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Symbiosis in the Ecosystem

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In 1935 Tansley[1] introduced the term "ecosystem" to comprehend the organisms, plant, animal and microorganism ; and the physical and chemical components of their immediate environment which together form a self-contained ecological entity. Ecosystems, in his view, tend to progress towards equilibrium wherever the factors at work are constant and stable enough for sufficiently long periods of time. He applied to ecosystems the expression " quasi-organism " which registered the fact that wherever conditions are the same and the same components are present, the same system will tend to reestatablish itself and progress in the same manner. It is perhaps one of the most important developments of modern ecology that the physiology of ecosystems is being actively studied.

The ideas behind such studies are relatively simple. The organisms of an ecosystem are classified according to their nutrition and physiological activities into groups like synthesizers, consumers, and decomposers. Inorganic substances enter the living part of the system as carbon dioxide, inorganic compounds of nitrogen, phosphorus, and sulphur and other essential elements, and are built by the synthesizers, mostly green plants, into their own body compounds. These form the food substrate for other organisms of the system which require organic carbon compounds, including amino acids, proteins or other preformed foods. In all stages in the consumption or decomposition of material initially produced by synthesis, carbon dioxide is released by the animals and heterotrophic plants such as fungi and bacteria. In the final stages, in addition to carbon dioxide, inorganic nutrients are released and may be reused by the synthesizers.

Although these processes are simple in outline they are very complex in detail and their study in quantitative terms is very difficult. It presents complex problems of definition, sampling and estimation. It has two essential aspects, quantity and rate of change. The first concerns the estimation of total of carbon, nitrogen and other substances present in various forms in both the living material and in the non-living phases of the system. The second requires the estimation of rates of absorption of substances into the living parts of the system, their rate of passage through complex consumption and decomposition cycles and their rates of release again in inorganic form.

Such investigations are so very difficult that detailed measurements have not yet been obtained for any land ecosystems, although good general estimates have been made in some cases. In this essay it is not proposed to review the subject of nutrient cycling itself but rather to consider some interesting close symbiotic relationships between heterotrophic and autotropoic organisms and their place in the physiology of ecosystems.

Forest Ecosystems

In forests, organic matter containing most essential elements for living organisms reaches the soil in large measure by the fall of leaves, stems, branches, bud scales, flower parts and by the abscission of roots. These are generally already attacked by microorganisms during their senescent phases, before they become detached.[2,3] These microorganisms, especially fungi and bacteria, bring about the early stages of degradation which are continued later by interaction in the soil by more diverse organisms, plant and animal. At first mineralization of the inorganic nutrients is slow especially in temperate climates. In the plant material carbon compounds are relatively plentiful but other nutrients are in relatively short supply because in the plant the skeletal matrix consists in large measure of carbohydrates such as cellulose. As a result the litter and highly organic horizons of the soil are regions where growth may be much limited by the availability of nitrogenous and other inorganic nutrients. In later stages of decomposition when much carbon has been utilized and carbon dioxide eliminated, the system including the bodies of the organisms becomes relatively richer in nutrients, and progressive mineralization accompanies decomposition. It is to be expected in climax communities which are approximately stable over long periods of time, that within one season the equivalent of the carbon in the materials returned to the soil in that period is eliminated as CO_2. The amount of organic matter which is present in the soil especially in the surface layers is not therefore an indication necessarily of the rate of breakdown. It is more an indication of the turnover rate of half-life of soil organic matter.

It has commonly been assumed that the soil is a region of intense activity of microorganisms especially in the horizons of high organic content. This arises in particular from the facts that very large numbers of many diverse species of fungi, bacteria, and actinomycetes may be isolated from it employing cultural procedures and that there appears to be a considerable reservoir of organic material within it. This last point is dubious because we have seen that the organic material is mainly in the process of breakdown rather than a reserve, even in temperate soils. The idea of large populations of microorganisms arises from the fact that most methods for their isolation do not distinguish between active organisms and dormant spores.[4,5] Hence most of the

methods used measure more the potential biological activity rather than the active biomass. The soil population of these microorganisms should be viewed in reality as consisting mainly of dormant spores and resting bodies ' lying in wait' for suitable substrates but given these, capable of great diverse activity.

The addition to a soil of a suitable substrate may call into activity a wide variety of dormant microorganisms which together in parallel or in series bring about decomposition.

This concept of the soil as a reservoir of potentially great biological activity but with a lower mean level of activity has been aptly emphasized by Gray and Williams.[6] They make two important points which have not previously received adequate stress.

First the amount of carbon falling as litter upon the soil, for instance in a forest ecosystem, is inadequate to maintain the growth of the apparently active heterotrophic organisms in that soil except on the average at a very slow rate. Secondly, the measured rate of CO_2 output from the soil may far exceed the apparent losses of carbon compounds from the soil estimated by analysis of litter disappearance. For example it would appear that Witkamp[7] and Rainers (1968) working in temperate forests were only able to account for about 60% and 30% respectively of the CO_2 emission from the soil by the carbon added to it as plant remains. A large part of the soil respiration must arise from some other source. Similarly Wiant[8] showed that even if CO_2 emission from a forest soil was assumed to continue at the lowest rate estimated during the year (0.20 g per M^2 per h) the litter fall would only maintain the rate for 136 days, not a full year. Such figures are so discrepant that if we were to suggest that they were due solely to errors of estimation of biomass or of CO_2 emission, it would be tantamount to calling into question the kind of evidence on which most of the existing ideas about carbon cycling are based. We must therefore look for other rational explanations whilst accepting that some degree of error is certain. Some have ascribed the excess of CO_2 production to the respiration of roots, but this does not seem sufficient to explain the large discrepancies.

One possible explanation is that there are particular sites where easily available supplies of organic compounds are present which are not derived from the fallen litter and abcised roots and on these active populations of microorganisms occur. The environs of plant roots, that is the rhizospheres and root surfaces of plants, seem to be possible examples of such sites.

The Rhizosphere

Rhizospheres contain numerically larger active populations of bacteria, actinomycetes, and fungi which differ from those of the rest of the soil both in number and in physiological type of microorganism. Measurements of various

chemical activities and concentrations of substances have led to the view that cellulose decomposition, nitrification, and solubilization of phosphate, release of simple nitrogen compounds and production of CO_2 may proceed faster in the rhizosphere due to the greater activities of the microorganisms.[9,10,11,12]

The explanation of this activity in the rhizosphere has been sought in the exudation of substances by roots, some of which may be of a vitamin or accessory nutrient nature and others may provide carbonaceous substrates. Indeed the study of exudations of roots, and the release of substances from them and from senescent root hairs, root cap cells etc., has shown them to contain a multiplicity of organic substances, carbohydrates, soluble nitrogen compounds, organic acids, vitamins and so on.[13]

Although the identification of the compounds has been possible, good estimates of their quantity have been difficult to obtain. Harmsen and Jager[14] give a table of values which are a little help. For instance vetch seedlings released the equivalent of 1.6 to 2.9 mg of carbon per 100 gms dry weight of root in six weeks when grown on soil. Gray and Williams[6] point out that this corresponds to the equivalent of 3.6% of the root mass in six weeks and must be a minimum because it is only that which has not been used by the rhizosphere microorganisms. In more recent work Dr D A Barber informs me that he has been able approximately to estimate the rate of exudation from young cereal roots in sterile conditions. In their first three weeks of growth, the rate of exudation may approach a quantity equal to 10% of the weight of the roots produced during the same period. He believes that Dr A Rovira in Adelaide has obtained rather similar rates. A very graphic impression of the amount of material released from the root cap is obtained from the work of Clowes.[15] He described the root cap of maize, which consists of about 10,000 cells, as being completely replaced by new cells every twenty-four hours. In addition the external cells of the cap secrete mucilage in the last stages of maturation which forms considerable interstitial layers between the cells[16] and constitutes an additional release of carbon to the substrate. The organic content of such exudates and sloughed cells serve to bridge the gap between measured CO_2 production from the soil and the estimated supply of carbon in the litter. But there is an additional more important bridge namely those mycorrhizal symbioses where the carbon currently fixed in photosynthesis by one of the partners supplies the needs of both.

Mycorrhizal Infection

The two commonest mycorrhizal infections are ectomycorrhiza (ectotrophic mycorrhiza) and vesicular-arbuscular mycorrhiza. In both kinds of infection fungal hyphae inhabit the root system and are connected to the mycelium in

the soil and in due season form fruit bodies within or upon the soil. The mycorrhizal fungi are known to intervene in the nutrition of their hosts and to derive carbon compounds from them. The extent of these interactions and their influence on carbon balance in the ecosystem as well as their effects on the growth of the photosynthetic partner are both considerable.

There has always been some doubt about the frequency and extent of mycorrhizal infections in natural conditions. They are indeed much more common than is often believed. For instance Dominik and Boullard[17] to take one example only, showed that 58% of all angiosperms in a single Fagetum were mycorrhizal and this agrees with the observation that most of the angiosperm families, all the gymnosperms and many of the pteridophyte group contain mycorrhizal species. To be more specific large numbers, perhaps most of the species of great forest trees of the world are mycorrhizal. Some, notably Pinaceae, Fagales, Eucalypts and some Dipterocarpaceae are ectotrophs. The remaining conifers and angiospermous trees have with few exceptions (amongst those examined) vesicular-arbuscular mycorrhiza. In addition vesicular-arbuscular mycorrhiza occurs in countless herbs and shrubs and it seems more usual for angiosperms and gymnosperms to be mycorrhizal than uninfected.

In the case of ectomycorrhiza there is strong experimental evidence for the direct supply to the mycorrhizal fungi of carbon from photosynthesis rather than from the soil. This has been summarized by Harley[11] and by Harley and Lewis[18]. Melin and his colleagues in an important series of papers showed that the fungi depended on simple carbohydrates and were not capable of using the lignin and cellulose of leaf litter and humus. Melin and Nilsson[19] demonstrated that during experiments of a few hours duration $^{14}CO_2$ provided to pine seedlings was photosynthetically fixed and ^{14}C labelled products translocated to the root system and out into the mycelium of the mycorrhizal fungus. Shiroya *et. al.*, Nelson[20] and Lister *et. al.*[21] and Reid[22] have performed similar experiments in some of which more ^{14}C labelled photosynthetic products were translocated per unit time to mycorrhizal root systems of *Pinus* than to non mycorrhizal ones. By a different method Lewis and Harley[23] showed that ^{14}C fed as sucrose to excised mycorrhizal roots of Fagus was translocated to the tip of mycorrhizas. After twenty-four hours some 60-75 percent of the sugar reaching the mycorrhizal apices had been incorporated into the fungal layer. Although the species of *Endogone* of endomycorrhizas have been shown to be selective in their absorptive physiology and not to be capable of growing in culture alone even when provided with soluble nutrients, simple carbohydrates and accessory factors, direct evidence for their being supplied from host photosynthesis has not yet been published. However in at least one laboratory experiment is in progress and seem to indicate a direct flow of photosynthate to the fungus.

It would seem therefore that respiration of mycorrhizal fungi must play an important part in the release of carbon dioxide from soil especially in natural habitats using current photosynthesis as a source of carbon.

Since the fungi involved in all these symbiotic unions are believed to be directly supplied with carbon from photosynthesis it is essential to make even a rough estimate of the quantities involved. Estimates based on ectotrophic mycorrhiza can be made in a number of ways and two examples are given in Table 1. Of the two separate estimates given, the first of these is based on a record of Romell[24] of the total dry weight of fruit bodies of the mycorrhizal fungus *Boletus bovinus* found in a spruce forest by I. Larsen. The second is based on the experimentally determined weight of fungal sheath and its respiratory CO_2 production. These two kinds of estimates are additive and must be taken together to give the order of magnitude of the drain on photosynthesis if the fungus were supplied with carbon by its host. There is in addition the mycelium, its maintenance growth and respiratory evolution of CO_2. A minimum conservative estimate might be of 500 Kg carbohydrate per hectare per year expended by the trees above of a beech forest, upon the mycorrhizal fungi and finding its way eventually to CO_2.

Tranquillini[25] made estimates of the carbon balance sheet in *Pinus cembra* woods in the Alps. Gasometric measurements showed that as much as 40% of the photosynthetically fixed carbon dioxide was unaccounted for and was believed to be lost as root exudates or used by mycorrhizal fungi (Table 2).

In addition, since so many of shrubs and herbs, as Boullard and Dominik[17] showed, also have vesicular-arbuscular mycorrhiza the total carbon dioxide evolution by all the mycorrhizal fungi in a woodland must be very great. Rough as the estimates must be with the present data, it is clear that it is likely to go some way to explain the discrepancy between carbon disappearing from leaf litter and humus and CO_2 release from the soil and merits further investigation.

Saprophytic Angiosperms

If the emphasis that has been put by Gray and Williams[6] on the relative lack of carbon to support the microorganisms of the soil and which has been elaborated above is credible, it would be expected that saprophytic angiosperms would be rare. In spite of this so called saprophytes are not uncommon. All Orchidaceae are non-photosynthetic during their early development and many lack photosynthetic equipment throughout life. In addition Gentianaceae, Monotropaceae, and Burmanniaceae and Triuridaceae and other families

contain examples of non-photosynthetic angiosperms. The bulky prothalli of *Lycopodium*, *Ophioglossum*, and Psilotaceae and the colourless bryophyte *Cryptothallus* are other examples of the same habit.

Nor are such so called saprophytes always small in size. Indeed some may be, like *Galeola hydra* described by Burgeff,[26] very large plants. All of them however are mycorrhizic and it has been assumed on much indirect experimental evidence that they, in contrast to ectomycorrhiza and vesicular-arbuscular derived their supplies of carbon via their mycorrhizal fungi from their substrates. The ability of *Dactylorchis purpurea* to absorb carbon in this way has been directly demonstrated by S. E. Smith.[27] This however does not solve the problem of the actual source of carbon under natural conditions. It is becoming progressively clearer that for such plants there are two possible sources commonly exploited.

The first was adumbrated by Kusano as long ago as 1911.[28] He showed that the orchid *Gastrodia elata* was associated mycorrhizally with the destructive fungal parasite *Armillaria mellea* through which it obtained nutrients including carbon from coniferous trees and other plants which *Armillaria* attacked and and parasitized. Burgeff[26] emphasized that the fungal symbionts of many tropical saprophytic orchids had the power of lignin and cellulose destruction and since then several destructive plant parasites have been implicated in orchid mycorrhiza. Hence they may well exploit resistant carbon sources of dead or living plants before incorporation in the soil. Ruinen[29] further showed that orchids epiphytic on living trees were connected with their hosts by fungal hyphae and their activities diminished the vigour of the host. In these examples therefore the organisms concerned were not dependent on the carbon compounds of the humus layer of the soil but upon carbon of living or dead hosts obtained by them by parasitic on destructive fungi.

The second mode of nutrition of saprophytes was demonstrated by Björkman[30] and later work has suggested the probability that it may be quite widespread.[31,32] Björkman showed that *Monotropa hypopithys*, a saprophyte shared a mycorrhizal fungus with *Picea* or *Pinus* under which it grew. ^{14}C-labelled glucose injected into the tree was translocated via the fungus to *Monotropa* plants 1-2 metres away. The experimental results indicated that *Monotropa* is essentially parasitic on the tree for carbon via the hyphae of the common mycorrhizal fungus.

Since Björkman's observations, a series of papers by Campbell has emphasized the complexity of these problems and the existence of the two forms of nutrition in saprophytes. In the genus *Monotropa* in America Campbell[33] found *Monotropa uniflora* to be associated with the parasite *Armillaria mellea* yet

Monotropa hypopithys was associated with a mycorrhizal fungus of neighbouring trees. However the latter association was not so harmonious as was implied by Björkman's work in Sweden because the cortical cells of the roots of the trees were short lived. Campbell's other work further illustrates the variability in metabolic behaviour both between and within genera of 'saprophytes'. In the genus *Gastrodia* in New Zealand,[34,35,36] *G. Cunninghamii* and *G. sesamoides* have mycorrhizal fungi which are parasitic on the hosts *Nothofagus* and *Acacia* respectively, but in *G. minor* the fungus is associated mycorrhizally, as in *Monotropa hypopithys*, with the host *Leptospermum*. The situation is similar in some ways in species of *Corallorhiza*[33] in Michigan where the mycorrhizal fungi were either weak parasites of tree roots or described as mycorrhizal with them. In *Yoania*[37] the fungus *Lycoperdon perlatum* once again seems to be both mycorrhizic with the host, *Beilschmiedia tarari* and also with the rhizome of the orchid, as in *Monotropa hypopithys*.

In any event these nutritive relationships serve to emphasize the dependence of many 'saprophytes' on living hosts via fungi mycorrhizal or parasitic on them, not dependent on humus or litter. These facts then fall into place when viewd alongside the observations of Gray and Williams.[6]

The Movement of Carbohydrates between Symbiotic Partners

In the saprophytes which we have been considering there is in most cases a visually obvious means by which substances could be transferred from the mycorrhizal fungus to its host. This is the destruction or digestion of the hyphae within the cells. This is an analogous process to that in which a necrotrophic fungal parasite destroys the cells of its host and absorbs their contents. The process of digestion in orchids and other saprophytes differs in the fact that the host cells may again be colonized by hyphae and destroy them a second or a third time. It has been described as parasitism of the fungus by the higher plant.[38] It is unlikely that this process is the only mode of interchange of material in such cases. Unlikely because in other examples of mycorrhiza, especially ectomycorrhiza, no digestion regularly takes place yet organic material moves from host into the fungus and inorganic materials from fungus into the host. In addition, in vesicular arbuscular mycorrhiza where digestion of the fungus occurs, carbon is believed to move from host to fungus rather than in the reverse direction.

Recent thoughts and experimental work on this problem have brought into juxtaposition a number of different kinds of symbiotic association in respect of the movement of carbon compounds between photo-synthesizing host and biotrophic partner[39]. Smith *et. al*[40], have emphasized the mechanistic

similarity of the carbohydrate movement between the partners in ectomycorrhiza, obligate fungal parasites (e.g. Erysiphales and Uredinales) and Lichens. In each case a particular photosynthetic product seems to move to the heterotrophic partner and to be built into a peculiarly fungal product such as an acyclic sugar alcohol (e.g. mannitol) or trehalose or glycogen. In biotrophic associations of other kinds, parasitic angiosperms and host, invertebrates and algae (e.g. corals) similar factors and indeed sugar alcohols play a part.

Indeed mutualistically symbiotic or biotrophic association of autotrophic and heterotrophic partners are common and widespread and it is becoming clear that their physiology is mechanistically similar. The mutualistic symbioses are especially developed in conditions of nutrient deficiency-mycorrhizas in deficient soil, coelenterate and algal symbioses in tropical waters, nitrogen fixing symbioses in pioneer and nitrogen deficient situations and lichens in barren habitats. All these are expected adaptations either to the direct use by heterotrophic biotrophs of carbon compounds currently fixed in photosynthesis, as in ectomycorrhiza, vesicular-arbuscular mycorrhiza, obligate parasites, corals and other coelenterates or the direct use of the carbon of resistant plant structures bipassing the processes of gradual breakdown by association with appropriate organisms as in higher plant saprophytes, ruminants, and many arthropods.

The Effect of Rhizosphere Organisms on their Hosts.

The populations of rhizosphere organisms and the mycorrhizal associates of roots are not only nourished by their host but also occupy a position in regard to them which may affect the availability and the rate of absorption of nutrients from the soil.

The rhizosphere populations have been extensively investigated over the last seventy years and their general features are well described. By and large they contain many organisms with special nutritional requirements for substances which are available in the products of living roots but not in the soil in general. They affect growth of their hosts sometimes in a positive sometimes in a negative manner. This arises from the balance of two sorts of circumstance. Many of the kinds of reaction detailed above which occur at increased rates in the rhizosphere, may increase the availability of nitrogenous, phosphatic, and other essential plant nutrients. On the other hand since the requirement of the microorganisms for trace elements as well as macronutrients is in broad lines similar to that of the host, they may in deficient circumstances successfully compete for these. The well known work of Gerretson[41] illustrates the possibility that rhizosphere organisms can increase phosphate availability. Yet

in some of his experiments this very increase of soluble phosphate seemed to diminish host growth by causing a deficit of available iron. By contrast Gerretson[42] and Timonin[43] showed that rhizosphere organisms might exacerbate manganese deficiency. Recent work using controlled experimental methods in solution culture[44,45,46,47] have served to illustrate the complexity of the effects of rhizosphere organisms and it is clear that broad generalizations of their effect on nutrition cannot be made.

In addition the rhizosphere and root surface populations have been shown to have a significant effect on disease incidence. As a result of much work since the 1920's, biological antagonism within the zone of the rhizosphere has been shown to exert some natural control over the spread of disease organisms. For instance it was early shown that the susceptibility of hosts to disease was highest in artificial sterile conditions and might be greatly diminished by the presence of normal soil populations[48]. The whole subject has been reviewed more recently in The Ecology of Soil-borne Plant Pathogens[49].

Mycorrhiza and nutrient absorption

The effects of mycorrhizal fungi upon nutrient absorption from the soil has been much more clearly characterized and defined. From the latter half of the nineteenth century for almost a hundred years there have been many experimental demonstrations that mycorrhizal infection, both ectotrophic and vesicular-arbuscular, may increase the growth of the host[11]. When this happens it is not always clearly realized that the activity of the fungal symbiont must affect some factor which is limiting the growth of the host. The majority of the host plants are quite capable of growing well uninfected provided that they are given appropriate cultural conditions. For instance food plants like maize, onion and tomato are grown for crop production in highly fertilized soils and develop well without mycorrhiza but there are good experiments to show that in nutrient deficient situations mycorrhizal plants of these very species grow much faster. The same is true for forest trees. Young trees grow perfectly well uninfected in artificially fertilized situations but in natural woodland soils infected plants develop well and uninfected plants poorly[11, 50].

The conclusion is therefore drawn that the fungi of ectomycorrhiza and vesicular-arbuscular mycorrhiza intervene in nutrient absorption. If one is seeking to explain the relative advantage of the mycorrhizal habit that has led to its persistence since Devonian times to the present day and its presence in so many plants one must seek it in the nutrition of the two partners. The fungi limited in their growth rate by carbon supplies escapes from the stagnation so

common to other soil organisms by extracting photo-synthetic products from their hosts. The hosts limited by inorganic nutrient supply for which they compete with soil organisms and with rhizosphere organisms in particular, obtain them from the mycorrhizal fungi.

To explain how the mycorrhizal infection improves nutrient supply to the host, the mechanism of absorption has been investigated using the same kinds of experimental method that have been used with roots[11]. By and large the same factors affect the process of absorption in much the same ways as they affect the absorption by other plant organs. Absorption of nutrients by mycorrhiza is dependent on the maintenance of normal metabolic processes within them. The rate is associated with respiratory turnover so that low oxygen supply, low carbohydrate concentration, low temperatures, metabolic inhibitors and the like diminish it. Rates of uptake are concentration dependent as are those of roots. Two points of difference from non-mycorrhizal roots have been demonstrated. The first is that the primary destination of absorbed material is into the fungus, in which considerable accumulation of absorbed inorganic nutrients may take place. The second is that the rates of uptake of nutrients by mycorrhizas is very often much greater than by uninfected roots.

These findings raise further problems which have been investigated to some degree.[18] The mechanism by which ions, accumulated in the mycorrhizal fungus, are released and shared with the host tissues has only been investigated in the case of phosphate in ectotrophic mycorrhizas. Phosphate is, perhaps the world over, the most conspicuous major nutrient which is deficient in natural habitats. It is the one whose uptake has so far been found to be most affected by mycorrhizal infection. Baylis in New Zealand[51] has pointed out that many native forest plants of that country are so conspicuously phosphate deficient in natural forest soils that they are unable to grow unless mycorrhizal. In the case of the European *Fagus sylvatica* not only are mycorrhizas several times more active in phosphate uptake per unit area than uninfected roots but also the fungus may pass accumulated phosphate to the host by a mechanism which is metabolically dependent. Similar mechanisms have not yet been successfully sought in the case of vesicular-arbuscular mycorrhizas although accumulation in the fungus has been demonstrated, nor has evidence yet accumulated on the mechanism of absorption of other nutrients than phosphate.

Three features go far to explain the high uptake rates of mycorrhizal systems. These are (1) that the fungus may modify the root system so that the extent of the absorbing surface is relatively increased, (2) that the hyphae which emanate

from the mycorrhizas into the soil are themselves an additional absorbing area in close physical contact with the soil, and (3) that the fungi themselves have a high avidity for nutrients and perhaps a potential for bringing them into solution.[38]

It is not proposed here to elaborate further on the nutritive activities of mycorrhizas which have been satisfactorily reviewed in the references already given and elsewhere. An important recent development is the demonstration that mycorrhizal fungi by virtue of their dominance in the root region and of their antibiotic activity play a part in the resistance of their hosts to disease. The possibility was emphasized by Zak,[52] and Marx and Davy.[53] Marx[54], has recently reviewed the later developments of this subject and has demonstrated experimentally the potential of ectomycorrhizas in this regard. The full importance of this process of antibiosis especially in the increase of efficiency of absorption by mycorrhizas by antagonism of competitors as well as disease organisms has not yet been demonstrated. Lewis[38] has attempted to put the problem in its context within the ecosystem.

Nitrogen Supply and Symbiosis.

Let us now turn to the question of the supply of nitrogen in the soil system. We have mentioned that inorganic nitrogen and other nitrogenous nutrients are released gradually from plant material in the later stages of decomposition when the ratio of carbon to nitrogen in the system has fallen. In the earlier stages in the decay of leaf litter, nitrogen deficit may limit the growth of microorganisms and animals so that an exogenous supply will increase this activity and so accelerate decomposition. Moreover the contention of Gray and Williams[6] that rates of growth of soil microorganisms are restricted by carbon availability is likely to apply with equal force to heterotrophic nitrogen fixation. Aerobic nitrogen fixing organisms, such as *Azotobacter* require much soluble organic matter because their rates of respiration are very high and hence the process of nitrogen fixation may be very inefficient with respect to carbon consumption.

As is well known such heterotrophic nitrogen fixers are not the only source of nitrogen compounds. Nitrogen fixation is more directly linked with photosynthesis in photosynthetic bacteria, in blue green algae and especially in nodulated angiosperms such as Leguminosae, *Alnus*, *Casuarina*, *Coriaria*, *Hippophae*, *Dryas*, and many others. These latter symbiotic systems are analogous to the mycorrhizal systems which we have been considering. The maintenance of the nodular tissue, the maintenance of the microorganism (bacterium or actinomycete) and the act of nitrogen fixation are all more or

less directly powered by photosynthesis. For instance in the experiments reported by van Schreven[55] additional light supply increased growth, nodulation, and nitrogen fixation per gram of nodular tissue, although excessive carbohydrate supply by sucrose addition and extra light diminished them.

The process of nitrogen fixation as well as the growth of the host plant are of course dependent on suitable inorganic nutrition as well as carbohydrate supply. It is therefore not unexpected perhaps that nodulated plants are often, perhaps nearly always, mycorrhizal in addition. This is certainly true of Leguminoseae where vesicular-arbuscular mycorrhiza has been reported in many of the herbaceous as well as in woody species. By contrast species of *Alnus* have ectotrophic mycorrhiza. There is no reason to doubt that the mycorrhizal infections of nodulated nitrogen fixing plants have a similar function to those of others. Asai[56] experimented with mycorrhizas of Leguminosae and showed reasonably convincingly that mycorrhizal infection stimulated nodulation and growth. Mejstrik and Benecke[57] described the ectotrophic mycorrhizas of *Alnus viridis* which forms nitrogen fixing nodules and showed that they had higher rates of phosphate uptake than uninfected roots.

We see therefore that the nodulated mycorrhizal plants may be adapted extremely well to habitats of low availability both of nitrogen and of other nutrients especially phosphate. An instructive example is found in glacial outwash gravels where symbiotic nitrogen fixers are of course conspicuous and species of Leguminosae and *Alnus* often play a pioneer role[12].

Conclusion.

In any ecosystem there is a gross cycling of carbon, from CO_2 fixed by autotrophic organisms through consumer and decomposer cycles which result in the release once again of carbon dioxide. In addition to this, there are tighter cycles of carbon utilization which involve, in the extreme cases, direct use of photosynthetic products by biotrophic heterotrophs. It is the burden of this essay to emphasize the potential importance in quantitative as well as in qualitative terms these tighter cycles. It has been shown, taking one example, that in terrestrial especially in forest ecosystems the tighter carbon cycle through mycorrhizal infections may afford an explanation of some of the discrepancies found in the study of their carbon turnover.

Many aspects of the subject have pointed to the need for knowledge of the mechanisms of interchange of material between symbiotic partners. This is not by any means an academic exercise for a number of reasons. Already there are clear indications that similar kinds of mechanism operate between partners of various mutualistic symbioses. Ectomycorrhizas, biotrophic

fungal parasites of green plants, coelenterates symbiotic with algae, and lichens have been shown in the papers of Smith *et, al.*[40], Harley[39], and in the works quoted by them to have carbon metabolisms which show many points of similarity. Comparative work will therefore have an important bearing on many ecologically and economically important subjects.

In the mutualistic symbioses the absorption of nutrients other than carbon is commonly the function of the heterotrophic partner. Hence the symbiosis is an adaptation to the absorption of nutrients by processes in the heterotroph powered by carbon compounds derived from the photosynthesis of the autotrophic partner. Diverse types of mutualistic symbiosis are therefore particularly adapted to nutrient deficient situations as are for instance the corals to trophical waters, mycorrhizal plants to deficient soils, and lichens to barren habitats.[50,11,12] It is common for angiosperms symbiotic with nitrogen fixing organisms, also to be mycorrhizic. In such cases the adaptation to habitats both deficient in nitrogen and other nutrients is quite clear and evident from ecological observations and involves tripartite symbiosis.

Finally it may be stressed that since mycorrhizal fungi are in general not closely specific it is possible that plants of different as well as the same species may be joined in a consortium by the mycelium of a common mycorrhizal species. This has been seen to occur in the case of the so-called angiosperm saprophytes which are parasitic in an indirect manner through a fungus which may be mycorrhizic or parasitic on a green host. The point was made by Lewis[50] that the cross nourishing of individuals by the same or different species having ectomycorrhiza or vesicular-arbuscular mycorrhiza through their common mycelium may also be possible and he quotes Reid and Woods[58] who demonsrated a carbon movement between individuals of *Pinus taeda* that were linked by a common mycelium.

All these considerations emphasize the possibility and importance of placing the results of experimental study of mutualistic symbioses in their ecological context.

PARTIAL ESTIMATES OF CARBOHYDRATE DRAIN ON HOST BY ECTOTROPHIC MYCORRHIZA

Based on sporophore formation. after Romell[24]

Spruce Forest

Dry weight *Boletus bovinus*	—	180 Kg/hectare/year
Carbohydrate required for formation	—	400 Kg/hectare/year
Equivalent volume of timber	—	1 m^3
Equivalent in medium quality spruce stand	—	10% of potential timber production

Beech Forest

Dry weight Fungal sheath of mycorrhiza	—	40% of dry wt. of feeding roots
CO_2 emission of this fungus	—	50% of CO_2 production of feeding roots
Feeding roots are	$\simeq$	10% of root mass
$\therefore$ Fungal Sheath	$\simeq$	4% of root mass
CO_2 from Fungal Sheath	$\simeq$	20-25% of total root CO_2
CO_2 emission per year (8-80 years) by Beech Root Systems	$\simeq$	500-900 Kg CO_2/hectare/year
CO_2 emission per year by Fungus	$\simeq$	100-250 Kg/hectare/year

(Based on Harley[11] and Möller *et. al.*[59])

PHOTOSYNTHESIS AND RESPIRATION IN PINUS CEMBRA

After Tranquillini[25]

All figures $MgCO_2$ per g dry weight of leaves.

Gross photosynthesis		7830 mg
Respiration in growing season :		
leaves	Day	1551 mg
	Night	556 mg
roots		447 mg
when snow covered		439 mg
Total loss per gram of leaf		2993 mg
Net synthesis		4837 mg
Equivalent dry weight of net synthesis		2.2 g/g leaves
Actual dry weight increment		0.65 g/g leaves
dry weight equivalent missing		1.65 g/g leaves

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