Plant Physiological Adaptations Induced by Low Rates of Photosynthesis

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Among the adaptory responses of plants to different ecological conditions the adaptation to low light intensities is one of the most important. This response, known as "shade adaptation", may, however, be similarly induced by decreasing the rate of photosynthesis in other ways. The partial inhibition of photosynthetic electron flow with herbicides has clearly been shown to induce shade-type plants; in the case of photosynthetic limitation by decreased CO_2-availability only certain aspects of the shade-type metabolism — namely the changes occurring in the nitrogen metabolism — have been demonstrated.

The capability of plants to respond to different light conditions is long known and has recently been summarized [1, 2]. Whole plants show characteristic responses to light of low intensities, but also single leaves may respond to their local light environment, *e. g.* by forming "shade leaves" in the interior of a tree's crown. Here, but also on the forest floor [3], the light intensity is not only lowered but also qualitatively changed [4]. It is interesting that some plants perfectly adapt in low intensities of white light but others do not [5, 6]. Because these plants do adapt under natural conditions and also in low intensities of green light, the participation of the phytochrome system in the induction process may have to be considered.

The adaptation of a plant to low light intensities includes morphological, ultrastructural, physiological and biochemical changes. Boardman [1] gives a synopsis of the morphological characteristics of shade leaves which includes

a) thinner leaves (shade: 3 – 4 cells; sun: 7 cells);
b) smaller mesophyll cells;
c) greatly reduced mesophyll surface area per unit leaf surface area (A_{mes}/A);
d) decreased CO_2-conductivity per unit leaf area;
e) however, unchanged CO_2-conductivity per unit mesophyll volume;
f) reduced stomata density.

This light adaptation not only occurs in developing leaves but also to a limited extent after leaf expansion is complete [7].

An interesting finding has been the observation, that plants treated with sublethal concentrations of photosynthesis-inhibiting herbitides resemble shade-adapted plants with respect to chloroplast anatomy (Table I) and also to chloroplast composition (Table II). Whereas the details may be taken from the Tables, mention should be made that one or the other parameter indicating a shade adaptation has not only been observed in flowering plants but also in algae [8, 9], mosses [10], ferns [11], selaginella [12] and conifers [13]. The changes of the grana/stroma lamellae ratio (Table I) and the changes of the pigment composition (Table II) are causally related, since grana lamellae are richer in xanthophylls, chlorophyll b and pigment system II [14, 15].

Table I. Chloroplast morphology and anatomy in plants adapted to low light intensities or treated with photosynthesis-inhibiting herbicides. +, as in low light; —, different from low light type; 0, no data available.

Low light	Ref.	Herbicidal treatment	Ref.
Swelling during isolation in 0.3 M medium	[2]	+	[18]
Stroma lamellae decreased	[16]	+	[6, 19]
Grana thickness increased	[3]	+	[20]
Grana/stroma ratio increased	[1]	+	[6]
Granal size increased, grana number decreased	[17]	+	[21]

The photosynthesis-inhibiting *s*-triazine herbicides induce physiological changes in plants which only partially agree with shade adaptory responses [42]. However, *s*-triazine herbicides have also been shown to possess plant hormone like activities [43, 44].

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Table II. Chloroplast pigment spectra and enzyme contents in plants adapted to low light intensities or treated with photosynthesis-inhibiting herbicides. Compare with Table I.

Low light	Ref.	Herbicidal treatment	Ref.
Chlorophyll (a+b) increased per fresh wt. and per chloroplast	[1, 2]	+	[18, 25, 26]
Chlorophyll ratio a/b decreased	[1, 2]	+	[18, 25]
Chlorophyll (a+b)/ β-carotine increased	[22]	+	[25]
Xanthophyll/β-carotine increased	[22]	+	[25]
Quinones decreased (plastoquinone, α-tocopherol)	[23]	+	[25, 27]
Cytochromes b and f and ferredoxin per chlorophyll decreased	[2]	o	—
P 700 and Q per chlorophyll unchanged	[2]	o	—
Carboxydismutase decreased	[24]	+	[27, 28]

Most of the work done on the physiology and biochemistry of shade adapted plants has concentrated on photosynthesis and on the composition of the chloroplast. However, other metabolic areas are changed, too; *e. g.*, in shaded plants the respiration rate will be lower while the transpiration rate is increased. Similar changes have been observed after herbicidal treatment. The transpiration rate, however, usually will be decreased shortly after herbicidal treatment because the stomata are closed after photosynthesis is inhibited and the internal CO_2-level is increased [45, 46]. Of special interest is the nitrogen-metabolism which shows dramatic changes (Table III). In low light intensities as well as in herbicidally treated plants the uptake and accumulation of nitrate is enhanced. The *in vitro* activity of nitrate reductase is similarly increased. This increase does not necessarily mean an increase *in vivo* [18], but in herbicide treated plants soluble amino acids and soluble proteins are generally also increased. Interestingly, similar changes may be obtained by reducing the photosynthetic rate via a decreased CO_2 availability. What shows up most clearly from these results is a strict negative correlation between the endogenous concentrations of nitrate and malate. This negative correlation has also been confirmed in nitrate reductase-less mutants of *Arabidopsis thaliana* (L.) [47]. Hageman *et al.* have suggested from these data that malate supplies the reducing equivalents for nitrate reductase *in vivo* [40]. The comparison given in Table III suggests that a strong coupling exists between the mechanisms of nitrate uptake and/or nitrate reduction and the rate of photosynthetic electron transport. All three ways of limiting the rate of photosynthesis – shade/low light, herbicides, CO_2 availability – led to a simultaneous increase of nitrate and decrease of malate in the tissue.

Change observed in low light	Ref.	Herbicidal treatment	Ref.	CO_2-deficiency	Ref.
Decrease of soluble carbohydrates	[29]	+	[18]	o	—
Decrease of malate concentration	[30]	+	[5, 35]	+	[40]
Increase of nitrate uptake	?	+	[36]	+	[41]
Increase of nitrate concentration	[30, 31]	+	[37]	+	[41]
Increase of nitrate reductase *in vitro*	[29]	+	[18, 37]	+	[41]
Increase of soluble amino acids	[18]	+	[18]	o	—
Increase [18, 34] or decrease of soluble protein	[29, 31, 32]	+	[37, 39]	+	—
Increase of stigmasterol, decrease of sitosterol	[33]	o	—	o	—

Table III. Metabolic changes – except those occuring in the chloroplast – in plants with reduced photosynthate production. Compare with Table I.

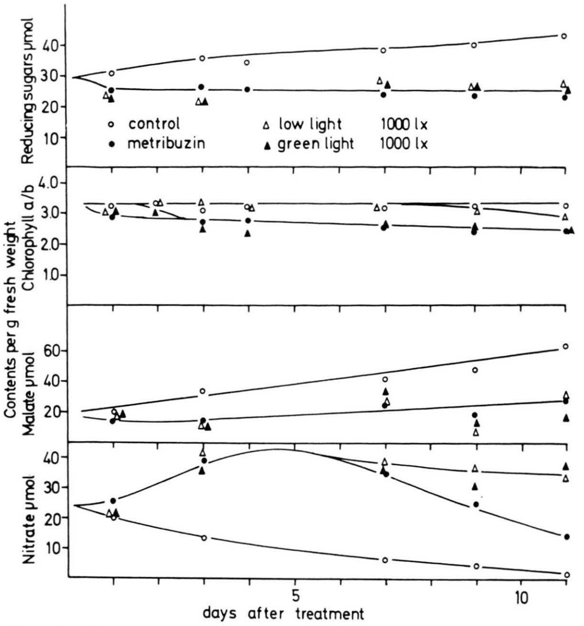

Fig. 1. Responses of soybean plants to low intensities of white and green light and to the photosynthesis-inhibiting herbizide metribuzin (3.7 µM) (compare [5]).

The question of the primary trigger(s) initiating the sequence of events eventually leading to the different shade adaptations remains unanswered. It is not even clear whether "shade adaptation" and "low light adaptation" are identical. Hitherto no differences have been found. However, individual species may differ in their induction requirements. As already stated, some species only adapt in low intensities of green light (Fig. 1). This, however, only applies to the chloroplast and not to the cytoplasm where the characteristic changes in the concentrations of malate and nitrate are also observed in low intensities of white light. Sofar we may only postulate that the rate of photosynthetic electron transport exerts some sort of a control. More specifically, a redox pair whose redox state is controlled by the rate of photosynthetic electron flow might function as a control valve. One possible candidate for a controlling redox compound is dehydro-ascorbic acid, whose concentration has been shown to be intimately controlled by the light intensity [48]. Still, different adaptory responses appear to be independently controlled, and the phytochrome system supposedly is involved in part of this control system. The final outcome for the plant is, of course, to save energy and carbon compounds in situations of light stress.

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