J Plant Growth Regul (2007) 26:222–228
DOI 10.1007/s00344-007-9009-4

Effect of Temperature on Growth and Phototropism of *Arabidopsis thaliana* Seedlings

Vladimir Orbović · Kenneth L. Poff

Received: 5 September 2006 / Accepted: 4 January 2007 / Published online: 21 August 2007

Abstract Seedlings of *Arabidopsis thaliana* grown at 25°C responded to a change in growth temperature by changing their elongation rate within the next 150 min. Regardless of whether the new temperature was higher or lower than 25°C, the seedlings grew slower after the transfer at all tested temperatures. When the seedlings were grown for 2 days at 11.5°C, 17.9°C, and 23.5°C and then transferred to the range of temperatures between 4°C and 38°C they exhibited maximum elongation in the temperature range between 18°C and 23°C. The kinetics of first positive phototropism in seedlings transferred from 25°C to 15°C differed from the kinetics exhibited by seedlings transferred from 25°C to 28°C. At 15°C, measurable curvature began 40–50 min after the blue light (BL) pulse and no straightening was evident within 150 min after the BL pulse. Seedlings transferred to 28°C exhibited kinetics of phototropism similar to the phototropic response of plants maintained at 25°C except that straightening began slightly faster in the seedlings at 28°C. Based on these results, it is concluded that changes in temperature conditions affect both the elongation rate of seedlings and a first positive phototropism and that phototropic curvature and subsequent straightening are independently controlled.

Keywords Phototropic curvature · Kinetics · Elongation · Hypocotyl

Introduction

Heat energy is an environmental factor that is present without interruption throughout the lifetime of all biological systems. Heat energy affects every molecule in every organism. Because it is not possible to provide conditions without heat energy, experiments in this field of research must be designed to test the effects of temperature gradients or temporal changes in temperature, a measure of heat energy.

When exposed to high- and low-temperature stress, plants respond by adapting to a new set of conditions. This adaptation response, called acquired tolerance to high and low temperature, is a complex trait as suggested by numerous breeding experiments directed toward crop improvement. However, based on results from molecular studies on characterization of the heat shock protein 100 family (Hsp100) and descriptions of its involvement in response to high temperatures in both prokaryotes and eukaryotes, it has been proposed that a limited number of factors contribute to development of thermotolerance (Hong and Vierling 2000; Queitsch and others 2000). Furthermore, an improvement in freezing tolerance has been achieved in transgenic plants by ectopic expression of a single gene, CBF1/DREB transcription factor (Jaglo-

In memory of Radomir Konjević (1 August 1946–22 July 2006), plant physiologist, teacher, mentor, and friend.

V. Orbović (✉)
Institute for Biological Research, 29 Novembra 142, Beograd 11000, Serbia
e-mail: orbovic@ufl.edu

K. L. Poff
Department of Horticulture, Michigan State University, East Lansing, Michigan 48824, USA

Present Address:
V. Orbović
Citrus Research and Education Center, University of Florida, 700 Experiment Station Rd., Lake Alfred, Florida 33850, USA

Ottosen and others 1998). However, a more detailed examination of genes involved in cold response revealed that not all of them are under the control of CBF/DREB factor (Fowler and Thomashow 2002), supporting the idea that temperature acclimation is controlled by multiple mechanisms and is therefore a complex trait.

The transduction chains for high- and low-temperature signals do not seem to overlap or share common elements (Sung and others 2003), although cell membranes seem to play a role in plant responses to either of the temperature extremes. Raison and Chapman (1976) used an Arrhenius plot to describe the elongation rate of mung bean plants at different temperatures and proposed that the change in slope of the Arrhenius plot at a particular temperature represented conditions at which phase transition occurred in the plasma membranes of the growing cells. Soon after it was proposed, this model was disputed by Bagnal and Wolfe (1978) who claimed that the process of plant elongation is more complex than processes described with the Arrhenius plot. However, more recent studies with genetic mutants deficient in fatty acid processing (Alfonso and others 2001) as well as freezing injury studies (Steponkus and others 1993) clearly indicated that membrane fluidity plays a pivotal role in perception of high- and low-temperature signals.

Phototropism and gravitropism of the young *A. thaliana* shoot result from unequal rates of elongation growth on two sides of the shoot. In the case of phototropism, light is screened from the shaded sides of the shoot by the shoot's opacity such that more photoproduct is formed on the light side than on the shaded side. This results in a decreased growth rate on the lighted side and an increased growth rate on the shaded side of the shoot with the consequence of curvature toward the lighted side (Orbović and Poff 1993). In the case of gravitropism of a shoot placed horizontally, the upward curvature is thought to be the consequence of an increased growth rate of the lower side of the shoot and a decreased growth rate of the upper side (Trewavas 1992). Auxins have long been implicated as regulators of both photo- and gravitropism as their unequal distribution on two sides of the responding organ appears to be prerequisite for differential growth and consequently development of curvature (Estelle 1996).

Because phototropism involves alterations in elongation growth and because growth is the end result of a large number of metabolic steps, each of which is directly affected by temperature, it follows that one should examine the effects of temperature on both elongation growth and phototropism. This work was undertaken to describe in detail the elongation rates of etiolated *A. thaliana* seedlings upon transfer from one temperature to another and the effects of temperature changes on kinetics of first positive phototropism.

Materials and Methods

Short-Term Experiments (STE)

Seedlings of the Estland race of *A. thaliana* were grown as previously described (Orbović and Poff 1991) in strips of microassay wells containing 0.7% (w/v) agar. The strips were incubated at 4 ± 1°C for 3 days and then transferred to white light (WL) at 22 ± 1°C for 19 h. Both chilling and the WL treatment were employed to potentiate and synchronize germination. Following the WL treatment, the strips were transferred into darkness at 25 ± 1°C for 2 days. At the end of this period, seedlings were put into a chamber set to the experimental temperature. Seedlings were permitted to equilibrate to the temperature in the chamber for 40 min before video recording began and they were given a blue light (BL) pulse (in phototropism experiments). Elongation rates were followed for the next 90–170 min.

A custom-built chamber was used to provide the different temperature conditions. The chamber consisted of a double-walled Plexiglas container enclosed in styrofoam for insulation. Copper tubing inserted between the walls of the chamber carried circulating liquid from a water bath. The desired temperature within the chamber was obtained by altering the temperature of the circulating liquid.

Long-Term Experiments (LTE)

For long-term experiments, seed germination was potentiated the same way as for the STE. After the WL irradiation, seeds sown in Petri dishes were transferred to a custom-built wooden chamber that was divided into ten well-insulated compartments. A heater was installed on one side of the chamber and the cooling mechanism on the other side. When both the heater and the cooler were turned on, a temperature gradient was established along the chamber so that a specific temperature was maintained within each compartment. For the first part of the experiments conducted in this chamber, three different batches of seedlings were incubated at 11.5°C, 17.9°C, and 23.5°C for 2 days. After this period, each batch of seedlings (one plate per temperature treatment) was transferred to the new range of temperatures for an additional 4 days after which they were collected for measurements. These experiments were repeated three times.

Temperatures inside the growth chambers were measured using a thermistor element connected to an electronic telethermometer YSI-42 SC (Yellow Springs Instruments, Co. Inc., Yellow Springs, OH, USA). Temperature variation was within ±1°C for individual experiments and within ±1°C for the group of experiments.

Light Sources

The white light (65 μmol m^{-2} s^{-1}) used to potentiate germination was provided by General Electric (Cleveland, OH, USA) DeLux Cool White fluorescent tubes. Phototropism was induced by a unilateral BL pulse. The BL source consisted of a projector equipped with a Sylvania (GTE Products, Danvers, MA, USA) 300-W ELH tungsten-halogen lamp and a 450-nm interference filter (PTR Optics, Waltham, MA, USA) with a half bandwidth of 10 nm. The fluence of BL used to induce phototropism was 0.3 μmol m^{-2} obtained in a single 0.9-s pulse at a fluence rate of 0.34 μmol m^{-2} s^{-1}. Fluence rates were measured with a Li-Cor (Lincoln, NE, USA) Li-190 SA quantum sensor in combination with a Li 1000 Data Logger. The duration of BL was controlled with a Uniblitz shutter (Vincent Associates, Rochester, NY, USA). The infrared irradiation used for video recording was described previously (Orbović and Poff 1991).

Data Collection

The video analysis system used for data collection and the method for data collection from STE were previously described (Orbović and Poff 1991, 1993). Length and curvature of seedlings were measured from the successive video recordings. Changes in length and curvature were calculated from these measurements and used for statistical analyses. Length of the seedlings grown in the LTE was measured similarly to how it was done for the STE with two modifications. The first modification was that images acquired by the video camera were not those of seedlings but of the images of seedlings that were inserted into a photographic enlarger. The second modification was that images were imported into the computer directly from the video camera.

Results

In the short period following the transfer from one temperature to another, etiolated seedlings of *A. thaliana* exhibited a change in elongation rate. Transfer from 25°C to both lower and higher temperature resulted in a decreased elongation rate (Figure 1). The elongation rate of seedlings was lowest at 9°C (Figure 1A), higher at 15°C and 36°C (Figures 1B and G), higher still at 20°C, 28°C, and 31.5°C (Figures 1C, D, E, F), and highest when the seedlings were both grown and measured at the same temperature of 25°C (Figure 1D). Lines were fitted to data points in Figure 1 by regression analysis of the Sigma Plot computer program.

The data points defining the elongation rates after transfer from 25°C to each temperature were averaged to obtain a single value representing the growth rate at that temperature. A plot of the average elongation rate as a function of temperature is a bell-shaped curve with a maximum at 25°C (Figure 2). Similar experiments were performed with seedlings initially grown at 11.5°C, 17.9°C, or 23.5°C and transferred to one in a range of temperatures between 4°C and 38°C. The highest hypocotyl elongation was recorded between 21°C and 29°C (Figure 3A) for seedlings previously grown at 11.5°C, between 17.9°C and 23.5°C for seedlings previously grown at 17.9°C, and between 17.9°C and 33°C for seedlings previously grown at 23.5°C. For the experiments described in Figure 3, the population of seedlings that had the highest average hypocotyl length was assigned a 100% value and

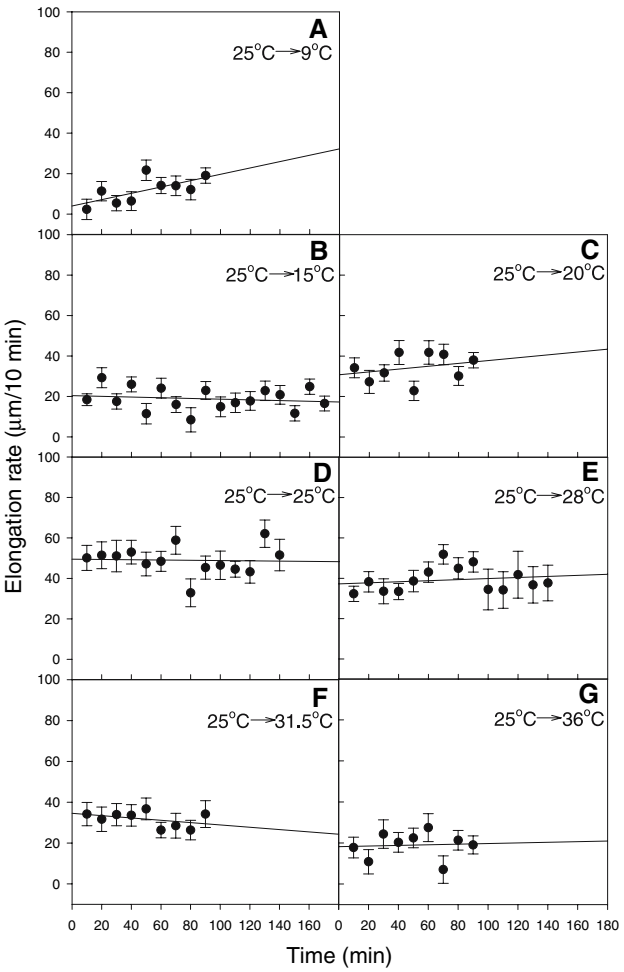

Fig. 1 Average elongation rate of seedlings transferred from 25°C to (**A**) 9°C, n = 29; (**B**) 15°C, n = 32–35; (**C**) 20°C, n = 29; (**D**) 25°C, n = 25–30; (**E**) 28°C, n = 11–35; (**F**) 31.5°C, n = 25; (**G**) 36°C, n = 21.Transfer of plants was done 40 min before the 0-min time point. Vertical bars represent ± 1 SE. The data shown in D are taken from Orbović and Poff (1993)

average lengths from different temperature conditions were expressed as a percentage of that value.

Seedlings that were grown at 25°C and kept at the same temperature following phototropic stimulation started curving toward the BL source 20 min after the pulse. Curvature increased linearly to its maximum over the next 40 min (0.60 deg min^{-1}). Curvature proceeded at a slower rate for an additional 20 min. About 80 min after the BL pulse, seedlings started straightening and continued to do so for the next 40 min (Figure 4A).

Upon transfer from 25°C to 15°C, seedlings first exhibited a curvature between 40 and 50 min following the BL pulse and then the curvature increased in a linear fashion for the next 40 min (0.44 deg min^{-1}). Curvature proceeded at a slower rate for an additional 30 min. Between 120 and 140 min after the BL pulse, curvature reached a plateau and remained unchanged (Figure 4B).

Seedlings transferred from 25°C to 28°C started curving toward the BL source 20–30 min after the pulse. Curvature increased linearly to its maximum over the next 30 min (0.68 deg min^{-1}). These seedlings subsequently started straightening and within the next 50 min reversed the previously attained curvature by about two thirds (Figure 4C).

Discussion

Research in the field of thermosensing and thermal responses is hampered by the difficulties centered round the nature of heat as a stimulus. First, heat energy non-specifically affects all the molecules that constitute living systems. Second, it is impossible to provide conditions in which heat energy is absent. Therefore, spatial and temporal changes in temperature have most frequently been used as thermal stimuli (e.g., Poff and others 1984). In this work, elongation rates and phototropism of *A. thaliana* seedlings were examined upon transfer from one temperature to another.

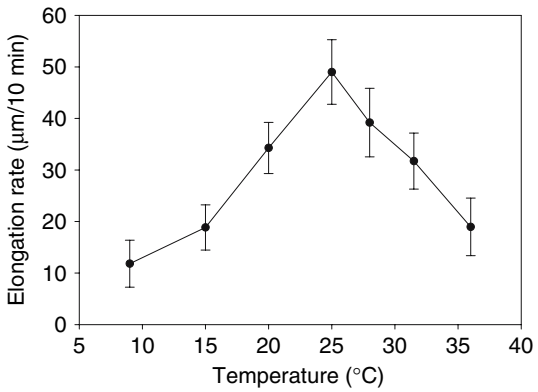

Fig. 2 Cumulative average elongation rate of seedlings incubated on 25°C and then transferred to different temperatures: at 9°C, $n = 9$; at 15°C, $n = 18$; at 20°C, $n = 9$; at 25°C, $n = 14$; at 28°C, $n = 15$; at 31.5°C, $n = 9$; at 36°C, $n = 9$. Vertical bars represent ± 1 SE

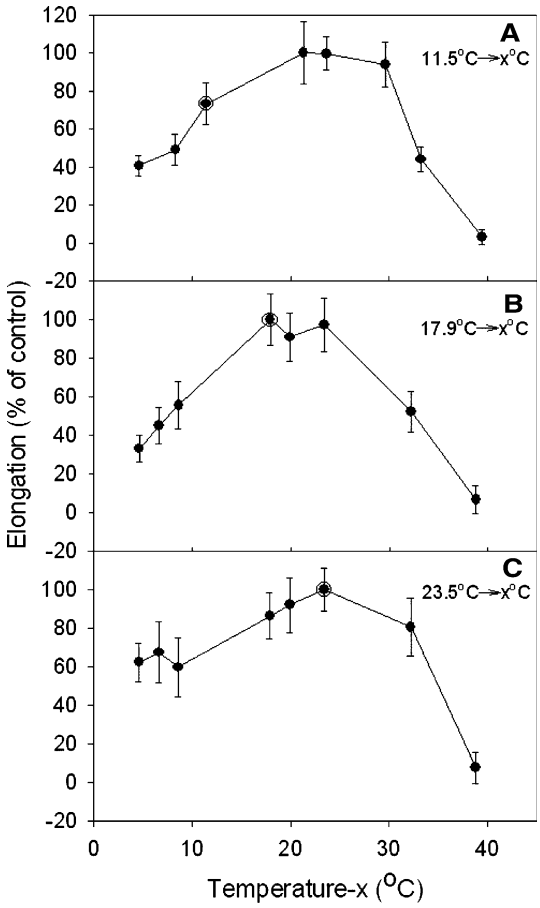

Fig. 3 Average elongation rate of seedlings grown at (**A**) 11.5°C, (**B**) 17.9°C, (**C**) 23.5°C and then transferred to different temperature. Data points representing the starting temperature in each of three treatments are circled. Vertical bars represent ± 1 SE

When etiolated seedlings of *Arabidopsis* were transferred from one temperature to another, the elongation rate was consistently reduced. The relationship between temperature and elongation rate is described by a bell-shaped curve (Figure 2). There are two possible explanations for these results. One possibility is that the seedlings were adapted to the first temperature at which they had grown (25°C) since germination. The growth conditions changed upon transfer to the second temperature, and the seedlings responded by slowing their elongation rate. Knowledge of adaptation to change in temperature conditions in plants is still obscure and elements of the adaptation mechanism and the rate at which adaptation happens remain largely unknown.

It was reported that stem length of *Arabidopsis* plants precultivated for 24 days at 22°C and then grown for 10–22 days in the range of average daily temperatures from 12°C

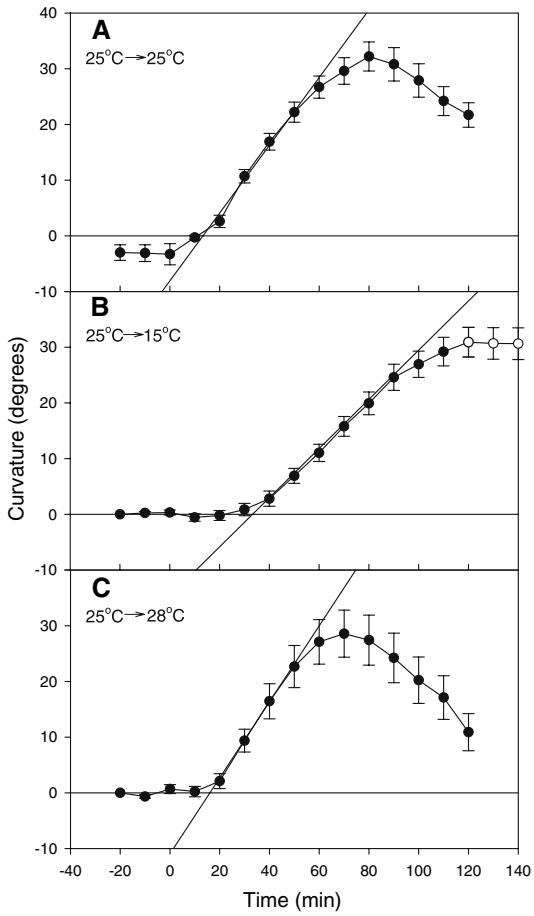

Fig. 4 The time course for development of average curvature of seedlings during the first positive phototropism upon transfer from 25°C to (**A**) 25°C, (**B**) 15°C, and (**C**) 28°C. Blue light was administered at the 0-min time point. Vertical bars represent ± 1 SE. The data shown in A are taken from Orbović and Poff (1993)

to 27°C increased linearly with the increasing temperature (Thingnaes and others 2003). In our study, transfer of *Arabidopsis* seedlings from one temperature to another led to deceleration of elongation (Figure 2). However, we conducted experiments only for 3–4 h, and it is hard to say if there was enough time for the adaptation to take place so that seedlings can resume growth at the same or possibly even a higher rate following temperature change. Nevertheless, exposure of *Arabidopsis* seedlings for 90 min to 38°C was sufficient to induce thermotolerance to subsequent exposure to 45°C (Hong and Vierling 2000).

The above-mentioned hypothesis could be tested by growing seedlings at temperatures other than 25°C and subsequently transferring them to a range of temperatures. If the growth curves obtained from such experiments were also bell-shaped with maximum elongation rates at temperatures corresponding to the initial temperatures, adaptation would be the likely factor controlling the growth response to thermal stimuli. However, in this present work, when seedlings were grown initially for 2 days at 11.5°C, 17.9°C, and 23.5°C and transferred to the range of different temperatures for an additional 4 days, elongation curves at the new temperatures did not have a maxima corresponding to the initial temperatures but to the temperatures close to 20–25°C (Figure 3). Similarly, it has also been shown that maize roots transferred from 16°C and 26°C to a range of other temperatures grew fastest at about 30°C (Fortin and Poff 1991).

A second possible explanation for the shape of the curves in Figures 2 and 3 is that the major processes controlling the elongation rate of *Arabidopsis* seedlings have optimum temperatures between 20°C and 25°C. In this case it would be expected that any change in temperature from the optimum would result in a decrease in the elongation rate, and, on the contrary, if plants were transferred from nonoptimal to optimal temperature conditions they would grow at the fastest rate. The data presented in Figure 3 support this hypothesis.

In related literature, a temperature of 25°C was found to be optimal for long-term culturing of the G-3 line of *Lemna gibba* plants (Rapparini and others 2002). The same authors also reported that the levels of free IAA found in tissue of the 3F7-11 line of *L. gibba* plants grown between 5°C and 35°C rose from 5°C to 20°C but decreased at higher temperatures. On the other hand, the growth rate of plants increased from 5°C to 30°C, so a direct correlation between free IAA levels and growth rate could not be established. These findings were attributed to (1) a change in auxin turnover that slowed down significantly at 25°C, and (2) the presence of a metabolic switch in production of IAA from the Trp-dependent to the Trp-independent pathway (Rapparini and others 2002). The presence of both Trp-dependent and Trp-independent biosynthetic pathways for auxins was confirmed in *Arabidopsis* (Jian and others 2000; Zhao and others 2002) but their role in temperature control of elongation of etiolated seedlings has not yet been studied.

Seedlings transferred from 25°C to other temperatures also exhibited an altered phototropic response (Figure 4). Upon transfer from 25°C to 15°C, seedlings required more than 40 min to exhibit measurable curvature toward the light source (Figure 4B). Although this might be attributed to heightened gravitropism at the lower temperature inhibiting the phototropic response, Wyatt and others (2002) reported that inflorescence stems of *Arabidopsis* did not respond to gravitropic stimulation at 4°C until they were subsequently transferred to room temperature, and that the inability of plants to respond to the signal when it was administered correlated well with the decreased basipetal transport of IAA (Wyatt and others 2002). We reported earlier (Orbović and Poff 1993) that the changes in elongation rates on opposite sides of *Arabidopsis*

seedlings following a unidirectional BL pulse at 25°C agree, in general, with the Cholodny-Went hypothesis, suggesting that phototropism is the consequence of unequal distribution of auxins along the responding plant organ. It is almost certain (for review see Liscum 2002) that one of the processes involved in growth distribution during phototropism of *Arabidopsis* seedlings is the redistribution of IAA within the hypocotyl such that there is a different concentration of IAA on the two sides of the seedling. The sensitivity of IAA transport mechanism(s) to different temperatures may be the cause of the difference in the kinetics of growth distribution during phototropism at 15°C and 25°C. The lower temperature could be affecting the rate of transport of auxin along and across the hypocotyl and thereby delaying the response of tissue to incoming auxin and decreasing the rate of phototropic bending. This hypothesis gets some support from recent publications describing lateral auxin transport and amyloplast sedimentation in *Arabidopsis* hypocotyls during tropisms (Friml and others 2002; Morita and others 2002). PIN3 protein is involved in lateral transport of auxins in the hypocotyl of *Arabidopsis* and *pin3* mutants display defects in differential growth. The presence of PIN3 was found to be higher in the lower side of columella, and pericycle cells in roots exposed to gravistimulation and redistribution within those cells took 2–5 min (Friml and others 2002). Friml and coworkers suggested that PIN3 protein moves via a membrane transport pathway closely associated with the cytoskeleton. Also, normal membrane traffic and vacuole organization in endodermal cells of *Arabidopsis* hypocotyls are necessary for sensing a gravity stimulus through sedimentation of amyloplasts (Morita and others 2002). Because the membrane system is at the core of these mechanisms, it is possible that changes in temperature conducive to decreasing membrane fluidity could also diminish the ability of amyloplasts and PIN3 to move, thereby interfering with sensing of stimulus as well as decelerating redistribution of auxins.

Nissl and Zenk (1969) showed that an increase in temperature from 21°C to 40°C resulted in a considerable decrease and near disappearance of the lag phase in the response of oat coleoptile segments to 5×10^{-3} M of exogenous IAA. In contrast, in this study the lag phase of the phototropic response of seedlings transferred from 25°C to 28°C did not appear shorter than the lag phase of seedlings kept all the time at 25°C (Figures 3A, C), and the bending rate was similar [0.60 deg min^{-1} (Figure 3A) and 0.68 deg min^{-1} (Figure 3C)] at the two different temperatures. Considering that temperature up to 37°C has no effect on the interaction of auxin with its receptor in *Arabidopsis* (Dharmasiri and others 2005) and by using reasoning similar to that employed for low temperatures, we can hypothesize that the increase in temperature from 25°C to 28°C led to a more rapid redistribution of auxin within the photostimulated seedlings resulting in a higher rate of curvature.

It should be noted that the magnitude of phototropic curvature was not affected strongly by temperature, while different temperatures had a pronounced impact on lag time and bending rate (Figure 4). These results clearly support the conclusion that there are multiple effects of temperature on phototropism.

It has previously been demonstrated that phototropic curvature in response to relatively long periods of irradiation, second positive phototropism, and phototropic curvature in response to relatively short periods of irradiation are manifestations of the same response network (Janoudi and others 1997). Second positive phototropism differs from first positive phototropism in that there is sufficient time during the irradiation in second positive phototropism for adaptation to the light stimulus. Thus, first positive phototropism and second positive phototropism differ only in the time permitted for adaptation to light. Although it would be technically possible to examine the temperature dependence of second positive phototropism, interpretation of the data would be confounded by the two separate adaptation processes, one to a change in temperature, and a second to a change in irradiation. Moreover, it is certainly possible that the second adaptation process, adaptation to light, is itself thermally dependent. For these reasons, the experiments reported here were deliberately designed for first positive phototropism in which adaptation to light is not known to occur.

At 28°C seedlings began to straighten almost immediately after they reached maximum curvature (Figure 4C). However, seedlings at 15°C did not exhibit any straightening within 30 min after attaining the maximal curvature (Figure 4C and data not shown). Although it is not possible from these data to estimate the time needed for initiation of straightening of seedlings at 15°C, it is clearly different from the time needed at 25°C and 28°C. A comparison of the lag phases preceding the initiation of curvature at 28°C and 15°C yields a ratio of about 1:2, whereas the ratio for the time needed for straightening at 28°C and 15°C is very different from 1:2 (Figure 4B, C). Based on this analysis, we suggest that phototropic curvature and subsequent straightening are independently controlled.

On the basis of these data it can be concluded that temperature affects both undirected and directed growth of *Arabidopsis thaliana* seedlings. The reduction in elongation rate in etiolated seedlings transferred from 25°C to different temperatures suggests that 25°C may be at or near the optimum temperature for growth. Transfers of seedlings to temperatures different from 25°C resulted in an altered phototropic response. Temperature affects

phototropism by changing the initial lag phase, the bending rate, and the time required for initiation of straightening.

Acknowledgment The authors thank Ms. Ivana Batak for help with LTE experiments.

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