PHYSIOLOGY AND MODE OF ACTION OF ETHYLENE

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The main evidence for a single mechanism of ethylene action is the observation that nearly all responses to the gas have the same dose response curve (8), suggesting a single type of receptor molecule. If so, the case is similar to that of phytochrome where one biochemical change produces a multitude of secondary changes resulting in a variety of physiological responses depending upon the tissue involved. We have chosen to use the etiolated pea seedling to investigate the primary and secondary actions of the gas because all parts of this plant have been extensively studied and are highly responsive to ethylene. When this seedling is exposed to ethylene stem growth slows, the hook tightens, the subapex swells and nutates horizontally, root growth slows and the zone of elongation swells, root hairs form, lateral root formation is inhibited, and the root tip bends plageotropically. The causes of these changes are to be found in the effects of ethylene on cell division, cell expansion, and auxin transport.

Effect of ethylene on cell expansion

Ethylene reduces the growth rate (increase in fresh wt) of the subapical zone of etiolated pea seedlings by about 65% (Fig. 1), but the tissue continues growing for at least 4 days, whereas these same cells in control plants cease growing within 1 or 2 days. Consequently, while ethylene initially retards growth it eventually stimulates it. The gas inhibits elongation of the subapex far more than rate of increase in fresh wt (Fig. 2), thus causing swelling, but elongation persists for the entire 4 day period in gassed tissue whereas again it stops in control cells within 1 or 2 days. The phenomenon of prolonged growth in ethylene treated plant cells can also be demonstrated using subapical sections cut from seedlings gassed with ethylene for 2 days. The control tissue, which 2 days earlier comprised the subapical 1 cm

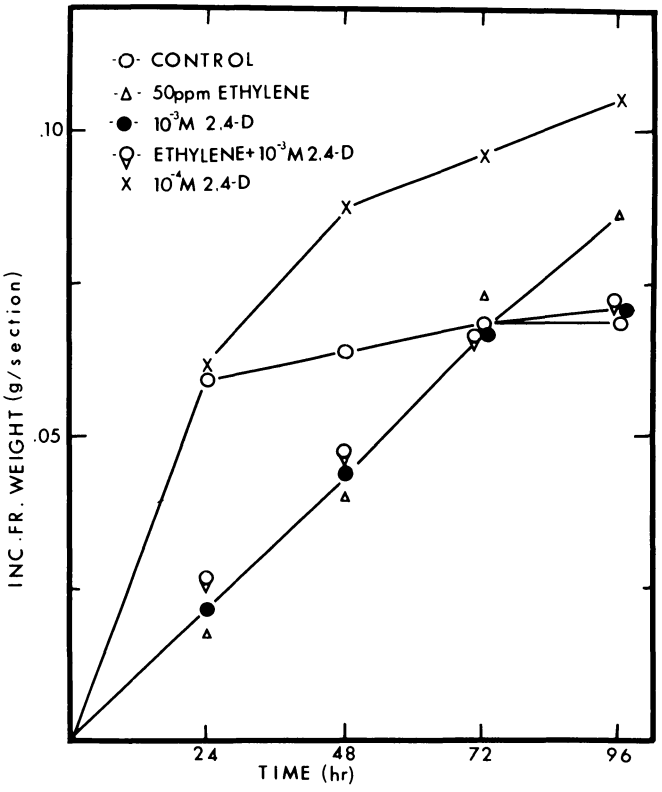

Fig. 1. Effect of ethylene (50 ppm), 0.1mM 2,4-D, 1 mM 2,4-D, and 1mM 2,4-D + ethylene (50 ppm) on the increase in fresh wt of the 7 day old etiolated pea subapical zone.

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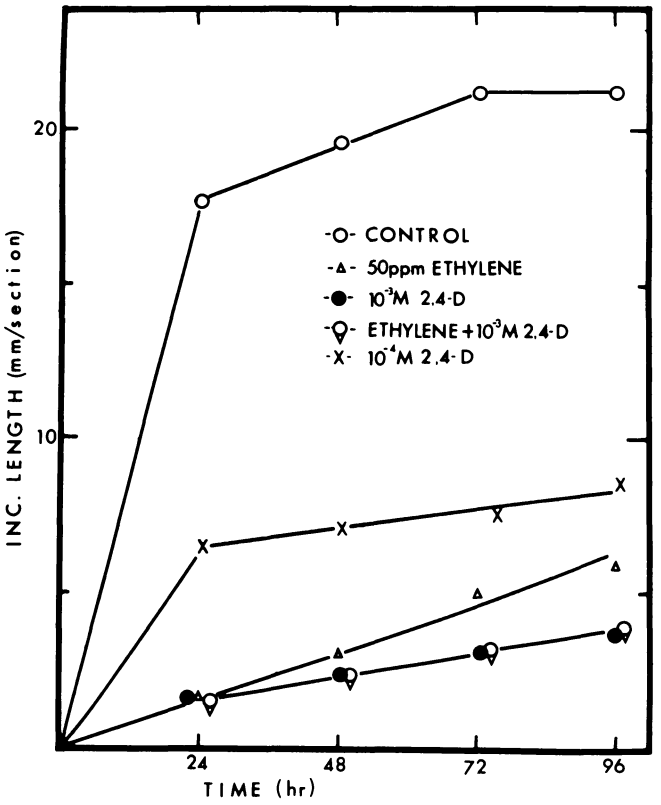

Fig. 2. Effect of ethylene (50 ppm), 0.1 mM, 2,4-D, 1 mM 2,4-D, and 1 mM 2,4-D + ethylene (50 ppm) on the elongation of the 7 day etiolated pea subapical zone.

zone, can no longer be stimulated to grow, whereas the same tissue cut from an ethylene treated stem increases in fresh wt and length at an appropriate indole-3-acetic acid (IAA) concn about as rapidly as it grows in the intact ethylene treated plant (Table 1). The same result is obtained regardless of whether ethylene is present or absent during the incubation, and the IAA dose-response curve (Table 1) is similar to that for etiolated subapical tissue treated with ethylene (3); i.e. it has the same dose-response curve as control tissue except that the ethylene-induced swelling response is lacking at high IAA concn, so there is no reduction in elongation at high auxin levels. Light microscope studies of fixed, stained and imbedded tissue indicate that no cell divisions occur in the subapical zone of control, 2,4 D or ethylene treated plants at any time during the 4 day treatment period (Table 2). Therefore only cell expansion need be considered, so these data indicate that the normal processes terminating growth and rigidifying the cell wall are impeded by ethylene.

According to the multinet hypothesis, for radial cellular expansion to occur the orientation of newly deposited microfibrils must be changed, for these normally are arranged transversely to restrain radial expansion and favor longitudinal growth (29,50). Since ethylene causes radial expansion, the effect of the gas on cell wall metabolism

Table 1. Growth of 1 cm. sections derived from the original 1 cm subapical zone of 7 day old etiolated pea plants treated with 10 ppm ethylene between the 7th and 9th day.

IAA Concn (μM)	% increase in 7 hr	
	Length	Fresh wt
0.1	9.0	18.2
1.0	18.0	29.9
10.0	22.0	36.2
100.0	21.5	34.1

Table 2. Effect of 24 hr pretreatment with 50 ppm ethylene or 100 μM 2,4-D on cell division frequency and incorporation of tritiated thymidine into nuclei.

Portion of etiolated pea plant	No. cell divisions			Labeled Nuclei/1000 Cells (after a 5 hr pulse feeding)	
	Control	Ethylene	2,4-D	Control	Ethylene
Apical Hook (avg of five 10 μ median longisections)	525	27	15	148	33
Subapical 1 cm (avg of five 10 μ median longisections)	0	0	0	88	2
Lateral Bud (avg of five 8 μ median longisections) - after 2 days treatment.	127	0	--	---	--
Root, 2 mm zone behind cap	142	52	8	138	64

was studied. The swelling response begins 3 to 4 hr after ethylene is applied to isolated subapical sections (3), but during 7 hr no change in the uptake or incorporation of C^{14}-glucose into the cell wall occurs. However, by 18 hr the label incorporated into wall protein of ethylene treated sections is 21-28% higher than the control value without a concomitant change in glucose uptake. This result may be associated with the previously noted prolongation of the growth phase in ethylene treated subapical cells. During the first 3 hr incorporation of C^{14}-proline and leucine into the cell wall is not influenced by ethylene, but between the 4th and 7th hr when swelling begins, proline incorporation into a pronase extractable wall fraction decreases by 35% (Table 3), leucine incorporation by 25%, and the hydroxyproline/proline ratio of the wall fraction but not the cytoplasm is markedly reduced without any concomitant change in the uptake of the isotopes. Chemical tests (17) indicate that the pronase extractable fraction is identical to extensin. These changes in cell wall metabolism are particularly striking because throughout an 18 hr period ethylene has no effect on total RNA, incorporation of ATP into RNA, respiration rate (5), size and rate of change of the sucrose, glucose and fructose pools (10), exosmosis (10), uptake of labeled-IAA, tryptophane, glucose, proline, leucine, ATP, arabinose and thymidine, total dry wt and wall wt (3), decarboxylation of C^{14}-IAA (3) and tryptophane, and permeability of the tissue to tritiated water (Table 4). Under the same conditions, as previously reported by others for several cases, we found that IAA markedly enhanced many of these processes, including respiration (5), changes in sugar pool sizes (10,15), incorporation of ATP into RNA (54), exosmosis (14), uptake of sugar and amino acids (16,47,48), incorporation of glucose (47), proline and leucine into the cell wall, and permeability of the tissue to tritiated water (Table 5). Therefore it is certain that had these changes occurred with ethylene they would have been detected by the methods used. The effect of ethylene in reducing the formation of hydroxyproline containing proteins in the cell wall may explain why the gas prolongs cellular expansion, for it has been proposed, by analogy with collagen, that hydroxyproline containing proteins give rigidity to the cell wall by cross linking polysaccharides (52). Cleland and Karlsnes (17) noted that these proteins increase markedly in the cell walls of pea epicotyls during the transition from rapid growth to non-elongating, mature tissue, and suggested that the increase in these proteins may be a factor in the cessation of cell expansion. This suggestion is supported by the data in Table 3 which show incorporation of C^{14}-proline into the wall to increase markedly between 4 - 7 hr, for these tissue sections stop growing after 8 - 12 hr (3). Consequently, when ethylene prevents synthesis of the hydroxyproline containing proteins it may lead to the opposite effect, a prolongation of the period of cell expansion.

Table 3. Effects of ethylene and IAA on distribution of ^{14}C label following ^{14}C-proline incubation of etiolated pea internode sections.

Treatment	Dpm/10 sections		
	Methanol extract	Pronase digest	Wall residue
	Isotope present 0 - 3 hr		
Control	9300	6300	1300
Ethylene (10 ppm)	8600	6100	1300
IAA (1 μM)	9400	8300	1900
Ethylene + IAA	9000	7400	1600
	Isotope present 4 - 7 hr		
Control	15,200	43,500	12,200
Ethylene (10 ppm)	14,300	27,500	9,600
IAA (1 μM)	16,700	60,000	17,100
Ethylene + IAA	16,000	41,900	13,600

Table 4. Effects of IAA and ethylene on the rate of efflux of ^3H_2O from etiolated pea subapical sections after 90 min incubation in ^3H_2O.

Treatment	Half-time (min) for equilibration
Control	15.2
IAA, 10^{-5}M	
Pre-treated, 0 hr	10.9
Pre-treated, 6 hr	7.6
Ethylene, 10 ppm	
Pre-treated, 6 hr	15.2

When ethylene causes cellular swelling it alters the optical birefringence pattern of the cell wall (7), producing a light and dark banding. This banding was first observed in pea subapical cells induced to swell by benzimidazole (45), and also occurs when the same cells swell in response to benzyl adenine or kinetin. In none of these cases, in spite of claims to the contrary (21), is the cause of the swelling induced ethylene production. Swelling always begins after 3 - 4 hr treatment, and is accompanied by a 35% decrease in proline incorporation. Colchicine and vinblastin-SO_4, agents which disrupt microtubules (43) and hence presumably the orientation of newly deposited microfibrils (25), also cause the pea subapex to swell after 3 – 4 hr treatment with a concomitant reduction in proline incorporation. In these cases the optical birefringence pattern is amorphous, just as in *Nitella* internodal cells treated with colchicine (25), presumably because of a random distribution of microfibrils. The common denominator in all these examples is a reduction in proline incorporation when swelling begins. The strict correlation between decreased proline incorporation and swelling is further indicated by the fact that subapical sections cut from plants pretreated with red light, which do not swell in response to ethylene (7), continue to incorporate proline at a control rate. Such tissue is not totally insensitive to ethylene, however, for the gas still prevents its stem from undergoing a geotropic curvature. This indicates that the swelling response is a secondary action of ethylene.

Probine (45) reported a correlation between the banded optical birefringence pattern and the distribution of labeled glucose in the cell wall of benzimidazole treated pea tissue, but our own studies with labeled glucose and proline, using both ethylene and benzimidazole, show a random distribution of isotope in radioautographs of cell walls. A banded optical birefringence pattern and reduction in proline incorporation also occur when pea subapical tissue swells in response to a high IAA concn, because this effect is due to auxin induced ethylene production (3). Veen, studying IAA induced swelling in pea tissue (56, 57), observed not only an optical birefringence change but also a change in the orientation of newly deposited microfibrils at the inner surface of the cell wall similar to that previously reported for the same tissue treated with benzimidazole (45), with the microfibrils directed in a longitudinal rather than radial direction. Thus when ethylene causes cells to expand isodiametrically it not only decreases the synthesis and/or type of hydroxproline rich protein formed, but in addition alters the orientation of newly deposited microfibrils, thus changing the optical birefringence pattern of the cell wall and removing the restraint on radial expansion.

Inhibition of growth and onset of the swelling response occur within a few hr in the intact subapex, and are accompanied by a reduction, eventually amounting to 90%, in the amount of IAA transported through that tissue (4). Consequently both the diffusible (38,55) and extractable (Table 5) auxin contents of the subapex

Table 5. Distribution of extractable IAA in 7 day old etiolated pea plants exposed to 10 ppm ethylene on the sixth day. (IAA assayed by the Nitsch *Avena* first internode test after methanol extraction, purification, and paper chromatography).

Plant part	IAA (meq/g fresh wt)	
	7 day old control	Ethylene (6-7 day)
leaf and apex	0.34	0.88
hook	0.68	0.42
subapex	0.27	0.07

decline by 70-80% within 18 hr, and possibly with a few hr as in *Vicia faba* (35). That this in part may be the cause of the inhibition of growth after ethylene application is indicated by the fact that applied 2,4 D, at 100 μM concn, maintains growth at a control level while stimulating ethylene production and swelling (Figs. 1 and 2); moreover, subapical sections increase in fresh wt at a normal rate when supplied with IAA in the presence of ethylene, although under these conditions elongation is markedly retarded and the tissue swells (3).

Effect of ethylene on cell division

Ethylene and 2,4-D markedly slow the growth of the apical hook, measured either as increase in fresh wt or length (Fig. 3 and 4). In the process the hormones stop almost all cell divisions, which normally occur with high frequency in control apices (Tables 2 and 6, and Fig. 5). Similarly, ethylene and 2,4-D retard cell divisions in the root tip, although 2,4-D stimulates divisions in the upper zone of the root and these ultimately give rise to numerous laterals (Table 2 and Fig. 6). Ethylene also prevents cell divisions in the lateral buds of decapitated pea plants (Table 2), thus explaining why the gas and applied auxins, which stimulate ethylene production (3), prevent these buds from expanding when the apical bud is removed (6). The effects of both ethylene and auxin on lateral bud growth are completely reversed by the cell division factor, kinetin (6, 58). Yet it has often been reported that ethylene breaks apical dominance (2); perhaps this only occurs after the gas has been removed, in which case the effect may be due to a secondary response such as lowering the diffusible auxin level (26,35,38,55). The gas inhibits cell division in the apex within 2 hr (Table 6), and the concn required is similar to that needed for induction of swelling and most other ethylene responses (39). Both in the apex and root (Table 2) incorporation of a pulse of tritiated thymidine into nuclei, measured by radioautography, is markedly inhibited in ethylene treated tissue in direct proportion to the effect of the gas on cell division, although total uptake of thymidine is not reduced by ethylene. The results with radioautography have been confirmed by direct extraction and analysis of DNA derived from treated and control apices. Thus a reduced rate of DNA synthesis is associated with, and perhaps the cause of the inhibition of cell division. Thymidine incorporation also is strongly inhibited by ethylene in the subapex (Table 2) where cell division is not occurring; in contrast ethylene does not effect RNA synthesis in this tissue. It is also plausible that ethylene induces swelling and inhibits cell division by the same mechanism, an alteration of the the microtubules, for these not only may order microfibril deposition, but in addition are essential for spindle formation during mitosis (42).

Rapid effects of ethylene on tropistic and epinastic behavior

Ethylene causes hook tightening in etiolated seedlings and prevents hook opening when the plants are exposed to red light (24,32,33). Endogenous ethylene production, largely restricted to the apical hook in etiolated pea seedlings (6 24), is inhibited by red light (7,24). Moreover CO_2, a competitive inhibitor of ethylene action (5), causes hook opening in the dark (32), while ethylene causes the hook to reform in the light after it has previously opened (7). Therefore it has been proposed (7) that endogenous ethylene is the cause of hook formation. There is no indication that cell divisions occur more frequently on the upper side of the hook (Fig. 5); to the contrary it is clear that the hook forms because of asymetric cell expansion, for the

Table 6. No. of metaphase figures in 50 μ (five 10 μ longisections) of the hook of the etiolated pea seedling after exposure to 50 ppm ethylene.

Hr Exposure to ethylene	% inhibition of cell division
2	27.0
4	40.0
6	47.5
8	67.5
10	82.0

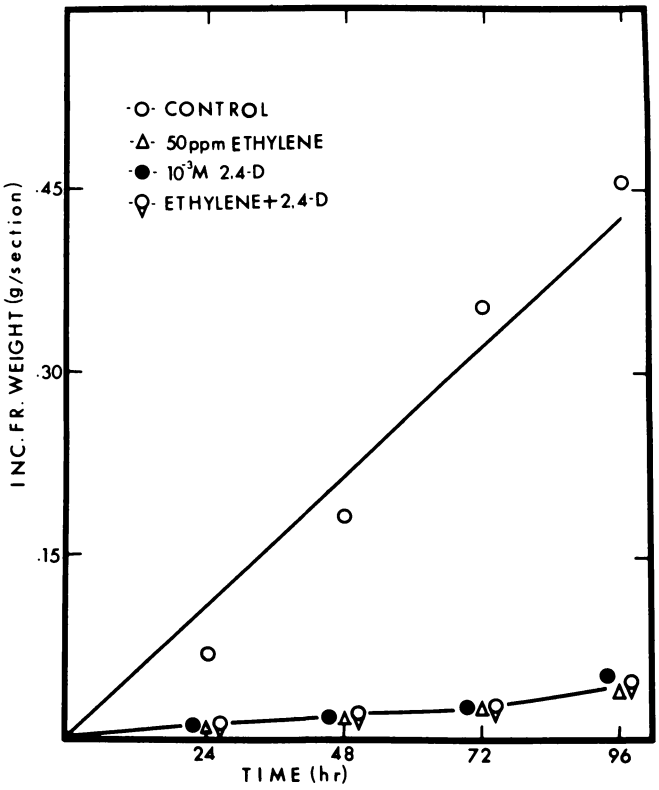

Fig. 3. Effect of ethylene (50 ppm), 1 mM 2,4-D, and 1 mM 2,4-D + ethylene (50 ppm) on the increase in fresh wt of the 7 day old etiolated pea apex.

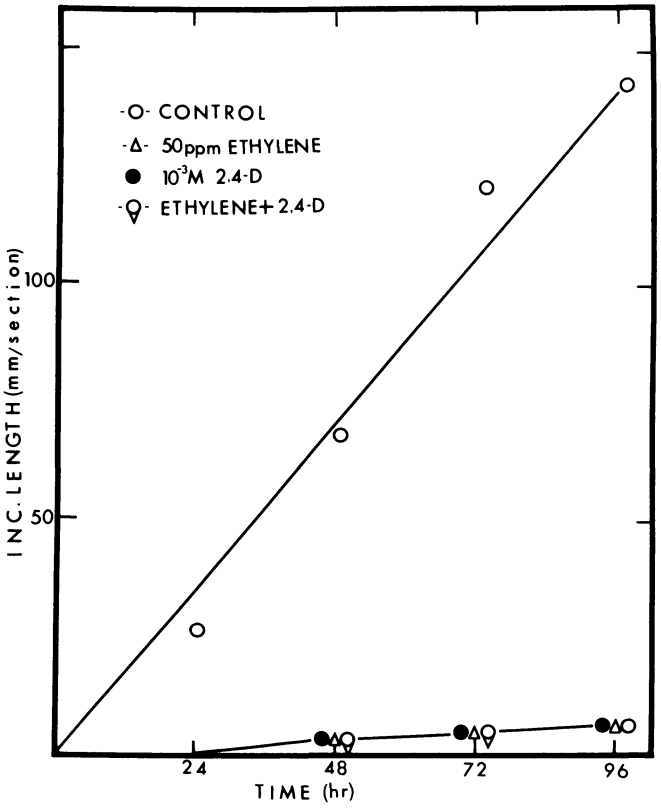

Fig. 4. (Lower right). Effect of ethylene (50 ppm), 1 mM 2,4-D, and 1 mM 2,4-D + ethylene (50 ppm) on the elongation of the 7 day old etiolated pea apex.

cells on the underside are smaller than those on the upper side and during hook opening those on the underside expand more rapidly (5). As hook formation is a typical example of epinastic growth, a clue to its mechanism may be sought in other cases of ethylene-induced epinasty. For example, when ethylene causes leaf epinasty it induces an asymetric expansion of cells on the upper side of the leaf petiole; and when the gas causes horizontal nutation in stems and plageotropism of roots, two other examples of epinastic growth, it does so by the same mechanism (36). During both horizontal nutation (35) and leaf epinasty (36) auxin accumulates on the upper side where it may cause rapid cellular expansion, even in old petioles which have ceased to grow (18). Reinitiation of growth in these mature cells which have stopped growing probably is not caused by the auxin asymetry, because usually overall auxin levels are decreased by ethylene; instead, it may be due to ethylene itself, while the asymetric growth rate which follows is caused by the auxin asymetry. Clinostat studies have shown that an excess of auxin accumulates in the upper side of a leaf petiole if gravity is prevented from transporting it to the lower side (36). Therefore the rapid and complete inhibition of lateral IAA movement, which has been demonstrated in ethylene treated pea subapical sections (3), is adequate to account for the subsequent asymetric distribution of auxin and the epinastic response of petioles. Yet it should be noted that leaf epinasty and horizontal nutation are not totally independent of gravity (19,41), for the magnitude of the response varies depending upon the orientation of the plant in space. Accordingly it has been argued that pea plants placed in a horizontal position in the presence of ethylene do not become ageotropic; rather they continue to grow horizontally because that is the direction they are actively seeking. This argument is not very convincing because the horizontal nutation takes 24-48 hr to develop; whereas gravitational curving is prevented by ethylene within 1-2 hr in intact pea roots and shoots, as well as subapical stem sections (3,11,12). Moreover the rapid phototropic curving of radish seedlings also is prevented by ethylene whereas the gas does not prevent either geotropic or phototropic curving of the coleoptiles of monocots such as *Avena* and corn, in which ethylene has no effect on lateral auxin movement (3), nor does the gas prevent phototropic curving of *Phycomyces* which apparently has the same light receptor system as that of higher plants but does not utilize auxin transport to mediate gravity perception. All of these examples indicate that when ethylene inhibits lateral auxin transport it renders plants ageotropic and aphototropic.

The cause of the asymetric distribution of auxin in the absence of gravitationally oriented auxin transport may depend upon an inherent morphological tissue asymetry. In the case of leaf petioles it is obvious that this exists for the underside normally contains larger cells than the upper side, but in the pea subapex there is no apparent difference between one side of the tissue and the other. Yet some asymetry must occur because the direction of the horizontal nutation is not random, but rather away from the side of the stem containing the leaf bract and bud. This is not readily apparent in a random sampling of plants including those with long internodes because the stem twists as it grows (23), so that while horizontal nutation invariably is unidirectional in plants having internodes shorter than 1 cm, it appears to become more and more random as the length increases (Table 7).

When pea stem sections are cut and placed in solution they undergo a spontaneous growth curvature or nutation which begins within 15 min and ultimately results in a bending of about 40° within 2 hr after which the sections again straighten (3). Ethylene acts very quickly to prevent this curvature, presumably by inhibiting lateral auxin transport, for the sections remain straight throughout the 2 hr period even though the gas has no effect on rate of elongation during that time. Concn of cycloheximide which half-inhibit the growth of the tissue do not interfere with this rapid action of ethylene, suggesting that it does not require protein synthesis, and that it may be close to the primary mechanism of action. That is no lasting product of the primary effect of ethylene is produced is also indicated by the rapid reversibility of many ethylene responses, including that on lateral auxin transport (3), abscission (22) and root growth (12).

Table 7. Direction of the horizontal nutation in etiolated pea seedlings treated with 10 ppm ethylene for 48 hr.

Internode length (cm)	Distribution (%)			
	Away from leaf bract	Towards leaf bract	To one side	No nutation
0-1	100	0	0	0
1-2	69	3	25	3
2-3	23	60	9	9

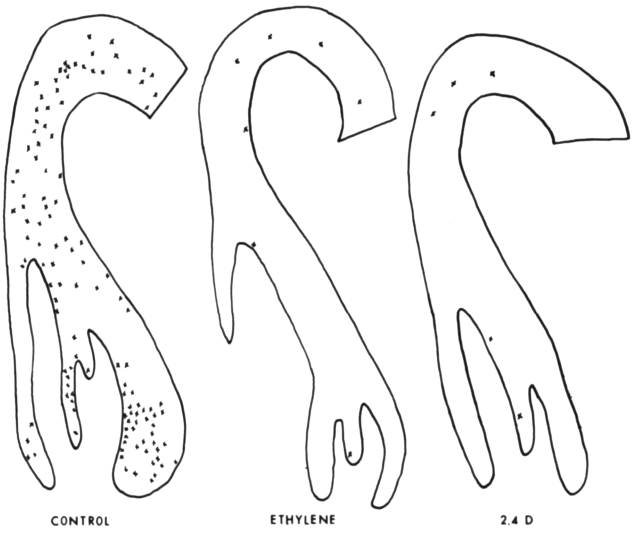

Fig. 5. (Upper). Location of cellular divisions in the median 10 μ (average of 5 median longisections, 10μ per section) of the apical zone of the stem of 8 day old *Pisum sativum*. Ethylene (10 ppm) or 2,4-D (10^{-4}M) was applied to 7 day old seedlings for 24 hr.

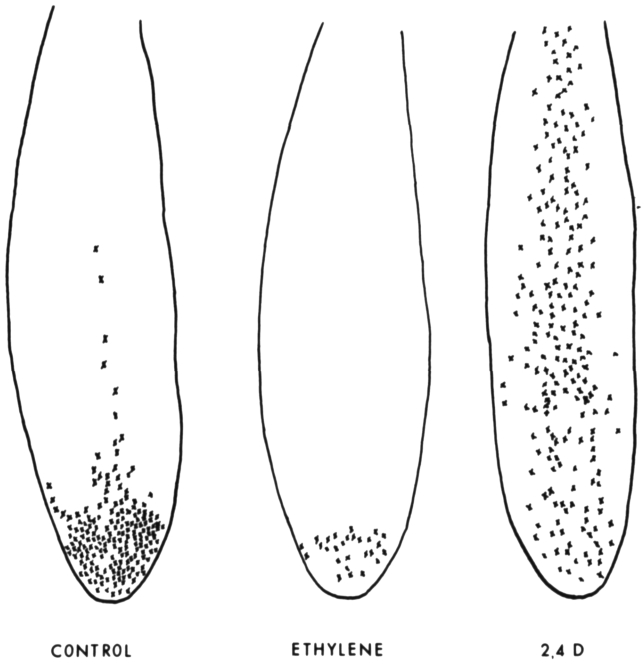

Fig. 6. (Lower). Location of cellular divisions in the median 35 μ (5 median longisections, 7 μ per section) of 5 mm root tips of 3 day old *Pisum sativum*. Ethylene (50 ppm) or 2,4-D (10^{-4}M) was applied for 24 hr to 2 day old roots.

To the contrary, both cycloheximide and actinomycin D prevent ethylene induced swelling (9), and therefore it apparently cannot take place without RNA and protein synthesis. The effect of ethylene on the spontaneous nutation resembles that of the gas on certain natural stem nutations in intact plants (18), which cease almost immediately after ethylene application.

Discussion

Analogue studies indicate that ethylene binds to a metal containing receptor having a specificity typical of a protein, and that this binding requires O_2 and is competitvely inhibited by CO_2 (5). The binding must occur through a non covalent linkage for it is readily reversible, and it probably occurs at one end of the molecule just as in model systems when olefines bind to metal (40). This explains why substitutions on the other end of the molecule hardly decrease activity if they are held linearly (5). The metallic binding site acts as if it is deeply buried within the protein structure and difficult to approach, for if substitutions are held at an angle to the unsaturated position they are capable of sterically impeding approach

of an analogue to the receptor. One of the immediate results of the binding appears to be an inhibition of lateral auxin transport. Other effects on active transport have been noted (31), and should not be confused with the often claimed stimulation by ethylene of passive permeability (44), for which there is little evidence (for example, see Tables 4 and 5). The "permeability' concept arose because ethylene is a highly fat soluble molecule which should concentrate in lipid phases such as membranes. But ethylene also has appreciable water solubility and some of its very active analogues, such as carbon monoxide (3), would not be expected to seek out lipid phases. Secondary results of ethylene action may include alteration of microtubule structure, microfibrillar orientation, cell wall metabolism and/or DNA synthesis, and cause an inhibition of cell division accompanied by radial cellular expansion, a marked prolongation of cellular growth, and inhibition of polar auxin transport. The effects of ethylene on call expansion, like those on abscission (1) require RNA and protein synthesis and in both cases it has been claimed that ethylene acts to stimulate RNA production (1,27). With pea tissue it is virtually certain that ethylene prolongs RNA synthesis, even if it does not stimulate it, for otherwise it is unlikely that the subapical cells could continue to expand. In other systems there is no doubt that various proteins ultimately are formed in response to ethylene (13,28,49).

The combined effects of ethylene on cell division and expansion explain a variety of effects, many of which have only recently been described. Thus ethylene, by inhibiting cell division, slows growth if applied during the stage of cell division to figs (37) or rice coleoptiles (34); it prevents pea buds (6) and potato sprouts (20) from growing; it inhibits secondary growth and lateral root formation in roots (46); and retards cell division in fern gametophytes (39). However, by prolonging or potentiating cell expansion and inducing radial growth, it stimulates growth of rice coleoptiles if applied after cell division has been completed (34), initiates the cell expansion phase in figs and possibly other fruits with sigmoidal growth curves (37) producing isodiametric cells, causes an increased cell size in fern gametophytes (39), stimulates root hair formation (2,11), and enhances growth in certain tissue cultures (53) and in pollen tubes (51). Since the gas normally is produced in the apex of plants, endogenous ethylene may also have a natural role not only in hook formation, but also in the control of cell division and expansion there, just as it does in roots where it appears to participate in the geotropic response (11,12) and also to influence normal expansion (11,12,46).

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PRACTICAL APPLICATIONS OF (2-CHLOROETHYL)PHOSPHONIC ACID IN AGRICULTURAL PRODUCTION

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In 1946 Kabachnik and Rossiiskaya (96) reported the chemical synthesis of "2-chloroethanephosphonic" acid and in 1963 Maynard and Swan (125) described the formation of ethylene from this compound. When (2-chloroethyl)phosphonic acid (ethephon; also variously cited as 2-chloroethanephosphonic acid, Amchem 66-329, CEPA and Ethrel® disintegrates, it releases ethylene and also chloride and phosphate ions (43,67,125,196,202) Ethephon is essentially stable in aqueous solutions below pH 4. When the presence of hydroxyl ions is increased and the pH rises above 4, disintegration of the chemical takes place. The pH of the cytoplasm of plant cells is generally greater than 4, so the plant growth activity of ethephon has been attributed primarily to its ability to release ethylene to plant tissues (14,43,132,195,196). Ethrel formulations provide a convenient way to apply ethylene without the need of gas-confining chambers.

The physiological effects of ethylene on plants are dramatic and commercially important (5,50,145). This paper correlates the known literature showing improved agricultural production which may accrue from the physiological influence of ethephon on flowering, vegetative growth and dormancy, abscission, ripening and maturity, freeze and disease resistance, and latex flow.

Influence on flowering

Flower induction is an essential part of production techniques in most areas where pineapples are grown, particularly during the season of long photoperiod when the duration of vegetative growth is extended abnormally. Spraying pineapple plants with ethephon at rates of 1 to 4 lb./acre has generally induced 100% flower formation (6,43,148). The flowering response is hastened with the higher rate of 4 lb./acre – these plants matured 2 to 3 weeks earlier than those treated with 1 lb./acre. Ornamental bromeliads, also members of the pineapple family, have been induced to flower after a foliage spray of ethephon at rates of 1000 to 2500 ppm or after ethephon solutions were placed in the cup-like throats (9,18,38,192,193).

Ethephon sprayed at 240 ppm has also induced flowering of the qualitative short-day plant *Plumbago indica* L. when grown under non-inductive short days (135).

Preliminary information indicates that foliar applications of 1000 ppm ethephon can promote earlier flowering of mangoes (60,134) and pistachio (6).

Fall and spring applications of 250 to 2000 ppm of ethephon to apple and pear trees have suppressed vegetative growth and subsequently promoted flowering in some cases (39,65,69,103,199). Ethephon treatments to induce flower bud formation may promote earlier bearing or control biennial bearing.

Producing hybrid cucurbit seed is costly when staminate flowers are removed by hand from seed parents to prevent self-pollination. Ethephon sprays can be an important hybridizing tool for suppressing anther development in cucurbit seed parents (120,126,154). Single or repeated foliar sprays of 125 to 250 ppm during the 1st to 5th true leaf stage can markedly increase earlier formation of pistillate or perfect flowers while decreasing or eliminating staminate flowers from the first 15 nodes (46,93,94,99,156,170). The flowering pattern of monoecious cucumbers treated with ethephon resembles that of gynoecious cultivars. Initially, ethephon-treated plants produce primarily pistillate flowers, then gradually revert to their original monoecious character after the 15th node. Ethephon applied to andromonoecious, monoecious and hermaphrodite muskmelon cultivars initiated a general flowering pattern characterized first by the production of pistillate flowers and later by increased frequency of hermaphrodite and staminate flowers (99,156). The marked increase in femaleness of ethephon-treated cucurbits has resulted in earlier and increased yields of some cucumber and squash cultivars (87,119,127,130,171,174,184,187) but not muskmelon (99).

The sex expression of staminate marijuana (*Cannabis sativa* L.) plants has also been modified. Staminate plants sprayed with 960 ppm developed 6.3, 69.9 and 23.8% staminate, pistillate and hermaphrodite flowers respectively (150).

Influence on vegetative growth and dormancy

Depending upon the crop, growth inhibition resulting from ethephon application may be important to induce or delay flowering or fruit maturing and to increase planting densities. Further, stopping terminal growth may stimulate lateral branching, thereby increasing sites for flower and fruit production.

Ethephon applications at rates of 100 to 5000 ppm have inhibited terminal growth and increased lateral branching of many ornamentals such as azalea, cotoneaster, hydrangea, petunia, poinsettia, zinnia, rose and pine (5,6,21,35,162,163,164,183). Ethephon has been a retardant when applied as a foliar spray or a soil drench. Combinations of ethephon with other growth retardant materials such as (2-chloroethyl)trimethylammonium chloride (chlormequat Cycocel) and succinic acid-2,2-dimethylhydrazide (SADH, Alar) have retarded vegetative growth of some resistant cultivars of poinsettias (164). The spray combination of ethephon at 2500 to 5000 ppm and a fatty acid chemical pinching agent at 2 to 5% stimulated lateral branching, and increased flower bud formation on florist-grown azaleas (21,163).

Rates of 1 to 4 lb./acre applied for pineapple flower induction inhibit vegetative growth, suggesting the possibility of increasing planting densities. The peduncle on which the fruit develops is shortened, reducing fruit tipping and subsequent sun scald (6,43).

Sprays of 125 to 1000 ppm ethephon applied to many cultivars of vegetables including sweet corn, beets, snapbeans, eggplants, garden peas, peppers and tomatoes have inhibited terminal growth (5,6,8,129). Treating onions at the 4 to 5 true leaf stage with 500 to 10,000 ppm ethephon at weekly intervals for 3 to 5 weeks initiated bulbs earlier, increased the frequency of bulbing and also accelerated their maturity (112).

Spraying small grains with 0.5 to 2.0 lb./acre of ethephon during the tillering stage generally increased the number of grain-producing tillers. Grain and grain heads were generally smaller so yields were not always increased (5,6).

Preventing lodging in small grains and other crops is important to insure maximum yield recovery at harvest. Sprays of ethephon at 0.25 to 1 lb./acre applied at the end of tillering or during the early boot stage reduced the extent of severity of small grains lodging by shortening stems or increasing straw stiffness (5,6,59). Growth inhibition and antilodging of corn following ethephon spray applications of 0.25 to 1 lb./acre may be important in some areas where high density planting would normally cause corn plants to be tall and thin (6,61,144). Ethephon rates of 0.5 lb./acre and less also appear to prevent soybean lodging (5,172).

Vegetative growth of tree fruits such as apple and pear has been suppressed with ethephon foliar sprays of 250 to 1000 ppm (39,67,69,103,199). On vigorous grape vines, reduced vegetative growth after mid-season foliar applications of 1000 ppm ethephon should reduce the labor required for pruning and stimulate more uniform cluster maturity as a result of better light penetration (6,197).

Foliar applications of ethephon at rates of 50 to 1000 ppm have stimulated rhizome production in lowbush blueberries. This should