Plant & Cell Physiol. 20(3): 583–592 (1979)

Regulation of lettuce hypocotyl elongation by gibberellic acid. Interaction of gibberellic acid and gibberellin synergists – dihydroconiferyl alcohol, pestalotin and a triazinone compound

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(Received December 22, 1978)

The effect of three gibberellin synergists on lettuce hypocotyl elongation was studied. Dihydroconiferyl alcohol isolated from lettuce plants and (−)-(6S, 1′S)-pestalotin isolated from *Pestalotia cryptomeriaecola* enhanced the promoting effect of gibberellic acid on hypocotyl elongation of lettuce seedlings with and without the cotyledons. On the other hand, TA, a triazinone compound, did not enhance the gibberellin effect. The action of (−)-(6S, 1′S)-pestalotin was strongly inhibited by competitive inhibitors of dihydroconiferyl alcohol such as caffeic, ferulic and *trans*-cinnamic acids. Of the two stereoisomers of pestalotin, (+)-(6R, 1′R)-pestalotin enhanced the gibberellin effect but (+)-(6R, 1′S)-epipestalotin did not. (+)-(6R, 1′S)-Epipestalotin strongly inhibited the action of (−)-(6S, 1′S)-pestalotin and dihydroconiferyl alcohol. TA did not affect the action of dihydroconiferyl alcohol.

Stress-relaxation analysis of the mechanical properties of the lettuce hypocotyl cell wall demonstrated that gibberellic acid caused cell wall loosening and dihydroconiferyl alcohol and pestalotin did not influence this gibberellin effect.

The action mechanism of gibberellin synergists is discussed based on these results.

Key words: Dihydroconiferyl alcohol — Gibberellin synergist — *Lactuca sativa* L. — Lettuce cotyledon factor — Lettuce hypocotyl elongation — Pestalotin — Triazinone compound.

The ability of the cotyledons to direct stem growth has been studied in relation to the action of gibberellins because removal of the cotyledons from intact plants depresses stem elongation, particularly that caused by gibberellins (*1*, *3*, *5*, *10*). Chemical messenger(s) named the cotyledon factor has been suggested to be involved in this correlation phenomenon (*5*).

Dihydroconiferyl alcohol was isolated from lettuce seedlings as the cotyledon factor active in enhancing the effect of gibberellic acid (GA) on hypocotyl elongation of decotylized lettuce seedlings (*3*, *16*). It hardly influenced hypocotyl elongation of decotylized lettuce seedlings when given alone, but synergistically enhanced the promoting effect of GA (*16*). Like GA-induced lettuce hypocotyl elongation, GA-induced hook elongation of decotylized pea seedlings was also reported to be synergist-

Abbreviations: GA, gibberellic acid; TA, 4-ethoxy-1-(*p*-tolyl)-*s*-triazine-2,6 (1H, 3H)-dione; T_0, minimum relaxation time.

ically enhanced by dihydroconiferyl alcohol (*12*). Furthermore, the presence of a dihydroconiferyl alcohol-like substance in pea cotyledons was demonstrated (*12*). These facts indicate that dihydroconiferyl alcohol plays an important role in the correlation phenomenon between the cotyledons and stem elongation caused by gibberellins.

In addition to dihydroconiferyl alcohol, pestalotin and triazinone compounds are known to be gibberellin synergists. Pestalotin was isolated from a phytopathogenic fungus, *Pestalotia cryptomeriaecola* Sawada (*7*, *18*). Triazinone compounds were chemically synthesized (*13–15*). Both pestalotin and triazinone compounds have been found to be active in synergistically enhancing the promoting effect of gibberellin on rice shoot elongation (*7*, *13–15*, *18*). These facts suggest that pestalotin and triazinone compounds can mimic dihydroconiferyl alcohol in synergistically enhancing the GA effect on lettuce hypocotyl elongation. The present study was carried out to test this possibility.

Materials and methods

Lettuce hypocotyl test

Growth experiments were carried out according to methods reported previously (*3*). Lettuce seeds (*Lactuca sativa* L., cv. Grand Rapids) were sown on filter paper moistened with distilled water in petri dishes and incubated for 2 days at 25.0±0.5°C under continuous light from fluorescence tubes (ca. 2000 lux at plant level). Seedlings were selected for size uniformity and the cotyledons were excised with scissors at the point below the cotyledon joint. Ten decotylized seedlings were transferred onto filter paper moistened with 4 ml of test solution in a petri dish (9 cm in diameter). Decotylized seedlings were grown for 2 days under the same conditions used in germination, then hypocotyl length was measured. In some experiments, seedlings with intact cotyledons were also used for the lettuce hypocotyl test.

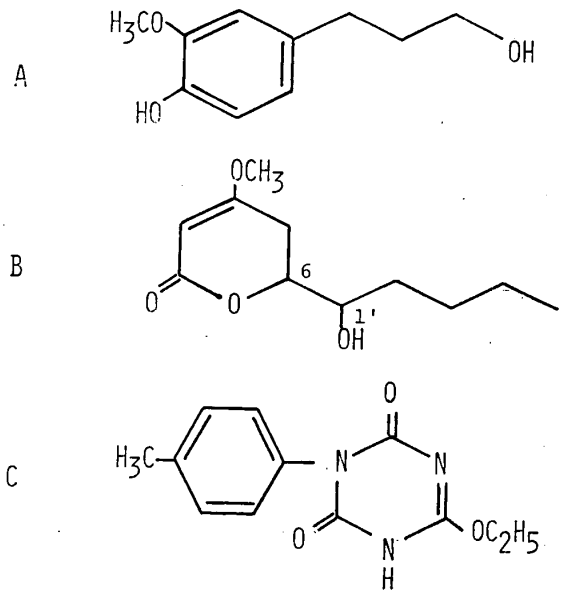

Fig. 1. *Chemical structure of gibberellin synergists.* A, dihydroconiferyl alcohol; B, pestalotin; C, TA.

Chemicals

Gibberellic acid (GA) was obtained from Kyowa Hakko Co. Ltd., Tokyo, Japan. (−)-(6S, 1'S)-Pestalotin, 6-(1-hydroxy pent-1-yl)-4-methoxy-5,6-dihydro-α-pyrone (Fig. 1B), was a gift from Dr. E. L. Patterson, Lederle Laboratories, American Cyanamid Co., New York, U. S. A. (+)-(6R, 1'R)-Pestalotin and (+)-(6R, 1'S)-epipestalotin synthesized by Mori et al. (*11*) were obtained from Dr. Y. Kimura, University of Tokyo, Tokyo, Japan. A triazinone compound, 4-ethoxy-1-(*p*-tolyl)-*s*-triazine-2,6 (1H, 3H)-dione (Fig. 1C), was obtained from Dr. M. Ogawa, Sankyo Co., Shiga, Japan. Dihydroconiferyl alcohol, 3-(3-methoxy-4-hydroxy) propan-1-ol (Fig. 1A), was synthesized by reducing dihydroferulic acid with lithium aluminum hydride in tetrahydrofuran (*4*).

Stress-relaxation analysis of the hypocotyl cell wall

The mechanical properties of the cell wall of the lettuce hypocotyl were measured by methods reported previously (*6*). Decotylized seedlings were treated with boiling methanol for 10 min, then the methanol was discarded. Methanol-killed seedlings were stored in fresh methanol at ca. 4°C until the stress-relaxation analysis (*19*). After being rehydrated with distilled water, the hypocotyl was fixed between two clamps (distance, 2 mm) of an Instron tensile tester (model TM-M) and stretched by lowering the bottom clamp (lowering rate, 20 mm/min). After the hypocotyl had received a load of 10 g, the clamp was stopped and the decay of the load was detected with a load cell and recorded with a Hitac-10II minicomputer (Hitachi) at various time intervals, minimum 10 msec. The load decay curve, i.e., the stress-relaxation curve was analyzed by simulating it to a continuous viscoelastic model consisting of infinite numbers of Maxwell components, then the minimum relaxation time (T_0) was determined from the equation: $S=b\cdot\log(t+T_m)/(t+T_0)$, where S is stress(g), T_0 is time (sec), b is a constant, and T_m is maximum relaxation time (sec).

Results

Effect of gibberellin synergists on lettuce hypocotyl elongation

Three gibberellin synergists were assayed for their ability to enhance GA-induced hypocotyl elongation of decotylized lettuce seedlings. As shown in Fig. 1B, (−)-(6S, 1'S)-pestalotin, originally isolated from *Pestalotia cryptomeriaecola*, synergistically enhanced the effect of GA on hypocotyl elongation of decotylized lettuce seedlings, as did dihydroconiferyl alcohol (Fig. 2A). The optimal concentration of pestalotin was around 10^{-6}–10^{-5} M. On the other hand, the triazinone compound (TA) in the concentration range from 10^{-7} to 10^{-4} M hardly influenced hypocotyl elongation in the presence or absence of exogenous GA.

The effect of gibberellin synergists on hypocotyl elongation was also tested using intact lettuce seedlings with the cotyledons (Fig. 3). Again, both dihydroconiferyl alcohol (Fig. 3A) and (−)-(6S, 1'S)-pestalotin (Fig. 3B) synergistically stimulated GA-induced hypocotyl elongation. But TA (Fig. 3C) showed no substantial effect on hypocotyl elongation of lettuce seedlings with the cotyledons in the presence or absence of added GA.

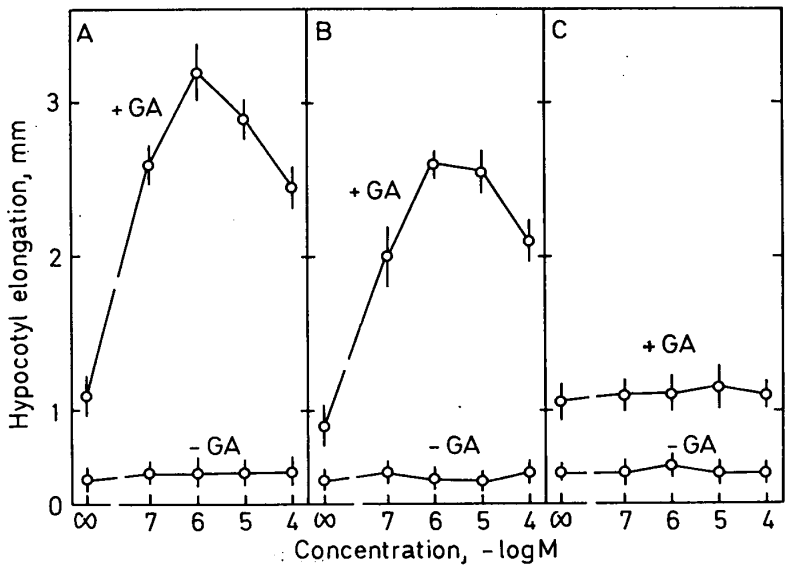

Fig. 2. *Effect of gibberellin synergists on GA-induced hypocotyl elongation of decotylized lettuce seedlings.* Decotylized seedlings were grown for 2 days in light in the presence or absence of 10^{-5} M GA with or without various concentrations of each gibberellin synergist. A, Dihydroconiferyl alcohol; B, (−)-(6S, 1'S)-pestalotin; C, TA. Vertical lines represent standard error.

Interaction between pestalotin and anticotyledon factors

As reported previously (*4*), the action of dihydroconiferyl alcohol on GA-induced lettuce hypocotyl elongation is competitively inhibited by anticotyledon factors such as *trans*-cinnamic, ferulic and caffeic acids. We studied whether or not the action of (−)-(6S, 1'S)-pestalotin on GA-induced hypocotyl elongation of decotylized lettuce seedlings is influenced by these factors. As shown in Fig. 4A–C, they hardly influenced hypocotyl elongation caused by 10^{-5} M GA but strongly inhibited the promoting effect of pestalotin on GA-induced hypocotyl elongation,

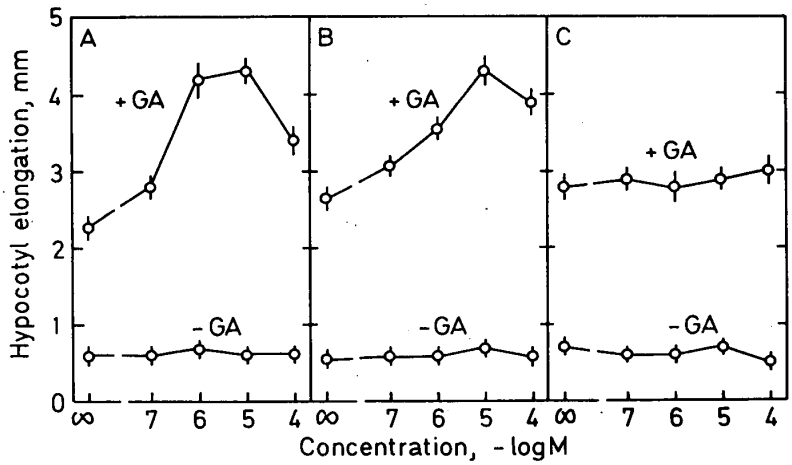

Fig. 3. *Effect of gibberellin synergists on GA-induced hypocotyl elongation of intact lettuce seedlings with the cotyledons.* Intact seedlings were grown for 2 days in light in the presence or absence of 10^{-5} M GA with various concentrations of each gibberellin synergist. A, dihydroconiferyl alcohol; B, (−)-(6S, 1'S)-pestalotin; C, TA. Vertical lines represent standard error.

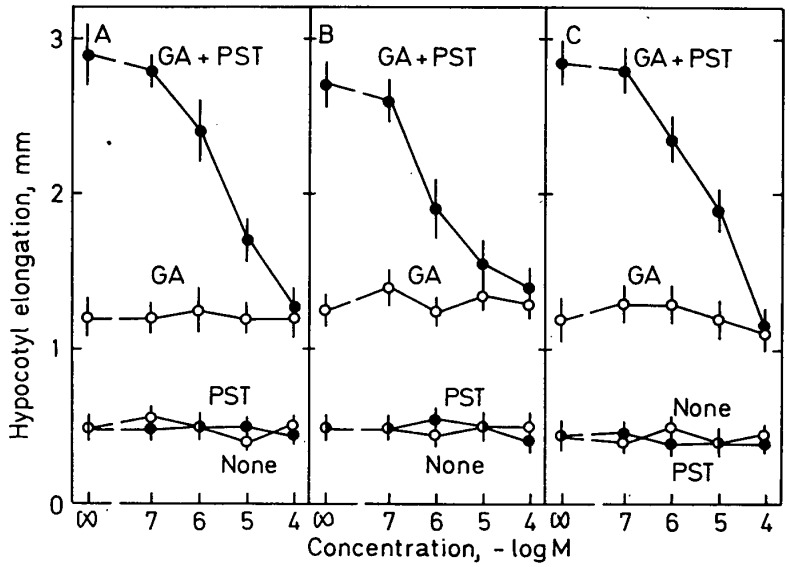

Fig. 4. *Interaction between (−)-(6S, 1'S)-pestalotin and anticotyledon factor in affecting GA-induced hypocotyl elongation of decotylized lettuce seedlings.* Decotylized seedlings were grown for 2 days in light in the presence or absence of 10^{-5} M GA and/or 10^{-6} M (−)-(6S, 1'S)-pestalotin (PST) with various concentrations of each anticotyledon factor. A, *trans*-cinnamic acid; B, ferulic acid; C, caffeic acid. Vertical lines represent standard error.

the action of 10^{-6} M pestalotin being almost completely eliminated by 10^{-4} M *trans*-cinnamic, ferulic or caffeic acid. These results suggest that both (−)-(6S, 1'S)-pestalotin and dihydroconiferyl alcohol function as gibberellin synergists in stimulating lettuce hypocotyl elongation by binding to the same cellular site.

Effect of stereoisomers of pestalotin

Stereoisomers of pestalotin were assayed for their ability to enhance the effect of GA on hypocotyl elongation of decotylized lettuce seedlings. (−)-(6S, 1'S)-Pestalotin is a natural product of *P. cryptomeriaecola* (*7*, *18*). Two of its stereoisomers, (+)-(6R, 1'R)-pestalotin and (+)-(6R, 1'S)-epipestalotin, which differ from natural pestalotin in the stereochemistry of C-1' and/or C-6 carbon(s), had been synthesized by Mori et al. (*11*). As shown in Fig. 5A, like (−)-(6S, 1'S)-pestalotin (Fig. 2B), (+)-(6R, 1'R)-pestalotin synergistically enhanced the effect of GA on hypocotyl elongation, its optimal concentration being around 10^{-6} M. On the other hand, (+)-(6R, 1'S)-epipestalotin showed no promoting effect on GA-induced lettuce hypocotyl elongation.

Next, we studied whether or not epipestalotin affects the action of (−)-(6R, 1'S)-pestalotin (Fig. 5B). It strongly inhibited the effect of (−)-(6S, 1'S)-pestalotin on GA-induced lettuce hypocotyl elongation, as observed with the anticotyledon factors (see Fig. 4). 10^{-4} M Epipestalotin completely cancelled the promoting effect of 10^{-6} M (−)-(6S, 1'S)-pestalotin.

Interaction between dihydroconiferyl alcohol and epipestalotin

(+)-(6R, 1'S)-Epipestalotin, in inhibiting the action of (−)-(6S, 1'S)-pestalotin, behaved as if it were the anticotyledon factor. This fact suggested that epipestalotin

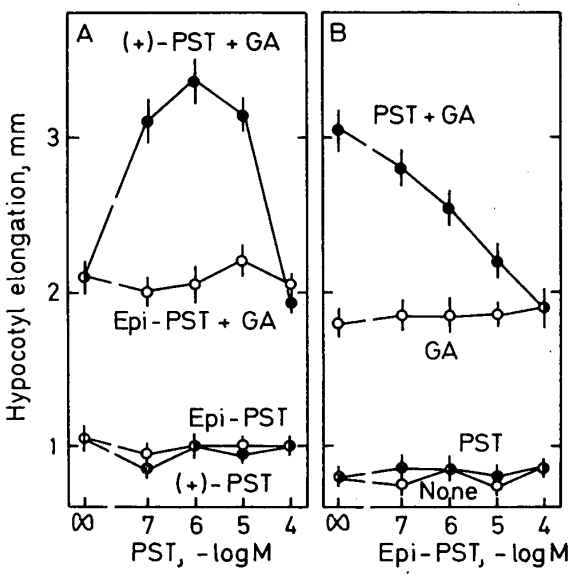

Fig. 5.

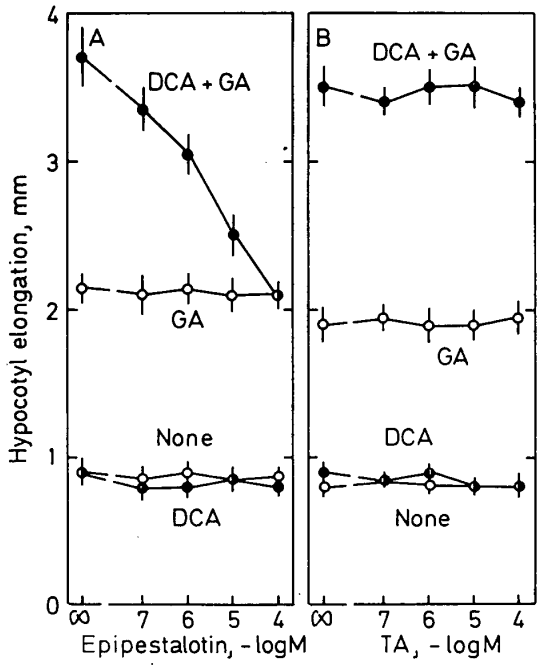

Fig. 6.

Fig. 5. *A. Effect of pestalotin stereoisomers on GA-induced lettuce hypocotyl elongation.* Decotylized seedlings were grown for 2 days in light in the presence or absence of 10^{-5} M GA with or without various concentrations of each pestalotin stereoisomer. (+)-PST, (+)-(6R, 1'R)-pestalotin; Epi-PST, (+)-(6R, 1'S)-epipestalotin. *B. Interaction between pestalotin stereoisomers in inducing lettuce hypocotyl elongation caused by GA.* Decotylized seedlings were grown for 2 days in light in the presence or absence of 10^{-5} M GA and/or 10^{-6} M (−)-(6S, 1'S)-pestalotin (PST) with or without various concentrations of (+)-(6R, 1'S)-epipestalotin (Epi-PST). Vertical lines represent standard error.

Fig. 6. *A. Interaction between dihydroconiferyl alcohol (DCA) and (+)-(6R, 1'S)-epipestalotin in inducing lettuce hypocotyl elongation caused by GA.* Decotylized seedlings were grown for 2 days in light in the presence or absence of 10^{-5} M GA and/or 10^{-6} M dihydroconiferyl alcohol with or without various concentrations of epipestalotin. *B. Interaction between dihydroconiferyl alcohol (DCA) and TA in inducing lettuce hypocotyl elongation caused by GA.* Decotylized seedlings were grown for 2 days in light in the presence or absence of 10^{-5} M GA and/or 10^{-6} M dihydroconiferyl alcohol with or without various concentrations of TA. Vertical lines represent standard error.

can inhibit the action of dihydroconiferyl alcohol on GA-induced lettuce hypocotyl elongation. Fig. 6A shows the interaction between 10^{-6} M dihydroconiferyl alcohol and epipestalotin in the concentration range of 10^{-7} to 10^{-4} M. As expected, epipestalotin strongly inhibited the promoting effect of dihydroconiferyl alcohol on GA-induced lettuce hypocotyl elongation. On the other hand, the triazinone compound TA showed no effect at all on the action of dihydroconiferyl alcohol (Fig. 6B).

Hypocotyl elongation and cell wall loosening

GA induces lettuce hypocotyl elongation by causing cell wall loosening represented as a decrease in minimum relaxation time (T_0) (*2*). The action of GA on cell wall loosening is closely correlated with the metabolism of polysaccharides in the lettuce hypocotyl cell wall (*6*). These facts suggested that gibberellin synergists

Table 1 *Effect of dihydroconiferyl alcohol and (−)-(6S, 1'S)-pestalotin on the mechanical property of lettuce hypocotyl cell wall*

Treatment	T_0 [a] (msec)	Hypocotyl elongation [b] (mm)
Initial	18.4±1.9	
Seedlings with cotyledons		
H_2O	33.2±2.0	0.40±0.12
DCA	33.5±1.2	0.40±0.10
PST	34.0±2.6	0.45±0.12
GA	19.7±1.9	3.90±0.25
GA+DCA	18.9±1.5	4.90±0.16
GA+PST	19.3±2.0	5.10±0.12
Seedlings without cotyledons		
H_2O	31.1±2.4	0.35±0.07
DCA	32.0±1.8	0.45±0.09
PST	29.8±3.1	0.45±0.11
GA	18.0±1.5	1.45±0.18
GA+DCA	19.1±0.8	3.30±0.21
GA+PST	17.0±1.6	3.45±0.11

Lettuce seedlings with or without cotyledons were grown for 2 days in light in the presence or absence of 10^{-5} M GA with 10^{-6} M dihydroconiferyl alcohol (DCA) or (−)-(6S, 1'S)-pestalotin (PST). Minimum relaxation time (T_0) was determined by the method described in **Materials and methods.**

[a] with standard error. n=20.

[b] with standard error. n=10.

enhance the action of GA on hypocotyl elongation by enhancing its effect on cell wall loosening. This possibility was examined in the next experiments (Table 1).

In the case of intact lettuce seedlings with the cotyledons, GA substantially decreased T_0, confirming our previous results (*2*). On the other hand, dihydroconiferyl alcohol and (−)-(6S, 1'S)-pestalotin hardly influenced the effect of GA on the decrease in T_0, although they synergistically enhanced GA-induced lettuce hypocotyl elongation. This was also the case for decotylized lettuce seedlings; neither dihydroconiferyl alcohol nor (−)-(6S, 1'S)-pestalotin modified the mechanical property of the hypocotyl cell wall caused by GA. These results suggest that the action site of gibberellin synergist is not in the cell wall.

Discussion

The present study demonstrated that dihydroconiferyl alcohol and pestalotin synergistically enhanced the effect of GA on lettuce hypocotyl elongation. The mode of action of pestalotin seems to be the same as that of dihydroconiferyl alcohol because 1) anticotyledon factors such as *trans*-cinnamic, ferulic and caffeic acids inhibited the promoting effect of pestalotin on GA-induced lettuce hypocotyl elongation (Fig. 4) and 2) epipestalotin, which had no effect on the GA action but strongly inhibited the action of pestalotin, completely eliminated the effect of dihydroconiferyl alcohol (Fig. 6A). These facts indicate that dihydroconiferyl alcohol and pestalotin

bind to the same cellular site when they function as gibberellin synergists in stimulating GA-induced lettuce hypocotyl elongation.

Kimura and Tamura (*8*) synthesized various compounds with modified side chains and the same pyrone ring structure as pestalotin and assayed them for their ability to enhance the effect of GA on rice shoot elongation. From these studies, they pointed out the importance of the side chain structure of pestalotin in the biological activity. Further evidence for the importance of the side chian structure of pestalotin came from experiments with stereoisomers of pestalotin. Kimura et al. (*9*) assayed (+)-(6R, 1'R)-pestalotin and (+)-(6R, 1'S)-epipestalotin, which differ from each other in the stereochemistry of C-1' and/or C-6 carbon(s), as gibberellin synergists for enhancing the effect of GA on rice shoot elongation, and found that (+)-(6R, 1'S)-epipestalotin was biologically active while (+)-(6R, 1'R)-pestalotin was inactive. On the other hand, as shown in Fig. 5A, in the case of lettuce hypocotyl elongation caused by GA, (+)-(6R, 1'R)-pestalotin was active as a gibberellin synergist while (+)-(6R, 1'S)-epipestalotin was not. These facts suggest that there is a subtle difference in the nature of the cellular binding site of pestalotin between lettuce and rice plants and that the side chain structure of pestalotin is important for the biological activity.

Shibata et al. (*17*) synthesized various compounds with aromatic substituents different from dihydroconiferyl alcohol and discussed the structure-activity relationships of dihydroconiferyl alcohol. Dihydroconiferyl alcohol has an aromatic ring, while pestalotin has a heterocyclic pyrone ring. Nevertheless, both compounds showed the same biological activity on GA-induced lettuce hypocotyl elongation. These facts suggest that the aromatic ring structure of dihydroconiferyl alcohol is not necessarily prerequisite for the biological activity of the lettuce cotyledon factor.

Ogawa et al. (*13*) demonstrated that lettuce hypocotyl elongation due to GA was not enhanced by the GA synergist 2-ethyl-3-methoxycarbonyl-(*p*-tolylcarbamoyl) isourea (IU), which is active in synergistically enhancing rice shoot elongation caused by GA. Later, they found that IU and TA had nearly equal biological activity for enhancing the GA effect on rice shoot elongation, and that IU was easily converted into TA in rice tissues after IU had been applied to rice plants (*14*). The present study showed that like IU, TA also did not enhance the GA effect on hypocotyl elongation of lettuce seedlings (Fig. 2C and 3C). And there was no interaction between dihydroconiferyl alcohol and TA (Fig. 6B). These results suggest that TA and pestalotin act differently when they enhance the GA effect on rice shoot elongation (*7*, *14*, *15*, *18*).

Pestalotin was isolated from a phytopathogenic fungus, *Pestalotia cryptomeriaecola*, as a gibberellin synergist active in enhancing the effect of GA on shoot elongation and α-amylase synthesis in rice plants (*7*, *18*). The fact that pestalotin can mimic dihydroconiferyl alcohol in stimulating GA-induced lettuce hypocotyl elongation suggests that dihydroconiferyl alcohol participates in the regulation of shoot elongation and α-amylase synthesis in rice plants, too. Further studies are needed to check this possibility.

One possible mechanism by which gibberellin synergists such as dihydroconiferyl alcohol and pestalotin stimulate lettuce hypocotyl elongation is enhancement of the GA effect on mechanical properties of the cell wall, because stress-relaxation analysis of the lettuce hypocotyl cell wall has demonstrated that GA stimulates hypocotyl

elongation by causing cell wall loosening represented by a decrease in T_0 (*2*, *6*). On the other hand, as shown in Table 1, GA caused a decrease in T_0 of the hypocotyl cell wall of lettuce seedlings with and even without the cotyledons. In addition, both dihydroconiferyl alcohol and pestalotin showed no significant effect on the GA-induced decrease in T_0 of the hypocotyl cell wall. These facts imply that the action of gibberellin synergists such as dihydroconiferyl alcohol and pestalotin is not directly correlated with the GA action of inducing cell wall loosening.

Dihydroconiferyl alcohol has been considered to be a chemical messenger responsible for the correlation phenomenon between the cotyledon and GA-induced lettuce hypocotyl elongation (*3*, *16*). On the other hand, another possible function of dihydroconiferyl alcohol may be alleviation of the injury effect due to cotyledon excision, resulting in the depression of GA-induced lettuce hypocotyl elongation. However, this possibility seems to be denied by the fact that dihydroconiferyl alcohol could synergistically enhance the GA effect on hypocotyl elongation of intact lettuce seedlings with cotyledons (Fig. 3A). This finding rather suggests that the endogenous level of dihydroconiferyl alcohol in the lettuce hypocotyl is suboptimal for exerting its maximum effect on hypocotyl elongation even in lettuce seedlings with cotyledons.

The author wishes to thank Prof. Y. Masuda and Dr. R. Yamamoto for their kind suggestions and discussions. The author is also indebted to Drs. E. L. Patterson, M. Ogawa and Y. Kimura for their kind gifts of gibberellin synergists.

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