Plant Physiol. (1969) 44, 831–838

Effects of Picloram and Ethylene on Leaf Movement in Huisache and Mesquite Seedlings[1, 2]

J. R. Baur and P. W. Morgan
Departments of Range Science and Plant Sciences, Texas A&M University, College Station, Texas 77843

Received December 30, 1968.

Abstract. **Application of 4-amino-3,5,6-trichloropicolinic acid (picloram) to roots stimulated the production of ethylene in both mesquite [*Prosopis juliflora* (Swartz) DC. var. glandulosa (Torr.) Cockerell] and huisache [*Acacia farnesiana* (L.) Willd.] seedlings. Herbicide levels rose in tissues before we detected increased ethylene production. Rates of ethylene production by various parts of the plant paralleled herbicide concentrations. In both species, picloram caused loss of leaf movement and epinastic curvature of leaves and stems. Only huisache was defoliated by picloram. Rates of ethylene production increased before we observed any leaf movement or defoliation responses. Fumigation of plants with levels of ethylene, calculated to approximate those in herbicide-treated plants at the initial loss of leaf movement, caused the same symptoms as picloram treatment. The time sequence of ethylene fumigation and loss of the ability for leaf movement is compatible with the hypothesis that there is a causal relationship between picloram and ethylene production and loss of leaf movement.**

We have observed that an early response of huisache [*Acacia farnesiana* (L.) Willd.] and mesquite [*Prosopis juliflora* (Swartz) DC. var. glandulosa (Torr.) Cockerell] seedlings to 4-amino-3,5,6-trichloropicolinic acid (picloram) applied to roots is loss of the ability of leaves to move in response to light and contact stimuli. In 1932 Crocker *et al.* (6) demonstrated that exposure to 2 ppm ethylene inhibited nutational movement in tomato (*Lycopersicon esculentum* Mill.) plants. Zimmerman and Wilcoxson (19) noted loss of leaf movement in *Mimosa pudica* L. plants enclosed with tomato plants that had been treated with indole-3-acetic acid. Picloram has been shown to possess growth regulator and auxin properties (9, 11, 12). Crocker later reported that *Mimosa pudica* (L.) leaves exposed to 0.5 % carbon monoxide lost the ability to respond to contact stimuli (5). He also reported that carbon monoxide is known to mimic many effects of ethylene (5). Stimulation of ethylene production, over a wide range of species, by several growth regulators is well documented (1, 3, 7, 10, 13, 17, 19).

The aim of our experiments was to determine the relationship of picloram treatment to ethylene evolution and leaf movement in huisache and mesquite seedlings. We studied the opening and closing of leaflets in response to light and dark, or their closing in response to a physical stimulus such as shaking or touching the plant.

Materials and Methods

Plant Materials. We dusted huisache and mesquite seeds with thiram (tetramethylthiuramdisulfide) and then germinated them at 22° between damp toweling in plastic refrigerator crispers. After germination (5 days), seedlings were transferred to half-strength nutrient solutions (15). Five seedlings were suspended by a piece of black Plexiglas[3] over a foil-wrapped one-half-pint freezer jar, so that the roots were in contact with the nutrient solution.

The seedlings were grown, treated and held for ethylene analysis in a plant growth room under the following conditions: light intensity, 1500 ft-c (supplied by a mixture of fluorescent and incandescent lamps); temperature, 22° constant; relative humidity, 40 % constant; day length, 15 hr.

Herbicide Treatment and Analysis. We treated 18-day-old seedlings (8–10 cm in height; 4–6 fully expanded leaves) by exposing their roots to

[1] Cooperative investigations of the Crops Research Division, Agricultural Research Service, United States Department of Agriculture and Texas Agricultural Experiment Station, Texas A&M University. Supported in part by Grant GB-5640 from the National Science Foundation.

[2] Preliminary reports of this study appear in Proceedings 22nd Annual Meeting, Southern Weed Conference, 1969 and Proceedings of 66th Annual Meeting, Association of Southern Agricultural Workers, 1969 (Southern Section, American Society of Plant Physiologists).

[3] Mention of a trademark name or a proprietary product does not constitute endorsement by the United States Department of Agriculture or Texas A&M University, and does not imply its approval to the exclusion of other products that also may be suitable.

4.13×10^{-6} M or 4.13×10^{-5} M (huisache and mesquite, respectively) picloram solutions for 24 hr. Treatment was accomplished by transferring the Plexiglas supports containing the plants to similar one-half-pint jars containing the treatment solutions. After 24 hr we removed the seedlings from the herbicide solution; dipped their roots 3 times in 1 % (v/v) NH_4OH to remove adsorbed picloram; and returned them to fresh nutrient solution. Previous studies have shown that these conditions kill approximately 60 % of the treated population.

Evaluation of Leaf Movement. We checked the response of seedlings to light and contact stimuli visually before each ethylene assay by moving the plants to a darkened area (or a lighted area for evaluation during the normal dark period). The first detection of a lack of movement following transfer from light to dark (or dark to light) was considered the onset of loss of leaf movement capability; complete loss was marked by a lack of response in all plants.

After each experiment, we determined picloram concentrations in leaf, stem and root fractions, utilizing the techniques of Merkle and Davis (14). The samples were weighed, ground in acidified acetone (4 ml HCl/l) and filtered. The filtrate was reduced to dryness, dissolved in 1 % (v/v) NH_4OH, washed twice with ether, acidified with HCl to pH 3 and re-extracted with ether. The picloram-containing ether fraction was reduced to dryness, methylated with methanolic boron trifluoride and taken up in hexane for gas chromatographic analysis (14).

Ethylene Analysis. To determine ethylene production by treated plants, we measured the ethylene content of 5 ml air samples periodically withdrawn from 12 liter bell jars that held groups of plants. The analysis of ethylene and verification of its identity was accomplished by gas chromatography as previously described (16). Immediately after analysis, all bell jars were flushed with air for 2 min to remove accumulated ethylene and then re-sealed.

Time-Course Experiments. Ethylene production by plants treated with picloram was measured at 6 hr intervals over periods of 24 and 36 hr (mesquite and huisache, respectively). We conducted 2 experiments, each consisting of 4, 12 liter bell jars for each species; 2 with treated plants and 2 with untreated, control plants. Each bell jar held 3 growth containers (a total of 15 plants).

Mesquite seedlings were enclosed 6 hr after initiation of treatment; huisache seedlings were enclosed upon removal from treatment solutions. The variation in time of enclosure was necessary to insure maximum uptake of herbicide prior to the loss of leaf movement that occurred at different times for each species.

Concurrent with the last time-course experiment, 8 groups (4 per species) of 3 growth containers were treated and held under the same conditions as plants in the bell jars. At 3, 6, 12, and 18 hr after treatment, 1 group (3 growth containers) of mesquite seedlings were harvested and fractionated. Four of the 5 plants from each growth container were divided into leaf, stem, and root fractions. Like fractions of all plants in each growth container were combined and placed in 125 ml Erlenmeyer flasks fitted with rubber vaccine caps. The fifth plant was kept intact and placed in a similar flask. Ethylene production by each fraction was determined 6 hr after fractionation, excepting plants divided at 3 hr which were analyzed 3 hr later. The same procedure was followed for huisache except that fractionation occurred at 18, 24, 30, and 36 hr after treatment.

Fumigation Experiments. We conducted 2 experiments to observe the effects of exogenous ethylene on huisache and mesquite plants not treated with picloram. Each experiment utilized 5 bell jars per species; each jar contained 3 growth containers (15 plants). For each species, the concentration of ethylene in 2 bell jars was maintained at a level calculated to result in the internal concentration present when herbicide-treated plants ceased to respond to light or contact stimuli. Ethylene levels in 2 additional bell jars were varied with time to approximate the time-course of internal ethylene

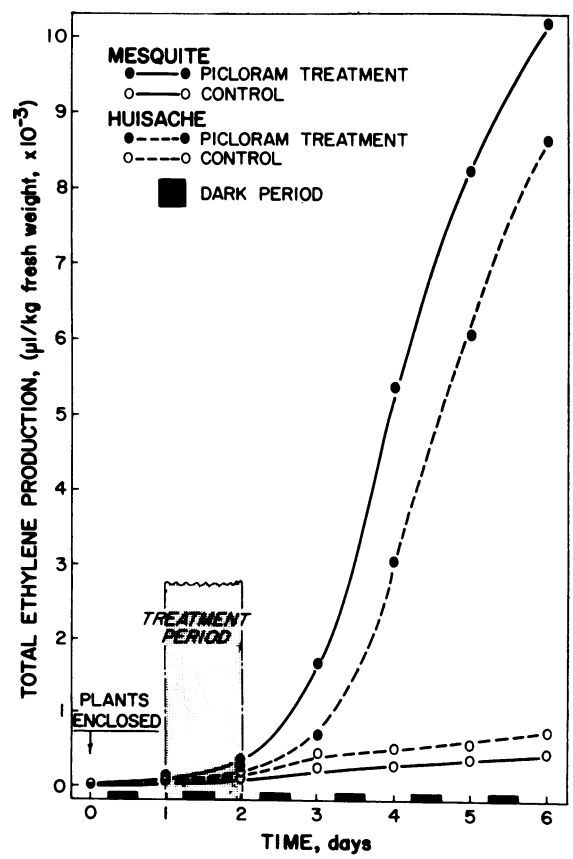

FIG. 1. Effect of picloram on total ethylene evolution by mesquite and huisache seedlings. Fifteen seedlings enclosed in 12-liter bell jars. Data are average of 2 replications of each treatment.

concentrations in picloram-treated plants. A final bell jar (not fumigated) served as control. At 6 hr intervals we observed the plants in all bell jars for leaf movement immediately before we measured ethylene content. Immediately after ethylene analysis, all jars were flushed with air and re-fumigated. We terminated each experiment after leaf movement ceased entirely.

We conducted a short-term fumigation experiment utilizing 14 bell jars containing huisache seedlings not treated with picloram. Six bell jars were fumigated with 3.2 ppm and 6 with 6.4 ppm ethylene. Two bell jars, not fumigated, served as control. Leaf movement was evaluated at 1 hr intervals for 5 hr.

Determination of internal ethylene concentrations was based on modification of a previously reported factor relating ethylene production rates to internal concentrations (2). Discussion of the conversion factor and its modification follow in the next section.

Results and Discussion

The effect of picloram on total ethylene evolution is shown in Fig. 1. Ethylene production by mesquite and huisache seedlings rose sharply after treatment with picloram, and an abnormally high production rate persisted for the duration of the experiment. Control plants not treated with picloram produced levels of ethylene near the lower limits of sensitivity of the measurement system. The sequence of visible responses attributed to picloram treatment were correlated with the air concentration of ethylene at the end of each collection period (Fig. 2). Ethylene production by both species began to increase significantly before exposure to picloram was terminated. Loss of leaf movement occurred in both species after ethylene levels in the air surrounding the plants had increased above the controls. Mesquite was first to demonstrate increased ethylene evolution and loss of

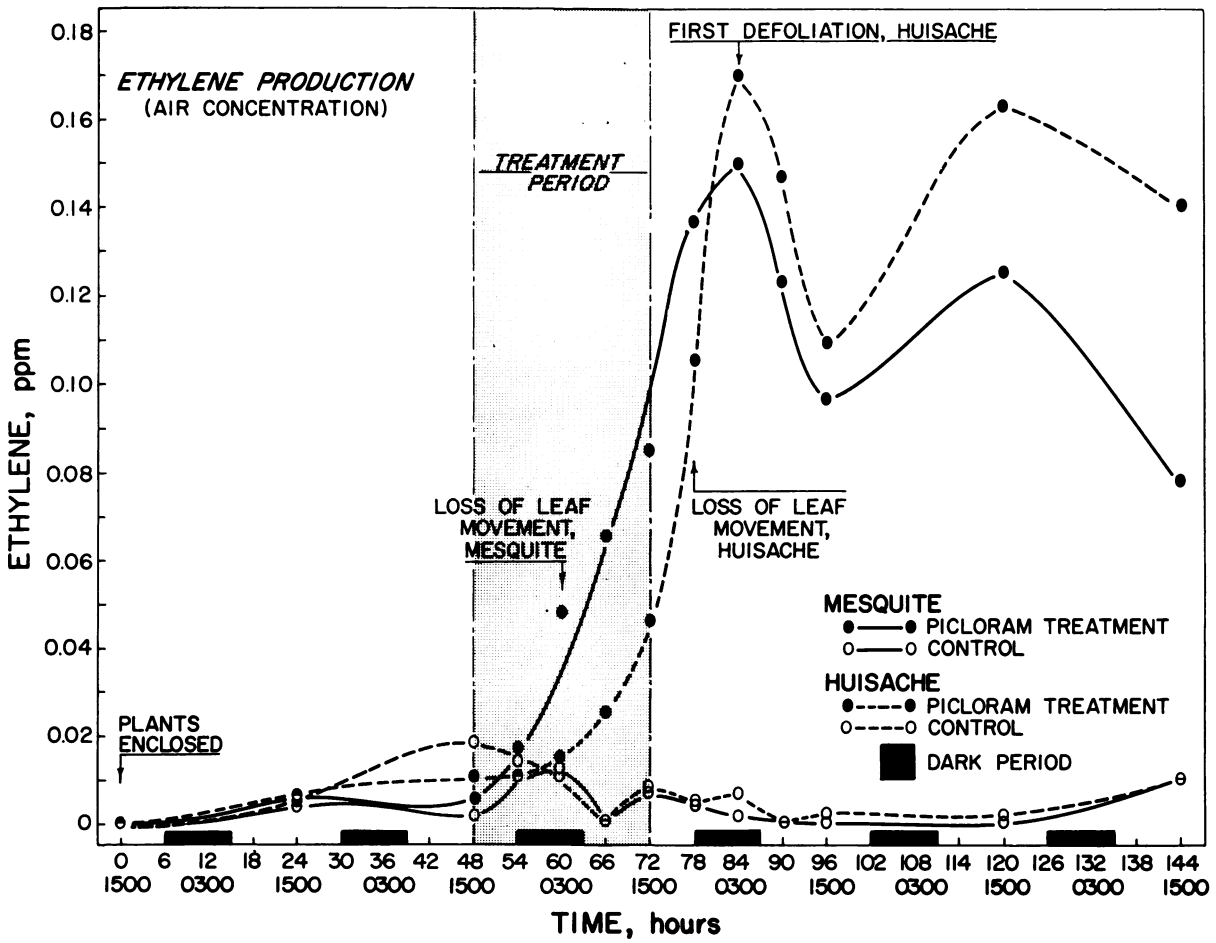

FIG. 2. The effect of picloram on the evolution of ethylene, loss of leaf movement and defoliation of mesquite and huisache. Ethylene levels in 12-liter bell jars at the end of various collection periods are indicated.

leaf movement due to picloram treatment. Maximum air levels of ethylene detected were in the 0.15 to 0.17 ppm range. Abscission of huisache leaves began at the time of maximum ethylene levels, which was only 6 hr after loss of leaf movement capability. Observations from this and other tests[4] revealed that mesquite does not defoliate in response to picloram; whereas, loss of leaf movement in huisache signals that defoliation will soon begin. Another response of both species to picloram was epinastic curvature of apical stems, apical leaves and eventually many leaves.

Since ethylene in the bell jars was removed by ventilation after each assay, a close approximation of production rates was calculated for each collection period in terms of μl/kg fresh wt/hr. To obtain an estimation of internal ethylene levels in various parts of mesquite and huisache seedlings, we applied a modification of Burg's (2) factor of 2 ppm internal ethylene for each μl $kg^{-1}hr^{-1}$ produced to the calculated production rates of intact plants enclosed in bell jars and detached plant parts enclosed in 125 ml Erlenmeyer flasks.

Burg's (2) conversion factor of 2 ppm μl^{-1} $kg^{-1}hr^{-1}$ was developed for apples and avocados having a surface-to-volume (S:V) ratio of approximately 1 cm^2/cm^3 (average value determined in our lab). The actual S:V ratios of the seedlings represented the fold increase in the ratio between seedling and fruit tissues. Consequently, the factor of 2 was divided by the S:V ratios of mesquite and huisache seedlings to give the factors used in subsequent experiments (table I).

We made surface and volume measurements on 4 representative seedlings of each species. Seedlings were divided into leaflet (pinna), petiole, stem and root fractions. The pinna were separated into 5 to 7 groups depending on size. We made detailed measurements (width, length, thickness) of representative samples from each group with a millimeter ruler and micrometer. Area and volume was calculated assuming the pinna to be 2 equal parallel elliptical surfaces. Area and volume of petiole, stem, and root segments were calculated assuming cylindrical shape.

The components of the intact plant varied in their S:V ratios and their contribution by weight to the total plant or leaf; therefore, we calculated composite S:V ratios for plants by weighting the S:V ratios of the individual components (Footnotes 2 and 3, table I).

The internal concentration of ethylene is critical to the question of whether the gas causes the initial symptoms which follow application of picloram. We were not able to measure internal levels directly and yet a conservative estimate of such concentrations would allow a conclusion on the probability that ethylene is the causal agent. The surface-to-volume correction of 2 ppm μl^{-1} $kg^{-1}hr^{-1}$ factor (2) is an attempt to account for an increase in exit area per volume of gas-producing cells if a fruit is compared to a leaf. It admittedly does not account for difference in resistance to diffusion offered by the epidermal layers of fruits *versus* leaves and stems. Similar calculations for pea epicotyl tissue resulted in a factor of 0.13 ppm μl^{-1} $kg^{-1}hr^{-1}$ (8). The accuracy of this factor (8) was supported by fumigation experiments involving levels of ethylene equal to those calculated to be present during treatment. An indirect method, based on auxin-induced ethylene synthesis and ethylene fumigation responses, allowed calculations of a factor of 0.2 ppm μl^{-1} $kg^{-1}hr^{-1}$ (3,4). These factors would estimate internal ethylene concentrations about 10-fold higher than would be estimated by our factors (table I). Our major purpose in the remaining experiment was to answer the question of whether the loss of leaf movement was due to ethylene. That we were able to answer the question affirmatively with a factor 10-fold more conservative than other available factors (4, 8), enhances the probability that our conclusion is correct. By reporting both the calculated internal levels and the factors (table I) we make it possible to convert our data to ethylene production rates.

In a more detailed study of the time-sequence of

Table I. *Surface to Volume Ratios of Various Fractions of Mesquite and Huisache Seedlings and Calculated Factors for Conversion of Observed Ethylene Production Rates to Internal Concentrations of Ethylene*

Species	Fraction	Surface:volume	Conversion factor[1]
Mesquite	intact[2]	90	0.022
	leaves[3]	82	0.024
	stems	78	0.026
	roots	126	0.016
Huisache	intact[2]	80	0.025
	leaves[3]	137	0.015
	stems	74	0.027
	roots	137	0.015

[1] Conversion factor obtained by dividing 2 ppm μl^{-1} kg^{-1} hr^{-1} by the observed S:V ratio. The conversion factor can then be multiplied times the μl ethylene kg^{-1} hr^{-1} to estimate internal concentrations of ethylene.

[2] Surface:volume ratio calculated by multiplying the S:V ratios of the individual fractions by the percent by weight that these fractions contribute to the total weight of the plant. These weighted values were then added to give the composite or average S:V ratio.

[3] Surface:volume ratio calculated by multiplying the S:V ratios of leaflets, cotyledons and petioles by the percent by weight that these fractions contribute to the total weight of the leaf fraction. These weighted values were then added to give the composite or average S:V ratio.

[4] Baur, J. R. and R. W. Bovey. Unpublished Data.

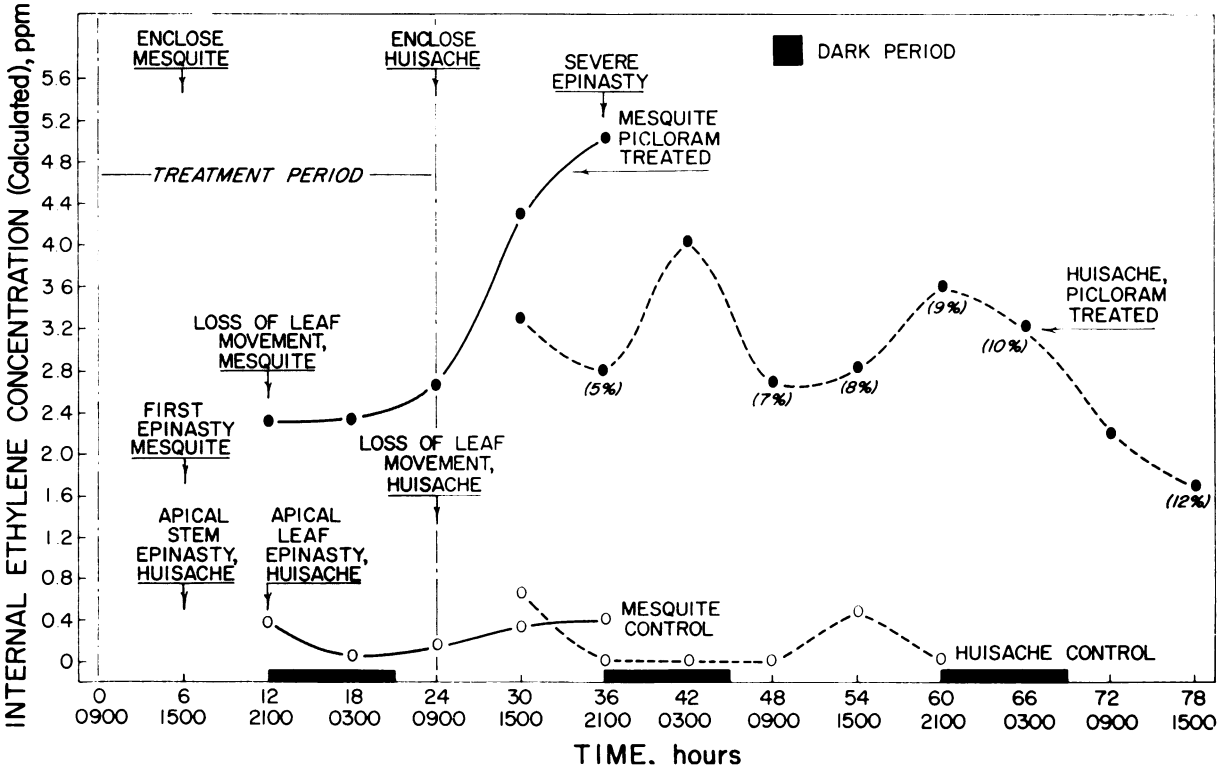

FIG. 3. Effect of picloram on internal ethylene levels (calculated) and other responses of mesquite and huisache seedlings enclosed in bell jars at the times indicated. Ethylene levels calculated from observed production rates using the conversion factors for intact plants in table I. Percent defoliation indicated in parentheses.

stimulated ethylene evolution and loss of leaf movement, we began exposure of the seedlings to picloram before they were enclosed, creating a condition which hastened the uptake and response to the herbicide (Fig. 3). Mesquite seedlings lost leaf movement capability 12 hr after they were exposed to picloram. During the 6-hr period prior to this response, the average internal level of ethylene was calculated to be about 2.4 ppm. The calculated internal level of ethylene eventually rose to 4.9 ppm in mesquite. Loss of leaf movement in huisache occurred 24 hr after the onset of exposure to picloram (Fig. 3). During the 6-hr period immediately following this response the average internal level of ethylene was calculated to be 3.2 ppm. Ethylene levels in huisache remained in the 2.8 to 4 ppm range until 72 hr after the plants were treated. Epinasty preceded loss of leaf movement in both species. Abscission was first observed 6 hr after huisache lost leaf movement ability. Air levels of ethylene in bell jars containing non-treated plants were occasionally too low to measure, but calculated ethylene levels in control plants were generally below 0.4 to 0.5 ppm.

Analysis of picloram in tissue from plants enclosed in bell jars revealed that the herbicide was predominantly in the tops of plants. Exposure of plants to picloram before they were enclosed increased the amount of herbicide recovered in the tissue. The longer period of treatment of huisache before enclosure apparently caused that species to take up more herbicide than mesquite.

Herbicide uptake and increased ethylene evolution was shown by plants that were fractionated during the second experiment. In mesquite (Fig. 4), picloram levels in the root increased first, followed by a sharp increase in stem tissue. Maximum herbicide concentration in the stem (2 μg/g fresh wt) occurred concomitantly with loss of leaf movement. There was no accumulation of picloram in leaf tissues. Roots and leaves both demonstrated a low but consistent increase in release of the gas. The dominant feature of the data was that the production of ethylene by stem tissue followed the rise in picloram levels in that tissue. Loss of leaf movement was first observed 12 hr after treatment. Internal ethylene levels in the stem at this time were calculated to be 3 ppm, eventually rising to over 8 ppm (Fig. 4).

Ethylene production by the first huisache samples fractionated in Experiment 2 was assayed 24 hr after the beginning of picloram treatment (Fig. 5). By this time picloram levels were high in leaves and remained at or above 2 μg/g fresh wt for the duration of the experiment. Picloram levels declined in roots from 24 to 36 hr. The last increase (36–42 hr) was correlated with a decline in the herbicide level in leaf tissues. Relatively little picloram accumulated in huisache stem tissue. As with mesquite, there was a direct correlation between the portion of

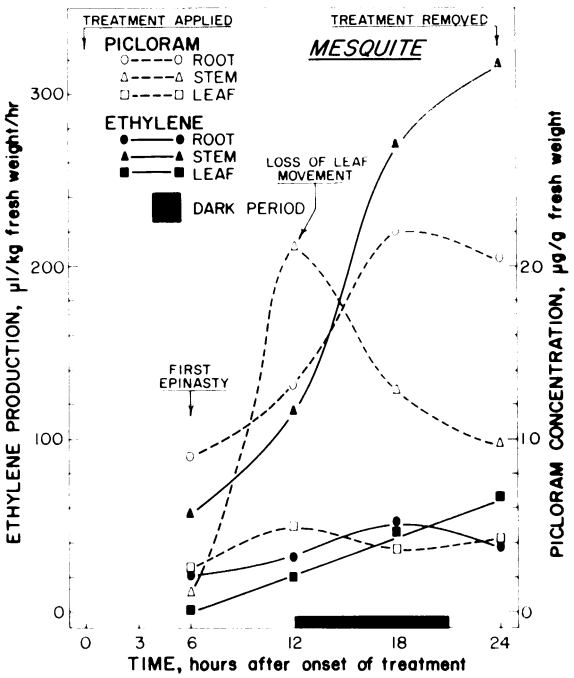

FIG. 4. Distribution of picloram levels and ethylene production rates in mesquite plant parts fractionated during the course of Experiment 2. Data plotted at the time of assay; fractionation occurred 6 hr previously.

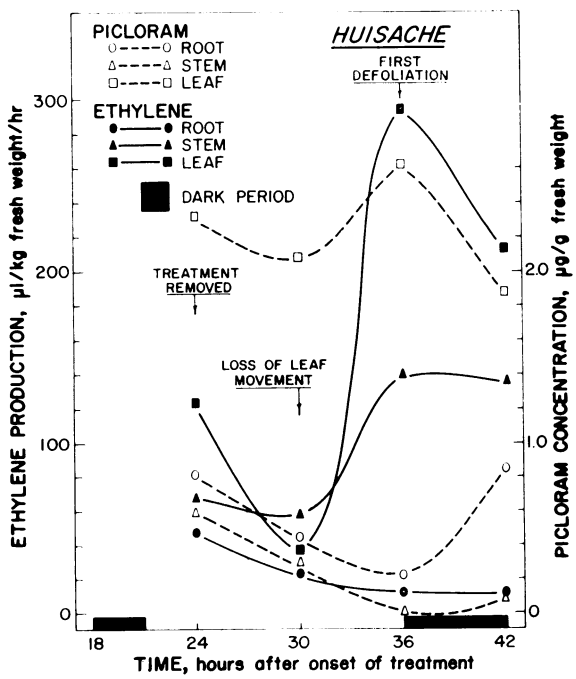

FIG. 5. Distribution of picloram levels and ethylene production rates in huisache plant parts fractionated during the course of Experiment 2. Data plotted at the time of assay; fractionation occurred 6 hr previously.

the plant containing the highest concentration of herbicide and the fraction releasing ethylene at the highest rate. Except for the unexplained reduction of ethylene production at 30 hr, huisache leaves released ethylene at the highest rates. While picloram levels in stem tissues were the lowest of all huisache fractions, ethylene production from this fraction was significant, especially during the 30- to 40-hr period when some redistribution of picloram between leaves and roots appeared to occur. This observation suggests 2 conclusions: A) the concentration of picloram necessary to stimulate ethylene synthesis in stem tissue is extremely low in that transitory levels appear capable of stimulation; B) movement of significant amounts of the herbicide through the stem to the leaves apparently does not inhibit or otherwise alter the capacity of the stem for subsequent ethylene production in response to picloram.

Production of ethylene by fractions of untreated seedlings of both species was negligible.

Maximum calculated internal ethylene levels in huisache leaves approached 6 ppm. The comparison of calculated ethylene levels and times of various responses in Fig. 4 and 5 is not as valid as it is for Fig. 3, because in the former case the movement of picloram into or out of a specific fraction is stopped at the time ethylene collection was started. In addition, ethylene was collected from a detached plant part rather than an intact plant. The approach did indicate the relative picloram levels and ethylene production rates in various plant parts during the experiment.

The major finding in Fig. 4 and 5 is that picloram levels and ethylene production rates are highest in mesquite stems and huisache leaves. The fact that the rate of ethylene production by huisache stems is out of proportion to herbicide level when compared to other fractions suggests that this tissue is relatively sensitive to the herbicide. It is interesting to note that while picloram causes inhibition of leaf movement and epinasty in both species, abscission occurs only in huisache, the species where the peak acceleration of ethylene production occurs in the leaves.

When we used the conversion factors in table I to calculate internal ethylene levels in fractionated plants, we found that all calculated values for leaves and some values for roots were lower, but of the same order of magnitude, as the levels of ethylene in the air surrounding these fractions. This observation could indicate that: (a) the conversion factors were too conservative or (b) enclosure of these fractions in 125 ml Erlenmeyer flasks for 3 or 6 hr allowed accumulation of ethylene above levels that would have been present internally, were the tissues not enclosed. Even if the latter explanation is correct, it would argue that the larger volume of the bell jars would prevent this error. In fact, we found that the calculated internal ethylene levels for bell jar plants were always much higher than the air levels of ethylene observed in these containers.

The data in Fig. 4 and 5 are in agreement with our conclusion that elevated ethylene production is a function of picloram level and that ethylene could function in the initial responses to the herbicide. We tested this hypothesis by fumigating plants (not treated with herbicide) with levels of ethylene calculated to be in treated plants at the time of their first loss of leaf movement. In 2 experiments, ethylene at 2.1 and 3.2 ppm removed or blocked the ability of mesquite and huisache leaves to respond to touch and light (table II). Epinasty was induced in both species by the added ethylene but defoliation occurred only in huisache plants. These responses, with 1 possible exception, exactly parallel the initial responses to picloram. Epinasty preceded loss of leaf movement with picloram treatment (Fig. 3), but the leaf movement response preceded or paralleled the appearance of epinasty following ethylene fumigation (table II). This sequence is reasonable because picloram results in a changing pattern of ethylene production (Fig. 4 and 5); whereas, ethylene fumigation results in uniform elevation of internal ethylene levels. The time required for ethylene to block leaf movement was between 6 and 12 hr for mesquite and 0 to 6 hr for huisache (table II). These times are brief enough to postulate that ethylene produced by the herbicide induced the loss of leaf movement in the picloram experiments (Fig. 2 and 3).

The order in which ethylene fumigation blocks leaf movement is reversed when compared to the sequence of herbicide-induced symptom production. It should be noted that the order in which leaf movements are blocked in the 2 species in response to picloram is actually a reflection of the order in which ethylene production is stimulated (Fig. 2 and 3).

Due to the rapidity of loss of leaf movement in huisache (table II), we fumigated an additional population of plants with 3.2 and 6.4 ppm ethylene. Hourly observations revealed that ethylene blocked this response between 2 and 3 hr after fumigation. Leaf movement capability was recovered after ethylene was removed. Since no abscission occurred following the 5-hr fumigation, it is obvious that loss of leaf movement precedes the induction of abscission. Induction of abscission may also be reversible or require a longer time than the leaf movement response before an irreversible stage is reached. Since there was no difference in the timing or severity of leaf movement at either level of ethylene, both concentrations probably saturate the response completely, suggesting that the response might occur at lower concentrations. A replicated test revealed that neither mesquite nor huisache lost leaf movement when fumigated with the air concentrations of ethylene observed at the time the movement response was noted in Experiment 1 (0.060 and 0.095 ppm, mesquite and huisache, respectively) (Fig. 2). Although fumigation with these concentrations did not produce the leaf movement response in mesquite and huisache, we observed some disorganization of leaflets and a slight but discernible slowing of leaf movement when plants were moved from light to dark or *visa versa*. Therefore, the minimum concentration of ethylene required to produce the leaf movement response must lie between 3.2 and 0.095 and 2.1 and 0.060 ppm for huisache and mesquite, respectively.

Table II. *Response of Mesquite and Huisache Seedlings Fumigated with 2.1 and 3.2 ppm Ethylene*

Time after onset of fumigation	Leaf movement response: Mesquite experiment I	Mesquite experiment II	Huisache experiment I	Huisache experiment II
hr				
0	Normal	Normal	Normal	Normal
6	Normal	Normal	Negative[1]	Negative[1]
12	Negative	Negative	Negative[2]	Negative[2]
18	Negative	Negative[1]	Negative[3]	Negative
24	Negative[1]	Terminate	Terminate	Negative[3]
30	Negative	...	...	Negative

[1] First epinastic response.
[2] Trace defoliation.
[3] 80 to 90% defoliation.

The results of our experiments strongly indicate that loss of leaf movement and other initial symptoms of picloram treatment of mesquite and huisache is exclusively or predominantly due to ethylene produced in response to the herbicide. This is essentially a restatement of the Zimmerman and Wilcoxon (19) hypothesis relating auxin treatments, auxin- and ethylene-induced plant responses, and the stimulated production of an emanation which causes epinasty. The hypothesis was re-introduced by Morgan and Hall (17) with direct proof of auxin-induced ethylene production. Subsequently, other workers have published evidence supporting a functional role for ethylene in several processes once thought to be caused by auxin (1, 3, 4, 13). Recently this phenomena was shown to be more generally applicable than just to the auxins. Morgan and Powell (18) reported that the growth promoter-inhibitor, coumarin, inhibited the light-induced growth of etiolated bean hypocotyl hooks *via* stimulation of ethylene production. At lower concentrations coumarin stimulated growth of hypocotyl sections. The present work further extends the applicability of the principle that plant regulators can exert one or more of their influences by causing the production of a physiologically active level of ethylene.

Apparently the only evidence lacking for complete proof that ethylene mediates the responses to picloram discussed here is whether the calculated internal ethylene levels are valid. Application to leafy seedlings of a factor developed to reflect on the diffusion of ethylene out of fruits is subject to criticism. In order to further clarify the role of ethylene, more critical methods for determining internal levels of the gas in vegetative tissue must be developed and applied to this and similar studies.

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