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Role of Gibberellins in the Environmental Control of Stem Growth in *Thlaspi arvense* L.

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ABSTRACT

Field pennycress (*Thlaspi arvense* L.) is a winter annual that requires a cold treatment for the induction of stem elongation. An inbred line was selected in which no stem elongation was observed in plants grown for 6 months at 21°C regardless of the prevailing photoperiod. Increased exposure time of plants grown initially at 21°C to cold (2°C) induced a greater rate of stem elongation when the plants were returned to 21°C. Moreover, longer cold treatments resulted in a greater maximum stem height and reduced the lag period for the onset of measurable internode elongation. The optimal temperature range for thermoinduced stem growth was broad: rates of stem growth in plants maintained for 4 weeks at either 2° or 10°C were virtually identical. However, a 4-week thermoinductive treatment at 15°C resulted in a greater lag period for the initiation of stem elongation and a decreased growth rate. The rate of cold-induced stem elongation was greater in plants subjected to long days than for plants subjected to short days following the cold treatment. Thus, photoperiod does not control the induction of stem elongation, but does regulate stem elongation in progress. Exogenous gibberellin A_3 (GA_3) was able to substitute for the cold requirement, but elicited a greater response in plants maintained under long days than short days. This indicates that photoperiod influences the plant's sensitivity to GAs. The GA biosynthesis inhibitor, 2-chloroethyltrimethyl ammonium chloride, inhibited low temperature-induced stem elongation, and this inhibition was completely reversed by exogenous GA_3. These results suggest that cold-induced stem elongation in field pennycress is mediated by some change in the endogenous GA status.

Field pennycress (*Thlaspi arvense* L.) is a winter annual weed that infests cultivated fields of the Northern Plains of the United States and the prairie provinces of Canada (4). Normally, the seeds of field pennycress germinate in the fall and develop into rosettes. After overwintering, rapid stem elongation occurs and the plants ultimately flower. As in other winter annuals and biennials, low temperature (0–15°C) is the environmental stimulus that induces these developmental changes when the plants are returned to temperatures more favorable for growth (1, 3, 10).

A series of investigations have been initiated in this laboratory on determining the molecular mechanisms for the environmental control of stem growth in field pennycress. In many rosette plants in which some environmental stimulus induces stem elongation, GAs[1] are thought to play a crucial role in mediating the response (2, 20). Thus, determination of the role that the endogenous GAs have in the environmental control of stem elongation in field pennycress is a logical starting point. In the following report, the stem elongation response to low temperature treatment by field pennycress is characterized in detail. Furthermore, photoperiod is shown to interact with thermoinductive temperatures in the control of stem growth. Finally, evidence is provided that low temperature-induced stem elongation is mediated, at least in part, by a change in the endogenous GA status.

MATERIALS AND METHODS

Plant Material and Culture. An inbred line of field pennycress (CR_1), which has a facultative requirement for a low temperature pretreatment before stem elongation can commence, was selected from seed collected locally in North Dakota. Seeds of CR_1 were germinated in Petri dishes in the light at 21°C. After 4 d, the seedlings were transferred to 10-cm plastic pots containing moist vermiculite. The plants were continuously subirrigated with one-fourth strength Hoagland solution (5). The plants were maintained at 21°C and 50% RH. Photoperiodic conditions during this phase of plant culture consisted of 8 h of light (300 μE m^{-2} s^{-1}, 400–700 nm) provided by fluorescent and incandescent lamps followed by 16 h darkness.

Thermoinductive and Photoperiodic Treatments. At age 6 weeks, plants were moved into a cold room (2–3°C) and received 8 h of light daily from fluorescent lamps (20 μE m^{-2} s^{-1}). In other experiments, plants received thermoinductive treatments at 10° C or 15°C in growth chambers. The light regimes were the same as in the 2°C treatments. After prescribed times, the plants were returned to the growth chamber at 21°C. One of two photoperiodic regimes was used: SD, which was described previously and LD, which consisted of the same 8-h illumination as in the SD treatment followed by 16 h of low intensity illumination (20 μE m^{-2} s^{-1}, 400–700 nm) from incandescent lamps.

Growth Measurements. Stem length measurements were taken from the basal leaf of the first measurably elongating internode to the last true leaf. Unless otherwise stated, stem length was measured daily until growth of the stem ceased. Growth of raceme continued several weeks thereafter.

Application of Chemicals. A solution containing 1 μg μl^{-1} GA_3 in 10% (v/v) aqueous acetone and 0.05% Tween 20 was applied to the apex and the youngest leaves. Ten μl were applied three times a week for a total of 10 applications. CCC was applied by incorporating it in the subirrigation nutrient solution at a concentration of 10 mM.

Extraction, Fractionation, and Bioassay of Endogenous GA-Like Substances. Following harvest, the plant material was frozen in liquid N_2, lyophilized, and stored at −15°C until extraction. The lyophilized plant material was extracted once with 80% (v/v) aqueous methanol and once with 100% methanol (500 ml of each per 10 g dry weight). The methanol was removed under

[1] Abbreviations: GA(s), gibberellin(s); CCC, 2-chloroethyltrimethyl ammonium chloride.

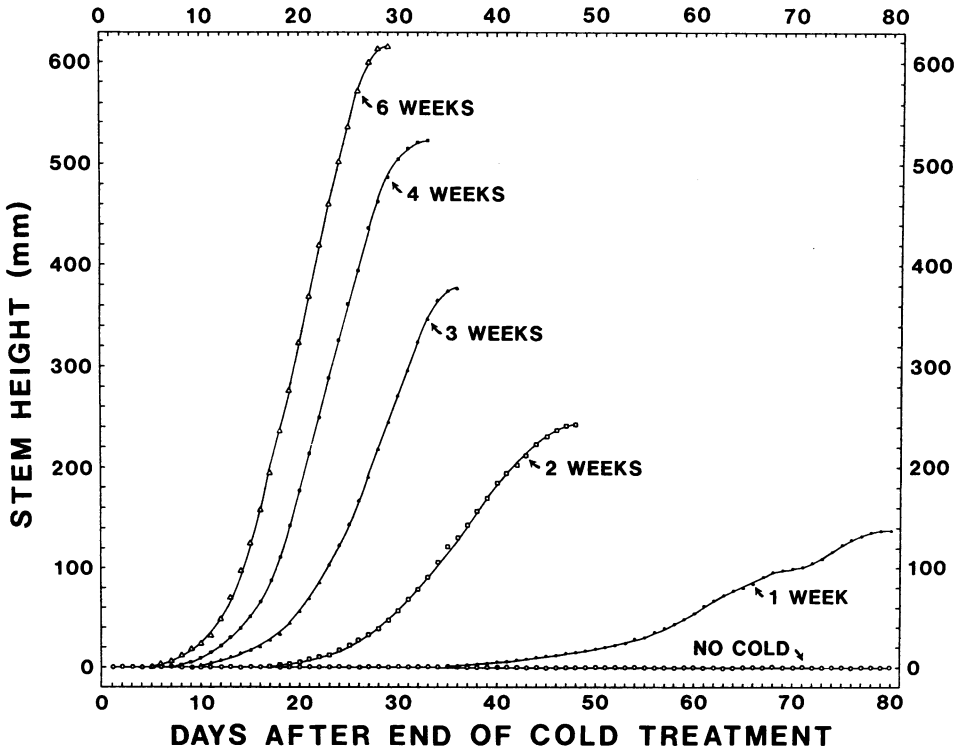

FIG. 1. The effect of different durations of low temperature pretreatment on stem elongation at 21°C. Each treatment had five replicates.

reduced pressure at 30°C and the endogenous GA-like substances were partially purified by solvent partitioning, charcoal adsorption, and silicic acid adsorption chromatography as described before (11).

The GA-enriched fraction was then fractionated by reversed phase HPLC. The HPLC system consisted of two Waters[2] 6000 A pumps controlled by a Waters model 720 System controller, U6K Universal injector, and a Waters Z-module radial compression system containing an 8-mm i.d. Radial-Pak C_{18} reversed phase cartridge. GAs were eluted from the column with a linear gradient of methanol (30–100%) in water in 20 min at 2 ml min^{-1}. The column was washed with 100% methanol for an additional 5 min. Both solvents contained 1% (v/v) acetic acid. One-min fractions were collected and dried overnight in a fume hood. The amount of GA-like substances in each fraction was estimated with the d-5 maize bioassay (11).

All experiments were repeated at least once with nearly identical results.

RESULTS

Relationship between Duration of Thermoinductive Treatment and Rate of Stem Elongation. Initially, the response of the CR_1 line of field pennycress to different lengths of low temperature was characterized. After 6 weeks at 21°C and SD, plants that were to receive 6 weeks cold were placed in the cold room at 2°C. Plants to receive shorter durations of thermoinductive treatment were sequentially subjected to the cold treatment so that all of the treatments ended simultaneously. The plants were then returned to 21°C and LD conditions, including a set of control plants that received no cold, and were maintained under SD conditions for 12 weeks before being transfered to LD. The effect of different durations of cold on stem elongation at 21°C is shown in Figure 1. Both the initiation and the rate of stem elongation were accelerated by increased duration of cold treatment. Furthermore, the final length of the stem was greater with increasing time in the cold treatment. No stem elongation was observed in 6-month-old plants that received no cold treatment. After 8 months, however, all of these plants exhibited some stem elongation (data not shown). Thus, the requirement for a low temperature treatment is not absolute, *i.e.* it is facultative.

Because of the experimental procedures, the plants in the various treatments were at different developmental stages, *viz.* had different numbers of leaves, when the low temperature treatments began. It is possible that at least part of the differences in the stem elongation response to different durations of the cold treatment is due to developmentally related changes in the plants' sensitivity to low temperature or the capacity for stem elongation. To test this possibility, plantings were sequentially arranged in a manner such that the plants in all of the treatments had the same number of leaves at the start of the thermoinductive treatment. This arrangement also allowed all of the cold treatments to end the same day. No differences were observed in the growth curves when the experiment was performed in this fashion and those presented in Figure 1 (data not shown).

Range of Effective Thermoinductive Temperatures. Plants were grown 6 weeks under SD at 21°C and were then subjected to one of four temperature regimes: 2°C, 10°C, 15°C, or 21°C. All treatments had the same photoperiodic conditions as described previously. After 4 weeks, the plants were returned to 21°C and LD. Stem growth was measured daily. The results are shown in Figure 2. The growth curves of plants receiving the 2°C or 10°C thermoinductive treatments were nearly identical. However, the capacity for stem elongation was greatly diminished in plants subjected to 15°C. The onset of measurable stem elongation occurred 10 d later in plants subjected to 15°C than those grown at 2°C or 10°C. Both the rate of stem elongation and the final height were less as well in plants receiving the 15°C thermoinductive treatment. No stem elongation was observed in plants maintained at 21°C.

Effect of Prevailing Photoperiod on Cold-Induced Stem Elongation. Plants were grown 6 weeks under SD at 21°C, given a 4-

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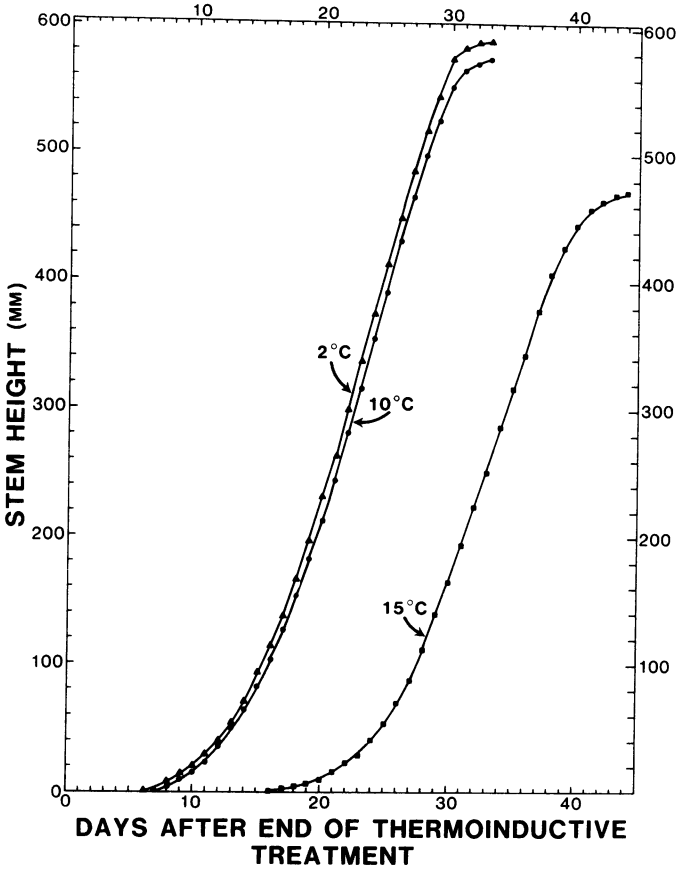

FIG. 2. Comparison of the effectiveness of four different temperature regimes on stem elongation at 21°C. Six-week-old plants, raised at 21°C and SD conditions, were treated for 4 weeks at 2°, 10°, or 15°C and then returned to the growth chamber at 21°C. Each treatment had five replicates.

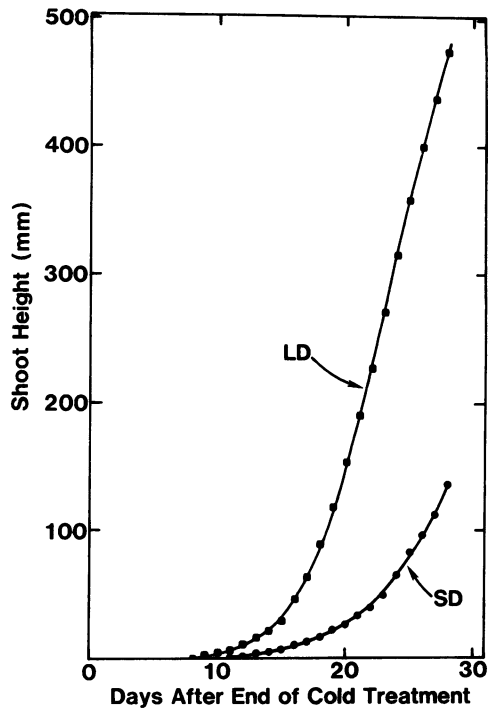

FIG. 3. The effect of day length on cold-induced stem elongation. Six-week-old plants, raised at 21°C and SD conditions, were treated for 4 weeks at 2°C and then returned to the growth chamber at 21°C under either SD or LD. Each treatment had five replicates.

week thermoinductive treatment at 2°C, and then returned to 21°C under LD or SD. Stem length was measured daily for 4 weeks. Stem growth was greater in plants maintained under LD than SD (Fig. 3). Moreover, the onset of measurable stem elongation was about 4 d earlier in the LD-treated plants than in plants maintained under SD.

The effect of photoperiod on stem growth was direct in contrast to the inductive effect of cold. There was little or no photoperiodic after-effect when elongating plants were transferred from one photoperiodic regime to the other (Fig. 4). When thermoinduced plants were grown under LD and then transferred to SD, the growth rate slowed to a level comparable to that observed in plants maintained entirely in SD following the cold treatment. Conversely, plants transferred from SD to LD exhibited increased growth rates. In other experiments, the photoperiodic conditions were varied prior to, or during the low temperature treatment. None of these treatments altered the growth response following the thermoinductive treatment (data not shown). Therefore, photoperiod does not directly control the initiation of stem growth, but it does appear to regulate stem elongation in progress.

Effect of Exogenous GA_3 on Nonthermoinduced Plants. In many rosette plants that require either an inductive low temperature treatment or LD for stem elongation, exogenous GAs can substitute for the environmental stimulus (2, 20). This possibility was tested in field pennycress. Plants were grown for 6 weeks under SD conditions at 21°C. At this time, plants were either transferred to LD or maintained under SD and given ten treatments of 10 μg of GA_3. The interaction of exogenous GA_3 and photoperiod on stem elongation in nonthermoinduced plants is shown in Figure 5. Exogenous GA_3 substituted for the thermoinductive treatment regardless of the prevailing photoperiod. The onset of measurable stem elongation was the same for both photoperiodic treatments—about 7 to 8 d following the start of the application of GA_3. However, the rate of stem elongation was substantially greater when GA_3 was applied to plants in LD, suggesting that photoperiod influences the plants' ability to respond to GAs.

The kinetics of stem growth in plants receiving exogenous GA_3 differed from that observed in thermoinduced plants (Figs. 1, 3, and 5). The GA_3-treated plants reached maximum growth rates (linear phase) more quickly than thermoinduced plants. Moreover, only in plants receiving 6 weeks of cold did initial growth rates exceed those exhibited by nonthermoinduced plants given GA_3 under LD (Figs. 1 and 5). Growth rates in the GA_3-treated plants under LD were initially higher than plants receiving 4 weeks of cold. By 16 d, however, this trend was reversed and the height of the plants in the two treatments was about the same after 23 d. The final heights were greater in plants receiving the 4-week thermoinductive treatment (Figs. 1, 3, and 5). A similar situation was observed in thermoinduced plants and plants receiving exogenous GA_3 under SD (Figs. 3 and 5).

Effect of CCC on Thermoinduced Stem Elongation. The previous results suggest that at least one part of the sequence of biochemical events resulting from thermoinduction and culminating in stem elongation is an alteration of the endogenous GA status. If this is true, then inhibition of GA biosynthesis should block thermoinduced stem elongation. To test this, 6-week-old plants were subjected to 2°C for 4 weeks. Upon return to 21°C and LD, the plants were treated continuously via the roots with CCC, an inhibitor of GA biosynthesis. After 2 weeks, half of the CCC-treated plants were given 10 μg of GA_3 six times over a 2-week period. Stem growth was measured daily for 4 weeks following the end of the low temperature treatment. CCC completely inhibited cold-induced stem elongation and this inhibition was reversed by exogenous GA_3 (Fig. 6). This indicates that

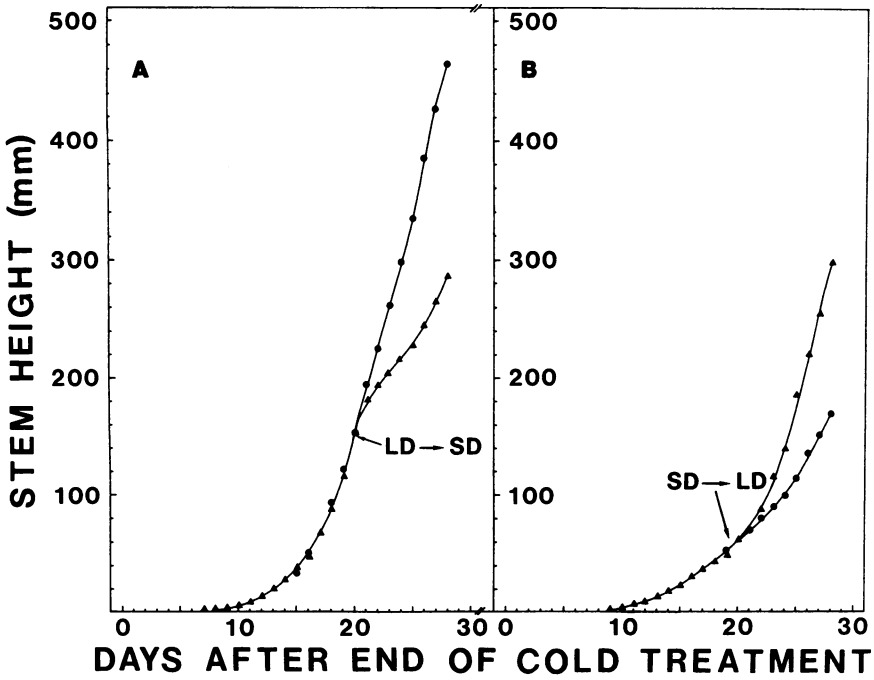

FIG. 4. The effect of a change in photoperiodic conditions on cold-induced stem elongation in field pennycress. Six-week-old plants raised at 21°C and SD conditions were subjected to 2°C for 4 weeks and then returned to the growth chamber at 21°C and SD or LD. After 20 d, half of the plants under LD conditions were transferred to SD (A) and half of the plants maintained under SD were transferred to LD conditions (B). Each treatment had five replicates.

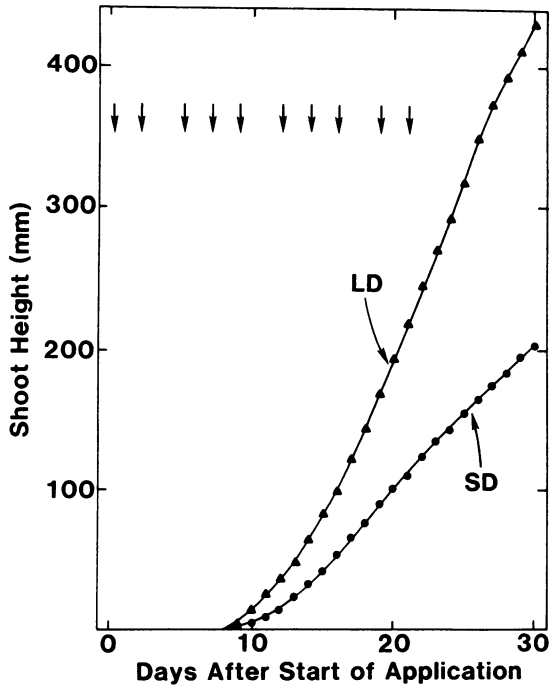

FIG. 5. The interaction of exogenous GA_3 and photoperiod on stem elongation in nonthermoinduced plants. Plants were initially grown for 6 weeks at 21°C and SD. Half of the plants were transferred to LD and half maintained under SD. The plants then received treatments of 10 μg GA_3 to the shoot tips 3 times a week for a total of 100 μg. Arrows denote days of application. Each treatment had five replicates.

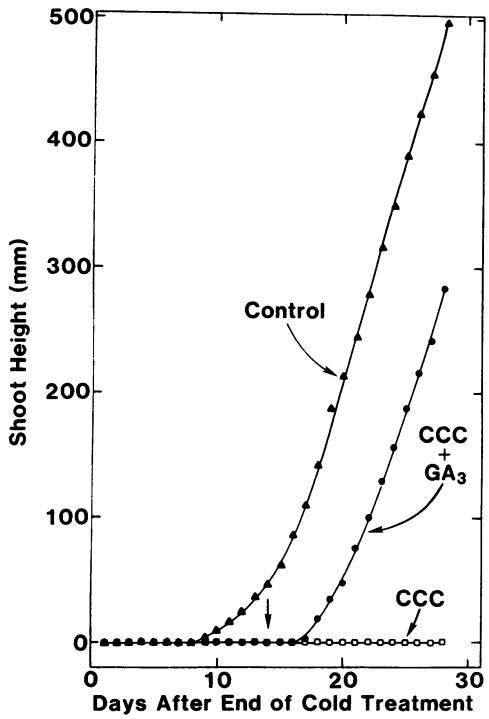

FIG. 6. Effect of CCC on thermoinduced stem elongation. Six-week-old plants received a 4-week thermoinductive pretreatment. Upon return to 21°C and LD, 10 plants were treated continuously via the roots with 10 mM CCC. After 2 weeks, half of the CCC-treated plants received six 10 μg treatments over a 2-week period. The arrow denotes the start of GA_3 treatments. Each treatment had five replicates.

GA biosynthesis is necessary for thermoinduced stem elongation. The lag period from the first application of GA_3 to the onset of measurable stem elongation in the CCC-treated plants was about 3 d—considerably shorter than the lag observed for nonthermoinduced plants treated with GA_3 (Fig. 5). Although the controls obtained a greater height than the CCC + GA_3-treated plants, the growth rates were essentially identical, suggesting that the exogenous GA_3 completely reversed the inhibition of stem growth by CCC.

Effect of Thermoinduction on Endogenous GA Levels. In preliminary work, the spectrum of GA-like substances was determined. Ten plants were extracted in methanol and the acidic ethyl acetate fraction was fractionated with gradient-eluted reversed phase HPLC. Four zones of biological activity were detected by the d-5 maize bioassay (Fig. 7). Zone A, the most polar, co-chromatographed with the dihydroxylated GAs, GA_1 and

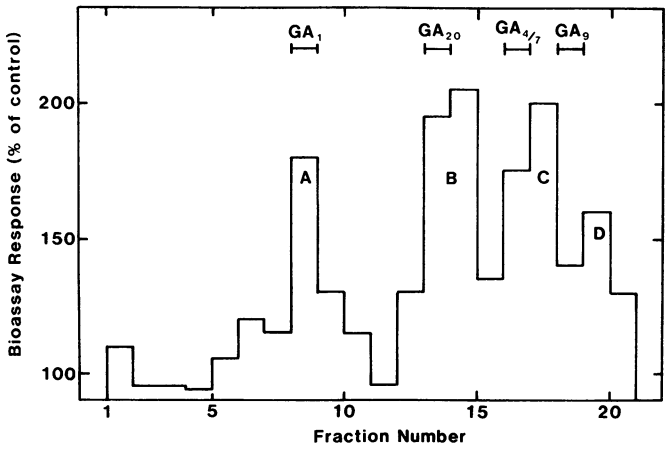

FIG. 7. The chromatographic behavior of GA-like substances present in a methanolic extract of lyophilized field pennycress shoots. Ten 6-week-old plants (dry weight, 21.2 g) received a 4-week thermoinductive treatment and 1 week of LD at 21°C. The partially purified acidic extract was fractionated by gradient-eluted reversed phase HPLC. Fractions were collected every minute and each fraction was assayed for the presence of GA-like substances by the d5 maize bioassay.

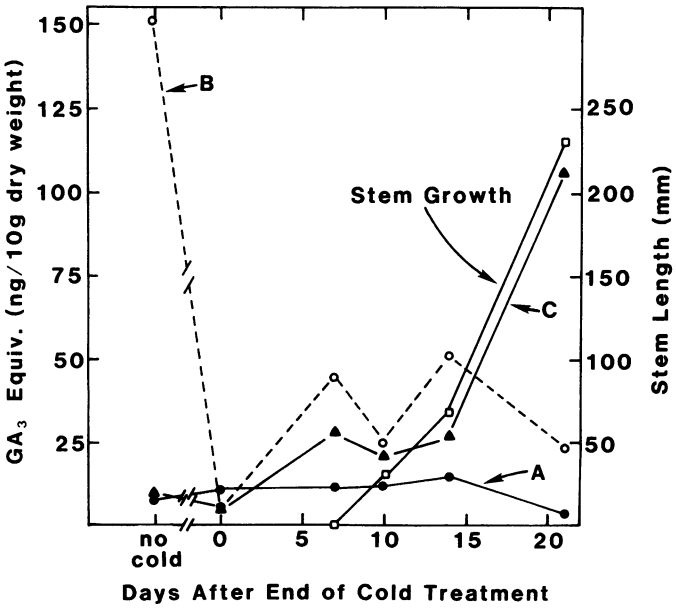

FIG. 8. The effect of low temperature pretreatment on the levels of endogenous GA-like substances and stem elongation. Ten plants from each treatment were lyophilized and extracted in methanol. The GA-like substances in the partially purified acidic extract were separated by reversed phase HPLC and quantitated by the d5 maize bioassay.

GA_3. In decreasing polarity, zones B and C had similar retention times as GA_{20} and $GA_{4/7}$, respectively. Zone D was less polar than GA_9.

These zones of biological activity were then quantitated as a function of time after the cold treatment. Six-week-old plants were subjected to 2°C for 4 weeks. Ten plants were harvested 0, 7, 10, 14, and 21 d after the end of the cold treatment, and the four zones of biological activity were isolated and quantitated by the d-5 maize bioassay. Also, 10 plants that did not receive the cold treatment were analyzed. These plants were 10 weeks old, the same age as plants harvested immediately after the end of the low temperature treatment. Thermoinduction caused dramatic changes in the levels of some of the endogenous GA-like substances (Fig. 8). However, none of the changes appeared to be related to thermoinduced stem elongation in a causal manner. High levels of B were observed in non-cold-induced plants, whereas plants of the same age but which received 4 weeks of cold treatment had a rather low level of B. The level of B increased somewhat following the return of the plants to warmer temperatures, but not to the level found in nonthermoinduced plants. The level of C remained low throughout most of the experimental treatment but increased dramatically in parallel with the increase in stem length. However, stem growth began about 1 week before the increase in the level of C. The levels of A and D (not shown) did not change appreciably following cold treatment.

DISCUSSION

The CR_1 inbred line of field pennycress has a strong facultative requirement for a low temperature treatment before stem elongation can commence (Fig. 1). Furthermore, the effect of low temperature is inductive; that is, growth occurs after the cold treatment. This is in contrast to the direct effect of LD on stem elongation in LD rosette plants which occurs only during LD treatment (1).

A quantitative relationship between the duration of the cold treatment and three parameters of stem growth (growth rate, final height, and the lag period before the onset of measurable elongation) was observed (Fig. 1). A similar effect by cold on both the growth rate and final stem height was observed in Brussels sprouts, a related species (18). Moreover, the optimal temperature range for cold-induced stem growth in field pennycress appears to be broad since the three parameters of stem growth were almost identical in plants subjected to 2° or 10°C (Fig. 2). However, it is possible that a more discrete optimal temperature exists since the effects of temperatures between 2°C and 10°C were not examined.

The three parameters of stem growth were not affected in the same way by the different thermoinductive treatments. Stems from plants that received a 4-week 15°C thermoinductive treatment grew at slightly higher rates and reached greater final lengths than in plants subjected to 2°C for 3 weeks (Figs. 1 and 2). In contrast, the lag period for the onset of measurable stem elongation was 7 d later in plants receiving the 15°C treatment (Figs. 1 and 2). This indicates that the control of cold-induced stem growth can be separated into two distinct processes: initiation and regulation of growth in progress. The dual nature of the control of stem growth was also observed in the effects of the prevailing photoperiod on stem growth. Although photoperiod regulates stem growth in progress (growth rate, final height), it does not directly control initiation (Figs. 3 and 4).

Evidence was obtained indicating that cold-induced stem growth in field pennycress is mediated, at least in part, by a change in the endogenous GA status. First, exogenous GA_3 substituted completely for the thermoinductive cold treatment (Fig. 5). Second, thermoinduced growth was inhibited completely by the GA biosynthesis inhibitor CCC (Fig. 6). These results are consistent with work on thermoinduced stem growth in other cold-requiring species (7, 13, 16). However, what is not clear is the mechanism(s) by which GAs mediate thermoinduced growth. Perhaps the key to resolving this question lies first in determining the role of GAs in regulating the two aspects of stem growth, *viz.* initiation and growth in progress.

Another important question is which aspect of the GA status is altered by low temperatures. Although thermoinduction resulted in alterations of endogenous GA levels in extracts of whole shoots, no increases were correlated in a causal manner with stem elongation (Fig. 8). Thus, it does not appear that cold-induced stem elongation is mediated by simple quantitative or qualitative changes in the endogenous GAs. However, at this point, one cannot rule out the possibility that extraction of whole

shoots does not give an accurate picture of quantitative changes occurring at the sites of growth. This would be especially true if the site of perception of low temperature in field pennycress is in the apical region of the shoot as is the case in other species which have a cold requirement for stem elongation (1, 2). Important quantitative changes occurring in the apical region could be masked by much larger, but fairly stable levels of GAs in the more mature leaves.

Thermoinduction may affect another aspect of the GA status: tissue sensitivity to the endogenous GAs (17). Indeed, low temperature treatments confer GA sensitivity to hormonally insensitive genotypes of wheat aleurone tissue (14, 15). Furthermore, the ability of certain LD rosette plants to respond to exogenous GAs is substantially enhanced when the plants are transferred from SD to LD, suggesting a role for hormone sensitivity in the regulation of stem growth in these plants (6, 8, 19). In an analogous manner, low temperature treatment may induce a quantitative increase in GA sensitivity in field pennycress. Consistent with this hypothesis is the observation that the lag period for the initiation of measurable stem elongation after the start of GA_3 applications was shorter in thermoinduced plants treated with CCC for 2 weeks prior to the first application of GA_3 than in nonthermoinduced plants (Figs. 5 and 6). This suggests that thermoinduction resulted in increased sensitivity to GAs. Despite this, GA sensitivity does not appear to be the limiting factor for stem elongation in noninduced plants since these plants responded to exogenous GA_3 with lag periods and initial stem growth rates comparable to those receiving 4 weeks of cold (Figs. 1 and 5). Moreover, thermoinduced plants treated with GA_3 had higher growth rates than plants receiving the cold treatment alone (data not shown).

Another possibility is that thermoinduced stem elongation is controlled by the rate of turnover of the endogenous GAs rather than by absolute levels. This is similar to the hypothesis of Jones and Zeevaart (9) concerning the photoperiodic control of stem elongation in *Agrostemma githago*. It is clear that thermoinduction causes changes in the levels of some of the endogenous GAs, indicating an alteration in the regulation of GA metabolism (Fig. 7). However, one cannot infer from these data that a change in the overall turnover rate of GAs occurred. Furthermore, it is not known exactly how an increase in the turnover rate of a plant hormone might regulate developmental processes.

Photoperiod was shown to interact with thermoinductive temperatures in the control of stem growth (Fig. 2). Since photoperiodic control of stem elongation in LD rosette plants is mediated by GAs (6, 8, 19), it is reasonable to suspect that photoperiod influences stem growth in field pennycress through some effect on the GA status. In both spinach and *A. githago*, GA metabolism is regulated by the prevailing photoperiod, and it is believed that this regulation mediates LD-induced stem growth in these species (9, 12). Whether a similar situation exists in field pennycress is not known. Regardless, it is clear that photoperiod affected tissue sensitivity to exogenous GA_3 (Fig. 4). But since the biochemical basis for hormone sensitivity is unknown, it is difficult to determine if it really relates to GA action in the regulation of stem growth *per se*. It is possible that photoperiod regulates other biochemical processes involved in stem elongation, and that these processes limit, to varying degrees, GA-mediated thermoinduced growth.

Some answers to these questions lie in a better understanding of the regulation and localization of pathways for GA biosynthesis and metabolism. To this end, present work in this laboratory is directed towards chemical identification of the endogenous GAs in field pennycress. At least nine GAs have so far been identified.

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