converged the attention of agricultural scientists to innovate and implement methods for boosting yield using agricultural, physiological and biotechnological tools. Among other factors, the use of plant growth regulators and management of plant canopy have a proven potential in modulating plant function and improving nutrient use and the source-sink relationship. The present review discusses the factors and the prospects of employment of gibberellic acid and removal of lower leaves as a tool for improving the source-sink relationship in mustard.

Keywords: *Brassica juncea*, carbonic anhydrase, defoliation, gibberellic acid, nitrogen, plant growth regulators

Abbreviations: ABA, abscisic acid; **GA$_3$**, gibberellic acid; **IAA**, auxin; **N**, nitrogen; **PAR**, photosynthetically active radiation; **PGR**, plant growth regulator; **Rubisco**, ribulose 1,5 bisphosphate carboxylase; **S**, sulfur

CONTENTS

INTRODUCTION........ 10
FACTORS AFFECTING SOURCE-SINK RELATIONS........ 11
  Plant growth regulators........ 11
  Carbon and nitrogen balance........ 12
IMPROVING SOURCE-SINK RELATIONSHIP IN MUSTARD........ 12
  The role of gibberellic acid........ 13
  The importance of defoliation........ 13
CONCLUSION........ 15
REFERENCES........ 15

INTRODUCTION

Photosynthetic activity, translocation of photoassimilates from source (leaf) organ to sink (seed) and accumulation of photosynthates in the sink determine the source-sink system. Apart from direct control of photosynthesis by light and carbon dioxide, others factors like nitrogen availability and a balance between carbon and nitrogen play a vital role in determining photosynthetic capacity. Carbon metabolism is essentially linked to nitrogen metabolism and any effect of a change in carbon abundance influences nitrogen metabolism and vice-versa (Noctor and Foyer 2000; Lewis *et al.* 2000). Nitrogen regulates the activity of the photosynthetic machinery as it is a constituent of chlorophyll, thylakoid proteins and enzymes of the Calvin cycle. Moreover, the physiological state that regulates photosynthesis and coordinates the plant carbon and nitrogen balance also determines photosynthetic and storage capacity. The source activity should be responsive to the sink metabolism and thus, optimal use of carbon and nitrogen resources (Paul and Foyer 2001). Plants with a higher sink/source ratio exhibit higher photosynthesis, increased translocation from source 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). Moreover, artificially induced changes in the demand for photosynthesis may influence carbon partitioning. There are reports where the export of carbon from leaves has been positively correlated with photosynthesis. Ho (1976, 1978) demonstrated a strong positive relation between photosynthesis and carbon export in tomato. Komor (2000) reported that total plant productivity relied on appropriate carbon assimilation rate and the export of carbon from source leaves. Similar correlation between photosynthesis and the export of carbon has been shown for a range of plant species including cotton (Hendrix and Huber 1986), sugarbeet (Servaites *et al.* 1989), sorghum and ryegrass (Wardlaw 1990). Fader and Koller (1983) studied the relationship between carbon assimilation, partitioning and export in leaves of soybean and found that rate of accumulation of dry matter and export increased as CO_2 assimilation rate increased. Grodzinski *et al.* (1998) using ^{14}C labeling of leaves examined twenty-one C_4 versus C_3 species and found that export rate was closely correlated with photosynthesis and sucrose concentration. The studies of Faville *et al.* (1999) and Bai and Kelly (1999) found a positive correlation between light saturated photosynthesis and spear yield among asparagus cultivars. They suggested that it might be source supply rather than sink demand that played a major role in the regulation of carbon export in asparagus. In leaves, sucrose synthesized within the cytosol is the form of carbohydrate translocated via the phloem to sink organs along a concentration gradient, whereas starch synthesized in the chloroplast serves as the immediate deposit for photoassimilate. In sink tissue, sucrose is acted upon by the enzyme sucrose synthase or invertase and metabolized to starch or lipids. The assimilate flow within the phloem is driven by a pressure difference generated by loading of os-

Received: 27 February, 2007. Accepted: 13 April, 2007.

Invited Review

motically active carbohydrates within the source and their unloading in the sink (Turgeon 2000). Guo *et al.* (2002) reported that sucrose concentration increased continuously through the light period even the rate of photosynthesis declined in the afternoon. The reason for the increase in sucrose concentration in the afternoon was attributed to the greater assimilation compared to carbon export.

The improvement of available carbon to the harvested organ signifies the crop harvest index. For many crops the increase in harvest index reaches a plateau and a further increase is not possible without an increase in the efficiency of carbon harvesting and the translocation to the sink. Therefore, the control of increase in carbon fixation, translocation and storage of assimilate to the sink form the basis on which crop yield is based (Neales and Incoll 1968; Herold 1980). Phytohormones have been implicated in various aspects of the control of photosynthesis and distribution of photosynthates to sink. They have been found engaged in increasing photosynthetic and yield potential of several crops, and increasing source-sink interactions. Apart from this the management of plant canopy also increases assimilate balance and improves source-sink growth. Several reviews have covered different aspects of source/sink relations, like the control of source or sink capacity or the regulation of photosynthetic machinery and sink system (Gifford and Evans 1981; Sonnewald and Willmitzer 1992; Paul and Foyer 2001). The present article focuses on the factors affecting source-sink interactions and the possible role of gibberellic acid (GA_3) and the influence of removal of lower leaves on leaf photosynthetic potential, nitrogen (N) use and yield of mustard, an oleiferous crop third in importance as a source of vegetable oil in the world.

FACTORS AFFECTING SOURCE-SINK RELATIONS

Plant growth regulators

Plant growth hormones are naturally occurring or chemically synthesized organic substances, acting at a low concentration to influence physiological and biochemical processes. They are also referred as phytohormones or plant growth regulators (PGRs). The action of PGRs in plants includes various developmental phases ranging from seed germination to seed set. It is now known that PGRs regulate expression of the intrinsic genetic potential of plants involving mechanism both at transcriptional and translational levels. For some phytohormone, receptors and binding proteins on the surface of membrane have been indentified (Sisler *et al.* 2006).

Plant growth regulators have been employed to improve the physiological efficiency of plants by modifying the balance between photosynthesis and respiration (Arteca and Dong 1981; Zerbe and Wild 1981; Makeev *et al.* 1992), affecting stomatal aperture or the activity of photosynthetic enzymes (Khan 1996a, 1996b; Foroutan-Pour *et al.* 1997; Khan 2005). The photosynthetic response of crops to phytohormones varies from one extreme to the other.

Gibberellins (GAs) have been shown to influence photosynthesis in various crops. GAs are a large family of diterpene acids, isolated as metabolites of the fungus *Fusarium moniliforme*, the imperfect stage of *Gibberella fujikuroi*. Stodola *et al.* (1955) and Brian *et al.* (1954) working with large scale preparation of GAs from fungus cultures isolated an entirely new compound, which was named as “Gibberellin X” by the former team while the latter opted the name “Gibberellic acid” which is universally accepted and retained.

GAs are essential growth factors affecting various aspects of plant developmental processes (Hoaley 1994). The number of identified GAs has crossed over hundred but only few like GA_1, GA_3, GA_4 and GA_7 are known to have biological activity. The regulatory mechanisms of GAs include reception, signal transduction and gene expression (Richards *et al.* 2001). The major studies on GA are related to induction of enzymes during the germination of certain grass seeds. GA induces the aleurone cells of barley seeds to produce α-amylase which is then transported to the endosperm where it helps in the production of soluble sugars from starch. The other aspect of GA studies is the promotion of elongation of stem. GA activates cell division in the intercalary meristem assisting in the change of rosette plants in long stem and bolting.

Application of GA_3 results in an increase, decrease or no change in the photosynthetic process (Hayashi 1961; Gale *et al.* 1974; Sanhla and Huber 1974; Little and Loach 1975; Erkan and Bangerth 1980; **Table 1**). It has been observed that the treatment of GA_3 increased photosynthetic rate in leaves of bean (Alvim 1960), rice and tomato (Hayashi 1961), maize (Nenova and Stoyanov 2000), cotton (Kumar *et al.* 2001), soybean (Yuan and Xu 2001) and wheat (Ashraf *et al.* 2002). However, the mechanisms for the increased photosynthetic rate were not clear. The treatment of plants with GA_3 could lead to the changes in plastid development and chloroplast structure (Wellburn *et al.* 1973). There are some contradictory reports showing the stimulatory (Treharne and Stoddart 1968; Popova *et al.* 1982; Nath and Mishra 1990) or inhibitory (Treharne *et al.* 1970; Huber and Sankhla 1974) effect of GA on ribulose 1,5 bisphosphate carboxylase (Rubisco) activity. It is still uncertain whether GA-induced Rubisco activity is responsible for the increase of photosynthetic rate. GA_3 at certain concentrations has been shown to be beneficial for the physiology and metabolism of many plants (Sinelnikova *et al.* 1972; Banyal and Rai 1983), since it may provide mechanisms to regulate physiology, biochemistry-growth and development as a function of water availability (Davies *et al.* 1986). The studies published about the effect of GA on photosynthesis are contradictory (Biemelt *et al.* 2004), and possibly were due to different ways of measuring and calculating photosynthesis as well as the different experimental system used (Nagel and Lambers 2002).

Similar varying response of other phytohormones has also been observed. Foliar application of auxin (IAA) enhanced the photosynthetic rate in maize (Nenova and Stoyanov 2000) and cotton (Kumar *et al.* 2001) whereas no significant effect (Robinson *et al.* 1978) or reduction (Erkan and Bangerth 1980) was noted. In a very like manner the effects of ethylene or ethylene-releasing compounds on photosynthesis was observed. Promoting or inhibitory effects of ethephon, an ethylene-releasing compound on photosynthesis were observed depending on the rate of ethylene release. A low concentration of ethylene increases photosynthesis (Buhler *et al.* 1978; Grewal *et al.* 1993; Khan *et al.* 2000; Khan 2004, 2005). Contrarily, a high concentration of ethylene inhibits photosynthesis (Kays and Pallas 1980; Rajala and Peltonen-Sainio 2001; Khan 2004, 2005). The increase in photosynthesis has been attributed to a variation in stomatal conductance (Gunderson and Taylor 1991; Kamaluddin and Zwiazek 2002; Khan 2004). In addition to the effect of ethylene on photosynthesis via the control of stomatal conductance, it also regulates photosynthesis through leaf area expansion and sugar metabolism. The down-regulation of the Calvin cycle enzymes by carbohydrate end products is another mechanism that controls photosynthetic activity and gene expression (Paul and Pellny 2003).

The application of cytokinins has stimulatory effects (Borzenkova 1976; Dong and Arteca 1982). Cytokinins have been reported to increase the expression of genes for light-harvesting chlorophyll a/b binding protein (Flores and Tobin 1989), carbonic anhydrase (Sugiharto *et al.* 1992), Rubisco (Lerbs *et al.* 1984) and phosphoenolpyruvate carboxylase (Suzuki *et al.* 1994). Abscisic acid (ABA) is also involved in photosynthetic responses via sugar metabolism and the regulation of gene expression (Davies and Jones 1991; Arenas-Huertero *et al.* 2000; Finkelstein and Lynch 2000). Studies on *A. thaliana* mutants showed that ABA plays a direct role in mediating photosynthesis via sugar signaling. Kumar *et al.* (2001) found a decrease in photosynthesis due to ABA application in cotton.

Table 1 Photosynthetic characteristics and phytohormone treatment.

Plant	Phytohormone	Characteristics	Response	Reference
Abies balsama	GA_3	Photosynthesis	0	Little and Loach 1975
Aspen	Ethylene	Stomatal conductance	+ +	Kamaluddin and Zwiazek 2002
Brassica juncea	GA_3, ethylene	Carbonic anhydrase activity, photosynthesis Stomatal conductance	+ +	Khan 1996, 2004, 2005
Glycine max	GA_3, ethylene	Photosynthesis, stomatal conductance	+ +	Yuan and Xu 2001; Gunderson and Taylor 1991
Gossypium hirsutum	IAA, GA_3	Photosynthesis, stomatal conductance, carboxylation efficiency	+ +	Kumar *et al.* 2001
Gossypium hirsutum	ABA	Photosynthesis, stomatal conductance, carboxylation efficiency	– –	Kumar *et al.* 2001
Lycopersicon esculentum, *Oryza sativa*	GA_3	Photosynthesis	+ +	Hayashi 1961
Pennisetum typhoides	GA_3	Photosynthesis	– –	Huber and Sankhla 1974; Sanhla and Huber 1974
Phaseolus vulgaris	GA_3	Rubisco activity	+ +	Treharne *et al.* 1970
Plantago major	GA_3	Photosynthesis	– –	Dijkstra *et al.* 1990
Trifolium pretense	GA_3	Rubisco activity	– –	Treharne and Stoddart 1968
Triticum aestivum	GA_3	Photosynthesis	+ +	Gale *et al.* 1974; Ashraf *et al.* 2002
Triticum aestivum	Ethylene	Photosynthesis	– –	Rajala and Peltonen-Sainio 2001
Zea mays	IAA, cytokinin	Photosynthesis, carbonic anhydrase activity, phosphoenol pyruvate carboxylase activity	+ +	Sugiharto *et al.* 1992; Suzuki *et al.* 1994; Nenova and Stoyanov 2000

+ +, increase; – –, decrease; 0, no change

The synthetic growth regulators, triazole, mixtalol, paclobutrazol, uniconazole and triadimefon considerably enhance the rate of photosynthesis (Child *et al.* 1987; Liu 1987; Zhou and Xi 1993; Yang *et al.* 1994; Zhou and Ye 1996). The GA_3-antagonist, cycocel has been reported to cause stimulation in the activity of Rubisco (Pando and Srivastava 1985), enhancement in hill reaction activity and total chlorophyll contents (Bashist 1990).

Sink potential is determined after growth and flowering and phytohormones have a prominent role in modifying it. The improvement in harvest index of different crops in response to phytohormones was observed by Ries *et al.* (1977) and Menon and Srivastava (1984). Phytohormones have also been found to be engaged in the assimilate translocation towards reproductive parts of plants (Pando and Srivastava 1985; Khan *et al.* 1996). Foliar spray of *N*-triacontanol to mustard (Ghosh *et al.* 1991) and NAA to Egyptian cotton (Sawan *et al.* 1989) brought an improvement in seed yield. Similarly, winter rape exhibited an increase in seed yield in response to uniconazole (Zhou and Ye 1996) and mixtalol (Zhou and Xi 1993). Cycocel has also been found to increase sink potential. Improvement in seed yield of *Brassica juncea* in response to cycocel application was observed by Khan *et al.* (2003). Contrarily, Scarisbrick *et al.* (1982) and Grewal *et al.* (1993) could not find an increase in seed yield of oilseed rape due to cycocel application. This was because a high concentration of cycocel was used. In other crops like triticale (Naylor and Stephen 1993), sunflower (Pando and Srivastava 1985), and sesame (Saxena *et al.* 1991), the application of PGRs has been found to increase sink potential. Differential responses of plants to ethephon application on yield were observed. Several investigators reported about the beneficial effects of ethephon on yield of winter wheat (Dahnous *et al.* 1982; Leary and Oplinger 1983; Wiersma *et al.* 1986), mustard (Grewal *et al.* 1993; Khan 1996a; Khan *et al.* 2001), while others claimed a reduction in yield with the use of ethephon (Nafziger *et al.* 1986; Simmons *et al.* 1988).

It is apparent that crop responses to PGRs vary and that the response is dependent on the concentration of PGR used. A low concentration increases the photosynthetic potential of leaves and translocation of photosynthates to sink, while high concentration adversely affects these traits.

Carbon and nitrogen balance

Carbon and nitrogen metabolism are highly integrated and regulated processes. Managing N nutrition improves carbohydrate assimilation increasing photosynthetic potential of leaves. Photosynthate production and N supply interact to control the efficiency of leaves and the acquisition of N, which provides the dominant basis for sink strength (Paul and Foyer 2001). Net photosynthetic rate is a pre-requisite for growth and productivity. It is the process that maximizes the use of available light to optimize the use of limiting carbon and nitrogen resources. Therefore, alteration of photosynthetic rate may result in an increase in demand for N assimilation. Carbohydrate accumulation in leaves leads to N release, which can be used for growth process. N fertilization to *Festuca* resulted in increased shoot growth due to changes in carbon partitioning, faster leaf area development and greater light interception (Belanger *et al.* 1994). The rate of senescence and leaf N remobilization was related to the activity of carbon-fixing enzymes. These enzymes, representing a large proportion of leaf protein, tended to decline in relation to N loss (Crafts-Brandner *et al.* 1983). The mechanism that optimizes the whole plant carbon to nitrogen balance may become an important strategy in the improvement of carbon and nitrogen acquisition. It is possible therefore, that at different stages of growth with changing sink demand, there may be significant shifts in carbon flow through the leaf. The storage of photosynthates in the leaf and sink provides an important control in relation to partitioning of carbon in plants. Since source activity drives sink metabolism, and photosynthetic control must also be responsive to the needs of the whole plant, and optimal use of carbon and nitrogen resources (Thorne and Koller 1974; Paul and Foyer 2001). Rice plants with a 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). The source-sink interaction may be viewed as the photosynthate accumulation and partitioning to sink influenced by factors like nutritional status and hormonal changes.

IMPROVING SOURCE-SINK RELATIONSHIP IN MUSTARD

Mustard (*Brassica juncea* L. Czern & Coss.) is an important oilseed crop of the tropical and sub-tropical regions of the world (Weiss 1983). The oleiferous *Brassica* is the third most important source of vegetable oil in the world after palm and soybean oil (Zhang *et al.* 2003). The major mustard oil-producing countries include Canada, China, France, Germany, India and UK. According to a report of USDA, the world oilseed production is 397 Mt in 2006-07. This total production is an increase of 9 Mt, or 2%, on last season (http://www.hgca.com). About 90% of the total land under oilseed cultivation in India is occupied by *B. juncea*.

Photosynthetic leaves present in lower layers experience a shading effect and do not receive sufficient light and remain below the light photosynthetic compensation point. They contribute to the development of supra-optimal leaf area indices with accompanying self shading and also by other leaves within the plant axis. Later, at maturity, these lower leaves are shed. Their cost of maintenance exceeds the rate of production in terms of nutrients and water. Moreover, the requirement of N for mustard is high for higher yield. The roots are also able to increase their uptake rate capacity rapidly in order to compensate shoot N requirement, but only 50% of the applied N fertilizer is recovered in the harvested seeds (Schjoerring *et al.* 1995). This implies that there exists an inefficient N utilization together with significant losses of the applied N to the environment. The efficiency with which the leaf N is mobilized to seeds may be improved by increasing N assimilation capacity. The strategies that lead to improving N utilization with the loss of lower leaves early in plant development can lead to the development of better source-sink interactions.

The role of gibberellic acid

The information on the effect of GA_3 on photosynthesis in mustard has been reported in the literature. The mechanisms presumed to be operative in GA_3-mediated photosynthetic response are the induction of photosynthetic enzymes, effect on leaf area index and light interception, or enhanced use efficiency of nutrients. Application of 50 μM GA_3 at fully developed three leaf stage was found to increase the activity of carbonic anhydrase three-times at 50d, two-times at 70 d and 90 d after sowing (Khan 1996) an enzyme that catalyses the reversible interconversion of HCO_3^- and CO_2 and in the leaves of higher plants it represents 1-2% of total soluble protein (Okabe *et al.* 1984). Its distribution pattern is similar to that of Rubisco (Tsuzuki *et al.* 1985) and the co-localization of Rubisco and CA in the stroma suggested its role in photosynthetic CO_2 fixation (Raven 1995; Khan *et al.* 2004). A relationship between carbonic anhydrase activity and photosynthesis has also been established in mustard (Khan 1994). In a study on mustard, Khan *et al.* (1996) reported that the plants which were fed with sufficient nitrogen and treated with GA_3 showed higher activities of carbonic anhydrase and nitrate reductase, photosynthesis and leaf area index. Photosynthetic rate integrated over time and leaf area resulted in increased dry mass. Adequate concentration of GA_3 may be required for maximum plant response. Studies of Dijkstra *et al.* (1990) and Nagel *et al.* (2001) showed that a higher concentration of endogenous GA resulted in higher specific leaf area, and that a GA mutant had lower specific leaf area.

Comparing the stage of GA_3 application, i.e. pre-flowering, post-flowering or pod-fill it was found that plants responded maximally when GA_3 was applied at the pre-flowering stage. GA_3 spraying on mustard plants at the pre-flowering stage contributed 35.5% more leaf area (Khan *et al.* 1998). This led them to have a better chance of trapping more sunlight and producing more dry matter. The 35.5% increase in leaf area contributed to a 27.1% increase in dry matter production. Further, it was found that the pre-flowering stage for GA_3 spraying was the best for developping pods and seed yield.

GA_3 spraying was found to be more suitable than GA_3 soaking in enhancing photosynthetic capacity of mustard leaves and sink strength. GA_3 at 10 μM as spray was found to be superior than any other concentrations of GA_3. Spraying 10 μM GA_3 caused more cells to differentiate and as a result leaf area and photosynthesis were enhanced by 29.6 and 31.1%, respectively whereas the same concentration applied through seed soaking could enhance only leaf area and photosynthesis by 21.4% and 27.0%, respectively (Khan and Samiullah 2003). GA_3-sprayed plants translocated more photosynthates towards pods and resulted in higher pod dry mass than GA_3-soaked plants. Various reasons for higher efficiency of spray of GA_3 than soaking were put forth. GA_3 spray checks the flower fall and premature pod drop by maintaining hormonal balance, thus increasing sink capacity.

The increased use efficiency of nutrients, particularly nitrogen and sulfur (S) by GA_3 application may also result in increased photosynthetic efficiency of leaves. Nitrogen status affects photosynthetic rate as the enzymes of CO_2 assimilation and thylakoid proteins account for the majority of leaf N content (Makino *et al.* 1992). GA_3 enhances nitrogen uptake because GA_3-enhanced shoot growth requires more utilization of soil N. GA_3 enhanced nitrogen uptake results in increasing photosynthetic efficiency through maintenance of photosynthetic enzymes. GA_3 at 10 μM was found to increase carbon dioxide exchange rate, plant N and seed N, especially at optimal N. Supra-optimal N applied to crop was not utilized (Khan *et al.* 2002c). At optimal N plants receiving GA_3 made maximum use of available N due to enhancement of vegetative growth and development of more sink (Khan *et al.* 2002c). A similar concentration of GA_3 enhanced seed yield (Khan *et al.* 1997).

In addition to high N requirement, mustard has the highest sulfur requirement among various crops (McGrath and Zhao 1996) but the amount required is not met due to priority of use of N-based fertilizers (Zhao *et al.* 1993). It has been reported that on average a loss of every kg of S results in a potential loss of 15 kg of N (Schung *et al.* 1993). Thus, the shortage of S to the crop lowers the use of N, and decreases rate of photosynthesis and dry mass accumulation. Several studies have established regulatory interactions between N and S assimilation in *Nicotiana tabacum* and *Lemna minor* plants (Barney and Bush 1985; Kopriva *et al.* 2002). The application of 10 μM GA_3 to mustard plants receiving sufficient sulfur (200 mg S/kg soil) increased photosynthesis and dry mass and N and S accumulation. At a low sulfur level (100 mg S/kg soil) GA_3 could not improve photosynthesis and dry mass of mustard plants (Khan *et al.* 2005). It has been suggested that leaf N is not utilized when mustard plants are grown with insufficient sulfur. Stewart and Porter (1969) suggested that leaf N is not utilized when *Triticum aestivum*, *Zea mays* and *Phaseolus vulgaris* plants are grown with insufficient sulfur. The adequate supply of S increased the utilization of N in protein (Rubisco) synthesis enhancing photosynthetic rate. Moreover, S also helps to maintain integrity of enzyme structure. A two-fold increase in sulfur use efficiency of GA_3 treated plants was noted at sufficient S (200 mg S/kg soil). Application of S more than that required did not increase sulfur use efficiency (Khan *et al.* 2005).

It may be said that GA_3 enhances source and sink potential through increasing photosynthetic enzymes increasing leaf area for higher interception of photosynthetically active radiation (PAR) and enhancing use-efficiency of nutrients. The integrated mechanisms enhance source potential and redistribution of photosynthates by GA_3 results in increased sink strength.

The importance of defoliation

Photosynthetic efficiency of leaves and productivity of crops primarily depends on the canopy structure, leaf area index and the efficiency of conversion of light into biomass. It has been suggested that modification in canopy structure subsequently improved crop yield by the influence on light interception by plants. Any modification in crop canopy affects photons absorbed by the plants and thus photosynthesis of individual leaves (Duncan 1971; Norman 1980;

Beadle *et al.* 1985). In a plant, photosynthetic photon flux decreases from top to lower axis. Therefore, photosynthetic potential of lower leaves on plant axis is less in comparison to the upper leaves. In *B. juncea* these factors are more pertinent because the plant bears a large number of broader leaves whose orientation is such that they are horizontally inclined giving the plant a pyramidal shape (Weiss 1983). The broader leaves in the middle hinder light penetration into the lower layers. Thus, the leaves in the lower layers on the plant axis remain below the photosynthetic light compensation point for most of the day and contribute less to net photosynthesis. Moreover, such leaves senesce, abscise and shed at maturity by losing 30-50% of their dry mass (Nobel 1991). Also the large leaf surface causes leaf area indices to reach supra-optimal levels leading to a decrease in photosynthetic biomass accumulation and seed yield. Any strategy by which such leaves are removed and the photosynthesizing potential of the remaining leaves is increased may lead to enhanced biomass accumulation and seed yield. Defoliation (removal of leaves) is practiced by the Northern Indians since old times for the use of leaves as a green vegetable, condiment and spice without knowing its impact on subsequent plant morphological and physiological changes. Research on other crops has shown that defoliation affects growth and mobilization of carbon and N compounds, and influences the total carbon input and determines the biomass accumulation as new source-sink relationships are established between the organs remaining after defoliation and the regrowing leaves of *Lolium temulentum* and *Lolium perenne* (Ourry *et al.* 1996).

Since the pathways of carbon and N assimilation are linked in higher plants (Evans and Terashima 1988; Pace *et al.* 1990), carbon assimilation provides the driving force for N assimilation. Therefore, internal cycling of carbon and N compounds is of great importance during plant development, and also a pre-requisite for regrowth after defoliation (Ourry *et al.* 1996). Thus, the success of a plant within a given environment is dependent on the compromise within the carbon and N interaction (Foyer *et al.* 1995).

Photosynthetic rate is limited not only by the physical resistance to CO_2 diffusion but also by the levels of carboxylating enzymes in the leaf. Partial defoliation has rejuvenating effects on the remaining leaves, restoring their photosynthetic capacity to near the values of newly formed leaves (Wareing *et al.* 1968; Hodgkinson 1974). The ability of leaves to photosynthesize increases as they grow until they are fully expanded, then it begins to decrease. Mustard plants defoliating at a pre-flowering stage exhibited higher photosynthetic characteristics compared to leaves removed at the post-flowering stage (Khan and Lone 2005). The early stage of leaf removal reduces competition between the organs for efficient utilization of light, water and nutrients. Moreover, young leaves produced after defoliation were photosynthetically more active than those attained at a later stage of the plant cycle. The plants defoliated at pre-flowering showed enhanced efficiency and contributed significantly to CO_2 assimilation. The changes in photosynthesis following defoliation were triggered by altered stomatal and non-stomatal processes (Khan and Lone 2005). The increases in the activities of carbonic anhydrase and Rubisco were found upon removal of lower leaves (Khan 2002). Caemmerer and Farquhar (1984) reported an increase in the CO_2 assimilation rate and Rubisco activity following the removal of shaded leaves. Partial defoliation leads to increased levels of Rubisco and PEP carboxylase and a parallel increase in photosynthetic rate (Wareing *et al.* 1968). Hua and Qui (1998) found that defoliation increased the activities of Rubisco and sucrose phosphate synthase in flag leaves of rice. Contrarily, de Roover *et al.* (1999) reported a decrease in fructan metabolizing enzyme activity in *Cichorium intybus* immediately after defoliation, which increased at later stages. Moreover, crop photosynthesis depends on the distribution of PAR among layers and also on the remaining leaves, restoring their photosynthetic capacity (Wareing *et al.* 1968; Hodgkinson 1974). 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 light penetration, thereby increasing grain yield (Emam and Seghatoleslami 1999). Kruger *et al.* (1998) reported that defoliating *Populus* increased light penetration in the crop canopy.

Defoliation brings changes in nutritional status of plants, and increased photosynthetic rate is associated with the increase in N assimilation. Stockhoff (1994) proposed that foliar losses are balanced by increased irradiance of leaves after defoliation and N allocation pattern. Macduff *et al.* (1989) reported that response of plants to defoliation has important implications in the efficient utilization of fertilizer N. Adaptation to defoliation in many grass species involves capacity for remobilization of N compounds stored in roots (Volenec *et al.* 1996). In mustard, the application of N as 100 kg/ha at the time of sowing and 50 kg/ha at post-flowering to plants defoliated at pre-flowering influenced carboxylating enzymes and photosynthesis (Lone and Khan 2007). The increase in photosynthetic rate with this treatment was associated with increased content of plant N and activities of N assimilation enzymes. A positive correlation between photosynthetic capacity and N content of leaves has been reported (Evans and Terashima 1988; Evans 1989; Makino *et al.* 1992). Increased allocation of N with increased N supply has been found to increase the activities of carbonic anhydrase and Rubisco (Terashima and Evans 1988; Burnell *et al.* 1990; Khan *et al.* 1996).

Sink strength is a function of the production of assimilate by photosynthesis, translocation of assimilate to reproductive parts and its utilization by the developing sinks to produce the storage materials, that give the seed its econo-

Table 2 Comparison of per cent increase in photosynthetic characteristics and plant N at pod-fill, i.e. 80 d after sowing (DAS) and yield traits at harvest of mustard (*Brassica juncea* L.) due to defoliation of 50% leaves on lower layers of plant axis at pre-flowering, i.e. 40 DAS or post-flowering i.e. 60 DAS over no defoliation control.

Characteristics	Per cent increase over control due to	
	Defoliation at 40 DAS	**Defoliation at 60 DAS**
Carbonic anhydrase activity	13.6	3.4
Net photosynthetic rate	17.1	2.3
Stomatal conductance	2.4	1.2
Water-use efficiency	14.3	5.9
Plant N content	26.1	15.2
Pod number	12.8	10.3
1000 seed weight	10.3	4.7
Seed yield	16.1	6.6

Table 3 Comparison of per cent increase in photosynthetic characteristics and plant N at pod-fill, i.e. 80 d after sowing (DAS) and yield traits at harvest of mustard (*Brassica juncea* L.) due to defoliation of 50% leaves on lower layers of plant axis at pre-flowering, i.e. 40 DAS and treated with soil-applied 100 kg N/ha at the time of sowing and 50 kg N/ha at post-flowering, i.e. 60 DAS [BN100+N50 (60 d)] over no defoliation plants treated with soil-applied 150 kg N/ha at the time of sowing (BN150) or no defoliation plants treated with soil-applied 100 kg N/ha at the time of sowing and 50 kg N/ha at 60 DAS [BN100+N50 (60 d)].

Characteristics	Per cent increase due to Defoliation + [BN100+N50(60 d)] over	
	No defoliation + BN150	**No defoliation + BN100 + N50 (60 d)**
Carbonic anhydrase activity	18.2	12.5
Net photosynthetic rate	17.2	11.1
Stomatal conductance	2.2	0.8
Water-use efficiency	14.6	10.8
Plant N content	53.6	27.6
Pod number	19.9	11.7
1000 seed weight	31.0	15.1
Seed yield	22.6	12.9

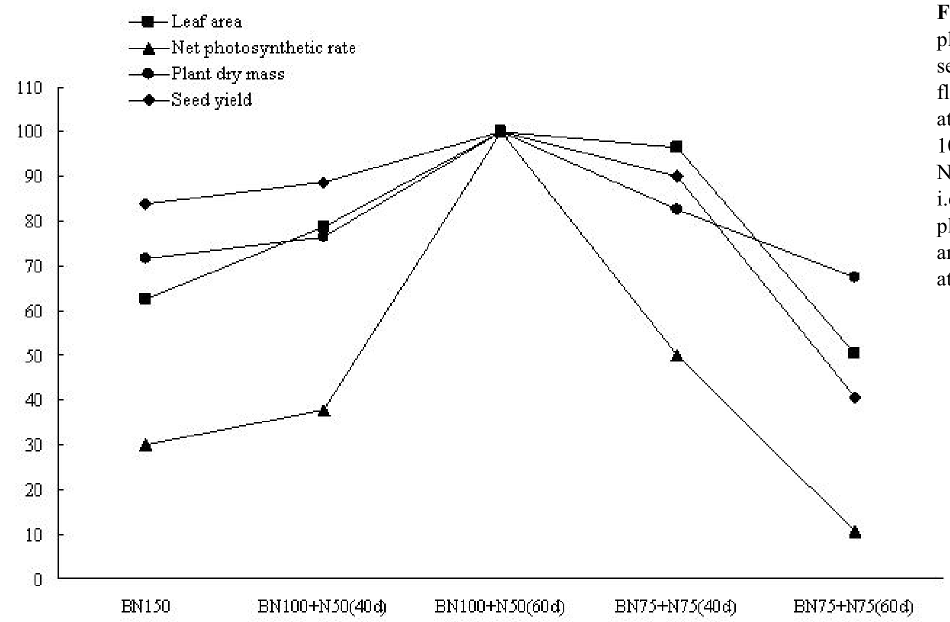

Fig. 1 Index of relationship among leaf area, plant dry mass, net photosynthetic rate and seed yield of mustard after defoliation at pre-flowering (40 d) and treated with 150 kg N/ha at the time of sowing (BN150), application of 100 kg N/ha at the time of sowing and 50 kg N/ha at 40d [BN100+N50 (40 d)] or at 60d, i.e., post-flowering [BN100+N50 (60 d)], application of 75 kg N/ha at the time of sowing and 75 kg N/ha at 40d [BN75+N75 (40 d)] or at 60d [BN75+N75 (60 d)].

mic value. The mustard plants which were defoliated at pre-flowering showed higher photosynthetic rate than the plants defoliated at post-flowering also exhibited enhanced sink strength (**Table 2**). Higher seed productivity of *B. juncea* on the removal of lower leaves has been reported (Raut and Ali 1986; Khan and Ahsan 2000; Khan *et al.* 2002a, 2002b). Becker *et al.* (1997a, 1997b) also found that defoliation at the pre-flowering stage is important in increasing plant dry mass and seed yield. The reduction in seed yield following defoliation at post-flowering is attributed to a lower number of pods per plant and seed weight at this stage of defoliation (**Table 2**). The post-flowering stage of defoliation coincided with the start of pod setting and the requirement for carbon and nitrogen was high but was not available to the seeds. Tayo and Morgan (1979) and Pecham and Morgan (1985) also showed a reduction in the number of pods and seed yield of *Brassica napus* due to leaf removal at anthesis because of reduced carbon assimilation. Raut and Ali (1986) also reported a decrease in seed yield on defoliation of mustard at post-flowering. A part of the nitrogen (50 kg N/ha) application at post-flowering and 100 kg N/ha at the time of sowing to plants subjected to defoliation at pre-flowering resulted in greater increase in the source-sink strength in mustard than no defoliation and one time application of 150 kg N/ha at the time of sowing or no defoliation and the application of 100 kg N/ha at the time of sowing and 50 kg N/ha at post-flowering (**Table 3**). The assimilate availability plays an important role in determining seed yield as the massive N remobilization takes place from the vegetative part to provide N to growing seeds (Schjoerring *et al.* 1995). An index of the relationship among leaf area, plant dry mass, net photosynthetic rate and seed yield showed that the treatment of N as 100 kg/ha at the time of sowing and 50 kg/ha at post-flowering to mustard plants subjected to defoliation at pre-flowering caused maximum increase in photosynthetic rate and seed yield (**Fig. 1**). This supported the argument that greater regrowth followed utilization of soil N more efficiently and enhanced photosynthetic rate, dry mass and finally seed yield.

CONCLUSION

Photosynthate accumulation and translocation to the sink during plant ontogeny are the main determinants of sink strength. The information on photosynthetic activity during leaf development and senescence and on the carbon and nitrogen status of different tissues will provide a means to enhance photosynthesis and crop productivity. The photosynthetic activity of leaves can be enhanced by identifying molecules that provide signals for the loss of lower leaves at an early stage of plant development. Moreover, translocation of photosynthates from source organ to sink may involve complex mechanisms which integrate the expression of the different enzymes involved in carbohydrate partitionning and sink metabolism. A clear understanding of these mechanisms is essential for manipulating source-sink interactions. The interaction study of plant growth regulators on the regulation of source-sink transitions may be fruitful as a single hormone may only act as an inducer for other hormones to set a cascade in motion.

REFERENCES

Alvim PDT (1960) Net assimilation rate and growth behaviour of beans as affected by gibberellic acid urea and sugar sprays. *Plant Physiology* **35**, 285-288

Anten NPR, Ackerly DD (2001) Canopy-level photosynthetic compensation after defoliation in a tropical understorey palm. *Functional Ecology* **15**, 252-262

Arenas-Hucrtero F, Arroyo A, Zhou L, Sheen J, Leon P (2000) Analysis of Arabidopsis glucose-insensitive mutants *gir 5* and *gir 6*, reveals a central role of the plant hormone ABA in the regulation of plant regulative development by sugar. *Genes and Development* **14**, 2085-2096

Arteca RN, Dong CN (1981) Stimulation of photosynthesis by application of phytohormones to the root systems of tomato plants. *Photosynthesis Research* **2**, 243-249

Ashraf M, Karim F, Rasul E (2002) Interactive effects of gibberellic acid (GA_3) and salt stress on growth, ion accumulation and photosynthetic capacity of two spring wheat (*Triticum aestivum* L.) cultivars differing in salt tolerance. *Plant Growth Regulation* **36**, 49-59

Bai Y, Kally JF (1999) A study of photosynthetic activities of eight asparagus genotypes under field conditions. *Journal of the American Society of Horticultural Science* **124**, 61-66

Banyal S, Rai VK (1983) Reversal of osmotic stress effects by gibberellic acid in *Brassica campestris*: recovery of hypocotyls growth, protein and RNA levels in the presence of GA_3. *Physiologia Plantarum* **59**, 111-114

Barney PE Jr., Bush LP (1985) Interaction of nitrate and sulfate reduction in tobacco. I. Influence of availability of nitrate and sulphate. *Journal of Plant Nutrition* **8**, 505-515

Bashist DP (1990) Effect of growth retardant – (2-chloroethyl)-trimethyl ammonium chlorine on NO^-_3 uptake and nitrate reductase activity in *Sesamum* seedlings. *Acta Botanica Indica* **18**, 55-58

Beadle CL, Long SP, Imbamba SK, Hall DO, Olembo RJ (1985) Photosynthesis in relation to plant production in terrestrial environments. *Natural Resources and the Environment Series*, No. 18, 156 pp

Becker GF, Busso CA, Montani T (1997a) Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: axillary bud viability and growth. *Journal of Arid Environments* **35**, 233-250

Becker GF, Busso CA, Montani T, Orchansky AL, Brevedan RE, Burgos MA, Flemmer AC (1997b) Effects of defoliation *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: tiller demography and growth. *Journal of Arid Environments* **35**, 251-268

Bélanger G, Gastal F, Warembourg FR (1994) Carbon balance of tall fescue (*Festuca arundinacea* Schreb.): Effects of nitrogen fertilization and the growing season. *Annals of Botany* **74**, 653-659

Biemelt S, Tschiersch H, Sonnewald (2004) Impact of altered gibberellin metabolism on biomass accumulation, lignin biosynthesis, and photosynthesis in transgenic tobacco plants. *Plant Physiology* **135**, 254-265

Brian PW, Elson GW, Hemming HG, Radley M (1954) The plant growth promoting properties of gibberellic acid, a metabolic product of the fungus *Gibberella fujikuroi*. *Journal of the Science of Food and Agriculture* **5**, 602-612

Buhler B, Drum H, Mohr H (1978) Investigations on the role of ethylene in phytochrome-mediated photomorphogenesis. II. Enzymes levels and chlorophyll synthesis. *Planta (Berlin)* **142**, 119-122

Burnell JN, Suzuki I, Sugiyama T (1990) Light induction and the effect of nitrogen status upon the activity of carbonic anhydrase in maize leaves. *Plant Physiology* **94**, 384-387

Caemmerer SV, Farquhar GD (1984) Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced p(CO$_2$) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. *Planta* **160**, 320-329

Child RD, Butler DR, Sims IM, Johnson W, Thorn M (1987) Control of canopy strucuture of oilseed rape with growth retardants and consequences for yield. *BPCC Monograph No. 36*, *Symposium on Plant Growth Regulators*, pp 21-35

Crafts-Brandner SJ, Below FE, Harper JE, Hageman RH (1983) Metabolism of carbon and nitrogen by soybean seedlings in response to vegetative apex removal. *Plant Physiology* **73**, 6-10

Dahnous K, Vigue GT, Law AG, Konzak CF, Miller DG (1982) Height and yield response of selected wheat, barley and triticale cultivars to ethephon. *Agronomy Journal* **74**, 580-582

Davies WJ, Jones HG (1991) *Abscisic acid: Physiology and Biochemistry*, Bios Scientific Publishers, Oxford, UK, 266 pp

Davies WJ, Metcalfe J, Lodge TA, Costa AR (1986) Plant growth substances and the regulation of growth under drought. *Australian Journal of Plant Physiology* **13**, 105-125

de Roover J, van Laere A, van den Ende W (1999) Effect of defoliation on fructan pattern and fructan metabolizing enzymes in young chicory plants (*Cichorium intybus*). *Physiologia Plantarum* **106**, 158-163

Dijkstra P, ter Reegen H, Kuiper PIC (1990) Relationship between relative growth rate, endogenous gibberellins, and response to applied gibberellic acid for *Plantago major*. *Physiologia Plantarum* **79**, 629-634

Dong CN, Arteca RN (1982) Changes in photosynthetic rates resulting from phytohormone treatments to the roots of tomato plants. *Photosynthesis Research* **3**, 45-52

Duncan WG (1971) Leaf angles, leaf area and canopy photosynthesis. *Crop Science* **11**, 482-485

Emam Y, Seghatoleslami MJ (1999) The effect of defoliation on the pattern of dry matter accumulation and grain yield in hybrid maize (*Zea mays* L.). *Iranian Journal of Agricultural Sciences* **30**, 215-223

Erkan Z, Bangerth F (1980) Investigations on the effect of phytohomones and growth regulators on the transpiration, stomata aperture and photosynthesis of pepper (*Capsicum annuum* L.) and tomato (*Lycopersicon esculentum* Mill.) plants. *Journal of Applied Botany* **54**, 207-220

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C$_3$ plants. *Oecologia* **78**, 9-19

Evans JR, Terashima I (1988) Photosynthetic characteristics of spinach leaves grown with different nitrogen treatments. *Plant Cell Physiology* **29**, 157-165

Fader GM, Koller HR (1983) Relationships between carbon assimilation, partitioning and export in leaves of two soybean cultivars. *Plant Physiology* **73**, 297-303

Faville MJ, Silvester WB, Green TGA, Jermyn WA (1999) Photosynthetic characteristics of three asparagus cultivars differing in yield. *Crop Science* **39**, 1070-1077

Finkelstein RR, Lynch TJ (2000) Abscisic acid inhibition of radicle emergence but not seedling growth is suppressed by sugars. *Plant Physiology* **122**, 1179-1186

Flores S, Tobin EM (1989) Cytokinin modulation of LHCP mRNA levels: the environment of post-transcriptional regulation. *Plant Molecular Biology* **11**, 409-415

Foroutan-Pour K, Ma BL, Smith DL (1997) Protein accumulation potential in barley seeds as affected by soil- and peduncle-applied N and peduncle-applied plant growth regulators. *Physiologia Plantarum* **100**, 190-201

Foyer CH, Valadier MH, Ferrario S (1995) Co-regulation of carbon and nitrogen assimilation in leaves. In: Smirnoff N (Ed) *Environment and Plant Metabolism: Flexibility and Acclimation*, Bios Scientific Publishers, New York, pp 17-33

Gale MD, Edrich S, Lupton FGH (1974) Photosynthetic rates and the effects of applied gibberellin in some dwarf, semidwarf and tall wheat varieties (*Triticum aestivum*). *Journal of Agriculture Science (Cambridge)* **83**, 43-46

Ghosh BK, Mandal BK, Chatterjee BN (1991) Effect of growth regulators on the productivity of some major oilseed crops. *Journal of Agronomy and Crop Science* **167**, 221-228

Gifford RM, Evans LT (1981) Photosynthesis, carbon partitioning, and yield. *Annual Review of Plant Physiology* **32**, 485-509

Grewal HS, Kolar JS, Cheema SS, Singh G (1993) Studies on the use of growth regulators in relation to nitrogen for enhancing sink capacity and yield of gobhi sarson (*Brassica napus*). *Indian Journal of Plant Physiology* **36**, 1-4

Grodzinski B, Jiao J, Leonardos ED (1998) Estimating photosynthesis and concurrent rates in C$_3$ and C$_4$ species at ambient and elevated CO$_2$. *Plant Physiology* **117**, 207-215

Gunderson CA, Taylor GE (1991) Ethylene directly inhibits foliar gas exchange in *Glycine max*. *Plant Physiology* **95**, 337-339

Guo J, Jermyn WA, Turnbull MH (2002) Carbon assimilation, partitioning and export in mature cladophylls of two asparagus (*Asparagus officinalis*) cultivars with contrasting yield. *Physiologia Plantarum* **115**, 362-369

Hayashi T (1961) The effect of gibberellin treatment on the photosynthetic activity of plants. *Sixth International Conference on Plant Growth Regulation*, pp 579-587

Hendrix DL, Huber SC (1986) Diurnal fluctuations in cotton leaf carbon export, carbohydrate content, and sucrose synthesising enzymes. *Plant Physiology* **81**, 584-586

Herold A (1980) Regulation of photosynthesis by sink activity-the missing link. *New Phytologist* **86**, 131-144

Ho LC (1976) The relationship between rates of carbon transport and of photosynthesis in tomato leaves. *Journal of Experimental Botany* **27**, 87-97

Ho LC (1978) The regulation of carbon transport and the carbon balance of mature tomato leaves. *Annals of Botany* **42**, 155-164

Hodgkinson KC (1974) Influence of partial defoliation on photosynthesis, photorespiration and transpiration by lucerne leaves of different ages. *Australian Journal of Plant Physiology* **1**, 561-576

Hoaley R (1994) Gibberellins: perception, transduction and responses. *Plant Molecular Biology* **26**, 1529-1555

Hua PX, Qui WX (1998) Influence of sink-source ratio alteration on photosynthesis, assimilate translocation and partitioning and leaf senescence of rice. *Acta Agronomica Sinica* **24**, 821-827

Huber W, Sankhla N (1974) Effect of gibberellic acid on the activities of photosynthetic enzymes and ^{14}CO$_2$ fixation products in leaves of *Pennisetum typhoides* seedlings. *Zeitschrift Pflanzenphysiologie* **71**, 275-280

Kamaluddin M, Zwiazek JJ (2002) Ethylene enhances water transport in hypoxic aspen. *Plant Physiology* **128**, 962-969

Kays SJ, Pallas JE Jr. (1980) Inhibition of photosynthesis by ethylene. *Nature* **285**, 51-52

Khan NA (1994) Variation in carbonic anhydrase activity and its relationship with dry mass of mustard. *Photosynthetica* **30**, 317-320

Khan NA (1996a) Response of mustard to ethrel spray and basal and foliar application of nitrogen. *Journal of Agronomy and Crop Science* **175**, 331-334

Khan NA (1996b) Effect of gibberellic acid on carbonic anhydraase, photosynthesis, growth and yield of mustard. *Biologia Plantarum* **38**, 145-147

Khan NA (2002) Activities of carbonic anhydrase and ribulose-1,5-bisphosphate carboxylase, and dry mass accumulation in *Brassica juncea* following defoliation. *Photosynthetica* **40**, 633-634

Khan NA (2004) Activity of 1-aminocyclopropane carboxylic acid synthase in two mustard (*Brassica juncea* L.) cultivars differing in photosynthetic capacity. *Photosynthetica* **42**, 477-480

Khan NA (2005) The influence of exogenous ethylene on growth and photosynthesis of mustard (*Brassica juncea*) following defoliation. *Scientia Horticulturae* **105**, 499-505

Khan NA, Ahsan N (2000) Evaluation of yield potential of defoliated mustard cultivars. *Tests of Agrochemicals and Cultivars* **21**, 33-34

Khan NA, Ansari HR, Mobin M (1996) Effect of gibberellic acid and nitrogen on carbonic anhydrase activity and mustard biomass. *Biologia Plantarum* **38**, 601-603

Khan NA, Ansari HR, Samiullah (1998) Effect of gibberellic acid spray during ontogeny of mustard on growth, nutrient uptake and yield characteristics. *Journal of Agronomy and Crop Science* **181**, 61-63

Khan NA, Javid S, Samiullah (2004) Physiological role of carbonic anhydrase in CO$_2$ fixation and carbon partitioning. *Physiology and Molecular Biology of Plants* **10**, 153-166

Khan NA, Khan M, Ansari HR, Samiullah (2002a) Auxin and defoliation effects on photosynthesis and ethylene evolution in mustard. *Scientia Horticulturae* **96**, 43-51

Khan NA, Khan M, Samiullah (2002b) Changes in ethylene level associated with defoliation and its relationship with seed yield in rapeseed-mustard. *Brassica* **4**, 12-17

Khan NA, Lone PM (2005) Effects of early and late season defoliation on photosynthesis, growth and yield of mustard (*Brassica juncea* L.). *Brazilian Journal of Plant Physiology* **17**, 184-186

Khan NA, Lone NA, Samiullah (2000) Response of mustard (*Brassica juncea* L.) to applied nitrogen with or without ethrel spray under non-irrigated conditions. *Journal of Agronomy and Crop Science* **183**, 1-4

Khan NA, Mir R, Khan M, Javid S, Samiullah (2002c) Effects of gibberellic acid spray on nitrogen yield efficiency of mustard grown with different nitrogen levels. *Plant Growth Regulation* **38**, 243-247

Khan NA, Mobin M, Samiullah (2005) The influence of gibberellic acid and sulfur fertilization rate on growth and S-use efficiency of mustard (*Brassica juncea*). *Plant and Soil* **270**, 269-274

Khan NA, Mobin M, Mir R, Samiullah (2001) Phytohormones and nutrients interaction on growth and productivity of crops. In: Khan NA, Samiullah (Eds) *Phytohormones in Crop Productivity under Different Environments*, Scientific Publisher, Jodhpur, India, pp 167-178

Khan NA, Samiullah (2003) Comparative effect of modes of gibberellic acid application on photosynthetic biomass distribution and productivity of rapeseed-mustard. *Physiology and Molecular Biology of Plants* **9**, 141-145

Khan NA, Singh S, Khan M, Samiullah (2003) Interactive effect of nitrogen and plant growth regulators on biomass partitioning and seed yield in mustard: mediation by ethylene. *Brassica* **5**, 64-71

Komor E (2000) Source physiology and assimilate transport: the interaction of sucrose metabolism, starch storage and phloem export in source leaves and the effects on sugar status in phloem. *Australian Journal of Plant Physiology* **27**, 497-505

Kopriva S, Suter M, Ballmoos PV, Hesse H, Krahenbuhl U, Rennenberg H, Brunold C (2002) Interaction of sulphate assimilation with carbon and nitrogen metabolism in *Lemna minor*. *Plant Physiology* **130**, 1406-1413

Kruger EL, Volin JC, Lindroth RL (1998) Influence of atmospheric CO_2 enrichment on the responses of sugar maple and trembling aspen to defoliation. *New Phytologist* **140**, 85-94

Kumar B, Pandey DM, Goswami CL, Jain S (2001) Effect of growth regulators on photosynthesis, transpiration and related parameters in water stressed cotton. *Biologia Plantarum* **44**, 475-478

Leary WP, Oplinger ES (1983) Effect of plant growth regulators and nitrogen on the agronomic performance of small grain crops. *Proceedings of Plant Growth Regulators Society of America* **10**, 277-286

Lerbs S, Lerbs W, Klyachko NL, Romanko EG, Kulaeva ON, Wollgichn R (1984) Gene expression in cytokinin and light mediated plastogensis of cucurbita cotyledons: ribulose-1, 5-biphosphate carboxylase-oxygenase. *Planta* **162**, 289-298

Lewis CE, Noctor G, Causton D, Foyer CH (2000) Regulation of assimilate partitioning in leaves. *Australian Journal of Plant Physiology* **27**, 507-519

Little CHA, Loach K (1975) Effect of gibberellic acid on growth and photosynthesis in *Abies balsamea*. *Canadian Journal of Botany* **53**, 1805-1810

Liu HL (1987) Practical rape cultivation, Sanghai Sci and Tech Press, Shanghai, 500 pp

Lone PM, Khan NA (2007) The effects of rate and timing of N fertilizer on growth, photosynthesis, N accumulation and yield of mustard (*Brassica juncea*) subjected to defoliation. *Environmental and Experimental Botany* **60**, 318-323

Macduff JH, Jarvis SC, Mosquera A (1989) Nitrate nutrition of grasses from steady-state supplies in flowing solution culture following nitrate deprivation and/or defoliation. II. Assimilation of NO_3 and short-term effects on NO_3 uptake. *Journal of Experimental Botany* **40**, 977-984

Makeev AV, Krendeleva TE, Mokronsov AT (1992) Photosynthesis and abscisic acid. *Soviet Plant Physiology* **39**, 118-126

Makino A, Sakashita H, Hidema J, Mae T, Ojima K, Osmond B (1992) Distinctive responses of ribulose-1,5-bisphosphate carboxylase and carbonic anhydrase in wheat leaves to nitrogen nutrition and their possible relationships to CO_2-transfer resistance. *Plant Physiology* **100**, 1737-1743

McGrath SP, Zhao FJ (1996) Sulphur uptake, yield response and the interactions between N and S in winter oilseed rape (*Brassica napus*). *Journal of Agricultural Science* **126**, 53-62

Mei TN, Yun GC (1999) Effects of leaf-cutting treatments on source-sink relation of rice during panicle initiation. *Journal of Hunan Agriculture University* **25**, 430-436

Menon KKG, Srivastava HC (1984) Increasing plant productivity through improved photosynthesis. *Proceedings of the Indian Academy of Sciences (Plant Science)* **93**, 359-378

Nafziger ED, Wax LM, Brown CM (1986) Response of five winter wheat cultivars to growth regulators and increased nitrogen. *Crop Science* **26**, 767-770

Nagel OW, Konnings H, Lambers H (2001) Growth rate and biomass partitioning of wildtype and low-gibberellin tomato (*Solanum lycopersicum*) plants growing at a high and low nitrogen supply. *Physiologia Plantarum* **111**, 33-39

Nagel OW, Lambers H (2002) Changes in the acquisition and partitioning of carbon and nitrogen in the gibberellin-deficient mutants A70 and W335 of tomato (*Solanum lycopersicum* L.). *Plant Cell and Environment* **25**, 883-891

Nath N, Mishra D (1990) Changes in RUBP case activity of developing and sensing barley leaves and its alteration by plant growth regulators. *Indian Journal of Experimental Biology* **28**, 665-670

Naylor RFL, Stephen NH (1993) Effect of nitrogen and the plant growth regulator chloromequat on grain size, nitrogen content and amino acid compositions of triticale. *Journal of Agricultural Science* **120**, 159-169

Neales TF, Incoll LD (1968) The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: a review of the hypothesis. *Botanical Review* **34**, 107-125

Nenova VR, Stoyanov IG (2000) Effect of some growth regulators on young iron deficient maize plants. *Biologia Plantarum* **43**, 35-39

Nobel PS (1991) *Physicochemical and Environmental Plant Physiology*, Academic Press, San Diego, 461 pp

Noctor G, Foyer CH (2000) Homeostasis of adenylate status during photosynthesis in a fluctuating environment. *Journal of Experimental Botany* **51**, 347-356

Norman JM (1980) Interfacing leaf and canopy light interception models. In: Hesketh JD, Jones JW (Eds) *Predicting Photosynthesis for Ecosystem Models* (Vol 2), CRC Press, Boca Raton, Florida, pp 49-67

Okabe K, Yang S, Tsuzuki M, Miyachi S (1984) Carbonic anhydrase: Its content in spinach leaves and its taxonomic diversity studied with anti-spinach leaf carbonic anhydrase antibody. *Plant Science Letters* **33**, 145-153

Ourry A, Macduff JH, Ougham HJ (1996) The relationship between mobilization of N reserves and changes in translatable message following defoliation in *Lolium temulentum* L. and *Lolium perenne* L. *Journal of Experimental Botany* **47**, 739-747

Pace GH, Volk RJ, Jackson WA (1990) Nitrate reduction in response to CO_2-limited photosynthesis: Relationship to carbohydrate supply and nitrate reductase activity in maize seedlings. *Plant Physiology* **92**, 286-292

Pando SB, Srivastava GC (1985) Physiological studies on seed set in sunflower III. Significance of dwarfing the plant size using growth regulator. *Indian Journal of Plant Physiology* **28**, 72-80

Paul MJ, Foyer CH (2001) Sink regulation of photosynthesis. *Journal of Experimental Botany* **52**, 1383-1400

Paul MJ, Pellny TK (2003) Carbon metabolite feedback regulation of leaf photosynthesis and development. *Journal of Experimental Botany* **54**, 539-547

Pecham PA, Morgan DG (1985) Defoliation and its effects on pod and seed development in oil seed rape (*Brassica napus* L.). *Journal of Experimental Botany* **36**, 458-468

Popova LP, Dimitrova OD, Vaklinova SG (1982) Effect of gibberellin (GA_3) on the chlorophyll content, on the intensity of photosynthetic CO_2 fixation and on the activity of carboxylating enzymes in C_3 and C_4 plants. *Doklady Bolgarskoi Akademii Nauk* **35**, 797-800

Rajala A, Peltonen-Sainio P (2001) Plant growth regulator effects on spring cereal root and shoot growth. *Agronomy Journal* **93**, 936-943

Raut MS, Ali M (1986) Studies on defoliation and detopping in mustard under rainfed conditions. *Indian Journal of Agronomy* **31**, 252-255

Raven JA (1995) Photosynthetic and non-photosynthetic roles of carbonic anhydrase in algae and cyanobacteria. *Phycologia* **34**, 93-101

Rawson HM, Hofstra G (1969) Translocation and remobilization of ^{14}C assimilated at different stages by each leaf of the wheat plant. *Australian Journal of Biological Sciences* **22**, 321-331

Richards DE, King KE, Ali TA, Harberd NP (2001) How gibberellin regulates plant growth and development: a molecular genetic analysis of gibberellin signalling. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**, 67-88

Ries SK, Wert V, Sweely C, Leavitt RA (1977) Triacontanol, a new naturally occurring plant growth regulator. *Science* **195**, 1331-1341

Robinson SP, Wiskich JT, Paleg LG (1978) Effects of indoleacetic acid on CO_2 fixation, electron transport and phosphorylation in isolated chloroplasts. *Australian Journal of Plant Physiology* **5**, 425-431

Rogers A, Bryant JB, Raines CA, Long SP, Blum H, Frehner M (1995) Acclimation of photosynthesis to rising CO_2 concentration in the field. Is it determined by source/sink balance? In: Mathis P (Ed) *Photosynthesis: From Light to Biosphere* (Vol V) Proceedings of the Xth International Photosynthesis Congress, Montpellier, France, 20-25 Aug. 1995, pp 1001-1004

Sanhla N, Huber W (1974) Eco-physiological studies on India and arid zone plants. IV. Effects of salinity and gibberellin on the activities of photosynthetic enzymes and CO_2 fixation products in leaves of *Pennisetum typhoides* seedlings. *Biochemie Physiologie Pflanzen* **166**, 181-187

Sawan ZM, Ramadan AS, Fouad AA (1989) Effect of 1-naphthaleneacetic acid on seed, protein, oil and fatty acids of Egyptian cotton. *Journal of American Oil Chemists Society* **66**, 1472-1474

Saxena HK, Tripathi RS, Singh OP (1991) Effect of plant growth substances on growth and yield of Til (*Sesamum indicum* L.). *Proceedings of International Conference on Plant Physiology*, pp 203-205

Schjoerring JK, Bock JGH, Gammelvind L, Jensen CR, Mogensen VO (1995) Nitrogen incorporation and remobilization in different shoot components of field-grown winter oilseed rape (*Brassica napus* L.) as affected by rate of nitrogen application and irrigation. *Plant and Soil* **177**, 255-264

Schnug E, Haneklaus S, Murphy D (1993) Impact of sulfur fertilization on fertilizer nitrogen efficiency. *Sulphur in Agriculture* (The Sulphur Institute, Washington, DC) **17**, 8-12

Scarisbrick DH, Daniels RW, Noor Rawi AB (1982) The effect of chloromequet on the yield and yield components of oilseed rape. *Journal of Agriculture Science Cambridge* **99**, 453-456

Servaites JC, Fondy BR, Li B, Geiger DR (1989) Sources of carbon for export from spinach leaves throughout the day. *Plant Physiology* **90**, 1168-1174

Simmons SR, Oelke EA, Wiersma JV, Lucschen WE, Warnes D (1988) Spring wheat and barley responses to ethephon. *Agronomy Journal* **80**, 829-834

Sinelnikova VN, Romanova LV, Udovenko GV (1972) Effects of salinization and physiological active substances on growth and level of endogenous growth regulators in potato. *Soviet Plant Physiology* **19**, 50-55

Sisler EC, Grichko VP, Serek M (2006) Interaction of ethylene and other compounds with the ethylene receptor: agonists and antagonists. In: Khan NA (Ed) *Ethylene Action in Plants*, Springer, pp 1-29

Stewart BA, Porter K (1969) Nitrogen-sulphur relationship in wheat (*Triticum* *aestivum*) corn (*Zea mays*) and heaps (*Phaseolus vulgaris*). *Agronomy Journal* **61**, 267-271

Stockhoff BA (1994) Maximization of daily canopy photosynthesis: effects of herbivory on optimal nitrogen distribution. *Journal of Theoretical Biology* **169**, 209-220

Stodola FH, Raper KB, Fennell DI, Conway HF, Sosns VE, Langford CT, Jackson RW (1955) The microbial production of gibberellins 'A' and 'X'. *Archives of Biochemistry and Biophysics* **54**, 240-245

Sugiharto B, Burnell JN, Sugiyama T (1992) Cytokinin is required to induce the nitrogen dependent accumulation of mRNAs for phosphoenol pyruvate carboxylase and carbonic anhydrase in detached maize leaves. *Plant Physiology* **100**, 153-156

Suzuki R, Cretin C, Omata T, Sugiyama T (1994) Transcriptional and post transcriptional regulation of nitrogen responding expression of phosphoenol pyruvate carboxylase gene in maize. *Plant Physiology* **105**, 1223-1229

Tayo TO, Morgan DG (1979) Factors influencing flower and pod development in oil seed rape (*Brassica napus* L.). *Journal of Agricultural Sciences* **92**, 363-373

Terashima I, Evans JR (1988) Effects of light and nitrogen nutrition on the organization of the photosynthetic apparatus in spinach. *Plant Cell Physiology* **29**, 143-155

Thorne JH, Koller HR (1974) Influence of assimilate demand on photosynthesis, diffusive resistance, translocation and carbohydrate levels of soybean leaves. *Plant Physiology* **54**, 201-207

Treharne KJ, Stoddart JL, Pughe J, Paranjothy K, Wareing PF (1970) Effects of gibberellin and cytokinin on the activity of photosynthetic enzymes and plastid ribosomal RNA synthesis in *Phaseolus vulgaris* L. *Nature* **228**, 129-131

Treharne KJ, Stoddart JL (1968) Effect of gibberellin on photosynthesis in red clover (*Trifolium pretense* L.). *Nature* **220**, 457-458

Tsuzuki M, Mijachi S, Edwards GE (1985) Localization of carbonic anhydrase in mesophyll cells of terrestrial C_3 plants in relation to CO_2 assimilation. *Plant Cell Physiology* **26**, 881-891

Turgeon R (2000) Plasmodesmata and solute exchange in the phloem. *Australian Journal of Plant Physiology* **27**, 521-529

Volenec JJ, Ourry A, Joern BC (1996) A role of nitrogen reserves in forage regrowth and stress tolerance. *Physiologia Plantarum* **97**, 185-193

Wardlaw IF (1990) The control of carbon partitioning in plants. *New Phytologist* **116**, 341-381

Wareing PF, Khalifa MM, Treharne KJ (1968) Rate-limiting processes in photosynthesis at saturating light intensities. *Nature* **220**, 453-457

Weiss EA (1983) *Oilseed Crops*, Longman Inc., New York, 660 pp

Wellburn FAM, Welburn AR, Stoddart JL, Trehane KJ (1973) Influence of gibberellic and abscisic acids and the growth retardant CCC, upon plastid development. *Planta* **111**, 337-346

Wiersma DW, Oplinger ES, Guy SO (1986) Environment and cultivar effects on winter wheat response to ethephon plant growth regulator. *Agronomy Journal* **78**, 761-764

Yang D-L, Yang J-X, Hu H-W (1994) Effects of S-3307 on some physiological characteristics of rape seedlings. *Plant Physiology Research Communications* **30**, 182-185

Yuan L, Xu D-Q (2001) Stimulation effect of gibberellic acid short-term treatment on the photosynthesis related to the increase in rubisco content in broad bean and soybean. *Photosynthesis Research* **68**, 39-47

Zerbe R, Wild A (1981) The effect of indole-3-acetic acid on photosynthesis apparatus of *Sinapis alba*. *Photosynthesis Research* **1**, 71-81

Zhang G-Q, Zhou W-J, Gu H-H, Song W-J, Momoh EJJ (2003) Plant regeneration for the hybridization of *Brassica juncea* and *Brassica napus* through embryo culture. *Journal of Agronomy and Crop Science* **189**, 347-350

Zhao F-J, Evans EJ, Bilsborrow PE, Syers JK (1993) Influence of S and N on seed yield and quality of low glucosinolate oilseed rape (*Brassica napus* L.). *Journal of the Science of Food and Agriculture* **63**, 29-37

Zhou W, Xi H (1993) Effects of mixtalol and paclobutrazol on photosynthesis and yield of rape (*Brassica napus*). *Plant Growth Regulation* **12**, 157-161

Zhou W, Ye Q (1996) Physiological and yield effects of uniconazole on winter rape (*Brassica napus* L.). *Plant Growth Regulation* **15**, 69-73