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Further Characteristics of an Anomalous Temperature Response of Hypocotyls in Some Soybean Cultivars[1]

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Some soybean cultivars exhibit a bimodal temperature response. Their hypocotyls elongate normally at 20 and 30 C but are inhibited at 25 C. The inhibition is inducible. It manifests itself, or continues to be manifest, after seedlings are transferred to 20 or 30 C. Sensitivity to 25 C is limited to early seedling development and disappears about 6 days after seeds are supplied with water.

INDEX DESCRIPTORS: bimodal temperature response, *Glycine max*, soybean seedling, hypocotyl.

The anomalous temperature response of seedlings of certain soybean cultivars, first reported by Grabe and Metzer (1969), has been studied with regard to agronomic significance (Grabe and Metzer, 1969, Fehr, Burris, and Gilman, 1973), genetic basis (Grabe and Metzer, 1969; Fehr, 1973), and physiological basis (Burris and Knittle, 1975, Samimy and LaMotte, 1976). The peculiar symptoms observed in seedlings grown at 25 C are less pronounced at temperatures differing only a few degrees from 25 C and are absent at 20 and 30 C (Gilman, Fehr, and Burris, 1973). Seedlings grown at 25 C exhibit short, swollen hypocotyls and enlarged root systems. These symptoms result from an abnormally high rate of ethylene production in the tissues of these cultivars (Samimy and LaMotte, 1976) and in most respects resemble the "triple response" of legume seedlings exposed to exogenous ethylene (Abeles, 1973).

In assessing the time course of these temperature-dependent changes, two kinds of experiment have been performed (Samimy, 1970; Gilman *et al.*, 1973; Samimy and LaMotte, 1976): (1) growth curves for hypocotyls and roots of seedlings at constant temperatures have been determined and (2) effects of temperature sequencing on hypocotyl elongation have been assessed. In none of the papers cited above have these observations been interpreted in terms of the growth dynamics involved, nor have they been compared in detail with other such temperature-induced phenomena in plants. The purposes of this paper are (1) to present some original temperature-sequencing results, (2) to demonstrate the persistent effects of an early, transient exposure to one temperature on growth rates at another temperature, and (3) to discuss these and other published findings in the context described above.

MATERIALS AND METHODS

Seeds of Clark soybean, *Glycine max* (L.) Merr., a cultivar which shows the abnormal pattern of development at 25 C, were selected and planted between 31 × 31 cm sheets of germination paper. The sheets were rolled into a cylinder and stood in water as previously described (Burris and Fehr, 1971; Samimy and LaMotte, 1976). Seedlings were grown in darkness in growth chambers for 9, 10, or 11 days, after which measurements of hypocotyl lengths were made. Details were provided earlier by Samimy and LaMotte (1976).

To study the effect of a low temperature seed pretreatment on seedling development at 25 C, seeds were soaked in water at 4 C for 2, 11, and 30 days, then were planted and grown at 25 C in the usual manner. Control seeds were planted directly at 25 C without prior soaking.

Four temperature-sequencing experiments were performed in which seeds were germinated and seedlings grown at one temperature for

varied periods of time, then were transferred to another temperature for the remainder of a 9 or 11 day period. The four regimes studied were 20 to 30 C, 20 to 25 C, 25 to 30 C, and 30 to 25 C. Hypocotyl lengths were measured at the end of the period. Constant temperature controls were included in each such experiment.

RESULTS AND DISCUSSION

Response to a 4 C Pretreatment. The inhibition of hypocotyl elongation by a temperature of 25 C is illustrated in Figures 1 and 2. Pretreating seeds at 4 C before planting at 25 C did not prevent this inhibition (Table 1). In fact, when administered for 11 or 30 days such pretreatment further reduced the elongation observed later at 25 C. The 11-day pretreatment at 4 C caused a 29% decrease in elongation relative to those receiving no pretreatment. The 30-day pretreatment caused a 20% decrease in elongation.

Response to a 25 to 20 C Sequence. At the end of the experiment the shortest hypocotyls were those which had been held at 25 C for 6.5 days or longer. Such hypocotyls were only 35% as long as those grown at continuous 20 C (Fig. 1). The maximum slope of the curve (Fig. 1) suggests that the inhibitory effect of 25 C was greatest between 2 and 5 days. This is of interest as the inhibition does not manifest itself until later (Samimy and LaMotte, 1976). As shown in our earlier paper, plants grown for 5 days at 25 C have an average hypocotyl length of 7 cm; those grown at 20 C require 6.5 days to reach this same length. When kept at 20 C for the next 6 days the growth of these two kinds of 7-cm seedlings is quite different. Hypocotyls of those having reached this length at 25 C increase only 4 cm in length at an average rate of 0.7 cm/day (Fig. 1). Those having reached this length at 20 C (*i.e.*, those grown throughout at 20 C) increase at least 10.5 cm in length at an average rate of at least 1.7 cm/day (Samimy and LaMotte, 1976). These results show that a temperature of 25 C during germination and early stages of seedling development induces changes which later result in inhibition of hypocotyl elongation. This inhibition becomes evident even if seedlings are transferred to 20 C before the rate of elongation declines.

Response to a 20 to 25 C Sequence. Increasing the duration of time at 20 C results in a progressive stimulation of hypocotyl elongation as measured after 11 days' growth (Fig. 1). The stimulatory effect of 20 C is greatest between 2 and 5 days just as was the inhibitory effect of 25 C. As shown earlier (Samimy and LaMotte, 1976), hypocotyls of Clark seedlings grown at 20 C reach an average length of 4 cm at 5 days. When such 4-cm seedlings are transferred to 25 C and grown for 6 more days, their hypocotyls increase 15 cm in length at an average rate of 2.5 cm/day (Fig. 1). On the other hand, seedlings grown continuously at 25 C reach a hypocotyl length of 4 cm at 3.5 days and during the next 6 days their hypocotyls increase only 7 cm in length at an average rate of 1.2 cm/day (Samimy and LaMotte, 1976). Therefore, the growth of 4-cm hypocotyls at 25 C is very much dependent on the temperature at which they reach this length. Hypocotyls grown to this length at 20 C elongate approximately twice as much and twice as fast at 25 C as those

Figure 1. *Final lengths of hypocotyls of Clark soybean seedlings grown for varied times at one temperature, then transferred to another temperature for the remainder of an 11-day period.*

Each point represents a mean of 29-30 hypocotyl lengths. Standard errors of the means range from 0.5-1.1 cm; coefficients of variation (standard error × 100 divided by the mean) range from 4.0-9.7%.
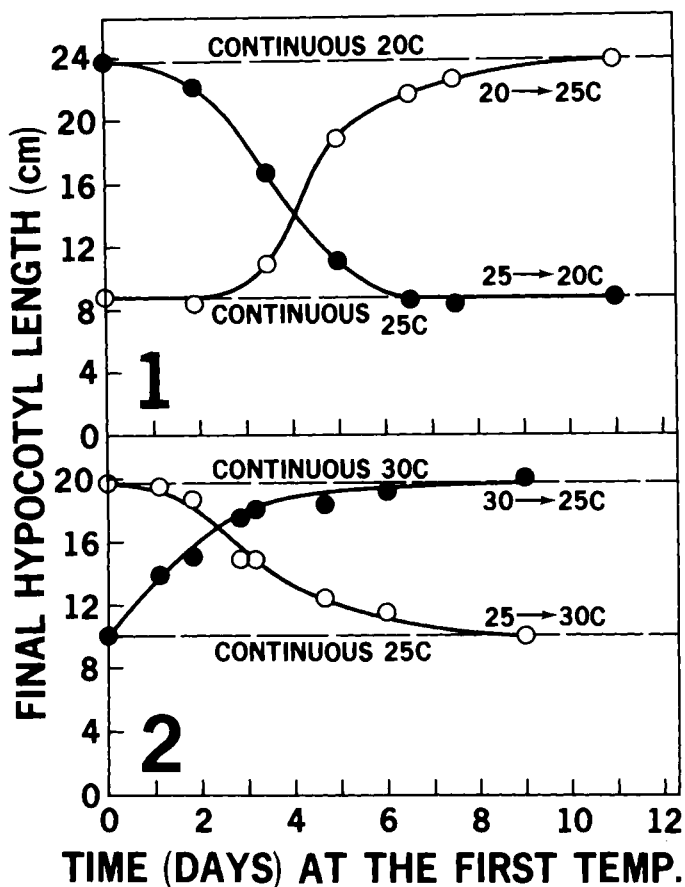
Figure 2. *Final lengths of hypocotyls of Clark soybean seedlings grown for varied times at one temperature, then transferred to another temperature for the remainder of a 9-day period.*

Each point represents a mean of 21-67 hypocotyl lengths. Standard errors of the means range from 0.2-0.8 cm; coefficients of variation range from 1.5-7.0%.

grown to this length at 25 C.

Response to a 25 to 30 C Sequence. Growth at 25 C resulted in a progressive inhibition of hypocotyl elongation as the duration at 25 C was increased (Fig. 2). Continuous growth at 25 C resulted in maximum inhibition (51% inhibition relative to growth at continuous 30 C). The inhibitory effect of 25 C was greatest between 1.8 and 2.8 days (Fig. 2).

Response to a 30 to 25 C Sequence. An increasing duration at 30 C resulted in a progressive stimulation of hypocotyl elongation judging from the lengths at the end of the 9-day period (Fig. 2). The stimulatory effect was most pronounced during approximately the first 3 days. Comparison of elongation in this sequence with that at continuous 25 C (Samimy and LaMotte, 1976) further illustrates the persistent inhibitory effect of 25 C during the first few days of seedling development. In a

Table 1. *Effect of a 4 C pretreatment of seeds on development of seedlings at 25 C.*

Time (days) at 4 C	Hypocotyl mean length (cm)[1]	n	p (%)[2]
0	10.1	40	—
2	11.9	19	>10
11	7.2	27	0.1
30	8.1	28	<2.5

[1]*After 10 days of growth at 25 C.*
[2]*Probability level for statistical significance of the difference between treatment and control means based on Student's 't' test. P > 5% is considered not statistically significant.*

manner similar to that observed in comparing effects of early exposure to 20 and 25 C, hypocotyls grown to a length of 6 cm at 30 C subsequently elongate at 25 C more than twice as fast as those grown to a 6-cm length at 25 C.

GENERAL DISCUSSION

Results reported here for Clark cultivar are similar to those reported for Ford and Amsoy cultivars by Gilman et al. (1973), but differ quantitatively from those reported for Clark by them. Clark seedling hypocotyl elongation was more strongly inhibited by 25 C in our tests than in theirs. This probably derives from differences in seed batches. We have observed such differences in a controlled experiment involving two different batches of Clark seed (unpublished results).

The anomalous temperature response of the soybean cultivars has three noteworthy characteristics: (1) It is bimodal. Two temperature optima for hypocotyl elongation are observed: one above 25 C, the other below it (Grabe and Metzer, 1969; Samimy, 1970; Gilman et al., 1973). (2) It involves an induced state which persists in absence of the inducing temperature. (3) It involves a period of temperature sensitivity which is peculiar to germination and the early stages of seedling development and persists for only a few days. Each of these characteristics is discussed below.

Bimodality. Other examples amongst plants are known but their physiological bases remain obscure. Germination of seeds of *Brassica arvensis* (mustard: Went, 1957) shows a bimodal response similar to that of soybean hypocotyl growth. Seed germination in *Jussiaea suffruticosa* (Wulff et al., 1972) is also bimodal but its response modes occur at higher temperatures than the corresponding modes for soybean and mustard. Vegetative growth by plants of Cuban White tobacco exhibits bimodality with respect to night temperature when grown at a constant day temperature of 26 C (Camus and Went, 1952; Went, 1957). Growth is slower and flowering is later at 17 C than at higher and lower night temperatures. Bimodal growth responses are also known in fungi (*Neurospora:* Mitchell and Houlahan, 1946) and in bacteria (putative *Clostridium:* Oppenheimer and Drost-Hansen, 1960).

Induction by Temperature. Changes induced by temperature during one stage of development which manifest themselves in a later stage are well known in plants. Vernalization, loss of seed dormancy during stratification, cold hardening (Leopold and Kriedemann, 1975), and increased heat tolerance (e.g., Schroeder, 1963) are changes of this kind. Amongst phenomena encompassed by the ecologists' term acclimation (or acclimatization), changes in assimilative capacity induced by prior exposure to various temperatures have been the most extensively studied (Billings, 1974). Such changes vary with the ecotype tested and appear to be of adaptive significance.

Lang (1963) has grouped such environment-induced phenomena into three categories based primarily on relative duration of persistence. The phenomenon demonstrated in soybean appears to be intermediate to the

first, which includes phenomena such as coleoptile geo- and photo-tropism, and the second, which includes phenomena such as ". . .thermo- and photoinduction of flower formation in many plants in which the response persists for extended periods of time but which still, upon transfer to non-inductive conditions, may revert to vegetative growth." The soybean phenomenon differs from the first in persisting for several days instead of several hours. It differs from the second in having shorter duration, in lacking susceptibility to reversal after full induction, and in being limited in persistence by the transient and determinate nature of hypocotyl development itself. Lang's third category includes phenomena "which last for the remaining life of the individual." The persistence of some such induced states is truly remarkable. The temperature-induced dwarf morphology of peach seedlings (Pollack, 1959) has been shown by Flemion (1956) to persist for at least ten years.

In Clark soybean seedlings the temperature-induced state is characterized by an abnormally high rate of ethylene evolution whose onset precedes the decline in rate of hypocotyl elongation after 5 days at 25 C (Samimy and LaMotte, 1976). Measurements of diffusible auxin in Clark seedlings grown in darkness at 20 and 25 C suggest that the enhanced rates of ethylene evolution are caused by supraoptimal auxin levels in hypocotyls of the 25 C-grown seedlings (unpublished findings). In any case, it appears that an abnormal hormone status characterizes and maintains the induced state. It may also have a causal role in bringing about this state. Further assessment of the time course of such temperature-induced changes in hormone status should narrow the scope of searches for the temperature-sensitive biochemical event(s) and enzyme(s) involved in catalysis.

Short-lived Sensitivity. In the anomalous soybean cultivars sensitivity to 25 C persists for less than a week (about 6 days). It disappears before hypocotyl elongation is complete and becomes diminished before hypocotyl elongation is half complete. In embryos and young seedlings of peach, sensitivity to temperatures capable of inducing dwarf morphology is similarly brief. They become sensitive 2-3 days after water is supplied and become insensitive 6 days later. After-ripening at 5 C reduces but does not completely alleviate the dwarf symptoms expressed upon germination at 25 C. Moreover, it does not change the duration of the 25 C-sensitive period (Pollack, 1962). Seeds of mustard show a similarly brief duration of susceptibility to inhibition by a temperature of 26 C. According to the interpretation of Went (1957), they are sensitive only during the earliest stages of germination.

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