Plant Physiol. (1986) 82, 653–657
0032-0889/86/82/0653/05/$01.00/0

The Response of Foliar Gas Exchange to Exogenously Applied Ethylene[1]

Received for publication March 12, 1986 and in revised form June 30, 1986

GEORGE E. TAYLOR, JR.*, AND CARLA A. GUNDERSON
Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831

ABSTRACT

The responsiveness to ethylene of net photosynthesis and stomatal conductance to water vapor in intact plants was investigated in 13 herbaceous species representing seven plant families. Exposures were conducted in an open, whole-plant exposure system providing controlled levels of irradiance, air temperature, CO_2, relative humidity, and ethylene concentration. Net photosynthesis and stomatal conductance to water vapor in units of moles per square meter per second were measured on recently expanded leaves in control and ethylene-treated plants using a remotely operated single-leaf cuvette. The ethylene concentration was either 0 or 210 micromoles per cubic meter and was maintained for 4 hours. Species varied substantially in the response of their foliar gas exchange to ethylene. In 7 of the 13 species, net photosynthesis was inhibited statistically by 4 hours of ethylene exposure. As a function of the rate in control plants, the responses were most pronounced and statistically significant in *Arachis hypogaea* (−51.1%), *Gossypium hirsutum* (−31.7%), *Glycine max* (−24.8%), *Cucurbita pepo* (−20.4%), *Phaseolus vulgaris* (−18.4%), *Setaria viridis* (−17.5%), and *Raphanus sativus* (−4.4%). Whereas the responsiveness of net photosynthesis to ethylene among the 13 species showed no specific taxonomic associations, the responsiveness was positively correlated with the intrinsic rate of net photosynthesis. Stomatal conductance to water vapor after 4 hours of ethylene exposure declined statistically in 6 of the 13 species. As a function of control rates, the most marked and statistically significant responses of stomatal conductance were in *Glycine max* (−53.6%), *Gossypium hirsutum* (−51.2%), *Arachis hypogaea* (−42.7%), *Phaseolus vulgaris* (−38.6%), *Raphanus sativus* (−26.8%), and *Solanum tuberosum* (−23.4%). Although ethylene-induced changes in net photosynthesis and stomatal conductance were positively correlated, there were species-specific exceptions in which net photosynthesis declined after 4 hours of exposure without a concurrent change in stomatal conductance, stomatal conductance declined without a change in net photosynthesis, and the decline in stomatal conductance substantially exceeded the corresponding decline in net photosynthesis. Thus, the responsiveness to ethylene of net photosynthesis and stomatal conductance to water vapor were not consistently synchronous or equivalent among the 13 species. It is concluded that foliar gas exchange is responsive to exogenously applied ethylene in many plant species. The sensitivity of foliar gas exchange to ethylene may play a role in general plant response to environmental stress in which one of the physiological sites of action for endogenously produced stress ethylene in the leaf is the plant's photosynthetic capacity and/or stomatal conductance to water vapor.

Although a variety of plant physiological processes at the biochemical, cellular, and whole-plant level are responsive to trace levels of ethylene, the degree to which foliar gas exchange responds to exogenous levels of this phytohormone in a variety of plant species is not well documented. Transpiration is reportedly nonresponsive to exogenously applied ethylene in both herbaceous (2, 17) and woody (11) species. In contrast, other researchers (8, 12, 19) observed significant responses in T_r[2], P_n, and/or $g_{s\cdot H_2O}$ to ethylene in several herbaceous species. *Arachis hypogaea*, one of the most responsive species, exhibited incipient ethylene-mediated effects on P_n after a 1.5-h exposure to an ethylene concentration[3] in the gas phase of 10.5 μmol/m^3 (12). With longer exposure times (*e.g.* 5 h), the minimum gas phase concentration of ethylene influencing P_n may be as low as 1.0 μmol/m^3 for ethylene-responsive species (27). This estimated threshold value is comparable to that which elicits the well documented suite of ethylene-induced hormonal responses (*e.g.* characteristics of premature senescence and/or cell elongation) observed in plants inhabiting both terrestrial (1) and semiaquatic (16) habitats. If P_n and $g_{s\cdot H_2O}$ are responsive to ethylene in a variety of species, foliar gas exchange may be an additional physiological site of ethylene action in vascular plants.

The dissimilar conclusions regarding the responsiveness of P_n and $g_{s\cdot H_2O}$ to ethylene may be accountable to the experiment-specific selection of plant species, conditions for growth and exposure, and subthreshold ethylene concentrations or exposure times. The principal objective of this study was to investigate the responses of P_n and $g_{s\cdot H_2O}$ to exogenously applied ethylene in a variety of species representing different taxonomic affinities. In an attempt to resolve some of the reported inconsistencies in the responses of P_n and $g_{s\cdot H_2O}$ to ethylene, many of the selected species were common to those used in previous investigations. The second objective was to investigate the relationship between ethylene-induced changes in P_n and $g_{s\cdot H_2O}$ to determine if the changes in $g_{s\cdot H_2O}$ and P_n were correlated and proportional.

MATERIALS AND METHODS

Plant Materials and Growth Conditions. To characterize the importance of interspecific variation in governing the response of foliar gas exchange to ethylene, 13 taxonomically diverse herbaceous species were selected, representing seven families and seven orders of angiosperms and including both monocots and dicots (Table I). Most were domesticated, with the exception of *Atriplex patula* and *Setaria viridis*. Two of the species, *Zea mays* and *S. viridis*, exhibited C_4 metabolism, as verified through

[1] Research sponsored by the Office of Health and Environmental Research, United States Department of Energy, under Contract No. DE-AC05-840R21400 with Martin Marietta Energy Systems, Inc. Publication No. 2796, Environmental Sciences Division, Oak Ridge National Laboratory.

[2] Abbreviations: T_r, transpiration; P_n, net photosynthesis; $g_{s\cdot H_2O}$ and $g_{s\cdot CO_2}$, stomatal conductance to water vapor and carbon dioxide, respectively, NBS, National Bureau of Standards; A_{mes}/A, ratio of internal cell surface to external leaf area; CV, coefficient of variation.

[3] Concentration units for ethylene are μmol/m^3, where 40.9 μmol/m^3 = 1 μl/L at standard temperature and pressure.

measured mean CO_2 compensation points of 287 μmol/m^3 (7 μbar) and 410 μmol/m^3 (10 μbar), respectively. Species common to other studies of ethylene effects on foliar gas exchange were *Solanum tuberosum*, *Z. mays*, *Pisum sativum*, *Phaseolus vulgaris*, *Arachis hypogaea*, and *Glycine max*. Taxonomic nomenclature followed that of Fernald (7).

Plants were grown from seed or tubers in Promix BX (Premier Brands, Inc., New Rochelle, NY) in approximately 1000-cm^3 plastic pots, and were thinned to one per pot after germination. Plants were maintained in a glasshouse at maximum day/minimum night temperatures of 35/18°C, naturally varying photosynthetic photon flux density of 0 to approximately 2000 μmol m^{-2} s^{-1}, and daytime RH of 45 to 85%. The natural photoperiod was extended to 15 h with high intensity discharge sodium vapor lamps, which provided a maximum of 540 μmol m^{-2} s^{-1} of PAR at the top of the canopy. Plants were watered daily and fertilized weekly with a full-complement liquid fertilizer (Peters Fertilizer, W. R. Grace Co., Allentown PA). Studies were conducted 3 to 8 weeks after germination and were made on recently expanded leaves.

Exposure System. Ethylene exposures were conducted in an open gas-exchange system operating in a controlled environment (30). Air entering the system was charcoal-filtered, particle-filtered, and conditioned to a dewpoint of 13°C. The whole-plant exposure chamber (1.08 m^3 volume with a 4.5 min air exchange) was equipped with ceiling-mounted turbulator blades to provide continuous mixing of the air reservoir and maintain slight leaf flutter. Using the energy budget approach, Taylor *et al.* (29) estimated the boundary layer conductance to H_2O vapor in *G. max* and *P. vulgaris* to be >3800 mmol m^{-2} s^{-1}, indicating that this component did not significantly impede foliar gas exchange. Gloved ports provided access to the chamber during the exposure for remote operation of a single-leaf cuvette, gas-exchange system without inadvertent modification of the atmosphere. The range of environmental conditions unique to this study during the exposure period were as follows: air temperature of 26 to 30°C, leaf temperature of 26 to 32°C, PAR of 300 to 510 μmol m^{-2} s^{-1}, photoperiod of 15 h, and leaf-to-air vapor pressure deficit of 1.7 to 2.3 kPa.. The suite of environmental conditions was favorable for plant physiological processes, as evidenced by the rates of P_n and $g_{s\cdot H_2O}$ in the 13 species (Table I) that were comparable to the range reported by Korner *et al.* (14) as being reasonable for herbaceous species grown in a variety of environments.

Concentrated ethylene was dispensed from a cylinder (1% v/v, ethylene in nitrogen, Matheson Gas Products, Secaucus, NJ) and diluted with charcoal-filtered and particle-filtered air prior to entering the chamber. Chamber air was sampled at the outlet port through continuously exhausted Teflon sample lines. The ethylene concentration was monitored continuously using a flame-ionization detector (model 400 Hydrocarbon Analyzer, Beckman Instruments, Inc., Fullerton, CA) calibrated with an NBS reference material (Certified Standard; ethylene in hydrocarbon-free air, Scott Specialty Gases, Plumsteadville, PA).

Foliar Gas-Exchange Measurements. Gas-exchange measurements were made with a portable photosynthesis system (model LI-6000, LI-COR, Inc., Lincoln, NE) that measured the transient (<1 min) exchange rates of H_2O vapor and CO_2 in a closed system. A single leaf or group of leaves (recently expanded) was enclosed in a 4000-cm^3 Margard chamber for 30 to 60 s, during which the depletion of CO_2 and the increase in H_2O vapor over time were monitored in conjunction with leaf temperature, air temperature, and flow rate. Concentrations of CO_2 and H_2O vapor were measured by an IR nondispersive analyzer and Vaisala sensor, respectively, and the detectors were calibrated using NBS traceable materials. Leaf area (one surface) was determined prior to exposure (model LI-3000 Portable Area Meter, LI-COR Inc., Lincoln, NE). Estimates of P_n (μmol m^{-2} s^{-1}) and $g_{s\cdot H_2O}$ (mmol m^{-2} s^{-1}) were the mean of 10 interval measurements over the ≤60-s enclosure period.

Experimental Design and Data Analysis. All gas-exchange measurements for each individual plant were made over a 2-d period. On the day preceding an experiment, the pots of two to six plants of two to three different species were watered to drip point and placed in the exposure chamber to acclimate for 18 h, of which 9 h were in the dark. On each of the subsequent 2 d, gas-exchange measurements were made at 4-h intervals (time t_0 and t_4) with the t_0 measurement being 4 h after photoperiod initiation (immediately prior to ethylene addition on d 2). For each individual plant the measurements on d 1 served as the reference to evaluate the effects of ethylene exposure recorded on d 2. Replicate readings were made for each leaf at each time interval, and the mean was used in all subsequent data analysis. The selection of a 4-h measurement interval beginning 4 h after photoperiod initiation was based on an initial study to identify sources of variability and patterns in the response over time of P_n and $g_{s\cdot H_2O}$ in both control and ethylene-treated plants of *G. max* and *G. hirsutum* (Fig. 1). Notable features of this study that influenced the experimental design were (a) a consistent initial lag time of >1 h before ethylene-induced changes in P_n and $g_{s\cdot H_2O}$ were detectable, (b) a highly consistent response asymptote or saturation phenomenon observed only after 2 to 3 h of exposure, (c) a tendency for P_n and $g_{s\cdot H_2O}$ to increase gradually over the 4-h period in control plants (Fig. 1), and (d) an increase in the mean rates of P_n and $g_{s\cdot H_2O}$ at t_0 from d 1 to d 2 in 11 of the 13 species. Many of these trends in control plants were consistent with those reported for rapidly growing plants maintained in the same controlled exposure system (15, 27).

Given the species-specific, gradual increase in P_n and $g_{s\cdot H_2O}$ over the 4-h measurement period in the absence of ethylene, this quantitative effect on gas exchange was accounted for by estimating the t_4 rate of P_n and $g_{s\cdot H_2O}$ on d 2 based on the % increase for each parameter per plant recorded on d 1. The effect of ethylene on a species' rate of P_n and $g_{s\cdot H_2O}$ was evaluated statistically by comparing the estimated and observed values using a paired t-test (23, 26). The number of paired observations (value of n in the paired t test) ranged from 4 to 10 (Table I). All statistical evaluations were conducted at $P \leq 0.10$.

RESULTS AND DISCUSSION

The 13 species varied substantially in their intrinsic rates of P_n and $g_{s\cdot H_2O}$ in the absence of ethylene (Table I). Mean P_n rates ranged by a factor of 1.6 from 8.71 (*Z. mays*) to 14.05 (*R. sativus*) μmol m^{-2} s^{-1}, and the average CV among species was 39% (ranged from 63% in *A. hypogaea* to 21% in *T. aestivum*). At the interspecific level, $g_{s\cdot H_2O}$ was more variable than P_n, ranging by a factor of 7.3 from 77 mmol m^{-2} s^{-1} in *Z. mays* to 561 mmol m^{-2} s^{-1} in *R. sativus*. At the interspecific level the variability (CV) in $g_{s\cdot H_2O}$ was only slightly greater than that of P_n, averaging 49% among all species. The correlation between intrinsic P_n and $g_{s\cdot H_2O}$ was positive but not statistically significant.

Relative to the control rate, P_n in plants exposed to ethylene for 4 h declined in 11 of the 13 species, and the mean % decline across all species was −15.4% (Table I). The P_n response to ethylene was statistically significant in seven of the species. The most marked and statistically significant responses were in *A. hypogaea* (−51.1%), *G. max* (−24.8%), *G. hirsutum* (−31.7%), *C. pepo* (−20.4%), *P. vulgaris* (−18.4%), *S. viridis* (−17.5%), and *R. sativus* (−4.4%). Of the seven families of plants represented, five had species whose P_n rate was influenced by ethylene. The responsiveness of P_n also differed within a single family, as evidenced by the interspecific variability in the Leguminosae and Gramineae (Table I). In the two C_4 species P_n declined −17.5% in *S. viridis* but was statistically unaffected in *Z. mays* (+14.0%).

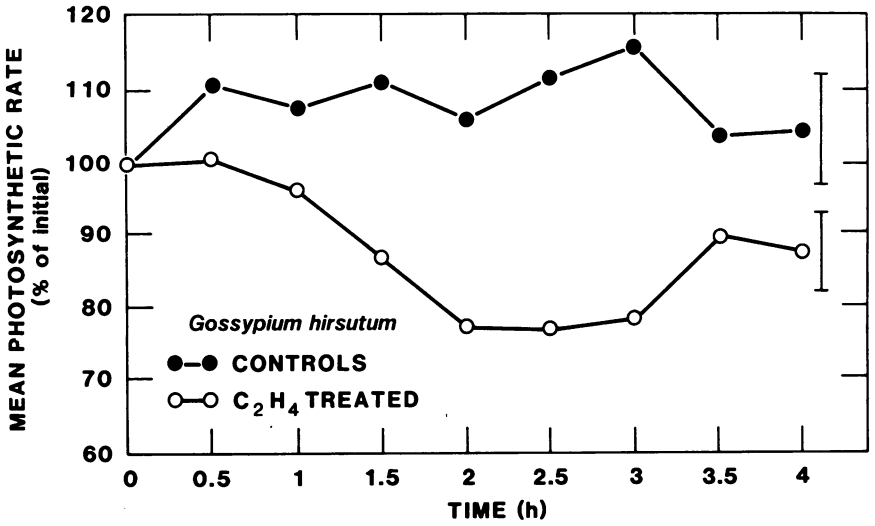

FIG. 1. The change over time of P_n in control and ethylene-exposed plants of *G. hirsutum*. Exposure to ethylene began immediately after the initial P_n rate (t_0) was determined. The error bar is the average SE in control and ethylene-treated plants.

Table I. *Foliar Gas-Exchange Parameters of the Herbaceous Species*

Family, species, cultivar, and P_n and $g_{s\cdot H_2O}$ in control and ethylene-treated plants of each species. The number of independent observations contributing to the mean of P_n and $g_{s\cdot H_2O}$ is the value of *n*.

Family	Genus and Species	P_n				$g_{s\cdot H_2O}$			
		n	Control	Ethylene[a]	Change	*n*	Control	Ethylene	Change
			($\mu mol\ m^{-2}\ s^{-1}$)		%	($mmol\ m^{-2}\ s^{-1}$)		%	
Chenopodiaceae	*Atriplex patula* L.	8	12.10	11.30	−6.6	6	195	162	−16.9
Cruciferae	*Raphanus sativus* L. cv Crimson Giant	6	14.05	13.39**	−4.4	4	561	411***	−26.8
Cucurbitaceae	*Cucurbita pepo* L. cv medullosa	7	12.38	9.86*	−20.4	7	199	148	−25.6
Gramineae	*Triticum aestivum* L. cv Oasis	8	8.67	8.88	+2.5	6	300	238	−20.0
	Setaria viridis L.	8	12.09	9.98**	−17.5	8	122	126	+3.5
	Zea mays L. cv Early Golden Giant	6	8.71	9.93	+14.0	4	77	80	+4.2
Leguminosae	*Arachis hypogaea* L. cv Jumbo Virginia	4	9.37	4.59*	−51.1	4	132	75*	−42.7
	Glycine max L. (Merr) cv Davis	10	11.91	8.95*	−24.8	8	168	78***	−53.6
	Phaseolus vulgaris L. cv Blue Lake 274	8	12.79	10.44**	−18.4	6	249	153***	−38.6
	Pisum sativum L. cv Alaska	7	12.47	11.43	−8.3	7	344	327	−4.9
Malvaceae	*Gossypium hirsutum* L. cv Delta Pine 61	8	13.22	9.03***	−31.7	6	206	103***	−51.2
Solanaceae	*Lycopersicon esculentum* L. cv Tiny Tim	10	12.07	8.69	−28.0	8	137	140	+2.1
	Solanum tuberosum L. cv Kennebec	8	8.75	8.26	−5.5	8	204	158*	−23.4

[a] Statistically significant differences reported at $P \leq 0.1$ (*), ≤ 0.05 (**), and ≤ 0.01 (***).

Although the responsiveness of P_n to ethylene was not clearly associated with taxonomic affiliation, the propensity to respond was correlated with a species' intrinsic rate of P_n. The scatter diagram relating ethylene sensitivity to intrinsic P_n rate showed a reciprocal relationship (Fig. 2) with a statistically significant correlation coefficient of −0.64 ($P < 0.05$). A similar relationship was observed by Pallas and Kays (19) at the intraspecific level in *A. hypogaea* cultivars differing in their sensitivity to ethylene. However, in comparison with the other 12 species' coordinates in Figure 2, the coordinate positions of *A. hypogaea* are unusual and well outside the calculated 95% confidence region for this correlation, according to the principal axis method (26). Consequently, the coordinates from *A. hypogaea* are regarded as being from another bivariate population. The mechanism underlying the correlation between a species' intrinsic P_n rate and its responsiveness to ethylene may be associated with leaf morphology (*e.g.* stomatal distribution, A_{mes}/A ratio), physiology (*e.g.* $g_{s\cdot H_2O}$), or biochemistry (*e.g.* number of ethylene binding sites per cell, membrane-associated features of CO_2 carboxylation and quantum efficiency).

The patterns in the response of $g_{s\cdot H_2O}$ to ethylene among the 13 species exhibited many of the same features as the response patterns of P_n. At the end of the 4-h exposure, $g_{s\cdot H_2O}$ was less than that of the control rate in 10 of the 13 species. Stomatal conductance declined statistically following ethylene exposure in 6 of the 13 species (Table I), and the % change in $g_{s\cdot H_2O}$ in each of the responsive species was ≥23%. The species in which $g_{s\cdot H_2O}$ were most affected were *G. max* (−53.6%), *G. hirsutum* (−51.2%), *A. hypogaea* (−42.7%), *P. vulgaris* (−38.6%), *R. sativus* (−26.8%), and *S. tuberosum* (−23.4%). Stomatal conductance was responsive to ethylene in four of the seven families, but the responsiveness was not common to all species within a single

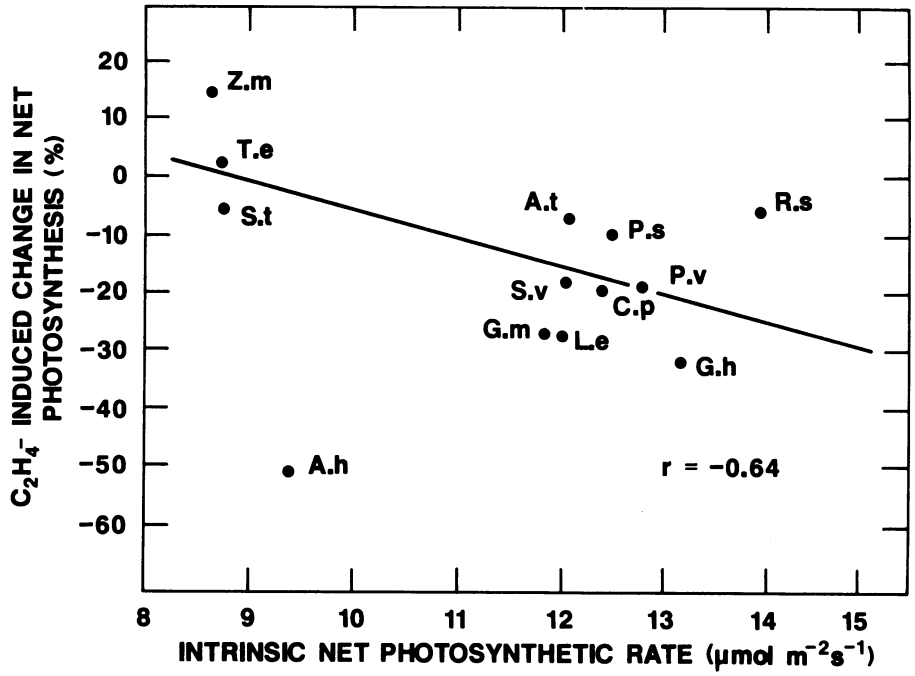

FIG. 2. The correlation between ethylene-induced changes in net photosynthesis (P_n) and intrinsic net photosynthetic rate. The regression line and the correlation coefficient (r = 0.64) are for the correlation analysis excluding the coordinates of *A. hypogaea* as explained in the text. Species abbreviations: *A. patula*, A. t; *R. sativus*, R. s; *C. pepo*, C. p; *T. aestivum*, T. a; *S. viridis*, S. v; *Z. mays*, Z. m; *A. hypogaea*, A. h; *G. max*, G. m; *P. vulgaris*, P. v; *P. sativum*, P. s; *G. hirsutum*, G. h; *L. esculentum*, L. e; and *S. tuberosum*, S. t.

family (*e.g.* Leguminosae). With the exception of *S. tuberosum*, a statistically significant effect of ethylene on $g_{s\cdot H_2O}$ was observed only in those species that also exhibited a significant P_n response.

Although these data are suggestive of a linkage between ethylene-induced changes in P_n and $g_{s\cdot H_2O}$ in responsive species, further analysis revealed some independence in the response of the two gas-exchange parameters. In four of the 13 species, the change in $g_{s\cdot H_2O}$ with ethylene exposure exceeded −38%, while the simultaneous % change in P_n was of equal or greater magnitude in only one species (*A. hypogaea*). For most of the seven species that exhibited an ethylene-induced decline in both P_n and $g_{s\cdot H_2O}$ (*i.e.* those in quadrant III, Fig. 3), the % decline in $g_{s\cdot H_2O}$ exceeded the % decline in P_n, as demonstrated by the displacement of species' coordinates above the 1:1 line in Figure 3. Among the same seven species, the average % decline in P_n and $g_{s\cdot H_2O}$ was 26 and 43%, respectively. In several species (*G. max*, *P. vulgaris*, and *R. sativus*), the % decline in $g_{s\cdot H_2O}$ exceeded by more than a factor of 1.6 the corresponding % inhibition of P_n. In one species (*S. viridis*) in quadrant IV of Figure 3, the statistically significant ethylene-induced decline in P_n of −17.5% occurred without any concurrent change in $g_{s\cdot H_2O}$. Conversely, $g_{s\cdot H_2O}$ declined 23.4% in the presence of ethylene in *S. tuberosum*, while P_n was unaffected (Table I). Thus, while the decline in P_n was positively correlated (r = +0.62) with a change in $g_{s\cdot H_2O}$ in the responsive species, the magnitude of response tended to be proportionally greater for $g_{s\cdot H_2O}$.

The unusual position of the *A. hypogaea* coordinates in Figure 2 is not clearly explicable. Among the 13 species evaluated, foliar gas exchange in *A. hypogaea* was consistently the most variable in the presence of ethylene, exhibiting the highest CV for both P_n (74%) and $g_{s\cdot H_2O}$ (90%). Whereas the CV for foliar gas exchange in *A. hypogaea* was greater in the presence of ethylene,

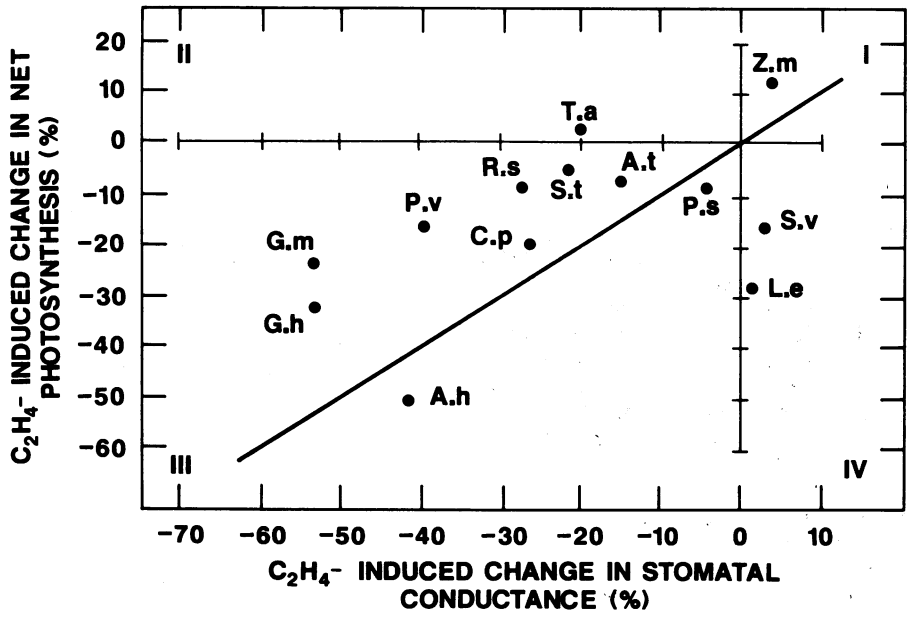

FIG. 3. The relationship between ethylene-induced changes in net photosynthesis (P_n) and ethylene-induced changes in stomatal conductance ($g_{s\cdot H_2O}$) in all species. The diagonal line through the origin represents equivalent changes (1:1) in P_n and $g_{s\cdot H_2O}$. Species abbreviations: *A. patula*, A. t; *R. sativus*, R. s; *C. pepo*, C. p; *T. aestivum*, T. a; *S. viridis*, S. v; *Z. mays*, Z. m; *A. hypogaea*, A. h; *G. max*, G. m; *P. vulgaris*, P. v; *P. sativum*, P. s; *G. hirsutum*, G. h; *L. esculentum*, L. e; and *S. tuberosum*, S. t.

this same statistic (CV) tended to be less in the other six responsive species following ethylene exposure. In spite of this unusually high degree of variability in *A. hypogaea* in the presence of ethylene, our data corroborate the major conclusions offered by Pallas and Kays (19) regarding the responsiveness in this species of both P_n and $g_{s \cdot H_2O}$ to ethylene and the equivalency in response of $g_{s \cdot H_2O}$ and P_n. As reported by Pallas and Kays (19), some features of foliar gas exchange in *A. hypogaea* are unusual relative to other species, including the high adaxial to abaxial surface ratio of $g_{s \cdot H_2O}$ (18) and the preferential sensitivity of stomata on the abaxial surface to closure during ethylene exposures (19). The uniqueness of the species' response to ethylene may be associated with its unusual features of foliar gas exchange.

Although the data associating ethylene-induced changes in P_n and $g_{s \cdot H_2O}$ are suggestive of stomata as the physiological site of ethylene action on P_n in at least some species (*e.g. G. hirsutum, G. max, R. sativus, P. vulgaris*), this hypothesis must be regarded as untested because the dynamics of response in $g_{s \cdot H_2O}$ and P_n over the 4-h exposure period were not intentionally characterized in this study. Specifically, the temporal changes in $g_{s \cdot H_2O}$ and P_n at time periods <4 h require investigation to identify sites of ethylene response. It is possible that the initial site of ethylene action is in the mesophyll cells affecting CO_2 carboxylation or quantum efficiency, which would increase the partial pressure of CO_2 in the intercellular space of the leaf interior, a well-documented forward feedback on $g_{s \cdot H_2O}$ (5). Moreover, the quantitative significance that changes in $g_{s \cdot H_2O}$ play in regulating P_n can only be addressed through careful manipulative experiments that characterize concurrently the leaf's P_n capacity, partial pressure of CO_2 in the intercellular space of the leaf interior, and $g_{s \cdot CO_2}$ (6, 33). This type of analysis is being pursued in *G. max*, one of the most ethylene-responsive species (28).

In response to a variety of biotic (*e.g.* pathogens) and abiotic (*e.g.* air pollution, drought, chilling temperature) stresses of both natural and anthropogenic origin, plants produce ethylene in excess of normal basal concentrations (1). Induction times are commonly <30 min (34) and may be as short as 12 min (9). Although the rate of ethylene production under stress varies as a function of plant species, environmental conditions, and intensity of the stress (1), increases of 10 to 100 times the basal rate are common for chemical stresses whose site of toxicity is the leaf (*e.g.* 13, 20, 32). With the exception of a few specific situations, the physiological significance of ethylene production under stress is not resolved (4), and none of the physiological mechanisms of action address the possibility that the immediate physiological site of action for ethylene produced in the leaf is the plant's capacity to assimilate CO_2 or govern T_r. All proposals assume that any role played by ethylene is mediated in a chronic fashion through the phytohormone's prolonged effect on growth processes in general and either premature senescence in aerobic environments (21, 22, 31) or renewed growth and development in anaerobic habitats (10, 16). Sojka and Stolzy (25) speculated that the stomatal closure observed in a variety of herbaceous species growing in poorly aerated soil could be a consequence of ethylene production under stress in the leaf and the phytohormone's subsequent effects on guard cell physiology. The proposal that ethylene may play a chemical role in mediating the effects on P_n or $g_{s \cdot H_2O}$ of multiple stress agents of natural and anthropogenic origin must be regarded as untested until the criteria for hormonal involvement are documented (3), with specific characterization of the relationship between ethylene concentration in the gas phase and that in the liquid phase at the physiological sites of action (24). This proposal has many features in common with that offered by Burschka *et al.* (4) for the role played by ABA in mediating the characteristic midday depression of foliar gas exchange in *Arbutus unedo* in a dry, hot habitat.

In summary, the results indicate that foliar gas exchange is affected by exogenously applied ethylene in a variety of vascular plant species. There is variability between species in their response to ethylene. The response parameters include P_n and $g_{s \cdot H_2O}$, and the magnitude of change in $g_{s \cdot H_2O}$ generally exceeds that of P_n. Whereas a species' responsiveness is independent of taxonomic affiliation and occurs in plants exhibiting either C_3 or C_4 metabolism, the propensity to respond is positively correlated with intrinsic rate of P_n. Some of the species-specific responses indicate that the ethylene-induced changes in $g_{s \cdot H_2O}$ and P_n are not necessarily coupled.

LITERATURE CITED

1. ABELES FB 1973 Ethylene in Plant Biology. Academic Press, New York
2. AHARONI N 1978 Relationship between leaf water status and endogenous ethylene in detached leaves. Plant Physiol 61: 658–662
3. BEYER EM JR, PW MORGAN, SF YANG 1984 Ethylene. *In* WB Wilkins, ed, Advanced Plant Physiology. Pitman, London, pp 111–126
4. BURSCHKA C, OL LANGE, W HARTUNG 1985 Effects of abscisic acid on stomatal conductance and photosynthesis in leaves of intact *Arbutus unedo* plants under natural conditions. Oecologia 67: 593–595
5. FARQUHAR GD 1978 Feedforward responses of stomata to humidity. Aust J Plant Physiol 5: 787–800
6. FARQUHAR GD, TD SHARKEY 1982 Stomatal conductance and photosynthesis. Annu Rev Plant Physiol 33: 317–345
7. FERNALD ML 1970 Gray's Manual of Botany, Ed 8. D. Van Nostrand Co, New York
8. GOVINDARAJAN AG, BW POOVAIAH 1982 Effect of root zone carbon dioxide enrichment on ethylene inhibition of carbon assimilation in potato plants. Physiol Plant 55: 465–469
9. HOGSETT WE, RM RABA, DT TINGEY 1981 Biosynthesis of stress ethylene in soybean seedlings: similarities to endogenous ethylene biosynthesis. Physiol Plant 53: 307–314
10. JACKSON MB 1985 Ethylene and responses of plants to soil waterlogging and submergence. Annu Rev Plant Physiol 36: 145–174
11. JOHNSON JD 1984 The effects of ethylene on stomatal conductance and transpiration at various levels of water stress. Plant Physiol 75: S-129
12. KAYS SJ, JE PALLAS JR 1980 Inhibition of photosynthesis by ethylene. Nature 285: 56–57
13. KIMMERER TW, TT KOZLOWSKI 1982 Ethylene, ethane, acetaldehyde, and ethanol production by plants under stress. Plant Physiol 69: 840–847
14. KORNER C, JA SCHEEL, H BAUER 1979 Maximum leaf diffusive conductance in vascular plants. Photosynthetica 13: 45–82
15. NORBY RJ, DD RICHTER, RJ LUXMOORE 1985 Physiological processes in soybean inhibited by gaseous pollutants but not acid rain. New Phytol 100: 79–85
16. OSBORNE DJ 1984 Ethylene and plants of aquatic and semi-aquatic environments: a review. Plant Growth Regul 2: 167–185
17. PALLAGHY CK, K RASCHKE 1972 No stomatal response to ethylene. Plant Physiol 49: 275–276
18. PALLAS JE JR 1980 An apparent anomaly in peanut leaf conductance. Plant Physiol 65: 848–851
19. PALLAS JE JR, SJ KAYS 1982 Inhibition of photosynthesis by ethylene—a stomatal effect. Plant Physiol 70: 598–601
20. PEISER GD, SF YANG 1979 Ethylene and ethane production from sulfur dioxide-injured plants. Plant Physiol 63: 142–145
21. REID DM, KJ BRADFORD 1984 Effects of flooding on hormone relations. *In* TT Kozlowski, ed, Flooding and Plant Growth. Academic Press, New York, pp 195–219
22. RICH S 1969 Ozone damage to plants. Annu Rev Plant Physiol 2: 253–266
23. SAS Institute 1982 SAS User's Guide: Statistics. SAS Institute Inc, Cary, NC
24. SMITH AR, MA HALL 1984 Mechanism of ethylene action. Plant Growth Regul 2: 151–165
25. SOJKA RE, LH STOLZY 1980 Soil-oxygen effects on stomatal responses. Soil Sci 130: 350–358
26. SOKAL RR, FJ ROHLF 1969 Biometry. WH Freeman, San Francisco
27. SQUIER SA, GE TAYLOR JR, WJ SELVIDGE, CA GUNDERSON 1985 Effect of ethylene and related hydrocarbons on carbon assimilation and transpiration in herbaceous and woody species. Environ Sci Technol 19: 432–437
28. TAYLOR GE JR, CA GUNDERSON 1986 Ethylene effects on photosynthesis in *Glycine max*: a nonstomatal site of action. Plant Physiol 80: S-50
29. TAYLOR GE JR, SB MCLAUGHLIN, DS SHRINER, WJ SELVIDGE 1983 The flux of sulfur containing gases to vegetation. Atmos Environ 17: 789–796
30. TAYLOR GE JR, DT TINGEY, CA GUNDERSON 1986 Photosynthesis, carbon allocation, and growth of sulfur dioxide ecotypes of *Geranium carolinianum* L. Oecologia 68: 350–357
31. TINGEY DT 1980 Stress ethylene production—a measure of plant response to stress. HortScience 15: 630–633
32. TINGEY DT, C STANDLEY, RW FIELD 1976 Stress ethylene evolution: a measure of ozone effects on plants. Atmos Environ 10: 969–974
33. VON CAEMMERER S, GD FARQUHAR 1981 On the relationship between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153: 376–387
34. YANG SF, NE HOFFMAN 1984 Ethylene biosynthesis and its regulation in higher plants. Annu Rev Plant Physiol 35: 155–189