

Zeitschrift: Archives des sciences et compte rendu des séances de la Société
Herausgeber: Société de Physique et d'Histoire Naturelle de Genève
Band: 48 (1995)
Heft: 2: Archives des Sciences

Artikel: How do land plants respond to stress temperature and stress light?
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DOI: <https://doi.org/10.5169/seals-740251>

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Archs Sci. Genève	Vol. 48	Fasc. 2	pp. 135-146	Septembre 1995
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HOW DO LAND PLANTS RESPOND TO STRESS TEMPERATURE AND STRESS LIGHT?

BY

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(Ms reçu le 14.2.1995, accepté après révision le 3.5.1995)

ABSTRACT

Light-driven chlorophyll *a* fluorescence intensity was used to measure the photochemical activity of photosystem II (PSII) after heat and light stress. Pea plants grown at 22°C show a dramatical decrease in the activity of PSII when exposed to high temperature (above 40°C). High light exacerbates the damage of PSII when exposed together with high temperature. But the low light strongly affect the response of the photosystem, acting as an efficient protector of the photochemical activity against its inactivation by heat. Heat protection was also triggered by exposing the leaves to moderately elevated temperature (30°C) before exposing them to high temperature (40°C). Photoinhibition resistance was induced by exposing leaves to high temperature for 15 min before illuminating them to high light intensity. The experimental results show the existence of an adaptive mechanism of land plants to protect themselves against heat and strong light, the usual changes during the diurnal cycle of the day. A comparable behaviour has not been found in algae. Aquatic higher plants respond individually. Some were able to protect themselves with low light against heat stress but this phenomena was totally absent in others.

Key-words: Chlorophyll *a* fluorescence, Heat stress, time course of the day, Pea (*Pisum sativum*).

INTRODUCTION

Any system at given environmental conditions works in its optimal way and attains a thermodynamically stable state. But the biosphere, lithosphere, hydrosphere and the atmosphere of the earth are in a dynamic stationary state; each is changing and affects the others in the sequence of naturally occurring events. Over the last decades plant biologists have become increasingly aware of the importance and complexities of interactions between the environment and the physiological processes of the plants (see for reviews in Baker & Long, 1986). Normally wild type plants are well adapted to their environmental conditions but the need for increased food and biomass production requires the development of more efficient plants, which should also resist to various environmental stress conditions. There are now reasonable agreements that the photosynthetic apparatus can exhibit adjustment (acclimation) to modest changes in the

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climate. For example during the time course of the day there are tremendous changes in light intensity, heat and the water deficit but the plants resist to these natural phenomena. This indicates that the response of the photosynthetic machinery to particular environmental constraints are controlled by the combination of different physico-chemical parameters of the environment. A combination of different stress factors can result in intensification, overlapping or reversal of the stress.

In a leaf, photosynthesis is highly sensitive to heat. For a given plant material, the thermolability of PSII has been reported to vary substantially due to the influence from various environmental factors. In general, bright light strongly magnify the heat damage of PSII, as it does for injuries from other physico-chemical stresses such as chilling, freezing or drought (for review, see Kyle *et al.*, 1987). This effect has been attributed to the decreased rate of photosynthesis caused by these various stresses, which predisposes stressed leaves to photoinhibition. On another hand low light has been shown to markedly reduce damage to PSII during heat stress (Havaux *et al.*, 1991, Schreiber & Berry, 1977). The heat protection by light depends on the intensity and spectral characteristics of the light (Havaux & Strasser, 1990, 1992). Other physico-chemical stresses such as high salinity (Larcher *et al.*, 1990), hypertonic stress (Kaiser, 1984) or leaf water potential (Seeman *et al.*, 1986, Havaux, 1992) have also been reported to increase heat tolerance of PSII in intact leaves. These observations suggest the existence of antagonistic interactions between environmental stresses, with one stress enhancing the tolerance of photosynthesis towards another. During the time course of the days heat stress is often combined with strong light. For this reason, we have examined the effects of heat and light on PSII activity of the plants by measuring Chl *a* fluorescence as a signal. Our results show that the phenomenon of heat protection by low light is a unique feature of the land plants. Training the plants with moderate temperature can also protect the plants to strong light and high temperature.

MATERIAL AND METHODS

Plant Material and Stress Treatment:

The land plants (*Pisum sativum*, *Lycopersicum esculentum*, *Camellia sp.*) were grown in glass house (day/night temperature approximately 22/18°C) under natural sunlight conditions. The swimming plants (*Salvinia natans* and *Pistia stratiotes*) and submerged plants (*Elodea sp.* and *Potamogeton sp.*) were obtained from the Botanical Garden of the University of Geneva, Geneva. Unicellular organisms (*Chlorella sp.*, *Chlorella rubrum* and *Scenedesmus sp.* in modified Detmer medium (Pringsheim, 1951) as described by Calderon (1991)) and *Chlamydomonas reinhardtii* (in tris-acetate phosphate medium (Gorman & Levine, 1965)) were grown in liquid medium with constant shaking in growth chamber at 25°C and illuminated for 12 hours by a fluorescent lamp (white light). To apply thermal stress, leaf discs were placed on a

moist filter paper on a metal block. The temperature of the block was modified by the circulation of water from a thermostated water bath (Colora Messtechnik, Lorch/Württ., Germany). Temperature was monitored with a Digi-Sense 8528-20 thermocouple thermometer (Cole-Parmer Instruments, Chicago, IL, USA) stuck on the lower surface of the leaf. Submerged plants were heated in distilled water and the unicellular organisms were heat stressed in their respective medium in DW-1 Hansatech cuvette (Hansatech Ltd., King's Lynn, Norfolk, England). The temperature was maintained by circulating the water from the thermostated water bath. During heating, the plants were either kept in darkness or illuminated with moderate (30 Wm^{-2}) or high (900 Wm^{-2}) broad band blue light (400 to 600 nm) intensity supplied by a halogen lamp (KL1500 light source; Schott, Mainz, Germany with Corning filter, CS 4-96) via fiber optics.

Chlorophyll a Fluorescence Measurement

After the stress treatment, the leaf discs were dark adapted for 10 minutes at room temperature. The Chl *a* fluorescence induction curve was monitored by a Plant Efficiency Analyzer (PEA, manufactured by Hansatech Ltd., King's Lynn, Norfolk, England) with 600 Wm^{-2} of light intensity. Illumination was provided by an array of 6 light emitting diodes (peak, 650 nm), focused on the sample surface to provide a homogeneous illuminated light spot of about 4 mm in diameter as described in detail by Strasser *et al.* (1995).

RESULTS AND DISCUSSIONS

Thermal sensitivity of PSII in pea leaves in presence of low and high light

In vivo Chl *a* fluorescence was measured in pea leaf discs which were briefly exposed to heat (15 min at 42°C) in dark or in presence of either low (30 Wm^{-2}) or high blue light (900 Wm^{-2}). When the control dark adapted leaf discs were excited by 650 nm of 600 Wm^{-2} of light, a typical O-J-I-P fluorescence induction transient was obtained. The fluorescence transient starts from an initial F_o intensity and increases to a maximum peak P through two intermediate steps between F_o and F_p labelled as J and I (Fig. 1). The first rise from O to J occurs within 2 ms. The second intermediate steps I levels in about 20 ms and the final peak in about 200 ms (for more detail see Strasser *et al.*, 1995). Heating the leaf discs for 15 min at 42°C in total darkness resulted in a large decrease in the variable Chl *a* fluorescence ($F_p - F_o$). The typical fluorescence kinetics O-J-I-P transformed in to an O-K-J-I-P transient with a new peak "K" at about 200 μs (Fig. 1 and for more detail see Guissé *et al.*, 1995). It has been shown earlier that PSII is more sensitive to heat stress in comparison to PSI (Berry & Björkman, 1980, Quinn & Williams, 1985). An early symptom of the heat injury is the loss of O_2 evolution activity and has been correlated with the deactivation of PSII due to denaturation of certain functional proteins (Thompson *et al.*, 1989), dissociation of light harvesting

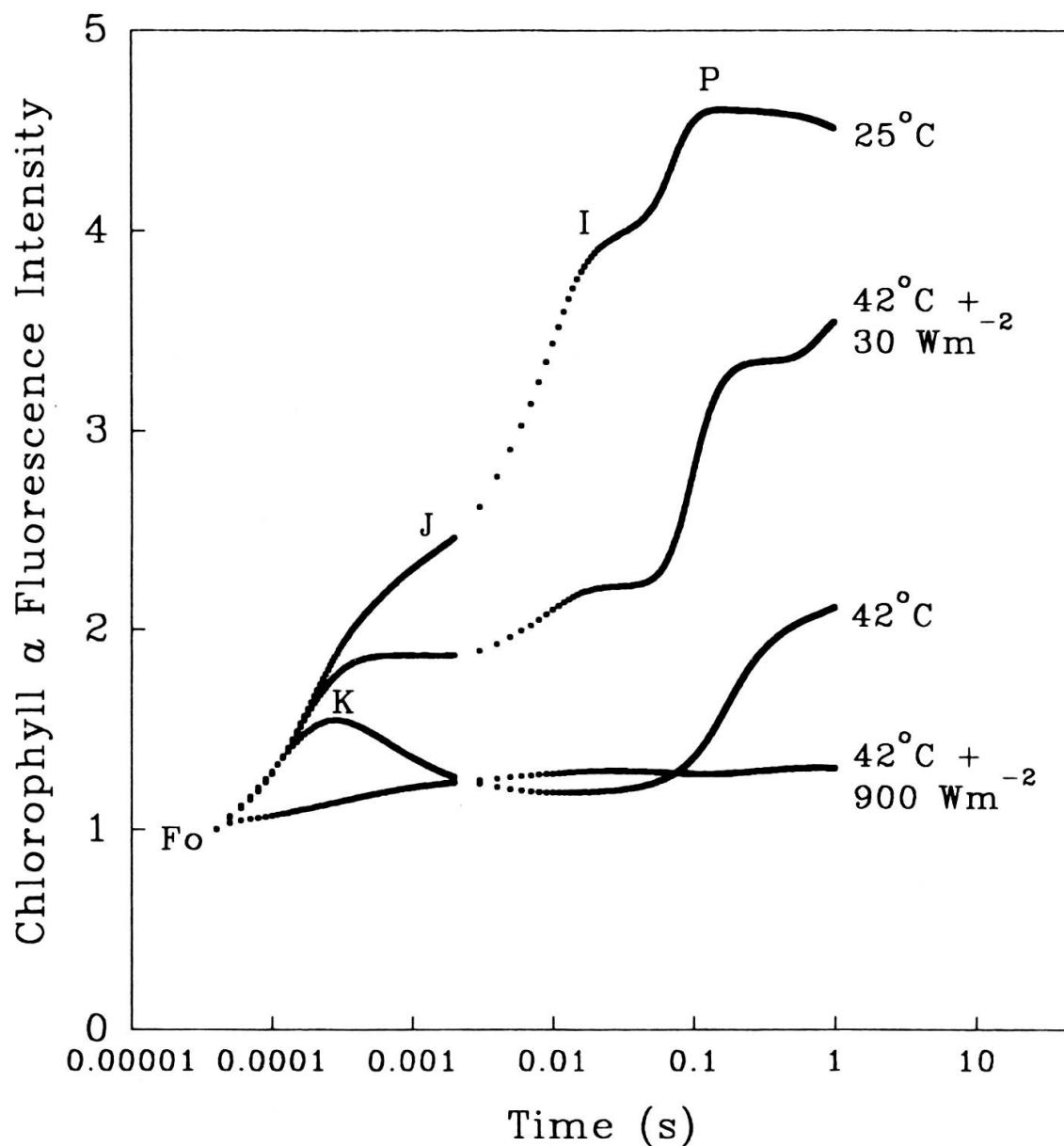


FIG. 1.

Chlorophyll *a* fluorescence induction kinetics of pea leaf discs. Leaf discs were treated with the conditions as given with each trace. All the treatments were done for 15 min and dark adapted for 10 min at room temperature before the measurements.

pigments and the PSII complex (Schreiber & Berry, 1977, Armond *et al.*, 1978, 1980; Gounaris *et al.*, 1984, Sundby *et al.*, 1986), and release of the functional Mn from the PSII (Nash *et al.*, 1985).

When the leaf discs were exposed to heat (42°C) in the presence of high light (900 Wm⁻²) a further decrease in the variable Chl *a* fluorescence was observed (Fig. 1). For example, after heat treatment in dark, the maximum variable fluorescence was reduced

by 54% whereas in the presence of high light and stressed temperature the reduction of the variable fluorescence was extended upto 72% (Fig. 1). This effect is a clear synergistic effect of heat and light.

In contrast to high light, when the heat treatment was imposed together with low light (30 Wm^{-2}) the decrease in variable Chl *a* fluorescence observed, was only about 24%, showing a protection of PSII activity by low light (Fig. 1). A similar type of result was reported earlier (Havaux & Strasser, 1990, Havaux *et al.*, 1991). The mechanism by which the low light protects PSII is still unclear. However, Weis (1982a, b) has suggested the importance of proton and metal cation concentrations of the medium for the heat stability of the isolated chloroplasts. It is possible that light stabilizes the thylakoid membranes by creating a proton gradient and maintaining ionic equilibrium. Al-Khatib & Wiest (1990) showed that elevated temperatures induce the conformational changes in the PSII reaction centers that facilitate thermal energy dissipation. When leaves were heated in the presence of low light, the heat induced alterations in the PSII reactions were considerably alleviated indicating that light efficiently protected the photochemical apparatus and photosynthesis against heat inactivation.

Acquirement of PSII thermal tolerance in pea leaves

Figure 2 shows the Chl *a* fluorescence transient of the pea leaf discs heated in dark either directly at 40°C for 15 min or pre-heated with mild temperature (30°C for 15 min) before exposing them further for 15 min at 40°C . Leaves heated with 30°C show a typical O-J-I-P fluorescence transient like control leaf discs but when the leaves were heated directly at 40°C a well defined K peak can be seen. About 50% decrease in variable fluorescence was observed in comparison to the control plants which were kept at 25°C . If the leaf discs were exposed to 40°C after a mild pre-heat treatment (30°C for 15 min) the Chl *a* fluorescence transient was more like the control one without the K peak (Fig. 2).

However, we found that pre-heat treatment (40°C for 15 min) results as well in a protection of the photosynthetic mechanism exposed to the synergistic effect of high light and high temperature (40°C and 900 Wm^{-2}) (Fig. 2). Long term adaptation of the photosynthetic apparatus to changes in growth temperature is a well-documented phenomenon. These adaptations are associated with re-organization of the thylakoid membranes, probably involving de-novo synthesis of membrane components (Berry & Björkman, 1980, Quinn & William 1985, Yordanov *et al.*, 1986). In the field, Lu *et al.* (1994) showed that heat resistant Pima cotton plants have modified themselves by reducing the size of their leaves and by increasing stomatal conductances, thus resulting in lowering the leaf temperature by evaporative cooling. It is also well documented that seasonal changes provoke the thermal resistance of the photosynthetic apparatus, with summer plants being noticeable more heat-resistant than winter plants (Downton *et al.*, 1984, Seeman *et al.*, 1986). But the duration for these types of adaptation is of the order of days or more.

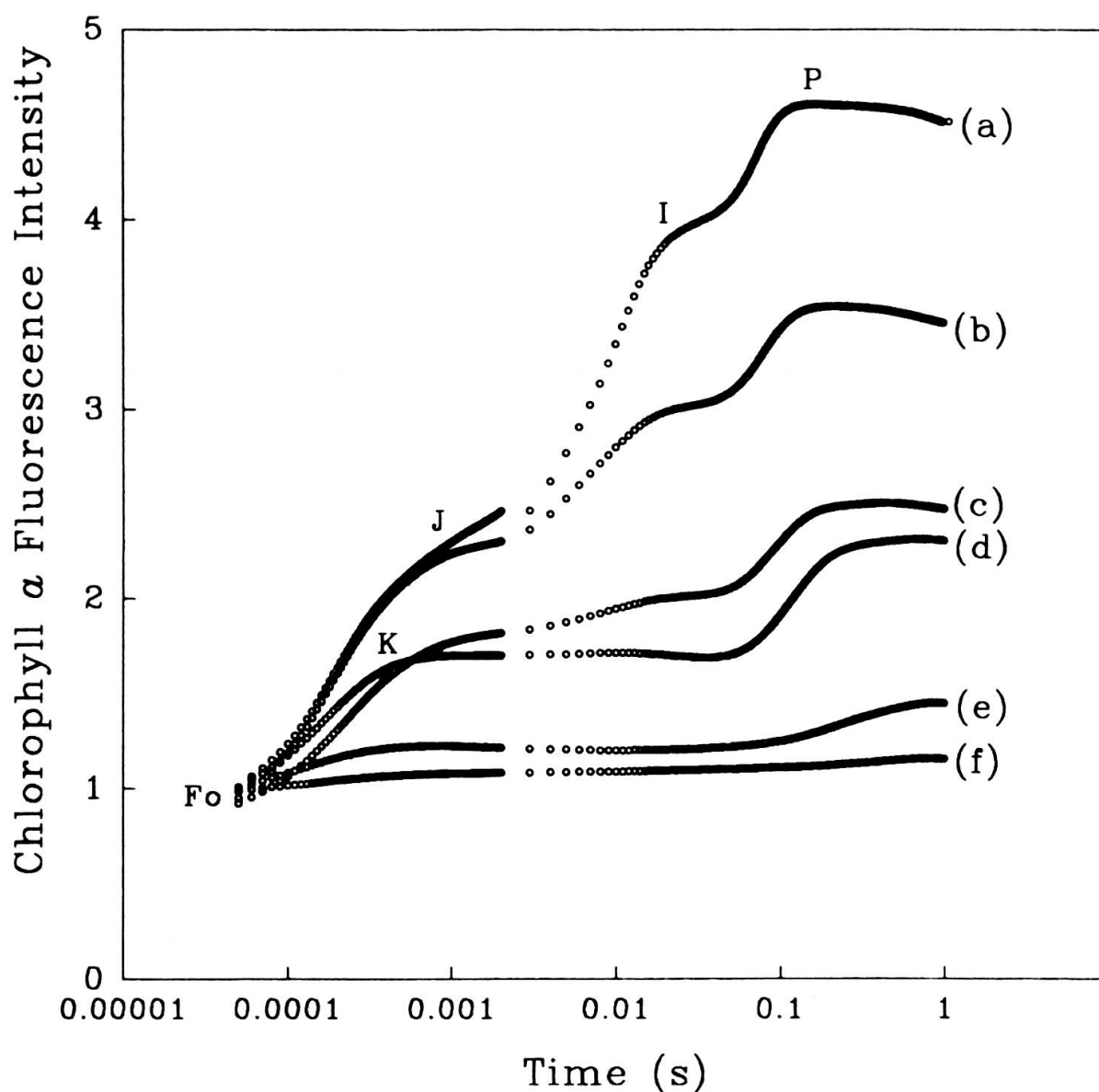


FIG. 2.

Chlorophyll *a* fluorescence induction kinetics of pea leaf disc at room temperature. Each treatment was done for 15 min. Trace (a): Chl *a* fluorescence transient of a control leaf disc. (b) Heated at 30°C. (c) First heated at 30°C and then transferred to 40°C. (d) Directly heated at 40°C. (e) First heated at 40°C and then exposed to 40°C together with 900 Wm⁻² light intensity. (f) Directly exposed to 900 Wm⁻² together with 40°C.

The present paper shows that, besides these long term processes, the most thermo-labile component of the photosynthetic apparatus, PSII, can rapidly adjust the level of its resistance to temperature stress within minutes. Additionally, it was observed that slight changes in leaf temperature (e.g., 30°C) was enough to trigger some thermal adaptation of PSII. The exact mechanism by which PSII thermostability can rapidly increase in leaves exposed to mild heat-stress conditions remains to be elucidated. But

one can speculate that the fast adaptive changes in PSII complex may be either due to conformational changes in PSII or changes in the surroundings of the chloroplastic membranes as suggested by various *in vivo* (Havaux, 1993, 1994) and *in vitro* studies (Weis, 1982a, b, Seeman *et al.*, 1986, Inoué *et al.*, 1987). Irrespective of the exact molecular mechanism for the observed changes, this paper confirms the thermal plasticity of PSII *in vivo*. Clearly the reported changes in PSII indicate a rapid process for photosynthetic adaptation to daily temperature variation of the environment. During the time course of the day, the usual increase in temperature can be quite high and the variation can be as high as 20°C (Lu *et al.*, 1994). One can put the possible scenario during the course of the day as in Fig. 3. In the morning, plants acclimatize themselves

DEVELOPMENT OF STRESS TOLERANCE OVER DAILY TIME COURSE

A REAL ADAPTATION PHENOMENON

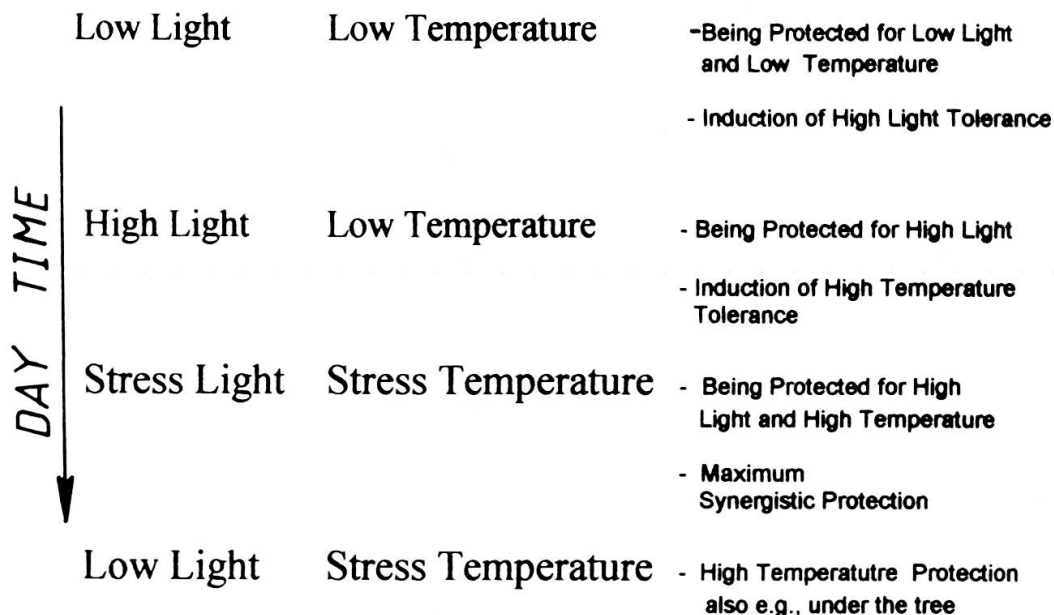


FIG. 3.

A model showing the changes in light intensities and temperature and the development of possible stress tolerance by the plants during the time course of the day.

by low temperature for high light, which protects them during mid-day when the light is very intense. In early afternoon, when the temperature also starts to rise, some plants protect themselves by closing the stomata and decreasing the rate of photosynthesis like mid-day depression (Wise *et al.*, 1991). In late afternoon, although the temperature is quite high, the plants can protect themselves due to the presence of low light.

An evolutionary trend of the protection of heat stress by low light

The aquatic plants have several advantages over their terrestrial counterparts. A major advantage is that the presence of water is in abundance and the variation in temperature is not so high as on the land. But free floating members of the aquatic flora are on the surface of the water and most of their parts are exposed to light and heat like the land plants. We have studied the heat protection effect by low light phenomena in different categories of these plants. Table 1 shows that all the land plants have the capacity to protect themselves against heat stress in the presence of low light. The free floating water-plants also showed the same response like the land plants. The submerged water-plants acted differently. Some times they were able to protect themselves with low light against heat stress but some times this phenomenon was totally absent. The variation in response could be due to the depth of the water tank. In contrast to all these terrestrial and aquatic plants, the unicellular organisms totally lack this behavior. These results suggest that the terrestrial plants have developed this unique feature for protecting themselves from heat stress during the evolution of the land plant.

TABLE 1.

Heat protection mechanism by low light in different organisms. For experimental details, see the text.

Land Plants	
<i>Pisum sativum</i>	++++
<i>Lycopersicum esculentum</i>	++++
<i>Camellia</i>	++++
Swimming Plants	
<i>Salvinia natans</i>	++++
<i>Pistia stratiotes</i>	++++
Submerged Plants	
<i>Elodea</i>	++—
<i>Potamogeton sp.</i>	+—
Unicellular organisms	
<i>Chlorella sp.</i>	—
<i>Chlorella rubrum</i>	—
<i>Chlamydomonas reinhardtii</i>	—
<i>Scenedesmus</i>	—

+ represents the relative heat protection by low light.

— indicates absence of heat protection mechanism by low light.

CONCLUSION

In conclusion, the presented data illustrate the complexity of the photosynthetic responses to environmental stresses with the effect of a given stress being markedly modulated by the other environmental factors. This study demonstrates the antagonism/synergism between the two main variables of the day, the temperature and the light, and shows that a combination of heat and light elicit less injurious effects on the *in vivo* PSII function than heat stress alone. As a result, the *in vivo* PSII activity could be substantially more heat resistant in the field than previously estimated from the laboratory experiments. The interaction between stressors also suggests that the stress effects on the plants monitored under controlled environmental conditions in the laboratory, where the effects of a defined stress are studied in a "one factor-one response" test, might be quite different from the plant's responses in the field, where several factors usually change simultaneously and interact. The results also indicate that plants have adapted themselves, for their best, for any given environmental conditions. The thermal protection by low light and by training the plants with pre-mild heat treatment suggests that the present terrestrial plants are well tuned for their natural inhabitant for every changes in the present daily cycle of the earth, for example heat and light, as discussed here.

ACKNOWLEDGEMENT

We thank Dr. Merope Tsimilli-Michael for critically reading the manuscript. This work was supported by the Swiss National Fund grant number 31.33678.92.

RÉSUMÉ

L'intensité de la fluorescence de la chlorophylle *a*, induite par la lumière, a été utilisée pour mesurer les effets d'un stress à la chaleur et à la lumière sur l'activité photochimique du photosystème II (PSII). L'exposition de plantes de pois cultivées à 22°C, à la chaleur (température supérieure à 40°C) a provoqué une forte baisse de l'activité du PSII. La présence d'une intensité lumineuse forte durant ce traitement a eu pour effet d'augmenter les dégâts causés au PSII. Au contraire, une intensité lumineuse faible a eu pour effet de protéger efficacement l'activité photochimique contre son inactivation par la chaleur. Une protection contre la chaleur a également été observée lorsque les feuilles avaient été acclimatées à une température de 30°C avant d'être exposées à un stress à 40°C. Une résistance à la photoinhibition a été induite en exposant les feuilles à une température élevée, pendant 15 min, avant de les illuminer avec une forte lumière. Les résultats des expériences indiquent que les plantes terrestres possèdent des mécanismes d'adaptations leur permettant de se protéger contre des stress à la chaleur et à la lumière, situations qui surviennent régulièrement durant la journée et

auxquelles les plantes doivent faire face. Un comportement semblable n'a pas été observé pour les algues. Les plantes aquatiques doivent être considérées de cas en cas. En effet, certaines d'entre elles ont été en mesure de se protéger contre un stress à la chaleur, en présence d'une intensité lumineuse faible, alors que ce phénomène était totalement absent pour d'autres espèces aquatiques.

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