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Effects of temperature on growth, morphology, and photosynthesis in wheat

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Abstract

Several morphological characteristics differed when wheat (*Triticum aestivum* L. cv. Doha 88) was grown under a cool (10 °C), warm (20 °C), and hot (30 °C) regime. Development of leaves was linearly related to shoot meristem temperature, and the time between appearance of successive leaves on the main culm was independent of growth temperature. Area and dry mass of leaves and roots increased exponentially with time, and variations between growth temperature regimes were reduced when plants were compared at a similar developmental age. In isolated thylakoids thermal stability of photosystem 2 and of whole electron transport chain was enhanced with the increase in growth temperature. Therefore this cultivar is able to acclimate to contrasting temperature regimes.

Key words: chlorophyll content, dry mass, leaf area, root area, photosystem 2, *Triticum aestivum*, whole chain electron transport

Introduction

Temperature is an environmental factor that cannot be manipulated in the field, and crops are often selected for a given region on the basis of their responses to temperature conditions in that region (Chowdhury and Wardlaw 1978). In areas of the world with mild winters and hot summers, wheat is sown in the autumn as temperatures are falling, and harvested in early summer. Late sowing results in reduced yield because grain filling takes place during hot summer (Sofield *et al.* 1977, Radley 1978, Buhullar and Jenner 1983), while early sowing curtails vegetative growth (Bagga and Rawson 1977).

Work presented in the present paper was carried out to investigate developmental and morphological responses of the wheat cv. Doha 88 to different growth temperature regimes. To avoid changes resulting from ontogeny, plants grown at different temperature were compared at a similar developmental age (Clarkson *et al.* 1988) using time-scale based on accumulated thermal time (White *et al.* 1990).

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It is well documented that shoot development in cereals is ordered on a phyllochron (time between appearance of successive leaves on the main culm) basis (Klepper *et al.* 1984), and that the rate of leaf appearance on the main culm is linearly related to shoot meristem temperature (Ong 1983). Therefore, the phyllochron, and the basal temperature for leaf appearance on the main culm were determined. Moreover, responses to high temperature of photosynthetic activities in chloroplasts isolated from leaves have been described.

Materials and methods

Wheat (*Triticum aestivum* L. cv. Doha 88) was grown on vermiculite and irrigated with modified Hoagland's nutrient solution (Johnson *et al.* 1957) in *Fitotron 600* growth cabinets (*Fisons*, Leics., UK). Plants were grown at a constant temperature of 10 °C (cool regime), 20 °C (warm regime), and 30 °C (hot regime) and a photon flux density of 250 μmol m^{-2} s^{-1} in 12 h day/night cycles.

Ten plants were sampled. Main culm leaf number (Haun 1973), and length were determined. Leaf area was measured by using a leaf area meter (*Delta/T Devices*, Cambridge, UK). Root area was measured by using *VIDS* software which combines TV camera video output, a computer graphics display, and a *Calcomp* digitizing tablet (*Analytical Measuring Systems*, Essex, UK). Shoots and roots were freeze dried, and dry mass was determined. Basal temperature for leaf appearance, and phyllocron were determined after White *et al.* (1990).

Total chlorophyll content of the first leaf was determined according to Arnon (1949). Thylakoids were isolated (Leegood and Malkin 1986) from fully expanded first leaves of 18-, 16-, and 14-d-old plants of cool-, warm-, and hot-grown plants, respectively. Aliquotes (50 μl) of thylakoid suspension were pre-treated at different temperatures for 3 min prior to measurement of electron transport at 25 °C and photon flux density of 850 μmol m^{-2} s^{-1}. The gramicidin-uncoupled PS 2 activity was assessed by measuring absorption changes associated with the flow of electrons from water to 2,6-dichlorophenol indophenol (Sayed *et al.* 1989b). The ammonium chloride-uncoupled whole-chain electron transport was measured as the rate of oxygen uptake associated with the flow of electrons from water to methyl viologen (Allen and Holmes 1986) by an oxygen electrode (*Hansatech Ltd.*, Norfolk, UK). Each measurement was repeated five times, and data were presented as percentage of control measurements made after heat treatment for 3 min at 25 °C. Results were expressed as mean ± SE.

Results

The number of leaves on the main culm increased linearly with time in plants grown under all three regimes, with a negative offset from the origin (Fig. 1A). The rate of leaf appearance on the main culm decreased in the order hot-grown (HG) plants > warm-grown (WG) plants > cool-grown (CG) plants. Extrapolation (Fig. 2A) showed that the apparent basal temperature for leaf appearance was 5.5 °C. The phyllochron was independent of growth temperature and attained a value of about 120 °C d for the three regimes applied (Fig. 1A). Areas of both leaves and roots increased with time, the total recorded leaf area and root area decreased in the order HG plants > WG plants > CG plants (Fig. 1B,C), and areas of leaves and roots were highly correlated in plants grown under the three regimes (Fig. 2B).

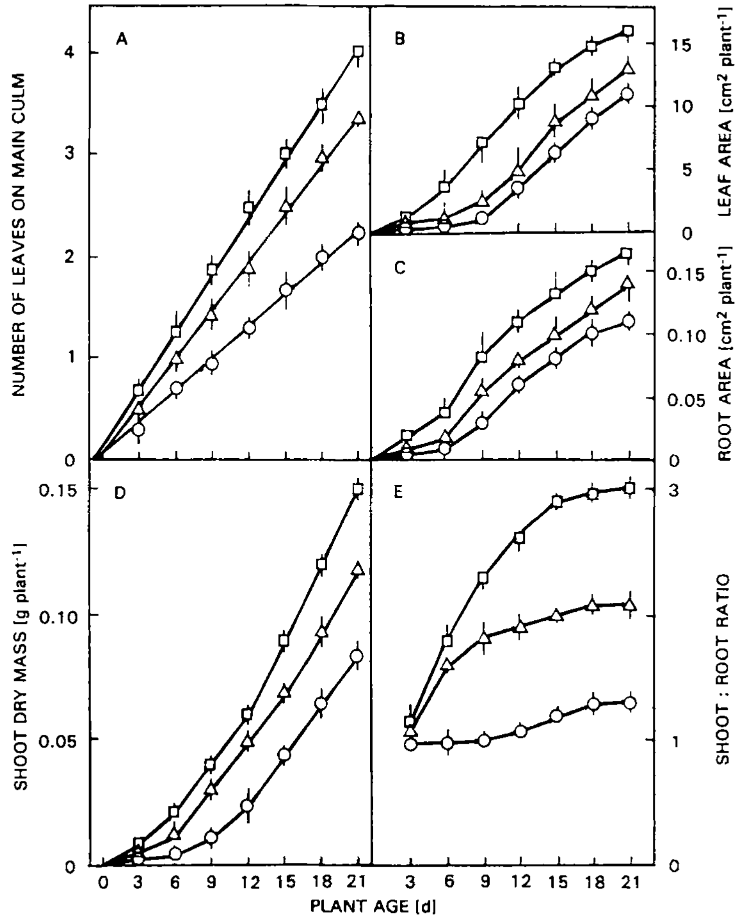

Fig. 1. The relationship between plant age and main culm leaf number (*A*), leaf area (*B*), root area (*C*), shoot dry mass (*D*), and shoot/root dry mass ratio (*E*) in the wheat cv. Doha 88 grown under cool (*circles*), warm (*triangles*), and hot (*squares*) regimes (mean ± SE, n = 10).

Shoot dry mass increased exponentially throughout 21d of the experiment, with the total mass being higher the higher the growth temperature was applied (Fig. 1D). However, when data were expressed on a developmental time-scale, differences between growth regimes were significantly reduced (Fig. 1E). The allometric relationship between shoot dry mass and root dry mass on a log scale was linear (Fig. 2D).

The length and chlorophyll content of the first leaf increased with time and reached maximum values at about 18 d, 16 d, and 14 d, in CG, WG, and HG plants, respectively (Fig. 3A,B). These fully expanded leaves were consequently used for thylakoid isolation. The uncoupled activity of PS 2 (Fig. 3C) and whole chain electron transport (Fig. 3D) were inhibited with increased heat pre-treatment

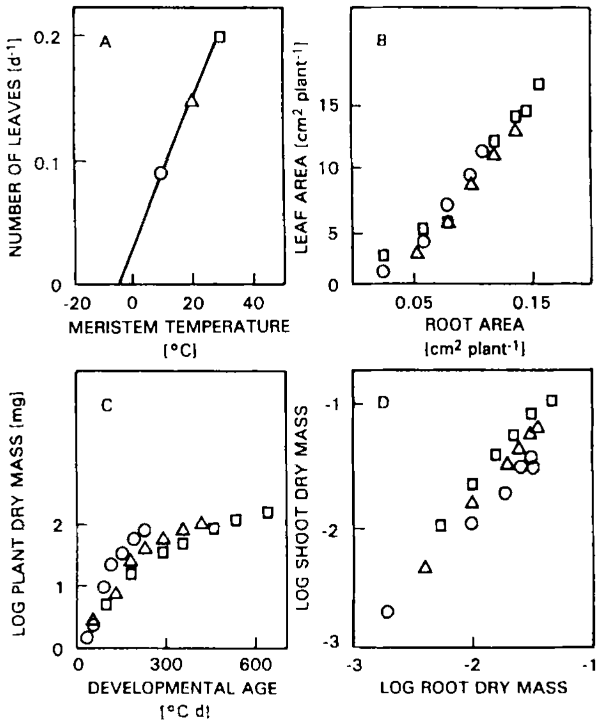

Fig. 2. The relationship between the rate of leaf appearance on main culm and shoot meristem temperature (*A*), the correlation between leaf area and root area (*B*), dry mass accumulation expressed on a log-scale and a developmental time scale (*C*), and the relationship between $\log_{10}$ shoot dry mass and $\log_{10}$ root dry mass (*D*) of the wheat cv. Doha 88 grown under cool (*circles*), warm (*triangles*), and hot (*squares*) regimes (regression lines not shown for clarity).

Table 1. Effect of growth temperature on the heat pre-treatment temperature causing 50 % reduction (T_{50}) in PS 2 activity and whole-chain electron transport in the wheat cv. Doha 88 grown under three temperature regimes (mean ± SE, n = 5).

Growth regime	T_{50} [°C] PS 2	whole-chain
Cool	40 ± 0.5	40 ± 0.3
Warm	42 ± 0.8	45 ± 0.7
Hot	45 ± 0.1	46 ± 0.4

temperature. An upward shift in the temperature causing 50 % inhibition of PS 2 activity and whole electron transport chain (T_{50}) was observed (Table 1).

Discussion

A linear relationship between the number of leaves on the main culm and shoot meristem temperature was observed in the wheat (*Triticum aestivum* L. cv. Doha 88 - Fig. 2A). Such a linear relationship has previously been reported in many cereals (Baker *et al.* 1980, Warington and Kanemasu 1983, Ong 1983, Baker *et al.* 1986, White *et al.* 1990). This linearity allowed calculation of the phyllochron which was constant for the three regimes applied. The calculated phyllochron value of 120 °C d compared to values reported for other *T. aestivum* cultivars (Baker *et al.* 1980, Baker *et al.* 1986, Masle *et al.* 1989, White *et al.* 1990), and for other temperate grasses (Kirby *et al.* 1982, Rooney *et al.* 1989). The estimated value of the basal temperature

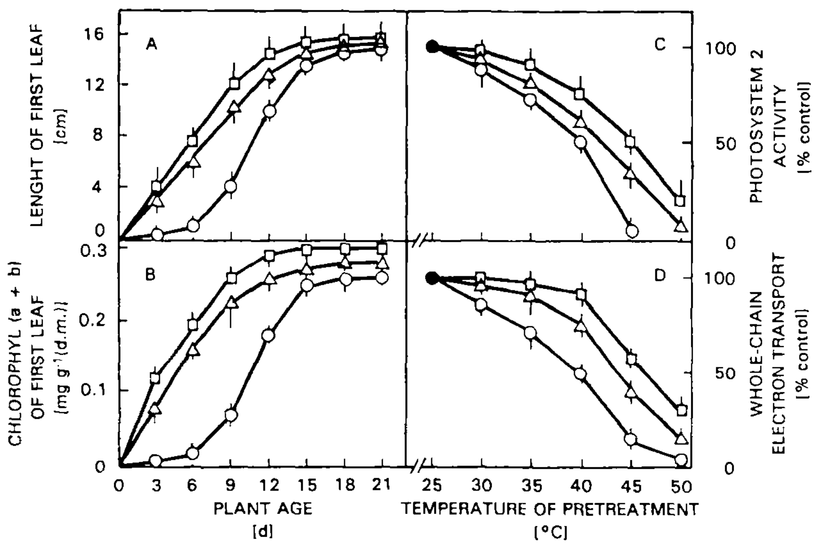

Fig. 3. Elongation (*A*), and total chlorophyll content (*B*) of the first leaf (mean ± SE, *n* = 10), and the effect of pre-treatment temperature on PS 2 activity (*C*), and whole-chain electron transport (*D*) in thylakoids isolated from the wheat cv. Doha 88 grown under cool (*open circles*), warm (*triangles*), and hot (*squares*) regimes (mean ± SE, *n* = 5). The 100 % rates (*closed circles*) at 25 °C (no heat pre-treatment) were 0.111 μmol DCPIP photoreduced mg^{-1}(Chl) s^{-1}, and 0.028 μmol (O_2 consumed) mg^{-1}(Chl) s^{-1}, for PS 2 and whole-chain electron transport, respectively.

for leaf appearance on the main culm of 5.5 °C was in agreement with previously reported data for other *T. aestivum* cultivars (Baker *et al.* 1980, 1986, White *et al.* 1990), and other temperate grasses (Kirby *et al.* 1982, Rooney *et al.* 1989).

Areas of leaves and roots increased with time, their values were higher the higher the growth temperature (Fig. 1B,C), and they appeared to be highly correlated

(Fig. 2B). A similar effect of growth temperature on development of shoots and roots in *T. aestivum* has previously been reported (Sayed *et al.* 1989a). The total accumulated plant dry mass increased with time and was higher the higher the growth temperature (Fig. 1D). These differences observed between plants grown under different regimes were significantly reduced when data were expressed on a thermal-time basis (Fig. 2C). Accumulation of shoot dry mass was highly correlated with that of roots (Fig. 2D), and the shoot/root ratio decreased in CG plants (Fig. 1E), as has previously been reported for several other cereals (Clarkson *et al.* 1988).

The observed thermal susceptibility of PS 2-mediated electron transport (Fig. 3C) has long been recognized (Santarius 1975, Sayed *et al.* 1989b). This susceptibility was attributed to a possible heat-induced functional separation of PS 2 light harvesting complexes from the rest of the PS 2 complex (Wies 1982). Support for this hypothesis stemmed from phase-separation of non-bilayer lipids, and physical dissociation of antennae complexes from core complexes of PS 2 (Quinn and Williams 1985). Moreover, heat stress dramaticaly inhibited whole-chain electron transport (Fig. 3D), an effect reported in a number of investigations (Stidham *et al.* 1982, Sayed *et al.* 1989b). Heat sensitivity of the water-splitting apparatus of PS 2 is thought to be responsible, at least in part, for this inhibition (Sayed *et al.* 1989b). It is important, however, to emphasize that there was an evident upward shift in the value of T_{50} (Table 1) denoting enhanced thermal stability of electron transport reactions in plants grown at higher temperatures. Enhanced thermal stability of electron transport and photophosphorylation in *T. aestivum* grown at high temperature has previously been reported (Sayed 1992). It can, therefore, be concluded that although several morphological characteristics were affected when the wheat cv. Doha 88 was grown under contrasting temperature regimes, no apparent differences in development were observed upon expressing data on an accumulated thermal time basis. It can also be concluded that this wheat cultivar possessed an ample degree of potential acclimation to grow in a wide range of temperatures and is, therefore, suitable for growth in Qatar.

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