Growth Promotion in Pea Stem Sections. II. By Natural Oils & Isoprenoid Vitamins [1, 2]

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The elongation of pea stem sections brought about by indoleacetic acid (IAA) and gibberellic acid (GA_3) can be increased considerably by trace quantities of a large number of fatty acid esters and chemically related compounds (19, 21). The emulsifying technique used for these alkyl lipids has permitted the study of the effect of some natural oils and of fat-soluble vitamins on pea stem section growth for the first time. In this paper it is shown that vitamins K_1 and E, and some related isoprenoid compounds, are like the alkyl lipids studied earlier in that they stimulate pea section growth in a similar manner and do so at even lower concentrations. No simple theory has yet been found adequate to explain this effect, but the results are compatible with the earlier suggestion (20, 23) that activation of the cytochrome system best explains the synergism of these compounds with auxins and GA_3.

Materials & Methods

Pea seeds (*Pisum sativum* L.) were soaked for about seven hours in a layer of water just thin enough to cover them, together with 0.3 % (of seed weight) Phygon (a United States Rubber Co. fungicide, active ingredient 2,3-dichloro-1,4-naphthoquinone), while being agitated gently on a shaker. Plastic basins 14 × 11 × 4½ inches were filled ¾ full with moist vermiculite (previously washed Mica-Gro, type B-3, California Products Corp.); the soaked peas were spread thinly on it and covered to a depth of 1 cm. Then the basins were placed under a red light source (see below) in the dark room at 23 C and 80 % relative humidity, and remained undisturbed for 7 days except for one watering of 2 liters per basin on the 2nd day. The dwarf variety Laxton's Progress was used initially, but its decreasing availability made it necessary to substitute a similar strain, Progress Number Nine, in later experiments. Stabilized emulsions of fat-soluble substances were prepared as described earlier (21); these were made up on the day of the test. Pluronic F-68 (Wyandotte Chemical Corp.) was added as an emulsion stabilizer, usually at a final concentration of 0.004 %. The acetonitrile normally used to make the emulsions never exceeded an initial concentration of 0.2 M and was markedly less in the test solutions (21). Concentrations are stated in the usual weight per volume basis, but it should be noted that since emulsions were used the amount of lipid in true solution, in most cases, must have been considerably less. The basal medium was 1.5 % sucrose + 50 μM $CoCl_2$ + 5mM KH_2PO_4 (pH 5.5) unless otherwise stated. With the addition of 1.8 μM IAA + 0.3 μM GA_3, this medium gives maximal extension of pea stem sections under our conditions. Percentage elongation of ten initially 10 mm long sections taken from the apical part of the third internode was measured after 20 to 24 hours in 20 ml of solution in a petri dish slowly rotated at 23° in a dark room. Least significant differences were assessed by analysis of variance.

Results

► Effect of Red light: In previous experiments the seedling plants always were grown in weak red light (19). As a consequence of moving the work to this laboratory it has been discovered (22) that sections from peas grown in complete darkness and handled only with weak green illumination failed to show significant stimulation of hormone action in any test of the previously active lipids (table I). It may be noteworthy that the lipids doubled the standard deviation without changing the mean length obtained. The quantity of red light, as stated earlier (19), was not critical; the continuous illumination used here was a

Table I

Effect of Exposing Seedling Plants To Red Light During Development*

	Dark-grown**	Red-grown***
Basal medium	38.8 ± 10.8	44.9 ± 8.2
1.8 μM IAA + 0.3 μM GA_3	72.9 ± 11.1	72.4 ± 12.1
Ditto + triolein 10 μM	71.6 ± 23.2	87.2 ± 13.3
Ditto + triolein 20 μM	71.5 ± 22.8	97.1 ± 10.0
Ditto + triolein 30 μM	77.4 ± 20.6	101.2 ± 7.9

* Average of the percentage increase in length from (**) 10, (***) 28 experiments, standard deviations of the mean cited. Basal medium as in text, Progress Number Nine peas.

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Table II

Effect of Natural Fats on Pea Stem Section Elongation*

Basal medium	28.7			25.5		
1.8 μM IAA + 0.3 μM GA_3	78.1			82.9		
+	*Coconut oil*	*Peanut oil*	*Mustard oil*	*Olive oil*	*Linseed oil*	*Butter*
8.4 mg/l Fat	85.7	86.0	83.5	98.3***	94.3***	101.3***
17 " "	91.9**	89.7**	88.1	93.4***	92.1***	91.2***
25 " "	95.0***	96.5***	92.0**	103.4***	102.1***	94.4***
34 " "	97.4***	100.9***	95.5***	100.8***	101.9***	105.0***
	Average of 10 experiments M.S. error 159.5 LSD (5 %) 11.1, (1 %) 14.6			Average of 2 experiments M.S. error 103.7 LSD (5 %) 6.4, (1 %) 8.4		

* Percentage elongation of Progress No. 9 pea stem sections, basal medium as in text.
** Significant at 5 % level compared to IAA + GA_3 control.
*** Significant at 1 % level compared to IAA + GA_3 control.

1 w NE-30 neon bulb in a white reflector housing, filtered through ⅛ inch thick pieces of 2444 Red and 2074 Smoky Grey Plexiglas plastic, and 170 cm from the surface of the vermiculite. This provided approximately 0.1 ergs/cm²/sec from neon emission lines largely in the region between 600 and 800 mμ. Progress Number Nine pea plants grown under these conditions have a final second internode length of about 25 mm. In several exploratory experiments varying the intensity of illumination within a range from about 10 times greater than to 100 times less than this value did not markedly change section sensitivity to lipids, although final intact plant internode lengths showed the anticipated decrease in length with increased light intensity throughout this range. Giving red light to the sections during or after cutting them did not sensitize sections from dark-grown seedlings to lipids; it was shown by a brief study that the red light must be given to the intact seedlings at least a day or two before the sections are to be cut.

This need for red light during the growth of the seedling is not unique to this bioassay. Kent and Gortner (13) have shown that red light is also necessary when peas are to be used for the Went split pea curvature assay, an observation which has been confirmed in this laboratory.

During late July and August of 1960, it was impossible to elicit lipid responses under the conditions cited above which have given consistent and significant growth increments at other times. It is suspected that atmospheric pollution was responsible for this failure of the plants to react, but as the phenomenon has not recurred it has not yet been possible to test this suggestion.

► Natural Oils: The results reported earlier (21) infer that most natural fats and oils should enhance gibberellin and auxin action. The tests of a number of such substances are reported in table II. The substances were obtained from commercial sources, and from semi-quantitative gas chromatography of the methyl esters obtained from them by transesterification it has been confirmed that their fatty acid composition was within normal limits (6). The activity of all these fats is essentially the same as that of other alkyl lipids studied earlier.

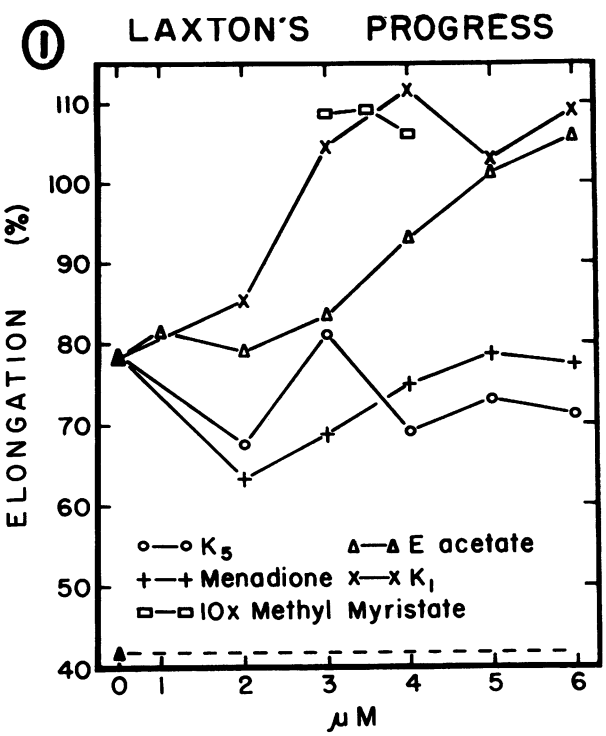
► Fat-Soluble Vitamins: Although it was concluded from the extensive earlier work that only certain fatty acid esters and closely related substances could increase the pea stem section elongation induced by hormones, the emulsification method in use made it possible to test some fat-soluble vitamins. Accordingly, vitamin D_2, E (α-tocopheryl acetate), and K_1, as well as β-carotene (the latter required tetrahydrofuran for emulsification), were emulsified and tested on the pea sections (table III). Vitamins E and K_1

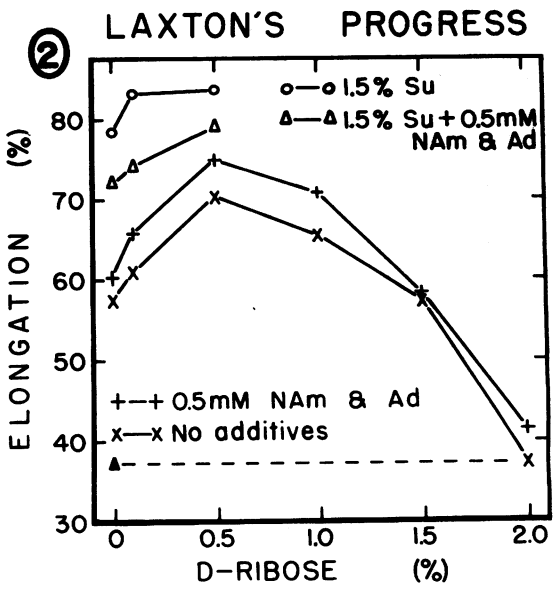
Table III

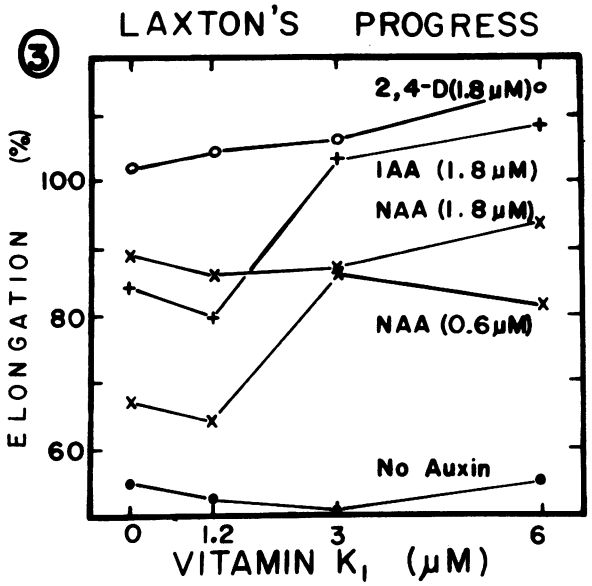
Growth Promotion by Fat-Soluble Vitamins*

Controls		μM	D_2	E	K_1	β-Carotene
Basal Medium	48.5	3	70.1	101.5***	74.6	64.4
IAA (1.7 μM)	74.7	10	61.7	96.8***	100.3***	74.6
+ GA_3 (0.3 μM)		30	65.5	98.1***	100.0***	62.2
+ Methyl linoleate (41 μM)	103.6***	100	60.8	81.8	83.4**	68.3

* Percentage increase in length of Laxton's Progress pea stem sections. Basal medium 1.25 % sucrose, otherwise as in text. All except the basal medium control were also 1.7 μM IAA + 0.3 μM GA_3. Significant growth promotions are indicated at the 5 % (**) and 1 % (***) levels, compared to IAA + GA_3 control. M.S. error 82.9, LSD (5 %) 8.1, (1 %) 10.6.







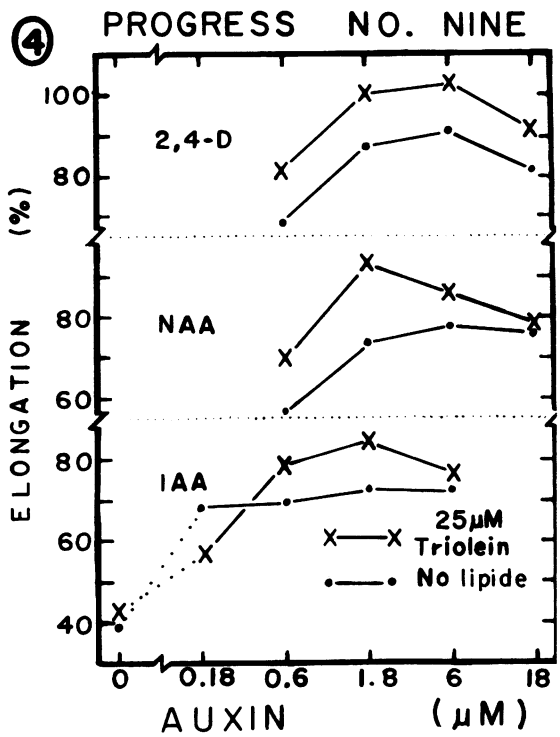


Fig. 1. Comparison of the effect of isoprenoid vitamins with the side chain lacking K analogs K_6, and menadione. Methyl myristate is at concentrations ten times greater than the scale. Basal medium as in text; its effect is indicated by lowest black triangle. At all other points 1.7 μM IAA + 0.3 μM GA_3 was added. Points from a single experiment, comparable results were obtained from various modifications of these conditions. M.S. error 88.57, LSD (5%) 8.3, (1%) 10.9 for comparison of growth promotions with IAA + GA_3 controls (vitamin E values could not be included in this statistical analysis).

Fig. 2. The effect of ribose on pea stem section growth in the presence of 1.5% sucrose (Su) and/or 0.5 mM niacinamide (NAm) and adenine (Ad). Basal medium as in text, its effect indicated by black triangle. At all other points 1.7 μM IAA + 0.3 μM GA_3 were also present in this one experiment. Comparable results were noted in other tests.

clearly enhanced pea section growth to the same extent as the alkyl lipid, methyl linoleate. But this test, as well as others of vitamin D_2 and β-carotene, failed to show growth promotion by these latter compounds. Vitamin A acetate also was inactive. To see if the activity of vitamins E and K_1 was similar in character to that of the alkyl lipids, tests reported elsewhere (20, 23) have been carried out. The response to these vitamins, like that to the alkyl lipids, required IAA and was greatest in the presence of both IAA and GA_3. Although the lower limit of activity has varied from test to test, it is clear that both vitamins E and K_1 are active at lower concentrations than are the alkyl lipids.

► K Vitamin Analogs: The only K vitamin known to occur in higher plants is K_1 (phylloquinone), but the presence of other, chemically different Ks, is a distinct possibility. A number of simpler synthetic substances, which lack the phytyl side chain, are known to have vitamin K activity in animals (12). Among these are vitamin K_5 (2-methyl, 4-aminonaphthol) and menadione (K_3 or 2-methyl, 1,4-naphthoquinone). These compounds, tested as the hydrochloride and sodium bisulfite addition products, respectively, are compared to vitamins E and K_1 in figure 1. In this test, as well as others, the K analogs show no valid activity, nor have they increased the response to vitamin K_1 or methyl linoleate when tested with these active compounds.

It thus appears that the activity of vitamin K_1, and perhaps that of vitamin E as well, lies in its side chain. A test of compounds similar to the vitamin side chains, namely phytol and farnesol, is shown in table IV. Phytol can cause elongation as great as does vitamin K_1, but requires higher concentrations to do so. Farnesol although active at statistically significant levels did not cause comparable elongations. However, the matching of farnesol to the side chain of vitamin E is not as close as phytol is to that of vitamin K_1. The inference from these results is that pea sections cannot synthesize the isoprenoid side chains which are responsible for the activity of vitamin K_1 and possibly vitamin E.

► Cofactors of Isoprenoid Synthesis: To check this assumption, a test of freshly prepared potassium mevalonate and mevalonic acid lactone, which are known to be precursors of farnesol (3), and probably of phytol as well, was made at 5, 8, 10, 20, and 50 μM. No significant stimulation of pea growth either in the presence or absence of 10 μM menadione was noted and the combination did not imitate vitamin K_1. In another test, mevalonolactone had no effect even at 3mM. In as much as diphosphopyridinenucleotide (DPN) is a cofactor of farnesol synthesis (3), its constituents, adenine and niacinamide, were also tested with mevalonolactone, but no statistically valid increase in growth was noted.

Table IV

Effect of Isoprenoid Alcohols on Pea Stem Section Elongation*

Basal medium only			25.5
Basal + 1.8 μM IAA + 0.3 μM GA_3			67.5
μM	*Phytol*	*Farnesol*	*Vitamin* K_1
10	...	89.1**	86.5**
20	...	...	99.1***
30	...	72.7	98.8***
60	86.4**	86.8**	...
80	89.2**	...	...
90	...	85.4**	...
100	104.5***	...	...

* Percentage elongation of Laxton's Progress pea stem sections, basal medium as in text, except that Pluronic F68 was 0.008 %. All but the basal medium control were 1.8 μM IAA + 0.3 μM GA_3. Starred data are significant at the 5 % (**) and 1 % (***) level as compared to the IAA + GA_3 control. M.S. error 375.7 LSD (5 %) 17.2, (1 %) 22.8.

Since ribose might similarly be needed for DPN synthesis, the effect of the sugar on sections was also tested. In figure 2 is demonstrated the fact that D-ribose stimulated growth both in the presence and absence of sucrose up to a concentration of 0.5 %, and thus was apparently available to metabolism of the sections. Concentrations in the absence of sucrose above this level were inhibitory. It is noteworthy that although 1½ % sucrose stimulated growth somewhat more than did ribose, ribose stimulated growth even more in the presence of sucrose. Adenine and niacinamide, although never stimulating growth to a statistically significant level, were consistent in slightly increasing growth with ribose at every experimental point, although with sucrose, decreases were noted. In other experiments more pentoses were tested. D-Galactose and D-mannose similarly increased growth above that of sugar-free controls up to the 0.5 % level and were inhibitory above it. L-Arabinose had no stimulatory powers, although it also inhibited growth at concentrations greater than 0.5 %. The fact that some other pentoses could also stimulate growth makes less likely the original idea that ribose was acting here via DPN promotion of isoprenoid synthesis in pea stem sections.

Fig. 3. The effect of vitamin K_1 on various auxins. Basal medium as in text. 0.3 μM GA_3 was added to all sections in this single experiment, similar results were obtained in other assays. The vitamin K_1 promotion of IAA and 0.6 μM NAA at 3 and 6 μM was significant at the 1 % level compared to the no vitamin K_1 points.

Fig. 4. The effect of 25 μM triolein on various concentrations of three auxins. Basal medium as in text, no GA_3 was used. Points are the average of one (18 μM), two (all other ° — °), and three (all other ×–×) experiments, respectively. The abscissa is a log scale. For one of these experiments for which a simplified statistical treatment was possible the growth promotion for each auxin at 1.8 μM by triolein was significant at the 1 % level.

► Auxin Specificity of Lipid Growth Promotion: To establish whether or not the lipid enhancement of IAA action is specific to this auxin, tests were also carried out with α-naphthaleneacetic acid (NAA) and 2,4-dichlorophenoxyacetic acid (2,4-D). In figure 3 are the results of one such test in which vitamin K_1 markedly increased the activity of IAA and also that of the lower concentration of NAA used. Growth at the higher NAA concentration and with 2,4-D was not convincingly enhanced in this experiment. As concentration of the auxin appeared to be a factor, several tests of this variable were carried out with triolein; their averages are plotted in figure 4. Here it is clear that at all but one auxin level tested the effect of triolein is a stimulatory one. The lipid growth stimulation is, thus, probably to be found when pea sections are treated with any auxin.

Discussion

These results amplify those of the first paper in this series, indicating that in nature fats and isoprenoid vitamins may act to enhance or modify auxin induced processes. Gross lipid involvement in major plant physiological changes has been shown many times, but in only a few cases can a link to auxin action be directly inferred. A number of these publications have been discussed earlier (21, 23).

More recently, the extensive work of Bernfeld (2) is noteworthy in demonstrating that a large number of natural fats can induce tumors in several plants. His active principle was not identified but was believed to be in the non-saponifiable fraction. He also reviewed a number of papers which may be interpreted as indicating that fats can modify plant growth. Worthy of special mention is the ancient horticultural practice of bringing figs more rapidly to full development with a drop of olive oil (5). Since the fig fruit is derived from stem tissue this is analogous to the response of pea stem sections reported here.

In addition, Beal et al. (1) have shown that the application of the fatty acid ester detergent Tween 20 to the soil at the base of Datura plants led to a 40 % increase in their final dry weight, though oddly enough a direct spray treatment had no such effect. The direct spray might have led to overdoses being applied. Westwood & Batjer (25) found that Tween 20 increased the epinastic effect of NAA under conditions where cuticular penetration was not a factor. Sironval, noting that the lipid content of cells of strawberry leaves increased with the long day treatments favorable to floral initiation (16), later showed that application of the crude unsaponifiable extract from such leaves led to increased internode and petiole elongation as well as to an increase in flowering (17). The flowering response was attributed to vitamin E (see below), but the effect of this substance on internode and petiole length was not stated.

Although the augmentation of auxin-induced pea stem growth by vitamins K_1 and E was an unanticipated outcome of this work, it is not a new discovery. Hey and Hopf published in 1951 (9, 11) a theory that auxin herbicides are most effective on plants with high vitamin K content and suggested that this explains their relative ineffectiveness on cereals and other plants with low vitamin K levels. The vitamin K assay used for the figures in their table was not specified, and the commonly employed animal nutrition tests have a broad specificity (12). Furthermore, they stated that NAA plus vitamin K increased the yield of a large number of crops. Their data on radishes show striking increases in gross weights obtained by such treatments, but the data for large scale commercial crop experiments are much more variable. Six additional tables of their data appeared in reprint form, but were not published in the journal. Unfortunately, assessment of these data is complicated by the fact that the precise regimen of the treatments is not given, and vitamin K is not defined. In fact, it is clearly implied that mixtures whose composition was a commercial secret were employed. A later paper states that menadione (K_3) was used to increase the parthenocarpic effect of NAA on apples (10), and that it also increased frost resistance.

Independent confirmation of the principal thesis of their work has been provided by Hemberg (7), who tested vitamin K and vitamin H′ supplied by Hey and Hopf on the rooting of bean cuttings. He found that these did augment auxin action by increasing the rooting of bean cuttings, and only in the presence of IAA. This work was then extended to intact Datura plants which were increased in dry weight by menadione sprays (8). In this latter case the addition of NAA did not enhance the response to menadione, but usually reduced it. Percentage of alkaloids was relatively unaffected but capsule number was significantly increased. Lowén (14) repeated these field experiments with slight modifications and confirmed the marked increase in dry weight and capsule number caused by menadione spraying. He noted that the cell area was nearly doubled in sections of leaves taken from treated plants; presumably, then, the size difference was largely attributable to increased cell enlargement. However, in the case of vitamin E, Booth and Hobson-Frohock (4) recently concluded that leaf growth rate is inversely proportional to vitamin E content, both in parts of the same plant and in different species.

Possibly related are the observations of Schwarzenbach (15), who found that a wide range of carotenoids could promote or inhibit the germination of Cyclamen pollen. The inhibitory effect of some of these, particularly β-carotene, could be reversed by IAA, which by itself was ineffective on this material. Vitamin K_1, and to a lesser extent vitamin E, could similarly reverse the effect of β-carotene inhibition of pollen germination. He suggested that similar interactions may be at the basis of pollen incompatibilities. Sironval has implicated vitamin E

as a factor in flower formation of strawberries, after deducing that it was the active principle in his unsaponifiable extract (17). He found that pure material (α-tocopherol) could increase flowering in strawberries grown under short day conditions where little flower initiation occurred. Considering the low concentrations found to be effective in our work, it is noteworthy that he found vitamin E acted in very small amounts within a narrow range, namely on the order of two to four micrograms per plant. Doubling the latter amount led to no effect and higher values were inhibitory to growth. He has further support for the natural role of this vitamin in flower initiation in that he showed it to increase in plants which are normally photoinduced (18). However, his assay has been criticized as non-specific (4).

Thus, it is evident that lipids of both the fatty acid ester and isoprenoid vitamin type in trace quantities can mimick or enhance auxin or gibberellin action in a number of different ways. As cited above, these lipids can enhance internode lengths, dry weight yields, and rooting of cuttings, cause epinasty, influence pollen germination and fruit formation, and promote flower formation. Furthermore, in some of these cases an interaction with or requirement for auxin was also shown. It would be unwise to draw many inferences from such a miscellany of observations, but they do make clear the fact that our results are not an isolated example of plant hormone-lipid interaction.

The mechanism underlying these phenomena cannot be established by the data presented here. We have suggested elsewhere (20, 23) that lipid activation of the cytochrome system could explain the results observed. It should be noted that an oxidation-reduction role in the usual sense would not be involved. As Weber, Gloor, and Wiss have pointed out (24), the activation of mitochondrial cytochrome systems requires a hydrocarbon chain within certain length limitations. This is compatible with our data indicating that it is the isoprenoid moiety of vitamins K_1 and E that is effective in increasing stem section growth, and with the earlier results (21) indicating that fatty acid esters equal to or greater than C_{12} chain length could so act. Presumably then, these compounds must fit into some lipid-requiring matrix, probably in the mitochrondrion, in order to be effective in some part of the cytochrome oxidation chain which produces at least some of the energy for auxin and gibberellin action.

If this hypothesis is true, it implies that red light can modify the cytochrome system of peas in such a way as to make the energy supply for auxin and gibberellic acid induced processes partially lipid dependent. Whether lipids can act naturally in such a way as cell growth stimulating hormones (i.e. via the synergism with auxin & gibberellin) in vivo cannot yet be stated. Proof of these suggestions must await more information on the natural lipids of the pea and their localization, an investigation which is now being undertaken.

Summary

► Auxin and gibberellic acid treated pea stem sections will not show the additional growth response caused by lipids unless the plants from which they were cut were exposed to red light a day or more previously.

► A number of natural fats and oils are capable of potentiating the additional section growth.

► Among the fat soluble vitamins tested, vitamins E and K_1 were as effective as alkyl lipids in augmenting auxin induced growth, and did so at even lower concentrations. Vitamins A and D_2, and β-carotene were inactive.

► The vitamin K analogs lacking a side chain, namely menadione and vitamin K_5, were inactive, even in the presence of mevalonic acid and co-factors of isoprenoid synthesis. Phytol and farnesol were active. It is concluded that pea stem sections are incapable of synthesizing isoprenoid vitamins and that the results are compatible with the previous suggestion that active compounds may act via cytochrome activation.

► D-Ribose, D-galactose, and D-mannose stimulated pea stem section growth in a manner suggesting they are available for metabolism. L-Arabinose was only inhibitory.

► The lipid stimulation of IAA action is probably general to auxins, since growth induced by NAA and 2,4-D is also susceptible to lipid enhancement.

► A number of observations in the literature indicate that auxin-lipid interactions may be widely distributed both as to species and to function in plants.

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