

Photosynthetic acclimation to high temperatures in wheat

O. H. SAYED

Department of Botany, Faculty of Science, University of Qatar, P.O. Box 2713, Doha, Qatar

SUMMARY

Growth and photosynthetic performance were assessed for the Finnish wheat *Triticum aestivum* L. var. APU under a cool (13/10°C day/night) and a warm (30/25°C day/night) regime. Plants exhibited a certain degree of acclimation to warm growth conditions. This acclimation appeared to involve enhanced performance of both photosystem II and whole-chain electron transport. Enhanced thermal stability of photophosphorylation was also observed in warm-grown plants.

Key-words: acclimation, growth temperature, photophosphorylation, *Triticum aestivum*, wheat.

INTRODUCTION

Temperature is one of the major ecological variables that determine plant distribution. Cereal crops are often selected for a region on the basis of their responses to temperature conditions prevailing in that region (Choudhury & Wardlaw 1978). Much of the work on the effect of temperature on wheat yield has concentrated on the period of grain development (Radley 1978; Bhullar & Jenner 1983). Although grain development is sustained by current photosynthesis, little attention has been given to this aspect of crop plants. It has been shown that certain plants possess considerable phenotypic plasticity in photosynthetic performance (Percy *et al.* 1977). This plasticity involves photosynthetic acclimation of functional properties of the plant to local environmental conditions (Berry & Bjorkman 1980). Moreover, there are some reports on the effect of growth temperature on key components of the photosynthetic machinery (Chapman *et al.* 1984; Leong & Anderson 1984). In a previous study the Finnish wheat var. *Triticum aestivum* APU was shown to exhibit an upward shift in the optimum temperature for CO₂ exchange (Sayed *et al.* 1989a) and an enhanced thermal stability of electron transport via the two photosystems (Sayed *et al.* 1989b) when grown under warm conditions. The objective of this paper was to test potential acclimation of this wheat variety and modulation of photophosphorylation by growth under warm conditions.

MATERIALS AND METHODS

The Finnish wheat (*Triticum aestivum* L.) variety APU (Plant Breeding Institute, UK) was grown on vermiculite and irrigated with modified Hoagland's solution (Johnson *et al.* 1957). Plants were raised under a cool (13/10°C) or a warm (30/25°C) regime with 12-h day/night cycles and an irradiance of 60 Wm⁻². Dry weights were determined after oven drying at 70°C for 3 days and leaf area was measured by using a Delta-T leaf area meter

Table 1. Growth parameters of the Finnish wheat var. *Triticum aestivum* APU when raised under a cool (13/10°C) and a warm (30/25°C) regime for 16 days (mean \pm SE, $n=5$)

Growth parameter	Cool-grown	Warm-grown
Shoot dry wt (g/plant)	0.02 \pm 0	0.04 \pm 0
Shoot:root ratio	1.40 \pm 0.1	2.80 \pm 0.3
Area of 1st leaf (cm ²)	4.00 \pm 0.4	6.00 \pm 0.1
Chlorophyll of 1st leaf (mg g ⁻¹ fresh wt)	0.28 \pm 0.1	0.42 \pm 0.2

(Delta-T Devices, UK). Growth criteria were assessed for 16-day-old plants, the time when first leaves of cool-grown plants had maximum expansion and chlorophyll content. For other purposes, first leaves of 16-day-old cool-grown and 43-day-old warm-grown plants were used as test materials.

Responses of the *in-vivo* chlorophyll fluorescence to growth temperature were monitored using a portable fluorometer (Plant Productivity Meter SF 10, Richard Branker Res. Ltd, Canada). Diurnal changes of the prompt fluorescence transient kinetics were measured as F_R , the maximal of the induced rise in chlorophyll fluorescence (Smillie & Hetherington 1983) after 10 min dark incubation of leaf segments at 25°C.

Chloroplasts were isolated (Nolan & Smillie 1976), chlorophyll content was determined (Arnon 1949) and aliquots (50 μ l) were heat pretreated for 3 min at different temperatures (as indicated in Figs 2 and 3) prior to measurements. After heat pretreatment, all assays were performed at 25°C and an irradiance of 200 Wm⁻².

The ammonium chloride-uncoupled whole-chain electron transport (5 mM NH₄Cl) was measured as the rate of oxygen uptake associated with the flow of electrons from water to methyl viologen (Allen & Holmes 1986) by an oxygen electrode (Hansatech Ltd, UK). Rate of non-cyclic photophosphorylation was calculated from data of photosynthetic control (State 3–State 4 transition) and ADP/O ratio (Allen & Holmes 1986). Cyclic photophosphorylation was induced in the presence of the co-factor *N*-methyl phenazonium methosulphate and the ATP synthesized was determined by the Luciferine/Luciferase technique (Mills 1986) and bioluminescence was measured using a luminometer (LKB Wallac, Finland). Chlorophyll content of chloroplast suspension was 100, 80, and 20 μ g ml⁻¹ for whole-chain electron transport, non-cyclic and cyclic photophosphorylation, respectively.

RESULTS

Development of the variety APU was profoundly influenced by growth temperature. Warm-grown plants accumulated higher amounts of dry matter in their shoots, attained higher shoot:root ratio, had a larger first leaf area, and contained more chlorophyll in their first leaves than cool-grown plants (Table 1).

Monitoring F_R at 25°C for 3 consecutive days revealed the presence of diurnal fluctuations in which F_R followed a declining trend as the day progressed, reaching a minimum at midday and an increasing trend in the afternoon and during the night reaching a maximum at midnight (Fig. 1). However, the values of F_R of leaf segments from warm-grown plants were always higher than those in leaf segments from cool-grown plants.

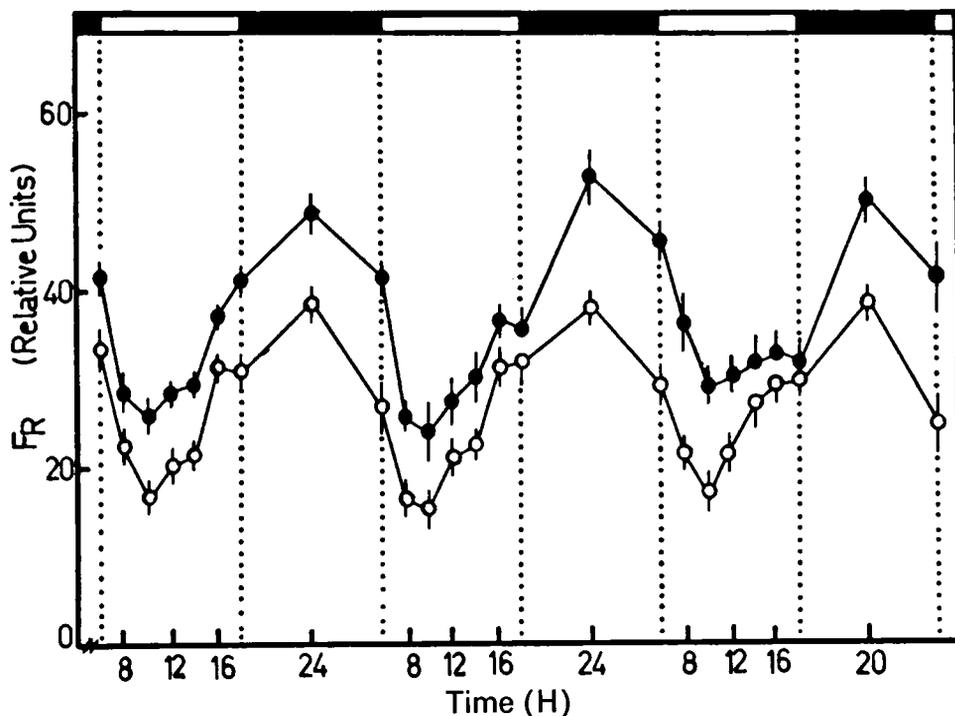


Fig. 1. Diurnal changes of F_R measured at 25°C in leaf segments of cool-grown (○) and warm-grown (●) plants of the wheat variety APU (mean ± SE, $n=4$).

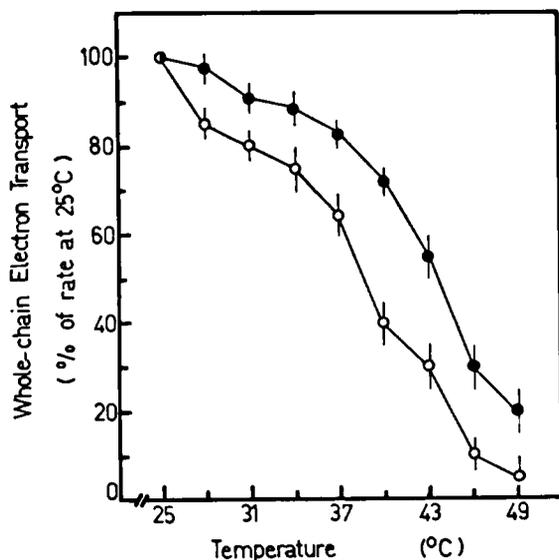


Fig. 2. Effect of heat stress on the ammonium chloride-uncoupled whole-chain electron transport in thylakoids isolated from cool-grown (○) and warm-grown (●) plants of the wheat variety APU. The 100% rate at 25°C (no heat treatment) was 100 $\mu\text{mol O}_2$ consumed mg^{-1} Chlorophyll h^{-1} (mean ± SE, $n=4$).

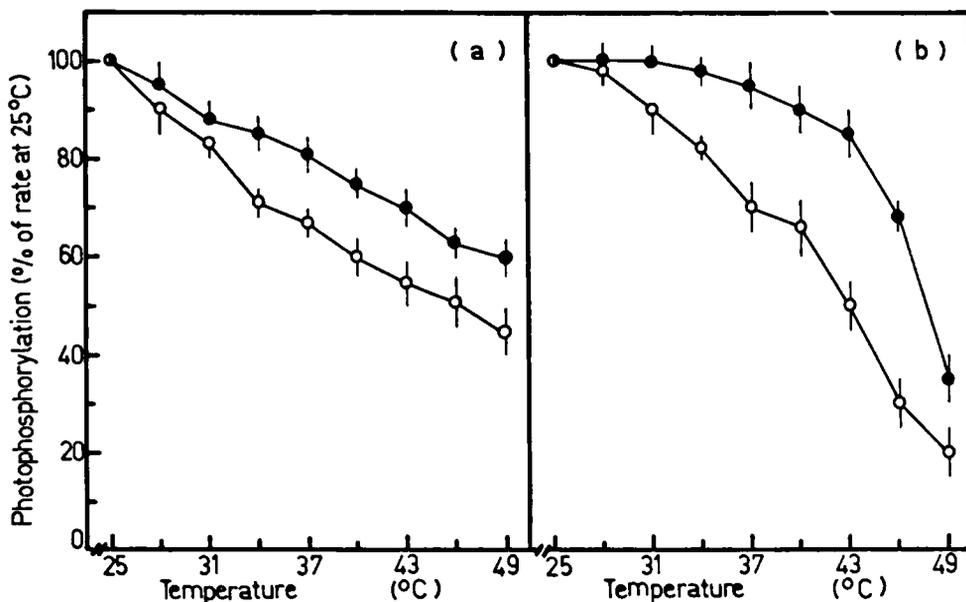


Fig. 3. Effect of heat stress on non-cyclic (a) and cyclic (b) photophosphorylation in thylakoids isolated from cool-grown (○) and warm-grown (●) plants of the wheat variety APU. The 100% rates at 25°C (no heat treatment) were 100 and 300 $\mu\text{mol ATP mg}^{-1}$ chlorophyll h^{-1} for cyclic and non-cyclic photophosphorylation, respectively (mean \pm SE, $n=4$).

Rates of the ammonium chloride-uncoupled whole-chain electron transport (Fig. 2), non-cyclic (Fig. 3a) and cyclic photophosphorylation (Fig. 3b) were expressed as percentages of rates measured after pretreatment at 25°C. These rates were higher and more stable towards heat stress in chloroplasts isolated from warm-grown plants than in those isolated from cool-grown plants. Moreover, non-cyclic photophosphorylation appeared to be more sensitive to heat stress than cyclic photophosphorylation in cool-grown plants up to 43°C.

DISCUSSION

The Finnish wheat var. *Triticum aestivum* of APU grew well under the cool regime and appeared to have a certain degree of potential acclimation to warm growth conditions. This acclimation was reflected as enhanced shoot dry-matter accumulation and increased area and chlorophyll content of first leaves of warm-grown plants. It was also accompanied by enhanced photosynthetic performance as indicated by data of F_R . Changes in F_R have previously been used to assess thermotolerance in crop plants (Smillie & Hetherington 1983) and the reduction or loss of F_R was considered to be a manifestation of heat injury on the donor side of photosystem II (Havaux & Lannoye 1984). Continuous monitoring of F_R revealed the presence of diurnal fluctuation in which high values of F_R recorded during the night could be due to long dark incubation prior to stimulation. Diurnal fluctuations of the variable component of chlorophyll fluorescence have been attributed to changes in the stoichiometry of the amounts of electron carriers between the photosystems (Everson *et al.* 1983). However, when measured at 25°C F_R was higher in

leaf segments of warm-grown plants than in those of cool-grown plants which reflects enhanced thermal stability of electron transport via photosystem II in warm-grown plants. Moreover, photosystem I-mediated electron transport has repeatedly been reported to be stable towards heat stress (Quinn & Williams 1985; Thomas *et al.* 1986) and this was confirmed for the wheat variety APU (Sayed *et al.* 1989b). Therefore, enhanced thermal stability of whole-chain electron transport in warm-grown plants is, at least in part, due to an enhanced performance of photosystem II.

Furthermore, two native coupling sites are known to exist within the photosynthetic electron-transport chain in thylakoid membranes (Jagendorf 1977). The site which is close to photosystem II was reported to be sensitive to heat stress (Santarius 1975) which may account for the observed heat sensitivity of non-cyclic photophosphorylation. On the other hand, photosystem I-mediated cyclic photophosphorylation driven by the co-factor *N*-methyl phenazonium methosulphate involved an artificial energy conservation site. Accordingly, the reduced co-factor shuttles electrons across the membrane generating a proton gradient upon being oxidized by the electrogenic photosystem I (Trebst 1980). The relative heat stability of this artificial site perhaps accounts for the differential heat sensitivity to heat stress of non-cyclic and cyclic photophosphorylation. Enhanced heat stability in warm-grown plants suggests modulation by growth temperature of the electron flow/photophosphorylation assembly. Therefore, it seems reasonable to suggest that conformational changes in the thylakoid membranes during acclimation to high temperature may be relevant to the observed improved thermotolerance of electron transport and photophosphorylation.

REFERENCES

- Allen, J.F. & Holmes N.G. (1986): Electron transport and redox titrations. In: Hipkins, M.F. and Baker N.R. (eds): *Photosynthetic Energy Transduction*. 103–141, IRL Press, Oxford.
- Arnon, D.I. (1949): Copper enzymes in isolated chloroplasts. Polyphenol-oxidase in *Beta vulgaris*. *Plant Physiol.* **24**: 1–15.
- Berry, J. & Bjorkman, O. (1980): Photosynthetic responses and adaptation to high temperature in higher plants. *Ann. Rev. Plant Physiol.* **31**: 491–543.
- Bhullar S.S. & Jenner C.P. (1983): Responses to brief periods of elevated temperatures in ears and grains of wheat. *Austr. J. Plant Physiol.* **10**: 549–560.
- Chapman D.J., De-felice J. & Barber J. (1984): Lipid, protein and Plastoquinone-A content of chloroplast thylakoids: Effect of plant growth temperature. In: Cybesma, C. (ed.): *Advances in Photosynthesis Research* 275–278, M. Nijhoff Dr. Junk Publishers, The Hague.
- Choudhury, S.I. & Wardlaw, I.F. (1978): The effect of temperature on kernel development in cereals. *Austr. J. Agric. Res.* **29**: 205–223.
- Everson, G., Chen, S. & Black, C. C. (1983): Diurnal variations in leaf fluorescence induction kinetics. *Plant Physiol.* **72**: 455–460.
- Havaux, M. & Lannoye, R. (1984): Effect of chilling temperatures on prompt and delayed chlorophyll fluorescence in leaves. *Photosynthetica* **18**: 117–127.
- Jagendorf, A.T. (1977): Photophosphorylation. In: Trebst, A. and Avron, M. (eds): *Encyclopaedia of Plant Physiology*, New Series. Vol. **5**, 307–337, Springer-Verlag, Berlin.
- Johnson, C.H., Stout, P.R., Broyer, T.C. & Carlton A.B. (1957): Comparative chlorine requirements of different plant species. *Plant Soil* **8**: 337–353.
- Leong, T. & Anderson, J.M. (1984): Effect of temperature during growth on the distribution of chlorophyll-protein complexes, coupling factor CF₁ activity and photosynthetic rates in two cultivars of sunflower. In: Cybesma, C. (ed.): *Advances in Photosynthesis Research* 267–270. M. Nijhoff/Dr. Junk Publishers, The Hague.
- Mills, J.D. (1986): Photophosphorylation. In: Hipkins, M.F. and Baker, N.R. (ed): *Photosynthetic Energy Transduction* 143–187, IRL Press, Oxford.
- Nolan, W.G. & Smillie, R.M. (1976): Multi-temperature effects on Hill reaction activity of barley chloroplasts. *Biochim. Biophys. Acta* **440**: 461–475.
- Pearcy R.W., Berry, J.A. & Fork, D.C. (1977): Effect of growth temperature on the thermal stability of the photosynthetic apparatus of *Atriplex lentiformis* (Torr.) Wats. *Plant Physiol.* **59**: 873–878.
- Quinn, P.J. & Williams, W.P. (1985): Environmentally induced changes in chloroplast membranes

- and their effects on photosynthetic function. In: Barber, J. and Baker N.R. (eds): *Photosynthetic Mechanisms and the Environment*, Vol. 6, 1-47. Elsevier, Amsterdam.
- Radley M. (1978): Factors affecting grain enlargement in wheat. *J. Exp. Bot.* **29**: 919-934.
- Santarius M. (1975): Sites of heat sensitivity in chloroplasts and differential inactivation of cyclic and noncyclic photophosphorylation by heating. *J. Thermal Biol.* **1**: 101-107.
- Sayed O.H., Emes M.J., Earnshaw M.J. & Butler R.D. (1989a): Photosynthetic responses of different varieties of wheat to high temperature. I. Effect of growth temperature on development and photosynthetic performance. *J. Exp. Bot.* **40**: 625-631.
- Sayed O.H., Earnshaw, M.J., & Emes, M.J. (1989b): Photosynthetic responses of different varieties of wheat to high temperature. II. Effect of heat stress on photosynthetic electron transport. *J. Exp. Bot.* **40**: 633-638.
- Smillie R.M. & Hetherington S.E. (1983): Stress tolerance and stress-induced injury in crop plants measured by chlorophyll fluorescence *in vivo*. *Plant Physiol.* **72**: 1043-1050.
- Thomas, P.G., Quinn, P.J. & Williams, W.P. (1986): The origin of photosystem I-mediated electron transport stimulation in heat-stressed chloroplasts. *Planta* **167**: 133-139.
- Trebst A. (1980): Inhibitors in electron flow. Tools for the functional and structural localisation of carriers and energy conservation sites. In: San Pietro, (ed.): *Methods In Enzymology*. Vol. **69**, 675-715. Academic Press, New York.