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## The behaviour of plants in various gas mixtures

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The effects of the composition and pressure of the ambient gas mixture on the diffusive gas exchange of leaves, and the effects of carbon dioxide and oxygen on respiration and photosynthesis are described. When photosynthesis is limited by the rate at which carbon dioxide reaches the chloroplasts, the net rate of photosynthesis of many (but not all) plant species depends on the ambient oxygen partial pressure. The effect of oxygen may be principally to stimulate a respiratory process rather than to inhibit carboxylation. However, when photosynthesis is not limited by the carbon dioxide supply, this respiratory process seems to be suppressed.

The gas exchange of plant communities responds to the aerial environment in the way expected from measurements on single leaves, but the growth response to a given difference in gas composition is smaller than expected because of adaptation, notably in the ratio of leaf dry mass to leaf area.

It is concluded that the growth rate of higher plants in given illumination will be independent of the partial pressure of oxygen and of other gases likely to be used to dilute it, provided that the carbon dioxide partial pressure is so adjusted (probably to not more than 2 mbar (200 Pa)) that the rate of photosynthesis is not limited by the rate of diffusion to the chloroplasts.

### INTRODUCTION

As Mr Pirie has said in his introductory remarks, some of the first photosynthesis experiments were made by Priestley in the context of the recycling of mammalian excreta (see Loomis 1960). Priestley's thinking was hampered by the theory of phlogiston, but at least he had to contend only with gas mixtures at atmospheric pressure and with nitrogen always much the largest component. Presumably, the frame of reference for the present paper should include gas mixtures of any pressure and composition likely to be readily tolerated by man, as well as the somewhat modified mixtures that might be possible were men and plants separated, when the volume of gas associated with the plants would probably at least equal that associated with the men. So it will be inconvenient to provide the plants with gas partial pressures greater than those provided for the men, for whom pure oxygen, or oxygen with up to 5% carbon dioxide, at a total pressure of 130 to 340 mbar (13 to 34 kPa) have been mentioned as suitable (Latterell 1966; Pirie 1967).

Presumably, the artificial environment to be created is one in which plants are to thrive, so the effects of harmful gases will not be considered here. It is assumed that the plants will be well supplied with water and possible indirect effects of the water vapour content of the air on photosynthesis via the effect of transpiration rate on leaf water potential will not be discussed.

It is presumably desired to maintain rapid growth, so succulent plants, which grow only slowly, will not be discussed here, although their gas exchange is of great physiological interest.

We shall be concerned primarily with photosynthesis in the leaves of higher plants, but the requirements of the roots must be considered also. In principle, there is little difficulty in providing the roots and shoots with different gas environments, but this is probably unnecessary. Various estimates have been made of the minimum oxygen partial pressure required in the root environment for good growth. These range from 80 to 100 mbar (8–10 kPa) mentioned by Carr (1961) as the minimum suitable for many species in soil or water culture, down to 25 mbar (2.5 kPa) found by Williamson & Splinter (1968) to be adequate for roots of *Nicotiana tabacum* growing in mist culture. At the other extreme, 1000 mbar (100 kPa) oxygen has detrimental effects (Carr 1961; Stiles 1960). However, root metabolism presumably depends on the oxygen concentration within the tissue, which in turn depends on the rate at which the gas is being metabolized, the diffusion pathway and the concentration in the external medium. Currie (1971) considered diffusion in the porous medium in which the roots may be growing, and Luxmoore, Stolzy & Letey (1970) developed a theory of oxygen transport and use within the roots, including diffusion from the shoots, but the subject is much less well developed than that of the gas exchange of leaves and Carr's conclusion probably remains the one of most practical use in creating a root environment suitable for good growth.

To complete this introduction, the discussion that follows will be put into a practical context by anticipating the main conclusion. This is that the photosynthesis and growth of higher plants in given illumination will be independent of the partial pressures of oxygen and of other gases likely to be tolerated by man, provided that the carbon dioxide partial pressure is suitably adjusted. The justification for the inclusion here of a detailed discussion of gas exchange at sub-optimal carbon dioxide partial pressures, apart from its intrinsic physiological interest, is that maintenance of the optimum may be practically inconvenient. At the other extreme, detrimental effects of excess carbon dioxide on shoot growth are improbable until the partial pressure is in the order of 10 mbar (1 kPa) (Carr mentions 70 mbar (7 kPa)) and roots with adequate oxygen will tolerate 200 mbar (20 kPa) (Williamson & Splinter 1968). Partial pressures as large as this are probably intolerable to man.

#### DIFFUSIVE GAS EXCHANGE OF LEAVES

In ordinary air, the net rate of carbon dioxide uptake,  $F$  g cm<sup>-2</sup> s<sup>-1</sup>, during light-saturated photosynthesis depends on the rate at which carbon dioxide diffuses to the chloroplasts from the ambient air and on the rate of carboxylation at the chloroplasts. We shall be concerned with the effects of the composition and pressure of the gas mixture on the diffusion process.

The pathway (effective length  $L$  cm) for diffusion of gases (with a coefficient of diffusion  $D$  cm<sup>-2</sup> s<sup>-1</sup>) between the walls of the mesophyll cells of a leaf and an ambient gas mixture ('air') can be considered to provide a diffusion resistance,

$r_{aw} = L/D$  s cm<sup>-1</sup>. This can be subdivided (Maskell 1928) into a boundary layer resistance,  $r_{as}$ , between air and leaf surface, and a stomatal resistance,  $r_{sw}$ , between leaf surface and mesophyll cell walls. (So defined,  $r_{sw}$  includes small cuticular and intercellular components which we shall neglect for the present.) This concept is accurate enough for our purpose, but for more exact calculations it is necessary to allow for the fact that the diffusion is accompanied by mass flow of gas (Parkinson & Penman 1970).

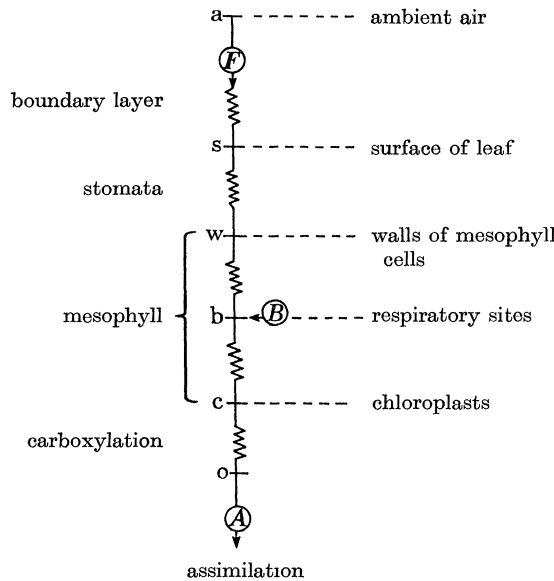


FIGURE 1. Electrical analogue of the carbon dioxide exchange of a leaf in bright light.

The pathway for diffusion in the cytoplasm between the mesophyll cell walls and the chloroplasts can be assigned a resistance,  $r_{wc}$ , in the same units as are used for diffusion in the gas phase. Finally, the inverse of the rate constant of the carboxylation process can be treated as an equivalent resistance to diffusion,  $r_{co}$ , as suggested by Maskell, and if the concentration of carbon dioxide beyond the carboxylation step is set at zero it follows from a simple series resistance electrical analogue (figure 1) that

$$F = \frac{\rho\phi_a - B(r_{bc} + r_{co})}{r_{as} + r_{sw} + r_{wc} + r_{co}} \text{ g cm}^{-2} \text{ s}^{-1}, \quad (1)$$

where  $\phi_a$  and  $\rho$  are the volumetric concentration and density of the ambient carbon dioxide. Note that  $\rho\phi_a = 10^{-3}\rho'p_a$ , where  $p_a$  is the partial pressure of carbon dioxide and  $\rho'$  is its density at 1000 mbar (100 kPa). The term  $B(r_{bc} + r_{co})$  allows for the effect of respiratory carbon dioxide entering the resistance chain at an intracellular site denoted by the subscript b.

Moss (1970) pointed out that, for plants in ordinary air in bright light, an upper limit to the rate of photosynthesis per unit leaf area is set by the denominator in

equation (1). Thus the smallest published values of  $r_{as}$  and  $r_{sw}$  for carbon dioxide are about 0.5 and 1.0 s cm<sup>-1</sup>, so that  $r_{aw}$  (min.)  $\approx$  1.5 s cm<sup>-1</sup> and for a plant with mesophyll and carboxylation resistances which are together  $\ll$  1 s cm<sup>-1</sup>,  $F$ (max.)  $\approx$   $0.7 \rho \phi_a = 150$  mg dm<sup>-2</sup> h<sup>-1</sup>. In practice,  $r_{wo}$  is not negligible and the greatest published values of  $F$  in ordinary air are about 100 mg dm<sup>-2</sup> h<sup>-1</sup> (Hesketh 1963), with more usual rates being in the range 20–50 mg dm<sup>-2</sup> h<sup>-1</sup> (Bull 1969). Useful lists of values of the various resistances for a range of plants are given by Bull, by Holmgren, Jarvis & Jarvis (1965) and by Laisk, Oja & Rahi (1970).

#### *Diffusion in the gas phase*

The partial pressure of carbon dioxide in a gas mixture of practical interest is unlikely to exceed 10 mbar (1 kPa) (1 mbar (100 Pa) is the value usually used in the glasshouse industry), so that, when the total pressure in the system is between 100 and 1000 mbar (10 and 100 kPa), the relative concentration of carbon dioxide will be negligibly small and its coefficient of diffusion will be independent of the properties of the diluting gas.

Nevertheless, there is experimental evidence to suggest that the nature of the diluting gas may affect the diffusion of gases during the anaerobic respiration of seeds (Latterell 1966) and during the aerobic (50 mbar (5 kPa) oxygen) growth of fungal hyphae (Schreiner, Gregoire & Lawrie 1962), but these phenomena are so far unexplained.

The boundary layer resistance of a fluid flowing over a plate of effective length  $d$  at a speed  $u$  is given theoretically by

$$r_{as} = (\eta d / \rho u)^{\frac{1}{2}} D^{-1} \quad (2)$$

where  $\eta/\rho$  is the kinematic viscosity.

Experimentally, for a leaf in air, Thom (1968) has found (his equation (16), rearranged)

$$r_{as} = 0.71(d/u)^{\frac{1}{2}} D^{-\frac{2}{3}} (\eta/\rho)^{\frac{1}{6}} \quad (3)$$

and this gives values of  $r_{as}$  which are 0.7 to 0.8 times those calculated from equation (2). Allowing for the effects of total pressure,  $P$ , on  $D$  and  $\rho$ , it follows from either equation that

$$r_{as} \text{ (air)} = r'_{as} \sqrt{P}, \quad (4)$$

where the prime refers to the value at a pressure of 1 bar (10<sup>5</sup> Pa).

The stomatal resistance depends simply on the inverse of the diffusion coefficient, so that

$$r_{sw} = r'_{sw} P. \quad (5)$$

However, stomatal resistance also depends on the composition of the gas mixture, as most stomatal movements, even the unusual ones observed in succulents (Neales, Patterson & Hartney 1968), can be explained, at least in part, by the hypothesis that stomatal closure increases with increasing intercellular carbon dioxide partial pressure (Meidner & Mansfield 1965; Heath & Mansfield 1969). There is no known effect of oxygen (Gauhl & Bjorkman 1969; Ludlow 1970) or of any other common gas.

*Diffusion in solution*

Although gases differ greatly in their solubility in water (Henry's Law constant for oxygen is 25 times that for carbon dioxide), their coefficients of diffusion in solution differ comparatively little. Diffusion in solution is much slower than in the gas phase. For example for carbon dioxide at 20 °C,  $D$  (in water)/ $D$  (in air) =  $1.1 \times 10^{-4}$ . By contrast with  $D$  (in air),  $D$  (in water) is nearly independent of the total pressure in the range 100 to 1000 mbar (10–100 kPa) at the gas/liquid interface, and this will have a bearing on our analysis of the effect of total pressure on photosynthesis.

The diffusion of carbon dioxide in water is complicated by the formation of bicarbonate ions. At pH < 4, carbon dioxide effectively acts as an inert gas, but at pH 7, the diffusion from the gas/liquid interface to a site in the liquid is enhanced by the concomitant diffusion of bicarbonate ion (Hoover & Berkshire 1969). With the enzyme carbonic anhydrase present (e.g. in leaf cytoplasm), the chemical equilibration between the dissolved gas and bicarbonate ion is greatly facilitated and the enhancement caused by bicarbonate diffusion is increased. Longmuir, Forster & Woo (1966) found that  $D$  in a solution buffered to pH 7.9 and containing carbonic anhydrase was 1.6 times  $D$  in pure water.

Given an appropriate value for  $D$  of carbon dioxide in cytoplasm the diffusion resistance,  $r_{wc}$ , between the walls and the chloroplasts of photosynthesizing cells, could be estimated from measurements of the relevant areas and distances (Rackham 1966; Laisk *et al.* 1970), but as the thickness of a chloroplast often exceeds the distance separating its surface from the cell wall, the estimate is likely to be less accurate than ones based on measurements of gas exchange via equation (1). However, the calculations of Laisk *et al.* make it plain that leaves with many small mesophyll cells will have a relatively small value of  $r_{wc}$  and gas exchange measurements by Wilson & Cooper (1970) confirmed this.

When a leaf is immersed in water, a liquid boundary layer is formed and equation (4) can be used to give an approximate estimate of the resistance to diffusion in this layer. It is remarkably great; e.g. for a given leaf in air or in water flowing at the same speed, the ratio of the resistances to the diffusion of carbon dioxide in the laminar boundary layers is  $r_{as}$  (water)/ $r_{as}$  (air)  $\approx$  3300. For small submerged plants or ones with greatly dissected leaves, and for thin roots,  $d$  in equation (4) may be small enough for  $r_{as}$  (water) to become more favourable for gas exchange, but even so, Bristow (1969) found that the finely divided leaves of submerged amphibious plants required a carbon dioxide partial pressure in the order of 10 mbar (1 kPa) for good growth. Many aquatic plants use bicarbonate for photosynthesis, but we are concerned here with the efficient recycling of carbon dioxide gas and it seems that, for this purpose, plants with submerged leaves, or even with floating ones, will be at a great disadvantage compared with those with leaves in air.

*The effect of pressure on leaf gas exchange*

As we have seen, diffusive resistance to leaf gas exchange depends on the total pressure of the gas mixture and it may be necessary to allow for this in estimating the effect of letting a given gas mixture expand from a small compartment containing men into a larger one containing plants, or more generally, to interpret experiments done at a total pressure of one atmosphere in the context of artificial environments where the pressure may be smaller, e.g. because nitrogen is not a component of the gas mixture.

To account for the effect of total pressure,  $P$ , on light-saturated photosynthesis, equations (1), (4) and (5) give

$$F = \frac{10^{-3}\rho' p_a - Br_{\text{bo}}}{r_{\text{as}}\sqrt{P} + r_{\text{sw}}P + r_{\text{wc}}}, \quad (6)$$

where the primes refer to values measured at 1 bar ( $10^5$  Pa). If the volumetric concentration of carbon dioxide is so adjusted that  $P_a$  is held constant when  $P$  changes, then

$$\frac{F}{F'} = \frac{r'_{\text{as}} + r'_{\text{sw}} + r_{\text{wo}}}{r'_{\text{as}}\sqrt{P} + r'_{\text{sw}}P + r_{\text{wo}}} = (\text{say}) \alpha^{-1}. \quad (7)$$

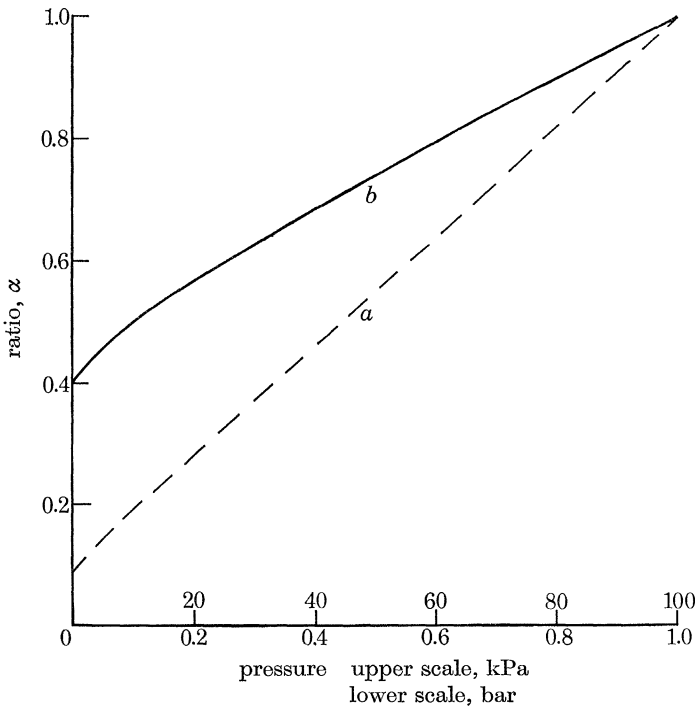


FIGURE 2. Effect of the total pressure,  $P$ , on the diffusion of carbon dioxide from the ambient air during photosynthesis. The ratio,  $\alpha = r_{\text{ao}}(P)/r'_{\text{ao}}$ , where  $r_{\text{ao}}$  is the sum of the diffusion resistances and the prime refers to the resistance at a total pressure of 1 bar ( $10^5$  Pa). Component resistances taken as:  $r'_{\text{as}} = 0.5 \text{ s cm}^{-1}$ ;  $r'_{\text{sw}} = 10.0 \text{ s cm}^{-1}$  (curve  $a$ ) or  $1.0 \text{ s cm}^{-1}$  (curve  $b$ );  $r_{\text{wo}} = 1.0 \text{ s cm}^{-1}$ .

When the liquid phase resistance is dominant, the effect of pressure is negligible; when the gas phase resistance dominates,  $r'_{sw} \geq r'_{as}$  in all practical cases and in the range 0.2 to 1.0 bar (20–100 kPa)  $\alpha$  is then nearly linear with  $P$  (figure 2).

Thus, if the nitrogen component is removed from ordinary air, leaving the partial pressures of oxygen and carbon dioxide unchanged,  $P$  becomes 0.21 bar (21 kPa) and photosynthesis is increased;  $F/F' = \alpha^{-1} = 3.4$  (curve *a*) or 1.7 (curve *b*) in the two examples of figure 2. However, if the composition of the gas mixture is unchanged, but the total pressure is decreased from 1.0 to 0.21 bar (100 to 21 kPa),  $p_a$  in equation (6) will change, and neglecting  $Br_{bo}$  as a first approximation, photosynthesis is diminished;  $F/F' = P/\alpha = 0.72$  (curve *a*) or 0.37 (curve *b*) in the two examples of figure 2. Gale (in the press) has done experiments at various pressures to simulate the effect of altitude on photosynthesis and transpiration. Using *Phaseolus vulgaris* and *Zea mays*, he demonstrated good agreement between measured and calculated effects of total pressure in the range 0.4 to 1.0 bar (40–100 kPa), but he gives insufficient details of his method of calculation for a comparison with the present analysis.

#### EFFECTS OF CARBON DIOXIDE AND OXYGEN ON RESPIRATION AND PHOTOSYNTHESIS

The rate at which carbon dioxide is lost from leaves by dark respiration is affected only slightly by the partial pressure of oxygen in the range 10 to 1000 mbar (1–100 kPa) (Forrester, Krotkov & Nelson 1966), although there may be detrimental effects when a large partial pressure is maintained for long periods (Stiles 1960). A small effect of carbon dioxide at partial pressures close to zero has been detected occasionally (*e.g.* by Forrester *et al.* 1966; Begg & Jarvis 1968), but the large effects of carbon dioxide, which are made use of in the so-called gas storage of fruits, are not encountered until the partial pressure is in the order of 100 mbar (10 kPa) (Stiles 1960).

It is not certain whether dark respiration persists during photosynthesis, but when carbon dioxide uptake is limited by the diffusion of carbon dioxide rather than by light, then in many, but not all, species of plants an additional respiratory process takes place, which is stimulated by oxygen. Dr Coombs will be discussing the group of 'Kranz-type' plants (Tregunna *et al.* 1970) in which this process has not been observed.

The oxygen-stimulated respiratory process is not detectable when the ambient carbon dioxide concentration is enough to saturate the photosynthetic demand, *i.e.* when light rather than the supply of carbon dioxide is limiting photosynthesis (Jolliffe & Tregunna 1968). When the illumination is increased a little, so that carbon dioxide is no longer saturating, the rate of net photosynthesis then responds to light, oxygen and carbon dioxide; an unsolved problem is to write equations that satisfy the measured response curves in this region. When the illumination is increased greatly, so that light is no longer limiting, equation (1) can be modified to



describe the interacting effects of oxygen and carbon dioxide then observed. Koller (1969) and others (reviewed in Jackson & Volk 1970) suggested that the effect of oxygen is not to stimulate respiration, but rather to inhibit the carboxylation process, but the most recent evidence seems to support the respiration hypothesis. Thus Mulchi, Volk & Jackson (1971) measured the effect of oxygen concentration on the rate at which labelled oxygen is taken up by leaves of *Glycine max* under conditions when there was no net carbon dioxide uptake (i.e. at the carbon dioxide compensation point,  $I'$ ) and their results have been replotted in figure 3 to show a linear relation.

Forrester *et al.* (1966) and others have shown that both  $I'$  and  $d\phi_a/dF$  (see equation (1)) also increase linearly with oxygen concentration, and a possible

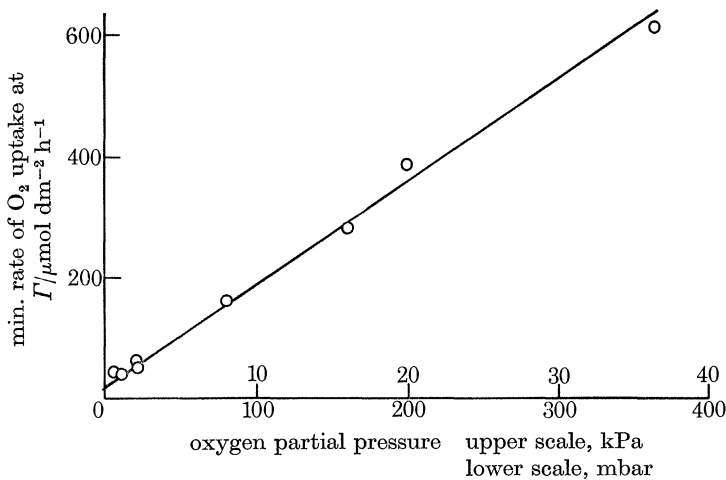


FIGURE 3. Effect of the partial pressure of oxygen on the rate of uptake of oxygen by a leaf of *Glycine max* in bright light. Carbon dioxide was at the compensation point,  $I'$ , (no net carbon dioxide exchange). Nitrogen brought the total pressure to 1 bar ( $10^5$  Pa). Plotted from measurements made by Mulchi *et al.* (1971).

explanation for all these phenomena is that during photosynthesis, in addition to the dark respiratory process (rate  $B_0$ ), a second respiratory process (rate  $B_1$ ) takes place that is linearly proportional to the gross rate of assimilation at the chloroplasts ( $A$  in figure 1), i.e.  $B_1 = \gamma A$  (Lake & Slatyer 1970), where  $\gamma$  depends (non-linearly) on the oxygen concentration. Then if all the respiratory carbon dioxide enters the circuit of figure 1 at position b, equation (1) becomes

$$F = \frac{\rho\phi_a(1-\gamma) - B_0r_{b0}}{r_{ab}(1-\gamma) + r_{b0}}. \quad (8)$$

The support for this reasoning, which differs somewhat from that of Lake & Slatyer, will be discussed more fully elsewhere; it is sufficient to note here that  $\gamma$  is often large (Lake & Slatyer found  $\gamma \approx 0.4$  for cotton leaves in ordinary air), but its effect is of no practical consequence if  $r_{b0}$  is small enough for the terms

containing it in equation (8) to be negligible. This is probably so in the Kranz-type plants, although it is also possible that in such plants  $\gamma$  is zero.

The failure of oxygen to affect the rate of net photosynthesis when there is an abundant supply of carbon dioxide may be accounted for by supposing that the supply of photosystem I reductant is used first to reduce carbon dioxide and only any remaining amount can be used for oxidation by oxygen (Mulchi *et al.* 1971). When photosynthesis is limited by light, i.e. by the rate at which reductant is produced, oxygen can have no effect.

It would be useful to know the relation between illumination and the ambient carbon dioxide partial pressure that just suffices to saturate photosynthesis, but few measurements have been made in very bright light. Hesketh (1963) showed that net photosynthesis of leaves of *Helianthus annuus*, *Zea mays*, *Nicotiana tabacum* and *Ricinus communis* in air (210 mbar (21 kPa) oxygen), and illuminated at about  $500 \text{ W m}^{-2}$  (wavelength 400 to 700 nm), increased with carbon dioxide partial pressure over the whole range up to 1 mbar ( $10^5 \text{ Pa}$ ). Brun & Cooper (1967) found that *Glycine max* responded in a similar way up to 1.7 mbar (170 Pa) carbon dioxide. At these values the response curves were beginning to flatten off, and one may conjecture that there would be little further effect beyond 2 mbar (200 Pa) if the total pressure in the system was 1 bar ( $10^5 \text{ Pa}$ ).

However, the conjecture is not fully supported by a consideration of the maximum possible rate of photosynthesis of Hesketh's maize leaves. If the energy associated with 1 mg of carbon dioxide assimilated was 10 J, if the photosynthetic efficiency was 0.2, close to the possible maximum, and if the leaf absorbed 85% of the incident light (400 to 700 nm), then  $500 \text{ W m}^{-2}$  should have given a carbon dioxide uptake rate of  $300 \text{ mg dm}^{-2} \text{ h}^{-1}$ , compared with the  $100 \text{ mg dm}^{-2} \text{ h}^{-1}$  measured by Hesketh, so at some stage factors other than light and carbon dioxide begin to limit net photosynthesis.

Hesketh's results are of direct relevance to our topic, as the intensity of the solar radiation just outside the Earth's atmosphere is near  $1400 \text{ W m}^{-2}$ , of which only one half is in the photosynthetically useful waveband, and the maximum fraction of this likely to be transmitted to the plants inside an extra-terrestrial transparent enclosure is about 0.8, giving  $0.8 \times 0.5 \times 1400 = 560 \text{ W m}^{-2}$ —close to the illumination used by Hesketh.

If, for some practical reason, the ambient carbon dioxide partial pressure,  $p_a$ , has to be increased beyond the value required to saturate net photosynthesis, the stomata will close in response to the increasing value of  $p_w$ , the intercellular partial pressure, and the question arises as to whether the photosynthesis will then slow. In the limit, with the stomata fully closed, gas exchange takes place through the leaf cuticle. The cuticular resistance to carbon dioxide transport has not been studied, but the resistance to water transport has been measured and ranges widely, with typical minimum values for plant species of temperate origin being around  $50 \text{ s cm}^{-1}$  (Holmgren *et al.* 1965). To make progress, we assume that this transport is by diffusion in the vapour phase and multiplying by  $D_{\text{H}_2\text{O}}/D_{\text{CO}_2} = 1.7$ ,

we get  $r_{\text{cuticle}} = 85 \text{ s cm}^{-1}$ . Then the value of  $p_a$  required to sustain a net rate of carbon dioxide uptake of  $150 \text{ mg dm}^{-2} \text{ h}^{-1}$  (half the theoretical upper limit) can be calculated from  $F \approx 10^{-3} \rho' p_a / r_{\text{cuticle}}$ , giving  $p_a = 18 \text{ mbar}$  (1.8 kPa). This is not great enough to cause known harmful effects on plants, except in so far as transpiration would be very slow, being limited to the cuticular rate, with unknown consequences to the plants but with possible significance for their management in an extra-terrestrial crop production system.

#### EFFECTS OF CARBON DIOXIDE AND OXYGEN ON GROWTH

It remains to consider whether the gas exchange and resulting growth of whole plants and plant communities responds to the ambient gas mixture in the way expected from experiments with single leaves. Almost all the published work on this has been done at atmospheric pressure and with nitrogen as the dominant component of the gas mixture.

In a community, the resistances to gas exchange of the individual leaves arranged above unit area of ground can be considered as being connected in parallel (as a first approximation) so that when the leaf area index exceeds unity, the equivalent resistance of the foliage is smaller than the resistances of the individual leaves. An expected consequence is that the increase in net photosynthesis in bright light, resulting from a given increase in ambient carbon dioxide concentration, should be greater for a community than it is for an individual leaf, and published results verify this. For example, the rates of net photosynthesis of a community of *Glycine max* (Egli, Pendleton & Peters 1970) and of a single leaf of the same species (Brun & Cooper 1967) increased respectively from 4 to 40 and from 2 to 20  $\text{mg dm}^{-2} \text{ h}^{-1}$  when the ambient carbon dioxide partial pressure was changed from 0.1 to 0.3 mbar (10–30 Pa). The results of Egli *et al.* also show how the rate at which a community transpires declines as ambient carbon dioxide concentration increases, presumably because of the effect of the intercellular concentration on stomatal aperture; carbon dioxide is the only known transpiration suppressant that enhances photosynthesis rather than diminishes it (Gale & Hagan 1966), and this may be of interest in the recycling of water in an artificial environment containing plants and men.

The effects of ambient carbon dioxide on the growth of horticultural plants are well documented and since about 1963 carbon dioxide enrichment to about 1 mbar (100 Pa) has become a part of commercial glasshouse practice (see, for example, Wittwer & Robb 1964; Krizek 1970), the chosen amount representing some compromise between the cost of supplying the gas and the extra crop growth expected as the response curve flattens out between 1 and 2 mbar (100–200 Pa). However, the gains in growth rate over a period of weeks are not always as great as expected from crop gas exchange measurements made over a period of minutes. The response of *Glycine max* will again serve as an illustration. Cooper & Brun (1967) sampled plants after 21, 38 and 92 days' growth in air with two concentrations of

carbon dioxide. After the first 21 day period the dry mass of plants at 1.35 mbar (135 Pa) carbon dioxide was 80 % greater than at 0.35 mbar (35 Pa), but thereafter the relative growth rates were nearly identical at the two concentrations. Thus adaptation to the carbon dioxide enrichment occurred and this was mainly in the form of an increase in the ratio of leaf mass to leaf area, offsetting any beneficial effect of the carbon dioxide on net assimilation rate. Nevertheless, much of the growth difference established during the first 21 days persisted and the seed yield was increased by nearly 60 %. Results of the same kind have been obtained with *Lycopersicon esculentum* (Hurd 1968) and with *Callistephus chinensis* (Hughes & Cockshull 1969).

The effect of oxygen on the gas exchange of whole plants has not been studied in any detail, but the effects on growth are consistent with leaf gas exchange measurements. Thus Bjorkman *et al.* (1967) grew plants of *Mimulus cardinalis* for 10 days in ordinary air and in air with the oxygen partial pressure diminished to 50 mbar (5 kPa), and their results show that the relative growth rates were respectively 0.18 and 0.24 g/day, an enhancement of 30 %, compared with the 40 % enhancement of leaf carbon dioxide exchange caused by a similar depletion of oxygen in a separate experiment (Bjorkman 1967). Bjorkman *et al.* (1969) showed that the effect of oxygen on growth lessened as the carbon dioxide partial pressure was increased from 0.11 to 0.64 mbar (11–64 Pa); this is consistent with leaf gas exchange measurements and the effect of oxygen could be expected to disappear when the carbon dioxide partial pressure was increased still further, to between 1 and 2 mbar (100 and 200 Pa). Also consistent with leaf gas exchange studies was the observation that the total dry mass increase of the Kranz-type species *Zea mays* showed no significant response to oxygen.

The measurements by Bjorkman *et al.* (1967) indicate that adaptation to oxygen depletion resembles adaptation to carbon dioxide enrichment, i.e. the leaves became thicker. There was also an increase in the ratio of the dry masses of roots and shoots and in the ratio of shoot dry mass to shoot fresh mass. These last two phenomena were detectable, surprisingly, in *Zea mays*.

#### CONCLUSION

The main technical conclusion has already been stated in the Introduction. It remains to emphasize that our knowledge of the subject is limited by the fact that most of the relevant research has been done in the context of the aerial environments encountered in terrestrial ecosystems. A discussion of the present kind provides a valuable stimulus to extend our vision.

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