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Comparative physiology of plant and arthropod land adaptation

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Plants related to aquatic Charophycean green algae were probably terrestrial by the early to mid Silurian; these plants were the ancestors of the vascular plants that have dominated the Earth's flora since the Devonian. The arthropods have been the major herbivores and carnivores in many terrestrial communities since the Devonian: they arose from a number of aquatic arthropod stocks which invaded the land from the Silurian onwards. The vascular plants and arthropods conduct their basic metabolism in the same way as their aquatic counterparts, but in the aerial environment which differs greatly from the aquatic in the exchange of materials, momentum and heat between organisms and their environment. Terrestrial organisms differ from their aquatic relatives in (*inter alia*) the water vapour loss attendant on the exchange of gases in photosynthesis and respiration; the potential for large and rapid changes in body temperature; and differences in the structural requirements for maintenance of posture and, in animals, locomotion. The (putatively) adaptive responses to these problems of terrestrial life show a number of important parallels between the vascular plants and arthropods, including internalization of gas-exchange surfaces, regulation of gas diffusion between the gas-exchange surfaces and the outside air, a wax layer over the general body surface which restricts non-respiratory and non-photosynthetic water loss, and the importance of rigid skeletal members (present in the ancestral aquatic arthropods, but not in algae). At the biochemical level many of the prerequisites for the special structures and functions found in terrestrial organisms can be traced in their algal and aquatic arthropod relatives. The seductive argument that increasing O_2 levels in the atmosphere in the Siluro-Devonian were of great significance in permitting larger phototrophs (absence of restriction of plants to shaded habitats to avoid ultraviolet, and increased bulk of non-photosynthetic parts permitted by greater O_2 availability) and larger and more active phagotrophs (as a result of greater O_2 availability) is, alas, very difficult to test quantitatively.

Introduction

To understand the evolution of terrestrial organisms from aquatic ancestors we must consider, *inter alia*, the physiological interactions of the organisms with their aquatic or terrestrial environment. In this paper an attempt is made to relate our knowledge of extant and Siluro-Devonian environments to that of extant and Siluro-Devonian vascular plants and arthropods to clarify the (putatively) adaptive responses of the earliest terrestrial vascular plants and arthropods to their 'new' environment.

The juxtaposition of these two groups in a single article may be defended on such grounds as the dominant roles played by vascular plants and arthropods as, respectively, the major primary producers and the major phagotrophs on land since the Siluro-Devonian; the co-evolution of the two groups; and the many similarities of the ways in which the two groups handle common problems of life on land.

Relevant aspects of the Siluro-Devonian environments

This section of the paper briefly analyses the differences between the aquatic and terrestrial environment with respect to both extant and Siluro-Devonian habitats.

Solar radiation

The maximum photosynthetically active solar radiation (400–700 nm) that reaches the surface of the land or sea today is 2 mmol m^{-2} s^{-1} (noon in the tropics); this was probably similar to the Siluro-Devonian level (Newman 1980). There was probably a higher ultraviolet photon flux density at the Earth's surface in the Siluro-Devonian, largely as a result of the lower O_2 and O_3 levels (cf. Canuto *et al.* 1982).

Atmospheric composition

The Siluro-Devonian atmosphere probably had a similar content of rare gases and of N_2 as does the extant atmosphere; the oxygen content was somewhere between one-fifth and one-half of the extant value (Broecker 1970; Hart 1980). The *mean* atmospheric CO_2 content over the last 4×10^8 years was probably close to the extant (pre-industrial) value (Holland 1965; Hart 1978), although there were probably considerable fluctuations over time scales of 10^4 to 10^7 years (Neftel *et al.* 1982; Broecker 1982; Berner *et al.* 1983). The atmospheric pressure in the Siluro-Devonian was at least 0.85 of the extant value (Hart 1978; Broecker 1970).

A comparison of water and air as habitats

Table 1 compares some biologically important properties of water and air (based on extant atmospheric composition) which will be used below to analyse the behaviour of a hypothetical attached plant or non-moving animal subjected to a bulk-phase fluid velocity (u) of 1 m s^{-1}. Such a fluid movement over a small (20 mm long) streamlined organism would involve effective boundary layer thicknesses (δ) of 10^{-3} m in air and 10^{-5} m in water (Jones 1983; Raven *et al.* 1982).

Table 1. Some properties of air and of water that are relevant to the functioning of aquatic and of terrestrial organisms

property	value in air	value in pure water
diffusion coefficient for H_2O (D_{H_2O})/(m^2 s^{-1})	2.42×10^{-5}	2.4×10^{-9}
diffusion coefficient for CO_2 (D_{CO_2})/(m^2 s^{-1})	1.47×10^{-5}	1.8×10^{-9}
diffusion coefficient for O_2 (D_{O_2})/(m^2 s^{-1})	2.02×10^{-5}	2.0×10^{-9}
thermal diffusivity (D_H)/(m^2 s^{-1})	2.15×10^{-5}	144×10^{-9}
kinematic viscosity (D_M)/(m^2 s^{-1})	1.51×10^{-5}	1010×10^{-9}
specific heat capacity (C_p)/(J m^{-3} °C^{-1})	1.22×10^3	4.17×10^6
density (ρ)/(kg m^{-3})	1.204 (dry) 1.194 (water-saturated)	998.4
[H_2O] in water-saturated air or in pure water/(mol m^{-3})	0.972	5.55×10^4
[CO_2] in air (30 Pa CO_2 in 100 kPa total pressure) or in water in equilibrium with air as specified	0.0125	0.0117
[O_2] in air (20.8 kPa O_2 in 100 kPa total pressure) or in water in equilibrium with air as specified	8.65	0.262

Data from Jones 1983; Monteith 1973; Riley & Skirrow 1975*a*, *b*. All values for 20 °C.
Pure water indicates water containing only the solutes (CO_2 or O_2) specified.

Material exchanges between organism and environment in air and in water

The diffusive flux between the bulk phase and the surface of the organism ($J/(\text{mol m}^{-2}\text{ s}^{-1})$) and the diffusion coefficient for the molecular species diffusing ($D/(\text{m}^2\text{ s}^{-1})$) is given by (Jones 1983):

$$J = (D/\delta)\,\Delta C \tag{1}$$

where ΔC is the difference in concentration (in moles per cubic metre) of the diffusing solute between the bulk phase (C_b) and the surface of the organism (C_s).

For a photosynthetic organism taking up CO_2 over its entire surface, C_b at 20 °C is 11.7 mmol m^{-3} in water and 12.5 mmol m^{-3} in air (table 1). A reasonable value for C_s during steady-state photosynthesis in air or water is 7 mmol m^{-3} (Raven *et al.* 1982), giving J_{CO_2} equal to 8×10^{-7} mol m^{-2} s^{-1} in water and 8×10^{-5} mol m^{-2} s^{-1} in air. The predicted J_{CO_2} is similar to that achieved in aquatic plant photosynthesis (Raven *et al.* 1982). For the plant in air the predicted J_{CO_2} could only be achieved with some amplification of the area of gas–water interface, for example by the presence of an internal gas distribution system, if the potential CO_2 flux to the surface is to be matched by the capacity for aqueous-phase diffusion and for CO_2 assimilation in individual photosynthetic cells (Raven 1977, 1984*a*).

For respiration by animals, or by non-photosynthesizing tissues of plants, an even larger difference between terrestrial and aquatic organisms is seen. For the respiratory substrate O_2 at 20 °C, C_b is 0.262 mol m^{-3} in water and 8.65 mol m^{-3} in air. Since a C_s value of 50 mmol m^{-3} can saturate respiration in organisms of the size we are considering (Raven 1984*b*), the potential flux (J_{O_2}) is 4.2×10^{-5} mol m^{-2} s^{-1} in water and 0.17 mol m^{-2} s^{-1} in air. A cylindrical organism 20 mm long and with a radius of 1 mm, respiring in air at 0.17 mol O_2 m^{-2} s^{-1}, would use all of its organic C in 10–20 s, that is, it has an enormous over-provision of O_2 supply to its surface.

While photosynthetic and, especially, respiratory gas supply is much favoured in terrestrial relative to aquatic organisms, the land-dwellers have a problem of water loss by evaporation (transpiration) from the photosynthetic or respiratory surfaces. Such surfaces are necessarily moist, since no natural or synthetic material is known that has a substantially higher permeability to CO_2 or O_2 than to H_2O. If the gas-exchange surface is saturated with water vapour at 20 °C ($C_s = 0.972$ mol m^{-3}) and the bulk air has a relative humidity of 50% at 20 °C ($C_b = 0.486$ mol m^{-3}), the transpiratory water loss from our terrestrial organism is 0.0118 mol H_2O m^{-2} s^{-1} (provided that the heat balance maintains the surface at 20 °C while supplying the latent heat of evaporation of water). On this basis, a terrestrial phototroph loses 140 moles of water per mole of CO_2 fixed in photosynthesis, while a terrestrial chemo-organotroph (or a phototroph in the dark) loses 0.065 moles of water per mole of O_2 used (CO_2 produced) in respiration. Correcting for respiratory carbon loss in plants during growth, and respiratory costs of movement as well of synthetic processes during growth of animals, a terrestrial plant loses at least 200 moles of H_2O per mole of C gained in plant material, while a terrestrial animal loses at least 0.065 moles of H_2O per mole of C gained in animal material (cf. Cowan 1977; Raven 1983; Schmidt-Nielsen 1983).

The analysis thus far has assumed the extant atmospheric composition. A lower O_2 content of the Siluro-Devonian atmosphere reduces the potential rate of respiration of our model organism in both water and in air, and the respiratory O_2 consumption per unit H_2O lost in terrestrial organisms. Variations in the atmospheric CO_2 content also alter the potential rate of photosynthesis and the quantity of C that can be assimilated per unit water lost: if the

Siluro-Devonian atmosphere had the higher CO_2 content suggested for the Cretaceous, these values would be higher than those computed on the basis of the extant atmosphere, while the lower CO_2 levels found during Pleistocene glaciations would reduce both values.

A final point concerns the significance of internalization of gas-exchange surfaces in terrestrial organisms. We have seen that the capacity for O_2 supply to the whole body surface of our hypothetical terrestrial organism far exceeds the respiratory demand for any feasible growth rate and level of activity. Assuming a respiratory rate of 1/10000 that calculated above (appropriate to a generation time of about two days), the use of the whole body surface as a respiratory gas-exchanger would give a water loss per unit carbon assimilated of 650 mol H_2O (mol C)$^{-1}$.

Internalization of the gas-exchange surface, with diffusive connection to the bulk air through a pore of variable aperture, in conjunction with a general body surface of very low permeability to O_2, CO_2 and H_2O, permits diffusive supply of O_2 to the respiratory surface to be reduced (via an increase in the D/δ term in equation (1) in parallel with metabolic demand at constant C_s), and the H_2O lost per unit C assimilated could approach the low value of 0.065 quoted above for a terrestrial animal. Internalization as a means of increasing the respiratory surface area is important as size increases, since surface area per unit biomass and respiratory rate per unit biomass tend to change as the $-\frac{1}{3}$ and $-\frac{1}{4}$ powers of the biomass respectively (Peters 1983).

We have seen that internalization of the photosynthetic gas exchange surface is necessary to realize the potential for photosynthesis conferred by diffusive CO_2 supply to the surface of our hypothetical terrestrial plant: this benefit of internalization sets in at a smaller size of organism that is the case for chemoorganotrophs as a result of the much smaller diffusion gradients that can be realized with CO_2 than with O_2. As with the animals, the water use efficiency of plants can be maximized by the occurrence of variable resistance pores between the bulk atmosphere and the internal aeration system, in parallel with a gas-impermeable external plant surface (Cowan 1977; Raven 1977, 1984*a*).

Momentum exchange between organism and environment in water and in air

The transfer of momentum (τ/kg m^{-1} s^{-2}) between organisms and their fluid environment is related to the kinematic viscosity of the medium (D_M/m^2 s^{-1}) by the relationship (Jones 1983)

$$t = (D_M/\delta)\,\rho u, \tag{2}$$

where ρ is the density (in kilograms per cubic metre) of the medium. For the values of u (1 m s^{-1}), δ_{water} (10^{-5} m) and δ_{air} (10^{-3} m) used above in calculation of material transfer, we find that τ is 101 kg m^{-1} s^{-2} for our hypothetical organism in water and 0.018 kg m^{-1} s^{-2} in air, that is, a water:air ratio of 5600. These momentum transfers represent skin friction, the tangential force acting on a surface due to fluid flowing over it. An additional and, for non-streamlined organisms, major drag force is the form drag, τ_f, given by (Jones 1983)

$$\tau_f = C_D \tfrac{1}{2}\rho u^2, \tag{3}$$

where C_D is a dimensionless factor that relates the *actual* drag to the maximum potential force ($\frac{1}{2}\rho u^2$) that could be exerted if all of the flow were completely stopped. For $C_D = 1$, τ_f is 500 kg m^{-1} s^{-2} in water and 0.60 kg m^{-1} s^{-2} in air, a water:air ratio of 833.

These water:air ratios of τ_f and τ mean that the forces tending to wash away an aquatic benthic organism are much greater than those tending to blow over or blow away a terrestrial organism of similar form exposed to the same u. In addition to their effects on stationary organisms, surface and form drag are relevant to energy requirements for locomotion, feeding and respiratory ventilation in animals. The differences in air density between the extant and the Siluro-Devonian atmosphere (see above) would only serve to increase the water:air ratios of drag forces by 1.08-fold for τ_f and by 1.15-fold for τ.

Gravitational forces are much greater in posture maintenance in terrestrial than in aquatic organisms of similar size and form. Gravitational forces are largely mitigated in water by the small difference in density between aquatic organisms and water relative to that between terrestrial organisms and air, the aquatic:aerial ratio of the density differences being of the order of 0.1. The likely difference in density between the extant and the Siluro-Devonian atmosphere has a negligible effect on the ratio of density differences.

In terms of the responses of organisms to frictional and gravitational forces, benthic aquatic plants have a firm attachment *to* a coarse-grained substratum (haptophytes) or *in* a fine-grained substratum (rhizophytes). The main forces on the plant (from currents, tides, etc.) are those tending to extend it (tensile forces): the plant consists of turgid-walled cells with an intercellular matrix which is often very readily deformed. Terrestrial macrophytes (all of which are rhizophytes) are subject to large gravitational as well as lateral (wind) forces, which produce compression as well as tension within the plant body. Terrestrial plants of low stature (tens or hundreds of millimetres in height) can subsist mechanically with turgid cells (with a less deformable matrix than in many aquatics). Taller (and stouter) plants use *rigid* compression-resistant structural elements: these lignified cell walls probably originated as implosion-resistant structures in the water-conducting xylem (Wainwright 1970; Raven 1977).

In animals, muscular and ciliary movement demand the absence of pressure-resistant walls around individual cells (see Gunning & Robards 1976). Aquatic arthropods maintain their posture, and execute locomotory, feeding and respiratory movements, with a hydrostatic skeleton (fluid-filled cavities pressurized by muscular activity) with supplementation (or essentially complete replacement) by a rigid exoskeleton to which muscles are attached. Hydrostatic skeletons of animals are predicated upon pressure-resistant, deformable structural elements surrounding the compression-resistant but deformable fluid compartment. The arthropod exoskeleton consists of articulated plates of rigid materials which can resist both tension and compression: motility is achieved by antagonistic muscle action and, in some cases, by deformation of the hydrostatic skeleton by muscular activity elsewhere in the organism (Little 1983). These two skeletal systems co-exist in terrestrial arthropods, with (as in aquatic examples) a very significant role for the exoskeleton. Hydrostatic skeletons are important in the terrestrial larvae of insects, in Onychophorans, and in all terrestrial arthropods during ecdysis (Little 1983), despite suggestions that gravitational effects militate against the efficacy of hydrostatic skeletons in terrestrial animals.

Heat exchange between organism and environment in water and in air

Heat transfer (C/J m^{-2} s^{-1}) between an organism and its fluid environment is related to the thermal diffusivity of the medium (D_H/m^2 s^{-1}) by the equation (Jones 1983)

$$C = (D_H/\delta)\, C_p \Delta T,$$

where C_p is the specific heat on a volume basis (J m^{-3} °C^{-1}) and ΔT is the temperature difference between the organism and its environment (in degrees centigrade). For an organism at 20.5 °C in a medium at 19.5 °C, the δ values used in the calculations above yield C values of 6.05×10^4 J m^{-2} s^{-1} in water and 25.8 J m^{-2} s^{-1} in air, so that $C_{\text{water}}/C_{\text{air}}$ is 2345. Accordingly, when the rate of diffusive (conductive) heat loss to fluid flowing at 1 m s^{-1} is equal in our hypothetical aquatic and terrestrial organisms, the temperature difference between the organism and the bulk water will be 1/2345 that between the organism and bulk air, if all other factors are equal. An important additional process that dissipates heat from terrestrial, but not aquatic, organisms is the latent heat of evaporation (transpiration) of water: whether or not it is 'needed' in temperature regulation, transpiration is an inevitable concomitant of CO_2 and O_2 exchange in terrestrial organisms and causes a decrease in the temperature of an organism relative to that of a non-transpiring, but otherwise similar, organism.

THE STRUCTURE, FUNCTION AND EVOLUTION OF VASCULAR PLANTS

The sporophyte generation of vascular land plants typically comprises above-ground axes concerned with photosynthesis (involving photon absorption and CO_2 uptake from the atmosphere) and below-ground axes concerned with the uptake of water and of nutrient elements other than C. In addition to these vegetative functions, the above-ground portion of the plant also serves a propagatory and recombinatory role through spore production. The distribution of vegetative functions between the above-ground and below-ground portions of the plant has obvious analogies to the division of labour in submerged rhizophytic plants; both kinds of plant obtain photons and most of their CO_2 through the shoot, and most of their nutrients through the root or rhizoid. Accordingly, both types of plant require transport systems whereby shoot products (photosynthates) move to the root or rhizoid and root or rhizoid products (nutrients absorbed from the soil or sediment) move to the shoot. Accordingly, submerged rhizophytes (whether primarily aquatic, such as many algae, or secondarily aquatic, such as certain vascular plants) share with terrestrial rhizophytes the occurrence of plasmodesmata and cytoplasmic streaming (see Raven 1981, 1984*b*).

A major change in resource acquisition in terrestrial plants concerns the supply of water: this can only be obtained in large quantities from the soil, and the fluid medium surrounding the shoots is a sink for water rather than a source (as is the case for submerged rhizophytes). The large transpiratory demand for water attendant on the absorption of both light energy and CO_2 by the shoot is the likely selective pressure that favoured the evolution of xylem tissue as a means of transferring large quantities of water from the soil to the transpiring surface under modest driving forces in terms of water potential. Xylem tissue has about a 10^6-fold greater specific conductance to water than does live parenchyma tissue (Raven 1977).

The other major vegetative attribute of the terrestrial vascular plant shoot is the internal gas distribution (air space system) together with the stomata and the waxy cuticle. These attributes not only increase the capacity for photosynthesis of a shoot system per unit volume or per unit surface area, but also permit regulation of gas exchange between the shoot and the atmosphere. When water supply via the xylem is abundant relative to the evaporative potential of the atmosphere, stomata are open and CO_2 assimilation can occur in the light, albeit at the expense of substantial water loss. When water is less readily available the stomata are partly or completely closed, restricting water loss and the rate of photosynthesis. An essential part of this mechanism is a water-impermeable cuticle: permeabilities as low as 10^{-6} m s^{-1} for CO_2 ($\equiv 10^{-5}$ m s^{-1} for H_2O?) have been reported (Keeley *et al.* 1984). A few micrometres of cutin plus tens of nanometres of wax impede the movement of water molecules as much as a metre of completely still water!

The combination of xylem, cuticle, gas distribution system and stomata permit vascular plant sporophytes to *grow* when water is available, and *survive* periods (years for some species) of water shortage in the hydrated state: the homoiohydric condition. The evolutionary potential of homoiohydry can be appreciated by noting the competition between phototrophs for light in otherwise well-provisioned environments, and the desirability of disbursing propagules into the more turbulently moving fluid at, or near, the top of the plant canopy. These two requirements constitute possible selective advantages of increased plant height in both aquatic and terrestrial environments (Raven 1984*a*, *b*, *c*). A height of 1–2 m is the maximum that has been reported for land plants that are capable of recovery from vegetative desiccation. This height limitation probably relates to problems of refilling the xylem elements of large desiccated plants (Bewley & Krochko 1982), rather than by an intrinsic inability of the cytoplasm of tall plants to withstand massive water loss, since vascular plants of all sizes that are desiccation-intolerant in the vegetative state can have desiccation-tolerant spores or seeds (Raven 1977, 1984*a*, *c*).

Terrestrial phototrophs with a canopy height of more than a few hundred millimetres require the homoiohydric water transport and gas exchange regulation system: it is only the vascular plants which have (or have had) such a system. The increased height of terrestrial plants permitted by homoiohydry requires additional structural components, particularly those that can resist compression without deformation: lignified tissues are the major elements involved here.

Reproduction has only been mentioned in relation to propagule (spore, seed) dispersal. All vascular plants have an alternation of generations, with the sporophyte dominant. Tracheophyte evolution has involved, in several parallel evolutionary lines, heterospory and the seed habit, with the result in flowering plants and in many gymnosperms of essential independence of external water for sexual reproduction (Cohen 1977). However, like many vegetative features (for example, leaves differentiated from stems in the shoot system), heterospory is not common to all vascular plants, and is not considered in this survey which attempts to identify, and propose selective values for, the features that are common to *all* extant terrestrial vascular plants. The earliest fossil vascular plants were homosporous.

The origin and evolution of vascular land plants

The vascular land plants, and the bryophytes, undoubtedly originated from algae closely related to the extant class Charophyceae of the Division Chlorophyta: Charophycean algae are indeed known from the Upper Silurian (see Stewart & Mattox 1975; Raven 1984*a*). We do not know the route by which the presumed macrophytic algal ancestors of the vascular plants became established on land: by using the terminology of Little (1983), cases have been made for the marine littoral (Church 1919), the fresh-water (Fritsch 1945) and the soil or interstitial (Stebbins & Hill 1980). Fossil evidence suggests that the earliest known Charophyceae were marine (Racki 1982), although on grounds of both morphology (the giant-celled habit) and age these could not have been the immediate precursors of vascular plants. The habitat of the earliest known erect, fertile *Cooksonia*-type plants (which may not have been vascularized) is not clear (Edwards *et al.* 1983).

Indirect argument based on the physiology of extant plants suggests that origin of vascular plants from emergent marine algal rhizophytes is unlikely: coping with transpiration from a

TABLE 2. ORDER OF ACQUISITION OF TERRESTRIAL PLANT CHARACTERS AND THEIR PROBABLE FUNCTIONS

characteristic	function	possible origin	comments
aerially dispersed spores	dispersal; survival of desiccating conditions	meiospores of submerged algal ancestors? Sporopollenin found in extant Characeae (Charophyceae), an algal family related to the ancestors of vascular plants	provides some of the earliest evidence for terrestrial macrophytes. Sporopollenin an anti-biophage material in algae
cuticularized surface	water-repellency facilitates CO_2 diffusion from air to plant surface; decreases grazing and parasitism. Reflects ultraviolet?	cutin derived from long-chain fatty acids which are common components of membranes and triglycerides. Wax esters on surface similar to those used as energy store/fermentation product in the alga *Euglena* (not a close relative of the Charophyceae!)	the alleged functions seem to be compatible with relatively high permeability to metabolic gases, provided wax layer (for which there is no fossil evidence) is not continuous
xylem (dead, lignified cells)	provides a high-conductance pathway for liquid water from subterranean organs to transpiring (and growing) parts of aerial organs	pre-programmed cell death common in algae; lignin biosynthetic pathway has precedents in phenolic synthesis and polymerization in walls of some algae of the Division Chlorophyta: used in protection against biophages and possibly as an ultraviolet-absorber	lignin initially used as a rigid (compression-resistant) wall component in dead water-conducting cells whose contents were under tension; later used as compression-resistant structural material for support of large aerial parts
intercellular air spaces and stomata	intercellular air spaces increase area for CO_2 absorption from the gas phase while minimizing the aqueous-phase diffusion path to the enzyme ribulose biphosphate carboxylase-oxygenase. Stomata regulate permeability of epidermis to CO_2, O_2 and H_2O (*via* systems sensing light, water and CO_2 availability)	algal intercellular spaces are generally not closely similar to vascular plant air spaces in their ontogeny; the limited schizogeny that produces the air spaces and stomatal pores may be analogous to mechanisms of spore production in some terrestrial algae of the Division Chlorophyta. Reversible changes of intracellular osmolarity (such as occur in stomata guard cells) occur in Characeans (Charophyceae) such as the euryhaline *Lamprothamium*, although the signal there is turgor change with changed extracellular osmolarity rather than the guard cell signals which can change turgor at constant extracellular osmolarity. Turgor regulation and maintenance may have been secondarily acquired by soil algae, euryhaline Characeans, and vascular plants whose freshwater ancestors were osmoregulators *sensu strictu* (Reed 1984; Raven 1984*b*)	surface area amplification by external furrowing (for example, in Polytrichaceous moss gametophytes) is less amenable to regulation of gas exchange between wall–air interface and bulk air than is an invaginated mechanism of amplification. Development of full homoiohydry possible at this stage, provided that there is a waxy epicuticle with a very low permeability to water (waxy layers do not fossilize well!)

From Raven 1977, 1983, 1984*a*, *b*, *c*, *d*, *e*.

saline rooting medium is a complex undertaking in extant halophytic flowering plants, and many of the mechanisms used seem to be derived from glycophytic terrestrial ancestors. It is, however, significant that terrestrial vascular plants, together with many marine algae, and some soil and freshwater algae have mechanisms that tend to keep cell *turgor* constant when environmental water potential changes, while the freshwater characeans maintain their intracellular osmolarity, but not turgor, constant (Bisson & Bartholomew 1984; Reed 1984). The euryhaline Characean *Lamprothamnium* regulates turgor rather than osmolarity, is probably secondarily halotolerant (Raven 1984*b*), and thus may constitute a precedent for re-acquisition of the capacity to regulate turgor by freshwater characeans such as would be required if vascular plants were to have evolved from freshwater Charophyceans (Reed 1984). There is nothing intrinsically implausible about the suggestion (Stebbins & Hill 1980) that terrestrial vascular plants arose from soil-dwelling microalgae. More evidence is needed as to the distribution of turgor regulation and of osmolarity regulation in Charophycean algae and in pteridophytes if arguments analogous to those employed by Little (1983) to suggest the routes to land used by various animal taxa are to be used for plants.

A likely sequence of acquisition of vascular plant characters, based on the Silurian and Devonian fossil record (Chaloner 1970; Chaloner & Sheerin 1979; Banks 1980; Edwards 1980; Edwards *et al.* 1983), has been interpreted from an ecophysiological viewpoint by Raven (1977, 1984*a*). It is possible to rationalize the order of acquisition of vascular plant characters in terms of sequential environmental challenges to terrestrial rhizophytes as their size increases: this evidence is summarized in table 2, which also presents possible evolutionary origins of the various features. It is clear that, by the lower to middle Devonian, vascular plants had all of the structural features associated with homoiohydry in extant vascular plants. It is not possible to tell from the fossil evidence whether these plants were desiccation-tolerant in the vegetative state. The association of poikilohydry with desiccation tolerance, and of homoiohydry with desiccation intolerance, is by no means complete (Raven 1984*c*, *d*).

The structure, function and evolution of terrestrial arthropods

The arthropods have a number of features in common with annelids, and particularly polychaetes, including metameric segmentation, with (primitively) a single pair of appendages on each segment, an anterior brain and a ventral nerve cord. The major structural factor in 'arthropodization' is the chitinous exoskeleton. The roles of the hydrostatic skeleton relative to direct muscle attachment to the exoskeleton has been commented on above in relation to motility and posture maintenance. The extent of hydrostatic pressure influence on motility based on muscles attached to an articulated exoskeleton will tend to be greater in organisms that rely on pressure-driven blood (haemocoel fluid) circulation to supply O_2 to the tissues, that is, organisms with gills or lungs, frequently associated with respiratory pigments in the blood, rather than tracheae.

The major arthropod divisions used follow Manton (1973). These are the Crustacea (marine; some freshwater; several independent invasions of the land), the Chelicerata (mainly terrestrial, with few extant marine representatives) and the Uniramia (predominantly terrestrial). In an analysis of locomotion in terrestrial arthropods, Manton (1977) showed that, in the Uniramia, the multitudinous walking legs of the Onychophora and Myriapods have been reduced to but three pairs in the Hexapoda, and that there is also a tendency to a reduction from four to three pairs of walking limbs in the terrestrial Chelicerata. Flight has only evolved in the Hexapoda.

Respiration in terrestrial arthropods involves lungs (gas-exchange surfaces that involve distribution of O_2 to the tissues through the blood; analogous to, and sometimes homologous with, the gills of aquatic arthropods) and tracheae (gas-exchange surfaces that transmit O_2 in the gas phase to the O_2-consuming tissues): some gas exchange occurs over the general body surface when this is not rendered relatively gas-impermeable by epicuticular wax. Internalization of the gas-aqueous phase transition for respiratory gases can help to reduce water loss per unit O_2 consumed under given environmental conditions if it is allied to *both* a relatively gas-impermeable epicuticle *and* a variable-permeability pore (spiracle) connecting the external atmosphere to the internalized respiratory surface. The extent to which this 'ideal' of minimizing respiratory water loss per unit O_2 consumption is achieved varies greatly between terrestrial arthropods (Edney 1977). In both the Chelicerata (some ticks, mites, scorpions and spiders) and the Uniramia (some insects) there is epicuticular wax that reduces the permeability coefficient for H_2O to as little as 10^{-6} m s^{-1} (cf. similar values achieved by plants: see above) and various mechanisms for changing the permeability of the spiracular aperture: many of these mechanisms respond to CO_2 in that a build-up of respiratory CO_2 increases the aperture (cf. enhanced opening of plant stomata by *decreased* intercellular CO_2 concentrations: table 2).

A much-discussed contributor to water conservation in terrestrial animals is nitrogen excretion in the form of the relatively insoluble uric acid (or guanine) rather than as the much more soluble urea or the very soluble (and toxic) ammonia. Edney (1977) and Little (1983) point out that the correlation between xeric environments and the use of insoluble nitrogen excretion products is not as clear as is sometimes asserted, although many terrestrial arthropods *do* excrete uric acid or guanine. Edney (1977) makes the significant point that uricotely, while conserving water, is expensive in terms of energy use. This raises the whole question of what resources limit the growth, and jeopardize the survival, of terrestrial arthropods: Mattson (1980) presents very strong evidence that animal growth on live or dead material is essentially nitrogen-limited rather than energy-limited, while it is clear that certain phytophagous arthropods have an excess of water in their diet (Edney 1977; Raven 1983). Accordingly, we must beware of assuming that water use efficiency for growth (and the associated water use efficiency of nitrogen excretion) is of paramount importance in all terrestrial arthropods. We may note that the capacity to survive complete desiccation is not common among terrestrial arthropods (unlike the situation in nematodes, rotifers and tardigrades, the latter phylum possibly being closely related to the Arthropods): (Edney 1977; Rolfe 1980).

While many species of terrestrial arthropods are 'specialist' feeders, there are also many 'generalist' species: biophages (herbivores, carnivores and some parasites) and necrophages (detritivores and some parasites). Generalization on nutrition of terrestrial arthropods are accordingly difficult: however, by comparison with aquatic arthropods, it would seem that extraorganismic digestion is commoner in the terrestrial members of that phylum. Extraorganismic digestion is presumably favoured in environments in which the secreted digestive enzymes, and the products of digestion, are less likely to diffuse away in solution, that is, on land as opposed to under water (see Manton 1977).

Finally, we note that internal fertilization, while common in aquatic arthropods, is commoner in terrestrial arthropods (Cohen 1977).

The origin and evolution of terrestrial arthropods

The immediate ancestors of arthropods were polychaete-like annelids. There is still controversy as to the mono- or polyphyletic nature of the Arthropoda (Barnes 1980; Little 1983): Manton (1973, 1977) argues very persuasively for a polyphyletic origin. Regardless of this, it is clear that the invasion of land by the arthropods has occurred several times and by diverse routes. Table 10.1 of Little (1983) indicates the marine littoral and the freshwater routes adopted by Crustacea, the marine littoral route taken by the Chelicerata and the (probably) marine interstitial route of the Hexapoda (and other Uniramia?). These assertions as to the routes taken are based on a wide range of evidence discussed by Little (1983).

Fossil evidence on the timing of the invasion of land by various taxa of arthropods is discussed by Rolfe (1980) and Little (1983). Rolfe (1980) notes that, among the Chelicerata, the Upper Silurian and Lower Devonian euripterids (an extinct taxon) and scorpions were primarily aquatic: extant scorpions are all terrestrial. Fossils of truly terrestrial Chelicerates (Arachnids) occur in the Rhynie Chert (Rolfe 1980) Among the Uniramia, the Diplopoda (millipedes) were possibly terrestrial in the Upper Silurian; they, and the Collembola (apterygote Hexapoda) were certainly terrestrial in the lower Devonian (Rolfe 1980). Crustacea were, apparently, later invaders of the land (Little 1983).

Little can be deduced about respiratory and water-conserving features from the earliest fossils of terrestrial arthropods. An exception is the very good preservation of a lung-book in an arachnid from the Rhynie Chert: internalization of respiratory surfaces had clearly occurred by the Lower to mid Devonian (Rolfe 1982). Although there is good preservation of the exoskeleton in many Siluro-Devonian terrestrial arthropod fossils, it is not easy to deduce the gas (CO_2, O_2, H_2O) permeability of such structures, especially in the absence of any indication of the occurrence, extent and composition of epicuticular wax (cf. table 2). The likely earliest terrestrial arthropods, that is, the Diplopoda, have extant relatives which are not generally noted for their ability to restrict cuticular and respiratory water loss: this is not surprising in view of the habitat and diet, that is, plant litter, of many millipedes (Edney 1977; Manton 1977; Little 1983).

Turning to possible precedents in their aquatic ancestors for the features that are 'unique' to terrestrial arthropods (cf. table 2 which attempts to summarize such precedents in plants), the following points may be briefly made.

The chitin–protein exoskeleton characteristic of arthropods was probably present in the aquatic ancestors of all of the transmigrant taxa: there is probably most dubiety on this point for the Uniramia. Extant annelids have collagen-based cuticles, but have chaetae whose chitin–protein composition is similar to that of the arthropod cuticle.

A very significant addition to the cuticle in many terrestrial arthropods in the Uniramia and Chelicerata (and probably the Crustacea: Little 1983) is wax ester in the epicuticle (Hadley 1981). The function of the epicuticular wax in small terrestrial arthropods in which respiratory gas exchange occurs over the whole body surface, for example, in some Collembola, appears to be in preventing accumulation of liquid water on the organism (water-repellancy), thus aiding O_2 diffusion to the body surface, with the caveat that such a layer must be discontinuous if it is not to impede greatly O_2 movement through the cuticle (Little 1983; cf. table 2). A function for the surface wax in those terrestrial arthropods that inherited specialized respiratory surfaces from aquatic ancestors (Crustacea; Chelicerates), or developed them subsequent to terrestrialization (Uniramian and Chelicerate trachaea), is in reducing water permeability of the general body surface (water resistance *sensu* Crisp 1963). The capacity to produce wax esters within the body as an energy store is characteristic of many planktonic marine crustacea (Benson *et al.* 1972), so that at least the Crustacean line of arthropod colonization of the land possessed the biochemical capacity for wax ester synthesis, albeit without the spatial aspect of this metabolism which is needed for wax ester deposition in the epicuticle.

Turning to the internalized respiratory surfaces that characterize many terrestrial arthropods, the lungs (respiratory surfaces exchanging gases between air and haemocoel) of many terrestrial Crustaceans and Chelicerates are generally homologous with the gills of their aqueous ancestors. Pseudotracheae and tracheae, which are found in all three subphyla of terrestial arthropods and which partly or completely take over (by gaseous diffusion and mass flow) the role of lungs plus mass flow of blood containing dissolved O_2 in supplying O_2 to the tissues, are without obvious precedent in primitively aquatic arthropods (see Wigglesworth 1983).

The nature of nitrogenous excretory products is an aspect of the water relations of terrestrial animals that has attracted considerable attention (Edney 1977; Little 1983). While we have already seen that the excretion of relatively insoluble purine-based nitrogenous compounds is a water-sparing stratagem that has energetic penalties (see Edney 1977), and is not universally found in terrestrial Uniramians and Chelicerates, it is significant that Crustacea are, apparently, unable to synthesize purines (Claybrook 1983). The small fraction of the total N excreted from even terrestrial Crustaceans as uric acid, that is, not more than 5% (Claybrook 1983), presumably reflects the disposal of dietary purines absorbed in excess of metabolic requirements. The inability to synthesize purines, and hence use purines or purine derivatives as vehicles for N excretion, may have limited the capacity of Crustaceans to invade xeric terrestrial habitats.

The final point to be mentioned in relation to evolution of terrestrial characteristics is that of osmoregulation. Little (1983) has used the 'normal' osmolarity of the tissues of terrestrial arthropods, the solutes generating this osmolarity, and tolerance of perturbations of this osmolarity, in deducing the paths by which the various terrestrial arthropod taxa invaded the land, further comparative investigations of osmoregulation in aquatic and terrestrial arthropods should prove rewarding, as should further investigations of acid-based balance (Edney 1977; Little 1983; Mantel & Farmer 1983; Truchot 1983).

Conclusions

There are a number of important characteristics shared by terrestrial vascular plant sporophytes and most terrestrial arthropods. These similarities include internalization of the air–water interfaces across which the exchange of gases involved in photosynthesis and respiration occurs; a pore of regulatable aperture (stomata or spiracles) which controls the exchange of gases, including water vapour, between the internal and external gas phases; the presence of a wax layer over the general body surface, severely restricting water loss through the 'cuticular' pathway; and the general lack of desiccation-tolerance of the organisms (excepting certain perennating structures). These attributes are all related to the potential for water vapour loss from terrestrial organisms to an unsaturated atmosphere.

The vascular plants apparently differ from the arthropods in that the major rigid, compression-resistant structural element of the plants, that is lignin, only appeared *after* plants had migrated onto land (table 2): the sclerotized protein–chitin cuticle of the arthropods first appeared in their aquatic forebears. The likely selection pressure favouring lignin was the tension developed in the lumina of water-conducting xylem elements, an essentially terrestrial phenomenon requiring a rigid structural element. Evolution of the arthropod cuticle was probably related to compressive forces in the solid skeleton which replaced a hydrostatic skeleton in an aquatic environment where maintenance of posture in a low-density medium was not required. Despite having originated in these diverse ways, both lignin and the arthropod exoskeleton were subsequently involved in posture-maintenance in terrestrial vascular plants and arthopods respectively, and owe their rigidity to three-dimensional covalent bonding involving phenolic compounds. Rigidity of vascular plant cuticle is related to covalent cross-links between lipid molecules (Hadley 1981).

This partial list of attributes of terrestrial vascular plants and arthropods shows that analogous solutions were found for analogous problems of growth on land, and that, at least at the biochemical if not at the anatomical level, there were precedents for many of these solutions in their aquatic ancestors. The 'pre-adaptive' biochemical background against which the evolution of the structures and functions appropriate to terrestrial phototrophy and phagotrophy took place in vascular plants and arthropods, respectively, suggests that the anatomical and physiological changes that were required to produce successful terrestrial organisms could have occurred by random mutation at some time previous to the late Silurian, granted a suitable environment.

Turning now to the environment, an obvious constraint on the colonization of land by organisms that were large enough to adopt a homoiohydric rather than a poikilohydric response to the water-relations problems of terrestrial existence (that is, the mainly desiccation-intolerant vascular plant sporophytes, and arthropods, rather than the frequently desiccation-tolerant non-vascular land plants and nematodes, rotifers and tardigrades) was the atmospheric O_2 concentration and the related (via O_3 levels) ultraviolet flux. Raven (1984*c*) discusses the 'autocatalytic' effect which increased atmospheric O_2 levels (paralleled by burial of the other product of photosynthesis, organic C) could have on the potential size of the phototrophs which produced the O_2. The decreased flux of ultraviolet relative to photosynthetically active radiation would permit plants to grow in environments of higher photon flux density, with a corresponding extra energy input that permits the growth of larger plants with, necessarily, more non-photosynthetic structural and conducting material as a fraction of the total biomass, while the higher O_2 concentration permits the aerobic growth and maintenance of bulky plant organs. However, it is difficult to quantify these effects for extant plants, and it is accordingly difficult to predict what atmospheric O_2 levels would have been needed to permit the evolution of land plants that were capable of growing large enough to become homoiohydric. For arthropods, it is clear that the most active extant arthropods (flying insects) require essentially the present atmospheric level of O_2 for their full activity: flight at lower O_2 levels in the atmosphere would require a greater tracheal volume in the flight muscle, which could only occur by displacement of other desiderata, that is, actomyosin and mitochondria (Wigglesworth 1983; Pennycuik & Rezende 1984). However, flying insects appeared almost contemporaneously with the earliest fossil charcoal, suggesting that atmospheric O_2 was at least 0.3 of the present atmospheric level (Cope & Chaloner 1980; Little 1983). We cannot yet quantify the atmospheric O_2 level at which terrestrial vascular plants and arthropods could have first occurred: even where this O_2 level known, there is still considerable dubiety over the timing of the attainment of any particular O_2 level in the pre-Carboniferous Palaeozoic.

On how many separate occasions did arthropods, and the ancestors of vascular plants, invade the land? Many non-vascular plants were terrestrial in the Silurian (Edwards 1980); of these, only Charophycean green algae gave rise to vascular plants. The tracheophytes and bryophytes thus appear to have resulted from a single transmigratory event by algae. It is still not clear if the tracheophytes are themselves monophyletic, that is, are all descended from a single, vascularized, *Cooksonia*-type ancestor. A major problem is the terminal position of sporangia in the rhyniophyte–trimerophyte line, by contrast with their lateral position in the zosterophyllophyte line.

For the arthropods, it is clear that terrestrialization took place in at least two subphyla (Chelicerata and Uniramia) in the Siluro-Devonian, with Crustacean invasion of the land occurring later in a number of taxa independently. Once on land, the occurrence of aerially dispersed spores in the plants, and of terrestrial and, later, aerial motility (through wings in insects and gossamer in arachnids) would have helped to spread the organisms over the continents.

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REFERENCES

Banks, H. P. 1980 Floral assemblages in the Siluro-Devonian. In *Biostratigraphy of fossil plants: successional and palaeoecological analyses* (ed. T. N. Dilcher & T. N. Thomas), pp. 1–24. Stroudsberg, Pennsylvania: Dowden, Hutchinson & Ross.

Barnes, R. D. 1980 *Invertebrate zoology*, 4th edn. Philadelphia: Saunders College.

Benson, A. A., Lee, R. F. & Nevenzeel, J. C. 1972 Wax esters: major marine metabolic energy sources. *Biochem. Soc.* (*Lond.*) *Symp.* **35**, 175–187.

Berner, R. A., Lasaga, A. C. & Garrels, R. M. 1983 The carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. *Am. J. Sci.* **283**, 641–683.

Bewley, J. D. & Krochko, J. E. 1982 Desiccation-tolerance. In *Encyclopedia of plant physiology*, new series, vol. 12B (ed. O. Lange, P. S. Nobel, C. B. Osmond & H. Ziegler), pp. 325–378. Berlin: Springer Verlag.

Bisson, M. A. & Bartholemew, D. 1984 Osmoregulation or turgor regulation in *Chara*. *Pl. Physiol.* **74**, 252–255.

Broecker, W. S. 1970 A boundary condition on the evolution of atmospheric O_2. *J. Geophys. Res.* **75**, 3553–3557.

Broecker, W. S. 1982 Ocean chemistry during glacial time. *Geochim. Cosmochim. Acta* **46**, 1689–1705.

Canuto, V. M., Levine, J. S., Augustsson, T. R. & Imhoff, C. L. 1982 U.V. radiation from the young sun and oxygen and ozone levels in the prebiological atmosphere. *Nature, Lond.* **296**, 816–820.

Chaloner, W. G. 1970 The rise of the first land plants. *Biol. Rev.* **45**, 353–377.

Chaloner, W. G. & Sheerin, A. 1979 Devonian macrofloras. In *The Devonian System*: special paper in palaeontology **23**, 145–161. London: The Palaeontological Society.

Church, A. H. 1919 *Thalassiophyta and the Subaerial Transmigration*. Oxford Botanical Memoirs Number 3. Oxford: Clarendon Press.

Claybrook, D. L. 1983 Nitrogen metabolism. In *The biology of Crustacea*, vol. 5 (ed. L. H. Mantel), pp. 163–213. New York: Academic Press.

Cohen, J. 1977 *Reproduction*. London: Butterworths.

Cope, M. J. & Chaloner, W. G. 1980 Fossil charcoal as evidence of past atmospheric composition. *Nature, Lond.* **383**, 647–649.

Cowan, I. R. 1977 Stomatal behaviour and environment. *Adv. Bot. Res.* **4**, 117–228.

Crisp, D. J. 1963 Waterproofing mechanisms in animals and plants. In *Waterproofing and water-repellancy* (ed. J. L. Moilliet), pp. 416–481. Amsterdam: Elsevier.

Edney, E. B. 1977 *Water balance in land arthropods*. Berlin: Springer Verlag.

Edwards, D. 1980 Early land floras. In *The terrestrial environment and the origin of land vertebrates* (ed. A. C. Panchen), pp. 55–85. London: Academic Press.

Edwards, D., Feehan, J. & Smith, D. G. 1983 A late Wenlock flora from Co. Tipperary, Ireland. *Bot. J. Linn. Soc.* **86**, 19–36.

Fritsch, F. E. 1945 Studies on the comparative morphology of the algae. IV. Algae and Archegoniate Plants. *Ann. Bot.* **9**, 1–30.

Gunning, B. E. S. & Robards, A. W. (eds.) 1976 *Intercellular communication in plants: studies on plasmodesmata.* Heidelberg: Springer Verlag.

Hadley, N. F. 1981 Cuticular lipids of terrestrial plants and arthropods: a comparison of their structure, composition and waterproofing function. *Biol. Rev.* **56**, 33–47.

Hart, M. H. 1978 The evolution of the atmosphere of the earth. *Icarus* **33**, 23–39.

Holland, H. D. 1965 The history of ocean water and its effect on the chemistry of the atmosphere. *Proc. natn. Acad. Sci. Wash.* **53**, 1173–1182.

Jones, H. G. 1983 *Plants and microclimate.* Cambridge: University Press.

Keeley, J. E., Osmond, C. B. & Raven, J. A. 1984 *Stylites*, a vascular land plant without stomata absorbs CO_2 via its roots. *Nature, Lond.* **310**, 694–695.

Little, C. 1983 *The colonisation of land: origins and adaptations of terrestrial animals.* Cambridge: University Press.

Mantel, L. H. & Farmer, L. C. 1983 Osmotic and ionic regulation. In *The biology of Crustacea*, vol. 5 (ed. L. H. Mantel), pp. 54–161. New York: Academic Press.

Manton, S. M. 1973 Arthropod phylogeny – a modern synthesis. *J. Zool.* **171**, 111–130.

Manton, S. M. 1977 *The Arthropoda: habits, functional morphology, and evolution.* Oxford: Clarendon Press.

Mattson, W. J. Jr 1980 Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol. Syst.* **11**, 119–161.

Monteith, J. L. 1973 *Principles of environmental physics.* London: Edward Arnold.

Neftel, A., Oescheger, H., Schwander, J., Stauffer, B. & Zumbrunn, R. 1982 Ice core sample measurements give atmospheric CO_2 content during the last 40000 years. *Nature, Lond.* **295**, 220–223.

Newman, M. J. 1980 The evolution of the solar constant. *Origins of Life* **10**, 105–110.

Pennycuik, C. J. & Rezende, M. A. 1984 The specific power output of aerobic muscle, related to the power density of mitochondria. *J. exp. Biol.* **108**, 377–392.

Peters, R. H. 1983 *The ecological implications of body size.* Cambridge: University Press.

Racki, G. 1982 Ecology of the primitive charophyte algae: a critical review. *N. Jb. Geol. Paläont. Abh.* **162**, 388–399.

Raven, J. A. 1977 The evolution of vascular land plants in relation to supracellular transport processes. *Adv. bot. Res.* **5**, 153–219.

Raven, J. A. 1981 Nutritional strategies of submerged benthic plants: the acquisition of C, N and P by rhizophytes and haptophytes. *New Phytol.* **88**, 1–30.

Raven, J. A. 1983 Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Adv. ecol. Res.* **13**, 135–234.

Raven, J. A. 1984*a* Physiological correlates of the morphology of early vascular plants. *Bot. J. Linn. Soc.* **88**, 105–126.

Raven, J. A. 1984*b* *Energetics and transport in aquatic plants.* New York: A. R. Liss. (In the press.)

Raven, J. A. 1984*c* Evolution of plant life forms. In *On the economy of plant form and function* (ed. T. V. Givnish). Cambridge: University Press (In the press.)

Raven, J. A. 1984*d* Physiology and biochemistry of pteridophytes. *Proc. R. Soc. Edinb.* B (In the press.)

Raven, J. A. 1984*e* Trees as producers of exudates and extractives. In *Attributes of trees as crop plants* (ed. M. G. R. Cannell). London: Academic Press. (In the press.)

Raven, J. A., Beardall, J. & Griffiths, H. 1982 Inorganic C-sources for *Lemanea*, *Cladophora* and *Ranunculus* in a fast-flowing stream: measurements of gas exchange and of carbon isotope ratio and their ecological implications. *Oecologia* **53**, 68–78.

Reed, R. H. 1984 Use and abuse of osmo-terminology. *Plant, Cell Environ.* **7**, 165–170.

Riley, J. P. & Skirrow, G. (ed.) 1975*a* *Chemical oceanography*, vol. 1, 2nd edn. London: Academic Press.

Riley, J. P. & Skirrow, G. (ed.) 1975*b* *Chemical oceanography*, vol. 2, 2nd edn. London: Academic Press.

Rolfe, W. D. I. 1980 Early invertebrate terrestrial faunas. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 117–157. London: Academic Press.

Rolfe, W. D. I. 1982 Ancient air breathers. *Field Mus. Nat. Hist. Bull.* **53**, 12–16.

Schmidt-Nielsen, K. 1983 *Animal physiology: adaptation and environment*, 3rd edn. Cambridge: University Press.

Stebbins, G. L. & Hill, G. J. C. 1980 Did multicellular plants invade the land? *Am. Nat.* **115**, 342–353.

Stewart, K. D. & Mattox, K. R. 1975 Comparative cytology, evolution and classification of the green algae with some consideration of the origin of other organisms with chlorophylls *a* and *b*. *Bot. Rev.* **41**, 104–135.

Truchot, J. P. 1983 Regulation of acid-base balance. In *The biology of Crustacea*, vol. 5 (ed. L. H. Mantel), pp. 431–457. New York: Academic Press.

Wainwright, S. A. 1970 Design in hydraulic organisms. *Naturwiss.* **57**, 321–330.

Wigglesworth, V. B. 1983 The physiology of insect tracheoles. *Adv. Insect Physiol.* **17**, 85–148.

Note added in proof (*5 September* 1984). A high uric acid content (16% of the body mass) has been reported for a land crab (Gifford 1968; Powers & Bliss 1983) so that the suggestion that crustacea lack the purine biosynthetic pathway (Claybrook 1983) does not seem to be valid in all cases. A re-evaluation of the constraints on the form in which nitrogen is excreted from terrestrial animals has recently appeared (Atkinson 1982).

References

Atkinson, D. E. & Camien, M. N. 1982 *Curr. Top. Cell Regulation* **21**, 261–301.

Claybrook, D. L. 1983 Nitrogen metabolism. In *The biology of Crustacea*, vol. 5 (ed. L. H. Mantel), pp. 163–213. New York: Academic Press.

Gifford, C. A. 1968 Accumulation of uric acid in the land crab, *Cardisoma guanhumi*. *Am. Zool.* **8**, 521–528.

Powers, L. W. & Bliss, D. E. 1983 Terrestrial adaptations. In *The biology of Crustacea*, vol.8 (ed. F. J. Vernberg & W. B. Vernberg), pp. 271–333. New York: Academic Press.