Biochemical and Ecological Similarities in Marsh Plants and Diving Animals

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Higher plants which can survive flooding have certain ecological and biochemical similarities with diving reptiles, birds, and mammals. The ecological similarities arise from the fact that these wet-land plants and diving animals are all terrestrial organisms which have re-entered the aquatic habitat as a retreat or ecological refuge free from interference by dry-land species. To survive in the wet-land or aquatic habitat species of terrestrial origin have to restrict their metabolic rate in the absence of oxygen and exploit a wide range of metabolic products to aid proton disposal and avoid the dangers of cell toxicity due to the accumulation of an excessive oxygen debt. In some plants metabolic adaptation to anoxia (low oxygen supply) resembles that found in animal parasites. It is a striking example of metabolic co-evolution that the retreat of so many terrestrial species of both plants and animals back to the low-oxygen habitat has been made possible by the exploitation of similar biochemical control mechanisms and pathways.

Fig. 1. The Egyptian water lotus (*Nymphaea lotus* L.), a typical example of the Nymphaceae; a dicotyledonous family living in aquatic habitats and showing the simplification of vegetative structure which is characteristic of all higher plants that have returned to the aquatic habitat

Evolution and the Tolerance of Anoxia

After the millions of years of evolution which were necessary for plant and animal life to make the transition from an aquatic to a terrestrial existence it is a curious paradox of evolutionary advancement that so many species have returned from land to the aquatic habitat. For species that are able to survive the hazards of inundation and submersion, water provides an ecological niche safe from the interference and predation of dry-land competitors. In animals the advantages of the aquatic habitat are clearly seen in turtles, crocodiles and other marine reptiles, for without the possibility of a sub-aquatic retreat it is unlikely that any of these species would be alive today. Even birds exploit the aquatic refuge as is evident from the large numbers of diving ducks, grebes, cormorants, and auks.

Among plants the fundamental division into monocotyledons and dicotyledons, first made by John Ray (1628–1705), has long been thought to have resulted from the return to the aquatic habitat of land-adapted species. Although taxonomic opinion differs in detail, there is general agreement that the modern monocots have evolved from a premonocot dicotyledonous group not unlike the modern Nymphaeales [1]. In a typical aquatic plant of the Nymphaeaceae such as the Egyptian water lotus (*Nymphaea lotus* L. Fig. 1) many of the vegetative structures essential for life in terrestrial plants have either degenerated or else are much simplified. These reductions include loss of secondary thickening, simplification of leaf structure, suppression of main root development and the reduction of the conductance system. These same vegetative

Fig. 2. An Indomalayan aquatic grass (*Hygroryza aristata* Nees.) which illustrates in its simplified leaf form the suitability of grasses to the aquatic habitat

Fig. 3. A marsh in the Orkney Islands colonized by cotton-grass (*Eriophorum angustifolium* Honck.) illustrating one example of the dominant role of monocotyledonous species in the development of wet-land vegetation

simplifications are also typical of monocot structure (Fig. 2). Although some authors dispute that the ancestors of the modern monocots were wholly aquatic, they do concede that they were at least amphibious, i.e, marsh plants capable of enduring a period of submersion. It is a striking corollary of this supposed evolutionary theory that so large a portion of the World's wet-land flora belongs to the monocots. Reeds, bamboos, rushes, and sedges constitute the bulk of the vegatation-mass in most of our swamps, fens, and bogs (Fig. 3).

The simplified structure of aquatic angiosperms in addition to promoting a greater physical flexibility

for life in lakes and marshes also aids the physiological fitness of the plants for these sites. The hollow stem, adventitious roots, and well developed aerenchyma which are common features in wet-land vegetation all aid the diffusion of oxygen from the photosynthesizing shoot to the submerged root. Nevertheless, in winter and when growth first resumes in spring, as well as in the germination of submerged seeds and at other times when unfavourable climatic conditions can limit photosynthesis, the metabolic activity of the submerged parts of these plants will depend on their ability to survive in the absence of oxygen. In dry-land plants any restriction of oxygen supply to either roots or seeds can be fatal if prolonged for many hours. The ability to survive in flooded soils will therefore require metabolic as well as morphological adaptation.

Metabolic Hazards of Anoxia

The return to the aquatic or wet-land habitat by either plants or animals has to resolve two basic biochemical problems; namely the disposal of protons in the absence of oxygen and the low energy yield from anaerobic as opposed to aerobic respiration. In purely aquatic species such as fish and marine algae the large surface contact between tissues and water as in the gills of the fish and the thallus of the sea-weed ensures a minimal tissue resistance to the diffusion of oxygen inwards and the outward diffusion of the waste products of respiration. This diffusive exchange process is impeded in terrestrial species by their more compact morphology. In higher plants and air-breathing animals submersion inevitably leads to the accumulation of an oxygen debt which has to be controlled and eventually repaid. Proton disposal under anaerobic conditions is thus limited by the potentially toxic effect of an accumulating oxygen debt. Ethanol is highly toxic to plants and there is a limit to the abilities of animal tissues to withstand the fall in blood pH due to the production of lactic acid. The capacity for prolonged submersion and lactic acid accumulation reaches its peak in diving turtles. The red-eared turtle (*Pseudemys scripta*) can not only dive for 2 weeks at 16–18 °C but tolerates a lactic acid concentration in its blood of 100 mM and a fall in pH from 7.9 to 6.8 [2].

Anaerobic respiration, due to its low energy yield, will also lead to tissue starvation if metabolic rates are not limited and if there is not an adequate supply of carbohydrate reserves during the period of immersion. As we shall see the tolerance of anoxia in plants as well as animals is always linked with controlled

metabolic rates and the provision of considerable stores of carbohydrate reserves.

Apart from the internal metabolic hazards of anoxia, plants face the additional danger caused by the presence of reduced toxic ions in anaerobic soils. Once a soil has been flooded, oxygen quickly disappears to be followed in sequence by the reduction of nitrate to nitrite, manganic to manganous ions, ferric to ferrous and sulphate to sulphide [3]. In the reduced condition these ions are not only more soluble but are also highly toxic to plant roots. Continued survival in flooded soil requires the possession of some detoxication mechanism which will either sequester or oxidize the reduced ions and prevent their reaching toxic concentrations in the plant roots.

Internal Metabolic Damage to Roots during Anaerobiosis

The first process to suffer from the depletion of the oxygen supply to the roots is the respiratory metabolism of the root itself. Although some oxygen diffuses from shoot to root in all plants, it is purely a physical process and as such takes the path of least resistance and diffuses out of the root into the surrounding medium without necessarily satisfying the oxygen demands of the denser meristematic regions of the root tip. The fact that oxygen diffuses out of the root does not necessarily mean that there is an excess of the gas for respiratory activity. Careful measurement of the oxygen loss by diffusion with the respiratory
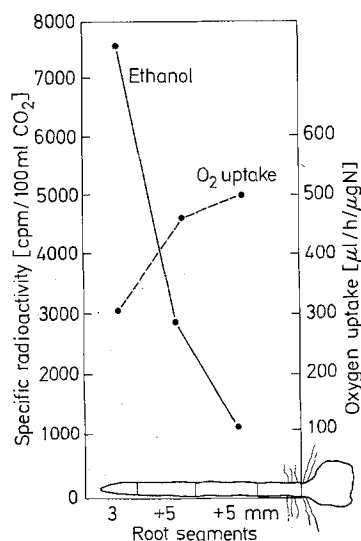
need of the root has so far shown that diffusion can account for only 8–25% of root oxygen uptake [4]. Furthermore, in all roots, both terrestrial and aquatic, there is a zone of natural anaerobiosis to be found in the apical 3–5 mm even when the roots are growing in an atmosphere of 21% oxygen (Fig. 4). When the oxygen concentration around the root falls there is an inevitable extension of the zone of natural anaerobiosis backwards from the root tip. The ability of plants to tolerate anoxia and hence flooding can be related to their metabolic reaction to the extension of this zone of natural anaerobiosis. In plants intolerant of flooding the extension of the anaerobic zone initiates a rapid acceleration of glycolysis, a pronounced Pasteur effect and as a consequence of this an increase in ethanol beyond the level at which the root can either metabolize or rid itself of this metabolite by diffusion (Fig. 5). This same accumulation of ethanol also distinguishes seeds that can withstand prolonged flooding from those that lose their viability when submerged for more than a few hours (Fig. 6). It is a characteristic feature of flood-intolerant plants that when ethanol production increases there is a simultaneous induction of alcohol dehydrogenase (ADH) activity (Fig. 7). This ADH activity comes

Fig. 4. Specific radioactivity of the combusted ethanol distillate from root segments of maize that were incubated with 0.05 M 3-^{14}C-pyruvate for 4 h under air, together with the oxygen consumption of the same segments
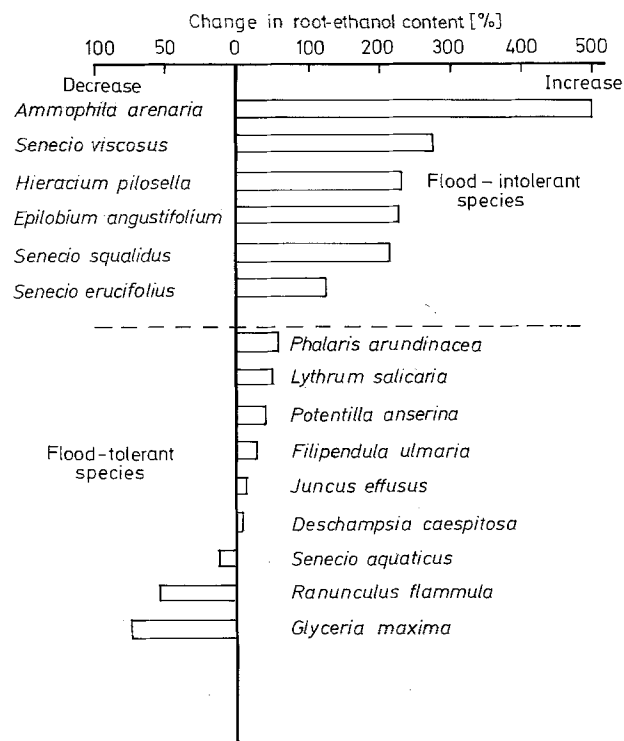

Fig. 5. Changes in ethanol production in roots of 15 species of higher plant of varying flooding tolerance after they had been flooded in sand culture for one month as compared with unflooded controls. Ethanol production was determined in excised roots incubated with 2.5% glucose under nitrogen (data from [5])
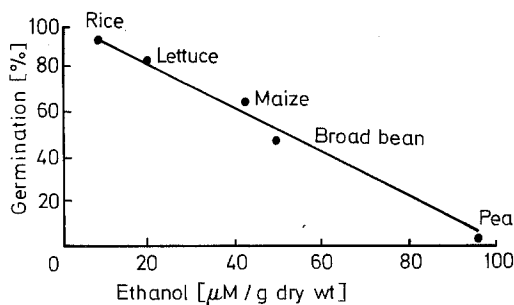
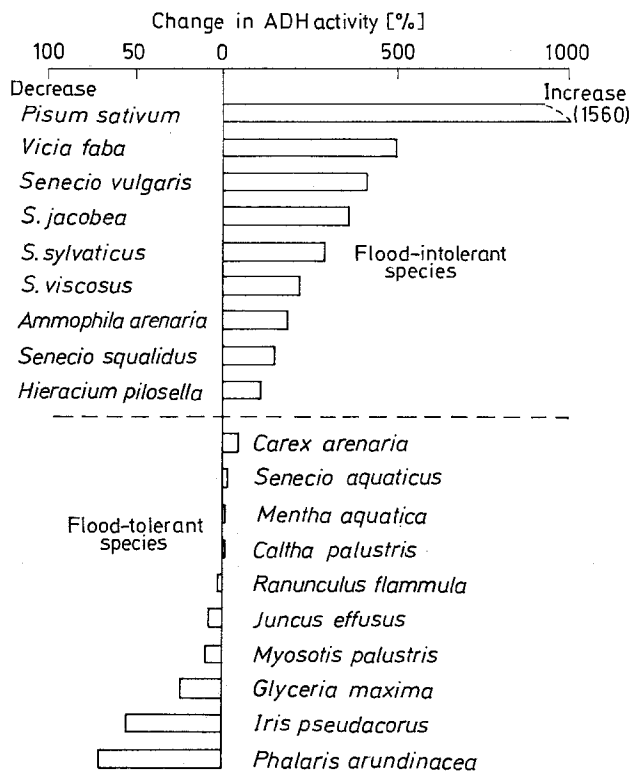Fig. 6. Relationship between ethanol content of seeds after 72 h soaking with viability (data from [23])

Fig. 7. Changes in alcohol dehydrogenase (ADH) activity of 19 species after flooding in sand culture for one month as compared with unflooded controls. Enzyme activity was calculated on a soluble-protein basis [7]

from a de-novo synthesis of new enzymatic material with increased activity and low K_m values [7]. From an agricultural viewpoint it is noteworthy that these differences in wild plants also occur in varieties of crop plants. In maize, narrow-leaved lupins, subterranean clover and soft-brome grass; flood-intolerant varieties can be distinguished from tolerant strains by the induction in the former of a highly active ADH iso-enzyme [8–11].

In all these studies the presence or absence of an inducible ADH iso-enzyme and the possession or not

of flooding tolerance has been shown to be under the control of one set of alleles. The use of flood-inducible ADH activity as a laboratory screening test for flooding tolerance is therefore a practical possibility both in growing crops and germinating seeds. The Gramineae, for reasons connected with their evolutionary history, discussed above, appear particularly suitable for selection for flooding tolerance on the basis of the above genetic engineering of ADH activity.

There is a striking similarity in many flood-sensitive plants in that they react to anoxia with the production of large quantities of ethanol (for exception see p. 196). By contrast, plants that survive flooding, although they are similar in controlling their metabolic rate in the absence of oxygen, show a wide-range behaviour in the manner of disposal of their oxygen debt. Flooding tolerance therefore needs further discussion as it is here that many similarities are to be found between flood-tolerant plants and animals tolerant of anoxia.

Metabolic Adaptation of Flood-tolerant Plants

Recent research in animal physiology has emphasized the biochemical ingenuity of animals in adapting their carbohydrate metabolism to survive prolonged periods of anoxia. These adaptations can be grouped under three headings:
1. the regulation of metabolic rate,
2. the diversification of the end-products of glycolysis,
3. the provision of adequate carbohydrate supplies.

Metabolic Regulation

In the regulation of metabolic rate under anoxia there is a clear parallel between diving animals and flood-tolerant plants. In the alligator the heart-rate may decline from a pre-diving value of 41/min to 2–3/min after 10 min of submergence. This phenomenon of pronounced bradycardia on submersion exists in all species of diving mammals, birds (Fig. 8), and reptiles and was first observed by Paul Bert [12] when he showed that in the diving duck the heart-rate fell from 100 to 14 beats per minute. Cardiac retardation is also accommpanied by muscle ischaemia which results in these tissues respiring by purely anaerobic means. In diving mammals where submersion is rarely prolonged beyond 1–2 h the onset of anoxia produces a pronounced Pasteur effect which presumably ensures continued muscular activity during the period of the dive [13]. However in bivalve molluscs, which
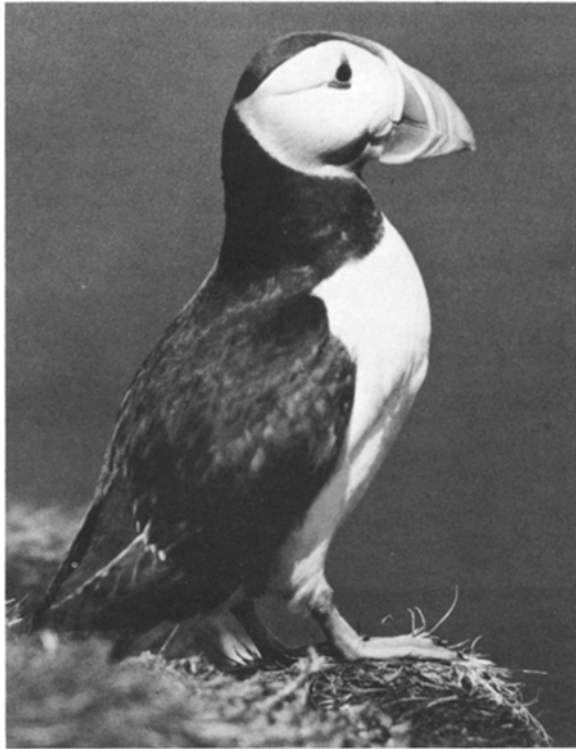
Fig. 8. A puffin (*Fratercula arctica*); a member of the auks (Alcidae) one of the groups of sea birds that make frequent use of diving. In birds capable of prolonged submersion there is a pronounced slowing of the heart beat (bradycardia) during the period of the dive (see text)

Fig. 9. Relationship between viability after 72 h soaking and (a) anaerobic respiration rate $QCO_2^{N_2}$ (μl CO_2 mg^{-1} dry weight h^{-1}) and (b) Pasteur effect as determined from CO_2 evolution (data from [23])

although primarily aquatic are subjected to anaerobiosis when buried in mud or exposed to air at low-tide, there is an ability to withstand much longer periods of anaerobiosis. In these species there is little muscular activity during the period of anoxia and a Pasteur effect is not readily demonstrated. In some species there may be an initial Pasteur effect on the onset of anoxia but this will disappear after a few hours [14].

In plants the ability to survive anoxia is also clearly associated with a control of anaerobic respiration. Roots of herbs and trees which can withstand flooding do not increase their anaerobic respiration on submersion; a feature that contrasts markedly with intolerant species where there is always an increase in glycolytic rate on flooding. In seeds there are close correlations between soaking tolerance and low rates of anaerobic respiration and soaking tolerance and the minimization of the Pasteur effect and the limitation of ethanol accumulation (Fig. 9). Seeds which can lie fully imbibed in wet soils, but are still capable of germination when soil-flooding subsides show the same traits of anaerobic metabolic control as bivalve molluscs during anoxia.
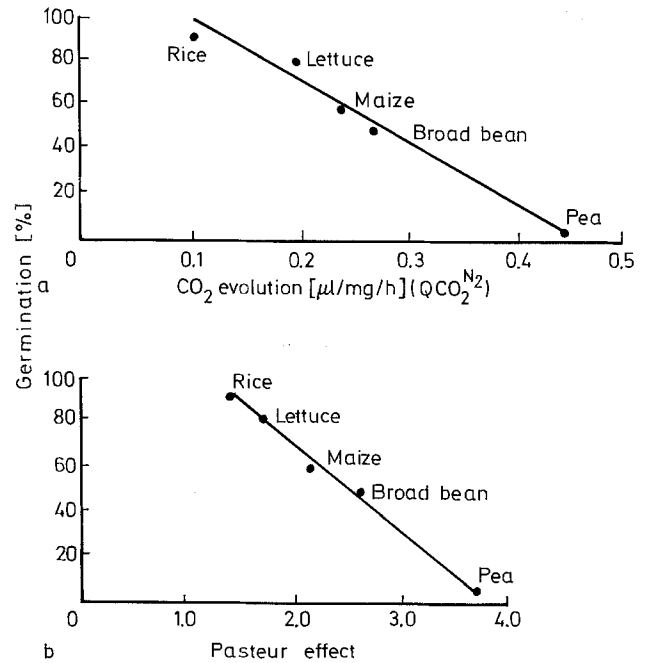
Diversification of the End-products of Glycolysis

The importance of multiple end-products of anaerobiosis in facilitating the tolerance of anoxia first came to light in studies on anaerobic micro-organisms. A discussion of the metabolic adaptations of mixed fermentations in microbial anaerobiosis is given by Krebs [15]. In animals the list of substances used for accumulating the oxygen debt grows steadily longer [13, 14]. In plants, due to the practice of working with non-flood-tolerant crop species for physiological experiments the biochemical diversity of anaerobic adaptation has remained largely unexplored. It is now 20 years since Mazelis and Vennesland [18] first suggested on theoretical grounds of enzyme equilibria that malate and not ethanol should be the natural end-product of glycolysis in higher plants, occupying the same position as lactate in animals. The lack of evidence at that time to support this view was due largely to the fact that most plant physiologists worked with non-flood-tolerant crop plants. However, when a selection of flood-tolerant herbaceous plants was subjected to partial anoxia [16] it was found that these accumulate malate as predicted by Mazelis and Vennesland. Malic acid also occurs in certain animal parasites as an end-product of anaero-

Table 1. Substances reported to accumulate under anaerobic conditions in higher plants and animals. (References are intended only as a source of further information and do not indicate priority of discovery or complete range of occurrence)

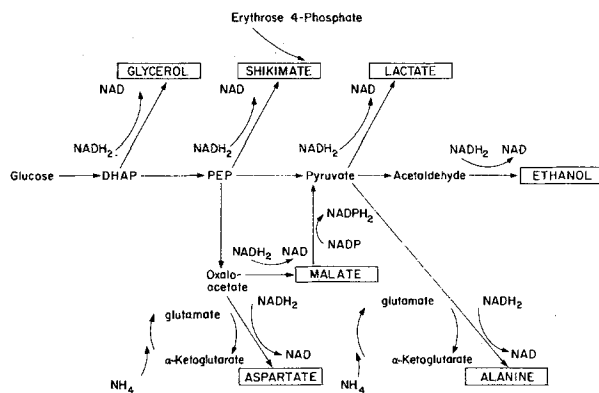| Substance	Animal occurrence	Plant occurrence
Lactic acid	Vertebrate skeletal muscle [2]	Germinating seeds [37], tubers [24]
Pyruvic acid	Vertebrate skeletal muscle [2]	Willow roots [21]
Formic acid	Parasitic helminths [17]	—
Acetic acid	Bivalve molluscs, cestodes [31]	—
Acetoin	Hematodes [17]	—
Propionic acid	Molluscs, cestodes [17]	—
Butyric acid	Parasitic protozoa [17]	—
Succinic acid	Bivalve molluscs [13]	Seeds [37]
Malic acid	—	Roots of marsh plants [16]
Shikimic acid	—	Iris and water-lily roots [20]
Glycolic acid	—	Willow roots [21]
Ethanol	Parasitic protozoa, helminths [17]	Flood-tolerant roots and seeds [6, 20, 23]
Sorbitol	Insects [19]	—
Glycerol	Insects [19]	Alder roots [20]
Alanine	Sea turtles [13], molluscs [14]	Flood-tolerant roots [21]
Aspartic acid	Marine annelids [33]	Flood-tolerant roots [21]
Glutamic acid	Marine annelids [33]	Flood-tolerant roots [6, 21]
Serine	—	Flood-tolerant roots [21]
Proline	—	Flood-tolerant roots [21]
Octopine	Cephalopods [34]	—
α-Amino-butyric acid	—	Tomato roots [36] Radish leaves [38]
α-Methyl butyrate	Parasitic nematodes [32]	—
α-Methyl valerate	Parasitic nematodes [32]	—
α-Glycerophosphate	Insects [19]	—
Hydrogen	Parasitic protozoa [17]	—
Ethylene	—	Roots and fruits [35]

Fig. 10. Summary diagram illustrating the various means of proton disposal and the range of end-products of glycolysis found in plants capable of enduring prolonged periods of partial or total anoxia
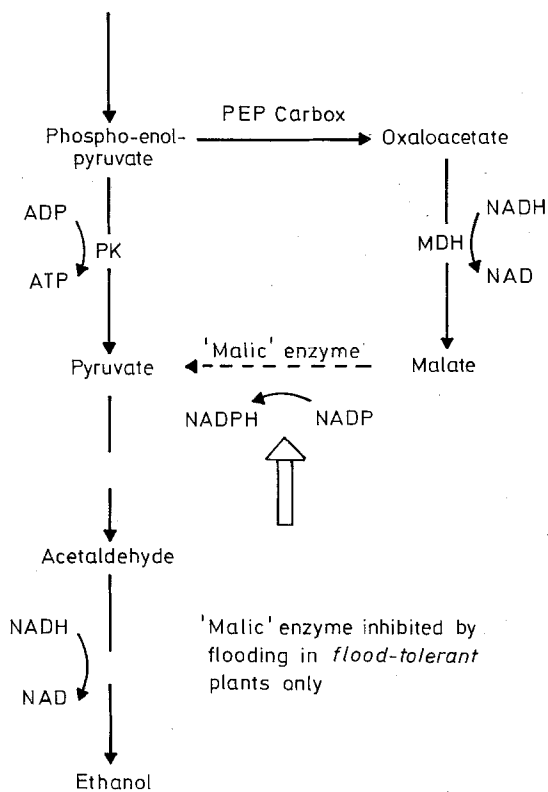

Fig. 11. A possible metabolic differentiation between flood-tolerant and non-flood-tolerant plants. In intolerant species there is an acceleration of glycolysis and malic enzyme is not inhibited and ethanol is the exclusive end-product of glycolysis. In flood-tolerant species there is no acceleration of glycolysis and malic enzyme is inhibited allowing malate to accumulate a proportion of the oxygen debt

biosis [17] although in most animal species it is further metabolized to succinate with the generation of an additional molecule of ATP. This last stage has not yet been demonstrated in flood-tolerant plants.

Continued experimentation on the products of anaerobiosis in both plants and animals is adding yet further examples to the list of substances known to accumulate during periods of anaerobiosis. A comparison of the metabolites that accumulate with the oxygen debt in plants and animals is given in Table 1. The system of carbon flow allowing the regeneration of NAD from NADH by plants in the absence of oxygen is shown in Fig. 10. As can be seen there are several striking similarities between plants and animals in metabolite accumulation under anoxia. Glycerol for example is produced by blood-inhabiting African trypanosomes [18] where it can account for 50% of the glucose utilized. It is also accumulated at diapause by silkworms and in the adipose tissue

of hibernating [19] hedgehogs. In plants it can be found to increase in alder roots (*Alnus incana*) after 8 days flooding [20]. Alanine also occurs in insects and molluscs during periods of anaerobiosis as well as in the roots of flooded trees [21, 22].

Little information is as yet available on the control mechanisms which determine the nature of the products of glycolysis under anoxia. The change from ethanol to glycerol production in alder takes about a week and this time delay suggests the induction of an adaptive enzyme system. The production of lactate in flood-tolerant seeds is favoured by low metabolic rates [23] and is influenced by pyruvate concentration and cell pH [24]. Enzyme deletion was originally proposed to account for the accumulation of malate instead of ethanol in flood-tolerant marsh plants [7]. The absence of malic enzyme in the carboxylation and decarboxylation by-pass of pyruvate kinase which is thought to operate in most plant tissues would allow malate to accumulate at the expense of ethanol (Fig. 11). It now appears that malic enzyme is not absent from these marsh species [25] but that it is inhibited by flooding in flood-tolerant plants [26]. In experiments with potato it has been shown that oxalic acid is a powerful inhibitor of malic enzyme and this may play a role in the differential response of flood-tolerant and non-flood-tolerant plants to periods of anaerobiosis [27].

Provision of Adequate Carbohydrate Supplies

All animals that are capable of enduring prolonged periods of anaerobiosis accumulate during the pre-stress period considerable supplies of glycogen, which are then used to support glycolytic activity during the period of anoxia. The large supplies are necessary as glycolysis is a less efficient producer of metabolic energy than aerobic respiration. This energetic inefficiency is the price these species have to pay for the priviledge of using the aquatic habitat. Similarly those species of higher plant that have returned to the aquatic or marsh habitat are frequently characterized by the possession of large tubers and well-developed rhizomes which lie submerged in anaerobic mud throughout the winter resting period and serve as carbohydrate reserves for periods of anaerobiosis. Plants like animals appear to indulge in this energy extravagance in order to enter the aquatic or marsh habitat. The carbohydrate reserves of these well-developed submerged organs are used by anaerobiosis in the early stages of the growing season when growth is first resumed and shoots are renewed. Before shoot-renewal there will be no means of submerged tissue aeration and the early growth of these aquatic plants

must be supported by anaerobic respiration. A similar pattern can be observed in trees. The xylem parenchyma of many tree roots accumulates large quantities of starch in the early autumn and this energy reserve is mobilized in the spring during the period of sap rise and bud burst.

Detoxification of Anaerobic Soils

Higher plants with their specialization of nutrient uptake by roots encounter further difficulties in returning to the aquatic or wet-land habitat in that many of the reduced soil mineral ions are phytotoxic. In mineral-rich lakes it is possible for the submerged plants to absorb ions through their leaves, but in nutrient-poor waters the root still serves as the major mineral-capturing site of the higher plants. It is a curious feature of many wet-land species that in spite of the abundance of water in their soils they exhibit many of the xeromorphic features which are characteristic of drought-adapted plants. The reduction of leaves in the genus *Juncus* and the hairy folded leaves of the cross-leaved heath (*Erica tetralix*) are two typical examples. Reduction of the water requirements of wet-land plants will reduce the in-flow of water to the root and with it, the arrival at the root surface of reduced phytotoxins. The detoxification rate that is necessary to protect the root will therefore be reduced and it appears that it is the downward diffusing oxygen from the shoot to the root that is the principal means of oxidizing reduced ions. The importance of control of water uptake for the survival of bog plants has been demonstrated with the use of anti-transpirants [28]. Spraying the leaves of *Erica cinerea* (a flood-sensitive heath) not only increases the ability of this species to survive flooding but reduces its iron content. The experiments illustrate the underlying cause of the effect well known in farming, that rushes not only grow in wet places, but make them still wetter. The reduced transpiration of the rush will allow the water table to rise and favour the competitive power of the rushes against the original dry-land vegetation.

Alternative Causes of Death and Means of Survival in Higher Plants

It would be both presumptious and erroneous to extend the present comparisons to cover the reactions of all plants to flooding. In many species, particularly in fruit trees the bark is rich in cyanogenic glycosides, flooding of these plants can cause death within 24 h.

In these species death is so rapid that no comparison can be made of ethanol production in tolerant and intolerant varieties. In plants with adventitious roots in direct contact with free water, as in rice, over 95% of the ethanol produced in the roots will diffuse quickly into the surrounding medium. In these cases an acceleration of glycolysis may not necessarily be harmful to the growing plant [29], whereas in the germinating rice seed before rupture of the testa the limitation of ethanol production was associated with tolerance of anoxia. Similarly when swamp tupelo trees (*Nyssa sylvatica* var. *biflora*) are grown as seedlings in water culture there appears to be a ready diffusion of ethanol out of the roots so that increased glycolytic rates do not produce toxic quantities of ethanol in the plants tissues [30]. However, in the majority of perennial aquatic plants with thickened roots, rooted in anaerobic muds, or in the perennating tubers and rhizomes of marsh plants as well as in germinating seeds, ethanol is not readily lost by diffusion and in these species just as with animals the control of glycolysis is regularly associated with tolerance of anoxia.

Conclusions

Co-evolution has long been recognized as a general morphological rule in areas of environmental stress. The desert plants of the Old and New World resemble each other in form even though they are taxonomically distinct. The adaptations that occur in plants and animals in relation to anoxia give a striking example of co-evolution at the molecular level. The remarkable fact that molecular evolution has selected the same mechanisms in such widely different groups as plants and animals shows that there can be only a few efficient metabolic solutions to any particular environmental stress. It must be expected that similar situations exist in other areas of plant and animal metabolism. Further biochemical investigations into the success or failure of organisms in relation to environmental stress will bring a new dimension into ecology and allow practical field studies to benefit from the recent advances that have been made in molecular biology.

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