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Aging Progression Involving Dwarfism and Its Acceleration by Red Light in Bean Hypocotyls

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ABSTRACT

The effect of red light on the aging progression of the bean (*Phaseolus vulgaris* L.) hypocotyl segment unit was examined in relation to dwarfism using Kentucky Wonder (tall) and Masterpiece (dwarf) varieties. In both plants, red light promoted the elongation of younger zones and inhibited that of mature zones. The zone exhibiting maximum elongation was shifted to the younger zones by red light irradiation regardless of the plant type, but its extent was greater in the dwarf than in the tall. Thus, red light hastens both the beginning of elongation in the younger portion and its termination in the mature portion of the hypocotyl, particularly of the dwarf plant. These red light responses in each zone of both the tall and dwarf hypocotyl units were reversed by subsequent exposure to far red light regardless of the duration and intensity of red light, thus indicating that the hastened aging progression of the hypocotyl by red light is mediated by phytochrome. However, there is no difference in the rate of decay of Pfr between the tall and dwarf hypocotyls.

The increased expression of bean dwarfism seems to result from a concerted action of red light upon the maturation of younger portions of the hypocotyls, which is more rapid in the dwarf than in the tall, and upon the elongation of the relatively matured portion, which is more severely inhibited in the dwarf.

We have reported that dwarf expression in the early growth of bean seedlings may be a reflection of a difference in gibberellin content between the tall and dwarf varieties (6, 8). The cotyledons and embryonic axes of the dwarf contain much less gibberellins than those of the tall, although there was no appreciable qualitative difference in the kind of extractable and diffusible gibberellins. We have not detected any significant difference between the two plant types in the gibberellin contents of the leaves and shoots during the vegetative growth stages after the cotyledons fall off (unpublished). This suggests that not only gibberellins but also other factors may be involved in the dwarf expression of bean plants.

Most cultivars of the dwarf beans belong to the early variety and have shorter life spans compared to the tall varieties. Some experimental results suggest that light actions differ in degree (17) or direction (10, 18) according to the physiological age of the plant tissues: light promoted elongation in the very young stem, but suppressed the active growth of the younger stem, acting to increase the rate of cell maturation (16). We also confirmed this with bean hypocotyl (7). Moreover, many researchers have showed that growth responses of dwarf plants to light differ from those of the tall varieties (1, 3, 5, 11, 14, 15). These findings suggest a relationship between the dwarf expression and physiological aging of a shoot system. The present study demonstrates the involvement of a light-mediated tissue aging in the dwarfism of beans.

MATERIALS AND METHODS

Two bean cultivars, a tall (*Phaseolus vulgaris* L. cv. Kentucky Wonder) and a dwarf (*P. vulgaris* cv. Masterpiece), were used for comparison in all experiments. The general procedures followed that described previously (7): the seed coat was cracked carefully near its hilum with a razor blade in order to ensure an even water absorption rate between the two plant types, and the seeds were germinated in vermiculite moistened by Knop's solution at 25 C in the dark for 5 days. Hypocotyl units were prepared from the etiolated seedlings selected for 6 to 7 cm in height (Fig. 1). Just before experiment, they were marked by India ink dots in 3-mm intervals to distinguish their different aged zones: AI, AII, B, CI, CII, CIII, CIV, and CV. The marked hypocotyl units were placed vertically to a depth of about 8 mm in 0.8% agar in which Nitsch's solution (13), exclusive of sugar, was included. The agar was renewed daily. One group of 15 hypocotyl units per a 9-cm Petri dish was used for each experiment, and the dishes were placed in a transparent acrylic case (40 × 20 × 20 cm). Then the cases were sealed and exposed to red and/or far red light and incubated in the dark or in red light at 25 C. The red light sources consisted of either six red fluorescent tubes (40 w) at about 32,000 ergs·cm^{-2}·sec^{-1} and λ_{max} 660 nm of 610 to 720 nm, or, for the experiments of red-far red reversion, 10 red fluorescent tubes (20 w) filtered through a sheet of red Plexiglas at about 5000 ergs·cm^{-2}·sec^{-1}. Far red light was supplied from four medical far red lamps (120 w, λ_{max} 1350 nm of above 600 nm) lighted at 80 v, passed through a 10-cm water layer and a sheet of blue plastic filter, the intensity being about 5000 ergs·cm^{-2}·sec^{-1}. In order to avoid the effects of endogenously evolved ethylene, 0.25 M mercuric perchlorate solution was put in the case. The elongation was represented by the increase in distance between the marks delimiting each zone, which was measured with 0.5 mm accuracy after necessary incubation periods. All manipulations were carried out under a dim green safelight.

RESULTS

Different Aging Progression between Tall and Dwarf Hypocotyl Units. The time courses of elongation of the bean hypocotyl units are shown in Figure 2, in which a difference in the initial (0 day) length between the tall and dwarf units is due to the longer hook region of the tall seedings. In the dark, dwarfism was hardly expressed in the hypocotyl units used in the present study, although intact seedlings exhibited a weak dwarfism. In red light, the growth rate of the tall unit surpassed that of the dwarf, and dwarfism was clearly revealed. Photoinhibition was manifested from the 2nd day in the dwarf and from the 4th day in the tall. Little difference was observed in the duration of the rapid elongation period between the two plant types both in the dark and in red light.

Figure 3 shows the daily growth patterns in the hypocotyl units of the tall and dwarf beans incubated in darkness or in red light.

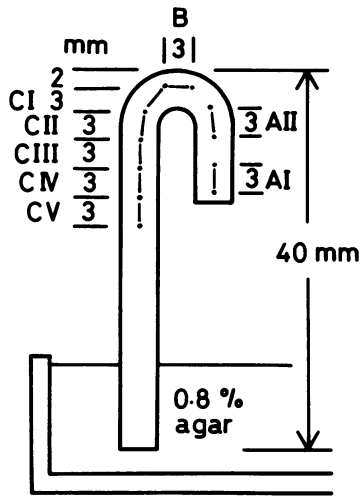

FIG. 1. Diagram of a hypocotyl segment unit showing the zones marked by India ink and measured for elongation.

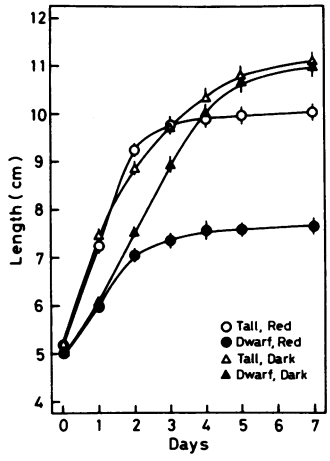

FIG. 2. Time courses of elongation of hypocotyl units of the tall and dwarf beans. Hypocotyl units were allowed to grow on 0.8% nutrient agar in the dark or in red light (about 32,000 ergs·cm^{-2}·sec^{-1}). Vertical bar through each point indicates SE of the mean.

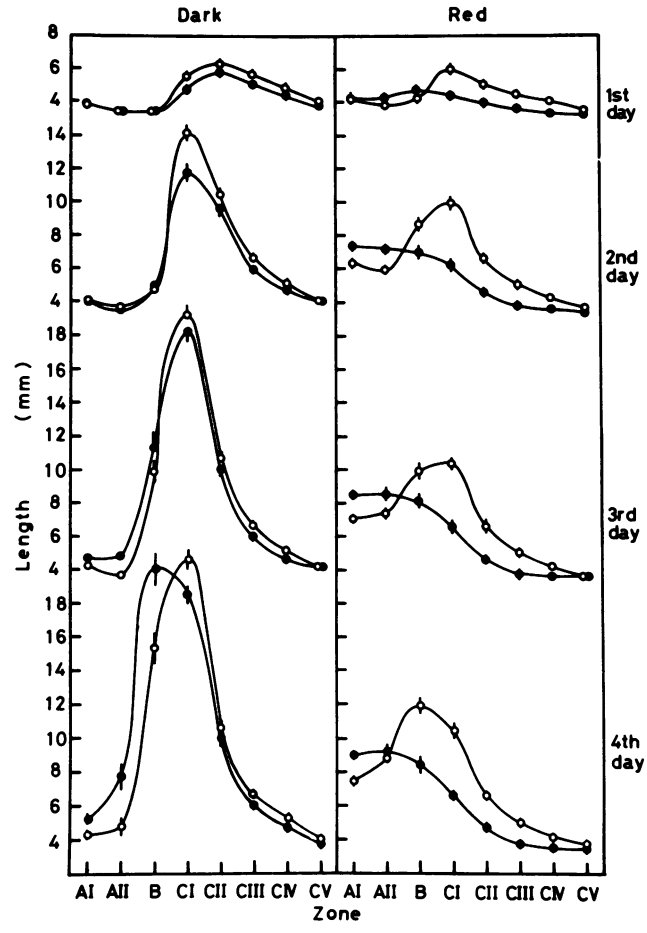

FIG. 3. Growth pattern of the tall (O) and dwarf (●) hypocotyl units measured daily for incubation in darkness and in red light (about 32,000 ergs·cm^{-2}·sec^{-1}). Vertical bar through each point indicates SE of the mean.

From a comparison of the length in each zone of the hypocotyl units incubated in the dark and in red light, it was apparent that red light was inhibitory to the elongation of older zones below CI, and conversely it was promotive in younger zones above B at the 2nd day of incubation. The elongation of the very young AI and AII zones in red light surpassed that in the dark even on the 4th day, although the relative difference in elongation of the B zone began to diminish by the 3rd day in both the tall and dwarf plants. In the dark, there was no significant difference in the growth pattern between the tall and dwarf plants until 3 days of incubation, both of which exhibited a maximum elongation in the CII zone at the 1st day, and in the CI zone at the 2nd and 3rd day. The rapidly elongating zone in the dwarf shifted to the B zone at the 4th day, although that in the tall remained at the CI zone. This indicates that in the dwarf units the beginning of the elongation in the younger zones and termination of it in the mature zone occurred sooner than those of the tall units. In red light, the growth patterns of the two plants were already different after the 1st day of incubation: the dwarf showed no maximum elongation zone, in contrast to the tall which exhibited the maximum elongation in the CI zone. After 2 days, the maximum elongation in the irradiated dwarf occurred at the youngest AI zone, while that in the tall shifted only to the B zone. These results indicate that the rapidly elongating zone of the hypocotyl moves toward the younger region in red light-treated plant, and suggest that red light may hasten a sequential aging of the whole hypocotyl tissue, with the rates of both processes being greater in the dwarf than in the tall plants. The faster progression of aging in the dwarf, as expressed by a rapid transfer of the zone of the maximum elongation, proceeds also in the dark, as evidenced by a different growth pattern between the two plant types at the 4th day of incubation.

These phenomena are more clearly demonstrated in Figure 4, in which the daily elongation patterns of the hypocotyl unit incubated in red light are presented as a per cent of the corresponding dark controls. In the dwarf, the zone responsive to the red light reached the AI zone at the 3rd day of incubation, while the tall needed 4 or more days. In the dwarf, moreover, red light stimulated the elongation of the youngest AI zone at the 4th day, but it was inhibitory in every zone on the 7th day, when little elongation occurred. In the tall, on the other hand, red light promoted the elongation of the AI and AII zones even 7 days later. Moreover, the degree of photoinhibition in the CI and CII zones was greater in the dwarf than in the tall within the period of experiment. The typical manifestation of dwarfism under red light may finally be due to less or no promotion and severer inhibition of elongation by light in the younger and the older zones of the dwarf hypocotyl, respectively, compared to those of the tall. From these results, it is conceivable that the dwarfism in intact hypocotyls is a reflection of summing up different growth responses in each zone to light and is partially ascribable to the

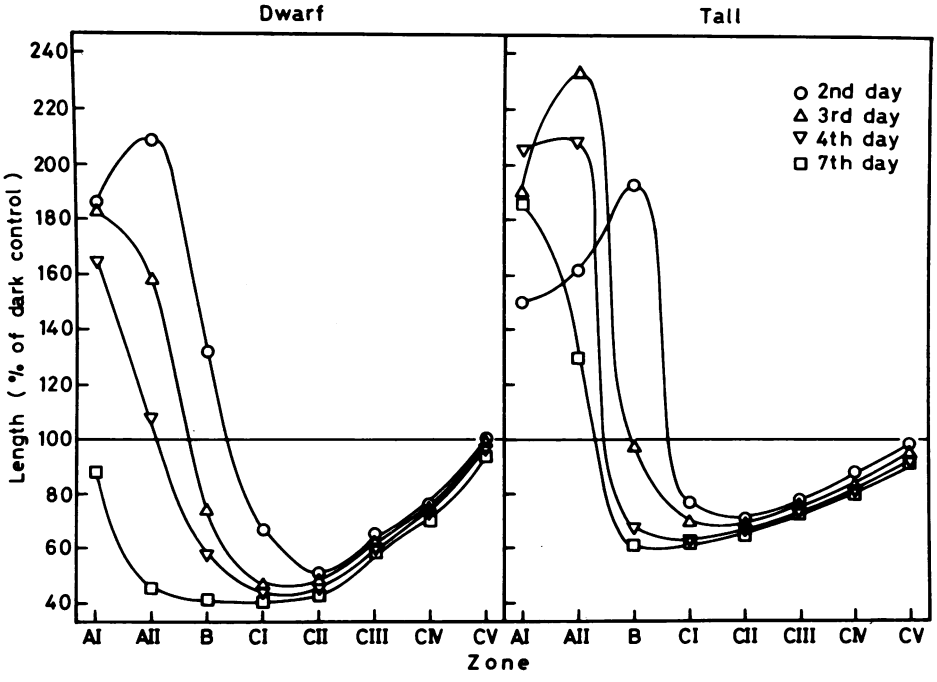

FIG. 4. Effect of red light (about 32,000 ergs·cm^{-2}·sec^{-1}) on the elongation of different zones of the tall and dwarf hypocotyl units. Length of each zone is presented by per cent of corresponding dark control.

earlier growth termination in the irradiated younger zones of the dwarf plant.

Effect of Exposure Time and Intensity of Red Light on Aging Progression of Hypocotyl Unit. Experiments were done to examine more precisely the effect of red light on the dwarf expression and the aging progression. Figure 5 shows the effect of exposure times to red light on the elongation of each zone of the dwarf and tall hypocotyl units. In both plants, growth of the AI and B zones was increased by red light irradiation up to 20 min, but its promotive effect on growth (except for the B zone of the dwarf) became less when irradiation was more prolonged than 20 min. The decrease of growth promotion in the B zone of the dwarf by red light over 20 min may be due to the more rapid aging progression in the dwarf than in the tall. Photoinhibition in the CII growth was also increased rapidly by shorter irradiation until 20 min and then slowly by further irradiation in both plants. These results imply that rapid responses of each zone to shorter light exposure may be mediated by phytochrome, while the slower responses to the prolonged irradiations may result from the aging of the hypocotyl tissues which may be controlled through the action of the high intensity light.

In experiments shown in Figures 6 and 7, the light intensity was changed by placing the hypocotyl units at various distances from a red light source. The continuous exposure to relatively high intensity (about 32,000 ergs·cm^{-2}·sec^{-1}) slightly advanced the maximum elongation zone to the younger zones as compared with the low intensity (about 2000 ergs·cm^{-2}·sec^{-1}): the youngest AI zone in the dwarf and AI and AII zones in the tall elongated more rapidly in the high intensity than in the lower intensity. It is obvious that the intensity of red light affects the aging progression of the hypocotyl units. In another experiment, red light of various intensities was given for 10 min (Fig. 7). The extent of photoinhibition of elongation in the relatively aged CII zone increased gradually with the light intensity, equally between the two plant types, and the CI zone did not exhibit any significant growth responses, regardless of the intensity of red light. The dwarf and tall plants were different in the response of the younger AI zone to the red light: the growth of the former increased in proportion to increased intensities, while in the

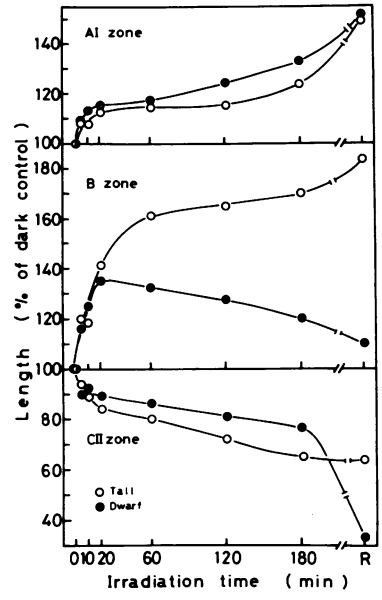

FIG. 5. Effect of irradiation time of red light (about 32,000 ergs·cm^{-2}·sec^{-1}) on the elongation of each zone of the tall and dwarf hypocotyl units. Red-irradiated hypocotyls were incubated in the dark for 2 days. R: Continuous irradiation of red for 2 days.

latter the red light at 4000 to 6000 ergs·cm^{-2}·sec^{-1} was sufficient to ensure its maximum elongation. Such a strong dependency on the light intensity of the elongation of the AI zone in the dwarf seems to result from the more rapid proceeding of aging in the dwarf hypocotyl than that in the tall one. In any case, this high responsiveness of the dwarf to light intensity may suggest the participation of an additional photoresponsive system (other than phytochrome) in the growth regulation of the dwarf hypocotyl.

Involvement of Phytochrome System in Aging Progression of Hypocotyl. Both the growth promotion by light in the younger

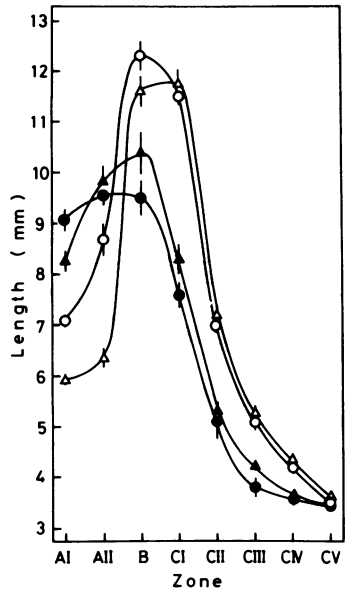

FIG. 6. Growth of different zones of the tall and dwarf hypocotyl units after 3-day incubation in two intensities of red light. Vertical bar through each point indicates SE of the mean. Tall (○); dwarf in about 32,000 ergs·cm^{-2}·sec^{-1} (●); tall (△); and dwarf in about 2000 ergs·cm^{-2}·sec^{-1} (▲).

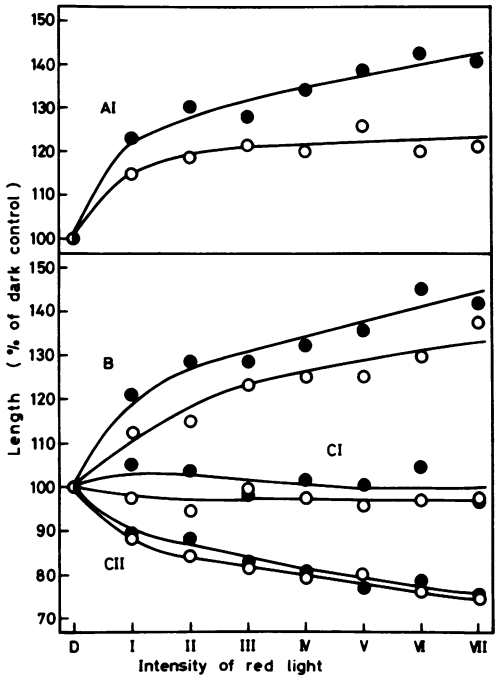

FIG. 7. Effect of intensity of red light on the elongation of AI, B, and CII zones of the tall (○) and dwarf (●) hypocotyl units. Hypocotyls were irradiated with various intensities of red light for 10 min and then incubated in the dark for 2 days. Intensity of red light (X 10^3 ergs·cm^{-2}·sec^{-1}); I: 2; II: 4; III: 6; IV: 8; V: 10; VI: 18; and VII: 32. D: Continuous dark control.

hypocotyl tissue and the growth inhibition by light in the older tissue were shown to be regulated by the phytochrome system since far red light could reverse the effects of a previous red light treatment (Fig. 8). In a short time irradiation of 20 min at 5000 ergs·cm^{-2}·sec^{-1}, far red light nullified both the red light-stimulated growth in the younger AI, AII, and B zones and the red

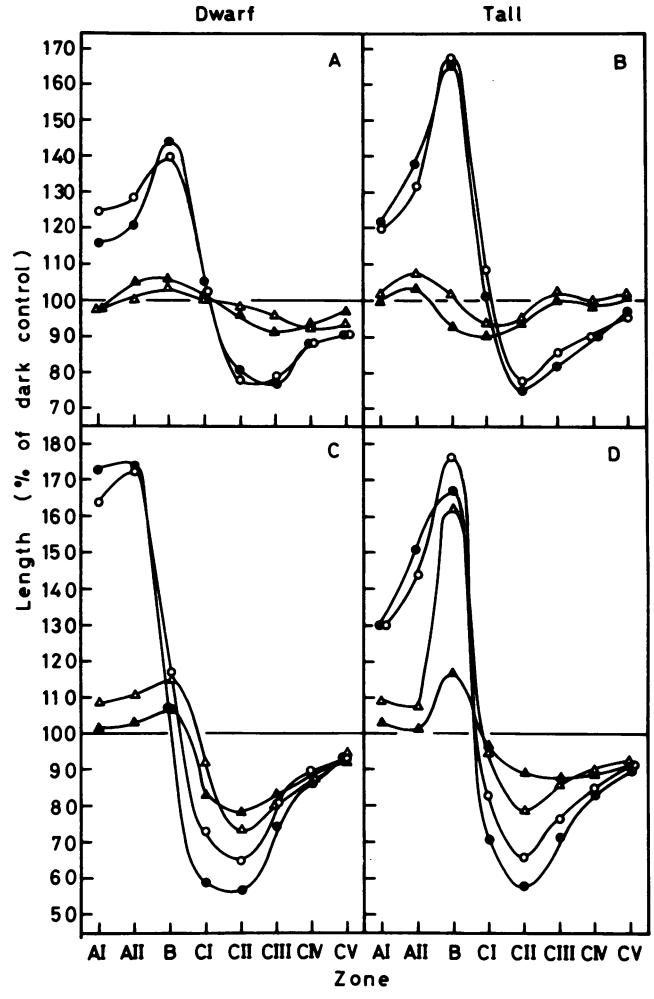

FIG. 8. Red-far red reversibility of elongation of each zone of the tall and dwarf hypocotyl units. Hypocotyls were incubated for 48 hr in the dark following red and/or far red irradiation. Data are presented with per cent of dark control. A and B: 20 min-light treatment; C and D: 6 hr-light treatment. Far red (about 5000 ergs·cm^{-2}·sec^{-1}) (▲); red (about 5000 ergs·cm^{-2}·sec^{-1}) (○); red-far red (△); and far red-red (●).

light-inhibited growth in the CII, CIII, and CIV zones. There was only a slight difference in the responding patterns between the dwarf and tall hypocotyls, with the exception that growth promotion by the red light in the B zone of the dwarf (Fig. 8, A and B) was less. The CI zone, which was situated at an inflection point between the opposite effects of the red light, did not exhibit any response to the light, and so, it appeared as if no phytochrome system participated in the zone. Similar results were obtained with high intensity irradiation at 32,000 ergs·cm^{-2}·sec^{-1} (data not shown). Unlike the case of a 20-min irradiation in Figure 8, however, a 6-hr red light exposure eliminated the red-far red reversibility in the B zone, and conversely rendered the CII zone more responsive to red and far red lights (Fig. 8, C and D). Such a loss of the red-far red reversibility in the B zone seems to result from the advanced aging in the hypocotyl tissue subjected to prolonged irradiation. There was little difference between the tall and dwarf plants in their response to red-far red reversible irradiations, regardless of the duration of the irradiations. These results suggest that the elongation of the dwarf hypocotyl, as well as that of the tall, may be controlled by the phytochrome system.

Data in Figure 9 have offered the alternative possibility that another high energy-requiring photoreceptor system, besides the phytochrome system, may be involved in the photostimulation of

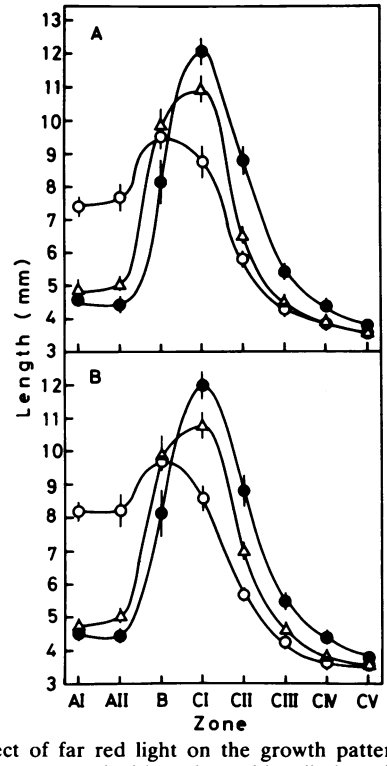

FIG. 9. Effect of far red light on the growth pattern of the dwarf hypocotyl units pretreated with prolonged irradiation of red light. After irradiation, the hypocotyls were incubated in darkness for 2 days. (A): about 5000 ergs·cm^{-2}·sec^{-1}; (B): about 32000 ergs·cm^{-2}·sec^{-1}. Dark control (●); 6 hr red (○); and 6 hr red- 6 hr far red (△). Vertical bar through each point indicates SE of the mean.

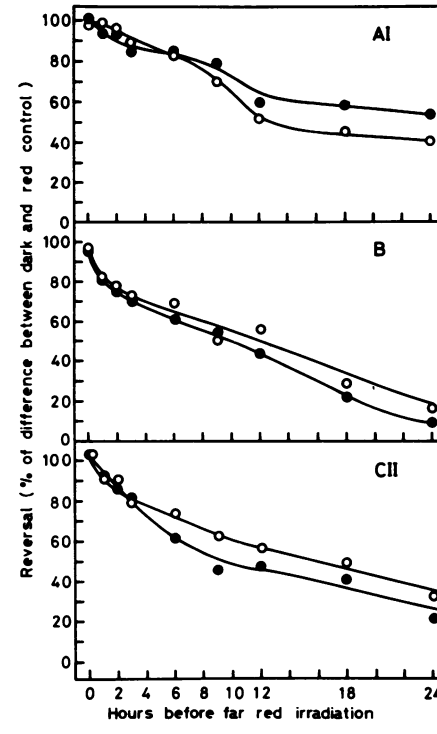

FIG. 10. Decays of reversibility of the red light promotion (AI and B zones) and inhibition (CII zone) by far red light in the hypocotyl units of the tall (○) and dwarf (●) beans. Marked hypocotyl units were irradiated by red light (about 5000 ergs·cm^{-2}·sec^{-1}) for 20 min at zero time, irradiated to far red light (about 5000 ergs·cm^{-2}·sec^{-1}) for 20 min after various periods of dark incubation, and measured at 48 hr.

elongation in the younger zones of the dwarf hypocotyls, and it may act to accelerate their tissue aging. A 6-hr red light-induced shift toward the younger zones of a portion which exhibits the maximum elongation in the dwarf hypocotyl unit was completely reversed by a 6-hr far red light at 5000 ergs·cm^{-2}·sec^{-1} administered immediately after the red light irradiation, regardless of the intensity of red light applied (Fig. 9). It seems likely that the phytochrome system itself not only mediates the photostimulation in the younger zones of the hypocotyl and the photoinhibition in the older zones, but also participates directly in accelerating tissue aging.

Stability of Pfr State of Phytochrome. A further experiment was performed to examine whether the rate of decay of Pfr was different between the tall and dwarf hypocotyl units (Fig. 10). Reversal by a subsequent far red light of both the red light-induced growth promotion in the AI and B zones and the red light-induced growth inhibition in the CII zone was reduced gradually as the dark period inserted between the red and far red irradiations was prolonged. The degree of escape from reversibility was similar between the tall and dwarf plants in every zone of the hypocotyl unit, indicating that there is no difference in the stability of the active Pfr state of phytochrome in the hypocotyl.

DISCUSSION

Genetic dwarfism of bean plants is most fully expressed in the light, suggesting that the dwarf expression is mediated by the phytochrome system and/or by a system which requires high light intensity or prolonged light exposure. This view is compatible with the suggestion by Vince (19) that at least two photochemical responses, the red-far red reversible phytochrome system and the second system which becomes functional only when irradiation is prolonged, are probably involved in the growth responses. Recently, Black and Shuttleworth (2) demonstrated a morphological separation of spectral sensitivity in the extension growth of cucumber hypocotyls: the major part of the inhibition of elongation by red light is mediated through the cotyledons, which transmit the effect to the hypocotyl, while the inhibitory effect of blue light results from a direct action upon the hypocotyl. In the present experiments, decotylized hypocotyl segment units (Fig. 1) were used in order to remove the cotyledon effects. The typical dwarf expression in the hypocotyl units under red light involves the response of the hypocotyl itself to red light, which may be one of the causes for the genetic dwarfism of bean plants.

There have been several reports that red light acts against the stem growth differently according to the tissue age (7, 10, 16-18). In the bean hypocotyl unit, red light promoted the elongation of younger portion (AI-B zone of the hypocotyl), but inhibited that of mature portion (CI-CIII zone) (Fig. 4). The magnitude of the promotion was greater and that of the inhibition was less in the tall than in the dwarf, which seems to contribute partially toward the enhancement of the dwarf expression. There was no significant difference in the red-far red reversibility of hypocotyl growth between the two plant types: regardless of the intensity and duration of red light (Figs. 8 and 9), the photoresponses of each zone of both the tall and dwarf bean hypocotyl units to red light were almost completely reversed by subsequent exposure to far red. These results apparently indicate that the growth of bean hypocotyls may be mediated only by the phytochrome system, although the direction of the response changes with tissue age. McArther and Briggs (12) also demonstrated that the action of phytochrome reflects the tissue age: the Pfr present in young pea epicotyl tissue following red light was converted mostly to Pr when the epicotyl was placed in the dark, while with older tissue, the level of reverted Pr was reduced by destruction of Pfr. However, the red-far red reversible responses in opposite directions in the differ-

ently aged zones of the bean hypocotyl units suggest that the limiting factor for cell growth is different according to the age of tissues, and is not associated with the stability of Pfr. This view is compatible with our previous results that the controlling factors or hormones for stem elongation are different along the physiological ages of the bean hypocotyl unit (7).

There are some reports that light accelerates the maturation of stem tissues (4, 16, 17). Bean hypocotyl tissue aging was accelerated by red light, as evidenced by the observation that the maximum elongation zone was shifted forward to younger zones more rapidly by red exposure than in continuous dark (Fig. 3). This shift induced by red may also be attributed to the phytochrome action, since it was prevented by subsequent far red irradiation regardless of the intensity of red light (Fig. 9). An important fact is that the extent of the shift was greater in the dwarf than in the tall (Fig. 3).

It has been reported that the growth response of dwarf plants to light is much more pronounced than that of the tall plants with the result that the marked photoinhibition of stem growth in the dwarf leads to the typical dwarf growth habit (5, 9). We obtained similar findings with bean hypocotyl units which were grown under continuous red light (Fig. 2). On the other hand, Russel and Galston (14) have concluded that there is no difference in energy required to activate phytochrome between the tall and dwarf pea epicotyls, but that the Pfr form remains stable and active in the dwarf but decays rapidly in the tall. In this study with bean hypocotyls, the extent of Pfr decay, which was estimated by the loss of the reversal of the red effect by subsequent far red irradiation, was similar between the tall and dwarf plants in both the younger and the more aged portions of hypocotyl (Fig. 10). This result suggests that the expression of dwarfism mediated by red light in the bean hypocotyls, in contrast to pea, may be due to the rapid progression of some irreversible metabolic process rather than to the stability of Pfr in the dwarf; *i.e.* the Pfr-activated metabolic process may become irreversible more rapidly in the dwarf than in the tall hypocotyl. Lockhart (11) mentioned that the cause of dwarfism in beans in contrast to that in peas is not the result of a difference in the steady state condition of the phytochrome. Rather, it is due to another "fundamental process." Our study suggests his fundamental process is identical with the rapidity of aging of the hypocotyl tissues.

The aging of the dwarf hypocotyl progressed more rapidly than that of the tall not only in red light but also in darkness (Fig. 3), although the difference in the rate of aging between the tall and dwarf hypocotyl tissues was markedly amplified when the Pr form of the phytochrome was converted to Pfr. Consequently, the elongation period of the younger AI and AII zones of the dwarf was drastically reduced by red, compared with the tall, and their growth was terminated earlier than that of the tall. We concluded that the more rapid maturation of the younger portion of the dwarf bean hypocotyl, together with the more pronounced photoinhibition of the older portion, results in the enhanced dwarfism observed when phytochrome is maintained in the Pfr state, even though there are no quantitative or qualitative differences in the Pfr state between the hypocotyls of the two plant types.

LITERATURE CITED

1. Barendse, G. W. M. and A. Lang. 1972. Comparison of endogenous gibberellins and of the fate of applied radioactive gibberellin A_1 in a normal and dwarf strain of Japanese morning glory. Plant Physiol. 49: 836–841.
2. Black, M. and J. E. Shuttleworth. 1974. The role of the cotyledons in the photocontrol of hypocotyl extention in *Cucumis sativus* L. Planta 117: 57–66.
3. Cheng, K-C. and H. V. Marsh, Jr. 1968. Gibberellic acid promoted lignification and phenylalanine ammonia-lyase activity in a dwarf pea *(Pisum sativum)*. Plant Physiol. 43: 1755–1759.
4. Downs, R. J. and H. M. Cathey. 1960. Effects of light, gibberellin, and a quaternary ammonium compound on the growth of dark-grown red kidney beans. Bot. Gaz. 121: 233–237.
5. Gorter, C. J. 1961. Dwarfism of peas and the action of gibberellic acid. Physiol. Plant. 14: 332–343.
6. Gotô, N. and Y. Esashi. 1973. Diffusible and extractable gibberellins in bean cotyledons in relation to dwarfism. Physiol. Plant. 28: 480–489.
7. Gotô, N. and Y. Esashi. 1974. Differential hormone responses in different growing zones of the bean hypocotyl. Planta 116: 225–241.
8. Gotô, N. and Y. Esashi. 1975. Gibberellins in embryonic axes of tall and dwarf beans. Plant Cell Physiol. 16: 759–766.
9. Kende, H. and A. Lang. 1964. Gibberellins and light inhibition of stem growth in peas. Plant Physiol. 39: 435–440.
10. Klein, W. H., R. B. Withrow, V. Elstad, and L. Price. 1957. Photocontrol of growth and pigment synthesis in the bean seedling as related to irradiance and wavelength. Am. J. Bot. 44: 15–19.
11. Lockhart, J. A. 1958. The influence of red and far-red radiation on the response of *Phaseolus vulgaris* to gibberellic acid. Physiol. Plant. 11: 487–492.
12. McArther, J. A. and W. R. Briggs. 1971. *In vivo* phytochrome reversion in immature tissue of the Alaska pea seedling. Plant Physiol. 48: 46–49.
13. Nitsch, J. P. 1951. Growth and development in vitro of excised ovaries. Am. J. Bot. 38: 566–577.
14. Russel, D. W. and A. W. Galston. 1968. Comparative analysis of phytochrome-mediated growth responses in internodes of dwarf and tall pea plants. Planta 78: 1–10.
15. Sale, P. J. M. and D. Vince. 1960. Effects of light and gibberellic acid on internode growth in *Pisum sativum*. Physiol. Plant. 13: 664–673.
16. Thomson, B. F. 1950. The effect of light on the rate of development of *Avena* seedlings. Am. J. Bot. 37: 284–291.
17. Thomson, B. F. 1954. The effect of light on cell division and cell elongation in seedlings of oat and peas. Am. J. Bot. 41: 326–332.
18. Thomson, B. F. 1959. Far red reversal of internode stimulating effect of red light on peas. Am. J. Bot. 46: 740–742.
19. Vince, D. 1964. Photomorphogenesis in plant stems. Biol. Rev. 39: 506–536.