DOI: 10.1007/s11099-012-0029-3 PHOTOSYNTHETICA 50 (2): 161-170, 2012

REVIEW

# Analyzing the significance of defoliation in growth, photosynthetic compensation and source-sink relations

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## Abstract

Leaf canopy plays a determining role influencing source-sink relations as any change in source activity (photosynthesis) affects sink metabolism. Defoliation (removal of leaves) influences growth and photosynthetic capacity of plants, remobilizes carbon and nitrogen reserves and accelerates sink metabolism, leading to improved source-sink relations.

The response of plants to defoliation could be used to manipulate source-sink relations by removing lower and senescing leaves to obtain greatest photosynthetic capacity and efficient carbon and nitrogen metabolism under optimal and stressful environments. The present work enhances our current understanding on the physiological responses of plants to defoliation and elaborates how defoliation influences growth, photosynthetic capacity and source-sink relations under optimal and changing environmental conditions.

*Additional key words*: carbon, defoliation, nitrogen, photosynthetic potential, sink, source.

## Introduction

Productivity of crop plants depends on the efficiency of photosynthesis, translocation of assimilates and formation of active sinks. Photosynthetic green organs (leaves), the machinery for assimilate production, act as source while seeds is one of the most important sinks. There are several factors affecting source-sink relations. For example, the efficiency of photosynthetic machinery (*e.g.*, the efficiency of photosynthetic conversion of intercepted light into biomass), the availability of nitrogen (N) and balance between carbon (C) and N all play a vital role in determining source potential. The source activity drives sink metabolism and is related to the optimal use of C and N resources (Paul and Foyer 2001). A sink is generally supplied with photosynthate from a nearby source organ (leaves) and as growth proceeds new sources develop and the photosynthetic rate of older leaves declines (Wardlaw 1990). Older leaves have reduced photosynthetic functions and serve as a source of N and other nutrients for the plant.

Leaves play an important role in determining photosynthetic potential and have significant effect on yield responses (Lawlor 2001). Any modification in plant canopy (the aboveground portion of plant) affects photons absorbed by plants and thus photosynthesis of individual leaves (Beadle *et al.* 1985). In a plant canopy, light-use efficiency decreases from apex to lower axis. Therefore, the photosynthetic potential of lower leaves on a plant axis is less than that of the upper leaves. Thus, one aspect of crop improvement is to maintain a critical leaf number and leaf area for the greatest photosynthetic capacity and most efficient metabolism (Lone *et al.* 2008). The critical leaf number or leaf area may be maintained by the partial removal of leaves. The removal of leaves, partial or complete, has been defined as defoliation, an old practice in many parts of world. It provides an opportunity for the photosynthetically active younger leaves to grow, efficiently utilize available water and mineral nutrients and influence source-sink relations (Khan *et al.* 2007). Several reviews have covered different aspects of source-sink relations, such as the control of source/sink capacity or the regulation of photosynthetic machinery and sink system (Austin and Edrich 1975, Koide and Ishihara 1992, Nakano *et al.* 1995, Paul and Foyer 2001, Khan *et al.* 2007). The present review

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*Received* 4 August 2011, *accepted* 6 March 2012.

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*Abbreviations*: ABA – abscisic acid; C – carbon; CA – carbonic anhydrase; Chl – chlorophyll; DAS – days after sowing; $g_s$ – stomatal conductance; HI – harvest index; IAA – indole-3-acetic acid; LA – leaf area; LDM – leaf dry mass; LFM – leaf fresh mass; N – nitrogen; NR – nitrate reductase; P – phosphorus; $P_N$ – net photosynthetic rate; PEP – phospho*enol*pyruvate; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; SLA – specific leaf area.

focuses on various physiological responses of plants to defoliation and the influence of defoliation in the regulation of source-sink relations under optimal and changing environmental conditions.

## Lower leaves as photosynthetic sink

Photosynthetic capacity of leaves is dependent on their position on the plant axis. Studies on mustard (*Brassica juncea* L.) have shown that leaves in the middle layer of plant axis caused overshadowing effect on the lower leaves, which received less light (Khan *et al.* 2002b). *B. juncea* is characterized by large number of broad, oblong-shaped leaves present in the lower layer of the plant axis (Weiss 1983). Murchie *et al.* (2002) reported that in $C_3$ grasses in the upper layer leaf age acts as a limiting factor for photosynthesis, while acclimation to light was the dominant factor for the lower canopy layer. Leaves make a substantial contribution to seed yield up to flowering and at later stage the other green tissues take up the ability to compensate for the leaf removal by increasing their photosynthetic rate (Freyman *et al.* 1973, Clarke 1978). The removal of lower leaves increases the source-sink ratio, *i.e.*, photosynthate production: photosynthate consumption, by reducing the competition for light and increasing the relative demand for photosynthates on the remaining leaves. Gautier *et al.* (1999) reported that competition for light reduced the light interception by plant and also changed the spectral composition of light. Such a change in light quality results in morphogenetic responses in plants mediated through different photoreceptors and photosynthetic pigments.

A number of studies have shown that defoliation of older and senescing leaves allows the growth of functional and efficient leaves (Hortensteiner and Feller 2002, Carlos 2006, Khan *et al.* 2007). This increases the photosynthetic potential of the remaining leaves and leads to enhanced biomass accumulation and seed yield. Khan and Ahsan (2000) working on *B. juncea* showed that eliminating the cost of maintaining senescing leaves by leaf removal may lead to increased plant yield.

## Physiological changes associated with defoliation

**Compensatory growth** is defined as the restoration of morphological and physiological changes that occur in plants following defoliation (Collin *et al.* 2000).

Root system experiences the imbalance in growth and allocation of reserves following defoliation. Following defoliation root growth is reduced, while leaf regrowth is maintained by the increase in the allocation of reserves from root to shoot (Ourry *et al.* 1988). Studies on ryegrass (*Lolium perenne* L.) showed defoliation-induced reduction in root growth, diversion of assimilates (Ennik and Hofman 1983) and remobilization of N compounds from root and stubble to leaf (Millard *et al.* 1990).

Moderate defoliation overcoming a threshold value results in the emergence of new leaves with modified assimilatory capacity and stimulates relative growth rate (Oesterheld 1992, Zhao *et al.* 2008). Alados *et al.* (1997) reported an enlargement of the stem, increase in leaf and flower number, greater vegetative growth and inflorescence length in albaida (*Anthylis cylisoides* L.) after 10% and 50% leaf removal by clipping. In white clover (*Trifolium repens* L.), defoliation of 1, 2, and 4 leaves for 36 days increased stolon elongation rate, leaf area, root mass, leaf number, and stolon number, but total nonstructural carbohydrate decreased with the lower supply of phosphorus (P). However, the loss was restored by increasing P supply (Singh and Sale 1997).

Various mechanisms have been proposed for compensatory growth, such as higher photosynthetic rate, stomatal conductance and delayed senescence (Striker *et al.* 2008). Defoliation reduces the photosynthetic ability of plants and it is restored through compensatory growth which allocates more C to the aboveground biomass. Zhao *et al.* (2008) have shown compensatory growth of clonal tissues (rhizomes) in chinese lyme grass [*Leymus chinensis* (Trin.) Tzvelev] after partial defoliation of 20% and 40% leaves. Defoliation up to 40–50% in *T. repens* increased the emergence and the development of young leaves at maturity (Marriott and Haystead 1990). An increase in leaf number and leaf area with partial defoliation (4 and 8 mature leaves) in burnet (*Sanguisorba minor* Scop.) was reported (Doughlas *et al.* 1994). The source and sink restriction due to defoliation (removal of both leaf and flower at full flowering stage) is compensated for by enhanced flowering in soybean (*Glycine max.* L.) (Saitoh *et al.* 2001). Defoliation of 50% lower leaves on plant axis at preflowering, *i.e.*, 40 d after sowing (DAS), in *B. juncea* resulted in enhanced photosynthesis and growth in the remaining leaves (Khan *et al.* 2002a). Quentin *et al.* (2011) have reported that removal of 45% of leaf area of blue gum (*Eucalyptus globulus* Labill.) was compensated by the increased photosynthetic rate, improved water relations and increased utilization of carbon assimilates.

Compensating for tissue removal, especially after intense defoliation, requires large amounts of energy investment (Reichman and Smith 1991), which is derived from reallocating energy stored in the remaining leaves, shoots, and roots of the damaged plants (Liu *et al.* 2007). The defoliation for 3–5 d at sufficient N supply resulted in the increase in protein content and total nonstructural carbohydrate in roots of red fescue (*Festuca rubra* L.) Paterson and Sim 2000); it also leads to increased reallocation to aboveground parts, allowing them to grow faster. Schnyder and Visser (1999) reported that rapid regrowth was associated with the transient changes in water-soluble carbohydrates and C:N ratio with the removal of eight mature tillers in *T. repens*. During regrowth P remobilization may be another factor to compensate for the loss due to defoliation. P remobilization from stubble, crown and root compartments to the regrowing tissues after defoliation (removal at 4-cm height) in grasses resulted in compensatory growth under P deficiency (Oyarzabal and Oesterheld 2009).

Compensatory growth may also occur through synthesis of carbohydrates. Kim *et al.* (1993) reported that shoot removal in alfalfa (*Medicago sativa* L.) at 6 d resulted in the decrease in N-fixation and starch reserves in tap roots. However, shoot regrowth started after 14 d and starch content recovered to 50% of the initial value on day 24. In grasses, the compensatory regrowth occurred through the preferential allocation of assimilate and remobilization of C storage compounds, from leaf blades, crowns and roots to support recovery of photosynthetic capacity (Johansson 1993). A study by Pammenter and Allison (2002) has shown that defoliation of alternate fully emerged laminae of sugarcane (*Saccharum officinarum* L.) at 155 d decreased the laminae area by 40% and also resulted in proportional partitioning of assimilate in leaves and stem with increased accumulation of sucrose.

**C and N allocation**: C and N metabolisms are highly integrated and regulated processes (Huppe and Turpin 1994, Noctor and Foyer 2000, Khan *et al.* 2007). Defoliation results in change in the demand for photosynthesis and may influence C partitioning. C export in leaves has been found to be positively correlated to photosynthesis in different plant species including cotton (*Gossypium hirsutum* L.) (Hendrix and Huber 1986), sugar beet (*Beta vulgaris* L.) (Servaites *et al.* 1989), sorghum (*Sorghum bicolor* L.) and *L. perenne* (Wardlaw 1990). The responses of plants to shortage of C brought about by defoliation (moderate or heavy) generally increases allocation of resources to shoot growth than root growth (Yang and Midmore 2004). After heavy defoliation, daily carbon gain of the whole plant is reduced, and the plant allocates available C to the actively growing leaves and stems to strengthen the shoot sink (Wilsey 1996). Priority allocation of C and N resources to active shoots sink is the main adaptive response of plants to frequent defoliation, which results in regrowth after defoliation (Khan *et al.* 2007). Besides, plants undergoing partial defoliation require large amount of N to compensate for the growth and maintenance of new leaves. However, N remobilization and mineral N uptake during recovery after defoliation depend on N reserve status (Louahlia *et al.* 1999).

The internal cycling of C and N compounds is of great importance during plant development and is also a prerequisite for regrowth after defoliation. In *B. juncea*, N uptake capacity of roots increased in order to meet the shoot N requirement, but only 50% of the applied N fertilizer recovered in the harvested seeds (Lone and Khan 2007). To increase N utilization efficiency the availability of photosynthate is an important requirement. In a study on *B. juncea* the supply of 100 kg(N) $ha^{-1}$ at the time of sowing and 50 kg(N) $ha^{-1}$ after flowering in plants defoliated at preflowering (40 DAS) has been shown to increase the activity of carbonic anhydrase and photosynthetic activity compared to no-defoliation plants (Khan and Lone 2005). Terashima and Evans (1988) have shown that the increase in the activity of carboxylating enzymes and photosynthetic activity was due to increased N content and N assimilation enzymes. Craft-Brandner *et al.* (1983) and Khan *et al.* (2007) reported an increased N allocation with the increase in N supply and increased activity of carbonic anhydrase and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). The mechanism that optimizes the whole plant C to N balance may become an important strategy in the improvement of C and N acquisition (Khan *et al.* 2007).

**Photosynthetic functions**: The maximum photosynthetic rate is a function of growth form and is inversely related to the leaf longevity (Archer and Tieszen 1980). The removal of the unproductive leaves earlier in seed development changes the assimilate balance within the plant and increases the photosynthetic activity in the remaining leaves. Photosynthetic responses of plants following defoliation are summarized in Table 1.

Studies on *B. juncea* have shown that removal of shaded leaves (50% of lower leaves at 40 DAS) increases the supply of assimilate more than demand and thus improves growth and photosynthetic potential of the rest of the leaves (Khan *et al.* 2002b). Anten and Ackerly (2001) reported that partial defoliation (50 and 66% of leaves removed) in palm (*Chamaedorea elegans* Mart.) significantly increased the light available to the remaining leaves and light-saturated photosynthesis per unit leaf area by 10–18%. Recently, Li *et al.* (2010) reported that defoliation at flowering in chickpea (*Cicer arietinum* L.) when crop canopy is closed allows light penetration into deeper canopy and improves photosynthesis.

Partial defoliation has rejuvenating effect on the remaining leaves, restoring the photosynthetic capacity to near the value of newly formed leaves (Wareing *et al.* 1968, Khan *et al.* 2008). The plants after defoliation require more assimilates for regrowth which is balanced by the increased leaf assimilatory capacity and efficient N use (Lone and Khan 2007). Ryle *et al.* (1985) reported that recovery of $N_2$ fixation in *T. repens* after removal of half of the shoot tissue was related to the re-establishment and increased photosynthetic capacity after 5, 6, or 9 d of regrowth.

Joudi *et al.* (2006) reported that source restriction by defoliation of winter wheat (*Triticum aestivum* L.) increased net photosynthetic rate and chlorophyll (Chl) content of leaves, although the increase depended on the

Table 1. Response of photosynthetic characteristics to defoliation treatment in plants. (+) indicates positive effect and (-) indicates negative effect on plant characteristics. $P_N$ – net photosynthetic rate; $g_s$ – stomatal conductance; Chl – chlorophyll.

| Characteristics | Plant | Defoliation | Response | Reference |
|---|---|---|---|---|
| $P_N$, $g_s$ | *Medicago sativa* | Partial defoliation | + | Hodgkinson (1974) |
| Rubisco | *Phaseolus vulgaris* | Partial defoliation after full expansion of leaf | + | von Caemmerer and Farquhar (1984) |
| $P_N$ | *Trifolium repens* | Defoliation by removing half their shoot tissue | - | Ryle *et al.* (1985) |
| Rubisco | *Betula pendula* | Half of leaf lamina removed | + | Ovaska *et al.* (1993) |
| Carbonic anhydrase, Rubisco | *Brassica juncea* | 30% defoliation in lower layers of plant | + | Khan (2002) |
| $P_N$, $g_s$ | *Triticum aestivum* | Defoliation at late tillering | + | Zhu *et al.* (2004) |
| Photosynthesis | *Vitis vinifera* | Two-third defoliation from shoot lower part | + | Chanishvili *et al.* (2005) |
| $P_N$, $g_s$ | *Brassica juncea* | Defoliating 50% of leaf from lower half of the plant | + | Khan and Lone (2005) |
| $P_N$ | *Acacia melanoxylon* | 50% of tree foliage | + | Medhurst *et al.* (2006) |
| $P_N$, plant mass | *Alnus tenuifolia* | Defoliation of 15, 25, or 40% leaf | - | Ruess *et al.* (2006) |
| $P_N$, $g_s$, Chl | *Triticum aestivum* | Defoliating all leaves except the flag leaf or flag and penultimate leaf | + | Ahmadi and Jaudi (2007) |
| Rubisco | *Eucalyptus globules* | 50–70% defoliation | + | Turnbull *et al.* (2007) |
| Photosynthesis, $g_s$ | *Eucalyptus pilularis, Eucalyptus cloeziana* | 50% of green crown length | + | Alcorn *et al.* (2008) |

type of cultivars. Further, Ahmadi and Joudi (2007) have reported positive effect of various intensities of defoliation performed at booting, anthesis and 20 d after anthesis in winter wheat. They found that Chl content and N remobilization in defoliated wheat plants increased at 20 d after defoliation compared to nondefoliated plants. The removal of all leaves at anthesis stage even did not reduce grain yield and grain protein significantly. It was found that spike photosynthesis and increased photoassimilate partitioning towards grain were responsible for sustained grain growth in this condition. Turnbull *et al.* (2007) reported increased leaf N content and photosynthesis of *E. globulus* following partial defoliation. An increase in Chl concentration was suggested as a reason for photosynthetic rejuvenation induced by partial defoliation (Wareing *et al.* 1968).

An increase in stomatal conductance ($g_s$) (Belesky and Hill 1997) and activity of Rubisco (Wareing *et al.* 1968) are other reasons for the increase in leaves photosynthetic rate following partial defoliation. However, Khan and Lone (2005) reported that the higher increase in net photosynthetic rate ($P_N$) in *B. juncea* plants defoliated at preflowering in comparison to the nondefoliated plants was due to mesophyll rather than stomatal effects. The increase in carbonic anhydrase (CA) activity and a constant ratio of intercellular $CO_2$ concentration to atmospheric $CO_2$ concentration suggested that the increase in net photosynthesis was due to mesophyll effects. The increase in CA activity increased Rubisco activity by increasing carboxylation reactions (Khan and Lone 2005). Both CA and Rubisco were higher by 71.7% and 140.0%, respectively over control after 30% defoliation of lower leaves at 40 DAS in *B. juncea* (Khan 2002). The increased carboxylating activity has been shown to be due to increased enzyme synthesis and higher leaf protein content after defoliation. This was due to reduced competition between leaves for mineral nutrients and metabolites supplied by the roots (Wareing *et al.* 1968). The increase in Rubisco (in $C_3$ plants) and PEP carboxylase activity (in $C_4$ plants) following partial defoliation and a parallel increase in net photosynthesis suggests that saturating levels of these enzymes were not present in the leaves of the control plants (Wareing *et al.* 1968). Defoliation influences the growth of $C_3$ and $C_4$ species differently. Boryslawski and Bentley (1985) reported that the regrowth biomass of western wheatgrass-rosana (*Agropyron* smithii Rydb.) ($C_3$ species) shoots was 38% lower in clipped plants than in unclipped plants, compared to only 9% lower in blue grama (*Boutelou gracilis* L.) ($C_4$ species). $C_4$ plants accumulate greater quantities of carbohydrate than $C_3$ plants (Downton 1971). This 'extra' photosynthate could be used for regrowth following defoliation. An added advantage of the $C_4$ system is that its net photosynthesis, compared to $C_3$ plants, is greatest in young foliage (Long *et al.* 2006). Thus, the new foliage produced in response to defoliation would replenish the carbohydrate reserves more rapidly in $C_4$ species than in $C_3$ species.

**Sink strength**: The term 'sink strength' refers to the capacity of phloem in the sink region to import assimilates from other parts of the plants and to release the imported substances into the sink apoplast. Photosynthates and N supply interact to control the development of leaves and the whole plant N acquisition provides the dominant basis for sink strength (Paul and Foyer 2001). Marcelis (1996)

Table 2. Response of biochemical, growth and yield characteristics to defoliation treatment in plants. (+) indicates positive effect and (-) indicates negative effect on plant characteristics. LA – leaf area, LFM – leaf fresh mass, LDM – leaf dry mass, NR – nitrate reductase, HI – harvest index, RGR – relative growth rate, SLA – specific leaf area.

| Characteristics | Plant | Defoliation | Response | Reference |
|---|---|---|---|---|
| Seed yield | *Vigna mungo* | Partial defoliation at vegetative and/or reproductive stage | - | Pandey and Singh (1981) |
| LA, LFM, LDM, NR activity | *Capsicum annuum* | Removal of all but one leaf | + | Vann *et al*. (1986) |
| Grain yield and biomass | *Gossypium hirusitum and Zea mays* | Defoliation of 33% leaf (twice) | - | Yang and Midmore (2004) |
| Grain yield and HI | *Triticum aestivum* | Defoliation at late tillering stage | + | Zhu *et al*. (2004) |
| Leaf N and P content | *Eucalyptus pilularis and Eucalyptus cloeziana* | 50% of green crown length | + | Alcorn *et al*. (2008) |
| Nitrogen assimilation | *Brassica juncea* | Defoliation of 50% leaves from lower half of plant | + | Lone *et al*. (2008) |
| Higher RGR and compensatory photosynthesis | *Leymus chinensis* | Defoliation by 20% and 40% of arial mass removed | + | Zhao *et al*. (2008) |
| Regrowth and biomass production | *Agropyron spicatum* | Defoliation by 20% at 3 leaf stage and 50% at peak standing crop | + | Sheley and Svejcar (2009) |
| Regrowth of vegetative tissue | *Cicer arietinum* | Defoliation at vegetative growth | + | Li *et al*. (2010) |
| LA and SLA, soluble sugars | *Eucalyptus globulus Labilladière* | Removal of 45% leaf area | + | Quentin *et al*. (2011) |

reported that formation of sink organs, *i.e*., tissues that receive nutrients, sugars and amino acids from other tissues determines partitioning of dry matter.

The sink organs receive photoassimilates from source in the form of sucrose along a concentration gradient created by the uploading of osmotically active carbohydrate within the source and unloading in the sink (Turgeon 2000). Manipulation of the source:sink ratio in *T. aestivum* during seed filling by defoliation provided evidence that plants experienced periods during the growing cycle when yield was mainly limited by the source strength, the sink capacity, or colimited by both (Borrás *et al*. 2004). Barimavandi *et al*. (2010) showed that yield response of maize (*Zea mays* L.) to defoliation depends on the intensity of defoliation, leaf position and stage of crop growth. Moser and Perry (1983) found reduction in total seasonal yield and tiller numbers of sand lovegrass (*Eragrostis trichodes* Nutt.) with multiple defoliation (seven harvesting treatment). Pandey (1984) reported that the removal of leaves subtending flowers and pods in *C. arietinum* during the reproductive phase resulted in a 40–60% reduction in seed yield compared with control plants, while removal of leaves below the flowering nodes decreased the seed yield by 25%. In contrast, complete defoliation resulted in a seed yield reduction to about 90%. In sunflower (*Helianthus annuus* L.), increase in defoliation (50% to 75%) at flowering stage resulted in decrease in seed yield because of the decrease in photosynthetic surface (Abdi *et al*. 2007). Removal of upper leaves in *B. juncea* caused decrease in yield whereas lower leaves removal increased seed yield (Khan *et al*. 2002a). Zhu *et al*. (2004) found that early-sown late maturity *T. aestivum* responded to defoliation at late tillering with an increased grain yield by 7.3% through increased harvest index by 10.7% and grain water-use efficiency by 22% compared to the control, but defoliation at booting stage had negative effects on almost all components. In *B. juncea* defoliation at preflowering stage caused greatest positive effects on yield compared to other stages of defoliation (Khan *et al*. 2002b, Khan and Lone 2005). Pecham and Morgan (1985) and Raut and Ali (1986) also showed a reduction in the number of pods and seed yield of rapeseed (*Brassica napus* L.) due to leaf removal at anthesis because of reduced carbon assimilation. The assimilate availability plays an important role in determining seed yield as massive remobilization takes place from the vegetative part to provide N to growing seeds. Ahmadi and Jaudi (2007) attributed the increase in grain yield in wheat to the enhanced photoassimilate partitioning towards grain and spike even under drought conditions. Effects of defoliation on biochemical, growth, and yield components are summarized in Table 2.

## Significance of defoliation under stress

Partial defoliation has significant importance in photosynthetic compensation and source-sink relations under changing environment, and the relationship between source and sink differs among genotype (Wang *et al*.

1994). Under elevated $CO_2$, defoliation has been reported to increase photosynthetic activity and nonstructural carbohydrate (sucrose) in Mediterranean grassland and forest trees (Korner and Miglietta 1994) and influence source-sink relations (Arp 1991). Plant species with strong sinks or with the ability to increase sink size have been shown to be more responsive to elevated $CO_2$ (Poorter 1993). Fischer *et al.* (1997) found that the response of *L. perenne* to elevated $CO_2$ was restricted by a carbon-sink limitation due to accumulation of carbohydrate. In their study on free air carbon dioxide enrichment (FACE) they showed that defoliation approximately 5 cm above the ground at regular interval of 4 to 6 weeks increased assimilate concentration in shoots of *L. perenne*. This reflects a change in the balance between source and sink activity, which was due to stimulation of carbon assimilation. The photosynthetic rate did not increase in nondefoliation plant under elevated $CO_2$, but the rate increased in the remaining leaf of partially defoliated plant. The increase in photosynthesis under higher $CO_2$ was due to reduced source activity by partial defoliation, whereas in intact plants the increase in $CO_2$ increased source activity and photosynthesis remains unchanged. Takagi *et al.* (2009) have shown that net photosynthesis of the defoliated plant increased by elevated $CO_2$ (100 Pa) by about 35% relative to that in the ambient air and down regulation was not observed during the 14-day experimental period in tomato (*Lycopersicum esculentum* L.). Plants may respond positively to moderate defoliation under elevated $CO_2$, but responsiveness decreases with high frequency of defoliation (Wand and Midgley 2004).

Defoliation could act as a potential method to reduce water stress. Partial defoliation in maize resulted in reduced leaf area (LA) and water transpired (Crookston and Hicks 1988). In a study on *T. aestivum* under wet and dry conditions, Shao *et al.* (2010) studied the effect of defoliation (mild, moderate, and severe) at heading and anthesis and found that defoliation helped in crop survival under dry conditions and the reduction in grain production was lesser in defoliated plants under dry conditions than wet conditions. Defoliation reduced the seasonal water use with the increase in net photosynthesis of leaves remaining after defoliation. Defoliation has also been found to reverse the salinity-induced reduction in stomatal conductance in *L. esculentum* and improved plant resistance to salinity stress (Takagi *et al*. 2009).

Low temperature during early growth is one of the major environmental factors limiting *Z. mays* range of growth (Cutworth and Shaykewich 1990). Defoliation (complete removal of leaf blades) during *Z. mays* kernel development has been shown to induce tolerance to cold of germinating seeds (Frascaroli *et al*. 2005). The effects of complete defoliation at maturation in *Z. mays* positively influenced seed vigor (TeKrony and Hunter 1995) and seed germination at low temperature (Martin and Zinselmeier 1996).

## Hormonal control of defoliation

Hormones produced by the plants regulate the physiological efficiency of plants by modifying the balance between photosynthesis and respiration (Arteca and Dong 1981), stomatal aperture or the activity of photosynthetic enzymes (Khan 2005). Defoliation causes morphological and physiological changes in plants which are regulated by the plant hormones (Gifford and Evans 1981, Liu and Zhang 1992, Khan *et al.* 2002b). RongQi and LeiYan (2000) reported the accumulation of abscisic acid (ABA) in leaves of *G. hirsutum* on following infection with defoliating strain of *Verticillium dahlia*. The ABA levels in *G. hirsutum* cultivars, Tangmian 2 and Ejing 1, were 1.3 and 4.2 times more than in plants inoculated with nondefoliating strains. Khan (2003) found decreased auxin content and increased ethylene level after defoliation in *B. juncea*. The increase in defoliation (by excising all the 1-year-old and older needles at the time when the current shoot (apical meristem) was fully elongated, but when current-year needle growth was just started) resulted in the production of phenolics as a protection mechanism (Roitto *et al.* 2008). The production of phenolics has been shown to increase IAA oxidase activity leading to decreased auxin concentration (Yang *et al.* 1990, Khan 2003). Thus, auxin and ethylene are found to have inverse relationship during defoliation. It may be said that ethylene plays a central role in regrowth process following defoliation as ethylene has been involved in leaf expansion, photosynthesis process, biomass production and seed traits (Abeles *et al.* 1992, Khan 2003). Ethylene-induced abscission is associated with the expression of polygalacturonase and β-1,4 glucan hydrolase in the vicinity of distal abscission zone (Dolan 1997). Exogenous and endogenous supply of auxin is known to stimulate ethylene production (Abeles 1966, Sakai and Imaseki 1971, Khan *et al.* 2002a) and young leaves produce more ethylene due to higher concentration of auxin (Morgan and Hall 1964, Khan *et al.* 2002a). Moreover, ethylene concentration may account for changes in physiological characteristics and for leaves with higher photoassimilatory capacity (Khan *et al.* 2002b).

**Conclusion**: The review summarizes that defoliation influences growth, carbon gain, nutrients remobilization and source-sink relations. The response of plants to defoliation depends on the species, leaf position, timing of defoliation, and environmental conditions. The growth and photosynthetic ability of plants after defoliation are associated with the synthesis of auxin, abscisic acid, and ethylene. However, a clear understanding of the interaction of defoliation and phytohormones in augmenting source-sink relations needs investigation, as single hormone may not be responsible for defoliation effects and only act as an inducer for the other hormone to set a cascade in motion. Defoliation could also be used to increase growth and photosynthetic rate in plants under abiotic stress conditions. However, further research is required to strengthen the role of phytohormones in the induction of defoliation and the response of plants to defoliation and source-sink relations under abiotic stress conditions.

## References

Abdi, S., Fayaz, M.A., Ghadimzade, M.: Effect of different levels of defoliation at reproductive stage on grain yield and oil percent of two hybrid sunflower. – Agri. Nat. Res. Sci. Tech. **11**: 245-255, 2007.

Abeles, F.B.: Auxin stimulation of ethylene evolution. – Plant Physiol. **41**: 585-588, 1966.

Abeles, F.B., Morgan, P.W., Saltveit, M.E.: Ethylene in Plant Biology, 2$^{nd}$ Ed. – Acad. Press, San Diego 1992.

Ahmadi, A., Joudi, M.: Effects of timing and defoliation intensity on growth, yield and gas exchange rate of wheat grown under well-watered and drought conditions. – Pak. J. Biol. Sci. **10**: 3794-3800, 2007.

Alados, C., Barroso, F.G., Garcia. L.: Effects of early season defoliation on above-ground growth of *Anthyllis cytisoides*, a Mediterranean browse species. – J. Arid Environ. **37**: 269-283, 1997.

Alcorn, P.J., Bauhus, J., Smith, R.G.B., Thomas, D., James, R., Nicotra, A.: Growth responses of following green crown pruning in plantation-grown *Eucalyptus pilularis* and *Eucalyptus cloeziana*. – Can. J. Forest Res. **38**: 770-781, 2008.

Anten, N.P.R., Ackerly, D.D.: Canopy-level photosynthetic compensation after defoliation in a tropical understorey palm. – Funct. Ecol. **15**: 252-262, 2001.

Archer, S., Tieszen, L.L.: Growth and physiological responses of Tundra plants to defoliation. – Artic Alpine Res. **12**: 531-552, 1980.

Arp, W.J.: Effects of source-sink relations on photosynthetic acclimation to elevated $CO_2$. – Plant Cell Environ. **14**: 869-875, 1991.

Arteca, R.N., Dong, C.N.: Stimulation of photosynthesis by application of phytohormones to the root system of tomato plants. – Photosynth. Res. **2**: 243-249, 1981.

Austin, R.B., Edrich, J.: Effects of ear removal on photosynthesis, carbohydrate accumulation and on the distribution of assimilated 14C in wheat. Ann. Bot. **39**: 141-152, 1975.

Barimavandi, A.R., Sedaghathoor, S., Ansari, R.: Effect of different defoliation treatments on yield and yield components in maize (*Zea mays* L.) cultivar of S.C7042. – Aust. J. Crop Sci. **4**: 9-15, 2010.

Beadle, C.L., Long, S.P., Imbamba, S.K., Hall, D.O., Olembo, R.J.: Photosynthesis in Relation to Plant Production in Terrestrial Environments. – Tycooly Publishing Ltd., Oxford 1985.

Belesky, D.P., Hill, N.S.: Defoliation and leaf age influence on ergot alkaloids in tall fescue. – Ann. Bot. **79**: 259-264, 1997.

Borrás, L., Slafer, G.A., Otegui, M.E.: Seed dry weight response to source-sink manipulations in wheat, maize and soybean: a quantitative reappraisal. – Field Crops Res. **86**: 131-146, 2004.

Boryslawski, Z., Bentley, B.L.: The effect of nitrogen and clipping on interference between $C_3$ and $C_4$ grasses. – J. Ecol. **73**: 113-121, 1985.

Carlos, P.: Efficiency of nutrient use by crops for low input agro-environments. – In: Singh, R.P., Shankar, N., Jaiwal, P.K. (ed.): Nitrogen Nutrition in Plant Productivity. Pp. 277-328. Studium Press, Houston 2006.

Chanishvili, S., Badridze, G.S., Barblishvili, T.F., Dolidze, M.D.: Defoliation, photosynthetic rates, and assimilate transport in grapevine plants. – Russ. J. Plant Physiol. **52**: 448-453, 2005.

Clarke, J.M.: The effects of leaf removal on yield and yield components of *Brassica napus*. – Can. J. Plant Sci. **58**: 1103-1105, 1978.

Collin, P., Epron, D., Alaoui-sosse, B., Badot, P.M.: Growth responses of common ash seedlings (*Fraxinus excelsior* L.) to total and partial defoliation. – Ann. Bot. **85**: 317-323, 2000.

Craft-Brandner, S.J., Below, F.E., Harper, J.E., Hageman, R.H.: Metabolism of carbon and nitrogen by soybean seedlings in response to vegetative apex removal. – Plant Physiol. **73**: 6-10, 1983.

Crookston, R.K., Hicks, D.R.: Effect of early defoliation on maize growth and yield: an eleven-year perspective. – Crop Sci. **28**: 371-373, 1988.

Cutforth, H.W., Shaykewich, C.F.: A temperature response function for corn development. – Agr. Forest Meteorol. **50**: 159-171, 1990.

Dolan, L.: The role of ethylene in the development of plant form. – J. Exp. Bot. **48**: 201-210, 1997.

Doughlas, G.B., Robertson, A.G., Chu, A.C.P., Gordon, I.L.: Effect of plant age and severity of defoliation on regrowth of sheep's burnet during substrate moisture depletion. – Grass Forage Sci. **49**: 334-342, 1994.

Downton, W.J.S.: Adaptive and evolutionary aspects of $C_4$ synthesis. – In: Hatch, M.D., Osmond, C.B., Slatyer, R.O. (ed.): Photosynthesis and Photorespiration. Pp. 3-17, Wiley-Interscience, New York – London – Sydney – Toronto 1971.

Ennik, G.C., Hofman, T.B.: Variation in the root mass of ryegrass types and its ecological consequence. – Neth. J. Agr. Sci. **31**: 325-334, 1983.

Fischer, B.U., Frehner, M., Hebeisen, T., Zanetti, S., Stadelmann, F., Luscher, A., Hartwig, U.A., Hendrey, G.R., Blum, H., Nosberger, J.: Source-sink relations in *Lolium perenne* L. as reflected by carbohydrate concentrations in leaves and pseudo-stems during regrowth in a free air carbon dioxide enrichment (FACE) experiment. – Plant Cell Environ. **20**: 945-952, 1997.

Frascaroli1, E., Casarini, E., Conti S.: Response of maize inbred lines to a defoliation treatment inducing tolerance to cold at germination. – Euphytica **145**: 295-303, 2005.

Freyman, S., Charnetski, W.A., Crookston, R.K.: Role of leaves in the formation of the seed in rape. – Can. J. Plant Sci. **53**: 693-694, 1973.

Gautier, H., Varlet-Grancher, C., Hazard, L.: Tillering responses to the light environment and to defoliation in populations of perennial ryegrass (*Lolium perenne* L.) selected for contrasting leaf length. – Ann. Bot. **83**: 423-429, 1999.

Gifford, R.M., Evans, L.T.: Photosynthesis, carbon partitioning, and yield. – Annu. Rev. Plant Physiol. Plant Mol. Biol. **32**: 485-509, 1981.

Hendrix, D.L., Huber, S.C.: Diurnal fluctuations in cotton leaf carbon export, carbohydrate content, and sucrose synthesizing enzymes. – Plant Physiol. **81**: 584-586, 1986.

Hodgkinson**,** K.C.: Influence of partial defoliation on photosynthesis, photorespiration and transpiration by Lucerne leaves of different ages. – Aust. J. Plant Physiol. **1**: 561-576, 1974.

Hortensteiner, S., Feller, U.: Nitrogen metabolism and remobilization during senescence. – J. Exp. Bot. **53**: 927-937, 2002.

Huppe, H.C., Turpin D.H.: Integration of carbon and nitrogen metabolism in plants and algal cells. – Annu. Rev. Plant Physiol. Mol. Biol. **45**: 577-607, 1994.

Johansson, G.: Carbon distribution in grass (Festuca pratensis L.) during regrowth after cutting-utilization of stored and newly assimilated carbon. – Plant Soil **151**: 11-20, 1993.

Joudi, M., Ahmadi, A., Poustini, K., Shrifzadeh, F.: Effect of leaf elimination on the effectiveness of flag leaf photosynthesis and seed growth in bread wheat. – Iranian J. Agr. Sci. **2**: 203-211, 2006.

Khan, N.A.: Activities of carbonic anhydrase and ribulose- 1,5-biphosphate carboxylase, and dry mass accumulation in *Brassica juncea* following defoliation. – Photosynthetica **40**: 633-634, 2002.

Khan, N.A.: Changes in photosynthetic biomass accumulation, auxin and ethylene level following defoliation in *Brassica juncea*. – Food Agr. Environ. **1**: 125-128, 2003.

Khan, N.A.: The influence of exogenous ethylene on growth and photosynthesis of mustard (*Brassica juncea*) following defoliation. – Sci. Hort. **105**: 499-505, 2005.

Khan, N.A. Ahsan, N.: Evaluation of yield potential of defoliated mustard cultivars. – Tests Agrochem. Cultivars **21**: 33-34, 2000.

Khan, N.A., Anjum, N.A., Nazar, R., Lone, P.M.: Activity of 1-aminocyclopropane carboxylic acid synthase and growth of mustard (*Brassica juncea*) following defoliation. – Plant Growth Regul. **56**: 151-157, 2008.

Khan, N.A., Khan, M., Ansari, H.R., Samiullah.: Auxin and defoliation effects on photosynthesis and ethylene evolution in mustard. – Sci. Hort. **96**: 43-51, 2002a.

Khan, N.A., Khan, M., Samiullah.: Changes in ethylene level associated with defoliation and its relationship with seed yield in rapeseed-mustard. – Brassica **4**: 12-17, 2002b.

Khan, N.A., Lone, P.M.: Effects of early and late season defoliation on photosynthesis, growth and yield of mustard (*Brassica juncea* L.). – Braz. J. Plant Physiol. **17**: 181-186, 2005.

Khan, N.A., Singh, S., Nazar, R., Lone, P.M.: The source-sink relationship in mustard. – Asian Aust. J. Plant Sci. Biotechnol. **1**: 10-18, 2007.

Kim, T.H., Ourry, A., Boucaud, J and Lemaire G, Partitioning of nitrogen derived from $N_2$ fixation and reserves in nodulated *Medicago sativa* L. during regrowth. – J. Exp. Bot. **44**: 555-562, 1993.

Koide, K., Ishihara, K.: Effects of ear removal on photosynthesis of the flag leaf during grain filling of the flag leaf during grain filling in wheat. – Jap. J. Crop Sci. **61**: 659-667, 1992.

Korner, C., Miglietta, F.: Long term effects of naturally elevated $CO_2$ on mediterranean grassland and forest trees. – Oecologia **99**: 343-351, 1994.

Lawlor, D.W.: Photosynthesis. – Bios Sci. Publ., Oxford 2001.

Li, L., Gan, Y.T., Bueckert, R., Warkentin, T.D.: Shading, Defoliation and Light Enrichment Effects on Chickpea in Northern Latitudes. – J. Agron. Crop Sci. **196**: 220-230, 2010.

Liu, H.D., Yu, F.H., He, W.M., Chu, Y., Dong, M.: Are clonal plants more tolerant to grazing than co-occurring non-clonal plants in inland dunes? – Ecol. Res. **22**: 502-506, 2007.

Liu, X.B., Zhang, Q.Y.: [Source-sink relationships in crops.] – Syst. Sci. Compar. Stud. Agr. **8**: 131–134, 1992. [In Chin.]

Lone, P.M., Khan, N.A.: The effects of rate and timing of N fertilizer on growth, photosynthesis, N accumulation and yield of mustard (*Brassica juncea*) subjected to defoliation. – Environ. Exp. Bot. **60**: 318-323, 2007.

Lone, P.M., Nazar, R., Singh, S., Khan, N.A.: Effects of timing of defoliation on nitrogen assimilation and associated changes in ethylene biosynthesis in mustard (*Brassica juncea*). – Biologia **63**: 207-210, 2008.

Long, S.P., Zhu, X.G., Naidu, S., Ort, D.R.: Can improvement in photosynthesis increase crop yields? – Plant Cell Environ. **29**: 315-330, 2006.

Louahlia, S., Macduff, J.H., Ourry, A., Humphreys, M., Boucaud, J.: Nitrogen reserves status affects the dynamics of nitrogen remobilization and mineral nitrogen uptake during recovery of contrasting cultivars of *Lolium perenne* from defoliation. – New Phytol. **142**: 451-462, 1999.

Marcelis, L.F.M.: Sink strength as a determinant of dry matter partitioning in the whole plant. – J. Exp. Bot. **47**: 1281-1291, 1996.

Marriott, C.A., Haystead, A.: The effect of defoliation on the nitrogen economy of white clover: regrowth and the remobilization of plant organic nitrogen. – Ann. Bot. **66**: 465-474, 1990.

Martin, B.A., Zinselmeier, C.: Improvement of seed vigor in maize by pre-harvest defoliation. – Agronomy Abstracts. Pp 137-137. Amer. Soc. Agron., Indianapolis 1996.

Medhurst, J.L., Pinkard, E.A., Beadle, C.L., Worledge, D.: Increases in photosynthetic capacity of plantation-grown *Acacia melanoxylon* after form pruning. – Forest Ecol. Manag. **233**: 250-259, 2006.

Millard, P., Thomas, R.J., Buckland, S.T.: Nitrogen supply affects the remobilization of nitrogen for the regrowth of defoliated *Lolium perenne* L. – J. Exp. Bot. **41**: 941-947, 1990.

Morgan, P.W. Hall, W.C.: Accelerated release of ethylene by cotton following application of indolyl-3-acetic acid. – Nature **201**: 99-99, 1964.

Moser, L.E., Perry, L.J.: Yield, vigor and persistence of sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood] following clipping treatments. – J. Range Manage. **36**: 236-238, 1983.

Murchie, E.H., Hubbart, S., Chen, Y., Peng, S., Horton, P.: Acclimation of rice photosynthesis to irradiance under field conditions. – Plant Physiol. **130**: 1999-2010, 2002.

Nakano, H., Makino, A., Mae, T.: Effects of panicle removal on the photosynthetic characteristics of the flag leaf of rice plants during ripening stage. – Plant Cell Physiol. **36**: 653-659, 1995.

Noctor, G., Foyer, C.H.: Homeostasis of adenylate status during photosynthesis in a fluctuating environment. – J. Exp. Bot. **51**: 347-356, 2000.

Oesterheld, M.: Effect of defoliation intensity on aboveground and belowground relative growth rates. – Oecologia **92**: 313-316, 1992.

Ourry, A., Boucaud, J., Salette, J.: Nitrogen mobilization from stubble and roots during regrowth of defoliated Perennial Ryegrass. – J. Exp. Bot. **39**: 803-809, 1988.

Ovaska, J., Walls, M., Vapaavuori, E.: Combined effects of partial defoliation and nutrient availability on cloned *Betula pendula* saplings. I. Changes in growth, partitioning and nitrogen uptake. – J. Exp. Bot. **44**: 1385-1393, 1993.

Oyarzabal, M., Oesterheld, M.: Phosphorus reserves increase grass regrowth after defoliation. – Oecologia **159**: 717-724, 2009.

Pammenter, N.W., Allison, J.C.S.: Effects of treatments potentially influencing the supply of assimilate on its partitioning in sugarcane. – J. Exp. Bot. **53**: 123-129, 2002.

Pandey, R.K.: Influence of source and sink removal on seed yield of chickpea (*Cicer arietinum* L.). – Field Crops Res. **8**: 159-168, 1984.

Pandey, R.K., Singh, V.B.: Influence of partial defoliation on dry-matter production and seed yield of urd bean (*Vigna mungo* L. Hepper). – J. Agr. Sci. **97**: 437-443, 1981.

Paterson, E. Sim, A.: Effects of nitrogen supply and defoliation on loss of organic compounds from roots of *Festuca rubra*. – J. Exp. Bot. **51**: 1449-1457, 2000.

Paul, M.J., Foyer, C.H.: Sink regulation of photosynthesis. – J. Exp. Bot. **52**: 1383-1400, 2001.

Pecham, P.A., Morgan, D.G.: Defoliation and its effects on pod and seed development in oil seed rape (*Brassica napus* L.). – J. Exp. Bot. **36**: 458-468, 1985.

Poorter, H.: Interspecific variation in the growth response of plants to an elevated ambient $CO_2$ concentration. – Plant Ecol. **104/105**: 77-97, 1993.

Quentin, A.G., Beadle, C.L., O'Grady, A.P., Pinkard, E.A.: Effects of partial defoliation on closed canopy *Eucalyptus globulus* Labillardière: Growth, biomass allocation and carbohydrates. – Forest Ecol. Manag. **261**: 695-702, 2011.

Raut, M.S., Ali, M.: Studies on defoliation and detopping in mustard under rainfed conditions. – Indian J. Agron. **31**: 252-255, 1986.

Reichman, O.J., Smith, S.C.: Responses to simulated leaf and root herbivory by a biennial, *Tragopogon dubius*. – Ecology **72**: 116-124, 1991.

Roitto, M., Rautio, P., Markkola, A., Julkunen-Tiitto, R., Varama, M., Saravesi, K., Tuomi, J.: Induced accumulation of phenolics and sawfly performance in scots pine in response to previous defoliation. Tree Physiol. **29**: 207-216, 2008.

RongQi, X., LeiYan, S.: [Dynamics of plant endogenous hormone of cotton leaves infected by *Verticillium dahlia*.] – Acta Gossypii Sin. **12**: 310-312, 2000. [In Chin.]

Ruess, R.W., Anderson, M.D., Mitchell, J.S., McFarland, J.W.: Effects of defoliation on growth and N fixation in *Alnus tenuifolia*: Consequences for changing disturbance regimes at high latitudes. – Ecoscience **13**: 404-412, 2006.

Ryle, G.J.A., Powell, C.E., Gordon, A.J.: Defoliation in white clover: regrowth, photosynthesis and $N_2$ fixation. – Ann. Bot. **56**: 9-18, 1985.

Saitoh, K., Isobe, S., Sequchi, Y., Kuroda, T.: Effects of source and/or sink restriction on the number of flowers, yield and dry matter production in field-grown soybean. – Japanese J. Crop Sci. **70**: 365-372, 2001.

Sakai, S., Imaseki, H.: Auxin induced ethylene production by mung bean hypocotyl segments. – Plant Cell Physiol. **12**: 349-359, 1971.

Schnyder, H., de Visser, R.: Fluxes of reserve-derived and currently assimilated carbon and nitrogen in perennial ryegrass recovering from defoliation. The regrowing tiller and its component functionally distinct zones. – Plant Physiol. **119**: 1423-1436, 1999.

Servaites, J.C., Fondy, B.R., Li, B., Geiger, D.R.: Sources of carbon for export from spinach leaves throughout the day. – Plant Physiol. **90**: 1168-1174, 1989.

Singh, D.K., Sale, P.W.G.: Defoliation frequency and the response by white clover to increasing phosphorus supply 1. Leaf dry matter yield and plant morphology responses. – Aust. J. Agr. Res. **48**: 111-118, 1997.

Shao, L., Zhang, X., Hideki, A., Tsuji, W., Chen, S.: Effects of defoliation on grain yield and water use of winter wheat. – J. Agr. Sci. **148**: 191-204, 2010.

Sheley, R.L., Svejcar, T.J.: Response of bluebunch wheatgrass and medusahead to defoliation. – Rangeland Ecol. Manage. **62**: 278-283, 2009.

Striker, G.G., Insausti, P., Grimoldi, A.A.: Floodings effects on plants recovering from defoliation in *Paspalum dilatatum* and *Lotus tenuis*. – Ann. Bot. **102**: 247-254, 2008.

Takagi, M., El-Shemy, H.A., Sasaki, S., Toyama, S., Kanai, S., Saneoka, H., Fujita, K.: Elevated $CO_2$ concentration alleviates salinity stress in tomato plant. – Acta Agr. Scandinavica, Sec. B: Plant Soil Sci. **59**: 87-96, 2009.

TeKrony, D.M., Hunter, J.L.: Effect of seed maturation and genotype on seed vigor in maize. – Crop Sci. **35**: 857-862, 1995.

Terashima, I., Evans, J.R.: Effects of light and nitrogen nutrition on the organization of the photosynthetic apparatus in spinach. – Plant Cell Physiol. **29**: 143-155, 1988.

Turgeon, R.: Plasmodesmata and solute exchange in phloem, Aust. J. Plant Physiol. – **27**: 521-529, 2000.

Turnbull, T.L., Adams, M.A., Warren, C.R.: Increased photosynthesis following partial defoliation of field-grown *Eucalyptus globulus* seedlings is not caused by increased leaf nitrogen. – Tree Physiol. **27**: 1481-1492, 2007.

Vann, D.R., Fletcher, J.S., Acchireddy, N.R., Beevers, L.: Influence of partial defoliation of green pepper on the senescence, growth, and nitrate reductase of remaining leaf. – Plant Soil **91**: 357-361, 1986.

von Caemmerer, S., Farquhar, G.D.: 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, 1984.

Wand, S.J.E., Midgley, G.F.: Effects of atmospheric $CO_2$ concentration and defoliation on the growth of *Themeda triandra.* – Grass Forage Sci. **59**: 215-226, 2004.

Wang, S., Wang, J., Liang, Z.: Study on basic performance of source-sink in hybrid wheat. – Acta Agron. Sin. **20**: 426-431, 1994.

Wardlaw, I.F.: The control of carbon partitioning in plants. – New Phytol. **116**: 341-381, 1990.

Wareing, P.F., Khalifa, M.M., Treharne, K.J.: Rate-limiting processes in photosynthesis at saturating light intensities. – Nature **220**: 453-457, 1968.

Weiss, E.A.: Oilseed Crops. – Longman Inc., NewYork 1983.

Wilsey, B.J.: Urea additions and defoliation affect plant responses to elevated $CO_2$ in a C3 grass from Yellowstone National Park. – Oecologia **108**: 321-327, 1996.

Yang, C., Chong, K., Qui, Q.: [Study on physiological reactions during senescence of detached leaves of broad bean.] – Acta Bot. Bor. Occident. Sin. **10**: 197-202, 1990. [In Chin.]

Yang, Z., Midmore, D.J.: Experimental assessment of the impact of defoliation on growth and production of water-stressed maize and cotton plants. – Exp. Agr. **40**: 189-199, 2004.

Zhao, W., Chen, S.P., Lin, G-H.: Compensatory growth responses to clipping defoliation in *Leymus chinensis* (Poaceae) under nutrient addition and water deficiency conditions. – Plant Ecol. **196**: 85-99, 2008.

Zhu, G.X., Midemore, D.J., Radford, B.J., Yule, D.F.: Effect of timing of defoliation on wheat (*Triticum aestivum* L.) in central Queensland. 1. Crop response and yield. – Field Crops Res **88**: 211-226, 2004.