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Friend or Foe? Exploring the Factors that Determine the Difference Between Positive and Negative Effects on Photosynthesis in Response to Insect Herbivory

John Paul Délano Frier[1],
Carla Vanessa Sánchez Hernández[2] and Axel Tiessen[1]
[1]*Unidad de Biotecnología e Ingeniería Genética de Plantas, Cinvestav - Irapuato, Guanajuato,*
[2]*Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Jalisco, México*

1. Introduction

Photosynthesis is a central process for the survival of plants, providing essential elements for growth and reproduction. As its name implies, the excitation of chlorophyll by photons, initiates an electron current that results in the generation of NADPH and ATP, which are subsequently used by the plant to sustain growth and development. However, precise and challenging energy equilibrium between the synthesis of NADPH and ATP and the downstream reactions that consume them must be maintained to ensure that the photosynthetic process runs efficiently. This balancing act is not trivial considering the necessity to integrate extremely rapid, temperature-independent photochemical reactions with relatively slow, temperature-dependent biochemical reactions. In addition, the equilibrium can be perturbed with relative ease when plants face adverse ambient conditions, including biotic stresses, leading to negative effects on the photosynthetic apparatus and concomitant disruption of the orderly transfer of electrons to their proper final acceptors. To avoid or minimize damage, plants have developed several strategies to maintain stability, the details of which will be explored in this chapter.

Together with many other biotic stresses, insect herbivory is known to alter photosynthetic activity and/or photosynthetic gene expression levels in affected plants. The effects are predominantly negative, although compensatory responses are not uncommon. Both positive and negative effects can be detected in injured and adjacent, intact, plant tissue, which may include, in some species, photosynthetically active stems in addition to leaves. Indirect effects on photosynthesis have been clearly demonstrated with the use of fluorescence and thermal imaging system techniques. The negative insect herbivory-derived effects on photosynthesis are frequently explained by a theoretical framework constructed on the argument that the resource-rich photosynthetic apparatus is sacrificed to provide the metabolic precursors and energy needed for the proper deployment of the resource-

demanding defense responses, although the concept of a down-regulated photosynthetic apparatus as a protective measure against oxidative damage has also been proposed. Jasmonic acid (JA), frequently interacting with ethylene, is recognized as the primary regulator of the defense response against defoliating insects and is strongly associated with the down-regulation of photosynthesis genes. Conversely, the mechanism(s) responsible for the compensatory photosynthetic activity that allows increased plant growth or fitness after insect herbivory are not well understood. Experimental evidence gathered to date suggests that the onset of compensatory photosynthesis may be dependent on many factors. The timing of herbivory injury, which also influences the plant's source/sink relationships along its phenology, is important. Also influential are the type of tissue damaged, the type and extension of damage, which in turn may be influenced by highly specific factors such as the composition of the herbivore´s saliva and the type of endosimbiotic bacteria colonizing the insect´s gut, the development stage of the herbivore, its feeding guild and even differences within guilds. Finally, the tolerance capacity of the plant to injury, the environmental conditions surrounding the plant, and the type of defense produced, if any, in response to herbivory, will also define whether a given assault on the plant leads to compensatory responses. The suggested role for phytochrome as a regulator of resource allocation between plant growth and anti-herbivore defense also implies its participation as a signaling element in herbivory-dependent changes in photosynthesis. Moreover, emerging data suggest that stress acclimation and chloroplast-to-nucleus signaling is mediated by phytohormones acting via AP2/EREBP transcription factors, which are believed to play a major and diversified role in environmental signal integration.

The overall perspective on the varying factors that influence the effect that insect herbivory may have on photosynthesis is that of complexity. This chapter will also concentrate on the description of these multiple factors, including emerging data that have shed light on the poorly understood mechanisms that regulate photosynthesis-related gene expression or that define how herbivore damage is interpreted by the plant, either as a "friendly" jolt to increase photosynthesis and stimulate growth and promote fitness or as an "act of war" leading to austerity measures to privilege a defense effort.

2. Photosynthesis under stress: How a vital process copes with a permanently changing environment

Photosynthesis constitutes a highly integrated process involving four multi-subunit membrane-protein complexes: photosystem II (PSII), photosystem I (PSI), cytochrome *b6f* and F-ATPase (Nelson & Yocum, 2006) that is exquisitely designed to funnel the electron current initiated by photon absorption to the reducing reactions that generate NADPH from $NADP^+$. The process of electron transport also generates an electrochemical proton gradient that powers ATP synthesis. The reductive power and ATP generated are then employed to reduce inorganic sources of carbon, nitrogen and sulfur needed for the synthesis of carbohydrates, amino acids and proteins used to maintain cellular homeostasis and growth respiration for cell division and expansion (Paul & Foyer, 2001). The need to balance the light energy absorbed by the photosystems with the energy consumed by metabolic sinks of the plant renders the photosynthetic process highly sensitive to any disturbing change in environmental conditions, such as fluctuating illumination, limitation of CO_2 fixation by low temperatures, salinity or low nutrient or water availability, and biotic stress. Several

molecular short-term and long-term acclimation mechanisms are deployed by photosynthetic organisms (predominantly green algae and land plants) to maintain or restore photosynthetic efficiency under adverse conditions and counteract stresses (Öquist & Huner, 2003; Ensminger et al., 2006). On a time scale of minutes, organisms can reduce the efficiency of energy transfer to PSII either by redistributing light energy to PSI at the expense of PSII through state transitions or by dissipating excess energy as heat by non-photochemical quenching associated with the light-harvesting complex (LHC) antenna (Hüner et al., 1998; Szyszka et al., 2007). Alternatively, it has also been proposed that quenching of excess energy may occur at the reaction centers, in addition to zeaxanthin-dependent antenna quenching (Krause & Weis, 1991; Bukhov et al., 2001; Matsubara & Chow, 2004; Ivanov et al., 2006). Long-term acclimation responses include alterations in light harvesting antenna size and adjustments of PSI: PSII stoichiometry that balance the excitation light energy absorbed by the two photosystems (Yamazaki et al., 2005; Ozaki et al., 2007, Solanke & Sharma, 2008; Muramatsu et al., 2009). A significant body of experimental evidence indicates that redox signals from photosynthetic electron transport and reactive oxygen species (ROS) or ROS-scavenging molecules play a central role in the regulation of acclimation and stress responses (Foyer & Noctor, 2009; Pfannschmidt et al., 2009; Mubarakshina et al., 2010).

2.1 Short-term acclimation mechanisms

2.1.1 State transitions

State transitions represent a short-term response, occurring within a time-frame of seconds to minutes, required to balance the light excitation energy between the antennae systems of PSII and PSI which preferentially absorb 650 and 700 nm light, respectively. Because of these differences in light absorption properties, changes in light conditions, such as those happening under shaded or light-limiting conditions, or as a consequence of shifts in the spectral filtering properties of leaf canopies, can lead to unequal excitation of the two photosystems (Allen & Forsberg, 2001; Haldrup et al., 2001; Wollman, 2001; Dietzel et al., 2008; Pesaresi et al., 2010). Preferential excitation of PSI leads to the oxidation of the plastoquinone (PQ) pool and to state 1. In state 1 the mobile light-harvesting antenna is bound to PSII and the photosynthetic electron transport chain acts mostly in a linear mode generating NADPH and ATP. Preferential excitation of PSII relative to PSI leads to a reduced state of the PQ pool and thus to the docking of plastoquinol to the Qo site of the cytochrome *b6f* complex. It is the PQ redox state only, acting independently of photoreceptors (Fey et al., 2005), that then activates the so-called redox-sensitive thylakoid LHCII kinase needed to phosphorylate the peripheral LHCII "mobile pool", which then migrates laterally, as a consequence of charge repulsion, from PSII to PSI (state 2) (Lunde et al., 2000). Chemical cross-linking and RNA interference approaches performed in Arabidopsis plants maintained in state 2 have provided evidence for an association of LHCII polypeptides to a specific PSI docking domain composed of subunits PsaL, PsaH and PsaO (Lunde et al., 2000; Zhang et al., 2004; Pesaresi et al., 2010), whereas a gentle mechanical fractionation of the thylakoid membranes showed that the lateral movement of phosphorylated LHCII might be confined to a very limited portion of the thylakoid membranes, more precisely to the grana margins (Tikkanen et al., 2008). Regardless of the mechanism, the re-distribution of the light-harvesting chlorophyll to PSI at the expense of

PSII results in a balanced excitation of PSII and PSI to ensure optimal quantum efficiency for photosynthetic electron transport. Under PQ oxidizing conditions the LHCII kinase is inactive, LHCII is or becomes dephosphorylated and is relocated to PSII (state I). The identity of the redox-independent and constitutively active protein phosphatase that presumably dephosphorylates LHCII during the transition from State 2 to 1 was the subject of intense research and remained unknown until recently. The search finally yielded fruit with the identification of a LHCII-specific phosphatase, called PPH1/TAP38. This enzyme dephosphorylates LHCII upon a transition from state 2 to state 1 (Pribil et al., 2010; Shapiguzov et al., 2010), by specifically dephosphorylating the major trimeric Lhcb1 and Lhcb2 proteins. It is a chloroplast protein that is mainly associated with the stromal membranes of the thylakoid membranes and belongs to the family of monomeric PP2C type phosphatases. Its regulatory role was demonstrated in experiments where the loss of PPHI/TAP38 gave rise to an increase in the antenna size of PSI and strongly impaired state transitions.

2.1.2 The nature of the redox-sensitive thylakoid LHCII kinase

LHCII kinase activity was first reported in 1977 (Bennett, 1977, 1979), a finding that also triggered an intensive search for its identity. A first approximation of its nature came from a screening for proteins capable of interacting with the N-terminal region of the light-harvesting proteins known to contain the amino-acid targets for phosphorylation during states 1–2 transition. This approach led to the identification of a small family of three kinases, called TAK kinases (for thylakoid associated kinases) in *Arabidopsis thaliana* (Snyders & Kohorn, 1999), whose exact role in state transitions regulation remains undefined until now, notwithstanding biochemical and genetic experimental evidence showing that TAKs do indeed participate in LHCII phosphorylation (Snyders & Kohorn, 2001). Moreover, the failure to identify TAK orthologs in the green motile unicellular alga *Chlamydomonas reinhardtii* either suggests that the TAK kinases perform a role which is specific to land plants or that a considerable diversion of these kinases happened as a result of evolutionary divergence between green algae and plants.

Later, advantage was taken of the large chlorophyll fluorescence changes that occur during a transition from states 1 to 2 in *C. reinhardtii* (that can be efficiently measured with a fluorescence video imaging system) to screen insertional mutants that could lead to the identification of the LHCII kinase and other factors of the signal transduction pathway leading to state transitions (Fleischmann et al., 1999; Kruse et al., 1999). This strategy permitted the isolation of the *state transition-deficient mutant 7* (*stt7*), which was found to encode a thylakoid-associated Ser-Thr protein kinase, and of another protein kinase of unknown function but related to Stt7, called Stl1. Orthologs of these two proteins, called STN7 and STN8, respectively, were subsequently found in Arabidopsis, rice and in marine algae (Depége et al., 2003). Utilization of Arabidopsis T-DNA insertion lines with disruptions in the *STN7* or *STN8* genes helped elucidate the function of these proteins. Thus, STN7 was found to be required for state transitions and for the specific phosphorylation, under state 2 conditions, of several LHCII proteins that did not include the major thylakoid proteins CP43, D1 and D2 (Bellafiore et al., 2005). An additional site directed mutagenesis approach provided conclusive evidence demonstrating that the kinase activity of STN7 is essential for state transitions. It is now known that Stt7 and STN7 are both structurally and functionally related.

The recent characterization of Stt7 in *C. reinhardtii* revealed a structural organization in which a transmembrane helix separates its stroma-exposed catalytic domain from its lumen-located N-terminal end. This organization permits the co-localization of the catalytic site with the target sites on the LHCII proteins. It also identified two conserved cysteine residues that are critical for its activity (Lemeille et al., 2009). In addition, co-immunoprecipitation assays have shown that Stt7 interacts with Cyt *b6f*, PSI and LHCII, suggesting that all these protein complexes might be clustered together, possibly in very restricted areas of thylakoid membranes, such as the grana margins (Tikkanen et al., 2008; Lemeille et al., 2009; see above). The curious fact that the Qo site of the cytochrome *b6f* complex, which is critical for the activation of the kinase, is on the lumen side necessarily implies that a signal for kinase activation needs to be transported across the membrane. A mobile Rieske protein (Zhang et al., 1998; Breyton, 2000) and subunit V (also called PetO) from the cytochrome *b6f* complex, which is the only protein of the complex capable of under-going reversible phosphorylation during state transitions (Hamel et al., 2000), have been proposed as possible signal transducing candidates in a pathway model that suggests that sensing of the structural changes of the Rieske protein by the lumenal domain of PetO is transmitted through its trans-membrane region to its stromal domain in order to allow its interaction with the kinase. Another interesting feature found in Stt7 and STN7 involves the presence of two conserved Cys residues near the N-terminal end which could be the targets of thioredoxin (Rintamaki et al., 2000). The loss of state transitions and LHCII phosphorylation as the result of site-directed mutagenesis of either of the conserved Cys residues in both Stt7 and STN7 strongly suggests that these residues play an important role in the activation of the kinase. It is also likely that the high-light-induced reduction of this bond may occur through a trans-thylakoid thiol-reducing pathway driven by the ferredoxin-thioredoxin system which is also required for cytochrome *b6f* assembly and heme biogenesis (Lemeille et al., 2009). Therefore, it appears likely that STN7 kinase activity is regulated not by PQ alone, but by a complex network involving co-operative redox control by PQ and the Cyt *b6f* complex, as well as by the ferredoxin/ thioredoxin system in the stroma of the chloroplasts (Rintamaki et al., 2000; Lemeille et al., 2009)

Although it is clear that the Stt7/STN7 kinase is required for LHCII phosphorylation and for state transitions, it is not yet known whether it acts in a kinase cascade or recognizes LHCII as its direct substrate. Some of these uncertainties were dispelled by the findings of a recent study that compared the thylakoid phosphoproteome of the wild-type strain and the *stt7* mutant of *C. reinhardtii* under state 1 and state 2 conditions (Lemeille et al., 2010). The study revealed that under state 2 conditions several Stt7-dependent phosphorylations occur in the Lhcbm1/Lhcbm10, Lhcbm4/Lhcbm6/Lhcbm8/Lhcbm9, Lhcbm3, Lhcbm5, and CP29 proteins located at the interface between PSII and its light-harvesting system. One of the two Stt7-dependent phosphorylation sites detected specifically in CP29 under state 2 was proposed to play a crucial role in the dissociation of CP29 from PSII and/or in its association to PSI where it serves as a docking site for LHCII in state 2. Moreover, the Stt7-dependent phosphorylation of the thylakoid protein kinase Stl1 under state 2 conditions, suggested the existence of a thylakoid protein kinase cascade. Curiously, the auto-phosphorylation of Stt7 in state 2, was found not to be required for state transitions. Additional findings included the identification of redox (or state 2)-dependent but Stt7-independent, and redox-independent phosphorylation sites.

The existence of the conserved STN7/ STN8 and Stt7/Stl1 kinase couples in Arabidopsis and *Chlamydomonas* also suggests a possible functional interaction between STN7/Stt7 and STN8/Stl1. This is in accordance with data proposing that these proteins appear to act synergistically, since the de-phosphorylation phenotype of LHCII and PSII core proteins in the double mutant *stn7/stn8* is more pronounced than than those observed in the two single mutants (Bonardi et al., 2005; Vainonen et al., 2005). Moreover, field tests revealed that fitness, as measured by seed production, was significantly decreased in the double mutant whereas it was decreased to a smaller extent in *stn7* and not significantly affected in *stn8* mutants, respectively (Frenkel et al., 2007).

2.1.3 The importance of state transitions in flowering plants

The magnitude of state transitions is much larger in *C. reinhardtii* than in flowering plants, where displacements have been reported to involve up to 85% of the LHCII antenna from PSII in State 2. In contrast, only 20-30% of the total LHCII is mobile in green plants. Moreover, state transitions in green algae represent a unique adaptive mechanism that allows the organism to switch between linear (State 1) and cyclic (State 2) electron flow through PSI (Finazzi et al., 2001), whereas *C. reinhardtii* mutants unable to undergo state transitions, such as *stt7*, exhibit altered photosynthetic performance and a marked decrease in growth rate (Depége et al., 2003). Conversely, plant development and fitness under laboratory and field conditions have been found to be only marginally affected in Arabidopsis mutants impaired in state transitions (Lunde et al., 2000; Bonardi et al., 2005; Bellafiore et al., 2005; Frenkel et al., 2007). However, a marked decrease in growth rate relative to the parental single mutants, which was accompanied by a consistent drop in the effective quantum yield of PSII and an increase in the reduction state of the PQ pool, was detected in double Arabidopsis mutants affected both in the linear electron transport leading to an increased pool of reduced PQ (i.e. *psad1-1* and *psae1-3*), and state transitions (i.e. *stn7-1 or psal-1*) (Lunde et al., 2000; Pesaresi et al., 2009). This behavior implied that state transitions become critical for plant performance when linear electron flow is perturbed. Further spectroscopic analyses performed on the different genotypes led to the conclusion that, in flowering plants as in green algae, state transitions play an important role in balancing energy distribution between photosystems.

2.2 Long Term acclimation Responses (LTR)

2.2.1 LTR mechanisms

Besides inducing short term acclimation processes such as state transitions, changes in light conditions are known to lead to long term responses (LTR) characterized by changes in the amounts of the antenna proteins of PSII and PSI and in photosystem stoichiometry. These changes are implemented over periods lasting hours or days (Dietzel et al., 2008). This process is achieved through a signaling network involving coordinate gene expression in the nucleus and chloroplast (Pfannschmidt, 2003; Pfannschmidt et al., 2009). Most experimental evidence gathered to date indicates that STN7 is also required for triggering LTR (Allen & Pfannschmidt, 2000; Bonardi et al., 2005; Tikkanen et al., 2006), suggesting a dual role for STN7, acting as a common redox sensor and/or signal transducer for both state transitions and LTR responses. However, experimental evidence obtained with mutant or silenced Arabidopsis lines affected in various components required for state transitions (including the novel TSP9 protein, suggested to function in the signaling pathway due to its partial

dissociation from the thylakoid membrane upon phosphorylation (Pesaresi et al., 2009), showed that neither LHCII phosphorylation, nor the conformational changes in the thylakoid associated with state transitions themselves, appear to play any role in LTR (Carlberg et al., 2003; Pesaresi et al., 2009). This argued against the possibility that the signal pathways leading to state transitions and LTR were part of a hierarchically organized signaling cascade, with changes in PQ redox state first triggering state transitions and then LTR, via a STN7-dependent phosphorylation cascade. In order to conciliate the above data, an alternative hypothesis proposing that the PQ redox state must reach a still undefined threshold value to be able to induce the specific, and reversible, STN7-dependent phosphorylation steps that trigger the signaling events leading to LTR was considered (Pesaresi et al., 2010).

In most species investigated, the re-adjustment of photosystem stoichiometry involves an enhanced expression of the PSI reaction-center genes *psaA* and *psaB* (which encode the P700 apoproteins) upon active reduction of the PQ pool or repression of its oxidation. LTRs are also known to involve the regulated expression of the PSII reaction-center gene *psbA* (encoding the D1 protein) (Pfannschmidt, 2003) and changes in several other physiological and molecular parameters, including the chlorophyll *a/b* ratio, steady state chlorophyll fluorescence and structural modifications of the thylakoid membrane system (Bonardi et al., 2005; Tikkanen et al., 2006). Several proteins were recognized as possible regulators of photosystem stoichiometry in the cyanobacteria *Synechocystis* sp., including photomixotrophic growth-related and CO_2-concentrating-mechanism proteins, a probable esterase, cytochrome c oxidase subunits II and III and a hypothetical protein with a von Willebrand factor type A domain. The latter suggested a role for protein-protein interactions in the regulation of photosystem stoichiometry in these organisms (Ozaki et al., 2007). In addition, the depletion of the vesicle inducing protein in plastids 1 (Vipp1), believed to be essential for thylakoid membrane formation in Arabidopsis and cyanobacteria, was found to negatively affect photosystem stoichiometry in *Synechocystis* sp. This effect was associated with a concerted decrease in the number of thylakoid layers and associated photosystem I (PSI) complexes in individual cyanobacterial cells, and an enrichment of PSI monomeric species resulting from of PSI trimer destabilization (Fuhrmann et al., 2009).

More recently, photosystem stoichiometry adjustment in plants and algae, was found to be governed by a modified two-component sensor kinase of cyanobacterial origin, known as chloroplast sensor kinase (CSK) (Puthiyaveetil et al., 2011), acting together with chloroplast sigma factor 1 (SIG1) and a plastid transcription kinase (PTK). These findings confirmed previous data implicating CSK as a control of chloroplast gene expression (Puthiyaveetil et al., 2008), via its role as a sensor of the PQ redox state. Moreover, they confirmed the concept assigning different signaling pathways to state transitions and photosystem stoichiometry adjustments, with the two pathways sensing PQ redox state independently of each other (i.e the reduced and oxidized forms of the quinone recognized for state transitions and photosystem stoichiometry, respectively).

The LTR is also accompanied by dynamic changes in metabolite pools that depend to the prevailing illumination (Bräutigam et al., 2009). For instance, the propagation of plants under PSI-specific light is known to cause a lower accumulation of transitory starch. Moreover, contrasting light conditions have been observed to exert different co-regulation effects on biosynthetic pathways for organic acids and several amino acids linked to

secondary metabolism in plants. Thus, the LTR appears to contribute also to the adaptation of plant primary productivity to environmental conditions (Pesaresi et al., 2010).
All evidence gathered to data indicates that short- and long-term photosynthetic acclimation responses are triggered by changes in the redox state of the PQ pool and require the modulated activity of the kinase STN7. Due to its dual regulatory role, STN7 initiates a phosphorylation cascade that induces state transitions by phosphorylating LHCII and promotes the LTR process via the phosphorylation of as yet unknown chloroplast proteins. Beyond this point, the LTR signaling pathway is divided into two main branches: one is responsible for transcriptional regulation of chloroplast gene expression, while the other controls the expression of nuclear photosynthesis-related genes at transcriptional and post-transcriptional levels (see Figure 1) (Pesaresi et al., 2010).

2.3 Acclimation responses under high or excess excitation pressure

State transitions and LTR are acclimation responses that typically occur under low-light conditions and are controlled via redox signals. Under conditions resulting in high or excess excitation pressure other acclimation responses are activated, such as non-photochemical dependent antenna quenching, the D1 repair cycle or various other stress-response programs. These responses are also controlled via redox signals originating from the photosynthetic process (i.e. the PQ redox state and signals from the PSI acceptor side), but may also involve the participation of ROS such as hydrogen peroxide (H_2O_2) or singlet oxygen (Pfannschmidt et al., 2009).

2.3.1 Non-photochemical quenching

Non-photochemical quenching (NPQ) is a rapid de-excitation photo-protective quenching mechanism (qE) that involves dissipation of excess energy occurring upon short-term high light exposure. In addition, NPQ is considered to act as a ''light intensity counter,'' providing the photosynthetic membrane with a ''memory'' of the light-exposure history of the leaf (Horton et al., 2008; Foyer & Noctor, 2009). qE is induced by a low thylakoid lumen pH (i.e. a high ΔpH) generated by photosynthetic electron transport in excess light and involves the harmless thermal dissipation of excess energy in the chlorophyll (Chl) singlet excited states (^{1}Chl*) in photosystem II (PSII) of green plants and algae. qE is designed to minimize alternative reaction pathways that generate toxic photo-oxidative intermediates. It functions by activating a lumen-localized violaxanthin de-epoxidase enzyme that catalyses the conversion of violaxanthin to zeaxanthin via the intermediate antheraxanthin, in what is known as the xanthophyll cycle (which is completed by the conversion of zeaxanthin back to violaxanthin by means of a zeaxanthin epoxidase activated under limiting light conditions). The process also requires the protonation of PsbS, a PSII subunit that plays a role in the regulation of photosynthetic light harvesting and is also necessary for qE *in vivo* (possibly by establishing a binding site for zeaxanthin that facilitates the de-excitation of singlet excited chlorophyll via energy or electron transfer). Experimental evidence has shown that energy transfer from chlorophyll molecules to a chlorophyll-zeaxanthin heterodimer that undergoes charge separation is the main mechanism for excess energy dissipation during feedback de-excitation (Horton et al., 1999; Külheim et al., 2002; Niyogi et al., 2005; Holt et al., 2004, 2005). However, quenching of excess energy can also occur independently of zeaxanthin via a reversible inactivation of a fraction of photosystem II

(PSII) centers (Ivanov et al., 2006, 2008) or through conformational changes within the PSII antenna, as recently reported (Johnson et al., 2009).

2.3.2 D1 repair cycle

In addition to the D1 and D2 proteins that conform its core reaction center, PSII contains *a* and *β* subunits of cytochrome *b*559, the *psb*I gene product and a few low molecular weight polypeptides. The D1-D2 heterodimer within PSII binds all the electron carriers and cofactors necessary for electron transport (Nanba & Satoh, 1987; Mattoo et al., 1989). The reaction center protein D1 of PSII is also the primary target of photo-inhibition (Mattoo et al., 1984; Prasil et al., 1992). Due to its intrinsic vulnerability, the short-lived D1 protein must be constantly replaced by new copies via a complicated and evolutionary conserved process known as the PSII or D1 repair cycle, whose significance remains elusive (Mattoo et al., 1989; Andersson & Aro, 2001; Baena-Gonzales & Aro, 2002; Yokthongwattana & Melis, 2006; Edelman & Mattoo, 2008). Nevertheless, the process has an undoubted physiological importance considering that an accumulation of photo-inactivated PSII centers, leading to a decreased photochemical efficiency and the consequent photo-damage, occurs whenever its repair capacity is surpassed (Melis, 1999; Andersson & Aro, 2001).

D1 is a target of at least five post-translational modifications during its life cycle, including N-acetylation, palmitoylation and phosphorylation (Edelman & Mattoo, 2008). One or more of these post-translational modifications could potentially alter protein degradation kinetics, although the use of nitric oxide donors to inhibit *in vivo* phosphorylation of the D1 protein suggested that redox-dependent phosphorylation and D1 degradation in plants are not linked events (Booij-James et al., 2009). The DegP and FtsH proteases have been shown to be involved in D1 degradation *in vitro* (Haussuhl et al., 2001; Kanervo et al., 2003; Lindahl et al., 2000). The physiological significance of these specific proteases was demonstrated in the Arabidopsis *var2* (for *yellow variegated2*) or *var1* mutants, lacking the FtsH2 or FtsH5 membrane-bound metalloproteases, respectively, and the *fu-gaeri1* (*fug1*) mutant that suppresses interfering leaf variegation in *var1* and *var2*, all of which led to an inefficient degradation of the D1 protein and a concomitant increase in ROS levels that was connected to an enhanced susceptibility to photoinhibition (Bailey et al., 2002; Kato et al., 2009). Similar results were reported in cyanobacteria, where impaired D1 protein turnover was detected in an FtsH inactivation mutant (Silva et al., 2003). Moreover, experiments in which an increased transcription of two FtsH-coding genes and of FtsH protease activity was found to be induced upon transfer of cyanobacteria to high light, demonstrated that FtsH proteolysis is a light regulated process (Hihara et al., 2001; Singh et al., 2005).

2.3.3 Other stress-response programs

The accumulation of excitation energy produced when the rate of absorption of photons exceeds the rate of utilization of excitation energy in photosynthetic electron transport leads to an accumulation of reduced electron acceptors that eventually produce excited states of chlorophyll (i.e. triplet state). This process is presumed to predominantly occur in the PSII reaction center where quenching by carotenoids is less effective. Triplet state chlorophyll readily reacts with oxygen to give rise to singlet oxygen, a highly destructive excited oxygen species causing photo-oxidations (Triantaphylidés & Havaux, 2009) (Figure 1). Superoxide, H_2O_2 (produced via reduction or dismutation of superoxide) and hydroxyl radicals, all of which are more reactive than ground state triplet O_2, can also be produced by numerous

pathways in photosynthetic cells. It is generally accepted that PSI is the major site of superoxide generation in the photosynthetic electron transport (PET) chain (Asada, 2006) (Figure 1). In addition to production linked to PET and respiratory electron transport (RET) chains, the photorespiration pathway is a major producer of H_2O_2 (Peterhansel et al., 2010). Photorespiration is due to the oxygenase activity of ribulose-1, 5-bisphosphate carboxylase-oxygenase (Rubisco), which produces 2-phosphoglycolate. This small molecule is metabolized through a sequence of reactions that includes H_2O_2 production by glycolate oxidase. Thus, the implementation of protective/metabolizing systems to prevent the deleterious effects of ROS accumulation in plants, are essential to maintain the process of photosynthesis in the oxygen-rich atmosphere of this planet.

The perturbation of the equilibrium between ROS production and scavenging that is frequently produced in plants under stress, can result in a transient increase in ROS levels that is closely associated with the emergence of various disorders such as cell death, disease, and aging (Neill et al., 2002; Overmyer et al., 2003). ROS exert this effect either by reacting with, and irreversibly damaging, a large variety of bio-molecules or by altering the expression of genes that affect signal transduction pathways in a highly selective, specific, and sometimes antagonistic, manner (Apel & Hirt, 2004; Danon et al., 2005; Gadjev et al., 2006; Laloi et al., 2007; Lee et al., 2007). Strong evidence suggesting that H_2O_2 either directly or indirectly antagonizes singlet-oxygen-mediated signaling was obtained recently using a ingenious experimental approach in which Arabidopsis *flu* mutant plants, which generate singlet oxygen in plastids during a dark-to-light transition (see below), were found to produce a more intense stress responses when the H_2O_2 concentration was reduced non-invasively by the over-expression of a thylakoid ascorbate peroxidase (Murgia et al., 2004; Laloi et al., 2007). In addition, low molecular weight antioxidants (e.g., ascorbate, glutathione) serve not only to limit the lifetime of the ROS signals but also participate in an extensive range of other redox signaling and regulatory functions (Foyer & Noctor, 2009).

Considering the above, ROS are considered to be primary diffusible and reactive mediators of signaling linked to electron transport status. For instance, singlet oxygen was considered for many years as a highly toxic molecule with very limited diffusion. However, the utilization of specific probes capable of detecting singlet oxygen in the aqueous phase of isolated thylakoid suspensions and the cytoplasm of high light stressed cells of *C. reinhardtii*, strongly suggested that singlet oxygen can diffuse significant distances from its site of production to activate specific gene expression, such as the nuclear-encoded glutathione peroxidase homolog GPXH (Fisher et al., 2007). However, the physiological relevance of these findings remains questionable considering that the fraction of mobile singlet oxygen was probably small, was detectable only at very high light intensities and has been observed only in this species. H_2O_2 is also recognized as an important signaling molecule. Its role as a signal conveyor was reinforced by data, generated using spin trapping electron paramagnetic resonance spectroscopy and H_2O_2-sensitive fluorescence dyes, that showed that up to 5% of the total H_2O_2 produced inside the chloroplasts was able to diffuse out of the chloroplasts, and in the process evade the effective antioxidant systems located inside this organelle. Moreover, H_2O_2 diffusion was shown to increase concomitantly with light intensity and time of illumination (Mubarakshina et al., 2010). Additional observations have suggested that glutathione, whose synthesis is affected by changes in photosynthesis, may also act as a plastid signal that controls expression of stress defense genes in the nucleus (Wachter et al., 2005; Mullineaux & Rausch, 2005; Rausch et al., 2007).

Identifying ROS specific signaling pathways leading to changes in nuclear gene expression is hampered by the fact that several chemically distinct ROS are generated simultaneously during stress within the plastid compartment. This problem was partially solved by the generation of the *flu* mutant of Arabidopsis that generates singlet oxygen in plastids in a controlled and non-invasive manner (Meskauskiene et al., 2001; op den Camp et al., 2003). Thus, this mutant accumulates excess protochlorophyllide in the dark that, upon illumination, acts as a photosensitizer capable of generating singlet oxygen (Flors & Nonell, 2006; Hideg et al., 2006; op den Camp et al., 2003). Light induced generation of singlet oxygen has revealed a rapid change in nuclear gene expression that differs substantially from nuclear gene expression profiles activated by superoxide or H_2O_2, further supporting the proposal that superoxide/H_2O_2- and singlet oxygen-dependent signaling occur via distinct pathways (Laloi et al., 2006; op den Camp et al., 2003).

The high reactivity of singlet oxygen, together with its unlikely ability to leave the plastid compartment, suggested that its physiological impact depended on the generation of more stable second messengers within the plastid, which were assumed to activate a signaling cascade outside of the plastid compartment. Two components of singlet oxygen signaling, the EXECUTER 1 and 2 proteins localized in the chloroplast, were recently identified as additional signaling components of singlet oxygen (Wagner et al., 2004; Lee et al., 2007) (Figure 1). However, the mechanisms involved in singlet oxygen sensing and signal transduction to the nucleus remain to be characterized, although experimental evidence supporting a positive role for abscisic acid (ABA), ethylene-, salicylic acid (SA)- and JA-dependent signaling pathways in the singlet oxygen- induced response was recently reported (Danon et al., 2005; Ochsenbein et al., 2006). In addition, approximately 50 genes encoding putative transcription factors have been identified to be rapidly and strongly induced within 30 min of the release of singlet oxygen. These include ethylene responsive factors, WRKY transcription factors, zinc-finger proteins and several DNA-binding proteins. Many genes involved in putative signal-transduction pathways and calcium regulation, such as protein kinases, calcium and calmodulin-binding proteins, were also identified (Danon et al., 2005; Laloi et al., 2006; Lee et al., 2007; op den Camp et al., 2003).

As mentioned above, H_2O_2 activates a response program different from singlet oxygen which is also more stable. Its experimentally proven capacity to diffuse across the chloroplast envelope is believed to be a pivotal step in a model that involves an H_2O_2-dependent activation of a mitogen-activated protein kinase (MAPK) cascade in the cytosol that subsequently affects gene expression in the nucleus (Kovtun et al., 2000; Vranova et al., 2002; Apel & Hirt, 2004; Mittler et al., 2004) (Figure 1). However, the polar nature of H_2O_2, which would be expected to limit its capacity to diffuse across hydrophobic membranes unaided, has been a strong argument used to question this model. Alternatively, it has been proposed that H_2O_2 transport is mediated by aquaporin channels (Bienert et al., 2007; Dynowski et al., 2008). This proposal, is supported by the hypersensitivity to H_2O_2 observed in yeast cells expressing Arabidopsis aquaporins in the plasma membrane, but has yet to be demonstrated in plants. Another nebulous aspect of the model is the mechanism by which H_2O_2, produced in multiple cell sites and in response to various different stresses and stimuli, acquires the specificity needed to act as a reliable signal conveying information on the state of chloroplasts to the nucleus.

Further experimental support for the presence of independent redox signaling pathways acting via differentiated signaling cascades came from the characterization of the so called

redox-imbalanced (*rimb*) mutants, which were detected using an Arabidopsis reporter gene line expressing luciferase under control of the redox-sensitive 2-cysteine peroxiredoxin A (2CPA) promoter (Heiber et al., 2007). Valuable information shedding light on the nature of redox signaling should be expected when the identity of the RIMB genes and their biochemical function is determined.

2.3.4 Tetrapyrrole and metabolite signaling

Pioneering experiments designed to understand plastid signaling were based on the application of norflurazon. This bleaching herbicide was found to be a potent experimental tool by its ability to profoundly disrupt chloroplast function, due predominantly by its strong inhibition of carotenoid biosynthesis. It was also shown to trigger the release of ROS upon illumination and prevent the light-dependent induction of nuclear photosynthesis-related genes (Oelmuller & Mohr, 1986). The isolation and characterization of the so called *gun* mutants (for *genomes uncoupled*), most of which coded for proteins that are involved in tetrapyrrole biosynthesis, led some workers to suggest that tetrapyrrole intermediates serve as a plastid signal to regulate the expression of nuclear genes for photosynthetic proteins (Mochizuki et al., 2001; Larkin et al., 2003; Strand, 2003; Koussevitzky et al., 2007). However, the conclusive results derived from subsequent studies strongly suggested that tetrapyrrole pathway intermediaries are not directly linked to plastid signaling (Mochizuki et al., 2008; Moulin et al., 2008).

Conversely, the concept of metabolic signaling arose from the unlikeness that ROS or redox compounds themselves act as signaling molecules that traverse the cytosol (see above). In this context, messengers that are metabolically more inert and less readily inactivated during diffusion through the cell represent much more promising signaling candidates (Baier & Dietz, 2005). This alternative signaling pathway is justified on the informative nature regarding the metabolic state of the chloroplast that is contained in the relatively large exchange of primary metabolites, such as carbohydrates, or of the xanthophyll derivative abscisic acid (ABA) phytohormone, with the rest of the cell. In this regard, sugar-signaling pathways have been considered as likely candidates for the regulation of photosynthetic acclimation under various stress conditions. Moreover, the expression of nuclear encoded photosynthetic genes (e.g. *CAB2* and *rbcS*) was found to be inversely correlated with intercellular soluble sugar levels (Oswald et al., 2001).

Thus, one proposed scenario envisions that metabolite concentration changes could be sensed by cytosolic or nuclear receptors to regulate nuclear gene expression. One of these sensors could be the cytosolic hexokinase, known to be crucial for sensing and responding to glucose signals intra-cellularly (Figure 1). Alternatively, the transport of carbohydrates across the chloroplast membrane might directly communicate information on the redox state of the chloroplast by means of so called 'redox valves'. Two well-studied examples of carbohydrate shuttles that export reducing power from the chloroplast are the malate/oxaloacetate and triose-phosphate shuttles (Heineke et al., 1991). The 'malate valve' comprises the malate/oxaloacetate translocator (Taniguchi et al., 2002) together with the chloroplast and cytosolic isoforms of NAD(P)H malate dehydrogenase, and is thought to constitute the central mechanism for the export of excess reducing power from the chloroplast. The dihydroxyacetonephosphate/3-phosphoglycerate shuttle involves the triosephosphate translocator (TPT) (Flügge et al., 1989) that functions primarily as a dihydroxyl acetonephosphate/phosphate exchanger to maintain sucrose synthesis in the

cytosol, but that could also export both ATP and NADPH from chloroplasts into the cytosol (Figure 1). Interestingly, the altered nuclear gene expression detected in the *tpt* (Biehl et al., 2005) and *cue1* mutants, the latter affected in the phosphoenolpyruvate/phosphate translocator (PPT) in the inner chloroplast envelope (Streatfield et al., 1999) supports the proposed role played by metabolite exchange in redox signaling .

Finally, the role of ABA as a signal relying information on the chloroplast status to the nucleus can be explained by evoking the multiple effects that photosynthetic activity rates have on the biosynthetic ABA pathway that is partially localized in the chloroplast (Baier & Dietz, 2005). For instance, oxidative stress conditions leading to increased ABA through inductive effects on the synthesis of its xanthophyll precursor in the chloroplast, could provide a link between the redox state and ROS levels in the plastid and gene expression in the nucleus. In this respect, it has been speculated that the repressed photosynthetic gene expression produced by norflurazon treatment might be associated with reduced levels of ABA resulting from a depressed carotenoid biosynthesis (Kleine et al., 2009).

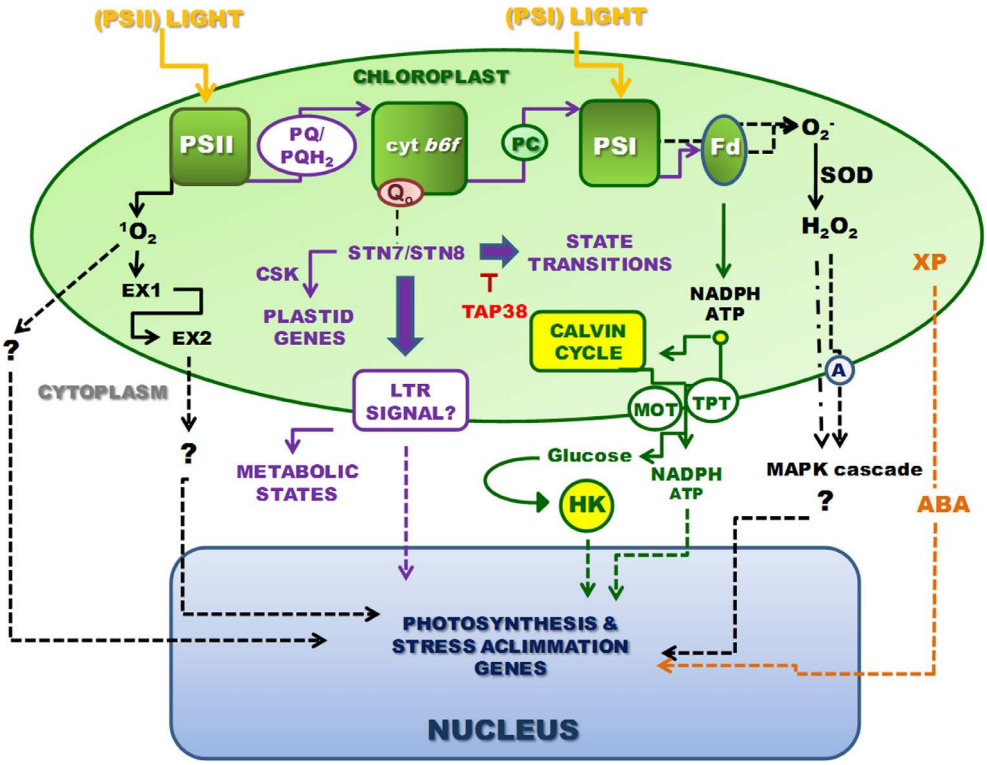

Fig. 1. Proposed plastid signal transduction pathways (redox, *metabolic* and ABA-dependent) involved in the regulation of acclimation responses to stress, including state transitions, long-term responses (LTR) and/or the activation/ repression of specific target genes in the chloroplast and nucleus. Redox signals are generated within the electron transport chain (purple) or by generation of reactive oxygen species (ROS) (black). The plastoquinone pool (PQ/PQH_2, in purple letters) is the origin for at least two redox

signaling pathways that are active under low or high light. These can lead to rapid state transitions, involving reversible association of the mobile pool of LHCII to PSI or PSII, or LTR. Qo (red oval) represents the docking site where plastoquinol binds to the cytochrome *b6f* complex. Both processes are dependent on the redox-regulated activity of the STN7 kinase (possibly in conjunction with STN8; purple letters). The TAP38 phosphatase (in red letters) regulates state transitions by specifically dephosphorylating LHCII. On the other hand, LTR involves chloroplast and nuclear gene expression (purple arrows). LTR-dependent plastid gene expression is believed to be regulated by the *Chloroplast Sensor Kinase* (CSK, in purple letters), while nuclear gene expression might require a putative LTR signal (in purple box). LTR-dependent changes in gene expression and protein accumulation can also lead to the establishment of two distinct metabolic states (purple letters, in *cytoplasm*) derived from the exposure to either PSI or PSII light (yellow letters and arrows). ROS are generated by transfer of electrons from PSI or reduced ferredoxin (Fd) to oxygen-generating superoxide (O_2^-, in black letters). This is detoxified by superoxide dismutase (SOD, in black letters) to hydrogen peroxide (H_2O_2; in black letters). Un-scavenged H_2O_2 might able to diffuse freely across the chloroplast envelope or through water channels (or aquaporins, A; blue letter in blue circle) and is thought to start MAP kinase cascades in the cytosol. Singlet oxygen ($^1O_2$; in black letters), is generated at PSII. Its high reactivity and short half-life require additional signaling components, such as Executer 1 and 2 (EX1, EX2, in black letters), although evidence in green algae suggests that $^1O_2$ might be able to diffuse out of the chloroplast. *Metabolic* plastid signaling has been proposed to require the activity of the malate/oxaloacetate (MOT; in green letters) and triosephosphate (TPT; in green letters) translocators needed for the export of excess reducing power and ATP from the chloroplast. Alternatively, metabolite concentration changes (e.g., glucose originated from the Calvin cycle; green letters) could be sensed by cytosolic or nuclear receptors (i.e. hexokinase; HK, green letters in yellow circle) to modify nuclear gene expression. Abscisic acid (ABA, in orange letters) whose synthesis is derived from ROS-sensitive xanthophyll precursors (XP, in orange letters) in the chloroplast, has also been proposed to act as a signal relying information on the chloroplast status to the nucleus. Dotted arrows represent pathways mediated by unknown components that have not been entirely elucidated. Tetrapyrrole and ROS-scavenging-associated signaling pathways are not shown (Adapted from Kleine et al., 2009, Pfannschmidt et al., 2009, and Pesaresi et al., 2010).

3. Photosynthesis under biotic stress: How is it regulated?

3.1 Integration of metabolic, hormonal and environmental signals in stress acclimation and retrograde signaling

Plants are able to integrate and evaluate a diversity of input signals to optimize acclimation responses to stressful environmental growth conditions and to ensure plant survival. Frequently observed adaptation responses are growth retardation, reduced metabolism and photosynthesis, reallocation of metabolic resources and increased antioxidant capacity. Cumulative evidence showing strong stress-related effects on ROS and auxin levels, coupled with the stress-induced morphogenetic changes often produced during adaptation, indicate that these physiologically active metabolites play a prominent role in the integration of the stress-regulatory networks, acting through mechanisms that remain poorly understood (Tognetti et al., 2011). The elaborate ROS signaling network is also known to act in concert with other hormonal networks and with plastid signaling to regulate developmental

processes, in addition to abiotic and biotic stress tolerance responses (Kleine et al., 2009; Tognetti et al., 2011). For instance, the local and systemic acclimation in Arabidopsis leaves in response to excess excitation energy associated with cell death and regulated by specific redox changes of the PQ pool, also caused a rapid decrease of stomatal conductance, global induction of genes involved in ROS scavenging and pathogen resistance, increased ROS production and enhanced ethylene signaling. In addition, evidence was provided which showed that multiple hormonal/ROS signaling pathways not only regulate the plant's response to excess excitation energy, but also control induced systemic acquired resistance and basal defenses to virulent bacterial pathogens. The balanced activity of the disease resistance and signaling-related proteins coded by the *LSD1*, *EDS1*, *PAD4*, and *EIN2* genes was found to be necessary to regulate the steps leading to programmed cell death, light acclimation, and defense responses that are initiated, at least in part, by redox changes of the PQ pool (Mühlenbock et al., 2008). Further evidence coupling chloroplast-controlled disease resistance with ROS accumulation was obtained with the Arabidopsis mutant *rph1* (for *resistance to Phytophthora 1*), which was found to be susceptible to the pathogen *Phytophthora brassicae* as a consequence of a reduced oxidative burst, a runaway cell-death response, and failure to properly activate the expression of defense-related genes. The finding that the *RPH1* gene encodes an evolutionary highly conserved chloroplast protein was in accordance with a prominent chloroplast-dependent role in the activation of immune responses to *Phytophthora*, not only in Arabidopsis but in potato, as well (Belhaj et al., 2009).

In addition, signal integration at the level of transcription factor (TF) activation appears to be majorly controlled by the family of APETALA 2/ ethylene response element binding protein (AP2/EREBP) TFs, which are abundantly represented in Arabidopsis, poplar and rice (Dietz et al., 2010). By dint of their activation of different innervating pathways, or their ability to bind to multiple target elements, AP2/EREBP TFs are known to integrate several signaling inputs. A couple of examples are the ERF1 TF, which is controlled by ethylene and JA (Lorenzo et al., 2004), and the dehydration-responsive element binding TF TINY, that connects abiotic stress signaling via DRE-dependent regulation to biotic stress signaling via ethylene response elements (Sun et al., 2008). It is considered that combinatorial target gene regulation by different signals may involve different mechanisms, including: (i) cross-talk in the signaling pathways; (ii) stimuli-dependent TF activation, e.g. by homo- or heterotypic dimer and oligomer formation, respectively; (iii) competition for the same or binding to different cis elements; and (iv) amplification cascades that can be modulated by interfering signals (Dietz et al., 2010).

3.2 The negative effect of abiotic and biotic stress on photosynthetic gene expression

The down-regulation of photosynthetic gene transcription is frequently observed in plants subjected to stress. Thereby, environmental stresses, including drought, salinity and low temperatures can negatively affect photosynthetic gene expression in addition to an induction of compensating physiological and biochemical alterations (Saibo et al., 2009; Chaves et al., 2009). Similarly, a whole gamut of biotic insults caused by arthropods, fungi, bacteria and viral pathogens triggers a uniform and apparently regulated reduction in transcription of nuclear genes coding for the major components of photosynthesis, regardless of the plant host. The widespread negative effect on photosynthesis caused by biotic stressors was recently evidenced by a meta-genomic analysis in which the transcriptome data from microarray experiments representing twenty two different forms of

biotic damage on eight different plant species (predominantly Arabidopsis, five other herbaceous species and two tree species) was performed. In this study, transcript levels of photosynthesis light reaction, carbon reduction cycle and pigment synthesis genes were decreased regardless of the type of biotic attack. Interestingly, down-regulation of photosynthesis-related genes contrasted with the corresponding up-regulation of genes coding for the synthesis of JA and those involved in the responses to SA and ethylene. This clear difference in expression patterns suggested that the up-regulation of defense-related biosynthetic genes could be part of the overall defense response responsible for re-allocating resources from growth to defense (see below; Bilgin et al., 2010).

Apparently, insect herbivory caused by chewing insects, had the weakest negative effect on photosynthetic gene expression as compared to other biotic stressors, whereas a general down-regulation of photosynthesis genes was observed in plants infested by aphids and the whitefly *Bemisia tabaci* (Bt) (Heidel & Baldwin, 2004; Zhu-Salzman et al., 2004; Voelckel et al., 2004; Qubbaj et al., 2005; Yuan et al., 2005; Kempema et al., 2007; Bilgin et al., 2010). Additional data pertaining modifications in gene expression produced by Bt larval feeding in tomato plants at different stages of development was generated using a suppression-subtractive-hybridization (SSH) approach (Estrada-Hernández et al., 2009). In addition to the identification of several genes whose expression was differentially modified at different larval phases during the infestation process, the study showed a down-regulation of photosynthetic gene expression which was in accordance to the general negative trend associated with biotic-stress. However, upon closer examination, it became apparent that a more or less defined phase-dependent change in photosynthetic gene expression occurred in response to Bt infestation, which favored an up-regulation of photosystem II genes in the late two phases of Bt development in detriment of genes coding for components of other photosynthetic complexes, and also of the oxygen evolving complex and the Calvin cycle. A similar behavior was observed in Bt-infested tomatillo (*Physalis* spp.) plants (C. Sánchez-Hernández, personal communication). This led to the proposal that the contrasting pattern of gene expression, which occurred concomitantly with an up-regulation of oxidative stress genes leading to tissue senescence, could represent an additional strategy used by Bt, besides their reported ability avoid plant defenses, to favor infestation, (Walling, 2008; Estrada-Hernández et al., 2009; Délano-Frier et al., 2009). Support for this proposal was recently provided by a study showing that the application of the bacterial toxin coronatine to tomato seedlings, led to a reduced expression of photosynthesis related genes and a 1.5- to 2-fold reduction in maximum quantum efficiency of PS II, which occurred concomitantly with ROS generation and necrotic cell death (Ishiga et al., 2009)

Mention should be made, however, that given the long functional lifetime of most photosynthesis-related proteins (the highly labile D1 protein is a notable exception, see above), reduced gene photosynthetic gene expression does not necessarily translate into an immediate loss of function. Such behavior is believed to permit reallocation of nitrogen to the defense response, due to repressed transcription, without significantly affecting the rate of carbon assimilation (Bilgin et al., 2010).

3.3 The role of JA in on photosynthetic gene expression and growth regulation

Jasmonates play a central role in regulating plant defense responses to herbivores (Howe & Jander, 2008; Spoel & Dong, 2008) and also inhibit growth and photosynthesis by participating in the down-regulation of photosynthesis-related genes (Creelman & Mullet,

1997; Wasternack & Parthier, 1997; Hui et al., 2003; Reymond et al., 2004; Giri et al., 2006; Zavala & Baldwin, 2006; Yan et al., 2007). Ample evidence demonstrating the direct and indirect negative effect on plant growth and/or photosynthesis exerted by JA is available. Early reports described that JA treatment of barley leaves inhibits activity of PSII electron transport (Maslenkova et al., 1999), whereas barley plants treated with methyl jasmonate (MeJA) suffered a repressed translation of transcripts coding for Rubisco small subunit, chlorophyll a/b binding protein and photosystem II proteins (Roloff et al., 1994). Moreover, plants treated with MeJA or genetically manipulated to accumulate higher JA concentrations were found to develop shorter petioles or have a reduced total seed production (Cipollini, 2007; Bonaventure et al., 2007), or suffer reduced root growth (Henkes et al., 2008). Also, induction by diverse types of herbivores of the lipoxygenase pathway, which represents the initial step of JA biosynthesis and jasmonate signaling, was found to be associated with reduced photosynthesis and vegetative growth (Heidel & Baldwin, 2004; De Vos et al., 2005; Kempema et al., 2007; Bilgin et al., 2010), similarly to experiments showing that herbivore-induced JA signaling suppressed re-growth and contributed to apical dominance (Zavala & Baldwin, 2006). It has been proposed that the above effects on plant growth are modulated by the gene *JASMONATE-ASSOCIATED1* (*JAS1*) (Yan et al., 2007). Moreover, a cross-talk between ABA- and JA-responsive gene expression in response to insect herbivory, mediated by the action of MYC and MYB TFs, has been proposed as a mechanism to coordinate the expression of defensive and dehydration-responsive genes (Yamaguchi-Shinozaki & Shinozaki, 2006). Such interaction is deemed to be needed by the plant in order to deal with the increased leaf dehydration and accompanying senescence produced by defoliating herbivores (Aldea et al., 2005; Lim et al., 2007; see below). The observed influence of light quality and perception by phytochromes on JA induced defense responses and resource allocation was also indicative of an indirect connection between JA and photosynthesis (Ballare, 2009; Moreno et al., 2009).

3.4 Main photosynthetic genes targeted by biotic stress

Curiously, the gene coding for the Rubisco enzyme, an absolutely vital component of the carbon assimilation machinery in plants, was found to be one of the primary photosynthetic genes targeted by herbivore attack, in addition to genes coding for the components of the antenna complexes in both photosystems (Logemann et al., 1995; Ehness et al., 1997; Hermsmeier et al., 2001; Hahlbrock et al., 2003; Hui et al., 2003; Montesano et al., 2004; Zou et al., 2005). Proteomic investigations provided further evidence of the vulnerability of the CO_2 fixing process to insect attack by showing that herbivory, or even the application of the insect´s saliva, also reduced the abundance of Rubisco activase (RCA) in *Nicotiana attenuata* and Arabidopsis (Giri et al., 2006; Thivierge et al., 2010). RCA is a key regulatory enzyme of photosynthetic carbon assimilation that modulates the activity of Rubisco by facilitating the removal of inhibiting sugar phosphates from its active site (Portis, 1995). Additional findings derived from the proteomic experimental approaches indicated that Rubisco large subunit and RCA, in addition to PS I P700 apoprotein A1 suffered several caterpillar-specific modifications, including the conversion of Cys192 in Rubisco to the the thiolate anion, which may lead to decreased enzyme activity and protein degradation, and adverse modifications, in RCA, of the protein domains involved in ATP binding (Thivierge et al., 2010).

A valid explanation for the slower growth and down-regulation of photosynthetic-related genes elicited by herbivore damage is that it may be required to liberate resources, e.g. the high proportion of leaf N that is invested in photosynthetic proteins, primarily Rubisco, for defense-related processes (Baldwin, 2001). Another possibility is that these changes could represent a variety of the *scorched earth* strategies used by plants to buffer the impact of herbivory, based on the premise that a reduction in growth and nutrient availability, resulting from the combined effects of decreased photosynthesis, inhibited nitrate assimilation and diminished levels of amino acids and of the main dietary protein (i.e Rubisco) in leaves, will reduce the nutritional quality of the plant to the feeding insect, and consequently, the degree of attractiveness for subsequent damage (Hermsmeier et al., 2001; Hahlbrock et al., 2003; Schwachtje et al., 2006).

Silencing of either *RCA* or *Rubisco* in *N. attenuata* suppressed photosynthetic capacity, as expected, but uncovered further refinements regarding the defensive role played by a reduced expression of these genes in plants subjected to insect damage (Giri et al., 2006; Mitra et al., 2008). Surprisingly, insect performance of both specialist and generalist insect pests was increased in RCA-silenced plants, a result attributed mostly to an impairment of the JA-Ile/leucine signaling pathway required for the expression of defense-related genes coding for trypsin protease inhibitors or for enzymes needed for biosynthesis of defensive metabolites such as diterpene glycosides (Mitra et al., 2008). The negative effect exerted by RCA silencing on JA-Ile/leucine signaling and related herbivore resistance traits was hypothesized to occur in response to reduced ATP levels produced in carbon and energy depleted plants having decreased photosynthetic rates, since ATP is needed for the adenylation of JA, the first step in the amino acid conjugation process needed to regulate this hormone's activity (Staswick et al., 2002). On the other hand, no negative effects on JA signaling were detected in Rubisco-silenced plants, which nevertheless suffered greater damage when confronted by larvae of a specialist insect. These were proposed to have a higher tolerance than generalist insects to the protein deficiency resulting from Rubisco silencing due to their improved ability to detoxify plant defenses (Green et al., 2001). One of the principal conclusions reached from the results of the above series of experiments was that the nature of the photosynthetic genes affected as a consequence of insect herbivory will have important repercussions in their relation to plant defense.

4. Plant responses to herbivory from the phostosynthetic perspective

4.1 The profound impact of insect herbivory on plants

Herbivory can negatively affect ecosystems by decreasing photosynthesis and net primary production. Estimates of global crop production losses caused by foliage-feeding insects typically range from 5% to 30%, with losses estimated to exceed 50% were it not for the widespread application of pesticides (Mattson & Addy, 1975; Oerke & Dehne, 1997). Additional losses range from 2 to 15% in forests and from 4 to 24% in old-fields and grasslands, while insect outbreaks have been known to reduce net primary productivity by 70% to 100% in some terrestrial ecosystems (Cyr & Pace, 1993). Insect herbivory reduces leaf area or depletes leaf fluids by mining and cell content feeding. It can also be selective, targeting other tissues such the phloem, xylem (Haile et al., 1999; Macedo et al., 2003a, b; Heng-Moss et al., 2006), or the stems (Macedo et al., 2005, 2007). Insect feeding typically reduces photosynthesis, although evidence showing positive or neutral effects (i.e. tolerance or compensatory responses; see below) on photosynthesis has also been reported. Most of

the time, this variability stems from characteristic factors of a given plant insect interaction, including damage intensity (e.g. total vs. partial defoliation; dispersed vs. concentrated damage; phloem feeding vs. defoliation) and location (e.g. proximity to veins), type of tissue that is preferentially damaged (as mentioned above) and the way tissue is damaged (e.g. chewing vs. scraping; crushing vs. piercing, etc.). Another important factor that influences the outcome of herbivory on photosynthesis has to do whether insect damage induces the accumulation of autotoxic defensive allelochemicals (see below).

4.2 Positive or neutral effects of insect herbivory on photosynthesis

Resistance and tolerance represent two general strategies of plant defense against herbivores, although interactions between these two strategies are assumed to occur under certain conditions, i.e. when the resources available for defense are limited or when both defensive strategies are physiologically costly (Leimu & Koricheva, 2006). Resistance involves the reduction of the amount of herbivore damage whereas tolerance leads to a reduction of the impact of herbivory on plant fitness (Rausher et al., 1993; Stowe et al., 2000). Resistance traits include mechanical and chemical characters that reduce herbivore performance (antibiosis) or preference (antixenosis). Conversely, proposed mechanisms for tolerance/compensation are re-growth stimulation, elevated rates of photosynthesis in remaining leaves of partially defoliated plants, increased branching through the release of apical dominance, alteration of phenology or plant architecture, production of new leaf area, utilization of high pre-herbivory stored carbon resources or the ability to reallocate them to less vulnerable tissues, resorption of nutrients from senescent/damaged leaves, especially nitrogen (N) and phosphorus (P), alteration of the external light environment and higher reproductive efficiency through increased percentage of fruit set (Mabry & Wayne, 1997; Hjalten et al., 1993; Strauss & Agrawal, 1999; Hochwender et al., 2000; Tiffin, 2000; Anten et al., 2003; Silla & Escudero, 2003; Leimu & Koricheva, 2006; Schwachtje et al., 2006). Compensatory ability in plants varies widely across species, and the degree in which it is manifested depends on the amount of leaf lost, with complete rather than fragmented defoliation usually being more conductive to an increased rate of net photosynthesis in the remaining or newly formed leaves (Welter, 1989). The mode of herbivore damage and herbivore type may also determine whether the overall effect on photosynthesis in the plant. This was elegantly evidenced in a recent report showing that herbivory on *N. attenuata* by *Tupiocoris notatus*, a cell-content feeder, (or by application on wounded plants of its salivary secretions), induced an elevated photosynthetic activity, and consequent CO_2 assimilation, that appeared to compensate for lost tissue and for the fitness costs associated with the deployment of direct and indirect defenses. This compensatory effect was shown to be specific for this insect, since feeding by chewing *Manduca sexta* larvae resulted in a strong down-regulation of photosynthesis (Halitschke et al., 2011).

Environmental conditions and the timing of the herbivory event are also influential factors. Thus, compensation to damage in terms of timing of herbivory is usually more effective when required early in the growing season or before the reproductive phase has started. For example, a study performed in Lebanese cucumber (*Cucumis sativus*) to compare the ability to compensate for foliar herbivory at both the pre-flowering and flowering stages found that damage produced before flowering allowed plants to compensate more efficiently, in terms of vegetative biomass and fruit production, for leaf losses that sometimes reached 80% of the total leaf area in the plant groups examined. Higher compensation was correlated with a

higher photosynthetic efficiency and capacity, and with less dissipation of light energy as heat, leading to the proposal that herbivore-damaged plants may be induced to use a greater proportion of the absorbed light energy for photosynthesis as a result of altered carbohydrate source-sink relationships (Thomson et al., 2003). In contrast, an experimental setting designed to test the effects of partial de-budding on photosynthesis, stomatal conductance and nitrogen in *Picea jezoensis* seedlings led to the conclusion that the enhanced photosynthetic rate observed in de-budded seedlings was the result of an increased root/leaf ratio that reduced the stomatal limitation of photosynthetic rate, rather than of an altered sink-source relationship or increased leaf nitrogen content (Ozaki et al., 2004).

A pair of studies aimed at determining the carbon costs of herbivory by phloem-feeding scale insects on tress found that infested trees had a greater annual photosynthesis, as determined by measuring parameters such as *Vc* max, the maximum rate of Rubisco-catalysed carboxylation, *J* max, the rate of electron transport when irradiance is saturating and/or chlorophyll fluorescence (Retuerto et al., 2004; Dungan et al., 2007). The small negative effect on tree growth and reproduction and increased photosynthetic efficiency observed were taken as an indication that damaged trees were able to compensate fully for the relatively large loss of carbon to herbivory caused by the honeydew insects. According to these workers, the amelioration of carbon loss resulting from the additional sinks for photosynthates created by scale insect feeding was achieved by increased photosynthetic rates. These results were in agreement with previous data suggesting that defoliation, as well as removal of reproductive and other vegetative sinks, may improve photosynthesis in remaining leaf tissue by increasing carboxylation efficiency and the rate of Rubisco regeneration (Holman & Oosterhuis, 1999; Thomson et al., 2003; Ozaki et al., 2004; Turnbull et al., 2007). However, they were in contradiction with data generated from the meta-analysis of a collection of reports showing that sap feeding insects have an almost universal negative effect on growth, photosynthesis, and reproduction of woody plants (Zvereva et al., 2010). The discrepancy detected was adjudicated to experimental biases introduced by the utilization of improper controls (e.g selective assignation as controls to undamaged plant sections that were avoided by herbivores or herbivore preference for hosts with higher rates of photosynthesis). Other important findings of the above meta-analysis were the following: i) sap-feeders did not change the resource allocation in plants; ii) mesophyll and phloem feeders produced stronger effects than xylem feeders, whereas generalist sap-feeders reduced plant performance to a greater extent than did specialists; iii) methodology (e.g. greenhouse vs. field settings; natural vs. imposed herbivory and short-term vs. long-term feeding) was a significant factor influencing the outcome of the experiments, and iv) sap feeding was more detrimental at higher temperatures. Thus, sap-feeders were considered to exert a more severe overall negative impact on woody plant performance than defoliators, mostly due to the latter's lower ability to compensate for sap-feeders' damage in terms of both growth and photosynthesis.

Another study in which the effect of high and low soil nutrient levels on biomass re-growth and photosynthetic up-regulation, among genotypes of the Mediterranean annual grass *Avena barbata* subjected to simulated herbivory, obtained rather unexpected results. They showed that tolerance in this species was positively correlated only with pre-defoliation photosynthetic efficiency at high nutrients, since no evidence for photosynthetic up-regulation in defoliated compared to control plants was observed regardless of nutrient treatment (Suwa & Maherali, 2008). In this context, a rather infrequent report describing compensatory responses to herbivory to the root system suggested a novel tolerance

mechanism for insect herbivory. This welcome contribution to the rather unexplored area of plant root-insect interactions was designed to understand the high tolerance to root herbivory by bio-control agents shown by *Centaurea maculosa*, an invasive North American plant species. The use of ^{15}N labeling indicated that infested plants were able to sustain growth and maintain a constant shoot N status under potentially devastating conditions characterized by a drastic reduction of whole plant and root N uptake as a result of herbivory, by shifting N allocation to the shoot, away from the reach of root herbivores (Newingham et al., 2007).

Compensatory photosynthesis is also deemed to play an important role in plants that utilize carbon-based defense strategies, by increasing the availability of carbohydrates that can potentially be allocated to defense. A recent report focused on the possible effects that diverse tritrophic interactions, involving browsing herbivores and several species of resident ants, could have on foliar photosynthetic rates, measured as net photosynthesis (Pn), transpiration and water use efficiency (WUE), and concomitant availability of carbon pools for metabolism and defense in *Acacia drepanolobium*. This species is an east-African, savannah-resident tree, that is known to exhibit carbon-based investments in direct defense (e.g. erection of physical barriers and accumulation of toxic chemicals), indirect defense (e.g. housing and feeding of beneficial ants that guard the plant from herbivores) and tolerance (e.g. stimulated rates of leaf and shoot growth) (King & Caylor, 2010). Their results, which represent the first evidence that indirect defenders of plants can also benefit plants by increasing their photosynthetic rates, indicated first, that *A. drepanolobium* trees exhibited elevated photosynthetic rates in response to browsing only when occupied by strongly mutualistic ants, and second, that this photosynthetic up-regulation mitigated the costs of herbivory by increasing pools of photosynthate available for additional defense or for re-growth of lost tissue.

A unique example of positive manipulation of plant photosynthesis by insect herbivores is represented by the so-called green-island phenotype induced by leaf-miners in deciduous leaves in the autumn season, and persisting long after leaf abscission. These green-islands are characterized by photosynthetically active green patches in otherwise senescing leaves, and correspond to regions with an increased concentration in cytokinins, which are hormones involved in a variety of biological processes, many pertinent to the phenomenon in question, such as the inhibition of senescence, maintenance of chlorophyll and control of source-sink relationships for nutrient mobilization, and maintenance of enriched nutritional environments (Gan & Amasino, 1995; Balibrea Lara et al., 2004; Walters & McRoberts, 2008; Giron et al., 2007). The concentrated levels of nutrients that characterize green-islands in senescent leaves favor growth and reproduction of the leaf miners with only a limited consumption of leaf tissues. This, in turn, allows areas of uneaten tissue to be employed for thermal regulation and parasitoid avoidance (Djemaï et al., 2000; Giron et al., 2007). However, the origin of cytokinins in leaf-miner systems has not yet been determined, although several lines of evidence initially suggested that cytokinins were derived from the insect. Such a concept was questioned by recent findings suggesting that cytokinins might originate from bacterial endosymbionts known establish an intimate association with leaf mining insects. This was evidenced by the negative effects on insect fitness derived from curing leaf-miners of their symbiotic partner, which also abolished green-island formation on leaves (Kaiser et al., 2010).

A number of selected examples in which insect herbivory has been shown to have a positive influence on photosynthesis, including many already described above, are shown in Table1.

Plant species	Herbivore species	Damage type/ feeding guild	Results	Method	Reference
Alder (Alnus incana, *A. glutinosa*) and birch (*Betula pendula)*	Alder beetle (*Agelastica alni*)	Foliage-chewing feeder	Photosynthetic rates of grazed leaves increased following herbivory in alder; by contrast birch exhibited a decline in net photosynthesis. Differences related to the beetle's feeding behavior that often cut midribs only in birch.	Gas exchange (GE)	Oleksyn et al., 1998
Willow tree (*Salix viminalis)*	Aphids (*Tuberolachnus salignus*; *Pterocomma salicis*)	Sap feeder (stem-feeding)	Photosynthetic rate and leaf nitrogen content were significantly raised by *T. salignus* feeding.	GE	Collins et al., 2001
Cucumber (*Cucumis sativum*)	Brown garden snail (*Helix aspersa*)	Foliage-chewing feeder	Higher compensation in terms of vegetative biomass and fruit production was correlated with an increase in photosynthetic efficiency and capacity, and with less dissipation of light energy.	Chlorophyll fluorescence (ChlF)	Thompson et al.,2003
European holly trees (*Ilex aquifolium*)	Scale insects (*Coccus* sp.)	Phloem feeder	Insect infestation increased photosynthetic efficiency; effect enhanced by high temperature and light. Insects altered the photosynthesis of leaves not directly affected by the insects.	ChlF	Retuerto et al., 2004
Ezo spruce *Picea jezoensis*	Manual de-budding (in nature *Choristoneura jezoensis*; aphids *Adelges japonicus*)	Bud feeder	Partial de-budding enhanced photosynthetic rates in 1-year-old needles but not in current-year needles. Greater photosynthetic rate was accompanied by increased stomatal conductance.	GE	Ozaki et al., 2004
Cotton (*Gossypium hirsutum*)	Cotton aphid (*Aphis gossypii*); thrips (*Thrips tabaci* and *Frankliniella schultzei*)	Phloem feeder	Photosynthesis, respiration rates or non-structural carbohydrates on leaves were not affected by short-term aphid feeding. No increase in net photosynthesis during thrips infestation or recovery phases revealed the lack of compensation in affected leaves.	GE	Lei & Wilson 2004; Gomez et al., 2006

Plant species	Herbivore species	Damage type/ feeding guild	Results	Method	Reference
Soybean (*Glycine max*)	Japanese beetles (*Popillia japonica*); corn earworm (*Helicoverpa zea*)	Foliage-chewing feeder	Herbivory increased transpiration without affecting carbon assimilation rates or photosynthetic efficiency. Reductions in net photosynthesis and stomatal conductance occurred only when midvein was disrupted.	GE, ChlF and thermal imaging (TI)	Aldea et al., 2005
Beech trees *Nothofagus solandri*	Scale insects (*Ultracoelostoma assimil)*	Phloem feeder	Infested trees had a greater annual photosynthesis measured as Vc max, J max and chlorophyll content. Consequently, annual canopy photosynthesis was 4% greater for infested trees.	GE	Dungan et al., 2007
Wheat (*Triticum aestivum*)	Armyworm (*Spodoptera frugiperda*)	Foliage-chewing feeder	Photosynthesis, intercellular CO_2 and transpiration of injured leaves were not significantly affected; however, stomatal conductance values were higher. Spatial pattern of defoliation differentially affected photosynthesis; leaves defoliated at the basal portion had lower rates.	GE and ChlF	Macedo et al., 2007
Acacia drepanolobium	Resident ants (*Crematogaster mimosa; C. nigriceps; C. sjostedti; Tetraponera penzigi*)		Trees exhibited elevated photosynthetic rates in response to browsing only when occupied by strongly mutualistic ants (*Crematogaster mimosa; C. nigriceps*). Photosynthetic up-regulation mitigated the costs of herbivory by increasing pools for additional defense or for re-growth of lost tissue.	GE	King and Caylor, 2010

Plant species	Herbivore species	Damage type/ feeding guild	Results	Method	Reference
Nicotiana attenuata	Mirid bugs (*Tupiocoris notatus*)	Foliage-chewing feeder	Elevated CO_2 assimilation rate was sufficient to compensate for loss of photosynthetic active tissue. Stomatal conductance and intercellular CO_2 were not affected. Mirid salivary secretions treatment also increased photosynthetic activity.	GE and fluorescence imaging (FI)	Halitschke et al., 2011

Table 1. Some examples of positive or neutral effects on photosynthesis after herbivory damage.

4.3 Negative effects of insect herbivory on photosynthesis

In the absence of compensatory mechanisms, insect herbivory causing removal and/or injury of plant tissues most frequently leads to a direct suppression of photosynthetic activity. A seminal report describing the outcome of an extensive examination of the pertinent literature available at the time, indicated that over 50% of all plant-insect interactions, predominantly involving leaf-mining, stem-boring, galling or sucking leaf injury, resulted in a loss of photosynthetic capacity, frequently manifested as decreased photosynthetic rate (Pn) (Welter, 1989). The reduction in chlorophyll content in response to insect damage, frequently reported in plants attacked by phloem feeding insects, has been also reported to result in a decrease in photosynthesis (Kaakeh et al., 1992; Cabrera et al., 1994), with even small reductions leading to a drastic reduction in the photosynthetic rate (Nagaraj et al., 2002). Interestingly, changes in leaf pigment composition caused by insect herbivory were found to have potential application for remote sensing pest detection in Australia. Thus, the reduction in leaf chlorophyll content occurring concomitantly with an increase in photoprotective pigments, known to be a sensitive indicator of plant stress caused by root feeding phylloxera grapevine pests, was exploited for the development of a phylloxera-specific remote detection system (Blanchfield et al., 2006). Additional factors contributing to decreased photosynthesis include changes in the nutrient status of leaves caused by competition between plant sinks and additional sinks created by insect herbivores, mostly sap-feeders or gall-formers (see above), decreased stomatal conductance, which is coupled to reduced WUE and altered water transport, stomatal aperture and/or sucrose transport and loading. Most of these conditions are also known to influence indirect suppression of photosynthesis, as described below.

However, as it has been mentioned already, a plant's response to herbivory is often variable and usually depends on the combined contribution of several factors including the type of tissue injured and the extent tissue damage. An illustrative example for this effect is given by reported data showing that the removal of leaf tissue from soybean by herbivores such as Japanese beetles (*Popillia japonica*), corn earworm caterpillars (*Helicoverpa zea*) (Aldea et al., 2005), cabbage loopers (*Trichoplusia ni*), and green clover-worms (*Plathypena scabra*) (Hammond & Pedigo, 1981; Ostlie & Pedigo, 1984) caused an increase in water loss from damaged tissue, but had a minimal effect on net photosynthesis. Conversely, chewing

damage by skeletonizing Mexican bean beetles (*Epilachna varivestis*) caused substantial losses of photosynthesis in the remaining leaf tissue (Peterson et al., 1998). It was hypothesized that the scraping and crushing of interveinal leaf tissue caused by feeding adults and larvae of Mexican bean beetles may have exacerbated localized water stress, ultimately causing tissue desiccation and photosynthesis repression. The timing of damage is also considered to be an important factor. In this regard, early season damage has been usually found to cause more pronounced changes in plants than late season damage, which is in accordance with the assumption that vigorously growing foliage has a greater capacity to respond to various stimuli, including damage. Also, seedlings are generally more susceptible to photosynthetic damage because of a shortage of reserves due to their smaller size or to limitations in nutrient acquisition (Nykänen & Koricheva, 2004; Hódar et al., 2008). A report recording the response of potted fruitless grapevines (*Vitis labrusca* var. Niagara) to early and late season mechanical and insect defoliation was in accordance with this concept by showing that growth, single leaf photosynthesis, and whole-vine photosynthesis were more tolerant to foliar injury late in the season than early in the season (Mercader & Isaacs, 2003). Similar results were obtained from a series of experiments performed to examine a possible trade-off between photosynthesis with defense or reproduction in the common milkweed *Asclepias syriaca*, which is a plant that accumulates toxic cardenolides in a constitutive or inducible manner and is also susceptible to insect damage during its relatively long reproduction period (Delaney et al., 2009). The results of this study showed that leaf Pn impairment after partial leaf defoliation had a seasonal pattern which correlated with *A. syriaca* reproductive phenology but not with cardenolide accumulation. In this regard, the small or absent Pn impairment occurring in leaves of pre-flowering or maturing seed pod plants, contrasted with the moderate to severe leaf Pn impairment detected in leaves of flowering and early seed pod formation plants. Such a behavior led the authors to suggest that a physiological 'cost of reproduction' might be an additional susceptibility factor leading to Pn impairment after herbivory injury on a leaf. Another important aspect to consider is that photosynthesis will be usually more affected when plants are attacked by generalist herbivores, against which they show a higher susceptibility. This is believed to be derived from the lack of a previous and selective co-evolutionary process leading to adaptation (Parker et al., 2006; however, see above). The plant's capacity to tolerate injury, its phenotypic plasticity and the type of environment with which the plant is interacting may be important factors too (Alward & Joern, 1993; Trumble et al., 1993; Delaney & Macedo, 2001; García & Ehrlén, 2002; Zvereva et al., 2010).

The nitrogen status of the plant is also considered to influence the way photosynthesis is affected by herbivory in plants. This is because of the strong positive correlation that is usually observed between photosynthesis rate and nitrogen concentration in plants, predominantly sequestered in the Rubisco enzyme (Field & Mooney, 1986; Evans, 1989; see above). It is not surprising then, that one of the mechanisms offered to explain why the localized decrease in N content negatively affects photosynthesis, a circumstance that has been frequently reported in damaged leaves of woody plants subjected to insect herbivory, is precisely that N deficiency directly affects CO_2 assimilation rates by lowering Rubisco levels (Reich et al., 1999; Mediavilla et al., 2001).

Another little studied aspect of plant-insect interations is the effect that insect oviposition might have on photosynthesis. Most of the available data suggest, however, that the effect is predominantly negative. A recent study reported that net photosynthetic rate, J max, and Vc max of pine needles laden with eggs of an herbivorous sawfly were lower than in egg-free

control plants that were not attacked. The negative effect was deemed to have occurred as the result of an egg deposition process that involved wounding of the plant tissue by the sawflies' ovipositor prior to the laying of eggs into its ovipositional wound (Schröder et al., 2005). In a more recent report, the oviposition and wounding effects were separated by employing two pentatomid insects (*Murgantia histrionica* and *Nezara viridula*) having different feeding habits but known not to cut or otherwise physically damage the host substrate during the oviposition procedure. In this process, the eggs are laid in clusters on the leaf surface and adhere to it by a sticky oviduct secretion (Bin et al., 1993; Colazza et al., 2004). Nevertheless, a surprisingly large inhibition of photosynthesis was detected in leaves of *Brassica oleracea*, one of the plant models employed together with common bean, in response to oviposition by *M. histrionica*, even when oviposition was not associated with feeding activity. High resolution chlorophyll fluorescence imaging revealed that the damage to photochemistry caused by feeding and oviposition was restricted to the affected areas, whereas an increase in photochemical yield detected temporarily in the neighboring intact areas of the attacked leaves, indicated the onset of a compensatory response. To date, the way(s) in which insect oviposition affects photosynthesis, occurring either with or without ovipositional plant wounding, remain(s) unknown. However, reduced diffusion rates of CO_2 in the mesophyll cells was suggested as a possible mechanism leading to photosynthesis inhibition during oviposition in the absence of plant wounding (Velikova et al., 2010).

4.4 Indirect effects of insect herbivory on photosynthesis

Leaf area removal not only affects photosynthesis in the damaged tissue but may have a *hidden* or indirect effect in tissues not directly damaged by the herbivore which undergo an additional reduction in photosynthetic capacity and alterations in transpiration (Welter, 1989; Zangerl et al., 2002; Aldea et al., 2006; Berger et al., 2007; Bilgin et al., 2008; Nabity et al., 2009). The discovery that herbivory-induced alterations to photosynthesis and transpiration propagate into remaining undamaged leaf tissue was greatly favored by the development of imaging techniques tools. These proved capable of performing spatially-resolved measurements of the component processes of photosynthesis across leaf surfaces in order to provide direct estimates of the magnitude of local and systemic damage in a quantitative, multi-layered or complementary and non-invasive way. The ability to measure chlorophyll fluorescence by imaging techniques was a pivotal development, considering that this is by far the most important indicator of photosynthetic stress and damage to the photosynthetic apparatus. Thus, chlorophyll fluorescence provides a precise measure of the quantum yield of photosystem II in light-adapted leaves (ΦPSII), which is, in turn, related to the rate of carbon fixation (Genty et al., 1989), and may be used to calculate the photosynthetic electron transport rate driving photosynthesis and photorespiration (Di Marco et al., 1990). Chlorophyll fluorescence data can also be used to assess damage to the photochemical aspect of photosynthesis by measurements of the quantum yield in dark-adapted leaves (by determining the ratio between variable and maximal fluorescence, Fv/Fm) and by the amount of photochemical energy lost as heat (by measuring the non-photochemical quenching of fluorescence, NPQ) (Genty & Harbinson, 1996). Fluorescence imaging, which more often than not correlates with photosynthetic capacity measured by gas exchange, further improved the already superior suitability of this technique to assess damage to the photosynthetic apparatus, by providing a topographical panorama of

damage in the leaf, including systemic damage produced in tissue sections not affected directly by the stressor (Chaerle et al., 2007). Moreover, this tool can be combined with thermal imaging, a powerful technique for mapping changes in temperature caused by variations in latent heat flux across leaf surfaces, which can be converted into maps of variable stomatal conductance (Omasa & Takayama, 2003; Jones, 2004; Bajons et al., 2005; Grant et al., 2006). Water limitations in leaves can result, for example, from the disruption in water transport caused by herbivore-damage of water-conducting xylem elements or by midrib vein cutting insects (Tang et al., 2006; Delaney & Higley, 2006; see below). Additional spatial patterning of other components of the photosynthetic machinery, including chlorophyll content and activation of the xanthophyll cycle can be mapped with a technique not frequently employed called hyper-spectral imaging (Nabity et al., 2009). The combined use of these techniques to measure changes in the same leaf in a given experiment, although technically challenging, has provided a deeper insight into the mechanisms by which herbivory indirectly reduces photosynthesis in the remaining undamaged leaf tissue, particularly if combined with physiological data, as reported in several related studies (Zangerl et al., 2002; West et al., 2005; Leinonen & Jones, 2004; Aldea et al., 2006; Tang et al., 2006, 2009).

The systemic suppression of photosynthesis in leaf tissues not directly damaged during insect herbivory has been found to extend to an area that greatly exceeds the actual leaf area removed or damaged by the herbivore. For example, the removal of only 5% of the area of an individual wild parsnip leaf by cabbage looper (*T. ni*) caterpillars reduced photosynthesis by 20 %, determined as ΦPSII and the rate of CO_2 uptake, in the remaining foliage (Zangerl et al., 2002). The indirect effect was observed to extend to a relatively considerable distance from the cut edges and was still detected for at least 3 days after the caterpillars were removed. Moreover, the size of the indirect effects was positively correlated with defense-related synthesis of auto-toxic furanocoumarins, suggesting that costs of chemical defense may be one factor that accounts for the deleterious indirect effects of herbivory on plants. Similarly, the decline in photosynthesis in the remaining leaf tissue of damaged oak saplings was equal to the decrease in photosynthesis associated with the actual removal of leaf tissue (Aldea et al., 2006). Chewing damage by cabbage looper larvae also caused substantial reductions in ΦPSII in Arabidospis' leaves at some distance from the tissue removed (Tang et al., 2006). Interestingly, this study demonstrated that the degree of photosynthetic impairment caused by herbivory depended on the nature of the damage inflicted. Therefore, damage caused by first instar larvae, which typically make small holes and avoid veins, led to photosynthetic depression in the remaining leaf tissue near the holes, whereas fourth instars, that make larger perforations while feeding, had little effect on photosynthesis (Tang et al., 2006). The workers concluded that both water stress, induced by the increased rate of water loss near the damaged tissues, and the reduced stomatal conductance produced in the tissues localized at some distance from the injuries, contributed to the inhibition of photosynthesis in the remaining leaf tissues, although subsequent data suggested that induction of defense responses in areas near the holes may have also contributed to the observed decrease in photosynthesis (Tang et al., 2009). The above studies provided evidence suggesting that defense induced auto-toxicity or defense-induced down-regulation of photosynthesis contributed to the indirect repression of photosynthesis. Another contributing factor to indirect suppression of photosynthesis is vasculature tissue severance, which generally leads to a disruption in fluid or nutrient transport, and altered sink

demand. The collected data indicates that the probable mechanisms responsible for reducing photosynthesis in remaining leaf tissues are multifaceted, ranging from disruptions in fluid or nutrient transport to self-inflicted reductions in metabolic processes. However, the magnitude of their contribution to indirect impairment of photosynthesis will vary depending in large part on the type of feeding damage and the mode of defense deployed by the plant under attack (Nabity et al., 2009). In this respect, chewing damage and fungal and gall infections were found to differentially affect the component processes of photosynthesis of nearby leaf tissue in several hard-wood tree species, with fungal infections and galls causing large depressions (>25%) of photosynthetic effciency (as ΦPSII) over extended areas of the leaf around the visible damage, whereas chewing damage resulted in minor (≈7%) depressions of ΦPSII that were restricted to a 1 mm perimeter around the perforations. Although similar in their effect on electron transport through PSII, the indirect effects of fungal and gall infections on photosynthesis were found to operate through different mechanisms. A reduction in stomatal conductance with an associated decline in intercellular CO_2 concentration may have contributed to the depression of ΦPSII around fungal spots but not in gall surrounding areas. On the other hand, the mild and localized suppressions of the photosynthetic efficiency in tissue surrounding chewing damage was attributed to the desiccation of tissue along the edges of damage, similarly to other reports (Aldea et al., 2005; Tang et al., 2006). One sobering conclusion reached by this study was that the indirect, negative, effects of photosynthesis caused by biotic stress on tress were exacerbated by elevated CO_2, exposing yet another damaging element of the ongoing global trend towards higher CO_2 levels in the earth's atmosphere.

Defoliation injury which severs venation indiscriminately (e.g by fouth instar, but not first instar, *T. ni* larvae; see above) can damage xylem and/or phloem, leading to altered water transport, stomatal aperture, and sucrose transport and loading. All these changes can strongly contribute to reduce photosynthesis in the remaining leaf tissue. Severing veins and inter-veinal tissue also alters the hydraulic construction of leaves as the result of an exponential reduction in resistance occurring with increasing damage (Nardini & Salleo, 2005). Long- or short-term leaf desiccation can also occur in the absence of alternative pathways for water transport. If insect feeding is subtle enough to avoid outright cell rupture (e.g. by phloem-feeders), modulation of nutrients sequestered by feeding will alter plant osmotica or sink/source relationships (Girousse et al., 2005; Dorchin et al., 2006). Feeding may physically obstruct fluid flow with insect mouthparts (stylets) or cell fragments and alter photosynthesis and water balance in remaining leaf tissue (Reddall et al., 2004; Delaney & Higley, 2006). A particular mechanism of plant vasculature disruption is midrib vein cutting, a little-known type of specialized herbivory suggested to have evolved as a strategy to avoid trapping leaf latex or toxic cardenolide defenses in plant species mostly restricted to the Asclepiadaceae (milkweed), Apocynaceae (dogbane), Polygonaceae and Fabaceae families. This type of damage was found to impair several leaf gas exchange parameters, but only downstream from the injury location. Photosynthesis impairment caused by midrib herbivory was more severe than manually imposed and actual insect defoliation, was relatively long-lasting and became most severe as the injury location came closer to the petiole (Delaney & Higley, 2006). As mentioned above, a form of defoliation in soybean plants known as skeletonization, is characterized by the removal of patches of tissue, reduced photosynthesis in remaining tissue on damaged leaves and on adjacent undamaged leaflets (Peterson et al., 1998). A related study reported results that

were in agreement with the high water losses associated with skeletonizing damage, by showing that the cut edges of soybean leaves damaged by Japanese beetles known to follow this mode of herbivory, suffered a very substantial dehydration (Aldea et al., 2005). However, their data showed that although damage to the inter-veinal tissue increased transpiration by 150 % for up to 4 days post-injury, it had no detectable effect on CO_2 exchange, and even induced a short-lived increase in photosynthetic efficiency in undamaged tissue of damaged leaves. Such a contradictory outcome was deemed to have happened as a result of a transient decoupling of photosynthetic electron transport from carbon assimilation caused by insect damage (Aldea et al., 2005). Regarding the above, it is not surprising to know that plants can increase WUE as a strategy to ameliorate the negative effects of herbivory, as was recently found in apple tress infested by leaf-mining moths (Pincebourde et al., 2006). Thus, WUE was found to be about 200% higher in the mined apple leaf tissues in comparison to intact leaf portions, prompting the proposal that minimizing water losses reduces the negative impact on photosynthesis derived from herbivore attacks, by avoiding severe reductions in the CO_2 assimilated to water loss ratio.

Autotoxicity by resident plant metabolites having potential biocidal properties that can directly affect the host plant may represent an important fitness cost. This adds to the investment in energy and C and N sources already employed for their synthesis, which could have otherwise been used for growth and reproduction (Zangerl & Bazzaz, 1993). Autotoxicity has been recorded in cases where secondary compounds having biocidal properties that severely affect the photosynthetic machinery of the plant are either released from specialized storage tissues that confine them (e.g. glands, trichomes or oil tubes) or accumulate as a consequence of leaf damage. An early study investigating autotoxicity in defense-related metabolites, linked nicotine toxicity to the reduction in photosynthesis in a number Solanaceous plants (Baldwin & Callahan, 1993). Some time later, the suppression of ΦPSII in regions of the leaf near the tissue removed by caterpillars was related to an increased production of toxic furanocoumarins (Zangerl et al., 2002; see above). A subsequent study tested the autotoxicity of several essential oil components, including several monoterpenes and sesquiterpenes and myristicin, an essential oil component derived from the phenylpropanoid pathway, in three plant species known to produce them (i.e. *Pastinaca sativa*, *Petroselinum crispum*, and *Citrus jambhiri*) (Gog et al., 2005). The toxic effects, which were assessed by quantifying reductions in photosynthetic capacity as measured by chlorophyll fluorescence imaging, were examined both by exogenous applications of pure compounds and by the release, by slicing, of endogenous essential oils known to contain these compounds, among others. Monoterpenes, but not the caryophyllene and farnesene sesquiterpenes or myristicin, produced a rapid and spatially extensive decline in photosynthetic capacity that was detected within a time frame of 200 s. On the other hand, the release of endogenous essential oils significantly reduced photosynthetic activity in all three plant species examined, an effect that was more pronounced in *P. sativa* and *P. crispum*. The auto-toxic effect of monoterpenes was assumed to be related to the loss of cell and organelle integrity associated with their known capacity to disrupt membranes (Harrewijn et al., 2001; Maffei et al., 2001). Conversely, coumarins and furanocoumarins have been long known to negatively affect photosynthesis in several plant species. Photo-phosphorylation uncoupling, energy transfer inhibition and/or Hill reaction inhibition have been identified as the probable mechanisms responsible for their suppression of photosynthesis in higher plants (Macías et al., 1999; Veiga et al., 2007).

A number of selected examples in which insect herbivory has been shown to directly or indirectly influence photosynthesis in a negative way, including many already described above, are shown in Table2.

Plant species	Herbivore species	Damage type /feeding guild	Results	Method	Reference(s)
Goldenrod (*Solidago altissima*)	Aphid (*Uroleucon caligatum*); beetle (*Trirhabda* sp.); spittlebug (*Philaenus spumarius*)	Phloem, foliage and xylem-sap feeders	Photosynthetic rates per unit area of damaged leaves were reduced by spittlebug feeding, but not by beetle or aphid feeding. Spittlebug feeding did not cause stomatal closure, but impaired C fixation within the leaf.	Gas exchange (GE)	Meyer & Whitlow, 1992
Barley (*Hordeum vulgare*)	Aphid (*Schizophis graminum*)	Sap feeder	Chlorophyll content and photosynthesis decreased 75 and 45% respectively after infestation.	GE	Cabrera et al., 1994
Cotton (*Gossypium hirsutum*)	Aphid (*Aphis gossypii*)	Phloem feeder	Photosynthetic depression and transpiration increase were quantitatively related to initial aphid infestation densities and to the length of feeding	GE	Shannag et al., 1998
Soybean (*Glycine max*); dry bean (*Phaseolus vulgaris*)	Mexican bean beetles (*Epilachna varivestis*)	Foliage-scraping chewing feeder (skeletonizer)	Adults and larvae reduced photosynthetic rates of the remaining tissue of the injured leaflet. A significant linear relationship between photosynthetic rate and percentage injury was observed. Light reactions of photosynthesis were not affected.	GE	Peterson et al., 1998
Cotton (*Gossypium hirsutum*)	Silverleaf whitefly (*Bemisia argentifolii*)	Phloem feeder	Photosynthetic rate was decreased 50%; associated with reductions in chlorophyll fluorescence and fluorescence yield. No changes were found in stomatal conductance, intercellular CO_2 concentration, and leaf chlorophyll content.	GE and chlorophyll content (ChlC)	Lin et al., 1999
Rice (*Oryza sativa*)	Planthopper (*Nilaparvata lugens*)	Phloem feeder	Suppressed photosynthetic rate after infestation, especially at lower leaf positions. Chlorophyll content and total plant dry weight were also reduced.	Carbon isotope ratios (CIR)	Watanabe & Kitagawa, 2000

Plant species	Herbivore species	Damage type /feeding guild	Results	Method	Reference(s)
Nicotiana attenuata, N. longiflora	Horn worm (*Manduca sexta*); *Tupiocoris notatus*; aphid (*Myzus nicotianae*)	Foliage-chewing, single cell- and phloem feeders	Up-regulation of defense-related genes and down-regulation of primary metabolism and photosynthesis-related genes. CO_2 assimilation and photosystem II efficiency reduced by 16% and 8% respectively in the remaining tissue of damaged leaves.	GE, fluorescence imaging (FI) and Microarray analyses (MA)	Hermsmeier et al., 2001; Izaguirre et al., 2003; Voelckel & Baldwin 2004a,b; Voelckel et al., 2004; Halitschke et al., 2003, 2011
Wild parsnip (*Pastinaca sativa*)	Cabbage looper (*T. ni*)	Foliage-feeder	Decreased efficiency of photosystem II that extended beyond the area directly damaged.	GE and chlorophyll fluore-scence (ChlF)	Zangerl et al., 2002
Tobacco (*Nicotiana tabacum*); soybean (*Glycine max*)	Tobacco budworm (*Heliothis virescens*); oblique-banded leaf roller (*Choristoneura rosaceana*)	Foliage-chewing feeder	Insect locomotion and herbivory across leaf surfaces reduced photosynthesis and increased production of ROS and signaling molecule 4-aminobutyrate.	ChlF	Bown et al., 2002
Soybean (*Glycine max*)	Soybean aphid (*Aphis glycines*); two-spotted spider mite (*Tetranychus urticae*)	Phloem feeder	Reduction up to 50% in photosynthetic rates was not the consequence of stomatal limitation and photoelectron transport was not impaired. Spider mites decreased photosynthesis, stomatal conductance, transpiration and clorophyll content.	ChlF, GE and CIR	Macedo et al., 2003a; Haile & Higley, 2003
Sorghum (*Sorghum bicolor*)	Greenbugs (*Schizaphis graminae*)	Phloem feeder	Photosynthesis-related genes were suppressed strongly by MeJA, and to a lesser extent by SA and aphids.	MA	Zhu-Salzman et al., 2004

Plant species	Herbivore species	Damage type /feeding guild	Results	Method	Reference(s)
Cotton (*Gossypium hirsutum*)	Two-spotted spider mite (*Tetranychus urticae*)	Mesophyll feeders or foliage-chewing feeder	Reduced light-saturated photosynthesis occurred only with high infestation levels. No significant reductions in photosynthetic rates were detected at all initial infestation levels. Photosynthesis declined with crop age and was faster in mite-infested leaves. A minor enhancement of photosynthesis was observed in bottom leaves due to greater light penetration in canopies severely defoliated by mite damage.	GE and photo-synthetic photon flux density	Reddall et al., 2004, 2007
Apple trees (*Malus domestica*)	European red mites (*Panonychus ulmi*); Spotted tentiform (*Phyllonorrycter blancardella)*	Mesophyll feeders	Feeding activity reduces leaf net CO_2 exchange rates; even when green patches maintain levels close to those in intact leaves. Stomatal conductance and hence transpiration rates were highly affected.	GE	Pincebourde et al., 2006
Conifer (*Picea sitchensis*)	Spruce budworms (*Choristoneura occidentalis*) white pine weevils (*Pissodes strobi*)	Floem feeders, stem boring or foliage-chewing feeder	Photosynthesis gene expression (e.g. photosystem I and II, chlorophyll a-b binding proteins and ferredoxin) was down-regulated by budworm feeding.	MA	Ralph et al., 2006
Hardwood saplings (*Carya tomentosa, C. glabra, Quercus alba, Q. velutina Ulmus ulata, Acer rubrum*)	Polyphemus (*Antheraea polyphemus*); redhumped caterpillar (*Schizura concinna*); wasps (*Caryomyia, Eriophyes, Cecidomyia* and *Cynipid* spp.)	Foliage-feeder or gall inductor	Decreased efficiency of photosystem II extended further form visible damage. Gall damage had the greatest depression and chewing rarely affected efficiency of photosystem II surrounding tissue over small distances.	ChlF and thermal imagining (TI)	Aldea et al., 2006

Plant species	Herbivore species	Damage type /feeding guild	Results	Method	Reference(s)
Arabidopsis thaliana	Cabbage looper (*T. ni*)	Foliage-chewing feeder	Decreased efficiency of photosystem II determined by the mode of feeding by different larvae instars and water stress associated with herbivore damage. Corresponding induction of defense gene expression (*cynnamate-4-hydroxylase*) with photosynthesis reduction, but photosynthetic damage spread further into surrounding wounded areas.	GE, ChlF and gene expre-ssion in trans-genic plants harboring a C4H:GUS fusion	Tang et al., 2006, 2009
Common milkweed (*Asclepias syriaca*)	Milkweed tussock (*Euchaetes egle*); monarch butterfly larvae (*Danaus plexippus*); salt marsh tiger moth (*Estigmene acrea*)	Foliage-chewing feeder	Partial tissue consumption by insect herbivores caused photosynthetic impairment on remaining tissue. Reduction in photosynthetic rates lasted >5 days. Neighboring uninjured leaves had a small degree (10%) of compensatory photosynthesis. Complete photosynthetic recovery observed at one day post-injury.	GE	Delaney et al., 2008
Tomato (*Solanum lycopersicum*)	Whitefly (*Bemisia tabaci*)	Phloem feeder	General repression of photosynthetic genes in an apparent infestation-stage-dependent mode.	SSH	Délano-Frier & Estrada-Hernández 2009; Estrada-Hernández et al., 2009
Wheat (*Triticum aestivum*)	Russian wheat aphid (*Diuraphis noxia*); bird cherry-oat aphid (*Rhopalosiphum padi*)	Phloem feeder	Both aphids negatively affected net photosynthesis; *D. noxia* had a greater impact than *R. padi*. Reduction was not related to the light reaction via pigment losses.	GE and ChlC	Macedo et al., 2009
Savoy cabbage (*Brassica oleracea*); Common bean *Phaseolus vulgaris*	harlequin cabbage bug (*Murgantia histrionica*); *Nezara viridula*	Sap feeder	Photosynthesis decreased rapidly and substantially by feeding and oviposition in the attacked areas. Stomatal conductance did not decrease with photosynthesis. Oviposition did not induce photoinhibitory damage.	ChlF and GE	Velikova et al., 2010

Table 2. Some examples of direct or indirect negative effects on photosynthesis after herbivory damage.

5. Conclusion

This chapter explored the highly complex mechanisms employed by plants to adapt to the ever-changing conditions of an environment that is becoming progressively more unpredictable as the consequences of global warming become painfully apparent. Much progress has been made in the identification of many important players in this vital regulatory process, but many areas remain obscure and will require active research to be elucidated. The manifold relationships between plants and insect herbivores from the photosynthetic perspective were also examined. From this perusal it is clearly evident that almost all contact with insects, even when no damage is involved, as in some oviposition processes or in tritrophic interactions that indirectly benefit the plant, will have an impact on photosynthesis. This highlights the importance of the photosynthetic process in plant-insect interactions, which can be variously manipulated to either favor or impair the plant, or the insect or both.

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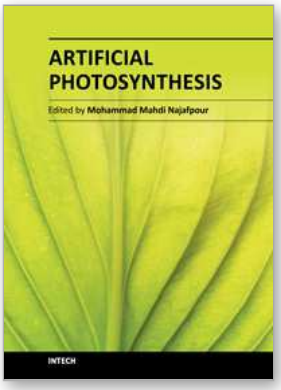

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Photosynthesis is one of the most important reactions on Earth, and it is a scientific field that is intrinsically interdisciplinary, with many research groups examining it. We could learn many strategies from photosynthesis and can apply these strategies in artificial photosynthesis. Artificial photosynthesis is a research field that attempts to replicate the natural process of photosynthesis. The goal of artificial photosynthesis is to use the energy of the sun to make different useful material or high-energy chemicals for energy production. This book is aimed at providing fundamental and applied aspects of artificial photosynthesis. In each section, important topics in the subject are discussed and reviewed by experts.

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Phone: +86-21-62489820
Fax: +86-21-62489821

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