Flooding: the survival strategies of plants

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River floodplains are attractive places to settle for plants, animals and, since the beginning of agriculture, people. Human habitation of floodplains is steadily increasing worldwide, as the benefits of living in a floodplain apparently outweigh the risks of flooding, a phenomenon that is also occurring increasingly throughout the world. The most common origin of flooding is heavy rainfall or rapid melting of snow upstream. Despite their seasonal component, the timing and duration of the natural inundation periods are often unpredictable. The probability of flooding is greatly increased by human activities such as removal of natural vegetation, improvement of drainage systems, overgrazing by cattle, and straightening of meanders to facilitate shipping. Precipitation reaches the stream system more directly and faster, often with a large load of sediment, enhancing the chance of flooding. To accommodate higher discharge, deepening and widening of the riverbed, as well as channelling, have been carried out in the upper reaches of many river systems. However, this causes increased downstream discharges and floodings.

Vegetation zones in the floodplain often reflect differences in flooding stress at the individual plant level. Only pioneer plants are able to establish in the open environment adjacent to the river stream itself. Species from the more elevated sites that are seldom flooded mainly belong to later successional stages. Species from the mid-successional stages occur in the intervening, regularly flooded zones. In flooding experiments, these species have tended to be overlooked because of the assumption that their characteristics are between those of early- and late-successional species[1]. In contrast, middle zones are included in descriptive and qualitative synecological methods that are used to develop models of establishment and regulation of river floodplain vegetation. Field studies and models show that wave action, current, flooding duration, exposure, fertility patterns and human intervention explain species composition in the floodplain (see Fig. 1)[2–4]. Also, physical soil characteristics in combination with flooding duration and frequency strongly determine the phytosociological position of floodplain vegetation[5].

In a recent study, vegetation types of riverine wetlands were distinguished according to a strategy concept[6] in three river areas encompassing much of the climatic range of Europe. The prediction of strategy at the vegetational level was possible on the basis of simple morphological trait data at the population level. Plant strategies of the riverine wetland plants were shown to be determined by competitiveness and stress tolerance, rather than by tolerance of disturbance (flooding and grazing).

Transient floods, particularly, induce vegetation zonation and small-scale spatial heterogeneity in terms of oxygen (O_2) and nutrient availability[7,8]. This permits multiple species coexistence[9] and enables us to study the adaptive re-

Floodplains and wetlands are highly suitable for plant ecological studies, whether for agricultural interests, nature conservation or basic science. Traditional work has entailed a descriptive approach at the community or individual plant level. Nowadays these studies are evolving into physiological research on relationships between flooding stress and vegetation zonation. Current experiments aim to unravel the adaptive mechanisms whereby terrestrial plants cope with the peculiar conditions of the floodplain, from the whole plant down to the cell.

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sponses of plants to flooding along two lines of research. The first is the 'more species – one habitat' approach. Many species are living together in one place; they all face similar environmental conditions, but they may possess different adaptive strategies. Part of this approach in floodplains is the comparison of the various zones, each with its own characteristic combination of species. Based on the knowledge obtained in community studies, the second line of research 'one genus – more habitats' can be followed. Species belonging to phylogenetically related groups, and growing in various zones in the floodplain, are facing contrasting environmental conditions. They all have their own survival strategies reflecting adaptations to their specific environment[10]. These species may serve as models in detailed experimental studies.

Alterations in soil–plant relationships

Apart from frequency, duration and timing, different depths of flooding can be distinguished, ranging from soil flooding or waterlogging to total submergence of the vegetation. Adaptive strategies of plants are directed to survival of these various conditions[11–13].

Gas diffusion is severely inhibited in flooded soils[14]. Oxygen remaining in the soil is consumed by aerobic processes in roots and soil organisms, resulting in a soil with a severely reduced O_2 partial pressure in which availability of nutrients for plants strongly decreases[15]. Under these conditions, important O_2-dependent microbial processes, such as nitrification, will no longer take place. Moreover, toxic substances accumulate[16] that originate from the anaerobic metabolism of plants or bacteria. Once the remaining O_2 is consumed, different groups of bacteria use inorganic compounds as electron acceptors in a well-defined sequence of anaerobic reduction oxidation processes, resulting in a further decrease of the soil redox potential.

The first anaerobic process to occur is the reduction of nitrate to nitrogen or ammonium ions, followed by the reduction of manganese and ferric oxides, respectively[15]. The reduced ions that are produced are toxic to plants. Thereafter, at redox potentials between −75 and −150 mV, sulphate is reduced by several genera of strictly anaerobic bacteria. The toxic sulphide enters the plant apparently without any control[16].

Another effect of flooding is a change in the physical status of the soil: waterlogging causes the breakdown of large aggregates into smaller particles[7]. As the water level declines, these small parts are rearranged in a more dense structure, creating smaller soil pore diameters, higher mechanical resistance to root penetration, low O_2 concentrations and the inhibition of resource use[7]. In spite of the flooded and compacted soil, many plants are able to escape from the adverse conditions in space and time, because of specialized life history strategies.

Life history adaptations to flooding

Many plants are able to avoid the adverse effects of submergence by timing of important life cycle events. Flooding influences seed dispersal, seedbank characteristics, germination, seedling emergence, establishment and survival, as well as growth and reproduction[17]. Water and (to a lesser degree) wind are the primary modes of dispersal of seeds in floodplains. Propagule floating capacities may last from minutes (e.g. *Scirpus lacustris*) to more than 1000 hours (*Iris pseudacorus*)[18]. Flood-related environmental factors are often responsible for seedling mortality of light-seeded, autumn-dispersing species, such as *Ilex decidua*, *Liquidambar styraciflua* and *Carpinus caroliniana*[19]. Some woody species, such as *Quercus nigra*, are able to avoid peak periods of flooding in winter and spring by producing heavy seeds late in summer. Species emerging in the early spring generally survive flooding in summer.

Spatial and temporal variation in seedling composition of riverplain forests result from (1) the interaction of emergence phenology with the occurrence of environmental disturbance by flooding, and (2) the ability to increase rapidly in numbers during favourable periods. Riverbanks are mainly inhabited by short-lived species, exhibiting strategies characterized by fast turnover rates. A comparison of the life histories of two of these species, *Chenopodium rubrum* (an annual) and *Rumex palustris* (a biennial), revealed that during the short period of water recession between two floods *Chenopodium* completes its life cycle very quickly and produces seeds that will survive the next flood. In contrast, *Rumex palustris* plants survive flooding in a vegetative state and postpone flowering and seed production to the next year[8].
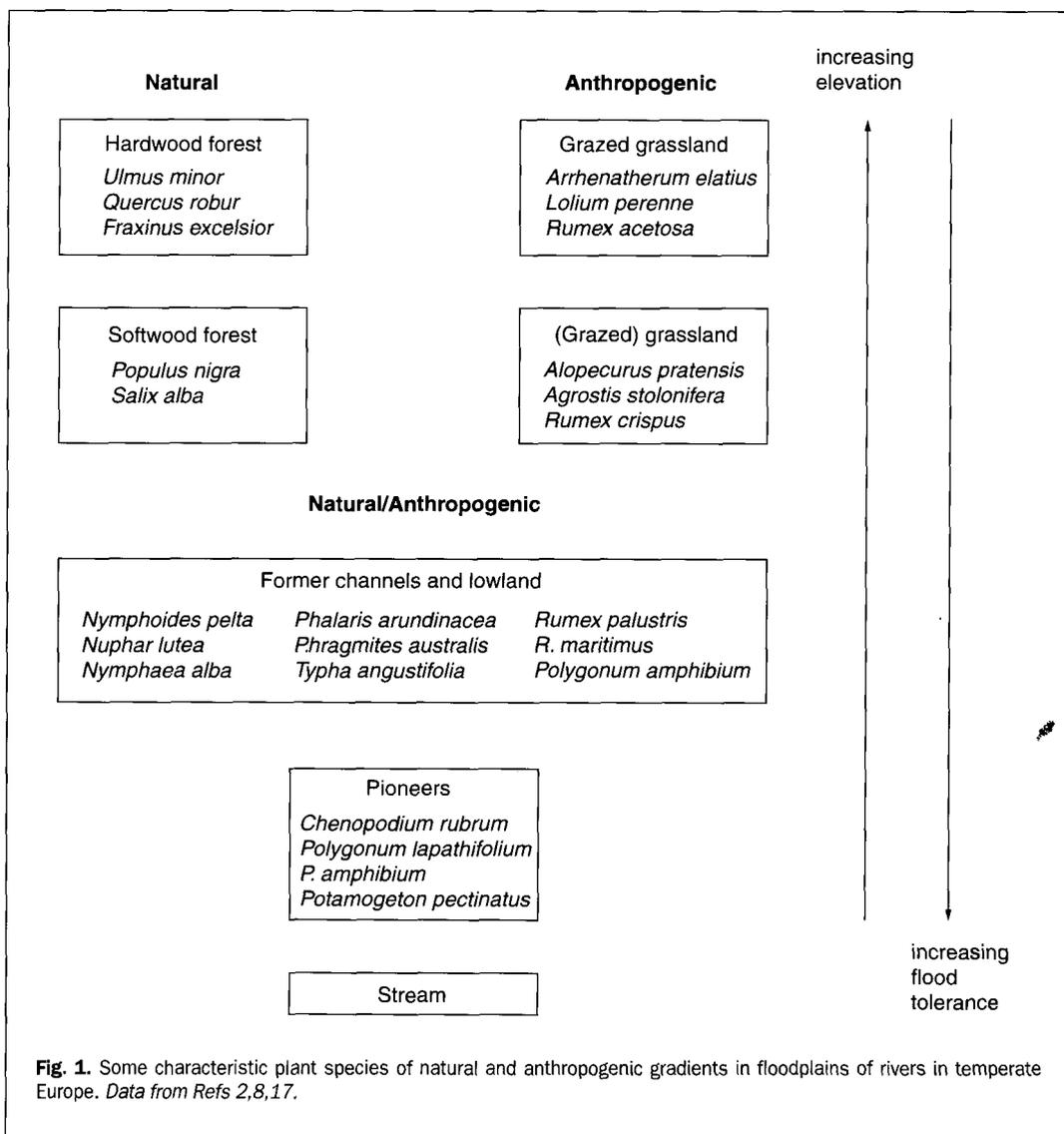
Short-term metabolic adaptation

The main effects of flooding on plant functioning can be mimicked by exposing roots to subambient partial pressures of O_2, indicating that O_2 shortage is one of the most important constraints during flooding[20,21]. Plants in floodplains display a range of mechanisms to live temporarily without O_2. Metabolic acclimation can help plants to tolerate O_2 stress for a relatively short period. The immediate consequence in higher plants is that ATP generation through aerobic respiration cannot continue. However, glycolysis can take place during anoxia in the plant as long as the generated NADH can be oxidized into NAD. There is increasing consensus that the main route for this in higher plants is ethanolic fermentation[22,23]. This metabolic pathway allows reoxi-

dation of pyrimidine nucleotides and (because of continued glycolysis) also some ATP production, although the rate of generation is much slower than under fully aerated conditions. At the molecular level, O_2 deficiency induces the production of a set of approximately 20 polypeptides, the so-called anaerobic stress proteins (ASPs)[24]. Several of these ASPs are enzymes of the glycolytic and fermentative pathway.

At complete submergence, plants not only face reduced gas exchange but also changed light conditions, which undoubtedly severely affects photosynthesis. In submerged terrestrial plants, photosynthesis will also be limited by the use of carbon dioxide (CO_2) as the only carbon source. Therefore, submerged plants that are able to photosynthesize at a low CO_2 level and to reduce their respiratory rate have a great advantage[25].

Some submerged terrestrial species (e.g. *Poa pratensis* and *Cardamine amara*) and many homophyllous amphibious species (e.g. *Veronica beccabunga* and *Myosotis palustris*) have photosynthetic rates exceeding $3.5\,mg\,O_2\,(gDW)^{-1}h^{-1}$, which allow growth under water. Photosynthetic rates in submerged leaves of heterophyllous amphibious plants (e.g. *Callitriche* and *Sparganium* species) exceed $7.9\,mg\,O_2\,(gDW)^{-1}h^{-1}$, which compares well with submerged aquatic macrophytes[26]. Submerged or floating leaves of heterophyllous species are flexible, thin and linear and have a thin cuticle and epidermal

Natural

Hardwood forest
Ulmus minor
Quercus robur
Fraxinus excelsior

Softwood forest
Populus nigra
Salix alba

Anthropogenic

Grazed grassland
Arrhenatherum elatius
Lolium perenne
Rumex acetosa

(Grazed) grassland
Alopecurus pratensis
Agrostis stolonifera
Rumex crispus

increasing elevation

Natural/Anthropogenic

Former channels and lowland		
Nymphoides pelta	*Phalaris arundinacea*	*Rumex palustris*
Nuphar lutea	*Phragmites australis*	*R. maritimus*
Nymphaea alba	*Typha angustifolia*	*Polygonum amphibium*

Pioneers
Chenopodium rubrum
Polygonum lapathifolium
P. amphibium
Potamogeton pectinatus

Stream

increasing flood tolerance

Fig. 1. Some characteristic plant species of natural and anthropogenic gradients in floodplains of rivers in temperate Europe. *Data from Refs 2,8,17.*
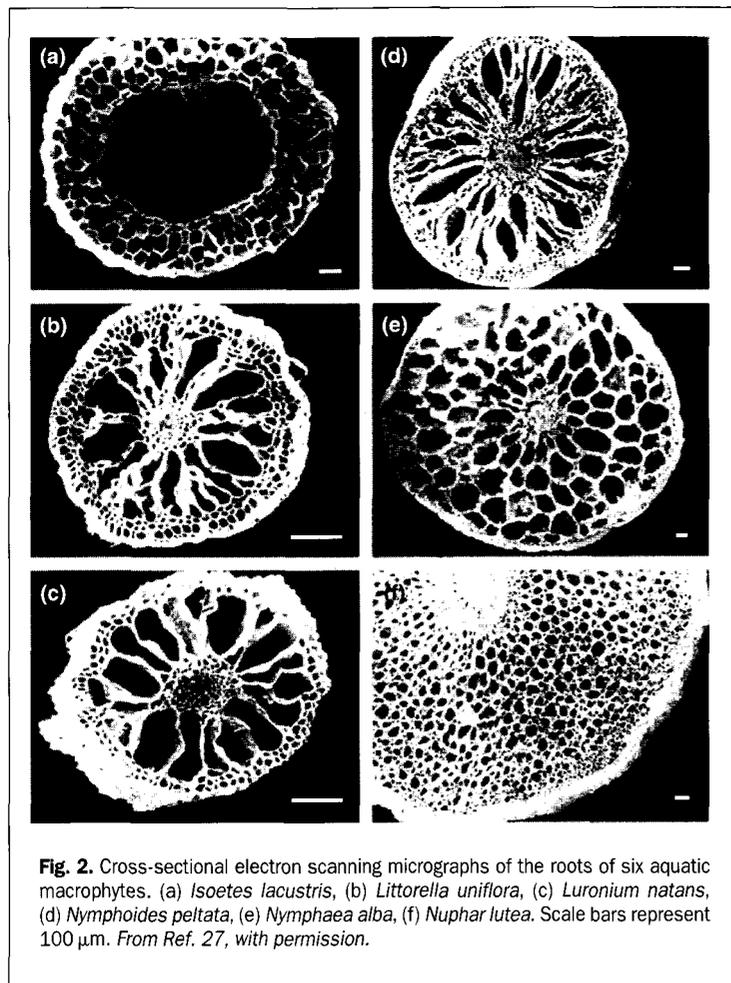
Fig. 2. Cross-sectional electron scanning micrographs of the roots of six aquatic macrophytes. (a) *Isoetes lacustris*, (b) *Littorella uniflora*, (c) *Luronium natans*, (d) *Nymphoides peltata*, (e) *Nymphaea alba*, (f) *Nuphar lutea*. Scale bars represent 100 μm. From Ref. 27, with permission.
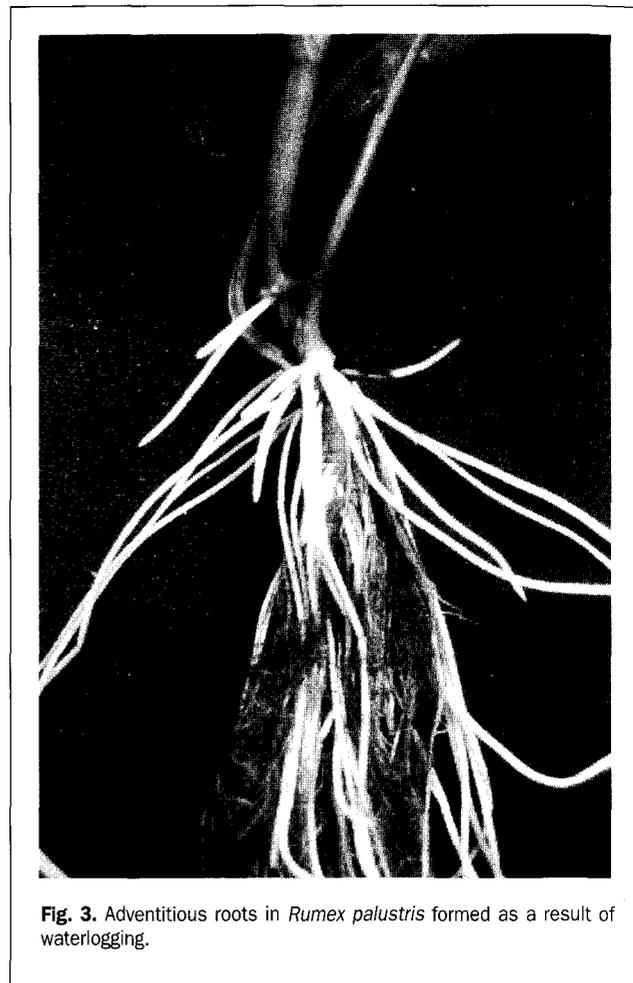

Fig. 3. Adventitious roots in *Rumex palustris* formed as a result of waterlogging.

chloroplasts, reducing resistance to CO_2 transport. The reduced photosynthesis at submergence in homophyllous, less adapted terrestrial and amphibious plants leads to an inadequate supply of carbohydrates to the plant, which strongly decreases the survival chances in the longer term.

Long-term responses in the root

Many flood-resistant plants are able to develop avoidance mechanisms to survive long-term floods. These adaptations are based on rapid changes in physiological processes, often displayed by shifts in anatomical and morphological characteristics. Upon flooding, the initial effects in plants are in the root system. The most important response in roots to extended periods of flooding is the formation of aerenchyma (aerated tissue) either by cell collapse (lysigeny) or by the enlargement of intercellular spaces resulting from cell separation without collapse (schizogeny)[14]. Aquatic plants such as *Nymphoides*, *Luronium* and *Littorella* species (but also *Zea mays*) possess the typical lysigenous form[27], and schizogeny can be found in wetland plants such as *Caltha*, *Rumex* and *Filipendula* species (see Fig. 2).

The primary lateral roots of most terrestrial plants are not able to develop effective adaptations towards flooding. They succumb during hypoxia and new, adventitious roots will develop within some days in flood-resistant plants[8,12,14]. These roots usually grow on the base of the shoot, the hypocotyl and upper part of the tap root and on stem nodes, mostly exploring the upper better aerated soil layers (Fig. 3).

The aerenchyma provides an interconnected system of air channels, enabling gases to diffuse or ventilate between plant organs. If plant parts emerge from the water surface, O_2 from the air reaches the roots and the rhizosphere. The downward supply of air, or photosynthetically derived O_2 and, in reverse, CO_2, ethylene and methane, are primarily physical processes.

Gas-phase diffusion can be measured by using microelectrodes to explore the longitudinal and radial distribution of O_2 in roots growing in stagnant anaerobic media. Models related to real measurements have been constructed for *Zea mays*[28]. Oxygen profiles appear to vary substantially with distance along the root (Fig. 4). These variations are, to a large degree, related to the O_2 supplying power of the cortex, which declines with the distance from the shoot. The experimental data showed a radial loss of O_2 from the cortex to the rooting medium; the O_2 concentration in the rhizosphere can be directly measured with a cylindrical platinum electrode[28]. Radial O_2 loss restores ion uptake and plant growth[7]. Plants with a shallow root system (e.g. *Betula* and *Picea* species) are less likely to suffer severe anaerobiosis, because they are growing above the deeper and wetter anaerobic soil region. An alternative mechanism is known from the mangrove genus *Avicennia*, which produces specialized roots that bend upwards to escape from the flooded soil[23].

Long-term responses in the shoot

Flooding of the upper plant parts may induce changes in physiology and morphology, often expressed as changes in growth patterns[8]. Some species immediately cease growth upon submergence, while others maintain or even increase biomass production. Shoot elongation that restores contact with the open air is a well-known adaptive response in flood-resistant plants[11,17,29,30], which restores or even accelerates growth and stimulates flowering and seed production[31]. Enhanced shoot elongation upon flooding is observed in

many semi-aquatic genera such as *Polygonum, Ranunculus* and *Rumex*[8,17,29,31–33]. The genus *Rumex* provides an excellent model for studying adaptation reactions upon flooding. Plants from dry sites all die upon flooding, whereas *Rumex* species from flood-prone habitats increase elongation rates of young petioles, laminae and internodes of bolting stems within a few hours and survive flooding[8,17,29,31].

Trade-offs between life history, growth and competitive efforts may affect flooding tolerance. *Polygonum lapathifolium*, an annual characterized by rapid initial growth rates with a high proportion of biomass allocated to shoots, does not react to flooding[32]. This species exhibits a short-term competitive advantage over perennials, which at least partly explains its ability to occupy unstable, recently disturbed areas with fluctuating soil-water levels. In contrast, *Polygonum amphibium*, a perennial thriving in standing water and waterlogged soils, shows increasingly higher shoot biomass at increasing flooding and strongly reduced growth in drained soils. In comparison with *P. lapathifolium*, this species is a weaker competitor regardless of flooding regime. So, short-term competitive performance, expressed as increased biomass production, was found to trade off with flood tolerance.
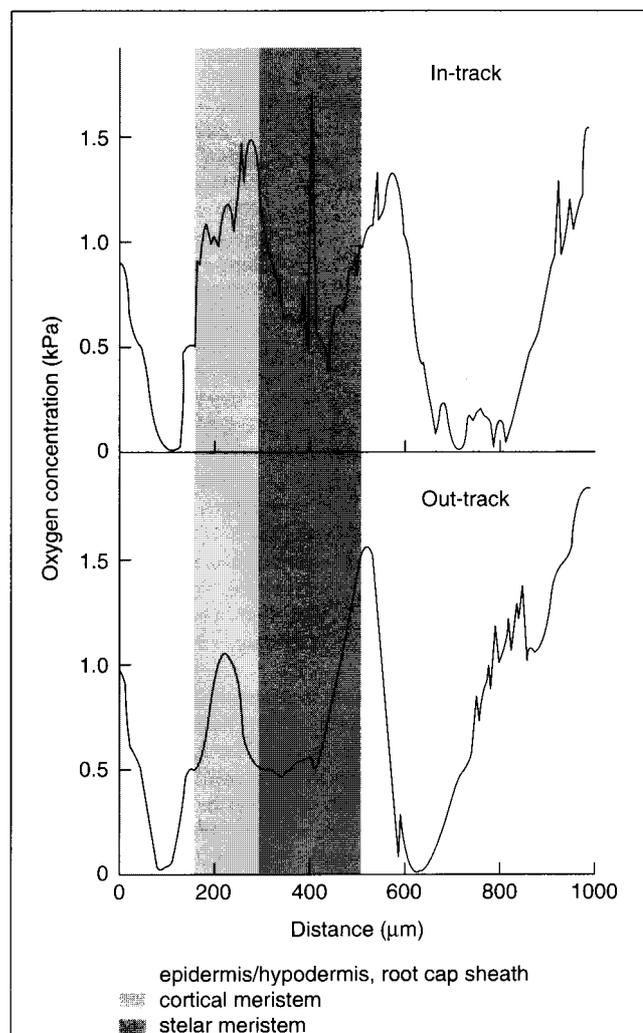

Fig. 4. Microelectrode polarographic 'radial' oxygen profile across primary root of maize (length approximately 90 mm) at an apical position within the zone of root cap sheathing of the meristem. 'In-track' refers to the movement of the electrode from the outside of the root to the central part of the root. 'Out-track' is the reverse movement. *From Ref. 28, with permission.*

Recent studies of biomass production of 20 wetland species raised under flooded, fertile and control conditions reveal clear competitive effect rankings that tend to be constant across environments, but are sensitive to the kind of neighbour[34]. Each vegetational zone in a gradient ranging from the riverbank to the non-flooded sites has its own characteristic group of species. The upper limits are determined by the competitive ability of co-occurring species, and the lower limits by their flooding resistances[8].

Hormonal regulation of adaptive responses

Phytohormones act as intermediates between environmental signals and the plant's responses to these stimuli. Because of its gaseous nature, the simple, 2-carbon hormone ethylene is well suited to signal a switch in the plant's environment from drained to overwet conditions (see Box 1)[29,35–39]. In submerged plants, ethylene levels rapidly build up, because the diffusion rate of this gas in water is approximately 10 000 times slower than in air, and because ethylene is hardly metabolized in most tissues[29,35,40,41].

Furthermore, the production rate of ethylene is stimulated by subambient partial pressures of O_2 (Refs 8,35). Ethylene promotes the formation of lysigenous aerenchyma in the cortex of roots of, for example, *Zea mays*. The programmed cell death in the cortex of maize roots is preceded by cell-wall degradation, which is linked to increases in the concentrations of cellulase (EC.3.2.1.4)[14]. The formation of schizogenous aerenchyma, characteristic of many wetland plants is, as far as we know, not under ethylene control. A new technique to measure ethylene is photoacoustic spectroscopy[41]. This technique makes it possible to measure endogenous ethylene concentrations and ethylene production rates in living plants, without physical perturbations (Box 2).

Ethylene is the key hormone in the initiation of enhanced elongation of leaves, petioles, internodes, coleoptiles and mesocotyls under submerged conditions[30,35,42] (Fig. 5). Growth rates of 25 cm per 24 h are recorded for certain floating-rice ecotypes, which may lead to a plant length of almost 7 m. The concerted action of low levels of O_2, ethylene, gibberellin and possibly abscisic acid regulates the fast growth of submerged stems in this species. A similar


Box 1. Ethylene biosynthesis and signal transduction

Ethylene, the simple 2-carbon phytohormone, is among the best-characterized regulators of plant growth and development. It plays a prominent role in processes such as germination, senescence, abscision, fruit ripening, and in the acclimation of plants to environmental stress. During overwet conditions, ranging from waterlogging to complete submergence, ethylene participates in the stimulation of shoot extension, the programmed cell death during aerenchyma formation and the initiation of adventitious root formation.

To unravel the adaptive mechanisms, the actions of two enzymes in the biosynthetic pathway of ethylene particularly determine the adaptive processes in higher plants. The enzyme ACC-synthase plays a role in the production of the intermediate 1-aminocyclo propane-1-carboxylic acid. The constitutive enzyme ACC-oxidase catalyses the conversion of ACC into ethylene. Environmental factors influencing these enzymes are flooding and reduced levels of oxygen.

Mutants of the annual crucifer *Arabidopsis thaliana* are an important tool in the elucidation of the ethylene signal transduction pathway. One of these mutants, the so-called ETR1 mutant, is insensitive to exogenously applied ethylene. The product of the *ETR1* gene, the ETR1 protein, probably acts very early in the ethylene signal transduction chain, perhaps as the receptor itself. The amino acid sequence of ETR1 shows a high similarity with a group of proteins very common in prokaryotic organisms, known as the two-component system. This communication module contains two proteins: a metal-containing sensor designed to sense ethylene and a response regulator that, indirectly, can affect gene expression[38]. The ETR1 protein also contains a hydrophobic domain demonstrating the membrane localization of this putative ethylene receptor[39].

Box 2. Laser-driven photoacoustic spectroscopy in flooding research
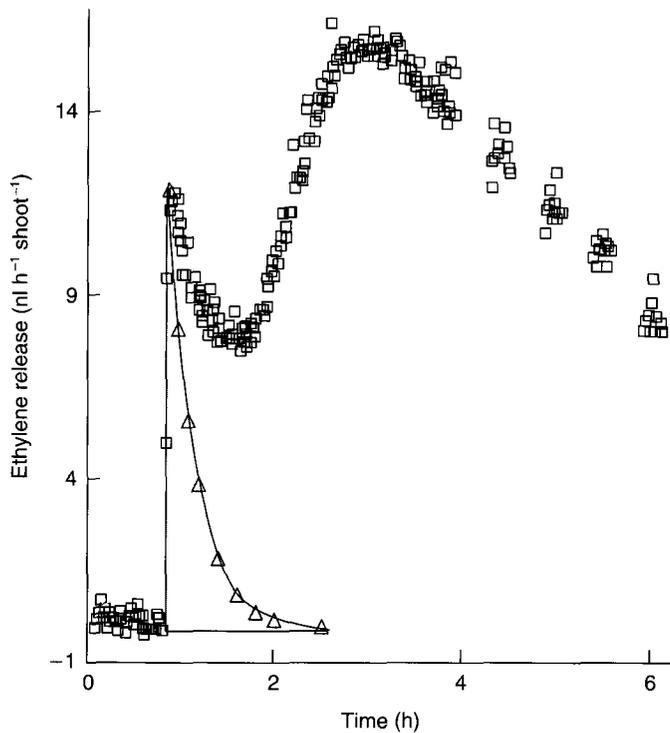
Laser-driven photoacoustic spectroscopy is a powerful technique to measure extremely low quantities of low molecular weight gases (e.g. ethylene) in living plants. Traditionally, ethylene production rates were measured by means of headspace analysis of accumulated gas evolved by excised tissue enclosed in small incubation vials. However, this procedure can disturb ethylene production by wounding, disruption of transport processes, gravitropic disorientation and changes in gas composition around the tissue[32]. The very high sensitivity of photoacoustic spectroscopy (10 pl l^{-1}) makes it possible to measure ethylene amounts directly evolved by plants growing in a cuvette and exposed to environmental stresses.

Photoacoustic spectroscopy was applied to measure accurately the endogenous ethylene concentration in shoots of Rumex palustris submerged for 24 hours. Submergence induces entrapment of ethylene due to its slow diffusion rate in water. However, upon de-submergence the accumulated ethylene will rapidly diffuse to the outside air owing to the very steep concentration gradient. De-submergence of shoots of R. palustris resulted in two ethylene release peaks, as shown in the figure. The first peak represents the endogenous concentration and corresponds with ethylene entrapped during the flooding period. (The shaded area represents ethylene concentration of 7.9 $\mu l\ l^{-1}$.) The ecological significance of this ethylene concentration is the accelerated growth of the plants in order to emerge above the water surface. The second peak was caused by increased biosynthesis of ethylene induced by de-submergence[41]. This extra ethylene increases the shoot height in the open air even more, which appeared to be positively correlated with the seed production[31].

Both peaks also provide information on the extent to which the endogenous ethylene production rate and concentration are regulated. It is important that we further our knowledge of the regulation of ethylene concentrations in plants in the near future because, to a large extent, ethylene economy determines the survival chances of plants in flooded areas.

Fig. 5. The length of Rumex petioles (white bars, R. acetosa; shaded bars, R. crispus; black bars, R. palustris) ($\pm$SE; $n = 12$) of different ages after (a) submergence, (b) exposure to an ethylene–air gas mixture (0.5 Pa), and (c) submergence in a silver nitrate solution, under laboratory conditions, expressed as percentages of controls grown in air. For each species and for each treatment, the length of the oldest (left) and youngest (right) petioles is given. The asterisk represents values that are significantly different from the control level [least significant difference (LSD); $P < 0.05$]; the asterisk in brackets represents values that are significantly different from submergence values (LSD; $P < 0.05$). From Ref. 42, with permission.

mechanism was suggested for elongating petioles of Rumex species[8,17,29,31].

In concert, both ethylene and auxin play important roles in the formation of adventitious roots. In contrast to experiments with cuttings[43], no accumulation of endogenous auxin is found in waterlogged intact plants of Rumex. Nevertheless, threshold levels of auxin appear to be essential for the induction of new roots, and recent experiments strongly indicate that ethylene sensitizes the root-forming tissue to auxin.

Screening of the hormonal regulation of adaptive responses in other species that occur in the various zones of the floodplain is a next step in flooding research. This
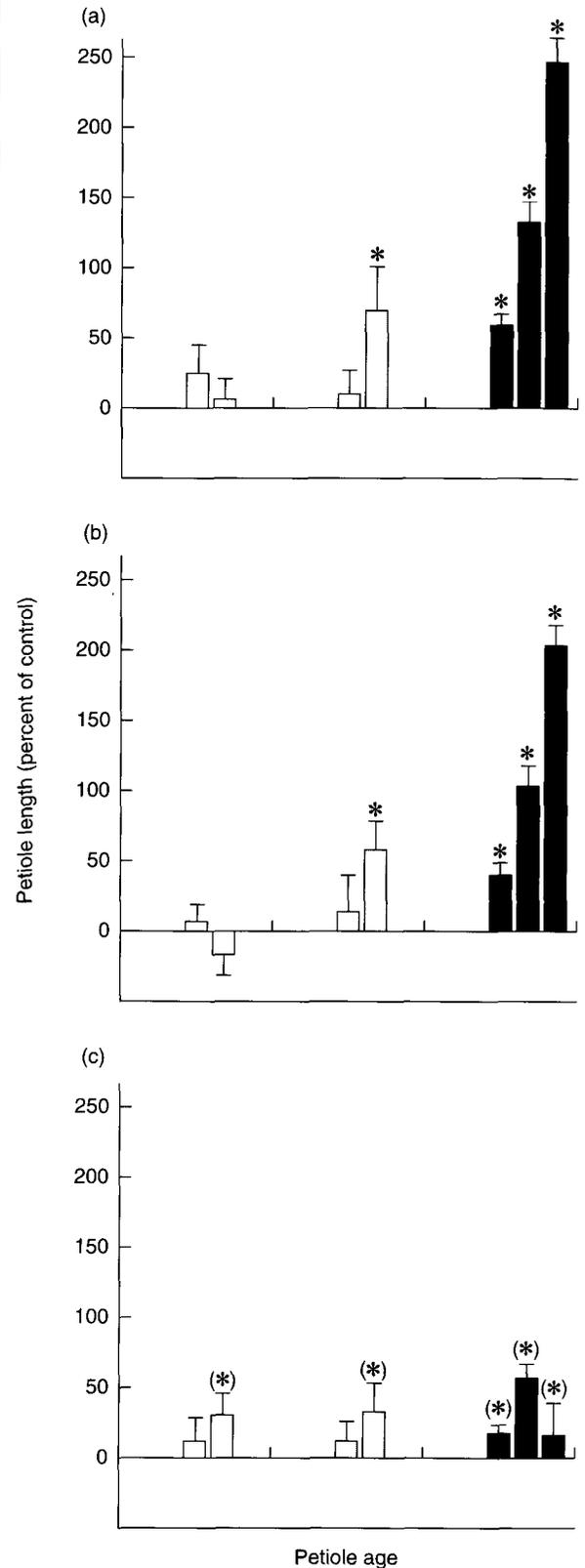
procedure will also validate the use of model species in plant ecology.

Future research

Increased insight into processes acting in plant communities under changing hydrological conditions will have valuable applications. Many areas all over the world suffer flooding disasters, and the restoration of damaged floodplains and the stocking of the river landscape with flood-resistant plants are topics of active research. Knowledge of adaptive responses of individual plants is necessary to understand the processes at the vegetation level. Many physiological and morphological reactions in plants are already known, but much has to be done on adaptive mechanisms at the cell level. Hormonal regulation plays an important role in the adaptation reaction, and in the near future we can expect progress in our understanding of combined actions of hormones. The photoacoustic technique is a powerful new instrument for measuring reactions of organisms living under environmental stress. Little is known about the signal-transduction chain upon flooding and about the genetic variation between plant populations that are exposed to long-lasting floods. Molecular biological techniques will be increasingly used to increase insight into these processes.

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