An Amalgamation Between Hormone Physiology and Plant Ecology: A Review on Flooding Resistance and Ethylene

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Abstract. Both distribution of terrestrial plants and species composition in flood plain communities are strongly influenced by flooding (waterlogging, partial submergence, or submergence). The interaction between a plant's flooding resistance and the seasonal timing, duration, depth, or frequency of flooding often determines plant distribution in flood plains. Flooding may be accompanied by marked physical changes in light, carbon availability, diffusion rate of gases, and density of the environment. Various physiological processes may be affected by these flooding-induced physical changes, including aerobic respiration, photosynthesis, and processes in which light acts as a source of information (e.g., phytochrome photoequilibrium). Certain plant species acclimatize and adapt to these physical changes to relieve the constraints imposed by the flooded environment. Underwater photosynthesis, enhanced shoot elongation, adventitious roots, and aerenchyma formation are typical adaptive responses which are believed to improve the oxygen status of submerged plants. Ethylene and other plant hormones play a central role in the initiation and regulation of most of these adaptive responses, which permit "escape" from anaerobiosis. Mechanisms of direct tolerance of anaerobic conditions, such as a vigorous fermentative respiratory pathway, are of particular importance when the plant is very deeply submerged, or during the night and when the water is sufficiently turbid to exclude light.

Studies on the cosmopolitan genus *Rumex*, distributed in a flooding gradient on river flood plains, have integrated plant hormone physiology with plant ecology. *Rumex* species showed a high degree of interspecific variation in ethylene production rates, endogenous ethylene concentrations, ethylene sensitivity, and ethylene-mediated growth responses. The field distribution of *Rumex* species in flooding gradients is explained in terms of a balance between endogenous ethylene concentrations and sensitivity towards this growth regulator ("ethylene economy"). Much data has been gathered using a recently developed laser-driven photoacoustic detection technique capable of detecting six parts of ethylene in 10^{12} parts air flowing continuously over the plant.

Flooding is common throughout the world (Kozlowski 1984). It can have a severe impact on terrestrial plant life and also interfere with human activities in these areas (Blom 1990A, Maltby 1991). Floods vary significantly in seasonal timing, duration, depth, and frequency (Voesenek 1990). When this is combined with the wide variation in the extent of flooding resistance among terrestrial plant species, one can expect a great influence on the occurrence and distribution of plant species (Blom et al. 1990). Various aspects of flooding and plant responses have been extensively reviewed in books (Crawford 1987, Etherington 1983, Hook and Crawford 1978, Hook et al. 1988, Jackson et al. 1991, Kozlowski 1984), special journal issues (Blom 1990B), and separate papers (Armstrong 1979, 1982, Armstrong et al. 1991, Blom 1990C, Crawford 1982, 1983, 1989, Davy et al. 1990, Drew 1983, 1990, Drew and Lynch 1980, Ernst 1990, Jackson 1982, 1985A, 1985B, 1987, Laanbroek 1990, Osborne 1984, Ridge 1985). These articles provide clear evidence that the physical changes accompanying flooding have a strong impact on plant hormones and that these in turn play a central role in the initiation and regulation of many acclimatic and/or adaptive responses of terrestrial plants upon flooding (see also Reid and Bradford 1984). In this context a key role is reserved for the gaseous plant hormone ethylene (Jackson 1985A, 1985B, 1987, 1990, Jackson and Pearce 1991, Ku et al. 1970, Mus-

grave et al. 1972, Osborne 1984, Ridge 1985, 1987). Only a few studies on ethylene and flooding, however, try to relate interspecific variation in physiological mechanisms to the ecology of those plant species. Ridge (1987) related two types of shoot elongation in response to submergence (large, rapid growth vs. small, delayed growth) with flooding regimes (predominantly aquatic vs. emergents in shallow waters, marshes, or in areas subjected to brief shallow floods). Ridge also presented a provoking analysis of both costs and benefits of the two types of ethylene-mediated shoot elongation. Mitchell (1976) and Osborne (1984) also attempted to relate the variation in shoot elongation under water of *Polygonum* species and *Ranunculus* species to their field distribution. Dodds and coworkers (1982) examined the relation between waterlogging resistance and ethylene metabolism in 21 different cultivars of *Vicia faba*. They suggested that the waterlogging resistance of the various cultivars was related to the ability to remove (metabolize) increased amounts of ethylene. Finally, Jackson and coworkers (1987) compared rice varieties of different submergence tolerance, with respect to their ethylene responses. Accumulated ethylene was casually related to fast leaf extension and chlorosis in the submergence-intolerant forms of rice. Pearce and Jackson (1991) compared submergence responses of Barnyard grass (*Echinochloa oryzoides*) and rice in relation to gaseous changes in the plants. The same changes (i.e., oxygen shortage, elevated ethylene, and carbon dioxide) brought about opposite effects in the two species growing in the same habitat. Poorly aerated solutions enhanced shoot growth in rice and inhibited it in *Echinochloa*. These two species probably have contrasting strategies for survival.

Overall, little is known about the hormonal regulation of ecologically significant processes in plant development. In a different area of plant physiological ecology, Dijkstra et al. (1990) showed a positive correlation between the relative growth rates of two inbred lines of *Plantago major* (the fast-growing *P. major* spp. *pleiosperma* and the slow-growing *P. major* spp. *major*) and their endogenous gibberellin concentrations. A reversion of the growth rate of both lines was realized by the application of exogenous GA_3 and addition of specific gibberellin inhibitors (Dijkstra and Kuiper 1989). The ecological significance of differences in growth rate is extensively discussed in Grime and Hunt (1975), Grime (1979), Chapin (1980), and Tilman (1988).

Up to now, although one was aware of the important role of hormones in adaptive responses of plants upon flooding, flooding resistance was re-

lated more to root porosity (aerenchyma) (Armstrong 1979, Justin and Armstrong 1987, Laan et al. 1989, Smirnoff and Crawford 1983) and to the terminal products of anaerobic respiration (McManmon and Crawford 1971, Roberts et al. 1984A) than to the role of hormones. In the present paper, the ethylene economy of several *Rumex* species, defined as the balance between endogenous ethylene concentration and sensitivity towards this growth regulator (see Voesenek 1990), will be related to the flooding resistance of the species. It is an intriguing possibility that plant distribution and flooding resistance in dry–wet gradients correlate with differences in hormone physiology. Firstly, the selection of the genus *Rumex* as a model for study will be discussed, followed by a survey of general environmental changes induced by flooding and the impact on terrestrial plants. The ethylene economy will be introduced by a description of a recently developed photoacoustic detection technique which can monitor ethylene levels as low as 6 ppt ($6:10^{12}$), and then will be discussed in relation to waterlogging, complete submergence, and field distribution of *Rumex* species.

Rumex as a Model

The present study concentrates on the correlative and possibly causal relationship between ethylene economy and flooding resistance and plant distribution. Three approaches were integrated, that is, ecophysiology, comparative physiology, and a study of the complete life cycle. Physiological ecology may provide insights into physiological mechanisms underlying acclimatic responses and adaptive traits of plants under stress. When comparing closely related plant species distributed along a stress gradient, a species' position within such a gradient can be linked directly to specific "fitness-increasing" physiological mechanisms (Blom 1987, Osmond et al. 1987). Since stress may have different effects on consecutive stages in the life cycle, studying several stages in the life cycle is a prerequisite to achieve complete understanding of plant distribution (Grime 1979).

The choice of the cosmopolitan genus *Rumex* as a model to study the relation between ethylene economy and flooding resistance is based on the following arguments:

1. Eight *Rumex* species occur in Dutch river flood plains within a clearly defined range of the flooding gradient (Fig. 1). This suggests differential
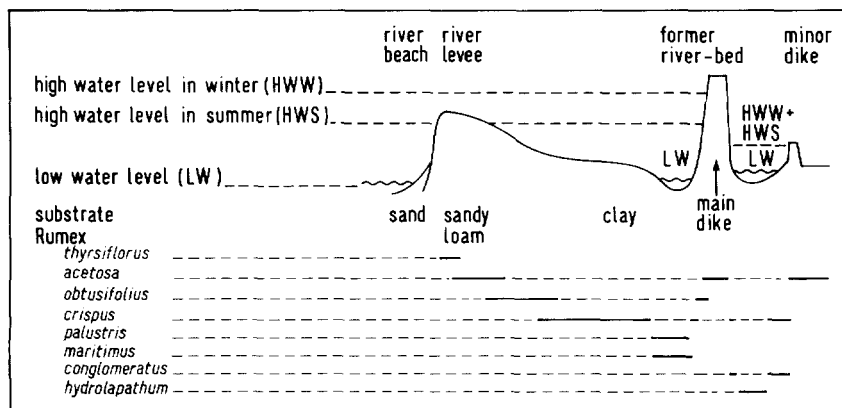
Fig 1. The zonation of eight *Rumex* species in the river flood plains of the river Rhine in The Netherlands.

resistance towards abiotic and biotic factors existing in this gradient.

2. *Rumex* species are very suitable for an experimental approach due to (a) the large amounts of seeds which can be collected directly in the field, (b) almost 100% germination in petri dishes exposed to a 12-h photoperiod at 25°C alternating with a 12-h dark period at 10°C (Voesenek et al. 1992A), (c) a high relative growth rate (>150 mg g^{-1} day^{-1}) (Poorter and Remkes 1990, Voesenek et al. 1989), and (d) the manageable size of seeds, seedlings, and adult plants.

The flood plains of river areas where *Rumex* is found range from nearly permanent flooded parts to erratically, infrequently inundated regions. Such river areas are highly dynamic ecosystems governed by strongly fluctuating water levels. The basic water discharge of the Rhine system is characterized by elevated levels during the winter and spring and relatively low levels during the late summer and autumn months; a pattern closely related to increases in rainfall in the winter and melting snow in spring. Superimposed on this basic pattern are the unpredictable high drainage peaks that occur throughout the year. These peaks in water level are related to excessive precipitation in the Rhine catchment area and may result in flooding of adjacent riparian habitats in both winter and summer. Riparian habitats of Dutch river areas are characterized by a distinct pattern of natural and man-made depressions and elevations, such as former river channels, sand, clay and gravel pits, river levees, and dikes. The continuum existing between depressions and elevations creates different flooding regimes and, as a consequence, gradients in intensity and extent of environmental stress and disturbance (see Grime 1979).

The Impact of Flooding on Terrestrial Plants

Flooding-Induced Environmental Changes

Historically, most research on flooding was concentrated on soil waterlogging-induced changes in plant growth and metabolism. Therefore, flooding tolerance is often used as synonymous with waterlogging tolerance. We prefer to use the general terms flooding and inundation to designate increased water levels without specific reference to the height of the water level. Flooding may result in inundation of soil and roots only (waterlogging), in complete inundation of roots and shoots (submergence), or in any level in between (partial submergence). This section will focus mainly on environmental changes and acclimatic responses of terrestrial plants induced by complete submergence; less attention will be paid to waterlogging.

As soon as a soil is flooded and all pores are filled with water, gas exchange between the soil and the atmosphere is strongly hampered (Jackson and Drew 1984, Ponnamperuma 1984). The trapped oxygen in the soil is chemically reduced to water by the terminal step in the respiratory electron transport chain of microorganisms and plant roots. After complete oxygen depletion, anaerobic microorganisms use various oxidized soil components as electron acceptors, leading to a sharp decline in the soil redox potential (Etherington 1983). The electrochemical changes in the soil, induced by overwet conditions, result in an increase of potentially toxic components (e.g., Mn^{2+}, Fe^{2+}, H_2S) (Ernst 1990). These electrochemical changes in flooded soils, and related processes of anaerobic decomposition of organic matter, have been extensively reviewed by Ponnamperuma (1984).

Submergence has also a dramatic impact on the aerial part of terrestrial plants as the whole plant is

suddenly surrounded by water. This environmental change significantly affects the quantity and quality of irradiation, carbon availability, diffusion rate of gases into and out of the plant, and density of the plant's immediate surroundings.

The water covering a shoot causes an exponential decline of photosynthetically active radiation (PAR) with increasing water depth (Spence 1981). At solar elevation angles of less than 41.4°, direct solar radiation is completely reflected by a smooth water surface (Weinberg 1976). This will result in a dramatic decrease in the photon flux density at plant level (Holmes and Klein 1987). A third factor which causes an attenuation of radiation under water is turbidity. Suspended particles cause a decline of radiation by both scattering and absorption (Holmes and Klein 1987). When radiation passes into both clear and turbid water, the red/far-red ratio increases with depth. In turbid water the penetration of UV A and B wavebands is strongly reduced. In addition, a proportionally greater depletion of far-red light, compared to red light, is observed (Holmes and Klein 1987).

A further factor that differs significantly from an aerial environment is carbon availability (Setter et al. 1987). Submerged shoots of terrestrial plants are exposed to three different interchangeable forms of dissolved inorganic carbon (DIC), occurring in a well-defined equilibrium: $CO_2 <=> HCO_3^- <=> CO_3^{2-}$. This equilibrium is shifted to the right by increasing pH and to the left by decreasing pH (Bowes 1987, Sand-Jensen 1987). In submerged, as well as aerial shoots, carbon has to dissolve before fixation can take place. However, the diffusion resistance for CO_2 in an aqueous solution is high due to the 10^4 times slower diffusion rate and the long pathway that is many times greater than in an aerial environment (Bowes 1987). It should be born in mind that both wave action and water currents do have a strong influence on the diffusion resistance for CO_2 and O_2, due to their impact on the boundary layer around the shoot. The low diffusion rate of gases in water also strongly interferes with diffusion of ethylene, leading to entrapment of this gaseous growth regulator in the plant tissue under submerged conditions (Musgrave et al. 1972, Ridge 1987).

The phenomenon of heterophylly gives a very clear idea of the very large impact the problem of diffusion resistance can have on plant development in aquatic environments. Plants exhibiting this phenomenon can form two very different types of leaves, often on the same stem: aerial leaves and submersed leaves. The latter are characterized by a small, thin, and/or finely dissected morphology and a lack of stomata and cuticle. This morphology

maximalizes the surface area/volume ratio to favor gas diffusion. In an aerial environment, however, such a submersed leaf would easily desiccate (Bowes 1987).

The high density of water causing the relatively low diffusion rate of gases is not just detrimental for a flooded plant, but its density also provides the flooded plant with support and buoyancy, thereby allowing a reduction of investment in structural components (Bowes 1987, Sculthorpe 1967). Since a submerged plant is literally surrounded by nutrient solution, it may function nearly independent from roots and an adequate transport system (Bowes 1987).

Flooding-induced Strains and Acclimatizations

So far we have described the physical changes of the environment that occur when a plant is flooded. This section addresses the physiological processes in the plant affected by these flooding-induced physical changes and how plants acclimatize and adapt physiologically to flooding.

Under aerobic conditions respiration generates most of its ATP via the transfer of electrons from cytochrome oxidase to oxygen (the respiratory electron transport system). Since cells of all higher plants are obligate aerobes (Vartapetian et al. 1978), oxygen is a prerequisite for aerobic respiration to provide energy for ion uptake, growth, and maintenance. Anaerobic soil conditions, as induced by flooding, completely prevent the synthesis of ATP via the respiratory electron transport system (Crawford 1989). However, a net yield of 2 mole of ATP can still be produced under anaerobic conditions through the action of the glycolysis (Jackson and Drew 1984). This restricted yield of energy is predominantly used for maintenance processes, while growth and active ion uptake are probably switched off (Jackson and Drew 1984, Setter et al. 1987). According to Setter and coworkers (1987) the balance between carbohydrate supply, maintenance respiration, and growth respiration is important in estimating the flooding tolerance of a terrestrial plant. Lack of oxygen is probably the most important factor limiting growth and survival of terrestrial plants in habitats with frequent floods (ap Rees et al. 1987).

Under conditions of waterlogging or partial submergence both wetland and nonwetland plants may develop new, adventitious roots (Hook 1984, Kramer 1951), which are often highly porous (Justin and Armstrong 1987, Laan et al. 1989). Waterlogging or partial submergence may induce longitudinal, interconnected gas spaces (aerenchyma) in both old and new roots. It reduces the resistance of

roots and shoot parts to internal passage of oxygen and other gases (Armstrong 1979, Crawford 1982, Konclová 1990, Laan et al. 1989). Two types of aerenchyma can be distinguished: the first type develops through separation of cells (schizogenous aerenchyma), while the partial lysis of cortical cells is involved in the second type (lysogenous aerenchyma) (Crawford 1983, Jackson and Drew 1984). Little is known about the mechanisms of aerenchyma formation (Justin and Armstrong 1987). Some evidence exists with respect to the physiological processes leading to cell lysis in maize roots in response to hypoxia. The breakdown of cortical cell walls is induced by enhanced endogenous ethylene levels. Both stimulated ethylene biosynthesis in response to low oxygen concentrations (hypoxia) and entrapment of produced ethylene within submerged roots explain the significant increase of the internal ethylene concentration in a flooded root (Drew 1987, Jackson 1982). It is also possible that exogenous ethylene, most probably of microbiological origin, enters the roots (Jackson and Pearce 1991). Jackson and coworkers (1985A) demonstrated that aminoethoxyvinylglycine (AVG), an inhibitor of ethylene biosynthesis, blocked the induction of aerenchyma development. Simultaneous addition of 1-amino-1-cyclopropanecarboxylic acid (ACC), the rate-limiting ethylene precursor, overruled the inhibitory effect of AVG: aerenchyma was again induced in roots, demonstrating that AVG did not act as a general inhibitor of plant metabolism.

In order to have functional significance, aerenchyma must permit internal aeration (i.e., supply of oxygen from the atmosphere or photosynthesis via aerial shoot parts to roots) (Laan et al. 1989, 1990). Experimental evidence for the process of internal aeration is reviewed by Jackson and Drew (1984). Very recently, Laan et al. (1990) showed that an increase in root porosity significantly enhanced the internal oxygen transport in two terrestrial *Rumex* species from frequently flooded habitats (*R. crispus* and *R. maritimus*). They also showed that the internal aeration was positively correlated to the total leaf area of *Rumex* plants protruding above the water surface.

It is possible, however, that despite aerenchyma and internal aeration, insufficient oxygen may be present throughout the root tissue to maintain aerobic respiration at a rate that can be compared to the fully aerobic tissues (Drew et al. 1985). The dependence of the final oxygen concentration in the root apex and elsewhere (e.g., stele) on factors such as root length, root porosity, root radius, stelar radius, oxygen consumption of the soil, and the root respiration rate has been modeled by Armstrong (1979) and Armstrong and Beckett (1987). Internal

aeration will also depend on the generation and utilization of oxygen produced by underwater photosynthesis, and the enhanced shoot elongation in response to complete submergence. The latter will allow the shoot to gain access to atmospheric oxygen if the shoot reaches the water surface. Since most oxygen will enter the plant via stomata (Gaynard and Armstrong 1987) or via micropores (see Nouchi et al. 1990), the importance of a large leaf area regaining a position above the water surface is undoubted (Laan et al. 1990, Van der Sman et al. 1991, Voesenek 1990). In order to achieve this shoot–atmosphere contact, petioles and/or internodes must maintain or enhance their elongation rate. Shoot elongation, mediated by the gaseous plant hormone ethylene, has been described for various aquatic, amphibious, and terrestrial plants (Ku et al. 1970, Musgrave et al. 1972, Osborne 1984, Ridge 1987). However, in spite of the close functional relationship between shoot elongation and aerenchyma development, almost no research has concentrated on the correlation between these two phenomena (see Jackson 1989). It may be expected that plant species which are able to elongate shoot parts also exhibit relatively high root and shoot porosities. According to Smirnoff and Crawford (1983) high root porosities are defined as those exceeding 10%. A literature survey in Table 1, in which data on root porosity and shoot elongation capacity of both aquatic and terrestrial plants are compiled, showed that elongation capacity always is accompanied by high root porosities thus confirming our expectation. However, under conditions of very deep water layers covering a flooded plant, during night periods or at high turbidity, it is likely that aeration stress in the roots cannot be relieved (Waters et al. 1989). A switch to anaerobic metabolism, induced during a transient hypoxic phase (Johnson et al. 1989, Saglio et al. 1988, Waters et al. 1991), will then be a preprequisite for survival.

During anaerobiosis, glycolysis can take place only as long as the generated NADH can be oxidized to NAD. This can be effected by various fermentative pathways, each having its own terminal product (e.g., glycerol, shikimate, lactate, malate, aspartate, ethanol, alanine) (Crawford 1978, Jackson and Drew 1984, ap Rees et al. 1987). The fermentative pathways generating ethanol, lactate, and alanine yield net ATP, although the amounts are very limited (Jackson and Drew 1984). Furthermore, these routes are characterized by an extremely inefficient use of substrate and the environmental loss of carbon-containing end products, particularly ethanol which diffuses out into the surrounding water. This may avoid accumulation of the potentially toxic terminal product ethanol (ap

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Table 1. A survey of plant species which can elongate shoot parts under water and their root porosity [root porosity of all plants was measured by pycnometry (Jensen et al. 1969)].

Species	Root porosity				Shoot elongation	
	%	Growth conditions[a]	Root type/part[b]	Reference[c]	Organ	Reference[c]
Callitriche stagnalis	14.6	CF	RL	1	Internodes	2
Rumex crispus	18.8–20.6	CF,GSW	RL,NR	1,3	Petioles/internodes	4
Rumex conglomeratus	21–26.1	GSW,CF	NR,RL	3,1	Petioles	5
Rumex maritimus	12.3–30	CF,GSW	RL,NR	1,3	Petioles/internodes	6
Ranunculus ligua	19.0	?	PR	16	Petioles	7
Epilobium hirsutum	22.2	CF	RL	1	Internodes	7
Caltha palustris	23.8	SF	RL	8	Petioles	7
Oenanthe fistulosa	23.9	CF	RL	1	Petioles	7
Aster tripolium	25.6	CF	RL	1	Petioles/laminae	15
Apium nodiflorum	28.1	CF	RL	1	Petioles	7
Ranunculus flammula	29.7–36.0	CF,SF	RL	1,8	Petioles/internodes	7
Rumex hydrolapathum	29.9	CF	RL	1	Petioles	5
Oryza sativa	35.1	CF	RL	1	Coleoptiles/mesocotyls/internodes	9,10,11
Carex hirta	36.3	CF	RL	1	Laminae	15
Nymphoides peltata	43.1	GMS	AS	12	Petioles	13,14
Nymphaea alba	57.0	GMS	AS	12	Petioles	13
Phragmites australis	51.9	CF	RL	1	Internodes	15

[a] Growth conditions: GMS, greenhouse, mineral sediment, submerged; GSW, greenhouse, sand culture, waterlogged; SF, sand culture, flooded; CF, John Innes no. 2 compost, flooded.

[b] Root type/part: AS, apical segments (2–4 cm length); NR, newly developed roots on the tap root or on the root–shoot junction, apical parts of 20–30 cm length; PR, primary roots; RL, root samples, laterals removed.

[c] 1, Justin and Armstrong (1987); 2, McComb (1965); 3, Laan et al. (1989); 4, Voesenek and Blom (1989A); 5, personal observation, Voesenek; 6, Van der Sman et al. (1991); 7, personal observation, Ridge and Amarasinghe; 8, Smirnoff and Crawford (1983); 9, Ku et al. (1970); 10, Suge (1971); 11, Metraux and Kende (1983); 12, Smits et al. (1990); 13, Funke and Bartels (1937); 14, Ridge and Amarasinghe (1984); 15, personal observation, H. van de Steeg; 16, Crawford (1983).

Rees et al. 1987), although the toxicity is probably too low to be harmful or fatal. Two theories, explaining metabolic differences between flood-tolerant and intolerant plant species, have developed during the last decades: the metabolic theory of flood tolerance of Crawford (1978) and a theory concentrated on the regulation of cytoplasmic acidosis (Davies et al. 1974, Roberts et al. 1984A, B).

According to Crawford (1978), plants that are intolerant to flooding respond to hypoxic environmental conditions with a significant increase in Pasteur effect and/or alcohol dehydrogenase activity. The increased production of ethanol accumulates in the root tissue and causes cell death. Flood-tolerant plants, however, are able to avoid the production of potentially toxic ethanol. In these plants the less toxic malate was assumed to accumulate. Arguments that counteract the Crawford theory concentrate on the high rates of ethanol production in flood-tolerant plants (Smith and ap Rees 1979A), the lack of evidence that ethanol is sufficiently toxic (Jackson et al. 1982), the small net ATP production of this route (Jackson and Drew 1984), the presence of malic enzyme in flood-tolerant plants (Smith and

ap Rees 1979B), and the very limited evidence that these plants actually accumulate malate.

The theory of Davies and Roberts indicates that roots respond to hypoxia with a transient lactic fermentation. As a consequence the cytoplasmic pH declines, triggering ethanolic rather than lactate fermentation. Consequently, no further cytoplasmic acidosis occurs when escape of CO_2 to the environment is not prevented (Davies et al. 1974, Roberts et al. 1984A, B). Variation in flood tolerance may be explained in part by differences in ethanolic fermentation. Roots with a limited ethanol production undergo significant lactic fermentation causing cytoplasmic acidosis and cell death (see Sieber and Brändle 1991). Recently, Menegus et al. (1989) demonstrated that flood-tolerant species like rice exhibit a limited lactate production and thus less cytoplasmic acidification than nontolerant species like maize and wheat. Interspecific differences in flooding resistance can also be related to variation in permeability of the tonoplast to protons (Roberts et al. 1984A). Finally, prevention of CO_2 escape can significantly increase cytoplasmic acidosis in certain plant species and this could lead to earlier cell

Table 2. Length of root tips (N = 20; ± SE) after a hypoxic incubation of several hours (6, 9, 12, 15, 18) followed by an aerated regrowth period of 7 days at 20°C.

Species	Exposure time (h) to hypoxia	Length of root tips (mm)	Ethanol concentration (μmol gDW^{-1})
Rumex acetosa	6	6.4 ± 0.2	30 ± 0
	9	5.1 ± 0.1	50 ± 5
	12	5.1 ± 0.1	60 ± 5
	15	5.0 ± 0.1	70 ± 10
	18	5.0 ± 0	70 ± 0
Rumex crispus	6	8.5 ± 0.2	260 ± 5
	9	6.3 ± 0.2	330 ± 5
	12	5.4 ± 0.1	370 ± 30
	15	5.1 ± 0.1	420 ± 35
	18	5.0 ± 0	480 ± 40
Rumex palustris	6	8.0 ± 0.2	220 ± 10
	9	7.5 ± 0.3	330 ± 50
	12	6.9 ± 0.1	380 ± 75
	15	5.6 ± 0.2	420 ± 40
	18	5.0 ± 0	470 ± 20

The excised root tips had a length of 5.0 mm before hypoxic incubation (when no regrowth occurred root tips were assumed to be dead; this was confirmed by tetrazolium staining). The cumulative ethanol concentration (N = 2; ± SE) in hypoxic solutions of 10 ml filled with 150–300 mg primary root tips (see Voesenek et al. 1992B).

death (Roberts et al. 1985, ap Rees et al. 1987). Additional evidence for this last theory was gathered in a recent comparative study of three *Rumex* species: *R. acetosa, R. crispus,* and *R. palustris* (see section *Rumex* as a Model). Survival of excised root tips under hypoxic *in vitro* conditions was positively correlated with ethanolic fermentation rate, measured as ethanol production (Table 2). Root tips of *R. acetosa* showed a low tolerance towards hypoxia accompanied by low alcoholic fermentation, whereas the opposite was observed in both *R. crispus* and *R. palustris* (Voesenek et al. 1992B).

Besides the shift in metabolism from oxidative phosphorylation to predominantly ethanolic fermentation, the pattern of gene expression dramatically alters under anaerobic conditions. At the molecular level the normal protein synthesis is repressed, whereas the expression of anaerobic polypeptide (ANP) genes is induced. ANPs most probably facilitate the metabolism of carbohydrates and contribute to the survival of the plant cell during anoxia (Walker et al. 1987).

Anaerobic injury is not only restricted to the actual period of anoxia, but damage can also occur after restoration of the normal oxygen conditions (Crawford 1989). This postanoxic injury is probably

related to a burst in superoxide radical production due to the shift from anaerobic to aerobic conditions (Toai and Bolles 1991). Superoxide dismutase is assumed to be an important enzyme in the free radical-scavenging pathway and thus important in the protection of plant cells against oxygen toxicity (Crawford 1989). Additionally, accumulated metabolites, such as ethanol, can be oxidized to potentially harmful products, such as acetaldehyde (Crawford 1989, Studer and Brändle 1987).

Dramatic changes in both light and carbon availability strongly interfere with the process of underwater photosynthesis. This photosynthesis can have a significant impact on the continuation of various processes:

1. It produces carbohydrates essential for sustaining shoot elongation (Raskin and Kende 1984A) and increased glycolytic rates (Setter et al. 1987).

2. The oxygen produced may assist internal aeration (Gaynard and Armstrong 1987, Laan and Blom 1990, Voesenek et al. 1992B, Waters et al. 1989).

The supply of carbon is rate-limiting for photosynthesis and growth of submerged aquatic plants (Sand-Jensen 1987). It is likely that this direct limitation restricts carbon fixation rates more than reduced irradiation (Black et al. 1981). Submerged aquatic plants, which during evolution returned from a terrestrial to an aquatic environment can be seen as a highly specialized group of plants (Sculthorpe 1967). They have developed an array of adaptations to relieve the constraints of carbon limitation. As mentioned before many aquatic plants have thin, finely dissected leaves with a thin cuticle to optimize plant–water contact (Sand-Jensen 1987). A rather specialized group of aquatic plants growing in CO_2-poor waters, can use CO_2 directly from the sediment. The carbon dioxide is "piped" via a longitudinally interconnected system of gas channels to the leaves (Bowes 1987). An adaptation which is especially advantageous in water with a high pH is the direct use of bicarbonate (HCO_3^-) as the main carbon source (Bowes 1987, Sand-Jensen 1987, Smits et al. 1988). Other CO_2-concentrating mechanisms which can operate in submerged aquatic plants are linked to C_4 and CAM metabolism (Bowes 1987, Keeley 1987). Since pH indirectly affects photosynthesis via the carbon equilibrium, it must be an adaptive trait that some submerged aquatic macrophytes can regulate the pH of the aqueous boundary layer around their leaves (Prins et al. 1982). Finally, it is also possible that a submerged aquatic plant develops aerial leaves

which photosynthesize at high rates once these leaves gain a surface position (Bowes 1987). Ethylene-mediated shoot growth to reposition leaves above the water surface can therefore not only be seen as a mechanism which restores root aeration, but it may play a significant role in the restoration of the carbon gain after submergence.

All of these adaptations with regard to carbon availability, which are fully documented for various aquatic plants, are only scarcely investigated for occasionally flooded terrestrial plants. However, there is some evidence that amphibious plants are poor HCO_3^- users (Spence and Maberly 1985). There are some indications that elongated petioles and leaves of submerged terrestrial plants dessiccate rapidly after lowering of the water level (Ridge 1987, Voesenek and Blom 1989A). This might be related to thinner cuticles under water, which can enhance underwater photosynthesis.

Plants use light both as a source of energy (photosynthesis) and as a source of positional and temporal information (Holmes and Klein 1987). As far as we know no data are available concerning the use by terrestrial plants of the information embedded in changes in light quality with increasing water depths. There is, however, evidence that the phytochrome photoequilibrium plays a significant role in the induction of aerial leaves in amphibious plants (Spence et al. 1987).

The high density of the flooding medium can be of significance. The reduced investment in, for example, lignin, often observed in submerged amphibious plant species (Ridge 1987), might have an important impact on the potential investment in an alternative process, such as shoot elongation.

With regard to the gaseous growth regulator ethylene, both waterlogging and submergence have a severe impact on production rates and concentrations in root and shoot tissues. Due to the low diffusion rate of gases in water, concentrations of oxygen, carbon dioxide, and ethylene may significantly change in response to flooding. Regardless of daily fluctuations and circadian rhythms, carbon dioxide and ethylene levels generally increase under submerged conditions, whereas oxygen concentrations decrease (Van der Sman et al. 1991, Stünzi and Kende 1989, Voesenek et al. 1990A). The elevated ethylene levels may stimulate formation of lysigenous aerenchyma and enhanced shoot growth to restore leaf–atmosphere contact after submergence. Both acclimatizations improve the oxygen status of the plant, whereas an increase in aerial photosynthesis, due to shoot elongation, may relieve the strong carbon limitation of terrestrial plants under water.

Photoacoustic Detection of Ethylene

The photoacoustic effect was first reported by Alexander Graham Bell in 1880 (Bell 1880, 1881). He discovered that thin disks (e.g., selenium, carbon, hard rubber) emitted sound when exposed to a rapidly interrupted beam of sunlight. Very soon, however, the interest in the photoacoustic principle declined. Renewed attention was gained by the invention of powerful lasers.

The photoacoustic effect (e.g., the transformation of light energy into acoustic energy) is based on the fact that molecules absorb electromagnetic radiation. As a consequence they are excited to a higher energy level. Excited molecules can fall back to their original ground state via two processes: radiative decay and nonradiative decay. In the infrared region this leads almost exclusively to nonradiative decay. De-excitation or relaxation increases the kinetic energy and temperature of all the gas molecules around the excited molecules. When this process takes place in a constant volume it increases the pressure. When the light source is chopped at an audiofrequency, pressure fluctuations of the same frequency occur inside that constant volume (Harren 1988).

Depending on the structure of a molecule, vibrational absorption bands are distributed over the entire range of the infrared wavelength region (1–50 μm). These bands can occur as narrow peaks or be spread out over several wavelengths. The CO_2 wavelength laser region (9–11 μm), however, covers only a small part of the infrared wavelength region. Molecules without a vibrational absorption in this region (e.g., CH_4, C_2H_6) therefore cannot be detected by CO_2 lasers. Molecules that do absorb in this region (e.g., C_2H_4, NH_3, O_3, H_2O) show a highly specific and unique absorption pattern (Harren et al. 1990A, Meyer and Sigrist 1990). For these molecules distinct fingerprint-like absorption spectra can be observed for the 90 discrete laser transitions in the 9–11 μm infrared wavelength region (see Fig. 3). Due to strong absorption by ethylene at the CO_2 laser wavelengths it has been possible to detect very low ethylene concentrations in air (Harren et al. 1990A, Van der Sman et al. 1991, Voesenek et al. 1990A, Woltering and Harren 1989, Woltering et al. 1988). To improve the sensitivity of the photoacoustic system further, the acoustic cell was placed inside the CO_2 laser cavity. The accompanying increase in laser power to approximately 150 W resulted in a detection limit of six parts of ethylene in 10^{12} parts of air (Harren et al. 1990B).

During application of this method in plant physiological experiments, intact plants were placed in
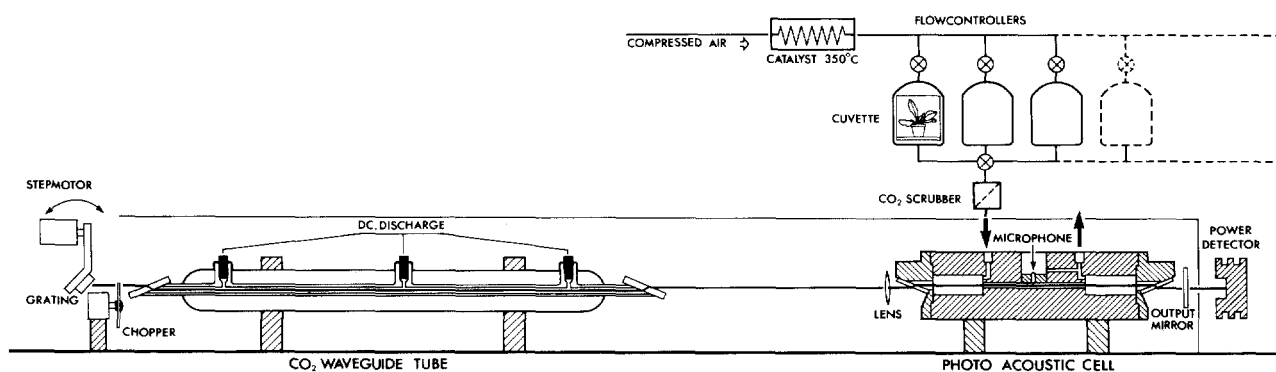
Fig. 2. The experimental assembly of a continuous flow system in line with a laser-driven intracavity photoacoustic detection system to monitor ethylene production of plants. For more information see Harren (1988).

small glass sample cells (200–600 cm^3) with inlet and outlet ports. To avoid the influence of changed oxygen, carbon dioxide, and ethylene levels on the ethylene production by plants, the sample cells were continuously flushed with air at 0.5–4.5 L/h after passing over a catalyst to remove traces of hydrocarbons. The catalyst consisted of a copper tube (length: 6 m) filled with platinized Al_2O_3 pellets heated at a temperature of 400°C. Under these conditions nearly all hydrocarbons dissociate into carbon dioxide and water. Between the plant-holding cell and the photoacoustic cell, a KOH-based scrubber eliminated CO_2 without influencing the ethylene concentration (Fig. 2). Almost complete removal of CO_2 is essential, since it coincides exactly with the laser transitions of the CO_2 laser.

The strongest ethylene absorption in the CO_2-laser wavelength region (9–11) μm) was observed at the 10P14 CO_2 laser line (10.53 μm), a much weaker absorption was observed at the 10P12 line (10.51 μm) (Brewer et al. 1982) (Fig. 3). During one measurement cycle, absorptions and the accompanying microphone signals were determined on both laser lines and recalculated to correct for the background signal. A stepmotor-driven grating regulated the transfers between both laser lines. The laser power on both lines was maximized during every measurement cycle with the aid of a computer-controlled piezo.

The higher sensitivity of photoacoustic detection of ethylene compared to gas chromatographic techniques allowed the use of continuous flow systems without collection traps. Ethylene can be measured directly in the effluent of the sample cells. The photoacoustic principle allowed, for the first time, registration of fast, short-lasting changes in ethylene production, such as the fast release of ethylene after
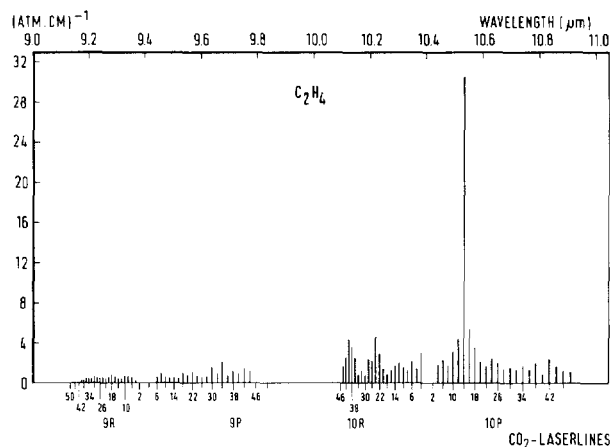

Fig. 3. Absorption strength of ethylene at CO_2 laser wavelengths in the 9–11 μm region. The identification of the individual laser-lines is deduced from molecular spectroscopy. It indicates which rotational and vibrational quantum states are involved in the laser transitions.

de-submergence of plants (Voesenek et al. 1992C).

Ethylene and Waterlogging

The general plant responses towards long-term soil waterlogging, in terms of survival, indicate that all *Rumex* species are relatively resistant. *Rumex acetosa, R. crispus,* and *R. palustris* (for field distribution, see Fig. 1) can survive waterlogging under greenhouse conditions (day temperature, 20–30°C) for at least 9 weeks. A relatively large interspecific variation in biomass increment was detected during such a waterlogging period. Reduced growth under these conditions was observed in *R. acetosa* within 40 days of waterlogging. Species from wet field sites

(i.e., *R. maritimus, R. palustris,* and *R. crispus*) showed a slightly increased shoot biomass after flooding of the soil (Van der Sman et al. 1988, Voesenek et al. 1989). The root biomass of *R. crispus* and *R. palustris,* however, was characterized by an inhibited biomass increase under these conditions. All *Rumex* species under study were able to develop a new root system in response to waterlogging (Laan et al. 1989, Van der Sman et al. 1988, Voesenek et al. 1989). These new roots can be divided into two morphological types: (1) strongly branched, thin, superficially growing roots; and (2) thick, white, hardly branched roots, which penetrate into deeper waterlogged soil layers (Voesenek et al. 1989). The high surface area/volume ratio of the thin roots might be adaptive in relation to the exploitation of oxygen from the upper water/soil layers (Armstrong et al. 1991). The seldomly flooded dry land species (i.e., *R. acetosa* and *R. thyrsiflorus*) developed very few new roots, with a maximum new growth of 10% of the length of the original primary root system. In contrast, extensive production of these roots was observed in species found in frequently flooded localities (i.e., *R. maritimus, R. conglomeratus, R. palustris,* and *R. crispus*). Here, up to 50% of the original root length was regenerated (Laan et al. 1989, Voesenek et al. 1989). These latter species developed a schizogenous type of aerenchyma in the new roots (Laan et al. 1989). These longitudinally interconnected gas-filled channels are functionally related to the use of aerial oxygen for energy acquisition via aerobic root respiration (Laan et al. 1990).

The slight increase of shoot biomass in *R. maritimus, R. crispus,* and *R. palustris* in response to waterlogging is related to a significant increase in lamina and petiole length (Van der Sman et al. 1988, Voesenek et al. 1989). In addition, stimulated stem growth in response to soil flooding was observed in generative *R. maritimus* plants (Van der Sman et al. 1988). Rumex from seldomly flooded field locations, such as *R. acetosa,* showed a different type of response in which no growth enhancement of the existing petioles occurred, whereas petioles which developed entirely during the waterlogging treatment showed a small, but significant, increase in length (Voesenek et al. 1990A).

The role of ethylene in the physiology of flooded roots has not been extensively studied for *Rumex* species. However, in flooded maize roots there is convincing evidence that the lysigenous type of aerenchyma is induced by enhanced ethylene levels (Drew et al. 1979, Konings 1982). The role of ethylene in the lysigenous breakdown of cortical cells in rice seems to depend on the type of cultivar: Jackson and coworkers (1985B) found no effect of

ethylene, whereas a small promotion of aerenchyma formation was demonstrated by Justin and Armstrong (1991) in another cultivar; flooded conditions are known to increase porosity in some cultivars (Armstrong 1971). Nothing is known about the inductive mechanisms in the schizogenous type of aerenchyma, which develops extensively in flooding-resistant *Rumex* species (Armstrong et al. 1991). It will be worthwhile to study whether ethylene promotes aerenchyma formation in *Rumex* and also whether interspecific differences in gas-channel development, as observed in this genus, are related to differences in internal ethylene concentrations and/or sensitivities towards this gaseous growth regulator.

It is well known that ethylene influences the rate of root extension. Under well-aerated conditions, low ethylene levels (0.02–0.1 ppm) stimulate root extension, whereas high concentrations (1–10 ppm) inhibit root growth in rice and tomato (Jackson 1985B). Interspecific variation between both species was observed in the ethylene concentration that actually stimulates root growth and in the degree of growth inhibition at high ethylene levels (Jackson and Pearce 1991). The internal ethylene concentration of a flooded root depends on its ethylene production level, the surface area/volume ratio, the permeability of the surface layers, the root porosity, and the depth of the covering water layer (Konings and Jackson 1979). The final responses in terms of root extension will also depend on the sensitivity of the root tissue to partial pressures of ethylene (Jackson and Pearce 1991). Laan (1990) related the interspecific variation in root growth of primary and newly formed laterals in the genus *Rumex* to differences in root porosity and the concomitant ability to use internal aeration. In addition, it is important to broaden our knowledge on the role of the ethylene economy in the process of root extension of waterlogged *Rumex* species.

According to criteria formulated by Jacobs (1959) and Jackson (1987), there is convincing evidence that ethylene plays an important role in the regulation of *Rumex* shoot growth in response to waterlogging. The enhanced petiole growth in *R. crispus* and *R. palustris* is accompanied by a significant increase in the ethylene production of the shoot. This production increase starts within a few hours after the onset of the waterlogging treatment. It reaches its highest production rate after 5–6 h. After a sharp decrease, the production again gradually increases up to approximately $10 \ nl \ gDW^{-1} \ h^{-1}$ after 7 days of waterlogging (control production, $0.5–1.5 \ nl \ gDW^{-1} \ h^{-1}$). During this second increase, a distinct circadian rhythm was observed in the formation of ethylene. *Rumex acetosa,* showing no stim-

ulation of growth by the youngest petiole, increased its production level by only twofold during the same time course. The difference in ethylene production in response to waterlogging between *R. acetosa* and *R. palustris* correlates well with changes in ACC levels in the shoots of these species. Additionally, a slight, but reproducible, increase in the activity of the ethylene-forming enzyme (EFE), catalyzing the conversion of ACC to ethylene, was observed in all species (Voesenek et al. 1990A). Bradford and Yang (1980, 1981) showed (for waterlogged tomato plants) that ACC accumulates in the roots and subsequently is transported to the shoot where conversion to ethylene takes place. It is possible that such a process occurs in waterlogged *Rumex* plants, but some movement of ethylene from the root to the shoot via aerenchyma channels cannot be ruled out (see Jackson and Cambell 1975, Zeroni et al. 1977).

The stimulation of petiole growth in *R. crispus* and *R. palustris* in response to soil flooding can be mimicked by exposing air-grown plants to elevated levels of ethylene. A partial pressure of 0.5 Pa was necessary to saturate the response. *Rumex acetosa* showed a very different response to exogenous ethylene. High concentrations significantly inhibited petiole growth; low partial pressures (0.1 Pa), however, demonstrated a trend towards a slight growth stimulation (Voesenek and Blom 1989A).

Ethylene production in *Rumex* plants under waterlogged conditions was significantly reduced when they were pretreated with AVG, an inhibitor of ethylene biosynthesis. This treatment also significantly reduced the stimulated petiole growth. Identical results were obtained with Ag$^+$ ions, inhibitors of ethylene action (Voesenek et al. 1990A).

The regulating role of ethylene in the shoot growth of waterlogged *Rumex* species has also relevance to higher levels of organization. Both *R. crispus* and *R. palustris* increased their petiole length in response to excess water under field conditions. *Rumex acetosa*, on the other hand, showed no significant growth stimulation (Voesenek and Blom 1989A).

Rumex species differ strongly in their ethylene economy. The growth of petioles of *R. acetosa* is inhibited by high ethylene concentrations. High levels in the shoot of this species are probably prevented under waterlogged conditions since the ethylene production increases only slightly. Low momentary internal ethylene concentrations may even slightly stimulate the growth of newly developed petioles. This is in accordance with the occurrence of *R. acetosa* in moist hayfields with high ground water levels. Both *R. crispus* and *R. palustris* are characterized by enhanced petiole growth in response to high ethylene levels. If we assume that

elongating petioles is an adaptive trait under waterlogged conditions, a strong enhancement of the ethylene production must be favorable to this growth response. The petiole growth is probably functionally related to an increase of the photosynthetic area and maximal diffusion of oxygen to the oxygen-deficient roots, if a large part of the shoot protrudes above the raised water level. Since both *R. crispus* and *R. palustris* commonly grow in frequently flooded parts of Dutch river areas, where waterlogging is a transient phase between periods with drained soils and periods with complete submergence, their ethylene economy corresponds well with their field distribution.

Ethylene and Submergence

Within a few hours after complete submergence the laminae and petioles of wetland *Rumex* species like *R. maritimus, R. palustris, R. crispus* alter their orientation from prostrate to vertical. This is accompanied by a significant stimulation of the growth rate of both petioles and laminae. The strongest growth enhancement is achieved in the youngest petioles (Laan and Blom 1990, Van der Sman et al. 1991, Voesenek and Blom 1989A, B). This shoot elongation response is observed in many other species occurring in the interface regions between land and water (see Table 1; Osborne 1984, Ridge 1987, Schwegler and Brändle 1991). In *Rumex* species this petiole elongation can, to a great extent, be attributed to increased cell expansion (Voesenek et al. 1990B). In other plant species, like *Ranunculus repens* and *Nymphoides peltata,* with comparable petiole responses to submergence, a relatively great contribution of cell division to the total elongation response was demonstrated (Ridge 1985). *Rumex acetosa,* a representative from infrequently flooded field sites, showed no stimulated shoot extension in response to complete submergence (Voesenek and Blom 1989A).

The enhanced shoot growth is functionally related to the restoration of contact between the shoot and the atmosphere. This enables the continuation of aerobic respiration, aerial photosynthesis, and wind- or insect-mediated pollination (Jackson 1985A). Lower shoot, taproot, and lateral root biomass were observed in continuously submerged *R. maritimus* plants when compared with plants with their leaf tips protruding (7 cm) above the water. When the water surface was not reached under greenhouse conditions, all *R. maritimus* plants died within 4 weeks (Laan and Blom 1990). In an experiment, presented in Table 3, survival of three *Rumex* species, with different field locations in a

Table 3. The survival (%; N = 8) of *Rumex* species after 1 week of complete submergence followed by various durations of partial (2–4 cm of the leaf tips protruded above the water surface) and complete submergence.

Species	Duration (weeks)	Partial submergence	Complete submergence
R. acetosa	3	88	38
	6	0	0
	9	0	0
R. crispus	3	100	100
	6	100	38
	9	100	13
R. palustris	3	100	100
	6	100	50
	9	100	0

flooding gradient, was studied under partially submerged conditions (leaf tips protruded 2–4 cm above the water surface), as well as complete submergence. All plants of *R. crispus* and *R. palustris* survived under the partially submerged conditions, whereas severe mortality occurred when no leaf parts protruded from the water surface. In *R. acetosa* no survival was observed after prolonged partial and complete submergence. The long diffusion pathway under partially submerged conditions, in combination with a limited development of aerenchyma, presumably prevented any improvement in oxygen status of the roots in this species. In summary, shoot–atmosphere contact is of the utmost importance for the survival of flooded *Rumex* plants, but the efficiency in which this enhanced shoot growth can aerate the root system and can contribute to an increased survival, depends on the porosity of both shoot and root systems.

Rumex maritimus behaves as an annual when it germinates before the end of June. However, plants that germinate in April and May will give the largest seed production (Van der Sman et al. 1991). Since seed germination in *Rumex* is obligately aerobic (Voesenek 1990), timing of seedling emergence in the field depends on withdrawal of the flood water. Highly elevated sites will be characterized by tall *R. maritimus* plants that flower early, while the lower zones contain mainly short rosette plants due to delayed germination. Unpredictable flooding in the middle of the growing season will lead to submergence of *R. maritimus* in various stages of the life cycle, such as rosette, bolting stage, or at flowering. These stages strongly differ in petiole and stem (internode) elongation responses to complete submergence (Fig. 4). The rosette stage was characterized by a rapid extension of petioles. This elongation was much less in the bolting stage, although a strong growth enhancement was observed in the in-
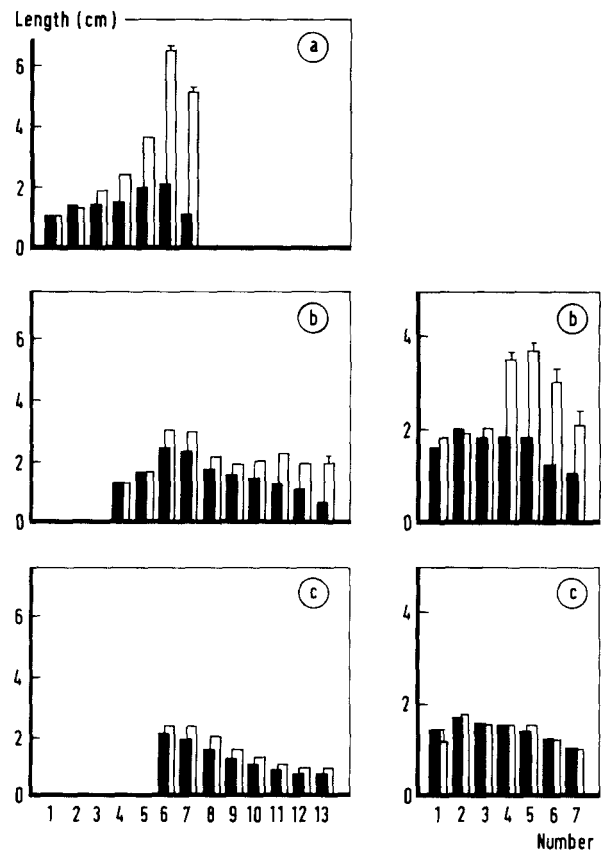

Fig. 4. Petiole (left) and internode (right) lengths (+ 1 SE; SEs ⩽ 1 mm are not indicated) of *Rumex maritimus* plants after 4 days of submergence (open bars), in comparison with nonsubmerged plants (closed bars), in three stages of development: (a) rosette; (b) bolting; (c) flowering. Numbers indicate leaves and internodes in the order of appearance with the first internode stretched between leaves 6 and 7. The last two leaves and the last internode in stages (a) and (b) were initiated during the treatment.

ternodes. In the flowering stage, extension of both petioles and internodes was almost nonexistent (Fig. 4). This shift from extension of petioles to elongation of internodes and the decrease of the enhanced growth response upon flooding in the course of the development of a flowering plant stresses the importance of studying all parts of the life cycle (see Blom 1979, Grime 1979). Because of its short life cycle, *R. maritimus* is very suitable for studies on the impact of stem elongation on seed production. This fitness-related parameter was significantly reduced in flooded plants, when compared with drained ones (Fig. 5). The amount of shoot elongation, expressed as final stem length, was positively correlated with seed output. Very low seed production was recorded for plants that exhibited little or no elongation and therefore be-
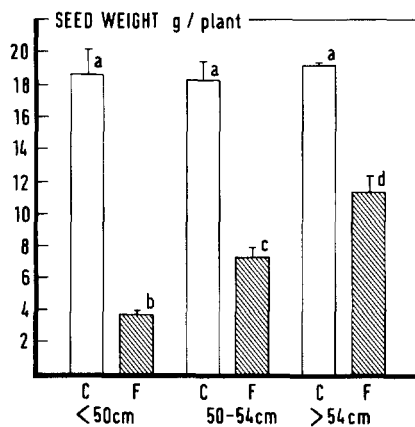
Fig. 5. The seed output of three length classes of *Rumex maritimus* (g/plant; N = 3–5; +1 SE) in response to drained (C) and flooded (F) conditions. During this last treatment, ethylene-mediated internode elongation occurred during the bolting stage. Means with the same letters are not significantly different.

longed to length class <50 cm. Intermediate seed production was observed in the 50–54 cm length class, whereas most seeds were produced by plants with the largest amount of shoot tissue above the water surface (Fig. 5). This effect cannot simply be explained by variation in biomass since no significant differences in seed output were observed between the same length classes grown under non-flooded conditions (Fig. 5).

Both petiole and stem elongation in *Rumex* species under submerged conditions can be correlated with increased internal concentrations of the gaseous plant hormone ethylene (Van der Sman et al. 1991, Voesenek and Blom 1989A, Voesenek et al. 1992C). The growth rate of *R. crispus* and *R. palustris* petioles increases within 5 hours; this matches the kinetics of the rise in the endogenous ethylene levels (Voesenek and Blom 1989B). The internal ethylene concentrations are enhanced in all studied *Rumex* species, including those with no growth stimulation. Experiments with the laser-driven photoacoustic detection technique showed us that large differences in endogenous ethylene levels can occur between and within the various *Rumex* species, after 24 h of submergence. *Rumex palustris* showed an internal concentration of 3–5 nl/ml under these conditions. *Rumex acetosa*, a representative from seldomly flooded locations, contained 1.5–6 nl/ml. Since enhanced ethylene levels in submerged plans are partly a consequence of the 10,000 times slower diffusion rate in water compared to air, the influence of water depth and surface area/volume ratio cannot be ignored. Deeper water and thicker tissue increase the entrapped ethylene levels (Jackson

1985B). Neither water depth nor surface area/volume ratio were, however, a source of variation in the experiments comparing the internal ethylene concentrations of *R. acetosa* and *R. palustris* under submerged conditions. The endogenous ethylene concentration is determined not only by the efflux of this gas to the external environment, but also by the rate of production. Preliminary results with two-compartment cuvettes, which separate the ethylene produced by shoot and root, indicate that neither *R. palustris* nor *R. acetosa* increase their rates of ethylene production in the shoot during a 24-h submergence period (Voesenek, unpublished observations). However, an enhanced ethylene biosynthesis in the shoot under submerged conditions can occur as was demonstrated for deep water rice (Cohen and Kende 1987, Kende et al. 1984, Raskin and Kende 1984B). Extra ethylene production, above the level induced by submergence, was observed after de-submergence of *R. maritimus* in the bolting stage (Van der Sman et al. 1991) and *R. palustris* in the rosette stage (Voesenek et al. 1992C). It is possible that accumulated ACC, due to submergence, was only partly converted to ethylene. The remaining ACC may have been converted to ethylene after de-submergence (Van der Sman et al. 1991).

The presence of other hormones, such as auxin, gibberellin, or abscisic acid, seems essential for ethylene- or submergence-induced shoot elongation. This aspect of the physiology of "depth accommodation" is extensively studied and discussed for various plant species (Cookson and Osborne 1978, Hoffmann and Kende 1991, Horton and Samarakoon 1982, Jackson 1985A, Jackson and Pearce 1991, Malone and Ridge 1983, Musgrave et al. 1972, Osborne 1984, Raskin and Kende 1984C, Ridge 1987, Walters and Osborne 1979). There is experimental evidence that gibberellin is involved in petiole elongation of *R. palustris* in response to exogenous ethylene and submergence (Fig. 6). Paclobutrazol, an inhibitor of the gibberellin biosynthesis at the ent-kaurene to ent-kaurenic acid conversion step, partly inhibits petiole elongation during submergence and external ethylene application. Under submerged conditions this effect could be reversed by addition of GA_3.

Shoot elongation in response ethylene may also interact with CO_2 concentration, O_2 concentration, light quantity and quality, buoyant tension, and the availability of water (Ridge 1987). These factors provide a reasonable explanation for the slightly reduced elongation response in *Rumex* and deep-water rice in response to exogenous ethylene compared to growth under submerged conditions (Raskin and Kende 1984B, Van der Sman et al. 1991, Voesenek and Blom 1989A).
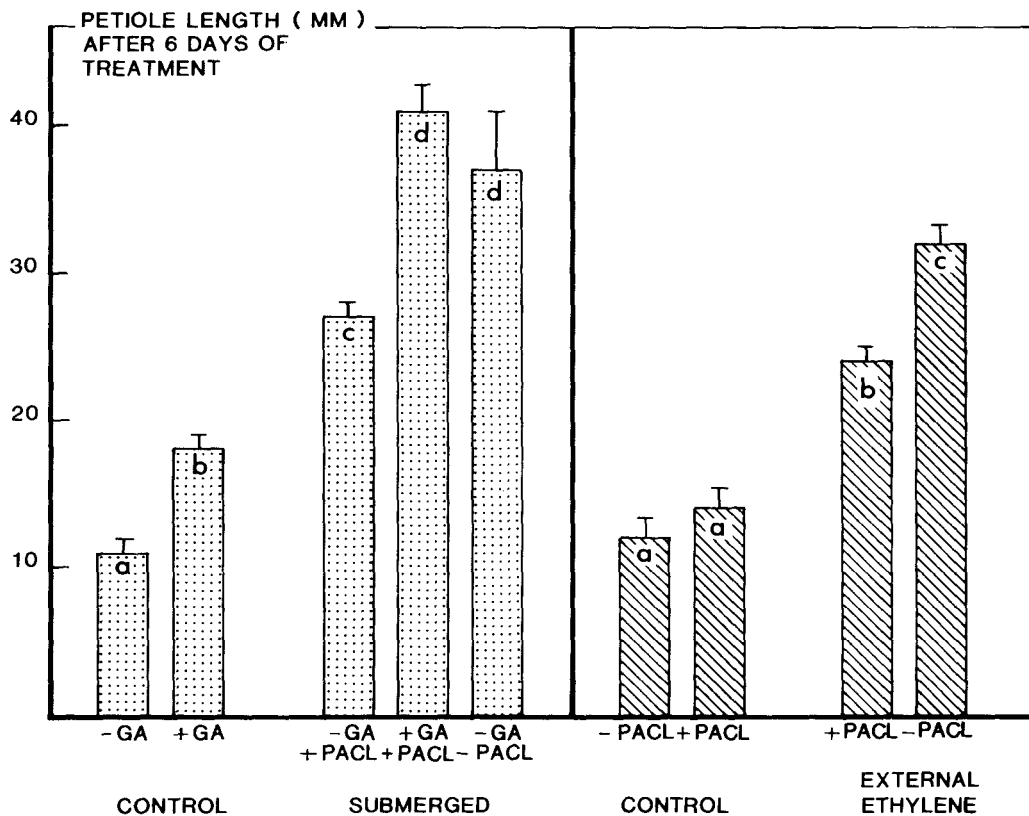
Fig. 6. Petiole length of *Rumex palustris* (N = 9–13; +1 SE) in response to addition of GA$_3$ (5 µM) and/or paclobutrazol (1 µM pretreatment of 4 days and 0.1 µM in the flooding water) under control and submerged conditions and under exogenous ethylene application. Means with the same letter within the submergence and ethylene experiment are not significantly different.

In response to submergence, wetland *Rumex* species accumulate large amounts of ethylene in their intercellular spaces and probably also in their cells. These high levels can to a great extent be explained by entrapment due to the slow diffusion of ethylene in water. In accordance with the ethylene sensitivity of petioles, stems, and laminae, these high concentrations lead to a rapid restoration of the shoot–atmosphere contact in these species, whenever the flooding is not to deep. Since these species occur in frequently flooded areas, in which 70% of the floods in the growing season do not exceed a maximum water depth of 100 cm (AJM van der Sman, personal communication), their ethylene economy corresponds well with their field distribution. The extra ethylene production after de-submergence, essential to maintain a high internal ethylene concentration, might be related to a continuation of growth to establish a substantial part of the shoot above the water surface (Van der Sman et al. 1991).

Growth-inhibitory high levels of ethylene can oc-cur in *R. acetosa*, a species from seldom-flooded field sites.

It is our belief that these two groups of *Rumex* species (group I, *R. acetosa* and *R. thyrsiflorus;* group II, *R. palustris, R. crispus,* and *R. maritimus*) from contrasting sites in a flooding gradient, illustrate two examples in a continuum of strategies, in which the ethylene economy of plant species plays an important role in flooding resistance and field distribution. Species group I is probably not at one extreme of such a continuum. An intriguing question and one of the research goals for the future is how the balance between ethylene sensitivity and internal concentration is tuned in species that are even more intolerant of flooding than *R. acetosa* and *R. thyrsiflorus.*

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