

Mycorrhizas in the Kakadu region of tropical Australia

II. Propagules of mycorrhizal fungi in disturbed habitats

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Abstract

Bioassays were used to provide estimates of both the distribution and abundance of mycorrhizal fungus propagules in soils from mine sites and natural habitats in tropical Australia. These bioassays measured mycorrhizal formation by bait plants that were grown in intact cores of soil collected along a transect at each site. The mine sites included, had sparse, patchy or dense vegetation cover on waste-rock materials that would initially have been devoid of mycorrhizal fungus propagules. The natural habitats included eucalypt savanna sites which had been subjected to hot annual fires for 4 years or remained unburnt. Propagules of vesicular-arbuscular mycorrhizal (VAM) and ectomycorrhizal (ECM) fungi occurred in all sites, but were sporadically distributed in highly disturbed areas, where they were associated with patches of vegetation. Both the relative abundance and frequency of occurrence of inoculum of VAM and ECM fungi increased with vegetation cover in older disturbed sites. Propagules of VAM fungi were substantially more numerous in some mine site habitats with dense vegetation cover, than in adjacent natural habitats. The presence of substantial amounts of phosphorus, released from weathering rock, in mine waste rock materials may have reduced the requirement of plants for mycorrhizal associations during vegetation establishment in mine sites. In woodland sites, hot annual fires appeared to restrict ECM fungi to infrequent patches in the surface horizon, while ECM fungus inoculum was much more frequently detected in soil from the unburnt site. These fire regimes apparently had less effect on the distribution or quantity of VAM fungus inoculum.

Introduction

Most plants in natural ecosystems have mycorrhizal associations which involve three-way interactions between fungi, soil and plants (Brundrett, 1991). Consequently, the impact of soil disturbance on these associations will depend on the nature of fungal propagules and changes to soil conditions, as well as the influence of any surviving vegetation. Most studies of mycorrhizal associations in highly disturbed habitats

such as mine sites have found reduced levels of mycorrhizal propagules (Danielson, 1985; Jasper et al., 1992; Pflieger et al., 1994). Less severe forms of soil disturbance, including agricultural tillage, soil animal activities, fire and erosion, can also have a detrimental effect on mycorrhizal associations (Habte et al., 1988; O'Halloran et al., 1986; Read and Birch, 1988; Vilariño and Arines, 1991).

The capacity of propagules of mycorrhizal fungi to persist in soil without roots, tolerate disturbance, resist predation by soil organisms and disperse to new locations will determine the outcome of disturbance

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on mycorrhizal associations, but are not well understood (Malajczuk et al., 1994). In undisturbed natural communities a network of hyphae is believed to be primarily responsible for the spread of mycorrhizal fungi to new roots (Brundrett, 1991; Read and Birch, 1988). However, we would expect severe soil disturbance to eliminate most of these hyphae and the efficacy of any surviving portions of the hyphal network to be further curtailed by the absence of host plants to provide energy (Jasper, 1994; Malajczuk et al., 1994). For vesicular-arbuscular mycorrhizal (VAM) and ectomycorrhizal (ECM) fungi, propagules with at least some capacity to survive soil disturbance are thought to include spores, mycorrhizal root fragments, pieces of rhizomorphs and sclerotia (Ba et al., 1991; Brundrett, 1991; Jasper et al., 1991). We would expect fungi which do not produce these resistant propagules to be lost immediately following disturbance, but other fungi with more resistant propagules may decline due to attrition of their propagules during subsequent periods when soil is devoid of vegetation. Propagules of mycorrhizal fungi are consumed or parasitised by a wide range of microorganisms and larger animals (Brundrett, 1991). Dramatic changes to soil conditions such as temperature extremes and anaerobic conditions, which may occur in stockpiled topsoil, may themselves be responsible for the death of fungal structures and further attrition could be caused by the ageing of propagules, or by their premature germination (Malajczuk et al., 1994). Typical changes that occur when soil is disturbed and stockpiled, include the loss of organic matter and nutrients, as well as structural and biological components (Abdul-Kareem and McRae, 1984; Danielson, 1985). There are also cases where the substrate to be revegetated (such as waste rock dump material) would initially be devoid of soil organisms.

Spores or other propagules of VAM fungi are dispersed by the activity of animals, wind and other soil transportation processes (Allen, 1991; Brundrett, 1991; McGee and Baczocha, 1994). In natural communities, ECM fungi are dispersed by airborne spores that are seasonally produced in vast numbers or by the activity of animals which feed on subterranean structures that contain spores (Claridge and May, 1984). In a disturbed habitat, the effectiveness of these natural vectors will depend on the quality and proximity of undisturbed habitats containing suitable fungi (and their associated animals) as well as the seasonality of fruiting of fungi. There is little information about the

effectiveness of, or time required for these processes to occur in disturbed habitats in Australia.

This paper represents the second part of a study which aimed to characterise the role of mycorrhizal associations and their inter-relationships with habitat characteristics in undisturbed and disturbed habitats in the Alligator Rivers Region (ARR) of the Northern Territory of Australia. Here results of bioassay experiments which examined the capacity of propagules of VAM and ECM fungi to form associations in soils from disturbed and undisturbed habitats in the Region are presented. This information is required to determine if the activity of mycorrhizal fungi is likely to be a limiting factor for achieving revegetation goals on the disturbed sites. This experiment used similar methods to a preliminary survey of natural habitats in the ARR Region (Brundrett et al., 1996), but involved more comprehensive sampling of fewer sites to provide information about the spatial variability and the abundance of inoculum of mycorrhizal fungi. The disturbed habitats sampled included partially vegetated waste rock material at Ranger Uranium Mine, Coronation Hill and Nabarlek Uranium Mine. Two woodland sites with contrasting fire management histories were also included in the study.

Materials and methods

Intact soil cores, soil samples and root material were collected from disturbed mine sites and natural sites (Figure 1) in the wet season (February–March) of 1992. This survey used similar procedures to the earlier study of natural habitat in the same region (Brundrett et al., 1996) which contains further details of methods. Mycorrhizal fungus inoculum potential bioassays were used to determine the average level and spatial variations in VAM and ECM fungus propagules of sites. Bioassays used 20 intact soil cores which were taken at 5 m interval along a 100 m transect at each of the 10 sites described in Table 1. This number of samples was found to be optimal for measuring mycorrhizal fungus propagules in disturbed habitats in Australia (D Jasper, unpublished data). Sampling occurred on rock overburden from open pit mining operations, which is referred to as waste rock dump (WRD) material. Habitats where varying amounts of vegetation was established on WRD material were sampled at Ranger Uranium Mine, an abandoned mine at Coronation Hill and Nabarlek Uranium Mine, with or without vegetation cover, were sampled. Two sites with contrasting fire

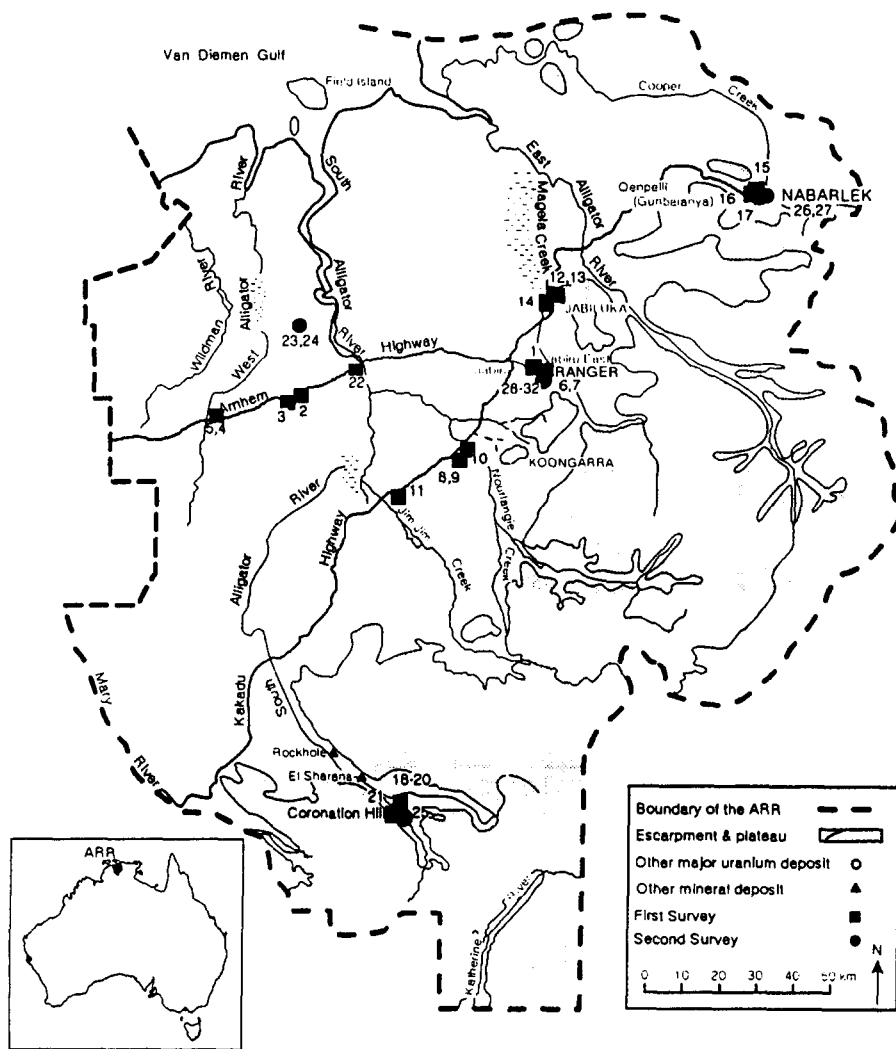


Figure 1. Map of the Alligator Rivers Region, which consists of Kakadu National Park and adjacent parts of Arnhem Land, showing the location of sample sites.

management histories at CSIRO's Kapalga Research Station were compared and an undisturbed woodland site, that was also sampled in part I of this study, was included as a control (Figure 1, Table 1).

Intact soil cores (12 cm diameter \times 12 cm deep) were collected and placed in 1 L plastic buckets for storage, transport and subsequent bioassays. Clover seeds (12) with rhizobium inoculum were planted into intact cores along with germinated *Eucalyptus miniata* seeds (5). Plants were grown in a glasshouse for 4 weeks, watered to field capacity by weight every second day, and soil temperatures were maintained at 25°C. After 4 weeks, plants were harvested and 2 clover and all surviving eucalypt seedling root systems

were sampled from each core. Roots were cleared, stained with Chlorazol black E and assessed using the grid line-intercept method to measure the total and VAM root length of clover samples. For eucalypt seedlings, ECM formation was quantified by counting the total number of colonized root tips (relative to total root length).

The presence or absence of vegetation and important plant species present near each sampling location along the 100 m transects at each site was recorded. Surface soil samples (0–10 cm) were collected from within 1 m of an intact soil core, from both ends and the middle of each transect, to identify spores of VAM

Table 1. Location and descriptions of the vegetation, soil and habitat characteristics of sample sites

Site No.	Location	Habitat	Dominant vegetation		Vegetation cover ^a	Soil type ^b	Comments (slope, drainage, fire, age, etc)
			Upper storey	Lower storey			
23	Kapalga fire trail, block M	Woodland	Eucalypts	Herbs	Moderate	Loam, brown, gravel lag	Gentle slope, moderately drained, thick litter, kept unburnt ca. 5 year
24	Kapalga fire trail, block L	Woodland	Eucalypts, palms	Grass shrubs	Dense	Loam brown, gravel lag	Gentle slope, well drained, no litter, experimentally severely burnt annually for ca. 5 years
25	Coronation Hill minesite, old pit	WRD	<i>Terminalia</i>	<i>Sorghum</i> , herbs	Dense (ground cover)	Loam, reddish Brown, rocky	Very steep slope, highly disturbed ca. 5 years prior to sampling, frequently burnt, no top soil
26	Nabarlek minesite, hill WRD-grey	WRD	Melaleucas, acacias	Grasses, sedges, <i>Sylosanthus</i>	Sparse and patchy	Sandy, chloritic schist rocks, grey	Fat with depressions, partially weathered schist, no top soil, unburnt, ca. 10 years old
27	Nabarlek minesite, WRD material	WRD	Acacias, melaleucas	Grasses	Very sparse	Clayey, reddish, weathered schist rocks	Moderate slope, moderately drained, no top soil, unburnt, ca. 10 years old
28	Ranger minesite WRD capsite	WRD	Nil	Sedges, grasses	Very sparse and patchy	Loam-clay, grey, with weathered chloritic schist rocks	Flat with depressions, poorly drained, compacted, no top soil, unburnt, ca. 5 years old, capsite, no revegetation.

29	Ranger minesite, WRD WRD-batter slope (vegetation trials)	WRD	Acacias	Grasses	Sparse and dense (see comments)	Loam-clay, grey, weathered chloritic schist rocks	Moderate slope, free draining, compacted, no top soil, unburnt, ca. 5 years old, 1/3 in dense acacia plot, 1/3 in sparsely grassed area and 1/3 in densely grassed area.
30	Ranger minesite, WRD WRD-ripped site vegetation trial	WRD	Acacias	Grasses	Sparse	Loam-clay, grey, weathered chloritic schist	Flat, ripped at 2 m intervals after spreading a thin layer of top soil. Site 5 years old, moderately drained
31	Ranger minesite, WRD WRD-1984 old revegetated site	WRD	Eucalypts acacias	Grasses <i>Stylosanthes</i>	Dense	Clayey, reddish, highly weathered schist	Flat, ripped, fertilized, seeded with eucalypts, acacias, <i>Stylosanthes</i> , ca. 8 years ago and part site burnt ca. 3 years prior to sampling, no top soil
32	Undisturbed woodland near Ranger minesite	Woodland	Acacias, eucalypts	Shrubs with a few grasses	Moderate	Sandy loam, brownish	Gentle slope, low lying, poorly drained, infrequently burnt, same as site 6 in natural habitat survey included as a control

WRD-waste rock dump.

^aVegetation cover ranges from sparse→dense.

^bVisual impression only.

fungi (data presented elsewhere). A subsample of this soil was also used to determine extractable P, K, NH₄, NO₃ and reactive Fe concentrations, pH, conductivity and organic carbon content (see Brundrett et al., 1996).

Results

Mycorrhizal bioassays

Mycorrhizal bioassays using intact soil cores collected along a transect, allowed both the overall level and distribution of mycorrhizal fungus propagules within sites to be examined and allowed different sites to be compared. Propagules of VAM fungi were detected at all sites, but their distribution patterns within a site varied substantially (Figure 2). Fungi capable of forming ECM associations with *Eucalyptus* seedlings were less uniformly distributed than VAM fungi. ECM fungi occurred at most sites, but were absent from severely disturbed areas without suitable host plants (Figure 2). Bioassay results for individual sites and vegetation characteristics are summarized below and correspond to parts A to J of Figure 2 and Table 1.

- A. Site 23 was a woodland site which had been protected from fires for 4 years. This site had low or moderate levels of VAM in all cores, but ECM propagules were detected in more cores than from any other site (50 %).
- B. Site 24 was a woodland site which had been subjected to hot annual fires for 4 years. This site had similar levels of VAM propagules to site 23, but ECM fungi were only detected in one core.
- C. Site 25 was a dense almost pure stand of the annual grass *Sorghum stipoides* growing on WRD material at Coronation Hill mine site. This site had VAM propagules in all cores, often at high levels. Propagules of ECM fungi were not detected, but there were few host trees nearby.
- D. Site 26 was a WRD area at Nabarlek Uranium Mine with herbaceous plants, shrubs and trees in vegetated patches surrounded by bare WRD material. This site had abundant VAM propagules in cores taken from vegetation patches, but ECM fungi were detected in only one core.
- E. Site 27 was adjacent to Site 26, but had fewer scattered shrubs and herbaceous plants and had large expanses of bare WRD material. This site had abundant ECM fungus propagules in one core

from under *Acacia* sp. shrubs, but most other cores were devoid of VAM or ECM activity.

- F. Site 28 was a highly disturbed area of WRD material at Ranger Uranium Mine. This site had substantial VAM fungus activity in 4 cores taken from patches of low herbaceous plants (mostly sedges, *Trianthema* sp. and grasses), traces of VAM activity in 6 other cores and very limited ECM activity in 2 cores.
- G. Site 29 was adjacent to site 28, but had different revegetation trials on sloping WRD material. This site had sporadic VAM fungus inoculum in cores from a sparse grass stand (*Sorghum* sp.), but high levels of VAM in cores from under dense *Acacia* spp. at the other end of the transect (cores from 75–100 m). No ECM fungi that associate with eucalypt seedlings were detected.
- H. Site 30 was a vegetation trial where a thin topsoil layer had been spread onto WRD material at the Ranger site. This site had abundant VAM fungus propagules in half the cores, and traces of activity in others, while ECM fungi were only found in one core. The distribution of mycorrhizal activity apparently were associated with variations in plant cover along ridges and furrows in the WRD material.
- I. Site 31 was an older WRD area on the Ranger site with a comparatively dense cover of herbaceous plants (especially grasses and *Stylosanthes* sp.) shrubs and trees. This site had very high levels of VAM fungus propagules in all cores and also had substantial ECM activity in several cores. This habitat had the highest overall levels of VAM fungus propagules of any area included in this survey and a rainforest area was the only comparable natural site, of those sampled in the region (see Brundrett et al., 1996).
- J. Site 32 was an undisturbed open woodland area with shrub and grass understorey near the Ranger site. This site had VAM fungus propagules in all cores, often at substantial levels, and ECM fungi were detected in 4 cores. This site was also sampled in the earlier survey (site 6 in Brundrett et al., 1996) where a somewhat lower level of VAM fungus propagules was measured.

Bioassays detected inoculum of VAM and ECM fungi in some cores from disturbed habitats but not in others. There was a strong correspondence between the peaks in the distribution of mycorrhizal inoculum shown in Figure 2 and the observed position of patches of vegetation on disturbed sites. When the

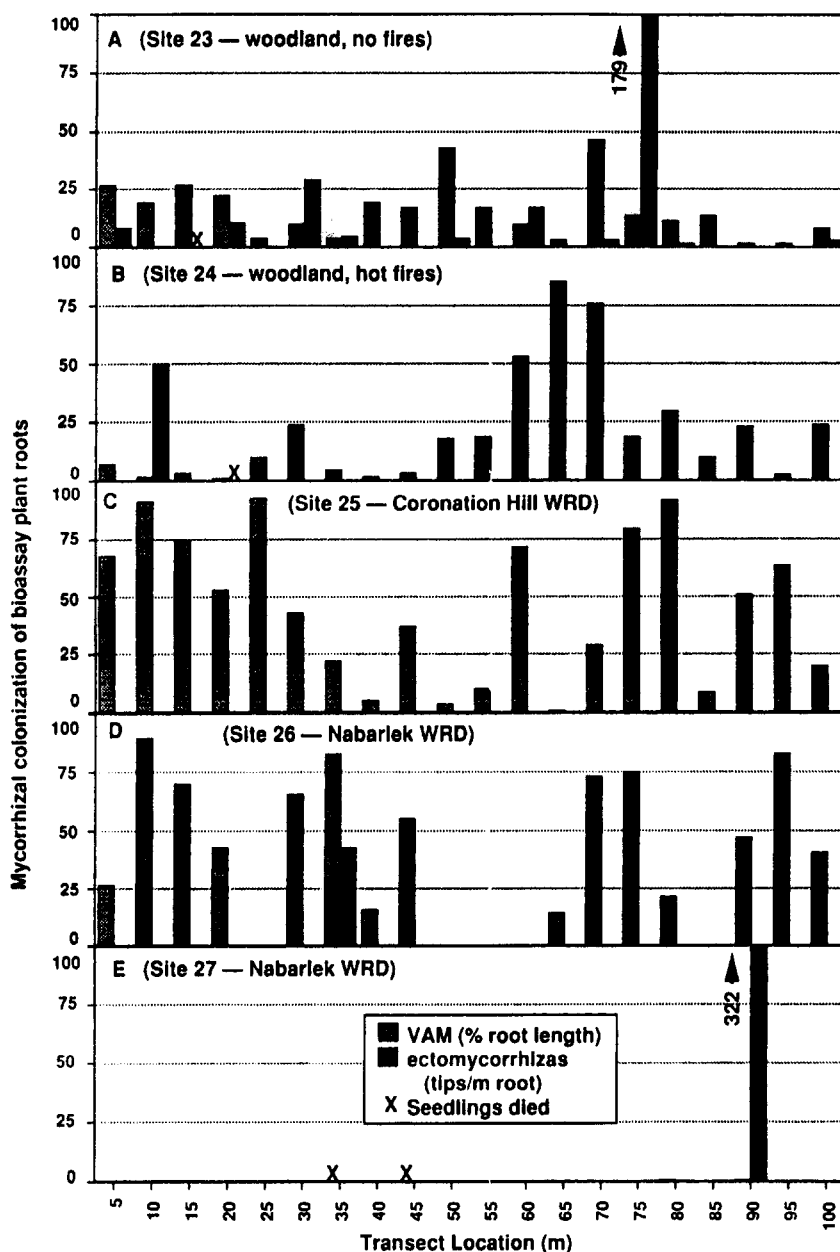


Figure 2. Spatial patterns in inoculum of VAM and ECM fungi at 10 sites, estimated by bioassays using clover (*Trifolium subterraneum*) and *Eucalyptus miniata* bait plants grown in the same intact soil cores. Soil cores were collected at 5 m interval along a 100 m transect at each site, to investigate spatial variability in mycorrhizal inoculum potential.

overall level of and distribution of mycorrhizal inoculum at each site is summarized (Figure 3), it can be seen that the probability of seedlings encountering VAM or ECM inoculum in disturbed habitats generally increased with plant cover. Numbers of VAM fungus propagules increased during plant succession on WRD sites, reaching exceptionally high levels in some fully

vegetated areas. These peaks in VAM fungus inoculum levels were substantially higher than those occurring in most of the undisturbed habitats included in this study (Figure 3), or the first part of this study (Brundrett et al., 1996). Inoculum of ECM fungi occurred sporadically in some sites and was associated with *Eucalyptus* or *Acacia* spp. Clover growth was inhibited by adverse

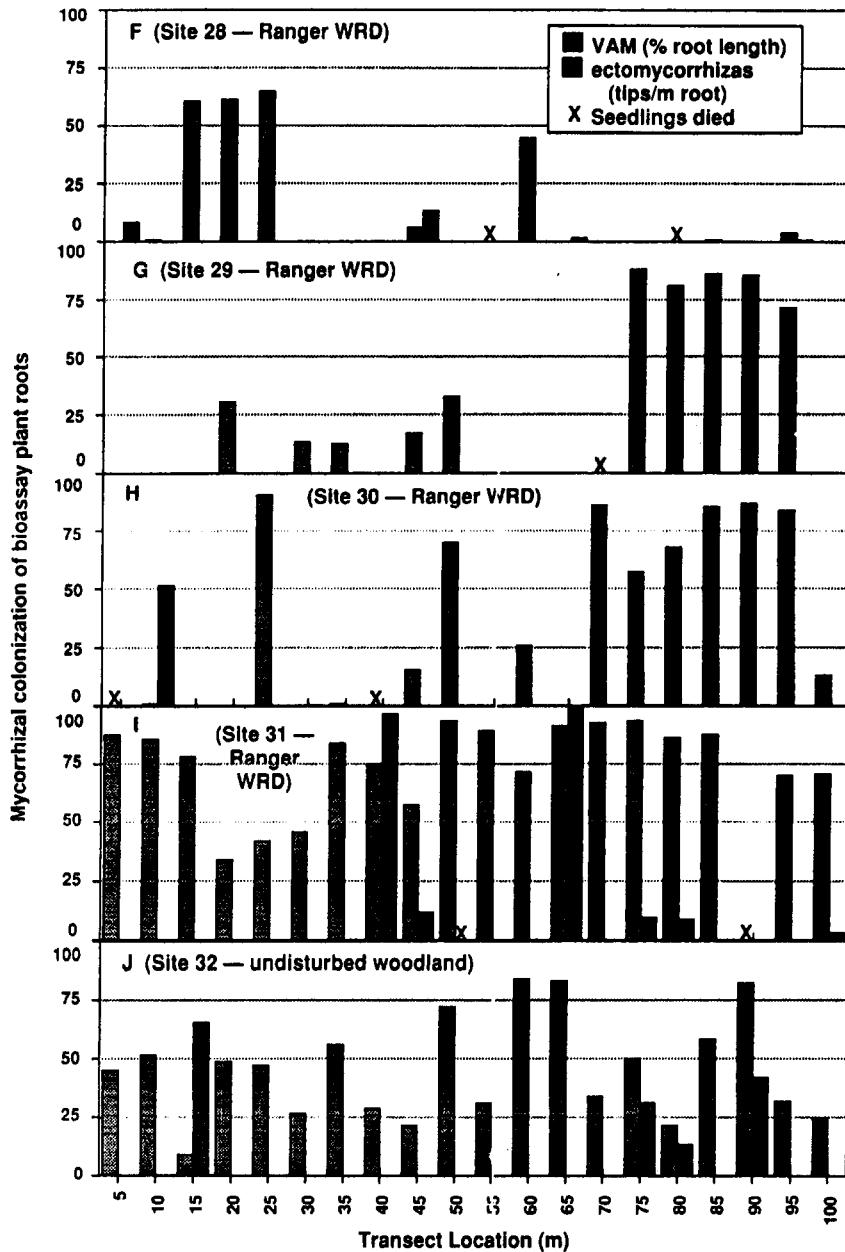


Figure 2. (continued)

physical or chemical soil properties in some soil cores from sites with sparse vegetation (dead seedlings are marked with an X in Figure 2).

Soil properties

The mine site soils sampled consisted of weathering rock material that included 50–60% gravel, 25–45%

sand and 10% or less silt or clay. Chemical properties of soils are summarized in Figure 4 with sites arranged in order of increasing vegetation cover, as in Figure 3. The macro-nutrients P and K were generally present in greater quantities, but there was less nitrogen in WRD soils, relative to those from natural habitats. Soil organic carbon content increased (from 0.1 to 0.7%) as vegetation developed in mine WRD

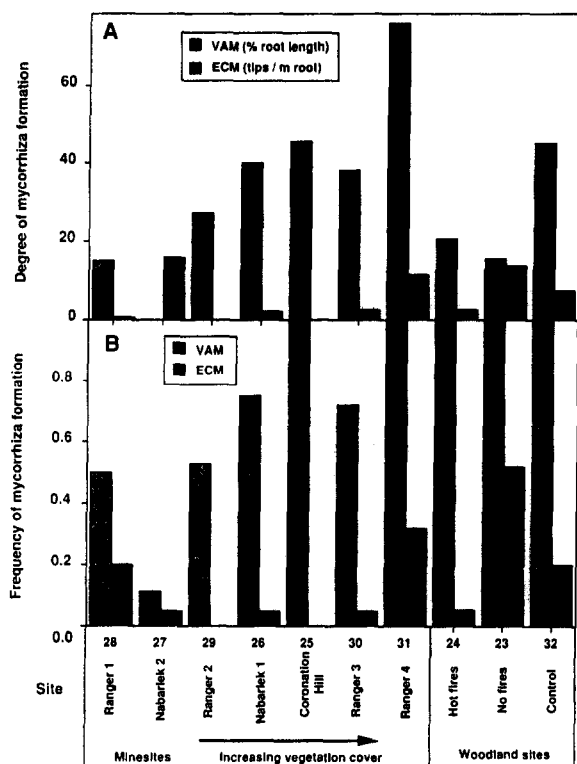


Figure 3. Mycorrhizal bioassay results using clover (*Trifolium subterraneum*) and eucalypt (*Eucalyptus miniata*) seedlings grown in intact soil cores to provide estimates of mycorrhizal inoculum potential for VAM and ECM fungi respectively. This procedure provided information on both (A) the average values for mycorrhizal colonization across each site and (B) the frequency of occurrence of mycorrhizas (number of soil cores with mycorrhizal seedlings).

soils, but was always lower than in soils from natural habitats (1.0–4.0%). Soil pH values of WRD soils were close to neutral (6.2–7.0), while soil in natural habitats were more acidic (5.9–6.1). Soil conductivity values of WRD soils were generally low ($4\text{--}8\ \mu\text{S m}^{-1}$), but were higher than those of woodland sites ($3\text{--}5\ \mu\text{S m}^{-1}$).

Discussion

Soil properties

There were substantial differences in soil properties between mine sites and natural sites. The soils in most mine habitats comprised weathering WRD material without applied topsoil. Soil organic matter content and nitrogen levels increased with site age and vegetation cover, when young sites with sparse vegetation were compared to older sites with dense vegetation,

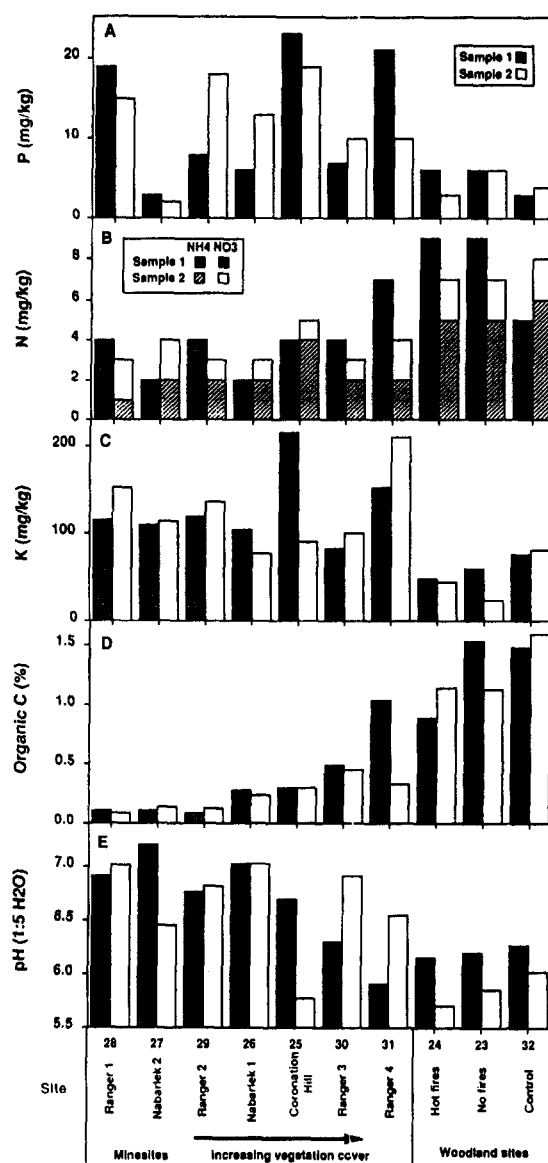


Figure 4. Extractable phosphorus (A), ammonium nitrogen (B), potassium (C), organic carbon (D), and pH (E) of soils from the disturbed sites and natural habitats examined.

or woodland sites. Levels of available phosphorus and potassium were substantially higher in soils derived from WRD material than in natural habitat soils. These elements would have been released by the weathering of WRD mineral components during soil formation and also occurred in higher concentrations in natural habitat sites with rocky soils than in those with less gravel or rocks (Brundrett et al., 1996). Correlations between soil nutrient levels and vegetation cover may also have been influenced by the uptake of nutrients by

vegetation. Similar values for available phosphorus, organic carbon and pH in Ranger WRD soils were also reported by Reddell and Milnes (1992) and Ashwath et al. (1993).

Measuring mycorrhizal inoculum potential

Results presented here and in earlier studies in Australian ecosystems (Brundrett and Abbott, 1995) suggest that information about spatial variability in the activity of mycorrhizal fungi can be much more important than average measurements of propagules of these fungi. This spatial variability was observed by using intact soil core bioassays and sampling at regular distances along transects (rather than randomly). Transect sampling also demonstrated that soil cores containing mycorrhizal fungi came from patches of vegetation in highly disturbed sites and that the intervening expanses of bare WRD material were largely devoid of mycorrhizal inoculum. Large gaps between patches of soil containing mycorrhizal fungus inoculum in highly disturbed sites may be important if seedlings have a limited capacity to find mycorrhizal fungi. Seedling roots may often fail to contact these fungi if patches are too large or frequent.

In all sites, spatial variability in ECM fungus inoculum was much larger than that for VAM fungi, suggesting that there may be little point in using average values for ECM fungus inoculum potential to compare sites. There may also be specificity problems with the use of eucalypt bioassays for ECM fungi, since mycorrhizas were not detected in cores from some stands of *Acacia* spp. or *Melaleuca* spp. which were ECM hosts (unpublished data). It is possible that these soils contained host-specific fungi that would not colonize the roots of eucalypt seedlings.

The effect of fire

Variations in burning regimes between two adjacent woodland sites had little apparent influence on the distribution or quantity of VAM fungus propagules, when compared to an unburnt site. Bellgard et al. (1994) found similar levels of VAM fungus inoculum in burnt and unburnt areas of sclerophyllous shrubland in Australia. Vilariño and Arines (1991) and Klopatek (1988) used bioassays to show that forest fires reduced inoculum levels of VAM fungi in soils. Vilariño and Arines (1992) also observed that mycorrhizal formation by propagules was inhibited by aqueous extracts from burnt soil.

The activity of ECM fungi appeared to have been encouraged by withholding fire for 4 years, relative to the site with hot annual fires where ECM fungus propagules were only detected in one core. However, inoculum of ECM fungi can also be detected in sub-soil layers (see Brundrett et al., 1996), so the main impact of intense fire regime may have been to change the depth at where these fungi are most active. Amaranthus and Trappe (1993) observed a greater reduction in inoculum of ECM fungi than of VAM fungi in a severely eroded burnt forest site. Different ECM fungi have often been observed to fruit in natural habitats after a fire (Watling, 1988), but fruiting may not be correlated with the activity of fungi in soils. The impact of fire on mycorrhizal fungi will result from (i) direct impacts on fungus propagules in soils, (ii) the loss of host plants and (iii) indirect effects on fungal habitats – such as the loss of litter from the soil surface, but little is known about the relative importance of these factors to ECM or VAM fungi.

Mycorrhizal fungi in successional habitats

Bioassays demonstrated that mycorrhizal fungi were generally present on mine WRD sites wherever suitable host plants had become established, even if it mostly comprised of nonmycorrhizal species, such as sedges and weeds. The probability of a plant becoming mycorrhizal in a disturbed habitat depends on the survival of propagules that remain after soil disturbance, or arrive as a result of dispersal processes, and which can adapt to prevailing site conditions (Brundrett, 1991; Jasper, 1994; Malajczuk et al., 1994). In the present study, the substrates in the mine sites sampled (rock material) would have initially been devoid of mycorrhizal fungi, so dispersal processes must have been responsible for their introduction. However, it was not possible to investigate the nature of, or the effectiveness of these vectors, without examining sites at regular intervals after their formation. The mine sites sampled were also re-disturbed many times, resulting in interruptions to vegetation development, making the sequence of events even more difficult to interpret.

In other studies, the action of wind and activities of animals have been thought to be responsible for the dispersal of mycorrhizal fungi (Allen, 1991). In the disturbed mine sites sampled there was a tendency for wetland species of herbaceous plants and shrubs to predominate early in succession (perhaps due to impeded drainage) and these species included many nonmycorrhizal plants (unpublished data). The absence of myc-

orrhizal fungus inoculum from disturbed habitats may not be a problem if dispersal of fungi to the site (by their natural vectors) is sufficiently rapid, if succession in a particular habitat normally involves species which are not highly dependent on mycorrhizal associations, or if phosphorus deficiency is not an important growth limitation at a particular site (Allen, 1991; Janos, 1980; Malajczuk et al., 1994).

In the mine soils sampled, inoculum of VAM fungi was found to be substantially more abundant in some dense patches of early successional vegetation than in adjacent climax plant communities. This enhanced mycorrhizal fungus activity likely resulted from greater plant productivity, which was perhaps due to the increased availability of phosphorus or water in the young soils. Plant productivity of these sites does not appear to be adversely affected by chemical or physical properties of the young WRD soils, such as reduced organic matter, or nitrogen contents, relative to natural habitat soils. However, we expect that there will be considerable variations between mine sites in the capacity for their soils to support vegetation establishment and the relative importance of mycorrhizal associations during this process.

In undisturbed habitats, a wide diversity of fungi can form ECM associations with one host species, but the diversity of these fungi in disturbed habitats is typically much lower and there are some species which are characteristic of disturbed soils (Danielson, 1985; Mason et al., 1987; Termorshuizen, 1991). There is also evidence that some species of VAM fungi are more likely to occur in disturbed habitats than others (Collins Johnson et al., 1991, 1992). These reductions in fungal diversity could result because disturbance itself eliminated many intolerant fungi, while others with more resistant propagules may not be effective because they had a limited capacity to adapt to the major changes to their environment (Brundrett, 1991; Malajczuk et al., 1994). Unfortunately there is insufficient information about the biology of mycorrhizal fungi to make robust predictions about the capacity of particular strains of these fungi to survive disturbance events or to adapt to radical changes in soil conditions following disturbance.

The questions outlined above, concerning the probability of seedlings encountering mycorrhizal inoculum, the capacity of fungi to adjust to site conditions and the mycorrhizal requirements of host plants must be answered to determine if introductions of mycorrhizal fungi will substantially improve plant establishment in a particular site. Some of these questions can be

answered by bioassay experiments, which detect fungus propagules and growth experiments which quantify mycorrhizal benefits for a particular combination of fungi, hosts and soil conditions. The benefit of mycorrhizal colonization varies between hosts and depends largely on phosphorus deficiency being the most important limitation to plant growth. Consequently, the phosphorus content of soils and the mycorrhizal dependency of plant species must also be considered. The absence of appropriate mycorrhizal fungi may also influence the outcome of competition between species by favouring species which are less dependent on these associations over other plants, and may thus reduce plant diversity in disturbed habitats.

Re-spreading fresh topsoil will often be the most effective method of reintroducing mycorrhizal fungi to disturbed sites, along with many other beneficial micro-organisms. Topsoil applications may have to be supplemented by, or replaced with the introduction of specific micro-organisms, if topsoil is not available or, lacks effective fungi. The decision to inoculate sites with mycorrhizal fungi, must consider all the factors outlined above, and will depend on the outcome a cost-benefit analysis which weighs the potential benefits of mycorrhizal inoculation against the difficulties involved in obtaining inoculum of appropriate fungi and the expense of introducing them at a particular site (Jasper, 1994; Malajczuk et al., 1994). There is a need for further research concerning the role of mycorrhizal associations in disturbed habitats in Australia. In particular, information is required on the mycorrhizal dependency of key plant species (such as eucalypts and acacias) in mine soils, the capacity of beneficial soil organisms to tolerate atypical soil conditions in disturbed habitats, and the timing of introduction of these microbes by natural vectors relative to the establishment of associated vegetation.

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