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For the purpose of this paper the term 'forest fauna' is taken to include both vertebrate and invertebrate forms. 'Nitrogen-fixing plants' are taken to be native leguminous plants with root nodules harbouring nitrogen-fixing organisms. It is accepted that there are other nitrogen-fixing plants, for example *Macrozamia reidlii* (Halliday and Pate 1976), *Casuarina* sp. and others, but these are not as widely distributed as the legumes and are therefore not treated in detail. Lastly, 'forest health' though it could be widely interpreted, is taken as referring primarily to the condition of the dominant tree species, the eucalypts, for it is these which essentially form the forest per se. In addition, this paper deals in particular with the dry sclerophyll jarrah (*Eucalyptus marginata*) forest of Western Australia.

## SUMMARY

Nitrogen is lost from the forest system during fires as a part of the natural process. It is believed to be returned largely by native legumes, the germination and development of which depends on fire. The type of fire, and the activities of animal grazers have a profound influence on germination and development.

The level of nitrogen in the system may influence sporocarp production in mycorrhizal fungi. These fungi are essential to maintain the health and vigour of the forest. Dispersal of the fungi is through the agency of mycophagous animals.

In recent times there have been changes to the forest ecosystem which may be affecting these natural processes. Thus the practice of regular and frequent cool prescribed burning for fuel reduction in the forest is reducing the legume component in the jarrah forest understorey. In addition the introduced fox has almost exterminated mycophagous animals in some forest areas. These two factors may affect the health and vigour of our forest ecosystem in the long term.

## LEGUMES, FIRE AND FOREST FAUNA

Australian forest soils are generally low in nutrients (Leeper 1970) and nitrogen is at a premium. Under such conditions, animals may select nitrogen rich foods (Leigh and Holgate 1979); indeed it has been proposed that the carrying capacity of the land, with respect to kangaroos and wallabies, may be defined by the amount of nitrogen fixed in the system (Main 1968). Grazing animals influence the survival of seedlings, in particular the nutritious legumes (Leigh and Holgate 1979). Both vertebrates, kangaroos, wallabies and wombats (Christensen 1977, Leigh and Holgate 1979, Oliver, pers. comm.), and invertebrates, principally native grasshoppers (Wheelan 1977), may be involved. As a consequence nitrogen rich leguminous plants are frequently under greater pressures from grazing animals than are other types of plants.

Fire is a natural factor in dry sclerophyll forest ecosystems such as the jarrah (Eucalyptus marginata) forests. Nitrogen is known to be released during fires. In the short term this is compensated for by an improved availability of nitrogen, the extent of which varies according to the degree of soil heating, the amount of ash produced, pH changes and other factors (Humphreys 1966, Raison 1976). In the long term, nitrogen-fixing bacteria in the roots of native leguminous plants appear to play an important role in maintaining the nitrogen status of the soil (Shea and Kitt 1976, Malajczuk pers. comm.).

The majority of native legumes possess 'hard seeds' which germinate most prolifically following fire (Christensen and Kimber 1975).

Under certain circumstances fire may compound the damaging effects of the herbivores (Wheelan 1977, Shea et al. 1979). The scrubby native legumes, unlike for example grasses, are not well adapted to grazing by herbivores, and the small seedlings are often damaged or destroyed. Thus following spring fires, which are generally of low intensity and germinate few legumes, the grazing pressure on the limited seedling resource may be extraordinarily high, resulting in the survival of very few seedlings (Wheelan 1977, Christensen 1977). Following fires of high intensity, when widespread prolific germination of seedlings occurs, grazing animals make little inroad on the vast germinant resource and a high proportion of seedlings survive (Christensen 1977).

The deleterious effects of low intensity fires are compounded because such fires have a tendency to burn unevenly, resulting in a mozaic of unburnt patches of understorey vegetation. Unburnt areas are known to provide a refuge during burns as well as centres from which populations of invertebrate grazers can rapidly expand following a fire (Wheelan 1977). Similarly the larger grazers, kangaroos and wallabies, utilize unburnt areas as refuges and centres from which to operate within recently burnt areas of forest. Under such circumstances grazing pressures may be at a maximum. Prescribed fires of low intensity occurring at regular and frequent intervals exaggerate these effects. Consequently, in areas under such a fire regime, we may expect the legume seed resource in the upper soil layers to become depleted over a period of time. There is some evidence that this is indeed occurring in the northern jarrah forest (Shea et al. 1979).

In the past, a natural balance between herbivores and leguminous plants was maintained by natural selection of adaptive traits which tended to reduce grazing pressures on these plants. One example is the common trait of hard-seededness referred to earlier. As a result of this trait, 'mass germination' of legumes occurs following intense fires. This has the effect of 'flooding the market' with food for the grazers, and ensuring that a high proportion of seedlings survive to maturity. In a similar manner the highly synchronized calving of species of African plains antelope protects the young from predation, ensuring that a high proportion of individuals survive to maturity.

In addition, many plants have developed unpalatable chemicals, for example alkaloid compounds which tend to deter grazing animals (Wheelan 1977). The widespread south-west genera Oxylobium and

Gastrolobium contain a highly poisonous compound, sodium fluoroacetate. Very small amounts of this compound is fatal to non-native grazing animals such as for example sheep. Native grazers, kangaroos, wallabies and others, have developed a very high level of tolerance to this compound, evidence which attests to the long association of grazing marsupials and native legumes in the south-west (Oliver et al. 1977). Despite the high tolerance of native herbivores the poison confers a high level of protection to the seedlings as the grazers may ingest only limited quantities of such plants.

These adaptive traits operate effectively under a system of natural fire diversity. Under natural conditions, should a succession of one or more cool fires occur, inevitably these will be followed by a fire of higher intensity sooner or later. The destruction and losses incurred as a result of a succession of cool fires would therefore have been balanced by the effects of the occasional more intense fire. The plants' adaptive traits may not be capable of coping with a continued regime of frequent cool fires without the occasional more intense fire to break the sequence. Hence we should be concerned about the current system of prescribed burning which may be affecting the relative frequency of occurrence of species of native legumes. There is already some evidence that the cumulative effects of prescribed fires and grazing by native fauna may have resulted in a reduced legume component in the understorey scrub layer of the northern jarrah forest (Shea et al. 1979).

In the long term, under a prescribed burning regime of regular and frequent cool fires, a lowering of the soil nitrogen status might be expected. On this point however, there is conflicting evidence, Floyd (1966) reported negligible available nitrogen production in soils under spotted gum (E. maculata) following eleven years of control burning as compared with unburnt soil. Hatch (1959) on the other hand found no significant differences between the nitrogen status of regularly burnt firebreaks and nearby unburnt jarrah forest.

# MYCORRHIZAE AND FOREST HEALTH

Microorganisms are an important link in the complex web of inter-relationships and inter-actions between forest plants, animals and nitrogen. Amongst the more prominent groups of microorganisms which play a role in the cycling of nitrogen, are the group of symbiotic hypogean fungi which form mycorrhizae with the roots of trees and woody plants. Mycorrhizae have been found associated with the roots of most families of the world's vascular plants and are considered to play an important role in plant nutrient uptake. Woody species of the Pinaceae, Fagaceae and Betulaceae in particular are known to be dependant on mycorrhizae, especially in nutrient deficient situations (Harley 1969; Marks and Kozlowski 1973).

In addition to their role in nutrient uptake, mycorrhizal fungi also play an important role in protecting the host roots against disease organisms. By shielding root tips with a protective mantle and producing metabolites that often inhibit pathogenic growth, mycorrhizae may protect rootlets from pathogens (Harley 1969; Marks and Kozlowski 1973).

Eucalypts are known to have distinctive mycorrhizal associations (Chilvers 1968, Malajczuk et al. 1980). In addition Malajczuk (1979) suggests that the differential susceptibility of the two major species of eucalypt, jarrah (Eucalyptus marginata) and marri (E. calophylla), to the plant root pathogen Phytophthora cinnamomi may be at least partially explained in terms of their mycorrhizae and associated microflora. It is perhaps pertinent that the plants most susceptible to this pathogen, Banksia sp., Macrozamia reidlii and Xanthorrhoea sp. do not form mycorrhizae (N. Malajczuk, pers. comm.).

Mycorrhizae therefore are of critical importance in tree nutrient uptake and in the tree's defence against disease organisms.

This association between fungi and the higher plants is a very ancient one indeed. Mycorrhizae occur in the oldest fossils of rooting structures, rhizomes of lycopods, from some 400 million years ago (Harley 1969). Sometime during this immense timespan there evolved a tri-partite relationship between mycorrhizal fungi, the vascular plants and animals. In one species, the West Australian rat kangaroo or woylie (Bettongia penicillata), this association has has been demonstrated to be a very ancient one indeed (Kinnear et al. 1979).

Animals eating the fruiting bodies of hypogean mycorrhizal fungi, which form an important food source for many mammals (Fogel and Trappe 1978; Christensen 1977, 1980a), in turn disperse the spores (Maser et al. 1978a, 1978b; Christensen 1980a).

Mammals in particular are important fungus eaters, and mycorrhizal fungi may account for 75% of small mammal mycophagy. Many animals are involved, a range of herbivores, carnivores, insectivores and omnivores all feed on different fungi. Some species rely on fungi as their primary food and there has evolved a high level of interdependence between fungi and animals in some cases (Fogel and Trappe 1978; Maser et al. 1978a; Christensen 1980a). The sporocarps, which they apparently detect by odour, are digested, but the spores pass through the alimentary canal and are deposited onto the soil in the animal faeces. A mechanism for long range dispersal also exists through the agency of native dung beetles, which can fly. Several species of these beetles have been shown to feed on the faeces of fungus eating animals (Christensen 1980a).

Maser et al. (1978b) hypothesize an obligatory symbiotic relationship between hypogean mycorrhizal fungi and most higher plants, together with mycophagous mammals which disperse their spores. The relationship, they maintain, is of critical importance to the optimum functioning of the coniferous forest ecosystem of North America. Christensen (1980a) suggests that a similar tripartite relationship may be of special significance under the peculiar conditions prevalent in Australian forests. Thus low soil nutrient levels, together with frequent fires, followed by rain, create conditions which might result in high nutrient losses, were there not some efficient mechanism such as mycorrhizal fungi for absorbing them quickly and retaining them in the system.

In recent years events which have made non-effective the dispersal mechanism of mycorrhizal fungi have occurred. Over the last 40-50 years dispersal of the spores of these fungi has been almost non-existent in the northern jarrah forests. The introduced European red fox (Vulpes vulpes) caused widespread disappearance of native mycophagous animals during the 1930s (Christensen 1980b). A new equilibrium has been established involving the fox, the introduced rabbit (Oryctolagus cunninculus), the rabbit disease myxomatosis, the rabbit flea (Spilopsyllus cuniculi), the rabbit poison 1080 and in some areas native poison plants of the genus Gastrolobium. This complex system of largely exotic species now apparently determines population levels of native phytophagous animals (Christensen 1980a, 1980b).

We may only speculate about the consequences of this lack of dispersal. For example, how essential is dispersal of the spores? If there is no dispersal, will a large proportion of the new roots produced by trees remain uninfected and therefore less effective in nutrient uptake and more susceptible to disease? It has been speculated (Christensen 1980b) that the lack of spore vectors from the northern jarrah forests over the last 30-40 years may be a factor in the spread of the forest tree disease (Phytophthora cinnamomi) in recent years.

In addition to the introduced fox, which is now a major factor regulating spore dispersal, nitrogen also appears to be a limiting factor in the spread and growth of mycorrhizal fungi. Both the sporocarps and the spores of mycorrhizal fungi contain very high levels of this element (Kinnear et al. 1979). Sporocarp production in the field has also been demonstrated to be most prolific under young vigorously growing stands of native legumes which have a high nitrogen fixing capacity (Christensen 1977, 1980a). High levels of soil nitrogen thus appears to favour sporocarp production and therefore their mycophagous animal vectors as well. Nitrogen therefore may be a further limiting factor in the growth and spread of mycorrhizal fungi.

## DISCUSSION

The relationship between nitrogen-fixing plant species, forest fauna and forest growth and health is a delicate one. The nitrogen status of the forest appears to depend in no small measure on fire diversity which affects the abundance of animal grazers and leguminous plants. Nitrogen levels ultimately influence mycorrhizal development and hence nutrient absorption, tree health and the mycophagous animals. Changes in the abundance of the animal spore vectors may in turn affect mycorrhizal distribution and growth.

In the short time since European settlement of the south-west, changes have occurred which may be altering former balances within the forest ecosystem. Fire is a natural agent in our forests (Christensen et al. 1980), but in recent times a new fire regime, broadscale cool spring prescribed burning on a short rotation has been introduced (Peet 1967). This new fire regime appears to be resulting in changes in the abundance of hard-seeded nitrogen-fixing leguminous understorey species in the jarrah forest. If such changes were to become irreversible it might adversely affect the nitrogen balance in the system with resulting problems in forest growth and health. Such a situation seems unlikely since there still appears to be a store of legume seeds at depth in the soil profile which may be made to germinate simply by introducing one intense fire (Shea et al. 1979).

Nevertheless how long can the system remain in temporary 'imbalance' without resulting in serious changes? There appears to be no answer to this question at the present time since there are too many imponderables. For example, are native legumes as important a factor in the total forest nitrogen budget as we believe they are? This is a difficult question. Certainly it may be demonstrated that they fix considerable quantities of nitrogen, but it has not yet been satisfactorily demonstrated that soil nitrogen declines significantly in their absence. The difficulty is to establish a 'natural' or 'base' level of nitrogen for the system. In the absence of concise pre-European fire history data, the relative frequency of occurrence of legumes in the forest and hence the rate of nitrogen fixation cannot be established with any degree of accuracy. As a consequence, there is nothing with which to compare present nitrogen levels and turnover rates in the jarrah forest in order to determine whether or not they are adequate. Nevertheless nitrogen levels could be measured on long term plots given different fire treatments resulting in a variety of legume populations. Such data would provide valuable information.

In addition to the lack of information concerning nitrogen input into the system, we also lack data on its real significance. For example, what are the precise relationships between spore production in mycorrhizal fungi and the levels and availability of nitrogen? Is the continuous distribution of the spores of mycorrhizal fungi essential to ensure adequate levels of root infection of forest trees? If it is, then the problem of the introduced fox and predation of spore vectors needs to be given more serious consideration.

To what extent is the capacity of eucalypts to take up nutrients and to resist disease affected by reduced mycorrhizal infections? Introduced plantation pines, for example, seem to manage throughout the entire life span with only one infection of mycorrhizae, carried out whilst they are in the nursery. Does the fungus in this case manage to spread by mycelial contact without the aid of animal vectors, or can the pines cope with lower levels of root infection only because of the artificially high nutrient levels?

To these and many other questions we do not yet have the answers. However, they are not impossible to test experimentally and this should be done. Having once done so we may find that for one reason or another the changes which we have imposed upon the forest ecosystem are causing no significant impact. On the other hand, if they should be found to be having harmful effects, it will still be possible to institute changes to negate or reverse these effects before they become irreversible and cause irreparable damage.

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