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The Contribution of Mitochondria to Energetic Metabolism in Photosynthetic Cells

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Mitochondria fulfill important functions in photosynthetic cells not only in darkness but also in light. Mitochondrial oxidative phosphorylation is probably the main mechanism to supply ATP for extrachloroplastic functions in both conditions. Furthermore, during photosynthesis mitochondrial electron transport is important for regulation of the redox balance in the cell. This makes mitochondrial function an integral part of a flexible metabolic system in the photosynthetic cell. This flexibility is probably very important in order to allow the metabolism to override disturbances caused by the changing environment which plants are adapted to.

KEY WORDS: Dark respiration; leaf mitochondria; oxidative phosphorylation; photorespiration; photosynthetic metabolism.

INTRODUCTION

In darkness a photosynthetic cell depends on respiratory metabolism oxidizing stored carbohydrates and with mitochondrial oxidative phosphorylation responsible for most of the ATP production. In light, on the other hand, photosynthetic cells produce ATP by photophosphorylation in the chloroplasts, thereby directly converting light energy into chemical energy. In photosynthetic metabolism this energy is used to fix CO_2 for production of carbohydrates which are directly used in the metabolism or stored to be used in subsequent dark periods. Plant respiratory metabolism uses the same main metabolic pathways as animal cells, i.e., glycolysis, tricarboxylic acid cycle, and the mitochondrial electron transport chain coupled to oxidative phosphorylation. However, in plants this is often referred to as "dark" respiration, since photosynthetic plant cells specifically contain a photorespiratory pathway, a series of metabolic reactions resulting in a light-dependent evolution of CO_2 and uptake of O_2. Photorespiration starts with an oxygenase reaction in the chloroplast stroma catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) producing 3-phosphoglyceric acid (3-PGA) and phosphoglycolate (Husic *et al.*, 1987). The 3-PGA enters the Calvin cycle whereas phosphoglycolate is dephosphorylated to glycolate and exported out from the chloroplast. Most of the carbon (75%) incorporated into glycolate is returned to the Calvin cycle as 3-PGA. This is achieved via a metabolic pathway known as the "glycolate cycle" which involves reactions in chloroplasts, peroxisomes, and mitochondria (Husic *et al.*, 1987).

A common view has been that the chloroplastic ATP production in light would be sufficient to supply the whole cell's ATP demand. Consequently, mitochondrial ATP production via oxidative phosphorylation would be superfluous in the light and the main function of leaf mitochondria would be to supply carbon skeletons for biosynthetic reactions (e.g., synthesis of amino acids). The direct exchange of adenylates across the chloroplast envelope membranes is slow (Woldegiorgis *et al.*, 1985), so during photosynthesis ATP would be indirectly exported from the stroma by metabolite shuttles (Flügge and Heldt, 1991).

However, during recent years results from several laboratories have indicated that mitochondrial oxidative phosphorylation produces ATP in the light. It has furthermore been shown that this is necessary in order

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to obtain maximal rates of photosynthesis (Krömer *et al.*, 1988). In this review we will discuss respiration in photosynthetic cells in the light in terms of effects on gas exchange and focus on recent results showing that mitochondrial ATP production and/or electron transport is crucial for optimal photosynthetic metabolism under a variety of conditions. In a recent review by Krömer (1995) the interactions between respiration and photosynthesis are treated in more general terms.

COMPONENTS OF GAS EXCHANGE

The gas exchange characteristics of photosynthetic tissues is very complex since both photosynthetic and respiratory processes with opposing CO_2/O_2 exchange take place simultaneously. The main metabolic reactions contributing to the gas exchange observed in photosynthetic tissue are summarized in Fig 1. During photosynthesis the dominating factors are CO_2 fixation by Rubisco and O_2 production from the water-splitting complex associated with PS II. Some CO_2 is also fixed by phosphoenol pyruvate carboxylase in the cytoplasm although this is usually less than 5% of the CO_2 fixed by Rubisco (Melzer and O'Leary, 1987; Raven and Farquhar, 1990). Carbon dioxide is also released from "dark" respiration occurring in the light as well as from photorespiration. The former reflects mainly decarboxylation reactions associated with the tricarboxylic acid (TCA) cycle and the latter glycine decarboxylation associated with the conversion of glycine to serine in the photorespiratory glycolate cycle. Some of the CO_2 released by respiratory reactions is refixed in photosynthesis, which can further complicate the evaluation of experimental results.

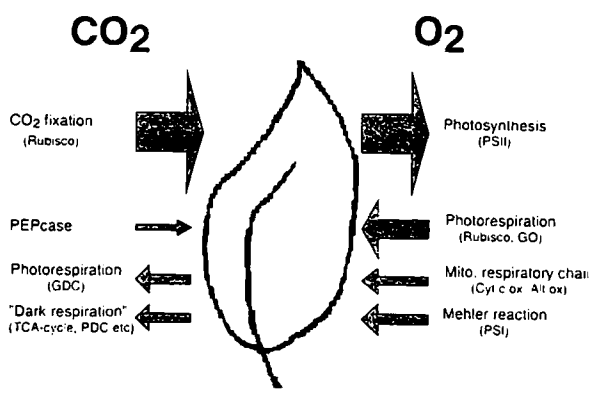

Fig. 1. Schematic representation of the gas exchange components of a photosynthesizing leaf.

Several O_2-consuming reactions occur in parallel to photosynthetic O_2 production. One is the photorespiratory O_2 uptake by Rubisco and glycolate oxidase. Oxygen is also taken up by the two terminal oxidases, cytochrome oxidase and the alternative oxidase, associated with the mitochondrial electron transport chain. In addition the so-called Mehler reaction associated with PS I in the thylakoid membranes results in O_2 uptake (Robinson, 1988). The Mehler reaction has often been regarded to be of minor quantitative significance (Wu *et al.*, 1991). However, recent findings indicate that the Mehler–ascorbate peroxidase reaction can be quantitatively significant and very important as a protective mechanism, especially at high light intensities (Osmond and Grace, 1995).

It is important to note that the gas exchange components of respiration are due to different metabolic reactions with respect to CO_2 release and O_2 uptake. Different factors are involved when respiration is measured as CO_2 evolution or as O_2 uptake, respectively. This can lead to confusion when respiration is discussed in general terms without reference to whether CO_2 evolution or O_2 uptake is considered.

EFFECTS OF LIGHT ON RESPIRATORY GAS EXCHANGE

It is not possible to directly measure respiratory CO_2 evolution in actively photosynthesizing cells since the net flux in the light is fixation of CO_2 in photosynthesis. However, several methods have been used to address this question, including indirect gas exchange methods (Villar *et al.*, 1994), mass spectrometric methods (Avelange *et al.*, 1991), and radioactive isotopes (McCashin *et al.*, 1988). In general, the results obtained agree in that respiratory CO_2 evolution continues in the light, indicating that the TCA cycle, or at least parts of it (Hanning and Heldt, 1993), is operating. However, it is commonly observed that CO_2 evolution from "dark" respiration is decreased in light as compared to darkness. The extent of this decrease depends on several factors such as species studied, leaf age, and light intensity (Avelange *et al.*, 1991; Villar *et al.*, 1995; Raghavendra *et al.*, 1994).

A different approach to determine intracellular decarboxylations has been taken by Keerberg and associates. By using a radiogasometric method a distinction

is made between four components of total decarboxylations depending on source (primary products or end products of photosynthesis) and decarboxylation pathway (linked to oxidase or oxygenase mechanisms) (Pärnik and Keerberg, 1995). The oxidase and oxygenase components are distinguished by the different oxygen affinities of the oxidases (cytochrome *c* oxidase and the alternative oxidase) and Rubisco. The results with this approach show a decreased rate of "dark" respiration in the light, defined as oxidase decarboxylation of end products of photosynthesis (Pärnik and Keerberg, 1995). Interestingly, this decrease was only observed at limiting CO_2 concentrations (photorespiratory conditions) and not at high CO_2 concentrations (nonphotorespiratory conditions) (O. Keerberg and T. Pärnik, personal communication). A possible mechanism for the inhibition of respiratory CO_2 release in the light is via a photorespiratory-dependent inhibition of the mitochondrial pyruvate dehydrogenase complex (PDC) as discussed below.

Experiments using mass spectroscopic determination of oxygen isotopes have indicated that respiratory O_2 uptake is not inhibited in the light to the same extent as CO_2 release (Avelange *et al.*, 1991). This aspect has been reviewed by Raghavendra *et al.* (1994). The differences in light inhibition of respiration obtained from measurements of CO_2 or O_2 exchange can be explained by the metabolic pathways involved. In the photorespiratory glycolate cycle glycine is produced in the peroxisomes and taken up by mitochondria. In the mitochondrial matrix glycine is oxidatively decarboxylized by the glycine decarboxylase complex which results in reduction of NAD to NADH (Douce and Neuburger, 1989). Direct measurements of subcellular NADH/NAD ratios in barley protoplasts showed that the mitochondrial NAD pool was more reduced in the light under photorespiratory conditions than under nonphotorespiratory conditions (Wigge *et al.*, 1993). In the photorespiratory glycolate cycle equimolar amounts of extrachloroplastic reductant is produced (in mitochondrial glycine oxidation) and consumed (in peroxisomal hydroxypyruvate reduction) (Husic *et al.*, 1987). Some of the NADH formed in the mitochondria can be shuttled out to the peroxisomes for hydroxypyruvate reduction via a malate/oxaloacetate exchange mechanism (Krömer and Heldt, 1991b). However, some NADH can be reoxidized by the mitochondrial electron transport chain leading to O_2 uptake. This oxygen uptake is connected to the mitochondrial electron transport chain and may therefore be regarded as a "dark" respiration. The CO_2 release is, on the other hand, a photorespiratory process since it is due to glycine oxidation in the glycolate cycle.

TRICARBOXYLIC ACID CYCLE ASSOCIATED ACTIVITIES IN THE LIGHT

The decrease in CO_2 release in light as compared to in darkness could be due to a lowering in activities of decarboxylation reactions of the TCA cycle or associated reactions in the matrix. The most studied of these decarboxylating enzymes is the pyruvate dehydrogenase complex (PDC) catalyzing the conversion of pyruvate to acetyl-CoA. PDC is thought to be an important step of control since it provides new carbon for the TCA cycle. The complex is allosterically inhibited by NADH and acetyl-CoA and also regulated by reversible protein phosphorylations/dephosphorylations (Randall and Miernyk, 1990). A PDH-kinase phosphorylates and inactivates the complex, while phospho-PDH phosphatase dephosphorylates and thus activates PDC (Miernyk and Randall, 1987). Steady-state PDC activity is thought to be the equilibrium between the kinase and phosphatase activities. PDH-kinase is strictly regulated, inhibited by, e.g., pyruvate (+TPP), acetyl-CoA, and NADH while NH_4^+ acts as an activator (Schuller and Randall, 1989). It has been shown that steady-state PDC activity decreases in the light in pea seedlings (Budde and Randall, 1990). This decrease might be due to photorespiratory glycine oxidation releasing NH_4^+, since inhibition of glycine decarboxylase (GDC) activity elevates the deactivation of PDC (Gemel and Randall, 1992). Furthermore, this is confirmed by the PDH-kinase-mediated deactivation of PDC in isolated mitochondria oxidizing glycine (Budde and Randall, 1988). The light-dependent deactivation of PDC has apart from in pea been reported in, e.g., zucchini, soybean, barley, tobacco, and maize (Gemel and Randall, 1992). However, PDC activities measured in mitochondria isolated from barley, wheat, and spinach are lower as compared to pea PDC (Gemel and Randall, 1992; Lernmark and Gardeström, 1994) and the distribution between the plastid and mitochondrial isoforms of the complex varies considerably between species (Lernmark and Gardeström, 1994; Krömer *et al.*, 1994). Thus, significant light-dependent changes might be difficult to detect or of lesser importance in some species, e.g., barley (Krömer *et al.*, 1994). Further experiments are needed to verify this

and to investigate if there are any species differences in regulation of PDC and its regulatory enzymes.

OXIDATIVE PHOSPHORYLATION IN THE LIGHT

A consequence of a decrease in TCA cycle-associated activities in the light is a lowered production of NADH from these reactions for oxidation by the electron transport chain to yield ATP. However, in photosynthesizing cells a significant amount of NADH is produced by photorespiratory glycine oxidation since in normal air one oxygenase reaction by Rubisco accompanies every two to three carboxylation reactions. The rate of NADH formation from glycine oxidation in the light is estimated to be higher than the rate of NADH formation from TCA cycle-linked reactions in darkness (Krömer, 1995). It is experimentally very difficult to measure to what extent NADH produced by glycine oxidation is reoxidized by the mitochondrial electron transport chain as compared to the amount exported to the cytosol *in vivo*. In experiments using isolated mitochondria under simulated *in vivo* conditions (with respect to substrate concentrations) it has been estimated that 25–50% of the NADH formed by glycine oxidation might be exported out from the mitochondria (Krömer *et al.*, 1992), mainly by a malate/oxaloacetate exchange mechanism (Ebbighausen *et al.*, 1985). This means that leaf mitochondria have a high potential for ATP production in light. However, it is complicated to evaluate the actual rate of oxidative phosphorylation in the light since plant mitochondria have a very flexible coupling between electron transport and ATP production. Oxidation of one NADH in the mitochondrial matrix can yield up to 3 ATP if the electron transport is coupled entirely to cytochrome oxidase (Douce and Neuburger, 1989). However, when the possibility of a bypass of complex I via a rotenone-insensitive pathway (Rasmusson *et al.*, 1993) and a bypass of complexes III and IV via the alternative oxidase (Douce and Neuburger, 1989) is taken into account, the yield of ATP can vary between 0 and 3 per NADH oxidized.

Direct measurements of subcellular ATP/ADP ratios by rapid fractionation of barley protoplasts has shown that the cytosolic ratio is higher in low CO_2 than in high CO_2 (Gardeström, 1987; Gardeström and Wigge, 1988). A photorespiratory-dependent ATP production was shown to contribute to the increased cytosolic ATP/ADP ratio in limiting CO_2 since inhibitors of mitochondrial glycine oxidation lowered the ratio (Gardeström and Wigge, 1988).

Photorespiration is often considered to be a wasteful process since the glycolate cycle consumes both ATP and reducing equivalents and at the same time releases recently fixed carbon (Husic *et al.*, 1987). However, most of the energy-consuming reactions are located in the chloroplasts. In the extrachloroplast compartments the reactions of the glycolate cycle are balanced with stoichiometric amounts of NADH produced in the mitochondria and consumed in the peroxisomes. Reducing equivalents can be shuttled out from the chloroplast by the combined action of NADP-malic enzyme (Scheibe, 1987) and a malate/oxaloacetate exchange across the envelope membranes (Hatch *et al.*, 1984) to support peroxisomal hydroxypyruvate reduction. This will make some of the NADH from photorespiratory glycine oxidation available for reoxidation by the respiratory chain coupled to oxidative phosphorylation. Thus, an effect of photorespiration can be a transfer of energy from the chloroplast to extrachloroplast compartments. A high flexibility in this system is likely to be beneficial to the plant by providing adaptability in the metabolism with respect to compartmentalized production and consumption of ATP and reducing power.

Oligomycin has proven to be a very useful inhibitor for studies of oxidative phosphorylation in the light. The inhibitor is very specific for mitochondrial ATPase as compared to chloroplastic ATPase (Krömer *et al.*, 1988). By using oligomycin, it has been shown that the cytosolic ATP/ADP ratio is always much lower after inhibition whereas the chloroplastic ATP/ADP ratio is unchanged or even increased. This has been shown to be the case under a variety of conditions of steady-state photosynthesis such as both limiting and saturating CO_2 and limiting and saturating light (Krömer *et al.*, 1993). Since oligomycin lowers the cytosolic ATP/ADP ratio also in nonphotorespiratory conditions, oxidative phosphorylation in light is not obligatory depending on photorespiratory activity. Thus, mitochondrial oxidative phosphorylation appears to be the normal mechanism for production of ATP for the cytosol in the light.

The phosphate/triose phosphate translocator in the inner envelope membrane of the chloroplast has generally been considered to be important for ATP export from the chloroplast to the cytosol (Flügge and Heldt, 1991). During steady-state photosynthesis the main function of this translocator is to export triose phosphates in exchange for inorganic phosphate for

sucrose synthesis in the cytosol (Flügge and Heldt, 1991). Triose phosphate can also be exported from the chloroplast in exchange for 3-phosphoglyceric acid. In the cytoplasm triose phosphate can be converted to 3-phosphoglyceric acid by two different routes, either producing ATP + NADH or only NADPH (Krömer, 1995). The NADPH-producing enzyme has higher affinity for its substrates than the ATP + NADH producing reactions which, considering the estimated substrate levels *in vivo*, makes this is the most likely route. However, in both situations reduced pyridine nucleotides must be reoxidized in the cytosol for the continued operation of the shuttle. Since plant mitochondria possesses external NAD(P)H dehydrogenases (Møller and Lin, 1986), they might fulfill this function, and ATP production coupled to this reoxidation would be produced. Also here NADPH is the most likely substrate *in vivo* based on the estimated cytosolic NADH as compared to NADPH concentrations (Heineke *et al.*, 1991) in relation to the affinity of the external dehydrogenases (Møller and Lin, 1986). However, recent results from experiments with transgenic plants with reduced content of the phosphate translocator protein obtained with anti-sense technique have shown that even a small reduction in its content leads to significant disturbances in the distribution of 3-phosphoglyceric acid between chloroplast and cytoplasm (Heineke *et al.*, 1994). This indicates that the activity of the translocator is not in excess with respect to its main function in triose phosphate export for sucrose synthesis. Thus, its activity may not be sufficient to be a major route for ATP export from the chloroplasts to the cytosol in conditions of steady-state photosynthesis.

It has been noted that the gradient in ATP/ADP ratio between cytosol and the mitochondria is larger in darkness than in light (Stitt *et al.*, 1982). This gradient in ATP/ADP ratio across the mitochondrial inner membrane might reflect the energization of the membrane due to the properties of the ATP/ADP exchange translocator catalyzing the export of ATP from the mitochondria to the cytosol in exchange for ADP (Douce and Neuburger, 1989). Since ATP is more negatively charged than ADP, the exchange results in a net transfer of one negative charge from the matrix side of the membrane to the cytosolic side. The exchange is therefore driven by the membrane potential across the inner mitochondrial membrane. A larger gradient in ATP/ADP ratio across the mitochondrial membrane in darkness as compared to light therefore suggests that the mitochondria are more energized in darkness than in light. Inhibition of the mitochondrial ATPase in light increased the gradient (P. Gardeström, unpublished results), as would be expected since oligomycin blocks the use of the protonmotive force by the ATPase but not its buildup via electron transport in the respiratory chain. Accepting this line of reasoning, mitochondria would operate closer to state 3 conditions in light as compared to darkness. However, the regulation of mitochondrial electron transport *in vivo* is very complex. Recent advances with respect to our understanding of the regulation of the alternative oxidase shows that it can play a much more active function in regulation of mitochondrial electron transport than previously realized (Siedow and Moore, 1993). This may suggest that it can have a function for regulation of the redox status of the mitochondrial electron transport chain (Umbach and Siedow, 1993). Furthermore, the substrate supply to the electron transport chain *in vivo* may be tightly regulated. Plant mitochondria have several NAD(P)H dehydrogenases associated with the electron transport chain in addition to Complex I, including a rotenone-insensitive bypass on the matrix side and NAD(P)H dehydrogenases on the outer surface of the inner membrane (Douce and Neuburger, 1989). Estimations of the *in vivo* reduction level of the mitochondrial ubiquinone pool has been done for nonphotosynthetic tissue (Wagner and Wagner, 1995). This type of experiments using photosynthetic tissues may answer some of the questions of regulation of electron transport at the cellular level.

MITOCHONDRIAL EFFECT ON CHLOROPLAST REDOX LEVELS

Photosynthetic Induction

When a leaf is abruptly transferred from darkness into light the metabolism will change from respiratory metabolism in darkness into photosynthetic metabolism in the light. This transition is associated with a lag phase involving light activation of stromal enzymes (Salvucci, 1989) as well as buildup of metabolite levels in the chloroplast stroma (Leegood and Walker, 1981). Immediately upon illumination of barley protoplasts the chloroplastic ATP/ADP ratio increased, reaching a maximum already after 5 sec, whereas the photosynthetic oxygen evolution started to increase after 1 min, reaching a maximal rate after several minutes (Gardeström, 1993). The lag in photosynthesis observed upon illumination is thus not due to lack of

chloroplastic ATP. The ATP/ADP ratio in the extrachloroplast compartments also increased quickly following illumination, and a maximum was reached after about 15 sec, which is well before high rates of photosynthesis were observed. Fluctuations in 3-PGA/triose phosphate content in the chloroplast and extrachloroplast compartments were consistent with the operation of a 3-PGA/triose phosphate shuttle across the envelope membranes (Gardeström, 1993). Alternatively a malate/oxaloacetate exchange can transport reducing equivalents from the chloroplast to the cytosol. This would be regulated by the activity of chloroplastic NADP-malic enzyme which in its turn is regulated by the ferredoxin/thioredoxin system and suggested to work as a valve for redox regulation (Scheibe, 1987). In any case pyridine nucleotides must be reoxidized outside the chloroplast. Recent experiments studying the effect of oligomycin on photosynthetic induction in isolated barley protoplasts suggests that the mitochondrial electron transport chain is involved in this reoxidation (P. Gardeström, S. Krömer, and V.M. Hurry, unpublished). Oligomycin caused a very pronounced delay in photosynthetic induction. The quick increase in the cytosolic ATP/ADP ratio was absent in protoplasts incubated with oligomycin, whereas the chloroplastic ATP/ADP ratio was unchanged. Furthermore, inhibition of oxidative phosphorylation caused a delay in the development of photochemical quenching. This indicates that the reason for the prolonged lag phase was due to an overreduction of the chloroplast electron transport chain. Thus, photosynthetic induction seems to be a very clear example where mitochondrial oxidation of excessive redox equivalents from chloroplast electron transport is important (Krömer and Heldt, 1991a).

The direct transfer of photosynthetic cells from darkness into saturating light is a very extreme treatment not occurring in nature. Future experiments will be designed to study what happens in fluctuating light, that is, situations with alterations in light intensities similar to light flecks caused by clouds and shadowing from other plants in a canopy (Pearcy, 1990).

Stress Conditions

Changes of environmental factors such as temperature, light intensity, water and nutrient availability, and so on, can cause stress situations for plants. In such situations the flexibility of plant metabolism may be very important. It is therefore potentially very interesting to study mitochondrial functions under such situations. In isolated protoplasts it has been shown that mitochondrial electron transport can be important to prevent photoinhibition which can occur when the electron carriers in the chloroplastic electron transport chain become too reduced and thereby limit electron transport between PS II and PS I (Saradedevi and Raghavendra, 1992). Here we will briefly describe some results relating to plant growth at low temperatures.

Some varieties of agricultural plants have been selected for survival at low temperatures, examples of which are winter varieties of cereals. The most resistant of these can, after cold-hardening, survive at temperatures of $-30°C$ or lower. In cereals like winter rye cold-hardening is associated with an increased photosynthetic capacity (Öquist and Huner, 1993) as well as increased respiration (Hurry and Huner, 1992). The adaptation is associated with increased activities of several enzymes of CO_2 fixation and sucrose synthesis as well as increased metabolic pools (Hurry *et al.*, 1995a). Photosynthesis in cold-hardened leaves was more sensitive to oligomycin inhibition than photosynthesis in nonhardened leaves. In the cold-hardened leaves oligomycin caused a dramatic decrease in metabolite pools which seemed to be associated with a decreased capacity to regenerate RuBP in the Calvin cycle (Hurry *et al.*, 1995b). The decrease in chloroplast metabolites was probably not directly associated with a decreased availability of cytosolic ATP but rather with alterations in the redox status of the chloroplast as revealed by fluorescence analysis (Hurry *et al.*, 1995b). Thus, also in this situation mitochondrial electron transport seemed to be important for the regulation of the redox situation of the photosynthesizing cell.

It seems clear that mitochondria fulfill important functions in photosynthetic cells also in the light. Mitochondrial oxidative phosphorylation is probably the main mechanism for supply of ATP to the cytosol in all conditions. An additional important function for leaf mitochondria is with respect to redox regulation in the cell during photosynthetic metabolism. The contribution of mitochondria to the metabolic flexibility of the photosynthetic cell will be a very important aspect in future studies on the integration of cellular metabolism. This will be of particular relevance in understanding metabolism under the fluctuating environmental conditions that plants encounter during growth in natural environments.

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