

Relationship between Leaf Water Status and Endogenous Ethylene in Detached Leaves¹

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ABSTRACT

The pattern of changes in the internal concentration of ethylene in response to water stress was investigated in species with leaves that do abscise and leaves that do not abscise. When leaves which abscise were detached and exposed to dry air for up to 6 hours, a continuous increase of internal ethylene was observed. In water-stressed leaves which do not abscise only a transient rise in ethylene occurred. The peak, which was attained after 30 to 120 minutes, depending on the species studied, was followed by a sharp decline to the initial level. The principal site of ethylene production in response to a short period of water stress was in the blades rather than the petioles in both types of leaves. The internal ethylene level in leaves was reduced by pretreatment with the ethoxy analog of rhizobitoxine (an inhibitor of ethylene biosynthesis) or by maintaining the leaves under subatmospheric pressure. The results obtained by these methods showed that ethylene was not involved in the mechanism of stomatal movement in either turgid or in stressed leaves. Also, the increase in leaf abscisic acid content and the depletion of gibberellins induced by water stress were not related to the internal concentration of ethylene in the detached leaf. The different patterns of drought-induced ethylene production observed in the blades of leaves which exhibit abscission compared with those which do not exhibit abscission may indicate the involvement of ethylene in a primary event in the process of leaf abscission induced by water stress.

The levels of phytohormones change when attached or detached leaves are exposed to drought and attempts have been made to correlate these changes with physiological processes induced in the stressed leaf. Leaf ABA content is known to increase in response to water stress (3, 4, 23, 28, 29). Since exogenous ABA causes stomatal closure, it has been concluded that the increase in ABA induced by water stress is part of a physiological mechanism causing reduced transpiration in the stressed leaves (15, 23). Gibberellin and cytokinin activity decline during leaf desiccation (3, 16). The marked retardation of stomatal closure observed in water-stressed leaves following treatment with either GA₃ or kinetin indicates that these hormones are also involved in regulating plant water balance (3, 20, 23).

Increased production of ethylene was found in leaves exposed to water stress. Studies of abscising leaves revealed that the drought-induced increase in ethylene may play a regulatory role in leaf abscission (5, 12, 18, 22). Some reports indicate that ethylene may reduce the amount of auxin transported out of the leaf blade (7, 9, 24). Ethylene was also reported to intensify auxin destruction (24). Although exogenous ethylene is reported as

enhancing the increase in ABA content and the decrease in GA activity (2, 13, 27), there is as yet no evidence that these alterations are directly due to ethylene.

The experiments reported here were undertaken to determine in several species the pattern of drought-induced ethylene in detached leaves bearing or not bearing a functional abscission zone. Further experiments were carried out to determine whether ethylene has any effect on the changes in leaf water status, stomatal aperture, and ABA and GA contents in detached leaves subjected to drought.

MATERIALS AND METHODS

Plant Material. The experiments were performed with detached leaves which were harvested during the period November to December, from plants or trees grown under field conditions, unless otherwise specified. Fully expanded leaves were grouped according to whether or not they abscise in nature. The leaves from species which exhibit abscission were harvested from: 12-week-old bean plants (*Phaseolus vulgaris* L.), 10-week-old pepper plants (*Capsicum annum* L.), 5-week-old kohlrabi plants (*Brassica oleracea* L. var. *Gongylodes*), old bushes of castor bean (*Ricinus communis* L.), and old trees of Shamouti orange (*Citrus sinensis* L. Osbeck). Leaves from species which do not exhibit abscission were harvested from 8- or 16-week-old romaine lettuce plants (*Lactuca sativa* L.), 5-week-old sugar beet plants (*Beta vulgaris* L. var. *Saccarifera*), 8-week-old tobacco plants (*Nicotiana tabacum* L.) grown in a greenhouse under controlled conditions, 9-week-old squash plants (*Cucurbita pepo*), and 6-week-old cabbage plants (*Brassica oleracea* var. *Capitata*).

Preconditioning and Chemical Treatment. Immediately after being detached, the leaves were transferred to high relative humidity for a period of 20 hr. The leaf petioles were immersed in water aerated by gently bubbling air. In one experiment (see Fig. 6), lettuce or orange leaves were pretreated with the ethoxy analog of rhizobitoxine, L-2-amino-4(2'-aminoethoxy)-*trans*-3-butenoic acid (kindly supplied by Hoffman-La Roche). The leaves were immersed in an aqueous solution of 0.1 mM rhizobitoxine analog for 10 min and subsequently were petiole-fed with this solution throughout the preconditioning.

Water Stress. Water stress was imposed by desiccating the detached leaves in several ways. (a) A mild stress was achieved by desiccating lettuce leaves in darkness while they were enclosed in 7-liter Perspex containers through which a current of 100 ml/min dry air (or humidified air in the controls) was passed. Various relative humidity levels in the containers were obtained by enclosing a different number of leaves (three to eight) and by drying the air with various amounts of CaCl₂ placed on the bottom of each container (Fig. 1, right). Respective air temperature and relative humidity are shown under "Results." (b) Severe water stress was imposed by placing the leaves horizontally on a table and exposing them for up to 6 hr to forced air (produced by an electric fan) under light supplied by cool white fluorescent lamps

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at an intensity of 2,500 lux (Fig. 1, left; and Figs. 2–6). Humidity levels were varied by using humidifiers, as well as by placing the leaves on moist filter papers (Fig. 1, left). (c) To reduce endogenous ethylene during desiccation, leaves were maintained in 10-liter desiccators under a subatmospheric pressure of 150 mm Hg through which pure O₂, predried with silica gel, flowed at a rate of approximately 1,000 ml/min (Fig. 5). The comparable non-stressed leaves were kept under the same experimental conditions but at a high relative humidity.

Determination of Leaf Water Status. The water status of the leaf blades was estimated by determining the water saturation deficit (WSD),³ according to the following equation:

$$\text{WSD} = \frac{\text{Water saturated wt} - \text{fresh or stressed wt}}{\text{Water saturated wt} - \text{dry wt}} \times 100$$

WSD was determined as described previously (3) in 5 to 10 replicates, each consisting of two leaf discs excised from two half-blades.

Stomatal Aperture. Stomatal diffusion resistance was determined on the adaxial side of the leaf blade by use of a diffusion porometer as described previously (3).

Ethylene Determination. Ethylene production rates in detached lettuce leaves were determined in four replicates by sampling 4 ml of air from the outlet of the containers through which dry air was streamed, as described for water stress (Fig. 1, right). The rates of ethylene production in lettuce leaves desiccated in room air (Fig. 1, left) were determined by enclosing them in 7-liter Perspex containers with an appropriate amount of CaCl₂ for maintaining the same relative humidity as in room air. Ethylene was allowed to accumulate for a 30-min period. Three separate groups, each comprising three leaves, were used for each reading.

Intercellular ethylene (Figs. 2–4, 6) was extracted by the vacuum method as described by Beyer and Morgan (8) except that a 50-mm Hg vacuum, for 3 min, was employed. Four to 6 ml of air were collected in three replicates, each consisting of a specific number of leaves, as follows: lettuce, 3; sugar beet, 3; tobacco, 3; squash, 3; cabbage, 6; bean, 25; pepper, 20; kohlrabi, 5; castor bean, 4; orange, 25. Ethylene concentration in the samples was determined with a Packard gas chromatograph equipped with an activated alumina column (1,800 × 6 mm) and a flame ionization detector. Calculations of ethylene production are expressed as $\mu\text{l/kg fresh wt} \cdot \text{hr}$, the fresh wt being determined before the initiation of desiccation.

GA and ABA Determination. After removal of the petioles and midribs, 8 to 10 leaf blades from each treatment were frozen in liquid N₂ and thereafter freeze-dried, ground, and stored desiccated in darkness at -18 C until analysis. The endogenous hormones were extracted and separated as described previously, using the barley endosperm bioassay and GLC for determination of GAs and ABA, respectively (3).

RESULTS AND DISCUSSION

Effect of Water Stress on Ethylene Production by Leaves Which Do Not Abscise. Exposing detached lettuce leaves to air at various levels of relative humidity, ranging between 50 and 75%, caused an immediate and large increase in the rate of ethylene emanation. The peak was reached after 60 min, irrespective of the severity of the stress, and was followed by a sharp decline (Fig. 1, upper curves). The extent of the increased ethylene emanation and its ultimate decline correlated positively with the degree of water loss as measured by leaf WSD (Fig. 1, lower curves). Such a pattern of modification in ethylene production induced by water stress differs from the patterns recently reported for other leaves. Peak ethylene production in water-stressed intact leaves of broad bean was reached after 24 hr and then was followed by a gradual

decline (12). A continuous increase of ethylene production was found in detached orange leaves during 50 hr of desiccation (5). The principal difference between lettuce and the other leaves studied was the absence of an abscission zone in the petiole. If the varying patterns of change in ethylene production are indeed due to this feature, similar patterns would be expected in other non-abscising, stressed leaves. Experiments performed with detached leaves of sugar beet, squash, cabbage, and tobacco support this assumption (Fig. 2). A similar pattern of drought-induced ethylene production was also found in excised wheat leaves (28).

Ethylene emanation in water-stressed lettuce leaves began to decline after the onset of stomatal closure (3). The same pattern of ethylene emanation was observed in nonabscising lettuce leaves here held in either light or darkness (Fig. 1) and was similar to the pattern of the internal ethylene (Figs. 2, 4B, and 6A). This indicates that the sharp decline of ethylene emanation in the stressed leaves is not due to reduced diffusion but is rather the result of a peculiar pattern of ethylene production in nonabscising

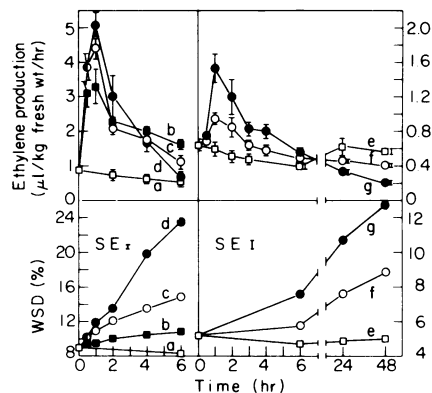


FIG. 1. Effect of severity and duration of desiccation on WSD and ethylene production in detached lettuce leaves. Left: leaves were exposed to room air at 25 C under illumination and relative humidity as follows: (a) 100%; (b) 70 to 75%; (c) 60 to 65%; (d) 50 to 55%. Right: leaves were kept in darkness at 25 C while they were enclosed in Perspex containers connected to an air flow system. Relative humidity was as follows: (e) 100%; (f) 70 to 75%; (g) 60 to 65%. Vertical lines represent the SE of three or four replicates of each treatment.

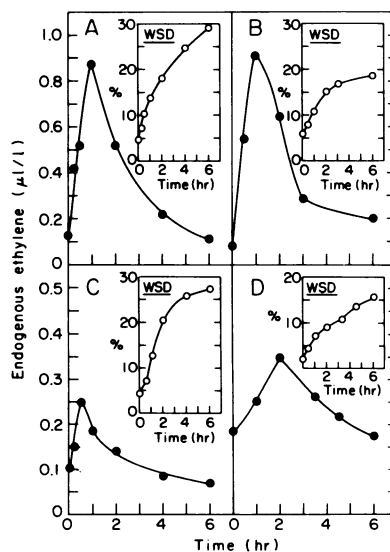


FIG. 2. Effect of duration of desiccation on WSD and endogenous ethylene concentration in leaves which do not abscise. Detached leaves were exposed to drought under light. Leaves of sugar beet (A) and cabbage (B) were held at 27 C and 45% relative humidity. Leaves of squash (C) and tobacco (D) were held at 22 C and 55% relative humidity.

³ Abbreviation: WSD: water saturation deficit.

water-stressed leaves. To verify that the inhibition of ethylene production in such leaves was not merely an experimental phenomenon, other leaves bearing a functional abscission zone were also examined under the same conditions. When detached leaves of kohlrabi, pepper, castor bean, and orange were exposed to dry air, a continuous rise in internal ethylene was observed during the 5 or 6 hr of the experiments (Figs. 3, 4A, and 6B).

Ethylene Production in Petioles and Blades. It has been questioned whether the differences in the ability of water-stressed leaves to produce a continuous rise in ethylene occur primarily in the leaf petiole (21, 22). The results shown in Figure 4 indicate clearly that the principal site of ethylene production in these species in response to a short period of water stress was in the blades rather than the petioles. This holds true both for leaves with an abscission zone (castor bean) and those without (lettuce). A similar observation was reported recently for intact cotyledons of water-stressed cotton seedlings (10). The continuous increase of internal ethylene in the stressed leaf blades may indicate the involvement of ethylene in a primary event in the process of leaf abscission. It has been reported that the leaf blade is the primary site of exogenous ethylene action in leaf abscission (7), apparently owing to the reduction of auxin transport from the leaf blade (7,

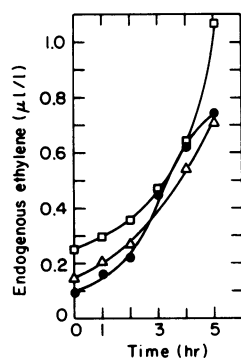


FIG. 3. Effect of duration of desiccation on endogenous ethylene concentration in leaves bearing a functional abscission zone. Detached leaves of kohlrabi (□), bean (Δ), and pepper (●) were exposed under light to 25 C and 50% relative humidity.

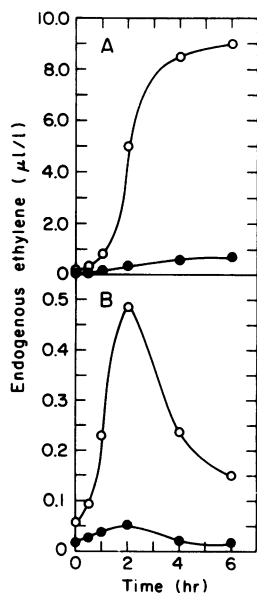


FIG. 4. Effect of duration of desiccation on endogenous ethylene concentration in blades (○) and petioles (●) of detached leaves. Castor bean (A) and lettuce (B) leaves were exposed under light to 25 C and 50% relative humidity. Endogenous ethylene was vacuum extracted from the petioles and blades within 5 min after cutting.

9). It is possible that the increased ethylene in the water-stressed leaf blade could reduce the auxin transport in the petioles as well as in the vascular tissue in the leaf blade itself. This assumption could be supported by the recent findings of Davenport *et al.* (11) showing that water stress reduced the basipetal transport of auxin in cotyledonary petioles of cotton seedlings.

The results of this work do not refute the evidence showing the role of ethylene, produced by the petioles, in leaf abscission. Jackson and Osborne (17) found a progressive increase in ethylene production by tissue surrounding the abscission zone prior to abscission. McMichael (22) first found a sharp rise of ethylene in leaf petiole which occurred as severe water deficit developed. The involvement of ethylene, produced by the petioles, as a regulator of leaf abscission in both water stress condition (5, 12, 18) and in natural senescence (9, 17), has been well documented. Beyer (7) has demonstrated that the initial effect of exogenous ethylene in abscission is in the leaf blade, but to induce rapid abscission, an ethylene treatment of the abscission zone was also needed. This indicates that leaf abscission following either natural senescence or water stress is connected with increased ethylene production in both the blade and the petiole.

Effect of Ethylene on Endogenous Level of ABA and GAs in Lettuce Leaves. The rise in ethylene which induces leaf abscission under drought conditions may well be considered part of the adaptation process leading to the reduction of foliage, thereby reducing the transpiration of the whole plant. It is still unclear whether the transient burst of ethylene which was found in nonabscising leaves is involved in the physiological mechanism of leaf adaptation to drought. Such a mechanism is demonstrated by the increased ABA content of water-stressed leaves which causes stomatal closure (23, 29). The rapid depletion of GAs (3) as well as cytokinins (3, 16) is also regarded as a mechanism designed to curtail water loss. The first change in the level of endogenous hormone in response to water stress (observed in detached lettuce leaves) was the transient rise in ethylene (Fig. 1) which was followed by reduced GA activity and increased ABA content (3). To study the possibility of increased ethylene in stressed lettuce leaves playing a causal role in the modifications occurring in GA and ABA levels, the internal ethylene was reduced by 80% by keeping the stressed leaves at subatmospheric pressure (150 mm Hg of pure dry O₂). This reduction did not affect the water stress-induced rise in ABA (Table I). Following 6 hr of desiccation, ABA content in leaves kept at either atmospheric or subatmospheric pressure increased about 10-fold. Since the GA level in the mature leaves used in these experiments was very low, the effect of ethylene removal during desiccation on GA activity was reexamined in young, expanding lettuce leaves which were found to have a relatively high GA content (2). In response to 3 hr of desiccation the GA activity disappeared almost completely in leaves desiccated in air or at subatmospheric pressure (Fig. 5). The lack of ethylene effect on either GA decrease or ABA increase during a short period of water stress was also found by gassing the desiccating lettuce leaves with ethylene at either 10 μg/l or 50 μl/l while the leaves were held at atmospheric or subatmospheric pressure, respectively (data not given). Wright (28), in comparing decreasing water potential in water-stressed wheat leaves with increasing levels of ethylene and ABA, concluded that there was no relationship between the levels of these hormones and it seems unlikely that the stress-induced ethylene evolution stimulated the accumulation of ABA in wheat leaves. Wright's conclusions are in agreement with the results of this work, in which the direct relationship between ethylene and ABA was examined.

Effect of Ethylene on Stomatal Aperture. In lettuce (Aharoni, unpublished data) and sorghum (4) stomatal closure induced by water stress preceded the rise in leaf ABA. Since the increased production of ethylene in water-stressed leaf blades occurred prior to and during stomatal closure, a possible influence of ethylene on the stomatal aperture, as measured by a diffusion porometer, was examined. Gassing the leaves with 10 μl/l ethylene during

Table I. Content of ABA and Leaf WSD in Detached Lettuce Leaves Subjected to Drought under Atmospheric or Subatmospheric Pressure

Leaves were kept in room air or in 10-liter desiccators with 150 mm Hg under light and at 25°C. Relative humidity was 50 to 60% in the desiccation treatments and 90 to 100% in the comparable controls. The ABA eluted from the 0.55–0.85 R_f zone (chromatography system of isopropanol:28% ammonia:water at 10:1:1 v/v), was methylated with diazomethane and determined by GLC.

Treatment	Experiment	Leaf WSD	ABA Content	ABA Increase
		%	ng/g dry wt	%
6-hr humidity	1	4.4	16.2	
	2	9.4	33.0	
6-hr humidity at subatmospheric pressure	1	3.8	14.2	
	2	9.0	21.5	
6-hr desiccation	1	24.3	153.9	850
	2	27.4	348.0	954
6-hr desiccation at subatmospheric pressure	1	28.5	163.3	1050
	2	22.0	249.0	1058

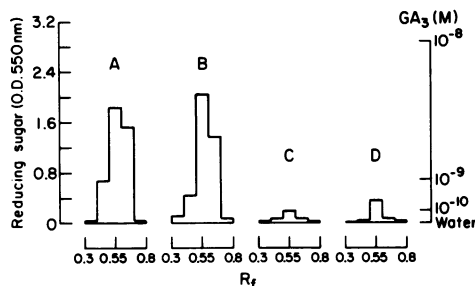


FIG. 5. Activity of GA-like substances in detached lettuce leaves subjected to drought under atmospheric or subatmospheric pressure. Level of GA activity was determined by the barley endosperm bioassay and is expressed as amount of reducing sugar determined spectrophotometrically. Dose response to GA_3 is shown on the right-hand ordinate. Extracts which were irradiated with UV light (for destruction of endogenous ABA) were loaded on strips of chromatography paper (200 mg dry wt/strip; four strips/treatment) and were separated by ascending chromatography in which isopropyl alcohol-28% ammonia-water (10:1:1, v/v) was used as developer. A: 3-hr humidity; B: 3-hr humidity under subatmospheric pressure; C: 3-hr desiccation; D: 3-hr desiccation under subatmospheric pressure. Expanding young leaves were exposed in room atmosphere or in 10-liter desiccators under light and at 25°C. Relative humidity was 90 to 100% in A and B, and 50 to 60% in C and D.

desiccation, or pretreatment with 100 μ l/l Ethephon, releasing ethylene in the plant tissue, had no effect on stomatal aperture in either turgid or desiccating leaves (data not given). These findings confirm previous reports of Pallaghy and Raschke (26) and of El-Beltagy and Hall (12).

Inhibition of Ethylene Biosynthesis and Its Effect on Leaf Water Status. To determine whether ethylene has an effect on leaf WSD in detached water-stressed leaves, an inhibitor of ethylene biosynthesis was used to reduce endogenous ethylene prior to and during water stress. Pretreatment with the ethoxy analog of rhizobitoxine at 0.1 mM, which is capable of antagonizing the utilization of methionine in the pathway of ethylene biosynthesis (14, 19, 25) reduced the concentration of ethylene in both turgid and desiccating leaves of lettuce and orange (Fig. 6). The maximum rate of inhibition of the water stress-induced ethylene was about 75%, corresponding with the inhibition of rhizobitoxine reported for other plant tissues (19). The ability of the rhizobitoxine analog to inhibit ethylene production in the stressed leaves indicates that

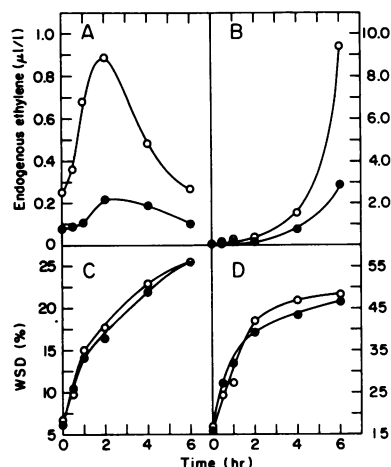


FIG. 6. Effect of rhizobitoxine analog on endogenous ethylene concentration (A and B) and on WSD (C and D) in detached leaves of lettuce (left) and orange (right) subjected to drought. Leaves were immersed for 10 min and subsequently were petiole-fed during the preconditioning with 0.1 mM rhizobitoxine analog (●) or H_2O (○). The leaves were desiccated under light, at 25°C and 50% relative humidity.

the methionine serves as the principal precursor of ethylene biosynthesis induced by water stress, as previously suggested for other stresses (1, 13). Although ethylene concentration was reduced in the rhizobitoxine analogue-treated leaves, no differences in WSD values were recorded during water stress (Fig. 6).

In conclusion, the different patterns of water stress-induced ethylene, found in the blades of leaves which do or do not abscise, strengthen the hypothesis that the increasing production of ethylene is directly connected with the ultimate abscission of stressed leaves bearing an abscission zone (5, 12, 18, 22). It was found that ethylene had no effect on the mechanism of stomatal closure and did not serve to trigger either the increase of ABA or the decrease of GAs occurring in the leaf blade in response to water stress. The results of this work, which was carried out with detached leaves, cannot ascribe any physiological role to the transient rise in ethylene observed in water-stressed leaves from species not exhibiting abscission. The possibility cannot be excluded that in intact leaves of certain plants which are exposed to drought, the transient burst of ethylene can probably change the orientation of the leaf blade toward incidental radiation and thereby reduce light interception which could affect the stomatal aperture. The sharp decline of the stress ethylene in nonabscising leaves could be a result of a deficiency in precursor or inducer. Another possibility is the existence of an inhibitory mechanism of ethylene synthesis which prevents the accumulation of this hormone in the leaf blade. Such a mechanism could be regarded as physiologically advantageous in plants with nonabscising leaves, which are subjected to drought, since the continuous increase of ethylene production can induce leaf senescence (2).

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