PHYSIOLOGICAL RESPONSES OF PLANTS TO WATERLOGGING[1]

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Waterlogging of the soil rapidly and dramatically alters both the physical and biological environment of plant roots. In response to environmental stimuli, physiological events occur within the plant which affect its growth and development. The purpose of this paper is to review certain aspects of the physiological responses of plants to waterlogging with respect to the response mechanisms and the subsequent adaptations in the growth and development of the whole plant. Many important aspects of the subject must be only briefly mentioned here, such as the effects of waterlogging on soil chemistry, nutrient availability and uptake, microbiology, pathology, and senescence. The reader is referred to recent literature for information on these topics (3, 13, 19, 21). The overriding effect of soil flooding is to limit the diffusion of oxygen to the root zone. The focus here, therefore, will be on the responses of plants to root anaerobiosis and some initial, rapid mechanisms of adjustment. Further information on long-term adaptation, especially in woody plants, can be found elsewhere (76).

The physiological responses to waterlogging represent a wide range of metabolic, hormonal, and developmental processes. Metabolic adaptations involving the accumulation of either ethanol or malate in anaerobic roots is an area of active research (15). All of the major plant hormones have been investigated for their involvement in the flooding syndrome. In this review, the role of ethylene in response to anaerobic conditions will be used as an example to illustrate the interrelationships between metabolism, growth regulators, and development. Ethylene has been established as an important mediator of many flood-induced plant characteristics such as leaf epinasty, aerenchyma formation, adventitious rooting, and leaf senescence (1, 18, 30). Recent advances in the biochemistry of ethylene synthesis have allowed a detailed characterization of the mechanism by which root anaerobiosis induces elevated ethylene levels in the shoot.

In keeping with the theme of this series of reviews, the effects of waterlogging on stomatal behavior and water relations of plants will also be discussed. Recent information on the relationship between root stress, leaf water potential (Ψ_{leaf}), and stomatal closure will be presented.

Ethylene and waterlogging

Role in leaf epinasty. One of the most rapid, visible responses of plants such as tomato (*Lycopersicon esculentum* Mill.) or sunflower (*Helianthus annuus* L.) to waterlogging is the downward growth of the petioles known as epinasty. This epinastic movement of the leaves is caused by more rapid expansion of the cells on the upper (adaxial) side of the petiole compared to the cells on the lower (abaxial) side (37). Epinasty is not associated with wilting or low Ψ_{leaf}, since it is a growth process which requires turgor for cell expansion. It has long been known that ethylene will induce epinasty even at very low concentrations (16). It has also been observed that waterlogged plants appear very similar to plants which have been gassed with ethylene (44, 72). Various studies have established that the ethylene levels in waterlogged plants exceed those in control plants (20, 31, 38). The ability of inhibitors of ethylene action such as silver ion (5) or benzothiadiazole derivatives (33) to prevent flood-induced epinasty confirms the role of ethylene in the response.

Several mechanisms have been proposed to account for the accumulation of ethylene in waterlogged plants. An exogenous source of the gas was suggested by the discovery that ethylene accumulated in anaerobic or flooded soils (65, 66). Further work has revealed that the soil ethylene is of microbial origin, although the exact organisms and substrates involved are still unclear (22, 23, 50). One problem that remains to be resolved is the pathway of ethylene synthesis in anaerobic soils, as oxygen is required for ethylene production in microorganisms as in higher plants (47). Since ethylene often accumulates to greater than 2 μl $liter^{-1}$ in waterlogged soils (27, 65), this may well serve as an exogenous source of the gas.

Kawase (39) found that ethylene levels rapidly increase in submerged tissues, or in tissues which were wrapped with a diffusion barrier such as plastic wrap. Since the diffusion rate of ethylene away from the root in the water phase is 10,000 times slower than in the gas phase, Kawase proposed that ethylene would build up in the root and move up the stem through the intercellular spaces, causing the characteristic responses. A drawback of this proposed mechanism is that the biosynthesis of ethylene requires oxygen (see below). The low oxygen levels in flooded roots would virtually stop the synthesis of ethylene, precluding the accumulation required for diffusion up the stem. However, it is possible that oxygen could diffuse internally through the intercellular spaces from the shoot and support some ethylene production in submerged tissues. Quantitatively, it is doubtful that ethylene production at the normal low rate in roots could account for the large increase in ethylene levels in the shoots of flooded plants solely by this accumulation mechanism (5, 9).

The hypotheses discussed above share the expectation that ethylene will move considerable distances into the nonsubmerged shoot. Radioactive ethylene supplied to tomato roots can be recovered unchanged from aerial stem tissue (31). However, the actual amount of ethylene transported was small, compared to the high concentration of ethylene applied. Zeroni and coworkers (84) found that unless diffusion from the plant was physically blocked, ethylene would move only a short distance internally. Consequently, ethylene entering the roots from the soil or synthesized within the roots could move within the submerged tissues to the water line, but should rapidly escape from the aerial organs. It is unlikely, therefore, that either of these mechanisms can account entirely for the epinastic response, although both may contribute under field conditions.

The importance of anaerobiosis as a factor in the epinastic response was established by Jackson and Campbell (33). When the roots of tomato plants, growing in nutrient solution, were made anaerobic with nitrogen gas, increased ethylene production and epinasty were observed in the shoot. Bradford and Dilley (5) performed similar experiments in which the ethylene production rates of both roots and shoots of individual plants could be simultaneously measured. When the root zones of tomato plants growing in porous media were made anaerobic with a flowing stream of N_2, the ethylene production rates of the shoots increased within 24 hr, and reached a maximum by 48 hr, a time course similar to that for waterlogged plants (Fig. 1). Ethylene emanation from the roots of the same plants, however, declined with increasing duration of the stress. Anaerobiosis of the roots is sufficient to cause elevated ethylene synthesis in the shoot, along with the associated epinasty. That the shoot injury is induced by the anaerobic root is easily demonstrated by simply removing the root system entirely. This does not result in epinasty or other injury symptoms, as was pointed out by Kramer (44).

Other evidence suggests that the factor which promotes ethylene synthesis is transported in the transpiration stream. For example, Jackson and Campbell (31) demonstrated that if the stem of a tomato plant is steam girdled to collapse the intercellular spaces but leave the xylem functional, the movement of ethylene gas from the root zone into the shoot is prevented. However, steam-girdled plants will develop epinasty and increase their shoot ethylene production in response to waterlogging (Bradford, unpublished). In other experiments, tomato plants were induced to develop two parallel root systems on cuttings with a vertically split stem base (30, 32). When only one of the root systems was treated anaerobically, epinasty and ethylene production increased asymmetrically in the shoot. Only those leaves with a direct vascular connection to the stressed roots exhibited marked epinasty. These observations led to the suggestion that some precursor or inducer of ethylene synthesis is transported from the anaerobic roots via the transpiration stream to the shoot (5, 18, 33). The resulting ethylene in the shoot then promotes the epinastic petiole growth, stem swelling, and adventitious rooting associated with waterlogging stress (see Kawase, these proceedings).

Identity of the Transported Signal. Ethylene production in plant tissues has long been known to require oxygen (10). When tissues are incubated anaerobically and then returned to air, a large burst of ethylene production occurs, suggesting that a precursor accumulates under anaerobiosis which is then converted to ethylene upon return to aerobic conditions (10). Adams and Yang (2) employed anaerobic incubation of apple tissue to identify this precursor as 1-aminocyclopropane-1-carboxylic acid (ACC). ACC accumulates to high levels in anaerobic tissue, but is rapidly converted to ethylene in air. As tomato roots show a similar inhibition of ethylene production under anaerobiosis, followed by a burst of ethylene synthesis when returned to air (35), ACC is a logical candidate to be the transported signal.

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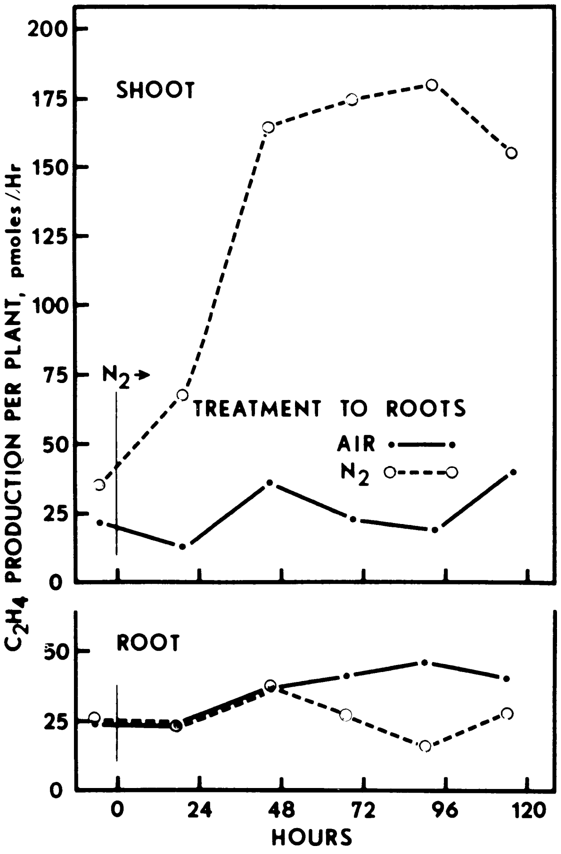

Fig. 1. Ethylene production by roots and shoots of intact tomato plants subjected to anaerobic conditions in the root zone only. From Bradford and Dilley (5).

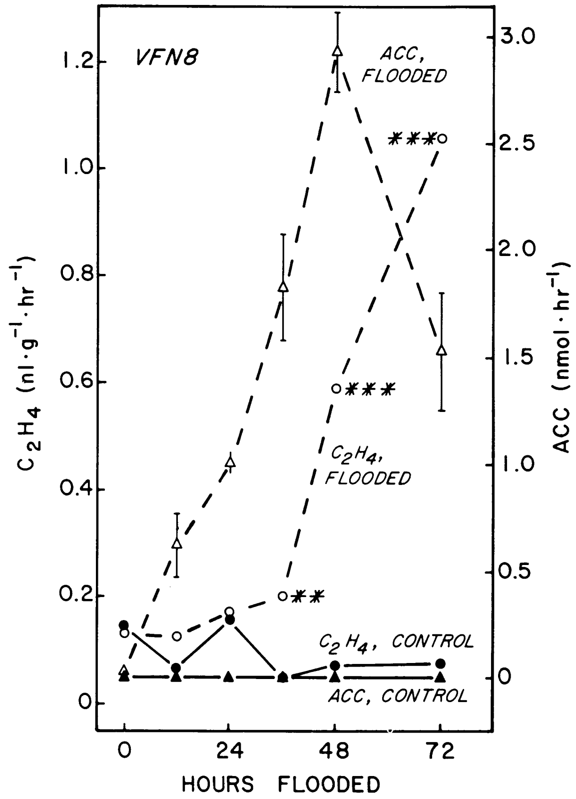

Fig. 2. Time course of ACC flux in the xylem and petiolar ethylene production of waterlogged tomato plants. From Bradford and Yang (9).

Bradford and Yang (9) measured the flux of ACC in the xylem sap of both flooded and control tomato plants by assaying the ACC content of the sap and multiplying by the rate of sap collection. This gives an indication of the rate at which ACC is being supplied to the shoot from the root. In all cases, ACC was virtually undetectable (<0.02 nmol hr^{-1}) in the xylem sap of control plants either in soil or in aerated nutrient solution. Sap from flooded roots or from root systems in anaerobic nutrient solution contained large amounts of ACC, with flux rates of up to 3 nmol hr^{-1} (Fig. 2). This rate of supply was sufficient to account for the increase in ethylene production by the shoots of the water-logged plants. The appearance of ACC in the transpiration stream always preceded the increase in ethylene production in the shoot and the development of epinasty (Fig. 2). When plants were flooded for 30 hr and then drained, readmitting oxygen into the root zone, the ACC flux declined immediately and was soon followed by a similar decline in petiolar ethylene production (8, 9,).

The enzyme converting ACC to ethylene appears to be constitutive in many plant tissues, so the reaction proceeds rapidly in the presence of oxygen (8, 9, 12, 41, 49, 81). When excised tomato shoots are supplied with ACC solutions via the transpiration stream at concentrations similar to those measured in waterlogged plants, ethylene production and epinasty are rapidly promoted (8,9).

Based on the rate of ethylene production in intact roots and the ACC flux rate, anaerobiosis must actually stimulate the production of ACC (8, 9). Thus, lack of oxygen not only blocks the conversion of ACC to ethylene, it also promotes ACC synthesis. This is consistent with the report of Kawase (40) of anaerobic stimulation of ethylene production in intact sunflower internodes. The localized anaerobic stress may have accelerated ACC synthesis in those cells where oxygen was below 1 or 2%. Movement of ACC to adjacent cells where the oxygen level was higher would allow conversion to ethylene to give a net increase in ethylene content over tissues which were not under stress.

Information on the regulation of ethylene biosynthesis provides further tests of the hypothesis that ACC from the anaerobic roots is responsible for accelerating shoot ethylene production. The pathway of ethylene biosynthesis from methionine (Fig. 3) has been demonstrated in both reproductive and vegetative tissues (2, 4, 36, 81). The key enzyme converting S-adenosylmethionine (SAM) to ACC has been extracted from tomato fruit and partially characterized (4, 82). Since this is the rate-limiting step in the sequence, factors such as indoleacetic acid (IAA), wounding, anaerobiosis, or senescence, which accelerate ethylene synthesis, have their primary effect on the activity of this enzyme, ACC synthase (for recent reviews, see 79, 80). In contrast, inhibitors of ethylene synthesis can act at either of the final 2 steps of the pathway (Fig. 3). Aminoethoxyvinylglycine (AVG) and aminooxyacetic acid (AOA) both inhibit ACC synthase (4, 82, 83), while cobaltous ion, uncouplers such as 2,4-dinitrophenol, and high temperatures, as well as

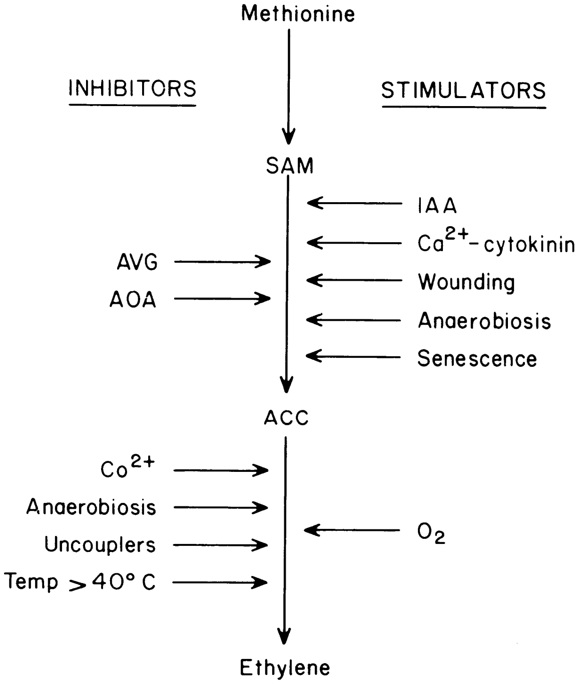

Fig. 3. Inhibitors and stimulators of the ethylene biosynthetic pathway, and the steps at which they act. For recent review, see Yang (80).

Table 1. Effects of aminoethoxyvinylglycine (AVG) on epinasty, ethylene production, and ACC flux in anaerobically stressed tomato plants.[z,y]

AVG (μM)	Aerating gas	Epinasty (degrees)	Ethylene (nl $g^{-1}hr^{-1}$)	ACC flux (nmol hr^{-1})
0	Air	−2.5 a	0.34a	0.05a
0	N_2	10.7 b	0.50b	3.6 b
10	Air	−2.3 a	0.04c	0.04a
10	N_2	−0.7 a	0.07c	0.11a

[z] AVG was added to the nutrient solution to give the final concentration indicated. Measurements were made after 24 hr of N_2 bubbling. "Epinasty" refers to the difference between initial and final petiole angles. "Ethylene" indicates the ethylene production rate from petioles during the first 30 minutes after excision. "ACC flux" is the rate of ACC transport in xylem sap collected with a vacuum.

[y] Mean separation in columns by Duncan's multiple range test, 5% level.

Table 2. Effects of cobaltous ion (Co^{2+}) on epinasty, ethylene production, and ACC flux in anaerobically stressed tomato plants.[z]

Co^{2+} (μM)	Aerating gas	Epinasty (degrees)	Ethylene (nl $g^{-1}hr^{-1}$)	ACC flux (nmol hr^{-1})
0	Air	0.6a	0.64a	<0.01a
0	N_2	28.9b	1.31b	2.5b
100	Air	4.7a	0.07c	<0.01a
100	N_2	4.3a	0.08c	1.1b

[z] For legends and symbols, see Table 1.

anaerobiosis, will block the synthesis of ethylene from ACC (80, 83). As predicted from Fig. 3, when AVG is supplied to anaerobic roots, the accumulation and transport of ACC is inhibited, ethylene production is reduced, and epinasty is prevented (Table 1)(7). On the other hand, Co^{2+} exerts little effect on the level of ACC in the xylem sap, but effectively inhibits both ethylene production and epinasty (Table 2)(7). These results are consistent with the proposed role of root-synthesized ACC in the etiology of the flooding syndrome.

Future research. While it seems clear that root-synthesized ACC must be considered as a significant component of the whole-plant response to waterlogging, there are questions remaining which should be addressed. For example, we have little quantitative data on the rate of ACC uptake from the xylem into the living cells of the stem, petiole and leaf. This could have important implications for the regulation of the shoot responses. Osborne (51) has described epinasty in terms of "target cells" on the adaxial side of the petiole which enlarge in response to ethylene. The transport of ACC in the vascular system offers the further possibility that certain cells may take up ACC more effectively, or convert it more efficiently to ethylene than others, thereby providing an additional means of distinguishing between "target cell types." The mechanism of regulation of ACC synthase in the root is also unknown. In vegetative tissues, ethylene production apparently is regulated by the level of endogenous IAA, which probably influences the rate of synthesis of ACC synthase (36, 81). The stimulation of ACC synthase due to wounding or anaerobiosis, however, seems to be independent of IAA action (8, 28). Our initial attempts to isolate the enzyme from tomato roots have been unsuccessful, and others have experienced similar difficulties in extracting it from vegetative tissues (36, 81). Another area of interest is the energy supply for ACC synthesis and possibly for enzyme synthesis under anaerobic conditions. To form ACC from SAM, the equivalent of three high-energy bonds are utilized for each ACC molecule. If ACC synthase is also synthesized *de novo*, this would represent an additional energy demand on the anaerobic system. The metabolic responses of plants to anoxia are quite diverse, however, and some species are able to maintain a high energy charge from fermentative processes (57). Some proteins, such as alcohol dehydrogenase, are known to be selectively synthesized in roots under anaerobic conditions (63). ACC synthase may represent a similar case; Imaseki and coworkers (26) showed indirectly that the ethylene-synthesizing enzyme system could be induced by IAA even at oxygen levels low enough to prevent the actual formation of ethylene. Of course, these proposals must be taken as speculation until it is possible to isolate and measure the enzyme activity.

In addition to these questions concerning the ethylene system itself, there is the larger problem which has been skirted thus far: how does ethylene interact with the other growth regulators to generate the entire gamut of morphological and anatomical changes which are observed in waterlogged plants? Whitlow and Harris (76) tabulated over 30 plant responses to flooding. Many of these are discussed by Dr. Kawase in the following article on anatomical adaptations to waterlogging. The reader is directed to recent reviews for further information on the role of growth regulators, other than ethylene, in the flooding syndrome (13, 17, 30, 34). It should be noted that much of the physiological research on waterlogging has been performed on only a few species such as tomato and sunflower, and extrapolations to other species may not be warranted. For example, pea plants (*Pisum sativum* L.) exhibit rapid dessication of the leaves upon waterlogging, a response that is not observed in most other plants (29). It is also possible that not all of the changes due to waterlogging are a result of root anaerobiosis, as the presence of water itself around the stem may induce effects, even when aerated (74, 75). The responses and adaptations of woody plants are also quite diverse and often different from those of herbaceous species (76). We hope that this discussion of ethylene physiology will be taken as a case history of how environment, metabolism, transport, tissue sensitivity, and growth response must all be integrated to produce an accurate picture of the plant adaptation. As similar case histories for the other growth regulators emerge, an overall understanding of how plants perceive and respond to environmental stresses can be developed.

Water relations and stomatal behavior during waterlogging

Since the anaerobic stress accompanying waterlogging occurs in the roots, but injury symptoms are readily apparent in the shoot, it is pertinent to consider the factors affecting transport of materials from the root to the shoot. In addition to ACC, the transpiration stream may also carry toxic compounds or ions generated in anaerobic soils (21, 56). Root-synthesized growth regulators such as cytokinins (CK) and gibberellins (GA), which are normally carried in the transpiration stream, appear at reduced levels in waterlogged plants (11, 61, 62). Water itself may be the most important component of the transpiration stream, as waterlogging stress is often considered to be a subset of water (drought) stress (20, 24, 70). It is certainly true that waterlogging can cause wilting, especially if the stress is imposed rapidly and transpirational demand is high (43). However, as was concluded by Kramer (44), "Although wilting of leaves is often observed after flooding, this is not the only nor even the most charactristic symptom of injury." Epinasty, hypocotyl swelling, and adventitious rooting are all growth processes requiring turgor, and are thus inconsistent with wilting or low Ψ_{leaf}. On the other hand, submerging the roots of a variety of plants has been reported to reduce transpiration and photosynthesis, implicating stomatal closure (14, 48, 53). The generally accepted explanation for this proposes the following sequence (24, 45): anaerobic stress reduces the permeability of the roots to water, increasing the resistance to water uptake; loss of water from the shoot exceeds the supply from the root, leading to a drop in Ψ_{leaf} and wilting; stomata close in response to the low Ψ_{leaf}, restricting transpiration and allowing recovery of turgor. In this scenario, waterlogging primarily affects the conductance of water through the root, and stomatal closure is a secondary response to low Ψ_{leaf}. It has been reported many times that rapid imposition of an anaerobic stress will reduce root conductance to water flow (e.g., 9, 46). However, in waterlogged plants, root conductance many remain identical to that of control roots or can change to a varying extent (35, 71). After longer periods of flooding (several days), root conductance often exceeds that of control roots (43; Bradford, unpublished). The lack of a consistent pattern in root conductance and the infrequency of wilting in waterlogged plants both raise questions about the role of water stress in flooding symptoms.

Numerous recent studies using porometric or gas exchange techniques have confirmed that waterlogging rapidly induces partial stomatal closure in a variety of woody and herbaceous species (6, 35, 42, 54, 60). Sunflower may be an exception, as stomatal conductance was reported to be unaffected by flooding in this species (70). However, in every case, Ψ_{leaf} of flooded plants was found to be equal to, or greater (less negative) than, that of control plants. Data reviewed by Sojka and Stolzy (67) show a clear positive relationship between oxygen diffusion rate (measured with the platinum electrode) in the root zone and stomatal conductance, but no correlation with Ψ_{leaf}. The time course of stomatal responses to flooding is illustrated in Fig. 4 (Bradford and Hsiao, unpublished). Stomata of waterlogged tomato plants still show a diurnal cycle, but maximal opening is only about 60% of the control. Stomata also tend to begin closing earlier on each successive day of flooding. While there is no detectable response on the first day of flooding, stomata simply do not open as widely beginning on the morning of the second day. Water potential measurements indicated that this was not due to a cycle of stomatal opening, transient wilting, and recovery. Such a cycle could be induced by waterlogging at the beginning of the dark period (Bradford and Hsiao, unpublished). In this case, the plants wilted within 30 min of illumination on the following morning, then recovered within the next 30 min. On subsequent days, the stomatal behavior was identical to that shown in Fig. 4. These data can be interpreted as indirect evidence of an effect of roots on stomatal behavior. When the stress was imposed in the morning, transpiration was occurring as the anaerobic conditions developed. This might allow transport of a "signal" from the roots which would limit the extent of stomatal opening on the next day. Stress imposed during the night, when transpiration is negligible, could reduce root conductance of water without the opportunity to communicate this event to the shoot. Thus, upon illumination, the stomata would open, loss of water would exceed uptake, and wilting would occur until the stomata closed sufficiently to equilibriate water loss and uptake. The timing of flooding stress may, therefore, be important in determining whether stomatal adaptation prevents or follows an episode of low Ψ_{leaf}.

Without delving too deeply into the mechanisms of stomatal regulation, some causes of the waterlogging effects on stomata can be proposed. While many points of contention remain, there is considerable evidence that abscisic acid (ABA) is involved in the endogenous control of stomatal aperture (58, 73). Increases in ABA content of leaves from waterlogged plants have been correlated with stomatal closure (78). Pierce and Raschke (55) have demonstrated that the accumulation of ABA in leaves is closely related to the loss of turgor, rather than to the total Ψ_{leaf}. We have failed to detect differences in turgor potential between leaves of flooded and control plants at a time when stomatal conductance is obviously affected (Bradford and Hsiao, unpublished). Consequently, if elevated ABA levels are responsible for stomatal closure, its synthesis or release must be due to stimuli other than loss of turgor. Further studies of the kinetics of ABA accumulation in waterloggred plants are clearly called for. On the other hand, it may be possible that stomatal closure is the result of a deficiency of factors from the root, such as CK and GA, which may promote opening. Hard evidence for their endogenous participation in stomatal regulation, however, is scant (25, 69). Jackson and Campbell (34) found that application of a mixture of benzyladenine and gibberellic acid increased the transpiration of both control and waterlogged tomato plants, often causing the flooded plants to wilt. Decreased export of CK and/or GA could act as a "signal" from the stressed root to reduce stomatal opening. When tomato roots are excised and the shoot cuttings are maintained in vials of water, stomatal closure occurs on the second day, as in Fig. 4 (Bradford and Hsiao, unpublished). This also implicates the roots in regulation of stomatal behavior. In woody plants, where stomatal responses are often slow to develop, K^+ deficiency may hamper stomatal action (60). An additional possibility is that waterlogging has a direct effect on the photosynthetic capacity of the plant. Wong and coworkers (77) showed that a reduction of photosynthetic capacity is paralleled by a decrease in stomatal conductance. The mechanism by which waterlogging could affect photosynthesis, as well as the connection between photosynthetic capacity and stomatal conductance, remains unknown. Since the time course of the stomatal effect coincides with that of epinasty, we tested whether ACC, when converted to ethylene, might induce stomatal closure. When ACC was fed to tomato shoot cuttings via the transpiration stream, no direct effect on stomatal conductance could be detected, even though epinasty was greatly stimulated (7). This is in agreement with earlier reports of the ineffectiveness of ethylene in modifying stomatal behavior (52). In conclusion, while stomatal closure is a common response to waterlogging, the underlying physiology remains at this point little more than speculation.

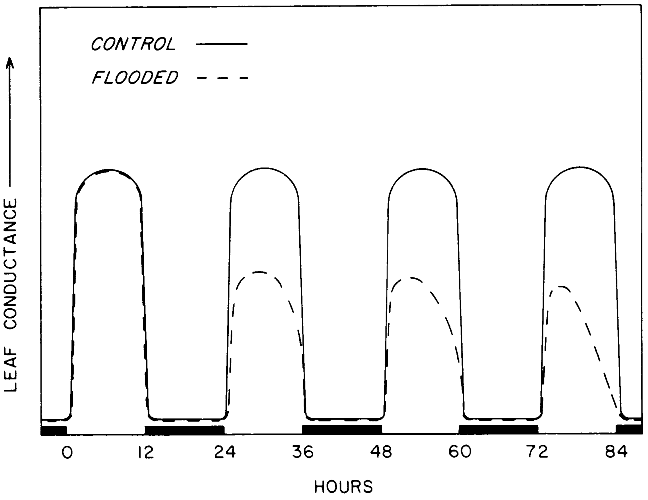

Fig. 4. Response of stomatal conductance of tomato plants to waterlogging at zero time. Bars on abscissa indicate dark periods. Schematized diagram based on numerous experiments using the diffusion porometer to estimate stomatal conductance (6; Bradford and Hsiao, unpublished).

One aspect of the water relations of flooded plants which has received little attention is whether the epinastic growth response has adaptive value. It could be that the import of excess ethylene from the root simply overpowers the normal mechanisms controlling leaf orientation (see 37). It is equally possible

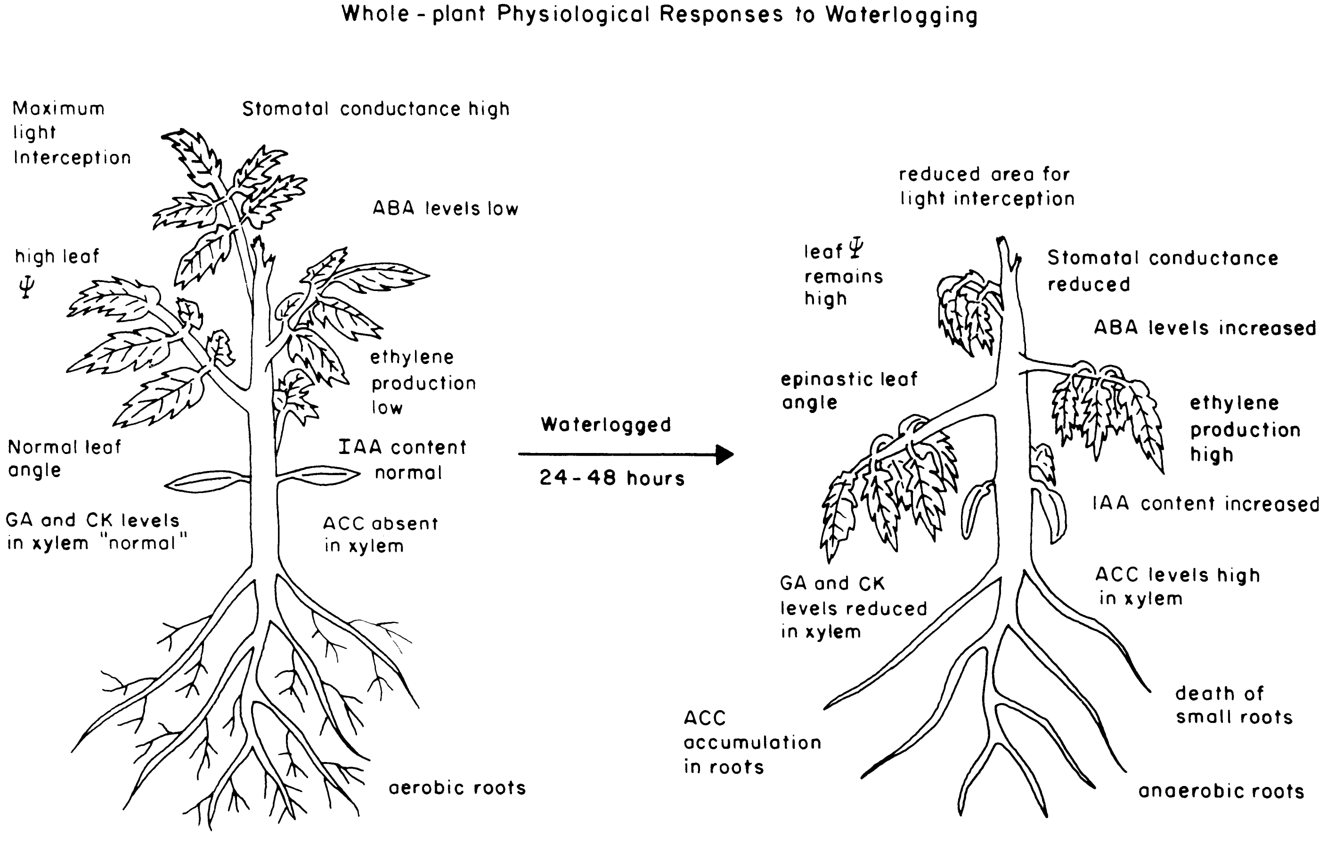

Fig. 5. Whole-plant physiological responses to waterlogging, as illustrated in the tomato.

that the anaerobic stimulation of ACC production, its export to the shoot, and the resulting epinasty have been preserved as responses to waterlogging because they confer an adaptive advantage on the plant. The adaptive significance of adventitious roots or aerenchyma is more apparent, and therefore these have been studied more carefully (see Kawase, these proceedings). Recent studies of adaptations to water stress suggest that epinasty may act to improve the water balance of the plant. In tomato, not only the main petiole, but also each individual leaflet assumes a more vertical position (see Fig. 5). This greatly reduces the horizontal surface area for light interception, especially when the sun is directly overhead and most intense. Studies of cowpeas (*Vigna unguiculata* L.), soybeans (*Glycine max* L. Merr.), and sunflowers all indicate that a vertical orientation of leaves during the afternoon can reduce water loss and increase water use efficiency (59, 64, 68). Epinasty may act in conjunction with partial stomatal closure to reduce the heat load on the leaf and limit transpiration, while still allowing much of the photosynthesis to continue. Methods exist for testing this hypothesis, but until the actual measurements are performed, the adaptive value of epinasty for plant water relations must remain in question.

Conclusions

Virtually all of the plant responses to flooding can be traced back to the limitation of oxygen diffusion to the root. For the case of ethylene biosynthesis, anaerobiosis has been found to stimulate the synthesis of the immediate precursor of ethylene, ACC, while at the same time blocking its subsequent conversion. This leads to an accumulation of ACC in the root, its export to the shoot, and its conversion to ethylene in tissues where the oxygen supply is adequate. Ethylene, in turn, promotes epinastic growth of the petioles and plays a role in other waterlogging responses. Thus far, this sequence of events has been demonstrated only in tomato, and the generality of this hypothesis awaits research with other species. The movement of ACC between plant organs does provide a new interpretation of many apsects of the flooding syndrome, as well as of plant growth and development in general.

Although the discussion of physiological responses to waterlogging was purposely restricted primarily to ethylene physiology, understanding the whole plant response requires attention to all aspects of plant-environment interactions. Metabolism, transport, and sensitivity to growth regulators, cell expansion, photosynthesis, root permeability, water relations, stomatal behavior, and morphology must all be considered and integrated to arrive at an accurate picture of plant adaptation to stress (Fig. 5). Experiments to test the adaptive significance of the various responses also need to be devised and performed. Current concepts in water stress physiology can provide useful models for research on waterlogging. However, important distinctions between drought and waterlogging stresses, such as the occurrence of anaerobiosis and changes in Ψ_{leaf}, must be recognized and appreciated.

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ANATOMICAL AND MORPHOLOGICAL ADAPTATION OF PLANTS TO WATERLOGGING[1]

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Most agricultural crops are mesophytes which require an environment which is neither too wet nor too dry for maximum growth and productivity. Once soil becomes waterlogged, air space is displaced with water. The O_2 remaining in the soil, either dissolved in water or trapped in air cavities, is quickly depleted by respiration of plant roots and soil microorganisms (69). O_2 replenishment in the soil is very inefficient because of the slow diffusion of atmospheric O_2 into the waterlogged soil. Root systems are thus suddenly plunged into an anaerobic condition by waterlogging. If waterlogging continues for a long period, the reducing processes in the rhizosphere aggravate the plant condition. Waterlogging does not necessarily occur only when the soil is inundated. Rather, waterlogging often occurs when water fills a critical proportion of the soil air spaces, depending upon the species of the plant involved. Such problems are prevalent in fields having poor drainage, that is, when underground and surface drainage is inadequate to remove water from the soil after a rain.

A great amount of literature covering the plant responses to waterlogging has been amply reviewed during the last decade (5, 6, 20, 22, 24, 25, 31, 40, 41, 70, 79). These reviewers contend that O_2 deficiency in the root system forces plants to switch their respiration from aerobic to anaerobic, inevitably resulting in low yield of ATP, accumulation of toxic end-products of anaerobic respiration, and rapid depletion of organic compounds. Absorption and translocation of water and nutrient in roots are slowed by the limited available energy. Synthesis and translocation of gibberellins and cytokinins in the roots are suppresssed by root injury resulting from waterlogging. Auxin concentration in stems increases as a result of blocked transport to roots or by inhibited IAA-oxidase activity in the stems. Ethylene concentration also increases in waterlogged plants.Anaerobiosis reduces the soil redox potential, changes soil pH, and increases the concentrations of toxic ions, metals, fatty acids, phenolic compounds, and ethylene found in the soil.

Symptoms of waterlogging injury described in these review articles are: leaf chlorosis, leaf epinasty, leaf abscission, decreased stem growth rate, stem hypertrophy, wilting of leaves and shoots, absence of fruits or decreased yields, adventitious root formation, decreased root growth, death of roots, increased susceptibility to attack by predators and pathogens, and finally death of plants.

The purpose of this paper is to review research related to anatomical and morphological adaptation, mainly of mesophytes, to waterlogging. The first and major effect of waterlogging is to reduce the availability of O_2 to the plant root system. Thus, any mechanism to supply O_2 to the roots and the reduced rhizosphere may be critical for the survival of plants under waterlogging conditions. Even hydrophytes, which grow partly or entirely submerged in water, have not evolved any specific biochemical mechanism of adaptation to shortage of O_2 (79). Adaptation to waterlogging in hydrophytes is centered mainly on their unique O_2 translocation system from the aboveground portion to the root system. For instance, *Spartina alterniflora*, a salt marsh grass growing along the southeast coast of the United States, has continuous gas spaces from the leaves to the tips of roots. Through this system, enough O_2 can be transported to supply the O_2 need of the roots and partially oxidize the rhizosphere (75). Anatomical or morphological adaptation should mainly, if not entirely, be evaluated by the capability in taking O_2 into the plant, translocating O_2 to the root system, and diffusing O_2 into the rhizosphere.

Plant adaptation to waterlogging is, of course, not limited only to anatomy and morphology. Review work cited earlier also discussed biochemical or metabolic adaptation (securing energy through anaerobic respiration and detoxification of the end-products of anaerobic respiration), rhizosphere oxidation (detoxification of the rhizosphere by oxygenation), and physiological

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