Aeration in Higher Plants

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I. INTRODUCTION

While there is a considerable volume of literature dealing with the diffusive influx of carbon dioxide and efflux of water vapour across leaf surfaces, the gas movements necessary to sustain respiratory activities throughout the plant body attract little comment in physiological texts. Historically, this can be attributed to the relative intensities of research in the two fields: whilst Browne and Escombe had by 1900 laid the foundation of the diffusion mathematics concerned with gaseous fluxes through stomatal surfaces, as recently as 1937 Conway was commenting that the general assumption of gas-phase continuity of intercellular spaces thoughout the wetland plant body had not yet been tested. A gas phase continuum in the cortical intercellular space system of non-wetland species was not even a general assumption ten years later. Brown (1947) concluded that longitudinal movements of nitrogen, oxygen and hydrogen which he could induce between shoot and root and vice versa in seedlings of *Cucurbita pepo* were not diffusion controlled but rather were dependent upon the active translocation of gases in solution. Brown was perhaps the first to demonstrate conclusively that there was oxygen leakage from root surfaces. We now know that in wetland and non-wetland plants alike, the major movements of respiratory gases between shoot and root occur in the gas-phase and are largely controlled by diffusion.

Current interest in whole plant aeration (but more particularly the aeration of below ground parts) can be traced back about 40 years, to experiments performed on wetland species. First Conway (1937), followed by Laing (1940) and the Dutch scientist Van Raalte (1941, 1944) convincingly demonstrated the continuity of the gas space of shoot and root, and the dependence of the submerged root upon the shoot for its oxygen supply. That the intercellular space system also provides for the escape of carbon dioxide was indicated by reverse-order gradients of concentration. Van Raalte (1944) also drew attention to the rhizosphere oxidizing activity of the rice root, an important property for counteracting the reduced nature of the wet soil and also dependent upon longitudinal oxygen flow from the aerial parts. The oxidizing activity of roots had been overlooked since the pioneer work of Molisch (1888), Raciborski (1905a, 1905b), Schreiner and Sullivan (1910) and Schreiner and Read (1909).

Van Raalte's findings were perhaps the greatest stimuli to further research and the oxidizing activities of root systems still continue to attract interest (Engler and Patrick, 1975; Green and Etherington 1977). Tracer studies gave the first proof of gaseous oxygen diffusion through non-wetland species (Evans and Ebert, 1960; Barber *et al.*, 1962), and this time marked the beginning of an upsurge in research activity concerned with both soil and root aeration. The earlier work of Buckingham (1904), Penman (1940), Van Bavel (1951) and others on gas movements in the soil was taken further (Currie,

1961a, b, 1965; Millington, 1959; Greenwood, 1961) and the application of diffusion mathematics to root aeration began (Lemon, 1962; Lemon and Wiegand, 1962; Kristensen and Lemon, 1962).

The following account is centred chiefly around developments since 1960 which have culminated in the modelling of the oxygen movements within the plant, and a recognition that internal oxygen transport in the mesophyte can be substantial. At the same time it has become apparent that root respiration and growth might proceed unimpaired at quite low internal oxygen pressures and under anoxic conditions some extraordinary "malformations" of mitochondrial structure have been observed recently (Vartapetian *et al.*, 1977). Since oxygen transport has been the foremost research topic during this period it is this which I have chosen to emphasize below. To this end I have attempted to collate the mathematical approaches to the aeration process and to explain the concepts of modelling in a manner which I hope may prove simple to understand.

As to the future, there is a pressing need to study further the responses of the roots, and their cells and organelles to sustained anoxia and low oxygen pressure, particularly in the intact plant. Hopefully this might result in a consensus on the role of anaerobic metabolism in the wetland condition; it might eventually lead to the discovery of what it is that enables the wetland plant to develop aerenchyma, perhaps the most teasing problem of all.

II. PRINCIPLES OF AERATION AND AERATION MODELLING

A. ENTRY AND DISPERSAL OF RESPIRATORY GASES

*1. Introduction**

The environment exerts a considerable influence on the directional flow of the respiratory gases within the plant and the directional exchange with the atmosphere.

Oxygen may enter the plant body in a variety of ways.

In non-aquatic species, where cuticularization and suberization lower the gas permeabilities of aerial surfaces, the internal gas-space system of the plant connects with the external environment through the stomata and lenticels which provide paths of low resistance for the entry and exit of both oxygen and carbon dioxide.

In submerged astomatal aquatics, surface permeabilities are sufficiently high to allow for the necessary gas transference across the epidermal layers by liquid-phase movement.

Plants rooted in unsaturated soils may be exposed to an oxygen-rich

* Note added in proof. For a broader view of transport processes in the plant the reader is recommended to consult the review by J. A. Raven (1978): The Evolution of Vascular Land Plants in Relation to Supracellular Transport Processes (*Adv. Bot. Res.* **5**, 153–219).

environment over the greater part of their shoot and root surfaces. In such circumstances there may be little longitudinal movement of gases within the plant: the leaves and shoots will be aerated by simple planar and radial gas exchange with the atmosphere; the oxygen requirements of the root system may be met largely by a diffusive transfer from the soil atmosphere supplemented by transpirational flow (p. 236). In most instances gaseous oxygen must enter the liquid-phase at a point external to the root and it is thought that its passage across the cellular layer(s) of the root wall occurs chiefly in the liquid phase. A substantial proportion of this will then pass into the gas phase of the intercellular space system at the outer perimeter of the root cortex.

In saturated soils the situation is very different: little or, more often, no oxygen is available for radial entry to the root system and it becomes essential for longitudinal transport to take place between shoot and root. There is potential for longitudinal gas transport in both the intercellular gas-space system and the stele and the relative merits of these paths are discussed in the following sections. Radial movements will tend to be bidirectional: from root cortex to stele and from root to soil. The latter, radial oxygen loss (ROL) may be of very great importance for the survival of plants in the wetland habitat (see p. 281).

Finally, oxygen enters the plant in the combined state as water. As water it is transported from root to shoot in the xylem where a proportion is finally released into the liquid phase within the chloroplasts during the photolysis stage of photosynthesis. At light intensities above the compensation point a net transfer of oxygen from the cellular liquid phase of the leaf to the gas-phase of the adjoining intercellular spaces will be ensured. The roles of light and darkness in the aeration process are considered in detail in Section II.C.2.

2. Longitudinal Transport

(*a*) *The gas-space system.* In the more complex animals oxygen enters and leaves an elaborate distribution network (the blood system) by means of diffusion, but within the distribution network itself movement is essentially a mass-flow energy-dependent process.

In contrast, most, if not all, of the steps in the gas flow process in the higher plant, including the major one of dispersal, are to a greater or lesser extent diffusion-dependent: gas-phase diffusion is the major mechanism for long-distance transport. Dispersal by diffusion is made possible because the higher plant has evolved as a porous structure with a labyrinth of intercellular gas-space. Diffusion in the gas-phase is extremely rapid (10^4 times more rapid than in an aqueous medium) and it is this which enables the higher plant to rely on diffusion for its gas exchange requirements to the extent it does.

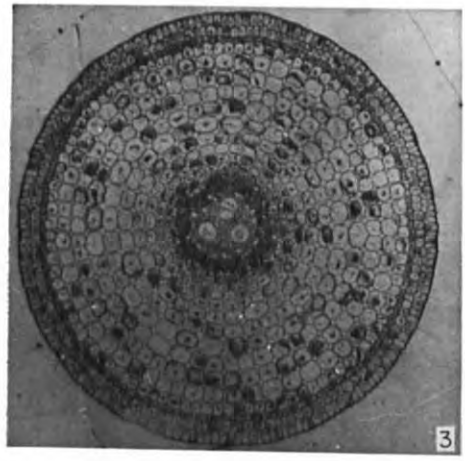
Intercellular gas-space is characteristic of most extrastelar ground tissues in the plant such as the mesophyll and palisade tissues of leaves, and the cortical parenchymas of stem and root, while pith within primary vascular cylinders may be similarly structured. Much ground-tissue gas-space interconnects and we find for example that herbaceous species are characterized by an uninterrupted gas-space continuum within the cortical ground tissues extending from the sub-stomatal cavities to within 20 μm of the root/root-cap junction (Plate I).

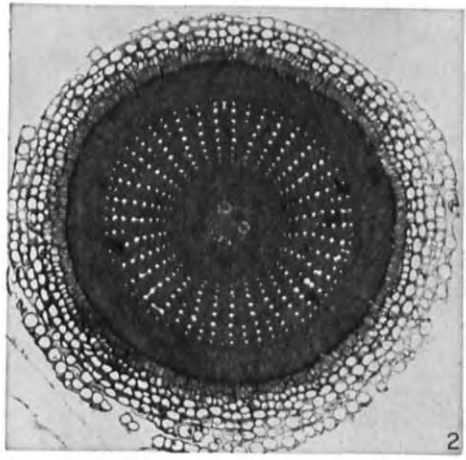
The volume *per cent* of the gas-space within an organ at any point is referred to as the porosity, and the proportion of gas-space within individual tissues and organs varies enormously: in wetland plants the porosities of roots, stems and leaves can be as high as 60%.

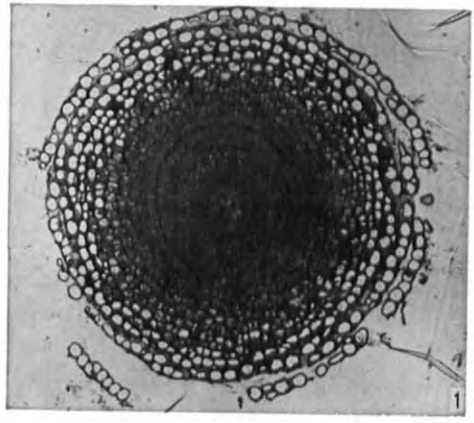
However, despite this, there are places within the plant structure which are not so liberally permeated; in other places adjacent gas-spaces may be separated by non-porous tissue barriers. Secondary growth can introduce areas of low or high porosity. In the primary plant body the stelar parenchymas most closely associated with the conducting tissues may have little if any significant gas-space. Likewise, the extremities of meristems are devoid of spaces. The endodermis is a tissue which is not usually traversed by gas-spaces and may be a significant barrier to gas exchange between stele and cortex in roots (and perhaps also in the stems of Gymnosperms and Pteridophytes). The primary vascular cambia may also have little if any permeating gas-space and may form a significant aeration barrier to both stem and root aeration in woody species. The compacted tissues of root–shoot and root–root junctions are potential dispersal barriers in gas exchange. The movement of gases through the individual cell and across aporous tissues is briefly discussed below under the heading "Lateral Transport".

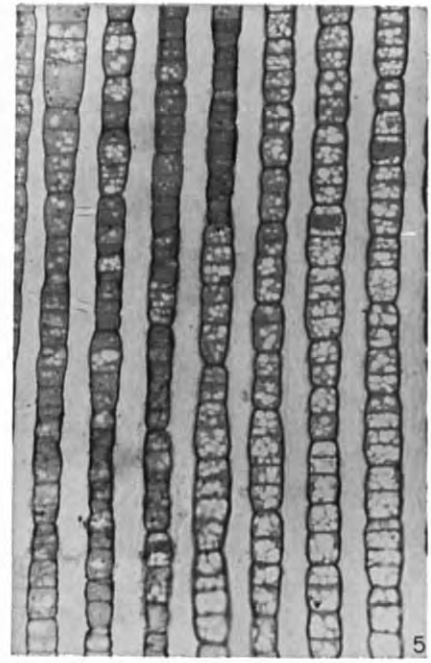
Although there is little doubt that the longitudinal movements of respiratory gases in the intercellular space systems of plants are essentially diffusional it is as well to realize that some mass-flow movement must occur: both the diffusion-exchange system itself and environmental factors such as temperature and barometric changes will tend to produce total pressure differences.

Wood and Greenwood (1971) have drawn attention to the probable induction of mass-flow in soils brought about by diffusional inequalities. The molecules of the three atmospheric gases oxygen, nitrogen and carbon dioxide have different weights and consequently different rates of random movement (Table I); also the total pressure at any point in the gas-phase is proportional to the number of molecules per unit volume irrespective of molecular species. In aerobic soils oxygen is consumed and carbon dioxide produced in approximately a 1 : 1 ratio. This induces a flow of molecules, and in general because of the different rates of oxygen and carbon dioxide diffusion, incipient differences in total pressure must arise which can only be









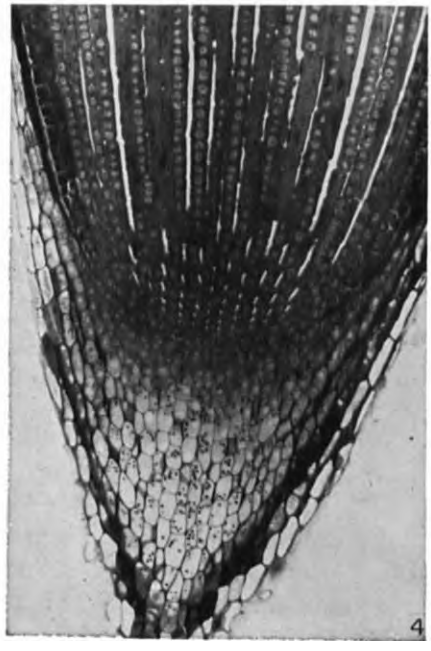


Plate I

balanced by mass-flow involving not only the oxygen and carbon dioxide, but also the nitrogen. By similar reasoning one can anticipate similar mass-flow effects within the plant.

Mass-flow supplementation of soil aeration in this way must be rather small but in roots the situation is more complicated because of the potential for carbon dioxide escape in the transpiration stream. (From simple solubility considerations it can be calculated that the water flow into the stele of a young root could be sufficient to accommodate much of the carbon dioxide efflux of stelar respiration.) Carbon dioxide removed in this way would further induce changes in total pressure and add to the mass-flow component in the aeration process. However, it is exceedingly difficult to estimate the likely magnitude of this effect; at this stage we can only assume it to be small. We know little of the relative respiratory rates of the different stelar zones or the diffusional characteristics of the tissues; the rate of carbon dioxide entry to the xylem will depend upon the carbon dioxide pressures generated within the stelar zones and upon the relative route resistances between the living stelar elements and the xylem elements and cortical gas spaces. Furthermore, in situations where this mechanism might assume some physiological importance, e.g. the wetland condition, it is by no means certain that there may not be a compensating inflow of carbon dioxide from soil to root in the transpiration stream.

A mass-flow of somewhat greater proportions is likely in tidally-inundated plants: a total pressure deficit of *c.* 0·05 atm in the roots of mangroves during periods of submergence has been reported by Scholander *et al.* (1955). This deficit is quickly corrected by mass-flow during the ebb-tide.

It is very unlikely that internal mass-flow induced by temperature or barometric fluctuations will be of any great significance in the overall aeration process. Undoubtedly mass-flow can be effected in this way: a 10°C fall in temperature can cause a mass-flow into soils of as much as 0·9 l O_2 m^{-2} (Bouyoucos 1915). For a varied range of soils Grable (1966) calculated this as sufficient to satisfy from 11–150% of the daily oxygen requirements of the soil population. How valuable such a recharging of the soil atmosphere might be will depend very much on the circumstances in particular soils. It seems reasonable to assume that a temperature-induced mass-flow within the plant would be of the greatest value for supplementing root aeration in

Plate I. Gas-space characteristics of wetland plants: Rice and *Eriophorum angustifolium*: Adventitious roots from waterlogged soils: transverse and longitudinal appearance of gas-spaces within the apex. (1)–(3) Rice: transverse sections at distances of 20 μm, 120 μm and 1·5 mm from the root/root cap junction (magnification × 120, × 122·5 and × 75). (4) Rice: tangential longitudinal section (magnification × 137·5). (5) *E. angustifolium*: longitudinal section through segment of cortex at a position which in rice would be approximately halfway between sections (2) and (3) (magnification × 500). Sections (4) and (5) both show clearly the lack of tortuosity in the cortical gas-spaces.

TABLE I

Diffusivities, Solubilities and Fractional Volumes in Air, of the Atmospheric Gases Nitrogen, Oxygen and Carbon Dioxide

1. Oxygen

Temp. (°C)	Fractional vol. in moist air at NP	Conc. in moist air at NP (10^{-6} g cm^{-3})	Solubility in pure water from moist air at NP (10^{-6} g cm^{-3}) *a*	(10^{-4} mol l^{-1}) *a**	(10^{-3} cm^3 cm^{-3}) *a**	Self diffusion coefficient (cm^2 s^{-1}) *b*	Diffusivity in air (cm^2 s^{-1}) *c*	Diffusivity in water (10^{-5} cm^2 s^{-1}) *d*
0	0·2086	297·9	14·63	4·57	10·25	0·181	0·178	0·99†
3	*0·2083*	*294·2*	*13·46*	*4·20*	*9·53*		*0·181*	*1·16†*
5	0·2081	291·7	12·77	3·99	9·11		0·184	1·27†
10	0·2074	285·6	11·28	3·52	8·19		0·189	1·54†
15	0·2064	279·3	10·07	3·15	7·44		0·195	1·82
20	0·2050	272·8	9·08	2·84	6·83		0·201	2·10
23	*0·2041*	*268·7*	*8·57*	*2·68*	*6·508*		*0·205*	*2·267*
25	0·2033	265·9	8·26	2·58	6·32		0·207	2·38
30	0·2011	258·7	7·57	2·36	5·88		0·214	2·67†

NB: The fractional volume of oxygen in dry air at NP is given as 0·2099 in the International Critical Tables (Humphries, 1926) and as 0·20946 ± 0·00002 in Weast (1974). The fractional volumes and concentrations of oxygen in moist air are based on the former of these two values.

2. Carbon dioxide

Temp. (°C)	Solubility in water. CO_2 gas source at a pressure of 760 mm: $(10^{-3}$ g $cm^{-3})$ *e**	$(10^{-4}$ mol $l^{-1})$ *e**	Self diffusion coefficient (cm^2 s^{-1}) *b*	Diffusivity in air (cm^2 s^{-1}) *c*	Diffusivity in water (10^{-5} cm^2 s^{-1}) *f*
0	3·29	747·7	0·0965	0·138	1·15†
3	2·98‡	677·3‡		0·141	1·24†
5	2·75‡	625‡		0·143	1·30†
10	2·28	518·8		0·148	1·46
15	1·94	440·7		0·153	1·63
20	1·66	377·3		0·159	1·77
23	1·52‡	346‡		0·162	1·86
25	1·44‡	327·3‡		0·164	1·92†
30	1·28	290·0		0·170	2·08†

3. Nitrogen

Fractional volume in dry air at NP:
0·7803 (Humphries, 1926)
0·7809 (Weast, 1974).
Solubility in water from N_2 source at a pressure of 760 mm: $18{\cdot}1 \times 10^{-6}$ g cm^{-3} @ 23°C (extrapolated from data of Kaye and Laby, 1966).‡
Self diffusion coefficient:
0·178 cm^2 s^{-1}.[b]
Other diffusivities are not comprehensively listed but closely approximate to those for oxygen.

NB: The fractional volume of carbon dioxide in dry air at NP is given as 0·0003 (Humphries, 1926) and 0·00033 by Weast (1974).

[a] Montgomery *et al.* (1964); [b] Chapman and Cowling (1939); [c] Boynton and Brattain (1929); [d] Millington (1959); [e] Kaye and Laby (1966); [f] Bruins (1929); * calculated from data given in a different form; † linear extrapolation from other data; ‡ curvilinear extrapolation from other data.

saturated soils. However it can be calculated that it would require many recharging operations within a 24 h period to satisfy the oxygen requirements of root systems, even in highly porous plants (see also p. 296).

(*b*) *The stele.* It might be thought that the specialized long-distance transport systems for water and solute movement in the plant could also play a significant role in the dispersal of oxygen to remote parts. For example, it might be particularly advantageous in wetland species if phloem were to provide a route for the transference of oxygen from the aerial shoot system to the submerged organs subject to the anoxia of the wetland soil regime. In such circumstances the reverse flow in the xylem might provide the escape route for carbon dioxide. Conversely it has been suggested that in non-wetland conditions the inner tissues of most broadleaved tree species may rely on oxygen dissolved in the transpiration stream (Hook *et al.*, 1972).

These possibilities are neither wholly supported nor contradicted in the specialist literature on phloem and xylem transport: phloem physiologists have divergent views on the oxygen relations of phloem transport. However, with the aid of some simple calculations, and taking a biased view from the literature I find myself drawn to the view that neither the phloem nor the xylem is likely to play a major role in the oxygen dispersal process.

(i) The phloem. Peel (1974) has noted that despite the difficulties encountered in making velocity measurements most workers in the field of phloem physiology would accept that solutes can be transported at speeds of up to 100 cm h^{-1}. Some experiments have indicated values greatly in excess of this (Nelson *et al.*, 1958), others considerably less (Canny, 1961).

Using this figure of 100 cm h^{-1}, consider a phloem bundle of length 100 cm and radius 0·005 cm. Assuming that the sieve tubes occupy approximately one-fifth of the total phloem volume (Peel, 1974) the total sieve tube volume will be (100/5) ($0{\cdot}005^2\,\pi$) or $1{\cdot}57 \times 10^{-3}$ cm^3. If the oxygen partial pressure at the loading site is 0·2043 atm and the oxygen solubility in the sieve tube cytoplasm approximates to that in water ($6{\cdot}5 \times 10^{-3}$ cm^3 cm^{-3}) then the maximum rate at which the phloem will conduct oxygen should be ($1{\cdot}57 \times 10^{-3}$) × ($6{\cdot}5 \times 10^{-3}$) or $10{\cdot}2 \times 10^{-6}$ $cm^3\,h^{-1}$. Assuming a density of 1·0 (Canny, 1973) the total fresh weight of the phloem strand would be $7{\cdot}85 \times 10^{-3}$ g. If the oxygen transported was freely available for phloem respiration the respiratory rate could not exceed $10{\cdot}2 \times 10^{-6}/7{\cdot}85 \times 10^{-3}$ or $1{\cdot}3 \times 10^{-3}$ cm^3 g^{-1} fw h^{-1}. A shorter phloem strand would naturally lead to an increase in the potential for respiratory activity: with a strand of 10 cm the value becomes 13×10^{-3} cm^3 g^{-1} fw h^{-1}. However even this contrasts markedly with the values for phloem respiration given in the literature: it is only one twentieth of the value cited by Canny (1973) as an acceptable mean level for oxygen consumption by phloem. With efficient oxygen extraction and a potential respiratory rate of 230×10^{-3} cm^3 g^{-1} fw h^{-1} up to 95% of the

10 cm phloem strand could become anaerobic; in a strand of 100 cm this could rise to 99·5%.

On this basis it would appear that the oxygen-carrying capacity of the phloem not only fails to meet the requirements for long-distance transport but is also inadequate for the vital activities of the phloem itself. Hence, although the velocity of solute movement in phloem can accord with that of gas-phase diffusion the suggestion that phloem might play a major role in gas transport appears to falter on the phloem's capacity in a gas-exchange role.

On the experimental side, a divergence of views emerges. Oxygen transport in the phloem has not been studied directly and there is even confusion concerning the phloem's own oxygen requirements and how these may be satisfied. Mason and Phillis (1936) found that provided they excluded oxygen from a sufficient length of stem, translocation of materials in the phloem could be reduced or stopped. However, the apparent difficulty experienced in actually excluding oxygen from the stem was taken as evidence for a special oxygen carrier in the phloem. (The evidence of later oxygen diffusion studies in plants would suggest that the difficulties in oxygen exclusion experienced by Mason and Phillis point to a rapid intra- or extra-stelar gas-phase diffusion of oxygen from more remote parts.)

The more recent findings of Quereshi and Spanner (1973) are particularly interesting in this respect. The movement of applied ^{137}Cs and naturally assimilated ^{14}C down the long uniform stolons of *Saxifraga sarmentosa* was strongly inhibited by confining 20–30 cm of stolon in an atmosphere of nitrogen but was readily reversed by re-exposure to air. The results (see Fig. 1) provide very convincing proof of the oxygen-dependence of the phloem transport phenomenon but offer little support for the oxygen carrier hypothesis of Mason and Phillis: the distance travelled within the N_2-treated portions is probably an indication of the length of stolon receiving adequate aeration from the untreated portion by diffusion along the gas-filled spaces within cortical tissues (see p. 256).

Ullrich (1961) whose work preceded that of Quereshi and Spanner favoured the carrier hypothesis of Mason and Phillis that an internal hydrogen acceptor, hydrogen peroxide (H_2O_2) or an organic peroxide, together with the peroxidase detectable in young uncallosed sieve tubes, could provide for the respiratory needs of the phloem. Ullrich's calculations show that *c.* 1·4 mg H_2O_2 g^{-1} fw h^{-1} would sustain the respiratory level of 230 × 10^{-3} cm^3 O_2 g^{-1} fw h^{-1}. Whether these levels of H_2O_2 are present in phloem is not known but the experiments on which Ullrich bases his hypothesis are open to alternative interpretation. The conclusions of Quereshi and Spanner seem less open to doubt and indicate the need for a constant lateral transference of molecular oxygen into the phloem along its whole length to sustain its activity.

(ii) The xylem. The likelihood of a significant transpirational dispersal of

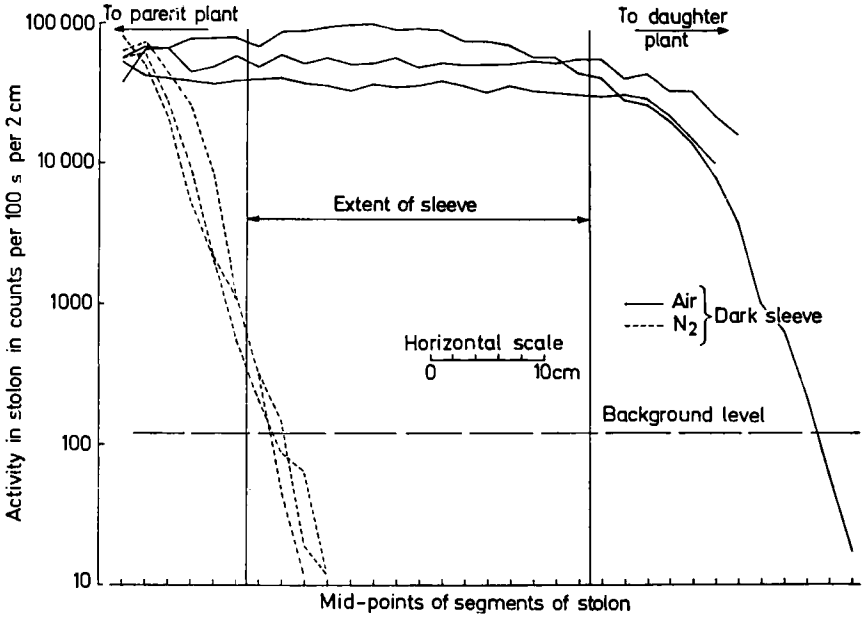


Fig. 1. The movement of ^{14}C labelled natural assimilates along the stolon of *Saxifraga sarmentosa* sleeved for part of its length in darkness and in atmospheres of either air or nitrogen. Dose of $^{14}CO_2$, 50 μCi. Temp. 25–32°C. Nitrogen treatment given 5 h, and $^{14}CO_2$ 4 h, before harvesting (after Quereshi and Spanner, 1973).

dissolved oxygen in roots located in unsaturated soils is probably as unreal as dispersal in the phloem.

It is as well to consider first the extent to which the transpiration flow may satisfy the respiratory needs of the roots themselves. If we accept a mean water uptake of 0·3 cm^3 day^{-1} cm^{-1} for young roots (r = 0·05 cm) (Nobel, 1974) water will enter one centimetre of root (vol.: 7·85 × 10^{-3} cm^3) at a rate of 3·5 × 10^{-6} cm^3 s^{-1}. If we assume a respiratory rate of 120 ng O_2 s^{-1} cm^{-3} fw root tissue the respiration of one centimetre of root will be 0·9425 ng O_2 s^{-1} (0·029 nmol s^{-1}). At air-saturation the oxygen in 3·5 × 10^{-6} cm^3 of water will amount to (3·5 × 10^{-6} cm^3) (8·57 × 10^{-6} g cm^{-3}) or 0·0299 ng O_2. Thus the influx of oxygen attributable to transpiration can at best satisfy only 3·2% of the root's requirements and in most instances the water entering the root will be below air-saturation. Clearly this cannot be the only source of oxygen for root metabolism and the major mechanism for entry and dispersal i.e., diffusion, is considered at length in subsequent sections. In unsaturated soils the diffusive flow of oxygen through the root wall can ensure high levels of oxygen throughout the root cortex (Section V). Consequently it remains possible that the water entering the stele may approach air-saturation and

micro-electrode analysis of oxygen pressure within the protoxylem elements of intact *Helianthus* roots (Bowling, 1973) supports this contention.

A stelar respiration of *c.* 200×10^{-3} cm^3 O_2 cm^{-3} fw h^{-1} in maize roots has been reported by Hall *et al.* (1971) and if the stele occupies approximately one quarter of the root volume used in the previous example it will have a potential rate of oxygen consumption of 0·117 ng O_2 s^{-1}. This is still four times greater than the rate at which the oxygen enters the stelar strand by transpirational flow and runs contrary to a direct oxygen transport role for the xylem.

However, the possibility remains that stelar parenchymas and phloem will be unable to compete effectively for this oxygen supply. Anatomical considerations must play a part here: the path from the endodermis into the non-respiring protoxylem and metaxylem elements is usually short and relatively non-tortuous and this could perhaps preclude any substantial oxygen loss from the inflowing water. In these circumstances some of the stelar oxygen requirements of basal regions of root or stem might be met by the transpirational flow. This effect could also be additive along the root to some extent as the radial water flow into subapical regions increases the velocity of water movement in the xylem and hence the potential rate of oxygen flow. The extent to which this might occur would depend greatly on the water permeability of the root in subapical regions and the efficiency with which the living stelar tissues can extract the oxygen from the tracheary elements. Nevertheless, it remains clear that if the stele is not to receive a supplementary oxygen supply from other sources much of it must experience the suboptimal aeration predicted by Crafts and Broyer (1938). The existence of supplementary oxygen sources for stelar aeration seems beyond doubt (e.g. liquid and gas-phase diffusion and symplastic cyclosis) and will be discussed later.

The transpiration stream has a vastly greater potential for carrying the carbon dioxide from respiratory sites than it has for oxygen transport: carbon dioxide solubility in pure water (346×10^{-7} mol cm^{-3} at 23°C) is 27 times greater than that of oxygen (Table I). Carbon dioxide carried from root to shoot in the transpiration stream could be either utilized in the photosynthetic process or escape to the atmosphere through the stomata. The total volume of carbon dioxide released per centimetre of root in the previous example would be (0·029 nmol s^{-1}) and a significant proportion of this could be accommodated in the transpiration fluid. However, although the carbon dioxide capacity of 3×10^{-6} cm^3 of water is (346×10^{-7} mol cm^{-3}) (3×10^{-6} cm^3) or 0·1038 nmol at a carbon dioxide partial pressure of 1 atm, this cannot be realized in aerated tissues. In the presence of oxygen the partial pressures of carbon dioxide are unlikely to exceed (or even approach) 0·2 atm and will lie within the range zero to 0·2 atm. Pressures will vary radially being highest in compact aporous stelar tissues and lowest in the

TABLE II

Surface Oxygenation in Saturated Soils (*see p. 281*)

The depth, x, at which the solution oxygen concentration falls to zero, has been computed for various combinations of potential soil oxygen consumption, M_s, and soil oxygen diffusivity, $D_{e(s)}$ (see equation 34). The solution oxygen concentration at the air:soil interphase was taken as $8{\cdot}57 \times 10^{-6}$ g cm^{-3} (20·41 %).

Soil oxygen consumption (g cm^{-3} s^{-1})	Depth of aeration (cm) Oxygen diffusivity in the wet soil (10^{-6} cm^2 s^{-1}) 0·56[a]	3·54[a]	10[b]
$5{\cdot}27 \times 10^{-8}$[c]	0·013	0·034	0·057
$5{\cdot}27 \times 10^{-9}$	0·042	0·107	0·180
$5{\cdot}27 \times 10^{-10}$	0·135	0·339	0·570
$5{\cdot}27 \times 10^{-11}$	0·426	1·073	1·803
$5{\cdot}27 \times 10^{-12}$	1·349	3·393	5·702

[a] Computed from the data of Currie (1965).
[b] Greenwood and Goodman (1967).
[c] From data of Teal and Kanwisher (1961).

cortex where gas-phase diffusion is an aid to dispersal. The complexity of the system makes it exceedingly difficult to predict the rate at which the carbon dioxide may pass into the tracheary elements of the young root and if carbon dioxide pressures were to approach 0·2 atm the harmful effects of high carbon dioxide concentration could be a further complication. Hence although significant carbon dioxide removal in the stele is an attractive and indeed a likely possibility it certainly could not fully accommodate the carbon dioxide production of whole-root respiration cited above. It might more realistically accommodate much of the carbon dioxide efflux of stelar respiration but it is still extremely difficult to estimate the proportion which could reasonably be expected to be transported in this way. One might anticipate that carbon dioxide escape in the xylem will increase in importance as root aeration becomes subnormal. It is known for example that the anaerobic by-product ethanol is translocated in the xylem (Fulton and Erickson, 1964) and similar claims have been made for other products of anaerobic metabolism, e.g. malic acid (Crawford, 1972).

In more normal circumstances carbon dioxide can probably escape equally or more readily from respiratory sites in roots and stems by alternative means, such as radial diffusive loss to the soil or gaseous diffusion in cortical gas spaces. In woody plants gas-filled pathways within secondary xylem may be a major route for both carbon dioxide and oxygen exchange (see p. 309).

3. Lateral Transport

The intercellular space system is an aid to lateral as well as longitudinal transport although within any particular tissue lateral resistance might differ

markedly from that in a longitudinal direction: the geometry of cortical intercellular space in roots is illustrative of this (see Plates I and III). Furthermore, whilst longitudinal transport occurs chiefly in the gas-phase, in lateral transport there is almost invariably a restrictive liquid-phase component. Even in porous tissues the transfer of gases between gas-space and mitochondrion and chloroplast are usually lateral movements occurring radially at right angles to the long axis of the cell. It would seem that in non-porous tissues gas movement must be restricted entirely to the liquid phase and normally this will tend to occur at right angles to the long axis of the organ in question. For the most part this will offer the route of least resistance between source and sink.

As with ion transport (Spanswick, 1976; Goodwin, 1976; Robards and Clarkson, 1976; Gunning and Robards, 1976) the manner in which gases are transported across aporous tissue blocks or even through the cytoplasm of individual cells is still far from being unequivocally resolved. There is a pressing need for a detailed analysis of the system and among other things to determine the relative contributions of cyclosis and liquid-phase diffusion in the aeration process. It is possible that gas transport might be enhanced by some as yet unidentified process.

High plasmalemma resistance to electrolytes has given rise to the view that ion movement may occur preferentially through the symplast via the plasmodesmata. However, although definitive values for plasmalemma or protoplasmic permeabilities to oxygen and carbon dioxide are apparently unavailable, oxygen is known to be highly lipid soluble and it is generally agreed (Collander, 1959; Nobel, 1974) that both gases are amongst the most rapidly penetrating of molecules (plasmalemma permeabilities $\geqslant 10^{-2}$ cm s^{-1}). Consequently the transfer from cell to cell in aporous tissue ought to be appreciable over the whole inter-cell interface although the partition of carbon dioxide between the dissolved gas and its ionic species adds a further dimension to the problem.

It is difficult to do more than comment briefly on the relative magnitudes of transport by cyclosis and diffusion: the problem is extremely complex. Pertinent literature may be found in Tyree (1970) and Robards and Clarkson (1976). We lack a knowledge of path characteristics such as streaming rates and directions and the examples which are known are very limited: for cyclosis an upper limit of 2×10^{-3} cm s^{-1} is often quoted. The protoplasmic diffusivities of carbon dioxide and oxygen are also uncertain although there are reasons for believing them to be close to those in water (Tyree, 1970). We are unaware of the path lengths and areas available for diffusion and cyclosis; if, as seems likely, the respiratory gases readily cross the tonoplast the diffusion path in the vacuolated cell might be substantially shorter than the path of cyclosis.

By adopting the most extremely simplistic view of the streaming process it

is possible to gain some appreciation of how cyclosis and diffusion might contribute to oxygen transportation across tissue barriers. Let the cytoplasmic streams between the two opposite sides X and Y of a hypothetical transport barrier be simplified as two parallel tubes, P and Q, of equal radius, through which water flows at constant velocity V, from X to Y in P, from Y to X in Q. If the side X behaves as an oxygen source at constant concentration C_0, and side Y behaves as an oxygen sink at constant, but lower, concentration C_1, there will be the potential for diffusive as well as mass flow of oxygen between X and Y. Within P the mass flow will act in conjunction with diffusion, within Q the two processes will be in opposition. (NB since the concern here is simply to elucidate the relationship between the diffusion and mass flow processes no attempt will be made to model the linkages between P and Q at the two surfaces X and Y.) For movement along the x-coordinate perpendicular to the surfaces X and Y we have the boundary conditions $C = C_0$ on $x = 0$, and $C = C_1$ on $x = l$. For the tube P the concentration C at any distance between $x = 0$ and $x = l$ is given by the equation:

$$C = C_0 - (C_0 - C_1)\left(\frac{e^{\lambda x} - 1}{e^{\lambda l} - 1}\right) \tag{1}$$

(see Appendix 1 for derivation).

where $\lambda = V/D$, D being the diffusion coefficient for oxygen in water.

The corresponding equation for tube Q is:

$$C = C_0 - (C_0 - C_1)\left(\frac{1 - e^{-\lambda x}}{1 - e^{-\lambda l}}\right) \tag{2}$$

For tube P the diffusive flux at $x = 0$ is given by the expression $V(C_0 - C_1)/(e^{\lambda l} - 1)$, at $x = l$ it is equal to $V(C_0 - C_1)\ (e^{\lambda l}/e^{\lambda l} - 1)$, whilst the total oxygen flux through P which is constant from $x = 0$ to $x = l$, is equal to $VC_0 + V\ (C_0 - C_1)/(e^{\lambda l} - 1)$; the corresponding expressions for tube Q are given in Appendix 1. If for C_0, C_1, V, and D in equation 1 we respectively substitute the values $8{\cdot}57 \times 10^{-6}$ g cm^{-3}, zero, 2×10^{-3} cm s^{-1}, and $2{\cdot}267 \times 10^{-5}$ cm^2 s^{-1}, and for path length l, we substitute distances which are multiples of average cell thickness, 30×10^{-4} cm, we obtain the series of oxygen concentration profiles 2–6 shown in Fig. 2. As the distance l increases so do the concentration profiles deviate the more from the linear relationship found where $V = 0$ and transport is entirely diffusive (Fig. 2, graph 1). Concentration gradient, dC/dx, is indicative of diffusion rate (p. 244), the steeper the gradient the greater is the flux, and hence it will be seen that when streaming is in conjunction with diffusion (curves 2–6, Fig. 2) it leads to a lowering of the diffusion rate close to the oxygen source whilst near to the sink the diffusion increases. Where the path length is the equivalent of 16

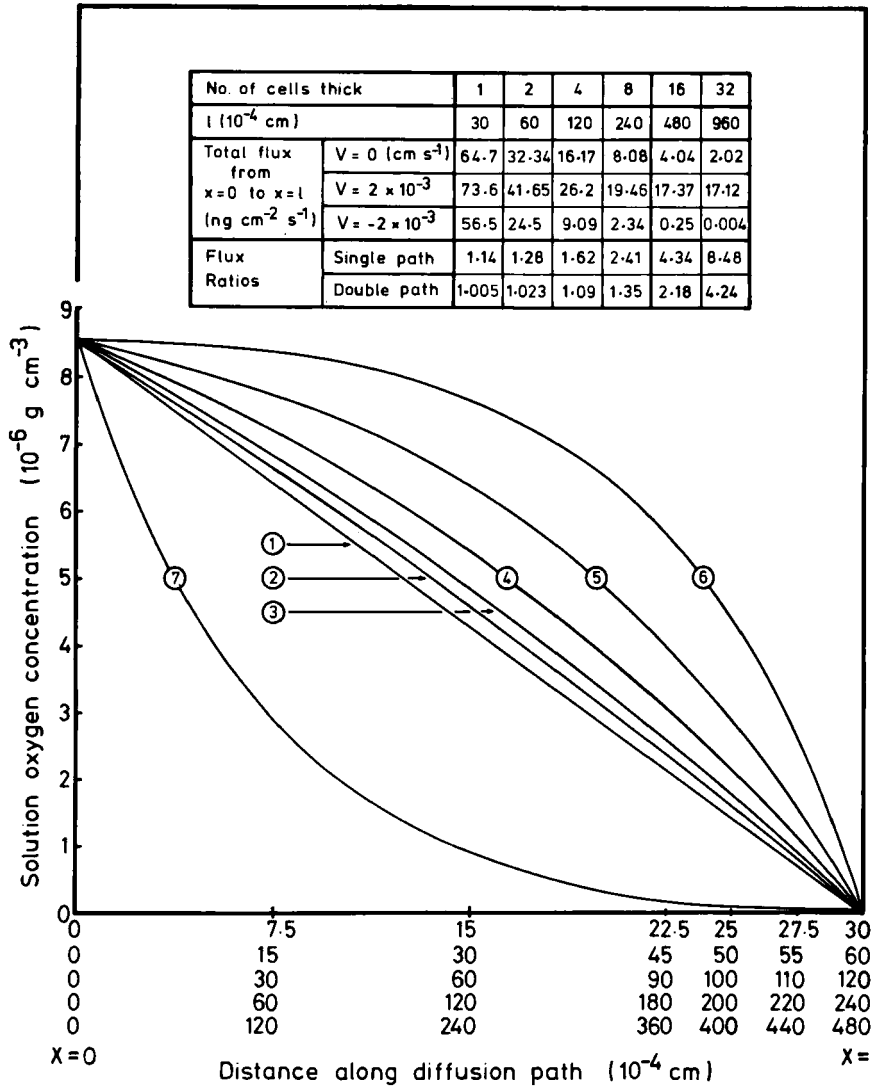


Fig. 2. To show how a stream of water having a constant velocity, V, numerically equal to that of cytoplasmic streaming (2×10^{-3} cm s^{-1}) can modify the oxygen concentration gradients of a simple source-sink diffusion system (plot 1), where $C = C_0 = 8{\cdot}57 \times 10^{-6}$ g cm^{-3} on $x = 0$, and $C = C_1 = 0$, on $x = l$. The effects of streaming both in the direction of diffusion (curves 2–6) and against it (curve 7) are shown together with the changes brought about by extending the source-sink path length from 30 μm (c. one cell thick, curve 2) to 480 μm (c. 16 cells thick, curves 6 and 7). The oxygen flux from source to sink ($x = 0$ to $x = l$) under the various circumstances is tabulated and the ratio, total flux with streaming: total flux without streaming, indicates how the enhancement of flux by streaming is reduced in the presence of a "return" flow (double path).

cells in thickness (curve 6, Fig. 2) the diffusive flux at $x = 0$ is only 0·25 ng cm^{-2} s^{-1}, whereas at $x = l$ it rises to 17·37 ng cm^{-2} s^{-1}. It is interesting to note that this is also the value attributable to the total flux at this point. In other words at $x = l$, the streaming component has been totally masked by the diffusive force. Where $V = 0$ diffusive flux is constant from X to Y at 4·04 ng cm^{-2} s^{-1}. Hence it can be seen that the combined streaming and diffusive movement increases the oxygen transport along P by a factor of (17·37/4·04) i.e. 4·34. Where the transport barrier is only one cell thick and $V = 2 \times 10^{-3}$ cm^2 s^{-1} (curve 2, Fig. 2) the oxygen flux at $x = l$ is 73·6 ng cm^{-2} s^{-1}; where $V = 0$ the value becomes 64·7 ng cm^{-2} s^{-1} and the fractional increase due to streaming is only 1·14.

When V is in opposition to the diffusive forces (equation 2) the concentration profiles obtained are as before but rotated through 180 degrees about an axis perpendicular to the plane of the graph (cf. curves 7 and 6, Fig. 2); diffusion is greatest near the oxygen source and is diminished towards the sink. For the path length, 480×10^{-4} cm, the final oxygen flux at $x = l$ is only 0·25 ng cm^{-2} s^{-1}; for the path length, 30×10^{-4} cm, it is 56·5 ng cm^{-2} s^{-1}.

If the oxygen movements from X to Y along P and Q are combined it seems that there is little advantage to be gained from the streaming process where path length is short: if the barrier is the equivalent of one cell in thickness the ratio between the streaming and non-streaming condition is as small as 1·005 : 1. However at eight times this thickness the ratio rises to 1·35 : 1, at sixteen times it becomes 2·18 : 1. Consequently it seems unlikely that cytoplasmic streaming will enhance the transport of oxygen across narrow cellular barriers but it is conceivable that it might enhance transport in thicker zones of aporous tissue.

B. DIFFUSION AND THE VENTILATING PROCESS

1. Introduction

Diffusion is the process by which matter is transported from one part of a system to another as a result of random molecular movement: if a chemical species j is present at concentration C'_j at some point in an isotropic medium and is present at a lower concentration C''_j elsewhere within the medium there will be a net transfer of material towards C''_j and this *net* transfer will continue until the two sites have attained the same uniform concentration. To appreciate this diffusion process the picture of random molecular motion has to be reconciled with the observed transfer of material from sites of higher to lower concentration. Consider a plane within an isotropic medium such that on opposite sides of the plane the species j is at the concentrations C'_j and C''_j. Although it is not possible to say in which direction any particular molecule of j will move in a given period, it can be said that, on average, be-

cause of random movement, a definite fraction of molecules will cross the plane from the area of high concentration, while the *same fraction* of molecules from the region of lower concentration will cross the plane in the opposite direction. Hence although the fractional movement from each region is the same, the total number of molecules moving from the higher concentration must exceed that from the lower concentration. It will also be apparent that the rate of net transfer must diminish with time as the concentration difference is reduced. The velocity of the random walk process within the isotropic medium is governed by the characteristics of the medium and sometimes by the concentration of the diffusing species. These find expression in a term which quantifies diffusivity, namely the diffusion coefficient (D). Diffusion coefficients are normally accorded the units $cm^2\ s^{-1}$; they vary with temperature and can vary with concentration (Crank, 1975), but for the diffusion of simple molecular species through gases or dilute aqueous solutions they may be considered to be relatively independent of concentration.

2. The Fundamental Diffusion Equations: Fick's Laws

The mathematical description of diffusive transfer originates from the researches of the Zurich Professor, A. von Fick (1855) who recognized that diffusion could be likened to the transfer of heat by conduction: the fundamental differential equation for diffusion attributed to Fick and commonly referred to as *Fick's second law* is a direct adaptation from the equation for heat conduction derived by Fourier (1822). In its simplest form for planar diffusion where diffusion is one-dimensional, i.e. there is a gradient of concentration only along the x-axis, the equation is:

$$\frac{\partial C}{\partial t} = D.\frac{\partial^2 C}{\partial x^2} \tag{3}$$

where C is concentration, t represents time and D is the diffusion coefficient for the species in question.

For diffusion to or from cylinders of radius r where diffusion is everywhere radial the equation becomes:

$$\frac{\partial C}{\partial t} = \frac{1}{r} \cdot \frac{\partial}{\partial r}\left(rD\frac{\partial C}{\partial r}\right) \tag{4}$$

while for spherical diffusion in which movement is again confined to the radial direction we get:

$$\frac{\partial C}{\partial t} = D\left(\frac{\partial^2 C}{\partial r^2} + \frac{2}{r} \cdot \frac{\partial C}{\partial r}\right) \tag{5}$$

Solutions of these equations can show how the concentration of a diffusate changes with position and time as a result of the diffusion process and the

various equations for steady-state diffusion may be derived from them (see later). Both steady-state and non-steady-state solutions have found application in the study of the aeration process although the former are by far the more commonly used.

The hypothesis upon which the differential equations are based is referred to as *Fick's first law.* This states that the rate of transfer of diffusing substance through unit area of section is proportional to the concentration gradient measured normal to that section. For diffusion in one dimension this can be expressed mathematically as:

$$J = -D\frac{\partial C}{\partial x} \tag{6}$$

where J is the rate of transfer per unit area of section, C is the concentration of diffusate, x is the space coordinate normal to the section and D is the diffusion coefficient for the diffusate in the medium concerned. The negative sign indicates that diffusion takes place in the direction away from increasing concentration; the partial derivative indicates that all but one of the possible independent variables is held constant.

In equation (6) ∂C can be likened to a "force" analogous in part to the potential difference in an electric circuit while the term $\partial x/D$ is a measure of the resistance to diffusion. From a consideration of the numerical values of D for the two respiratory gases (see Table I) it will be apparent that diffusive resistance in water is approximately 10^4 times greater than in air and that resistance to oxygen diffusion in air and water is *c.* 0·8 times that of carbon dioxide.

3. Planar Diffusion: The Simple Case

A number of stages in the aeration process in higher plants approximate in the short term to fairly simple steady-state one-dimensional diffusion systems in which there is no net lateral movement in y or z directions, and where a linear gradient of concentration is developed between a source of diffusible molecule and an adjacent or more remote sink. During darkness the entry of oxygen into leaves and the corresponding efflux of carbon dioxide probably deviates little from this diffusion pattern. Localized linear gradients may also arise in the longitudinal transport pathway under certain circumstances; they can be brought about by experimental techniques used to assess aeration parameters (Armstrong and Wright, 1975).

An equation describing the steady-state linear diffusion from planar source to planar sink of equal area, through an intervening isotropic medium in which there is no lateral loss or gain of the molecular species, can be derived from the differential equation for planar diffusion previously described: consider the case of one-dimensional diffusion through a plane sheet or membrane of thickness l and diffusion coefficient D whose surfaces, $x = 0$, $x = l$, are maintained at constant concentrations C_0 and C_1 respectively. After a

time a steady state is reached in which the concentration remains constant at all points of the sheet and provided that D is constant (and ignoring such effects as gravitation) the diffusion equation (3) in one dimension reduces to:

$$\frac{d^2C}{dx^2} = 0 \tag{7}$$

On integration we get:

$$\frac{dC}{dx} = A \tag{8}$$

where A is a constant > 0 confirming that the concentration must change linearly through the sheet from C_0 to C_1. Integrating a second time we obtain:

$$C = Ax + B \tag{9}$$

where B is a second constant of integration.

Applying the boundary conditions $C = C_0$ on $x = 0$ and $C = C_1$ on $x = l$ then $C_0 = B$ and $C_1 = Al + C_0$ and hence

$$A = \frac{dC}{dx} = \frac{C_1 - C_0}{l} \tag{10}$$

In the situation under consideration equation (6) can be written:

$$J = -D\frac{dC}{dx} \tag{11}$$

and substituting from (10) into (6) we get

$$J = D\left(\frac{C_0 - C_1}{l}\right) \tag{12}$$

where J, the one-dimensional *flux* of diffusate is constant throughout the length of the diffusion path from $x = 0$ to $x = l$. Graphically the plot of C against x for this system has the form illustrated in Fig. 3(a). J which has dimensions of quantity, area and time may also be written:

$$J = \frac{Q}{At} \tag{13}$$

where Q = grammes, moles or cm^3; A = cm^2 and t = seconds, hence equation (12) is often rearranged as

$$\frac{Q}{t} = DA\left(\frac{C_0 - C_1}{l}\right) \tag{14}$$

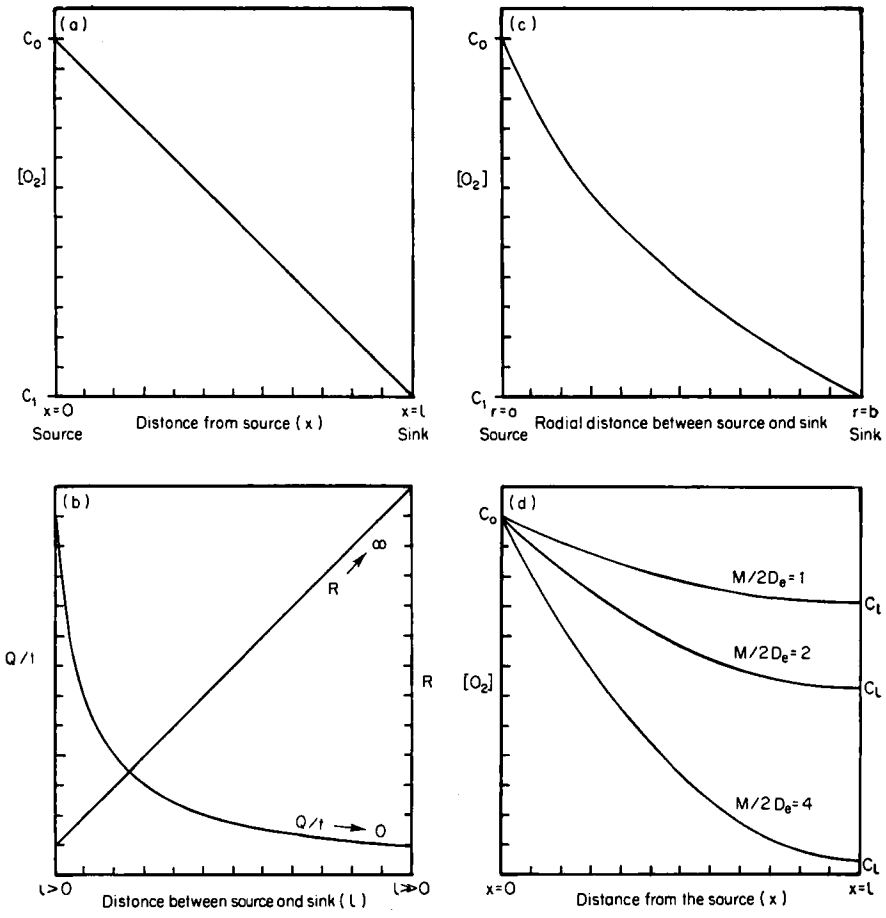


Fig. 3 (a). Linear diffusion gradient in simple planar source–sink system. Oxygen source, C_0, on x = 0 and sink, C_1, on x = l.

(b). Showing how a linear increase in the diffusive resistance between source and sink in a simple diffusive system is accompanied by a curvilinear decrease in flux.

(c). A curvilinear concentration profile characteristic of a diffusive system in which source and sink lie on concentric cylinders. The example given was computed for an oxygen source (r = 0·01 cm) at concentration C_0 (= $8{\cdot}57 \times 10^{-6}$ g cm^{-3}) separated from a concentric oxygen sink (r = 0·1125 cm) at concentration C_1 (= 0) by a "shell" of water in which, $D_{O_2\text{–}H_2O}$ was taken as $2{\cdot}267 \times 10^{-5}$ cm^2 s^{-1} (see equation 23).

(d) Curvilinear gradients characteristic of planar diffusion systems in which the diffusate is removed uniformly along the length of a homogeneous diffusion path (see equation 30).

where the term Q/t is referred to as the *diffusion rate* (g s^{-1}) for the finite system of planar sectional area A (cm^2).

4. Ohm's law and the Diffusion Analogy

In discussing equation (6) it was pointed out that the term $\partial x/D$ was a measure of the resistance to diffusion while ∂C could be considered as analogous with a force and hence the flux is the resultant of the interaction between "force" and "resistance". In equation (12) there is no restricting area term and the resistance l/D is simply a measure of the linear resistance between planar surfaces, providing that the areas of these surfaces are equal.

The units of l/D are

$$\left(\frac{cm}{1} \times \frac{s}{cm^2}\right)$$

or s cm^{-1} and the use of resistance in this form has found wide application in considering water vapour and carbon dioxide fluxes across leaf surfaces. Equation (14) specifies the area through which diffusion takes place and the resistance term becomes l/DA and has the units

$$\left(\frac{cm}{1} \times \frac{s}{cm^2} \times \frac{1}{cm^2}\right)$$

or s cm^{-3}. Resistance expressed in this form is of great value in considering the longitudinal transport of gases through shoot and root.

There are close similarities between equations (12) and (14) and the expression of Ohm's law for the conduction of electricity through a homogeneous conductor and it is often helpful to consider diffusion problems using such electrical analogues; it can also prove helpful to develop functional models of diffusion using electrical systems. In its expanded form Ohm's law may be written:

$$\frac{e}{t} = f\left(V_0 - V_1\right) \cdot \frac{O}{l} \qquad (15)$$

where e is the quantity of electricity (coulombs) flowing through a conductor in time t (seconds), l is the length of the conductor (cm), O is its sectional area (cm^2), V_0 and V_1 represent the electrical potential (volts) at the beginning and end of the conductor, and f is the conductivity constant, the value of which depends on the quality of the conducting material and on temperature. Comparing equations (14) and (15) it will be apparent that Q/t is analogous with e/t, D with f, $C_0 - C_1$ with $V_0 - V_1$, A/l with O/l, and that diffusive resistance l/DA is an analogue of electrical resistance $l/f.O$. In the condensed version of Ohm's law e/t is reduced to the term I (amperes), $V_0 - V_1$ reduces to V, and $l/f.O$ becomes R, the resistance of the conductor which is measured in ohms (Ω). Ohm's law is then written

$$I = \frac{V}{R} \tag{16}$$

and is equivalent to a condensed form of equation (14), i.e. $Q/t = \Delta C/R$, where ΔC represents $C_0 - C_1$ and R represents l/DA.

At this stage it may be useful to note that just as in an electrical circuit one may calculate the voltage drop (V') along any section of conductor by applying the relationship $V' = IR'$ where I is the current flowing through the whole conductor and R' is the resistance in the segment, in a diffusion system one may similarly calculate a localized concentration drop. For homogeneous conductors $R' = Rl'/l$ where l' is the length of the segment, l the length of conductor and R its total resistance.

For a number of conductors in series Ohm's law reads:

$$I = \frac{V}{R' + R'' + R''' + \ldots.} = \frac{V}{R} \tag{17}$$

Similarly, diffusive resistances in series become additive and, as with the flow of electricity where only as R approaches ∞ does I approach zero, so too with diffusion: Q/t remains finite at all values of $R < \infty$. This important principle is illustrated graphically in Fig. 3(b), where the change in diffusion rate consequent upon extending the distance between source and sink across an isotropic medium is plotted against the change in diffusive resistance. While diffusive resistance increases linearly with increasing path length the diffusion rate decreases in a curvilinear fashion.

Just as conductors in series are additive in their resistance to flow in both electrical and diffusion systems so do conductors in parallel effectively reduce the total resistance. For electrical conductors in parallel the total effective resistance is found from the equation

$$\frac{1}{R} = \frac{1}{R'} + \frac{1}{R''} + \frac{1}{R'''} + \ldots \tag{18}$$

and can be directly applied in the appropriate diffusional context. In long-distance oxygen transport to submerged roots the presence of several leaves arising on a condensed submerged axis can behave as parallel resistances and similarly the distribution of stomata is akin to a parallel resistance network.

5. Pore-space Resistance and Effective Diffusion Coefficient

The simplest analogue of linear (long-distance) gas transport in roots would be that of planar diffusion along a simple tube of uniform radius and having an impermeable wall. Equation (14) would suffice to describe gas flow in this system. Although such an analogue differs in many respects from the situation pertaining in roots, it serves to illustrate one particular point: that the physical resistance to diffusion in this system is a direct function of the length and

sectional area of the diffusion path, i.e. the diffusional impedance will be given by the term l/DA and will have units of s cm^{-3}. Although the linear resistance to diffusion along the whole tube would be effectively increased if the diffusate could leak away laterally through a permeable tube wall (see p. 305), nevertheless the term l/DA could be retained to represent the physical impedance of the linear path. In plants this particular feature of the gas-transport path may be termed the pore-space resistance, R_p. R_p can be categorized as a non-metabolic diffusive resistance to distinguish it from the resistance effects which arise from the metabolic usage of diffusate along the diffusion path.

Plant organs rarely if ever (see next section) fully approximate with the open-tube analogy and the gas-space volume can vary enormously (p. 290). The occlusion of potential "low resistance" pathways by cellular structures effectively increases the diffusional impedance and for any uniform segment the expression l/DA may be modified to $l/\epsilon DA$ to accommodate this, where ϵ is the fractional porosity of that part of the organ in question; A, its overall sectional area; and l its length. The value of ϵ may be determined in various ways and Jensen *et al.* (1969) have described a useful pycnometer method for assessing root porosities.

The geometry of the intercellular space system also contributes to the overall impedance of the diffusion path: the effective linear path along an organ such as a root may be made considerably longer than the organ itself because of the tortuosity of the channels. By convention tortuosity is considered as a modifying influence on D_0 the diffusivity of the respective gas in air. The porosity factor ϵ is considered likewise and the modified diffusivity term is known as the effective diffusion coefficient (D_e). To allow for tortuosity the fractional porosity may be raised to a power m, and from this we get the relationship:

$$D_e = D_0\epsilon^m \tag{19}$$

Alternatively D_0 may be multiplied by a tortuosity factor τ having some value <1. D_e is then given by

$$D_e = D_0\tau\epsilon \tag{20}$$

For diffusion through a system occluded by glass beads, Penman (1940) has established the relationship $D_e/D_0 = 2/3\epsilon$, while Jensen *et al.* (1967) have suggested that tortuosity may reduce gas diffusivity in roots by almost 60%: for roots of low porosity they estimate a value of $\tau = 0{\cdot}433$. Clearly however as porosity increases the value of τ must approach unity. In the following sections τ will be adopted as the tortuosity term with D_e derived as in equation (20).

6. Radial Diffusion: The Simple Case

For radial diffusion between cylinders the simple source–sink steady-state solution of equation (4) (analogous with planar solution 14) has been of considerable value in the study of soil and plant aeration (Lemon, 1962; Kristensen and Lemon, 1962; Letey and Stolzy, 1964; McIntyre, 1970; Armstrong and Wright, 1975). It forms the foundation for the assessment of data obtained using the cylindrical platinum technique reviewed in Section III.

Consider a medium in the form of a long hollow cylinder such that at the inner and outer radii (r = a, and r = b), a diffusible species is maintained at concentrations C_0 and C_1 respectively. The differential equation describing the steady-state condition for radial diffusion may be written:

$$\frac{1}{r} \cdot \frac{d}{dr}\left(r.D\frac{dC}{dr}\right) = 0 \tag{21}$$

Assuming that D is constant integration gives:

$$C = A + B \log r \tag{22}$$

where A and B are constants to be determined for the boundary conditions:

$C = C_0$ on $r = a$, $C = C_1$ on $r = b$ and $a \leqslant r \leqslant b$. Hence

$$B = -(C_0 - C_1)/\log\frac{b}{a}$$

and

$$A = (C_0 \log b - C_1 \log a)/\log\frac{b}{a}$$

On substituting for A and B in (22) we get

$$C = \frac{C_0 \log (b/r) + C_1 \log (r/a)}{\log (b/a)} \tag{23}$$

and differentiating with respect to r:

$$\frac{dC}{dr} = \frac{1}{\log (b/a)}\left(-\frac{C_0}{r} + \frac{C_1}{r}\right) \tag{24}$$

For the radial system the analogue of equation 6 is:

$$\frac{Q}{tA} = -D.\frac{dC}{dr} \tag{25}$$

and substituting from equation (24) we get

$$\frac{Q}{tA} = -D \cdot \frac{1}{\log (b/a)}\left(-\frac{C_0}{r} + \frac{C_1}{r}\right) \tag{26}$$

Finally on rearrangement this becomes:

$$\frac{Q}{t} = D.2\pi rh.\frac{(C_0 - C_1)}{r.\log(b/a)} \tag{27}$$

By analogy with equations (14) and (15) it may be noted that the resistance to radial diffusion is given by the term r.log (b/a)/DA_r, where A_r is the surface area of a cylinder of radius r. If our observations concern the diffusion incident upon the inner cylinder r = a, the resistance term becomes a.log (b/a)/DA_a, while for diffusion incident upon the surface r = b the term becomes b.log (b/a)/DA_b. The numerical value of the two terms is of course equal and has the standard units of diffusive resistance s cm^{-3}. However, we may also note that the terms a.log (b/a) and b.log (b/a) are analogous with *l* in equations (14) and (15); they may be thought of as the effective path lengths when diffusion is considered with respect to the particular surfaces concerned. Hence diffusion to or from the inner cylinder appears to be controlled by a path length shorter than the observed path length b–a. Diffusion to or from the outer cylinder is less than would have been expected for planar flow and the effective diffusion path length b.log (b/a) is greater than b–a. If we were concerned with flux only, our resistance terms would be a.log (b/a)/D and b.log (b/a)/D respectively and the units would be s cm^{-1}. For equal increments of the path b–a, the resistance component of r.log (b/a)/DA is distributed in a curvilinear manner and hence at equilibrium the concentration profile between b and a is also curvilinear (Fig. 3c). This contrasts with the linear profile in the corresponding planar system.

The simple case for spherical diffusion has been little used in plant aeration studies and its derivation will be omitted here. Mathematically it is similar to the linear case from which it can be derived by simple transformation. The final solution is:

$$\frac{Q}{t} = DA_r\frac{ab}{r^2(b-a)}(C_0 - C_1) \tag{28}$$

where $a \leqslant r \leqslant b$.

For diffusion to or from a sphere of radius r = a, the effective length of the diffusion path will be given by a(b – a)/b. The resistance in the radial direction (measured in s cm^{-3}) will be

$$\frac{b-a}{ab}/4\pi D$$

7. Respiration, Synergism and Effective Diffusive Resistance

(*a*) *Concept.* Consider a simple electrical circuit such as that in Fig. 4a in which we have a source of potential V (300 volts) and two conductors, B and C in series, each conductor having a resistance of 100 Ω. The current through the conductor path M–L given by V/R will be (300/200) or 1·5 amperes and the potential which will fall linearly from M to L will be 150 volts at N. If a

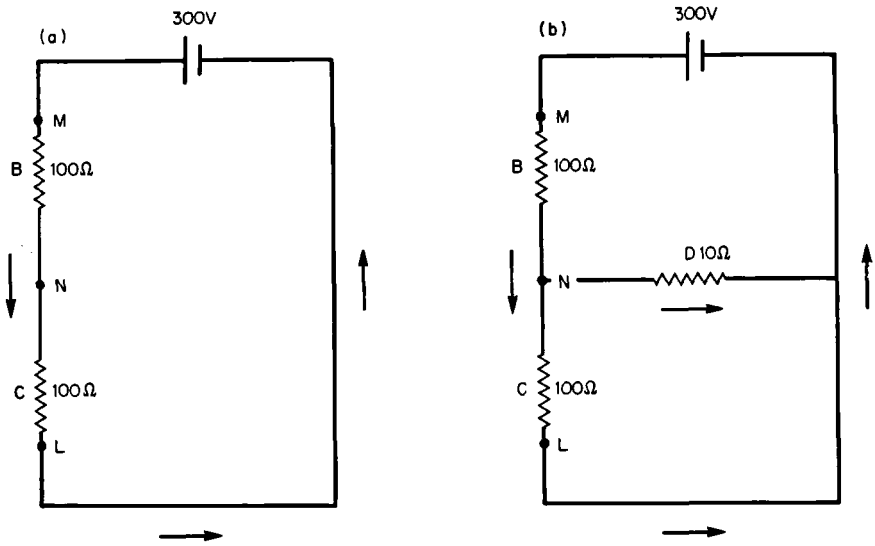


Fig. 4 (a) (b). See Section IIB (7).

third conductor (D) of 10 Ω resistance is now positioned "laterally" as shown in Fig. 4b the current will diverge at point N and flow in the directions indicated by the arrows. As conductors C and D are in parallel we find from equation (18) that their combined resistance is 9·09 Ω. The current through conductor B must therefore be (300/109·09) or approx. 2·75 amperes and hence the potential drop across B will be approx. (2·75 $\times$ 100) or 275 volts. The potential at N must therefore be 25 volts and the current flow through C is now only *c.* 0·25 amperes. If we could measure the current through C, (i.e. I_c), but were unaware of the existence of conductor D, and had no prior knowledge of the resistance values for B and C we should conclude that the combined resistance B + C was equal to V/I_c, i.e. 300/0·25, or 1·2 kΩ. In other words because of the shunting of electricity through D we gain the impression of a much greater resistance between M and L and this we could consider to be the *effective resistance* between the two points.

This simple principle is of major consequence in the plant aeration process whether we are concerned with oxygen uptake or carbon dioxide output. Such processes can be thought of respectively as lateral shunts or sources of potential which in effect contribute additively (in both instances) to the linear diffusive resistance. In the case of carbon dioxide, lateral sources of carbon dioxide would effectively reduce the rate at which the gas could escape from the sites more remote from the sink. The lateral "leakage" of oxygen whether it be for metabolic usage or, as in the case of radial oxygen loss (p. 281–284), for lateral diffusion to the external environment, acts *synergistically*

with the pore-space resistance producing what we might term the *effective diffusive resistance* of the linear diffusion path. We may express this effective diffusive resistance in the conventional resistance units s cm^{-3}.

It must be remarked upon at this stage that respiratory uptake of oxygen is not concentration dependent in the way that current flow through D was dependent upon a difference in potential: the rate of oxygen uptake can remain unaffected by concentration down to extremely low values (p. 286). Hence although the simple electrical model adequately serves to illustrate the principle of synergism in the diffusion path, if we truly are to simulate respiratory activity it becomes necessary to replace our lateral conductor with a constant current device. Furthermore as respiration can be more or less homogeneously distributed along the diffusion path a single constant current device could be a very inadequate means of simulating activity (p. 268).

Mathematical expressions which embrace the synergism between physical resistance and loss or gain of diffusible species can be derived from the differential equations (3), (4) and (5). A number of the solutions are particularly relevant to the problems of plant aeration and are considered at some length below.

(*b*) *Planar flow*. The differential expression for planar flow (equation 3) can be used to derive a solution describing the steady-state condition for linear diffusion through a medium in which the physical resistance to diffusion has an approximately homogeneous distribution and in which the sites for absorption of the diffusible species are also distributed homogeneously. The longitudinal acropetal gas-phase diffusion of oxygen which takes place in submerged roots can approximate in certain circumstances to this fairly simple diffusion model. Greenwood (1967b) considered such a case where the roots of intact plants were embedded in oxygen-free agar to the root/shoot junction and the stems were exposed to air. If, (a) no oxygen transfer occurs between the roots and the surrounding agar-medium, (b) the rate of oxygen uptake by the metabolic processes is homogeneously distributed in a linear direction and is unaffected by lowering of the oxygen concentrations until extremely low values are reached, and (c) there is a homogeneous distribution of pore space resistance in the longitudinal direction, then, when equilibrium is established between oxygen transport from the leaves and consumption by root metabolism, the distribution of oxygen concentrations along the root is given by solving

$$\frac{M}{D_e} = \frac{d^2C}{dx^2} \tag{29}$$

where M is the rate of oxygen uptake by the root (g O_2 cm^{-3} s^{-1}) and D_e is the effective diffusion coefficient for oxygen transport along the root (see equation 20).

On integrating with respect to x,

$$\frac{dC}{dx} = \frac{Mx}{D_e} + A$$

where A is a constant of integration.

On further integration with respect to x

$$C = \frac{Mx^2}{2D_e} + Ax + B \tag{i}$$

where B is a second constant of integration.

If the root is of length l, then on $x = l$

$$\frac{dC}{dx} = 0 = \frac{Ml}{D_e} + A$$

$$\text{and } A = -\frac{Ml}{D_e} \tag{ii}$$

If oxygen enters the plant at concentration C_0, we have $C = C_0$ on $x = 0$, and

$$C_0 = B \tag{iii}$$

Substituting in (i) for A and B gives

$$C - C_0 = \frac{Mx^2}{2D_e} - \frac{Mlx}{D_e} = \frac{Mx}{2D_e}(x \times 2l)$$

and on rearrangement

$$C = C_0 - \frac{Mx(2l - x)}{2D_e} \tag{30}$$

from which the concentration C at all distances of $x<l$ may be found, and when $C = C_1$ at the root apex ($x = l$),

$$C_1 = C_0 - \frac{Ml^2}{2D_e} \tag{31}$$

from which the concentration C_1 may be determined. If D_e is replaced by $D_0\tau\epsilon$ and C_1 can be measured experimentally it becomes possible to find the value of $\tau\epsilon$; if ϵ is known the tortuosity factor can be established. If root growth stops at some apical concentration C_1' then the maximum length of root growth (l') supported by longitudinal oxygen transport from the leaves will be given by:

$$l' = \sqrt{\left(\frac{2D_e(C_0 - C_1')}{M}\right)} \tag{32}$$

and if oxygen becomes zero on $x = l''$ and root growth stops when $C = 0$ the maximum length of root (l'') is:

$$l'' = \sqrt{\left(\frac{2D_eC_0}{M}\right)} \tag{33}$$

Similarly, if the oxygen concentration becomes zero at some distance (x_1) from the entry point the boundary conditions are $C = C_0$ on $x = 0$, and

$$C = \frac{dC}{dx} = 0$$

on $x = x_1$, and the distance x_1 is given by

$$x_1 = \sqrt{\left(\frac{2D_eC_0}{M}\right)} \tag{34}$$

Unfortunately these equations are of rather limited application experimentally. Although techniques are available for measuring the concentrations C_1 and detecting the location $C = 0$ (Greenwood, 1967a, b; Armstrong, 1967a; Armstrong and Wright, 1975), in practice there are probably few instances in which all the prior assumptions hold. Respiration perhaps never truly approximates to a uniform linear distribution in roots as apical respiration is invariably higher than elsewhere, porosity can vary considerably with length and, in oxygen-free media there will always be some oxygen leakage through the root wall. However, despite these inadequacies the equations can be used to illustrate a number of fundamental principles concerning the aeration of submerged roots and stems:

(a) If we solve equation (30) for C over a range of values of x we find that the distribution of oxygen varies curvilinearly from $x = 0$ to $x = l$ (Fig. 3d). This is the characteristic pattern for a system in which the diffusible species enters at one end of a tube and is then consumed over the whole length of the diffusion path. It contrasts with the linear distribution which was characteristic of the more simple planar system (cf. Fig. 3a).

(b) Equations (33) and (34) serve to illustrate how the synergism between oxygen uptake and pore space resistance can effectively make the diffusive resistance between $x = 0$ and $x = l$ appear to be infinite: in equation (34), the effective diffusive resistance has become infinite when $x = x_1$.

(c) If in equation (31) we were to substitute a zero value for M the whole of the right hand term becomes zero and hence $C_0 = C_1$, and this would be so even if $l \to \infty$. In other words, no matter how great is the physical diffusive resistance in a submerged organ, provided that there is no oxygen usage or leakage the oxygen concentration throughout the gas space system must remain equal to that at the point of entry. In practice of course such a situation can never arise although respiratory activity and leakage may reach extremely low values.

(d) Equation (33) also provides the opportunity to observe in some detail

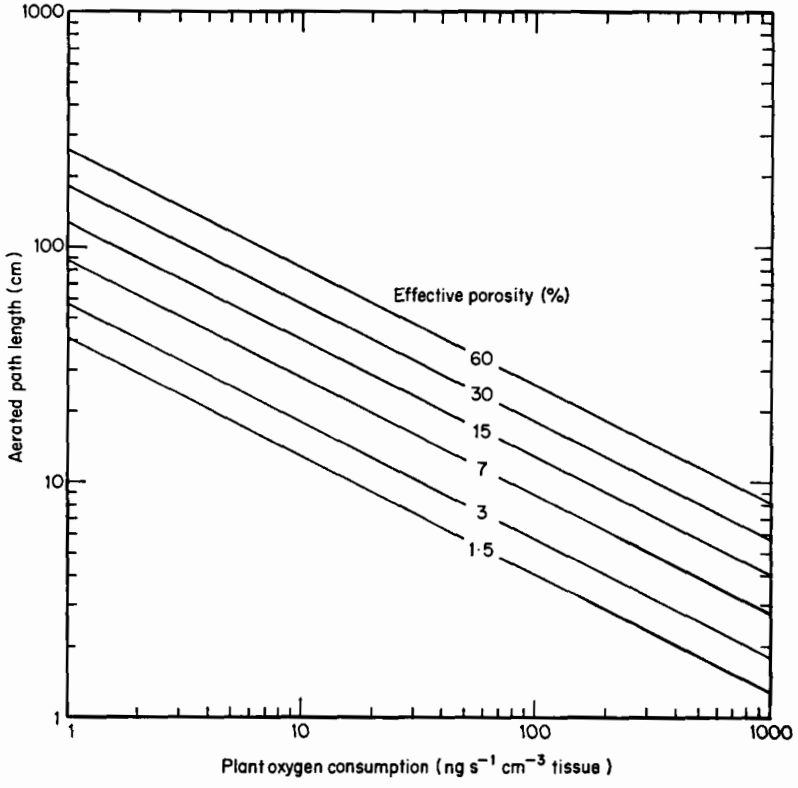


Fig. 5. Data computed from equation (33) predicting the maximum distance to which oxygen will diffuse longitudinally through plant organs in which there is uniformity of respiratory oxygen consumption and porosity along the diffusion path.

the relationship which exists between pore space resistance, respiratory activity and l', the potential length of aerated diffusion path. The line plots in Fig. 5 derived by substituting for M, D_e and l' in this equation are valuable as a general reference to the interaction of these parameters over the normal physiological range. For example a mean respiratory rate of *c.* 120 ng cm^{-3} s^{-1} and an effective porosity of *c.* 3% would be fairly representative for the roots of many non-wetland species; a glance at Fig. 5 is sufficient to demonstrate the potential inadequacies of internal aeration in such roots. Further references to this figure will be made later.

(*c*) *Radial flow: the cylindrical case.* Steady-state solutions for the cylindrical case in one dimension in which respiratory activity and pore space are distributed uniformly along the radial diffusion path are helpful in assessing certain aspects of root and rhizosphere aeration. Two basic situations have been considered: (1) the radial diffusion of oxygen from soil to root (Lemon,

1962; Lemon and Wiegand, 1962; Kristensen and Lemon, 1962; Griffin, 1968; Greenwood, 1969 and see below), (2) the converse of this, radial oxygen loss from root to soil (Armstrong, 1970). It may be noted that solutions in case (1) are also suitable for separately considering the oxygen diffusion across the stele.

Case (1): Consider a root segment of unit length within which diffusion is entirely radial and let the potential rate of oxygen consumption (M) and the effective diffusion coefficient (D_e) for oxygen be constant throughout the segment. For steady-state radial diffusion in cylindrical coordinates the diffusion equation is:

$$\frac{1}{r}\frac{d}{dr}\left(r\frac{dC}{dr}\right) = \frac{M}{D_e} \tag{35}$$

Multiplying throughout by r we get

$$\frac{d}{dr}\left(r\frac{dC}{dr}\right) = \frac{Mr}{D_e} \tag{36}$$

and on integrating both sides with respect to r then:

$$r\frac{dC}{dr} = \frac{Mr^2}{2D_e} + A \tag{37}$$

Dividing throughout by r gives

$$\frac{dC}{dr} = \frac{Mr}{2D_e} + \frac{A}{r} \tag{38}$$

and integrating both sides with respect to r we get

$$C = \frac{Mr^2}{4D_e} + A \log r + B \tag{39}$$

If $C = C_0$ at the perimeter of the root where $r = b$ then for roots in well stirred aerated water, C_0 would approximate to $8{\cdot}57 \times 10^{-6}$ g cm^{-3} at 23°C. Synergism between respiratory activity and diffusive impedance will lower the oxygen concentration radially across the root. If at some inner radius $r = a$ the oxygen concentration falls to some critical value $C = C_1$ such that on $r < a$ M becomes zero, then from $r = a$ to $r = 0$ the ratio $dC/dr = 0$. Summarizing these boundary conditions we get $r \geqslant 0 \leqslant a < b \geqslant r$ and

$$C = C_0 \text{ on } r = b$$
$$C = C_1, \frac{dC}{dr} = 0, \text{ on } r = a$$

From equation (39) we get

$$C_0 = \frac{Mb^2}{4D_e} + A \log b + B \tag{40}$$

and

$$C_1 = \frac{Ma^2}{4D_e} + A \log a + B \tag{41}$$

Subtracting (41) from (40) gives

$$C_0 - C_1 = \frac{M}{4D_e}(b^2 - a^2) + A \log (b/a) \tag{42}$$

Now as $C = C_1$, $\frac{dC}{dr} = 0$ on $r = a$

from (38) we get

$$\frac{Ma}{2D_e} + \frac{A}{a} = 0 \tag{43}$$

and

$$A = -\frac{Ma^2}{2D_e} \tag{44}$$

Substituting from (44) into (42) gives:

$$C_0 - C_1 = \frac{Ma^2}{4D_e}\left\{\frac{b^2}{a^2} + 2 \log \frac{a}{b} - 1\right\} \tag{45}$$

which may be solved to derive the radius $r = a$.

If we consider the situation where $C = C_1$ on $r = a = 0$ then equation (45) simplifies to

$$C_0 - C_1 = \frac{Mb^2}{4D_e} \tag{46}$$

and as oxygen consumption appears to continue at a constant rate down to extremely low concentrations such that $C_1 \approx 0$ then C_1 may be eliminated from equation (46) and on re-arranging we get:

$$b^2 = \frac{4D_eC_0}{M} \tag{47}$$

where b is now the critical radius of the root when the root is just wholly aerobic (e.g. see Table III). For fixed values of D_e, C_0 and M any increase in radius b will cause the development of a core of anaerobiosis within the root. If $C_1 = 0$ and is eliminated from equation (45) then the radius $r = a$ will be the estimated radius of this anaerobic core.

If we wish to predict the distribution of oxygen across a cylinder in which

all the prior assumptions have been met we require a solution in terms of C_0, C_1, C, r, b and a. The solution is:

$$C = \frac{M}{4D_e}\left\{(r^2 - b^2) - (b^2 - a^2)\frac{\log (r/b)}{\log (b/a)}\right\} + C_0 + (C_0 - C_1)\frac{\log (r/b)}{\log (b/a)} \quad (48)$$

but if $C_1 = 0$ and $dC/dr = 0$ on $r = a$ the equation simplifies to:

$$C = \frac{M}{4D_e}\left\{(r^2 - b^2) - (b^2 - a^2)\frac{\log (r/b)}{\log (b/a)}\right\} + C_0\left(1 + \frac{\log (r/b)}{\log (b/a)}\right) \quad (49)$$

This solution may be suitably modified for $a = 0$ (Equation 94, Appendix 2). Numerical solutions of equations (48) and (49) are best carried out by computer. Equation (46) appears extensively in the literature but to my knowledge solutions (45,) (48) and (49) have not previously been published in connection with root aeration although Currie (1961a) has presented spherical analogues of (45) and (49) (see Appendix 2).

Equations (45)–(49) must of necessity be treated with caution and they have very obvious limitations when applied to diffusion across the whole section of root: while respiratory activity might frequently approximate to a uniform distribution, diffusivity most certainly will not unless for some reason the intercellular space system has become flooded. In the intact root there will be a major change in diffusivity at the stelar boundary. Within the stele the effective diffusion coefficient may approach the diffusivity of oxygen in water; in the cortex it will more closely approach that for oxygen in air but modified by pore-space volume and tortuosity of the diffusion path. The latter is probably greater in the radial path but again, as with longitudinal diffusion, definitive values appear to be unavailable. Greenwood (1968, 1969) has used equation (46) to predict an overall value of D_e of approximately $1{\cdot}2 \times 10^{-4}$ cm^2 s^{-1} for "average" roots and has suggested that the critical value of C_0 for roots of radius 0·037 cm is very low, *c.* $2{\cdot}8 \times 10^{-4}$ ml/ml in water (approximating to a partial pressure of *c.* 0·01 atm). More will be said of this later (p. 313).

Case (2): Outward flux. Radial oxygen loss from roots into saturated soil encourages the formation of an aerated rhizosphere in which microbial activity may be aerobic and in which the by-products of anaerobic decomposition and metabolism may be oxidized. The diffusion equations describing the outward diffusion of oxygen from a root into a medium in which the potential rate of oxygen consumption (M) is constant radially and in which oxygen diffusivity (D_e) is also constant are identical in form with those for inward diffusion but the a, b notation is reversed: if we take as our boundary conditions: (a) $C = C_0$ on $r = a$ (root radius) and (b) $C = C_1$, and $dC/dr = 0$ on $r = b$, where $0 < a \leqslant r \leqslant b$ the solution equivalent to equation (45) is:

$$C_0 - C_1 = \frac{Mb^2}{4D_e}\left\{\frac{a^2}{b^2} + 2\log\frac{b}{a} - 1\right\} \quad (50)$$

Analogous solutions are available for equations (48) and (49); there are no corresponding analogues for equations (46) and (47). Equation (50) in an alternative form has been used to confirm the likelihood and extent of rhizosphere oxygenation in soils (Armstrong, 1970) and has provided the basis for an electrical simulation of soil sink activity around the root (p. 270).

C. THE OXYGEN SOURCE

1. Leaf Resistances

During the hours of darkness oxygen reaches the mitochondria of the leaf tissue by diffusive flow along a negative gradient of concentration which builds up between the external atmosphere and the tissues. In daylight the circumstances change: the leaf becomes an oxygen generator and this leads to a net efflux of oxygen across the leaf surface. Although the diffusion path between the leaf mesophyll and the turbulent atmosphere is in some parts non-planar (Brown and Escombe, 1900; Bange, 1953), when the various resistances in the path have been quantified the diffusion of carbon dioxide and water vapour across leaf surfaces can be treated in planar terms (Meidner and Mansfield, 1968; Nobel, 1974). The movements of oxygen can be treated likewise. Consequently, provided that we can identify and quantify the diffusive resistances and are aware of the rate of oxygen consumption, the simple steady-state solution for planar diffusion should enable us to compute the approximate gradient of oxygen concentration across the leaf surface during periods of darkness. Conversely, the net output of oxygen into the atmosphere during daylight can be used to predict the gradient of oxygen pressure from mesophyll surface to atmosphere.

The recognizable resistances to oxygen flow and their distribution in one dimension are indicated diagrammatically in Fig. 6; they are quantified below.

(*a*) *The boundary layer.* The thickness of the boundary layer of still air adjacent to the leaf varies with position on the leaf, with leaf shape, and with wind-speed and direction. Following normal convention we denote the average depth of the unstirred layer as δ^a and we may compute its approximate value from the expression:

$$\delta^a \approx 0{\cdot}4\sqrt{\left(\frac{l}{v}\right)} \tag{51}$$

where l is the linear dimension of the leaf in the downwind direction, and v is the ambient wind velocity in cm s^{-1}. Equation (51) is based on hydrodynamic theory for laminar flow adjacent to a flat surface, but has been modified from experimental observations to fit the leaf model (see Nobel, 1974). The magnitudes of δ^a for a wide variety of wind speeds and leaf dimensions are given in tabular form by Nobel and others: as l varies from 0·2 to 50 cm, and v from 10 cm s^{-1} ("still air") to 1000 cm s^{-1} (22 m.p.h.) δ^a

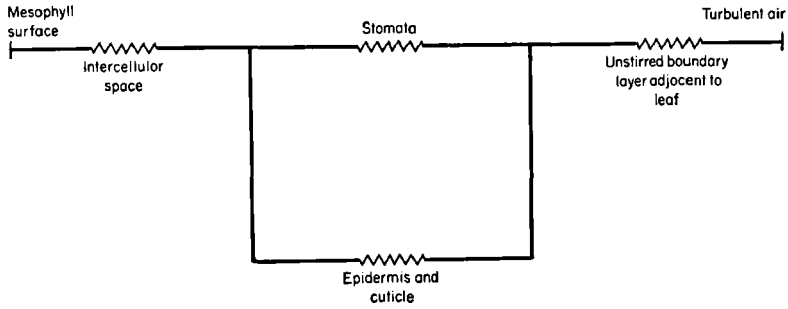


Fig. 6. Resistances involved in oxygen exchange between the leaf and external atmospheres.

ranges from 0·0057 to 0·89 cm. Accordingly by analogy with equation (12) we find that the resistance R^a must be given by δ^a/D and for oxygen in air at 23°C will vary between (0·0057/0·205) or 0·0278 s cm^{-1} and (0·89/0·205) or 4·34 s cm^{-1}. If we wish to express the resistance for a defined portion of the total leaf area we may use the expression l/DA (cf. equation 14) and for unit area of surface the two resistances would become 0·0278 and 4·34 s cm^{-3} respectively.

(*b*) *Leaf-wall resistance.* Leaf-wall resistance is dependent upon stomatal numbers, the degree of opening and the length, depth and other geometrical characteristics of the stomatal pore (Bange, 1953), but as the stomata approach the point of closure it becomes increasingly a function of cuticular and epidermal resistances. The relationships l/D or l/DA for resistance to one-dimensional planar flow (equation 12) can both be used to derive leaf-wall resistance.

(i) The stomatal component: Stomatal pore space (or rather the lack of it) modifies the value of D for oxygen transport across the leaf surface just as cellular occlusion of potential gas-space modifies the value of D in longitudinal transport (p. 249). Total resistance per leaf will be reduced still further if stomata occur on both leaf surfaces. In the following paragraphs it will be assumed that the stomata are confined to one surface and for convenience that the non-stomatal surface is impermeable to oxygen.

The fractional porosity (ϵ) of the stomatal leaf surface (area, A_l') is given by the expression $n \cdot a^{st}/A_l'$, where n is the number of stomata and a^{st} is the average area per stomatal pore; the effective diffusion coefficient $D^{st}_{e(ox)}$ is therefore given by $D_0 \cdot n \cdot a^{st}/A_l'$, (i.e. $D_0\epsilon$). For leaves with fully open stomata the value of ϵ generally varies from *c.* 0·004 to 0·02 depending upon the species and the corresponding maximum values of $D_{e(ox)}$ at 23°C are (0·004 × 0·205) or 8·2 × 10^{-4} cm^2 s^{-1} and (0·02 × 0·205) or 4·1 × 10^{-3} $cm^2 s^{-1}$. In practice we calculate ϵ from the relationship $n'a^{st}$ where n′ is the number of stomata per unit area of stomatal surface, and a^{st} is the average area per

stomatal pore. The measurable depth of the stomatal pore, d^{st}, is not strictly analogous with l in the expression l/DA and it is necessary to make an end correction to allow for the funnel-like diffusion patterns which occur immediately beyond each end of the pore. It has been shown that the pore usually has an effective depth equal to the observed depth (d^{st}) plus a distance equal to the mean radius of the pore r^{st}. The latter is given by

$$r^{st} = \sqrt{\left(\frac{a^{st}}{\pi}\right)}$$

and if there was but one stoma per unit area of leaf its effective resistance R′ (s cm^{-1}) would be given by:

$$R' = \frac{d^{st} + r^{st}}{D_0 \,.\, a^{st}/A_{l'}} \tag{52}$$

However stomata occur in extremely large numbers over leaf surfaces (Meidner and Mansfield, 1968) and behave collectively as a network of parallel resistances such that the greater their number and degree of opening the less will be the total resistance of a given leaf surface. If there are n stomata over a given leaf surface then the total stomatal resistance of that surface $R^{st}_{(ox)}$ (measured in s cm^{-1}) will be:

$$R^{st}_{(ox)} = \frac{d^{st} + r^{st}}{D_0\, n \,.\, a^{st}/A_{l'}} \tag{53}$$

or by analogy with equation (18) we may write

$$\frac{1}{R^{st}_{(ox)}} = n \,.\, \left(\frac{1}{R'}\right) \tag{54}$$

If the fractional porosity of the leaf surface were 0·02, d^{st}, 10μm and r^{st}, 5 μm, the value of $R^{st}_{(ox)}$ would be $15 \times 10^{-4}/4{\cdot}1 \times 10^{-3}$ or 0·365 s cm^{-1}. Taking the more extreme case where D_e is $8{\cdot}2 \times 10^{-4}$ cm^2 s^{-1} and d^{st} is 50 μm the resistance becomes 6·7 s cm^{-1}. Again, if we wish to use the analogue l/DA then for unit area of leaf surface the above resistances would take the units s cm^{-3}.

(ii) The epidermis. The leaf epidermis itself with its waxy cuticle forms a substantial impedance to the diffusional flow across the leaf surface. We may make an approximate lower estimate of the epidermal resistance by appropriate substitution in the expression l/D. If the liquid path across the epidermis is 40 μm and the coefficient for liquid phase diffusion of oxygen across the cell is approximately that in water, then at 23°C the resistance would be $(40 \times 10^{-4}/2{\cdot}267 \times 10^{-5})$ or 176 s cm^{-1}. Epidermal resistance *per se* is thus substantially greater than the stomatal term and as a resistance in parallel with the stomata will be insignificant providing that the stomata remain open.

(*c*) *Gas-space resistance.* This is probably the least significant resistance in

the diffusion path into the leaf. The effective length (i.e. average distance between the mesophyll surfaces and stomatal pores) of the diffusion path ranges between 100 μm and 1 mm for most leaves and hence the resistance R^{gs} will range from ($100 \times 10^{-4}/0{\cdot}205$), 0·049 s cm^{-1}, to 0·49 s cm^{-1}. The gas-space resistance will be ignored in the examples which follow.

2. Photosynthetic versus Atmospheric Oxygen Source

Having regard to the potential diffusional impedances outlined above it is now possible to perform a few simple calculations and from these to make a number of general statements of principle concerning the role of the leaf in whole plant aeration.

Consider firstly a leaf in which the diffusive resistances to planar flow are the greater of those computed above. Let the leaf have but one permeable and stomatal surface and let the non-stomatal path through the epidermis have a resistance of 200 s. cm^{-1}. The combined epidermal and stomatal resistance ($R_{l'}$) is 6·48 s cm^{-1} and is given by $1/R_{l'} = 1/6{\cdot}7 + 1/200$. If R^a is 4·34 s cm^{-1}, the resistance external to the gas space, R^e, will be 10·82 s cm^{-1}. If the leaf is in darkness, the stomata fully open, and respiration relatively high such that the oxygen flux into the leaf is 0·2 nmol cm^{-2} s^{-1} we can calculate the oxygen concentration in the gas-space of the leaf C_1 from a derivative of equation (12):

$$J = \frac{C_0 - C_1}{R^e} \tag{55}$$

where J is the oxygen flux and C_0 is the oxygen concentration in the atmosphere beyond the boundary layer. If we assume the atmosphere to be water saturated then C_0 may be taken as 269×10^{-6} g cm^{-3} (20·41 %) and C_1 will be $269 \times 10^{-6} - [10{\cdot}82\,(32 \times 0{\cdot}2 \times 10^{-9})]$ or $268{\cdot}93 \times 10^{-6}$ g cm^{-3} (20·40 %), a fall in concentration of only 0·01 %. If the stomata had been fully closed the total resistance would have been 204·34 s cm^{-1} and C_1 would have become $267{\cdot}7 \times 10^{-6}$ (20·31 %) which is still a very small fall in concentration (0·10 %).

Consider now the same leaf illuminated, supposing it to have a net inward flux of carbon dioxide from the atmosphere of 1·8 nmol cm^{-2} s^{-1}. If this represents approximately nine-tenths of the amount of carbon dioxide fixed by photosynthesis the other tenth being supplied as a respiratory by-product, then the photolysis process will supply the equivalent of 2·0 nmol cm^{-2} s^{-1} of oxygen and nine-tenths of this (1·8 nmol cm^{-2} s^{-1}) will escape to the atmosphere. If the stomata are now fully open the concentration of oxygen in the intercellular spaces will be $269 \times 10^{-6} + [10{\cdot}82\,(32 \times 1{\cdot}8 \times 10^{-9})]$ or $269{\cdot}62 \times 10^{-6}$ g cm^{-3} (20·46 %) a rise in concentration of as little as 0·05 % and hence the total fluctuation in the oxygen percentage within the leaf from darkness (stomata fully closed) to full illumination is only 0·15.

If leaf respiration can go unchecked at internal concentrations $\geqslant 2\,\%$ (see p. 286 and Yocum and Hackett, 1957) it will be clear from these examples

that for leaves in isolation the stomatal and other lateral resistances are of no consequence in the leaf aeration process during darkness, and in daylight they have virtually no restraining influence whatsoever on the escape of oxygen produced by the photolysis process. How then might these characteristics affect the aeration of submerged underground organs dependent for their oxygen supply upon the aerial parts of the plant? Clearly this must depend upon the morphology and growth characteristics of the plant concerned and upon habitat circumstances. If the water table is coincident with the soil surface and the growth habit of the plant is such that both stem and roots are below ground then during darkness the oxygen can only enter across the leaf surfaces. Because of the greater flux now required to supply the respiratory needs of the below-ground parts the fall in oxygen concentration across the leaf surface may be greater than previously indicated. How significant this might be will naturally depend upon the oxygen demand, leaf area, the degree of stomatal opening and upon cuticular and epidermal resistance; it could also depend to some extent upon resistances to "longitudinal" flow within the leaf. However, the concentration drop across a unit area of leaf having a total dark resistance of 204·34 s cm^{-3}, and supporting 125 cm of root ($r = 0{\cdot}05$ cm and mean respiratory rate 60 ng cm^{-3} s^{-1}) would be only 1·01 %. If the stomata were a tenth open (dark resistance 58·87 s cm^{-3}) the corresponding value would be only 0·29 %. If the leaf area was doubled the respective values would be 0·57 % and 0·16 %. If the stomata were 50 % open, resistance would be 16·9 s cm^{-3} and the concentration drop across unit area of leaf would be 0·08 %. A doubling of leaf area would give a concentration difference of as little as 0·05 %. It should be noted that the highest oxygen flux across the leaf will tend to occur at the point of least resistance from the sink, i.e. at ground level, consequently there will be a tendency for the fall in concentration across the leaf to be greatest at this point. However, this tendency will be immediately counteracted and minimized by longitudinal oxygen flow from more distal parts of the leaf.

If the stem is emergent, lenticels or stem-borne stomata will provide the route of least resistance to below-ground parts and again there will be the tendency for the surface oxygen flux and concentration drop to be greatest at soil level. From what has already been said we might again predict that relatively little emergent stem may be required to sustain the respiratory activity of submerged parts. Conversely if longitudinal resistance to flow is high, compensating movements from more distal parts will be restricted and this will tend to limit the effective entry point to basal regions.

Since all the examples chosen above have been deliberately weighted in favour of high leaf resistances one is forced to conclude that surface resistances at the point of oxygen entry to the plant must normally have an almost undetectable restraining influence on gas flow to more remote parts. Experimental support for this view is illustrated in Fig. 7. We can conclude also that

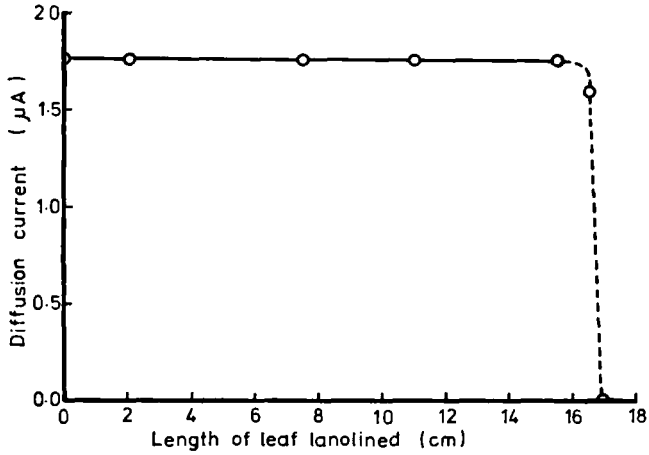


Fig. 7. Sequential basipetal occlusion of stomata in a single-leafed specimen of *Eriophorum angustifolium* and its effect upon the oxygen status of the root apex. Stomata occluded by painting the leaf with lanolin down to the submergence level. Oxygen status of the root apex indicated on the ordinate by the electrolysis current caused by polarographic electro-reduction of oxygen leaking from the root (after Gaynard, 1979).

unless some extra restraint can be placed upon the escape of oxygen from the leaves in daylight (see p. 297) photosynthesis will do no more than ensure a daytime oxygen source almost identical in pressure with that in the external atmosphere and the switch from atmospheric to photosynthetic source will be almost undetectable; this is borne out experimentally (T. J. Gaynard and W. Armstrong, unpublished). With increasing respiratory demand there will be a tendency for the daytime oxygen supply to include a significant atmospheric component and in parts of the leaf system there might be a net efflux and in others a net influx of oxygen. In species with non-photosynthetic woody stems atmospheric oxygen will normally remain the sole oxygen source at all times.

D. THE AERATION MODEL

1. Introduction

Some indication has been given already of the usefulness of mathematical modelling in the analysis of aeration problems. However, whilst the relatively straightforward mathematical solutions for planar and radial diffusion are valuable for evaluating certain specific aspects of the aeration process, individually they are somewhat limited in their scope and the development of more elaborate models which might integrate the many facets of plant aeration is a desirable goal.

In recent years two such models have been evolved, both intended primarily

for the study of root aeration by the internal path. The first of these (Luxmoore *et al.*, 1970, 1972) relies on the linking together into a continuity equation the individual equations describing diffusion in the various segments of the aeration path. The final continuity equation is manipulated using modern computation methods. This model devised by Soil Physicists at Riverside, California overcomes various of the deficiencies inherent in equation (27): uniformity of porosity and respiratory activity is no longer a requirement and both can vary in successive root segments. Radial oxygen loss from the root is allowed for, as is radial intake in the presence of a soil oxygen source, while provision is made for a concentration-dependent respiratory rate. The latter was perhaps an untimely refinement for the concentration dependence characteristics used (10% oxygen for $\frac{1}{2}$ max. respiration) have since been proved wrong. Recent studies indicate values considerably lower than this ($\leqslant 2{\cdot}5\%$ oxygen for maximum respiration, p. 286) and hence the published data from this model may need to be treated with some reserve. The principle limitations of the model lie in the provision made for "simulating" the radial oxygen loss from the root in a wetland environment and the radial oxygen intake in an unsaturated soil. In both instances simulation is based on the simple case for radial diffusion (equation 27). For inward diffusion (non-wetland soil) it is assumed that the root (radius $r = a$) for the whole of its length is surrounded by a shell of water ($r = b$) such that on $r = b$, $C = C_0 =$ 18% oxygen. No allowance is made for oxygen consumption within the liquid shell which would be analogous with soil oxygen consumption. For radial diffusion from the root (the wetland condition) it was assumed that on $r = b$, $C = C_1 =$ zero. Potential sink activity external to the root is therefore intensified by reducing the input radius of the liquid shell ($r = b$). This device is not a strict analogue of soil oxygen demand for no allowance is made for the distribution of oxygen demand along the diffusion path $a \rightarrow b$ and no soil respiratory rates were specified. An inbuilt assumption is that soil oxygen consumption will vary linearly with the internal oxygen concentration of the root while in reality the relationship is more likely to be curvilinear (p. 272). However the importance of such limitations has yet to be established and the errors introduced may yet turn out to be marginal. If not the model can undoubtedly be modified to accord more closely with reality.

The second of the two models, a functional electrical analogue was developed specifically to simulate root aeration in the wetland condition. In its original form (Armstrong and Wright, 1976a) it embodied the same deficiency found in the mathematical model, i.e. to simulate the soil "sink" it was assumed that the root for the whole of its length was bounded by a shell of water (radius $r = b$) such that on $r = b$, $C = C_1 =$ zero. This deficiency has now been rectified and the model has also been modified to accommodate the soil oxygen demand of the unsaturated (non-wetland) soil condition (p. 321).

For the average biologist the electrical analogue is undoubtedly the easier of the two models to understand and operate. The principles underlying its design are outlined below and in subsequent sections reference is made to its application.

2. The Electrical Analogue

(*a*) *The basic unit.* The similarities between electrical and diffusion laws demonstrated earlier provide the basis for the electrical modelling of diffusive aeration. These similarities are such that in a functional model electrical resistors may take the place of diffusional impedance (p. 247), resistors with "leakage" to "earth" can behave as diffusion sinks, and electrical "pressure", (EMF), substitutes for partial pressure and concentration differences of diffusate. In the functional model appropriate values are assigned to these simulators and both flow and partial pressure of diffusate at any point in the system can be respectively monitored by ammeter and electrometer (voltmeter) suitably scaled.

We can electrically simulate unit length of root–wet-soil system as shown in Fig. 8a; further identical circuit units are added in series to simulate an increasing length of root but, it may be noted that in the unit representing the apical segment of root the resistor $R_{P''}$ becomes superfluous (see Fig. 8b). Pore space resistance to longitudinal oxygen flow is represented by the equal resistors $R_{P'}$ and $R_{P''}$ and, on the assumption that respiratory activity is homogeneously distributed with length, the oxygen consumption by the root tissues is simulated by a single lateral current leak from between $R_{P'}$ and $R_{P''}$. This may be controlled by a simple variable resistor R_R as indicated but in practice it is more satisfactory and realistic for R_R to operate through a constant current (compensating) device. In this way the model automatically simulates the natural insensitivity of respiratory activity towards oxygen concentration (p. 286). Consequently once respiration has been programmed it is not readily upset by the changes in concentration induced by programming adjustments made elsewhere in the model.

Radial oxygen loss to the soil is also simulated by a lateral tapping between $R_{P'}$ and $R_{P''}$, controlled by another variable resistor R_S, and a realistic simulation of soil sink activity in the wetland environment is quite feasible with this simple device. The impedance of the root wall is simulated by resistor R_{WL}. It is recognized that this may not be an entirely satisfactory way of simulating the root wall, since it fails to take account of sink activity within the wall itself. It is felt that a truer simulation must await the results of further experimental and theoretical studies into the nature of root wall resistance.

Oxygen concentrations at positions P, G and T are measured by electrometers V_P, V_G and V_T. The use of the high impedance electrometer is necessary to ensure an insignificant lateral current loss through the measuring device. Respiratory activity and radial oxygen loss are measured on ammeters A_R

and A_s respectively and it is especially important in this model that these lateral current tappings should be taken at a point midway along the root segment. Only then will the concentration recorded at T be a true reflection of the concentration drop along a root segment in which respiratory activity and pore space resistance are distributed uniformly with length. The truth of this statement is easily demonstrated electrically as follows.

In unit length of root in which respiratory activity and pore space are distributed uniformly with length (and where the oxygen source is at one end) the oxygen profile along the root may be determined by solving equation (30). In electrical terms we could in theory simulate this root as a longitudinal resistor bearing an infinite number of lateral tappings extracting equal currents and summing to the total respiratory consumption. However it is impossible to construct such an analogue and in practice some compromise must be reached. With this in mind consider a 10Ω electrical resistor R_l with a source of potential V_P (100 volts) applied at one end, and let the current i_c taken from each of a finite number of lateral tappings (n) set equidistant along R_l be equal and, be such that the total current taken (Σi_c) is 5 amperes. In the arrangement shown in Fig. 8c, $n = 5$, $R_{l1} = R_{l2} = R_{l3} = R_{l4} = R_{l5} = 2\,\Omega$ and $i_c = 1$ ampere. The voltage drop across R_{l1}, given by ($\delta V' = \Sigma i_c \times R_{l'}$) is ($5 \times 2$) or 10 volts, and the voltage at Q is therefore ($100 - 10$) or 90 volts. The voltage drop across R_{l2} is given by $\delta V'' = (\Sigma i_c \times i_c) - R_{l2}$ and hence the voltage at S is $90 - (4 \times 2)$ or 82 volts. Continuing with this procedure it can be shown that the voltage at T (V_T) must be 70 volts. Again, by Ohm's law we can calculate that this same potential would have been realized had the current, Σi_c, been taken from a point R_{l*} along resistor R_l. The value of R_*, given by $(V_P - V_T)/\Sigma i_c$, is $(100 - 70/5)$ or 6 Ω and it may be noted that the ratio R_{l*}/R_l is 0·6. When $n < 5$ the ratio is larger and as n increases the ratio diminishes. If we plot R_{l*}/R_l against n we obtain a curve which is fitted by the equation $y = (0{\cdot}5/n) + 0{\cdot}5$ where $y = R_{l*}/R_l$ from which it is evident that as $n \longrightarrow \infty$ then $y \longrightarrow 0{\cdot}5$.

Hence provided that our major concern is with total concentration drop along unit length of root rather than with the concentration profile it is obvious that this may be satisfactorily achieved by extracting the total oxygen

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Fig. 8 (a). Detailed arrangement of resistances and meters to simulate the diffusion of oxygen in unit length of root–wet soil system: $R_P' = R_P'' = \frac{1}{2}R_P$, where R_P is the longitudinal pore-space resistance of the root segment; R_R, a variable resistor for setting the respiratory uptake of the root segment; R_{WL}, the diffusive resistance of the root wall; R_S, variable resistance for the control of soil sink activity. Electrometers, V, indicate oxygen concentration; meters, A, register oxygen consumption by root and soil.

(b). Alignment of root–soil units in a functional electrical analogue.

(c). Five electrical resistances in series, representing together the diffusive resistance in a unit length of root in which respiratory activity is represented by five equal current tappings (i_c). See Section II. D.2 (a).

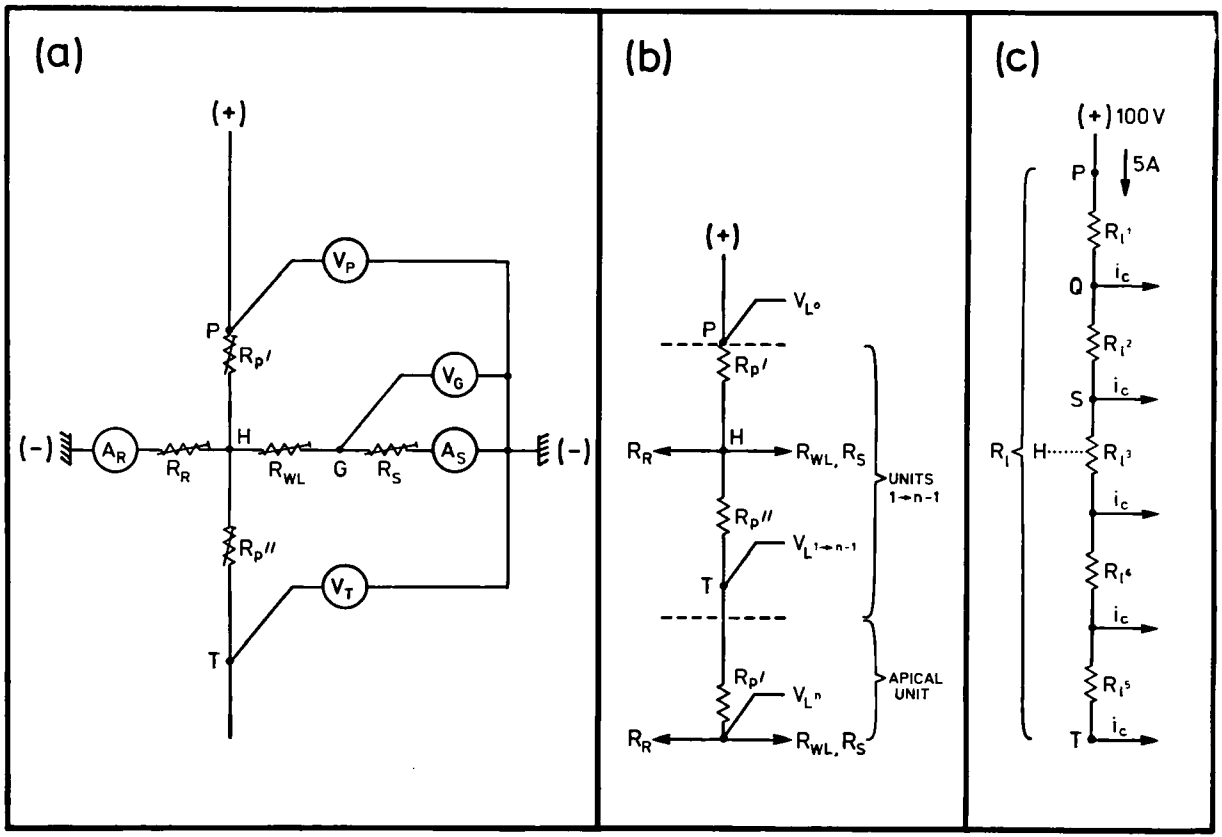

(a)
(+)
V_P
P
$R_{p'}$
V_G
(-)
A_R
H
A_S
(-)
R_R
R_{WL}
G
R_S
$R_{p''}$
V_T
T
(b)
(+)
V_{L^0}
P
$R_{p'}$
R_R
H
R_{WL}, R_S
UNITS 1→n-1
$R_{p''}$
$V_{L^{1\to n-1}}$
T
$R_{p'}$
V_{L^n}
APICAL UNIT
R_R
R_{WL}, R_S
(c)
(+) 100 V
5A
P
R_{l^1}
i_c
Q
R_{l^2}
i_c
S
R_l
H
R_{l^3}
i_c
R_{l^4}
i_c
R_{l^5}
i_c
T

Fig. 8

consumption at a point halfway along the pore-space impedance of the segment (H in Figs 8a, b and c).

(*b*) *Calibration.* To calibrate the model it is necessary simply to equate some value of electric potential (e.g. 20 V) with the atmospheric oxygen source, and similarly to choose some resistor value (e.g. $10^3\ \Omega$) to equate with a particular diffusive resistance (e.g. 10^4 s cm^{-3}). The electrometers may now be calibrated so that 20 volts will read atmospheric oxygen concentration near full scale deflection. Choosing the lesser of these two values, 20 volts might therefore equate with an oxygen concentration in the gas-phase of 269×10^{-6} g cm^{-3} at 23°C (see Table I). If this source ($C = C_0$) is separated from a sink ($C = C_1$ = zero) by the diffusive resistance, 10^4 s cm^{-3}, the diffusion rate will be ($269 \times 10^{-6}/10^4$) or 26·9 ng s^{-1}. The ammeters will read ($20/10^3$ amperes) or 20 mA and the linear scale of the meters may then be calibrated directly to read 26·9 ng s^{-1} at 20 mA or shunted so that 25 ng s^{-1} will read on an appropriate scale division. The diffusive resistances of the plant, R_P and R_{WL} (calculated from the expressions l/DA (p. 249) or a. log (b/a)/DA_a (p. 251) or derived experimentally (p. 276), may be assigned their respective analogue values (ohms) from the relationship R(ohms) = R(s cm^{-3}) $- 10^4/10^3$. Resistor values chosen for R_R and R_S are those necessary to programme for the appropriate ranges of root respiration and soil sink activity. The potential assigned to the atmospheric oxygen source is applied at the top of the series of current units as shown in Fig. 8.

(*c*) *The wetland soil sink.* To simulate the activity of the soil oxygen sink (whether wetland or non-wetland) it is convenient to adopt the oft-made assumption that the potential respiratory activity of the soil is constant along the radial diffusion path and is unaffected by oxygen concentration until this approaches zero (Greenwood, 1961, 1962, 1963). Similarly let us assume that the effective diffusion coefficient in the radial direction is a constant. Having made these assumptions we may approach the electrical simulation of wetland soil sink activity as follows:

Consider a unit length of internally aerated root (radius r = a) lying within a wet soil having a potential rate of oxygen consumption, M (g cm^{-3} s^{-1}). If the oxygen concentration at the root wall is C_{WL} then from equation (50) the radial distance (r = b) from the centre of the root at which the oxygen concentration in the soil must fall to zero is given by

$$C_{WL} = \frac{Mb^2}{4D_e}\left\{\frac{a^2}{b^2} + 2\log\frac{b}{a} - 1\right\} \tag{56}$$

and in unit time the quantity of oxygen, Q, consumed by the soil surrounding the root will be

$$\frac{Q}{t} = M\pi(b^2 - a^2) \tag{57}$$

Q/t is also the rate of oxygen diffusion from root segment to soil (i.e. the radial oxygen loss, g s^{-1}) and this value may be programmed into the analogue by adjusting the resistor R_S.

For any given value of M and a, the radial distance b–a varies as a curvilinear function of C_{WL} (and hence with the concentration within the root) (see Fig. 9a); radial loss from the root also varies in a curvilinear manner (Fig. 9b). The necessary programming adjustments for sink activity in any particular root segment are made by consulting the graph of C_{WL} and radial oxygen loss appropriate to the particular root radius and potential soil activity in question.

The modelling of soil sink activity in this way is clearly a simplification although not necessarily a serious one; it is also a compromise. Regarding the simplification it is by no means certain that soil respiration and effective diffusivity will be uniformly radially distributed. As values for M and D_e become known from experimental observation it may become necessary to adopt the method developed for simulating root aeration to the unsaturated soil (see p. 321) and separately model soil resistance and respiration in successive shells around the root.

If soil oxygen consumption varies in a curvilinear manner with C_{WL} in theory it must vary also in a curvilinear manner along a root segment. It would be a difficult matter to simulate this circumstance exactly and the compromise adopted, referred to above, is the tapping of soil activity midway along each circuit unit (cf. root respiration). It is felt that the error introduced by this procedure is small enough to be disregarded.

(*d*) *Programming.* Normally, one circuit unit represents unit length of root–soil system and to simulate the conditions required the model is programmed by making the necessary adjustments to the various resistors. Pore space and wall resistances are usually programmed first, followed by root respiration. As the oxygen consumed by the soil must depend on the oxygen concentration at the root wall this parameter is programmed last of all. Depending upon the procedure adopted to simulate sink activity (above and p. 321) it may or may not be necessary to make several successive adjustments to the resistor R_S to bring the model to equilibrium.

When fully programmed the model automatically integrates the interactions between the various impedances and sinks acting on the linear diffusion path, and the oxygen profile along the root is obtained by plotting the readings from meters V_L; V_{L° represents the concentration at the root base, $V_{L'}$ one centimetre from the base, and likewise V_{Ln} the concentration at the apex, where n = the number of circuit units.

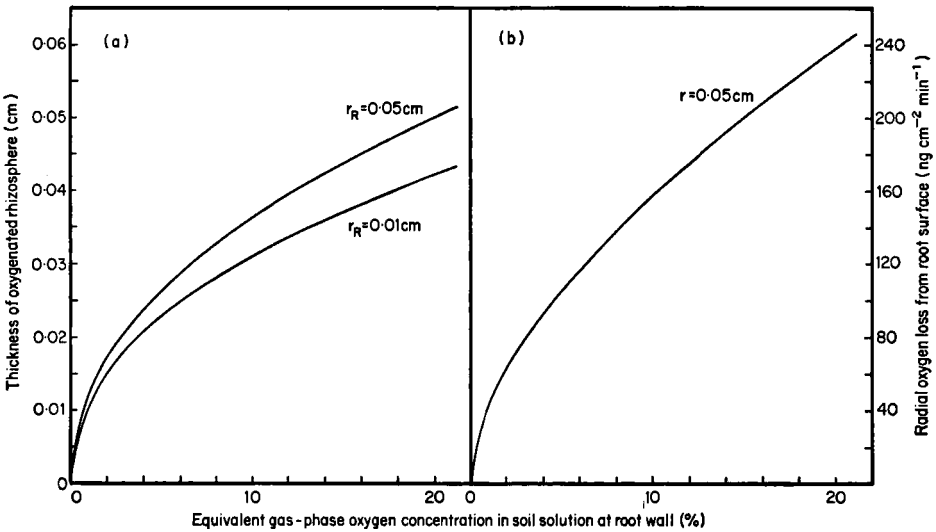


Fig. 9 (a). Thickness of oxygenated rhizosphere (b − a, equation 56) as a function of the oxygen concentration at the root wall and the root radius, a (a = 0·05 cm or 0·01 cm). Values computed assuming a uniform respiratory activity in the aerated soil of $5{\cdot}27 \times 10^{-8}$ g O_2 cm^{-3} s^{-1}, and a uniform oxygen diffusivity of 1×10^{-5} cm^2 s^{-1}.

(b). Radial oxygen loss from a root (radius, 0·05 cm) into wet soil, as a function of the oxygen concentration at the root wall. Soil characteristics as above.

III. THE CYLINDRICAL PLATINUM ELECTRODE TECHNIQUE

1. Introduction

The inadequate methods of analysis which for many years hampered the study of diffusive aeration in plant and soil have now been superseded by the more sophisticated tracer, GC and polarographic techniques (Lemon and Erickson, 1952, 1955; Barber *et al.*, 1962; Armstrong, 1964, 1967a; Greenwood, 1967a,b; Greenwood and Goodman, 1967; Jensen *et al.*, 1967; Armstrong and Wright, 1975, 1976b; Smith, K. A., 1977). The construction and use of cylindrical Pt electrodes for polarographically assaying the oxygen diffusion from roots in anaerobic media was first reported as a method for quantifying the differences in the rhizosphere-oxygenating activity of wetland plants (Armstrong, 1964, 1967a). Since then it has become apparent that "flux" data yielded by quite simple procedures can be successfully manipulated to quantify many aeration properties in both wetland and non-wetland plants (Armstrong and Wright, 1975). At present the cylindrical Pt electrode technique probably provides the least expensive and most versatile method for assessing the diffusive resistance to oxygen transport in roots: pore space resistance, root wall resistance, tortuosity, the synergism between root respiration, lateral leakage and pore space resistance may all be quantified,

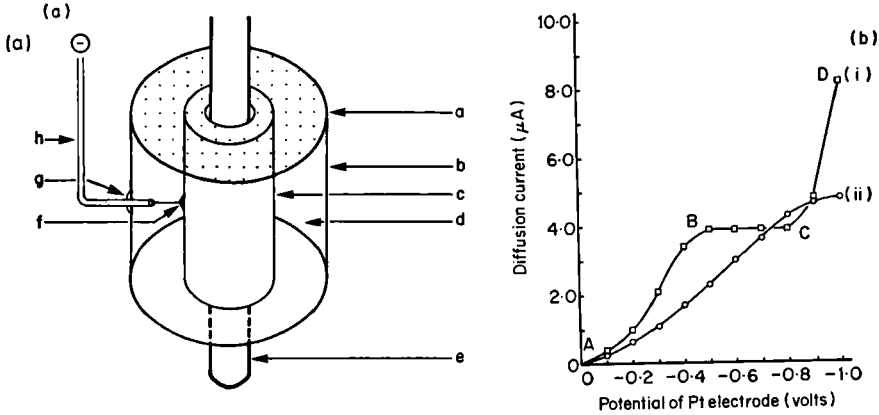


Fig. 10 (a). Cylindrical platinum electrode for assaying the oxygen flux from roots. Key: a, celluloid guide; b, perspex tube; c, platinum cylinder; d, epoxy-resin; e, root through electrode; f, solder joint; g, araldite; h, sleeved copper wire.

(b). Curve (i) represents a typical current voltage curve (polarogram) resulting from the electrolytic reduction of oxygen at a platinum cathode. Reactivity of the electrode increases from A to B when it achieves maximum efficiency. In the plateau region, B–C the rate of oxygen diffusion is the controlling factor. H^+ ion reduction begins at C and this process accelerates from C–D. In the absence of a supporting electrolyte the oxygen polarogram characteristics are lost (curve ii).

while aeration parameters in shoot and leaf and the dynamics of oxygen transport can also be assessed.

The essential features of the technique, described below, provide a useful background to much of the data presented in the following two sections.

2. The Polarographic Method

The polarographic determination of oxygen diffusion from roots is based on the characteristics of the current-voltage (c–v) curve obtained (Fig. 10b) when oxygen in aqueous solution is electrolytically reduced in a cell in which one electrode, the cathode, consists of a sleeve-insulated thermo-pure platinum tube (Fig. 10a) while the other is some standard half-cell (e.g. saturated Ag/AgCl reference electrode).

The reduction of oxygen at a Pt surface is thought to proceed in two stages (McIntyre, 1970). At pH 3·5 or above the overall reaction follows the equation: $O_2 + 2H_20 + 4e^- \rightarrow 4OH^-$, and for each molecule of oxygen reduced there is a current transfer of $4e^-$. At low potentials (applied EMF) this reaction is voltage dependent but with increased potential it becomes dependent on the rate of oxygen diffusion to the electrode surface. The c–v curve then assumes the form of a plateau (curve (i), Fig. 10b). If the applied voltage in the plateau region is sustained the current equilibrates to a value which is related to the rate of oxygen diffusion to the electrode according to the equation:

$$i_t = nF\, f_{x=0,t} \tag{58}$$

where i_t = the diffusion current in amperes at the time of equilibration, t,
n = the number of electrons required for the reduction of one oxygen molecule = 4,
F = The Faraday, 96 500 coulombs, and
$f_{x=0,t}$ = the oxygen flux at zero distance (x) from the platinum surface at time t (mol cm^{-2} s^{-1}).

Oxygen diffusion from roots is measured in oxygen-free liquid medium (+supporting electrolyte, see Fig. 10b). Roots are inserted through the Pt electrode as shown in Fig. 10a, and a shell of liquid (of uniform thickness) separates the root from the inner (reactive) electrode surface. Under the appropriate polarizing voltage the platinum acts as a sink for oxygen, (the oxygen concentration at the electrode surface is effectively maintained at zero) and a diffusion gradient is set up between root and electrode. At equilibrium the rate of oxygen loss from that portion of root lying within the electrode can be calculated from equation (58) which simplifies to the expression:

$$ROL = \frac{4{\cdot}974\, i_t}{60} \tag{59}$$

where ROL = the radial oxygen loss in ng s^{-1}, and
i_t = diffusion current (μA) with the root within the electrode, provided that the root is the only significant oxygen source.

3. Manipulation of "Flux" Data

(a) Calculating the diffusive resistance offered by the liquid shell between root and electrode. Reference to Section II.B.6 will show that at equilibrium the boundary conditions of the root-surface/electrode diffusion-system are those of the simple case for steady-state diffusion along radial coordinates. It follows that diffusion must conform with equation (27) and as C_1 (concentration at the electrode surface) is equal to zero the diffusion rate given by equation (59) above must also be that given by the expression:

$$Q/t = \frac{D_W^T A_R C_{WL}}{a \log (b/a)} \tag{60}$$

where Q/t is the diffusion rate in g s^{-1},
D_W^T is the diffusion coefficient for oxygen in water at the temperature T,
A_R is the surface area of the root within the electrode (cm^2),
C_{WL} is the dissolved oxygen concentration at the root surface (g cm^{-3}),
a is the root radius, and
b the electrode radius (cm).

In equation (60) the resistance of the liquid path between root and electrode

is expressed by the term $a \log (b/a)/D_W^T A_R$. However, the liquid shell between root and electrode may be considered as a lateral extension of the diffusion path within the root ($\equiv$ to R_S, Fig. 8a). To quantify the resistance of the shell relative to transport in the gas-phase of the root allowance must be made for the fall in oxygen concentration which occurs across the "air"-liquid interphase. Accordingly the effective resistance (s cm^{-3}) of the liquid shell becomes:

$$R_{sh}^T = \left[\frac{a \log (b/a)}{D_W^T A_R}\right] \frac{C_a^T}{C_{a-w}^T} \tag{61}$$

where C_a^T is the oxygen concentration in air at temperature T (g cm^{-3}) and C_{a-w}^T is the oxygen concentration in air-saturated water (g cm^{-3}). If a = 0·05 cm, b = 0·1125 cm and electrode length 0·5 cm, the value of R_{sh} is 3·570 $\times$ 10^5 s cm^{-3} at 23°C.

(*b*) *The overall diffusional impedance apparent at the apical root wall.* If the oxygen diffusion rate (Q/t) is measured over the submeristematic apical root segment (l = 0·5 cm) it is a simple matter to determine the total effective internal diffusive resistance (R_t) between the atmosphere and the root surface. From what has been stated previously it follows that diffusion rate from the root must be given by the expression:

$$\frac{Q}{t} = \frac{C_a}{R_t + R_{sh}} \tag{62}$$

and if Q/t is computed from equation (59) and R_{sh} from equation (61) the equation can be solved for R_t.

The term R_t is a measure of the total effective diffusive impedance between the oxygen source and the surface of the root apex. However, if the oxygen enters the plant at a point very close to the root base the term R_t can effectively represent the total synergistic resistance of the root at that particular temperature plus a wall resistance component. If the wall resistance component is insignificantly small R_t is then a measure of the total effective resistance to longitudinal diffusion within the root itself.

(*c*) *Root wall resistance.* What little data there is available suggests that the oxygen permeability of root walls can be surprisingly high in apical regions (Armstrong, 1967; Greenwood, 1967a; Luxmoore *et al.*, 1970). As the root "wall" forms only a small part of the lateral diffusion path between root and electrode cyclosis within the wall layers may considerably reduce their apparent diffusive resistance (p. 240). The diffusive resistance of the liquid shell will effectively enhance the effects of any streaming component in the wall and the natural diffusive resistance of the root wall will be masked.

Wall resistance can be estimated by measuring first the oxygen diffusion from the root apex and then extracting and analysing the gas from the intercellular spaces of the cortex (T. J. Gaynard and W. Armstrong, unpublished). The wall resistance is given by solving the equation:

$$Q/t = \frac{C_{ias}}{R_{WL} + R_{sh}} \tag{63}$$

where C_{ias} is the oxygen concentration within the root, and R_{WL} is the apparent resistance of the wall.*

The relationship found between wall resistance and total resistance in *Eriophorum angustifolium* using this method is shown in Fig. 11.

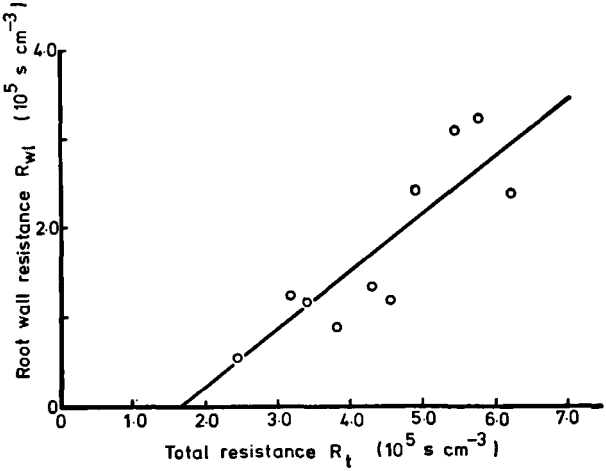


Fig. 11. *Eriophorum angustifolium.* Apical root wall resistance to radial oxygen diffusion, as a function of total plant resistance at 23°C (y = 0·6487x–1·089) (after Gaynard, 1979).

(*d*) *Synergism in the longitudinal path.* If effective wall resistance is derived by the procedure outlined above, the term $R_t - R_{WL}$ will give a total effective internal resistance to longitudinal transport between the oxygen source and the apical segment of the root. It is thus a measure of the synergism between pore-space resistance and the two "lateral" sinks: respiratory activity and subapical oxygen leakage through the root wall.

If radial oxygen loss cannot be detected at the root apex then provided that there is negligible wall resistance one may conclude that the effective internal resistance has become infinite (p. 255). In these circumstances some indication of wall resistance may be obtained by raising the concentration of the oxygen source until it is possible to apply procedure 3.

If the lateral leakage from subapical parts can be curtailed then $R_t - R_{WL}$ quantifies the synergism between the pore-space resistance (R_p) and the respiratory activity of the longitudinal path.

(*e*) *Pore-space resistance.* Since R_t is a corporate resistance in which lateral leakage and respiration mask the expression of R_p it becomes necessary to suppress these influences in order to quantify R_p.

* Provided that C_{ias} is sufficiently high (>5%), R_{WL} will normally approximate to the non-metabolic resistance of the wall.

In wetland plants lateral leakage is naturally suppressed by the impermeability of the root wall in subapical regions; with non-wetland plants leakage can be severely curtailed by embedding the subapical regions in thick agar (p. 303).

Respiratory activity can be curtailed by cooling (Armstrong, 1971a, 1971b) but for plants which still respire significantly at low temperatures an alternative method is required.

Greenwood (1969) has maintained that the respiratory sites in the root will be oxygen saturated at very low gas-phase concentrations (*c.* 1% or less) while Armstrong and Gaynard (1976) have shown that respiratory rate in whole roots remains constant provided that the concentration of oxygen maintained in the cortical gas-phase is in excess of 2–3%. Assuming that these observations are generally applicable then if lateral leakage can be satisfactorily suppressed the respiratory component may be masked and the magnitude of R_p obtained as follows.

Where radial oxygen loss from root to electrode (I′) indicates a cortical gas-phase oxygen concentration $>3\%$ we may write

$$I' = \frac{V'}{(R_p + R_{WL} + R_{sh})} - \text{Resp.} \tag{64}$$

where V′ is the concentration of the oxygen source in the atmosphere and Resp. is the respiratory component removed along the longitudinal diffusion path.

If the concentration of the oxygen source is now raised to a new value V″ we may express the new rate of apical oxygen loss I″ as:

$$I'' = \frac{V''}{(R_p + R_{WL} + R_{sh})} - \text{Resp.} \tag{65}$$

If respiratory oxygen demand is fully satisfied by concentrations of oxygen $>3\%$ the magnitude of the term Resp. will be common to both equations and hence on combining with respect to Resp. and re-arranging we obtain:

$$R_p = \frac{V'' - V'}{I'' - I'} - (R_{sh} + R_{WL}) \tag{66}$$

(*f*) *Effective diffusion coefficient.* It follows from Section II.B.5 that the pore-space resistance (as obtained above) can be manipulated to derive an effective diffusion coefficient for longitudinal transport in the root. In appropriate circumstances this effective diffusion coefficient may then be further manipulated to determine the tortuosity of the longitudinal path.

If the root is of uniform cross-section (A_x) and has linear uniformity of porosity the effective diffusion coefficient will be given by the expression:

$$D_e = \frac{l}{R_p A_x} \tag{67}$$

where l is the length of the root (cm). Tortuosity may then be computed from equation 20, such that $D_e = D_0 \tau \epsilon$ where ϵ is the fractional porosity determined separately by the method of Jensen *et al.* (1969), τ is the tortuosity factor and D_0 the diffusivity of oxygen in air at the temperature concerned.

IV. AERATION IN THE WETLAND CONDITION

A. THE WETLAND PLANT

1. Responses to Anoxia

(*a*) *Total anoxia.* Although wetland plants flourish in anoxic soils there is no convincing evidence that their roots are less sensitive to anoxia (oxygen stress) during normal growth than are species which frequent unsaturated soils; indeed, the converse might be true. Vartapetian (1970) observed destructive changes in the cell organelles of excised rice roots after only four hours in anoxic culture and after seven hours the ultrastructure had become grossly impaired. This contrasted with the effects observed in the non-wetland species, pumpkin, bean and tomato where mitochondrial ultrastructure remained intact for the first 24 h of anoxia. It has since been shown (Vartapetian *et al.*, 1976) that mitochondrial damage under anoxia can be delayed for two days in roots of freshly germinated rice if the whole seedling is kept in anoxia and similarly in excised roots if they are kept in 0·5% glucose solution. During this two day period the mitochondria develop parallel cristae and in the intact seedlings they increase in size. Changes such as these have been noted also by Morriset (1975) who described mitochondria with cristae in characteristically parallel arrangement in tomato roots after 72 h in anoxic culture. The failure of rice root mitochondria to be sustained longer than two days under anoxia contrasts markedly with the response found in the coleoptile and leaf. Intact coleoptiles kept in distilled water and excised coleoptiles in 0·5% glucose solution remained intact even after five days in a nitrogen atmosphere and again the mitochondria enlarge and develop parallel cristae. Leaf mitochondria were persistent and contained stacks of parallel cristae after five days but were less enlarged. Although they do not offer an explanation for the changed nature of the persistent mitochondria, Vartapetian *et al.* suggest that the capacity of rice coleoptiles to grow under anoxia and to preserve undamaged mitochondria and other organelles is not caused by the resistance of the cell organelles to oxygen deficiency. They consider it to be due rather to the ability of the seedling to transport organic compounds easily, even under the exclusion of oxygen, from the grain to the coleoptile where they can be utilized by glycolysis. The lower resistance to anoxia in the cells of rice roots is variously explained: there is the possibility of more active anaerobic metabolism which renders the sugar supply inadequate; alternatively it might be that the early disintegration of the root mitochondria in

an oxygen-free environment is caused by a failure of the root cells to develop glycolytic processes to an adequate degree; again it is possible that the root cells are less resistant to the products of anaerobic metabolism. Concerning the second of these suggestions it may be noted that at the tillering stage rice plants grown throughout in aerobic culture exhibit some glycolytic activity in the roots under anoxia (John and Greenway, 1976) but this is substantially lower than if the plants have been pretreated for several days with a supply of nitrogen in the rooting medium.

The effects of total anoxia on rice germination and early seedling development have been studied by Kordan (1974, 1975, 1976a, b, c, d, 1977). Kordan has demonstrated convincingly that initial coleoptile growth and the laying down of the first adventitious root primordia can take place under conditions of complete oxygen exclusion. He has shown also that for the further development of adventitious roots a supply of molecular oxygen is essential. So too is molecular oxygen necessary for chlorophyll development (Kordan, 1976b; Kirk and Tilney-Basset, 1967) and for normal vertical shoot growth.

Kordan's observations are in line with the general premise (Vartapetian *et al.*, 1976, and others) that the normal activities of higher plants require an external source of molecular oxygen. It is perhaps pertinent to stress at this stage that there is as yet no evidence to suggest that an oxygen requirement for root growth is not universally true. Anaerobic pathways of metabolism, the activity of which can be increased by oxygen stress, do not alone seem able to sustain growth.

(*b*) *Anaerobic metabolism.* Although there seems little reason to doubt that anaerobic metabolism sustains the submerged overwintering leafless rhizomes of some marsh species, the role of anaerobic metabolism in the wetland condition is not well understood. Information is scanty and contradictory and a number of basic questions remain unanswered (Rowe and Beardsell, 1973): particularly is there uncertainty concerning the possible auto-toxicity from fermentation by-products such as ethanol. Apart from cyanide poisoning in species containing cyanogenic glycosides (Rowe and Catlin, 1971) the chemical basis of death from anoxia has not been established. It is still not clear whether the roots of non-wetland plants are any more or less well-endowed with the potential for anaerobic metabolism than those of wetland plants; neither is it known whether they are more sensitive to anaerobic end products. It could be argued that because of aerenchyma formation wetland species might have less need for anaerobic metabolism.

In anaerobic conditions a small net production of energy can still be gained in plant tissues by fermentation which yields ethanol and carbon dioxide as end products. However, ethanol is potentially phytotoxic and it could be envisaged that the prolonged waterlogging of plants might lead to its accumulation in damaging quantities. Although no clear evidence for this has emerged, such considerations have stimulated the search for less toxic by-products in

wetland species, a search which has not gone entirely unrewarded. However, just as both wetland and non-wetland species possess the ability to respire anaerobically so are the less toxic products of anaerobic metabolism, e.g. lactate, succinate, malate, glycerol, shikimate, produced by both.

Mazelis and Vennesland (1957) were of the opinion that malic acid should be considered a principal end-product of anaerobic respiration in many, if not all, plant tissues. However, malate was not found in anoxic Iris rhizomes (Boulter *et al.*, 1963) and Effer and Ranson (1967) found that malate accumulation was associated with aerobic respiration in buckwheat seedlings and that its concentration declined under anaerobiosis. Ethanol and carbon dioxide were the major end-products in the buckwheat but significant quantities of lactate, succinate and free amino acids accumulated also. Crawford (1969) has suggested that malate forms preferentially in the roots of flood-tolerant plants, alcohol in the roots of intolerant species. The dark fixation of carbon dioxide which accompanies malate formation and the potentially less toxic nature of malic acid make the theory an attractive one and it has excited much interest. However, the supposition that ethanol is harmful to the plant is not borne out in practice and ethanol accumulation is known to occur in a number of tolerant species. Boulter *et al.*, (1963) found considerable quantities of alcohol in the rhizomes of *Iris pseudacorus* but no adverse effects were noted. Similarly ethanol accumulation without ill-effects has been noted also in the flood tolerant *Nyssa aquatica* and *Nyssa sylvatica* (Hook and Brown, 1973; Hook *et al.*, 1971). Alcohol production in rice is enhanced by pretreatment with lower oxygen concentrations (John and Greenway, 1976). There is no net yield of energy in Crawford's proposed scheme and the theory was based on the failure to detect malic enzyme in flood-tolerant plants (NB malic enzyme catalyses the conversion of malic acid to pyruvic acid). Highly active malic enzyme has now been found in some flood tolerant species (Davies *et al.*, 1974) including those studied by McMannon and Crawford (1971) and this must cast doubt on the validity of the proposals. However, it is still possible that malate might accumulate in some other way: it could be that malic enzymes may be inhibited in some flood-tolerant plants (Chirkova *et al.*, 1973; Crawford, 1976). Nevertheless, until more is known one can only warn against an uncritical acceptance of the suggested alternatives to alcoholic fermentation.

There is no evidence yet for any appreciable involvement of anaerobic respiration in growth activities, but there are grounds for believing that ethanol production is a self-regulating process. Ethanol may induce a quasi-dormant state in tissues (Rowe, 1966) and the rapid catabolism of ethanol and other end-products which follows re-aeration (Effer and Ranson, 1967; Rowe, 1966; D. V. Beardsell, personal communication) indicates that they can serve as a metabolic pool and may be non-toxic. In suitable circumstances ethanol vapour may be lost from tissues via the gas-space system or by

diffusion into the soil (Hook *et al.*, 1972), while the transpiration stream also can act as a carrier (Fulton and Erickson, 1964).

(*c*) *Gas-space development.* An enlargement of the gas space within the plant body improves internal ventilation. It lowers the resistance to gas flow, it also reduces the potential respiratory demand per unit volume of tissue and in its natural habitat the wetland plant is characterized by a gas-space system of exceptional proportions which extends even into the aerial parts. Tissues having abnormal amounts of gas space are often loosely referred to as aerenchyma and for detailed accounts of aerenchymatous structure and formation in wetland plants the reader may refer to Arber (1920), Sifton (1945, 1957) and Sculthorpe (1967).

Aerenchyma formation is an obvious adaptation to the wetland condition; it is at best only poorly developed by non-wetland species. Nevertheless, although we can readily demonstrate the superior ventilating efficiency of the wetland plant body (pp. 289–297) the chemical basis of aerenchyma formation remains obscure. The extensive gas-space development in the roots is an obvious response to conditions associated with soil anoxia and may be delayed, reduced or prevented if the soil is made aerobic (Van der Heide *et al.*, 1963; Armstrong, 1971a, b; Das and Jat, 1977). However, for the most part it seems that the wetland plant will not normally experience anoxia even within the cells of the root meristem (p. 294) and it becomes difficult to believe that the triggering stimulus for gas-space enlargement is anoxia within the root cells. It might be that certain processes within the wetland plant require higher than normal oxygen levels to function as in the non-wetland plant: the reactions concerned with the polysaccharide formation required to stabilize cell wall structure could be those affected perhaps (Van der Heide *et al.*, 1963) and in rice there is evidence that planes of discontinuity in the middle lamella arise at an early stage in cell maturation (Boëke, 1940). It is interesting to note that in rice, aerenchyma fails to develop in those sectors of cortex which lie adjacent to the lateral root initials (Armstrong, 1971a, 1971b).

2. Radial Oxygen Loss and Phytoxin Immobilization

(*a*) *General.* Aerobic conditions persist only in the surface of the wetland soil and one may illustrate this theoretically by substituting appropriate soil data for M and D in equation (33) (see Table II).* Where oxygen is unavailable facultative and obligate anaerobes proliferate. These organisms use oxidized mineral components or organic matter dissimilation products as respiratory electron acceptors and consequently the chemistry of the submerged soil differs considerably from that of its unsaturated counterpart (Ponnamperuma, 1972; Gambrell and Patrick, 1978). Nitrate, Mn(IV), Fe(III), SO_4^{2-}, and the dissimilation products CO_2 and N_2 give Mn(II), Fe(II), H_2S, methane, NH_3 and H_2; a host of organic compounds which emanate from the further reduction of pyruvic acid and which eventually are degraded

* See p. 238.

to methane, accumulate also. Notable examples of these include the lower alcohols, the highly volatile and phytotoxic lower fatty acids (formic, acetic, propionic and butyric) and the plant hormone ethylene.

Many of these substances are phytotoxic and the survival of plants in the wetland habitat is closely linked with an ability to transform soil-borne toxins to less harmful products (see Armstrong, 1975, 1978). Transformation is essentially oxidative in nature and species can be graded on the oxidizing abilities of their root systems. Those exhibiting the greatest oxidizing powers are the most tolerant of phytotoxins and prove not surprisingly to be the better ventilated.

The sites and means of toxin transformation are various although ultimately oxygen from the ventilating system is the major electron acceptor. The Fe^{2+} (soluble) $\rightarrow$ Fe^{3+} ("insoluble") conversion which can be effected by molecular oxygen alone or enhanced by enzymatic activities (Yamada and Ota, 1958), is the most readily observed example of toxin transformation. Insoluble iron residues may line the intercellular gas spaces within the root itself (Armstrong and Boatman, 1967), and this has recently been most elegantly demonstrated by Green and Etherington (1977) who have shown that the iron is deposited within the cell walls also. Deposits of ferric iron around the root bear witness to the protective role of oxygen leaking radially from root to rhizosphere (Armstrong, 1967b).

If internal aeration is adequate, metabolic activities within the root may destroy some potentially phytotoxic materials (e.g. the lower fatty acids, Sanderson and Armstrong, 1978), so too may the activities of the microbe populations within an oxygenated rhizosphere (Pitts *et al.*, 1972; Yoshida and Suzuki, 1975).

(*b*) *The oxygenated rhizosphere.* Although ventilating "power" affords protection in several ways the absolute quantity of oxygen available for phytotoxin immobilization must ultimately determine the total quantity which can be removed from circulation. However, it seems likely that the dimensions of the oxygenated rhizosphere which again depend upon the absolute quantities of oxygen available in the root may also play an important part in the protective process. The better ventilated the root the broader may this zone of oxygenation be and this should advantageously prolong the period in which slowly oxidizable compounds may be immobilized during their passage to the root.

Some indication of how the dimensions of the oxygenated rhizosphere might vary with ventilating power may be gained by solving equation (50) for appropriate values of D_e, M and a. Unfortunately, the various assumptions upon which this expression is based may be a poor approximation to conditions in the rhizosphere and the results must therefore be treated with some caution. Equation (50) depends upon the establishment of a state of quasi-equilibrium in the rhizosphere. It does not embrace the initial phase of

oxygenation which follows root penetration into reduced soil and during which any resident pool of reduced products would be oxidized (Teal and Kanwisher, 1961). It fails also to take proper account of the continuing diffusion of reduced substances into the rhizosphere. However, despite these drawbacks the predicted dimensions of rhizosphere oxygenation are comparable with the oxidized rhizosphere zones found in the wet soil (Armstrong, 1967b). The predicted relationship between root radius and the radius of oxygenated rhizosphere is interesting. Relatively broad zones of oxygenation are predicted for the narrower roots (Fig. 9a) and this again accords with practical observation: lateral roots ($r \leq 0{\cdot}01$ cm) often show zones of oxidation similar to those of the major root from which they originate. From considerations of phytotoxin exclusion alone it might be concluded therefore that in wetland conditions plants having narrower roots could be at a competitive advantage. Such an assumption would be incorrect, however, for since the narrow root can lose relatively more of its oxygen by leakage, the effective resistance to diffusion in the longitudinal path becomes correspondingly greater (p. 302). The oxygen balance must therefore become rapidly poorer with increasing length. Consequently, it is not surprising that the narrow roots of wetland species are laterals with a marked tendency to be short and borne on the basal regions of major roots where internal oxygen levels are relatively high. Lateral roots often display negative geotropism (positive aerotropism?) in wet soils.

(*c*) *Root wall permeability and rhizosphere dynamics.* Root wall permeability to oxygen in wetland species declines rapidly with distance from the apex (Armstrong, 1964, 1971b; Luxmoore *et al.*, 1970) and oxygen leakage may cease at distances $\geqslant 2$ cm from the apex. The effect that this has upon oxidation in the rhizosphere is evident from the changing pattern of iron deposits found there (Armstrong, 1967b). Where rhizosphere oxygenation is appreciable, major iron precipitates are usually remote from the root surface. With declining permeability the deposits may eventually be confined to the rhizoplane, subsequently to be re-solubilized if impermeability becomes complete.

It is natural to question the adaptive significance of this declining permeability. It has been suggested that there will be a conserving effect on the oxygen available for longitudinal "flow" to the root apex (Armstrong, 1967) but since the wetland root is aerenchymatous and diffusive resistance low (p. 293), the synergistic effects of oxygen leakage in subapical regions could be relatively slight; only in longer roots might there be a sufficient accumulation of diffusive resistance for the conserving factor to gain in importance; a significant effect may be noted in Fig. 16.

The impermeable root wall could be more important as a barrier to phytotoxin entry and this may be related to the dynamics of rhizosphere oxygenation. The oxygen supplying power of the wetland root apex can be simulated

to some extent by the oxygen permeable tubular Si-rubber apex of the model roots depicted in Fig. 12. The leuco-methylene blue in dye-impregnated wet soil will rapidly oxidize around the apex of these roots, eventually forming an oxidized halo of significant proportions (r = 0·3–0·4 cm). However, in water-logged loam we have found that the peak dimensions of the halo can be relatively short-lived: in time the oxidation boundary contracts and eventually approaches the root wall again. We suspect that this decline may be caused by a build-up of aerobic organisms in the rhizosphere immediately adjacent to the root. If the living wetland root did not quickly lose its permeability to oxygen and phytotoxins it is conceivable that such a contraction in the rhizosphere boundary might lead to a critical influx of phytotoxin. It is suggested therefore that the declining permeability of the root wall may be necessary to curtail the period over which oxygen is released to any fixed point in the soil.

3. Critical Oxygen Pressure

The relatively high oxygen status attained in the roots of wetland species by internal longitudinal transport can be readily demonstrated. Apical concentrations *c.* 10% or greater are not uncommon in roots up to 10 cm long (Armstrong, 1967a; Gaynard, 1979, in preparation). However, concentrations of this magnitude are not in themselves sufficient justification for assuming adequate internal aeration; it is necessary also to establish the relationship between respiration and oxygen concentration in the intact plant. Similarly one needs to know the optimal levels of oxygen required to achieve root growth (p. 288) and adequately oxygenate the rhizosphere (p. 282).

Unfortunately, little is known of the respiratory responses of intact plants for it has proved much more convenient to measure the oxygen uptake of excised blocks of tissue. In these circumstances oxygen uptake increases hyperbolically as the oxygen pressure is raised, until a point is reached, the critical oxygen pressure (COP, Berry and Norris, 1949), at which the respiration becomes constant. A search of the literature reveals few instances in which the COP obtained by *in vitro* methods lies below 0·10 atm (10% oxygen) and Luxmoore *et al.* (1970) have recorded values in excess of 0·2075 atm for rice root respiration.

However, one must seriously doubt the significance of COP data obtained by *in vitro* analysis. These methods usually cause the intercellular gas-space of the sample to be flooded and this infilling of gas-space will substantially raise diffusional impedance. In these circumstances an abnormally high oxygen pressure at the boundary of the sample will be necessary to sustain its respiratory activity; consequently an abnormally high COP must be recorded. Where lower values of COP have been found there is usually evidence to show that surface moisture on the sample has been minimal (Yocum and Hackett, 1957; Forrester *et al.*, 1966). In the intact plant the unflooded gas-

space system greatly enhances oxygen diffusivity. Consequently the COP of the *in vivo* condition should, in theory at least, be substantially lower than that normally detected *in vitro*. Some of our recent experiments (Armstrong and Gaynard, 1976) confirm that the COP for root respiration in the intact plant may be nearly an order of magnitude lower than that found by *in vitro* analyses.

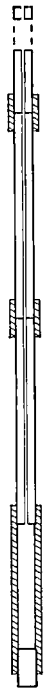


Fig. 12. An artificial root for simulating the radial leakage of oxygen from the living root. Glass micro-capillaries joined in series form the subapical parts of the root; the oxygen-permeable apex (hatched) is translucent silicone-rubber tube (O.D., 0·1 cm), sealed by a small bung at the free end. The length of the "root" and hence the internal resistance to diffusion may be varied by altering the length of glass capillary. After Armstrong, (1972).

The *in vivo* analysis which is entirely non-destructive is based on the premise that radial oxygen diffusion (I) from the intact root will be a linear function of the leaf oxygen pressure (V) provided that the internal oxygen concentration is everywhere greater than the COP. The relevant equation from Section III is

$$I = \frac{V}{(R_P + R_{sh} + R_{WL})} - \text{Resp.} \qquad (64)$$

If a gradient of oxygen pressure exists between leaf and root apex it follows

that if V is reduced it must bring the oxygen concentration in the root apex nearer to the COP. As Resp., R_P, R_{sh} and R_{WL} are constants in the short term then for any given root, I will fall linearly with V. If the concentration at the root apex falls below the COP the term Resp. will be no longer constant: it will decline, and hence the slope I : V will change. If Resp. declines linearly with V the I : V relationship will again be linear; if the decline is curvilinear the new relationship will be curvilinear. Whichever is the case the COP will be apparent from the inflexion point in the plot of I and V, and may be determined by substituting I for Q/t in equation (63).

In practice we have found without exception that the relationship between I and V has the bilinear character indicated in Fig. 13B (ii). The linearity above the COP is as forecast above but below the COP the curvilinear pattern had been anticipated. COPs (atm) for root respiration (together with standard deviations) calculated, from the oxygen flux at the inflexion point were: Rice cv. Norin 37, 0·026 ± 0·002 (5 plants), Rice cv. Norin 36, 0·024 ± 0·001 (6 plants) and *Eriophorum angustifolium* (cotton sedge), 0·02 ± 0·004 (10 plants).

An explanation for the unexpected bilinear character of the experimental plot and its inception with the abscissa was sought using the electrical root analogue described earlier (Section II.D.2). The experimental flux pattern was finally reproduced by making the following assumptions: firstly, that the COP was experienced within the apical 2 cm of root only; secondly, that respiratory rate and internal oxygen concentration for segments of intact root do not follow the hyperbolic *in vitro* form normally attributed to them, but adhere rather to the type of relationship outlined in Fig. 13A. Here it is assumed that the cortical cells accounting for 50% or more of the respiratory demand exhibit a very low COP (e.g. 0·001 atm or less) because of their close contact with the gas phase. Experiments on the dark respiration of whole leaves (Forrester *et al.*, 1966) and moist tissue slices (Yocum and Hackett, 1957) support this assumption. On the other hand the tissues accounting for the remainder of the respiratory activity in the apex, such as the central vascular core and meristem are devoid of gas-space; the assumption made was that the effective diffusion coefficient of these tissues is low enough for anaerobic centres to arise when the declining cortical oxygen concentration approaches 0·02–0·025 atm. It was also assumed that below the COP the decline in respiratory activity from the increasing volume of anaerobic tissue is a linear one with oxygen concentration (Fig. 13A). This does not accord with the simplest applications of equation (45) but suggests rather that the major respiratory demand in the stelar core is peripheral in location.

If these assumptions are correct we must conclude that the COP of the intact root is a property of extremely low porosity tissues. The indications are that COP for the intact porous cortical region *per se* is so low as to be extremely difficult to detect.

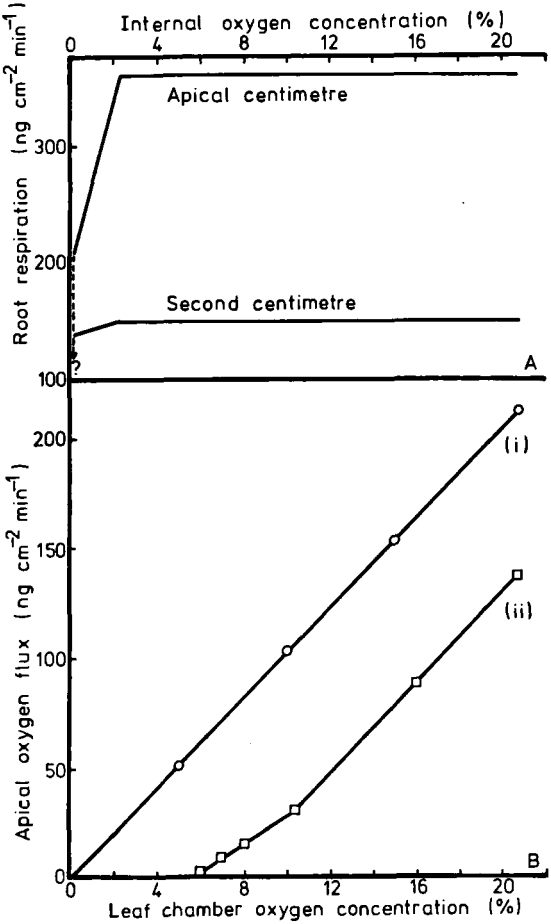


Fig. 13. Analogue simulation of oxygen concentration vs apical flux relationship. (A) Relationships between root respiration and internal oxygen concentration used to programme the analogue in order to reproduce the experimental flux pattern. (B) Analogue-predicted relationships between leaf chamber oxygen concentration and apical oxygen flux for a cooled (○) and uncooled (□) root. Programming details as follows:

Distance from apex, cm	0–1	1–2	2–3	3–4	4–5
Effective porosity, %	6	9	12	16	24
Potential respiration, ng min^{-1} cm^{-2} root surface	360	150	135	109	99
Potential oxygen leakage through root wall, % maximum	100	95	73	56	0

After Armstrong and Gaynard, 1976.

The attainment of full respiratory activity at such low oxygen pressures will undoubtedly be beneficial in anoxic soils and this will be enhanced by high oxygen diffusivity and low respiratory demand in wetland species.

4. Oxygen Pressure and Root Growth

Although Kordan's findings (p. 279) and those of Amoore (1961a, b) and others (Banath and Monteith, 1966; Huck, 1970; Vartapetian *et al.*, 1977) lend support to the premise that oxygen is an invariable requirement for root growth in both wetland and non-wetland species, nevertheless we know very little concerning the relationship between internal oxygen pressure and root growth.

Those who have sought to establish the relationship between oxygen pressure and growth have done so usually by measuring the response to oxygen pressure in the solution culture bathing the roots. Understandably many conflicting records have thus accumulated for it has not been appreciated until quite recently (Greenwood, 1967a, b; Luxmoore *et al.*, 1970; Healy and Armstrong, 1972) that even in non-wetland plants there may be a very significant (but undetected) internal oxygen supply. Furthermore, there has often been a failure to appreciate that the rate of stirring of culture solutions needs to be high if the concentration of oxygen at the root wall is to be equal to that in the bulk solution. Diffusion gradients between the bulk solution and the root can arise even with quite vigorous stirring (Greenwood, 1969). Consequently there is often something of an analogy between the studies *in vitro* of respiratory activity criticized earlier (see previous section) and those in which root growth is measured in relation to solution-culture oxygen-pressure.

At the cellular level somewhat different results have been obtained and Amoore (1961a, b) has shown that in excised pea roots mitosis will proceed unchecked at an oxygen concentration of 0·5% and above while mitotic activity is only arrested completely below 0·0005%.

Having found a way to control and monitor the internal oxygen pressure in roots (see previous section), we have recently carried out several trial experiments to examine the relationship between internal oxygen pressure and root growth in rice (T. J. Gaynard and W. Armstrong, unpublished). Although the work is at a very preliminary stage, parallels between the results obtained and the findin gs of Amoore are evident. Growth was apparently indifferent to oxygen pressures greater than the COP (*c.* 2·5%), while at all concentrations below the COP root growth ceased; the results accord with the development of anaerobic centres in the root at values immediately below the COP (see p. 286). The rapid cessation of growth at very low oxygen pressures indicates an effect upon the elongation phase; the less rapid decline at higher pressures suggests that perhaps the meristem only is affected. Normal growth activities always recommenced within ½–7 h after the original oxygen supply had been

restored, even after treatments in which oxygen was barely detectable at the root apex for 40 h. The time taken for recovery appeared to be related to the period and intensity of oxygen stress.

Interesting parallels have been found also with the work of Vartapetian *et al.* (1976, 1977). When whole plants were subject to anoxia for 20 h by replacing the leaf atmosphere with nitrogen, it was found on re-aeration that both roots and shoots were dead. However, the roots of plants subjected to this treatment after introducing a 4% glucose solution as the anaerobic rooting medium recommenced their growth within 1 h of re-aeration from the leaves; the leaf system itself appeared moribund. The obvious inference is that root viability had been maintained by anaerobic metabolism in the presence of a readily available substrate and, further, that this activity was insufficient for growth.

5. Aerenchyma and Aeration

If plants are to successfully exploit the wetland condition diffusive theory (Section II) demands that the total effective resistance to internal longitudinal oxygen transport should be minimized: pore-space resistance must be reduced together with the synergistic effects of respiration and lateral oxygen leakage (Fig. 5).

Pore-space resistance in the wetland plant is reduced by the formation of aerenchyma, so too is respiratory activity. Lateral leakage from the root is restricted by the basipetal decline in root wall permeability; leakage from submerged portions of leaves and stems is often restricted by the absence of stomata.

(*a*) *The aerenchymatous root.* Most roots, whether wetland or non-wetland, develop small but continuous intercellular gas-spaces in cortical parenchyma. In rice this pore space is first evident within a few cells of the root cap (see Plate I, 1, 4). As the cells mature the individual spaces as seen in T.S. enlarge (Plate I, 2) and when fully developed may occupy up to 12% or more of the total root cross-sectional area. In wetland grasses and sedges the normal intercellular space system rarely persists beyond 2–3 cm from the root apex under wetland conditions. At this point the separation and collapse of the cortical cells begins and the gas-space becomes considerably enlarged: aerenchyma is formed (Plate II and Fig. 14). Sometimes this collapse will be so extensive as to leave intact only those cells immediately adjacent to the endodermis and root cortex. However, the pattern of gas-space development does show genetic variation: the enlarged spaces may replace only the inner cortex in some species and it may be noted that the cell walls which persist in the aerenchymatous grass root are radially orientated (Plate II, 2) while in sedges they are tangential (Plate II, 1). In herbaceous species other than the grasses and sedges shizogeny without lysigeny is common: the number of cells is not reduced but rather a honeycomb structure is formed.

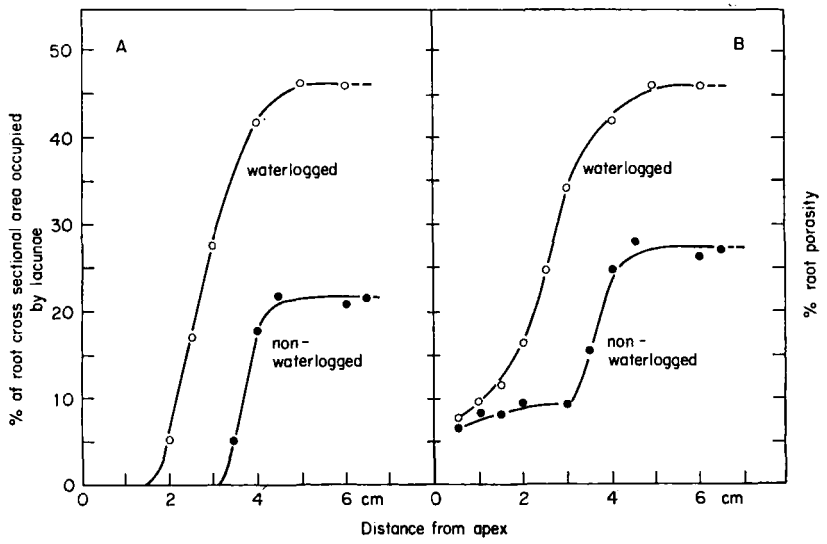
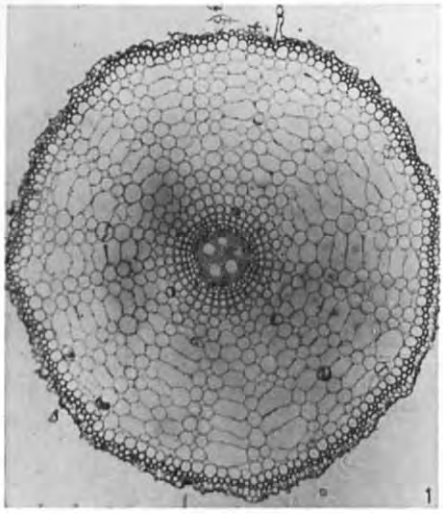


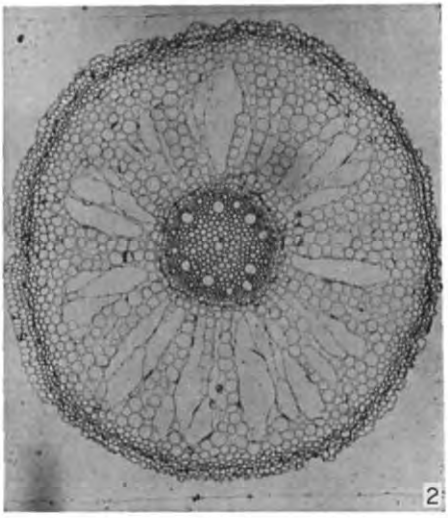
Fig. 14. Rice: A. Variation in position of initiation, and subsequent levels of lacuna production, in roots from waterlogged and non-waterlogged soil.
B. Total porosity changes along some roots. After Armstrong (1971b).

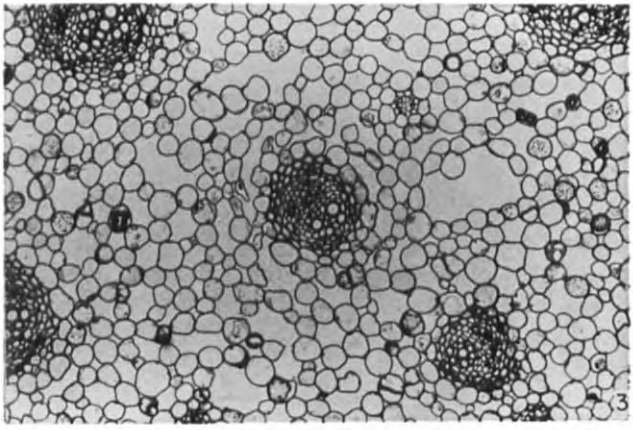
Again, in rice, we find that the gas-space of the non-aerenchymatous apex is non-tortuous (Plate I, 4). It is not clear whether this might be a general feature of the wetland plants. *Eriophorum angustifolium* also displays the same regularity of packing of the cortical cells found in rice and the impression gained is that regularity of packing evident in T.S. may always coincide with the superimposition of intercellular spaces over appreciable distances. A lack of tortuosity in the apex together with the continuous development of high subapical porosity is a most effective recipe for minimizing pore space resistance and at the same time ensuring that the vital functions of the root are maintained.

We may transform the pore space distribution pattern of the aerenchymatous root into the equivalent one of pore space resistance by the appropriate use of the expression $l/D_0\tau\epsilon A_x$ given earlier (p. 249). If we transform the

Plate II. Gas-space characteristics of wetland plants. (1) and (2), *Eriophorum angustifolium* and *Spartina* × *townsendii*: respectively showing the lysigenous aerenchyma characteristic of Cyperaceous and Graminaceous adventitious roots (sections at 4 cm and 6 cm from root apex; magnifications × 62·5 and × 40). (3) *Limonium vulgare:* T.S. petiole to show the honeycomb arrangement characteristic of schizogenous aerenchyma (magnification × 95). (4) *Spartina* × *townsendii:* T.S. aerenchymatous leaf sheath showing lacunae (magnification × 65). (5) *E. angustifolium:* T.S. leaf-aerenchyma diaphragm showing the unusual gas-spaces within adjoining cell walls (magnification × 1300).







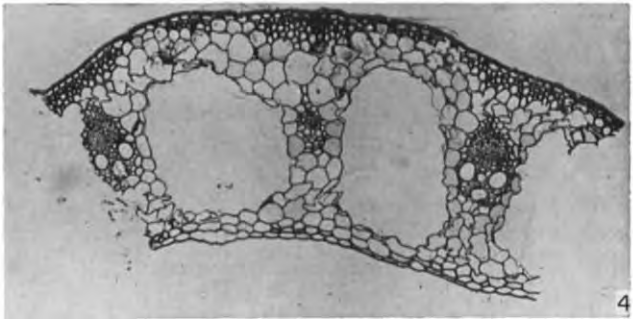


Plate II

data from Fig. 14 the tortuosity factor (τ) may be omitted (cf. Plate I, 4, 5). The resulting plot of pore space resistance and root length over 15 cm where r = 0·05 cm is shown in Fig. 15(i). If aerenchyma did not develop at 1·5 cm it can be seen that by 15 cm the accumulated resistance would have been nearly treble that in the aerenchymatous root; if porosity had not risen beyond the apical figure ($\epsilon = 0{\cdot}065$) and if the non-aerenchymatous path was tortuous (e.g. $\tau = 0{\cdot}66$) the resistance at 15 cm would be approaching a figure seven times that in the aerenchymatous root (Fig. 15 (iii)).

However, aerenchyma does not simply reduce the pore space resistance in the root: no matter how it forms it reduces also the respiratory demand of subapical parts; it is associated also (perhaps causally) with the declining permeability of the root wall. Luxmoore *et al.* (1970) have shown that in the rice root respiration declines from a peak of 360 ng cm^{-3} s^{-1} in the apical 0–0·5 cm to 180 ng cm^{-3} s^{-1} at 0·5–1 cm and becomes relatively constant (*c.* 60 ng cm^{-3} s^{-1}) beyond 5 cm. The same pattern occurs in *Eriophorum angustifolium* and with the extremes of aerenchyma formation found in rice and *Eriophorum* it follows that respiratory demand in subapical regions could be almost entirely stelar.

The wetland root as exemplified by rice and *Eriophorum* is thus most effectively adapted to the rigours of the submerged soil: the low pore space resistance in subapical regions in itself reduces synergism significantly; the low subapical respiratory activity and lateral leakage enhance the effect still further.

Using a 10 cm rice root as a template and the electrical analogue as a model we can illustrate the magnitude of these synergistic effects and assess in detail how the various properties of the aerenchymatous root influence its aeration status: oxygen concentration profiles with different degrees of respiration and leakage, and in the presence and absence of the aerenchymatous structure, are given in Fig. 16.

From these data the non-aerenchymatous root structure emerges as probably the biggest single obstacle to adequate root aeration in the wetland soil, although the respiratory and leakage characteristics of the non-aerenchymatous condition are of significance also. If both the respiration and leakage characteristics of the aerenchymatous rice root are imposed upon the non-aerenchymatous structure there is a moderate improvement in aeration (an increase in oxygen concentration of 3·3 % at a root length of 7 cm, cf. curves 5 and 8). However, with the leakage or respiratory characteristics of rice applied independently the improvement is approximately halved and hence is relatively small (cf. curves 6 and 8, 7 and 8). For the non-aerenchymatous root itself the indications are that growth would be limited to around 6·5 cm where the COP for growth is 2 %.

When the aerenchymatous structure is mated with non-aerenchymatous characteristics the oxygen status improves enormously (curves 2, 3 and 4). It

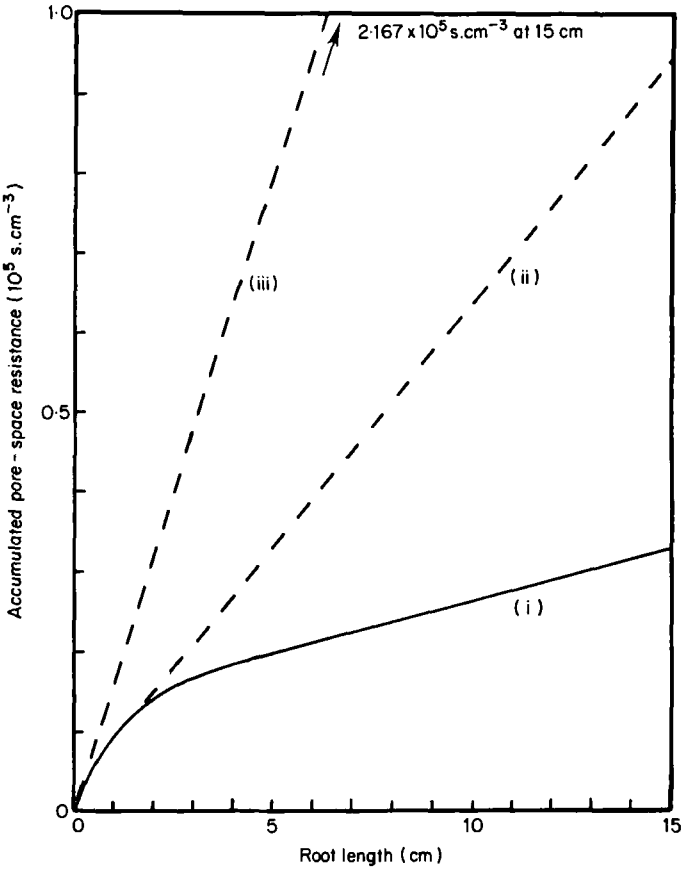


Fig. 15. Accumulated pore-space resistance as a function of root length: (i) wetland rice; (ii) a uniformly porous root (non-aerenchymatous, see Fig. 16), having an effective porosity equal to that in the apical centimetre of the rice root; (iii) uniformly porous root ($\tau\epsilon$ = 4·3%).

is interesting to note that the rise in apical concentration which accompanies the change from non-aerenchymatous respiration and leakage to the equivalent rice characteristics (curves 1 and 4) is similar in magnitude to differences already noted (curves 5 and 8). This type of effect will increase in magnitude the longer the root becomes and will apply also to conditions 2 and 3.

The characteristics used to simulate the rice place a limit on root growth of *c.* 30+ cm. This is in keeping with the normal growth habit of the rice plant which has a relatively shallow root system. Rice relies heavily on new nodal roots developing successively with plant growth to maintain the high oxygen status and strong oxidative powers of its functional roots (Okajima,

1964). At a length of 10 cm the rice root is losing approximately 30% of its oxygen supply to the rhizosphere (see Fig. 16), but this is concentrated in the apical region (41% in the apical centimetre) where the internal oxygen concentration is 11·1%. In contrast, the non-aerenchymatous root of length 7 cm loses approximately 41% of its oxygen supply to the rhizosphere but the apical rhizosphere receives the smallest part of this (7·6%) and the internal oxygen concentration of the apex is only 1·5%.

(*b*) *The leaf and stem.* The aerenchyma found in the leaf and stem of wetland plants generally differs structurally from that in the roots. The spaces occur as discrete chambers (lacunae) in longitudinal array. The lateral walls of the lacunae are often very thin and may be imperforate but the gas-space is always continuous through the thin end walls or diphragms: unwettable perforate cellular plates of multifarious design and very low porosity. Although septa of such low porosity increase the overall resistance of the longitudinal diffiusion path and indeed counteract to some extent the low path resistance of the lacuna body nevertheless their presence is essential. In the event of injury they form a most effective safeguard against internal flooding; they may be considered as the cofferdams of the gas-space system. Consequently, it seems likely that the presence of a diaphragm will be desirable no matter how small the lacunae; diaphragm frequency may be determined more by the mechanical needs of the organ.

Little but speculative comment concerning the diffusional resistance imposed by diaphragms is to be found in the literature. From experimental observations Teal and Kanwisher (1966) and Armstrong (1972) have concluded that they might not be a serious impedance to root aeration. The diffusional impedance imposed by diaphragms will be a function of their frequency, thickness and effective porosity. From visual observations, Coult (1964) has estimated "diaphragm" porosity in the *Menyanthes* rhizome as 0·6%; thickness is 40 μm and frequency *c.* 1 per 1·5 cm of aerenchyma channel. The diffusive resistance of the "diaphragm" thus approximates to 3·25 s cm^{-1} and the resistance of the lacuna body 7·317 s cm^{-1}. The resistance of a core of lacuna tissue 1·0 cm long and equivalent in cross-section to a root (radius r = 0·05 cm) would be 0·00894 $\times$ 10^5 s cm^{-3}. In the aerenchymatous root this would be equivalent to an overall porosity of 69%. In *Eriophorum angustifolium* we find that diaphragm resistance in the leaf

Fig. 16. An analogue analysis showing how the various characteristics of wetland (aerenchymatous rice root) and non-wetland (non-aerenchymatous) roots contribute to the oxygen status of the root in the wetland condition. The data were compiled on the assumption that the wetland soil, where aerated, consumes oxygen at the uniform rate of 5·27 $\times$ 10^{-8} g cm^{-3} s^{-1}, and that oxygen diffusivity in the soil was a uniform 1 $\times$ 10^{-5} cm^2 s^{-1}. It was assumed also that wall permeability to oxygen of the rice root declined from a maximum of 100% at the apex, to zero at 5 cm from the apex; in the non-aerenchymatous root the minimum value (60%) was attained at 6 cm.

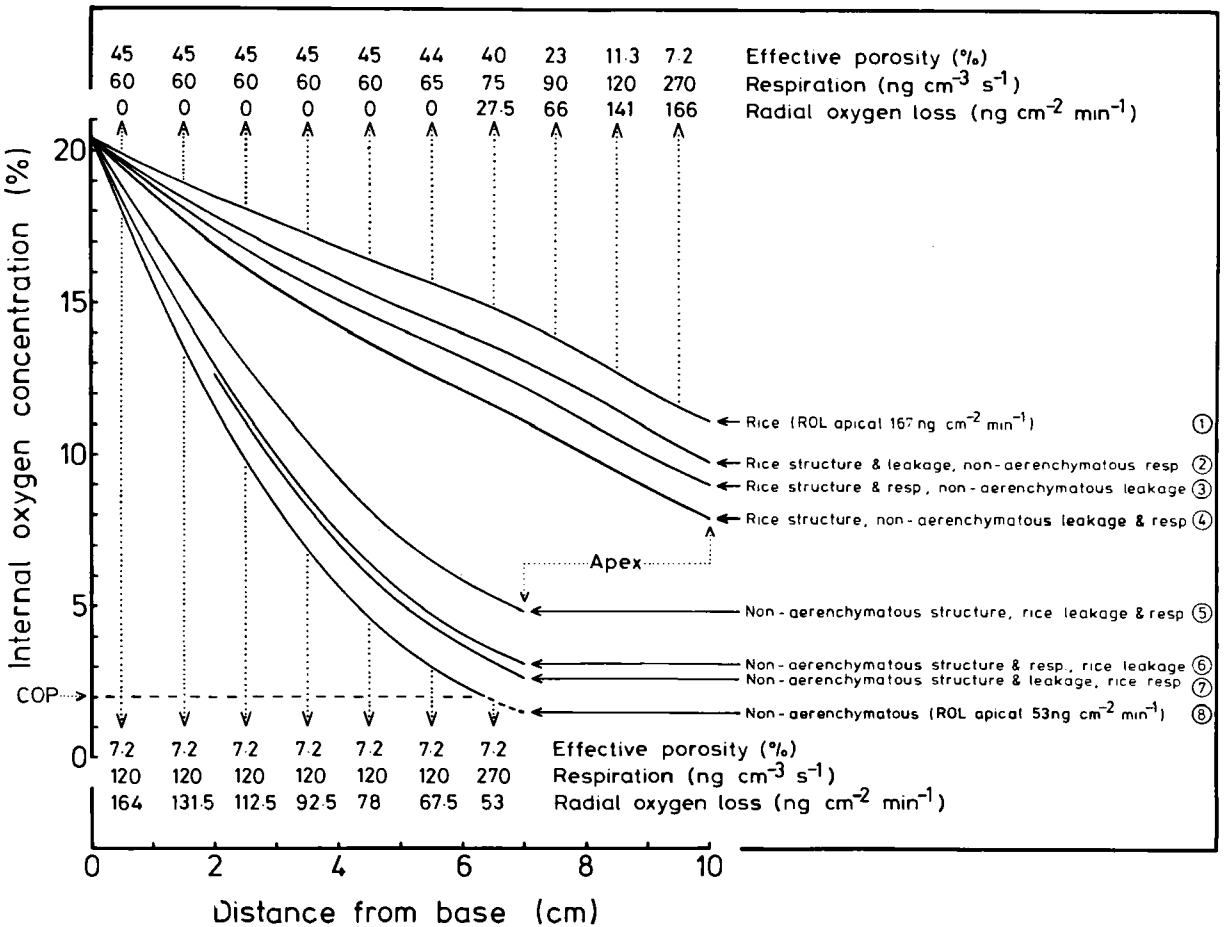

45 45 45 45 45 44 40 23 11·3 7·2 Effective porosity (%)
60 60 60 60 60 65 75 90 120 270 Respiration (ng cm⁻³ s⁻¹)
0 0 0 0 0 0 27·5 66 141 166 Radial oxygen loss (ng cm⁻² min⁻¹)
Internal oxygen concentration (%)
20
15
10
5
0
COP
Rice (ROL apical 167 ng cm⁻² min⁻¹) ①
Rice structure & leakage, non-aerenchymatous resp ②
Rice structure & resp, non-aerenchymatous leakage ③
Rice structure, non-aerenchymatous leakage & resp ④
Apex
Non-aerenchymatous structure, rice leakage & resp ⑤
Non-aerenchymatous structure & resp., rice leakage ⑥
Non-aerenchymatous structure & leakage, rice resp ⑦
Non-aerenchymatous (ROL apical 53ng cm⁻² min⁻¹) ⑧
7·2 7·2 7·2 7·2 7·2 7·2 7·2 Effective porosity (%)
120 120 120 120 120 120 270 Respiration (ng cm⁻³ s⁻¹)
164 131·5 112·5 92·5 78 67·5 53 Radial oxygen loss (ng cm⁻² min⁻¹)
0 2 4 6 8 10
Distance from base (cm)

Fig. 16

aerenchyma is somewhat greater (Gaynard, 1979). Leaf porosity ($\leq 60\%$) compares with an effective diaphragm porosity no greater than 0·4%, and the mean value recorded was *c.* 0·25%. The latter figure was obtained by assessing total pore space resistance in the longitudinal path (equation 66) before and after the excision of leaf segments. The number and area of the diaphragms within the segments were then determined and the pore space resistance attributable to the diaphragms estimated. Diaphragm thickness was *c.* 0·0058 cm, their frequency 2/cm/aerenchymatous channel and hence the resistance of 1 cm of leaf base of 0·05 cm^2 cross-section area and 63% porosity amounts to 874 s cm^{-3} and diaphragm resistance accounts for 82% of this total. 874 s cm^{-3} is the pore space resistance offered by 1 cm of root (r = 0·05 cm) having an overall porosity of 71%.

A further possible source of internal diffusive resistance is to be found within the root and shoot at the root/shoot junction. Coult (1964) was of the opinion that the cortical gas-space system of shoot and root became discontinuous at this point in *Menyanthes*. By assessing total pore space resistance prior to and after excision of the root/shoot junction in *Eriophorum angustifolium*, Gaynard (1979) has obtained values for the pore space resistance of the junction which range from 0·057–0·13 $\times 10^5$ s cm^{-3}. Neither figure suggests a discontinuity in the gas-space across the junction, rather do they indicate an effective porosity in the range 0·9–2%.

(*c*) *The functional significance of aerenchyma.* In a stimulating essay under this title Williams and Barber (1961) assessed the merits of what they chose to label respectively the Transport and Reservoir Theories which seek to explain the need for aerenchyma.

An acceptable theory, it was suggested, should satisfy each of four basic postulates:

1. The structure should be necessary for the successful growth of the plant in competition with others.
2. The structural provision should be adequate for the requirements of the function it is supposed to serve.
3. These requirements could not have been met with markedly greater economy by some other available means.
4. Provision should not be markedly more than is necessary to fulfil the functional requirements.

The Reservoir Theory assumes that the aerenchymatous structure is required as an oxygen reservoir to tide the plant over periods when stomatal closure or other events interrupt the gas-phase continuity of plant and atmosphere. For a variety of reasons Williams and Barber could not satisfy themselves on the validity of this argument, for different reasons neither can we: in our experiments with rice and other aerenchymatous species such as *E. angustifolium* (T. J. Gaynard and W. Armstrong, unpublished) the extensive lacuna systems support the respiratory needs of the plants for periods

rarely exceeding 60 min. The oxygen is consumed to extinction and hence the second of the four postulates is not satisfied.

The Transport Theory in summary states that "the normal intercellular space system of vascular plants is inadequate to transport oxygen at the necessary rate" in a wetland environment and "that the deficiency is redressed by the formation of aerenchyma". Williams and Barber dismiss this hypothesis on several grounds. Their principle objections concern the gas-space system of the leaf and shoot. The volume of the lacunae is they suggest more than necessary to fulfil the transport role (a contravention of postulate 4); a small increase in the pore-size of the diaphragms, they argue, would be vastly more effective in reducing the diffusional resistance than a large increase in chamber size. This cannot be disputed, but if diaphragm pore size is determined by the need to form a barrier to flooding (p. 294) this objection is perhaps less valid. Williams and Barber concluded that aerenchyma affords a mechanical-cum-metabolic compromise in the plant and the starting point of this hypothesis is the assumption "that the oxygen flow within the plant is not easily increased but that the oxygen requirement of the submerged portions can be reduced". "What is required . . . is a structure which for any given diameter provides the greatest possible strength with the least possible amount of tissue" and "this double requirement is met by the honeycomb, and by this only". The hypothesis is an attractive one but perhaps embraces something of an unnecessary over-reaction to the principles of the Transport Theory.

Of primary concern for the majority of aerenchymatous species is probably the need to maintain high levels of oxygen in the root systems to effect phytotoxin transformations in root and rhizosphere; perhaps also to support an aerobic microflora. In a previous section (Fig. 16, p. 295) we saw how important for this purpose was an aerenchymatous structure in the root: a reduction in metabolic activity to aerenchymatous levels in a non-aerenchymatous structure increased the oxygen status by a relatively small amount. It has been my contention that the scale of aerenchyma is perhaps primarily concerned with the achievement of high oxygen levels in the root system (Armstrong, 1972) and to this end high porosities are advantageous. If this is so, the aerenchymatous provision will not necessarily contravene Williams and Barber's fourth postulate and we may regard the Transport and Mechanical-cum-metabolic Theories as essentially complementary.

6. Photosynthesis and Aeration

As early as 1940, Laing reported increases in the oxygen pressure in the stems, roots and leaves of *Nuphar advenum* Ait., *Pettandra virginica* (L.) Kunth, *Typha latifolia* L., *Sparganium eurycarpum* Engelm and *Scirpus validus* (Vahl), during periods of illumination. In *Menyanthes trifoliata* L. Coult and Vallance (1958) recorded light/dark fluctuations in oxygen pressure

of *c.* 0·048 atm in the stem cortex and 0·033 atm in the root. In all of these cases it appears that the photosynthetic activity responsible for oxygen enrichment of the plant atmosphere took place in organs which were either submerged or astomatal or both. The oxygen build-up during illumination can thus be attributed to diffusional impedances preventing the rapid release of oxygen to the external atmosphere and this accords with the theory outlined in Section II.C.2.

In *Eriophorum angustifolium* we find that the extent to which photosynthesis enhances root aeration depends upon two factors: the degree of immersion of the leafy parts and the availability of free carbon dioxide at the submerged leaf surface. The bicarbonate ion is an ineffective carbon source where cuticular resistance is high. The sheathing leaf bases in *Eriophorum* are largely astomatal and non-photosynthetic and in unsubmerged plants or those submerged to the top of the outermost leaf sheath photosynthesis has an insignificant effect on root aeration even at light intensities of 100 μE m^{-2} s^{-1}. If submergence is extended to include the photosynthetic parts of the leaf system the oxygen pressure in the root system rises as a function of light intensity, carbon dioxide concentration and degree of immersion. At a solution concentration of 0·8 mM (CO_2) l^{-1} and a light flux of 100 μE m^{-2} s^{-1} the oxygen concentrations in the root apices of fully submerged plants can rise to 150% of the unsubmerged condition; at $\frac{3}{4}$ submergence the value falls to *c.* 140%; at $\frac{1}{2}$ submergence a figure of 110% has been recorded; at 300 μE m^{-2} s^{-1} the latter value rose to 120% of the unsubmerged condition. In the dark, oxygen levels in the root are depressed by all degrees of immersion which cover the stomatal surfaces of the leaf: the length of the internal diffusion path is extended and the total effective resistance is thus increased. Consequently, the advantages accruing from submergence in daylight could be countered during the subsequent dark period.

One may foresee circumstances where partial submergence in darkness could result in a lowering of the oxygen tension below the COP in more remote parts. Alternatively, the process of rhizosphere amelioration which could be enhanced by photosynthetic activity might be critically imbalanced by darkness. There are indications of the latter in the reported sulphide damage to rice during periods of sunless weather or deliberate shading (Vamos and Köves, 1972). It is possible that a thorough evaluation of the photosynthetic enhancement of root aeration in rice would indicate the need for reduced levels of submergence during periods of sunless weather.

B. THE NON-WETLAND PLANT

The vast majority of higher plants are confined to well-aerated soils. In general they respond unfavourably to sudden soil waterlogging, are extremely shallow rooting and non-competitive in wet soils and grow relatively poorly in solution cultures which lack forced aeration. Until quite recently little

consideration had been given to the likelihood of internal longitudinal oxygen transport in these species; it was not generally appreciated that the small cortical intercellular spaces of the roots might form a gas-filled continuum with the atmosphere. Only in the late 1950s and early 1960s was it conclusively demonstrated that oxygen could travel by gaseous diffusion through the cortical intercellular space system of the non-wetland root. Since then it has become increasingly apparent that internal oxygen transport is just as normal a feature of non-wetland species as it is of wetland plants. Where the two groups differ is in the degree of aeration afforded: root porosities are much lower and overall respiratory demand higher in the non-wetland root; there have also been suggestions that tortuosity might add significantly to the pore-space resistance (Jensen *et al.*, 1967). Neither the respiratory demand nor the root-wall permeability in the non-wetland root show the same marked basipetal decline met with in the wetland plant (Luxmoore *et al.*, 1970).

The critical oxygen pressures for respiration and root growth in non-wetland roots are known with even less certainty than for wetland species. Huck (1970) has noted that whereas tap-root elongation in soybeans and cotton ceases abruptly if the oxygen is purged from the soil gas-space, oxygen levels of 2–5 % resulted only in a temporary reduction in growth. Recent experiments of the kind performed on rice and cotton grass (p. 288) (Webb, 1978—unpublished), indicate that primary root elongation in pea can continue below the respiratory COP and even for some time after the oxygen pressure in the root apex has fallen so low as to become immeasurable. Roots have extended for up to 80 hours and by 7 mm under these circumstances, with the growth rate showing a progressive, if somewhat stepwise, decline before growth finally halted. However, several hours after growth ceased, re-aeration of the apex via the internal path has brought an almost immediate return to the initial growth rate. This could indicate that root growth had continued until some critical distance separated the apex from the still-oxygenated parts of the root; a critical distance perhaps limiting the supply of oxidizable substrates and alternative electron acceptors, or limiting the removal of metabolic by-products. That oxygen was still present but undetected because of high wall resistance is also a possibility which cannot be precluded at this stage.

At the cellular level the data of Vartapetian *et al.* (1977) and Morriset (1975), suggest that total anoxia may be less immediately damaging to the non-wetland root. On the other hand Huck reports that periods of soil anoxia exceeding 30 min resulted in a killing of tap-roots in cotton and soybean. Five hours of anoxia was sufficient to cause the tip-death of all tap-roots.

1. Adaptability

Non-wetland species show some improvement in their ventilating character-

istics in waterlogged soils. Nevertheless, the plasticity of response found in the wetland plant is lacking. Yu *et al.* (1969) grew several non-wetland crop species under a whole range of soil treatments which included full flooding, half-flooded and drained. Root porosities were always lower in the drained treatments and ranged from 3·5% (barley) to 7·5–11·5% in corn. From the diffusional point of view it is not surprising that such roots penetrated but a short distance below the water table of the half-flooded treatment. With the exception of barley most plants responded to full flooding by producing fresh roots of higher porosity. The porosity in corn rose to 15–18% and the roots penetrated up to 17 cm. In sunflower the porosity rose from 6% to *c.* 11% and some roots penetrated the wet soil to a depth of 15 cm. Porosity in barley varied little but the roots penetrated to 12 cm; root porosity in "Pato" wheat increased from 6 to nearly 15% but penetration was limited to about 5 cm.

Yu *et al.* interpret their data in terms of effective root ventilation; the apparent exceptions of barley and wheat they suggest were due respectively to exceptionally low and unusually high root respiration in these species.

2. Analogue Data

Electrical analogue studies of aeration in the non-wetland root type yield results which accord well with the observations of Yu *et al.* and the supposition that root penetration into wet soil reflects the sufficiency of internal aeration. However, the analogue approach makes it abundantly clear that root radius and the "sink" activity of the wet soil may substantially influence the root's oxygen status and potential for growth; it seems more than likely that differences in root radius will have contributed to the interspecific differences in growth recorded by Yu *et al.*

Analogue data presented in Fig. 17 (A–H) show how the internal oxygen supply to the apex of non-wetland roots ought to vary with length, radius, effective porosity, root respiration and soil oxygen demand. For convenience it has been assumed that the roots are devoid of laterals and are of constant radius (r = 0·05 cm, B, C, F and G; r = 0·01 cm, D and H). It has been assumed also that oxygen entry is at the root base; that root respiration and diffusivity ($D_0\tau\epsilon$) remain constant with distance from the root apex; and, (A and E excepted), that root wall permeability declines from a maximum (100%) at the apex to a minimum (60%) at 6 cm from the apex. For (A) and (E) the root wall permeability was set at zero to give zero soil sink activity. Root respiration is programmed at two levels: 120 ng cm^{-3} s^{-1} (A–D) is a moderately high rate, 30 ng cm^{-3} s^{-1} (E–H) is relatively low. Soil oxygen demand is represented at three levels: zero (A and E); 4×10^{-6} cm^3 cm^{-3} s^{-1} (B and F); and 4×10^{-5} cm^3 cm^{-3} s^{-1} (C, D, G and H); the oxygen demand of 4×10^{-5} cm^3 cm^{-3} s^{-1} is a high level of activity. Since the effective root porosity for non-wetland plants appears to lie within the range 1·5–15%,

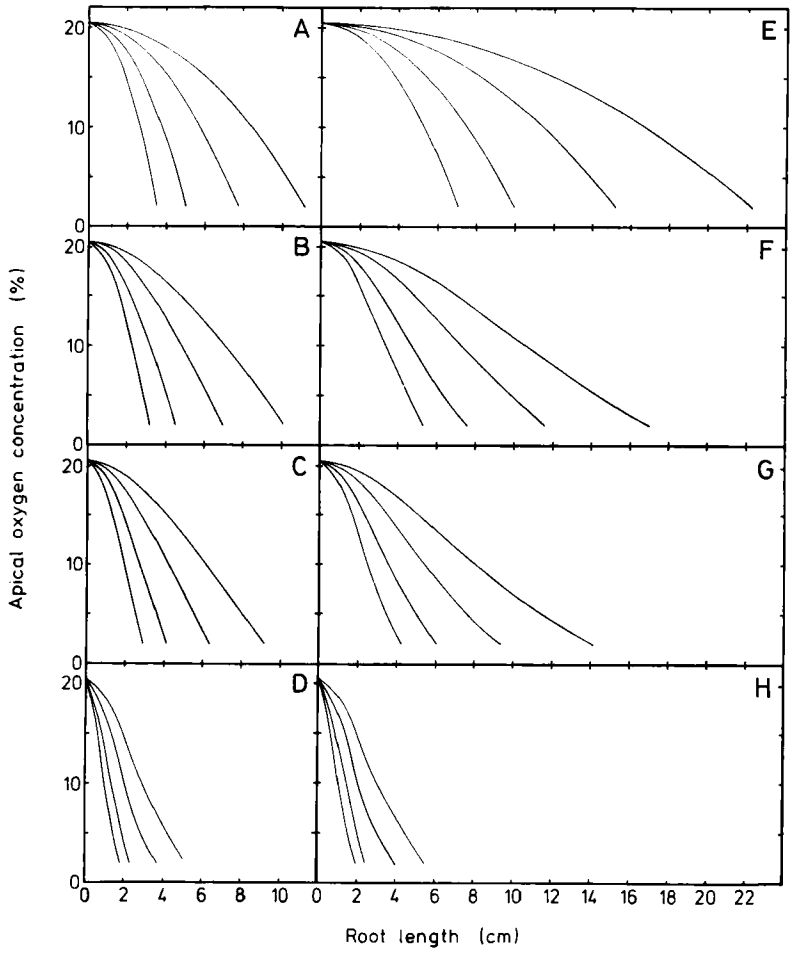


Fig. 17. Internal apical oxygen concentration in roots as a function of root length, root respiration, effective porosity, root radius and soil oxygen sink activity. Analogue data obtained by assuming (i) uniform respiratory activity in the roots, 120 ng cm^{-3} s^{-1} (A, B, C, D) and 30 ng cm^{-3} s^{-1} (E, F, G, H); (ii) uniform effective porosity throughout the roots: from left to right in each figure 1·5%, 3%, 7%, 15%; (iii) uniform oxygen consumption in aerated rhizosphere soil: B and F, $5{\cdot}27 \times 10^{-9}$ g cm^{-3} s^{-1}; C, D, G and H, $5{\cdot}27 \times 10^{-8}$ g cm^{-3} s^{-1}, but no oxygen leakage from root to soil in A and E; (iv) root wall permeability to decline from 100% at the apex to a minimum of 60% at 6 cm and beyond; (v) root growth ceases at an internal oxygen concentration of 2%. In B, C, F and G root radius (r) is 0·05 cm; in D and H, r = 0·01 cm; the data in A and E are independent of root radius.

these and two intermediate values (3% and 7%) have been programmed for each set of conditions.

Perhaps the most interesting point to emerge from these data is the very considerable influence exerted by the soil sink when root radius is low. Conversely, the respiratory activity of the root is of only minor importance under these circumstances; the maximum root length predicted in (H) is only 5·5 cm ($r = 0{\cdot}01$ cm; $\epsilon = 0{\cdot}15$; soil respiration 4×10^{-5} cm^3 cm^{-3} s^{-1}), and yet a four-fold increase in root respiration, (D), reduces this figure by only 0·3 cm. However if oxygen leakage to the soil is reduced to zero (as in E), the root can in theory attain a length of *c.* 22 cm before the hypothetical COP (2%) is reached. It is also interesting to note that an increasing effectiveness of the soil sink becomes apparent in a concavity of the appropriate curve (cf. E and G).

At the higher root radius ($r = 0{\cdot}05$ cm) soil sink activity has considerably less influence on the internal oxygen regime (cf. A, B, C and E, F, G); root respiration exerts a substantial effect which is approximately equalled by the effective root porosity. Where there is no lateral leakage of oxygen to the soil, (e.g. A and E), the internal oxygen regime becomes a function of porosity and root respiration only and the internal oxygen status becomes independent of radius. Under these circumstances the maximum attainable root length supported by initial aeration is predicted here as 22 cm ($\epsilon = 0{\cdot}15$ in E). This is several centimetres longer than the deepest recorded root penetration in the studies of Yu *et al.* and for non-wetland herbaceous species is possibly near the attainable limits of root penetration into wet soil; the lower limit is probably less than 2 cm (e.g. D, where $\epsilon = 0{\cdot}015$ and $r = 0{\cdot}01$ cm). If rhizosphere oxygenation and phytotoxin immobilization are taken into account it will be obvious that many of the predictions concerning attainable root length (B, C, D, F, G and H) may in practice never be realized. In the majority of cases the apical oxygen status declines rapidly with increasing root length and so too will the protection afforded by ROL rapidly diminish.

3. Oxygen Transport in Pea: An Experimental Study

In a recently completed study of oxygen transport in pea roots Healy (1975) has provided what appears to be the first experimental record of the changes in diffusional resistance which accompany root elongation in a non-wetland plant; the plants ranged in age from 1–55 days. Cylindrical Pt electrodes were used to monitor the oxygen flux from the apices of the primary roots and the diffusional resistances in the longitudinal path were calculated as described in Section III. Pore space resistance and the synergistic effects of respiratory activity and leakage were quantified as were the effects of secondary root production, and these results are summarized in Fig. 18 (curves a–e). Changes in the total effective resistance which could be attributed to a

decline in respiratory activity were noted and plumule resistance was demonstrated by submergence experiments. No evidence was found of significant stomatal resistance to longitudinal oxygen transport.

The peas were grown for the most part in sterile 1 % agar medium in 250 ml glass cylinders and the plants were removed for assay by extracting the agar core intact. To minimize the oxygen leakage from subapical regions of the roots, only the agar enclosing the primary apex was trimmed away before assay; plant and agar jacket were immersed in anaerobic liquid medium to the cotyledon junction before moving the Pt electrode to ensleeve the primary apex (Section III). The effects of subapical oxygen leakage were studied by trimming away the whole of the agar jacket; the influence of lateral (secondary) roots on the oxygen status of the primary root was determined by assaying the oxygen flux from the primary apex before and after excision of the laterals.

The relationship found between pore-space resistance and root length (Fig. 18a) illustrates one aspect of root aeration not stressed previously. During the early stages of root elongation (3·5 cm–8·5 cm) there is no observable gain in pore-space resistance. Upon further investigation it was found that this phenomenon could be attributed to the changing shape of the developing root. The final root shape is that of an elongated inverted cone and this may be of considerable benefit to the non-aerenchymatous uniformly porous root: as basal respiration declines with age the effective resistance of the base could decline very substantially, more so than in a root of uniform diameter. The oxygen status in the root apex would be enhanced accordingly.

The pore-space resistance in the pea cannot be entirely accounted for in terms of root shape and mean porosity (3·8 %) alone and it is tempting to suggest that the diffusion path may be a tortuous one. However, although longitudinal sections of the roots do not show the same continuity of channels evident in rice (cf. Plates III and I), the impression gained is that gas-space tortuosity might be relatively slight even in this species. Unfortunately, the data in Fig. 18a are inclusive of apical wall resistance; until we can establish the magnitude of this term it is not possible with any certainty to quantify the tortuosity.

Healy found that apical oxygen flux from the primary pea root always declined with increasing root length provided that the plants were no more than 10 days old ($l \leq 10$ cm approx.). In jacketed roots with excised laterals the oxygen flux showed a smooth curvilinear decrease with length. The corresponding increase in effective diffusional resistance ($8{\cdot}1 \times 10^5$ s cm^{-3} at 3 cm to $27{\cdot}2 \times 10^5$ s cm^{-3} at 10 cm; Fig. 18b) is attributable to the synergism between primary root respiration and pore-space resistance. The retention of secondary roots was associated with a bi-modal flux pattern. The initial decrease in flux was as before but during lateral emergence there followed a

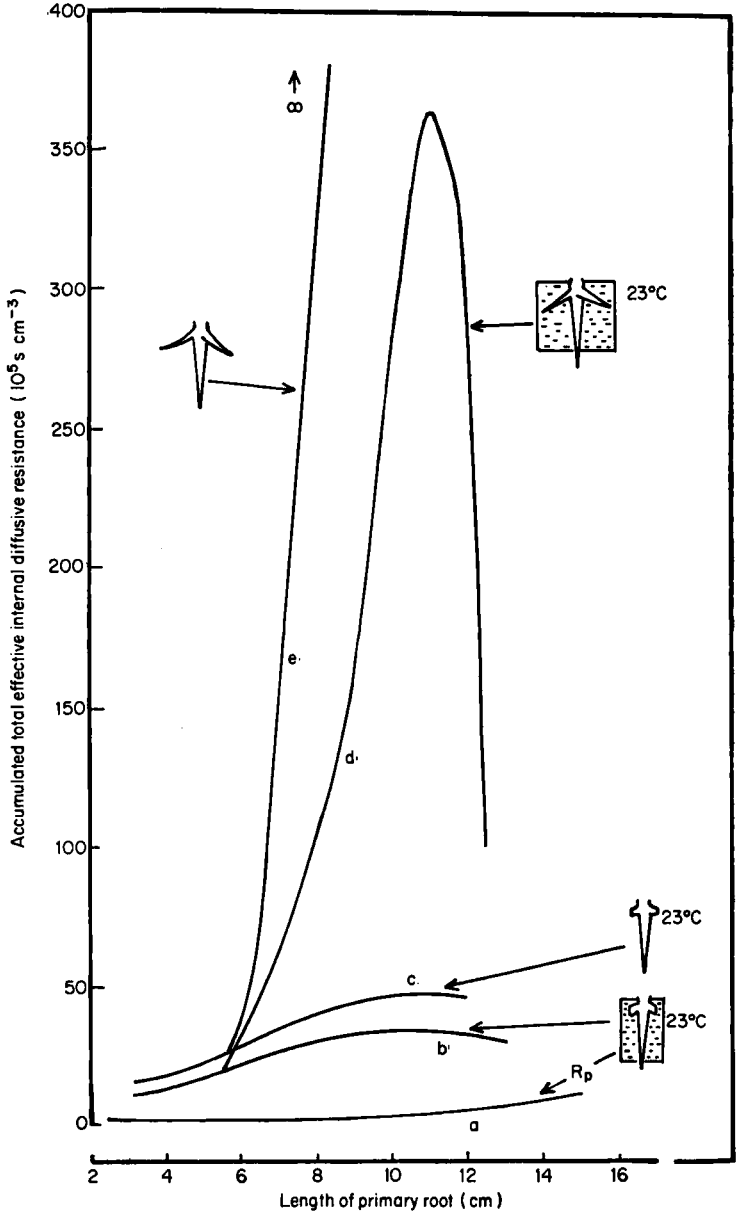


Fig. 18. Oxygen transport in the primary root of Pea; collective figure showing the changes in total effective diffusive resistance found during primary root elongation under the circumstances indicated. Compiled from Healy (1975) and Armstrong and Healy (unpublished).

steep decline in the apical oxygen status: effective diffusional resistance rose from *c.* $14{\cdot}1 \times 10^5$ s cm^{-3} at 5·5 cm, immediately prior to emergence, to a value of 294×10^5 s cm^{-3} at 10 cm (Fig. 18d). When leakage is permitted the role of the lateral roots becomes even more pronounced: the apical oxygen status of the primary became immeasurably small at *c.* 8 cm and hence the effective diffusional resistance approaches infinity (Fig. 18e). This is the first record of the possible influence of secondary roots on the internal ventilation of a major root and the effect can be seen to be substantial indeed.

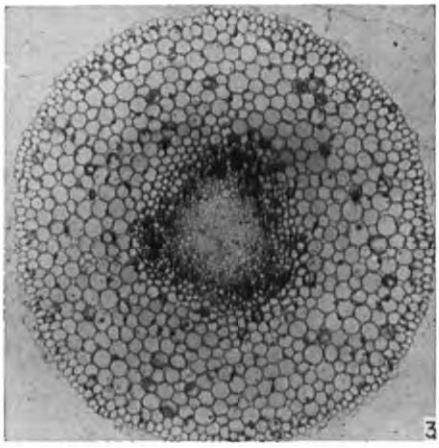
In periodically degassed liquid medium pea roots cease growth abruptly at 8·5–9 cm. This accords closely with the length at which the roots have accumulated infinite diffusional resistance. Consequently we have suggested that the initial 8–9 cm of root growth in pea will be sustained by internal ventilation provided that there is some impedance to radial oxygen loss (Healy and Armstrong, 1972) (provided also that the level of the culture solution does not come above the root-shoot junction). Static oxygen-free culture solution seems to fulfil this requirement. If growth is to proceed beyond 9 cm a more effective "jacketing" appears to be essential. Agar jelly (1 %) can fulfil this role but for prolonged growth it must eventually become necessary for the rooting medium to receive forced aeration.

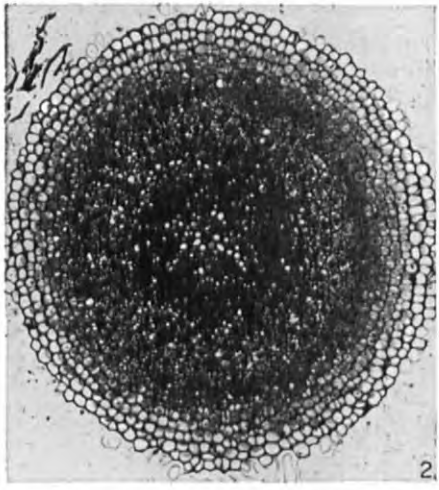
In saturated soils it seems unlikely that pea could initially attain a root length of 8–9 cm because of soil oxygen demand and it is interesting to note that in continuously degassed medium growth ceases at 4–5 cm (Healy, 1975). However, the final root length attained might depend also upon the ageing effects in the root system: in roots of 11 days and older Healy noted an increase in the apical oxygen concentration (Fig. 19). In periodically gassed culture solution this was accompanied by a resumption of growth for a short period.

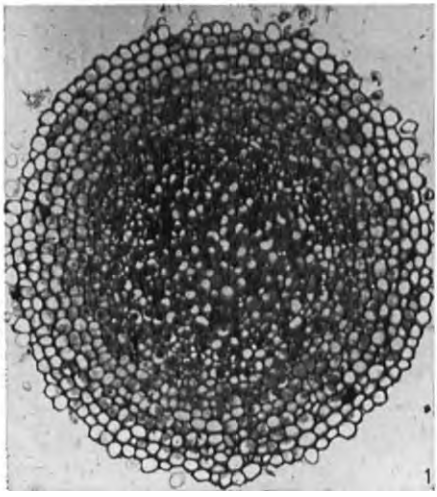
C. TREES

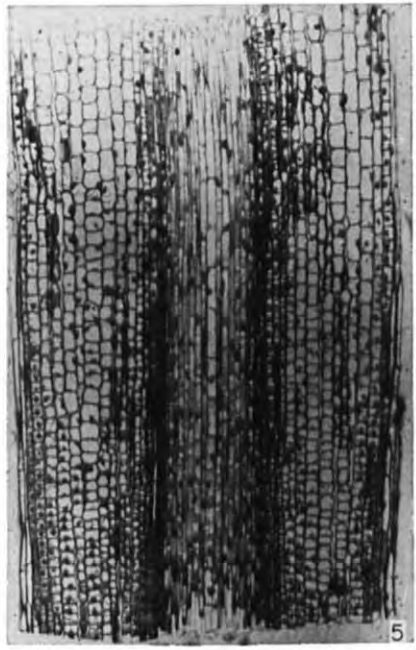
It is perhaps the economics of tree production and the deleterious effects of waterlogging which have done most to stimulate an interest in tree aeration and several reviews concerned chiefly with this topic have appeared recently (Rowe and Beardsell, 1973; Hook *et al.*, 1972; Gill, 1970; Coutts and Armstrong, 1976). The following is intended only as a supplement to these reviews.

It seems certain that much of what has been said already concerning the ventilation of herbaceous species applies equally well to woody plants. There are, however, characteristics peculiar to woody species which can create special problems for the ventilation of submerged parts and which reduce the competitiveness of tree species in wet soils. These features include: the development of secondary tissues with ensheathing and perhaps non-porous cambia; the loss of primary cortical tissues and their replacement by secondary cortex which with time occupies less and less of the total cross-section of









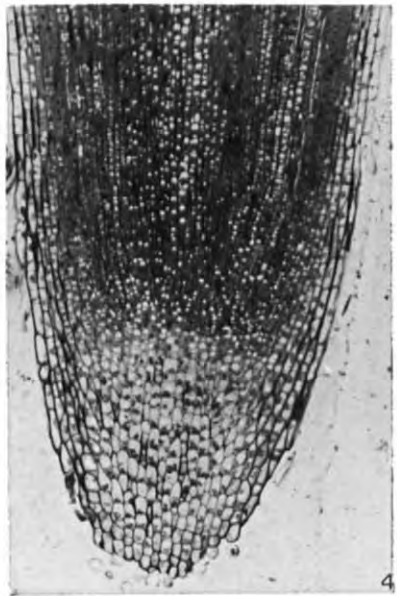


Plate III

the plant body; and last but not least the more massive dimensions of the woody plant body itself.

The part played by anaerobic metabolism in tree roots is very uncertain (Rowe and Beardsell, 1973) and there are as yet no firm grounds for believing that internal longitudinal oxygen transport is not just as necessary a requirement in submerged tree roots as it so obviously is in non-woody species.

The long distances over which oxygen might have to travel in trees when the roots or even the basal regions of the trunk have been inundated has led to speculation that internal oxygen transport may be insufficient to maintain viability in remote organs (Crawford, 1976). This may well be so (see below) but in such circumstances anaerobic metabolism is apparently equally insufficient to sustain the root system.

Gill (1970) observes that few, if any, temperate species can survive an indefinite period of partial inundation and it is interesting to note (D. D. Hook, personal communication) that even the roots of the Swamp Cypress may die back to near the trunk if the mature tree is submerged by flood-waters to a depth of 100–150 cm. Root activity recommenced in *Taxodium* by the production of new lateral roots which had their origin close to the trunk.

Secondary and adventitious root development in trees is a common response to soil flooding and there is every reason to suppose that these roots are aerated internally. Hook *et al.* (1970, 1971) found that swamp tupelo and water tupelo developed new lateral roots when inundated and these new roots oxidized their rhizosphere under anaerobic conditions, whereas the initial roots failed to do so. The newly formed roots differed from the initial ones in anatomy, rates of anaerobic respiration, and their ability to tolerate high concentrations of carbon dioxide in the flooded soil. Adventitious tree roots formed in response to flooding can be strongly aerenchymatous in the primary cortex (personal observation); they emerged from trunk lenticels which are themselves grossly hypertrophied with loose aerenchymatous tissue (Gill, 1970). Similar roots produced by cuttings receive oxygen by internal longitudinal transport (Armstrong, 1968) and will oxidize reduced media (Leyton and Rousseau, 1957). Extensive tracts of fused hypertrophied root and trunk lenticels within the soil and immediately above it are a common feature in Lodgepole Pine, one of the more wet-tolerant members of Pinaceae. The lenticel material is exceptionally hydrophobic and must ensure

Plate III. Pea: primary root apices: transverse and longitudinal appearance of cortical gas-space—plants grown in a nutrient 1% agar. (1)–(3), transverse sections at 30 μm, 90 μm and 4–5 mm from the root/root cap junction (magnification × 117·5, × 92·5, and 62·5); gas-spaces already visible in the differentiating cortex in (1). (4) and (5), radial longitudinal sections at extreme apex (magnification × 82·5), and at 0·2 cm from the apex (magnification × 67·5). Non-tortuous spaces extending for several cell lengths may be seen in both sections. The impression gained is that gas-space tortuosity is relatively slight in these roots.

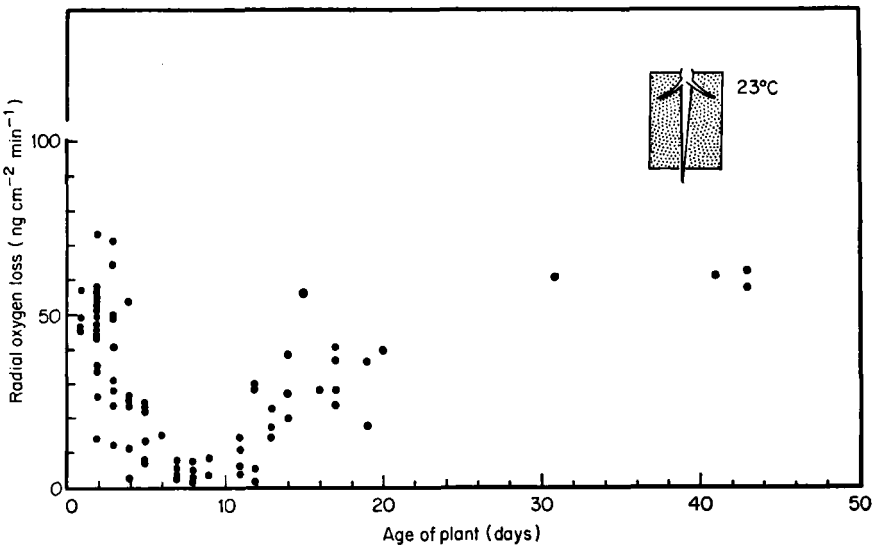


Fig. 19. Oxygen transport in the primary root of Pea: oxygen flux from the root apex as a function of plant age at 23°C. Roots jacketed in agar and laterals intact. After Healy (1975).

the gas-phase continuity between plant and soil atmospheres whenever the level of free water allows. Gas-phase continuity between root lenticels and gas-spaces in the root apices has been demonstrated by Coutts and Phillipson (1978a). There seems little doubt that the major sites of oxygen entry to the submerged roots of woody plants are the lenticels. Both Hook *et al.* (1971) and Armstrong (1968) have shown that obstruction of lenticels halts rhizosphere oxidizing activity and radial oxygen leakage from the roots. The unsubmerged lenticels lying closest to the water table will normally be those most closely involved with the aeration of the root system (Section II.C.2); it seems most unlikely that leaves will directly influence the aeration process unless they abut the water table or are submerged beneath it.

The diffusion path from lenticel to root apex is still somewhat uncertain (Hook *et al.*, 1972; Coutts and Armstrong, 1976): it probably very much depends upon species and age. Submergence experiments (Armstrong, 1968) suggest that the adventitious roots of cuttings may rely chiefly on transport in the secondary stem cortex but there are indications that in relatively wet-tolerant species gas-filled elements of the xylem might form a major route in the mature plant. Specialized xylem aerenchyma of secondary origin occurs infrequently (Arber, 1920) but extensive zones of unspecialized but gas-filled elements can form within the maturing secondary xylem of both Angiosperms and Gymnosperms.

Oxygen entering the xylem must cross the cambium and recent research shows that adequate gas-space continuity across the cambium may be a feature which characterizes only the more flood-tolerant of woody species (Hook and Brown, 1972). Effective porosities will normally be exceedingly low and longitudinal diffusive resistance correspondingly high if an impervious cambium and water-filled xylem confine longitudinal oxygen movements to the narrow secondary cortex of the woody stem and root. It has recently been suggested that the deeper penetration of waterlogged soil by Lodgepole Pine (LP) is due to internal oxygen transport in the stele; Coutts and Phillipson (1978b) found that the actively growing roots of LP would penetrate the water table to a depth of 20 cm at 10°C whereas Sitka Spruce (SS) made only shallow growth; they also found (1978c) that LP roots effect a greater degree of rhizosphere oxidation. Gas-filled elements are a more characteristic feature of the LP and gas-filled cavities in the secondary tissues of the pericycle were evident in those pine roots which penetrated the water table. These cavities which were absent from the spruce connected ultimately with the lenticels above the water table.

The roots of actively growing cuttings of LP and SS also react to soil flooding in a manner which suggests that aeration in the two species differs and is a major factor determining the responses (Coutts and Phillipson, 1978a, b): the responses varied with the period of waterlogging, temperature and depth below the water table (Fig. 20). Waterlogging for a period of seven days at 15°C killed all of the root apices in SS but 60% of the pine root tips survived. When the flood period was extended to 28 days only 38% of the pine root tips survived but dieback extended a relatively short distance from the apex. In spruce the only root tissues to remain alive were within 3 cm of the water table. A lower temperature (6°C) reduced dieback in both species but the greater tolerance of LP was still evident. Root regeneration from solution culture anoxia and phytotoxin treatments is also consistent with differences in the internal aeration of the species (Sanderson and Armstrong, 1978) and oxygen diffusion studies at low temperature confirm that LP is the better aerated (Sanderson, 1977). It is interesting to note however that the root apices of *Taxodium distichum* which produced primary root aerenchyma can survive a 100 μg cm^{-3} acetic acid treatment in which the apices of LP are killed; the roots of the strongly aerenchymatous herbaceous species *E. angustifolium* will even continue to grow under these circumstances but the response in pea parallels that of the SS and regeneration is by adventitious root production. Sanderson and Armstrong (1978) have summarized these observations as part of a more generalized scheme outlining the possible relationship between ventilating power and response to soil waterlogging (see Fig. 21).

Wall permeability in the tree root decreases markedly as secondary tissues develop (Sanderson, 1977) and in large organs such as mature tree roots

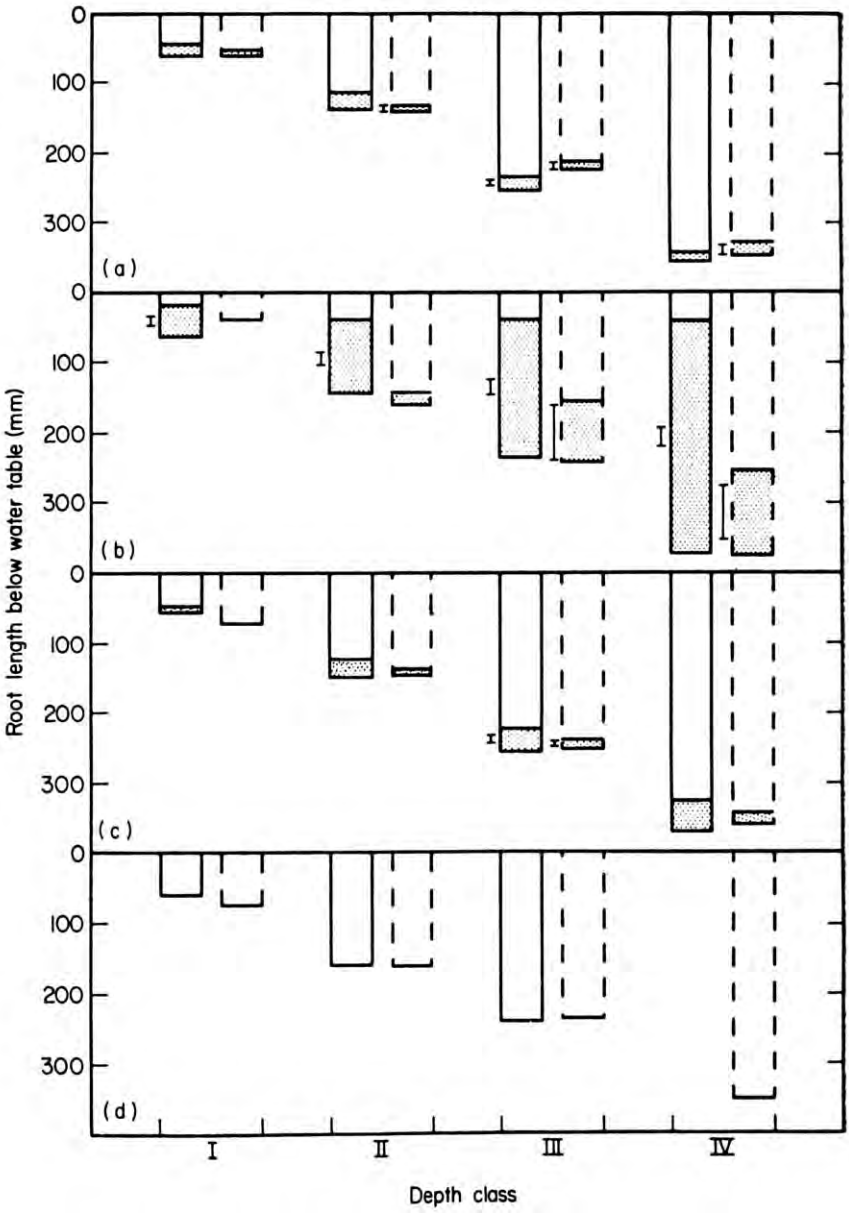


Fig. 20. Sitka Spruce (SS) and Lodgepole Pine (LP) after flooding of the soil: the dieback and survival of roots at different depths below the water table. The data are grouped into four depth classes along the horizontal axis; class I represents the mean of all roots extending 0–100 mm below the water table, class II, 101–200 mm, class III, 201–300 mm; and class IV, 301–400 mm. Four treatments (a–d) are represented. (a) Growing roots, 15°C, 7 days; (b) growing roots, 15°C, 28 days; (c) growing roots, 6°C, 28 days; (d) dormant roots, 6°C, 28 days. The left-hand column of each pair is Sitka spruce (solid columns), the right-hand, Lodgepole Pine (dashed columns). The stippled portion represents the mean extent of dieback; the unstippled portion, the length of root surviving. The vertical bars are the standard errors of the mean length of dieback, where they are of sufficient size to be represented. After Coutts and Phillipson (1978a).

lateral leakage to the soil should have little effect upon the aeration process (p. 301). Porosity, tortuosity and respiratory activity should be of major importance. The greater penetration of anaerobic soil by LP at 10°C than at 20°C (Coutts and Phillipson, 1978b) is consistent with a reduced respiratory demand and enhanced oxygen transport at the lower temperature. By substitution in equation (34) it is possible to make some tentative predictions concerning the aerated path length in woody organs. If the gas-filled parts of the xylem contribute to the internal diffusive path (Coutts and Armstrong, 1976) effective porosities might rise to 60% or greater in mature trees and if so, the overall respiratory demand will be relatively low, perhaps 10 ng cm^{-3} s^{-1} or even less. In these circumstances we find predicted an aeration path of 250 cm or greater. This is hardly adequate for the aeration of laterally spread root systems if the roots are completely inundated, but it might in appropriate circumstances make possible a sufficient anchorage of trees in wet soils. To maintain tree stability it is necessary for the roots to penetrate deeply. If gas-filled xylem abounds, substantial sinker root development might be possible from beneath the bowl or, (water table permitting), from the large laterals of the primary root system. The increasing proportion of gas-filled elements in the xylem of maturing LP could be responsible in part for its deeper rooting on wet sites when at the pole stage and beyond. Conversely, the serious losses from windthrow where Sitka Spruce has been used for afforesting wet sites (Fraser and Gardiner, 1967) may be attributed to, among other things, the relatively small proportion of gas-filled elements in the xylem. It is interesting to note that when sinker roots develop in wet soils they can be strongly carrot shaped (see p. 303).

Dormancy may help submerged roots to survive a period of flooding (Coutts and Philipson, 1978b). However, it would seem that to survive frequent inundation during non-dormant periods the laterally spread root system will require an internal oxygen path which by-passes the stem. In the mangrove *Avicennia nitida* snorkel-like lateral roots are produced (Scholander *et al.*, 1955). A single tree may produce several thousand of these; 20–30 cm high, 1 cm thick, soft and spongy, studded with numerous lenticels, they project from the mud and aerate the submerged radially spreading main roots. The "knees" of the Swamp Cypress may function similarly although Kramer *et al.* (1952) have cast some doubt on this.

In a section dealing with tree aeration it would be inappropriate if something was not said concerning internal aeration and mycorrhizal roots since these are of such particular importance in forest tree nutrition. The mycorrhizal fungi are strongly aerobic organisms and in ectotrophic associations can account for >50% of total respiratory demand. The bulk of the ectotrophic fungus lies outside the root and in aerated soils is undoubtedly oxygenated from the soil; indeed the mycorrhizal rootlets are a feature of the more aerobic soil horizons. Those hyphae which enter the root occupy the inter-

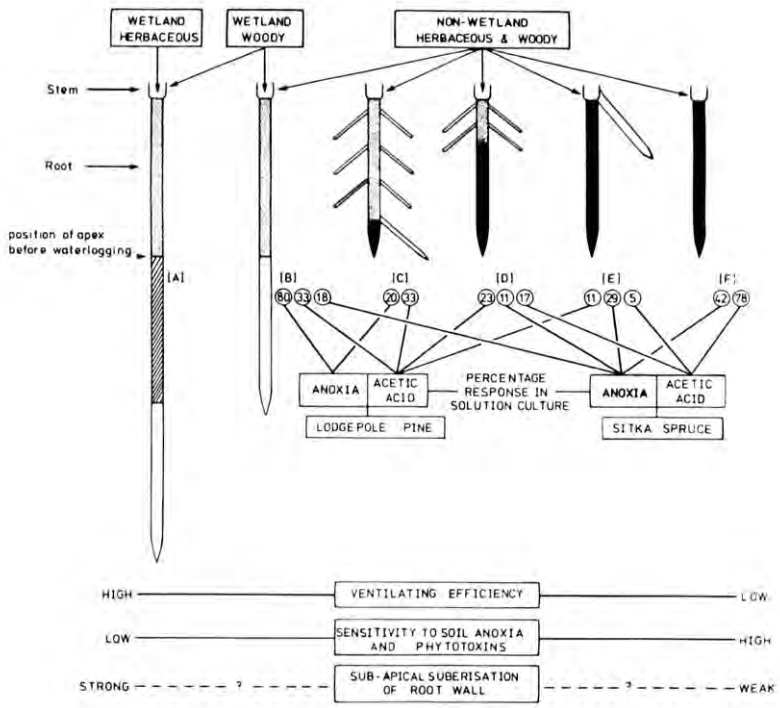


Fig. 21. Suggested relationship between internal root ventilation and the responses of wetland and non-wetland plants to a limited period of soil waterlogging. Root growth before and during, and regrowth after the end of, the waterlogged period is indicated as follows: before (and surviving) *dotted*; before but killed by the waterlogging *black*; during *shaded*; regrowth *white*. The figure also records how Sitka Spruce and Lodgepole Pine respond when exposed for a limited period to anoxia or to acetic acid (100 ppm) in solution culture. NB. Mature woody roots may at times substitute for the stem in the above scheme. After Sanderson and Armstrong (1978).

cellular spaces of the outer cortex and form what is called the Hartig "net". This must reduce oxygen diffusivity in the rootlet and although there is no direct supporting evidence we must suppose that it will adversely affect aeration of both root and fungus under conditions of submergence. Likewise, endotrophic mycorrhizal fungi must hinder the internal ventilation process in anoxic soils. Internal longitudinal oxygen transport can sustain mycorrhizal fungi in anoxic agar culture (Read and Armstrong, 1972) but it is perhaps unfortunate that the only experiments so far performed were with conifer seedlings where the internal diffusion path was short. In the same series of experiments it was found possible for the first time to induce ectotrophic "mantle" formation artificially on internally aerated Si-roots. These were introduced into an agar medium containing fungal macerate and the other essential growth factors. It is my opinion that this result could be open to

misinterpretation: it most probably indicates that mantle formation is a phenomenon requiring a point (radial) source of one of the essential growth factors upon which the other essential growth factors can impinge. In the field situation the roles will be reversed, the carbohydrates and vitamins will form a point source diffusing from the rootlet while the oxygen normally in surplus will diffuse in radially from the soil.

V. ROOT AERATION IN THE UNSATURATED SOIL

Whilst we now recognize that internal ventilation is a not insignificant property of mesophytic species, equally well do we recognize it as generally insufficient to sustain the activities of the extensive root systems found in unsaturated soils: in these circumstances its role is essentially supplementary to the radial movements of gases which can take place.

However, despite the gas-space continuity of soil and aerial environment and the maintenance of appreciable oxygen concentrations within the soil atmosphere, root aeration in the unsaturated soil is not always adequate: critical configurations of soil structure, water distribution and oxygen demand can combine to cause oxygen stress in both root and soil (see below).

The supplementary role of internal transport can be analysed only by resort to relatively complex mathematical or analogue techniques (see (3) below). However, with a knowledge of relevant soil and root diffusion characteristics it is possible to utilize relatively simple diffusion equations to assess the sufficiency of root aeration by the soil path.

1. The Soil Path

The effectiveness of the soil path is determined by numerous factors: its structural characteristics, the distribution of water, the distribution and respiratory activities of the microorganisms and the distribution, internal diffusivity, diameter and oxygen requirements of the roots themselves.

So far as aeration is concerned two primary structural soil types may be recognized: where sand predominates and the pore space follows a normal distribution the soils may be regarded as homogeneous; more generally, however, the soils contain some clay, their primary particles aggregate into distinct units and the pore-space distribution is strongly heterogeneous. In these soils distinct zones of relatively fine crumb pores are separated by a more continuous system of larger intercrumb pores (Currie, 1961a).

Since water offers a considerable resistance to diffusive gas exchange, soil structure affects root aeration chiefly by its influence on water distribution. In the homogeneous soil gas-space continuity throughout the pore space is established even at low suctions (Currie, 1961b): 80% or more of the pore space system of sand will drain at 10–20 mb suction and a single plateau plot of suction versus saturation is obtained. Consequently, diffusion to

depth in these soils will usually occur freely throughout the pore system with roots and microorganisms always closely adjacent to the soil atmosphere. The final stage of the diffusion path will be a relatively uncomplicated function of the water-film thickness around the root and the effective overall soil porosity within the water film. The microorganism respiratory component might be small enough to be ignored and on this assumption Kristensen and Lemon (1962) modified and combined the two diffusion equations (27) and (47) to describe root aeration by the soil path and to predict the limiting thickness of water film at which the root just remains wholly aerobic. The equation is:

$$\log \frac{a}{b} = \frac{D_e}{2D_i} - \frac{2D_eC_0}{Ma^2} \tag{68}$$

where a is the root radius (cm);

b is the critical radial distance from the centre of the root to the air–water interphase between the bounding water film and the soil atmosphere (cm) at which the root remains just wholly aerobic;

D_e is the effective diffusion coefficient for oxygen within the liquid film ($D_{O_2/H_2O}\tau\epsilon$) ($cm^2\ s^{-1}$) (NB for thin films the tortuosity factor will be effectively zero);

C_0 is the equilibrium oxygen concentration in the water film where it adjoins the soil atmosphere ($g\ cm^{-3}$);

D_i is the overall effective radial oxygen diffusion coefficient of the root ($cm^2\ s^{-1}$); and

M is the rate of root oxygen consumption ($g\ cm^{-3}\ s^{-1}$).

The equation is a useful one if a true value can be assigned to D_i: it would now seem that the value chosen by Kristensen and Lemon ($8 \times 10^{-6}\ cm^2\ s^{-1}$) might be substantially in error except at low temperatures and Greenwood has suggested a figure of $1{\cdot}2 \times 10^{-4}\ cm^2\ s^{-1}$. A more conservative estimate, $7 \times 10^{-5}\ cm^2\ s^{-1}$, is calculable on the basis of the COP data given earlier, assuming an effective root wall thickness of 35 μm.

Choosing this figure and considering a root of radius 0·035 cm, then if C_0 is $8 \times 10^{-6}\ g\ cm^{-3}$, $M = 2 \times 10^{-7}\ g\ cm^{-3}\ s^{-1}$ and D_e is $1 \times 10^{-5}\ cm^2\ s^{-1}$ (i.e. $D_0\epsilon$ where ϵ is 0·44: Kristensen and Lemon, 1962) we obtain a value of 0·0276 cm for the "critical" path length (water film thickness: b − a). This contrasts with the figure of 0·001 cm estimated by Kristensen and Lemon. Further estimates for different values of a, M and C_0 are shown in Table III together with values for the critical root radii under these conditions calculated from equation (68). Clearly, root radius is of major importance in aeration by the soil path and in contrast with the wetland condition the narrower the root the less likely is it to be made anoxic. However if we extrapolate from the data of Kemper and Rollins (1966) we find that water film thickness rarely exceeds 6×10^{-4} cm at suctions greater than 20 mb. Consequently,

unless waterlogging occurs or microorganism activity within the water films is found to be too great to be neglected, we can, for homogeneous soils, predict adequate aeration in all roots narrower than the critical radius. The intercrumb pores of the heterogeneous soil occupy up to 60% of the pore space system and, like the homogeneous soil, drain at extremely low water sections, < -10 mb (Currie, 1961b). Accordingly, the atmosphere within the intercrumb pore space is characterized by high concentrations of oxygen: Currie has suggested that intercrumb concentrations $< 15\%$ O_2 will be a rarity. Conversely the fine crumb capillaries drain much less easily and, at suctions less negative than field capacity, the crumbs can remain water-filled. At field capacity (pF 2·0) the crumbs will begin to empty, albeit slowly, and the bimodal nature of the system is confirmed by a double-plateau plot of suction and % soil saturation (Currie, 1961b). Since the saturated soil crumb is a respiring unit oxygen will decline in concentration inwardly from its surface as a function of respiratory demand and diffusivity. The saturation, narrowness and tortuosity of the capillaries are synonymous with low diffusivity and hence despite the high gas-phase oxygen levels of the intercrumb pore space there is a tendency for centres of anaerobiosis to develop within the wet crumb (Currie, 1961a; Greenwood and Goodman, 1967 and Appendix 2).

Currie (1965) obtained diffusivity values, (D_{CR}/D_0), for dry crumb material which ranged from 0·025 to 0·156 where crumb fractional porosities lay between 0·25 and 0·41; such values are indicative of the considerable tortuosity of the crumb capillaries. When translated into diffusivity for wet crumbs at 23°C we get $D_{CR} = 0{\cdot}025 \times 2{\cdot}267 \times 10^{-5}$ and $D_{CR} = 0{\cdot}156 \times 2{\cdot}267 \times 10^{-5}$ i.e. $0{\cdot}56 \times 10^{-6}$ cm^2 s^{-1} to $3{\cdot}54 \times 10^{-6}$ cm^2 s^{-1} where D_{O_2/H_2O} is $2{\cdot}267 \times 10^{-5}$ cm^2 s^{-1}. When fitted into the Currie:Greenwood equations describing crumb aeration (see Appendix 2) we find that for spherical crumbs the critical crumb radius (i.e. the maximum radius at which the crumb is just wholly aerobic) ranges from 0·023 cm to 0·59 cm where crumb respiration lies between $5{\cdot}27 \times 10^{-8}$ g cm^{-3} s^{-1} and $5{\cdot}27 \times 10^{-10}$ g cm^{-3} s^{-1} (i.e. 4×10^{-5} ml O_2 ml^{-1} s^{-1} and 4×10^{-7} ml O_2 ml^{-1} s^{-1}). Since aggregates >4 cm diameter are by no means uncommon (Smith, 1977) anaerobiosis might often be considerable within some unsaturated soils and phytotoxins may accumulate; however it is of interest to note that as the volume of anaerobiosis within the aggregates increases so too will the oxygen content of the intercrumb pore space because of the overall reduction in oxygen consumption.

Just as it was possible to calculate critical water film thickness in the homogeneous soil type we can readily derive an expression to describe the diffusion to a root lying within respiring wet aggregates if we assume these to be cylindrical rather than spherical: the particular solution required is the "critical thickness" of crumb material which will just bring the centre of the root to zero oxygen concentration. The problem is rather similar to that

TABLE III

Conditions Leading to Anoxia at the Centre of Roots in Non-aggregated Soil

(i) Critical soil water-film thicknesses, (b–a), at which roots would remain just wholly aerobic, predicted for various combinations of root oxygen consumption, M_R, and root radius, a (see equation 68). Root oxygen-diffusivity, D , 7×10^{-5} cm^2 s^{-1}; soil oxygen-diffusivity, D_e, 1×10^{-5} cm^2 s^{-1}; C_0, the solution oxygen concentration at the gas-liquid interphase in the soil on radius, b, either $8{\cdot}56 \times 10^{-6}$ g cm^{-3} (20·41 %) or $6{\cdot}18 \times 10^{-6}$ g cm^{-3}. (ii) Critical root radius, a_c, at which the root would be just wholly aerobic if the solution oxygen concentration at its surface was equal to C_0 (see equation 47).

	b–a (cm)					
	M_R 2×10^{-7} (g cm^{-3} s^{-1})		M_R 1×10^{-7} (g cm^{-3} s^{-1})		M_R 5×10^{-8} (g cm^{-3} s^{-1})	
a (cm)	C_0 $8{\cdot}56 \times 10^{-6}$ (g cm^{-3})	C_0 $6{\cdot}18 \times 10^{-6}$ (g cm^{-3})	C_0 $8{\cdot}56 \times 10^{-6}$ (g cm^{-3})	C_0 $6{\cdot}18 \times 10^{-6}$ (g cm^{-3})	C_0 $8{\cdot}56 \times 10^{-6}$ (g cm^{-3})	C_0 $6{\cdot}18 \times 10^{-6}$ (g cm^{-3})
0·01	$4{\cdot}85 \times 10^{1}$	4·52	$2{\cdot}53 \times 10^{5}$	$2{\cdot}19 \times 10^{3}$	$6{\cdot}9 \times 10^{12}$	$5{\cdot}22 \times 10^{8}$
0·02	$1{\cdot}38 \times 10^{-1}$	$6{\cdot}74 \times 10^{-2}$	1·325	$3{\cdot}9 \times 10^{-1}$	9·71	9·04
0·03	$4{\cdot}23 \times 10^{-2}$	$2{\cdot}55 \times 10^{-2}$	$1{\cdot}57 \times 10^{-1}$	$8{\cdot}04 \times 10^{-2}$	1·22	$4{\cdot}07 \times 10^{-1}$
0·04	$2{\cdot}35 \times 10^{-2}$	$1{\cdot}48 \times 10^{-2}$	$6{\cdot}85 \times 10^{-2}$	$4{\cdot}07 \times 10^{-2}$	$2{\cdot}76 \times 10^{-1}$	$1{\cdot}35 \times 10^{-1}$
0·05	$1{\cdot}55 \times 10^{-2}$	$9{\cdot}62 \times 10^{-3}$	$4{\cdot}23 \times 10^{-2}$	$2{\cdot}63 \times 10^{-2}$	$1{\cdot}33 \times 10^{-1}$	$7{\cdot}53 \times 10^{-2}$
0·06	$1{\cdot}08 \times 10^{-2}$	$6{\cdot}34 \times 10^{-3}$	$2{\cdot}98 \times 10^{-2}$	$1{\cdot}87 \times 10^{-2}$	$8{\cdot}46 \times 10^{-2}$	$5{\cdot}11 \times 10^{-2}$
0·07	$7{\cdot}61 \times 10^{-3}$	$3{\cdot}95 \times 10^{-3}$	$2{\cdot}24 \times 10^{-2}$	$1{\cdot}38 \times 10^{-2}$	$6{\cdot}11 \times 10^{-2}$	$3{\cdot}80 \times 10^{-2}$
0·08	$5{\cdot}14 \times 10^{-3}$	$2{\cdot}04 \times 10^{-3}$	$1{\cdot}73 \times 10^{-2}$	$1{\cdot}04 \times 10^{-2}$	$4{\cdot}79 \times 10^{-2}$	$2{\cdot}96 \times 10^{-2}$
0·09	$3{\cdot}13 \times 10^{-3}$	$4{\cdot}48 \times 10^{-4}$	$1{\cdot}35 \times 10^{-2}$	$7{\cdot}62 \times 10^{-3}$	$3{\cdot}79 \times 10^{-2}$	$2{\cdot}37 \times 10^{-2}$
0·10	$1{\cdot}43 \times 10^{-3}$	—	$1{\cdot}05 \times 10^{-2}$	$5{\cdot}36 \times 10^{-3}$	$3{\cdot}11 \times 10^{-3}$	$1{\cdot}92 \times 10^{-2}$
a_c	0·1095	0·093	0·1548	0·1316	0·2189	0·186

outlined in Section II. 7(c) except that at the boundary of the inner cylinder (in this case the root surface) respiration does not cease but changes in intensity. The respiratory characteristics of the root can be accommodated by specifying the critical oxygen pressure required at the root wall and defining the oxygen gradient at that point. Consider a root (radius = a) which lies at the centre of a cylindrical respiring soil crumb ($r > a$) in which respiration and pore space are homogeneously distributed radially. Let soil respiration be M and soil diffusivity be D_e, then from Section II. 7(c) we can write:

$$C = \frac{Mr^2}{4D} + A \log r + B \tag{69}$$

(equation 39, p. 257)

If $C = C_w$ on $r = a$, then

$$C_w = \frac{Ma^2}{4D_e} + A \log a + B \tag{70}$$

Suppose that $\frac{dC}{dr} = P$ at $r = a$, then from equation (38) we get:

$$P = \left(\frac{dC}{dr}\right)_{r=a} = \frac{Ma}{2D_e} + \frac{A}{a} \tag{71}$$

and therefore

$$A = \left(P - \frac{Ma}{2D_e}\right) a \tag{72}$$

Substituting for A in equation (70) gives,

$$C_w = \frac{Ma^2}{4D_e} + \left(P - \frac{Ma}{2D_e}\right) a. \log a + B \tag{73}$$

$$\therefore \quad B = C_w - \frac{Ma^2}{4D_e} - \left(P - \frac{Ma}{2D_e}\right) a. \log a \tag{74}$$

If C_w is the oxygen concentration at the root wall which will just maintain the root wholly aerobic, then substituting for A and B in equation (69) and solving the resulting form of (69) for r when $C = C_0$ we obtain

$$C_0 - C_w = \frac{M}{4D_e}(r^2 - a^2) + a \log \frac{r}{a}\left(P - \frac{Ma}{2D_e}\right) \tag{75}$$

where C_0 is the oxygen concentration at the outer surface of the soil crumb and r is the critical radius of the crumb cylinder. It may be noted that if M becomes zero the expression $M(r^2 - a^2)/4D_e$ disappears and we are left with equation (27) while if M is the same in both soil and root, the right hand

expression disappears and we are left with an equation which satisfies the boundary conditions $C = C_W$ and $dC/dr > 0$ on $a > 0$, and $C = C_0$ on $r = r$. When $a = 0$, $dC/dr = 0$ and the expression simplifies to equation (46).

In practice the oxygen gradient at the root surface, P, is given by the expression: flux/D_e where the flux is calculated from the root's respiratory rate and surface area, and D_e is the crumb diffusivity. Equation (75) is applicable both to "crumb" structured and homogeneous soil conditions but whereas in the homogeneous soil type our main concern is to predict critical film thickness ($r - a$), in the heterogeneous soil the critical aggregate diameter, $2[a + (r - a)]$ is the more important feature. The term $r - a$ is, in itself, of little relevance and indeed for comparative purposes can be highly misleading as reference to Table IV will show. The data in this table obtained by fitting various combinations of a, P, M and D into equation (75) (together with a C_0 value of $8{\cdot}56 \times 10^{-6}$ g cm^{-3}) indicate once again that in terms of $r - a$, narrowness of root is perhaps an advantageous feature in wet aggregated soils. However, when account is taken of the volume of aggregate occupied by the root itself the situation can be reversed. For example, when $D = 0{\cdot}56 \times 10^{-6}$ cm^2 s^{-1}, $M = 5{\cdot}27 \times 10^{-8}$ g cm^{-3} s^{-1} and $a = 0{\cdot}05$ cm, the critical aggregate diameter can be more than double that tolerated by the narrower root ($a = 0{\cdot}01$ cm). Only when D is higher ($3{\cdot}54 \times 10^{-6}$) and M lower (e.g. $5{\cdot}27 \times 10^{-10}$) do narrower roots achieve a significant advantage.

If soil aggregates much exceed a diameter of 1 mm there would seem to be a real danger of inadequate aeration in all roots having a radius $\leq 0{\cdot}05$ cm. However, if roots are sufficiently thick to occlude intercrumb pores this might effectively unite the surrounding aggregates into bigger units and cause problems of root aeration where crumb diameter is not obviously critical. Against this must be set the crumb draining powers of the roots and differences in aggregate shape: in spherical aggregates critical crumb diameter will be greater whilst the crumb draining activities of roots may be sufficiently rapid to prevent anaerobiosis being sustained for sufficiently long periods to cause injury.

The effects of introducing a respiratory term into the water film of the homogeneous soil types are also demonstrated in Table IV: critical water film thickness is very much reduced for the narrower roots but again there seems little likelihood of inadequate aeration if root radius is $\leq 0{\cdot}05$ cm.

2. Oxygen Flux in the Soil: Measurement and Interpretation

Since adequate root aeration in the unsaturated soil depends chiefly upon the characteristics of the final water-saturated stage of the diffusion path, an evaluation of conditions at the interface between the root surface and the soil system presents the greatest possibility of ascertaining the influence of soil aeration on plant growth. It was this rationale which motivated Lemon and Erickson (1952) to develop a polarographic method (the Pt-micro-

TABLE IV

Conditions Leading to Anoxia at the Centre of Roots in Aggregated and Non-aggregated Soil

Critical soil water-film thicknesses, r — a (cylindrical wet aggregates and non-aggregated soils), and critical diameter, 2 [a + (r — a)], of saturated cylindrical aggregates, for various combinations of soil oxygen consumption, M_s, root oxygen consumption, M_R, and soil path diffusivity, $D_{e(s)}$. Root radius, a, either 0·05 cm or 0·01 cm; C_0, the oxygen concentration at the gas-liquid interphase in the soil at radius r, taken as $8{\cdot}56 \times 10^{-6}$ g cm^{-3} (20·41 %). Data calculated using equation (75).

M_s (g cm^{-3} s^{-1})	$D_{e(s)}$ (cm^2 s^{-1})	M_R (g cm^{-3} s^{-1})	r — a where a = 0·05 cm (cm)	2 [a + (r — a)] where a = 0·05 cm (mm)	r — a where a = 0·01 cm (cm)	2 [a + (r — a)] where a = 0·01 cm (mm)
		2×10^{-7}	0·0007(5)	1·01	0·00153	0·303
	$0{\cdot}56 \times 10^{-6}$	1×10^{-7}	0·0017(2)	1·03	0·0087	0·374
$5{\cdot}27 \times 10^{-8}$		5×10^{-8}	0·0035(0)	1·07	0·0117	0·434
		2×10^{-7}	0·0047	1·09	0·034	0·88
	$3{\cdot}54 \times 10^{-6}$	1×10^{-7}	0·0107	1·21	0·036	0·92
		5×10^{-8}	0·0190	1·38	0·039	0·98
		2×10^{-7}	0·0007(7)	1·01	0·0060	0·321
	$0{\cdot}56 \times 10^{-6}$	1×10^{-7}	0·0017(5)	1·03	0·0156	0·512
$5{\cdot}27 \times 10^{-10}$		5×10^{-8}	0·0035(5)	1·07	0·0481	1·162
		2×10^{-7}	0·0050	1·10	0·1408	3·016
	$3{\cdot}54 \times 10^{-6}$	1×10^{-7}	0·0121	1·24	0·3046	6·29
		5×10^{-8}	0·0289	1·58	0·3904	8·00
		2×10^{-7}	0·0155		48·5	
Zero	1×10^{-5}	1×10^{-7}	0·0423	Not aggregated	$2{\cdot}53 \times 10^{5}$	Not aggregated
		5×10^{-8}	0·1330		$5{\cdot}22 \times 10^{8}$	
		2×10^{-7}	0·0143		0·0636	
$5{\cdot}27 \times 10^{-8}$	1×10^{-5}	1×10^{-7}	0·0291	Not aggregated	0·0686	Not aggregated
		5×10^{-8}	0·0439		0·0712	

electrode technique), for assessing the oxygen flux within the wet phase of the soil. The Pt micro-electrode comprises a short apical oxygen "sensor" of bare thermo-pure Pt-wire ($l \leq 1$ cm) which is embedded basally into a strong but narrow insulated rod where it fuses with a copper wire from the polarizing circuit (Armstrong and Wright, 1976b). Oxygen is "consumed" electrolytically at polarographic electrodes (p. 273) and when embedded in the soil the polarized Pt-wire micro-electrode, being dimensionally similar to a root apex, is in a sense analogous with the respiring root apex. However, whilst the root respires throughout its volume, electrode activity is a surface phenomenon: the oxygen concentration at the activated electrode surface is effectively zero but that at the root surface is always >0 provided that the effective diffusive resistance of the soil path is less than infinite. Consequently, the oxygen flux to an electrode will always be greater than to a root of equal radius lying within the same soil micro-zone. The flux at the micro-electrode surface will be the maximum possible flux to a cylindrical body of such dimensions at that particular location.

Although the Pt micro-electrode technique is a valuable agronomic and ecological tool and is widely used, it has been made very clear by McIntyre (1970) and others, that it must be used with a caution which has so far been noticeably lacking. Those wishing to use it should not neglect to study McIntyre's excellent review. A number of factors can interfere with the correct functioning of this technique; others can alter the current–voltage relations of the oxygen reduction process in a manner which is easily overlooked by those using fundamentally incorrect operating procedures. The use of constant applied voltage regardless of soil conditions is a procedure which can be particularly criticized: in poorly aerated or acidic soils plateau potentials become less negative; the fixed potentials in the range −0·6 to −0·8 V which have been employed by so many workers can then cause a reduction of H^+ ions in addition to oxygen. Because of this the literature abounds with suspect data.

The technique is at its most reliable in saturated conditions, and in well-drained aggregated soils appears to be applicable without complication only at moisture contents greater than field capacity (McIntyre, 1970). However, it could be argued that this is not a serious limitation since at tensions beyond field capacity aeration is much less likely to limit root activity.

Efforts to establish the critical oxygen flux for root growth from soil oxygen flux measurement have not unnaturally revealed enormous variation. To some extent this is due to differences in the oxygen requirements of the roots themselves: the flux requirement at the root wall is a function of root radius and respiratory demand and, as Table V shows, one may forecast a 40-fold increase in flux requirement (15–600 ng cm^{-2} min^{-1}) as root radius and oxygen demand are raised from 0·01 cm and 5×10^{-8} g cm^{-3} s^{-1} to 0·1 cm and 2×10^{-7} g cm^{-3} s^{-1}. However, there are other complicating

factors to be considered. These include the influence of electrode diameter, the use of inappropriate polarizing potentials, and aeration by the internal path (p. 305). As regards the polarizing potential McIntyre (1970) has suggested that the soil oxygen flux figure of 200 ng cm^{-2} min^{-1} claimed by some (Stolzy and Letey, 1964a, b; Letey and Stolzy, 1967) to be critical for most non-wetland species could be partly a result of H^+ ion reduction in nearly anaerobic media.

The effect of electrode diameter is such as to widen still further the range of soil oxygen flux which might be regarded as critical for root growth (see Table V). Consider a root of radius 0·1 cm and respiratory demand 2×10^{-7} g cm^{-3} s^{-1}; if the root lies within a water film (D_e, 1×10^{-5} cm^2 s^{-1}) of critical thickness $1{\cdot}43 \times 10^{-3}$ cm (Table III) the flux requirement of the root, 600 ng cm^{-2} min^{-1} will be satisfied. The Pt micro-electrodes most commonly used have diameters of 1·2 mm, 0·64 mm and 0·46 mm; if these electrodes were surrounded by the critical film thickness $1{\cdot}43 \times 10^{-3}$ cm the critical flux recorded (equation 27) would be 3634, 3671 and 3702 ng cm^{-2} min^{-1} respectively. At the other extreme (root radius 0·01 cm, respiratory demand 5×10^{-8} g cm^{-3} s^{-1}, and critical flux requirement 15 ng cm^{-2} min^{-1}) the same electrodes would register critical values of 2·6, 4·9 and 6·7 ng cm^{-2} min^{-1}. As electrode and root approach a common radius so does electrode flux more closely register the true oxygen availability to the root and hence there are good grounds for trying to match the electrode radius with some characteristic root radius of the plant species concerned. In aggregated soils the problem of diameter becomes even more acute and hence the matching of electrode sizes with characteristic root radii is almost a necessity.

3. Internal Oxygen Transport in an Aerated Soil

As soils drain, more and more oxygen will tend to enter roots via the soil path, and proportionately less will be provided by internal longitudinal transport from the aerial parts. The extent to which this will occur will depend chiefly upon the gas-phase oxygen concentration in the soil, upon soil diffusivity and metabolic activity in any saturated zone around the root, and upon root length, radius, pore-space resistance, and respiratory demand. Provided that the root is well within its critical radius, a_c (see Table III), and, in aggregated soils, the aggregates are not large or saturated, the soil path should predominate. However, as the following examples show, if aggregates remain saturated the internal path may continue to provide a significant proportion of the root's respiratory needs. These data were obtained using an electrical analogue suitably modified to simulate unsaturated as well as saturated soils. The introduction of a soil oxygen source made it necessary to devise new means for simulating soil sink activity and this was achieved by siting series of constant-current devices along the diffusion paths (diffusive resistances) between root and soil gas space; a digital-analogue-

TABLE V

Oxygen Flux at Pt-microelectrode When Surrounded by the Critical Soil-water Film Thickness Appropriate to Roots Having the Characteristics Shown

Predictions based upon an effective oxygen diffusivity of 1×10^{-5} cm^2 s^{-1} within the soil-water film and a solution oxygen concentration at the gas-liquid interphase in the soil of $8{\cdot}56 \times 10^{-6}$ g cm^{-3} (20·41%).

M_R	Root radius	Oxygen flux required at root wall	Observed flux at electrode lying within critical film thickness (ng cm^{-2} min^{-1})		
(g cm^{-3} s^{-1})	(cm)	(ng cm^{-2} min^{-1})	Electrode radius 0·06 cm	Electrode radius 0·032 cm	Electrode radius 0·023 cm
	0·01	60	12·8	21·9	29·2
2×10^{-7}	0·03	180	160	190·5	214
	0·05	300	372	406	433
	0·10	600	3634	3671	3702
	0·01	30	5·7	10·1	13·77
1×10^{-7}	0·03	90	66·6	90·4	108·5
	0·05	150	160	190	214
	0·10	300	530	565	593
	0·01	15	2·64	4·86	6·69
5×10^{-8}	0·03	45	27·9	43·7	55·9
	0·05	75	73	98	116·6
	0·10	150	205	236	261

TABLE VI

Root Aeration in Saturated and Unsaturated Soil

Comparative data compiled by electrical analogue simulation of a root (radius, a = 0·05 cm) lying within saturated soil aggregate (radius, b = 0·10 cm) such that the thickness of aggregate around the root is everywhere 0·05 cm (ie b – a). Other characteristics as follows: root length, 9 cm; $M_R = O_2$, 70 ng cm^{-3} s^{-1}, ie 33 ng min^{-1} cm^{-1}, ΣM_R = 297 ng min^{-1}; $D_{e\ (soil)} = 3{\cdot}54 \times 10^{-6}$ cm^2 s^{-1}; M_s = 5·27 ng cm^{-3} s^{-1}. Internal oxygen concentrations (a) and lateral oxygen exchange (b) across the root surface (influx, +; efflux, —), at the distances indicated (*) or (**) are given for the following circumstances: (i) no lateral transfer between root and soil—impermeable root wall; effective root porosity, 7%: (ii) soil acting only as an oxygen sink —fully permeable root wall; effective root porosity, 7%: (iii) soil oxygen-source (20·41%) introduced at aggregate boundary; effective root porosity, 7%: (iv) as for (iii) but effective root porosity, 5%.

Distance from root base (cm)		(i) a O_2 (%)	(i) b Lateral exchange (ng min^{-1} cm^{-1})	(ii) a O_2 (%)	(ii) b Lateral exchange (ng min^{-1} cm^{-1})	(iii) a O_2 (%)	(iii) b Lateral exchange (ng min^{-1} cm^{-1})	(iv) a O_2 (%)	(iv) b Lateral exchange (ng min^{-2} cm^{-1})
*	**	*	**	*	**	*	**	*	**
1	0·5	17·26	nil	16·68	—7·5	17·71	—1·7	16·89	—1·3
2	1·5	14·48	nil	13·43	—7·5	15·4	+0·6	13·97	+1·5
3	2·5	12·07	nil	10·60	—7·5	13·4	+2·2	11·45	+3·6
4	3·5	10·03	nil	8·2	—7·5	11·75	+4·0	9·39	+5·6
5	4·5	8·36	nil	6·24	—7·5	10·37	+4·9	7·72	+7·2
6	5·5	7·06	nil	4·76	—7·3	9·37	+6·0	6·44	+8·3
7	6·5	6·14	nil	3·73	—5·9	8·65	+6·9	5·55	+9·4
8	7·5	5·58	nil	3·08	—5·4	8·19	+7·1	5·01	+9·6
9	8·5	5·39	nil	2·85	—4·9	8·05	+7·6	4·83	+10·2

converter and display replaced the meters (Fig. 8a) of the original analogue system (E. J. Wright and W. Armstrong, unpublished).

Consider a root (length 9 cm, radius 0·05 cm, and oxygen demand, M_R, 7×10^{-8} g cm^{-3} s^{-1} (33 ng min^{-1} cm^{-1})), lying within saturated soil aggregates such that the thickness of aggregate material around the root is 0·05 cm: let the radial oxygen diffusivity of the aggregates, D_e, be $3{\cdot}54 \times 10^{-6}$ cm^2 s^{-1} and their rate of oxygen uptake, M_S, be $5{\cdot}27 \times 10^{-9}$ g cm^{-3} s^{-1}. If there was no leakage of oxygen between root and soil the root's respiratory needs would be met entirely by internal transport and the oxygen profile along the root could be readily computed from equation (30). For an effective root porosity of 7% the internal oxygen regime would be as shown in Table VI(i)a. If conditions were such that the soil behaved only as an oxygen sink (and there was no restriction on oxygen leakage through the root wall), internal oxygen transport would continue to fully support the root's respiratory requirements, but the oxygen regime would change to that in Table VI(ii)a. Radial oxygen loss to the soil would amount to 14·5% of that entering the root (Table VI(ii)b). The introduction of an oxygen source (20·41%) into the soil gas space, it is predicted, would modify the oxygen regime in the root to that shown in Table VI(iii)a. Oxygen leakage to the soil is now confined to the basal centimetre of the root. Thereafter the soil makes an increasing contribution to root aeration (Table VI(iii)b) but nevertheless, this does not exceed 13% of the total oxygen requirement. However, it can now be seen that the soil oxygen source is also acting as a buffer to the root's internal supply (see also p. 305).

A decrease in the effective porosity of the root increases the contribution made by the soil source: at an effective porosity of 5% the soil will provide *c.* 19% of the root's requirements (see Table VI(iv)b). A further lowering of porosity would lead to further increases in oxygen flux from the soil but whilst it might eventually provide the bulk of the oxygen consumed at this aggregate thickness it could never fully support the root's respiratory needs: root aeration would become inadequate as the effective root porosity approached 3%.

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APPENDIX 1. *The Transport of Diffusible Species in Media Moving by Mass Flow:* (a supplement to Section II.A.3)

(a) *The Complementary Condition*

Consider an idealistic model in which two planes X and Y within, of equal radius to, and normal to the long axis of, a water-filled tube P provide respectively, a source of diffusible species at constant concentration C_0, and an effective sink at a lower but constant concentration C_1. If water flows through P in the direction X, Y and at a constant velocity V, there will be the potential for diffusive as well as mass flow of diffusible species from X to Y, and the two processes will act in conjunction. If there is no lateral leakage of diffusate from P the differential equation for diffusion in one dimension can be written:

$$D\frac{\partial^2 C}{\partial^2 x} = V\frac{\partial C}{\partial x} + \frac{\partial C,}{\partial t} \tag{76}$$

where x is the space coordinate in the direction X to Y. The planes X and Y are given by $x = 0$ and $x = l$ respectively, and D is the diffusion coefficient of the diffusate in the water.

The time independent solutions satisfy $\partial C/\partial t = 0$, and have the form

$$C = A + Be^{\lambda x}, \tag{77}$$

where $\lambda = V/D$, and A and B are constants of integration to be determined for the boundary conditions $C = C_0$ on $x = 0$, and $C = C_1$ on $x = l$. The solution which satisfies these boundary conditions is:

$$C - C_0 = (C_0 - C_1)\frac{e^{\lambda x} - 1}{e^{\lambda l} - 1} \tag{78}$$

(equation 1, p. 240)

The diffusion rate per unit area (i.e. *the diffusive flux*) can be expressed as follows:

$$-D\frac{dC}{dx} = -BVe^{\lambda x} = \frac{V(C_0 - C_1)e^{\lambda x},}{e^{\lambda l} - 1} \tag{79}$$

Since the solutions are time independent we now use the ordinary differential notation and thus on $x = 0$,

$$-D\frac{dC}{dx} = V\frac{C_0 - C_1,}{e^{\lambda l} - 1} \tag{80}$$

and on $x = l$,

$$-D\frac{dC}{dx} = V(C_0 - C_1)\frac{e^{\lambda l}}{e^{\lambda l} - 1} \tag{81}$$

The *total flux* of diffusible species, the sum of *diffusive flux* and CV, is derived as follows:

$$\text{Total flux} = -B\text{V}e^{\lambda x} + \text{V}(A + Be^{\lambda x}) \tag{82}$$

$$= C_0 + \frac{(C_0 - C_1)}{(e^{\lambda l} - 1)}\text{V} \tag{83}$$

(b) *Diffusion and mass flow in opposition*

When the mass flow is negative the solution which corresponds with equation (78) is:

$$C = C_0 - (C_0 - C_1)\frac{1 - e^{-\lambda x}}{1 - e^{-\lambda l}} \tag{84}$$

where $\lambda = \text{V}/\text{D}$ as before. (equation 2, p. 240)

The *diffusive flux* is given by

$$-\text{D}\frac{dC}{dx} = \frac{\text{V}(C_0 - C_1)\,e^{-\lambda x}}{1 - e^{-\lambda l}} \tag{85}$$

and thus on $x = 0$

$$-\text{D}\frac{dC}{dx} = \frac{\text{V}(C_0 - C_1)\,e^{\lambda l}}{e^{\lambda l} - 1} \tag{86}$$

and on $x = l$

$$-\text{D}\frac{dC}{dx} = \frac{\text{V}(C_0 - C_1)}{e^{\lambda l} - 1} \tag{87}$$

Corresponding to (83), we have

$$\text{Total flux} = \text{V}\left(\frac{C_0 - C_1 e^{\lambda l}}{e^{\lambda l} - 1}\right) \tag{88}$$

(NB. Numerical solutions from equations (78) and (84) are plotted in Fig. 2.)

APPENDIX 2: *Radial Diffusion into Respiring Spherical Bodies*

Solutions describing the radial diffusion of gases within spherical bodies have been used extensively in connection with the aeration of soil aggregates (Currie, 1961a; Greenwood and Goodman, 1967). Spherical analogues of various of the solutions for radial diffusion into cylindrical bodies are given below and in each of these the spherical body is of radius $r = b$, and for all values of r, D_e is a constant.

(i) The spherical analogue of equation (49) is given by Currie (1961a) as

$$C_0 - C = \frac{M}{6D}(b^2 - r^2) - 2a^3\left(\frac{1}{r} - \frac{1}{b}\right) = \Delta r \tag{89}$$

where M is the oxygen uptake within the sphere ($\text{g cm}^{-3}\,\text{s}^{-1}$)

a is the radius at which aerobic respiratory activity ceases such that $dC/dr = 0$ on $r = a$, and $a > 0$. It is assumed that respiration is unaffected by oxygen concentration until extremely low values are reached and hence $C \approx 0$ on $r = a$.

C_0 is the oxygen concentration (g cm^{-3}) at the surface $r = b$.

C is the oxygen concentration at any radius r where $a \leq r \leq b$.

Δr is the oxygen deficit within the crumb at radius r.

(ii) The maximum radius at which the body is just wholly aerobic is given by putting $r = a = 0$ and is termed its critical radius b_c. The oxygen deficit, Δ_c, is then,

$$\Delta_c = \frac{Mb^2}{6D_e} = C_0 \tag{90}$$

(Currie, 1961a)

and is the spherical analogue of equation (47).
(iii) For all $b > b_c$ we get

$$\Delta_c = C_0 = \frac{Mb^2}{6D_e}\left\{1 - \frac{3a^2}{b^2} + \frac{2a^3}{b^3}\right\} \tag{91}$$

(Currie, 1961a)

which is the spherical analogue of equation (45).
(iv) If we combine equations (90) and (91) we obtain,

$$\left(\frac{b_c}{b}\right)^2 = 1 - \frac{3a^2}{b^2} + \frac{2a^3}{b^3} \tag{92}$$

(Currie, 1961a)

from which the fractional anaerobic volume can be calculated: at twice the critical radius 30 % of the sphere will be anaerobic; at four times the critical radius the figure rises to 60 % and when the radius is 10 b_c the anaerobic volume is 84 %. Currie (1961a) has noted that as the radius becomes very much greater than the critical value "the volume of the crumb which remains anaerobic becomes proportional to the surface area of the crumb", i.e. when $b \gg b_c$,

$$4/3\,\pi(b^3 - a^3) \rightarrow 4\,\pi\, b^2(b - a)$$

and

$$\left(\frac{b_c}{b}\right)^2 \rightarrow 3\left(1 - \frac{a}{b}\right)^2$$

(v) When $dC/dr = 0$ on $a = 0$ equation (89) simplifies to

$$C = C_0 - \frac{M}{6D_e}(b^2 - r^2) \tag{93}$$

(Currie, 1961a)

where $M(b^2 - r^2)/6D_e$ is the oxygen deficit between b and r. The cylindrical counterpart of this equation which has been given by Lemon (1962) is:

$$C = C_0 - \frac{M}{4D_e}(b^2 - r^2) \tag{94}$$

and defines the oxygen field within the cylinder, $r = b$, when M and D_e are distributed uniformly along r.

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NOTE ADDED IN PROOF

Since submission of this article the following relevant publications have appeared:

(*a*) *Starch metabolism*
Kaiser, W. M. and Bassham, J. A. (1979). *Pl. Physiol.* **63,** 105–108.
Mares, D. J., Hawker, J. S. and Possingham, J. V. (1978). *J. exp. Bot.* **29,** 829–835.
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(*b*) *Metabolite transport in intact chloroplasts*
Akamba, L. M. and Siegenthaler, P. A. (1979). *FEBS Letters* **99,** 6–10.
Flügge, U. I. and Heldt, H. W. (1978). *Biochem. Biophys. Res. Com.* **84,** 37–44.
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(*c*) *Ribulose-1,5-bisphosphate carboxylase regulation*
Heldt, H. W., Chon, C. J. and Lorimer, G. H. (1978). *FEBS Letters* **92,** 234–240.
Robinson, S. P., McNeil, P. H. and Walker, D. A. (1979). *FEBS Letters* **97,** 296–300.

(*d*) *Galactosyl transferase activity of chloroplast envelopes*
Dalgarn, D., Miller, P., Bricker, T., Speer, N., Jaworski, J. G. and Newman, D. W. (1979). *Plant Sci. Lett.* **14,** 1–6.

(*e*) *Amino acid composition of chloroplast envelopes*
Mackender, R. O. (1978). *Plant Sci. Lett.* **12,** 279–285.

(*f*) *Import of proteins into cell organelles*
Maccecchini, M. L., Rudin, Y., Blobel, G. and Schatz, G. (1979). *Proc. Nat. Acad. Sci. USA* **76,** 343–347.