Bryophytes and lichens at the Warra LTER Site. II. Understorey habitats in *Eucalyptus obliqua* wet sclerophyll forest

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Abstract

The lichen and bryophyte floras of major understorey habitats are described for a Eucalyptus obliqua wet sclerophyll forest community in southern Tasmania. Habitats were partitioned into smooth-barked trees, papery-barked trees, eucalypts, logs, rocks and inorganic soil. Most lichens occur as epiphytes above about 1–2 m from ground level whereas bryophytes are most abundant on the forest floor or as basal epiphytes, becoming more dispersed with increasing height up the trees. Smoothbarked trees represent the richest habitat and support the highest number of specialist species. The forest dominant, E. obliqua, has a relatively small but very distinct flora, especially with respect to lichens. Habitat specialists are seen as a particularly vulnerable component of the flora in these forests.

Introduction

This study of cryptogams (bryophytes and lichens) is part of an ongoing investigation by Forestry Tasmania into the impacts on forest biota of different logging and regeneration treatments (e.g. see Hickey and Neyland 2000, 2001; Jarman and Kantvilas 2001). To date, 144 bryophytes and 134 lichens have been reported from pre-logging surveys of a

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Eucalyptus obliqua wet forest community with a Gahnia/Bauera understorey (Jarman and Kantvilas 2001). In the present paper, we examine the cryptogamic flora of major understorey habitats in the same forest. Studies of this type are scarce in the Australian literature, but one by Ashton (1986) in Victoria is particularly relevant to the present work. It focussed mainly on bryophytes, and includes floristic composition and patterns of colonisation in the understorey of E. regnans wet forest. Many similarities (and differences) can be recognised between the flora of that forest and the E. obliqua forest examined here.

Methods

Details of the study area, cryptogamic plots and sampling methods are given in Jarman and Kantvilas (2001), along with a detailed description of the structure and vascular species composition of the forest. A brief summary of the vegetation is also included here because of its critical role in determining cryptogamic habitats. Nomenclature is consistent with that in the earlier paper except that three moss species, Rhaphidorrhynchium amoenum, Warburgiella leucocytus and W. macrospora, have been combined as Sematophyllum aggr. because of difficulties in routinely identifying them from vegetative material.



Photo 1. The general appearance of the understorey, with trunks of small understorey trees (at this site, mainly Melaleuca squarrosa) projecting above a dense layer of Gahnia grandis and Bauera rubioides.



Photo 2. Forest litter of leaves, bark, twigs and branches covers the forest floor where gaps occur in the Gahnia and Bauera layer. Cryptogams colonise substrates such as logs and rocks raised above the smothering effects of the debris.

Substrate classes

The categories used in habitat/substrate sampling were:

A. Epiphytes

- Smooth-barked hosts (Nematolepis squamea, Pomaderris apetala, Acacia verticillata and Banksia marginata);
- Papery-barked hosts (*Melaleuca* squarrosa, *Leptospermum lanigerum*, *L. scoparium*);
- Fibrous-barked hosts (Eucalyptus obliqua);
- · Living leaves.

B. Non-epiphytes

- (i) Sampled collectively
 - The forest floor (rotting stumps and logs of all sizes, branches, twigs, dead leaves, miscellaneous forest debris, rocks, inorganic soil and humus).
- (ii) Sampled separately
- Logs greater than 10 cm diameter;
- Rocks;
- Inorganic soil.

Forest structure and composition

The forest is dominated by mixed-age Eucalyptus obliqua which forms an open canopy over a dense tree layer of Nematolepis squamea, Leptospermum lanigerum and Melaleuca squarrosa. Less common trees include Leptospermum scoparium, Pomaderris apetala, Acacia verticillata and Banksia marginata. Understorey conditions vary from being brightly lit below canopy gaps in the low tree layer to very shady where the canopy cover is more continuous.

The medium to low understorey vegetation is dominated by *Bauera rubioides* and *Gahnia grandis* (Photo 1). The forest is relatively open between this layer and the dense crowns of the low trees, with the pole-like trunks of the latter contributing little foliage to the understorey. Apart from *Bauera*, shrubs are uncommon.

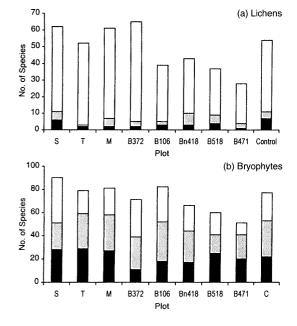


Figure 1. A comparison of the lichen and bryophyte floras on the sampled plots, showing the number of species occurring only as epiphytes (\Box) or non-epiphytes (\blacksquare) , with species that occur as both shown separately (\blacksquare) .

A thick blanket of eucalypt litter formed of leaves, bark and branches covers much of the soil surface in understorey gaps. Rocks, logs and mounds of inorganic soil raised above the litter provide suitable habitats for cryptogams, providing the surfaces are not densely shaded by *Bauera* or *Gahnia* (Photo 2).

Results

The flora is a mixture of ecologically tolerant species that are widespread across a range of habitats within wet forest, and more restricted species that show preferences for particular substrates (Appendices 1, 2). In the latter case, some species are confined to a single substrate, or almost so.

Lichens are mostly epiphytic (Figure 1a) and are generally the dominant plant group above about 1–2 m from ground level. Bryophytes are dominant on the forest floor and on buttresses, becoming more dispersed with increasing height up the trees, and are

virtually absent from the canopy. Their visual dominance in forest floor habitats suggests that species richness is greatest there but the epiphytic flora is equally rich (Figure 1b).

Many species can occur as both epiphytes and non-epiphytes (Figure 1). In the bryophytes, such species are represented by predominantly forest-floor colonisers that also occur on exposed roots, buttresses and the lower parts of trunks, providing the microclimate is suitable. In the lichen flora, such species are predominantly epiphytes that are found on the ground mainly around the buttresses.

A summary of species richness in the habitats surveyed is shown in Table 1. The total flora and the 'typical' flora are shown for each substrate. Species are considered 'typical' of a particular substrate if they occur there in three or more plots, irrespective of their abundance. Depending on the substrate, typical bryophytes range from one-half to about two-thirds of the total bryophyte flora recorded on any individual substrate. The proportions are lower among the lichens, with typical species ranging from just over one-third to just over one-half of the total lichen flora on individual substrates.

Table 1. Richness of major forest habitats surveyed in the study, based on nine plots. Figures in italics in columns three and four show the bryophytes divided into liverworts/mosses.

Habitat	Plant group	Total number of species	'Typical' species (found in≥3 plots)
Smooth bark	bryophytes	84 (54/30)	50 (30/20)
	lichens	84	38
Papery bark	bryophytes	69 (46/23)	35 (22/13)
	lichens	46	16
Eucalypts	bryophytes	27 (18/9)	14 (11/3)
	lichens	33	18
Leaves	bryophytes	-	-
	lichens	4	0
Total epiphytes	bryophytes	101 (66/35)	63 (41/22)
	lichens	126	56
Logs*	bryophytes	60 (42/18)	29 (20/9)
Rocks*	bryophytes	58 (40/18)	32 (19/13)
Inorganic soil*	bryophytes	44 (28/16)	24 (16/8)
Total forest floor	bryophytes	100 (69/31)	57 (37/20)
	lichens	22	9
Total community†	bryophytes	135 (91/44)	88 (60/28)
	lichens	132	59

^{*} For lichens, these substrates support so few species that they were not sampled separately.

[†] Community totals differ from those listed in Jarman and Kantvilas (2001) because some taxa have been combined (see Methods) and species that were not recorded within formal plots are omitted.

Tree trunks represent the major substrate for epiphytes in the forest. Understorey twigs, apart from those of *Bauera* which are poorly colonised, represent an uncommon habitat. The canopy flora of the trees was not studied in detail, but an examination of fallen trees near the plots, and of fallen twigs, indicates that it is composed predominantly of crustose lichens, with very scattered macrolichens represented by genera such as *Hypogymnia*, *Usnea* and *Menegazzia*. No bryophytes were observed from a cursory examination of canopy twigs.

Overall, smooth-barked trees support the richest epiphytic flora, followed by papery-barked trees and then eucalypts (Table 1). For the most part, the same trends are evident on a plot by plot basis (Figure 2) except that, for lichens, eucalypts are generally richer than papery-barked trees (Figure 2a).

1. Smooth-barked trees

Smooth-barked trees are represented mainly by *Nematolepis squamea*, *Pomaderris apetala*, *Banksia marginata* and *Acacia verticillata*. They have small girths, with the largest being about 20 cm diameter (dbh), although *Pomaderris* is typically smaller than the other species.

Nematolepis, partly because of its higher frequency in the plots, supports the greatest number of epiphytic species. However, our observations suggest that mature trees of *Pomaderris* are potentially richer but were too infrequent to enable a meaningful comparison to be undertaken. *Banksia marginata* is a very unfavourable substrate and *Acacia verticillata* is moderate for lichens and extremely poor for bryophytes. Within this general framework, the occurrence of lichens and bryophytes on individual trees is very variable.

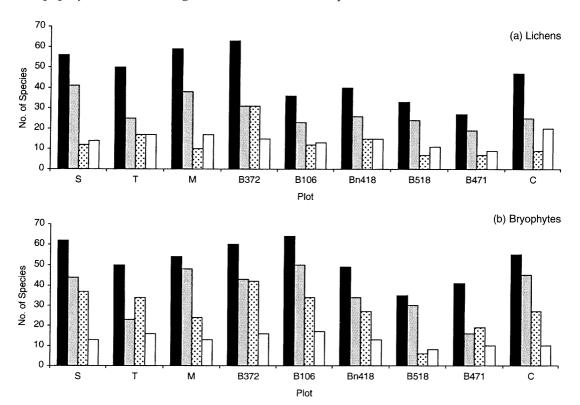


Figure 2. Richness (number of species) of epiphytic lichens (a) and bryophytes (b) for the three main substrate groups in each plot. (\blacksquare = total epiphytes; \blacksquare = smooth bark; \boxdot = papery bark; \Box = eucalypts)



Photo 3. Smooth-barked trunks, showing the mottled appearance produced by abundant crustose lichens. Dispersed patches of bryophytes are evident here as very dark-coloured areas.

Photo 4. The mainly bryophyte-covered lower trunk of a smooth-barked tree, with loose, rounded clumps of Ptychomnion standing out amongst the more appressed shoots of other bryophytes.



A total of 84 lichen species was recorded, with 38 comprising the typical flora (Table 2). Crustose lichens dominate, with the most conspicuous species including *Arthothelium* sp., *Coccotrema* cf. *cucurbitula*, *Micarea alabastrites*, *Micarea prasina* aggr. form A, *Mycoblastus* sp. 1, *Opegrapha stellata*, *Phlyctis* sp., *Thelotrema lepadinum*, *T. suecicum* and *T. subdenticulatum*. These species can produce a very mottled appearance on the trunks (Photo 3), especially on trees with dark-coloured bark that contrasts with the pale-

coloured lichens. There are also numerous other species, including *Arthonia* spp., *Bactrospora* sp. and *Melaspilea* sp. A, that are abundant but very tiny and inconspicuous.

The bryophyte flora comprised 84 species, with 50 being considered typical (Table 2). The flora is more conspicuous on smoothbarked trees than on papery-barked trees and more evenly distributed over the trunk. Forest-floor species that commonly occur as basal epiphytes include *Distichophyllum*

Table 2. Typical flora of smooth-barked trees (present in \geq 3/9 plots). Underlined bryophytes are predominantly basal epiphytes.

Mosses

<u>Cyathophorum bulbosum</u>, Daltonia splachnoides*, Dicranoloma billardierei, D. menziesii, D. robustum, D. setosum, <u>Distichophyllum pulchellum</u>, <u>Fissidens tenellus</u>, Glyphothecium sciurioides, <u>Hypnodendron comosum</u>, <u>Hypnum chrysogaster</u>, H. cupressiforme, <u>Hypopterygium didictyon</u>, Isopterygium limatum, Macromitrium archeri, Ptychomnion aciculare, <u>Rhizogonium novae-hollandiae</u>*, Sematophyllum aggr., Wijkia extenuata, Zygodon intermedius

Thallose liverworts

Metzgeria saccata, Metgeria sp., Riccardia aequicellularis, R. crassa, R. lobulata

Leafy liverworts

<u>Bazzania involuta</u>, Cheilolejeunea campbelliensis, C. mimosa, Chiloscyphus gippslandicus, C. muricatus, Colura saccophylla, Cuspidatula monodon*, Drepanolejeunea aucklandica, Frullania aterrima, F. rostrata, F. ?scandens, Gackstroemia weindorferi, Harpalejeunea latitans, <u>Heteroscyphus fissistipus aggr.</u>, <u>Kurzia hippurioides</u>, Lejeunea drummondii, Lepidozia ulothrix, Radula buccinifera, R. compacta, R. ratkowskiana, R. tasmanica, <u>Telaranea patentissima</u>, <u>Tylimanthus tenellus</u>, <u>Zoopsis argentea</u>, <u>Z. lietgebiana</u>

Lichens

Arthonia tasmanica, Arthonia sp. A, Arthopyrenia spp., Arthothelium sp., Bactrospora sp., Bunodophoron insigne, Cladia aggregata, C. schizopora, Cladonia ramulosa, C. rigida, Coccotrema cf. cucurbitula, Hypogymnia tasmanica, Loxospora solenospora, Megalaria pulverea, Melaspilea sp. A, Menegazzia confusa, Micarea alabastrites, M. cinerea, M. prasina aggr. form A, M. prasina aggr. form B, M. prasina aggr. form D, Mycoblastus sp. 1, Mycoblastus sp. 2, Neophyllis melacarpa, Opegrapha stellata, Parmeliella nigrocincta, Pertusaria jamesii, P. novaezelandiae, Phlyctis sp., Sarrameana albidoplumbea, Strigula albicascens, Thelotrema decorticans, T. lepadinum, T. subdenticulatum, T. suecicum, Thelotremataceae sp. A, Usnea sp., Species A

pulchellum, Heteroscyphus fissistipus aggr., Telaranea patentissima and Zoopsis lietgebiana. The large, fern-like moss Cyathophorum bulbosum was well developed in a few of the plots, mainly on buttresses of Pomaderris. Other common facultative epiphytes that extend further up the trunks (Photo 4) include Dicranoloma billardierei, Ptychomnion aciculare, Sematophyllum aggr., Wijkia extenuata, Riccardia aequicellularis, Metzgeria sp. and Lepidozia ulothrix.

Obligate epiphytes occur mostly above the buttress and are represented by species with closely appressed growth forms. The main families are the Frullaniaceae, Lejeuneaceae and the Radulaceae, and common species include Cheilolejeunea campbelliensis, C. mimosa, Frullania aterrima, F. rostrata, F. ?scandens, Drepanolejeunea aucklandica, Harpolejeunea latitans, Lejeunea drummondii, Radula compacta and R. ratkowskiana.

2. Papery-barked trees

Trees in this group (Melaleuca squarrosa, Leptospermum lanigerum, L. scoparium) have loose, flaky bark (Photos 5–7). Melaleuca has thicker and more spongy bark than the *Leptospermum* species, with a better moisture-holding capacity. Typically, its surface is densely colonised by cyanobacteria and microfungi that form a gelatinous, mucus-like film over the trunk after rain, increasing the bark's capacity to remain moist (Photo 5). Leptospermum species are predominantly single-stemmed but Melaleuca is often multi-stemmed from just above the buttress. Rotting debris often collects in the axils of Melaleuca stems, providing a habitat for some ground colonisers not normally found as epiphytes. The three papery-barked species are generally similar in girth to the smooth-barked trees.

^{*} Very small quantities

Photo 5. The loose, peeling bark of Melaleuca, covered with dark-coloured slime composed mainly of cyanobacteria.



Photo 6 (below). A poorly colonised papery-barked trunk (Leptospermum, right), with a richly colonised smooth-barked stem (small diameter) to the left.



Photo 7. The base of a Melaleuca colonised by the moss Hypopterygium didictyon, characterised by palegreen, fan-shaped shoots.

The flora of papery-barked trees is very inconspicuous above the bryophyte-dominated basal zone. *Melaleuca* supports the richest flora, larger trunks of *Leptospermum lanigerum* usually support a few species and *L. scoparium*, with its very unstable bark that is shed frequently, supports scarcely any species.

A total of 46 lichen species was recorded, with only 16 of these occurring in three or more plots (Table 3). The most common and obvious species on papery bark are ubiquitous epiphytes such as *Cladia aggregata*, various forms of *Micarea prasina*, and species of *Thelotrema*. However, several less conspicuous species show a distinct preference for *Melaleuca*, including *Dactylospora* sp., *Dimerella* cf. *pineti* and *Wawea fruticulosa*, and some uncommon but very unusual taxa were also recorded there, *viz. Steinia geophana*, *Glonium* cf. *stellatum*, *Porina impolita* and *Ramalodium* sp.

Table 3. Typical flora of papery-barked trees (present in \geq 3/9 plots). Underlined bryophytes are predominantly basal epiphytes.

<u>Bryum ?billardierei</u>, Dicranoloma billardierei, D. robustum, D. setosum, Distichophyllum pulchellum, <u>Fissidens tenellus</u>, <u>Hypnodendron comosum</u>, <u>Hypopterygium didictyon</u>, Isopterygium limatum, Macromitrium archeri*, <u>Ptychomnion aciculare</u>, Sematophyllum aggr., Wijkia extenuata

Thallose liverworts

Metgeria sp., Riccardia aequicellularis, Riccardia crassa, Riccardia sp.

Leafy liverworts

Chaetophyllopsis whiteleggei*, Cheilolejeunea mimosa, Chiloscyphus gippslandicus, Drepanolejeunea aucklandica, Frullania aterrima, F. rostrata, Gackstroemia weindorferi, Harpalejeunea latitans, <u>Heteroscyphus fissistipus aggr., H. knightii, Kurzia hippurioides, K. sexfida, Lejeunea drummondii, Radula buccinifera, R. compacta, Telaranea patentissima, Zoopsis argentea, Z. lietgebiana</u>

Lichens

Cladia aggregata, Cladonia ramulosa, C. rigida, Dactylospora sp., Dimerella cf. pineti, Lecidea sp. B, Megalaria pulverea, M. prasina aggr. form A, M. prasina aggr. form B, M. prasina aggr. form D, Mycoblastus sp. 1, Thelotrema decorticans, T. lepadinum, T. subdenticulatum, T. suecicum, Wawea fruticulosa

The bryophyte flora comprises 69 species, of which 35 occurred in three or more plots (Table 3). As with smooth-barked trees, a large component of the flora comprises facultative epiphytes, many of which are confined to the lower trunk. The latter include the distinctive 'large' dendroid mosses *Hypnodendron comosum* and *Hypopterygium didictyon* (mainly on *Melaleuca*) that can form very prominent patches (Photo 6). Three species on *Melaleuca* buttresses are considered unusual as epiphytes. These are *Fissidens tenellus*, *Bryum ?billardierei* and *Heteroscyphus knightii* which were otherwise found predominantly on rocks and inorganic soil.

Among the obligate epiphytes, *Radula* compacta is the most common species but several others, including *Cheilolejeunea* mimosa, *Drepanolejeunea* aucklandica, *Harpalejeunea* latitans, *Frullania* aterrima and *F. rostrata*, are widespread in small quantities.

3. Eucalypts

Only one species of eucalypt, *E. obliqua*, is present in the community. It occurs in a range of diameter classes, with the biggest

trees being well over 200 cm dbh. Due to their size, the largest trees have clearly defined wet and dry sides, as well as pronounced fluting on the buttresses, all of which are important in determining epiphyte distributions. The buttress and bole of the tree are characterised by a thick, fibrous bark, and there are patches of charcoal on most of the larger trees, providing another specialised habitat.

A detailed description of the flora of E. obliqua is currently being prepared for publication elsewhere. Four main communities have been recognised: the dense green 'sock' vegetation that encircles the buttress (Photo 8), dominated by Bazzania involuta and Rhizogonium novae-hollandiae; a community of smaller fine-leafed mosses, Orthodontium *lineare* and *O. pallens*, also on the buttress; a community above these dominated by small and inconspicuous lichens, including *Placynthiella icmalea* which is found mainly on charcoal, Micarea prasina aggr. form A and Cladonia rigida; and a community on the driest parts of the trunk, characterised by minute crustose lichens such as Chaenotheca hygrophila and species of Chaenothecopsis.

^{*} Very small quantities

Table 4. Typical flora of the eucalypts (present in \geq 3/9 plots). Underlined bryophytes are predominantly basal epiphytes, present near ground level.

Mosses

Orthodontium lineare, O. pallens, Rhizogonium novae-hollandiae

Thallose liverworts

Riccardia cochleata, R. crassa

Leafy liverworts

Acromastigum colensoanum, Bazzania involuta, <u>Kurzia hippurioides</u>, <u>K. sexfida</u>, Lepidozia ulothrix, Lepidozia sp. C, <u>Telaranea herzogii</u>, <u>T. patentissima</u>, <u>Zoopsis argentea</u>

Lichens

Chaenotheca hygrophila, Cladia aggregata, C. schizopora, Cladonia ramulosa, C. rigida, C. cf. murrayi, C. subsubulata, C. weymouthii, ?Icmadophila sp., Lecidea cf. botryosa, Melaspilea sp. B, M. prasina aggr. form A, M. prasina aggr. form C, M. prasina aggr. form D, Neophyllis melacarpa, Placynthiella icmalea, Trapeliopsis granulosa, Species C

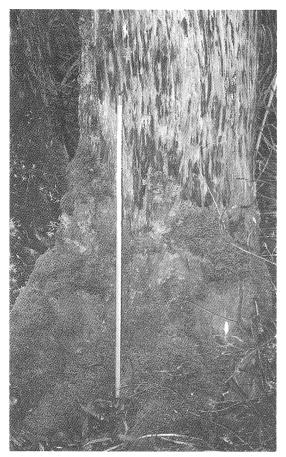


Photo 8. One of the larger regrowth eucalypts with a short basal 'sock' dominated by Bazzania. (Scale rod = 1 m)

Twenty-seven bryophytes and 33 lichens were collected from eucalypts, with 14 and 18 species respectively being considered 'typical' eucalypt colonisers (Table 4).

4. Leaves

Living leaves represent a major habitat for highly specialised lichens in some vegetation types throughout the world, especially tropical rainforest. The foliicolous lichen flora of Tasmania includes a significant assemblage of species, found mainly in certain wet sclerophyll and rainforest communities (McCarthy et al. 2001). In the study site, this component of the flora is extremely impoverished but, nevertheless, four species were recorded, albeit rarely: Aspidothelium cinerascens, Trichothelium assurgens, T. meridionale and Porina subapplanata. The first two of these are rare in a Tasmania-wide context.

Very few bryophytes in Tasmania are exclusively foliicolous and none of these was recorded in the *Gahnia/Bauera* community. However, some of the more ecologically tolerant forest species occur on *Blechnum wattsii* fronds where conditions are particularly moist and sheltered.

Achrophyllum dentatum, Bryum ?billardierei, Dicranoloma billardierei, D. dicarpum, D. menziesii, D. robustum, D. setosum, Distichophyllum pulchellum, Fissidens tenellus, Hypnodendron comosum, Hypnum chrysogaster, Hypopterygium didictyon, Isopterygium limatum, Leucobryum candidum*, Mittenia plumula, Ptychomnion aciculare, Rhizogonium novae-hollandiae, R. pennatum, Sematophyllum aggr., Wijkia extenuata

Thallose liverworts

Metgeria sp., Podomitrium phyllanthus, Riccardia aequicellularis, R. cochleata, R. crassa, R. lobulata, R. ?longiflora, Riccardia sp., Symphyogyna podophylla

Leafy liverworts

Acromastigum colensoanum, Adelanthus falcatus*, Balantiopsis diplophylla, Bazzania involuta, ?Cephaloziella sp. B, Chiloscyphus gippslandicus, Colura saccophylla*, Gackstroemia weindorferi, Heteroscyphus coalitus, H. fissistipus aggr., H. knightii, Kurzia fragilifolia, K. hippurioides, K. sexfida, K. tenax, Lepidozia procera, L. ulothrix, Radula buccinifera, R. compacta*, Schistochila lehmanniana, Telaranea centipes, T. herzogii, T. mooreana, T. patentissima, T. tasmanica, Zoopsis argentea, Z. lietgebiana, Z. setulosa

Lichens

Cladia aggregata, Cladia schizopora, Cladonia ramulosa, Cladonia rigida, Micarea prasina aggr. form A, Micarea prasina aggr. form D, Neophyllis melacarpa, Placopsis sp., Species A

B. THE FOREST FLOOR

The forest floor comprises a mosaic of habitats, including rocks, clay soil and humus, and logs, stumps and litter (branches, twigs, leaves and bark) in various stages of decay. Colonisation of these habitats by cryptogams is affected by the density of *Bauera* and *Gahnia*, and by the distribution of compacted eucalypt litter, especially leaves and bark, that can smother much of the substrate surface. Consequently, the best development of the flora is found on sites raised above the litter and in gaps in the shrub/sedge layer. The availability of such habitats varies from plot to plot.

In this study, clearly defined logs (> 10 cm diameter), rocks and patches of inorganic soil were sampled separately. A composite category, 'forest floor', was also included to incorporate all these substrates, as well as finer woody debris, rotting leaves, humus and any other substrates for non-epiphytes. This category was used to capture all the species of the forest floor without the need to identify the underlying substrate, a time-

consuming task where the substrates are small in area, mixed, and overgrown by a mosaic of bryophytes.

The cryptogamic flora on the forest floor is dominated by bryophytes, a fact attributed to the generally more protected and stable environment there, with higher humidity and lower temperatures than in the upper levels of the forest. Lichens, although present, are few in number and rarely abundant. Canopy lichens attached to fallen twigs and branches, and trunk species attached to decorticating bark can also be found on the forest floor. However, the chances of these surviving in their 'new' habitat appear negligible, and they are not considered typical of the forest floor.

A total of 105 bryophyte species was recorded from the forest floor (98 from the plots), the high number reflecting not only the suitability of this environment but also its heterogeneity. Typical forest floor species are given in Table 5. The most widespread and common mosses include *Dicranoloma billardierei*, *Distichophyllum pulchellum*, *Wijkia*

^{*} Very small quantities

Dicranoloma billardierei, D. robustum, Distichophyllum pulchellum, Hypnodendron comosum, Leucobryum candidum*, Ptychomnion aciculare, Rhizogonium novae-hollandiae, Sematophyllum aggr., Wijkia extenuata

Thallose liverworts

Podomitrium phyllanthus, Riccardia aequicellularis, R. cochleata, R. crassa, R. lobulata, R. ?longiflora

Leafy liverworts

Acromastigum colensoanum, Bazzania involuta, Heteroscyphus fissistipus aggr., Kurzia fragilifolia, K. hippurioides, K. tenax*, Lepidozia procera, L. ulothrix, Schistochila lehmaniana, Telaranea herzogii, T. patentissima, Zoopsis argentea, Z. lietgebiana

Lichens

Cladia aggregata, C. schizopora, Cladonia ramulosa, C. rigida, Micarea prasina aggr. form D, Neophyllis melacarpa

extenuata, Ptychomnion aciculare and Sematophyllum aggr., and Hypnodendron comosum can be locally common. Among the liverworts, the family Lepidoziaceae is very well represented, with several very small species being so abundant that they can dominate the flora locally (e.g. Kurzia hippuroides, Telaranea patentissima, Zoopsis argentea and Z. lietgebiana). Heteroscyphus fissistipus aggr. and several species of Riccardia (R. aequicellularis, R. cochleata, R. lobulata, R. crassa) are also widespread. A minute, possibly lichenised ascomycete (Species A in Appendix 2) is sometimes common on bryophyte leaves.

Twenty-two lichens were recorded on the forest floor but most of these are essentially epiphytes that extend onto raised ground in the vicinity of tree buttresses or persist on fallen logs. It is noteworthy that species typical of the forest floor in wet eucalypt forests in general, for example, *Peltigera dolichorhiza* and species of *Placopsis*, *Dibaeis* and *Baeomyces*, are absent or present in only very small quantities in the study site.

A specialised forest floor habitat for a few species is the rotting bases of *Gahnia* leaves and their associated soil. Two tiny, superficially similar lichens, *Gyalideopsis* hyalinescens and Dimerella cf. lutescens, are restricted to this habitat and a tiny, very fragile liverwort, Kurzia fragilifolia, is most common there. Another specialised habitat is that of animal droppings, which provide the main substrate for two mosses, Tayloria octoblepharum and the distinctive endemic T. gunnii. Given their substrate, it follows that the occurrence of these two species is rather unpredictable.

1. Logs (woody debris greater than 10 cm)

Logs exhibit various levels of decay, from a very advanced state which is almost humus to recently fallen trunks with very solid wood. All of the larger logs, some greater than 1.5 m diameter, are derived from eucalypts (Photos 9, 10).

Logs are generally well-colonised, except the most recently fallen ones or those overgrown by *Bauera* and *Gahnia*. The flora is overwhelmingly dominated by bryophytes but a few lichen species are also present. Where the logs are particularly large, leaf litter is able to accumulate on the broad upper surface, and as it becomes compacted, the cryptogams are eventually smothered and die. This same feature was noted by Ashton (1986) in *E. regnans* forests in Victoria.

^{*} Very small quantities



Photo 9. A solid log showing early colonisation by bryophytes.



Photo 10. An old log with a dense cover of bryophytes providing a moist bed for ferns.

Fifty-nine bryophyte species were recorded from the logs, of which 29 are considered typical (Table 6). Common bryophytes include several of the larger, more ubiquitous species listed in the forest floor category. Three thallose liverworts, *Podomitrium phyllanthus, Riccardia ?longiflora* and *R. cochleata*, and the leafy liverwort *Acromastigum colensoanum* are predominantly wood colonisers in this community. The

moss *Rhizogonium novae-hollandiae*, when not growing epiphytically, is common only on large logs (see below).

The lichens present on logs are almost exclusively species which also occur on eucalypt buttresses, for example, *Cladia aggregata*, *C. schizopora*, *Cladonia ramulosa*, *C. rigida*, *Micarea prasina* aggr. form D and *Neophyllis melacarpa*. Only one species, the uncommon *Micarea* sp., was recorded from logs but was not found on standing eucalypts.

Large logs compared to small logs.—Only a superficial comparison between small (less than 50 cm diameter) and large logs was undertaken. Whilst there appeared to be no significant differences in species composition, differences in species abundance and distribution are apparent. The curved sides (but not the top surface) of the very large logs usually support dense masses of *Rhizogonium novae-hollandiae*, a species that is very rare on small logs. The filmy fern *Hymenophyllum flabellatum* occupies a similar microhabitat but was found in only a few plots. It was not recorded on small logs.

Large 'mossy' logs also appear to play an important role in vascular plant succession. In several plots, seedlings and saplings of rainforest species such as *Eucryphia lucida*, *Phyllocladus aspleniifolius* and *Atherosperma moschatum* were found on large logs but were rare elsewhere in the community. These species are important in the vegetation succession from sclerophyll forest to rainforest and, although not common in any of the plots, their presence indicates the potential for significant long-term change in the vegetation in the absence of major disturbance.

2. Rocks

Small dolerite rocks occur in all the plots and vary greatly in number, prominence and level of colonisation (Photos 11, 12). Irrespective of species abundance, some rocks are dominated by only one or two species; others have more complex mixtures of several co-dominants. Lichens are almost

invariably poorly developed, being outcompeted by bryophytes.

Fifty-eight bryophyte species were recorded in the plots, and a further four were recorded from a large rock near plot B471 (see below). Thirty-two species are considered typical (Table 7), and most of the common ones are widespread in forest floor habitats. Species clearly associated with rocks include the minute moss Fissidens tenellus, which is rare elsewhere in the community except on some Melaleuca squarrosa buttresses. It normally grows on the steeper faces of the rocks, away from competition from the larger bryophytes that can easily overgrow it. Heteroscyphus knightii and Bryum ?billardierei are also associated with rocks, the former growing on the more sheltered sides and the latter occurring on the top surfaces. Several other species which were rare in the forest (e.g. Plagiochila ?baileyana, P. retrospectans and Adelanthus falcatus) were recorded only or mainly on rocks. These species are common in some rainforest communities.

Large rocks.—A single large rock, rising over three metres above the ground at its highest point, was examined near plot B471 (Photo 13). It supported a rich and very distinct flora (26 species; Table 8), indicating that large rocks can be very important sources of biodiversity. Several species present, including *Grimmia* sp., *Racomitrium* sp., *Polytrichum juniperinum*, *Jamesoniella colorata*, *Baeomyces heteromorphus* and ?Lepraria sp., were not found in the main plots. Three other very uncommon species (found once only in the plots) were also present (*Campylopus* sp., *Plagiochila retrospectans* and *Jamesoniella tasmanica*).

Further study of large rocks (and rockfaces) is needed to gain a better understanding of their flora. We would expect the flora to become more distinct with increasing size (height) of the rocks, as it becomes more distant from the cool humid conditions near the ground. The steepness of the rock surfaces is likely to be important also (Ashton 1986), since the greater the inclination, the

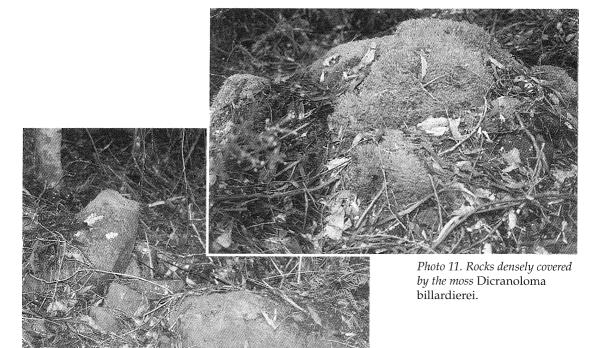
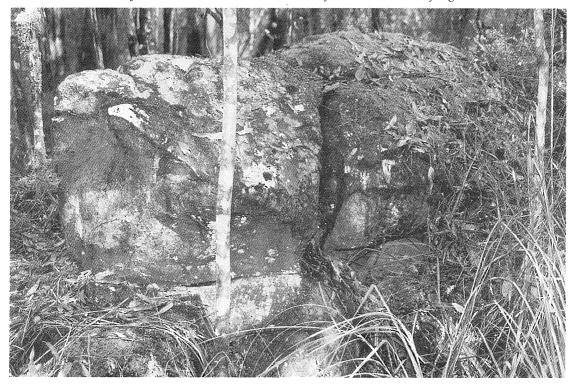


Photo 12. Several small rocks with few cryptogams present.

Photo 13. A large rock near plot B471, well-covered with cryptogams where the surface is not smothered by Bauera or litter. Note the densely colonised smooth-barked trees on the left (behind) and in the foreground.



Achrophyllum dentatum*, Bryum ?billardierei*, Dicranoloma billardierei, D. menziesii, Distichophyllum pulchellum, Fissidens tenellus, Hypnodendron comosum, Hypnum chrysogaster, Hypopterygium didictyon, Isopterygium limatum, Ptychomnion aciculare, Sematophyllum aggr., Wijkia extenuata

Thallose liverworts

Metzgeria sp., Riccardia aequicellularis, R. crassa, Symphyogyna podophylla

Leafy liverworts

Balantiopsis diplophylla, Bazzania involuta, Heteroscyphus fissistipus aggr., H. knightii, Kurzia hippurioides, K. sexfida, Lepidozia procera, L. ulothrix, Telaranea centipes, T. herzogii, T. patentissima, T. tasmanica, Zoopsis argentea, Z. lietgebiana, Z. setulosa.

Lichens

Placopsis sp.

Table 8. Species occurring on a single large rock near plot B471.

Mosses

Bryum ?billardierei, Campylopus sp., Dicranoloma setosum, Fissidens tenellus, Grimmia sp., Hypnum chrysogaster, Hypopterygium didyction, Isopterygium limatum, Polytrichum juniperinum, Racomitrium sp., Sematophyllum aggr., Thiudium sparsum, Wijkia extenuata

Thallose liverworts

Riccardia aequicellularis

Leafy liverworts

Adelanthus falcatus, ?Cephaloziella sp., Chiloscyphus gippslandicus, Gackstroemia weindorferi, Heteroscyphus fissistipus aggr., H. knightii, Jamesoniella colorata, J. tasmanica, Kurzia hippurioides, Lepidozia ulothrix, Radula compacta, Telaranea patentissima

Lichens

Baeomyces heteromorphus, Cladia aggregata, Cladonia rigida, ?Lepraria sp., Micarea prasina aggr., Placopsis sp.

less chance there is of litter accumulating to smother the plants or decomposing there in a thin layer of humus that would buffer the special characteristics of the rock surface. For the lichens, it is usually only the larger rocks that provide extensive bare surfaces for colonisation. The smaller ones, close to the ground surface, are readily overgrown by bryophytes.

3. Inorganic soil

Patches of exposed inorganic soil are present mostly as low mounds compacted after the

roots of windthrown trees have long since rotted, or as relatively dry, very shaded patches under logs. Where trees have fallen more recently, soil held amongst the upturned roots can be raised 2–3 m or more above the ground surface. Such habitats were under-represented in this study but observations elsewhere suggest that they can support a very distinct flora.

Forty-four bryophyte species were recorded from soil, 24 of which are considered typical (Table 9). Most are widespread across forest floor habitats but there is also a small suite

^{*} Very small quantities

Bryum ?billardierei*, Distichophyllum pulchellum, Fissidens tenellus, Hypnum chrysogaster, Mittenia plumula, Ptychomnion aciculare, Sematophyllum aggr., Wijkia extenuata

Thallose liverworts

Metzgeria sp., Riccardia aequicellularis, R. crassa, Riccardia lobulata, Symphyogyna podophylla

Leafy liverworts

Balantiopsis diplophylla, Bazzania involuta, Heteroscyphus fissistipus aggr., Kurzia hippurioides, K. sexfida, Telaranea centipes, T. herzogii, T. patentissima, T. tasmanica, Zoopsis argentea, Z. lietgebiana.

Lichens

nil

that shows a distinct preference for inorganic soil: Fissidens pallidus (uncommon), Balantiopsis diplophylla (widespread), Mittenia plumula (uncommon), Symphyogyna podophylla (widespread) and Telaranea centipes (widespread). Some of these have also been recorded in very small amounts from rocks.

Although soil lichens are common in more open eucalypt forest, the vegetation at the study site appears to be too moist and shaded for most species, and they are unable to compete with bryophytes. However, three rare and interesting species were found, mostly in marginally drier sites under logs (*Mycobilimbia* sp. and *Micarea sylvicola*) and on soil around *Gahnia* (*Gyalidea hyalinescens*).

Discussion

For lichens and bryophytes, a small patch of forest is equivalent to a landscape of different habitats for vascular species (Kantvilas 1990). Although the scale is different, the vascular and non-vascular floras respond similarly, with different associations of species characterising each habitat. Factors affecting the distribution of bryophytes and lichens have been discussed by many workers, and include microclimate, the physical and chemical nature of the substrates, forest continuity, and the dispersal

and competitive ability of the species (see, for example, Billings and Drew 1938; Richards 1984; Kantvilas 1988, 1990; Kantvilas and Minchin 1989; Laaka 1992; Söderström 1988a; Hallingbäck and Hodgetts 2000).

Habitat specialisation

The flora can be divided into two groups, ecological generalists and specialists, based on the level of habitat specialisation the species display. These terms are adapted from Northern Hemisphere studies (e.g. Cornelisson and ter Steege 1989; Andersson and Hytteborn 1991) and the broad concept has been applied by many authors (e.g. Hedenas and Ericson 2000; Cooper-Ellis 1998; Holien 1996). Generalists are the apparently indiscriminate colonisers that occur on a wide range of substrates (logs, rocks, soil, and bark of a variety of hosts), providing the microclimate is suitable. Specialists, on the other hand, are totally restricted to or display a clear preference for a particular substrate. The particular category a species is placed in is very much site-specific, and a species that is a generalist in one vegetation type may well occupy a narrower, specialist niche in another.

Generalist bryophytes are common in the study area (see Appendix 1) and include species such as *Ptychomnion aciculare*, *Wijkia*

^{*} Very small quantities

extenuata, Sematophyllum aggr., Bazzania involuta, and Lepidozia ulothrix. Lichens such as Cladia aggregata and Micarea prasina aggr. form A are also examples of generalist species. The relatively low number of generalists amongst the lichens (Appendix 2) compared to bryophytes is attributed mainly to their inability to compete successfully with bryophytes in the shady moist conditions of the forest floor.

Among the specialists, the degree and nature of specialisation varies. For some lichens in particular, specialisation appears to be linked to a physical attribute of the substrate. This has been observed previously among the epiphytes in Tasmanian rainforest (Kantvilas et al. 1985) and is the rationale behind the stratified sampling approach used in this study. The distribution of species is influenced by the physical nature of the bark—whether, for example, it is smooth or rough, spongy, fibrous or flaky, or consistently wet or dry. Thus, the preference of species of Chaenothecopsis for eucalypts is interpreted (on the basis of their occurrence elsewhere) as a preference for dry, old bark, a habitat available in the plots only on oldgrowth Eucalyptus obliqua.

Habitat specialisation is also apparent among the non-epiphytic species. For example, Fissidens pallidus, Mittenia plumula, Balantiopsis diplophylla, Symphyogyna podophylla and Telaranea centipes were common only on inorganic soil, and Heteroscyphus knightii and Bryum ?billardierei occurred mainly on rocks and inorganic soil. The lichens Gyalideopsis hyalinescens and Dimerella cf. lutescens are restricted to the rotting leaf bases of dead Gahnia plants and the associated soil, and the liverwort Kurzia fragilifolia is most common there. Two Tayloria species occurred only on animal droppings.

Some species considered specialists in the Warra plots show a less restricted distribution outside the study area. For example, *Wawea fruticulosa* can occur on any thick, wet spongy surface. In the Warra plots, it was restricted to *Melaleuca*, but it is known to colonise a range of substrates with similar attributes in other vegetation types. *Lopidium concinnum* and *Sarrameana albidoplumbea* were restricted to the smoothbarked tree *Pomaderris*, and *Zygodon intermedius* and *Daltonia splachnoides* show a distinct preference for it, but all of these species occur outside the study area on other smooth-barked hosts, or in some cases, even on other substrate types.

The relative richness of different substrates

Smooth-barked trees form the single, most important habitat in terms of supporting the greatest diversity of species. A combined flora of 170 lichens and bryophytes was recorded from this habitat, representing just over 60% of the species in the entire community. These trees also support the largest number of specialist species.

Papery-barked trees support a smaller flora, much of which is also present on smooth-barked trees. However, there are some species such as *Dactylospora* sp. and *Wawea fruticulosa* that were recorded only on this substrate and some which showed a preference for it, even though found in minute amounts elsewhere. No bryophytes were restricted to papery-bark trees but several forest floor species (e.g. *Riccardia* sp., *Heteroscyphus knightii*, *Bryum ?billardierei*) were only ever recorded as epiphytes on this substrate.

The flora of eucalypts is relatively small but very different from that of other trees. Seventy per cent of all lichens found on eucalypts and more than half (56%) of those considered typical of the habitat are specialists. A smaller proportion of the bryophyte flora of eucalypts are specialists but of the four most common species in the habitat, two are specialists and one is abundant only on standing eucalypts or on eucalypt logs. The low numbers and minute amounts of generalists on eucalypts is also intriguing. For example, even though many bryophyte generalists occur on the forest floor

and on buttresses of understorey trees, very few occur on the eucalypt buttresses in spite of the habitat being in the most suitable (for bryophytes) microclimatic zone of the forest.

It is difficult to compare the relative importance of the substrates on the forest floor because of very obvious differences in their proportional representation. However, each of the three habitats sampled separately supports some specialist species and makes a unique contribution to forest diversity. It is likely that the floras of rocks and inorganic soil in particular would be richer, and include higher numbers of specialist species, if the sampling were extended to include more examples of large rocks or windthrown trees with exposed soil on their upturned roots (see also Ashton 1986).

Management implications

Our results suggest some of the problems likely to be encountered in wood production forests that are also being managed for the conservation of species diversity or for ecological sustainability. The discussion here is directed at the harvested units, not the entire managed landscape.

Generalist species are likely to cause least concern for forest managers. A silvicultural regime that results in environmental conditions that broadly mimic those found in the interior of wet forests of the area is likely, in the long term, to accommodate their requirements because any one of several substrates will satisfy their needs.

Specialist species are likely to pose a more complex problem because of their more narrowly defined substrate requirements. Obligately epiphytic species are particularly vulnerable, especially those that show specificity for understorey trees or shrubs, since there is no emphasis on understorey regeneration in production forests. The extent of recovery of a wet sclerophyll understorey following logging and burning treatments is unknown. In mixed forest (eucalypt forest

with a rainforest understorey: Gilbert 1959), a study comparing 20-30-year old wildfire regeneration and silvicultural regeneration of the same age showed little difference in vascular plant composition and frequency of the common understorey plants (Hickey 1994). Regrowth from both sources is expected to eventually become mature mixed forest (in the absence of further disturbance). In the present study, the recovery after logging of an understorey similar in vascular plant composition and structure to that present before logging is considered critical in regaining the pre-logging cryptogamic flora, especially with respect to specialist species.

As a habitat for cryptogams, the eucalypts themselves are not without problems even though they are certain to be replaced in abundance in the regenerating forest. The fact that large, old trees support species not found on young ones (manuscript in prep.) is likely to result in changes in the epiphytic flora in short-rotation forests.

Other complications for the forest's epiphytes are apparent in the localised nature of certain species whose occurrence in the study site is linked not just to a particular microhabitat but to a particular individual tree on a plot (Jarman and Kantvilas 2001). Thus at our current level of knowledge, the occurrence of many of the rare species, or of species-rich host trees, seems to be a chance event, and to interpret the observed pattern more rigorously will require much study of the autecology of individual species.

Removal or disturbance of some forest floor habitats such as small logs, decaying litter, inorganic soil and rocks, will probably have little long-term impact on the flora. However, large logs, tall stumps and large windthrown trees (with soil elevated high above the ground) are potentially vulnerable habitats. Although few tall stumps were encountered in the plots, our observations from other wet eucalypt forests in Tasmania indicate that large, rotting stumps, whether

from wind damage or past logging, represent a special habitat for several drywood colonisers. With modern forestry methods, trees can be cut so low to the ground that the stumps do not project beyond the humid bryophyte-dominated zone of the forest, and dry-wood habitats required for certain lichen specialists are unlikely to develop. Furthermore, the forest floor can be cleared of recently felled eucalypt logs so efficiently that large logs will become increasingly scarce with successive rotations in production forests (Forestry Tasmania 1999). This is certainly of concern in Northern Hemisphere forests (e.g. Söderström 1988b; Andersson and Hytteborn 1991; Laaka 1992; Hallingbäck 1998; Rambo and Muir 1998) and has contributed to the recent establishment of a study on decaying logs by Forestry Tasmania (Forestry Tasmania 1999).

Where silvicultural treatments involve the use of hot burns that consume the vegetation, it can be assumed that most recolonisation by cryptogams takes place from propagules originating outside the coupe. All coupes in the present study are bordered on at least three sides by uncut forest likely to contain most of the species found on the plots. However, there are no data on the dispersal ability of Tasmania's wet forest cryptogams or on the conditions required for their establishment. There is no doubt that individual species will vary greatly in the time taken to move into the new forest, and some will be extremely slow, moving in a stepwise manner via vegetative reproduction. Those that can disperse successfully will only be able to establish if suitable habitats and micro-environments have developed, which is also likely to be a lengthy process. Timing of the next harvest in both the coupe and in the adjacent forest is therefore likely to be a critical factor in ensuring that there is no reduction in biodiversity at the coupe level as a result of the silvicultural treatment.

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References

Andersson, L.I. and Hytteborn, H. (1991). Bryophytes and decaying wood — a comparison between managed and natural forest. *Holarctic Ecology* 12: 121–130.

Ashton, D.H. (1986). Ecology of bryophytic communities in mature *Eucalyptus regnans* F. Muell. forest at Wallaby Creek, Victoria. *Australian Journal of Botany* 34: 107–129.

Billings, W.D. and Drew, W.B. (1938). Bark factors affecting the distribution of corticolous bryophytic communities. *American Midland Naturalist* 20: 302–330.

Cooper-Ellis, S. (1998). Bryophytes in old-growth forests of western Massachusetts. *Journal of the Torrey Botanical Society* 125 (2): 117–132.

Cornelissen, J.H.C. and ter Steege, H. (1989). Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology* 5: 131–150.

Forestry Tasmania (1999). Division of Forest Research and Development Annual Report 1998/1999. Forestry Tasmania, Hobart.

Gilbert, J.M. (1959). Forest succession in the Florentine Valley, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 93: 129–151.

Hallingbäck, T. (1998). Threats and protection of bryophytes in Sweden. *Journal of the Hattori Botanical Laboratory* 84: 175–185.

Hallingbäck, T. and Hodgetts, N. (compilers) (2000). *Mosses, Liverworts and Hornworts. Status Survey and Conservation Action Plan for Bryophytes.* IUCN, Gland, Switzerland, and Cambridge, UK.

- Hedenas, H. and Ericson, L. (2000). Epiphytic macrolichens as conservation indicators: successional sequence in *Populus tremula* stands. *Biological Conservation* 93: 43–53.
- Hickey, J.E. (1994). A floristic comparison of vascular species in Tasmanian oldgrowth mixed forest with regeneration resulting from logging and wildfire. *Australian Journal of Botany* 42: 383–404.
- Hickey, J.E. and Neyland, M.G. (2000). Testing silvicultural options for mixed forest (*Eucalyptus–Nothofagus*) regeneration in Tasmania. In: *Sustainable Management of Indigenous Forest* (eds G.H. Stewart, U. Benecke and J. Hickey), pp. 65–73. Proceedings of a symposium held at 'Southern Connection' Congress III, Lincoln University, Canterbury, New Zealand, 17–22 January, 2000.
- Hickey, J.E., Neyland, M.G. and Bassett, O.D. (2001). Rationale and design for the Warra silvicultural systems trial in wet *Eucalyptus obliqua* forests in Tasmania. *Tasforests* 13 (2): 155–182.
- Holien, H. (1996). Influence of site and stand factors on the distribution of crustose lichens of the Caliciales in a suboceanic spruce forest area in central Norway. *Lichenologist* 28 (4): 315–330.
- Jarman, S.J. and Kantvilas, G. (2001). Bryophytes and lichens at the Warra LTER site. I. An inventory of species in *Eucalyptus obliqua* wet sclerophyll forest . *Tasforests* 13 (2): 193–216.
- Kantvilas, G. (1988). Tasmanian rainforest lichen communities: a preliminary classification. *Phytocoenologia* 16: 391–428.
- Kantvilas, G. (1990). Succession in rainforest lichens. Tasforests 2: 167–171.
- Kantvilas, G., James, P.W. and Jarman, S.J. (1985). Macrolichens in Tasmanian rainforest. *Lichenologist* 17: 67–83.
- Kantvilas, G. and Minchin, P. (1989). An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. *Vegetatio* 84: 99–112.
- Laaka, S. (1992). The threatened epixylic bryophytes in old primeval forests in Finland. *Biological Conservation* 59: 151–154.
- McCarthy, P.M., Kantvilas, G. and Vezda, A. (2001). Foliicolous lichens in Tasmania. *Australian Lichenology* 48: 16–26.
- Rambo, T.R. and Muir, P.S. (1998). Bryophyte species associations with coarse woody debris and stand ages in Oregon. *The Bryologist* 101: 366–376.
- Richards, P.W. (1984). The ecology of tropical forest bryophytes. In: *New Manual of Bryology* 2 (ed. R.M. Schuster), pp. 1233–1270. The Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan.
- Söderström, L. (1988a). Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. *Nordic Journal of Botany* 8 (1): 89–97.
- Söderström, L. (1988b). The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in northeast Sweden. *Biological Conservation* 45: 169–178.

Appendix 1. Distribution of bryophyte species, shown as the frequency on different substrates in nine plots. The final column shows frequency irrespective of substrate. Brackets indicate a record outside the main plots.

	Smooth bark	Papery bark	Eucalypts	Logs	Rocks	Inorganic soil	Total forest floor	Total plots (all substrates)
Mosses	•							
Achrophyllum dentatum	1	2	-	1	4	_	7	8
Bryum ?billardierei	-	3	-	-	8	5	9	9
Calyptopogon mnioides	1	-	-	-	-	-	-	1
Campylopus sp.	-	-	-	-	1	-	1	1
Cyathophorum bulbosum	3	-	-	-	-	-	1	3
Daltonia splachnoides	5	_	-	-	-	-	-	5
Dicranoloma billardierei	9	9	2	8	8	2	9	9
Dicranoloma dicarpum	-	-	-	2	-	1	4	4
Dicranoloma menziesii	3	1	-	1	3	1	5	7
Dicranoloma robustum	4	3	-	5	-	1	7	8
Dicranoloma setosum	7	5	1	2	-	1	3	8
Dicranum trichopodum	1	1	-	-	-	-	-	1
Distichophyllum pulchellum	8	6	-	7	7	6	9	9
Distichophyllum rotundifolium	-	2	-	-	1	-	1	2
Fissidens pallidus	-	-	-	-	-	2	2	2
Fissidens tenellus	3	7	-	-	9	3	9	9
Glyphothecium sciuroides	4	-	-	-	-	-	-	4
Grimmia sp.	-	-	-	-	[1]	-	-	
Hampeella alaris	1	1	-	-	-	-	-	1
Holomitrium perichaetiale	-	-	-	-	-	-	1	1
Hypnodendron comosum	5	6	-	3	4	2	8	9
Hypnum chrysogaster	5	2	1	2	4	3	7	8
Hypnum cupressiforme	3	-	-	-	-	-	-	3
Hypopterygium didictyon	3	8	-	2	3	-	6	9
Isopterygium limatum	4	8	-	1	3	-	4	8
Leptostomum inclinans	1 1	1	-	-	-	-	-	1
Leptotheca gaudichaudii	1	_	- 1	4	-	-	- 4	1 5
Leucobryum candidum Lopidium concinnum	2	_	-	4	_	_	4	2
Macromitrium archeri	4	4	-	-	-	_	-	7
Mittenia plumula	-	-	_	_	1	4	4	4
Orthodontium lineare	_	_	9	1	-	-	2	9
Orthodontium pallens	_	_	9	-	_	_	1	9
Polytrichum juniperinum	_	_	_	_	[1]	_	_	
Ptychomnion aciculare	8	8	_	7	8	4	9	9
Racopilum cuspidigerum	-	-	_	-	1	_	1	1
Racomitrium sp.	_	_	_	_	[1]	_	-	Î
Rhizogonium novae-hollandiae	5	1	9	8	1	-	9	9
Rhizogonium pennatum	-	-	-	1	_	_	3	3
Sematophyllum aggr.	9	9	1	7	8	6	9	9
Tayloria gunnii	-	-	-	_	-	-	2	2
Tayloria octoblepharum	-	-	-	-	-	-	1	1
Thuidium sparsum	-	2	-	-	-	1	1	2
Weymouthia cochlearifolia	1	-	-	-	-	-	-	1
Wijkia extenuata	7	5	1	7	6	5	9	9
Zygodon hookeri	1	1	-	-	-	-	-	1
Zygodon intermedius	4	-	-	-	-	-	-	4

	Smooth bark	Papery bark	Eucalypts	Logs	Rocks	Inorganic soil	Total forest floor	Total plots (all substrates)
Thallose liverworts								
Hymenophyton flabellatum	-	-		-	-	1	1	1
Metzgeria saccata	5	1	-	-	-	-	1	7
Metzgeria sp.	9	8	1	2	5	3	9	9
Podomitrium phyllanthus	-	-	2	7	2	1	7	7
Riccardia aequicellularis	6	7	-	5	8	6	9	9
Riccardia cochleata	-	2	6	8	1	2	9	9
Riccardia crassa	3	4	6	8	8	7	9	9
Riccardia lobulata	4	1	-	3	2	4	7	7
Riccardia ?longiflora	-	-	-	4	2	1	6	6
Riccardia wattsiana	-	-	-	1	-	-	1	
Riccardia sp.	-	3	-	-	1	1	4	5
Symphyogyna podophylla	-	-	-	1	3	6	6	7
Treubia tasmanica	-	-	-	-	1	-	1	1
Leafy liverworts								
Acrobolbus concinnus	2	1	_	_	_	_	_	3
Acrochila biserialis	_	1	_	_	_	_	-	1
Acromastigum anisostomum	_	2	1	_	-	_	-	2
Acromastigum colensoanum	1	_	4	6	1	2	7	7
Acromastigum mooreanum	1	_	_	1	_	_	2	3
Adelanthus falcatus	-	-	-	-	2	-	3	3
Balantiopsis diplophylla	1	-	-	-	8	7	9	9
Bazzania involuta	7	2	9	8	6	3	9	9
Bazzania monilinervis	-	-	1	-	-	-	-	1
Bazzania ?novo-zelandiae	-	-	-	1	-	-	1	1
?Cephaloziella sp. A	3	-	-	2	1	-	1	
?Cephaloziella sp. B	4	1	-	-	-	1	3	
Chaetophyllopsis whiteleggei	2	3	-	2	-	-	2	5
Cheilolejeunea albovirens	1	-	-	-	-	-	-	1
Cheilolejeunea campbelliensis	6	2	-	-	-	-	1	6
Cheilolejeunea comitans	2	1	-	-	-		1	2
Cheilolejeunea mimosa	5	5	-	-	-	-	-	5
Chiloscyphus echinellus	2	1	-	-	2	-	2	4
Chiloscyphus gippslandicus	4	3	-	1	-	-	3	6
Chiloscyphus muricatus	2	2	-	-	-	-	-	4
Chiloscyphus semiteres	2	-	-	-	-	-	2	4
Chiloscyphus sp.	2	1	-	-	-	-	2	4
Colura saccophylla	5	2	-	-	-	-	4	6
Cuspidatula monodon	3	-	-	-	-	-	-	3
Drepanolejeunea aucklandica	5	4	-	-	-	-	1	6
Frullania aterrima	9	6	-	-	-	-	-	9
Frullania falciloba	1	-	-	-	-	-	-	1
Frullania probosciphora	1	1	-	-	-	-	-	2
Frullania rostrata	9	8	-	1	-	-	1	9
Frullania ?scandens	8	1	-	-	-	-	-	8
Gackstroemia weindorferi	8	5	-	2	1	-	4	8
Geocalyx caledonicus	-	-	-	1	-	-	1	1

	Smooth bark	Papery bark	Eucalypts	Logs	Rocks	Inorganic soil	Total forest floor	Total plots (all substrates)
Harpalejeunea latitans	5	6	-	 _	-	-	_	7
Heteroscyphus coalitus	-	-	-	-	1	1	4	4
Heteroscyphus conjugatus	-	-	-	1	-	-	1	1
Heteroscyphus cymbaliferus	-	-	-	[1]	-	-	-	
Heteroscyphus decipiens	-	-	-	1	-	-	1	1
Heteroscyphus fissistipus aggr.	8	8	-	4	8	6	9	9
Heteroscyphus knightii	-	4	-		-5	1	7	7
Heteroscyphus limosus	-	-	-	1	1	1	2	2
Jamesoniella colorata	-	-	-	-	[1]	-	-	
Jamesoniella tasmanica	-	-	-	-	1	-	2	2
Kurzia fragilifolia	-	-	-	3	_	-	6	6
Kurzia hippurioides	6	9	9	8	9	8	9	9
Kurzia sexfida	3	7	3	4	7	5	8	8
Kurzia tenax	-	-	-	3	-	-	5	5
Lejeunea drummondii	6	3	-	-	-	-	1	6
Lepicolea scolopendra	1	-	-	-	-	-	-	1
Lepidolaena brachyclada	1	-	-	-	-	-	- tal	1
Lepidozia glaucophylla	-	-	-	_	-	-	[1]	0
Lepidozia procera	2	2	-	6	4	-	9	9
Lepidozia ulothrix	8	2	7	8	6	2	9	9
Lepidozia sp. C	-	-	7	-	-	-	-	7
Lepidozia sp. L	-	-	-	1	1	-	1	1
Lepidozia sp. W	-	-	2	1	1	-	2	3
?Leptophyllopsis laxa	-	2	-	- 1	-	-	1	2
Marsupidium surculosum	-	-	-	1	2 1	-	2 2	2 2
Plagiochila?baileyana	1	-	-	-	1	-	1	2
Plagiochila ?fasciculata Plagiochila retrospectans	1	-	-	-	1	-	1	1
Radula buccinifera	8	5	-	-	1	-	3	9
Radula compacta	9	8	-	-	-	-	4	9
Radula multiamentula	1	-	-	-	-	-	+	1
Radula ratkowskiana	8	2	_	_		_	1	8
Radula tasmanica	5	_	_	_	_	_	1	5
Radula sp.	2	1	_	_	_	_	_	2
Saccogynidium decurvum	_	-	_	1	_	_	2	2
Schistochila lehmanniana	_	_	_	3	_	_	3	$\frac{2}{4}$
Telaranea centipes	_	_	_	_	6	8	9	9
Telaranea grossiseta	1	_	_	_	_	_	1	2
Telaranea herzogii	$\hat{1}$	2	4	3	3	7	8	8
Telaranea mooreana	_	_	_	2	_	1	6	6
Telaranea patentissima	9	6	6	8	9	8	9	9
Telaranea tasmanica	1	1	1	1	6	8	9	9
?Тетпота sp.	_	_	-	1	_	_	1	1
Tylimanthus diversifolius	_	-	-	-	1	-	1	1
Tylimanthus pseudosaccatus	_	_	-	-	_	-	[1]	
Tylimanthus tenellus	4	1	_	-	-	-	- 1	4
Zoopsis argentea	6	4	8	8	7	5	9	9
Zoopsis leitgebiana	5	4	-	6	8	8	9	9
Zoopsis setulosa	-	1	-	2	4	1	4	6
Unknown sp. 1	1	_	_	_	_	_	_	1

Appendix 2. Distribution of lichen species, shown as the frequency on different substrates in nine plots. The final column shows frequency irrespective of substrate. Brackets indicate a record outside the main plots.

	Smooth bark	Papery bark	Eucalypts	Ground	Leaves	Total plots (all substrates)
Anisomeridium aff. biforme	1	-	-	-	-	1
Arthonia apteropteridis	1	-	-	-	-	1
Arthonia ilicina	2	-	-	-	-	2
Arthonia subramulosa	1	-	-	-	-	1
Arthonia tasmanica	5	-	-	-	-	5
Arthonia sp. A	5	-	1	-	-	6
Arthonia sp. B	-	-	2	-	-	2
Arthopyrenia spp.	3	-	-	-	-	3
<i>Arthothelium</i> sp.	9	-	-	-	-	9
Aspidothelium cinerascens	-	-	-	-	1	1
Austroblastenia pauciseptata	1	-	-	-	-	1
Bactrospora sp.	4	-	-	-	-	4
Baeomyces heteromorphus	-	-	-	[1]	-	
Balpalmuia buchananii	2	2	-	1	-	3
Bunodophoron australe	1	1	-	-	-	2
Bunodophoron insigne	3	-	-	-	-	3
Catillaria sp. 1	1	1	-	-	-	2
Chaenotheca hygrophila	-	-	4	-	-	4
Chaenothecopsis cf. nana	-	-	1	-	-	1
Chaenothecopsis nigropedata	-	-	1	-	-	1
Chaenothecopsis pusilla	-	-	1	-	-	1
Chaenothecopsis savonica	-	-	1	-	~	1
Chaenothecopsis tasmanica	-	-	1	-	-	1
Chaenothecopsis sp.	-	-	1	-	-	1
Cladia aggregata	5	5	9	6	-	9
Cladia schizopora	3	1	8	6	-	9
Cladonia cf. murrayi	-	-	3	1	-	3
Cladonia ramulosa	3	3	4	4	-	7
Cladonia rigida var. rigida	6	4	9	7	-	9
Cladonia subsubulata	1	-	8	2	-	9
Cladonia ustulata	-	-	1	-	-	1
Cladonia weymouthii	-	-	3	-	-	3
Cliostomum griffithii	-	-	[1]	-	-	1
Coccotrema cf. cucurbitula	9	1	-	-	-	9
Coccotrema sp. A	-	2	-	-	-	2
Coccotrema sp. B	1	-	-	-	-	1
Dactylospora sp.	-	7	-	-	-	7
Dimerella cf. lutescens	-	1	-	2	-	2
Dimerella cf. pineti	1	6	-	-	-	7
Eopyrenula sp.	1	-	-	- 1	-	1
Glonium cf. stellatum	-	2	-	1	-	2
Graphis sp.	1	-	-	2	-	1
Gyalidea hyalinescens	1	-	- 1	2	-	3
Hypocenomyce foveata	-	-	1	-	-	1
Hypocenomyce scalaris	- 1	-	1	-	-	1
Hypogymnia lugubris	1	-	-	-	-	1

	Smooth bark	Papery bark	Eucalypts	Ground	Leaves	Total plots (all substrates)
Hypogymnia mundata	_	1		-	-	1
Hypogymnia tasmanica	4	2	-	-	-	7
Hypotrachyna sinuosa	1	-	-	-	-	1
?Icmadophila sp.	-	-	6	-	-	6
Jarmania tristis	1	-	-	-	-	1
Lecanora sp.	-	-	[1]	-	-	1
Lecidea cf. botryosa	-	-	7	-	-	7
Lecidea cf. pruinosa	-	-	[1]	-	-	1
Lecidea sp. A	-	1	-	-	-	1
Lecidea sp. B	1	3	-	-	-	4
Leifidium tenerum	1	2	-	-	-	3
?Lepraria sp.	-	-	-	[1]	-	
?Leprocaulon sp.	1	-	-	-	-	1
Leptogium victorianum	2	1	-	-	-	3
Loxospora solenospora	3	-	-	-	-	3
Marasmiellus affixus	-	-	1		-	1
Megalaria pulverea	5	4	-	-	-	8
Megalaria sp.	-	1	-	-	-	1
Megalospora lopadioides	1	-	-	-	-	1
Melaspilea sp. A	8	-	-	-	-	8
Melaspilea sp. B	-	-	3	-	-	3
Menegazzia confusa	3	-	-	-	-	3
Menegazzia norstictica	2	-	-	-	-	2
Menegazzia subpertusa	1	-	-	-	-	1
Micarea cf. adnata	-	-	2	1	-	2
Micarea alabastrites	8	2	-	-	-	8
Micarea cinerea	5	-	-	-	-	5
Micarea mutabilis	1	-	-	-	-	1
Micarea cf. mutabilis	-	-	1	-	-	1
Micarea prasina aggr.; form A	8	9	9	4	-	9
Micarea prasina aggr.; form B	4	4	-	-	-	6
Micarea prasina aggr.; form C	-	-	5	~	-	5
Micarea prasina aggr.; form D	3	6	5	6	-	8
Micarea prasina aggr.; form E	-	2	-	-	-	2
Micarea sylvicola	-	-	-	2	-	2
Micarea tubaeiformis	-	1	-			1
Micarea sp.	-	-	-	2	-	2
Microcalicium disseminatum	-	-	1	-	-	1
?Multiclavula mucida	1	-	-	-	-	1
Mycobilimbia sp.	-	-	-	2	-	2
Mycoblastus sp. 1	9	8	-	-	-	9
Mycoblastus sp. 2	5	2	-	-	-	6
Neophyllis melacarpa	3	1	9	4	-	9
Ochrolechia sp.	2	1	-	-	-	2
Opegrapha stellata	5	-	-	-	-	5
Parmelia protosulcata	1	-	-	-	-	1
Parmeliella nigrocincta	3	1				3

	Smooth bark	Papery bark	Eucalypts	Ground	Leaves	Total plots (all substrates)
Parmelina pseudorelicina	1	_		_	_	1
Peltigera dolichorhiza			_	1	_	1
Pertusaria gibberosa	1	-	_	-	_	2
Pertusaria jamesii	4	2	~	_	_	5
Pertusaria novaezelandiae	4	_	_	_	_	4
Phaeographis exaltata	2	_	_	_	_	2
Phlyctis sp.	6	_	_	_	_	6
Placopsis sp.	-	_	_	4	_	4
Placynthiella icmalea	_	_	8	_	_	8
Porina hyperleptalea	1	_	-	_	_	1
Porina impolita	_	1	_	_	-	1
Porina leptalea	1	_	-	_	_	1
Porina subapplanata	2	_	_	_	1	2
Pseudocyphellaria brattii	1	_	_	_	_	1
Pseudocyphellaria glabra	1	-	-	-	_	1
Psoroma microphyllizans	2		_	_	_	2
Pyrenula galactina	2	_	_	_	_	2
Pyrenula sp.	1	_	_	_	_	1
Pyrrhospora laeta	1	_	-	_	_	2
?Ramalodium sp.	1	1	_	_	_	2
Ramboldia brunneocarpa	2	2		_	_	4
Sagenidium molle	$\frac{2}{1}$	-	_	_	_	1
Sarrameana albidoplumbea	4	_	_	_	_	$\overset{\circ}{4}$
Steinia geophana	_	2	_	_		2
Strigula albicascens	3	-	_	-	_	3
Strigula indutula	1	_	_	_	_	1
Tephromela atra	_	1	_	_	_	1
Thelotrema decorticans	5	3	_	1	_	6
Thelotrema lepadinum	9	4	_	_	_	9
Thelotrema subdenticulatum	6	5	_	2	_	7
Thelotrema suecicum	8	3	-	_	_	8
Thelotremataceae sp. A	6	_	_	_	-	6
Topeliopsis muscicola	1	1	_	_	-	1
Trapeliopsis granulosa	_	_	8	_	_	8
Trichothelium assurgens	_	_	-	_	1	1
Trichothelium meridionale	_	_	-	-	1	1
Usnea sp.	4	1	_	_	-	6
Wawea fruticulosa	-	5	-	-	-	5
Species A	4	_	_	4	-	7
Species B	1	1	-	-	-	1
Species C	_	-	6	-	_	6

Tasforests