The Fate of Leaves in South Eastern Australian Terrestrial and Aquatic Environments:

Implications for taphonomic bias in the Tertiary macrofossil record

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Nothofagus cunninghamii dominated rainforest and stream near field site (David Greenwood, *with permission,* 1996).

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Abstract

An understanding of the taphonomic processes that form and possibly bias plant fossil assemblages is of central importance to understanding and interpreting some of the anomalies in the Australian Cenozoic plant fossil record. This study measured a variety of ecosystem processes in contiguous *Nothofagus cunninghamii* (Hook) Oerst. dominated cool temperate rainforest and *Eucalyptus regnans* F.Muell. dominated wet sclerophyll forest in southeastern Australian forest in order to find an ecological explanation for anomalies between the poor macrofossil record on the one hand, and high abundance of one of these taxa as pollen. From the examination of these two forests three sources of taphonomic bias between taxa were identified: 1) bias between standing crop and leaf biomass production between species; 2) bias in overland and riparian leaf transportation distance between species; and 3) bias in decay rates between species.

An analysis of the relationship between standing biomass and leaf litter production revealed that determining the relative proportions of the leaf area of each species or taxon in either forest floor litter or in a potential plant fossil deposit can serve as a proxy indicator of the relative proportions of standing biomass in the source vegetation. The analysis also indicated that, where there are substantial differences in leaf size between the leaf taxa found in a fossil flora or forest litter sample, the practice of counting leaves as a proxy indictor of standing biomass has the potential to incorrectly predict rank order.

The litter taxon makeup was found to vary between locations, both in species composition and in the proportions each species contributed to the forest floor litter. This

was linked to the distribution of individual taxa throughout the source vegetation. Such observations therefore point to the importance of the collection and analysis of fossil material from multiple locations within a bedding plane in order to address this variability.

It was observed that leaf material does not move great distances once it has come to rest, either after falling from a tree or upon entering high order streams. Factors such as the slope of the land had little overall effect upon the transport distances of leaves once they have fallen from a tree and come to rest. No leaf travelled over land more than 3.4 m in a six-month period. The leaves of tree species growing more than two or three tree heights away from a waterway or stream would have little chance of entering it except by wind blow in extreme weather events. For example, leaves of *Acacia dealbata,* one of the principal tree species found growing on the boundaries of the field site and which grew to a height of ~ 15 metres, contributed no leaves at all to the stream side leaf litter traps even though the trees were growing just 30 to 35 metres from the nearest of the stream side litter traps. This species and its counterparts in that particular vegetation association would therefore be excluded from the macrofossil record.

The prospect of differential transport in streams was also found to be significant. The likelihood of long distance transport was linked to size, weight per unit area, flexibility, flow rate and the number of obstructions in the stream. For Cumberland Creek, a high order retentive waterway, no leaf travelled more than 100 m in a six-hour period. The conclusion drawn from this observation was that fossil deposits derived from leaf litter preserved *in situ* in high order streams are highly likely to represent the leaf litter of the nearby taxa. It was also concluded that small leaves like *Nothofagus cunninghamii* have a much larger potential for transport than do large flexible ones like those of *Eucalyptus regnans*. These differences in transportation potential mean that fossil deposits derived from large rivers

and streams will most likely consist of locally derived taxa, and a larger regional flora consisting of those species, which have good transport potential.

Reconstructions of source vegetation based upon fossil deposits derived from either slow flowing low order rivers and streams or turbulent high order streams need to take into account the transport and differential sorting potentials between these systems.

The leaves from the various species used in this study were found to have strong decay rate bias between species. Some species such as *Atherosperma moschatum* Labill. decay rapidly, regardless of how ideal their burial conditions might be, while other species such as *Nothofagus cunninghamii* decayed more slowly when buried. The important indicator for decay rates is the lignin to nitrogen ratio. Species with high lignin to nitrogen ratios will have the lowest decay rates and the best chances of entering the fossil record.

The study suggested that taphonomic factors do not appear to offer an explanation for the paucity of *Nothofagus* leaf remains in the Australian Cenozoic record, however in the absence of data for subgenus *Brassospora*, the generality of this conclusion is speculative.

It was found that leaves of *Eucalyptus regnans* decay comparatively rapidly, on the ground or on the stream/sediment interface, transport poorly, and are underproduced relative to the standing biomass. This may explain their rarity in the Australian macrofossil record.

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma and, to best of my knowledge, contains no material previously published or written by any other person except where due reference has been made.

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List of abbreviations used in this thesis

CTRF	Cool Temperate Rainforest
Eqn	Equation
Eh	Reducing Potential
LDE1	Leaf Decay Experiment 1
LDE2	Leaf Decay Experiment 2
L:Nr	Lignin to Nitrogen ratio
MAT	Mean Annual Temperature
MYR	Millions of Years Ago
NLR	Nearest Living Relative
N.S.W.	New South Wales
PVC	Poly Vinyl Chloride
SE	Standard Error
spp	species
TNC	Total nitrogen content (%)
WSF	Wet Sclerophyll Forest
Yr	Year
Vic	Victoria
w/w	Weight for weight
Note 1:	Standard international (SI) units are used throughout this thesis unless otherwise stated.
Note 2:	All plant nomenclature for the Victorian plant species used in this thesis follows Foreman and Walsh (1996)

Chapter 1

General Introduction and Literature Review

1.1 Introduction

The fossilised remains of plants constitute a fundamental source of information on the evolutionary history of plant lineages. They also comprise a primary record of the past history of vegetation and climate (Spicer, 1989; Greenwood, 1994). Accurate reconstructions of past climates and ecosystem processes provide a window on how the Australian continent and its biota have responded to past climate change. Nonetheless, the Australian Cenozoic fossil record has numerous anomalies, which confound reconstructions of plant lineages, past vegetation patterns and climate. For example, *Nothofagus* Blume, a genus of forest trees which are frequently forest dominants in Australian cool temperate rainforest ecosystems, has an abundant Tertiary pollen record, yet has a sparse leaf and other macrofossil record, especially for *Nothofagus* subgenus *Brassospora* (Christophel & Blackburn, 1978; Hill, 1982; Christophel, 1981, 1989; Lange, 1982; Greenwood, 1991; Hill, 1994; Greenwood *et al.*, 2003). Other subgenera of *Nothofagus*, such as subgenus *Lophozonia* were rare both as pollen and leaves during the Tertiary, but less so in the Quaternary where they can be well represented (Hill, 1991; Jordan & Hill 1999; Jordan 1999; Hopf *et al.*, 2000; Rowell *et al.*, 2001). Likewise, *Eucalyptus* L' Hèr., and *Acacia* Mill., two plant genera that both dominate the modern Australian flora and landscape

(Barlow, 1981), have poor Cenozoic fossil records (Hill, 1994; Greenwood *et al.*, 2001). These observations prompt the question:

> Is the representation of these plant taxa in the Cenozoic macrofossil record a reflection of patterns in the vegetation or patterns in preservational potential of these genera as leaves?

Several studies have shown that the pollen rain in the complex rainforests of the Australian wet tropics reflects the spatial distribution and general floristic composition of these forests (e.g. Kershaw & Strickland, 1990; Kershaw & Bulman, 1994). However, Lauraceae pollen was absent from the pollen sum from these tropical rainforests, despite being well represented in the source forest canopy, while pollen from *Eucalyptus* and *Casuarina* from near by stands of sclerophyll forests made up at least 20% of the pollen sum (Kershaw & Bulman, 1994). These studies highlight that, whereas there is an understanding (albeit an incomplete one) of potential taphonomic bias in the pollen floras relative to the source forest, little is known about bias in the Australian leaf fossil record. The reliability of the fossil record as a source of data relies upon a detailed understanding of the processes that resulted in the formation of plant fossil assemblages. This study aims critically to identify and analyse the confounding factors that may distort the leaf fossil record.

One of the most significant of the potential confounding factors in the fossil record is species preservational bias (Ferguson, 1985; Spicer, 1981, 1989; Greenwood, 1991; Burnham *et al.*, 1992). This bias may arise whenever there is differential preservation among plant parts from different species, resulting in differential representation of these species in fossil assemblages. For example, Mathews and Kowalczewski (1969) found that European oak leaves (*Quercus robur*) decayed more slowly than did sycamore (*Acer* spp.) or willow leaves (*Salix* spp.). Similarly Greenwood (1991) found that leaves of the rainforest tree, *Doryphora aromatica* (Bailey) L.S. Smith, were under-represented in

stream-bed accumulations relative to the abundance of this species in forest-floor litter, whereas other species in the local area were equally represented as leaves in both forest-floor litter samples and in the stream-bed samples. Similar results to those of Mathews and Kowalczewski (1969) and Greenwood (1991) have been found in Australia for contrasting plants and environments such as sub-alpine shrub lands (Hill & Gibson, 1986), *Eucalyptus* forests (Pressland, 1982; Woods & Raison, 1983; Carpenter & Horowitz, 1988), subtropical to temperate rainforests (Blackburn & Petr, 1979; Lowman & Box, 1983; Madden & Turnbull, 1984; Lowman, 1988), and salt marshes (Van Der Valk & Attiwill, 1983). Differential decay rates within and between species are considered to be due to variation in the chemical composition or structural attributes of the leaves (e.g. Lowman & Box, 1983; Spicer, 1989; Thomas & Asakawa, 1993). These factors are thought to influence leaf processing by stream or forest-floor biota and potentially bias species representation (i.e. presence- absence, and abundance), in fossil assemblages (Spicer, 1981).

Much of the terrestrial Australian work on differential decay rates between species has been on forest-floor litter (e.g. Ashton, 1975; Attiwell *et al.*, 1978; O'Connell & Menage, 1983; Lowman, 1988). In contrast, studies of leaf decay in water bodies have focused on litter in streams as a source of organic matter for the biota (e.g. Bunn, 1986) or on the processes controlling the rates of decay (e.g.Campbell *et al.*, 1991; Campbell & Fuchshuber, 1995). The stream studies have consequently relied on leaves suspended in the water column or on the sediment surface interface where the majority of the leaf-processing biota are found. The current literature on leaf decay for Australian environments does not address the fate of leaves in potential plant fossil-forming environments. It is the fate of leaves at the sediment-water interface, and within alluvial sediments, which is pertinent to understanding preservational bias. Only three Australian studies have directly addressed the potential for species bias in the fossil record (i.e. Hill & Gibson, 1986; Carpenter &

Horwitz, 1988; Greenwood, 1991), however these studies only provided anecdotal evidence of differential representation and did not address experimentally the underlying processes.

This study examines the possible sources of bias in the fossil record by examining differential biomass production (Chapter 2), leaf transport (Chapters 3 & 4), and decay and deposition (Chapter 5), in situations that mimic sites of plant fossil deposition in a contemporary ecosystem (Figure 1.1). This ecosystem was examined as a potential source of plant fossils, and was used to assess and quantify the sources of bias. From such analyses, models were constructed to represent the impact that these potential sources of bias may have upon palaeoecological analyses of the plant fossil record.

Although there is no guarantee that any modern ecosystem is an exact analogue of a fossil ecosystem, it is possible to select modern ecosystems that are similar enough to ancient ones so that possible sources of bias can be discovered. This approach is essentially uniformitarian in that it focuses on processes rather than species. Species evolve over time, whereas ecological and physical processes can be considered to remain consistent over the Cenozoic. A large body of palaeontological data already exists making this possible, and it is plausible to identify and match such extant communities with fossil ones based upon the following three criteria:

(1) taxonomic representation;

(2) similar ecosystem processes; and,

(3) similar climate regimes.

A field site (Section 2.2), chosen for its near match to these criteria, was used to approximate the ecosystem dynamics of the fossil communities under investigation. A brief overview of the evolution of the climate and flora of Australia is given in section 1.2 and this will highlight anomalies in the representation of important plant genera, and why certain types of plant community were selected for examination.

1.2 The evolution of south eastern Australian climates and vegetation in the Cenozoic

Australian Cenozoic Climates

Over the Cenozoic era, the Australian continent separated from Antarctica and steadily moved towards the equator due to continental drift (Embleton, 1984; Quilty, 1984, 1994; Adam, 1992; Wilford & Brown, 1994 (Figure 1.2). This movement had a profound effect upon the climate and the evolution of the Australian flora (Quilty 1984, 1994; Frakes *et al.*, 1987; Adam, 1992). Multiple fossil deposits reveal that the Australian biota have responded to climate change in a dynamic manner for most of the Cenozoic (Barlow, 1981; Christophel, 1989; Hill, 1992; Greenwood *et al.*, 2003). The fossil rainforest taxa of southern Australia, in particular, show considerable evidence of a flora evolving in response to changes to temperature and rainfall, resulting in the range of vegetation we are familiar with today (e.g. Christophel, 1989; Christophel & Greenwood, 1989; Adam, 1992; Truswell, 1993; Greenwood & Christophel, 2004). Cenozoic floras have strong affinities to the modern flora, allowing for the direct application of ecosystem data gathered from extant communities to fossil ones, especially where floristics and forest structure are similar (Barlow, 1981).

At the beginning of the Cenozoic, Australia was covered by complex mosaics of megathermal and mesothermal vegetation (Table 1.1), which were similar to extant vegetation found in the tropical and subtropical regions of Australia today (Christophel & Greenwood, 1989; Truswell, 1993). The global climate of this period was very different from that of today in that southern Australia was located near the Antarctic circle, yet was covered with a thick mantle of complex perhumid meso- to megathermal vegetation, with forests extending to the south pole (Frakes *et al.*, 1987). This complex humid rainforest is thought to have resulted mostly from strong greenhouse warming and warm tropical sea

currents being deflected polewards by continental coastlines. These sea currents were highly effective in transferring heat polewards, thus creating a generally tropical global environment (Quilty, 1984, 1994; Frakes *et al.*, 1987; Greenwood & Wing, 1995).

Table 1.1 The definitions of the palaeoclimatic thermal regimes as mentioned in the text (Nix 1982).

Vegetation Type	Thermal Range
Megathermal	MAT > 24° C
Meso-Megathemal Interzone	MAT between 20 - 24° C
Mesothermal	MAT between 14 – 20°C
Microthermal	MAT < 14°C

The fossil record of the Australian vegetation covers most of the Cenozoic (Figures 1.3 & 1.4). Two of the oldest sites are the Late Palaeocene sediments of Lake Bungarby and Cambalong Creek in N.S.W., which contain diverse large leaved floras, and taxa with nearest living relatives found today in both microthermal and mesothermal rainforests (Hill, 1990, 1992; Greenwood *et al.*, 2003).

Other major Australian Eocene macrofossil sites include the Early and Middle Eocene Nerriga, Hotham Heights, Brandy Creek, Anglesea, Maslin Bay and Golden Grove localities (Figures 1.3 and 1.4 for locations). These Early to Middle Eocene floras represent closed rainforests of considerable diversity, including species from the Lauraceae, Elaeocarpaceae, Myrtaceae, Proteaceae, and Podocarpaceae (Lange, 1982; Greenwood, 1987; Hill, 1992; Greenwood *et al.*, 2003). The Anglesea site alone has over 100 different leaf types and physiognomically and floristically, resembles forests growing in the rainforests of north eastern Queensland today (Christophel, 1989; Christophel & Greenwood, 1989; Greenwood *et al.*, 2003). The pollen record for these sites indicates that *Nothofagus* was common in these forests, although *Nothofagus* leaves were rare or absent from the macrofloras (Christophel, 1989; Lange, 1982; Greenwood *et al.*, 2003; Table 1.2). For example, Scriven *et al.* (1995) recorded a single *Nothofagus* leaf out of many hundreds

of leaf fossils examined from the Middle Eocene Maslin Bay macroflora from South Australia. The disparity between the palynological and macrofossil records for this genus, particularly *Nothofagus* subgenus *Brassospora*, has caused considerable debate in the literature over the importance of *Nothofagus* in these Eocene floras (see Christophel 1989). Suggestions have ranged from large expanses of *Nothofagus* forest, to it having only an occasional or rare occurrence in the landscape (Barlow, 1981; Galloway & Kemp, 1981; Christophel, 1989; Truswell, 1993; Scriven *et al.*, 1995). This is not to suggest that *Nothofagus* macrofossils are always uncommon, as the genus has a good Tasmanian fossil record, with all four extent subgenera occurring in Tasmanian Paleogene sediments (Hill, 1994).

Palynological reconstructions of Late Eocene floras from the Murray Basin indicate that the forests were mostly dominated by *Nothofagus spp.* and *Lagarostrobos spp.* with rainforest species of Proteaceae present in a diverse flora (Martin, 1993). The presence of this forest indicates that inland climatic conditions were suitable for extensive rainforest communities. The Middle Eocene Nelly Creek Macroflora however has a foliar physiognomic signature that suggests the presence in central Australia of seasonally dry (possibly monsoonal) palaeoclimates, where mesic vegetation may have occurred in riparian corridors (Greenwood, 1994 & 1996). The evidence for a thick mantle of per humid forests in the Eocene is further augmented by macrofossil sites located at Vegetable creek in New South Wales and in Tasmania which include temperate rainforest species such as *Nothofagus, Eucryphia* and numerous conifer species (Hill, 1992). Kershaw *et al.* (1991), likewise indicated that *Nothofagus* comprised a major fraction of the pollen spectra of the regional component of Middle Eocene to Middle Miocene LaTrobe valley coals.

Table 1.2 The relative proportions (out of 100) of leaves and pollen grains or spores of major taxa collected from various fossil localities from around Australia. M= leaves and leaf fragments, S= spores or pollen. Note the disparity between the proportion of pollen grains collected for taxa such as *Nothofagus* as compared to the number and proportion of leaves recovered from the fossil sites listed. It is interesting that this disparity holds for Myrtaceous pollen versus *Eucalyptus* leaves, even though these two groups are strictly speaking, not equivalent. All spore and pollen values are counts of land plants and therefore exclude fungal and algal spores. The leaf counts are of leaves or leaf fragments. The macrofossil data was compiled by Dr. David Greenwood from various sources cited in Greenwood *et al.* 2003, Greenwood (1981) for the Yallourn Clays, and Pole *et al.*, (1993) for the Berwick Quarry. The microfossil or pollen and spore data was complied from various sources cited in Greenwood *et al.* 2003, Blackburn and Sluiter (1994) for the Yallourn clays, and Pole *et al.*, (1993) for the Berwick Quarry. Where there is no data a '--' is given.

Family/Group	Fossil Site/Locality															
	Cambalong Creek		Deans Marsh		Hotham Heights		Nerriga		Golden Grove		Anglesea		Berwick		Yallourn Clays	
	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S
Bryophytes	--	0.6	--	26.3	--	54.8	--	22.8	--	24.0	--	9.2	--	1.0	--	0.6
Gymnosperms	33.3	28.5	23.8	14.1	9.3	4.5	1.0	3.6	1.0	13.0	1.1	11.9	3.0	9.1	4.6	20.6
Gymnostoma	0.0	--	19.3	--	0.5	--	1.5	--	0.8	--	0.5	--	9.0	--	0.8	--
Casuarinaceae	--	0.1	--	16.1	--	2.2	--	3.3	--	9.0	--	5.1	--	3.0	--	5.4
Aquifoliaceae	--	3.1	--	1.0	--	0.6	--	0.0	--	0.0	--	0.0	--	0.1	--	0.0
Nothofagus	**0.0**	**24.9**	**0.0**	**4.0**	**0.0**	**3.3**	**0.0**	**7.7**	**0.1**	**11.1**	**0.0**	**17.2**	**17.9**	**81.5**	**2.0**	**18.4**
Proteaceae	18.2	10.6	7.6	12.9	9.3	3.3	0.0	20.3	3.2	13.6	1.0	9.2	2.2	0.5	2.9	1.9
Myrtaceae	--	0.0	--	0.0	--	0.6	--	4.3	--	0.1	--	7.9	--	1.0	--	17.8
Eucalyptus	0.0	--	0.0	--	0.0	--	0.0	--	0.0	--	0.0	--	2.0	--	0.0	--
Cunoniaceae/Elaeocarpaceae	3.0	--	0.0	--	3.7	--	0.0	--	27.0	--	11.4	--	37.3	--	5.8	--
Lauraceae	24.2		1.7		64.8		24.4		16.2		20.2		6.7		49.2	
Other Angiosperms	1.3	32.2	47.6	25.6	12.4	30.7	72.0	38.0	51.7	29.2	65.8	39.6	21.9	3.8	34.7	35.2

At the end of the Eocene to the beginning of the Oligocene there was a cooling of the prevailing climate (Shackleton & Kennett 1975; Wing, 1998; Zachos *et al.*, 2001; Greenwood *et al.*, 2003; Greenwood & Christophel, 2004). Tasmanian floras from this period exhibited a strong shift towards microthermal rainforests and a reduction in species diversity (Hill, 1990). Sites elsewhere in Australia, such as those of the La Trobe Valley in Victoria and Westdale in Western Australia, show a shift towards more sclerophyllous vegetation, possibly indicating a drier climate over inland Australia (Hill, 1992). The degree of climatic change for the humid continental margins such as the La Trobe Valley was much less than that seen for the interior, however, as the rainforest taxa such as the Podocarpaceae and *Nothofagus* continued to contribute significantly to the Oligocene pollen spectra (Kershaw *et al.*, 1991). The fossil record for sclerophyllous taxa such as *Casuarina* is primarily Neogene, although *Banksia* is known from the Middle Eocene and sclerophyllous *Banksia*-like leaves appear from the Late Paleocene (Christophel, 1989; Hill, 1992; Hill, 1994; Greenwood & Christophel, 2004).

The Oligocene and Miocene floras show a general climate change characterised by lower temperatures, less rainfall and possibly an increased mean annual range of temperatures. For example the use of nearest living relative analysis indicates that the presence of the subtribe Banksiinae and other taxa at Stuart Creek, Morris Creek and other sites in the Stuart Range is consistent with a lowering of the annual rainfall between the Middle Eocene and the Miocene for sites in the Lake Eyre region (Greenwood *et al.*, 2001). This transformation is thought to have been brought about by the widening of the strait between Australia and Antarctica allowing the formation of a circumpolar current (Christophel, 1989; Quilty, 1984; Frakes *et al.*, 1987). As this circumpolar current developed, the flow of warm water from the equator would have been disrupted, resulting

in less heat transfer from the equator to the higher latitudes. The result was a cooling high latitude climate, with decreasing humidity and rainfall.

Important Australian Cenozoic Taxa

Fossil *Eucalyptus* and *Acacia* leaves are rare from Oligocene and Miocene sediments. Considering the domination by these two genera of the form, structure, and ecology of almost every contemporary vegetation association on the Australian continent (Barlow, 1981), their scarcity in the fossil record is intriguing (Hill, 1992, 1994; Greenwood *et al.*, 2000). For example, the *Eucalyptus* macrofossil record essentially begins with the Late Oligocene Berwick Quarry flora of Victoria (Pole *et al.*, 1993), while its pollen record begins long before this (Martin, 1994). The oldest other macrofossil with eucalypt affinities is that of a tree stump enclosed in 21 million year old basalt in the Upper Lachlan Valley of New South Wales (Bishop & Bamber, 1985). Eucalypt bloodwood/*Angophora* type pollen has been recorded from the Paleocene/Eocene (Martin 1994), *Myrtaceidites tenuis* pollen (a primitive eucalyptoid type) occurred from the Middle to Late Eocene (Harris, 1965 (as cited in Hill, 1994); Macphail *et al.*, 1994).

The Australian fossil record for *Acacia* can at best be described as 'enigmatic' with its Australian microfossil record becoming well established from the Oligocene/Miocene (Martin, 1981), while macrofossils are rare in Australia and elsewhere (Christophel, 1989; Macphail & Hill, 2001). The few reliable Australian fossil occurrences include *Acacia* leaves from the Middle Miocene-Pliocene clays at Sentinel Rock, and the Pliocene Grange Burn sediments in Victoria (Cookson, 1954; Greenwood *et al.*, 2000). Other fossils include a fragment of *Acacia melanoxylon* wood from the Pliocene sediments at Stoney Creek, near Daylesford, Victoria (Cookson, 1954; Greenwood *et al.*, 2000) and another wood fragment of potentially dubious identification

from the Upper Lachlan Valley of New South Wales (Bishop & Bamber, 1985). *Acacia* phyllodes have also been found in the Early Pleistocene Rafted Mudstones from Regatta Point in western Tasmania (Hill & Macphail, 1985; Jordan, 1997).

The current evidence suggests that *Acacia* had its initial centre of evolution in Africa and was then spread around the world through the activities of migratory birds (Macphail & Hill, 2001). It most likely arrived in Western Australia first, around the Late Oligocene-Early Miocene, and arrived in Eastern Australia by the Early Miocene (Macphail & Hill, 2001). Macphail and Hill (2001) also suggest that the adaptive radiation and speciation of this genus in Australia probably occurred in the Late Neogene.

Hill (1994) in reviewing the available fossil evidence supported Lange's (1980) hypothesis that *Eucalyptus* was absent from the continental margins up to the Mid-Cenozoic, and that eucalypts contributed to the more xeric vegetation of the interior. However, no evidence of *Eucalyptus* in Australian interior Eocene macrofloras exists (Greenwood, 1996; Greenwood & Christophel, 2004), posing the question whether a taphonomic bias may provide the answer to the discrepancy between the pollen and macrofossil records. For example, Carpenter and Horwitz (1988) examined two Tasmanian creeks flowing into the Hunter River and found that *Eucalyptus* leaves do not normally enter depositional settings, even if they are the local forest dominants. In these forests *Nothofagus* and other rainforest species found in gullies were common in the stream's litter load, but *Eucalyptus* litter was rare or absent. This may have implications for reconstructions of Cenozoic eucalypt evolution, because Myrtaceae pollen has been recorded from the Palaeocene/Eocene throughout much of the Cenozoic, and eucalypt bloodwood/*Angophora* type primitive eucalyptoid pollen has been recorded since the Eocene onwards (Christophel, 1989; Martin, 1994).

The fossil record for the genus *Atherosperma* (Atherospermataceae), a canopy tree taxon that forms part of the cool temperate rainforest associations in south eastern Australia, is virtually non-existent with only a few isolated reports of wood, leaves and pollen from Australia and elsewhere are known (Nishida, 1984; Hill & Macphail, 1985; Collinson *et al.*, 1993; Mckenzie, 1997; Poole & Francis, 1999).

The general picture of the Australian climate is of high temperature and humidity with little variation in temperature in the Eocene, followed by a progressive cooling and drying of the climate from then on. As the climate deteriorated further, forests lost complexity and species richness as individual taxa became either locally extinct or followed the movement of their most suitable life zones northwards (Barlow, 1981; Hope, 1994; Christophel & Greenwood, 1989; Greenwood & Christophel, 2004). Some plant taxa followed the movement of their most suitable life zones northwards, such that they are now found no further south than New Guinea or Malaysia. For example contemporary populations of *Nothofagus* subgenus *Brassospora* are today found no further south than New Guinea and New Caledonia, even though they occurred in Tasmania in the Oligocene (Hill, 1991; Hill, 1994; Hill & Scriven, 1996). Indeed the coexistence of all four subgenera of *Nothofagus* in Tasmania during the Oligocene has led to the suggestion that the Tasmanian forests and climate of this period may have no modern analogue (Hill, 1994). Other species evolved locally to keep pace with climate change, though the severe glaciation of the most recent ice ages resulted in many species becoming extinct. One of the features of the south eastern Australian rainforest flora of the Cenozoic which has been lost in the severe glaciations of the Quaternary, is the high levels of inter and intra-generic diversity. Not only did Cenozoic rainforests have a high level of diversity of different plant groups right down to the generic level, but each plant genus usually had several representatives present in the forest, a feature that is uncommon in most south eastern

Australian forest catchments today. As such, genera like *Nothofagus,* and the giant conifers (e.g. *Araucaria*), appear to have been more diverse in the Cenozoic forests than they are today (Lange, 1982; Christophel, 1989; Hill, 1990, 1992).

1.3 The importance of taphonomy

The term taphonomy was originally coined by the Russian palaeontologist, Efremov (1940), and extended by later studies, including those mentioned above, to embrace the whole fossilisation process, from the biology of the organism that produced the fossil to the process whereby the fossil is extracted from the sediments that entomb it. Taphonomic bias assumes that the processes that affect fossilisation have different effects upon the preservation of different organisms or parts of organisms.

The notion of taphonomic bias as defined by Behrensmeyer and Kidwell (1985) and Spicer (1989,1991), has given rise to considerable debate about the reliability and accuracy of plant fossil-based palaeoclimatic and palaeoecological reconstructions (e.g. Ferguson, 1985; Spicer, 1989; Greenwood, 1991, 1992; Burnham *et al.*, 1992; Wing & Greenwood, 1993; Gastaldo, 1994; Greenwood & Wing, 1995). Taphonomic bias posits the likelihood that the fossil record may not contain an unbiased reservoir of fossil plant parts (Ferguson, 1985; Greenwood, 1991; Spicer, 1991). This thesis aims to quantify some of the potential sources of taphonomic bias in a modern Australian ecosystem with a view towards explaining some of the anomalies observed in the Australian plant fossil record (Section 1.2).

1.4 Plant palaeoecology

A basic assumption of this study of taphonomic bias is uniformitarianism: the presumption that the physical processes operating in the past, which controlled plant fossil formation (i.e. decay rates, deposition and plant matter processing in aquatic environments) continue to operate today. Plant palaeoecology utilises many types of evidence, based upon the uniformitarian principle, including; (1) the floristic composition of fossil floras, and (2) leaf characteristics, usually termed foliar physiognomy.

The floristic composition of a fossil flora can provide evidence on both the ecology of the ecosystems that formed it and the evolution of plant lineages. Most modern plant species have definable climatic ranges, reflecting their physiological and ecological restrictions (Nix, 1982). By identifying the nearest living relative (NLR) of a species identified in a fossil flora, the climate and ecological structure of the vegetation from which the fossils formed can be inferred from the modern relatives' range (e.g. Greenwood *et al.*, 2003).

This extrapolation using floristic analogy (or NLR) is reliant upon the uniformitarian principle that the ecological preferences of a fossil plant (such as the optimal temperature and rainfall required for growth) and its closest living relative are similar. This method is open to criticism as many species will have evolved, or altered their climatic ranges over the Cenozoic (Wolfe, 1978). Wolfe (1978) further noted that a major flaw with floristic analogy was the potential confounding effect of misidentifications, a problem not encountered with foliar physiognomy. Nevertheless, the floristic content of fossil macrofloras are commonly used to reconstruct vegetation type and make estimates of climate (e.g. Greenwood, 1994; Greenwood *et al.*, 2003). Some palaeobotanists suggest

that a tandem approach be used, which combines foliar physiognomic and floristic information (e.g. Wing & Greenwood, 1993; Greenwood, 1994; Greenwood *et al.*, 2003).

As a result of foliar physiognomic analyses of extant vegetation, it has become possible to predict the prevailing climate of a region using only the leaf physiognomy of the plant species which grow in that region (Bailey & Sinnott, 1916; Raunkiaer, 1934; Webb, 1959, 1968; Parkhurst & Loucks 1972; Webb *et al.*, 1976; Givnish, 1978; Wolfe, 1978, 1985; Webb *et al.*, 1984; Greenwood 1991, 1992).

When foliar physiognomic techniques are applied to Cenozoic fossil macrofloras, it is possible to reconstruct the climate, ecology and structure of the community that produced them (Greenwood, 1991, 1992; Wolfe, 1993, 1995). Reconstructions of Cenozoic climates and vegetation provide an opportunity to accurately examine climate change over time (Wolfe, 1971, 1990, 1993; Wolfe & Upchurch, 1987). For an accurate reconstruction to be made, the leaves must have come from plants local to the site, otherwise, the reconstruction may be confounded, due to the mixing of plant remains from distant and local communities (Christophel & Greenwood, 1989; Greenwood, 1991, 1992).

1.5 Sources of taphonomic bias

A detailed study of the taphonomic processes at work in a particular depositional setting provides an evaluation of how reliably a fossil assemblage represents the original plant community. There are many potential sources of taphonomic bias and they can be divided into three broad categories:

1. Bias in biomass production: the differential production of plant parts (leaves, reproductive organs and woody parts), both between plant taxa and between time of abscission.

2. Bias in transport; the differential transport and sorting of plant organs between species once they have been produced and shed from the parent plant.

3. Bias in differential decay and preservation of plant organs from different species.

A summation of many of the potential factors affecting the fate of leaves is given in Figure 1.5 and can found in Gastaldo (1988). The main factors are discussed in the following sections.

1.5.1 Bias in biomass production

The possibility that some plants produce and then shed biomass in differing amounts relative to their standing biomass has been known for some time. Some of the earliest field investigations in this area were carried out by Chaney (1924 & 1925), upon the Miocene Bridge Creek flora of central Oregon USA. These investigations examined the relationship between stem number and leaf number in modern Californian redwood forests, to develop a relative picture of the dominant taxa in the fossil flora and found a generally low correlation of 0.44. Other early examples of taphonomic work include MacGinitie (1941), Chaney (1959) and Hickey (1977).

The current emphasis on field based studies of taphonomy in contemporary ecosystems largely resumed with Drake and Burrows (1980) who studied the relationship between the composition (and basal area) of lakeside vegetation and the species composition of plant litter in lake sediments at Lady Lake in North Westland New Zealand. Drake and Burrows (1980) found a good qualitative representation of the forest vegetation and common taxa in the lake sediments, but made no effort to explain the

observed discrepancies by measuring the relative amounts of litter fall for the various species found growing around the lake.

Spicer and Wolfe (1987) revealed that the dominant forest taxa found in the vegetation around Trinity Lake, an artificial water storage in Northern California USA, were well represented in the drainage deposits of the major inflowing streams, while some riparian taxa were over represented. However, Spicer and Wolfe (1987) did not provide data on either basal area or crown cover for the individual plant taxa found in this vegetation, and were unable to generate quantitative relationships between the standing biomass and what was found in the various drainage deposits of Trinity Lake. The usual measure for determining the biomass of larger trees and shrubs is through basal area, due to the relative ease in its determination and widespread use in forestry literature (Catchpole & Wheeler, 1992).

The relationship between standing forest biomass and leaf litter composition was largely uninvestigated until the seminal work of Burnham (1989). This was in spite of the fact that it had long been recognised that there was a potential source of bias created by differential rates of leaf litter production between tree species relative to their standing biomass (Burnham, 1989). Burnham (1989) demonstrated that local floras are reliably reflected in litter samples when large sample sizes are used, with declining levels of reliability for regional floras. She also observed that the natural heterogeneity of the forest was well preserved in litter samples, and that more accurate models of regional vegetation were formed when litter samples were taken from a number of environments within the study area.

Burnham *et al.* (1992) investigated the relationship between leaf mass, leaf number, leaf area and stem basal area, and found that leaf area was highly correlated with stem basal area. They concluded that this measure could therefore be used to infer

dominance patterns in fossil floras. Turnbull and Madden (1983) also found a link between stem basal area and leaf litter production in an ecological study of *Nothofagus* and *Eucalyptus* regrowth forests in Tasmania, Australia.

Burnham *et al.* (1992) also observed that rare plant species were equally rare in litter samples, and that total species richness for an area of forest may be difficult to determine without replicate samples. They noted that some life forms, particularly vines and lianas, are over represented in the leaf litter, and commented upon the general applicability of these observations to fossil leaf floras (Burnham *et al.* 1992).

Later work by Burnham investigated whether leaf litter data can represent the species richness, diversity, composition and structure of the source vegetation. Burnham (1993) looked at the following three questions:

1. How is the richness of a source forest reflected in the parautochthonous leaf litter deposits?
2. How reliable are such estimates?
3. How large an area do you need to answer the above two questions?

She concluded that a single collection of 350-450 leaves of a temperate forest represents from 45 to 92 % of the tree species, with heterogeneous forests (3-4 dominants) having a richness reflected in the litter varying between 45-78%. While for homogeneous forests having at least 7-8 forest dominants, had a richness from a single collection varying between 53-92%. Burnham (1993), comments that litter samples having between 350-450 leaves represent an area of 0.1 to 0.125 hectares, and that three samples spaced at 25 m consistently include 85% (± 5 %) of the tree species in a temperate forest hectare.

Burnham's (1997) study again revealed that both dominant and subdominant tree species are well represented in the leaf litter, while the representation of rare taxa in leaf litter samples was highly variable. It was noted, however, that the relative abundance of various taxa such as *Quercus oleoides*, *Hymenaea courbaril* and *Manilkara zapota* in terms of basal area did *not* match the relative abundance in terms of leaf number or leaf mass. However, these measures did give reliable indications of which trees are dominant and which trees are not.

Two Australian taphonomic studies have examined the relationship between standing biomass and litter fall; Greenwood (1992), and Schimanski and Bergstrom (1998). Schimanski and Bergstrom (1998) dealt directly with the relationship between the species composition of leaf litter and stem number for a New South Wales rainforest. In common with standard ecological practice, Schimanski and Bergstrom (1998) defined 'richness' as the number of species in a given area and 'diversity' as the number and proportion of species in a given area. Schimanski and Bergstrom (1998) observed that *Nothofagus moorei* was overproducing leaf material relative to stem number and that richness of the source forest is reflected in the leaf litter, but not the diversity.

1.5.2 Time of Abscission or Seasonality

Abscission is the process whereby plants shed their leaves in response to an external or internal environmental stimulus. The timing of the leaf fall can have major effects upon the likelihood of those leaves entering the fossil record (Greenwood, 1991; Parrish *et al.*, 1998). Most plants shed their leaves due to seasonal cold (e.g. Northern Hemisphere temperate dicot trees), or dryness (e.g. tropical monsoon forest trees). Many plants considered 'evergreen' shed a proportion of their leaves seasonally, but do not have a seasonal leaf-less period (e.g. *Eucalyptus* spp. and many other Australian dicot trees)

(Howard, 1973b; Tracey, 1982; Whitmore, 1990; Adam, 1992; Barlow, 1994; Groves, 1994). In Australian rainforest communities, leaves fall in synchronised bimodal leaf flushes normally six months or so apart, the exact timing of which depends upon the forest type (Howard, 1973b; Bunn, 1986; Campbell & Fuchshuber, 1994, 1995).

In rainforests where the stream and river systems flow all year around, there is no shortage of potential depositional settings in which leaves may become trapped and ultimately preserved (Greenwood, 1991, 1992; Spicer, 1991). Such communities are common in Australia's fossil record as a result. If leaf fall occurs at a time of the year when decay is rapid and/or when the chances of preservation are low, this will significantly alter the occurrence of those leaves in depositional settings and ultimately the fossil record (Greenwood, 1994).

In southern Australian evergreen *Eucalyptus*-dominated communities, trees shed some of their leaves in late summer (e.g. Attiwell *et al.*, 1978; Lake, 1982; Pressland, 1982; Turnbull & Madden, 1983; Bunn, 1986). In late summer, when rates of decay can be very high and water flow low (Bren *et al.*, 1979; Lake *et al.*, 1985; Bunn, 1986; Department of Water Resources Victoria, 1989). There may thus be a preservational bias in *Eucalyptus* forests because the flow rates in local streams and rivers are at their lowest when leaf-fall occurs in mid summer. In such circumstances, these leaves will be unlikely to enter depositional environments because the streams are not active at the time of leaf-fall. However, in contradiction of this hypothesis, Boulton and Lake (1988, 1992) found that along the Werribee and Lerderderg rivers (Victoria, Australia), large amounts of leaf litter built-up in the river beds during the dry summers of the drought of 1982 and 1983 when the rivers dried up. Huge leaf dams formed later in the year when the rivers started flowing again. It is apparent then, that the chances of preservation in the fossil record must be altered in such a situation. At present, the effects of this potential bias in Australian forests

are unknown. Fossil *Eucalyptus* leaves are rare in the fossil record (Chapman, 1926; Lange, 1978, 1980; Christophel, 1989; Pole *et al.*, 1993; Hill 1992, 1994). This gives rise to the question as to why *Eucalyptus* leaves are not a major component of the fossil record before the Miocene, and whether this was due to taphonomic bias (Hill, 1992; Lange, 1982; Christophel, 1989; Greenwood, 1991).

1.5.3 Bias in differential transport and sorting

An important aspect of taphonomic bias is to establish how faithfully a particular deposit of fossil leaves represents the plant communities growing near the place of preservation. The accuracy with which a fossil leaf deposit represents a local flora depends upon how far its [no apostrophe] component leaves were transported before burial (Ferguson, 1985; Greenwood, 1991; Spicer, 1989, 1991). Complications arise if leaf material is brought in from afar, because such extraneous leaf material can be quite different from those plant communities found near the site of deposition (Ferguson, 1985; Spicer, 1989, 1991). This transport may also be biased for, or against, leaves of different plant taxa and their proximity to a preservational setting. It applies to both of the potential ways by which leaves may be transported after the initial abscission event. These are:

1. The redistribution of leaf material that has already fallen to the ground, termed 'overland transport' in this study.
2. The downstream transport of leaf material that has either fallen into watercourses during the initial abscission event, or entered them as a result or overland transport, here termed 'stream transport'.

When most leaves fall from their parent tree they will tend to fall within a few metres of the edge of the tree canopy (Burnham, 1994; Ferguson, 1985; Greenwood, 1991, 1992, Ferguson, 1995; Figure 1.6). Ferguson (1985), Spicer (1981, 1989, 1991) and

Greenwood (1991), have established that the distance leaves travel during abscission is a function of tree height, ambient air speed, the fall speed of the leaf, and the number of obstructions between the leaf and the ground. Most forest floor litter tends to faithfully represent the ranges of the canopies of the trees from which the leaves came. It is rare for leaves to be found more than two or three tree height radii from their parent tree; the number of leaves found upon the forest floor follows an exponential decay function, as distance increases away from the bole of the tree (Figure 1.6, Ferguson, 1985, 1995). Sun leaves may be blown substantial distances from the parent tree by the strong air currents that frequently occur above forests. Such leaves have little impact on the overall character and composition of forest floor leaf litter however, because leaves from local trees vastly outnumber them (Roth & Dilcher, 1978; Ferguson, 1985; Burnham *et al.*, 1992; Greenwood, 1992).

A difficulty with using forest-floor litter as an analogue of fossil assemblages is that litter on a forest floor may only rarely enter a depositional setting. It is therefore important to attempt to quantify how far leaves travel overland after the initial abscission event. Carpenter and Horwitz (1988) for example, found that in a Tasmanian rainforest that there was almost no lateral flow at all, resulting in the near complete exclusion of the forest dominant species (*Eucalyptus obliqua*) from the stream detritus.

In order for a fossil leaf assemblage to fairly represent the local flora, it must be derived from more than just the immediate riparian vegetation. Burnham (1989, 1994) suggests that to obtain a high fidelity representation of the autochthonous plant community for a given fossil site, samples should be selected from locations equivalent to the stream bed, stream bank and flood plain. Regrettably, it is not always possible to have such rigorous sample selection at fossil locations, as the sites may be too deeply buried, or the fossil assemblage may represent the stream bed only.

Spicer (1989, 1991) and Spicer and Wolfe (1987) found that long distance stream transport was unusual. They observed that most material was of local origin and had travelled less than 1.5 km from the site of abscission. Even in the mountainous landscape of Trinity Lake in California (USA), most plant material in the sediment load was of local origin. The only plant part transported some distance was a coniferous cone bract from an upstream forest 1.5 km away. In Australia, there have been few studies (e.g. Hill & Gibson, 1986; Greenwood, 1992) concerning the transportation distances of the leaves of native species, and data are required to quantify these distances.

Overland Transport

Leaf material can be redistributed after it has come to rest upon the ground because of the constant movement of wind currents through forests and over landscapes (Spicer, 1981, 1989; Ferguson, 1985; Burnham *et al.*, 1992). The movement of plant litter after the initial abscission event raises the following questions:

1. How effective is the wind in redistributing forest floor leaf litter?
2. What distance does leaf litter travel overland after the abscission event?
3. Do the leaves of different species travel different distances?

Available published research indicates that leaves are not spread far from the source plant and form easily identifiable leaf halos around the bole of the tree (see Spicer, 1981, 1991; Ferguson, 1985; Burnham *et al.*, 1992; Greenwood, 1992; Burnham, 1994, 1997). Ferguson (1985) posits that if leaves remain relatively mobile after abscission, then one would expect the forest floor leaf litter to become well mixed with time and become fairly homogeneous. Several studies (e.g. Ferguson, 1985; Burnham *et al.*, 1992; Greenwood, 1992; Burnham, 1994, 1997), have shown that this does not happen, and observed that within a given plot of forest, the boundaries between the leaf

halos of different tree species remain clear-cut even after periods of many months. Greenwood (1992) comments that in North Queensland, Australia, the taxonomic composition and relative abundance of leaves from local taxa in the leaf litter were strongly influenced by the nearest trees. The number of leaves of a given taxon more than 30 m from the bole of the parent tree was low, showing little evidence of overland transport (Figure 1.7).

Even for the leaves of *Fagus sylvatica*, which Ferguson (1985) classified as having mobile leaves, the levels of lateral transfer were low. In an experiment where 500 air dried leaves of *Fagus sylvatica* were spray painted with a bright fluorescent paint and placed in a pile in a closed woodland coppice of *Alnus glutinosa* (Alder), only one leaf had moved more than two metres after 98 days (Ferguson, 1985). France (1995) found that the average annual overland transport distance of coniferous pine needles and deciduous angiosperm leaves into a north-western Ontario lake, to be ~ 0.3 m and ~ 0.5 m respectively. Dudgeon (1982) mentions that light and 'flimsy' leaves such as those of *Liquidambar formosana* are easily moved by gusts of wind and suggests that they may potentially be subject to significant overland transport, but gives no experimental data. In theory, therefore, fossil deposits resulting from forest floor litter should provide a window as to what plants were growing at a particular location at a particular time.

Spicer (1981) investigated the various factors that may influence the extent to which a leaf is transported overland from its parent plant. These experiments used curled and flat *Fagus sylvatica* leaves and artificial leaves of various sizes, shapes and weights (Table 1.3). It was noted that flat shapes blown along the ground moved largely by saltation and rolling; with the greatest dispersion distances being associated with round shaped leaves that tended to 'roll' along. When folded to give a 'V' shape (as viewed

down the main axis) these shapes were transported increased distances for a given wind speed. A similar effect was noted for *Fagus* leaves, which had curled after drying.

Spicer (1981) found that size had no observable affect upon overland transport, and that weight was the major determinant in the lateral overland dispersal of leaf material. The transport distances travelled by the different weight classes of Spicer's artificial leaves were normally distributed (Figure 1.8). The heaviest leaves had the lowest mean transport distance, while the lightest leaves had the highest mean transport distances (Spicer, 1981). This is not surprising as one would expect heavier leaves to require more energy to be moved a given distance, therefore for a any given wind speed heavier leaves should travel the lowest mean distance.

Table 1.3 The combinations of paper, size and weight as used by Spicer & Ferguson in their investigations into effects of these parameters upon how far leaves can move via lateral dispersion (Spicer, 1981). In these experiments, Spicer blew the leaves along a flat plane surface using a ducted fan moved from side to side over a distance of three metres for a period of one minute so that all the leaves were blown equally.

Size Of Artificial Leaf	11 cm^2 22 cm^2 44 cm^2
Shape Used	Circular Equilateral Triangle Rhombic Shape1 (Length to breadth ratio 1.45:1) Rhombic Shape2 (Length to breadth ratio 6.9:1)
Weight of Paper Used	0.0030 g/ cm^2 0.0123 g/ cm^2 0.0346 g/ cm^2

The density of obstructions at ground level also has an effect on overland transport distances (Ferguson, 1985). These obstructions can act as obstacles which entrain leaves, while simultaneously slowing the wind speed at ground level by the creation of a boundary layer. Ferguson's PVC leaf shapes which moved little whilst on

the forest floor, moved great distances in an open meadow (Ferguson, 1985). Hence, areas exposed to high winds with little obstructing vegetation may be exposed to substantial lateral transfer of leaves.

Other authors such as van der Burgh (1994) indicate that long distance wind transport may be significant where catastrophic atmospheric events such as hurricanes and tornadoes are frequent. He notes that researchers need to be aware of the conditions under which their particular fossil deposit formed before commenting upon the floras from which the leaves came. Other studies give anecdotal evidence that leaves travel overland by wind blow or water wash under storm conditions (Drake & Burrows, 1980; Dudgeon, 1982; Greenwood, 1992).

The level of hydration also affects how far a leaf is dispersed overland as this affects the weight of the leaf; most leaves lose a mass of water roughly equal to two thirds of the leaf's initial wet weight during abscission (Ferguson, 1985). Hence, freshly fallen abscised leaves are much lighter than green leaves and have the potential to be blown greater distances. Additionally if the forest floor is moist or if the leaves are wetted while they are at rest, the cohesive properties of water will cause the leaves to adhere to each other, forming a clump resistant to movement due to its weight (Ferguson, 1985).

An additional factor affecting overland dispersal is the slope of the land. Fisher (1977) indicates there is a positive relationship between bank slope and lateral input into streams. For example Sedell *et al.* (1973), as cited in Fisher (1977), indicates that two thirds of the leaf litter input into a small Oregon stream (with banks of up to 90% (sic)) is attributable to lateral transport. Fisher and Likens (1973) likewise attribute 23% of total leaf input into a small New Hampshire stream, with bank slopes of up to 50% (sic) as being due to lateral transport by wind, while France (1995) comments that lateral

transport increases where slopes are steep. Forest floor litter may also be introduced into a stream because of bank collapse associated with the undercutting of steeper stream banks by running water, causing sections of the forest floor to fall into the stream. The localised nature of such collapses is unlikely to add leaf material from afar, as it will primarily affect riparian stands only.

The palaeobotanical implications of the above discussion suggests that woodland leaves may only be dispersed limited distances. Even the tallest tree species in a forest must normally be growing near a body of water to have a chance of becoming fossilised because its leaves will, in all probability, not travel much further than one tree height from the bole of the tree (Spicer, 1981; Ferguson, 1985, 1995; Greenwood, 1991). This relationship is best exemplified by Greenwood's (1991) study of North Queensland rainforests (Figure 1.7). If then, leaves remain more or less stationary after reaching the ground, one would expect that many fossil leaf assemblages would consist of mainly of riparian or wetland plants. In Australia, this is of some significance due to the general paucity of fossil leaves of the floristically significant sclerophyll taxa of *Eucalyptus* and *Acacia*, which are often not riparian plants, and the normally rainforest taxon, *Nothofagus cunninghamii* (Section 1.2; Lange, 1982; Hill, 1982, 1994; Greenwood *et al.*, 2000).

Stream Transport

The longitudinal transport of leaf material down streams is a key feature of the River Continuum Concept (Vannote *et al.*, 1980; Johnson *et al.*, 1995), and is also of importance in understanding the formation of plant fossil deposits in stream sediments (Spicer, 1981; Ferguson, 1985; Greenwood, 1991; Steart *et al.*, 2002). A key topic for palaeobotany would appear to be the differential sorting of plant material upon transport

in a riparian system. The leaves of different species vary in their anatomy and chemical composition, potentially influencing retention within a given stream section, buoyancy (and thus flotation time) and the distance travelled (Spicer, 1981). The differential transport and survival of leaves of terrestrial taxa will manifest itself in a biased contribution between stream reaches, and a biased leaf taxonomic composition in allochthonous leaf assemblages (Spicer, 1981; Greenwood, 1991; Steart *et al.*, 2002).

The River Continuum Concept, initially developed for undisturbed streams in forested watersheds in northern temperate regions, posits that streams possess a consistent longitudinal structure, which results from a clear gradient in physical forces. Inputs of coarse particulate organic matter – largely derived from terrestrial vegetation – dominate organic matter fluxes in low-order, forested headwater streams (Fisher & Likens, 1973; Cummins, 1974; Winterbourn, 1976; Neaves, 1978; Blackburn & Petr, 1979; Bunn, 1986; Campbell *et al.*, 1992a & b, Benson & Pearson, 1993; Campbell & Fuchshuber, 1994; Johnson & Covich, 1997). Physical forces and biological activity gradually break down these inputs of leaf, wood and bark, both microbial and invertebrate, into finer particles (Anderson & Sedell, 1979; Benfield & Webster, 1985). The processed organic matter – which comprises both large and small particles - is either retained or is translocated downstream and contributes markedly to the "energy income" for animal communities in the lower reaches (Vannote *et al.*, 1980 page 135).

A large number of studies have addressed the transport – or more specifically the retention – of allochthonous leaf material in streams (e.g., Newbold *et al.*, 1982; Speaker *et al.*, 1984; King *et al.*, 1987; Gurtz *et al.*, 1988; Smock, 1990; Stewart & Davies, 1990; Jones & Smock, 1991; Prochazka *et al.*, 1991: Snaddon *et al.*, 1992;; Webster *et al.*, 1994; Ractliffe *et al.*, 1995; Webster & Meyer, 1997; Koetsier & Mcarthur, 2000; Larned, 2000). These studies have (in the main) shown the overwhelming importance of

hydrology – especially stream velocity – in determining whether a leaf is translocated downstream or retained within a given stream section. Studies such as Newbold *et al.* (1982), emphasise the importance of stream reach in addition to velocity upon retention, suggesting that high order streams, or swamp streams, experience greater retention due to the presence of organic debris dams which can entrain leaves and reduce their transport distance. Other studies such as Koetsier and Mcarthur (2000) show that dense macrophyte beds in streams can also affect retention.

A number of studies have quantified the distance that individual leaves are translocated downstream. In many cases these distances are quite low. In one of the earliest reports, Young *et al.* (1978) quantified the distances travelled by maple (*Acer rubrum*), beech (*Fagus grandifolia*) and oak (*Quercus rubra*) leaves in a woodland stream in Pennsylvania (USA) and found that the distances ranged markedly, from ~100 m to over 1 km. Ehrman and Lamberti (1992) reported that the average distance travelled by *Ginkgo* leaves in a third-order woodland stream in Indiana (USA) ranged from 109 m to 168 m; while, wooden dowels travelled between 14 and 183 m. Other studies have indicated far more effective retention of leaves. Jones and Smock (1991), for example, reported that the mean transport distance of leaves in a first-order stream in Virginia (USA) could be as short as 1.6 m. Wallace *et al.* (1995) concluded that the maximum downstream movement of surrogate "leaves" (plastic sheets) in headwater streams in North Carolina (USA) was ~42 m per year. In the first-order Window Stream (South Africa) leaves could be retained within reaches as short as 50 m (Prochazka *et al.*, 1991).

A phenomenon linked to leaf transport in streams is leaf sorting, or the potential of leaves from different plant taxa to be selectively transported greater or lesser distances downstream. A number of studies deal with leaf sorting because of the importance of

being able to quantify the origins of fossil leaf material when analysing fossil leaf deposits and attempting reconstruction of the ecosystems that formed them (e.g., Drake & Burrows, 1980; Spicer, 1981; Ferguson, 1985; Spicer & Wolfe, 1987; Carpenter & Horwitz, 1988; Greenwood, 1992). Spicer (1981, 1989) noted that powerful sorting effects were brought about by variation in leaf flotation times, and that these times were affected by factors such as whether both leaf surfaces were wetted, the degree of turbulence, and the extent of gas saturation of the water body. With respect to leaf morphology, it has been shown that the thin papery leaves of deciduous trees, such as *Alnus glutinosa*, sink within hours in aquaria, whereas the thick coriaceous leaves of the broad-leaved evergreen *Rhododendron* sp. float for several days (Spicer, 1981; Ferguson, 1985). Variation in flotation times have been reported by Hill and Gibson (1986), who found that leaves of the sclerophyllous taxa, *Eucalyptus coccifera* and *Orites acicularis*, sank within two days, whereas the leaves of other taxa floated for much longer periods of time (See Table 1.4). Anecdotal evidence suggests also that large coriaceous leaves may be transported shorter distances in streams than small leaves within or between stands of tropical rainforest (Greenwood, 1992).

Differences in leaf retention among taxa will contribute to discrepancies in taxonomic composition of fossil leaf assemblages (Spicer, 1981, 1989; Ferguson, 1985; Greenwood, 1991, 1992). Taxa with poor transport potential will be under-represented or even absent in allochthonous fossil leaf assemblages, whereas taxa with high transport potential may be over-represented, distorting interpretations of species composition and relative abundance (Spicer, 1981, 1989, 1991; Spicer & Wolfe, 1987; Greenwood, 1991).

Table 1.4 The number of days taken for a given percentage of leaves to sink, for the eleven plant taxa reported in Hill and Gibson (1986). One hundred leaves of each species were used and the leaves were agitated for 10 seconds twice per day. The leaves were removed as they sank and the experiment was conducted over a period of 100 days.

Species	Time (days) Needed for		
	25% of leaves to sink	50% of leaves to sink	75% of leaves to sink
Athrotaxis cupressoides	0	0	1
Bauera rubioides	23	28	31
Cyathodes juniperina	12	18	26
Epacris sepyllifolia	19	28	39
Eucalyptus coccifera	0	0	0
Microstrobos niphophilus	4	92	>100
Leptospermum lanigerum	15	19	25
Nothofagus cunninghamii	11	15	36
Orites acicularis	0	0	1
O. revoluta	13	25	37
Trochocarpa cunninghamii	50	67	77

1.5.4 Bias in differential decay and preservation

Only a tiny fraction of the plant material ever produced has the opportunity to become fossilised, and the amount of material escaping the process of decay will clearly determine whether a species is recognisable in the fossil record (Spicer, 1981; Ferguson, 1985). The decay process includes all of the factors that effect the rate at which a leaf is degraded to the point of it becoming unrecognisable. It begins before the leaf is removed from its tree, and ends when the leaf has been completely destroyed. Of particular interest to the palaeobotanist is whether leaves from different plant taxa decay and fragment at the same rate. If some species decay more rapidly than others do, they may be under-represented in the fossil record (Spicer, 1981).

The phenomenon of differential decay rates has been acknowledged for some time, especially in the soil biology and limnological literature where significant differences in the comparative break down rates of leaf material have been observed

between species (e.g. Heath *et al.*, 1966; Edwards, 1977; Blackburn & Petr, 1979; Hayes, 1979). The most widely used mathematical descriptor to compare leaf litter decay rates, from different plant species and treatments is the single exponential model as reviewed by Olsen (1963). Other equations such the linear and asymptotic models have been soundly criticised by Wieder and Lang (1982) for their lack of biological reality. Quadratic models have been criticised for similar reasons and can have absolute decomposition rates that tend towards positive or negative infinity as time increases or when decay curves are extrapolated beyond the experimental data (Weider & Lang, 1982). The equation for the single exponential model is shown below.

Equation 1.1 $W_t = W_0 e^{-kt}$

In this equation W_t is mass remaining at time t, W_0 is the mass of material present initially and k is the exponential decay coefficient. The term t is usually measured as a fraction of a year. The value of k can be determined through the manipulation of the equation so that k is isolated. This is given in equation 1.2.

Equation 1.2 $-k = \ln(W_t/W_0)/t$

The exponential decay coefficient 'k' has frequently been used in the ecological literature to compare the decay rates of the leaves of different tree species. For this reason, this model has been used in the current study. Examples of some literature based k values are given in Table 1.5.

The outstanding palaeobotanical criticism of measuring leaf decay by weight is that it does not measure a quantity that can be easily applied to a fossil assemblage. Fossil leaf deposits can be measured in terms of the presence or absence of species, the number of leaves or dispersed cuticles of each species, or the cumulative area of leaves of each species (Greenwood, 1991; Wilf *et al.*, 1998; Greenwood *et al.*, 2003). In most

circumstances, it is not possible for palaeobotanists to either weigh the mass of their leaf samples, or to know the mass of the original leaf material they have collected from a fossil locality. One of the secondary aims of this study was to identify whether leaf decay rates, expressed as k values, can be correlated with the destruction of the leaf blade or lamina versus time. Should this be the case, then the extensive ecological literature which uses the k constant as a measure of decay can be used to indicate which taxa decay quickly, and which ones don't and thus potentially correct for their occurrence in reconstructions of palaeoecosystems.

Techniques used to measure leaf decay rates

Two of the common means of measuring leaf decay rate involve placing known quantities of leaves in single or mixed species leaf packs, or bags, of varying design and materials (Boulton & Boon, 1991). Some studies (e.g. Petersen & Cummins, 1974) have used single species leaf packs fastened by a nylon fastener. The packs were designed to mimic stream leaf accumulations often seen upstream of obstacles when temperate deciduous forests shed their leaves.

A major draw back of the leaf pack method is that leaf fragments are lost during the decay process (Woods & Raison, 1982). The other commonly used device used in leaf decay rate experiments is the 'leaf bag'. Generally leaf bags are made of plastic or nylon mesh, sewn into a pouch containing the leaves. Leaf bags have the advantage of retaining leaf fragments that result during the decay and disintegration of leaf litter because they are completely contained. Leaf bags can also regulate access of soil macrofauna to the leaf material by varying bag mesh size; the larger the mesh size, the larger the organisms able to access the leaf material (Woods & Raison, 1982). Boulton and Boon (1991) have criticised the use of leaf bags because they can deny access to large soil and stream invertebrates, alter water currents around the bags (thereby

Table 1.5 Examples of the range of annual literature derived *k* values, sorted by *k* value and clade. Decay values marked with an asterix, '*' were derived from daily decay rates multiplied by 365 to give annual decay rates; Values marked with '•' were given as daily rates in the publication, and then recalculated as annual decay rates from the publications decay rate data; Values marked with '⊗' were calculated from the published decay rate data.

Species	*K* Value	Type	Country	Source
Eucalyptus regnans[1,3,4]	4.95	Dicot	Australia	Blackburn & Petr (1979)
Melicytus ramiflorus (green leaves)	4.17⊗	Dicot	New Zealand	Enright & Ogden (1987)
Eucalyptus regnans[1,3,5]	4.18	Dicot	Australia	Blackburn & Petr (1979)
Nothofagus cunninghamii[1,3,5]	4.11	Dicot	Australia	Blackburn & Petr (1979)
Nothofagus cunninghamii[1,3,6]	1.77	Dicot	Australia	Blackburn & Petr (1979)
Melicytus ramiflorus (dead leaves)	1.44-1.85⊗	Dicot	New Zealand	Enright & Ogden (1987)
Ripogonum scandens	1.22⊗	Dicot	New Zealand	Enright & Ogden (1987)
Salix sp.	0.9819*	Dicot	Canada	Hodkinson (1975)
Eucalyptus brookerana	0.94-0.76	Dicot	New Zealand	Guo & Sims (1999)
Alnus glutinosa	0.908	Dicot	Portugal	Pereira *et al.* (1998)
Pseudopanax arboreus	0.81-0.96⊗	Dicot	New Zealand	Enright & Ogden (1987)
Eucalyptus globulus	0.808	Dicot	Portugal	Pereira *et al.* (1998)
Eucalyptus delegatensis	0.68	Dicot	Australia	Woods & Raison (1983)
Castanopsis wattii	0.6477	Dicot	China	Liu *et al.* (2000)
Lithocarpus xylocarpus	0.6211	Dicot	China	Liu *et al.* (2000)
Eucalyptus regnans (Mature forest)[1,2]	0.58-0.73	Dicot	Australia	Ashton (1975)
Eucalyptus pauciflora	0.53	Dicot	Australia	Woods & Raison (1983)
Elaeocarpus denatatus	0.53⊗	Dicot	New Zealand	Enright & Ogden (1987)
Eucalyptus marginata (In summer)	0.51-0.55*	Dicot	Australia	Bunn (1988)
Beilschmiedia tawa	0.50-0.53⊗	Dicot	New Zealand	Enright & Ogden (1987)
Lithocarpus chintungensis	0.4964	Dicot	China	Liu *et al.* (2000)
Acacia longifolia	0.486	Dicot	Portugal	Pereira *et al.* (1998)
Eucalyptus dives	0.47	Dicot	Australia	Woods & Raison (1983)
Eucalyptus marginata (In winter)	0.44-0.73*	Dicot	Australia	Bunn (1988)
Populus nigra	0.393	Dicot	Portugal	Pereira *et al.* (1998)
Eucalyptus diversicolor	0.37-0.57	Dicot	Australia	O'Connell (1987)
Eucalyptus diversicolor	0.37-0.57	Dicot	Australia	O'Connell (1987)
Cornus florida	0.366	Dicot	United States	Finzi *et al.* (2001)
Eucalyptus botryoides	0.36-0.24	Dicot	New Zealand	Guo & Sims (1999)
Myrtus communis	0.33-0.48	Dicot	Italy	Fioretto *et al.* (2000)
Cistus incanus	0.29-0.57	Dicot	Italy	Fioretto *et al.* (2000)
Acer rubrum	0.256	Dicot	United States	Finzi *et al.* (2001)
Eucalyptus regnans (Pole forest)[1,2]	0.25-0.83	Dicot	Australia	Ashton (1975)
Knightia excelsa	0.25⊗	Dicot	New Zealand	Enright & Ogden (1987)
Liquidambar styraciflua	0.246	Dicot	United States	Finzi *et al.* (2001)
Cercis canadensis	0.176	Dicot	United States	Finzi *et al.* (2001)
Deschampsia cespitosa	0.6680*	Monocot	Canada	Hodkinson (1975)
Juncus tracyi	0.4088*	Monocot	Canada	Hodkinson (1975)
Rhopalostylis sapida	0.31⊗	Monocot	New Zealand	Enright & Ogden (1987)
Agathis australis	0.35⊗	Conifer	New Zealand	Enright & Ogden (1987)
Pinus contorta	0.2154*	Conifer	Canada	Hodkinson (1975)
Phyllocladus trichomanoides	0.17⊗	Conifer	New Zealand	Enright & Ogden (1987)
Pinus taeda	0.083	Conifer	United States	Finzi *et al.* (2001)
Dicksonia squarrosa	0.32⊗	Fern	New Zealand	Enright & Ogden (1987)
Cyathea dealbata	0.21⊗	Fern	New Zealand	Enright & Ogden (1987)
Cyathea medullaris	0.17⊗	Fern	New Zealand	Enright & Ogden (1987)

Notes: 1 = experiments were conducted over three months only; 2 = variation in *k* values due to seasonality; 3 = decay rates measured in a stream; 4 = bag mesh size 3.9 mm; 5 = bag mesh size 1.3 mm; 6 = bag mesh size 0.5 mm

potentially altering microbial colonisation and attack), readily trap detritus, and alter rates at which leaves are physically abraded. On the other hand leaf bags are the only feasible means of tethering very small leaves such as *Nothofagus cunninghamii*, one of the key species to be used in this study (Boulton & Boon, 1991; p. 6). For this reason leaf bags will be used in this study inspite of the above mentioned criticisms.

There have also been a number of criticisms of the use of single-species leaf-packs and bags, in that the ecology of the organisms involved in leaf decay may be affected by the presence of only one food source (Woods & Raison, 1982; Boulton & Boon, 1991). Woods and Raison (1982) suggest that important interactions between litter-bed components will not be fully expressed when leaves of only one species are used in a litterbag. In contradiction to Woods and Raison (1982), other researchers such as Thomas (1968) indicate there is little difference between decomposition rates for pine needles in single and mixed litter bags of *Pinus taeda* (loblolly pine) and *Cornus florida* (dogwood), even though the number of litter faunal species was almost twice as high in mixed-species bags. The extra faunal species in the mixed-species leaf-bags apparently fed upon the high quality *C. florida* litter only, without affecting the observed decay rates (Thomas, 1968; Enright & Ogden, 1987). Enright and Ogden (1987) argue that such studies support the use of single-species leaf-bags and the calculation of separate decomposition rates where species specific decomposition rates are of interest.

The Decay Process

For any leaf which falls off a tree, three distinct phases of leaf processing are recognised (Cummins, 1974; Boulton & Boon, 1991), a general model for the decomposition of leaf material being given in Figure 1.9, as modified from Berg and Matzner (1997). Initially the leaf loses mass rapidly due to the leaching of water soluble

sugars and other cell components out of the leaf into the surrounding soil/litter environment via the movement of water through the leaf (Brinson, 1977; Blackburn & Petr, 1979; Woods & Raison, 1983). The loss of these soluble organic compounds can account for as much as 30% of the initial leaf mass, and the water soluble compounds can be leached out within a day for some leaves (Bunn, 1986; Petersen & Cummins, 1974; Pozo, 1993; Woods & Raison, 1983). Mass loss slows after a few days to a week, due to the loss of these water-soluble compounds. The initial mass loss from green leaves is frequently higher than for brown or abscissed leaves (Woods & Raison, 1983; Cornelissen, 1996), due to their higher initial levels of water-soluble nitrogen and phosphorus rich organic compounds. Higher levels of nitrogen and phosphorus increase the nutrient status of the leaf and hence its palatability to soil and stream microorganisms and macrofauna (Bunn, 1986). Brown or senescent leaves have few nutrients in them, as the plant has already removed most of the mobile nutrients prior to leaf abscission (Addicott, 1982). Such leaves take much longer to decay because the saprophytic organisms colonising the leaf have to obtain their nitrogen and phosphorus from sources outside the leaf (Bunn, 1986; Campbell, *et al.*, 1992b).

The second phase of leaf processing begins as the rapid leaching of organic compounds ceases, and is characterized by the colonization of the leaf by bacteria and hyphomycete fungi (Bunn, 1986). This period can be quite long for some leaves, and is generally called conditioning (Petersen & Cummings, 1974). The relative ratios of lignin, cellulose and hemicellulose play a major role in determining the length or even the presence of a conditioning period (Bunn, 1986; Wilson *et al.*, 1986), as does the presence of either condensed or hydrolysable tannins (Bernays *et al.*, 1989; Stout, 1989). The higher the initial lignin content of the leaf, the slower the decay rate becomes, with some authors indicting that when the lignin to cellulose ratio reaches a certain point, decay can almost cease (Berg

& Matzner, 1997; Berg, 2000; Wilson *et al.*, 1986; Figure 1.9). This is due, in part to the chemical complexity of lignin (Reese, 1977; Hayes, 1979; Lewis & Yamamoto, 1990; Aber & Melillo, 1991; Boulton & Boon, 1991; Berg & Matzner, 1997; Berg, 2000;).

The decomposition of lignin and cellulose is mainly mediated by bacteria and fungi, which secrete cellulose and lignin degrading enzymes into the medium they are digesting (Reese, 1977; Hayes, 1979). The organisms then absorb the degradation products across their cell membranes (Reese, 1977). Lignin and cellulose degradation is a strongly aerobic process, dependent upon the temperature, nitrogen and moisture content of the tissues (Whitkamp, 1966; Williams & Grey, 1974; Brinson, 1977; Reese, 1977; Harmon *et al.*, 1986; Eriksson *et al.*, 1990; Bernhard-Reversat, 1993; Berg & Matzner, 1997). Reese (1977) indicates that to prevent cellulose degradation, moisture contents need to be kept below fibre saturation point, or 24 to 32 % for most woods. Should a leaf therefore be deposited in either a dry, anaerobic, or cold place, the enzymatic decomposition of the lignin and cellulose in a leaf will be either prevented or strongly inhibited. Larger aquatic organisms such as freshwater invertebrates and fish are usually only involved in the mechanical decay of leaf matter by shredding the leaves, gaining their nutrition by digesting the microorganisms growing on the leaf (Cummins, 1973; Bunn, 1986).

The concentration of manganese is also thought to have an important positive effect in the decay of leaf material, especially lignin (Berg *et al.*, 1995; Fioretto *et al.*, 1998; Berg, 2000). This metal ion is essential for the activity of manganese peroxidase, a lignin-degrading enzyme (Perez & Jeffries, 1992). Manganese also stimulates the production of this enzyme and is involved in the regulation of other lignin degrading enzymes such as laccase and lignin peroxidase (Archibald & Roy, 1992; Perez & Jeffries, 1992). In many situations the decay process is enhanced via the increase in surface area

and creation of points of entry for microbial decomposition by the actions of the various organisms which shred and eat leaf material.

The third stage of decomposition involves the mechanical breakup of the leaf by stream or soil macrofauna, followed by rapid decay and decomposition as the conditioned microbial population builds up, and the leaves get eaten by invertebrates and shredders (O'Connell & Menage, 1983; Bunn, 1986; Campbell & Fuchshuber, 1994). In unlignified leaves this stage may occur without a significant period of conditioning, as invertebrate fauna begin feeding on the leaf and the microorganisms that are degrading it. Cellulose and hemicellulose are usually degraded by saprophytic micro-organisms before lignin, and unlignified leaves can follow a decay curve without an inflection point caused by a conditioning period (Bunn, 1986; Wilson *et al.*, 1986). The decay of the cuticle can be very slow (Spicer, 1991; Van Bergen *et al.*, 1995; Van Bergen, 2001). Frequently, rotted leaves are found in which only their lignified main vein and secondary veins enveloped in the leaf cuticle are observed (Spicer, 1989, 1991; Van Bergen *et al.*, 1995). Leaf cuticles are common fossils, as they are made from highly resistant materials, consisting chiefly of waxes and fats (Bold *et al.*, 1987; Spicer, 1989, 1991; Knox *et al.*, 1994; Van Bergen *et al.*, 1995). Some researchers have implied that cutin and hence cuticle thickness may slow decomposition (Gallardo & Merrino, 1993). Spicer (1981, pp 37-38) comments that cuticle thickness is commonly proposed as a major factor in the preservation of a leaf, though not as effective a barrier to microbial colonisation as is often assumed.

Decomposition can also be inhibited by a diverse class of compounds known called tannins (Bernays *et al.*, 1989). Tannins have molecular weights ranging from 300 to 3000 Dalton's, and are classed into four groups:

1. The condensed tannins or Proanthocyanidins.

2. The hydrolysable tannins.

3. The oxytannins.

4. The β-tannins.

The condensed tannins are the most ancient and widespread of these 4 groups, being thought to have evolved in the Carboniferous (Bate-Smith, 1974; Swain, 1976; Bernays *et al.*, 1989). They structurally resemble flavanoids, consisting of oligomers of flavon-3-ols, such as catechin, epicatechin or gallocatechin. It has been suggested that condensed tannins inhibit leaf decay due to their insoluble nature (Campbell & Fuchshuber, 1995), and ability to remain in the leaf for extended periods. The next most common class of tannins are the hydrolysable tannins, so called because they can be easily hydrolysed by mineral acids (Bernays *et al.*, 1989). They are restricted exclusively to dicots and are esters of glucose (or more rarely polyols) with gallic acid, hexahydroxydiphenic acids, or their derivatives (Swain, 1979).

Tannins are thought to protect leaves from herbivory by being toxic to insects and other grazing animals (Bernays *et al.*, 1989; Stout, 1989). High tannin concentration can cause liver and kidney damage in mammals, and lethal damage to the intestines of susceptible insects (Bernays *et al.*, 1980, 1989). Most tannins can complex with proteins and precipitate them (Asquith & Butler, 1985), and thus may have a significant impact upon the activity of extracellular enzymes (Bernays *et al.*, 1989; Serrano & Boon, 1991). The precise mechanism by which tannins protect the plant is still debatable (Bernays *et al.*, 1989). But what is known is that tannins and polyphenolic compounds influence the growth rates of fungi on or in the plant (Swain, 1979; Zucker, 1983), and that they inhibit decomposition in the soil by bacteria, fungi and arthropods (Harrison, 1971; Anderson, 1978; Cameron & LaPoint, 1978). Gonzalez-Farias and Mee (1988) have also demonstrated a seasonal inhibition of decay in a Mexican tannin and polyphenol rich mangrove swamp.

The high levels of tannins and other polyphenolic compounds found in many *Eucalyptus* species, *Acacias* and other Australian native plants are thought to have a significant impact upon slowing leaf decay rates in Australian forests and streams (Bunn, 1986; Boon & Johnstone, 1997). If this is the case then these compounds may have a positive impact upon the likelihood of leaves entering the fossil record by slowing decay rates or delaying decomposition until burial.

1.5.5 Deposition

For preservation to occur a leaf must be able to reach a place where the normal processes of plant decay are inhibited, and such places normally exist at sites of deposition (DiMichele & Wing, 1988; Spicer, 1989, 1991). The best sites of deposition are those which occur in a lacustrine setting where a stream or river is debouching into a lake, or in a riparian setting where there is significant deposition of silt along the rivers flood plain by a slow moving silt-rich river (Spicer, 1989, 1991). In lakes, the leaf can become incorporated into aggrading sediment fronts that are forming because of in-flowing rivers or streams depositing their sediment load. If the site of deposition is deep enough so that it becomes anoxic, and remains undisturbed, any buried plant material has a good chance of slowly fossilising.

The site of deposition must not be reworked, either by the disturbance of the basal sediments of lakes, or in a riparian setting, by erosion resulting from a change in the course of a river. Significant reworking can also occur as a result of the underground activities of soil invertebrates and plant roots, which tend to aerate soils and disturb sediments. The site should also be anoxic so that the normal saprophytic soil microflora have less opportunity to degrade the organic material *in situ.* This normally requires the site to remain permanently water logged so that oxygen levels remain low for extended periods. If

sufficient time passes to allow for the consolidation of the fossils embedding medium, then the object has a good chance of long term preservation.

1.6 Overview and statement of intent

From the above discussion and literature review, a number issues have been raised which this thesis aims to address. The main objective of this thesis is to examine potential sources of taphonomic bias in the relative abundance of the principal tree genera as leaves in fossil deposits, using modern stands of *Eucalyptus* and *Nothofagus* dominated forest. A secondary aim was to use these observations to assess whether an ecological –landscape model, or a taphonomic model, can be invoked to explain the paucity of *Nothofagus*, *Acacia, Eucalyptus* and other plant genera as macrofossils in the Australian Cenozoic fossil record. To discover the possible reasons for these anomalies in the Australian fossil record, four major experiments were conducted. They were based upon the uniformitarian assumption, that the ecological processes that operate in the modern world operated throughout the Cenozoic. The experiments were designed to identify the possible confounding factors that emerge from the three broad categories of taphonomic bias described in section 1.5. These are:

1. Bias in biomass production: the differential production of plant parts (leaves, reproductive organs and woody parts), both between plant taxa and time of abscission.
2. Bias in transport: the differential transport and sorting of plant organs between species once they have been produced and shed from the parent plant.
3. Bias in differential decay and preservation of plant organs from different species.

Chapter 2 of this study addresses the first of these categories of taphonomic bias. To determine the nature of any bias in biomass production in the ecosystem studied, the standing biomass had to be determined. To this end every plant taller than 1.8 metres in the field site had its diameter measured at breast height (1.5 m) and its basal area determined. Tree basal area is a widely used measure for standing biomass of self-supporting trees (Catchpole & Wheeler, 1992), but not lianas (Putz, 1983). Though Niklas (1994a & b), indicates that regression equations estimating height and other biomass measures can be calculated for most plant habits. As all the plant taxa examined in this study are self supporting trees, tree basal area was the measure of biomass used. The amount of biomass produced by the ecosystem had also to be measured. To this end 22 litter traps were constructed and deployed throughout the field site. The spatial, temporal and organ type production of each species was measured and the possible sources of taphonomic bias examined.

Chapters 3 and 4 address bias in transport. Because of the different physical processes that operate between leaves moving overland with the assistance of wind, and moving down a stream with the assistance of flowing water, this category was divided into overland transport (Chapter 3), and longitudinal transport in streams (Chapter 4). The distance that leaves travel from their parent plant during the initial abscission event has already been comprehensively explained by previous researchers (e.g. Spicer, 1981, 1989, 1991; Ferguson, 1985) and so was not dealt with here. To measure how far leaves move overland (Chapter 3), a number of leaves from each of the four canopy tree taxa found at the field site, and the tree *Lomatia fraseri* a member of the Proteaceae (a family with a good fossil record), were marked and distributed throughout the field site at 20 discrete locations. After six months these leaves were collected and the distances travelled by them noted. The measurement of the how far leaves travelled in a stream

(Chapter 4) was determined by releasing known numbers of leaves at different distances upstream from a set point along Cumberland Creek (See Section 2.2). The various distances at which leaves became entrapped were noted, and some of the physiognomic characters of the leaves such as size and weight tested in order to explain some of the phenomena observed.

Chapter 5 addresses bias in differential decay and preservation of plant organs for different species. To examine the magnitude of any differences in decay and preservational potential between the taxa used, leaves of each species were placed into leaf bags and deployed throughout the field site in each of the four locations that a leaf might possibly be expected to be found after falling from a tree (see Ferguson, 1985; Spicer 1989, 1991; Greenwood, 1991), that is:

1. The forest floor or autochthonous leaf fall (the most probable location for the bulk of the leaf material that falls from its parent tree to the ground, without subsequent long distance and or overland transport or entry into a watercourse).
2. Autochthonous burial in the sediments of the forest floor (possibly by a flash flood or other depositional event which deposits a layer of silt or soil which entombs leaf material lying upon the forest floor).
3. Parautochthonous accumulation on the surface of stream channels (a probable fate of many leaves upon entering the stream channel).
4. Allochthonous burial in the stream or lake sediments (the place preservation is most likely to occur).

These samples were collected monthly for a year and the differences in decay rates noted. The physiochemical makeup of the leaves was determined with a view towards using this information to explain the differences in decay rate observed. Chapter

5 was also designed to elucidate whether or not the widely used measures of foliar decay rates (the decay coefficient *k*) could be used as a means of identifying which species may decay rapidly or slowly from a taphonomic sense.

Finally Chapter 6 examines the findings from the experimental chapters, and offers an explanation as to various discrepancies in the Australian fossil record for the four genera of *Nothofagus*, *Acacia*, *Atherosperma* and *Eucalyptus*.

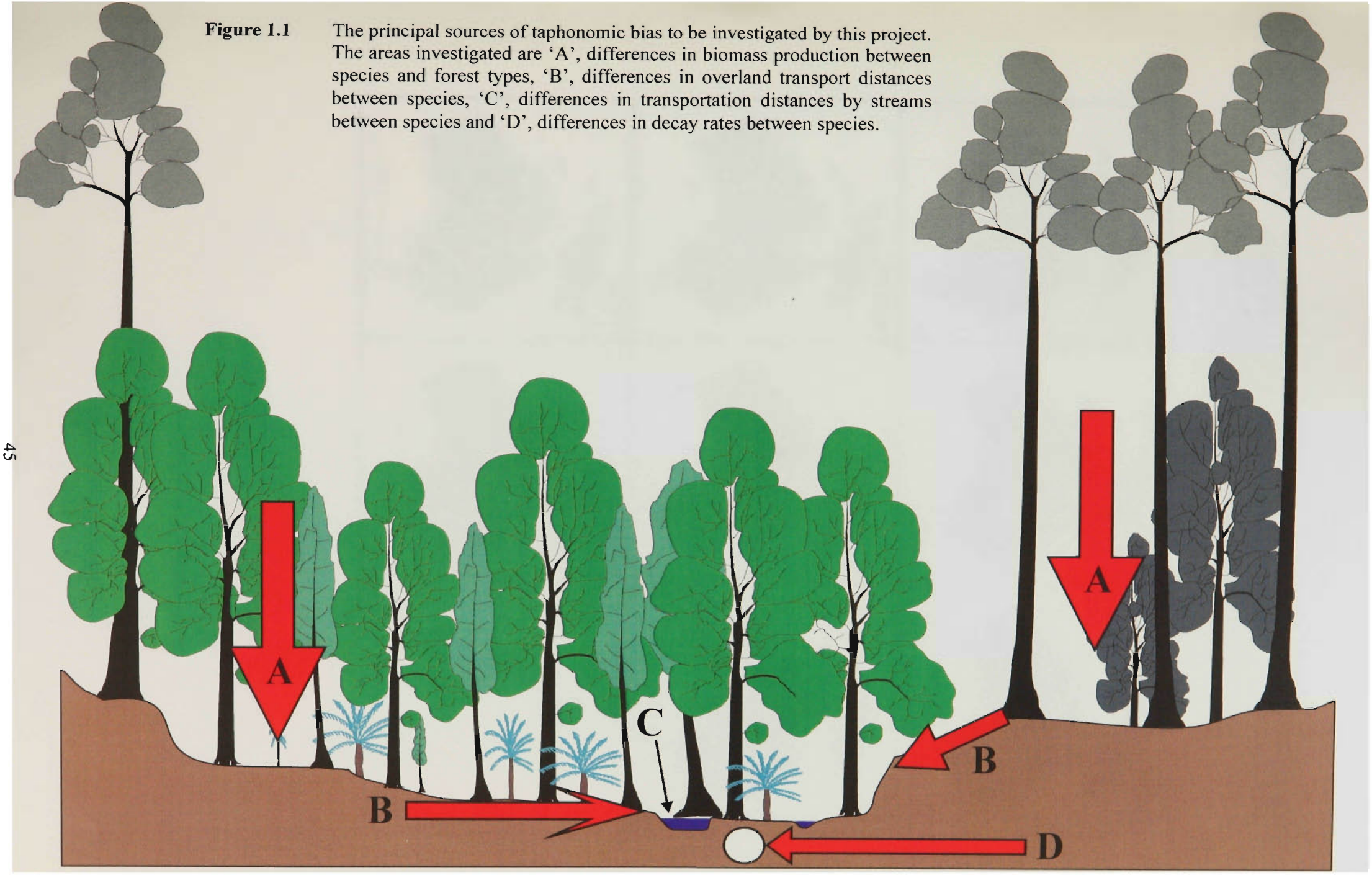


Figure 1.1 The principal sources of taphonomic bias to be investigated by this project. The areas investigated are 'A', differences in biomass production between species and forest types, 'B', differences in overland transport distances between species, 'C', differences in transportation distances by streams between species and 'D', differences in decay rates between species.

Figure 1.2 The Australian continent has changed its latitudinal position significantly during the Cenozoic period. The diagrams above indicate the relative position of the continent at the times marked. Note Ma equals millions of years ago (Modified from Embleton 1984 as cited in Adam 1992).

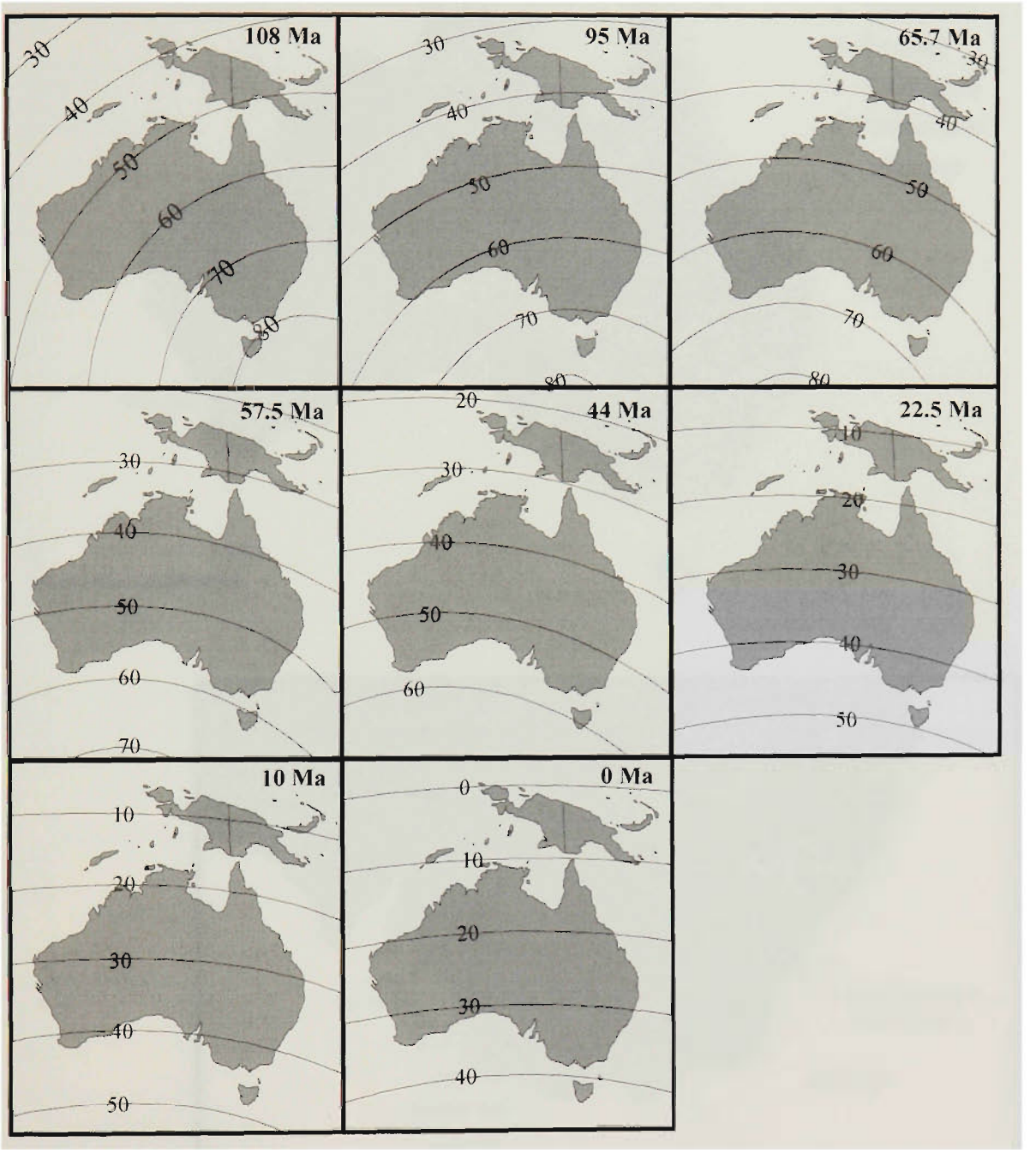


Figure 1.3 Map showing Australian Cenozoic macrofossil localities. Adapted from Greenwood *et al.*, (2000).

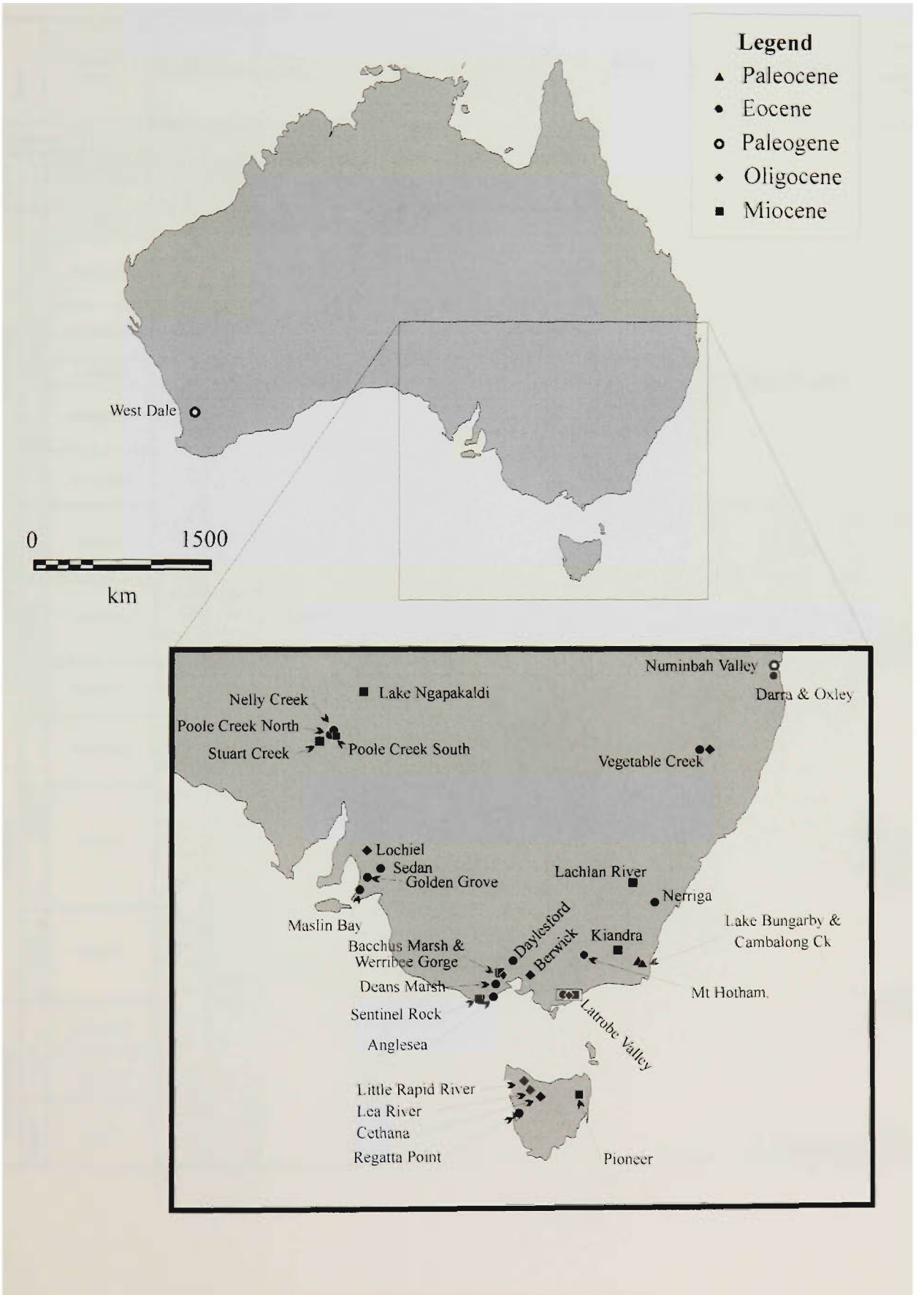


Figure 1.4 The stratigraphic ranges of selected Cenozoic South East Australian plant fossil localities (Greenwood, 2003 *pers comm.*).

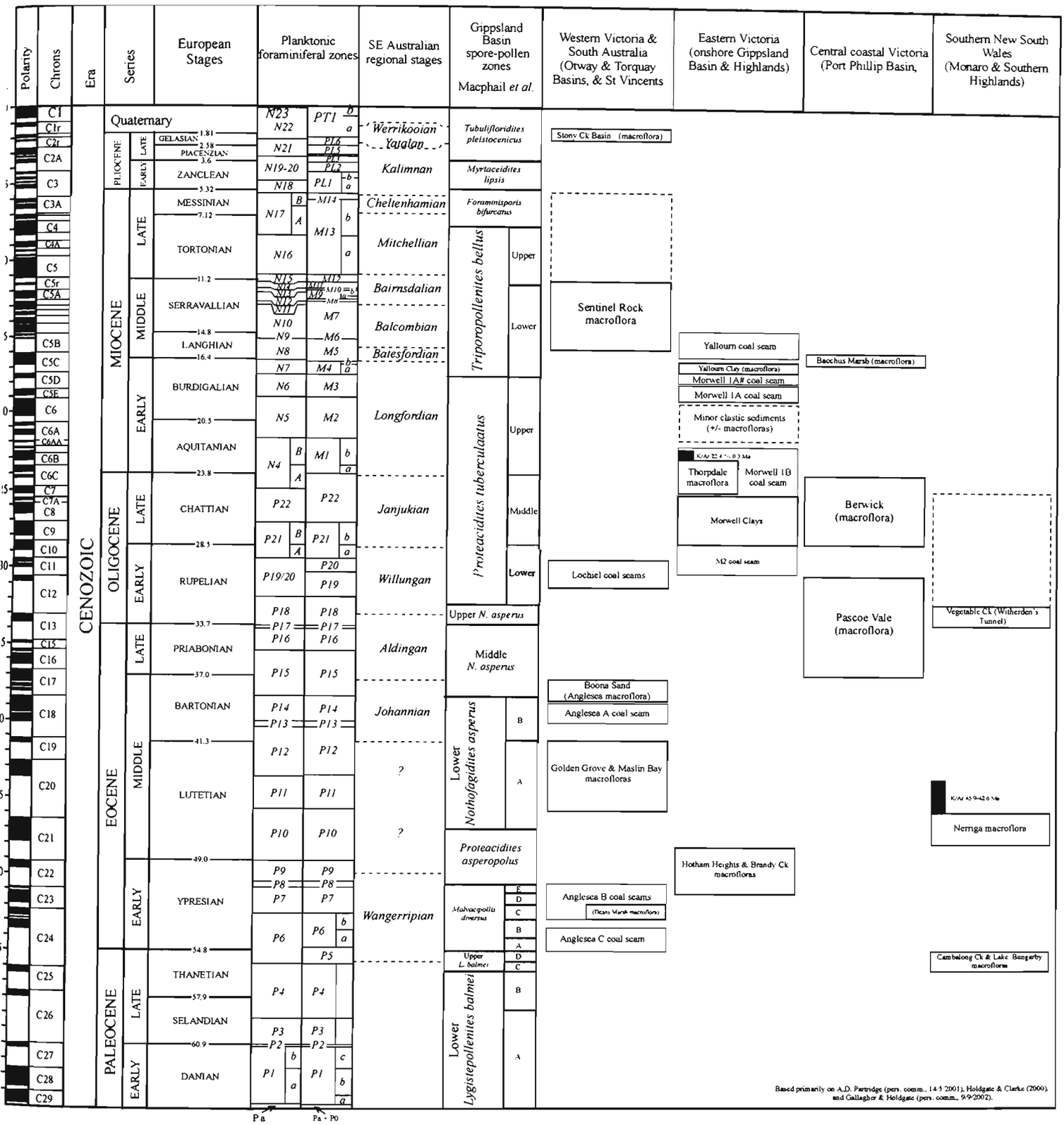


Figure 1.5 Generalised diagram outlining the fate of aerial canopy parts in terrestrial and aquatic ecosystems (Gastaldo, 1994).

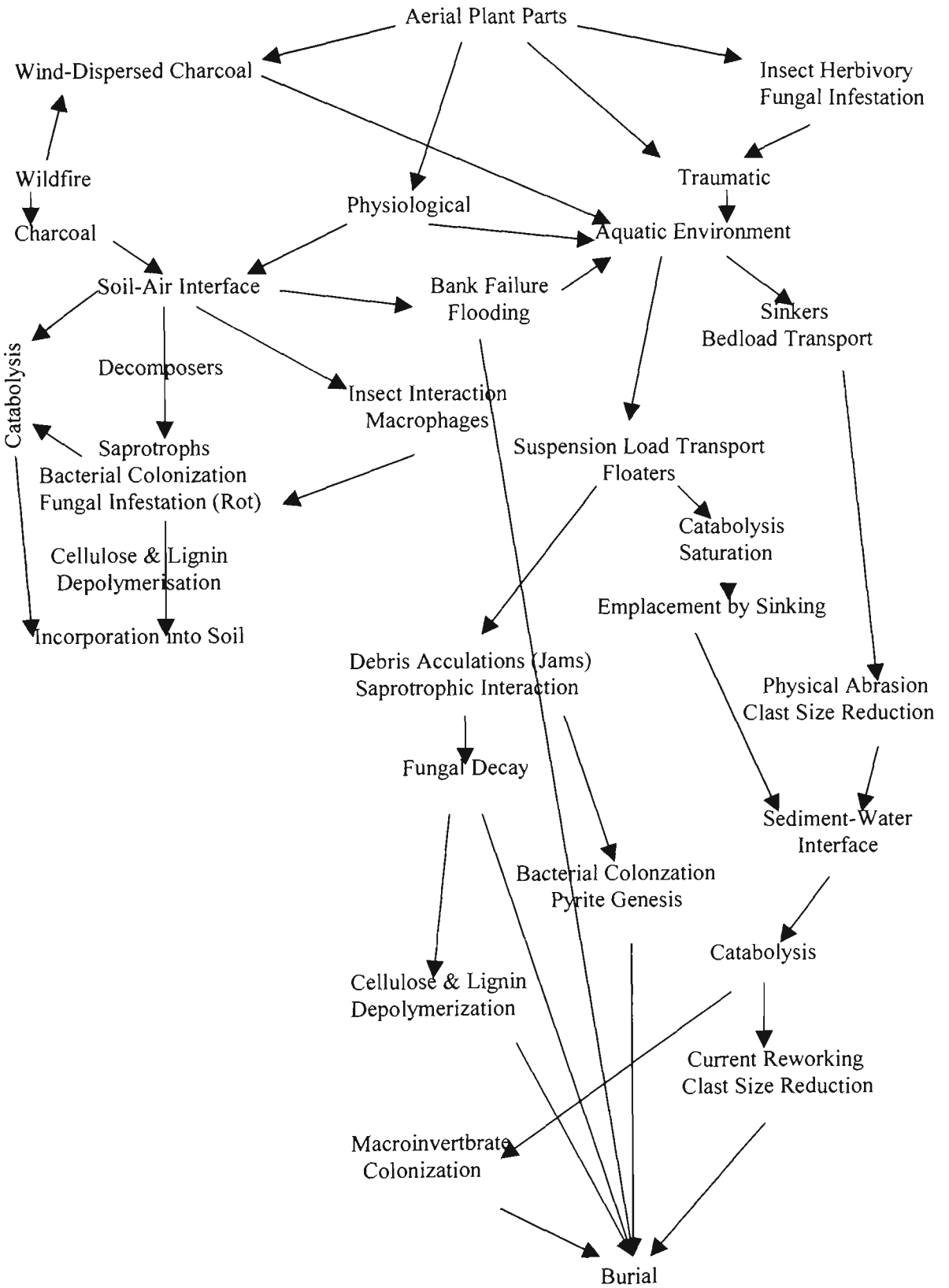


Figure 1.6 Graph illustrating the exponential dilution of detrital "rain" away from a source. Note that when twice as many plant parts are abscissed, the signal remains twice as clear even at some distance from the source (Ferguson, 1995).

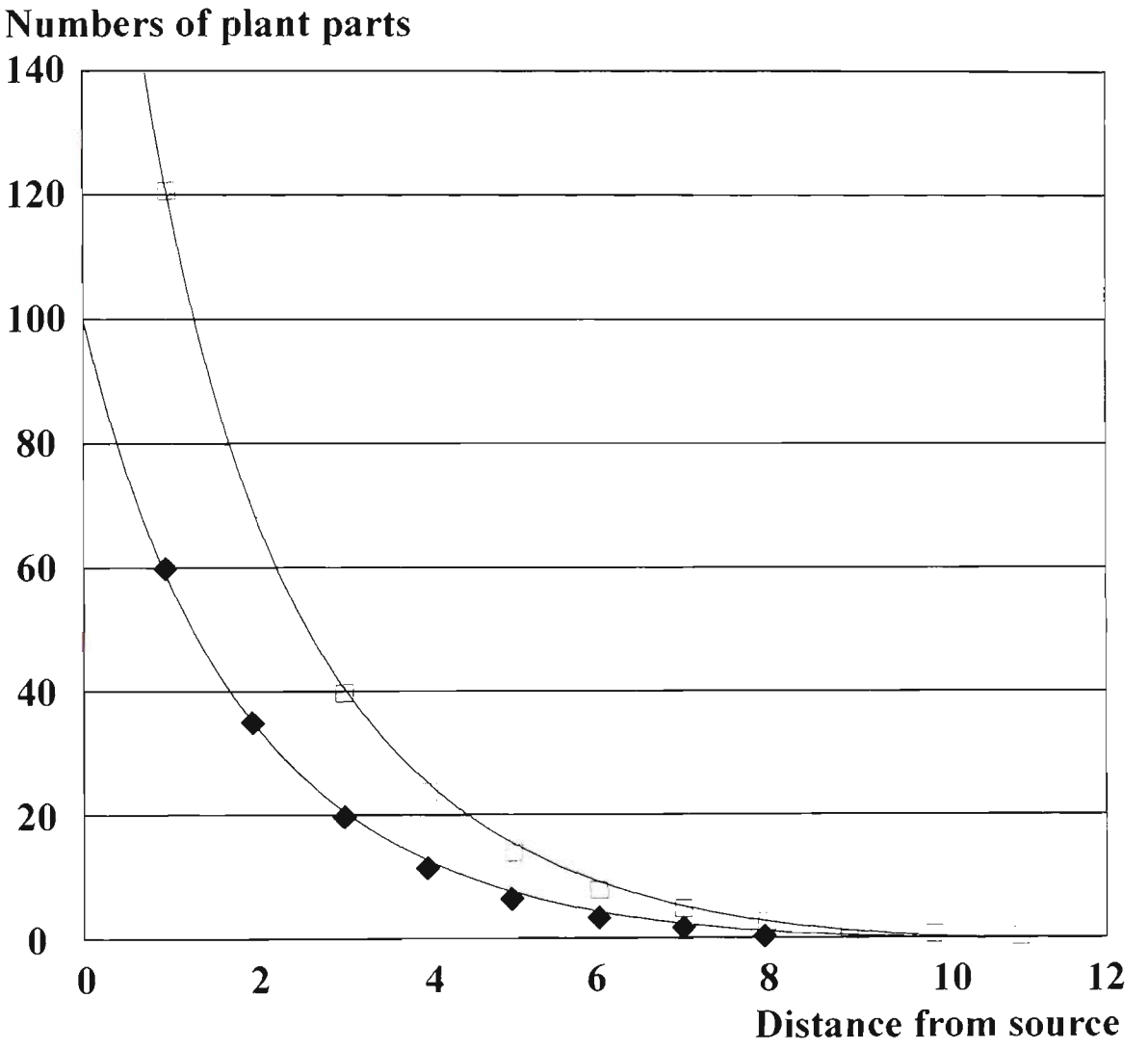


Figure 1.7 The number of leaves found in forest floor litter at distance from the source tree (*Prumnopitys amara* – Podocarpaceae) in 10 X 10 cm quadrats along two forest transects – upslope (■) and down slope (▲) in North Queensland (Australia) Complex Notophyll Vine Forest (*sensu* Webb, 1959). From Greenwood (1991).

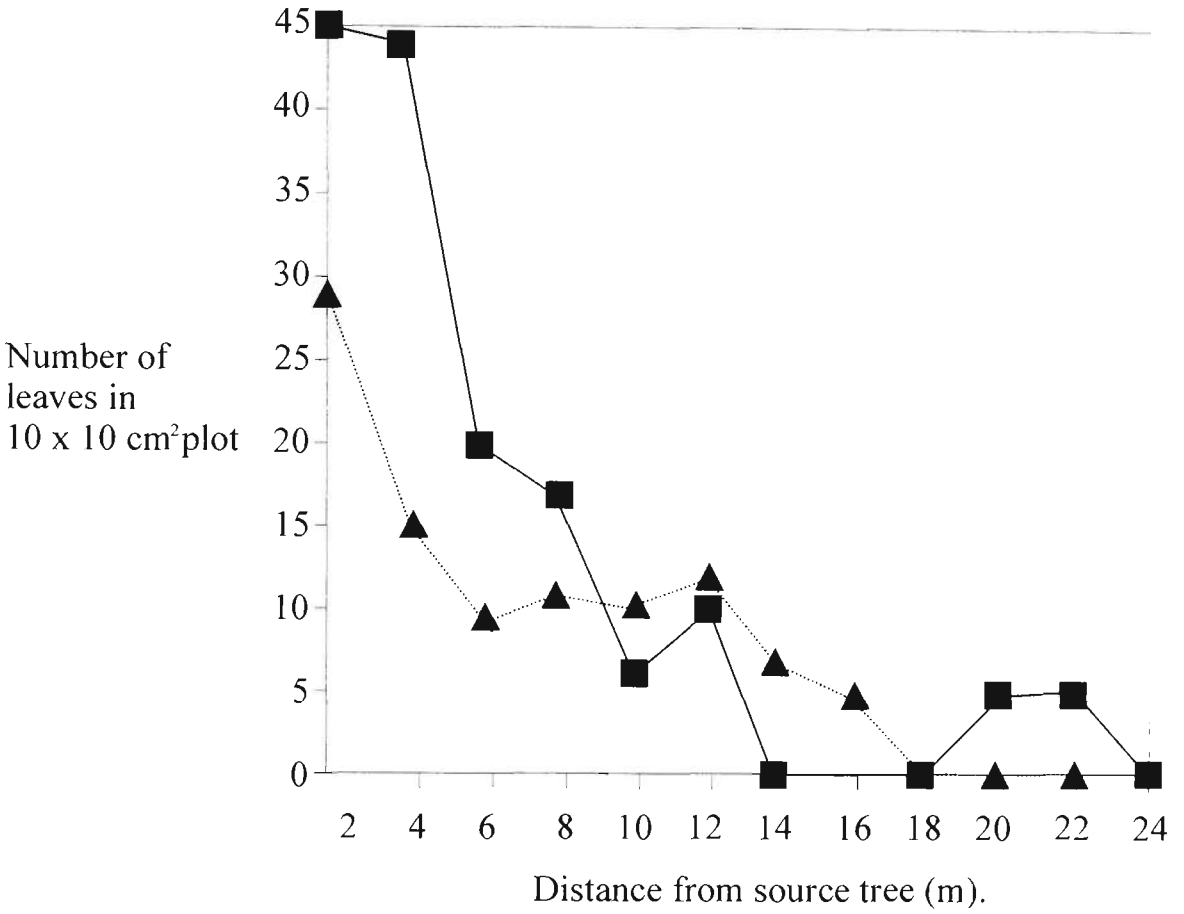


Figure 1.8 The lateral dispersal distances of different shape, size and weight of natural and artificial leaves as used by Spicer (1981). Graphs a) to c) Lateral blowing of flat rhombic paper leaves (length to breadth ratio 1.45:1) along a plane flat surface. The horizontal distance leaves will travel will be dependent on wind strength. The distance classes used were arbitrary. Graphs d) and e) Horizontal distances travelled by folded paper (0.0123 g/cm2) artificial leaves as compared with both flat and curled *Fagus* leaves under the influence of a given wind speed. Graph d) shows folded paper, Graph e) shows *Fagus* leaves. Note: Curled *Fagus* leaves appeared to be blown fractionally further than flat leaves, but imbrication marked positive skewness (Spicer, 1981).

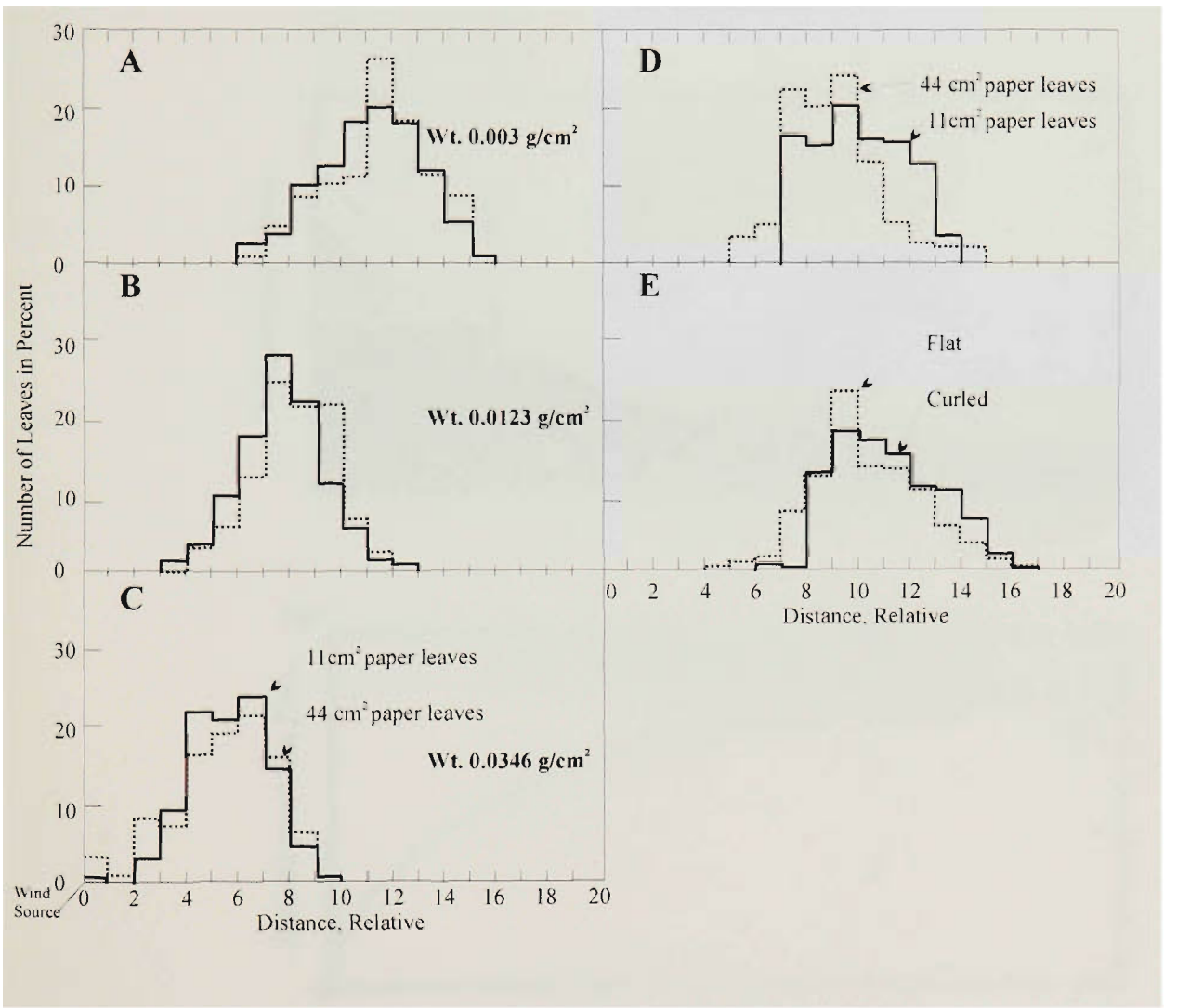
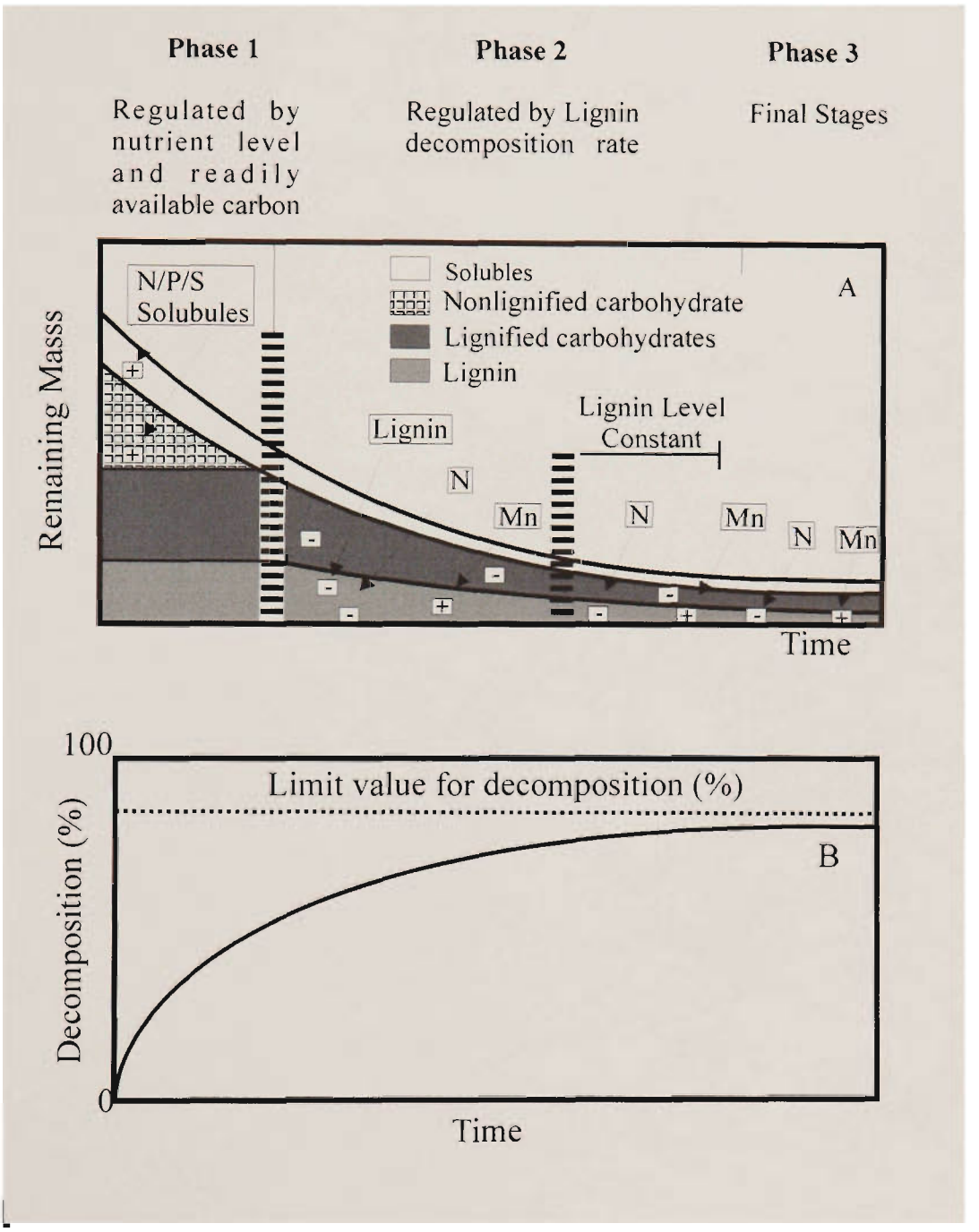


Figure 1.9 A model for the decay of leaf material. The initial rapid phase of mass loss is due mostly to the leaching of water soluble materials out of the leaf, followed by the decay of the most readily metabolised cell fractions. Decay slows down as only the intractable lignified cell wall components remain and eventually reaches a asymptotic limit as further decay becomes so slow as to be unmeasurable (Berg & Matzner, 1997).



Chapter 2

The Relationship between Standing Biomass and Leaf Litter fall

2.1 Introduction

The principal sources of species preservational bias in the plant macrofossil record (as recognised by Spicer, 1981, 1991; Ferguson, 1985; Burnham, 1989, 1993; Burnham *et al.*, 1992; and Greenwood, 1992 amongst others), can be summarised under the following three broad headings:

1. The differential production of plant parts (leaves, reproductive organs and woody parts), both between plant taxa and time of abscission;
2. The differential transport and sorting of plant organs between species once they have been produced and shed from the parent plant;
3. The differential decay and preservation of plant organs from different species.

Of these three points, the first, 'The differential production of plant parts (leaves, reproductive organs and woody parts), both between plant taxa and time of abscission', will be examined in this chapter. Specifically, this chapter addresses the relationship between the standing biomass and litter production, the null hypothesis being that the rank order of species dominance remains the same, regardless of the measure of biomass being used. The standing biomass of trees is measured as stem basal area, a standard measure of the relative contribution of each species to a forest (Catchpole & Wheeler,

1992). Litter production is measured as litter mass, leaf area, and leaf number, the latter being a standard way palaeobotanists measure the relative contribution of a taxon to a fossil flora (Burnham *et al.*, 1992). This chapter also has as a secondary aim, to contribute to an understanding of why certain plant genera, such as *Eucalyptus* and *Acacia*, which are key components of many modern Australian ecosystems, have a relatively sparse fossil record (Lange, 1980; Christophel, 1989; Hill, 1992, 1994, Hill *et al.*, 1999).

It is important to note that while leaf mass can not be directly calculated from a fossil deposit, an estimate of leaf area can be, by measuring the number and areas of preserved leaves of a species (counting only those fragments larger than half of one leaf to preclude counting the same leaf twice) and multiplying by the average leaf area of the whole leaf specimens for that species (Burnham *et al.*, 1992) or by counting dispersed leaf cuticles (Greenwood *et al.*, 2003).

2.2 Materials and methods

Field site description

Field experiments were undertaken at and around Cumberland Creek, in the Central Highlands of Victoria, south eastern Australia (145°52'40", 37°33'28" Figure 2.1). There are two contiguous forest types growing at the Cumberland Creek field site, the first being classified as Cool Temperate Rainforest (CTRF) and second as Wet Sclerophyll Forest (WSF); the latter is also termed tall open forest (Conn 1993). The term used here will be 'Wet Sclerophyll Forest'. These two forest types comprise a significant part of the temperate forests of south eastern Australia (Groves, 1994).

Cumberland Creek is a first order perennial stream, flowing in a shallow valley depression of two to four metres depth and 20 to 50 metres wide. The typical width of the stream is between 1.2 to 1.8 m with a maximum depth up to 0.8 m under average flow conditions (See Figure 2.2 for channel profile). The normal pH of the stream varies between 6.3 and 6.5. The stream channel generally weaves a complex path through the granitic substrata and deep, friable mountain loams. The study site is 880 m above sea level, has a mean annual precipitation of ~ 1,700 mm (Figure 2.1), a mean annual temperature of 9.6°C and is subject to occasional winter snowfall.

The site can be divided into two different types of terrain; the valley formed by the stream channel of Cumberland Creek, and the surrounding hinterland. The area surveyed amounts to 0.85 Ha, in which all plants higher than 1.8 m were plotted and had their diameter at breast height (1.5 m) recorded. The valley is covered by a CTRF and is surrounded by WSF (Figure 2.1 & 2.3). The cool temperate rainforest at Cumberland Creek is dominated by two tree species; *Nothofagus cunninghamii* (Hook.) Oerst. and *Atherosperma moschatum* Labill., both of which grow to a height of ~35 m with *Eucalyptus regnans* as emergent trees scattered through the rainforest (Figure 2.3). The ground vegetation, is dominated by two fern species; *Dicksonia antarctica* Labill., (soft tree fern), which grows in the low lying areas of the valley and *Blechnum wattsii* Tindale (hard water fern), which occupies the higher ground and the sides of the valley. The floor of the valley is typically marshy consisting mostly of deep (up to 120 cm), mildly acid soil (pH 5.3 to 6.0). There are also numerous granitic outcrops scattered throughout the valley floor. A shrub layer is virtually absent from the forest.

The WSF surrounding the rainforest is dominated by sub-mature *Eucalyptus regnans* F.Muell., ~ 50 m tall, with an under-storey of *Acacia dealbata* Link. and *Acacia melanoxylon* R.Br., which form a subcanopy of ~ 30 m height. This floristic pattern is

typical for these forest types in the region (Blackburn & Petr, 1979; Conn, 1993). The ground layer is a patchwork of either bare ground covered with thick deposits of leaf litter or areas covered with thick stands of *Olearia phlogopapa* (Labill.) DC. (dusty daisy bush), or grasses and sedges such as *Lepidosperma elatus* Labill. and *Dianella tasmanica* Hook. The fallen tree trunks of *E. regnans* occasionally bisect the area. The soils are relatively shallow, acidic (pH 4.0 to 4.4), hard, with numerous stones and low-lying granitic outcrops. The vegetation is open and is subject to regular strong gusts of wind throughout the year.

A number of aspects of *Eucalyptus* dominated WSF and CTRF (dominated by *Nothofagus cunninghamii*) and streams of the nearby Cement Creek and Keppel Creek catchments were described by Blackburn and Petr (1979) and Treadwell *et al.* (1997), respectively. Total litter fall near Cement Creek was six tonnes (dry weight) Ha^{-1} Yr^{-1}, of which leaves constituted 25% (*Eucalyptus regnans* leaves 11% of total litter by weight; *Nothofagus cunninghamii* leaves 5%; *Atherosperma moschatum*, leaves 6%). Leaf litter accumulated in the stream to form discrete aggregations, mainly of *Eucalyptus* leaves. Large amounts of wood were found in the stream also. Treadwell *et al.* (1997) reported that standing crop of wood (> 1 mm size) in Keppel Creek was 3.9 kg m^{-2}, whereas coarse and fine benthic organic matter accounted for only 0.13 kg m^{-2}. All of the woody species in both forest types are evergreen, but show seasonal leaf shedding behaviour with a late spring (October - November) peak in litter fall (Blackburn & Petr, 1979; Campbell & Fuchshuber, 1994). Large numbers of green and brown leaves of species from the WSF and the CTRF were observed in both litter fall and stream detritus at Cumberland Creek.

Mapping of field site

The field site was mapped by marking out a series of 20 x 20 m or 10 x 20 m quadrats (though other sizes were used as needed). Each quadrat was subdivided *in situ* into a series of one metre wide lanes that ran the length of the quadrat with builder's line. The position of every living plant higher than 1.5 m was measured from the start of each lane using a fibreglass tape measure and its position marked on a sheet of graph paper to within 25 cm accuracy.

Each plant was numbered, and with the exception of tree ferns (i.e. *Cyathea australis* (rough tree fern), or *Dicksonia antartica* (soft tree fern), had its girth and diameter at breast height (1.5 m) measured. Measurements of basal area were calculated from the diameters of each individual tree and by applying equation 2.1.

Equation 2.1 $BA = r^2\pi$

Where BA = Basal Area in square centimetres and r = the radius of the trunk of the tree in centimetres. All the map data was entered into Corel Draw™ 7.0 for map drafting.

Litter fall methods

Forest primary production was measured using 22 leaf litter traps. Eleven leaf litter traps were placed in the CTRF and 11 in the WSF sections of the Cumberland Creek Field Site (Figure 2.4). The leaf litter traps were placed randomly throughout the appropriate sections of the field site. The fully demountable leaf litter trap frames were assembled from 25 mm pressure pipe supplied by James Hardy Industries, Australia. Each frame had a 1.0 x 1.2 m collecting surface and stood one metre above the ground (Figure 2.5 a & b). These designs were modified from conceptual plans provided by Ian Campbell (*pers. comm.*, Monash University 1996).

The collecting surfaces were cut from 4 x 5 m tarpaulins made from triple layered polypropylene cloth. The various pieces were heat welded and sewn together to form the collecting surface. The collecting surface formed a four sided cone with a slope of 45° so that any litter material falling upon it would slide rapidly in to the collecting basket (Figures 2.5 a to d). At the centre and bottom of the cone, a reinforced 20 x 10 cm chute led directly to the collecting basket. The collecting basket was suspended from the bottom of the chute using Velcro strips and was made from 1mm fibreglass mesh. Each litter trap was numbered when it was placed in the field; traps 1 to 11 were placed in the CTRF and traps 12 to 22 were placed in the WSF.

All materials in the leaf litter traps were collected simultaneously at roughly one-month intervals, and transferred into appropriately labelled bags. The bags used were 10-litre heavy-duty polyethylene autoclave bags, chosen for their durability under field conditions. The bags were then taken back to the laboratory and refrigerated at 4°C (to slow decomposition), until processed.

The first stage of processing involved oven drying the samples at 70° C for 96 hours until completely dry samples in appropriately labelled 30 x 45 cm brown paper bags. This temperature was chosen to minimise the fire risk, as some trial samples spontaneously combusted at the recommended temperature (105°C) for drying plant materials (Allen 1989).

In the second stage of processing, the collected litter samples were separated into different species and organ types. The organ type classifications used were, leaves, reproductive organs (which were further separated into seeds and flowers) and structural materials (which were further separated into bark or stems and twigs). Smaller items (i.e. less than 10 mm in size) were sorted using 30 cm diameter sieves with mesh sizes of 10,

5, 2 and 1 millimetres. Sieved samples were then further separated with a pair of long nose tweezers, to ensure pure samples of species and organ type. All materials smaller than 1 mm in size were placed in the "unsorted" category. The only exceptions were *Nothofagus cunninghamii* seeds, which were produced in sufficient quantities to warrant their separation. These seeds were easily collected by a 1 mm size sieving grid and the sieved samples were on average 99% (w/w) pure seed. The resulting piles of plant material were then identified to species level, classified according to organ type, weighed on a top loading balance (Model Toledo PB3002) and placed into paper bags. The raw data can be found in Appendix 2.1

Table 2.1 Leaf characteristics of the major tree species found at the field site. For the purposes of this work, sclerophyllous leaves are defined as having a thick, leathery texture (due to the presence of abundant thickened cells and thick leaf cuticle), whereas the non-sclerophyllous leaves of the rainforest species have a papery texture. All leaf weights are measured in grams per square metre. The leaves of *Acacia dealbata* are bi-pinnate and for the purposes of this study, a 'leaf' refers to the entire rachis.

Species	Leaf size	Leaf texture	Margin type	Average Leaf Area (cm^2)	Average Weight ($g\ m^{-2}$)
Acacia dealbata	Notophyll/ Macrophyll	Sclerophyll	Entire	14.13	346
Acacia melanoxylon	Microphyll	Sclerophyll	Entire	8.43	183
Atherosperma moschatum	Microphyll	Non-sclerophyll	Toothed to rarely entire	10.34	94
Eucalyptus regnans	Notophyll/ Macrophyll	Sclerophyll	Entire	17.16	256
Lomatia fraseri	Notophyll	Intermediate	Toothed	34.19	121
Nothofagus cunninghamii	Nanophyll	Non-sclerophyll	Toothed	1.31	101
Tasmannia lanceolata	Notophyll/ Macrophyll	Intermediate	Entire	13.64	100

Calculations of leaf number and size

All of the leaf fall figures were then converted into measures of leaf number and leaf area using the conversion factors shown in Table 2.1. These conversion factors were calculated by randomly selecting 50 leaves of each species and measuring the areas and weights of the individual leaves to calculate average leaf weight and area. The area of each leaf was measured by using a Hewlett Packard Scanjet 6100c scanner to create a digital image of each leaf and using 'the calculate area' function of the Scion ™ digital analysis package (version 4.03) for MS Windows 98™. A sheet of metric graph paper was used to calibrate the scale measurements for the analysis package. The rank order abundance figures for each forest type was then graphed in Microsoft Excel ™, for basal area, number of stems, total leaf fall, number of leaves produced and total leaf area.

2.3 Results

Map of field site

The vegetation map of the field site (Figure 2.6a) marks out the two forest types in the study area. The boundary between them is marked on the map (Figure 2.6); the WSF occupies the north of the field site, the CTRF the south. The distribution of each of the major canopy tree species found at Cumberland Creek is displayed on the species specific maps (Figures 2.6 b, c, d, & e). The total number of stems for each tree species and the total basal area in square centimetres is shown in Table 2.2. The rainforest tree species *Nothofagus cunninghamii* and *Atherosperma moschatum* are mostly located within the confines of the riparian zone of Cumberland Creek (Figures 2.6 b & c).

The large number of *N. cunninghamii* saplings at periphery of the rainforest indicates that it may be expanding into the surrounding wet sclerophyll forest. The other

rainforest tree species, *A. moschatum* is entirely located within the confines of the rainforest zone (Figure 2.6c). The WSF *Eucalyptus regnans* is distributed throughout both forest types found at Cumberland Creek, though only late mature trees are found within the rainforest zone. There are no seedlings found in either forest type. Outside the rainforest zone, there is a greater distribution in the range of stem basal areas for *E. regnans*, indicating that there has been recruitment of new plants within the WSF zone within the last 60 - 70 years (Figure 2.6d). This agrees with the fire history of the site, where fire affected parts of the region in 1939, killing most mature *E. regnans* (Jeremiah & Roob, 1992).

Table 2.2 List of all woody angiosperms with a height greater than 1.5m found at the Cumberland Creek field site. All of the tree basal areas have been rounded to the nearest whole square centimetre.

Forest Type	Species name	Total Basal Area (cm^2)	Basal Area (%)	Total Number Of Stems	Total Stem number (%)
CTRF	*Acacia melanoxylon*	5.5×10^3	1.1	23	1.7
	Atherosperma moschatum	67.9×10^3	13.3	456	32.4
	Eucalyptus regnans	18.3×10^4	35.7	11	0.8
	Lomatia fraseri	2	>0.1	1	>0.1
	Nothofagus cunninghamii	25.6×10^4	50	894	64.1
	Polyscias sambucifolia	<1	>0.1	1	>0.1
	Tasmannia lanceolata	218	>0.1	10	0.7
Total		**512696**		**1395**	
WSF	*Acacia dealbata*	760	>0.1	8	1.8
	Acacia melanoxylon	82.5×10^3	15.8	191	41.8
	Atherosperma moschatum	231	>0.1	7	1.5
	Eucalyptus regnans	36.5×10^4	70	27	5.9
	Hedycarya angustifolia	3	>0.1	1	02
	Nothofagus cunninghamii	72.5×10^3	13.9	205	44.9
	Polyscias sambucifolia	57	>0.1	13	0.2
	Tasmannia lanceolata	428	>0.1	17	3.8
Total		**521049**		**457**	
Site Total		**1,033,745**		**1,856**	

The tree *Acacia melanoxylon* is found only in the WSF zone of the field site, with numerous dead boles in the ecotone between the two forests (Figure 2.6e). Trees that are uncommon within the mapped area are mostly located within the WSF zone

(Figure 2.6f, Table 2.2). *Acacia dealbata* for example is exclusively located towards the outer parts of the wet sclerophyll forest well away from the watercourse, while *Tasmannia lanceolata* (Poir.) A.C. Smith has an uneven occurrence throughout the field site although it is more common in the WSF zone. The other tree species found at Cumberland Creek are rare and contribute little in terms of stem number or basal area to the statistics of the field site (Table 2.2).

Litter Production

The litter production (of both forest types), was 481.9 (SE = ± 34.5) grams per square metre per year for the CTRF and 477.3 (SE = ± 65.8) grams per square metre per year for the WSF (Tables 2.3 & 2.4 and Appendix 2.1). These figures calculate out to 4.8 and 4.7 T/Ha^{-1} respectively for the litter production of both forest types. Globally, this falls in the midrange for litter production (Bray & Gorham, 1964) and is less than the figure of 6.0 T/Ha^{-1} recorded for Cement Creek a mountain stream located within the same general geographic region (Blackburn & Petr, 1979).

The percentage litter fall data in Figures 2.7 a to i, indicates that different forest types, tree species and individual tree species in different forest types, produce different proportions of their litter as leaves (Figure 2.7 a & e). In the CTRF (for example), *Nothofagus cunninghamii* sheds a total of 64.5 % of its litter fall as leaves, while *Atherosperma moschatum* and *Eucalyptus regnans* shed 42.5 % and 80.0 % of their total litter fall as leaves respectively (Figures 2.7 b, c & d). Differences in the proportions shed for other plant organs are also large, where *A. moschatum* produces 50.0 % of its nett litter fall as structural materials (i.e. branches and twigs), while just 7.0 % of the total litter fall of *E. regnans* is shed as structural materials (Figures 2.7 c & d). These

differences are sufficiently large to be noteworthy when calculating litter fall figures from leaves alone.

Table 2.3 Average annual litter and leaf fall of the 11 leaf litter traps *for all the species* that contributed to litter fall figures from the CTRF zone of the Cumberland Creek Field Site. The final category 'Unidentified fragments' consists of all the plant materials that were too small (less than 1 mm), to be identified.

Species Name	Annual Litter Fall (g/m^2)	Annual Leaf Fall (g/m^2)	Percentage of Annual Litter Leaves
Nothofagus cunninghamii	329.56	212.46	64.5
Atherosperma moschatum	71.61	30.41	42.5
Eucalyptus regnans	49.30	39.33	79.8
Acacia melanoxylon	1.03	0.95	92.2
Dicksonia Antarctica	2.19	2.13	97.3
Olearia phlogopapa	0.68	0.02	2.9
Blechnum wattsii	0.02	0.02	100
Tasmannia lanceolata	0.04	0.04	100
Polyscias sambucifolia	0.01	0.01	100
Unidentified fragments	27.5	N/A	N/A
Total	**481.94**	**285.37**	

Table 2.4 Average annual litter and leaf fall of the 11 leaf litter traps *for all the species* that contributed to litter fall figures from the WSF zone of the Cumberland Creek Field Site. The final category 'Unidentified fragments' consists of all the plant materials that were too small (less than 1 mm), to be identified.

Species Name	Ann Litter Fall (g/m^2)	Ann Leaf Fall (g/m^2)	Percentage of Annual Litter Leaves
Nothofagus cunninghamii	25.93	20.49	79.0
Atherosperma moschatum	0.78	0.04	5.1
Eucalyptus regnans	266.76	159.47	48.0
Acacia melanoxylon	114.64	73.48	64.1
Cyathea australis	0.04	0.04	100.0
Olearia phlogopapa	4.03	1.22	30.3
Tasmannia lanceolata	0.53	0.53	100.0
Acacia dealbata	8.59	7.75	90.2
Unidentified fragments	56.3	N/A	N/A
Total	**477.56**	**263.02**	

Differences in the proportions of litter shed as leaves were found in the WSF as well (Figures 2.7 f-i). The tree *Acacia dealbata* shed a total of 91% of its total litter production as leaves, while the other three important tree species found there (*A.*

melanoxylon, *E. regnans* and *N. cunninghamii*) shed between 48% and 79% of their litter as leaves. It is also interesting to note the major differences in the proportions of litter production shed as leaves for single species growing in both forest types (the trees *N. cunninghamii* and *E. regnans* exemplify this phenomenon). In the CTRF *N. cunninghamii* shed 64 % of its litter as leaves while shedding 79% of its total litter fall as leaves in WSF (Figure 2.7 b & f). *Eucalyptus regnans* exhibits the reverse pattern in that it shed 80% of litter as leaves in CTRF, and 59% of its litter as leaves in WSF (Figure 2.7 c & g).

The average proportions of litter production, produced as leaves differ slightly for each forest type. Fifty six percent of the wet sclerophyll forests total litter production is shed as leaves and 63% of the total litter production of the cool temperate rainforest is shed as leaves (Figures 2.7 a & e).

The CTRF was dominated by the three tree species *N. cunninghamii*, *E. regnans* and *Atherosperma moschatum*, with these trees having 50.0 %, 35.7% and 13.3% of the total basal area respectively (Figure 2.8a and Table 2.2). The rank order abundance for the woody angiosperms in this forest type is shown in Figure 2.8a, where basal areas are compared. This rank order abundance was not repeated when stem number was plotted (Figure 2.8b), as the bulk of the basal area for *Eucalyptus regnans* was represented by 11 very large trees, whereas many of the stems of *Nothofagus cunninghamii* were saplings and thus had small stem basal areas.

The rank order sequence of the tree species for stem basal area for the CTRF was unchanged for total leaf litter mass (Figure 2.8c). This matches with previously published literature such as Burnham *et al.* (1992) and Burnham (1997) who found that basal area and leaf mass production were highly correlated. One would expect a relationship between basal area and leaf litter production because the metabolic needs of the stem of a

tree and its root system should increase proportionately with its biomass and would therefore require a proportionately greater mass of photosynthetic tissue to sustain it.

The rank order sequence between basal area and total leaf number was also unchanged (Figure 2.8d), though there were far fewer leaves of *E. regnans* and *Atherosperma moschatum* than would be expected from their basal area. Conversely *N. cunninghamii* accounts for a far higher than expected proportion of the leaf production of the forest than would be indicated from basal area alone. This may in part be due to the average size of *E. regnans* leaves (17.16 cm^2) when compared to *N. cunninghamii* leaves (1.31 cm^2). The rank order sequence between basal area and total leaf area shed annually is also unchanged (Figure 2.8e). However, the leaf area shed by *N. cunninghamii* is much higher per unit of basal area than for the other species found in the CTRF. *Nothofagus cunninghamii* is therefore over producing leaves relative to standing biomass and is over represented in the forests leaf litter.

The basal area of the WSF is dominated by *E. regnans*, *Acacia melanoxylon*, and *N. cunninghamii* respectively (Figure 2.8f, Table 2.2). Most of the *N. cunninghamii* stems in the WSF are found near the ecotone between the two forest types (Figure 2.3b) and have a relatively small basal area. This suggests recent recruitment and raises the possibility the CTRF is invading into the WSF due to the continuing suppression of fire. There is no ecological reason (Howard, 1973 a & b; Read, 1995) why this should not be possible as *N. cunninghamii* can tolerate the conditions found in the WSF as long as fire is suppressed.

The rank order abundance data of the woody angiosperms in the WSF shows *E. regnans* as having approximately four times the basal area of *A. melanoxylon* and five times that of *N. cunninghamii* (Figure 2.8f & Table 2.2). When basal area and stem number are compared the dominance order for the three major tree taxa is reversed with

N. cunninghamii having the most stems (mostly saplings), *E. regnans* the least (mostly mature trees), with *A. melanoxylon* being in between (Figures 2.8 f & g, Table 2.2). The other WSF sub-canopy trees totalled less than 0.4% of the forests basal area, 7.5% of the total stem number, and produced negligible amounts of leaf litter production (Table 2.2 & Figure 2.8).

The WSF rank order sequence for basal area is unchanged for leaf mass production (Figure 2.8h). *Eucalyptus regnans* is the dominant contributor to the leaf mass production of the forest (46%t), where it produces fewer leaves in terms of mass relative to its basal area, than do the other trees found in the WSF. This low level of leaf production for *E. regnans* becomes quite pronounced in Figure 2.8i, where it is producing ~ 10.1% of the total number leaves counted and yet accounts for 70.0% of the basal area of the forest. By comparison, *A. melanoxylon* is producing near the expected number and *N. cunninghamii* is producing more leaves than its basal area would predict (Figures 2.9 f & i).

The WSF rank order sequences for leaf area production and stem basal area vary (Figures 2.9 f &j). The percentage leaf area produced by the three main canopy species are 37.6%, 43.8% and 18.6% for *E. regnans, A. melanoxylon* and *N. cunninghamii* respectively. Here, *N. cunninghamii* is producing a leaf area near its basal area (13.9%), *A. melanoxylon* is producing a greater than expected leaf area and *E. regnans* is again producing too little (Figure 2.8j & Table 2.2).

Seasonality

The annual and seasonal variability of leaf fall is quite pronounced in both forest types. Both forests are evergreen, so there is no period of the year in which the trees are leafless. The annual variation in litterfall for the CTRF is substantial (Figures 2.9 a to k and 2.10 a to j) with the quarterly patterns of leaf fall being shown in figures 2.10 a to k.

The CTRF has its lowest leaf fall in winter when temperatures and forest productivity are at their lowest (Figure 2.9g). Its leaf fall during the rest of the year is substantially higher with no particular major period of leaf fall. The WSF has periods of heavy leaf fall during summer and autumn and low periods of leaf fall during winter and spring (Figure 2.9a). The principal period for the production of reproductive materials is during spring and summer for both forest types.

The leaf fall cycle for *Eucalyptus regnans* is strongly seasonal for both forest types. It sheds its lowest number of leaves in winter and its highest number in summer (Figures 2.9 b & h). In the WSF *Acacia melanoxylon* has its maximum leaf fall in summer with low leaf fall figures during the rest of the year (Figure 2.9d). In the CTRF, the leaf fall rate of *A. melanoxylon* was highly variable and approximately 1% the rate for WSF, and probably associated with of heavy storms (Figure 2.9j & Appendix 2.2 for the weather data from the Marysville climate station).

Atherosperma moschatum has a regular seasonal cycle of leaf fall, which peaks during summer and falls to its lowest point in winter (Figure 2.9i). It does however shed large amounts of branches and twigs during winter, some of which entered the litter traps in the WSF, most of this material seems to be associated with severe winter storms (Figure 2.9c, Appendices 2.1 - 2.2 & *pers observ.*). *Nothofagus cunninghamii* has its minimum leaf fall in winter and a variable maximum of leaf fall spread throughout the other three seasons in the CTRF (Figures 2.9e). In the WSF, *N. cunninghamii* leaf fall is low in winter and spring and at its highest in summer and autumn. Seed production is at its peak during spring and summer, with the spring of 1997 and summer of 1998 being a mast year in which copious quantities of seed were produced throughout the field site. The tree *Acacia dealbata* has its maximum leaf fall in summer and autumn (Figure 2.9f).

Variability in litter fall between sites

The variability in leaf litter composition between litter traps is substantial as evidenced by the error bars in Figures 2.10 a - i. The average proportion of leaves found in an individual litter trap for a particular species can vary between zero to the total amount recorded for that quarter (See Appendix 2.1 in the CD ROM for the raw data). Overall, the variability lies in the general range of 20% to 30% for WSF and up to 50% or more for CTRF (Figures 2.10 a & b).

The variability in the proportions of *N. cunninghamii* leaves between locations was much larger in WSF than for CTRF; some WSF locations recorded almost no *Nothofagus* leaves in some seasons (Figure 2.10 c & d), while the CTRF traps collected *Nothofagus* leaves throughout the year. Whereas for *E. regnans* the opposite is true. The variation in *Eucalyptus* leaf fall between WSF locations is consistently lower where the species is the clear forest dominant, as compared to CTRF where it is codominant (Figures 2.10 g & h). All 22 litter traps recorded some *Eucalyptus* or *Nothofagus* leaf fall throughout the study however.

The variability in the leaf litter proportions in individual traps for species such as *Acacia melanoxylon*, *A. dealbata* and *Tasmannia lanceolata* was often quite large (Appendix 2.1), with individual trees contributing to several nearby litter traps (Figures 2.10 i to l). This is particularly true with *A. melanoxylon* in the CTRF (Figure 2.10 j), where the standard deviation exceeds the average leaf contribution to all the litter traps throughout the duration of the experiment, with many traps receiving no leaf fall from this species at all (Appendix 2.1). *Acacia dealbata* only contributed significant leaf litter to the traps placed near where the trees were growing, (Traps 12, 13, 17, 20 & 22). The same applies to *Tasmannia lanceolata*, which made limited contributions to the traps

located near where the trees were growing (Traps 9, 12, 17, 20 & 22), while contributing nothing at all to most trap locations. The quantity of *Atherosperma moschatum* leaves collected was also highly variable between the 11 CTRF (Figure 2.10f) and tended to reflect the distribution of larger trees throughout the field site. *Atherosperma moschatum* contributed little leaf litter to the WSF traps.

2.4 Discussion

Tree distribution

The distribution patterns of the four major canopy trees found within the two forest types show clear spatial differences from each other. The CTRF species (*Nothofagus cunninghamii* and *Atherosperma moschatum*) and the WSF species (*Acacia melanoxylon*) are found mostly within their respective forest types or in the ecotone between them. *Eucalyptus regnans* comprises a major part of the biomass in both forest types. The ecotonal boundary between the CTRF and the WSF is narrow, being in the order of five metres or less. This clear and distinct spatial separation of tree species found at the Cumberland Creek field site occurs over small scales and it would be expected to be seen in the leaf fall patterns within the field site (Spicer, 1981; Ferguson, 1985; Burnham, 1989; Burnham *et al.*, 1992).

Litter production

It has been observed in previous studies that trees form distinct leaf halos around the bole of the parent tree (Ferguson, 1985, 1995; Burnham, 1989; Burnham *et al.*, 1992), where the number of leaves found in the forest floor litter decreases in proportion with the distance from the bole of the parent tree. The clear difference in leaf litter composition between the CTRF and the WSF demonstrates this point. In the CTRF for

example, leaves from the WSF tree *Acacia melanoxylon* make up only a small proportion of the total leaf litter of the traps found in the CTRF even though stands of *Acacia melanoxylon* were within 20m. This localisation in litter composition is also exemplified by *A. dealbata*; its leaves only contribute to the leaf litter of closest litter traps (Traps 13, 17, 20 & 22). This observation reinforces the point raised by Burnham (1993) that sampling from at least three different locations spaced at roughly 25 metre intervals within a fossil lens (where possible), is essential if a representative picture of the source tree species richness of a fossil flora is to be developed.

There is also a link between basal area and leaf litter production, whereby the relative proportions of a forest's leaf litter production per species mirrors the relative proportions of the forest's basal area per species (Turnbull & Madden, 1983; Spicer, 1981; Ferguson, 1985; Burnham, 1989; Burnham *et al.*, 1992). These observations match what was seen at Cumberland Creek. The data (Figures 2.8 a, c, f & h and Table 2.2), clearly indicate that the differences in the relative proportions of basal area are also to be found in the relative proportions of leaf litter produced for each tree species.

The spatial differences in standing biomass can also be observed in the litter fall patterns throughout the field site (Figure 2.10). The standard deviations (Figures 2.10 a - l) from the average litter fall figures for the 11 traps found in each forest type are large, indicting that each trap represents the makeup of the local vegetation. The variation in leaf mass production is especially large for *Eucalyptus regnans* and *Acacia melanoxylon* in the CTRF, and for *Nothofagus cunninghamii* in the WSF. These variations in leaf litter composition between individual leaf litter traps reflect differing occurrences of canopy tree taxa near the traps and are similar to observations made by Burnham (1989, 1993, 1997) where the heterogeneity in the source vegetation showed up in forest floor leaf litter. These observations demonstrate the need for multiple litter samples to be collected

throughout the vegetation if a good reflection of the relative species importance is to be obtained (Spicer, 1988; Burnham, 1989, 1993, 1997). Single samples tend to give extremely localised pictures of the source vegetation with rare or uncommon species contributing strongly to some traps but not to others. It is therefore imperative when sampling fossil deposits, that great efforts be made to sample multiple areas from the same bedding plane in an effort to derive a true reflection of the composition of the source vegetation.

The data also show that relying on leaf number alone without reference to leaf size will potentially misinform when reconstructing the structure of a plant community from fossilised leaves (Figures 2.8 d & i). Previous findings that have observed low correlations between leaf number and stem number or basal area support this assertion (Chaney, 1924; Burnham *et al.*, 1992; Burnham, 1997; Schimanski & Bergstrom, 1998). If the data (Figure 2.8d) were used to reconstruct the structure of the source vegetation of the CTRF, it could be concluded that it consisted of a virtually pure stand of *Nothofagus cunninghamii*; as the other tree species found in this forest contribute just 1.03% of total litter fall by number but in reality comprise 50% of the total basal area of the forest. The relative sizes of leaves must therefore be taken into account. Burnham *et al.* (1992: p. 46) observed that leaf area gives a good approximation of stem basal area (Burnham *et al.*, 1992), and thus factoring in leaf size to give a measure of leaf area (Figure 2.8e) better reflects the relative importance of *Eucalyptus regnans* and *Atherosperma moschatum*.

The same observations can also be derived for the WSF where *Eucalyptus regnans* is the clear forest dominant (Figure 2.8f, Table 2.2). Any ecological or palaeoecological reconstruction of the source vegetation using leaf number alone (Figure 2.8 i), would relegate *E. regnans* to a relatively minor position in the forest's structure. In reality, it is a massive tree, growing to 80 or more metres in height and comprises 70 %

of the basal area for this forest. It is overwhelmingly the major biotic component of this vegetation. The importance of this species in the source vegetation only becomes evident when leaf size is factored in to the reconstruction (Figure 2.8j). Leaf area is thus a far more important measure of the relative importance of trees in a plant community than leaf number or species composition alone.

The differences between the amount of leaf and other litter produced relative to basal area between different species within and between forest types, (Figures 2.7 a & e) show that the different forests allocate differing amounts of primary production, to leaves, reproductive structures, structural materials and bark. Burnham *et al.* (1992) also found this, and a wide variability in the percentage of litter fall that fell as leaves was also found in the 51 forests in Bray and Gorham (1964) where total leaf and litter fall data are given. The data in Bray and Gorham (1964) indicate that forests produce between 47% and 94% of their litter as leaves with the world average being 69%. This figure compares well with the percentage litter fall that fell as leaves for the CTRF (63%) and WSF (56%), though these two forests are producing leaf litter at a lower percentage than many forests. Other reports such as Blackburn and Petr (1979) have WSF at Mt. Donna Buang, Victoria, Australia, producing as little as 25% of its total litter fall as leaves. These differences are thus highly likely to show up in the fossil record.

There are notable differences in the percentages of bark and reproductive structures between the CTRF and the WSF. The CTRF sheds 9% of its total litter fall as reproductive structures, while the WSF sheds 2%. On the other hand, the CTRF produces 2% of its litter as bark, and the WSF produces 16% of its litter as bark. Blackburn and Petr (1979) indicate that WSF at Mt Donna Buang produces as much as 22% of its total litter production as bark. These results indicate that different forests can have notably

different compositions of litter in terms of organ types and these differences therefore have the potential to show up in the fossil record.

These differences show up not only between different forest types, but also between different populations of a single species growing within different forest types (Figures 2.7 c & g, Table 2.5). *Eucalyptus regnans* for example, sheds about 48% of its litter as leaves in the WSF and between 80% and 52% of its litter as leaves in the CTRF. *Nothofagus cunninghamii* on the other hand sheds more of its litter as leaves in the WSF than the CTRF (Figure 2.7 b & f, Table 2.5).

Table 2.5 Comparison of percentage litter shed as leaves between this study and the two other reports which have comparable data in nearby forests for the species listed. These two other reports do not give estimates of species basal area

Forest Type	***Nothofagus cunninghamii***	***Eucalyptus regnans***
WSF (This Study)	79	48
CTRF (This Study)	64	80
CTRF (Howard, 1979)	42	52
WSF (Ashton 1975)	N/A	48

These differences have the potential to distort the fossil record. As one moves through different vegetation types the same species may be producing different proportions of its litter as leaves. Any palaeoecological studies that have such species preserved amongst the leaf fossils found in a particular location have the potential to wrongly elevate certain species to prominence in some vegetation types and lower them in others. These differences do not however dilute the general dominance patterns that such deposits may contain, when the forest wide leaf litter figures are compared (as in Figure 2.8). This again emphasises the need to collect multiple samples from a within the same bedding plane of a fossil locality if an accurate representation of the source vegetation is to be established.

There are also major differences in biomass production between species. *Eucalyptus regnans* consistently produced much less leaf matter compared to its basal area. In the WSF for example this species accounts for 70% of the total basal area for all trees in the area of forest mapped (Figure 2.6 & Table 2.2) and yet accounts for just 10.1% of the leaves produced in this forest (Figure 2.8). This underproduction also persists when leaf area is examined, where *E. regnans* is producing 37.6% of the total area of leaves shed by this forest. By comparison, *Acacia melanoxylon* and *Nothofagus cunninghamii* are producing more leaves than would be expected from their basal area alone. This phenomenon is even more obvious in the CTRF. Here *Nothofagus cunninghamii*, which represents 50.0% of the forest's basal area, is producing 98.9% of the total number of leaves produced and accounts for 89.8% of the total leaf area shed. Hence *Nothofagus cunninghamii* is definitely over producing leaves relative to its basal area. A similar observation was made by Schimanski and Bergstrom (1998), who found that *N. moorei* was over-represented in the leaf litter of a New South Wales rainforest relative to stem number. However Schimanski and Bergstrom (1998) did not include a measure of stem basal area and thus no quantitative relationship between standing biomass and leaf litter production could be made.

Palaeobotanical implications

The observation that some plant species may overproduce or underproduce leaf material relative to their standing biomass has significant implications for palaeobotany, and if consistent across whole genera needs to be determined and corrected for. For example, if *Nothofagus cunninghamii* was present in an area (as in the CTRF), its occurrence in the fossil record should not be restricted by the underproduction of leaf material. In the absence of data from subgenus Brassospora, this observation can not be used to explain the paucity of leaves of this subgenus in the Australian Cenozoic record.

Eucalyptus regnans however, accounts for a meagre 0.6% of the leaves shed and 6.8% of the leaf area shed for the same forest type. However, it represents 35.7% of the forest's basal area. If this underproduction of leaf material by *Eucalyptus regnans* is widespread throughout the genus *Eucalyptus*, then it could go some way towards explaining the relative paucity of *Eucalyptus* leaves in the fossil record. *Eucalyptus* trees could be present within a vegetation community that forms a fossil deposit, and yet produce sufficiently few leaves to bias the fossil record against their preservation in all but the most favourable circumstances.

This underproduction of leaves can also be found with *Atherosperma moschatum*, which accounts for 13.3% of the basal area of the CTRF. It's leaf production however accounts for only 0.5% of the total leaves produced and 3.4% of the leaf area shed. This also may potentially help explain why this genus has such a poor fossil record. Further studies would be helpful in the cool temperate rainforests of eastern Victoria, Australia (where *Atherosperma moschatum* is the dominant canopy tree), to determine whether or not this underproduction relative to basal area occurs in this vegetation type as well.

The pronounced seasonality of leaf litter production for these two forest types (Figures 2.9 a to k) is similar to that which has been observed for other Australian temperate forests (Howard, 1973b; Attiwell *et al.*, 1978; Lake, 1982; Pressland, 1982; Turnbull & Madden, 1983; Bunn, 1986). The dominant tree taxa in the CTRF tended to shed their leaves mostly in the growing season of either spring/ summer or autumn while shedding few leaves in winter. The WSF species (*E. regnans* and *Acacia melanoxylon*), tended to shed their leaves mainly in late summer and autumn (Figures 2.9 a to f). Some species also had their maximum leaf fall figures at different times of the year depending on forest type. In the CTRF, *N. cunninghamii* had variable leaf fall maxima occurring in

either spring or autumn, while in the WSF the maximum period of leaf fall was in late summer to autumn. These findings contrast with Howard (1973b), who found that maximum leaf fall of *N. cunninghamii* in CTRF at Mt. Donna Buang, Victoria, Australia occurred in autumn. The seasonal variations in leaf litter production between species observed in this study were however not sufficiently large to distort the mean species composition of the forest's leaf litter.

2.5 Conclusions

This study indicates firstly that using the relative proportions of leaf area in either forest floor litter or in a potential fossil deposit can serve as a measure of the relative biomass of tree taxa in the standing vegetation. Secondly, this study cautions against counting leaves and then relating the number of leaves per taxon to the importance of that taxon in the source vegetation, especially where leaf size differs. Small leafed taxa such as *Nothofagus cunninghamii* produce far more leaves than large leafed species, although they may have similar leaf area to biomass ratios. A reconstruction based upon leaf number has the potential to elevate the small leaved species to an unwarranted pre-eminence, while under-representing the role of large leaved species within a fossil flora. Thirdly, this study emphasises that variations in the proportions of each taxon in leaf litter makeup can vary widely between locations and that multiple locations need to be sampled in order to derive an accurate representation of the source vegetation. Fourthly, this study indicates that there are major differences in leaf litter production as measured by number of leaves, leaf mass and leaf area production relative to the basal area for different taxa. *Eucalyptus regnans* and *Atherosperma moschatum* are under producing leaves relative to basal area, while *Nothofagus cunninghamii* is over producing leaves relative to its basal area. One species, *Acacia melanoxylon*, produced leaf litter near the expected amount indicated by its basal

area. These differences are evident when either leaf mass, leaf number or area of leaves produced are examined.

The observed differences between taxa in this study show that differential organ production will introduce bias in the fossil record and may potentially explain or resolve some issues raised by the fossil record. This topic is considered later in the thesis.

Figure 2.1 Details of field site. (a) Map of the local region and location of the Cumberland Creek field site, Victoria, Australia. The map also shows the annual rainfall for the region (200 mm isohyets). (b) Detail of the field site area showing the aerial distribution of the main forest types, topography (50 m contours), stream courses, and outline of the field site.

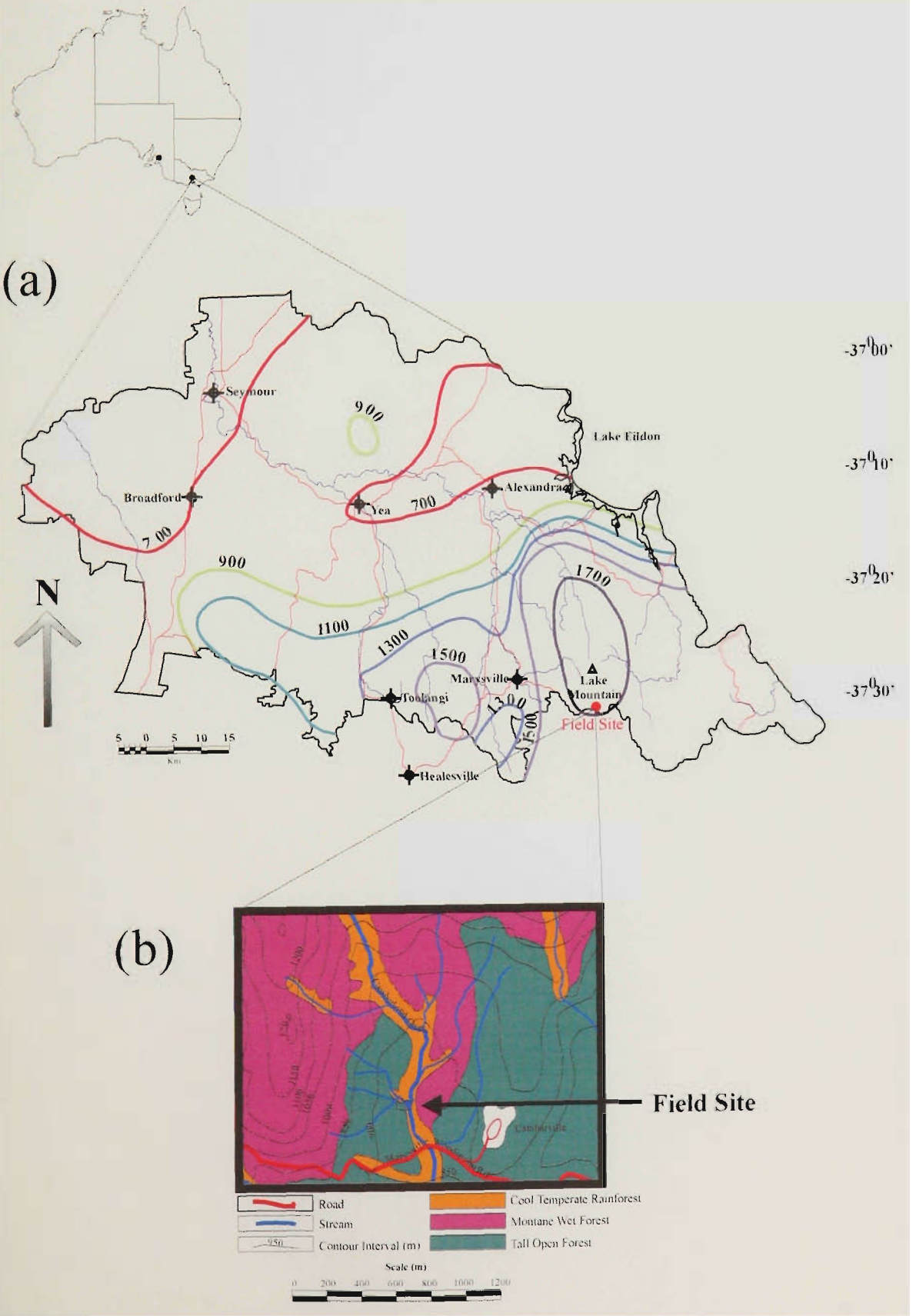


Figure 2.2 Channel profile of Cumberland Creek at the southern boundary of the field site. The channel profile is marked by a solid black line, the water level is marked by a dashed line. All units are in centimetres.

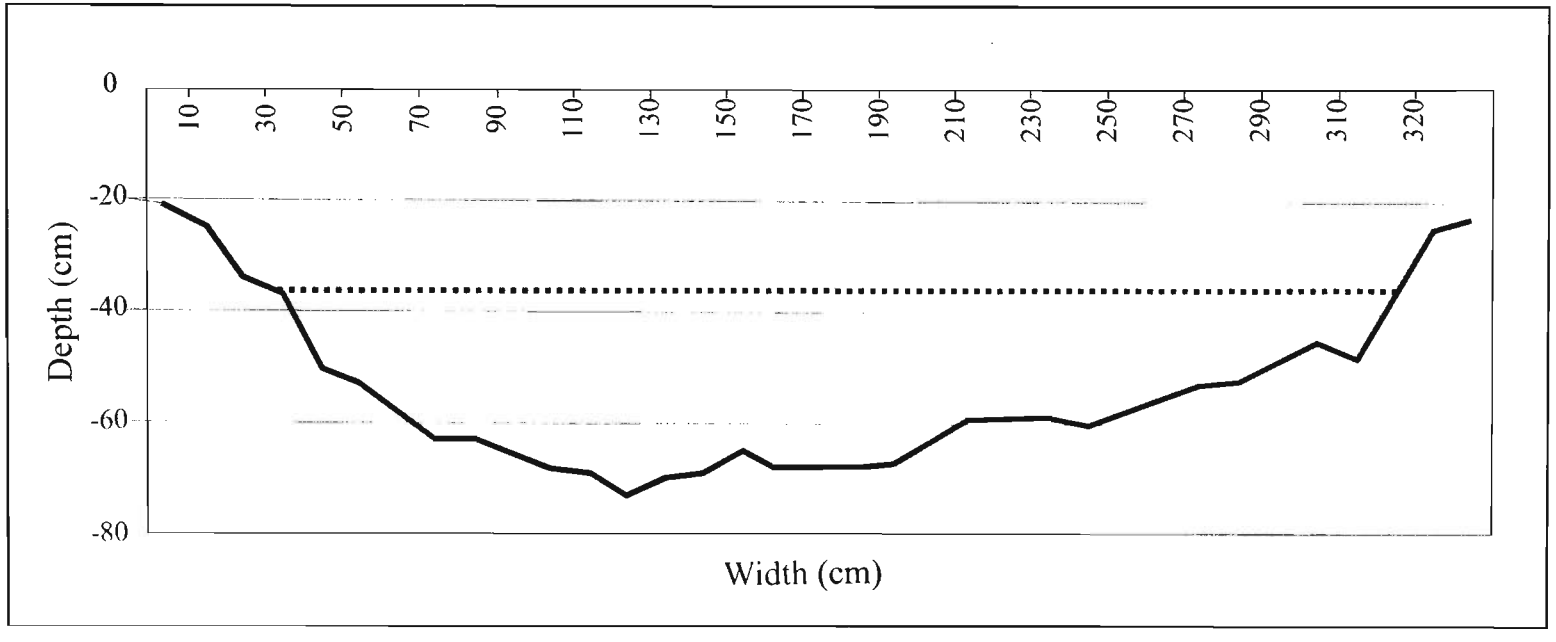


Figure 2.3 Generalised diagram showing the structure and profile of the vegetation (in cross section) at the Cumberland Creek Field Site. The vegetation of the site is composed of two vegetation types; Cool temperate rainforest, which is dominated by *Nothofagus cunninghamii*, and Tall Open Forest (synonymous with Wet Sclerophyll Forest) which is dominated by *Eucalyptus* regnans. D= *Dicksonia antartica, N = Nothofagus cunninghamii, At = Atherosperma moschatum, Am = Acacia melanoxylon, Er = Eucalyptus regnans* and *Bw = Blechnum wattsii*.

Figure 2.4 Position of leaf litter traps throughout the Cumberland Creek Field Site. Each Leaf Litter Trap (LLT), is labelled with its number.

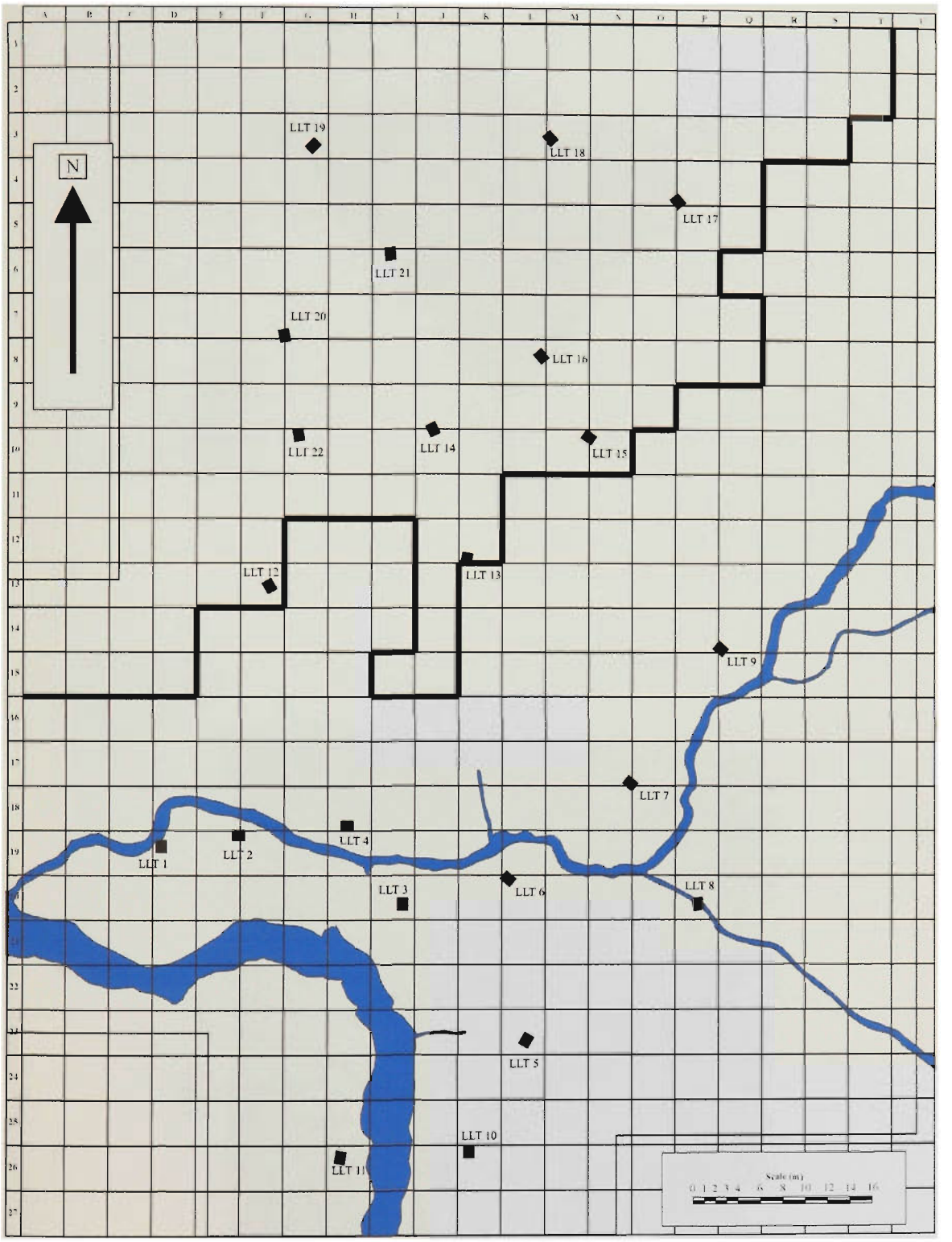
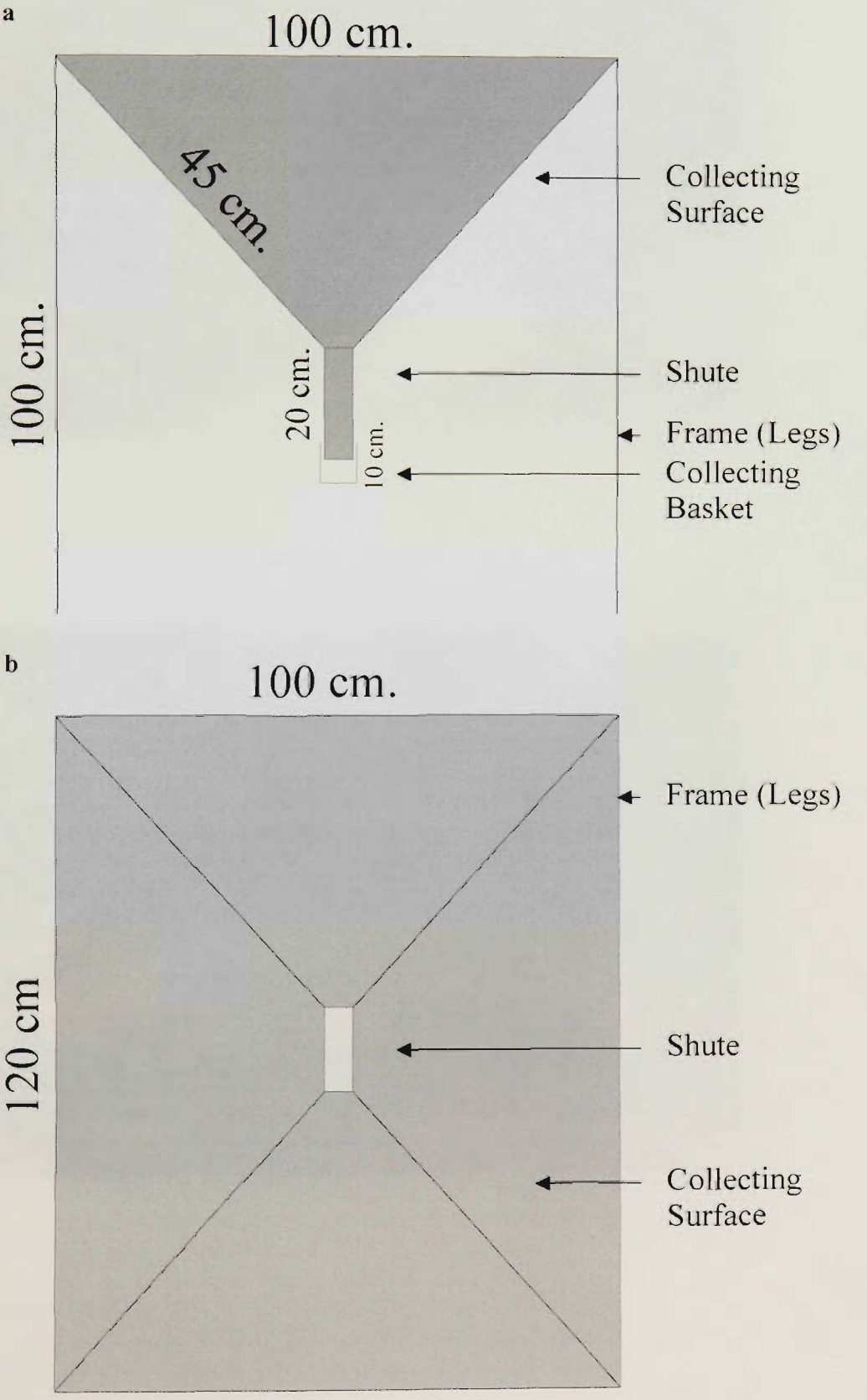


Figure 2.5 The design of the leaf litter traps. Figure 2.2 a shows the blueprints of the trap from the side, Figure b shows the trap from above, while figures c and d are photographs of the traps in operation at the field site (on following page).



c

d

Figure 2.6 Vegetation maps for the Cumberland Creek Field Site. Each tree marked was taller than 1.5 metres.

a Master vegetation map for the Cumberland Creek Field Site. All of the trees marked on the map were taller than 1.5 m and have been numbered. The positions of all the tree ferns (mostly *Dicksonia australis*) are also shown, as well as the major topographic features, the positions of litter traps and the other test locations used at the field site.

b Vegetation map showing the distribution of *Nothofagus cunninghamii* and topographic features only.

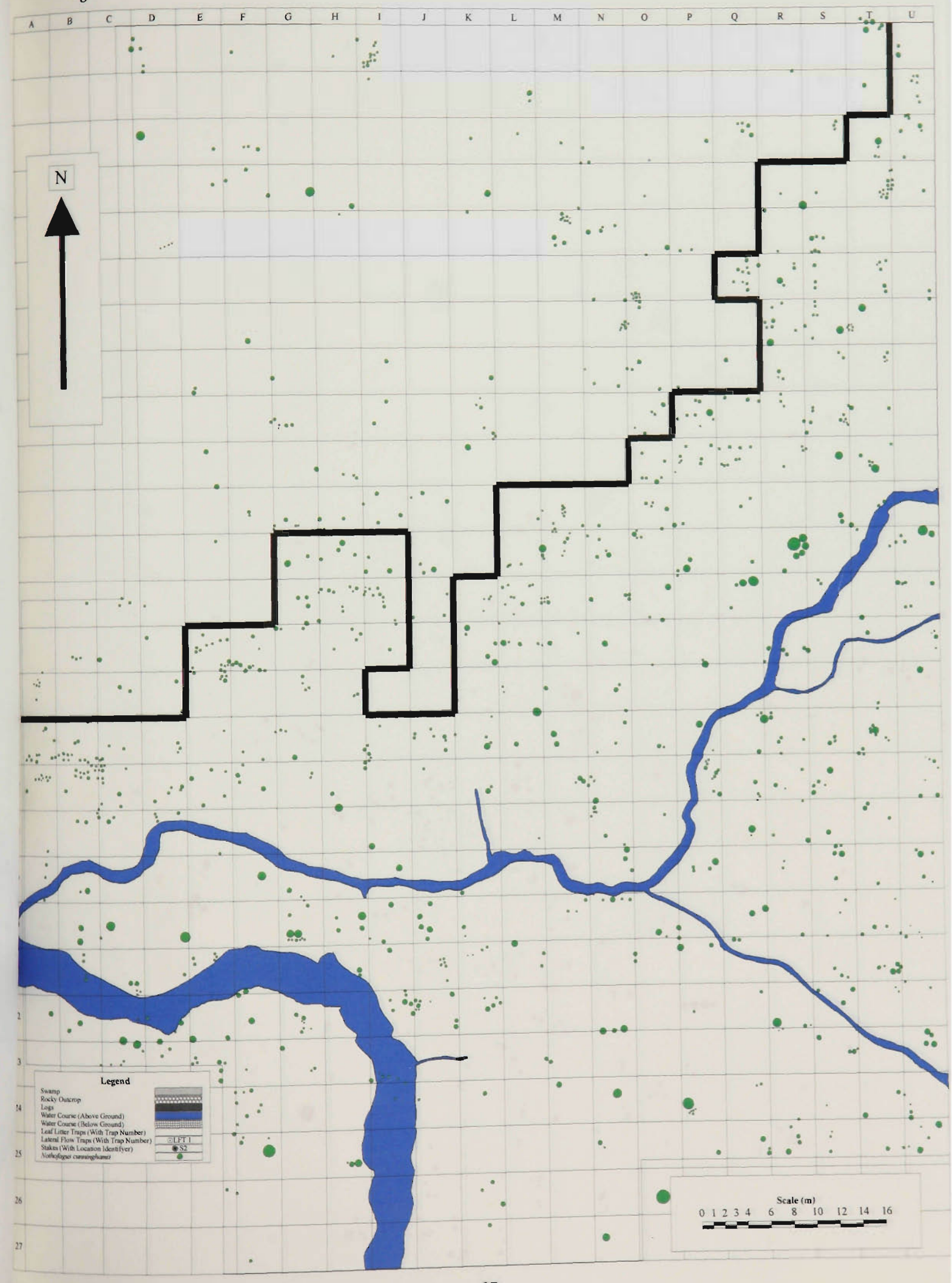
c Vegetation map showing the distribution of *Atherosperma moschatum* and topographic features only.

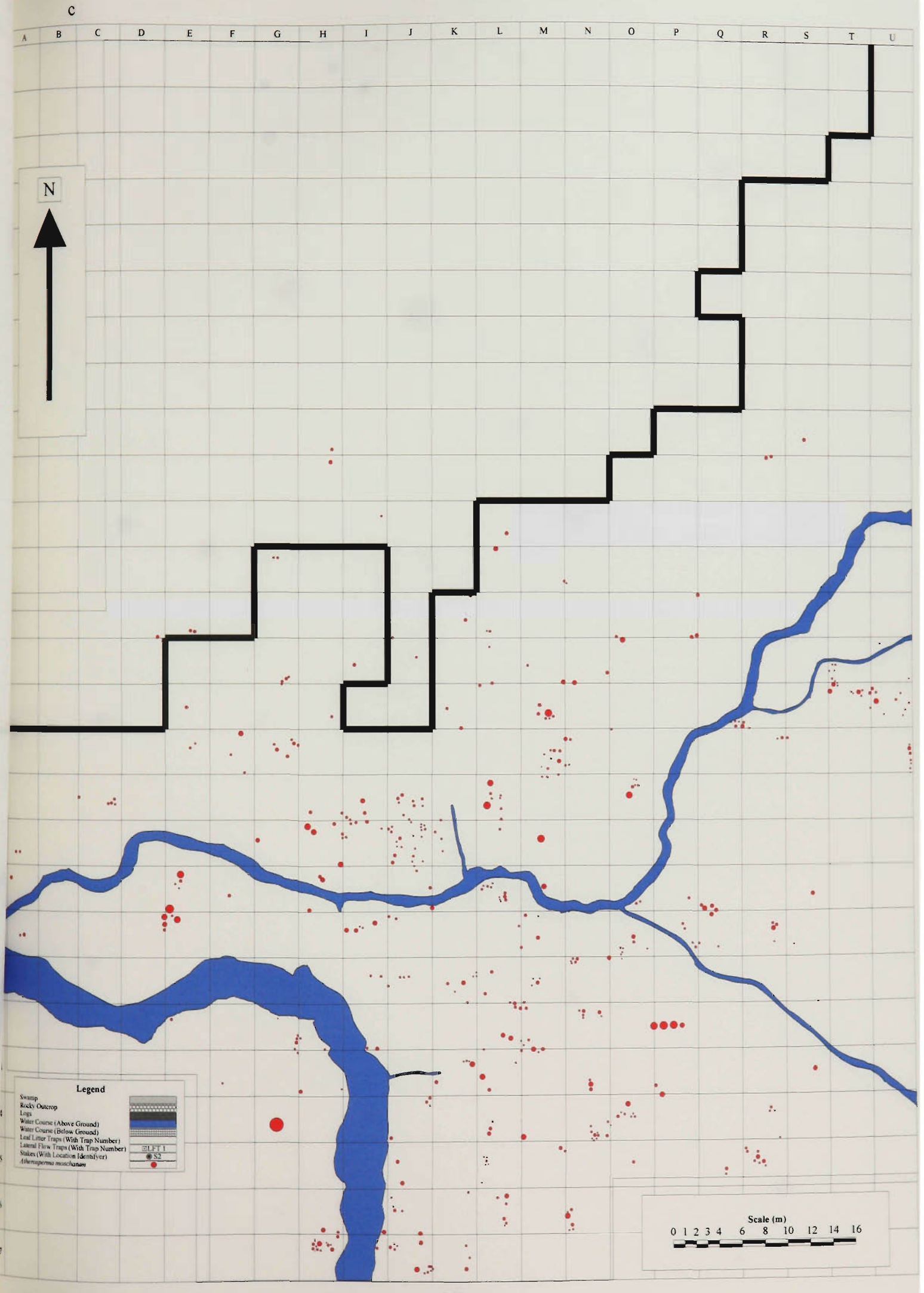
d Vegetation map showing the distribution of *Eucalyptus regnans* and topographic features only.

e Vegetation map showing the distribution of *Acacia melanoxylon* and topographic features only.

f Vegetation map showing the distribution of the rare trees and topographic features only.

b


A B C D E F G H I J K L M N O P Q R S T U
N
Legend
Swamp
Rocky Outcrop
Logs
Water Course (Above Ground)
Water Course (Below Ground)
Leaf Litter Traps (With Trap Number)
Lateral Flow Traps (With Trap Number)
Stakes (With Location Identifyer)
Nothofagus cunninghamii
LFT 1
S2
Scale (m)
0 1 2 3 4 6 8 10 12 14 16


C
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Swamp
Rocky Outcrop
Logs
Water Course (Above Ground)
Water Course (Below Ground)
Leaf Litter Traps (With Trap Number)
Lateral Flow Traps (With Trap Number)
Stakes (With Location Identifyer)
Alternaperma moschatum
LFT 1
S2
Scale (m)
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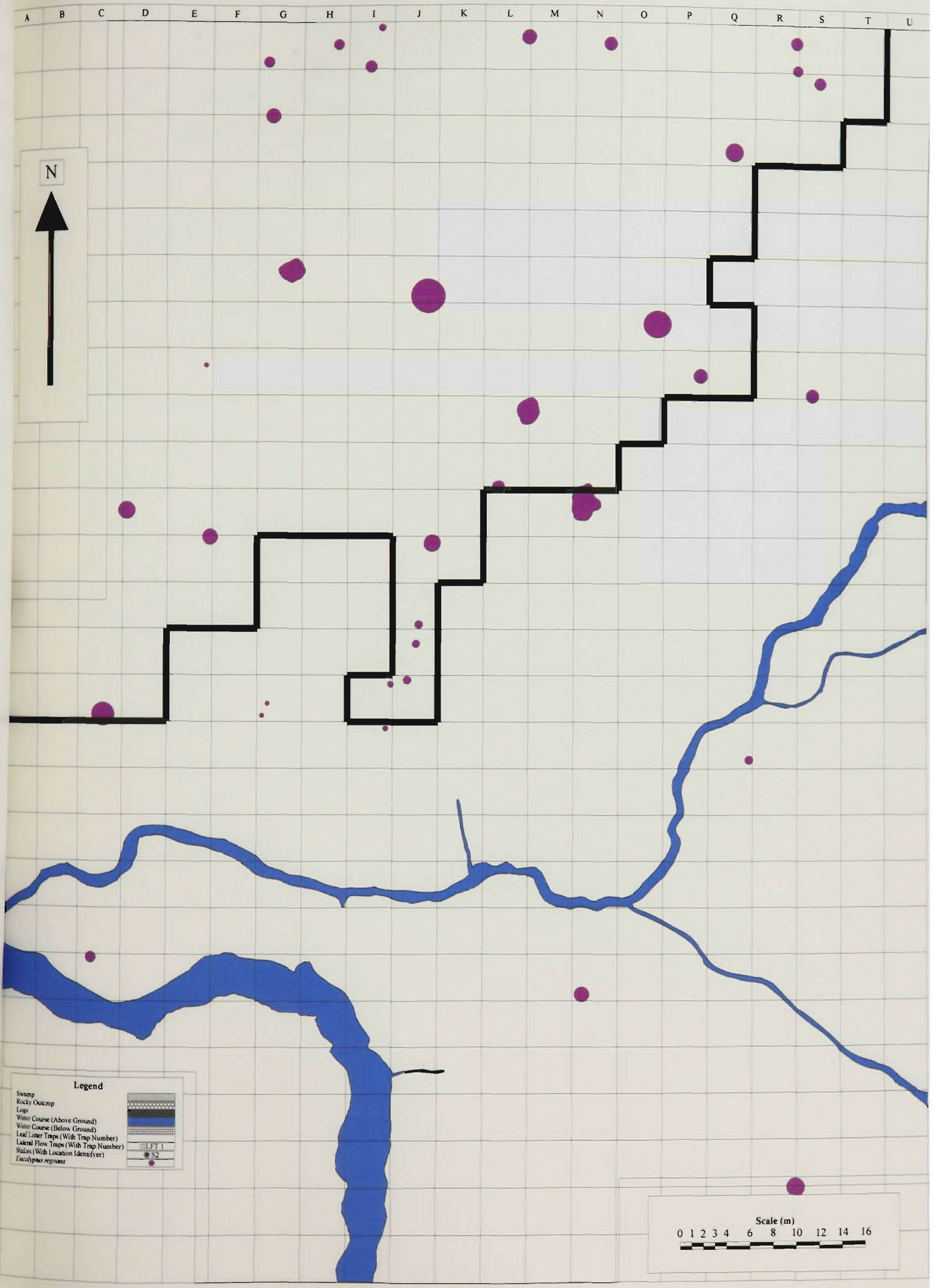
d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Lateral Flow Traps (With Trap Number)
Stakes (With Location Identifyer)
Eucalyptus regnans
LFT 1
S2
Scale (m)
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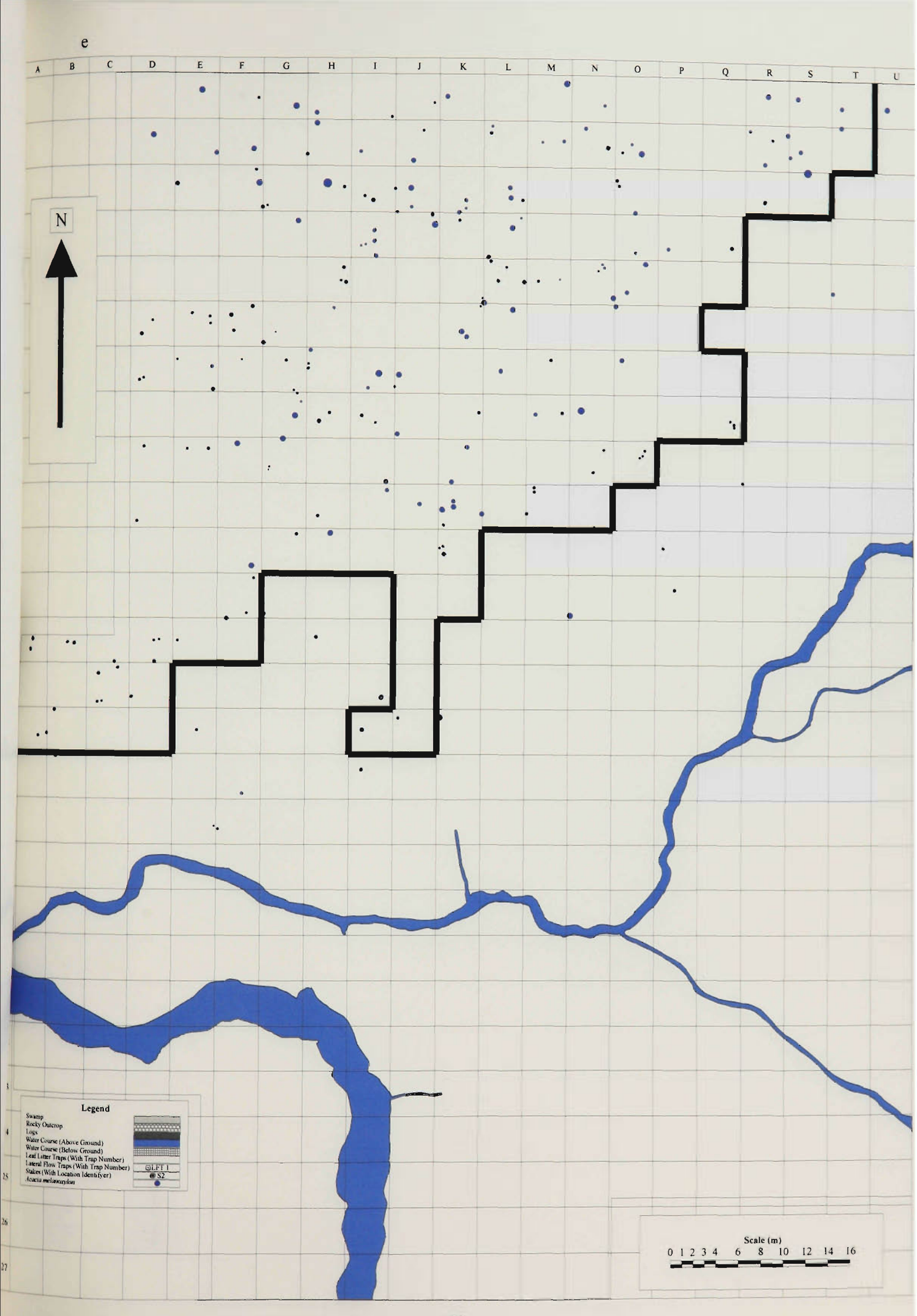
e
A B C D E F G H I J K L M N O P Q R S T U
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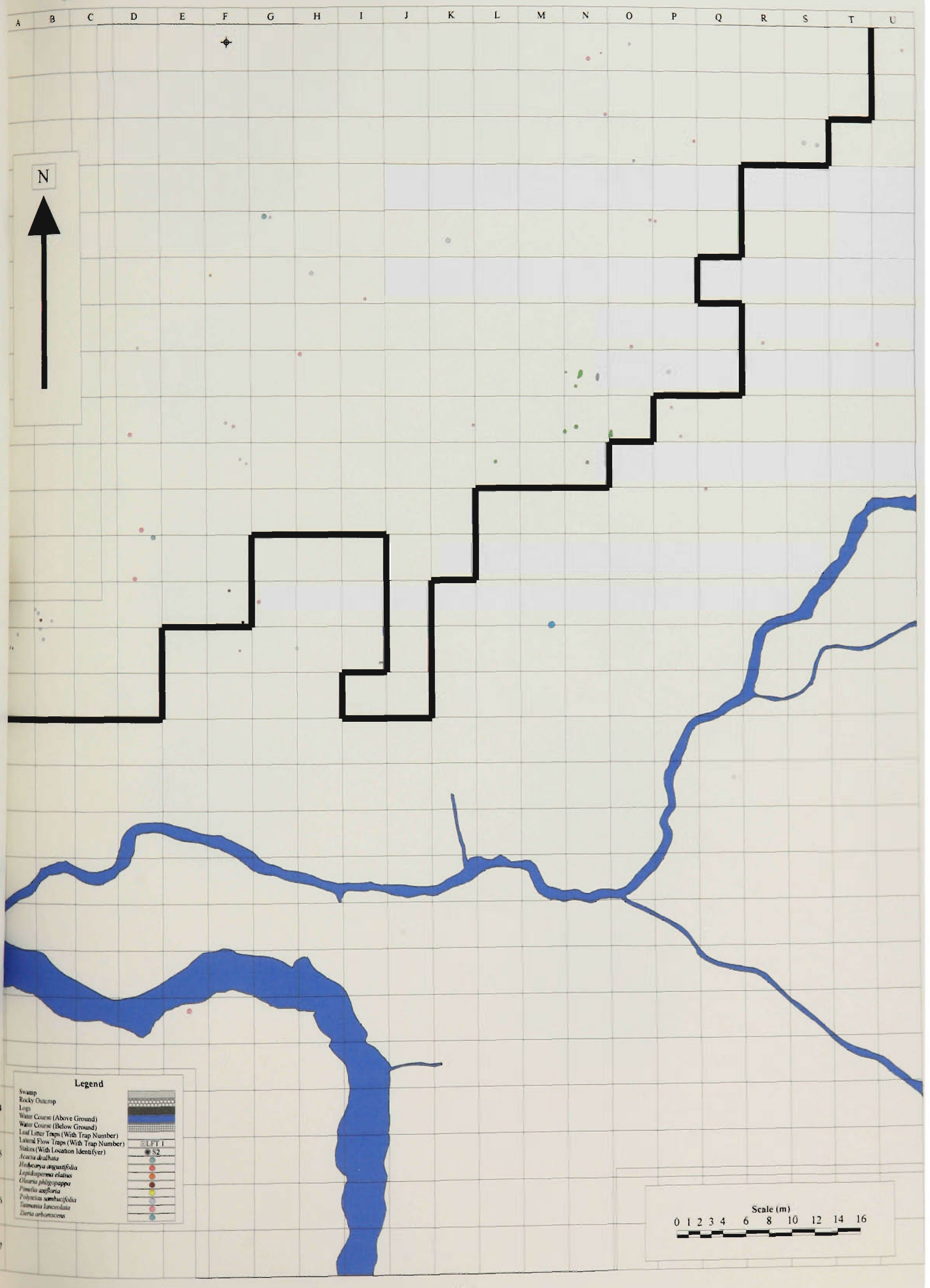
Rocky Outcrop
Logs
Water Course (Above Ground)
Water Course (Below Ground)
Leaf Litter Traps (With Trap Number)
Lateral Flow Traps (With Trap Number)
Stakes (With Location Identifyer)
Acacia melanoxylon
LFT 1
S2
Scale (m)
0 1 2 3 4 6 8 10 12 14 16

f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N
Legend
Swamp
Rocky Outcrop
Logs
Water Course (Above Ground)
Water Course (Below Ground)
Leaf Litter Traps (With Trap Number)
Lateral Flow Traps (With Trap Number)
Stakes (With Location Identifyer)
Acacia dealbata
Hovea arya angustifolia
Lepidosperma elatius
Olearia phlogopappa
Pimelia axiflora
Polyscias sambucifolia
Tasmania lanceolata
Zieria arborescens
LFT 1
S2
Scale (m)
0 1 2 3 4 6 8 10 12 14 16

Figure 2.7 The relative proportions of organ types produced by either forest types as a whole or the individual species within those forests. **Figures 2.7a to d** are for the cool temperate rainforest and species, and **Figures 2.7e to i** are for the wet sclerophyll forest and species. All figures are percentages.

Key:

Leaves 

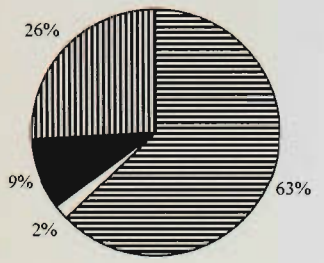
Bark 

Reproductive Structures 

Structural Materials 

a Cool Temperate Rainforest (Average).
b *Nothofagus cunninghamii.*
c *Eucalyptus regnans.*
d *Atherosperma moschatum.*
e Wet Sclerophyll Forest (Average).
f *Nothofagus cunninghamii.*
g *Eucalyptus regnans.*
h *Acacia melanoxylon.*
i *Acacia dealbata.*

a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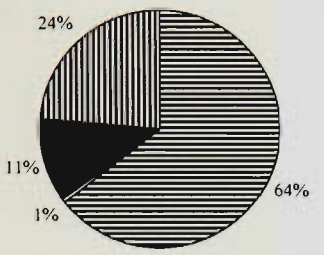
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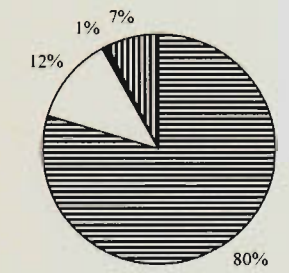
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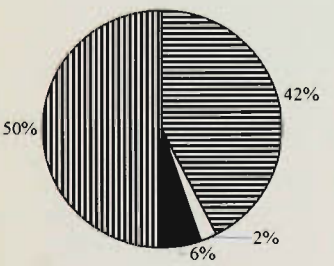
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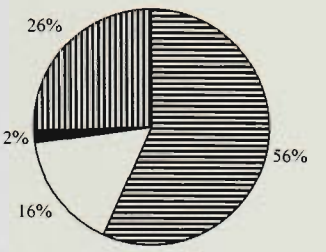
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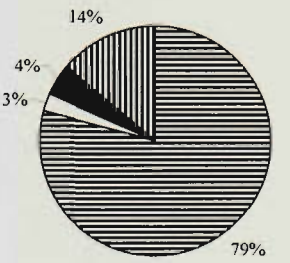
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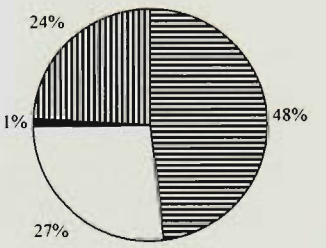
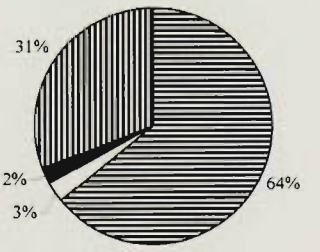
79%

g


24%
1%
48%
27%

h


31%
2%
64%
3%

i

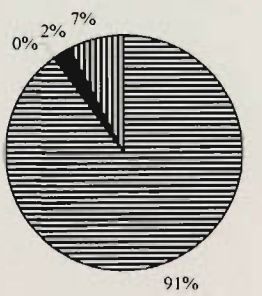
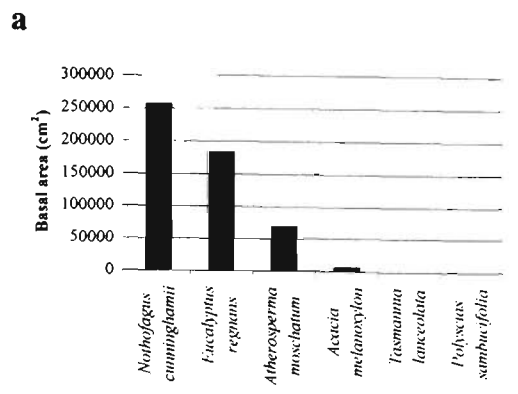

0%
2%
7%
91%

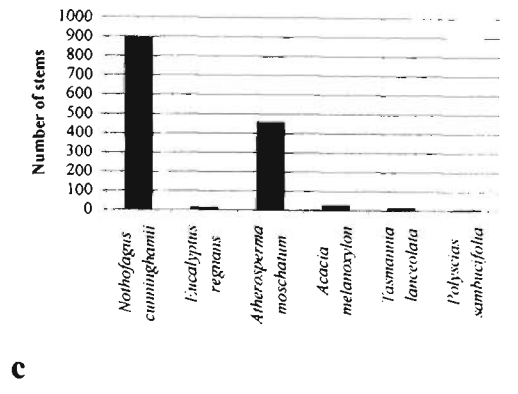
Figure 2.8 Rank order abundance histograms for the principal canopy tree taxa for the cool temperate rainforest and wet sclerophyll.

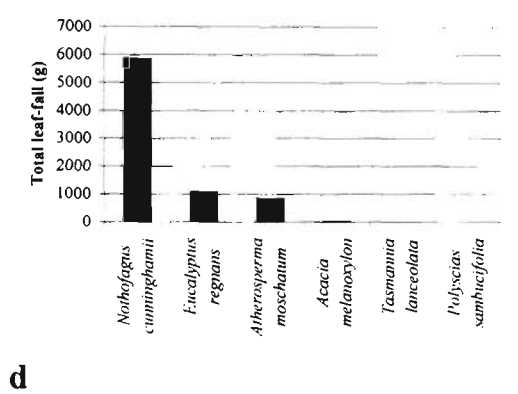
Key: Cool Temperate Rainforest 

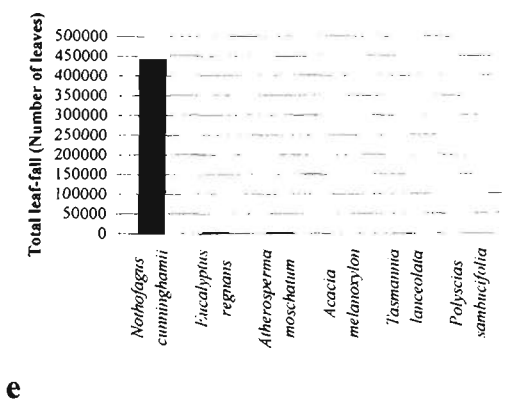
Wet Sclerophyll Forest 

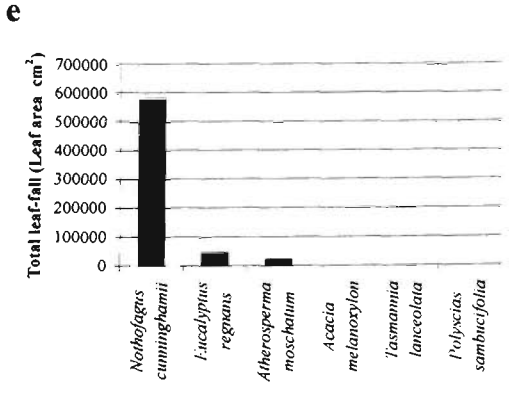
a **CTRF** Basal Area.
b **CTRF** Number of Stems.
c **CTRF** Total Leaf-fall (grams of leaf material).
d **CTRF** Total Leaf-fall (Numbers of leaves).
e **CTRF** Total Leaf-fall (Leaf area cm^2).
f **WSF** Basal Area.
g **WSF** Number of Stems.
h **WSF** Total Leaf-fall (grams of leaf material).
i **WSF** Total Leaf-fall (Numbers of leaves).
j **WSF** Total Leaf-fall (Leaf area cm^2).

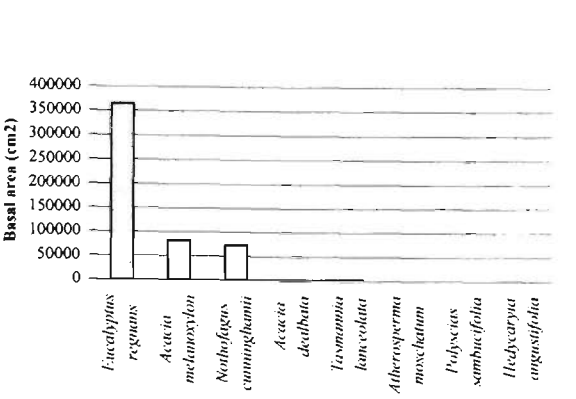

a
Basal area (cm²)
300000
250000
200000
150000
100000
50000
0
Nothofagus cunninghamii
Eucalyptus regnans
Atherosperma moschatum
Acacia melanoxylon
Tasmania lanceolata
Polyscias sambucifolia

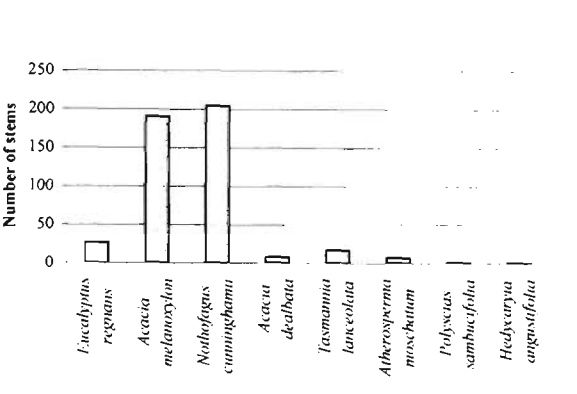

b
Number of stems
1000
900
800
700
600
500
400
300
200
100
0
Nothofagus cunninghamii
Eucalyptus regnans
Atherosperma moschatum
Acacia melanoxylon
Tasmania lanceolata
Polyscias sambucifolia

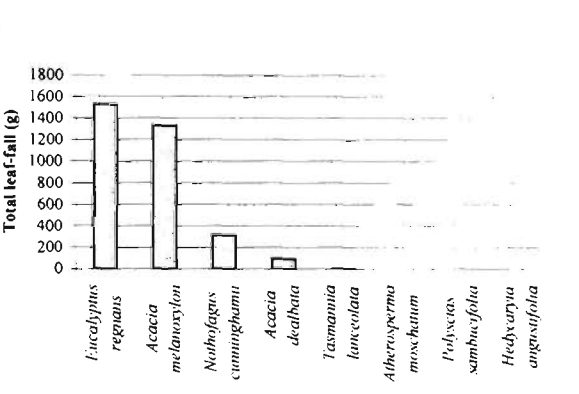

c
Total leaf-fall (g)
7000
6000
5000
4000
3000
2000
1000
0
Nothofagus cunninghamii
Eucalyptus regnans
Atherosperma moschatum
Acacia melanoxylon
Tasmania lanceolata
Polyscias sambucifolia

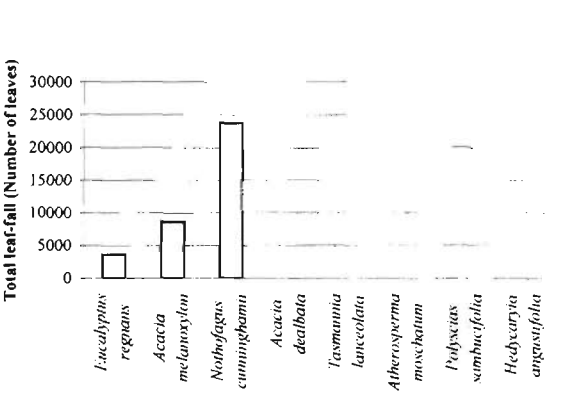

d
Total leaf-fall (Number of leaves)
500000
450000
400000
350000
300000
250000
200000
150000
100000
50000
0
Nothofagus cunninghamii
Eucalyptus regnans
Atherosperma moschatum
Acacia melanoxylon
Tasmania lanceolata
Polyscias sambucifolia


e
Total leaf-fall (Leaf area cm²)
700000
600000
500000
400000
300000
200000
100000
0
Nothofagus cunninghamii
Eucalyptus regnans
Atherosperma moschatum
Acacia melanoxylon
Tasmania lanceolata
Polyscias sambucifolia


f
Basal area (cm2)
400000
350000
300000
250000
200000
150000
100000
50000
0
Eucalyptus regnans
Acacia melanoxylon
Nothofagus cunninghamii
Acacia dealbata
Tasmania lanceolata
Atherosperma moschatum
Polyscias sambucifolia
Hedycarya angustifolia


g
Number of stems
250
200
150
100
50
0
Eucalyptus regnans
Acacia melanoxylon
Nothofagus cunninghamii
Acacia dealbata
Tasmania lanceolata
Atherosperma moschatum
Polyscias sambucifolia
Hedycarya angustifolia


h
Total leaf-fall (g)
1800
1600
1400
1200
1000
800
600
400
200
0
Eucalyptus regnans
Acacia melanoxylon
Nothofagus cunninghamii
Acacia dealbata
Tasmania lanceolata
Atherosperma moschatum
Polyscias sambucifolia
Hedycarya angustifolia


i
Total leaf-fall (Number of leaves)
30000
25000
20000
15000
10000
5000
0
Eucalyptus regnans
Acacia melanoxylon
Nothofagus cunninghamii
Acacia dealbata
Tasmania lanceolata
Atherosperma moschatum
Polyscias sambucifolia
Hedycarya angustifolia

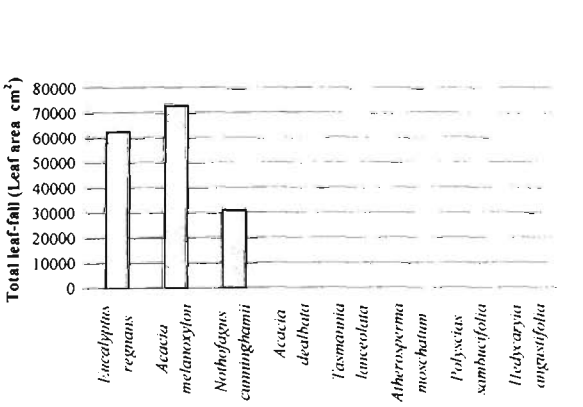
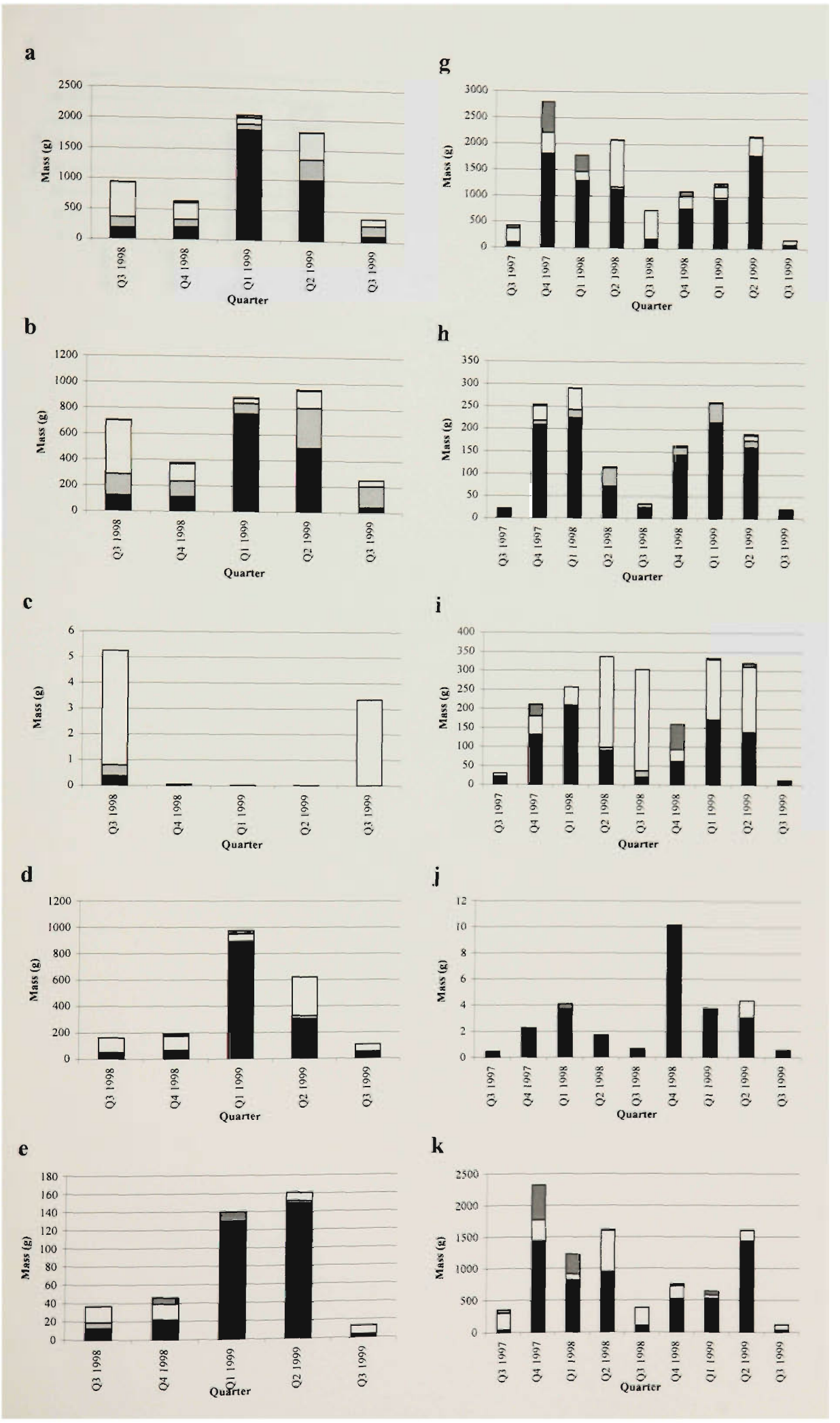

j
Total leaf-fall (Leaf area cm²)
80000
70000
60000
50000
40000
30000
20000
10000
0
Eucalyptus regnans
Acacia melanoxylon
Nothofagus cunninghamii
Acacia dealbata
Tasmania lanceolata
Atherosperma moschatum
Polyscias sambucifolia
Hedycarya angustifolia

Figure 2.9 The quarterly patterns of leaf fall for the Cumberland Creek Field site. For all the histograms Q1 equals summer, Q2 equals autumn, Q3 equals winter and Q4 equals spring.

a Wet Sclerophyll Forest (Total).
b **WSF** *Eucalyptus regnans.*
c **WSF** *Atherosperma moschatum.*
d **WSF** *Acacia melanoxylon.*
e **WSF** *Nothofagus cunninghamii.*
f **WSF** *Acacia dealbata* (on following page).
g Cool Temperate Rainforest (Total).
h **CTRF** *Eucalyptus regnans.*
i **CTRF** *Atherosperma moschatum.*
j **CTRF** *Acacia melanoxylon.*
k **CTRF** *Nothofagus cunninghamii.*


a
Mass (g)
2500
2000
1500
1000
500
0
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
b
Mass (g)
1200
1000
800
600
400
200
0
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
c
Mass (g)
6
5
4
3
2
1
0
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
d
Mass (g)
1200
1000
800
600
400
200
0
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
e
Mass (g)
180
160
140
120
100
80
60
40
20
0
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
g
Mass (g)
3000
2500
2000
1500
1000
500
0
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
h
Mass (g)
350
300
250
200
150
100
50
0
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
i
Mass (g)
400
350
300
250
200
150
100
50
0
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
j
Mass (g)
12
10
8
6
4
2
0
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
k
Mass (g)
2500
2000
1500
1000
500
0
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter

f


70
60
50
40
30
20
10
0
Mass (g)
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter

Figure 2.10 The variability in leaf litter composition between litter traps. The error bars indicate standard deviation from the mean production figures per litter trap. The average proportion of leaves found in an individual litter trap for a particular species can vary between zero to the total amount recorded for that quarter. For all the histograms Q1 equals summer, Q2 equals autumn, Q3 equals winter and Q4 equals spring.

Key:

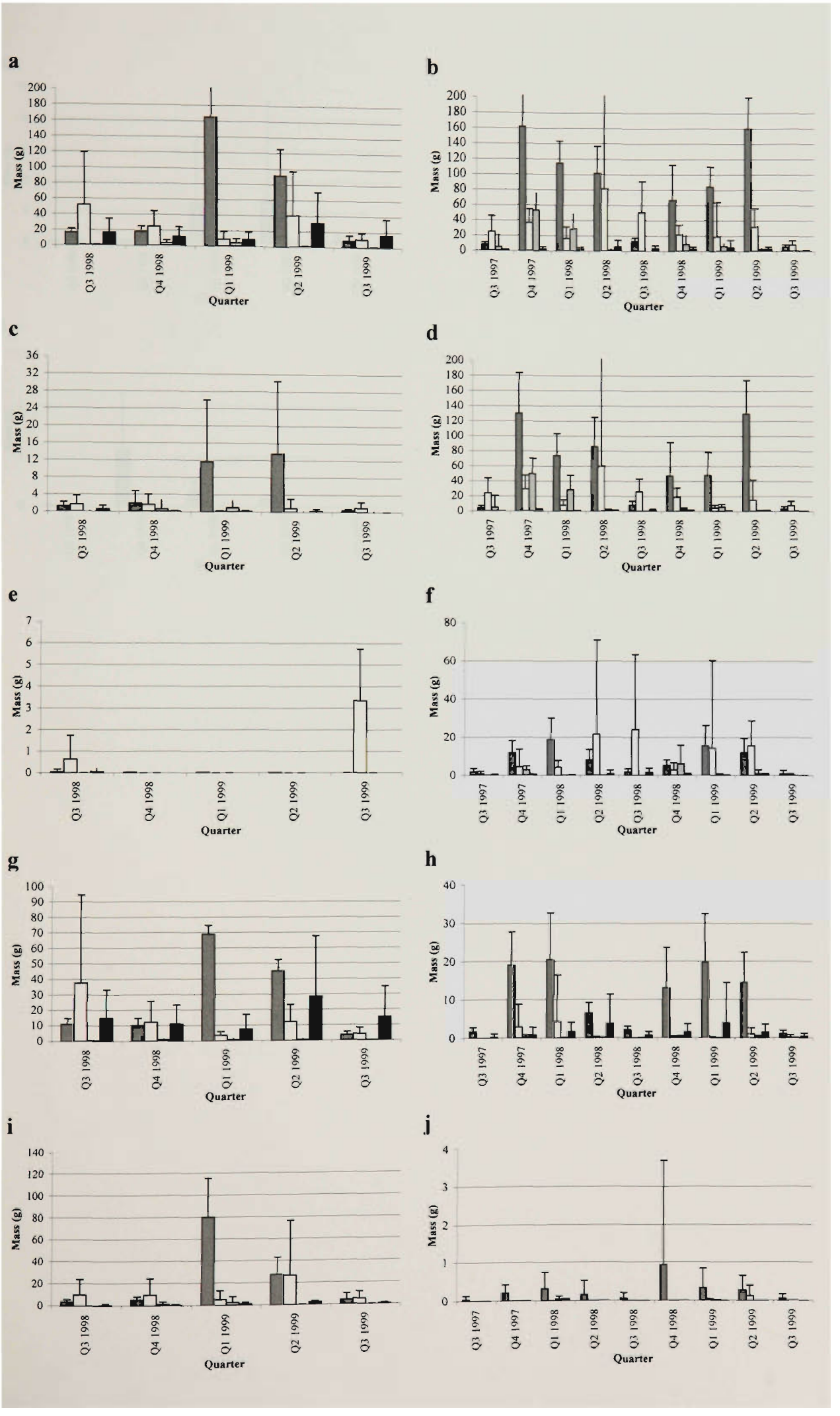
Leaves 

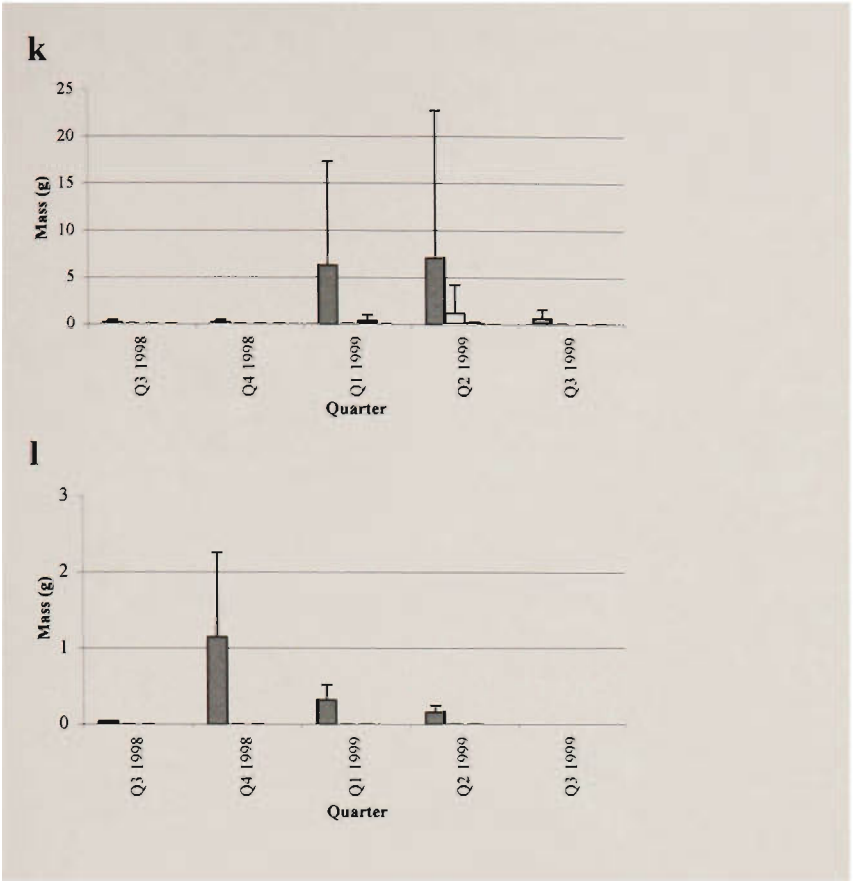
Structural Materials 

Reproductive Structures 

Bark 

a Wet Sclerophyll Forest (Summary for all Species).
b Cool Temperate Rainforest (Summary for all Species).
c **WSF** *Nothofagus cunninghamii.*
d **CTRF** *Nothofagus cunninghamii.*
e **WSF** *Atherosperma moschatum.*
f **CTRF** *Atherosperma moschatum.*
g **WSF** *Eucalyptus regnans.*
h **CTRF** *Eucalyptus regnans.*
i **WSF** *Acacia melanoxylon.*
j **CTRF** *Acacia melanoxylon.*
k **WSF** *Acacia dealbata* (on following page).
l **WSF** *Tasmania lanceolata* (on following page).


a
Mass (g)
Quarter
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
b
Mass (g)
Quarter
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
c
Mass (g)
Quarter
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
d
Mass (g)
Quarter
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
e
Mass (g)
Quarter
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
f
Mass (g)
Quarter
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
g
Mass (g)
Quarter
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
h
Mass (g)
Quarter
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
i
Mass (g)
Quarter
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
j
Mass (g)
Quarter
Q3 1997
Q4 1997
Q1 1998
Q2 1998
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999


k
25
20
15
10
5
0
Mass (g)
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter
l
3
2
1
0
Mass (g)
Q3 1998
Q4 1998
Q1 1999
Q2 1999
Q3 1999
Quarter

Chapter 3

The Overland Transport of Leaves

3.1 Introduction

As discussed in section 1.5.2, several studies have found that long distance overland transport of leaves was minimal (Spicer, 1981; Ferguson, 1985, 1995; Greenwood, 1992; Burnham *et al.*, 1992; Burnham, 1994, 1997; France, 1995). These studies commonly observed that most forest floor litter was of local origin, and that the heterogeneity of that litter was preserved well after leaf fall. Most leaves tend to fall close to the tree that produced them. What needs to be established therefore is:

1. How far do leaves travel once they reach the ground?
2. Do leaves of different species travel different distances?

This aspect of the thesis examines the effects of slope, ground cover and forest type on the overland transport of leaves from five tree species from the genera *Acacia*, *Atherosperma, Eucalyptus, Lomatia* and *Nothofagus*. The following hypotheses were tested:

1. Leaves do not travel any substantial distance (>5 m) after falling to the ground.
2. Where leaves are transported overland, factors such as the slope of the land, density of the ground level vegetation and the size and weight of the leaves affect the distances travelled.
3. Leaves travel greater distances in open forests such as the wet sclerophyll forest and shorter distances in closed forests such as cool temperate rainforest.

This hypothesis was raised to test the suggestion by Fergusson (1985) that differences in forest structure may impact upon leaf transport distances. Closed forests (CTRF) should have lower wind speeds than open forests (WSF) and lower leaf transport distances.

This study is also designed to help answer the question:

Can low levels of overland lateral transfer provide an explanation for the paucity of some plant genera in the Australian fossil record?

The answer to this question is of some interest from a palaeobotanical point of view because long distance overland transport of leaves could give rise to a situation when regional floras are merged into local riparian floras. Conversely, if the overland transport of leaves is insignificant then many fossil floras will tend to reflect local or riparian floras only.

3.2 Materials and Methods

Four hundred freshly abscissed leaves of the five tree species (Table 3.1) were collected from trees at the Cumberland Creek field site (Section 2.2). They were collected using fibreglass mesh nets suspended beneath trees of the appropriate species. Leaf collection took place weekly until sufficient leaves had been obtained and were air dried at a constant 50% humidity so they could be spray painted. The dried leaves were sprayed with a bright pink fluorescent paint and were numbered (to assist with their identification from other leaves of the same species found naturally on the forest floor). The paint used was White Night Highlight Paint. The colour was Super Bright Fluorescent Pink from an aerosol pressure pack. The leaves were then weighed and compared to the weight of freshly abscissed leaf material (Table 3.1). It was found that the paint added between 10% and 55% to the net dry weight of the leaves.

Table 3.1 The effect of spray painting upon the Dry Weight (DWt) and density of the leaves of the 5 species used in this study. All dry weights are given in grams per 50 leaves, all densities are given as grams per square metre.

Species Name	DWt. before spray painting (g/50 leaves)	Density before painting (g/m^2)	DWt. after spray painting (g/50 leaves)	Density after painting (g/m^2)	Change (%)
Lomatia fraseri	28.59	121	32.86	140	14.9
Eucalyptus regnans	22.03	243	24.23	268	10.0
Atherosperma moschatum	5.11	94	7.95	147	55.6
Nothofagus cunninghamii	0.68	101	0.99	151	45.6
Acacia melanoxylon	7.64	183	8.83	209	15.6

On January 3, 1999, 20 leaves of each species were placed in a pile, around a labelled maker stake at each of the 20 experimental locations throughout the field site (For locations refer to Figure 3.1). Five replicates each were placed upon areas of the cool temperate rainforest (CTRF) and the wet sclerophyll forest (WSF) forest floor devoid of ground or shrub level vegetation. Such areas were labelled bare ground, because of the absence of ground or shrub level vegetation. The replicates were at least five metres apart and on level ground. A typical example of the vegetation free ground cover in the WSF forest is shown in Figure 3.2a and the CTRF in Figure 3.2b.

The remaining 10 replicates were established on the sides of the valley. Two different slope classes observed along the valley sides were used. These were labelled as 'Steep' and 'Medium'. The gradient of the steep and medium slopes was between 45° to 50° and 20° to 30° respectively. The slopes were determined trigonometrically. Five replicates were set up upon the steep slope; the ground cover at these locations consisted of *Blechnum wattsii* and *Polystichum proliferum*, which formed a tangled mat of vegetation throughout the length of the steep areas of the valley. The remaining five replicates were placed in the medium slope areas. Three of these locations had dense coverings of the spreading fern *Blechnum wattsii* (Figure 3.2c), while two were placed

upon bare ground with no ground level vegetation. Such areas were atypical along the valley sides and there were only two suitable locations.

All of the sites were examined monthly for six months. After six months the distance each individual leaf had moved from its initial starting location was measured using a fibreglass measuring tape (Figure 3.3 a & 3.3 b). An area up to 10 m away from the marker stake was thoroughly searched for painted leaves and then all distances travelled were measured from the stake to the petiole of the leaf. Where any leaves had rotted away during the intervening six months, the distance from the marker to the shell of paint (where clearly identifiable) that remained after the leaf had decayed was measured instead. The paint was resistant to decomposition, and if undisturbed, remained intact even if the original leaf material had completely rotted away. In some cases, it was not possible to measure the position of the shell of paint because it had fractured into various small fragments. Data were initially analysed by a statistician (Dr. Neil T., Diamond; Victoria University of Technology, Department of Computer Science and Mathematics), using Minitab 12. Subsequently the analysis was reviewed by Associate Professor Gerry Quinn (Monash University, School of Biological Sciences) to determine whether there were any differences in lateral redistribution due to species, slope, leaf weight or size and density of ground cover. All data used were $\log_{10}$ transformed.

The mean distances travelled by the leaves of each species at each location were calculated and used in the analysis rather than the raw data. This was done because the sample sizes were unequal (Table 3.3), and this precluded the use of the raw data directly. The linear relationship between the means and standard deviations of each species and treatment suggested that a natural log transformation be taken. The data was then analysed using a two way ANOVA ($\alpha = 0.05$), where site and species were contrasted, with site being a random factor within each location category (Table 3.4).

Finally, a multiple regression analysis was run, in order to determine what variables influenced the differences between sites and species. The location variables tested were; a) forest type, b) the density of the ground level vegetation coverage, c) flat versus steep slope and d) medium versus flat and steep slope. The species variables tested were; a) leaf area and b) average leaf weight after painting.

3.3 Results

The number of leaves (out of the initial 400) recovered for each species varied between 391 leaves for *Lomatia fraseri* and 314 leaves for *Acacia melanoxylon* (Table 3.2). The leaves of *Lomatia fraseri* had the highest rate of recovery. This was possibly

Table 3.2 The total number of leaves from all locations found in each distance class. The zero distance column also includes the total number of leaves (in parenthesis) recovered for each species. It was assumed that the unrecovered leaves had rotted *in situ* as evidenced by the mass of paint fragments left at the bottom of the piles of leaves. These 'remains' were not included in the analysis

	Number of leaves which have travelled distance X (cm) over six months					
Species Name	0	0 - 9.9	10 - 19.9	20 – 29.9	30 - 39.9	>40cm
Lomatia fraseri	23(391)	96	187	50	14	21
Eucalyptus regnans	34(374)	121	131	52	20	11
Nothofagus cunninghamii	34(337)	138	106	35	6	18
Atherosperma moschatum	31(347)	129	113	51	11	12
Acacia melanoxylon	38(314)	127	100	40	5	4

	Percentage which have travelled less than 0.3m over six months
Lomatia fraseri	91
Eucalyptus regnans	90
Nothofagus cunninghamii	93
Atherosperma moschatum	93
Acacia melanoxylon	97

due to their large size, which made them easily identifiable from the other marked leaves even if all mesophyll tissue had decayed away. The entire leaf of some species had decayed to the point where the leaf was unrecognisable and could not be measured. This

applied mostly to *Acacia melanoxylon* leaves. In such cases, the leaves were recorded as being lost and not included in the analysis. The data (Table 3.2) indicate that over 40% of the leaves placed on the ground stayed within 0.1 m of their starting location, while 80% remained within 0.2 m of their starting location.

From the raw data (Appendix 3.1), the mean distance travelled by the leaves of each of the five species at each of the 20 sites was calculated and tabulated in metres in Table 3.3. Overall, transport distances were low (Table 3.3). The maximum mean

Table 3.3 The mean transport distances (in metres), of the leaves from their initial starting point to their final resting point after six months. The values for *n* are given in parenthesis after each mean. Note: **Loc** = Location, **SC** = Slope Class, **VC** = Vegetation Cover. The abbreviations in the **Loc** column are RF = Rain Forest, Euc = Eucalypt Forest, S = Slope; The abbreviations in the **SC** column are F= Flat, M=Medium, S=Steep; The abbreviations in the **VC** column are B=Bare, H=Heavy.

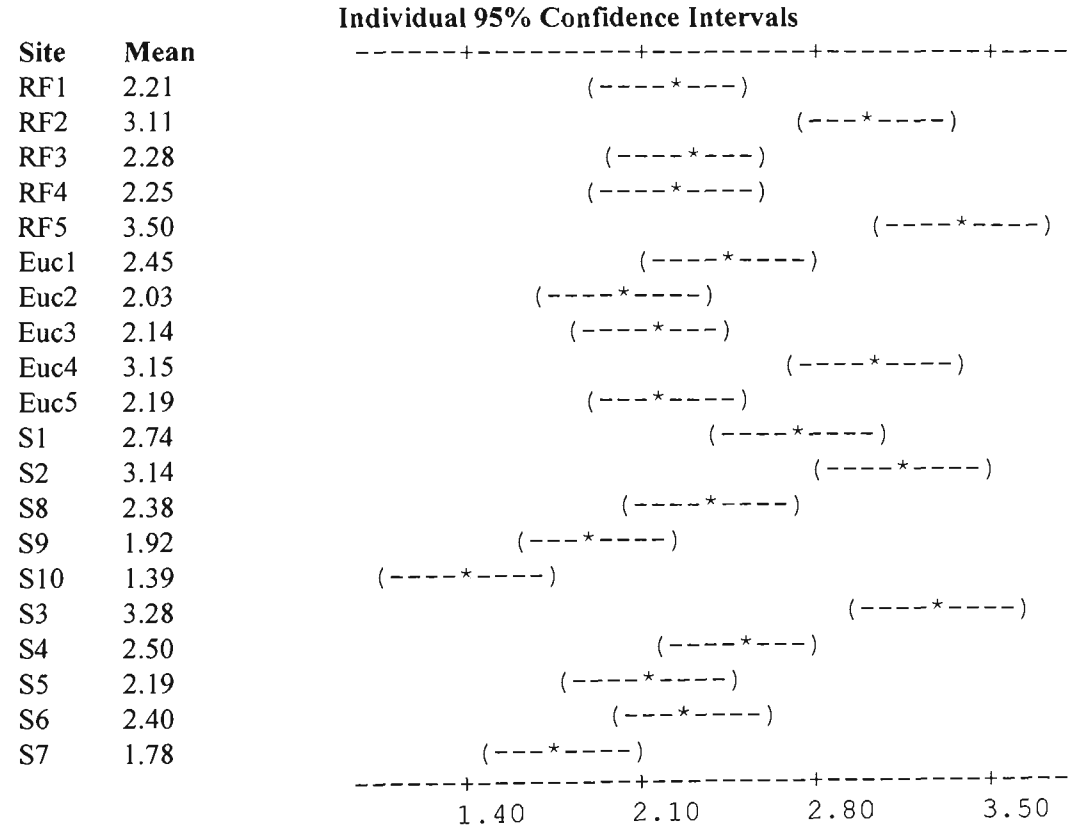
Loc	**Forest Type**	**SC**	**VC**	*Lomita fraseri*	*Eucalyptus regnans*	*Nothofagus cunninghamii*	*Atherosperma moschatum*	*Acacia melanoxylon*
RF1	CTRF	F	B	0.11 (20)	0.13 (18)	0.09 (19)	0.09 (19)	0.06 (17)
RF2	CTRF	F	B	0.24 (20)	0.20 (19)	0.17 (7)	0.23 (20)	0.28 (20)
RF3	CTRF	F	B	0.09 (19)	0.12 (19)	0.11 (19)	0.11 (15)	0.07 (20)
RF4	CTRF	F	B	0.08 (20)	0.10 (19)	0.09 (19)	0.13 (17)	0.08 (19)
RF5	CTRF	F	B	0.46 (17)	0.37 (14)	0.43 (20)	0.21 (10)	0.26 (12)
Euc1	WSF	F	B	0.13 (20)	0.13 (20)	0.12 (16)	0.12 (18)	0.09 (14)
Euc2	WSF	F	B	0.13 (18)	0.09 (19)	0.04 (19)	0.07 (20)	0.09 (5)
Euc3	WSF	F	B	0.11 (20)	0.06 (19)	0.12 (14)	0.05 (19)	0.10 (20)
Euc4	WSF	F	B	0.27 (20)	0.40 (20)	0.17 (20)	0.20 (17)	0.18 (18)
Euc5	WSF	F	B	0.14 (19)	0.05 (18)	0.07 (19)	0.12 (17)	0.10 (18)
S1	CTRF	M	B	0.16 (20)	0.19 (20)	0.12 (20)	0.18 (20)	0.13 (20)
S2	CTRF	M	B	0.25 (20)	0.14 (20)	0.46 (19)	0.23 (19)	0.18 (12)
S8	CTRF	M	H	0.06 (19)	0.17 (20)	0.10 (16)	0.14 (15)	0.11 (11)
S9	CTRF	M	H	0.08 (20)	0.04 (19)	0.11 (15)	0.15 (14)	0.03 (16)
S10	CTRF	M	H	0.08 (20)	0.06 (20)	0.06 (20)	0.04 (20)	0.01 (20)
S3	CTRF	S	H	0.35 (20)	0.37 (20)	0.18 (20)	0.31 (19)	0.19 (17)
S4	CTRF	S	H	0.12 (19)	0.12 (20)	0.14 (12)	0.10 (17)	0.13 (15)
S5	CTRF	S	H	0.14 (20)	0.07 (16)	0.08 (16)	0.06 (15)	0.13 (16)
S6	CTRF	S	H	0.14 (20)	0.17 (19)	0.08 (15)	0.13 (19)	0.06 (19)
S7	CTRF	S	H	0.06 (20)	0.06 (15)	0.07 (12)	0.05 (17)	0.06 (8)

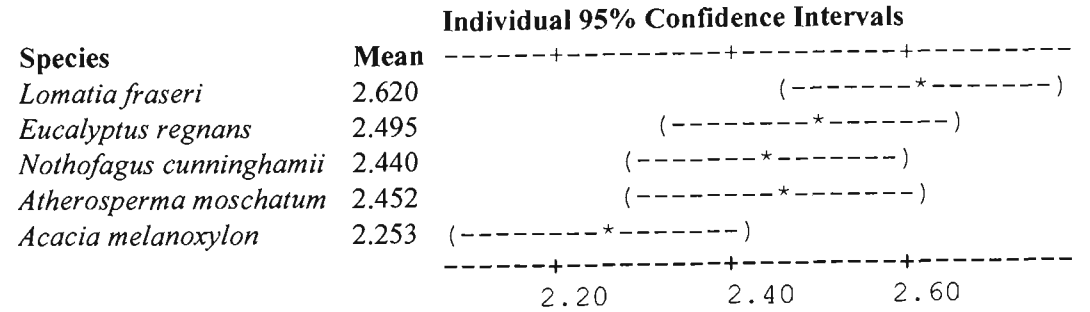
distance travelled was for *Lomatia fraseri* leaves at RF 5, where the leaves travelled 0.46 m. Most other mean transport distances were much lower e.g. *N. cunninghamii* at Euc4

with 0.2 m or *Atherosperma moschatum* at S1 with 0.2 m. No individual leaves were recorded as having as travelled more than 3.43 m during the entire six-month duration of the experiment. A lone *E. regnans* leaf from the Euc4 site was the only leaf to travel any significant distance overland (3.4 m). It is noteworthy that over 90% of the leaves recovered travelled no more than 0.30 m from their initial resting-place (Tables 3.2 & 3.3). Thus, the hypothesis that leaves do not travel substantial distances is credible.

Table 3.4 Results of the two way ANOVA where the means of site versus species were contrasted. The means were log transformed prior to analysis.

Source	DF	SS	MS	F	*P*
Sites	19	28.615	1.506	10.56	0.000
Species	4	1.399	0.350	2.45	0.053
Error	76	10.838	0.143		
Total	99	40.853			





The statistical analysis indicated significant differences among individual sites ($p < 0.001$) and significant differences between *Lomatia fraseri* and *Acacia melanoxylon*, but not between the other three species ($p = 0.053$, Table 3.4). Although it assumed that there was no interaction between site and species, there was no way to test this assumption.

The r^2 value returned from the multiple regression analysis was 0.227, and the only significant variables were the degree of vegetation coverage ($T = 2.79$, $p = 0.006$) and medium vs steep slope ($T=-4.441$, $p < 0.001$). A full quadratic model was tried to ascertain if the addition of crossproduct or squared terms would improve the regression model. Such addition did not improve the regression model and the only terms allowed in the analysis were quadratic terms for the leaf variables and interaction terms between the leaf variables and the location variables. Only the linear terms ($F_{6,83} = 2.66$, $p = 0.021$) were significant, while the quadratic terms ($F_{2, 63} = 0.68$, $p = 0.507$) and the interaction terms ($F_{8, 63} = 0.24$, $p = 0.982$) were not. Finally a best subset regression routine was run (Table 3.5).

Based on the Cp value, the best model is Model 7. However, it was decided that it was preferable to have both Flat versus Steep Slope and Medium versus Flat and Steep Slope in the model and hence Model 9 was chosen (Table 3.6). The regression equation for the model used, Model 9, is shown in equation 3.1 and its statistics in Table 3.6. Leaf weight was not included in the regression equation because it was correlated with leaf area.

Equation 3.1 $\quad \text{Log(Distance)} = 2.92 + 0.00763(\text{Leaf Area}) - 0.2803(\text{Forest Type}) + 0.4033(\text{Vegetation Coverage}) - 0.0437(\text{Flat versus Steep Slope}) - 1.0489(\text{Medium versus Flat/Steep Slope})$

Table 3.5 The results of the best subsets regression for the mean transport data shown in Table 3.3. Note: r^2 indicates the percentage of the variation in the data explained by the regression equation; r^2 adj is the adjusted r^2, which takes into account the number of variables in the regression; Cp is a measure of the predicted error of the regression equation; and S is the standard deviation. The included variables abbreviations are **LA** = Leaf Area, **LW** = Leaf Weight, **FT** = Forest Type, **VC** = Vegetation Coverage, **S1** = Flat versus Steep Slope, **S2** = Medium versus Flat and Steep Slope.

Model	r^2	r^2 adj	Cp	SD	Included Variables					
					LA	LW	FT	VC	S1	S2
1	8.1	7.2	14.6	0.61895						X
2	2.1	1.1	21.8	0.63879	X					
3	18.0	16.3	4.7	0.58780				X		X
4	12.7	10.9	11.1	0.60644			X			X
5	20.1	17.6	4.2	0.58319	X			X		X
6	19.8	17.3	4.5	0.68404			X	X		X
7	22.0	18.7	3.9	0.57931	X		X	X		X
8	21.1	17.7	5.0	0.58260		X	X	X		X
9	22.6	18.5	5.1	0.57983	X		X	X	X	X
10	22.0	17.9	5/8	0.58207	X	X	X	X		X
11	22.7	17.7	7.0	0.58262	X	X	X	X	X	X

Table 3.6 Statistics for regression equation 3.1, P values marked with an '*' are statistically significant at $P = 0.05$.

Variable	Standard Deviation	T-Statistic	*P*-Value
Leaf Area	±0.0046	1.60	0.112
Forest Type	± 0.1640	-1.71	0.091
Vegetation Coverage	±0.1440	2.80	0.006*
Flat Versus Steep Slope	± 0.048	-0.91	0.365
Medium versus Flat/Steep Slope	±0.2367	4.00	<0.001*

The statistical analysis of the regression equation indicates that both the density of the ground vegetation and medium versus flat/steep slope were significant. The leaves of all species were moving greater distances on the medium slope sites with no ground level vegetation than they were on medium slopes with heavy ground level vegetation (Table 3.3 & 3.6). The area of the leaves was found not to be statistically significant and neither were there any differences between the two forest types, and the flat and steep slopes.

3.4 Discussion

The results of the lateral overland transport experiments indicate that there is negligible transport of leaf material once it has fallen to the ground. The maximum distance any leaf moved form its starting location was 3.4 metres over six months, and about 90% of the leaves of the five species tested remained within 0.3 m of where they had been placed (Table 3.3). This accords with the findings of Spicer (1981), Ferguson (1985) and France (1995), who indicate that leaf redistribution occurs only over small distances, in the order of 0.5 m or less, once leaves fall to the ground. There was some expectation that the lateral overland transport of leaves in open forest and down the various slopes would have been greater than what was actually observed. There were no statistically significant differences in mean leaf transport distance between the two forest types; hence it can be concluded that the 'openness' of the WSF had no impact upon leaf transport distance. The hypothesis that leaf transport would be greater in the WSF versus the CTRF is thus untenable.

There was increased leaf transport down the medium slopes in the CTRF, but only where the slopes had no ground vegetation cover. The limited distances involved however indicates that the assertions made by Sedell *et al.* (1973) and Fisher and Likens (1973), of a strong positive relationship between slope and overland transport, must be questioned where ground vegetation is dense. Nevertheless, the effect of slope on leaf transport distance was small (Table 3.3), where the maximal mean distances between sites are in the order of tens of centimetres under the circumstances tested here. These results indicate that for the sides of steep vegetated valleys, overland transport is insignificant.

The effect of the density of the ground vegetation was significant, with the two way ANOVA and the regression model both indicating a statistically significant effect (Table 3.6). This result is largely in accordance with Ferguson (1985) who suggested that as ground vegetation became thicker, the likelihood of travel declined because there were more obstructions upon which leaves became captured. Thick ground vegetation would also have the effect of creating a wider boundary layer of still air above the leaves, and therefore further decrease the extent and distance of travel.

The small scale of movement in both the open vegetation of the WSF and in the closed vegetation of the CTRF also suggests that the transfer of leaf material through wind assisted lateral transfer is very low in these two forest types. It is possible that the high humidity and rainfall of both forest types played a role here. As both Spicer (1989) and Ferguson (1985) have noted, if the leaves become wetted or exist in conditions of high humidity they will tend to adhere to one another, creating a leaf mass that is resistant to transport due to its weight. This phenomenon was observed when the leaves were being removed for analysis; the leaves adhered quite strongly to each other and to other components of the forest floor litter.

The two way ANOVA with 95% confidence intervals for species (Table 3.4) indicates that there are significant differences in mean transportation distances for *Lomatia fraseri* and for *Acacia melanoxylon*, and no significant differences between the other three species. This raises the theoretical possibility of differential sorting between these species, though the results of regression analysis suggest that this is not linked to leaf area. In practice the effect in the forest ecosystems examined would be small; once the leaves have fallen to the ground, the leaves of all five species simply do not to travel sufficiently far for differential sorting to have a pronounced effect. In order for differential sorting to play any role in determining the taxonomic make up of a fossil leaf

flora, the leaves must have moved large enough distances for differential sorting to have an affect in the first place. The only likely location where there may be an opportunity for differential sorting to play a role in biasing leaf litter composition is on the actual banks of a stream or lake. These are locations where transport distances to a moving water body (and hence potential site of deposition), are very short and may cause a slight enrichment in terms of leaf number of one species as opposed to another.

From a palaeobotanical point of view, the results of this study are of interest. They indicate that for these forest types, the overall level of overland transport of leaf material is quite small. This would seem to apply regardless of the slope of the land and the degree to which the vegetation is open or closed (as in the case of WSF versus CTRF). There is a high probability that dense ground level vegetation may retard lateral overland transport of leaves. The implication here is that leaves of one vegetation community tend not to merge or travel into another vegetation community once they have actually completed their fall from their parent tree. Any intrusion of leaves from one vegetation type into another (at least in the ones studied here) will therefore occur mostly during the initial leaf fall (i.e. due to wind drift; see Ferguson 1985). Hence, if the leaves of the dominant trees of the surrounding vegetation types do not fall to ground within the confines of the riparian vegetation, then their likelihood of entering the riparian zone by overland lateral transport is small.

It is plausible to suggest therefore that in many streams and waterways, the leaf litter being transported would be mostly derived from the riparian vegetation growing along their banks. Hence, waterways flowing through vegetation communities which are mainly sclerophyllous in nature, but which have bands of mesic riparian forest following the watercourses, would have little input from the surrounding sclerophyllous vegetation. The possibility exists that any fossil deposits resulting from such communities would

give the impression of the vegetation being far more mesic than what it actually was. A tree only needs to be several times its own height away from a watercourse to be largely excluded from the riparian leaf litter (Ferguson 1985, 1995).

This effect may go a long way to explaining the relative paucity of *Eucalyptus* and *Acacia* leaves in the Australian plant fossil record. They may have been present, maybe even common, in the landscape from Oligocene/Miocene times onwards, as evidenced by the existence of their pollen records (Martin, 1994). However, if they grew on ridges and areas of land not immediately adjacent to the local watercourses, then macrofossils would be rare. If their leaves lack the power to disperse overland (as seems likely), they would be largely excluded from the macrofossil record.

3.5 Conclusions

The main conclusions that can be drawn from this chapter are firstly that leaves do not travel substantial distances once they have fallen to the ground. Secondly, the effects of phenomena such as the slope of the land and the density of the ground vegetation only have a limited impact on the distance leaves move once they have fallen to the ground after the initial abscission event. Thirdly, the potential exists for the selective overland transport of leaves from different plant taxa, but only in situations where overland transfer may be large such as the open grassy fields mentioned in Ferguson (1985). Fourthly, given that leaves don't travel far once they have fallen to the ground, plant taxa growing away from sites of water-born transport have little chance of entering a water body. Therefore, they have little chance of being carried to a site of deposition or preservation, except for those times when leaves are blown large distances in extreme weather events. Fifthly, the heterogeneity of the source vegetation is likely to be preserved in any *in situ* deposits of fossil forest floor litter, and sampling strategies need to account for this.

Figure 3.1 The locations of the twenty sites where leaves were positioned for the overland transport experiment. Note: Where a location is labelled RF(number) this corresponds to Rainforest site one, two, three etc, where a location is labelled Euc(number) this corresponds to Wet Sclerophyll Forest site one, two, three etc and where a location is labelled S(number) this corresponds to 'Slope' site one, two, three etc. See Table 3.2 for further details.

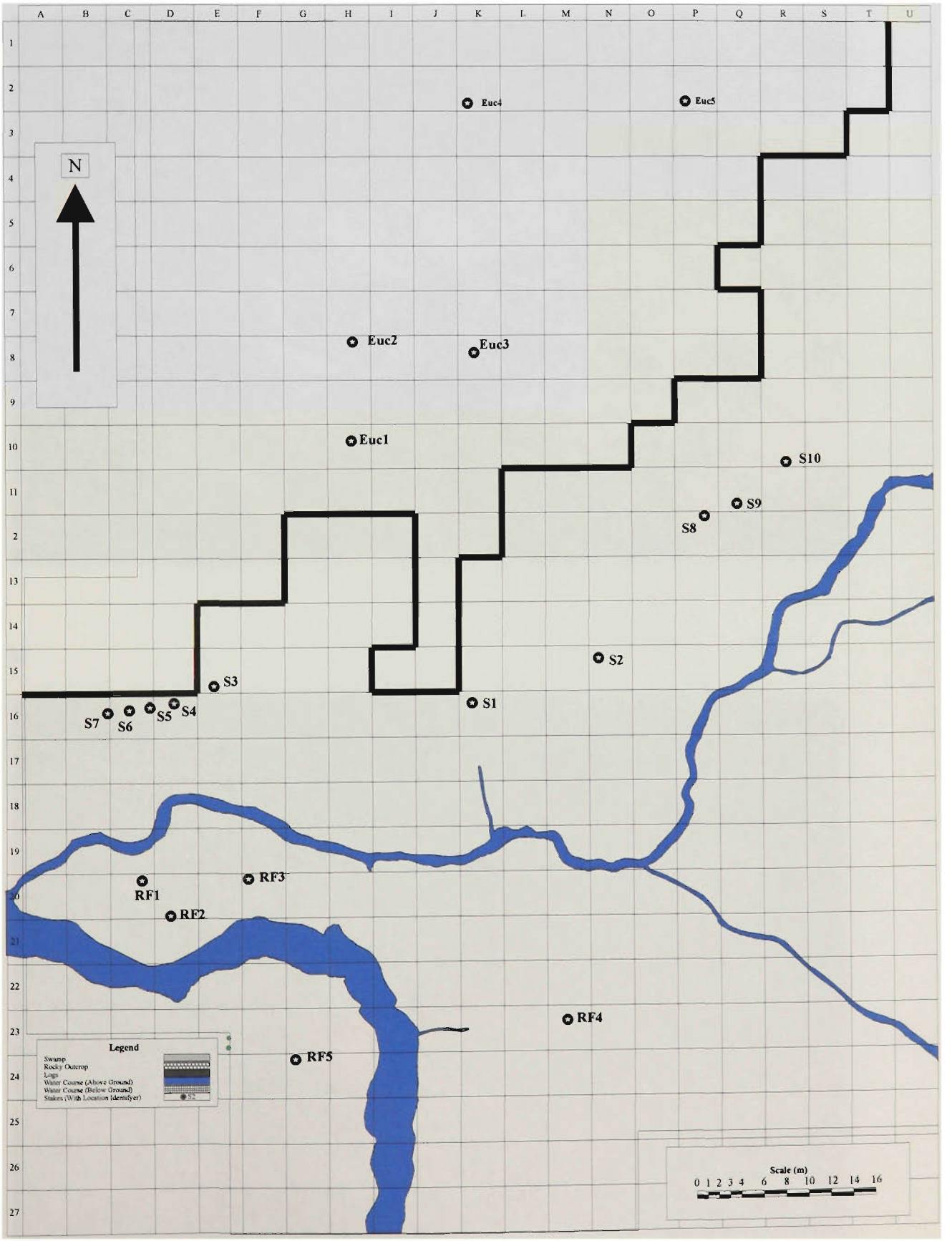


Figure 3.2 The forest floor litter in the wet sclerophyll forest (a) was mostly composed of a dense mat of litter, dominated equally by bark leaves and twigs. Leaves and twigs dominated the forest floor litter in the cool temperate rainforest (b). Bark was virtually absent. The slopes of much of the valley were covered by a thick mantle of ground fern *Blechnum wattsii* (c).

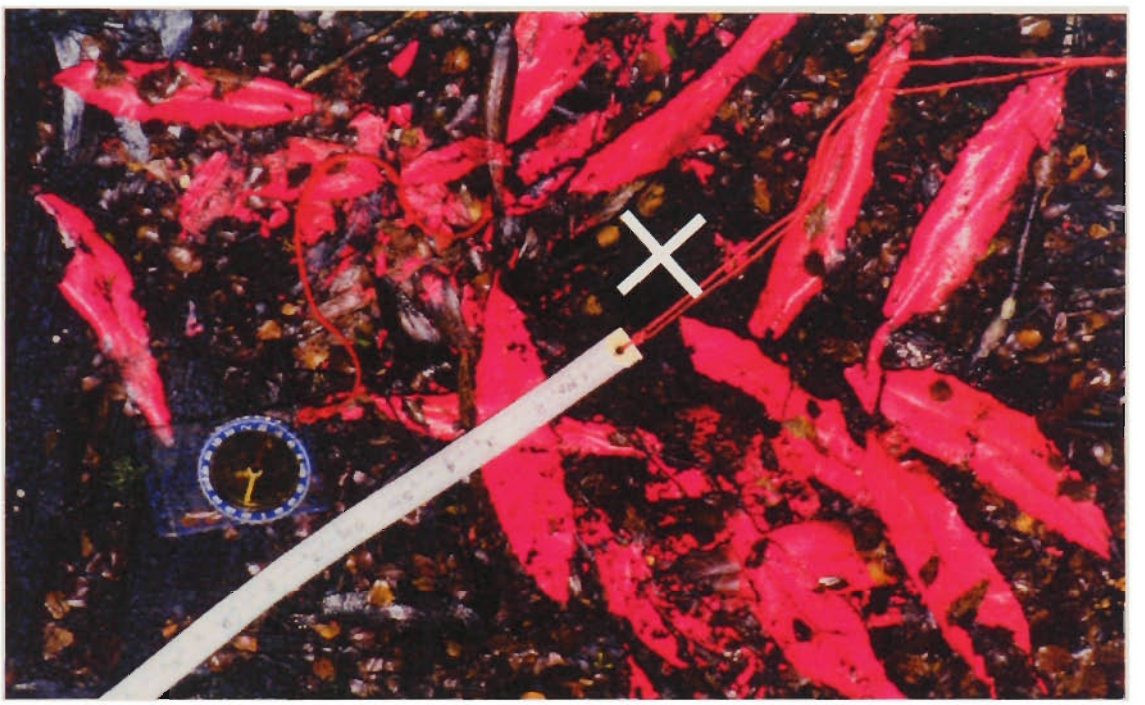
a

b

c

Figure 3.3 The recovery of the marked leaves was accomplished by individually measuring the distance each leaf had moved from its starting point. The location of the starting point is indicated by a white 'X'. Figure a (top) and b (bottom) shows the leaves *in situ* prior to removal and data collection.

a



b

Chapter 4

Transport of leaf litter in upland streams

4.1 Introduction

The studies mentioned in section 1.5.3, found that long distance riverine transport was unusual. They observed that most material was of local origin and had travelled less than 1.5 km from the site of abscission. Even in the mountainous landscape of Trinity Lake in California, most plant material in the sediment load was of local origin. The only plant part transported some distance was a coniferous cone bract from an upstream forest 1.5 km away (Spicer & Wolfe, 1987). The potential distortion caused by this specimen was small when compared with the vast number of locally derived plant parts that would dilute out its impact. In Australia there have been few studies (e.g. Greenwood, 1992; Hill & Gibson, 1986) concerning the transportation distances of the leaves of native species, and data are urgently required to quantify these distances.

In this study, the following hypotheses were tested:

1. Leaves do not travel long distances in high order streams.
2. That leaves from plant taxa in different forest types would be transported different distances downstream.

3. Differential transport of leaves between species is related to leaf density; heavy leaves will travel smaller distances downstream than light papery leaves
4. Differential transport of leaves between species is related to size; smaller leaves will travel longer distances downstream than large leaves.

Temperate rainforest in south eastern Australia typically occurs as riparian stands, usually dominated by myrtle beech, *Nothofagus cunninghamii* (Conn, 1993). The surrounding areas are typically dominated by tall open forest dominated by one or more species of *Eucalyptus*, although individuals of the common species of both forest types may be found throughout the riparian and non-riparian areas. The leaves of the main woody taxa in these forests vary from chartaceous (e.g. some rainforest species) to markedly sclerophyllous (e.g. *Eucalyptus* spp.), offering marked differences in leaf anatomy by which to assess the influences of leaf anatomy on transport behaviour. In particular, it was of interest whether the transport behaviour of woody rainforest taxa and woody sclerophyllous taxa differed and whether flow regime and leaf morphology played a significant role in determining leaf flotation, transport and retention. To this end, laboratory experiments were conducted to compare the flotation behaviour of five species of leaves. These experiments were complemented with field observations, using marked leaves, to quantify the distances travelled downstream by the various leaf types.

4.2 Methods

Field site

Field experiments were undertaken at Cumberland Creek, in the Central Highlands of Victoria, south eastern Australia (Section 2.2, Figure 2.1). Cumberland Creek is a first order perennial stream, with a typical width of 1.2 to 1.8 m, and a

maximum depth up to 0.8 m deep under average flow conditions (Figure 2.2). The stream bed consists of coarse sand with occasional pebbles and larger rocks. There are also many large submerged logs and smaller branches and twigs embedded in the stream channel which weaves in a complex way through the granitic substrata and deep, friable mountain loams.

4.2.1 Laboratory experiments on leaf flotation

Leaves from five tree species were used in the laboratory experiments: two CTRF taxa (*Nothofagus cunninghamii* and *Atherosperma moschatum*), two sclerophyllous taxa (*Acacia melanoxylon*, and *Eucalyptus regnans*) and one taxon from the ecotone between the two forest types (*Lomatia fraseri*). Table 4.1 shows the morphological characteristics of the leaves of the different tree species.

Table 4.1. Leaf characteristics of the six tree species used in this study. For the purposes of this work, sclerophyllous leaves are defined as having a thick, leathery texture (due to the presence of abundant thickened cells and thick leaf cuticle), whereas the non-sclerophyllous leaves of the rainforest species have a papery texture. All leaf weights are measured in grams per square metre.

Species	Leaf class size	Average leaf Area (cm^2)	Leaf texture	Margin type	Average Weight (gm^{-2})
Nothofagus cunninghamii	Nanophyll	1.3	Papery	Toothed	101
Atherosperma moschatum	Microphyll	10.8	Papery	Toothed to rarely entire	94
Lomatia fraseri	Notophyll / Macrophyll	36.2	Intermediate	Toothed	121
Eucalyptus regnans	Notophyll	17.2	Sclerophyll	Entire	243
Acacia melanoxylon	Microphyll	8.4	Sclerophyll	Entire	183

Flotation times of leaves were determined in twelve 90 L aquaria, kept at a constant 10°C. The dimensions of the tanks were 60 cm x 30 cm x 45 cm (length x width x height). All species were found locally in or near the field site.

Three flow regimes were used to examine the effect of turbulence on leaf flotation: i) a high flow rate-regime, with an aquarium turnover time of 4 min and surface flow rate of ~ 25 cm s^{-1}; ii) a low flow-rate regime, with a turnover time of 11 min and surface flow rate ~ 5 cm s^{-1}; and iii) still water. Commercially available aquarium pumps were used to circulate the water and were run continuously for the duration of the experiment. Each aquarium contained either 100 brown or 100 green leaves of each species. The green leaves were freshly picked the day before they were used. The brown leaves consisted of recently abscised leaf litter that was air dried at 20°C and 45 - 55 % relative humidity for two weeks before deployment in the tanks. All leaves were placed carefully onto the surface water of each tank at the commencement of each experiment to avoid clumping and leaves sticking to the sides of the tank. The leaves of all species circulated freely in a circular motion within the tank, without clumping or adhering to the sides.

The number of leaves that had sunk in the tanks was recorded each day for the first seven days, then at 5 and 10 day intervals until day 110. This counting strategy was used after a trial experiment indicated that leaves tended to either sink in the first week of the experiment or remain buoyant over a period of months.

Statistical analysis

The mean time before sinking (MTBS) was determined using the statistical software, Minitab Version 11 (Minitab for Windows, Release 11), to enable a comparison of the sinking times for each leaf population.

4.2.2 Field experiments on leaf transport

A gill net (mesh size: 4 mm) was deployed across Cumberland Creek and this was set as the collection point for any leaves washed down stream. Marker stakes were placed upstream of this point at intervals of 1, 2, 5, 10, 20, 50, 100 and 200 m. Twenty green and 20 brown leaves of each species were released at each marker stake, giving a total release for each species of 160 leaves. Each leaf was given a mark that corresponded to each one of the distances. The marks were made with small dots of Liquid Paper™ (a water-insoluble typing and correction fluid, Gillette Australia Pty. Ltd) before being dropped gently into the centre of the stream. The time taken by each leaf and number of leaves that reached the net were recorded until all the leaves for either that distance had been accounted for, or the onset of twilight ended each day's observations. Only one release for each species was completed for each distance. Brown leaves were released in a dry state, as this is the typical condition when washed into the stream by summer storms. These experiments were conducted in July-August 1999 and lasted six hours each. Experimental days were chosen to reproduce as much as possible the same conditions, with the stream flow ~ 1.5 $m^3 s^{-1}$, and stream velocity (at the gill net) between 0.5 and 0.7 $m s^{-1}$ and the day length was ~ 8 hrs.

Statistical analysis

The mean time before sinking (MTBS) was determined using the statistical software, Minitab Version 11 (Minitab for Windows, Release 11), to enable a comparison of the sinking times for each leaf population. The sedimentation curves for each leaf population were then assessed for optimal curve fitting using Minitab (Minitab for Windows, Release 12.23), SPLUS (SPLUS 2000 Professional Release 1) and SPSS (SPSS for Windows Release 10.0.5). A log normal distribution best described the data.

4.3 Results: Laboratory experiments on leaf flotation

The leaf flotation experiments clearly indicated that there were differences in flotation times among leaves of the five plant species (Table 4.2; Figure 4.1). When the sinking times of green leaves from all five tree species are examined, green leaves from the rainforest species, *Nothofagus cunninghamii* and *Atherosperma moschatum*, floated

Table 4.2. Flotation times determined under laboratory conditions for combinations of each of the six tree species, leaf type, and flow-rate combinations. Leaf colour (green or brown) refers to whether leaves were used fresh (green) or from dead material (brown). MTBS (Mean Time Before Sinking) is shown in days.

Group	Species	Flow rate	Leaf colour	MTBS (days)
1	*Nothofagus cunninghamii*	Still Water	Green	132
2	*Nothofagus cunninghamii*	Low	Green	67
3	*Nothofagus cunninghamii*	High	Green	10
4	*Nothofagus cunninghamii*	Still Water	Brown	207
5	*Nothofagus cunninghamii*	Low	Brown	18
6	*Nothofagus cunninghamii*	High	Brown	8
13	*Atherosperma moschatum*	Still Water	Green	88
14	*Atherosperma moschatum*	Low	Green	97
15	*Atherosperma moschatum*	High	Green	129
16	*Atherosperma moschatum*	Still Water	Brown	70
17	*Atherosperma moschatum*	Low	Brown	7
18	*Atherosperma moschatum*	High	Brown	4
7	*Lomatia fraseri*	Still Water	Green	64
8	*Lomatia fraseri*	Low	Green	22
9	*Lomatia fraseri*	High	Green	2
10	*Lomatia fraseri*	Still Water	Brown	13
11	*Lomatia fraseri*	Low	Brown	13
12	*Lomatia fraseri*	High	Brown	5
25	*Eucalyptus regnans*	Still Water	Green	29
26	*Eucalyptus regnans*	Low	Green	1
27	*Eucalyptus regnans*	High	Green	<1
28	*Eucalyptus regnans*	Still Water	Brown	137
29	*Eucalyptus regnans*	Low	Brown	2
30	*Eucalyptus regnans*	High	Brown	<1
19	*Acacia melanoxylon*	Still Water	Green	18
20	*Acacia melanoxylon*	Low	Green	1
21	*Acacia melanoxylon*	High	Green	1
22	*Acacia melanoxylon*	Still Water	Brown	4
23	*Acacia melanoxylon*	Low	Brown	2
24	*Acacia melanoxylon*	High	Brown	2

for the longest time, irrespective of flow regime. Green leaves from the two sclerophyll species, *Eucalyptus regnans* and *Acacia melanoxylon*, have markedly shorter floating times, with flow regime having a significant effect on flotation time with leaves from these species sinking most rapidly in the two moving-water regimes (Table 4.2; Figure. 4.1). Thus, all 100 of the green *Eucalyptus regnans* leaves in the high-flow rate treatment sank within 24 hours, as did all the green *Acacia melanoxylon* leaves. The fifth species, *Lomatia fraseri*, had a floating behaviour that was intermediate between the two groups.

The analysis of the laboratory experiments in detail confirms that flotation times were significantly different across tree species, leaf colour and degree of turbulence. The two rainforest species, *Nothofagus cunninghamii* and *Atherosperma moschatum,* (represented by Groups 1 - 6 and 13 - 18 of Table 4.2), are clustered to the right and centre of Figure. 4.2, where many of their Bonferroni confidence limits overlap. This overlap signifies that their flotation behaviour is not significantly different from each other. The Bonferroni confidence limits of the rainforest groups do not overlap with the confidence limits of leaves from the sclerophyll species, which cluster to the left of Figure 4.2. This statistically significant separation indicates that leaves from the rainforest species in general, had significantly different median log normal floating times compared to leaves from the sclerophyllous taxa.

When the rainforest species *Nothofagus cunninghamii* and *Atherosperma moschatum* were examined, it was evident that flow regime had an influence on flotation times of both brown and green leaves. For example, the MTBS values of *Nothofagus cunninghamii* green leaves (Groups 1 - 3) declined from 132 days for the still water treatment to 10 days for the high flow-rate treatment (Table 4.2). In Figure 4.2, there is a confidence limit overlap between Groups 1 and 2, but neither overlaps with Group 3. Group 3 was subject to turbulent conditions in the high flow treatment and both sides of

the leaf were wetted whereas this did not occur in the other two treatments. Therefore green *Nothofagus cunninghamii* leaves subject to high turbulence, sink rapidly. A different pattern is seen with brown leaves of *Nothofagus cunninghamii*, where the MTBS values of the moving-water treatments (Groups 4 and 5) are similar with overlapping confidence limits. There is no confidence limit overlap between moving water Groups 4 and 5 and the still water treatment (Group 6). This suggests that, for brown leaves of this species, the presence or absence of turbulence in the water column *per se* is more important than the intensity of the turbulence.

The MTBS values for *Atherosperma moschatum* green leaves (Groups 13, to 15, of Table 4.2 and Figure 4.2) were close and consistently high, varying between 88 and 129 days. The lack of statistical difference between these three groups indicates that green leaves from *Atherosperma moschatum* floated well, regardless of water turbulence (Figure 4.2). In contrast, differences in flow rate had a clear impact upon the MTBS values for brown leaves of this species (Groups 16, to 18 of Table 4.2 and Figure 4.2). As with *Nothofagus cunninghamii* brown leaves, the main differences were between the two moving-water treatments (Groups 17 and 18) versus still water (Group 16), a result indicating that a key determinant in floating times for *Atherosperma moschatum* brown leaves was the presence or absence of turbulence in the water column.

Quite different flotation patterns were found for sclerophyllous leaves. The MTBS values of the sclerophyll species, *Eucalyptus regnans*, and *Acacia melanoxylon*, indicate that leaves from the sclerophyllous species all had much shorter flotation times than leaves of rainforest taxa (Table 4.2); the MTBS values for leaves of the sclerophyllous tree taxa were generally shorter than for the rainforest taxa. Only two groups (Groups 25 and 28) floated for longer than 20 days, with the mean flotation times for the others being less than 10 days in 9 of the 12 cases shown in Table 4.2. In

comparison, seven of the 12 rainforest groups showed mean flotation times of > 60 days. Figure 4.2 shows that the sclerophyllous leaf groups (Groups 19 - 30) cluster towards the centre and left-hand side of the graph, in contrast to the grouping of the rainforest taxa (Groups 1 to 6 & 12 to 18). The extreme outlier value for Group 28 was so variable, with such a large Bonferroni confidence limit that it was left out of the analysis.

The three remaining sclerophyll forest groups (Groups 21, 27, & 30) could not be analysed statistically, as their leaves sank in less than one day and in many cases in less than one hour. These three groups therefore had insufficient data points for further analysis (see also Table 4.2). In any case, further analysis is barely needed, as the effect of the high flow treatment is self-evident (Figure 4.1).

The fifth species, *Lomatia fraseri*, is a plant often found growing near or in the ecotone of the rainforest, where the sclerophyll forest and rainforest overlap, or in shaded gullies with permanent water. Based on the very clear distinction between flotation times of leaves from the two forest types, it would be expected that this species would have MTBS values that were midway between those of the rainforest and the sclerophyll forest taxa. This prediction was largely supported, in that all six of the *Lomatia* groups (Groups 7 - 12) occur in the mid-region of Figure 4.2. As with a number of other taxa, however, leaves in still water floated the longest, while those in flowing conditions sank more quickly, especially if the water was highly turbulent.

Field experiments on leaf transport

From the analysis of the results of the sinking behaviours of the green and brown leaves of the three tree species under laboratory conditions (Figure 4.1 & Table 4.2), predictions can be made about which leaves are likely to travel significant distances under field conditions. Those species most likely to travel significant distances are (in

order); *Nothofagus cunninghamii* brown and green leaves followed by *Atherosperma moschatum* green leaves and brown leaves, followed by the sclerophyllous taxa.

Table 4.3. Percentage recovery of leaves after six hours at various distances under field conditions. n = 20 for each taxon and each leaf colour for each distance travelled.

		Percentage recovery of leaves						
		Distance travelled (m)						
Species	**Leaf colour**	**1**	**2**	**5**	**10**	**20**	**50**	**100**
Nothofagus cunninghamii	Green	100	100	100	100	25	10	0
	Brown	100	100	100	85	55	20	0
Atherosperma moschatum	Green	100	100	100	100	35	0	0
	Brown	100	100	100	75	60	10	0
Lomatia fraseri	Green	100	100	100	75	15	0	0
	Brown	100	100	100	100	40	0	0
Eucalyptus regnans	Green	100	100	100	75	15	0	0
	Brown	100	100	100	100	40	0	0
Acacia melanoxylon	Green	100	100	90	45	0	0	0
	Brown	100	100	100	70	40	0	0

The *in situ* stream transport experiments showed differences in transport distance among the leaves of the plant species that largely matched these predictions (Table 4.3). After six hours, 20% of the *Nothofagus cunninghamii* brown leaves, 10% each of the *Nothofagus cunninghamii* green and *Atherosperma moschatum* brown leaves had travelled 50 m. Green leaves of *Acacia melanoxylon*, a sclerophyllous species with the shortest overall flotation times, were the first to be filtered out, and significant filtering (55% loss) became noticeable over distances as short as 5 m. The next species and leaf colour combination to be filtered out was *Acacia melanoxylon* brown leaves, followed by *Lomatia fraseri* green and brown leaves, and *Eucalyptus regnans* green and brown leaves. Collectively, these three latter species all began to be filtered out over distances as short as 10 m and none travelled more than 20 m in the six hour duration of the field experiments (Table 4.3). This result supports the contention that leaves of species that do not float well do not travel significant distances downstream.

4.4 Discussion

A number of observations can be drawn from the results presented in this chapter. First, Cumberland Creek was highly retentive of particulate organic detritus, and leaves of no taxon travelled downstream more than 100 m in six hours. Presumably this was a consequence of the sinuous nature of the stream, the large number of obstacles (often large woody debris) in the stream channel, and the relatively low discharge rate. It is well known that discharge rate plays a major role in determining the retentiveness of stream ecosystems and that leaf retention in headwater streams decreases dramatically as discharge increases (e.g. Speaker *et al.*, 1984; Cuffney & Wallace 1989; Snaddon *et al.*, 1992). The effects of discharge on leaf retention were not investigated in this study. Nevertheless, some indication of the importance of discharge can be gauged by the influence of turnover time and water turbulence in the laboratory experiments on leaf sinking times. These studies indicated that leaf sinking rates could increase by an order of magnitude if the flow rate were increased from still water to one of 25 cm/s. Note that the stream velocity at the gill net of Cumberland Creek during the field experiments was between 50 and 70 cm/s.

Second, the downstream transport of leaf material was highly selective, due to the very poor transport of leaves of sclerophyllous taxa, such as *Eucalyptus* and *Acacia*, and the considerably greater transport of leaves from the rainforest taxa, *Nothofagus* and *Atherosperma*. The primary difference between these species groupings is leaf morphology and chemistry; namely, the markedly leathery texture and thickened cuticles and cell walls (and concomitant richness in phenolic compounds) of the sclerophylls versus the papery (chartaceous) character of the leaves of the rainforest species.

This result has clear limnological and palaeobotanical implications for the selective export of leaf material from forested catchments. A central plank of the River Continuum Concept for streams draining forested catchments is the downstream transport and ongoing processing of particulate organic matter into progressively finer particles (Vannote *et al.*, 1980). The results of this study indicate that the export of leaves may occur to a greater extent from catchments vegetated with rainforest (or other riparian vegetation with chartaceous leaves) than with sclerophyllous vegetation. To date, neither of these vegetation types has featured prominently in studies of leaf transport and organic matter budgets (e.g., see papers following Webster & Meyer, 1997). Sclerophyllous shrub lands and forests surrounding non-sclerophyllous riparian stands are a feature of Mediterranean type climates in South Africa (e.g. Stewart & Davies, 1990; Prochazka *et al.*, 1991) and elsewhere. Furthermore, species of both *Eucalyptus* and *Acacia* are common plantation species and even woody weeds in California, Portugal, sub-Saharan Africa, India, parts of South America and some Pacific island nations (Savill & Evans, 1986; Evans, 1992). The present study therefore informs on the relative transport potential of the native and introduced sclerophyllous species, and riparian chartaceous species, to contribute to the organic budgets of streams in these areas.

Clearly, leaves that have poor powers of dispersal have a high probability of becoming entrained, whereas leaves with good dispersal ability can travel downstream (Spicer, 1981, 1989; Ferguson, 1985). This may result in allochthonous leaf assemblages found in stream bed sediments reflecting differential transport in response to hydrodynamic sorting, rather than the ecological patterns that make up the local vegetation (Spicer, 1989; Greenwood, 1991). Importantly in an Australian setting, the transport of the dominant sclerophyllous canopy-tree taxon – *Eucalyptus* – and the

dominant cool temperate rainforest canopy-tree taxon – *Nothofagus* – are significantly different. Hill and Gibson (1986) suggested that the relative paucity of *Eucalyptus* leaves in the fossil record might be linked to their poor dispersive ability. Such a discrepancy in dispersive ability could be expressed in the leaf fossil record of the different taxa, although data on the behaviour of additional species of *Eucalyptus* and *Nothofagus* are required before generalisations can be made.

Third, the pattern of downstream transport observed *in situ* could be predicted quite accurately on the basis of median leaf flotation time, as quantified in laboratory aquaria. In addition to the very clear distinction between leaves from rainforest taxa and sclerophyll taxa, there were a number of other relationships apparent between gross leaf characteristics and leaf buoyancy and transport distances in the field. There was evidence for the smallest leaves to be transported most easily and the largest leaves the least easily - *Nothofagus cunninghamii* and *Atherosperma moschatum* are nanophyllous and microphyllous respectively, whereas both *Acacia melanoxylon* and *Eucalyptus regnans* are notophyllous and *Lomatia fraseri* is notophyllous-macrophyllous. Dance (1981) and Greenwood (1992) also indicated that small leaves travel further than large ones.

Prochazka *et al.* (1991) emphasised that flexibility was a significant factor in differential retention times between *Cunonia capensis* L. and *Brabejum stellatifolium* L., both of which are Afromontane elements of the fynbos biome, a sclerophyllous vegetation type. The leaves of *Cunonia capensis* are far more flexible than leaves of *Brabejum stellatifolium*, and as suggested by Young *et al.* (1978), flexible leaves become easily entwined and wrapped abound twigs, sticks and other obstacles. This effect is mirrored in this study, where the most flexible leaf types (green leaves of *Eucalyptus regnans* and *Acacia melanoxylon*) became entrained first, usually by becoming wrapped

around twigs and branches embedded in the sides of the channel. Moreover, the less flexible brown leaves travelled a greater distance down the stream than did the more pliant green leaves, regardless of plant taxon (Table 4.3). In contrast, whether the leaf margins were entire or toothed was not a good predictor of *in situ* transport, even though it might have been anticipated *a priori* that toothed leaves would be caught more readily on surfaces of in-stream obstacles.

Spicer (1981) clearly linked flotation time to the degree of turbulence of the surface water, and found that thin papery leaves such as *Alnus glutinosa* sank readily. This study found the opposite pattern: the most papery leaves were green leaves of *Atherosperma moschatum*, and these tended to float well regardless of the degree of turbulence in the laboratory experiments. A precautionary note is needed here though, as all the taxa in our study were evergreen, whereas a number of those in Spicer's studies were deciduous. Spicer (1981) noted that because of their thicker cuticles leaves from evergreen species are more resistant to water uptake and thus float longer than those from deciduous taxa. The clear difference between rainforest and sclerophyll taxa in both relative buoyancy and observed transport also could be a function largely of different cuticle thickness and composition, and thus of leaf wettability.

Fourth, these results are in broad agreement with the few other published studies that have examined relative buoyancy and transport of leaves in Australian fresh waters. For example, Hill and Gibson (1986), studying leaf flotation in Lake Dobson (Tasmania), reported that *Eucalyptus coccifera* leaves sank very rapidly and were poorly dispersed. Carpenter and Horwitz (1988) reported that *Atherosperma moschatum* leaves readily floated in Tomalah Creek, a Tasmanian stream broadly similar to Cumberland Creek, and seemed to break down more quickly than leaves of *Nothofagus cunninghamii*. Leaf material found drifting in Tomalah Creek was overwhelmingly *Nothofagus cunninghamii*

(62 % of all whole leaves found), with a lesser representation of *Atherosperma moschatum*, and the virtual absence of *Eucalyptus obliqua* leaves. This pattern is consistent with our finding that *Nothofagus cunninghamii* leaves floated well under all but the most turbulent conditions, while *Eucalyptus regnans* sank rapidly. The organic-matter retentiveness of Cumberland Creek is also consistent with the finding that the nearby Keppel Creek accumulates organic matter at a rate of ~2.5 kg AFDW m^{-2} y^{-1} (Treadwell *et al.*, 1997).

4.5 Conclusions

The main conclusions that can be drawn from this work are firstly that most leaves travel limited distances in high order streams. The observation that no leaves travelled more than 100 m in six hours would suggest that not only is Cumberland Creek highly retentive, but that under normal flow conditions most plant fossil deposits resulting from such a stream would reflect local riparian floras only. There would be little input of intact leaf material from plant communities substantially up-stream, as they would become rapidly entrained. Secondly downstream transport is selective. The light papery leaves of *Atherosperma moschatum* float for longer periods of time than heavy sclerophyllous leaves creating a bias against the transport of such taxa. Thirdly downstream transport may also be size related, with small leaves such as *Nothofagus cunninghamii* being able to flow between obstacles that larger leaves such as those of *Lomatia fraseri* would become entangled in. Fourthly flexible leaves such as those of *Eucalyptus regnans* become entangled upon streambed obstacles like twigs and branches more easily than rigid leaves, which flowed around them.

NB: This chapter has been published as Steart, D.C., Boon, P.I., Greenwood, D.R. & Diamond, N.T. (2002): Transport of leaf litter in upland streams of *Eucalyptus* and *Nothofagus* forests in south-eastern Australia. – Archiv für Hydrobiologie. **156**: 43-61. See end papers.

Figure 4.1 Flotation behaviour of leaves of *Acacia melanoxylon*, *Atherosperma moschatum*, *Eucalyptus regnans*, *Lomatia fraseri* and *Nothofagus cunninghamii* under laboratory conditions. All six flow-rate versus leaf colour type combinations are shown. **Key:** *Nothofagus cunninghamii* ◇; *Atherosperma moschatum* △; *Lomatia fraseri* □; *Eucalyptus regnans* ○; *Acacia melanoxylon* ✕.

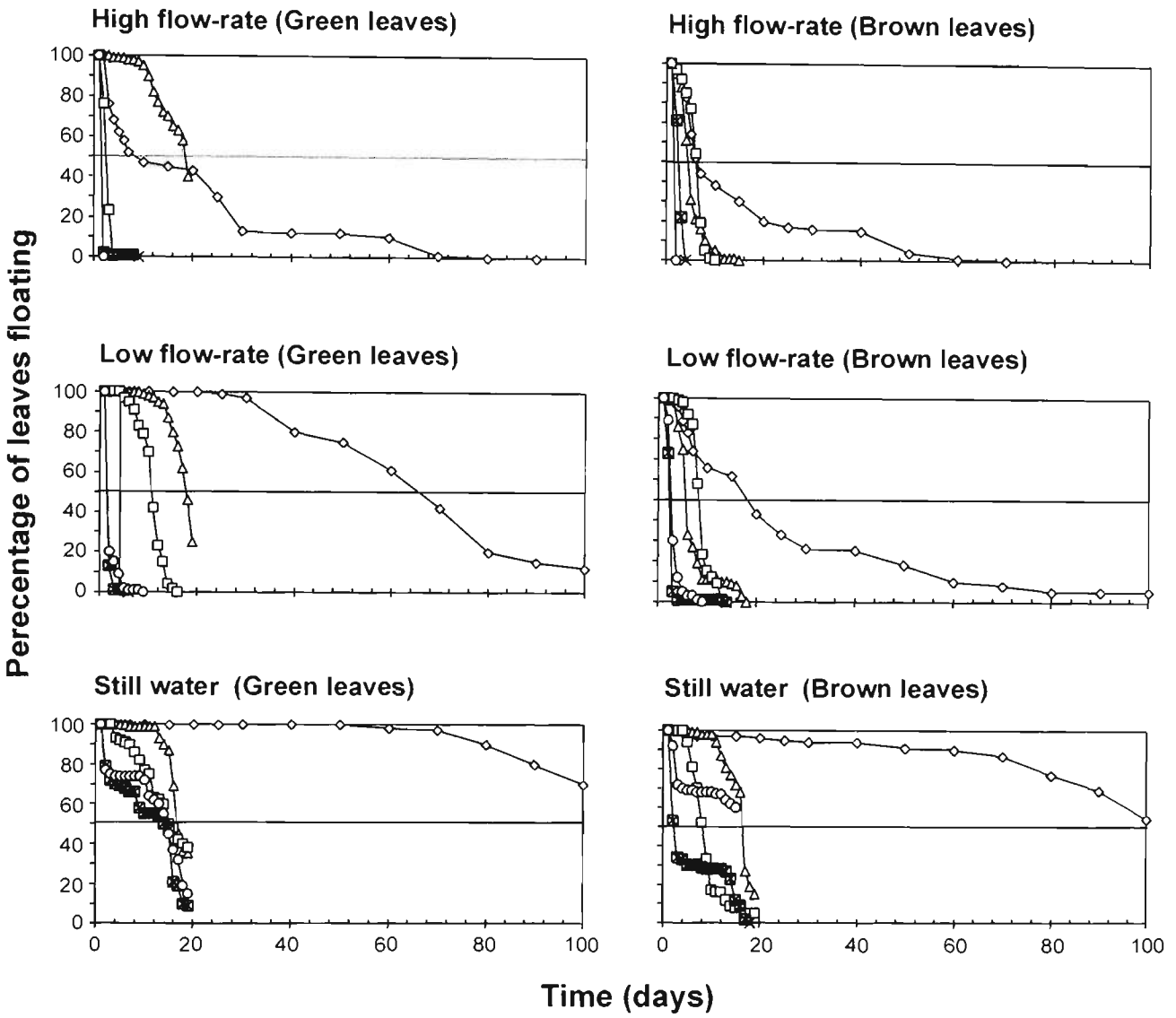
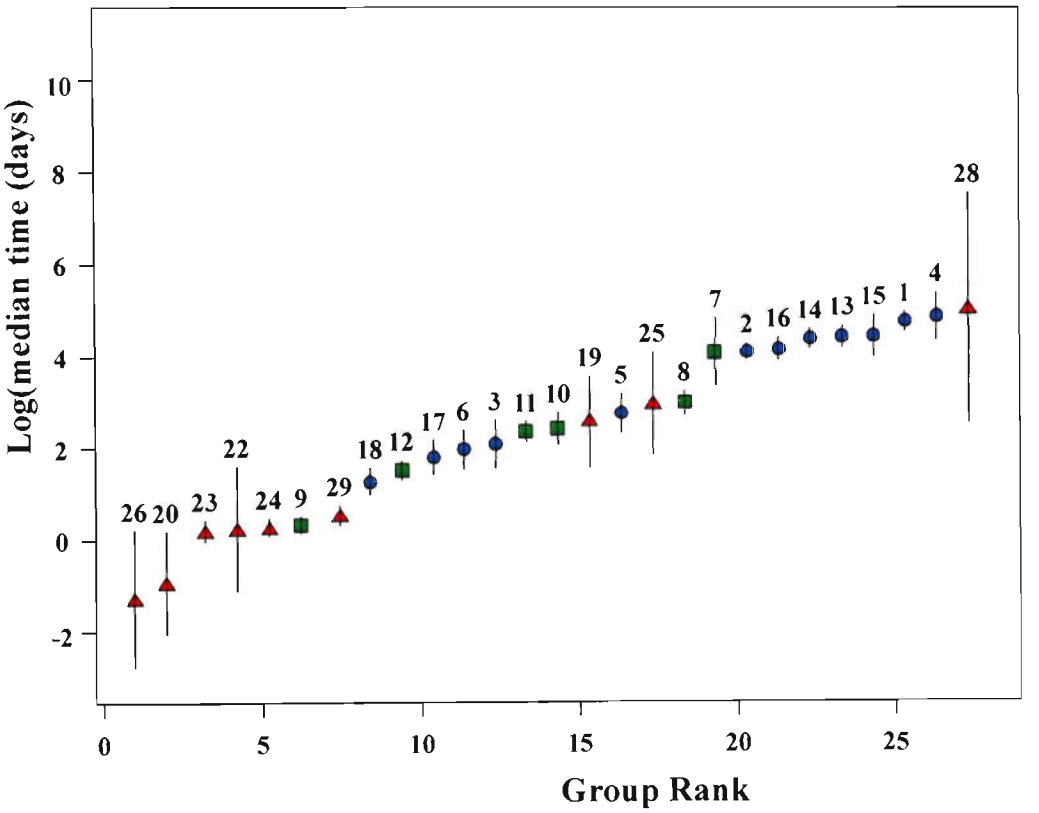
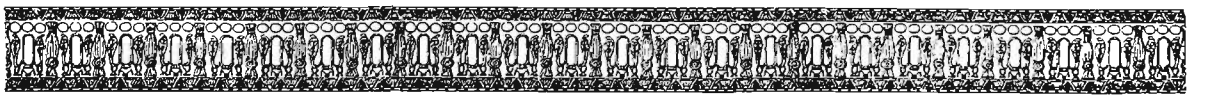


Figure 4.2 Diagrammatic summary of flotation behaviour of leaves under laboratory conditions. The values shown are the median times for leaves to remain floating; bars are joint 95% Bonferroni confidence intervals for the median parameters. Groups 21, 27, 30 and 33 have not been included (too few data points for reliable estimation). The coding of group numbers is the same as in Table 4.2. Key: Rainforest taxa ●; sclerophyllous taxa ▲; intermediate taxa ■.



Chapter 5

The Decay of Leaves



5.1 Introduction

Of particular interest to the palaeobotanist is whether leaves from different plant taxa decay and fragment at the same rate and whether they do so predictably across different depositional settings (Spicer, 1981; Greenwood, 1991, 1992). For the purpose of this chapter, depositional setting is defined as that place where a leaf comes to rest after abscission. The four places where leaves are likely to be found or deposited after abscission, are; autochthonous forest floor litter, autochthonous burial in forest floor sediments, parautochthonous leaf accumulations on stream beds and allochthonous burial in riparian or lacustrine sediments (Section 1.6; Ferguson, 1985; Spicer, 1989, 1991; Greenwood, 1991).

Few taphonomic or ecological studies have examined the effect of different depositional settings upon leaf decay either in terms of weight loss or loss of leaf blade area, in spite of its likely ecological and taphonomic significance. This chapter examines differential decay rates between species under the four depositional settings listed above. It examines some of the leaf physiochemical factors (such as initial nutrient content, lignin content and cuticle thickness) and a number of physical factors (such as environmental moisture regime, temperature and oxygen availability) that may determine these differences in decay rates (Williams & Gray, 1974). One of the factors thought to aid in the preservation of plant materials is their burial in anaerobic or reducing

sediments where the decay process is slowed down or stopped by the exclusion of oxygen (Spicer, 1991). The Cumberland Creek field site had such deposits, all of which emitted hydrogen sulfide (H_2S) when disturbed. The presence of H_2S in these sediments indicates that they are reducing soils with a low Eh (Bohn, 1971). The leaves placed on the surface of the forest soils and the stream channel should have no restrictions to the oxygen supply needed by aerobic decay organisms. The buried leaves thus should have lower decay rates due to restricted oxygen supplies and the absence of the aerobic saprophytic soil macro- and microfauna.

The soil biology and limnological literature has recognised the phenomenon of differential decay for some time, where many researchers have compared the comparative break down rates of leaf material, often observing significant differences among species (e.g. Heath *et al.*, 1966; Edwards, 1977; Blackburn & Petr, 1979; Hayes, 1979; Campbell & Fuchshuber, 1995). There are few experiments, however, which test the decay rates of different species under different depositional settings. If some species decay more rapidly than others under fossil forming conditions, they may be under represented in the fossil record (Spicer, 1981; Greenwood, 1991).

Two of the most important predictors of leaf decay rates are the lignin and cellulose content of the leaf material and the initial lignin to nitrogen ratio (Section 1.5.3; Berg & Matzner, 1997). It is thought that as the lignin content of plant material rises the quality and digestibility of the material declines in equal measure. A number of reports link high initial lignin and nitrogen ratios (L:Nr) and reduced decay rates for leaves (e.g. Melillo *et al.*, 1982; Gallardo & Merino, 1999; Moore *et al.*, 1999). The data in Table 5.1 supports this supposition. The current thinking is that for partly decomposed leaf litter, low molecular weight nitrogen compounds will react with lignin during decay, creating more refractory aromatic compounds (Berg, 2000). The higher the initial lignin and

nitrogen concentrations, the higher will be the eventual concentration of nitrogen recalcitrant forms (Fioretto *et al.*, 1998).

High initial nitrogen content can also enhance decay due to increased consumption by soil meso and macrofauna (Bernhard-Reversat, 1993). Plant materials high in nitrogen (and phosphorus) decay more rapidly than plant materials low in these nutrients (Woods & Raison, 1983; Gallardo & Merino, 1999). One of the reasons given for this is that the bacteria and fungi involved in the decay process can degrade cellulose and lignin more easily when there are sufficient supplies of these elements in the substrate being degraded. Many reports also indicate that nitrogen and phosphorus enrichment increases decay rates as well (Kaushik & Hynes, 1971; Howarth & Fisher, 1976; Elwood *et al.*, 1981; Meyer & Johnson, 1983; Vogt *et al.*, 1986; Royer & Minshall, 2001). The data in Table 5.1 display a selected list of published figures for leaf lignin and nitrogen content, including those of *Acacia melanoxylon* (34.9% & 26.8%, respectively). When compared with other species included in Table 5.1, *Acacia melanoxylon* leaves have a comparatively high lignin content and should thus decay slowly.

The widely used mathematical descriptor of decay rates for leaves, the single exponential model, has been used to compare the comparative break down rates of the five tree species mentioned above (Section 1.5.3, p. 31; Olsen, 1963). The world-wide use of exponential decay coefficient '*k*' throughout the ecological literature to compare leaf decay rates for various tree species justified its use in the current study. One of the minor aims of this study was to identify if leaf decay rates expressed as a *k* value can be matched with leaf area loss versus time. Should this be the case then the extensive ecological literature which uses the *k* constant as a measure of decay rate can be used to indicate which taxa are likely to decay quickly or slowly and correct for their occurrence

in reconstructions of palaeoecosystems. Examples of some literature based *k* values are included in Tables 1.4 and 5.1. The decay rates of *Nothofagus cunninghamii* and *Lomatia fraseri* were further investigated, in triplicate, with six sets of single variable mesocosms. These two species were chosen so as to compare two phylogenetically unrelated taxa to see if the leaf decay rates varied significantly with different environmental conditions. The laboratory mesocosm experiments were designed to test the effect of nutrient enrichment, temperature, and anaerobic conditions upon decay rate. The principal hypotheses behind the decay rate, leaf physiochemistry, and mesocosm experiments are therefore that:

1. The decay rates of leaves buried in anaerobic riparian and lacustrine sediments will be lower than those in aerobic conditions.
2. The decay rates of leaves placed in aerobic ever wet conditions (the surface of the stream channel) will be higher than those placed in aerobic occasionally dry conditions (the forest floor).
3. The leaves of the five tree species used in this study decay at different rates (see Table 4.1 for list).
4. The relative order of decay rates for the five tree species will be similar in all four depositional settings tested.
5. Leaves high in initial lignin should decay the slowest, while leaves low in lignin should decay rapidly (e.g. Hayes, 1979; Singh *et al.*, 1999; Wedderburn & Carter, 1999).
6. Leaves with a high lignin to nitrogen ratio will decay more slowly than leaves with a low lignin to nitrogen ratio (Berg & Matzner, 1997).

7. The differences in decay rates between these five species will be determined by the leaf physiochemistry of each leaf species.

8. Leaves with a high initial nitrogen concentration will decay more rapidly than those with low initial nitrogen concentration.

9. Leaves will decay more rapidly in comparatively warm conditions (15°C) as opposed to leaves in comparatively cold conditions (5°C).

10. Leaves in nutrient rich or aerobic conditions will decay more rapidly than leaves in nutrient poor or anaerobic conditions.

In order to study the comparative break down rates of *Acacia melanoxylon*, *Atherosperma moschatum*, *Eucalyptus regnans*, *Lomatia fraseri* and *Nothofagus cunninghamii* at the Cumberland Creek field site single species leaf bags were used. Single species leaf bags allowed for the easy comparison of fragmentation rates of individual leaf species without loss of leaf fragments, under constant conditions, without the difficulty of identifying and sorting leaf fragments by species (Section 1.5.3).

Table 5.1 A selected list of percentage lignin, lignin to nitrogen ratios and *k* values derived from the literature. Values marked with an asterix, '*' were calculated from data in the papers cited, an 'X' indicates that the values were not given nor could they be computed from the given data, while values marked with a '♦' were klason lignin to nitrogen ratios. An '-' sign indicates that the value was not given in the paper and an '⊗' indicates the publication was citing literature based values.

Species	Lignin (%)	L/N Ratio	*k* value	Source
Acacia melanoxylon	34.9	19.7	-0.34*	Wedderburn & Carter (1999)
Alnus glutinosa	19.8	8.1	-1.91*	Wedderburn & Carter (1999)
Quercus rubra	25.3	36.8	-0.36*	Wedderburn & Carter (1999)
Eucalyptus nitans	34.9	19.7	-0.42*	Wedderburn & Carter (1999)
Acacia melanoxylon	26.8⊗	11.5*	X	Bunn (1986)
Eucalyptus camaldulensis	15.1⊗	11.7*	X	Bunn (1986)
Eucalyptus maculata	24.0⊗	24.7*	X	Bunn (1986)
Eucalyptus ovata	21.8⊗	15.4*	X	Bunn (1986)
Prunus pensylvanica	19.3	16.1	-0.35	Melillo *et al.* (1982)
Fagus grandifolia	24.1	26.8	-0.08	Melillo *et al.* (1982)
Acer saccharum	10.1	16.8	-0.25	Melillo *et al.* (1982)
Fraxinus americana	12.2	13.6	-0.47	Melillo *et al.* (1982)
Acer rubrum	10.1	14.4	-0.42	Melillo *et al.* (1982)
Betula papyrifera	14.5	16.1	-0.34	Melillo *et al.* (1982)
Eucalyptus spp.	22-25	34-37	-0.61	Bernhard-Reversat (1993)
Acacia auriculiformis	34	22	-0.96	Bernhard-Reversat (1993)
Acacia mangium	31	19	-1.20	Bernhard-Reversat (1993)
Azadirachta indica	18.0±(0.26)	18.0±(0.29)	-1.31*	Singh *et al.* (1999)
Dalbergia sisso	23.0±(0.26)	19.9±(0.10)	-1.14*	Singh *et al.* (1999)
Pongamia pinnata	26.0±(0.30)	21.5±(0.25)	-0.89*	Singh *et al.* (1999)
Shorea robusta	30.0±(0.38)	41.7±(0.5)	-0.69*	Singh *et al.* (1999)
Halimium halimifolium	8.9	27	-0.13	Gallardo & Merino (1999)
Cistus libanotis	8.8	21.5	-0.18	Gallardo & Merino (1999)
Quercus suber	18.1	22.3	-0.13	Gallardo & Merino (1999)
Quercus canariensis	15.6	22.3	-0.24	Gallardo & Merino (1999)
Quercus pyrenaica	14.3	15.4	-0.31	Gallardo & Merino (1999)
Fraxinus angustifolia	10.5	11.3	-0.56	Gallardo & Merino (1999)
Populus tremuloides	-	21.4♦	-0.19*	Moore *et al.* (1999)
Fagus grandifolia	-	39.4♦	-0.11*	Moore *et al.* (1999)
Pteridium aquilinum	-	37.4♦	-0.15*	Moore *et al.* (1999)
Picea mariana	-	38.7♦	-0.19*	Moore *et al.* (1999)
Pseudotsuga menziesii	-	43.3♦	-0.13*	Moore *et al.* (1999)
Festuca halii	-	15.7♦	-0.29*	Moore *et al.* (1999)
Pinus banksiana	-	25.6♦	-0.17*	Moore *et al.* (1999)
Larix laricina	-	40.6♦	-0.14*	Moore *et al.* (1999)
Betula papyrifera	-	33.3♦	-0.24*	Moore *et al.* (1999)
Tsuga heterophylla (wood)	-	122.6♦	-0.04*	Moore *et al.* (1999)
Thuja plicata	-	55.5♦	-0.09*	Moore *et al.* (1999)

5.2 Materials and Methods:

5.2.1 Field Experiments

Leaf Decay Experiments

Two leaf decay experiments were conducted. Leaf Decay Experiment one (LDE1), used leaves from four tree species, (*Acacia melanoxylon, Atherosperma moschatum, Lomatia fraseri* and *Nothofagus cunninghamii*). LDE1 lasted for 333 days, commencing on 15/06/1997 and ending on 15/05/1998. The experiment was terminated at 333 days when the remaining samples became unrecoverable after the plastic streaming tape that marked their position had been buried after a recent flood.

Leaf Decay Experiment Two (LDE2), added *Eucalyptus regnans* as an additional species. *Eucalyptus regnans* was not used in LDE1 due to difficulties in obtaining leaves from the 60 m high forest canopy, a problem which was resolved when a mature *E. regnans* tree blew over near the field site in a severe mid winter storm shortly after LDE1 had begun. LDE2 lasted for 365 days, commencing on 23/08/1998 and ending on 22/08/1999. All field data can be found in Appendix 5.1

Ten kilograms (fresh weight) of green leaves were collected at the field site from each of the tree species used in the two leaf decay experiments. The leaves were dried for three weeks at room temperature (20°C) at ~ 50% humidity (as measured by a humidity logger), until a constant weight had been achieved. Five grams of air dried leaves were then placed into 15 x 15 cm fibreglass single-species leaf bags with a 2 mm mesh size and the bags heat welded shut; 300 bags of each leaf species were made. Each leaf bag had a securely tied one-metre length of nylon builder's line attached to one corner. A different coloured thread was used for each species to enable species identification after deployment without disturbing the leaf bags (Table 5.2).

Six leaf bags of the same species were secured to 45 cm steel tent pegs by the nylon builder's line. Brightly coloured plastic flagging tape (25 mm in width) was then tied to each peg, to be used later in locating and recovering the leaf bags. The pegs and leaf bags were subsequently deployed through out the rainforest section of the field site in the four depositional settings in which fallen leaf material was likely to find itself (Section 1.6). The specific locations used throughout the field site were:

1. The rain forest floor, (representing autochthonous leaf fall, referred to as 'Land Surface' or 'LS');
2. The forest floor sediments (representing autochthonous burial, referred to as 'Land Buried' or 'LB');
3. The sediment water interface of the stream channel (representing parautochthonous leaf accumulations on stream beds, referred to as 'Stream Surface' or 'SS');
4. The deep anaerobic fluvial deposits along the stream channel (representing allochthonous burial in riparian or lacustrine sediments, referred to as 'Stream Buried' or 'SB').

The buried samples were covered to a depth of at least 50 cm with adjacent soil. The pegs were used to hold the surface samples in place so that they would not be washed away by floods etc, and were spaced to maximise the distance between samples. Six leaf bags of each species were collected from each depositional setting on a monthly basis for the experimental period. The leaf bags were recovered at random from the total pack population for each species and treatment. They were stored at 4°C for transport to the laboratory. When returned to the laboratory, the packs were gently rinsed in distilled water to remove excess soil, opened and rinsed again to remove the remaining soil particles. The leaf material was then placed into brown paper bags, dried in a drying oven

at 70°C until a constant dry weight was obtained (~ four days) and weighed. The 70°C drying temperature was used after a trial sample spontaneously combusted at the recommended drying temperature of 105°C (Allen, 1989). The balance used was a Mettler 'Toledo' PB 3002 top loading balance.

Sub-samples of ~ 1.0 g of dry leaf where weighed on an 'A and D HR-200' analytical balance and placed into 45 ml crucibles. These sub-samples were subsequently placed in a muffle furnace, heated at 550°C for two hours (to remove the organic matter), the remaining ash weighed and the ash free dry weight of the original samples calculated. All the LDE1 samples, and the LDE2 3, 6, 9 and 12-month samples, had their ash-free dry weight determined.

Table 5.2 The colour coding scheme for labelling the leaf bags deployed at the field site. Each bag had a 1 m coloured nylon tether tied to it. Six leaf bags of the same species were tied to a 45 cm steel tent peg by the tether along with a 1m length of flagging tape. When deployed, the six leaf bags were arranged hexagonally at ≈ 1 m distances from the tent peg. Fifty centimetres of flagging tape was left exposed for all buried leaf bags to enable their location and recovery.

Species	Treatment	Flagging Tape Colour	Colour of Nylon Tether
Nothofagus cunninghamii	Stream Buried	Fluorescent Orange	Antique Green
Nothofagus cunninghamii	Stream Surface	Fluorescent Yellow	Antique Green
Nothofagus cunninghamii	Land Buried	Fluorescent Pink	Antique Green
Nothofagus cunninghamii	Land Surface	Fire Engine Red	Antique Green
Atherosperma moschatum	Stream Buried	Fluorescent Orange	Fluorescent Orange
Atherosperma moschatum	Stream Surface	Fluorescent Yellow	Fluorescent Orange
Atherosperma moschatum	Land Buried	Fluorescent Pink	Fluorescent Orange
Atherosperma moschatum	Land Surface	Fire Engine Red	Fluorescent Orange
Acacia melanoxylon	Stream Buried	Fluorescent Orange	White
Acacia melanoxylon	Stream Surface	Fluorescent Yellow	White
Acacia melanoxylon	Land Buried	Fluorescent Pink	White
Acacia melanoxylon	Land Surface	Fire Engine Red	White
Eucalyptus regnans	Stream Buried	Fluorescent Orange	Fluorescent Pink
Eucalyptus regnans	Stream Surface	Fluorescent Yellow	Fluorescent Pink
Eucalyptus regnans	Land Buried	Fluorescent Pink	Fluorescent Pink
Eucalyptus regnans	Land Surface	Fire Engine Red	Fluorescent Pink
Lomatia fraseri	Stream Buried	Fluorescent Orange	Fluorescent Yellow
Lomatia fraseri	Stream Surface	Fluorescent Yellow	Fluorescent Yellow
Lomatia fraseri	Land Buried	Fluorescent Pink	Fluorescent Yellow
Lomatia fraseri	Land Surface	Fire Engine Red	Fluorescent Yellow

Measurements of Soil Eh

The soil Eh was determined using a saturated calomel reference electrode, and a platinum electrode calibrated against Zobell's Solution (See Appendix 5.2; Chemicals and Solutions). The Eh measurements were measured with a battery operated dual function Orion™ 520 'Laboratory Instrument' pH and millivolt meter. The soil Eh was tested by inserting the 10 cm platinum electrode and the calomel reference electrode into the soil. Readings where taken after 15 minutes, or when the Eh values had stabilised. The platinum electrode was checked before and after use to see if it had became 'poisoned' with a build up of organic material by checking its electro-potential against the Zobell's calibration standard. Un-poisoned electrodes returned a reading near 186 mV (± 5mV) before and after they were used. The 3.3 mM potassium ferricyanide and 3.3 mM potassium ferrocyanide (in 0.1 M KCL) calibration standards were made separately before use and were mixed in equal proportions (in a glass beaker) at the field site prior to use as the calibration solution. Poisoned electrodes were cleaned with 10% v/v sulphuric acid.

Determination of the decay coefficient k and predicted decay times

The decay curves were described mathematically in the manner of Olsen (1963). The equations used are defined in Equations 1.1 and 1.2, with high k values equating to rapid decay rates and low k values equating to low decay rates. The negative sign of the k value has been kept (refer to Equation 1.2).

The effects of decay time upon leaf area

Leaves from the first, second, fourth and eighth month samples of LDE2 were used to measure the changes in leaf blade area as the process of leaf decay continued. For this reason these samples were not subsampled for the ash free dry weight

determinations. Ten leaves were sampled randomly from the total population of recovered leaves. Each leaf was imaged on a Hewlett Packard digital scanner (HP 5100 C) in black and white using the Scion ™ image analysis package (Beta Release, Ver. 4.0.2). A 10 cm standard scale was used to calibrate the dimensions of each scanned image.

Statistical analysis of field data and decay rates

The results of the leaf decay experiments were analysed using SPSS™ for Windows™ ver 11.0.1. The decay curves were compared using the Univariate ANOVA and repeated measures ANOVA procedure of the general linear model. In all cases, the SPSS™ software reported p values to the third decimal place only (and is reported as such in the relevant tables). Wherever a p value of 0.000 was cited in the text it was recorded as $p \leq 0.001$, a p value of absolute zero being deemed unlikely. All p values cited are Tukey HSD post hoc tests. For both the univariate and repeated measures analysis, the model used was either treatment by species or species by treatment. For the repeated measures ANOVA, the within subject factor was collection date (labelled d1, d2 etc.), with 12 levels for LDE1, and 5 levels for LDE2. The between-subjects factors were species and treatment. The fit of the decay curve data to the single exponential model was checked using regression analysis in Microsoft Excel™. The decay values predicted by the single exponential model for each collection date were compared against the actual values and the adjusted r^2 values included in Table 5.3 along with significant p values being marked by an '*'.

5.2.2 Analysis of leaf chemistry

Determination of initial leaf nutrient status

Fresh leaf samples of each species were air dried at room temperature and 50% humidity until a constant weight had been reached. Then 10 g samples of the leaves were frozen with liquid nitrogen and ground until a finely divided powder was obtained. The labelled samples were then sent to the Victorian Government 'State Chemistry Laboratory' for analysis. The samples were analysed using a Leco™ furnace for the following elements, total nitrogen, phosphorus, potassium, sulphur, calcium, magnesium, sodium, copper, zinc, manganese, iron and boron.

Measurement of Leaf Cuticle Thickness

Leaf cuticle thicknesses were determined by randomly selecting five fresh leaves of each of the tree species used and excising three 2 x 2 mm sections from each leaf. The sections were placed into labelled tissue cassettes and dehydrated in an alcohol concentration series of 30%, 50%, 70%, 90% and 100% using an automatic tissue processor. The samples were subsequently infiltrated with paraffin by being cycled through 50% and 100% molten paraffin solutions overnight. The samples were removed from the tissue cassettes the next day, embedded in paraffin blocks and cut in cross-section. The best sample thickness for measuring cuticle was determined to be 4 μm while 6 μm was used for those samples which crumpled under the cutting knife of the microtome. The microtome used was a Microtom™ 2 microtome, using disposable microtome blades. The sections were mounted on glass slides and examined under a Carl Zeiss™ Axioplan 2 microscope. Digital images of each section were then taken using a Carl Zeiss AxioCam at times 400 magnification and an image resolution of 1300 x 1030

pixels. The cuticle thicknesses were measured five times for each image using the measure length tool of the Carl Zeiss™ Axioplan image analysis software (Ver 3.01). The source images are in Appendix 5.3. The cuticle measurements were entered into Microsoft Excel 97™, averaged and the standard deviation calculated for each species.

Lignin Determination

The leaf lignin contents were determined using the method described in Allen (1989). This method, based upon the widely used procedure developed by Ritter & Barbour (1932), uses 72% sulphuric acid hydrolysis. The lignin determination involves three pre-extractions followed by the lignin assay. Each determination was conducted in duplicate upon leaves that were air dried at room temperature and ground into a fine powder using a Kambrook 'Classic' electric blender and a mortar and pestle. Then ~ 1.0 g of each leaf sample was weighed out on to labelled, pre-weighed 90 mm diameter glass fibre filter paper dried at 105°C. The sample weights, filter papers and all other weighed items in this procedure were determined on a 'A and D HR-200' analytical balance. The samples and filter papers were then tied into a bundle with Terylene thread for use in the first pre-extraction.

A soxhlet apparatus was used for the first pre-extraction to remove the ether soluble cell fractions from the leaf samples, including, fats, lipids and some polyphenols. The samples were refluxed for six hours at 36°C with diethyl ether as the extractant. When finished, the samples were removed from the soxhlet and the ether evaporated from the samples at room temperature for least two hours. The samples were dried at 40°C overnight to remove the remaining traces of the ether and weighed.

The second pre-extraction removed water-soluble carbohydrates and cell components. Approximately 0.8 g of each sample from the soxhlet extraction was

weighed into a labelled 600 ml beaker. To each beaker 400 ml of distilled water was added and the contents gently brought to the boil. Each beaker was covered with a watch glass to limit evaporation and boiled gently for three hours and maintained at a constant volume. The third pre-extraction (which removed the remaining proteins) involved adding 22 ml of 10% sulphuric acid (v/v) to each of the above beakers, which were then boiled gently for another one hour.

The beakers were then allowed to cool and the samples settle. The supernatant fluid of each beaker was removed (using a separate pre-weighed number 2 Pyrex sintered glass filter stick for each beaker), and discarded. The samples and filter sticks were left in the beakers, which were covered and dried at 40°C over night. When dry, the beakers and filter sticks were placed in a 12-15°C water bath and 15 ml of 72% (w/v) sulphuric acid added. The samples were wetted with the acid by stirring with the filter stick. After one minute, the temperature of the water bath was increased to 18-20°C and the samples digested for two hours. They were stirred at regular intervals with the filter sticks.

After two hours the strength of the acid was reduced to 3% (w/v) by adding 560 ml of double distilled water, any remaining particles of sample on the filter stick were washed off and the filter sticks removed. Finally the beakers were then covered with watch glasses, heated until the contents were boiling gently and boiled for four hours at constant volume. After being allowed to cool the contents of each beaker was poured through numbered, pre-weighed, number 2 sintered glass crucible to catch the residue. The residue caught in the crucibles was washed with hot distilled water to remove excess acid and the crucible (and contents), dried at 105°C for three hours, cooled and weighed. The samples were corrected for mineral content, by ashing at 550°C for two hours.

Statistical analysis

The decay rates of each treatment for both LDE1 and LDE2 were correlated against initial nitrogen content, total phosphorus, manganese, lignin and lignin to nitrogen ratio in a one tailed Pearson Correlation matrix. The software used was SPSS™ for Windows™ ver. 11.0.1. The relationships that were indicated as significant were regressed against treatment. In all regressions the dependent variable was decay rate (treatment) and the total phosphorus, manganese, lignin or lignin to nitrogen ratio were set as the independent variables.

5.2.3 Mesocosm Experiments

Two species were used in the mesocosm experiments *Lomatia fraseri* and *Nothofagus cunninghamii*. The mesocosms used were 60 cm long, 45 cm deep and 30 cm wide. Each mesocosm had a 30 cm depth of a 10:1 mix of builder's sand and soil from the Cumberland Creek field-site added to it, and was then filled to within 5 cm of the top with aged tap water. After two weeks (to allow the soil biota from the field-site time to acclimatise to the mesocosm environment), 18 leaf packs of both species of the same size and construction used in the leaf decay experiments were buried in each mesocosm. The following variables were tested:

1. Excess nitrogen and phosphorus, where 50 g of Osmocote™ slow release fertiliser was added to give an effective nitrogen and phosphorus loading of ~530 kg N $Ha^{-1}$and 120 kg P Ha^{-1} to the sand soil mix as the mesocosm was being filled;
2. Aerobic soils at 10°C, in which the water over the sediment was aerated with an aquarium air pump (Conducted with duplicate sets of mesocosms);
3. Aerobic soils at 15°C, in which the water over the sediment was aerated with a aquarium air pump;

4. Aerobic soils at 5°C, in which the water over the sediment was aerated with a aquarium air pump;

5. Unaerated anaerobic soils at 10°C. To each of these mesocosms, 25 ml of 0.1 M Cystine.HCl was added to the sediment as a reducing agent. Glucose solution was added to the water over the sediment to de-oxygenate it and assist with the generation of anaerobic conditions in the sediment.

At roughly two monthly intervals for 18 months, six leaf packs (two leaf packs bi-monthly from each of the three mesocosms for each treatment) for each species were removed, washed free of sand and grit, dried at 70°C until no further weight loss occurred and weighed. The experiment began on 28/01/1998 and ended on the 28/09/1999. After the experiment was completed, the results were analysed using SPSS ver. 10.0.5 for Windows, using a repeated measures analysis of variance. The soil Eh (Table 5.3) was determined using the method described in section 5.2.1; p. 145.

Table 5.3 The average Eh (reducing potential) of the sediments used in the mesocosm experiments. The Eh of each mesocosm was measured prior to the removal of the leaf packs from the tanks, the standard deviation of the Eh readings is given in brackets after the average value.

Species	Treatment	Mesocosm Number	Average Eh (mV)
Lomatia fraseri	Excess Nitrogen & Phosphorus	1	437 (±9)
Lomatia fraseri		2	439 (±8)
Lomatia fraseri		3	442 (±11)
Lomatia fraseri	Aerobic 10°C	4	268 (±16)
Lomatia fraseri		5	285 (±32)
Lomatia fraseri		6	347 (±68)
Lomatia fraseri	Aerobic 10°C	7	206 (±160)
Lomatia fraseri		8	333 (±66)
Lomatia fraseri		9	255 (±44)
Nothofagus cunninghamii	Anaerobic 10°C	10	-79 (±14)
Nothofagus cunninghamii		11	-153 (±25)
Nothofagus cunninghamii		12	-112 (±4)
Nothofagus cunninghamii	Aerobic 5°C	13	297 (±105)
Nothofagus cunninghamii		14	245 (±10)
Nothofagus cunninghamii		15	298 (±34)
Nothofagus cunninghamii	Aerobic 15°C	16	339 (±48)
Nothofagus cunninghamii		17	193 (±7)
Nothofagus cunninghamii		18	139 (±117)

5.3 Results

5.3.1 Field Experiments

Leaf decay experiments

The leaf decay curve data for LDE1 and LDE2 showed significant differences between species and between treatments. This is clearly shown in the decay coefficients (Table 5.4) and the predicted times for 50% and 95% mass loss (Figures 5.5a-d) for each species and treatment combination.

Table 5.4 List of the '*k*' values determined for the leaf species used in decay experiments one and two. All *k* values were derived from the sample weights obtained at the beginning and end of the leaf decay experiments. The species average was calculated from the mass of all the leaf packs concerned. The adjusted r^2 values (in parenthesis) measure the fit of the single exponential model to the decay curve data. An '*' indicates a significant relationship between the model and decay data.

Species	Treatment	'*k*' values for leaf decay experiment one	'*k*' values for leaf decay experiment two
Atherosperma moschatum	Stream Buried	-1.30 (0.88)*	-1.36 (0.69)
Atherosperma moschatum	Stream Surface	-1.70 (0.87)*	-2.50 (0.98)*
Atherosperma moschatum	Land Buried	-1.25 (0.89)*	-1.03 (0.79)*
Atherosperma moschatum	Land Surface	-1.31 (0.87)*	-1.43 (0.60)
Average		-1.17	-1.45
Acacia melanoxylon	Stream Buried	-0.35 (0.67)*	-0.93 (0.81)*
Acacia melanoxylon	Stream Surface	-0.65 (0.79)*	-1.24 (0.97)*
Acacia melanoxylon	Land Buried	-0.37 (0.80)*	-0.28 (0.47)
Acacia melanoxylon	Land Surface	-0.87 (0.93)*	-0.87 (0.82)*
Average		-0.51	-0.77
Eucalyptus regnans	Stream Buried	N/A	-0.58 (0.84)*
Eucalyptus regnans	Stream Surface	N/A	-1.24 (0.86)*
Eucalyptus regnans	Land Buried	N/A	-0.63 (0.83)*
Eucalyptus regnans	Land Surface	N/A	-1.35 (0.97)*
Average			-0.96
Lomatia fraseri	Stream Buried	-0.47 (0.78)*	-0.71 (0.86)*
Lomatia fraseri	Stream Surface	-0.58 (0.64)*	-1.39 (0.97)*
Lomatia fraseri	Land Buried	-0.67 (0.92)*	-0.59 (0.67)*
Lomatia fraseri	Land Surface	-0.63 (0.93)*	-0.71 (0.92)*
Average		-0.55	-0.79
Nothofagus cunninghamii	Stream Buried	-0.24 (0.68)*	-0.38 (0.86)*
Nothofagus cunninghamii	Stream Surface	-1.54 (0.62)*	-1.10 (0.96)*
Nothofagus cunninghamii	Land Buried	-0.50 (0.86)*	-0.40 (0.62)
Nothofagus cunninghamii	Land Surface	-0.61 (093)*	-0.80 (0.93)*
Average		-0.57	-0.74

The decay coefficients shown in table 5.4 were entered into equation 1.1 (page 31) and the mass of the leaves remaining at the sample collection dates predicted by the single exponential model and the actual mass obtained compared via a regression analysis. In most cases the single exponential model gave a satisfactory fit to the actual data and the decay coefficient generated by this model could therefore be used to describe the decay curves. Alternative linear and quadratic models were tried. Either their r^2 values were lower than those of the single exponential model (as was the case for the linear models), or the predictive capabilities of the models were not helpful and lacked biological reality (as was the case with the quadratic models). These observations are in general agreement with those made by Weider and Lang (1982 & Section 1.5.3).

The scale of difference between the k values of the different species and treatments is quite substantial, indicating that different species decay at different rates, and that different treatments have significant impacts upon decay rate (Tables 5.4 & 5.5). The *Atherosperma moschatum* samples had high k values and showed the least response to treatment; all the samples decayed quickly (Table 5.4). This is evident in the LDE1and LDE2 decay curve data, where *A. moschatum* is decaying more rapidly than the other species used in the decay experiments (Figures 5.1a-d & 5.3a-d, Tables 5.4 & 5.5).

Table 5.5 The decay rate order of the various leaf species used in the two decay experiments. The species at the top of each group had the slowest decay rate and the species at the bottom the fastest.h *Acc.* = *Acacia melanoxylon*; *Ath.* = *Atherosperma moschatum*; *Euc.* = *Eucalyptus* regnans; Lom. = *Lomatia fraseri*; *Noth.* = *Nothofagus cunninghamii*; SB = Stream Buried; SS = Stream Surface; LB = Land Buried; LS = Land Surface.

	Overall	**SB**	**SS**	**LB**	**LS**
LDE1	Acc	Noth	Lom	Acc	Noth
	Lom	Acc	Acc	Noth	Lom
	Noth	Lom	Noth	Lom	Acc
	Ath	Ath	Ath	Ath	Ath
LDE2	Noth	Noth	Noth	Acc	Lom
	Acc	Ecu	Euc	Noth	Noth
	Lom	Lom	Acc	Lom	Acc
	Euc	Acc	Lom	Euc	Euc
	Ath	Ath	Ath	Ath	Ath

The minimum time for any species to achieve 50% or 95% mass loss was the *A. moschatum* stream surface treatment in LDE2, with 100 (± 11) days and 437 (± 47) days respectively (Figures 5.5c-d). The LDE2 land buried treatment had the slowest decay rate for *A. moschatum* with a k value of –1.033, or 244 (± 7) days being needed for 50% mass loss. The greatest difference in time needed for 50% mass loss between treatments for *A. moschatum* samples was therefore 144 days, the lowest difference between treatments in either LDE1 or LDE2. Generally the *A. moschatum* decay curves differ significantly, the only exceptions being the LDE1 SB x LB, SB x LS and the LDE2 SB x LS curves (Figure 5.2b & 5.4b and Table 5.6). This indicates a small but significant impact of treatment with the surface treatments decaying more rapidly than the buried treatments (Table 5.4).

Nothofagus cunninghamii had significantly different decay curves from those of the other species ($p \leq 0.001$ in all cases). In LDE1, decay rates for *N. cunninghamii* were higher than those of *Lomatia fraseri* and *Acacia melanoxylon*. In LDE2, *N. cunninghamii* had the slowest overall decay rate. However it must be noted that in LDE1 and LDE2, *N. cunninghamii, A. melanoxylon* and *L. fraseri* had similar average decay rates (Table 5.4 & Table 5.6). In LDE1, *L. fraseri* and *A. melanoxylon* had statistically similar decay curves ($p = 0.580$) and different curves in LDE2 (Table 5.6).

The decay rate data for *N. cunninghamii* indicate that this species responds very strongly to treatment (Figure 5.5a-d; Tables 5.4 and 5.5). For example, in LDE1 the k values for *N. cunninghamii* ranged from a low of -0.242 in the stream buried treatment to a high of –1.537 for the stream surface treatment (Table 5.4). The predicted times for 50% mass calculated from these k values were the largest in either decay experiment at 1042 (± 21) days and 164 (± 23) days for the stream buried and surface samples respectively (Figure 5.5a). In both leaf decay experiments the stream surface samples had high k values and the stream buried samples had low k values (Table 5.4).

Table 5.6 Summary of the SPSS data output for the ANOVA's between species and treatment for leaf decay experiments one and two. All numbers given are *p* values and those marked with an '*' are significant at 0.05 confidence. **AT** = All Treatments; **SB** = Stream Buried; **SS** = Stream Surface; **LB** = Land Buried; **LS** = Land Surface.

Leaf decay experiment one.

Species (i)	Species (j)	AT	SB	SS	LB	LS
Atherosperma moschatum	*Nothofagus cunninghamii*	0.000*	0.000*	0.991	0.000*	0.000*
	Acacia melanoxylon	0.000*	0.000*	0.000*	0.000*	0.000*
	Lomatia fraseri	0.000*	-	0.000*	-	0.000*
Acacia melanoxylon	*Nothofagus cunninghamii*	0.000*	0.000*	0.000*	0.050	0.016
	Atherosperma moschatum	0.000*	0.000*	0.000*	0.000*	0.000*
	Lomatia fraseri	0.580	-	0.985	-	0.026
Lomatia fraseri	*Nothofagus cunninghamii*	0.000*	-	0.000*	-	1.000
	Atherosperma moschatum	0.000*	-	0.000*	-	0.000*
	Acacia melanoxylon	0.580	-	0.985	-	0.026*
Nothofagus cunninghamii	*Atherosperma moschatum*	0.000*	0.000*	0.991	0.000*	0.000*
	Acacia melanoxylon	0.000*	0.000*	0.000*	0.050*	0.016*
	Lomatia fraseri	0.000*	-	0.000*	-	1.000

Leaf decay experiment two.

Species (i)	Species (j)	AT	SB	SS	LB	LS
Atherosperma moschatum	*Nothofagus cunninghamii*	0.000*	0.000*	0.001*	0.000*	0.000*
	Acacia melanoxylon	0.000*	0.027*	0.004*	0.000*	0.000*
	Eucalyptus regnans	0.000*	0.000*	0.341	0.000*	0.984
	Lomatia fraseri	0.000*	0.000*	0.023*	-	0.000*
Acacia melanoxylon	*Nothofagus cunninghamii*	0.000*	0.000*	0.967	0.003*	0.933
	Atherosperma moschatum	0.000*	0.027*	0.004*	0.000*	0.000*
	Eucalyptus regnans	0.000*	0.009*	0.258	0.000*	0.000*
	Lomatia fraseri	0.000*	0.157	0.955	-	0.349
Eucalyptus regnans	*Nothofagus cunninghamii*	0.000*	0.169	0.079*	0.000*	0.000*
	Atherosperma moschatum	0.000*	0.000*	0.341	0.000*	0.984
	Acacia melanoxylon	0.000*	0.009*	0.258	0.000*	0.000*
	Lomatia fraseri	0.218	0.682	0.642	-	0.000*
Lomatia fraseri	*Nothofagus cunninghamii*	0.000*	0.010*	0.673	-	0.802
	Atherosperma moschatum	0.000*	0.000*	0.023*	-	0.000*
	Acacia melanoxylon	0.000*	0.157	0.955	-	0.349
	Eucalyptus regnans	0.218	0.682	0.642	-	0.000*
Nothofagus cunninghamii	*Atherosperma moschatum*	0.000*	0.000*	0.001*	0.000*	0.000*
	Acacia melanoxylon	0.000*	0.000*	0.967	0.003*	0.933
	Eucalyptus regnans	0.000*	0.169	0.079	0.000*	0.000*
	Lomatia fraseri	0.000*	0.010*	0.673	-	0.802

Notes:

1. The minimum *p* value given by the SPSS program was 0.000, these values have been reported as such here, even though they have been written as $p < 0.001$ in the text.
2. The LDE2 Land Buried *Lomatia fraseri* samples could not be analysed.

Table 5.7 Summary of the SPSS data output for the repeated measures ANOVA of species by treatment for leaf decay experiment's one and two. All numbers given are *p* values resulting from a Tukey HSD test and those values marked with an '*' are significant at 0.05 confidence. *Acc.* = *Acacia melanoxylon*; *Ath.* = *Atherosperma moschatum*; *Euc.* = *Eucalyptus regnans*; Lom. = *Lomatia fraseri*; *Noth.* = *Nothofagus cunninghamii*; SB = Stream Buried; SS = Stream Surface; LB = Land Buried; LS = Land Surface. An 'X' indicates the species was not included in the experiment and an '-' indicates that a statistical analysis was not possible for that species and treatment combination.

Leaf decay experiment one[1]						
Treatment (i)	**Treatment (j)**	*Acc.*	*Ath.*	*Euc.*	*Lom.*[2]	*Noth.*
SB	SS	0.000*	0.000*	X	0.000*	0.000*
	LB	0.136	0.954	X	0.980	0.000*
	LS	0.000*	0.955	X	0.104	0.000*
SS	SB	0.000*	0.000*	X	0.000*	0.000*
	LB	0.000*	0.000*	X	0.000*	0.000*
	LS	0.215	0.000*	X	0.000*	0.007*
LB	SB	0.136	0.954	X	0.980	0.000*
	SS	0.000*	0.000*	X	0.000*	0.000*
	LS	0.000*	0.000*	X	0.208	0.121
LS	SB	0.000*	0.955	X	0.104	0.000*
	SS	0.215	0.000*	X	0.000*	0.000*
	LB	0.000*	0.000*	X	0.208	0.121

Leaf decay experiment two[1]						
Treatment (i)	**Treatment (j)**	*Acc.*	*Ath.*	*Euc.*[3]	*Lom.*[2]	*Noth.*[3]
SB	SS	0.000*	0.000*	0.000*	0.000*	0.000*
	LB	0.000*	0.000*	0.990	0.929	0.811
	LS	0.000*	0.543	0.000*	0.919	0.000*
SS	SB	0.000*	0.000*	0.000*	0.000*	0.000*
	LB	0.000*	0.000*	0.000*	0.000	0.000*
	LS	0.053	0.000*	0.410	0.000*	0.000*
LB	SB	0.000*	0.000*	0.990	0.929	0.811
	SS	0.000*	0.000*	0.000*	0.000	0.000*
	LS	0.000*	0.001*	0.000*	0.627	0.000*
LS	SB	0.000*	0.543	0.000*	0.919	0.000*
	SS	0.053	0.000*	0.990	0.000*	0.000*
	LB	0.000*	0.001*	0.000*	0.938	0.000*

Notes:

1. The minimum *p* value reported by the SPSS program was 0.000, these values have been reported as such, and written as $p < 0.001$ in the text.
2. The LDE1 *L. fraseri* decay curves were compared at 10 months and LDE2 *L. fraseri* decay curves were compared at nine months due to the final samples becoming unrecoverable as the result of the burial location markers due to a minor flood at the end of each experiment.
3. The *E. regnans* and *N. cunninghamii* decay curves in LDE2 could not have their month three decay values included in the analysis due to the loss of the samples before analysis.

The stream buried and surface decay curves were statistically different from each other in both experiments (Table 5.7). The LDE1 LB x and LS decay curves were not statistically different from each other (Figure 5.2d & 5.7).

The *Acacia melanoxylon* samples had a variable decay rate response to treatment between the two leaf decay experiments and generally decayed slowly (Figure 5.5a-d; Tables 5.4 & 5.5). In LDE1 there was a clear impact of treatment upon *k* values and decay times (Table 5.4 and Figures 5.5a-b). The 'buried' treatments had low *k* values, while the 'surface' treatments had higher *k* values (Figures 5.5a-b & Table 5.4). The LDE1 buried and surface decay curves also were statistically different from each other (Tables 5.4 & 5.7). In LDE2 the decay rate and mass loss times for stream buried and surface *k* values were higher than LDE1 (Table 5.4 and Figures 5.5 c & d). Only the LDE2 LS x SS decay curves were statistically different each other (Table 5.7). The land 'buried' and 'surface' *k* values were similar between the two experiments (Table 5.4).

The overall decay rate for *Eucalyptus regnans* was comparatively fast, and there were large differences between treatments (Table 5.4). The overall decay rate was significantly different from *Nothofagus cunninghamii* and *Atherosperma moschatum* but not *Acacia melanoxylon* and *Lomatia fraseri* (Figures 5.4c & 5.5c-d and Tables 5.4 & 5.6). In LDE2 *E. regnans* stream buried treatment, the decay rate was the second slowest (Tables 5.4 & 5.5). The stream and land surface treatments had high *k* values and 50% mass loss times of 204 (±35) and 186 (±17) days; while the stream and land buried treatments had low *k* values and 50% decay times of 435 (±37) and 404 (±27) days (Figures 5.5c-d). The stream buried decay rate was the second lowest for LDE2 and the surface and buried treatments were statistically different from each other (Tables 5.5 & 5.7).

The *k* values for the LDE1 *Lomatia fraseri* decay curves were low and fairly close in value, indicating that treatment had little effect upon decay rate (Table 5.4). The only species it was statistically different from regardless of treatment was *Atherosperma moschatum* (Table 5.6). The LDE1 stream surface *L. fraseri* decay rate was significantly slower than the other three treatments, while the other treatments were not significantly different from each other (Tables 5.5 & 5.7). The LDE2 decay curves had similar weak responses treatment, with the exception of the stream surface treatment whose *k* value increased from –0.582 to –1.394 (Table 5.4 and Figure 5.5a-d). The corresponding 50% and 95% decay times for the stream surface samples fell from 433 (+/-79) and 1881 (+/-344) days to 180 (+/-24) and 785 (+/- 107) days respectively for LDE1and LDE2.

The effects of decay time upon leaf area

There were substantial differences between species in the rate at which the leaves either fragmented or lost leaf blade area. The leaves of *Acacia melanoxylon* tended to lose weight without significant loss of leaf blade area (Figures 5.6a i-iv). In general *A. melanoxylon* phyllodes became more brittle as they decayed with the ends becoming cracked and fragmented as the time progressed. The stream and land buried leaves (Figure 5.6a (i & iii)) showed the least alteration after eight months, while the land and stream surface leaves showed the highest degree of alteration after eight months (Figure 5.6a(ii & iv)). The low levels of alteration for the land buried leaves coincide well with the low *k* value for this treatment, as do the high *k* values for the two surface treatments (Table 5.4). An anomaly exists between the high degree of preservation for the stream buried leaves after eight months and the *k* value of –0.931, which is higher than that of land surface leaves (k = -0.872) which showed far higher level of alteration (Figure 5.6a (i & iv) and Table 5.4). Thus mass loss equals leaf area loss in some but not all cases for this species.

The leaves of *Atherosperma moschatum* (Figures 5.6b (i-iv)), were generally skeletonised rapidly and had lost structural integrity after eight months. In a number of cases the cuticle remained *in situ* after having become detached from the leaf blade as the mesophyll decayed (Figures 5.6b (i-ii)). Only the land buried leaves were well preserved after eight months. These levels of preservation coincide with the decay rate data listed in Table 5.4, where the land buried samples had a lower decay rate than the other three treatments. Some of land buried leaves did show signs invertebrate grazing by having neat round holes in the leaf margins (Figure 5.6b (iii); leaves 12, 13, 16 & 28). The land surface leaves showed signs of invertebrate grazing by the first month, with many leaves having only the skeleton and cuticle remaining by four months (Figure 5.6b (iv)). The stream surface leaves had even higher levels of alteration, all the leaves being partially for fully skeletonised after four months (Figure 5.6b (iii)).

The general pattern of decay for *Eucalyptus regnans* leaves involved a loss of rigidity and structural integrity when wet (and increased brittleness when dry), followed by rapid fragmentation and the tendency to disintegrate into a slimy mass (not shown) (Figures 5.6c (i-iv)). Often the leaf cuticle became completely detached from the leaf blade prior to the disintegration of the mesophyll. The stream buried leaves had the least alteration, while the land buried leaves had greater areas of blade loss (Figures 5.6c (i & iii)). By eight months the land buried leaves were either essentially intact or reduced to a leaf base and petiole.

Leaves from the *E. regnans* stream and land surface treatments had high levels of leaf area loss by eight months and tended disintegrate without leaving a leaf skeleton or extensive areas of cuticle (Figures 5.6c (ii & iv)). Often only a petiole remained by eight months (Figure 5.6c (iii); Leaves 31-40). The rapid fragmentation of the land surface *E. regnans* leaves became notable after two months (Figure 5.6c (iv) leaves 11-20). The

levels of leaf area preservation again mostly coincide with the decay rate values in Table 5.4. The rapid fragmentation and leaf area loss observed for the surface treatments match the *k* values. The comparatively rapid fragmentation and leaf area loss of *E. regnans* compares poorly with species such as *Atherosperma moschatum* however because its leaves lose area far more rapidly inspite of having generally lower decay rates (Table 5.4).

The leaves of *L. fraseri* proved to be highly brittle from the outset of the experiment, this being due to their large size, thinness and tendency to curl upon drying. The brittleness of these leaves increased with time, and they became more prone to fracturing as the decay process progressed (Figures 5.6d (i-iv)). Generally *L. fraseri* leaves decayed either by fracturing into small pieces along the main-vein (or at right angles to it), or by invertebrate grazing characterised firstly by cuticle separation with numerous small 'circles' of missing mesophyll near the leaf margins, which then progressed towards the mid-vein of the leaf.

The stream buried leaves fractured mostly during their removal from the leaf bags, undergoing limited *post mortem* alteration until the fourth month, when grazing began to occur (Figure 5.6d (i)). The land buried leaves had high levels of alteration by eight months a fact at variance with the *k* value (-0.587), which was lower than that of the stream buried samples (k = -0.705) which had lower levels of damage (Figures 5.6d (i & iii); Table 5.4). The *L. fraseri* stream surface leaves had the most leaf area loss after eight months (Figure 5.6d (ii)). The land surface leaves had the next greatest leaf area loss by eight months, while the buried treatments had the least (Figure 5.6d (ii-iv)). This agrees well with the decay rate data where stream surface *k* values of –1.394 is higher than the land surface *k* value (-0.705) and those of the buried treatments (Table 5.4).

Nothofagus cunninghamii leaves showed little *post mortem* alteration throughout the duration of the experiment (Figure 5.6e (i-iv). No leaf from any leaf pack showed signs of either cuticle separation, or skeletonisation. The leaves from the stream and land buried treatments turned black with time (at around four months), but otherwise remained unaltered. This coincides well with the LDE2 low decay rates measured for these treatments (Table 5.4). Both sets of leaves became slightly more brittle after eight months, becoming easier to break when pressed or crushed.

The stream surface specimens (Figure 5.6e (ii)) had the greatest overall loss of leaf blade area, with minor leaf blade loss beginning at four months. This agrees well with the highest *N. cunninghamii* LDE2 k value of −1.100. The land surface *N. cunninghamii* leaves became thin and tended to turn a light yellow with time but did not lose leaf area. This is consistent with the k value (-0.799), which is higher than the buried treatments, but lower than the stream surface treatment (Table 5.4). The decay rate values for *N. cunninghamii* and the four species thus tend to coincide with the rates at which leaf area is lost.

5.3.2 Analysis of leaf chemistry

Leaf cuticle thickness

The measurements of leaf cuticle thickness are given in Table 5.8. Of the five species tested, the two rainforest species *Nothofagus cunninghamii* and *Atherosperma moschatum* had the thinnest cuticles, with an average cuticle thickness of 2.2 (± 0.6) μm and 1.3 (± 0.3) μm respectively. That *N. cunninghamii* had the thicker cuticle is consistent with the fact that it is more tolerant of water stress than is *A. moschatum* (Howard 1973a).

The two sclerophyll forest species, *Eucalyptus regnans* and *Acacia melanoxylon* had the thickest leaf cuticles with average values of 6.9 (± 1.9) μm and 4.4 (± 1.1) μm respectively. The remaining species '*Lomatia fraseri*' had a cuticle thickness value closer to that of the sclerophyll forest species at 4.1 (± 1.6) μm than it did to the rainforest species. *E. regnans* had the thickest cuticle thicknesses at 11.2 μm (Appendix 5.3). The lowest value was for *Atherosperma moschatum* at 0.8 μm (Appendix 5.3).

Table 5.8 The average cuticle thickness of the five tree species used in this study. All thicknesses are given in μm. The source photomicrographs can be found in Appendix 5.3.

Species	Average Cuticle thickness (μm)	Standard Deviation (μm)	Number of Measurements	Number of Leaf Sections
Acacia melanoxylon	4.4	1.1	95	19
Atherosperma moschatum	1.3	0.3	101	20
Eucalyptus regnans	6.9	2.0	109	22
Lomatia fraseri	4.1	1.6	99	20
Nothofagus cunninghamii	2.2	0.6	95	19

Initial leaf nutrient status

The initial elemental composition data of the leaf material of each species is shown in Table 5.9. *Acacia melanoxylon* had the highest total nitrogen at 2.7% (w/w). The total nitrogen figures for the other four species varied between 1.2% to 1.7%. The total phosphorus figures for the five tree species were similar, ranging between 0.07 to 0.09% (w/w). Sulphur levels varied widely between species, with *Nothofagus cunninghamii* having the lowest (0.09 mg/g) while *A. melanoxylon* had the highest at 0.33 mg/g. *Atherosperma moschatum* had the highest manganese concentration (1600 μg/g) and *Eucalyptus regnans* the lowest (210 μg/g), an eight fold difference.

Table 5.9 Elemental analysis of fresh green leaves of the five tree species used. *Acc.* = *Acacia melanoxylon*; *Ath.* = *Atherosperma moschatum*; *Euc.* = *Eucalyptus regnans*; *Lom.* = *Lomatia fraseri*; *Noth.* = *Nothofagus cunninghamii*.

Results	**Units**	*Acc.*	*Ath.*	*Euc.*	*Lom.*	*Noth.*
Total Nitrogen	% (w/w)	2.70	1.70	1.80	1.20	1.40
Total Phosphorus	% (w/w)	0.07	0.09	0.09	0.07	0.09
Total Potassium	% (w/w)	0.54	1.20	0.48	0.74	0.58
Total Sulphur	% (w/w)	0.33	0.01	0.12	0.12	0.09
Total Calcium	% (w/w)	0.57	1.10	0.27	0.74	0.47
Total Magnesium	% (w/w)	0.23	0.24	0.16	0.14	0.18
Total Sodium	% (w/w)	0.17	0.04	0.06	0.01	0.04
Total Copper	µg/g	4	5	8	4	4
Total Zinc	µg/g	12	14	11	7	26
Total Manganese	µg/g	460	1600	210	1200	520
Total Iron	µg/g	53	93	57	170	130
Total Boron	µg/g	23	19	14	10	16

Lignin content

The lignin contents varied considerably between species, with the lowest figures being recorded for leaves of *Atherosperma moschatum* and *Eucalyptus regnans* at 21.0% and 25.7% respectively (Table 5.10). The low lignin concentrations for these two species also matches the rapid decay rates seen in Figures 5.6 c & d. The lignin determination for *Acacia melanoxylon* was 31.9% which is near a previously published value of 34.9% (Wedderburn and Carter 1999). The highest figure was for *N. cunninghamii* (at 35.0%); *L. fraseri* had a lignin content of 28.2%.

Table 5.10 The percentage of ether soluble extracts and the lignin content for the five species used in LDE2. All samples were done in duplicate.

Species Name	**Ether Soluble Extracts (%)**	**Crude Lignin Content (%)**	**Lignin to Nitrogen Ratio**
Atherosperma moschatum	11.2	21.0	12.4
Acacia melanoxylon	7.0	31.9	11.8
Eucalyptus regnans	22.5	25.7	14.3
Lomatia fraseri	7.1	28.2	23.5
Nothofagus cunninghamii	7.9	35.0	25.0

The percentage of ether soluble materials in the leaf samples was also varied greatly (Table 5.10). The figure of 22.5% for *E. regnans* was nearly twice the value of the species with next highest value, *Atherosperma moschatum.* The other three species had values that were close to each other, ranging from 7.0% to 7.9%.

Relationships between chemical variables and decay rate

The Pearson Correlation analysis indicated that different leaf physiochemical factors were important for different treatments (Table 5.11). For the stream buried treatment, phosphorus (r = -0.586; p = 0.049) and Lignin to Nitrogen ratio (L:Nr) (r = -0.654; p = 0.028) were negatively correlated with decay rate. The higher the phosphorus and L:Nr levels in the leaves the lower the decay rate. In the stream surface treatment none of leaf physiochemical characters were significant, though nitrogen concentration was the closest factor to significance (r = -0.520; p = 0.076). In the land buried treatment phosphorus was significant (r = -0.782; p = 0.006) and in the land surface treatment L:Nr was significant (r = -0.745; p = 0.011). In no case was manganese found to be significant.

When the significant factors were entered into a multiple regression against treatment, a number of highly significant relations ships were found. For the land and stream buried treatments the regression of total phosphorus and L:Nr gave a high r^2 and was statistically significant (Table 5.12). For the land surface treatment, L:Nr alone was regressed against decay rate and was found to be significant.

Table 5.11 Results of the one tailed Pearson Correlation analysis. The *r* value is followed an '*' were a significant relationship was found. SB = Stream Buried; SS = Stream Surface; LB = Land Buried; LS = Land Surface.

Factor	Treatment			
	SB	SS	LB	LS
Total P	-0.586*	-0.359	-0.782*	0.073
Manganese	-0.184	-0.548	-0.542	-0.077
Lignin	0.027	0.461	0.418	-0.445
Lignin to Nitrogen ratio	-0.654*	-0.308	-0.344	-0.745*
Total Nitrogen	0.115	-0.162	-0.342	0.580

Table 5.12 Results of the multiple regression analysis of the significant factors indicated in table 5.10 against treatment. All values marked with an '*' were significant. SB = Stream Buried; SS = Stream Surface; LB = Land Buried; LS = Land Surface; P = total phosphorus, L:Nr = lignin to nitrogen ratio

Factor	Treatment			
	SB	SS	LB	LS
Factors included	P; L:Nr	None	P; L:Nr	L:Nr
r^2	0.711	-	0.689	0.555
Adjusted r^2	0.615	-	0.586	0.491
Significance (*P*)	0.024*	-	0.030*	0.021*

5.3.3 Mesocosm Experiments

The decay curves for the *Lomatia fraseri* and *Nothofagus cunninghamii* samples are given in Figures 5.7a-b. Graphical comparisons between the two species for each treatment are given in figures 5.8a-f. The statistical analysis indicates that there were significant differences between the decay curves of each treatment (Tables 5.13 and 5.14). The decay curves of each species were also significantly different ($p \leq 0.001$). When both *L. fraseri* and *N. cunninghamii* are compared graphically, *L. fraseri* is decaying more rapidly in all of the treatments (Figures 5.8 a-f and Table 5.14).

Of the six treatments, only the aerobic 5°C treatment was significantly different from all the others ($p < 0.001$), where the low temperature was suppressing the decay rates of both species (Table 5.14, Figure 5.7a & b). The aerobic 15°C treatment was

Table 5.13 Summary of the SPSS data output for the Tukey HSD ANOVA's between treatment and species for the mesocosm decay curve data. All numbers given are *p* values and those marked with an '*' are significant at 0.05 confidence.

Treatment (i)	Treatment(j)	Significance
Excess N & P	Aerated 10°C	0.058
	Aerated 10°C(a)	0.970
	Anaerobic 10°C	0.995
	Aerobic 5°C	0.000*
	Aerobic 15°C	0.000*
Aerated 10°C	Excess N & P	0.058
	Aerated 10°C(a)	0.291
	Anaerobic 10°C	0.187
	Aerobic 5°C	0.000*
	Aerobic 15°C	0.180
Aerated 10°C(a)	Excess N & P	0.970
	Aerated 10°C	0.291
	Anaerobic 10°C	1.000
	Aerobic 5°C	0.000*
	Aerobic 15°C	0.000*
Anaerobic 10°C	Excess N & P	0.995
	Aerated 10°C	0.187
	Aerated 10°C(a)	1.000
	Aerobic 5°C	0.000*
	Aerobic 15°C	0.000*
Aerobic 5°C	Excess N & P	0.000*
	Aerated 10°C	0.000*
	Aerated 10°C(a)	0.000*
	Anaerobic 10°C	0.000*
	Aerobic 15°C	0.000*
Aerobic 15°C	Excess N & P	0.000*
	Aerated 10°C	0.180
	Aerated 10°C(a)	0.000*
	Anaerobic 10°C	0.000*
	Aerobic 5°C	0.000*

Table 5.14 The decay rate coefficients for *Nothofagus cunninghamii* and *Lomatia fraseri* for the mesocosm decay experiments.

Treatment	*Nothofagus cunninghamii*	*Lomatia fraseri*
Excess N & P	-0.150	-0.314
Aerated 10°C	-0.164	-0.345
Aerated 10°C(a)	-0.162	-0.310
Anaerobic 10°C	-0.158	-0.310
Aerobic 5°C	-0.108	-0.230
Aerobic 15°C	-0.159	-0.345

statistically different from all the others except the aerobic 10°C samples (p = 0.180; Table 5.13). The *L. fraseri* curve was more obviously different from the other *L. fraseri* curves, than was the *N. cunninghamii* curve from its counterparts (Figure 5.7a & b). As would be expected, the two sets of aerobic 10°C samples had no statistical differences between them (p = 1.000; Table 5.13). The impact of oxygen exclusion was statistically insignificant between the 10°C treatments (p = 0.187 < x > 1.000), regardless of the fact that the soils of the anaerobic 10°C mesocosms were strongly reducing. They had Eh readings between –323 (±14) mV to –397 (±25) mV, while the other 10°C treatments were oxidising (Table 5.3). The impact of excess Nitrogen and Phosphorus was fairly low, with no statistical differences between it and the other 10°C treatments (Table 5.13). None of the 10°C treatments differed statistically from each other with temperature alone having a statistically significant impact upon decay rates.

5.4 Discussion

Decay rates

The leaves of the five tree species, *Acacia melanoxylon*, *Atherosperma moschatum*, *Eucalyptus regnans*, *Lomatia fraseri* and *Nothofagus cunninghamii* decayed at vastly different rates (Tables 5.4 & 5.5). In LDE1 the overall order of decay rates were *Acacia melanoxylon* < *Lomatia fraseri* < *Nothofagus cunninghamii* < *Atherosperma moschatum*, with the first three species having very close k values. In LDE2 the order was *Nothofagus cunninghamii* < *Acacia melanoxylon* < *Lomatia fraseri* < *Eucalyptus regnans* < *Atherosperma moschatum*. The overall LDE2 decay curves for *Eucalyptus regnans* and *Lomatia fraseri* where not statistically different from the other curves. There is thus clear evidence supporting hypothesis 3 (Section 5.1) that the five different species decay at different rates. Spicer (1981) also found that leaves of different European tree

species decayed at different rates. Decay rates were faster in LDE2 than in LDE1, and the decay rates were faster for surface treatments than the buried treatments, supporting hypothesis 1, that oxygen restricted buried samples would decay more slowly than the aerobic surface samples.

The leaves of *Atherosperma moschatum* decayed the most rapidly irrespective of treatment (Figures 5.1a-d, 5.2b, 5.3a-d, 5.4b, and Tables 5.4 & 5.5). It was the only species whose k value exceeded –1.0, for all treatments and its k values fell in the upper range of the values in Tables 1.4 and 5.1.

The decay coefficients (Table 5.4) for *Acacia melanoxylon* leaves fell into the mid-range of values shown in Tables 1.4 and 5.1, and the impact of treatment was greater than for *Atherosperma moschatum*, varying between –0.351 and –0.866 for LDE1 and –0.931 and –0.280 for LDE2. The k values for the *A. melanoxylon* treatments demonstrate the impact of the 'surface' verses the 'buried' treatments for LDE1 (Figure 5.5a & b and Table 5.4). The surface samples, in their oxygen rich environment, decay more rapidly than the anaerobic, buried samples (Tables 5.4 & 5.5). The high lignin content of these leaves is the most likely cause of this difference. Lignin degradation requires oxygen and in anaerobic environments decay rates should be lower (Brinson, 1977; Reese, 1977; Eriksson *et al.*, 1990; Bernhard-Reversat, 1993; Berg & Matzner, 1997). Harmon *et al.* (1986; p. 172) commented that oxygen was required for significant rates of microbial decomposition of lignin, and while fungal decomposition has been observed in anaerobic conditions it occurs at rates are far lower than under aerobic conditions.

Few literature based decay rates are available for *Acacia melanoxylon,* the main studies being Campbell *et al.* (1992b) and Wedderburn and Carter (1999). Of these reports only the later has a decay rate coefficient that is directly comparable to the current study (k = -0.34; Table 5.1). Wedderburn and Carter (1999) used leaf bags (1 mm

mesh size) on a forest floor in high rainfall conditions north of Hamilton, New Zealand. This decay rate was lower than the equivalent land surface samples measured here (k = -0.866 & -0.872), with leaf bags of 2 mm mesh size suggesting large variations between locations. Bag mesh size may be important, as the larger mesh size used in the current study would have allowed larger soil meso and macro fauna entry into the leaf bags enhancing grazing damage and decay rate.

The decay rates for *Eucalyptus regnans* leaves showed a definite 'buried' versus 'surface' response, with the oxygen restricted buried samples decaying more slowly than the surface decay samples (Table 5.4 and Figures 5.4c). There are two literature based decay rates for *E. regnans* comparable to the current study, both originating from forests in similar climates, within 100 km of the Cumberland Creek field site. The first, Ashton (1975) is comparable with the *E. regnans* land surface treatment. The rate measured in the current study (k = -1.345) is higher than those published by Ashton (1975; k = -0.25 to -0.83; Table 1.5), who buried green *E. regnans* leaves 5 mm below the forest floor litter and found strong seasonal variations in decay rate. The stream surface value (k = -1.238) is comparable and lower than the calculated values from Blackburn and Petr (1979), (k = 4.94 & 4.18) who examined leaf decay in a stream near the field site in southern Victoria.

The higher of the decay rates calculated from Blackburn and Petr's (1979) data (k = -4.95), was for leaf bags (in a stream) with a large mesh size of 3.9 mm. The lower value (k = -4.18) was for leaf bags with a mesh size of 0.5 mm, where as this current study used a 2 mm mesh size, allowing larger invertebrates to graze upon the leaves than Blackburn and Petr's later samples. The wide differences in decay rate measured between Blackburn and Petr (1979) and the current study are thus unlikely to be related to differences in bag mesh size, but more to differences in processing rates between

locations and seasons. That the leaves from the stream surface treatment had large round holes in many of the leaves (indicating that large particle feeders were able to access the leaf bags), suggests minimal exclusion of those large aquatic organisms responsible for shredding leaf material and accelerating decay rate. Large particle feeders tend to leave large round holes in the leaf blade, while small particle feeders remove predominantly intercostal tissue (Yonge, 1928; Petersen & Cummins 1974).

For *Lomatia fraseri* the LDE1 stream buried samples had a lower *k* value (-0.467) than the other three *L. fraseri* treatments, which also decayed at similar rates and were not statistically different (Tables 5.4 & 5.7). In both experiments, one of the buried treatments had the lowest decay rates (Table 5.4).

The LDE1 *Nothofagus cunninghamii* samples had the most pronounced response to treatment. The stream and land surface samples all decayed more rapidly than the stream and land buried samples. For example in LDE1, the stream buried treatment had a *k* value of -0.242, taking twice the time to reach 50% mass loss as the land buried treatment and three and six times longer than the land and stream surface treatments (Figure 5.5a-b).

Comparable literature based decay rates for *Nothofagus cunninghamii* can be calculated from Blackburn and Petr (1979). The *k* values, calculated from mass loss figures for leaf bags equivalent to the stream surface samples, were -4.11 and -1.77 for *N. cunninghamii* leaves in leaf packs with mesh sizes of 3.9 mm and 0.5 mm respectively. The size used here was 2 mm, so the size exclusion seen in Blackburn and Petr's 0.5 mm samples should not have occurred. Thus, as for *E. regnans*, the decay rate for *N. cunninghamii* leaves is variable between locations and the relative difference between species can be found at other locations. The *k* value of -1.537 for LDE1 stream surface samples approached that of the *N. cunninghamii* leaves in the 0.5 mm packs, but no

samples used in this experiment approached the rates seen in Blackburn and Petr's (1979) 3.9 mm packs.

In light of the above, the field data support hypothesis (1) that leaves buried in anaerobic sediments will generally decay more slowly than leaves in aerobic conditions. The hypothesis that leaves will decay more rapidly in aerobic ever wet conditions such as the stream channel as opposed to occasionally dry conditions (hypothesis 2) is also supported. The stream surface leaves consistently decayed more rapidly than leaves subjected to the other three treatments. The variance in the relative order of decay rates is dependent upon species and treatment, with *Atherosperma moschatum* always decaying rapidly (Tables 5.4 & 5.5). Hypothesis 4, that the relative order of decay rates will be the same in all depositional settings is therefore only partly proven, only *Atherosperma moschatum* has the same relative decay rate (the most rapid), regardless of treatment. The relative order of the other species tested is treatment dependent with *Acacia melanoxylon, Eucalyptus regnans, Lomatia fraseri,* and *Nothofagus cunninghamii* all having relative decay rates that vary with treatment.

The mesocosm experiments (Figures 5.7 and 5.8) indicated that temperature was the major factor involved in the acceleration or deceleration of decay rates (Tables 5.13 and 5.14). This is in general agreement with assertions made Whitkamp (1966) and later researchers that an increase in temperature accelerates decay rate (e.g. Kaushik & Hynes, 1971; Petersen & Cummins, 1974; Williams & Gray, 1974; Gallardo & Merino, 1993). The 5°C samples decayed more slowly than the 15°C samples, thus supporting hypothesis nine, that the 15°C samples will decay more rapidly than the 5°C samples.

Interestingly, the Eh of the mesocosms (Table 5.3) had no statistically significant effect upon the decay rate of the 10°C samples, and neither did the addition of exogenous

nitrogen and phosphorus (Table 5.13). The lack of statistical effect for the anaerobic treatment at 10°C is at variance with the field data, where the anaerobic buried treatments had a generally negative effect upon decay rate. The lack of effect of high levels of exogenous nitrogen and phosphorus upon decay rate is at variance with a body of literature that suggests decay rate is positively linked to nutrient levels (Kaushik & Hynes, 1971; Howarth & Fisher, 1976; Elwood *et al.*, 1981; Meyer & Johnson, 1983; Vogt *et al.*, 1986; Royer & Minshall, 2001). The hypothesis that sediments rich in nutrients such as nitrogen and phosphorus (hypothesis ten) is thus untenable.

Leaf area loss and decay rate

The rate of leaf area loss generally mirrored the rate of leaf mass loss measured by the decay rate coefficients; a pattern also found by Ferguson (1985). Generally the species and treatment combinations which lost mass rapidly also lost leaf area rapidly and those species with low k values lost leaf area more slowly. This result suggests that k values can be used as an indicator as to which species are likely to preserve and enter the fossil record. For example, *Atherosperma moschatum* leaves quickly lost structural integrity with time, the pattern of rapid leaf area loss mirroring that of leaf mass loss (Table 5.4 & Figures 5.6a (i-iv)). Similarly, the rate leaf area loss and fragmentation for *Eucalyptus regnans* and *Lomatia fraseri* leaves mirrored the pattern of leaf mass loss in response to treatment (Table 5.4 & Figures 5.6c & d (i-iv)), while the rate of leaf area loss for *Acacia melanoxylon* and *Nothofagus cunninghamii* generally reflected their lower mass decay rates. These species tended to undergo little *post mortem* change in leaf blade area, remaining recognisable to the eight month mark, probably due to their high lignin content. The stream surface samples of these two species with their high k values showed some signs of deterioration after eight months, often involving the large

rounded holes indicative of large particle feeders (Yonge, 1928; Petersen & Cummins, 1974; Figure 5.6a (ii) & 5.6e(ii)).

Leaf chemistry and decay rate

The correlation and regression analyses indicated that different leaf physiochemical factors were important for different treatments. For the stream buried treatment, phosphorus and L:Nr were negatively correlated with decay rate (Tables 5.11 & 5.12). The higher the phosphorus and L:Nr levels in the leaves the lower the decay rate. In the stream surface treatment none of leaf physiochemical characters were significant, though nitrogen concentration was the closed factor to significance (r = -0.520; p = 0.076). In the land buried treatment, phosphorus was significant and in the land surface treatment L:Nr was significant. In no case was manganese found to be significant. These findings are in general agreement with the published literature that initial L:Nr and phosphorus are good predictors of decay rate (Cortez *et al.*, 1996; Berg & Matzner, 1997; Gallardo & Merino, 1999; Liu *et al.*, 2000).

A number of authors have suggested that leaves with a high manganese concentration and low lignin concentration will decay more rapidly than those with low levels of manganese and high lignin concentrations (Hayes, 1979; Berg *et al.*, 1996; Fioretto *et al.*, 1998; Singh *et al.*, 1999; Wedderburn & Carter, 1999; Berg, 2000). The lack of correlation between decay rate and initial manganese concentration of any of the samples tested here would suggest that initial manganese concentrations are probably not important in determining decay rate of these species at Cumberland Creek. It is important to note that the initial tissue manganese concentrations are higher for the species tested at Cumberland Creek, than in the species for which the assertion that low initial tissue manganese concentrations predict low decay rates was initially made. For example

Fioretto *et al.* (1998) made the link between low decay rate and a low manganese concentration for *Pinus pinea* L. (Stone pine) at a manganese concentration of 53 μg/g. This manganese concentration is one quarter the lowest value found in the current study (Table 5.9). It is therefore possible that none of the Cumberland Creek samples had low enough manganese concentrations to inhibit decay rate.

The low L:Nr found in *Acacia melanoxylon* of 11.8 is at some variance with the idea that low a L:Nr equates to rapid decay rates. In LDE1 *Acacia melanoxylon* was the species decaying most slowly and was the second slowest decaying species in LDE2. However as Fioretto *et al.* (1998) commented, a higher concentration of lignin determines a greater proportion of nitrogen in recalcitrant forms (See also Berg, 1986). It is thus probable that the initial lignin concentration of 31.9% was sufficient to render the leaf material unpalatable to most organisms except under the conditions of the stream surface of LDE2, where many aquatic invertebrates capable of shredding the leaves presumably existed. The only literature based value for the L:Nr of *Acacia melanoxylon* was in Wedderburn & Carter (1999). This value was higher (L:Nr = 19.7) than for the current study and had a *k* value that was lower (-0.34), suggesting that the low L:Nr and high nitrogen status of *Acacia melanoxylon* leaves used in this study may have increased their palatability and their decay rates.

The lignin content of *Eucalyptus regnans* was 25.7 % and its L:Nr was 14.3 (Table 5.9). The lignin to nitrogen ratio for *E. regnans* is higher than for *Atherosperma moschatum* or for *Acacia melanoxylon*, and still falls within the low to mid range of the lignin and L:Nr values given in Table 5.1. The L:Nr ratio also sits well within the ranges of the three other *Eucalyptus* species listed in table 5.1. The low lignin content and relatively low lignin to nitrogen ratio for *E. regnans* again supports the idea that leaves low in lignin with low lignin to nitrogen ratios have rapid decay rates. The initial L:Nr's

for *L. fraseri* and *N. cunninghamii* (Table 5.11) are the highest of the five species examined.

The reduction in decay rate observed for the buried samples of the above species also agrees well with the literature based expectation that decay rates would be slower in anaerobic environments as opposed to aerobic ones (Whitkamp, 1966; Williams & Gray, 1974; Reese, 1977; Berg & Matzner, 1997). This phenomenon was expected because the metabolic activity of the aerobic white rot fungi needed to break down the lignin in the buried leaves would be greatly inhibited due to the lack of oxygen in the field sites anaerobic soils. In the absence of white rot fungi, the only available lignin degrading organisms are bacteria whose lignin decomposition rate is much slower (Leisola & Garcia, 1989). The decay rate suppression observed for buried samples of lignin rich leaves such as *Nothofagus cunninghamii* would also be expected, once the water soluble leaf fractions had leached out of the leaf, due to a lack of alternative energy substrate. No organism is known to use lignin as a sole energy source despite its potentially high energy content (Leisola & Garcia, 1989). This is what was found; for most of the species, especially *Nothofagus cunninghamii,* at least one of the buried treatments had the lowest decay rate. The surface samples on the other hand were not oxygen limited. Decay was more rapid, and the L:Nr's of the leaves would have had only a limited inhibition upon decay rate.

There is thus clear support for both hypotheses 5 and 6 that leaves high in lignin or which have a high L:Nr decay more slowly than leaves with relatively low lignin concentrations or low L:Nrs. The moderation of decay rates seen in those species with high L:Nrs, (except for the stream surface treatments) and the statistical significance of the findings suggest that L:Nr in particular is important in determining decay rate, thus supporting hypothesis six (Berg & Matzner, 1997; Gallardo & Merino, 1999; Berg,

2000). It is important to note the synergistic effect of phosphorous as well, where in combination with a high L:Nr it has a strong negative effect upon the decay rates of leaves subjected to the buried treatments. Leaf physiochemistry thus has a strong effect upon decay rate (hypothesis 7). In no case was nitrogen alone found to be an important predictor of decay rate. Therefore, hypothesis eight which predicted that leaves with a high initial nitrogen concentration will decay more rapidly than those with low initial nitrogen concentration is untenable (Table 5.11).

The impact of cuticle thickness upon decay rate was determined to be largely unimportant, as the species which had the thickest cuticle, *E. regnans* (6.9 μm), also happened to be one of the species which had the highest decay rates (Table 5.3 & Figure 5.5c-d). While the species with the second lowest cuticle thickness *Nothofagus cunninghamii*, had some of the lowest decay rates. The thin cuticle and rapid decay rate of *Atherosperma moschatum* may indicate that these two phenomena are linked, but if so, why did *N. cunninghamii* have decay times and 'k' values so much lower? The tacit hypothesis, that leaves with thicker cuticle have a low decay rate is therefore not valid.

Palaeobotanical implications

The high decay rates seen for *Atherosperma moschatum* under all four treatments may explain why this genus has a sparse fossil record. Few *Atherosperma* fossils are known, including those of the Plio-Pleistocene mudstones of Regatta Point, Tasmania and atherospermataceous wood from Cretaceous sediments of James Ross Island, Antartica (Hill & Macphail, 1985; Poole & Francis, 1999). If *A. moschatum* leaves decay rapidly under most preservational conditions, as suggested here, then its leaves would be rare in the fossil record. Of course it might be the case that no one has actually looked for leaf fossils of this genus.

The decay rate and leaf physiochemistry data raise the question of why *Acacia* fossils are comparatively rare. If the low decay rates and high lignin contents measured for *A. melanoxylon* hold for the genus, then *Acacia* phyllodes have the potential to preserve well under the right circumstances. Comparable L:Nr and k values exist for *Acacia auriculiformis* (L:Nr = 22; k = -0.96), and *A. mangium* (L:Nr = 19; k = -1.20) for land surface decay rates (Bernhard-Reversat, 1993). The decay rates are similar to those calculated for *A. melanoxylon* here (k = -0.866 & -0.872) and if the decay rates for buried leaves were also similar then preservation should occur under anaerobic burial. The fossil record for this genus is sparse with only a few localities recording its presence (Cookson, 1954; Martin, 1981; Hill, 1992; Macphail & Hill, 2001). The possibility exists therefore that the genus *Acacia* was either not a major part the Australian flora until the Neogene as suggested by Macphail and Hill (2001), or that it grew in places well away from water, where the chances of preservation were slim. Such locations would not need be far from a water course (i.e. tens to hundreds of metres), as the data in Chapter 3 indicate that overland transport of leaves after abscission is very restricted as is transport in high order or turbulent streams (Chapter 4).

The absence of a good fossil record for the genus *Eucalyptus* again can not be linked to leaves that decay rapidly when buried, as the stream and land buried decay rates were low (for *E. regnans* at least). As in the case of *Acacia*, the possibility exists that *Eucalyptus* as a genus grew in stands at a distance from nearby watercourses and thus didn't have the opportunity to become preserved. The propensity for *Eucalyptus* dominated vegetation to encourage fire may also be involved. Leaf material would probably not enter the fossil record if it were totally combusted before its preservation, though numerous examples of charcoalified leaves do exist (Spicer, 1991).

From a palaeobotanical point of view leaves of *Nothofagus cunninghamii* should also become preserved under the right circumstances because they have such low decay rates under anaerobic conditions (Figure 5.5a-d & Table 5.4). Even the *post mortem* changes in leaf area are small, as the leaves do not fragment and show few signs of attack by soil macro-fauna in any of the four treatments examined in LDE2 (Figures 5.6e (i-iv)). The only observable impact of the decay process was that the land surface leaves became thinner and more translucent as time progressed. The expectation therefore is that the leaves should preserve well upon burial, and their paucity in the fossil record may imply that the genus *Nothofagus* was either absent from those locations where preservation could occur, or rare in the landscape generally. The generality of this supposition is limited by the lack of lignin and nitrogen data for subgenus *Brassospora*, the taxon common as pollen in Australian Paleogene floras.

The possibility remains that there are significant ecological and leaf physiochemical differences between decidious and evergreen members of the genus and between the different subgenera of genus *Nothofagus*. In the absence of additional ecological and physiochemical information for the different subgenera and habits of *Nothofagus,* it is plausible to suggest that the rarity of *Nothofagus* leaves in many Australian Tertiary fossil floras may indeed best be explained by:

1. The trees not being major components of the source vegetation, or;
2. The trees grew in stands far enough away from water courses so as to not normally become preserved in stream, swamp and lake sediments.

5.5 Conclusions

Five main conclusions can be drawn from these results. First, leaves from the different plant species examined decay at different rates. Species bias in decay rates must be considered when fossil floras are analysed and their source vegetation reconstructed.

Secondly, the decay coefficients reported in the extensive forestry, ecology and limnological literature have the potential to enable the quantification of these sources of decay bias. These biases in decay rates may well be predictable across taxa and the well established practice of Nearest Living Relative (NLR) analysis could be used to quantify (in general terms), what these biases are, athough further work is needed (e.g. *Nothofagus* subgenus *Brassospora*).

Thirdly, where decay rate coefficients are lacking in the literature, lignin and lignin to nitrogen ratios can be used from the fossil taxon's NLR's to again quantify the magnitude of decay based species bias in fossil floras.

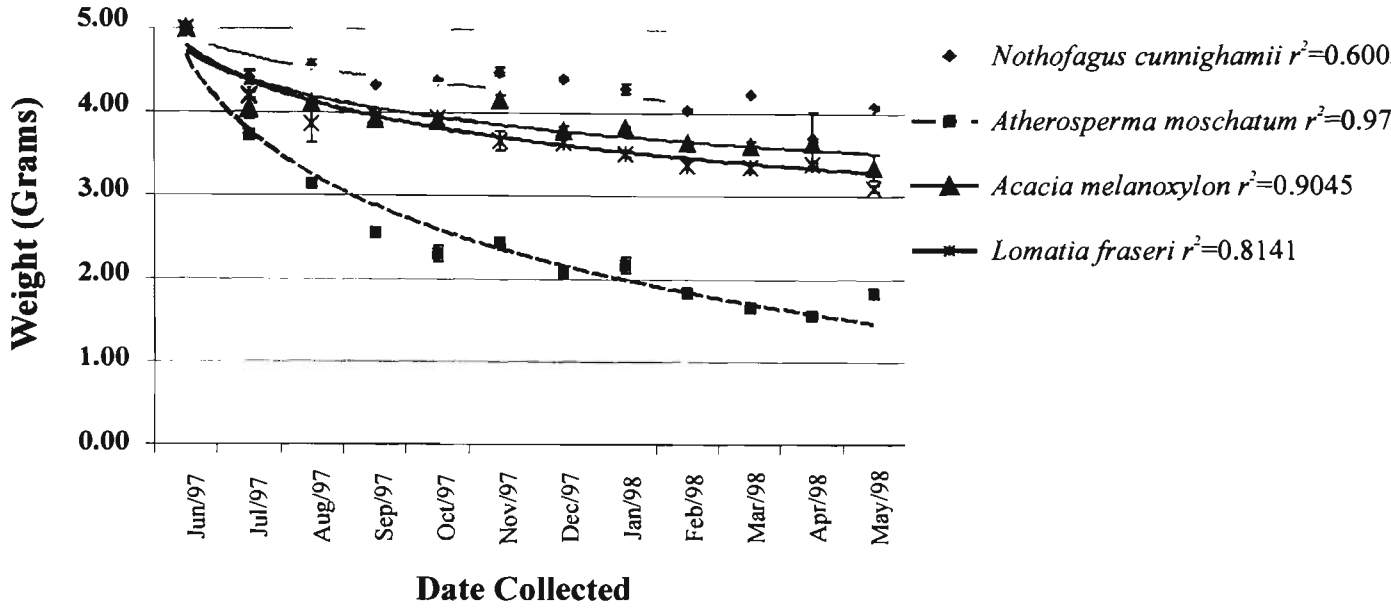
Fourthly, given that the leaves of *Nothofagus cunninghamii* may serve as a potential indicator for decay rate behaviour for the whole genus, then *Nothofagus* leaves should preserve well. In the event this assertion holds, then it would largely resolve the disparity between the macro and micro flora histories of this genus.The generality of this statement is not assessable in the absence of data for additional subgenera.

Fifthly, temperature seems to have more of an effect upon decay rate than other factors such as Eh or excess nitrogen and phosphorus.

Figure 5.1 The decay curve data for the LDE1 samples. The error bars for each data point show the standard error between the six samples collected for each data point. All five species tested in LDE1 are included on each graph of treatment versus time. The r^2 values indicate how closely the exponential trend lines, fit the data points.

Figure 5.1a Stream Buried
Figure 5.1b Stream Surface
Figure 5.1c Land Buried
Figure 5.1d Land Surface (over page)

a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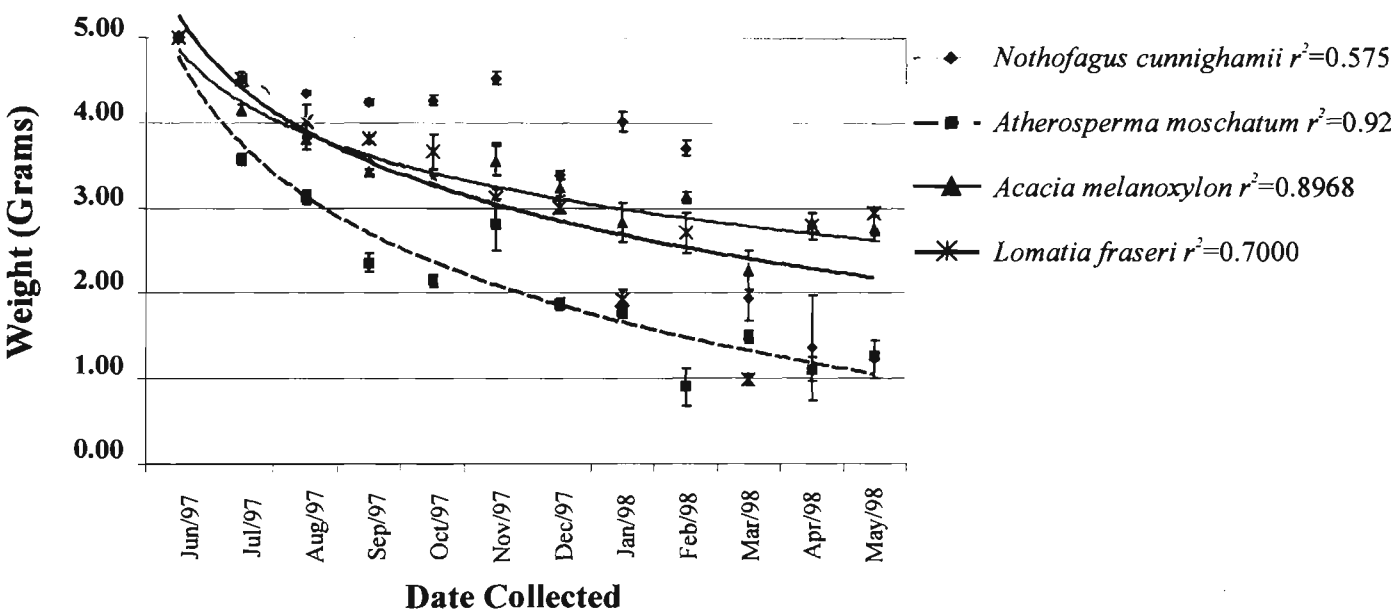
Date Collected
Nothofagus cunnighamii r²=0.600
Atherosperma moschatum r²=0.97
Acacia melanoxylon r²=0.9045
Lomatia fraseri r²=0.8141

b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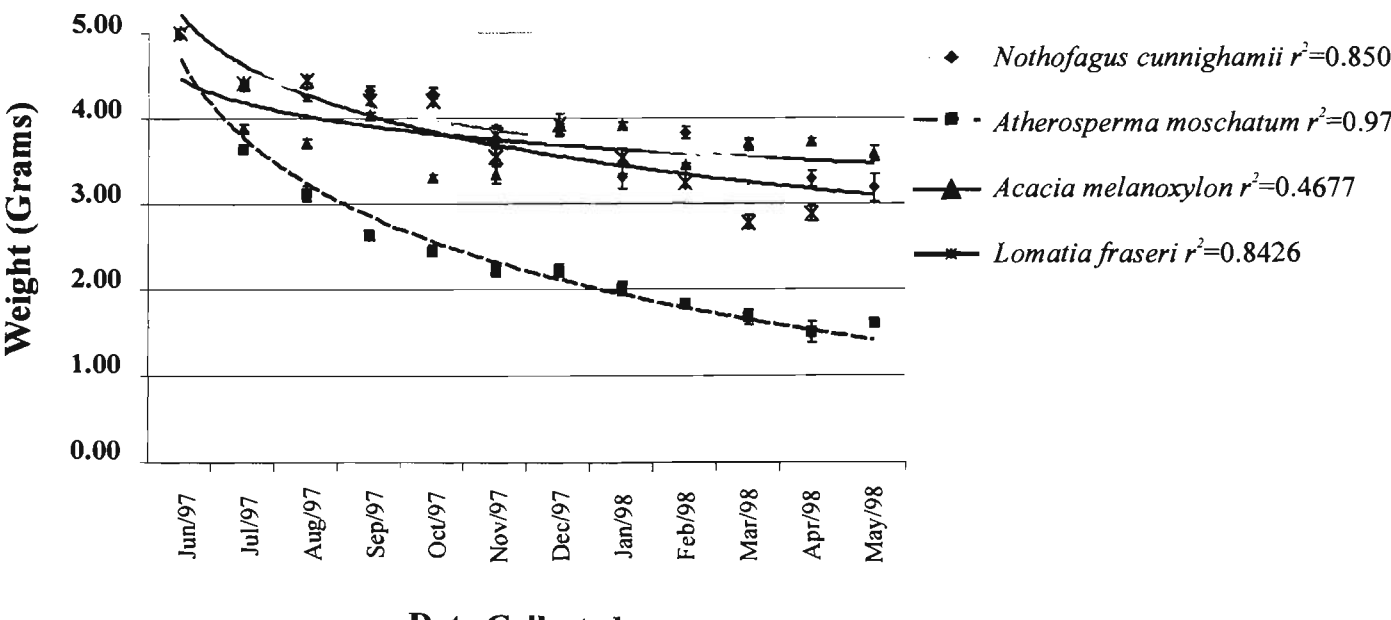
Date Collected
Nothofagus cunnighamii r²=0.575
Atherosperma moschatum r²=0.92
Acacia melanoxylon r²=0.8968
Lomatia fraseri r²=0.7000

c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Date Collected
Nothofagus cunnighamii r²=0.850
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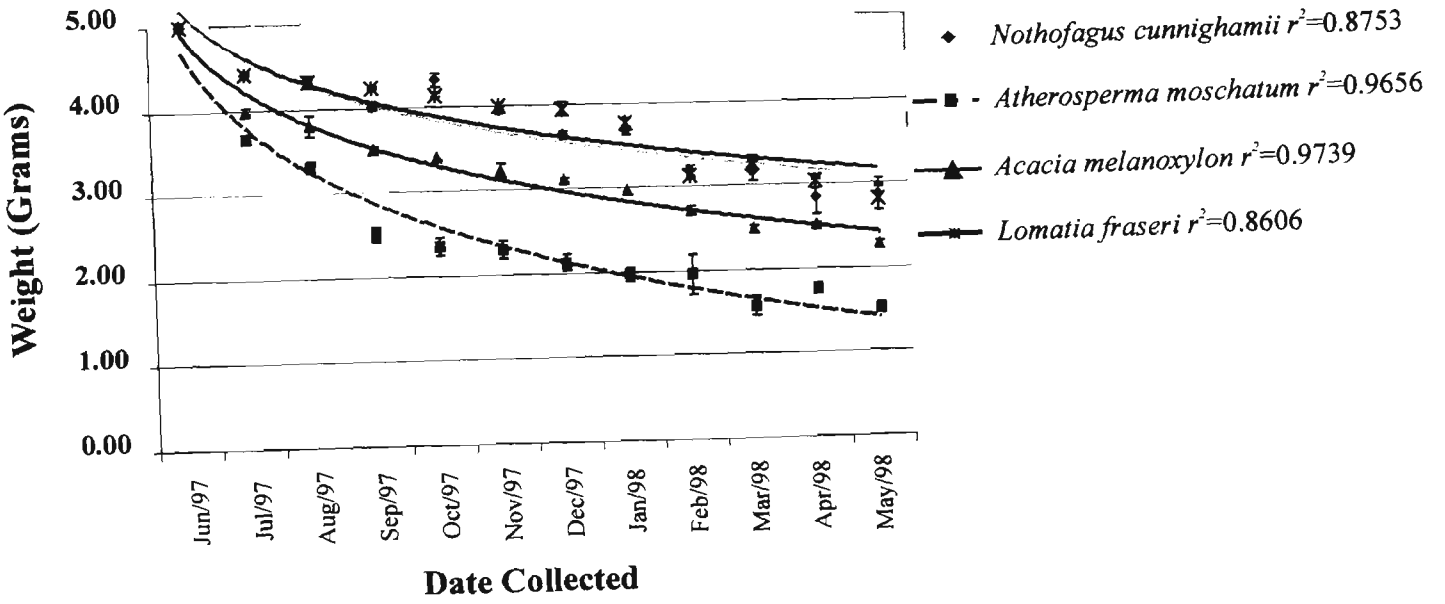
Acacia melanoxylon r²=0.4677
Lomatia fraseri r²=0.8426

d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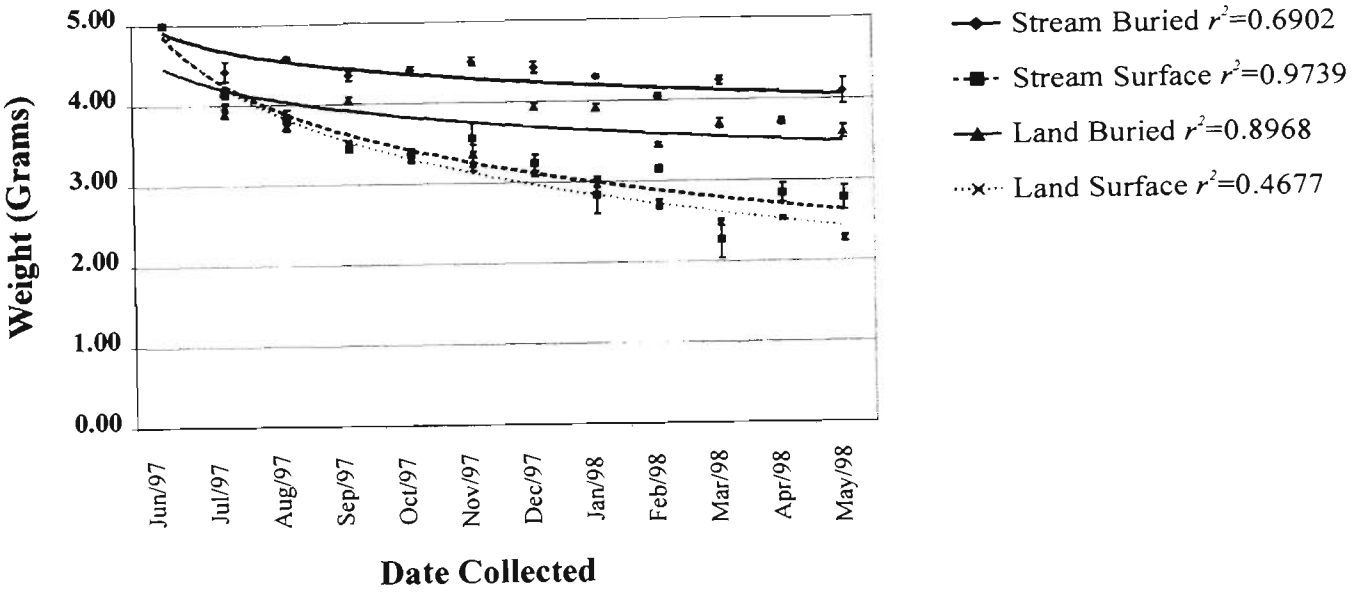
Date Collected
Nothofagus cunnighamii r²=0.8753
Atherosperma moschatum r²=0.9656
Acacia melanoxylon r²=0.9739
Lomatia fraseri r²=0.8606

Figure 5.2 The decay curve data for each species versus all four treatments for LDE2. The error bars for each data point show the standard error between the samples collected for each data point. The r^2 values indicate how closely the exponential trend lines, fit the data points.

Figure 5.2a *Acacia melanoxylon*
Figure 5.2b *Atherosperma moschatum*
Figure 5.2c *Lomatia fraseri*
Figure 5.2d *Nothofagus cunninghamii* (over page)

a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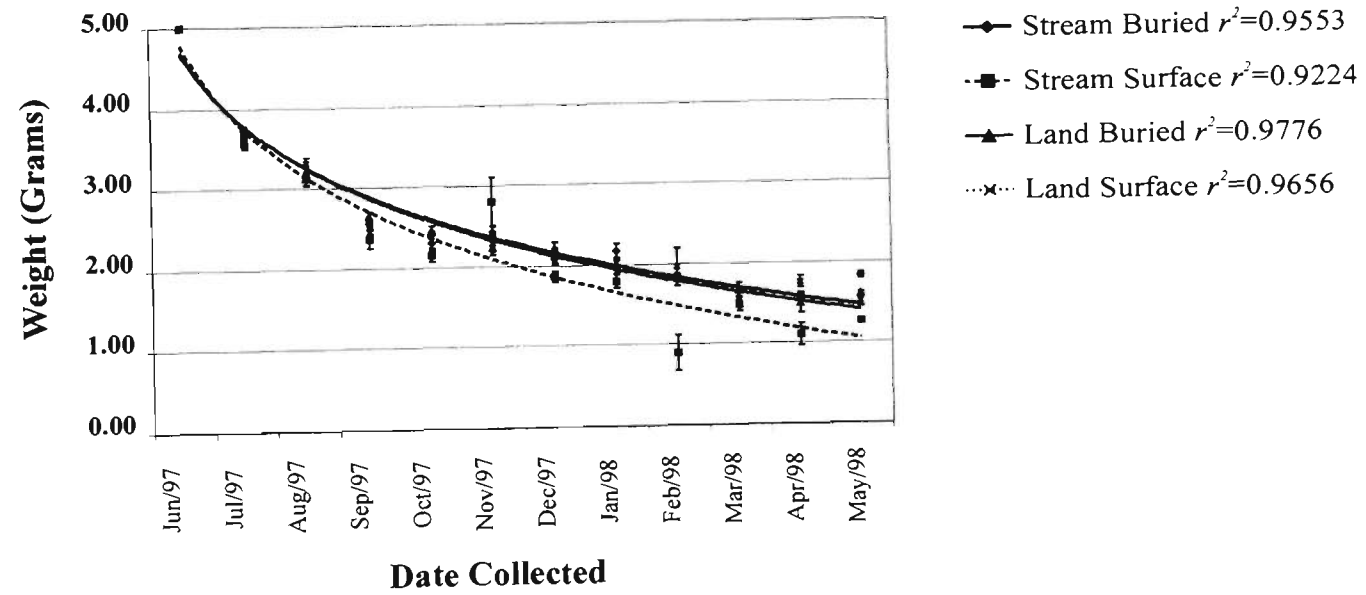
Date Collected
Stream Buried r^2=0.6902
Stream Surface r^2=0.9739
Land Buried r^2=0.8968
Land Surface r^2=0.4677

b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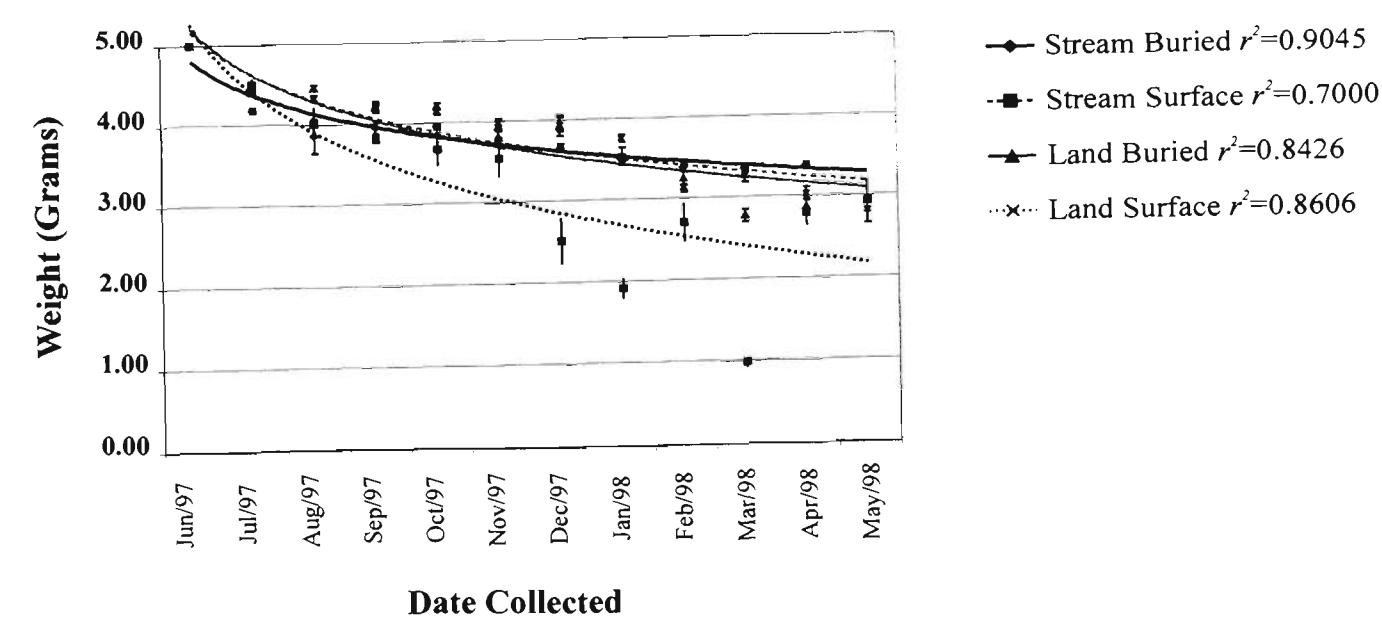
Date Collected
Stream Buried r^2=0.9553
Stream Surface r^2=0.9224
Land Buried r^2=0.9776
Land Surface r^2=0.9656

c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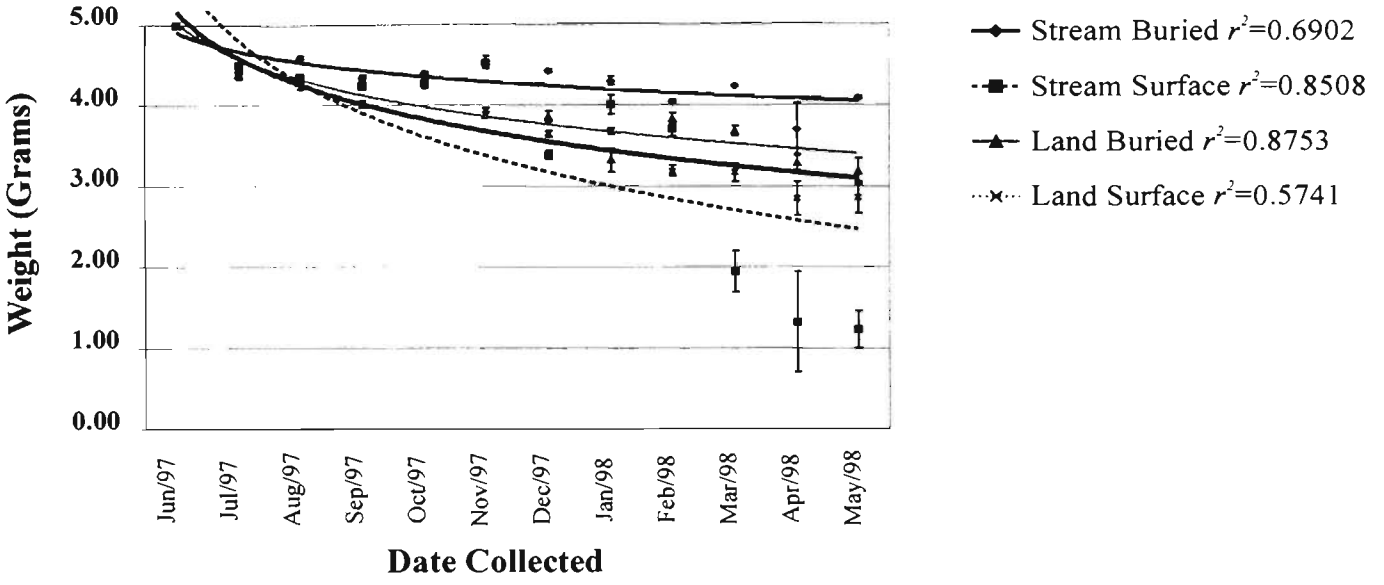
Date Collected
Stream Buried r^2=0.9045
Stream Surface r^2=0.7000
Land Buried r^2=0.8426
Land Surface r^2=0.8606

d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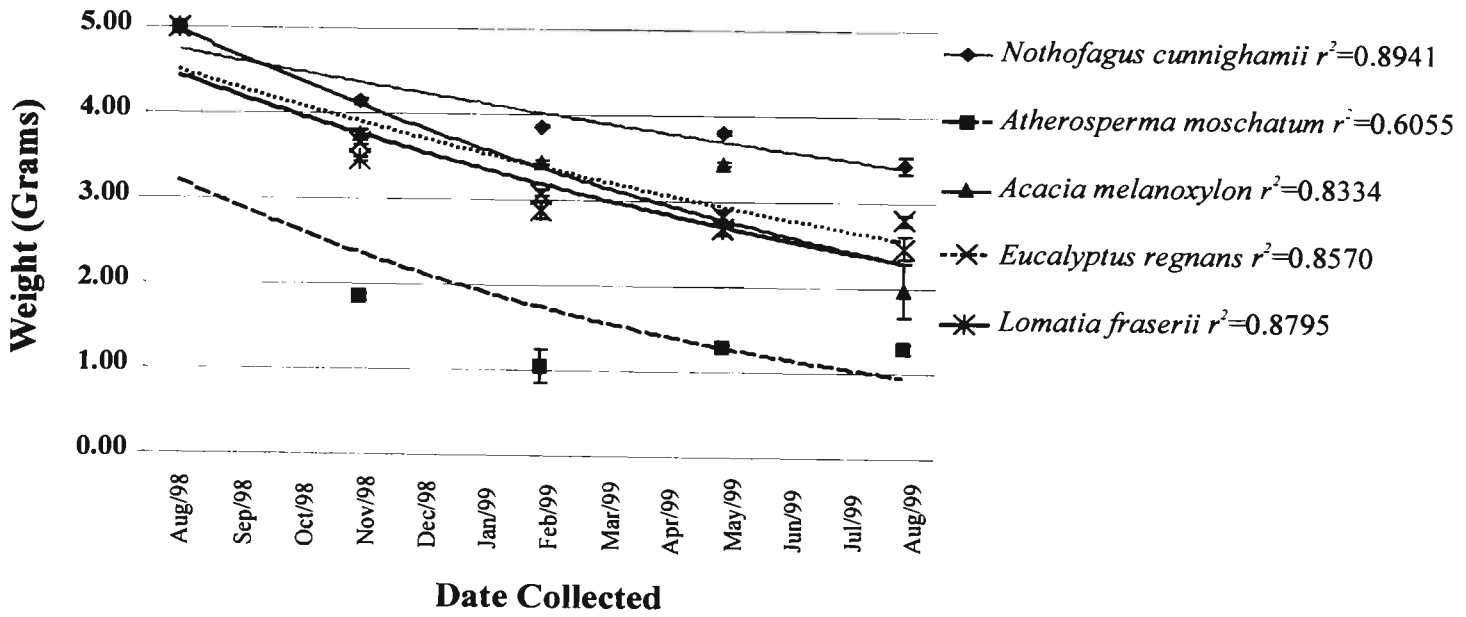
May/98
Date Collected
Stream Buried r^2=0.6902
Stream Surface r^2=0.8508
Land Buried r^2=0.8753
Land Surface r^2=0.5741

Figure 5.3 The decay curve data for the LDE2 samples. The error bars for each data point show the standard error between the six samples collected for each data point. All five species tested in LDE2 are included on each graph of treatment versus time. The r^2 values indicate how closely the exponential trend lines, fit the data points.

Figure 5.3a Stream Buried
Figure 5.3b Stream Surface
Figure 5.3c Land Buried
Figure 5.3d Land Surface (over page)

a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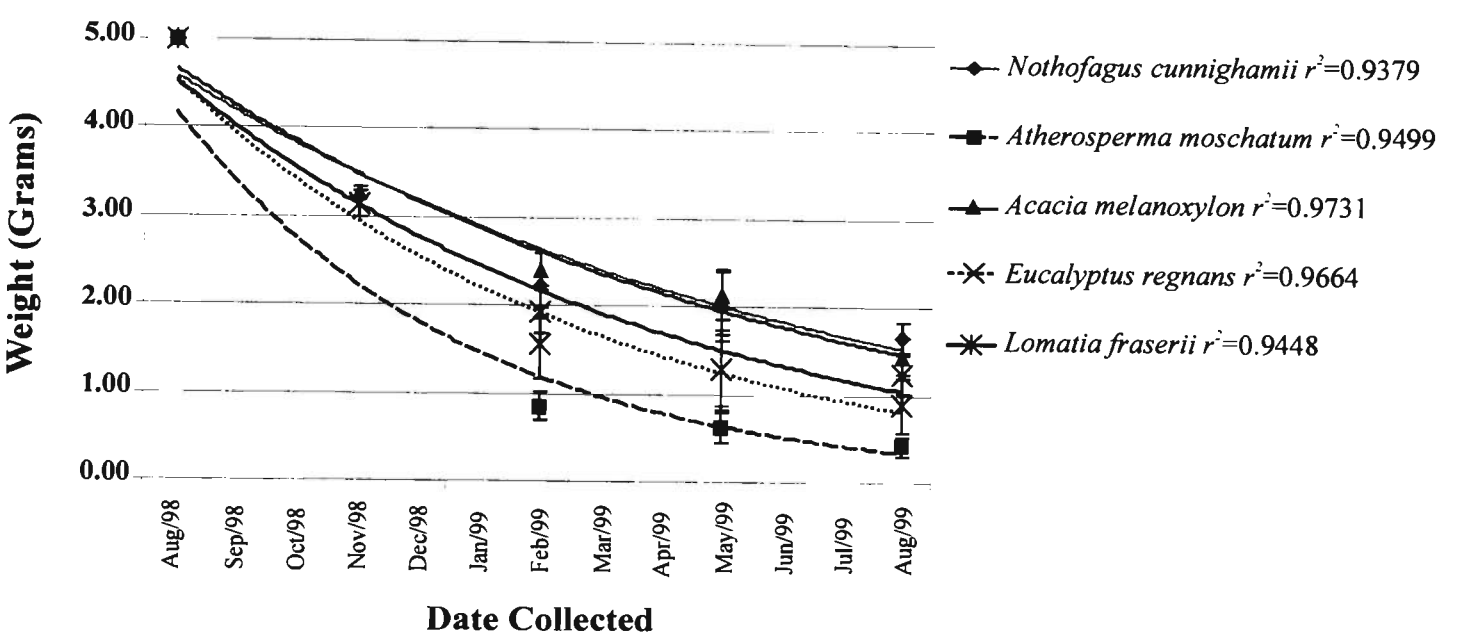
Date Collected
Nothofagus cunnighamii r²=0.8941
Atherosperma moschatum r²=0.6055
Acacia melanoxylon r²=0.8334
Eucalyptus regnans r²=0.8570
Lomatia fraserii r²=0.8795

b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Date Collected
Nothofagus cunnighamii r²=0.9379
Atherosperma moschatum r²=0.9499
Acacia melanoxylon r²=0.9731
Eucalyptus regnans r²=0.9664
Lomatia fraserii r²=0.9448

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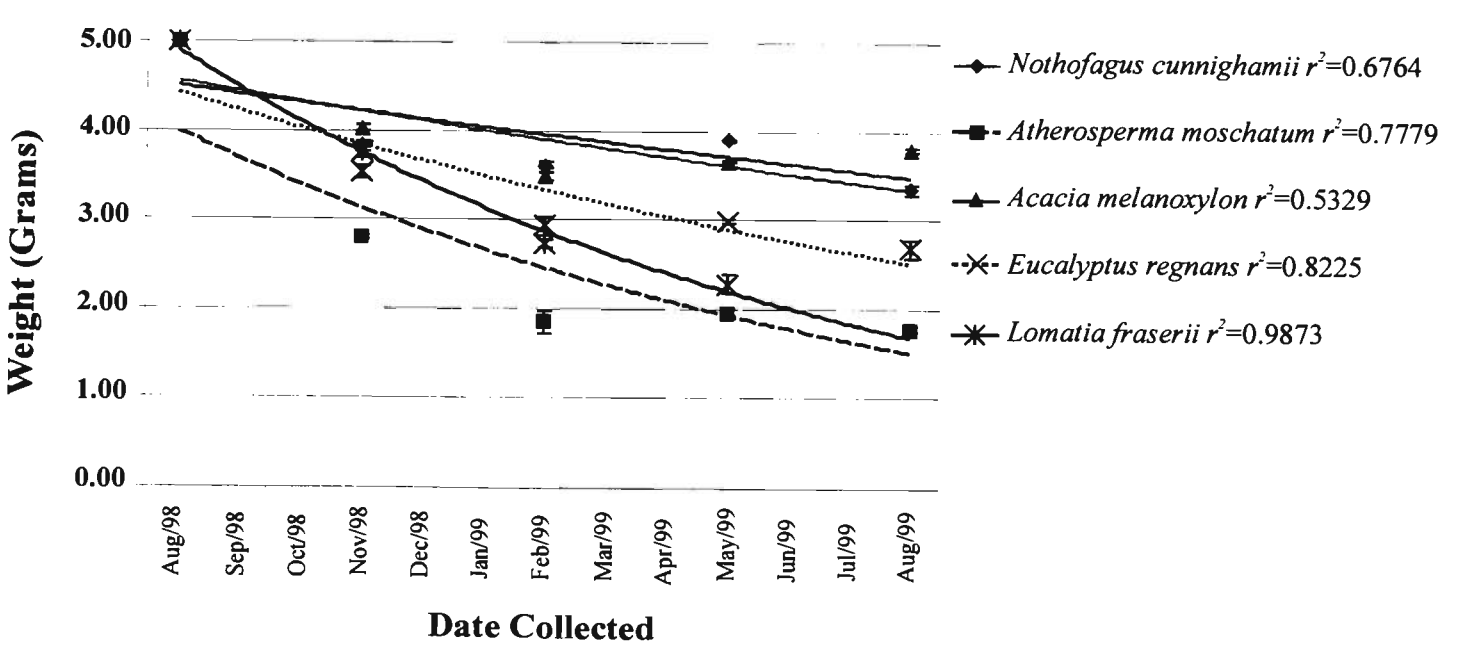
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Weight (Grams)
Aug/98
Sep/98
Oct/98
Nov/98
Dec/98
Jan/99
Feb/99
Mar/99
Apr/99
May/99
Jun/99
Jul/99
Aug/99
Date Collected
Nothofagus cunnighamii r²=0.6764
Atherosperma moschatum r²=0.7779
Acacia melanoxylon r²=0.5329
Eucalyptus regnans r²=0.8225
Lomatia fraserii r²=0.9873

d

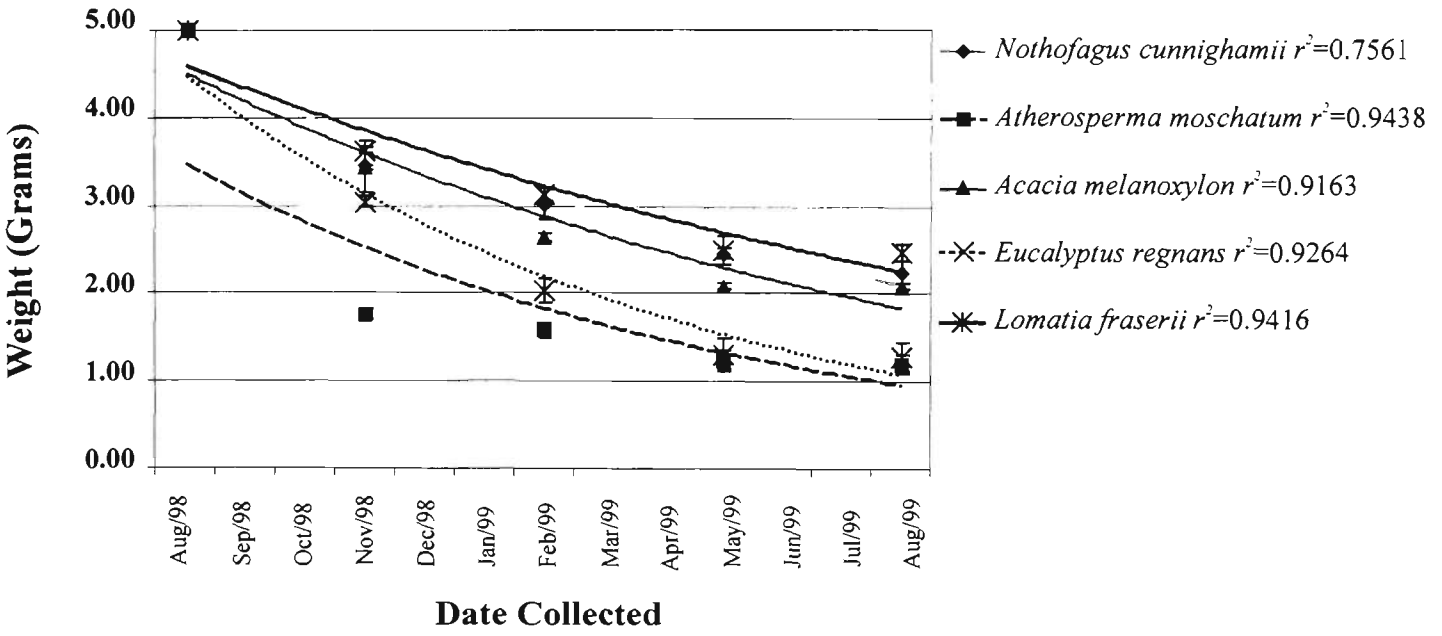
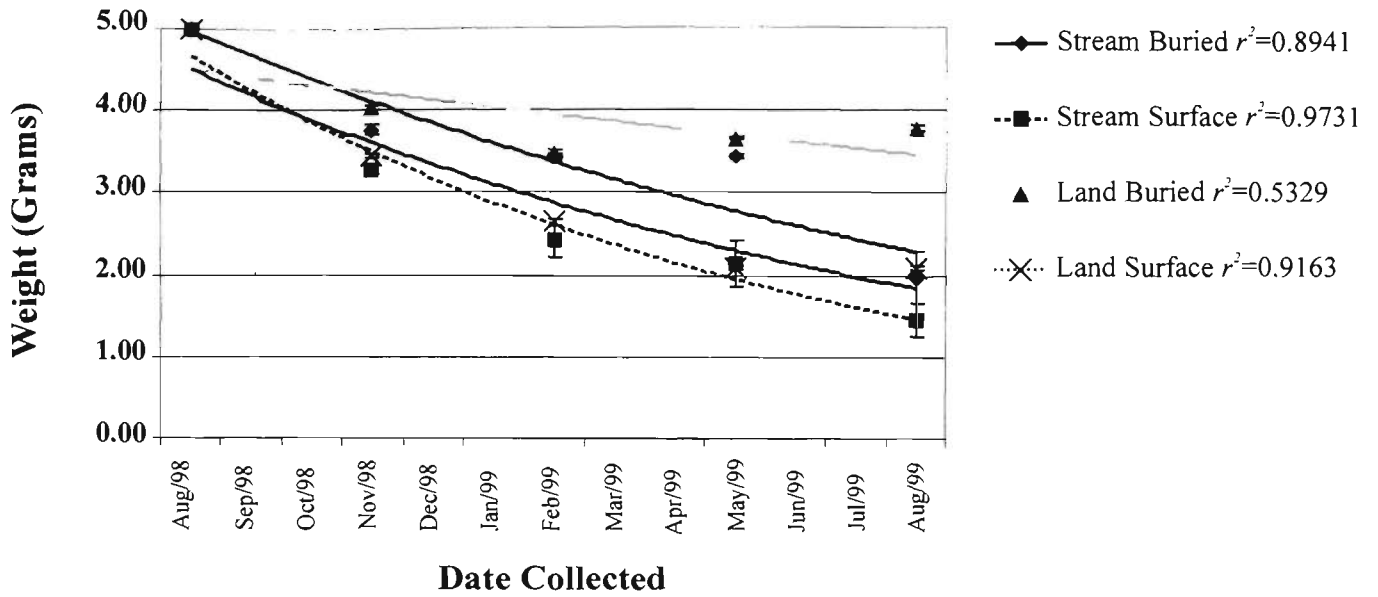

5.00
4.00
3.00
2.00
1.00
0.00
Weight (Grams)
Aug/98
Sep/98
Oct/98
Nov/98
Dec/98
Jan/99
Feb/99
Mar/99
Apr/99
May/99
Jun/99
Jul/99
Aug/99
Date Collected
Nothofagus cunnighamii r²=0.7561
Atherosperma moschatum r²=0.9438
Acacia melanoxylon r²=0.9163
Eucalyptus regnans r²=0.9264
Lomatia fraserii r²=0.9416

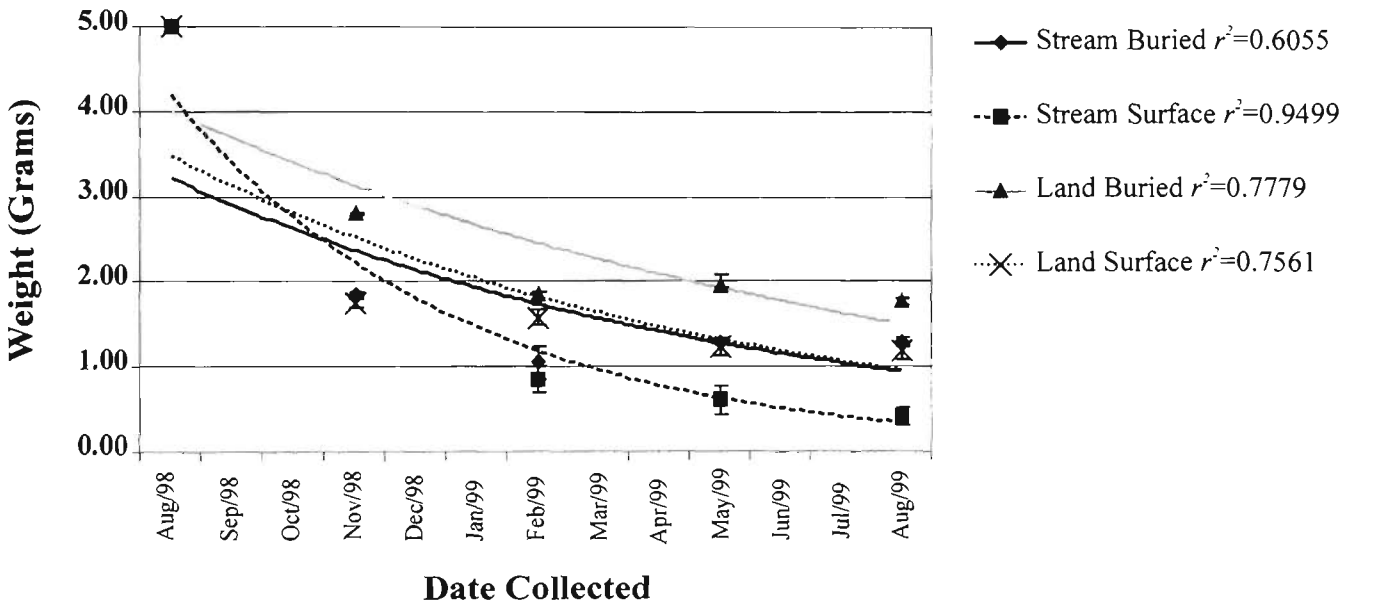
Figure 5.4 The decay curve data for each species versus all four treatments for LDE2. The error bars for each data point show the standard error between the samples collected for each data point. The r^2 values indicate how closely the exponential trend lines, fit the data points.

Figure 5.4a *Acacia melanoxylon*
Figure 5.4b *Atherosperma moschatum*
Figure 5.4c *Eucalyptus regnans*
Figure 5.4d *Lomatia fraseri*
Figure 5.4e *Nothofagus cunninghamii* (over page)

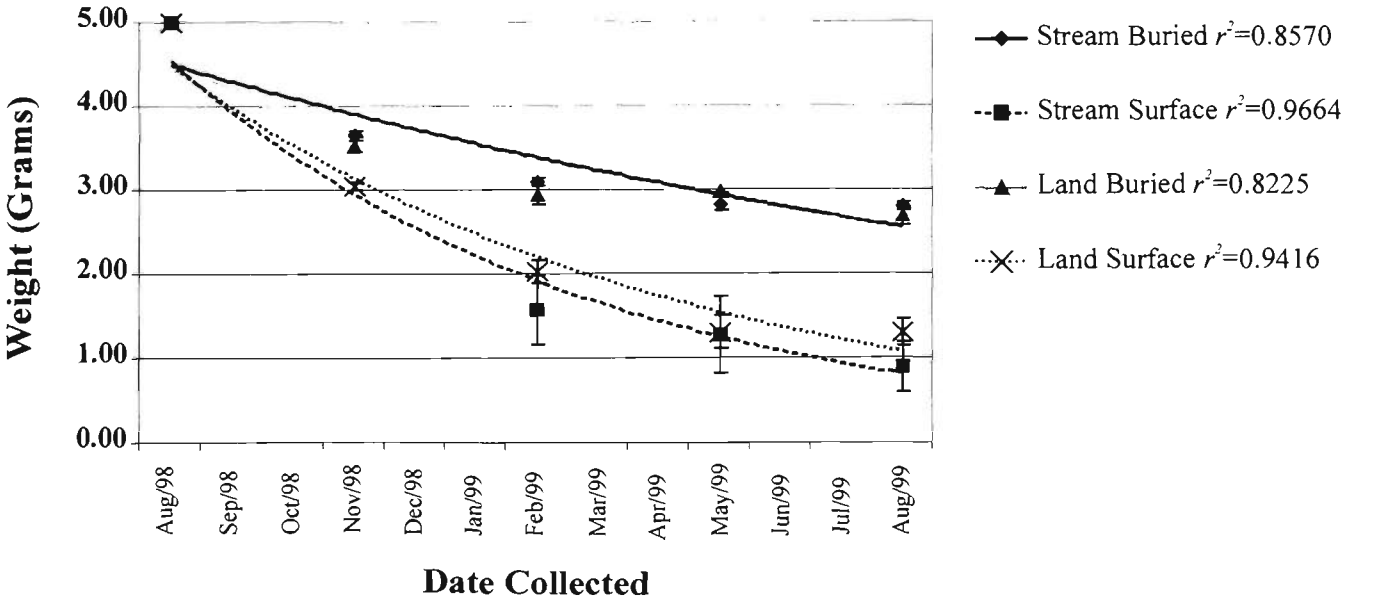
a


5.00
4.00
3.00
2.00
1.00
0.00
Weight (Grams)
Aug/98
Sep/98
Oct/98
Nov/98
Dec/98
Jan/99
Feb/99
Mar/99
Apr/99
May/99
Jun/99
Jul/99
Aug/99
Date Collected
Stream Buried r^2=0.8941
Stream Surface r^2=0.9731
Land Buried r^2=0.5329
Land Surface r^2=0.9163

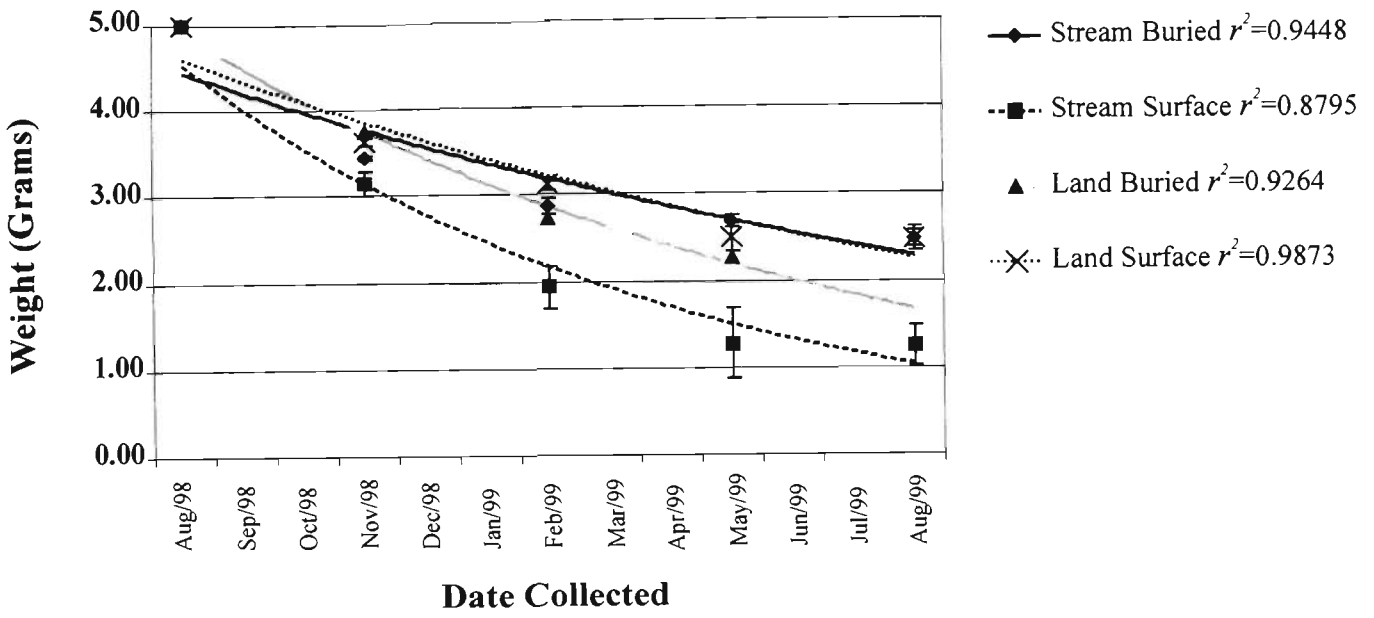
b


5.00
4.00
3.00
2.00
1.00
0.00
Weight (Grams)
Aug/98
Sep/98
Oct/98
Nov/98
Dec/98
Jan/99
Feb/99
Mar/99
Apr/99
May/99
Jun/99
Jul/99
Aug/99
Date Collected
Stream Buried r^2=0.6055
Stream Surface r^2=0.9499
Land Buried r^2=0.7779
Land Surface r^2=0.7561

c


5.00
4.00
3.00
2.00
1.00
0.00
Weight (Grams)
Aug/98
Sep/98
Oct/98
Nov/98
Dec/98
Jan/99
Feb/99
Mar/99
Apr/99
May/99
Jun/99
Jul/99
Aug/99
Date Collected
Stream Buried r^2=0.8570
Stream Surface r^2=0.9664
Land Buried r^2=0.8225
Land Surface r^2=0.9416

d


5.00
4.00
3.00
2.00
1.00
0.00
Weight (Grams)
Aug/98
Sep/98
Oct/98
Nov/98
Dec/98
Jan/99
Feb/99
Mar/99
Apr/99
May/99
Jun/99
Jul/99
Aug/99
Date Collected
Stream Buried r^2=0.9448
Stream Surface r^2=0.8795
Land Buried r^2=0.9264
Land Surface r^2=0.9873

e

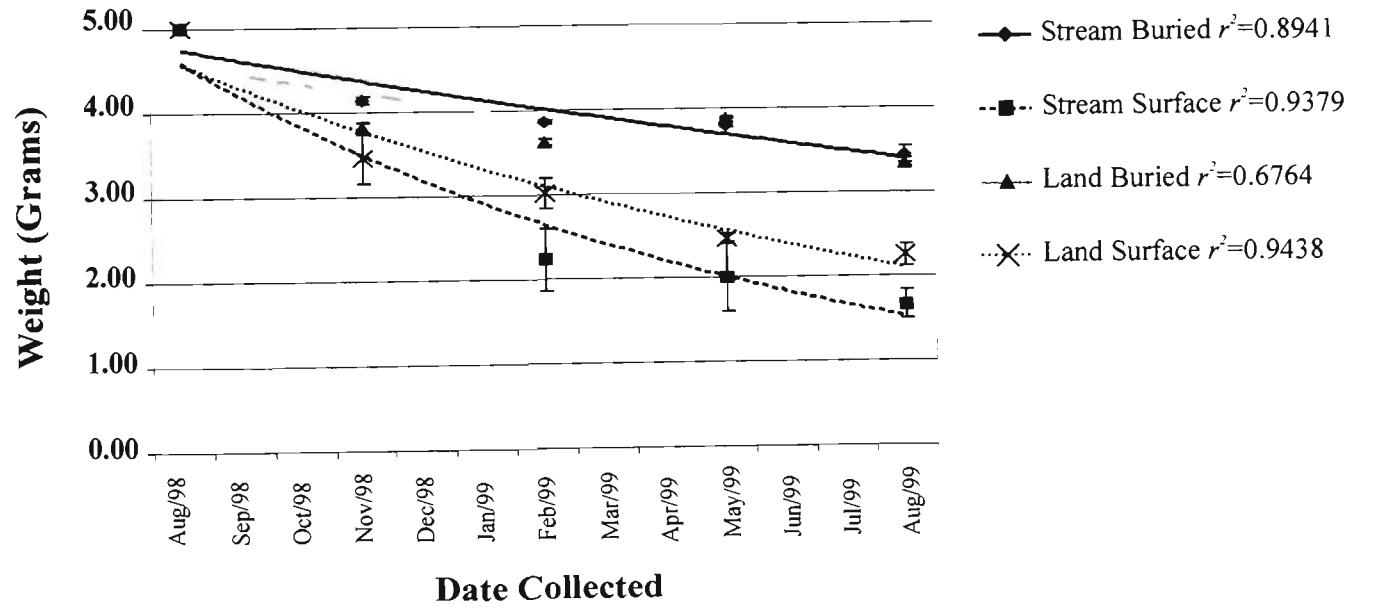
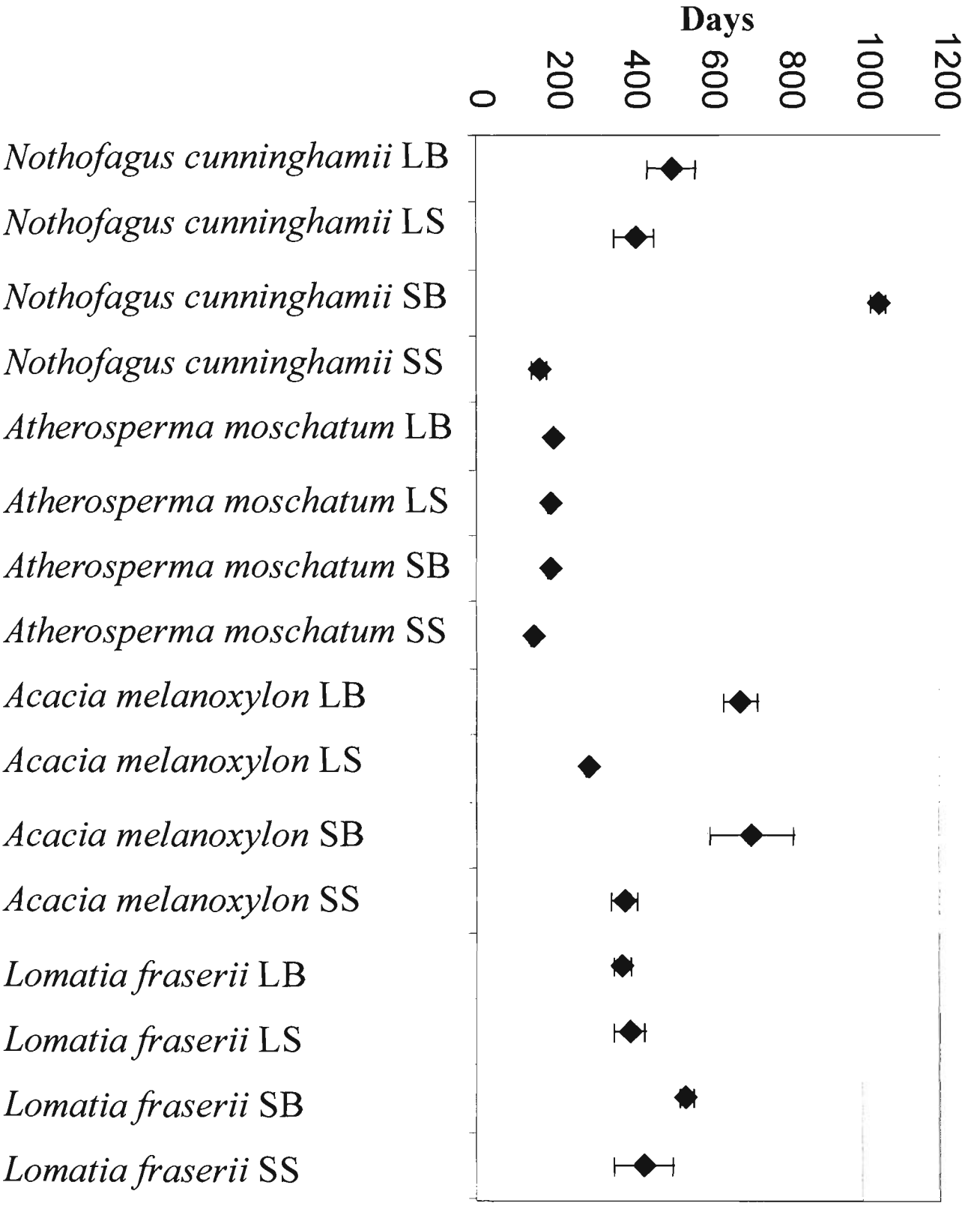

5.00
4.00
3.00
2.00
1.00
0.00
Weight (Grams)
Aug/98
Sep/98
Oct/98
Nov/98
Dec/98
Jan/99
Feb/99
Mar/99
Apr/99
May/99
Jun/99
Jul/99
Aug/99
Date Collected
Stream Buried r^2=0.8941
Stream Surface r^2=0.9379
Land Buried r^2=0.6764
Land Surface r^2=0.9438

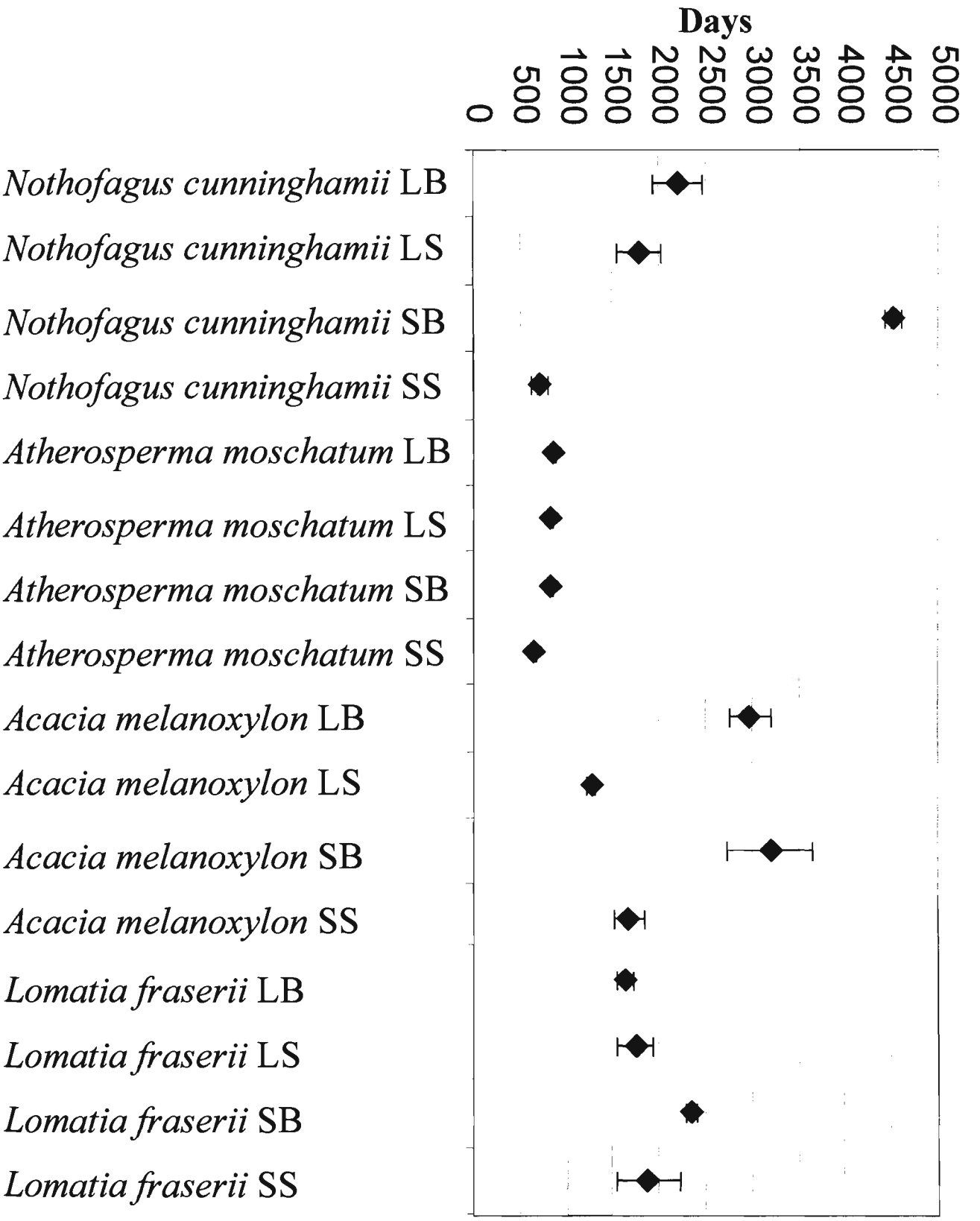
Figure 5.5 The calculated time in days needed for 50% and 95% mass loss. These times were calculated using the single exponential model. Error bars were determined by calculating the standard deviation for the group of samples used to collect the data point and entering them into the single exponential model to give upper and lower estimates of decay time.

Figure 5.5a The calculated time for 50% mass loss for LDE1 samples
Figure 5.5b The calculated time for 95% mass loss for LDE1 samples
Figure 5.5c The calculated time for 50% mass loss for the LDE2 samples
Figure 5.5d The calculated time for 95% mass loss for the LDE2 samples

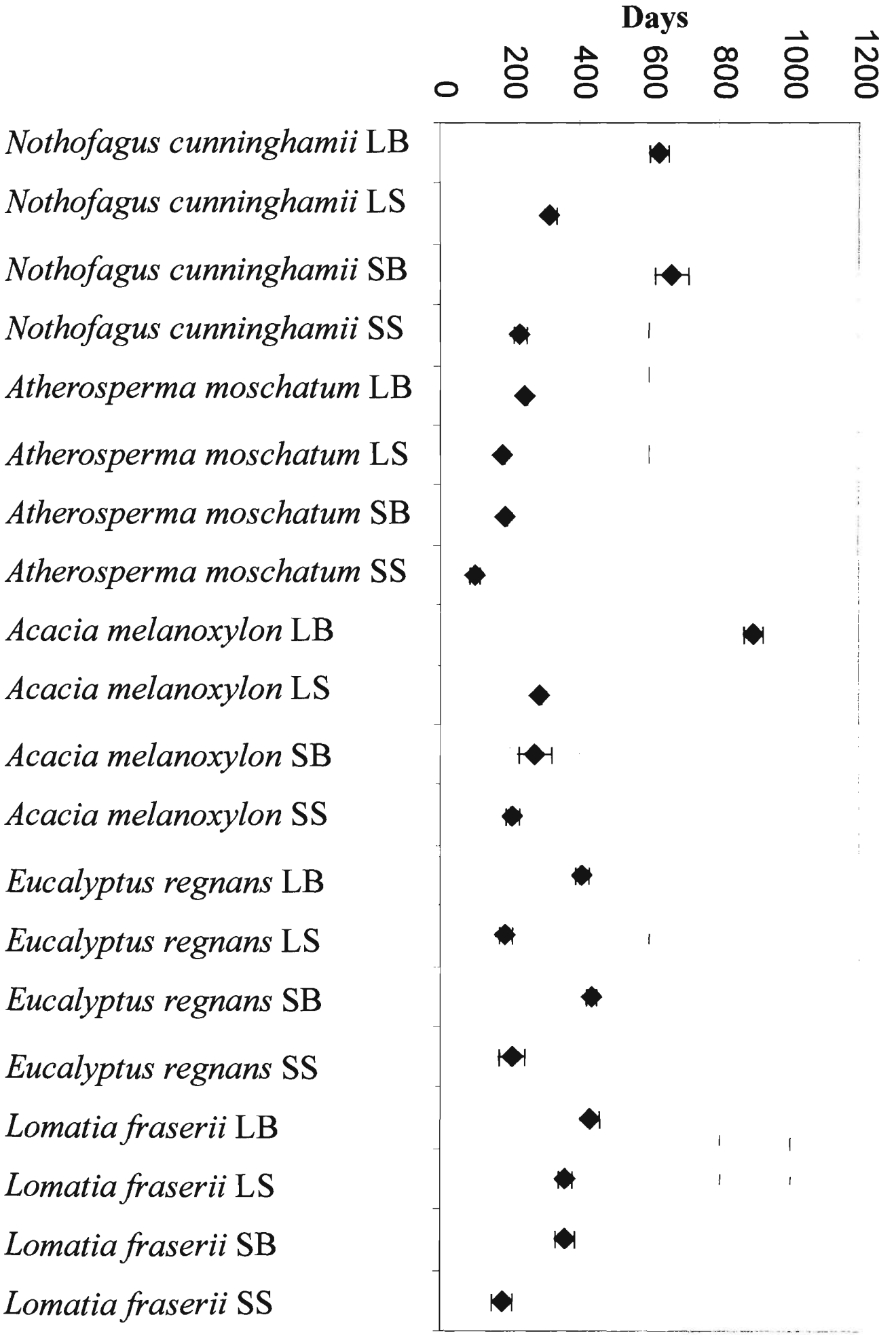
a **Predicted Time for 50% Mass Loss**



b **Predicted Time for 95% Mass Loss**



c


Predicted Time for 50% Mass Loss
Days
0
200
400
600
800
1000
1200
Nothofagus cunninghamii LB
Nothofagus cunninghamii LS
Nothofagus cunninghamii SB
Nothofagus cunninghamii SS
Atherosperma moschatum LB
Atherosperma moschatum LS
Atherosperma moschatum SB
Atherosperma moschatum SS
Acacia melanoxylon LB
Acacia melanoxylon LS
Acacia melanoxylon SB
Acacia melanoxylon SS
Eucalyptus regnans LB
Eucalyptus regnans LS
Eucalyptus regnans SB
Eucalyptus regnans SS
Lomatia fraserii LB
Lomatia fraserii LS
Lomatia fraserii SB
Lomatia fraserii SS

d **Predicted Time for 95% Mass Loss**

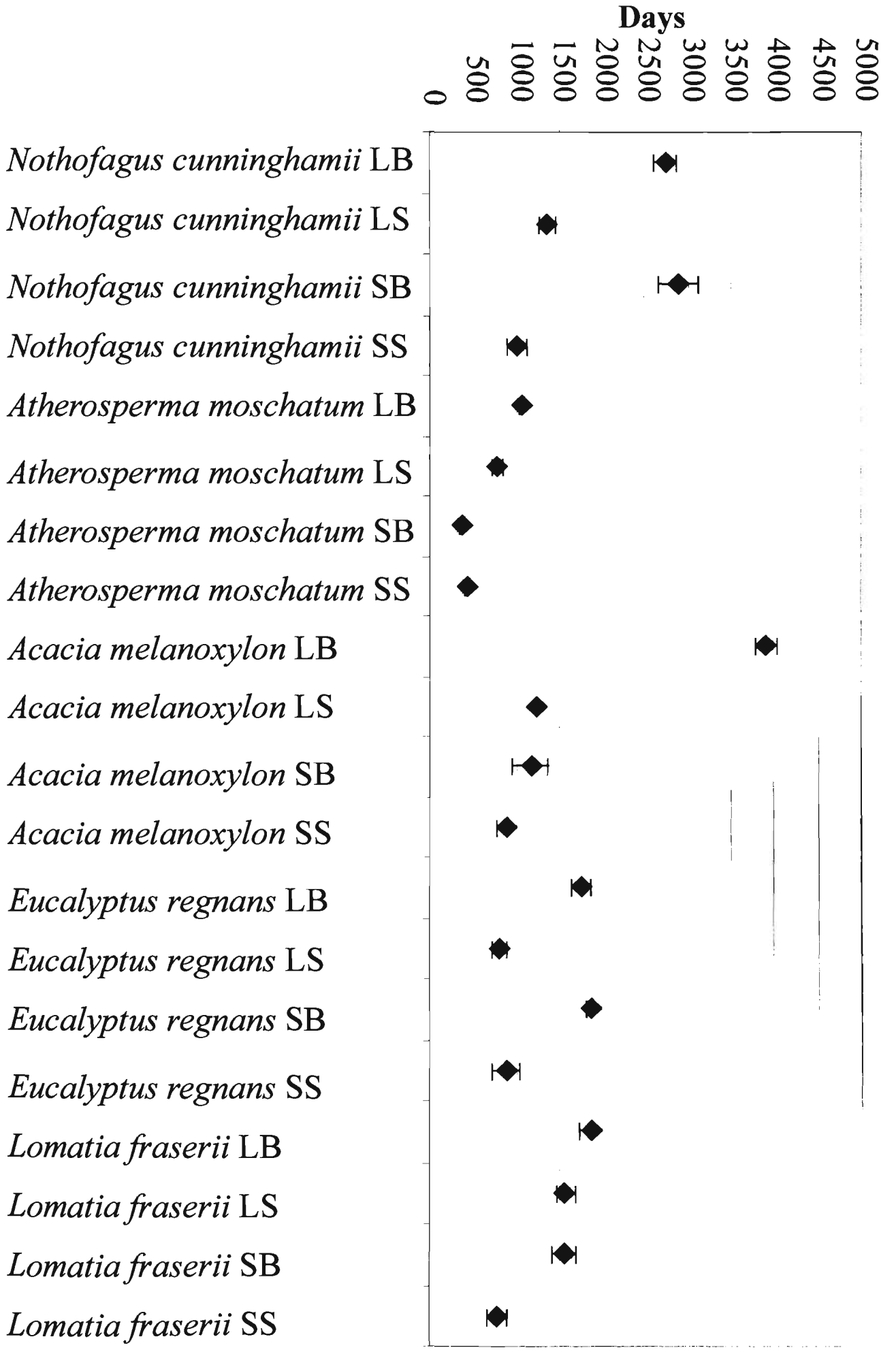


Figure 5.6 Scanned images of the leaves used in the Effects of Decay Time upon Leaf Area experiments. Leaves 1-10 are leaves that have been buried for 1 month, 11-20 are leaves that have been buried for two months, 21-30 are leaves that have been buried for four months and 31-40 are leaves that have been buried for eight months. If a monthly collection is not shown, then those samples were unable to be collected. For each species, four treatments are shown.

Figure 5.6a *Acacia melanoxylon.* Figure 5.6a(i) stream buried; Figure 5.6a(ii) stream surface; Figure 5.6a(iii) land buried; Figure 5.6a(iv) land surface.
Figure 5.6b *Atherosperma moschatum.* Figure 5.6b(i) stream buried; Figure 5.6b(ii) stream surface; Figure 5.6b(iii) land buried; Figure 5.6b(iv) land surface.
Figure 5.6c *Eucalyptus regnans.* Figure 5.6c(i) stream buried; Figure 5.6c(ii) stream surface; Figure 5.6c(iii) land buried; Figure 5.6c(iv) land surface.
Figure 5.6d *Lomatia fraseri.* Figure 5.6d(i) stream buried; Figure 5.6d(ii) stream surface; Figure 5.6d(iii) land buried; Figure 5.6d(iv) land surface.
Figure 5.6e *Nothofagus cunninghamii.* Figure 5.6e(i) stream buried; Figure 5.6e(ii) stream surface; Figure 5.6e(iii) land buried; Figure 5.6e(iv) land surface.

Figure 5.6a(i)

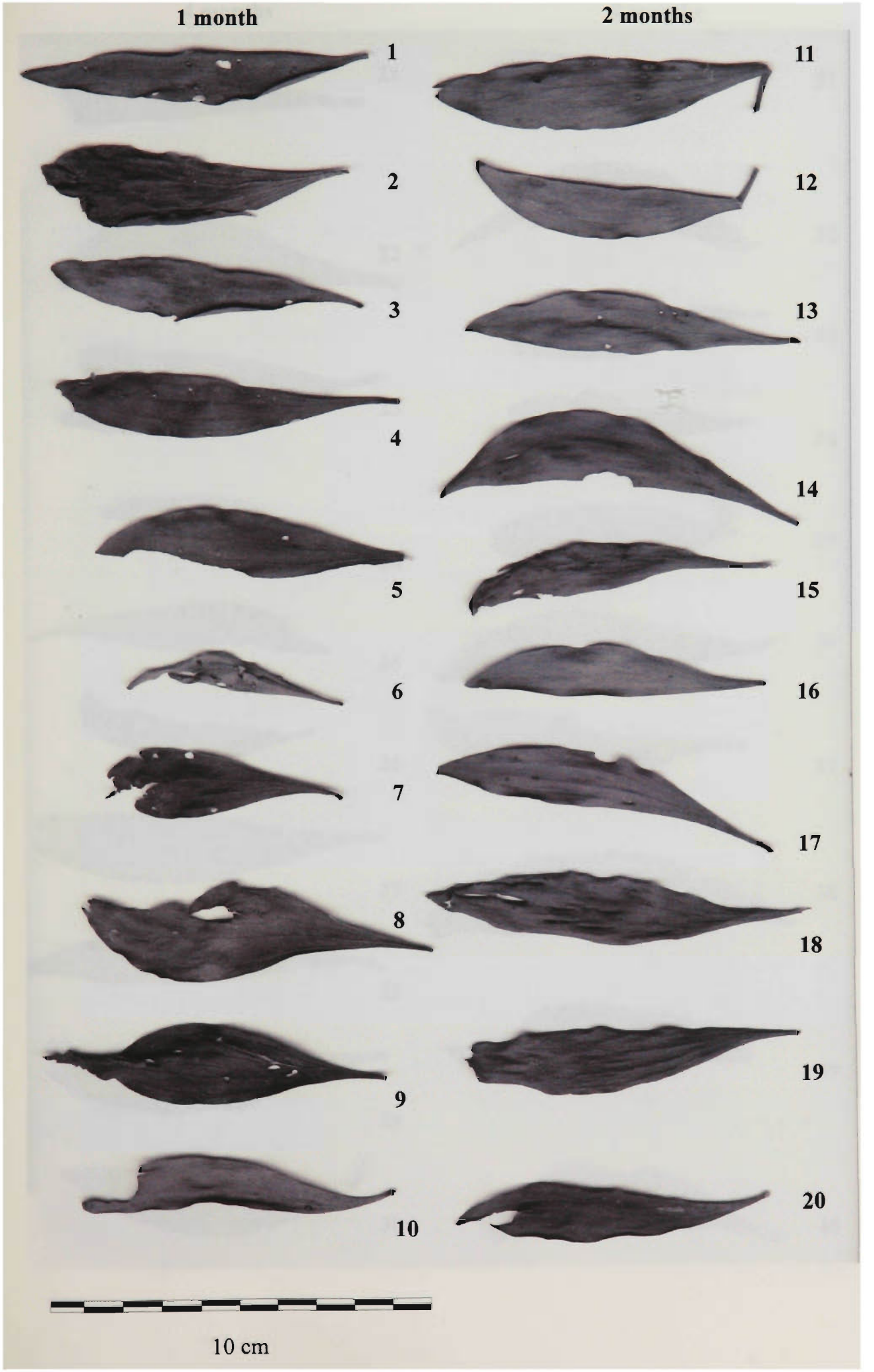


Figure 5.6a(i)

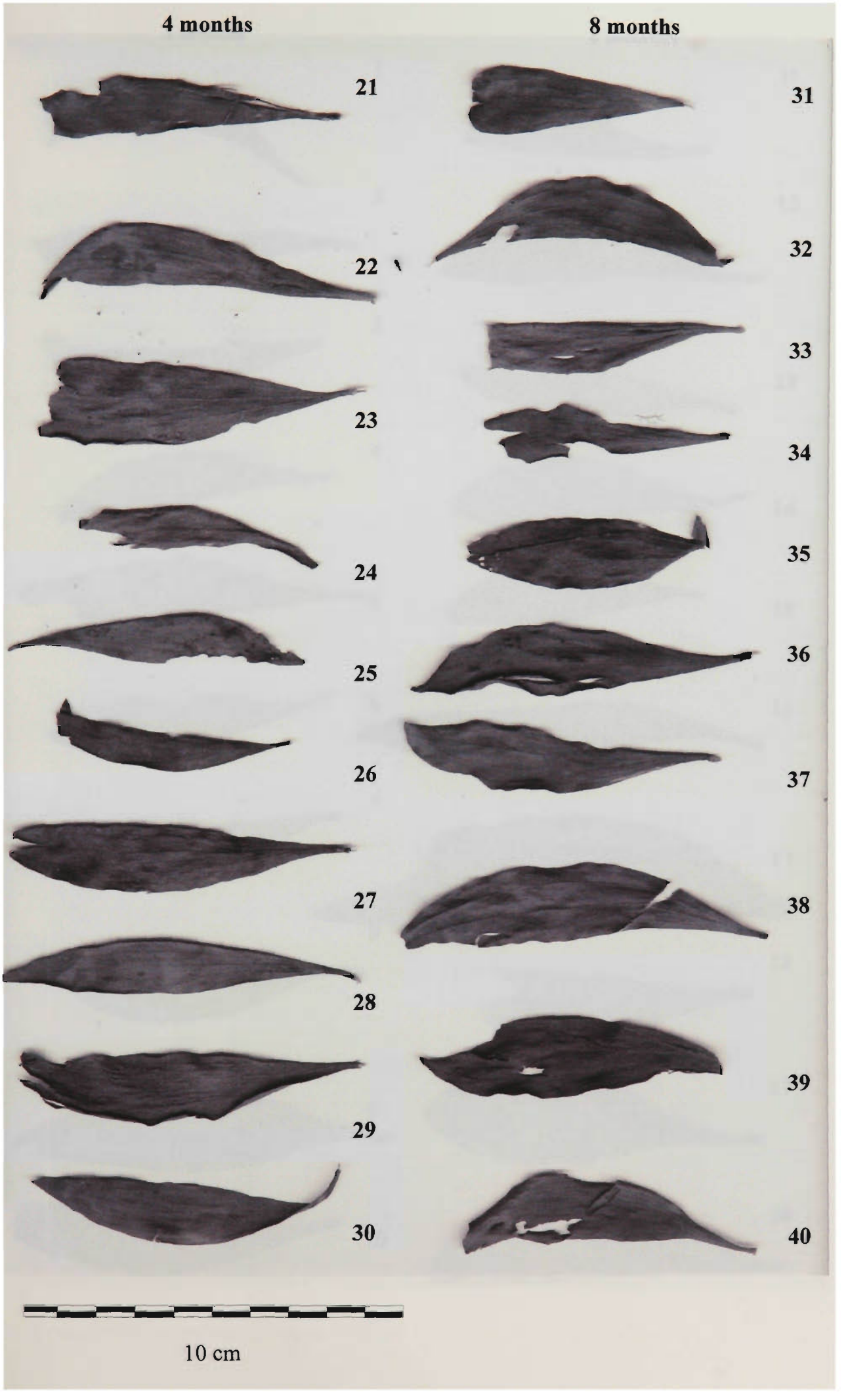

4 months
8 months
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
10 cm

Figure 5.6a(ii)

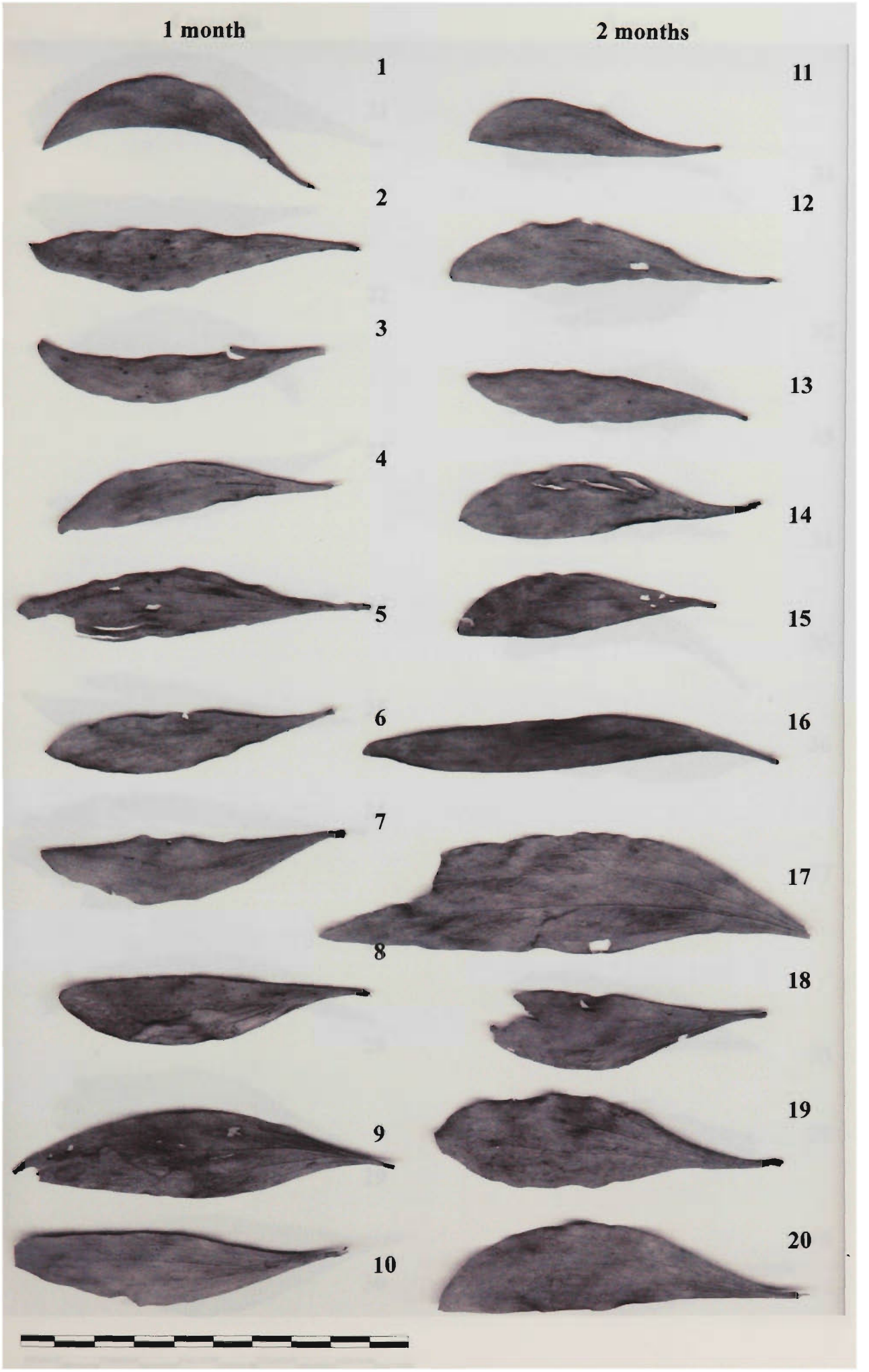


Figure 5.6a(ii)

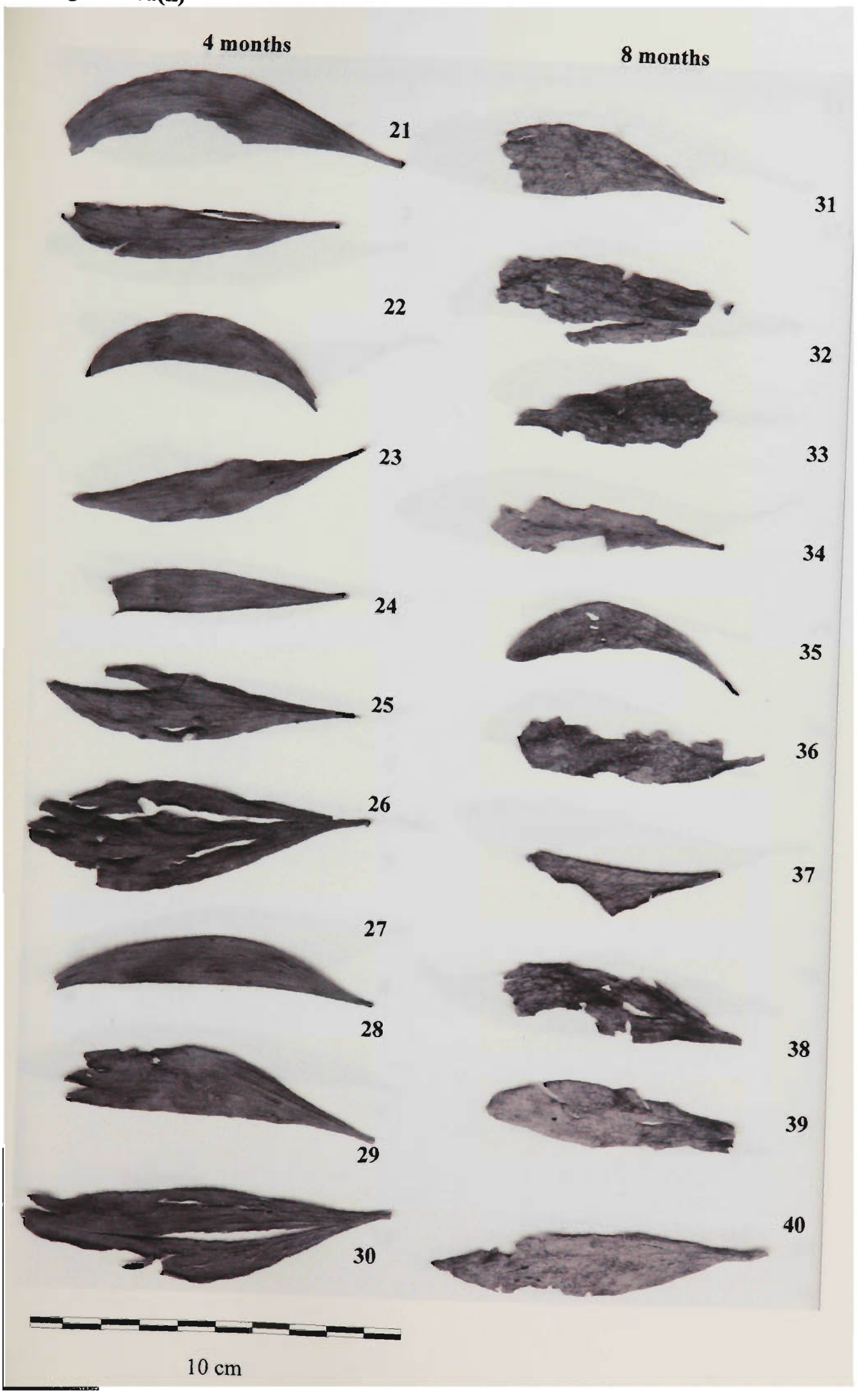


Figure 5.6a(iii)

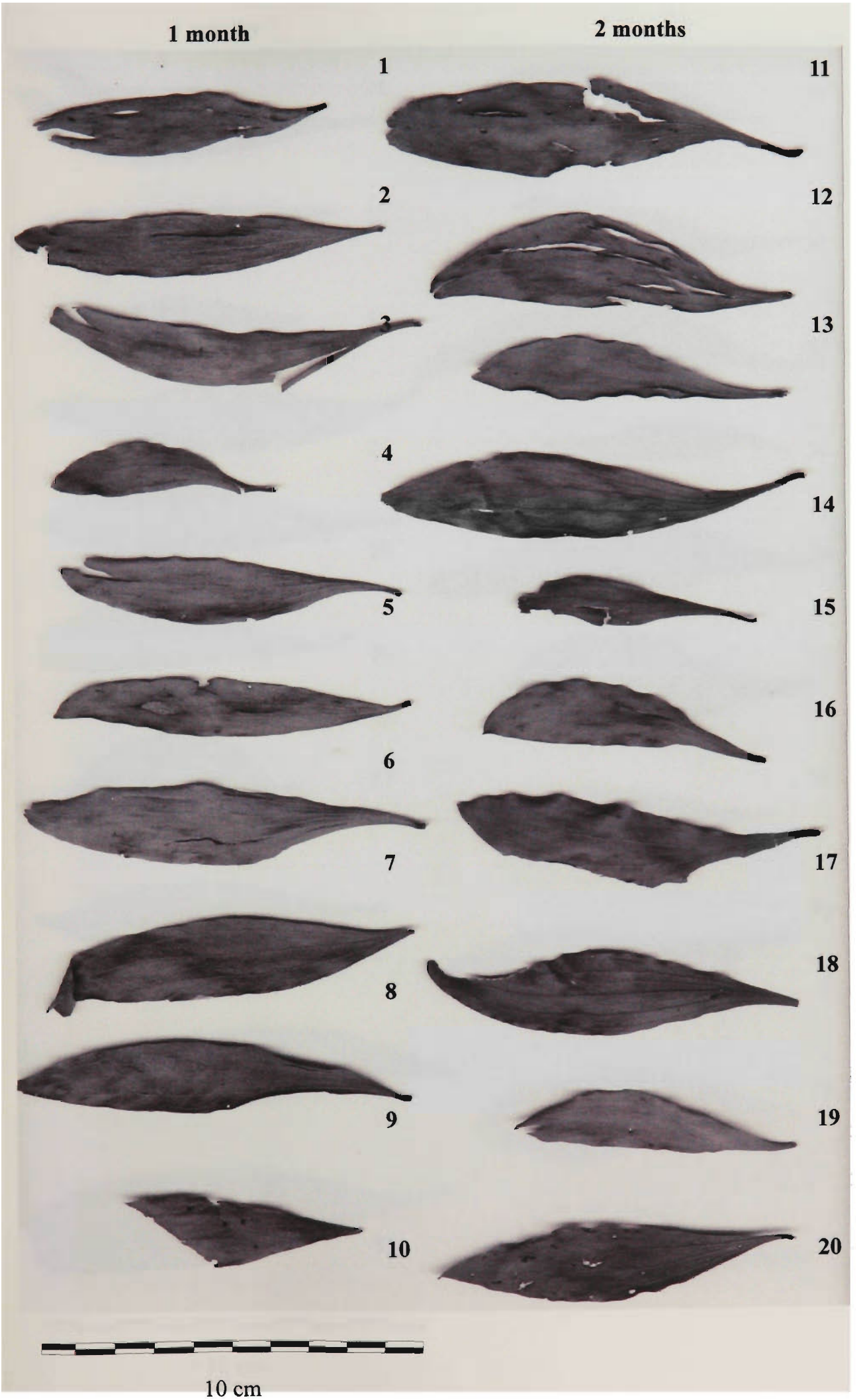


Figure 5.6a(iii)

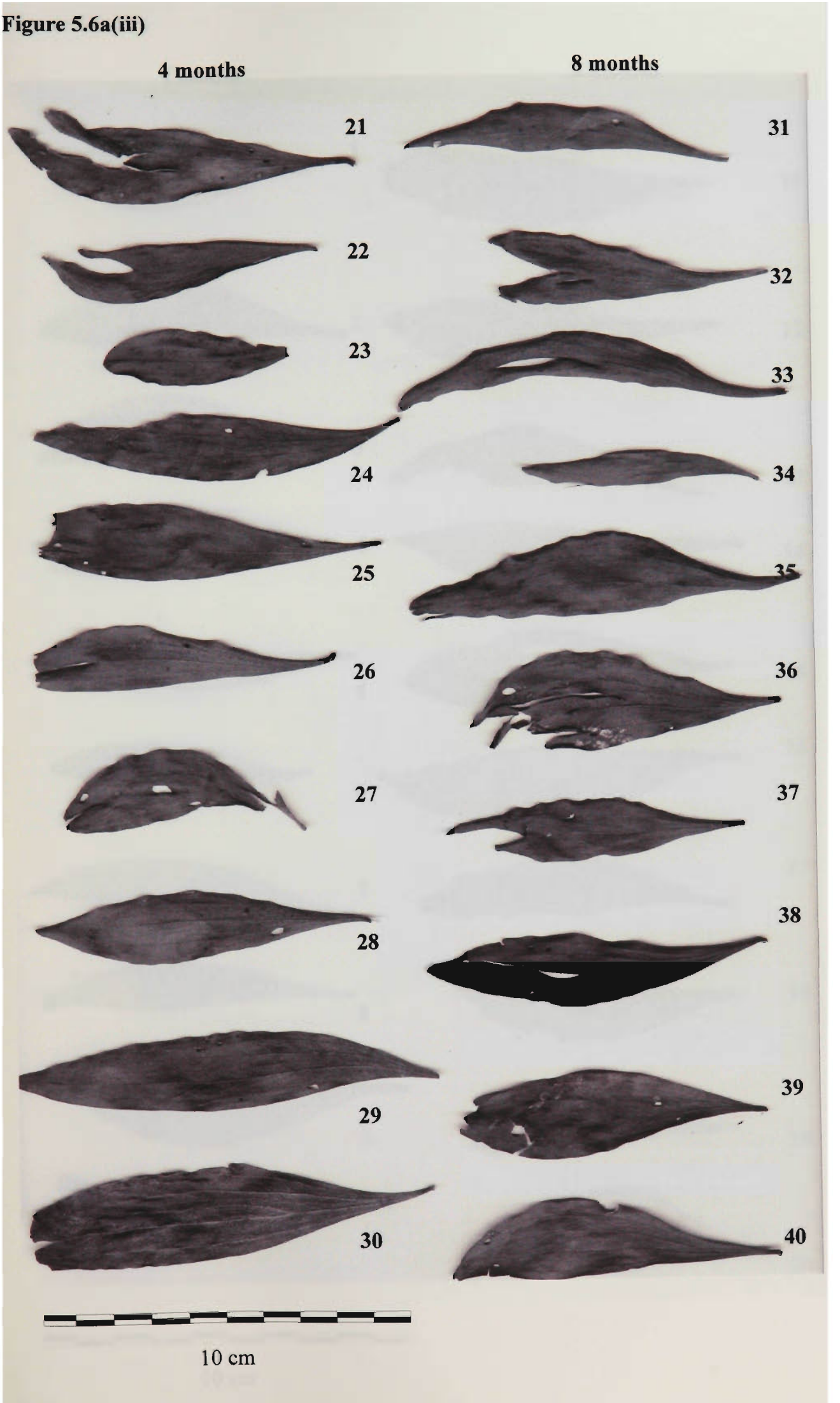


Figure 5.6a(iv)

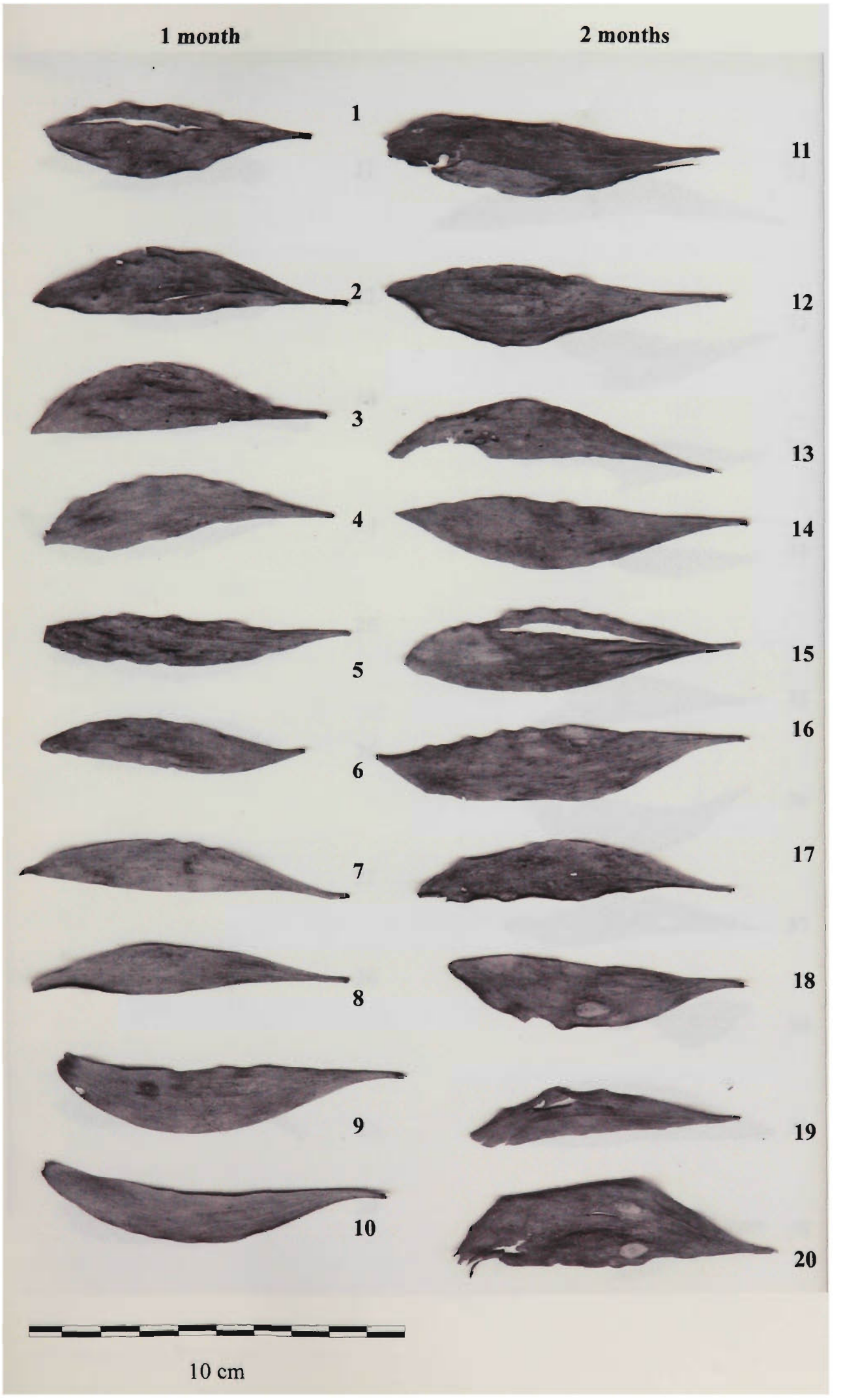


Figure 5.6a(iv)

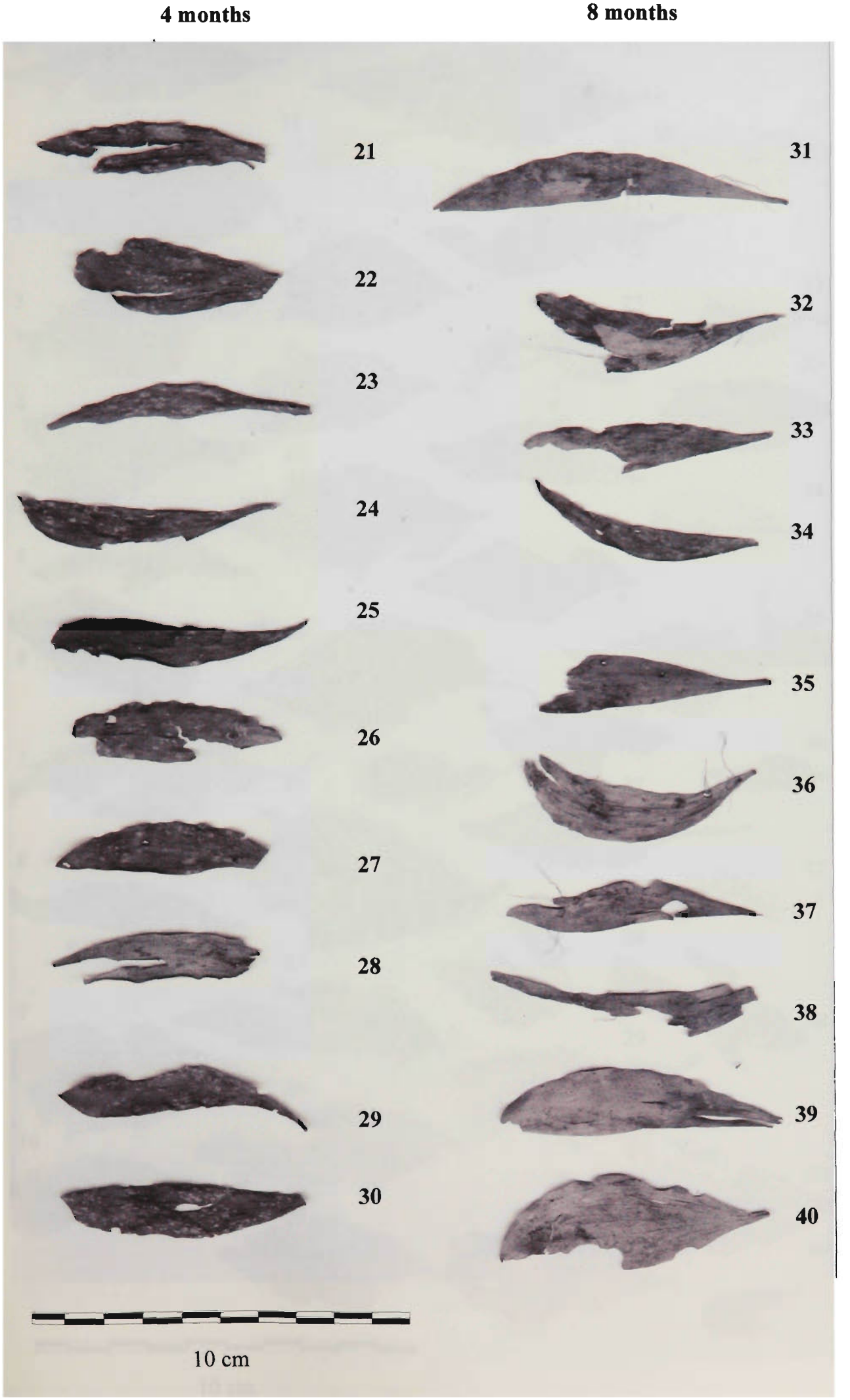


Figure 5.6b(i)

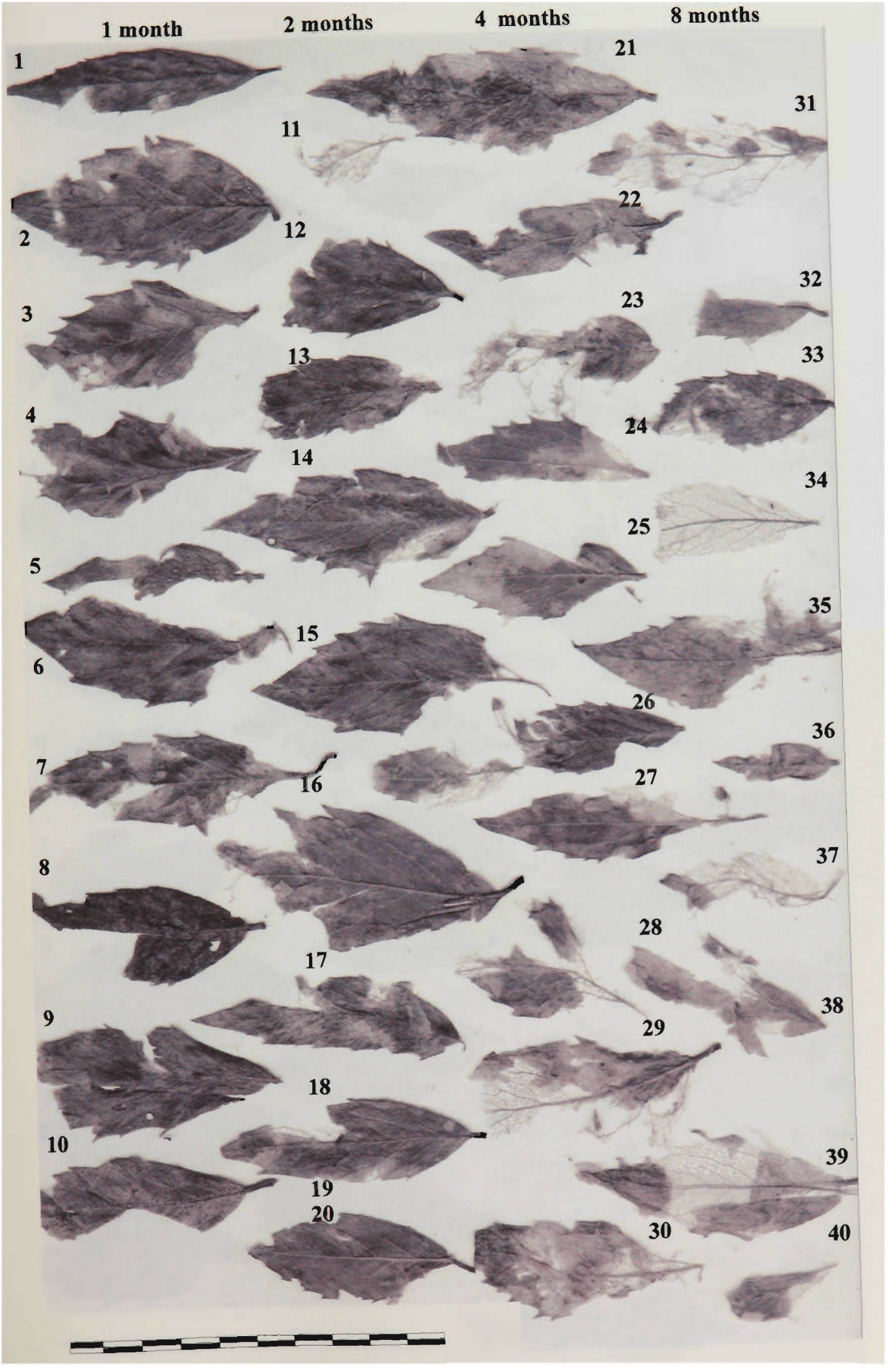

1 month
2 months
4 months
8 months
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
10 cm

Figure 5.6b(ii)

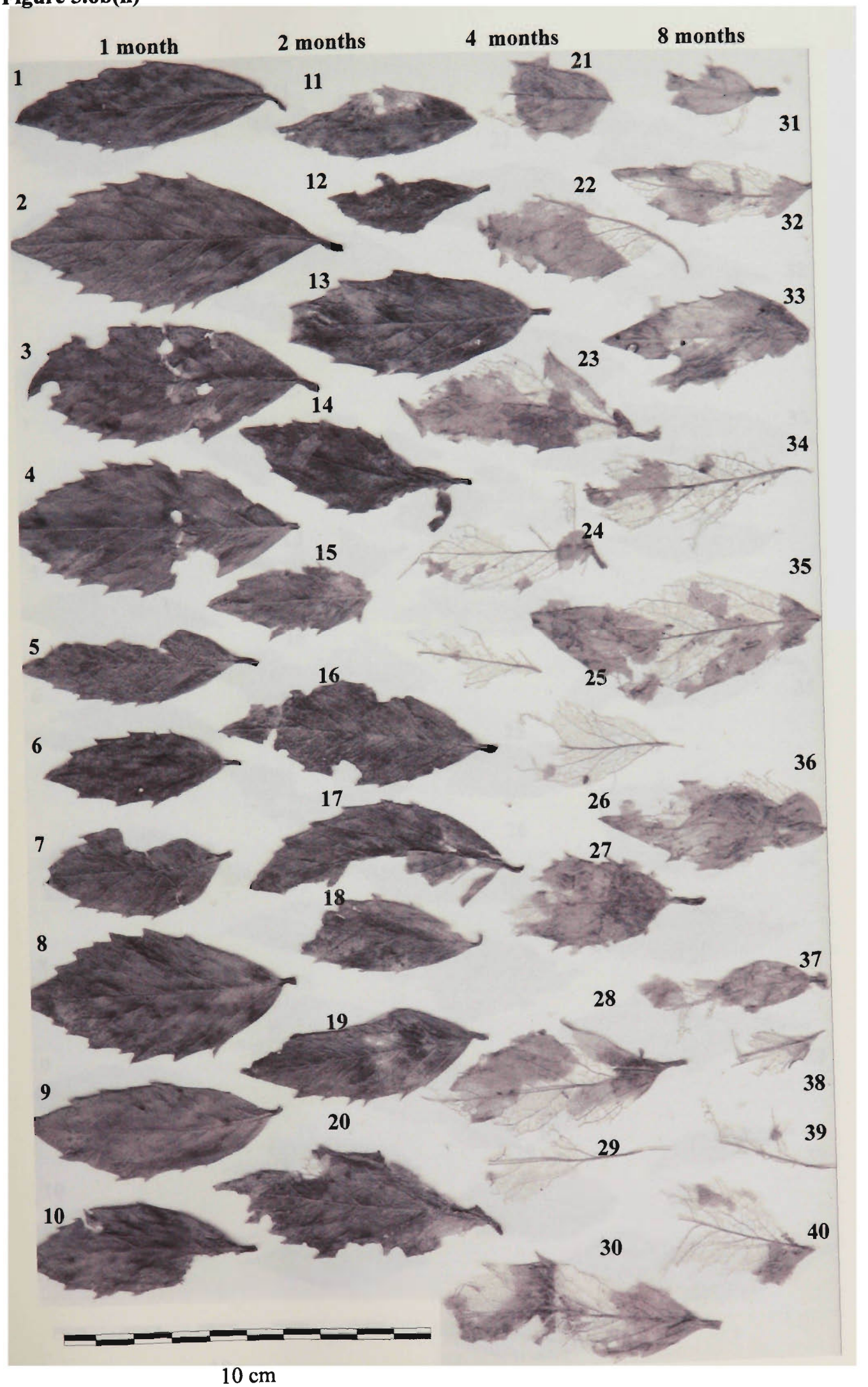


Figure 5.6b(iii)

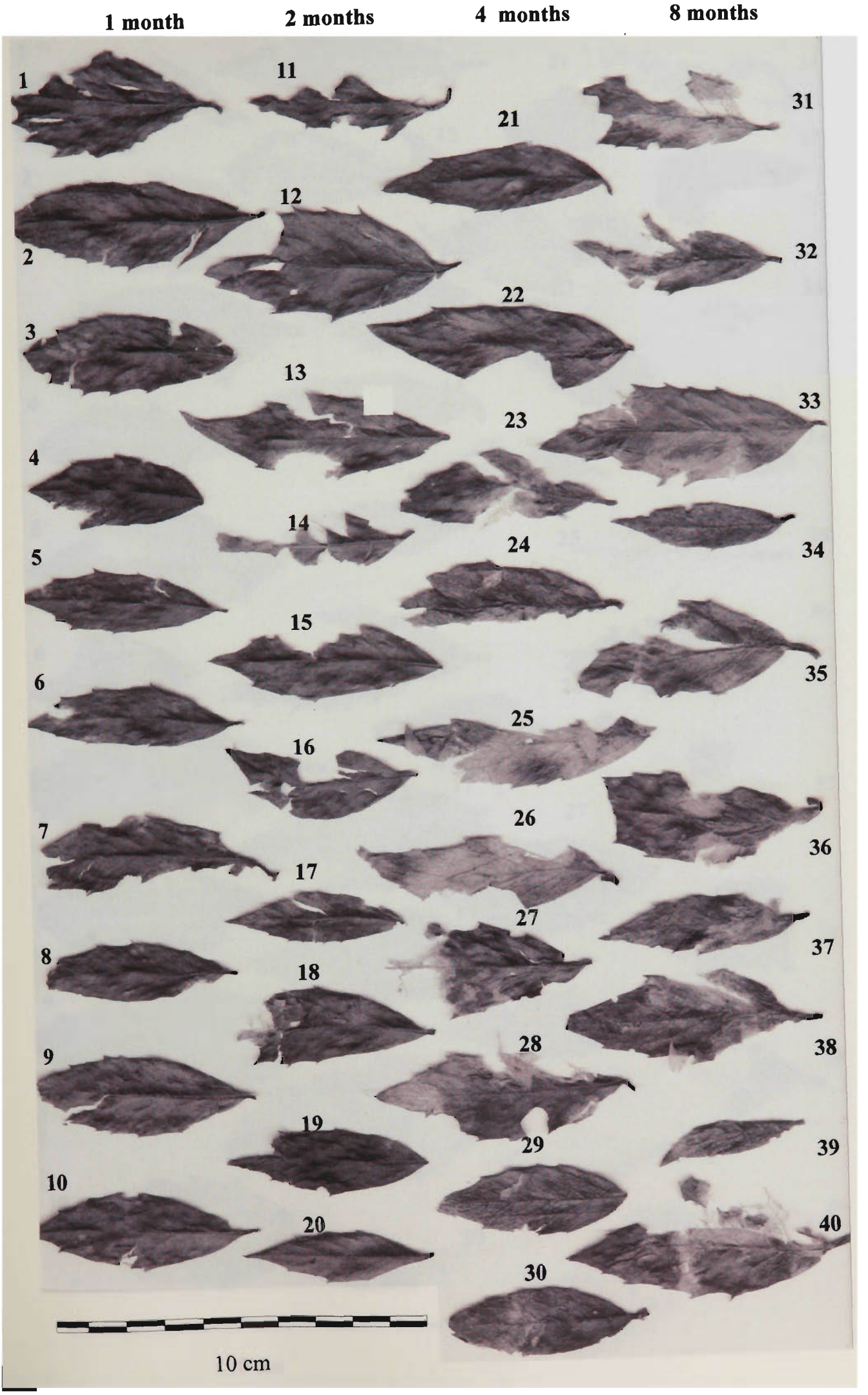


Figure 5.6b(iv)

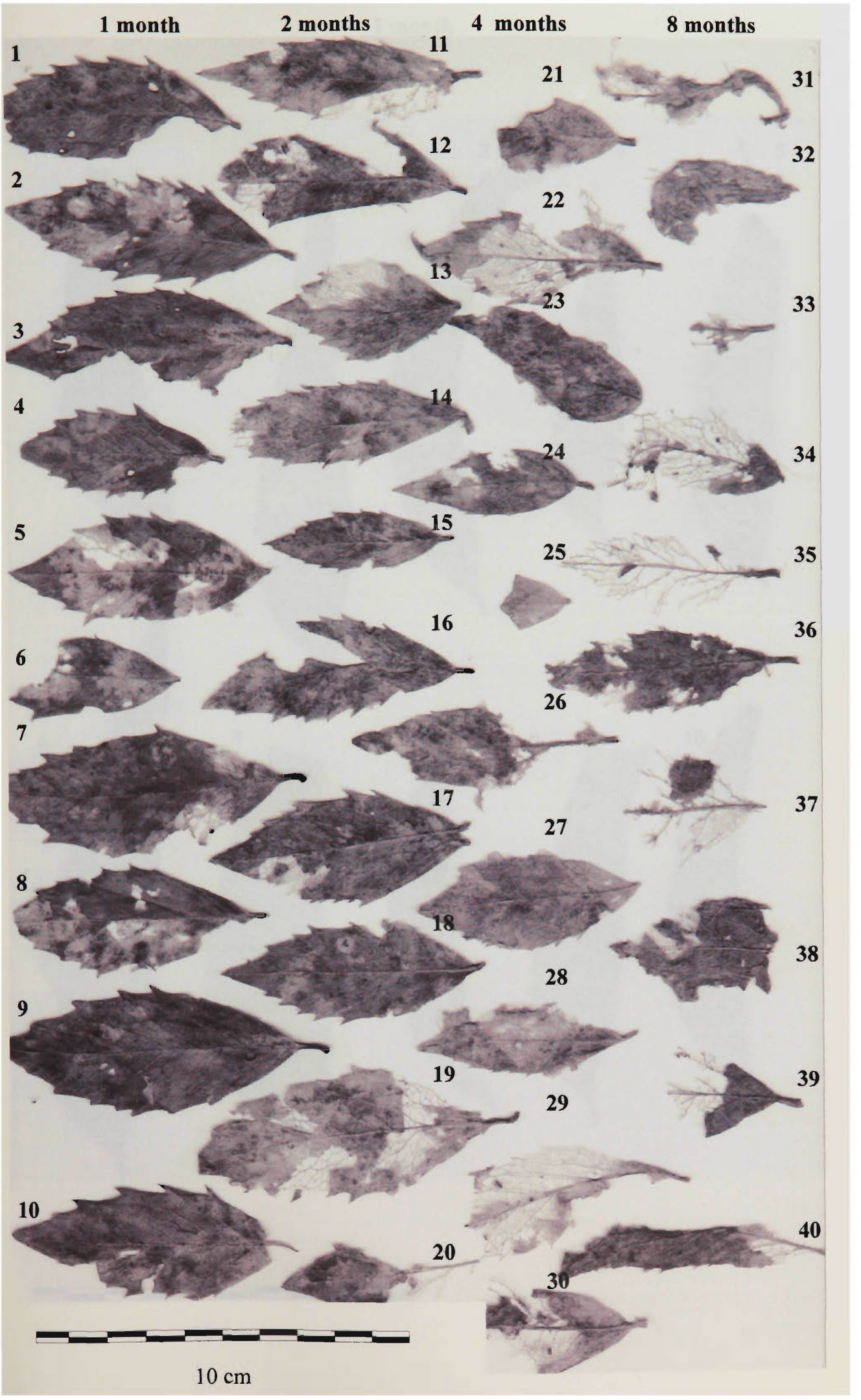


Figure 5.6c(i)

1 month

Figure 5.6c(i)

2 months

Figure 5.6c(i)

4 months

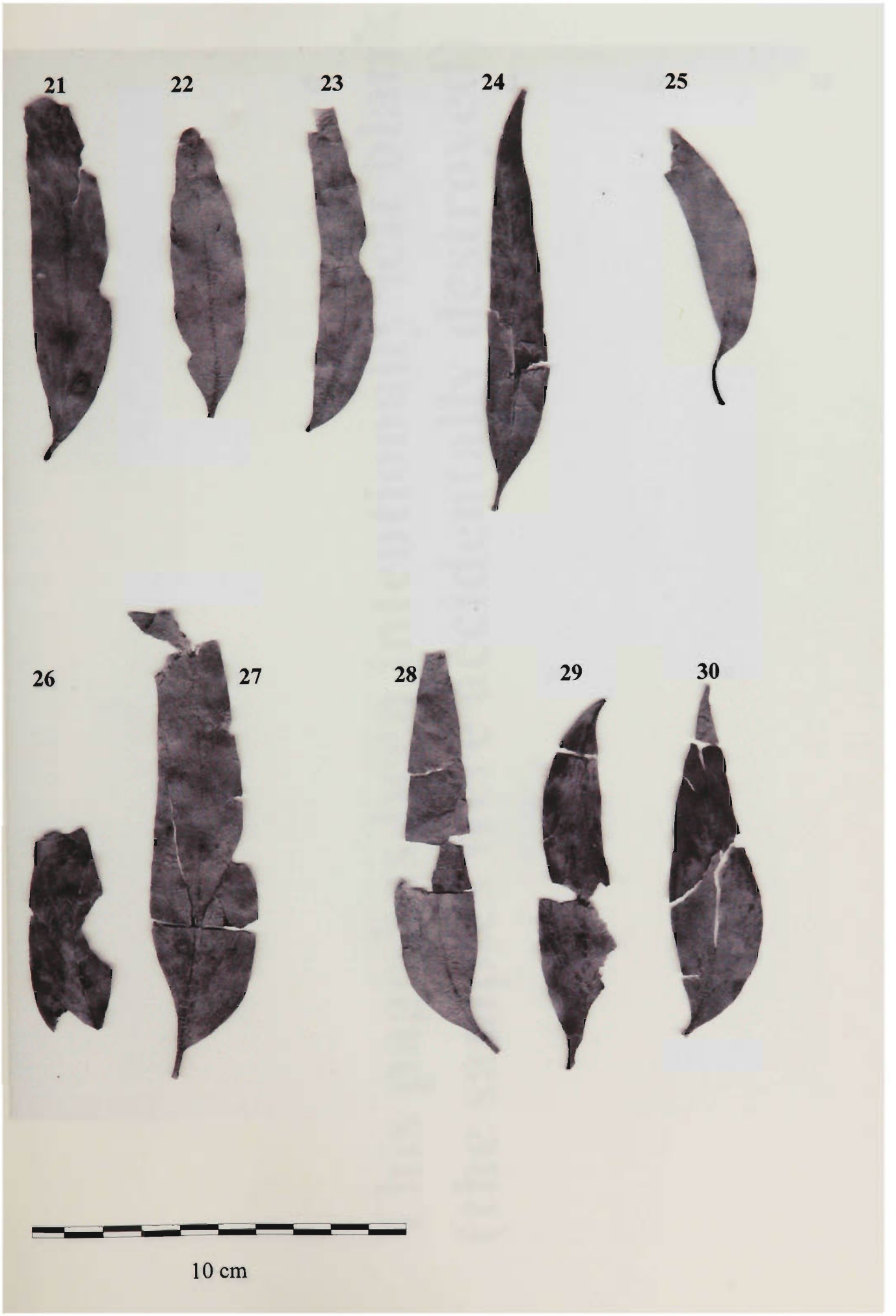


Figure 5.6c(i)

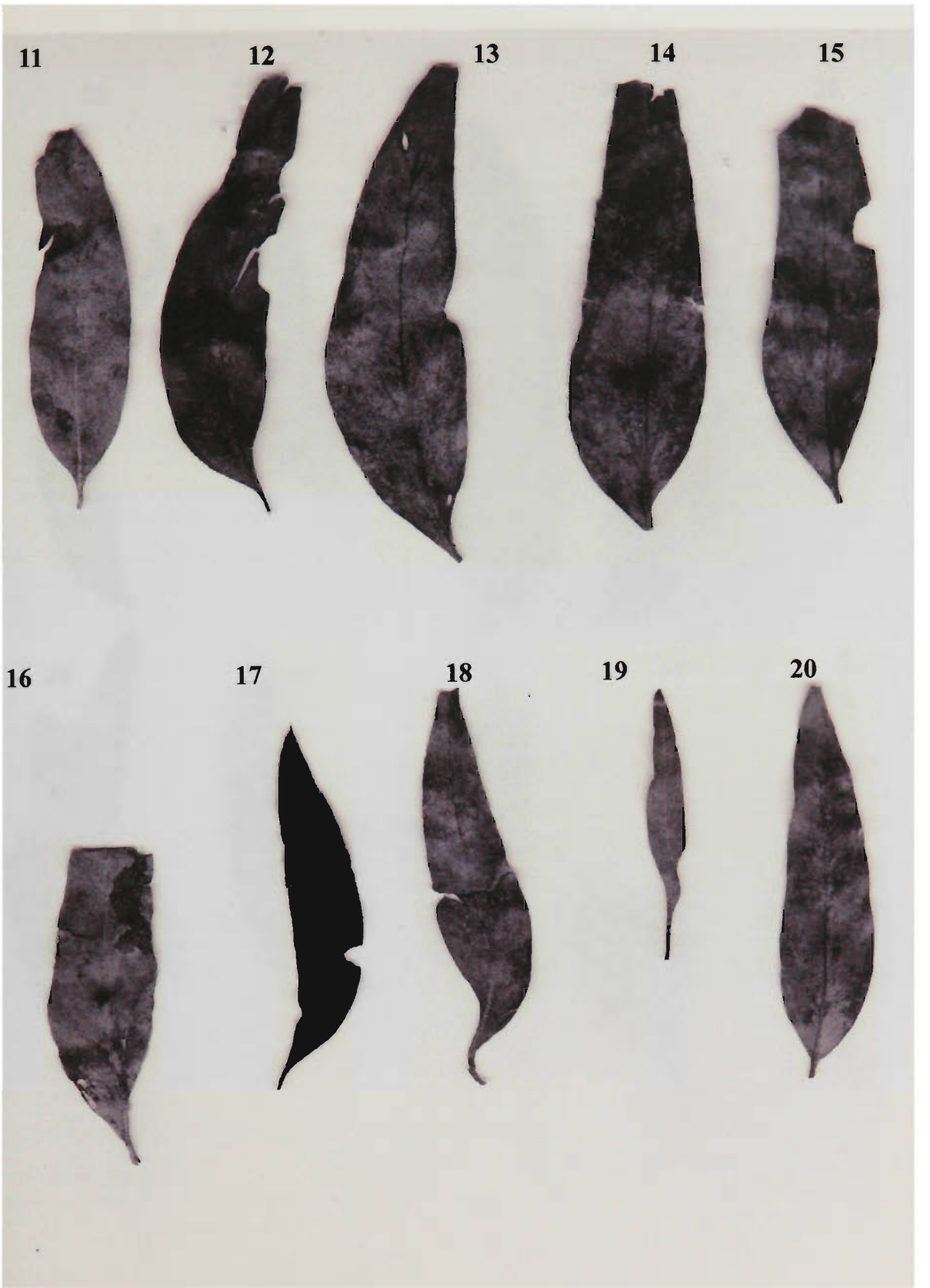
8 months

Figure 5.6c(ii)

1 month

Figure 5.6c(ii)

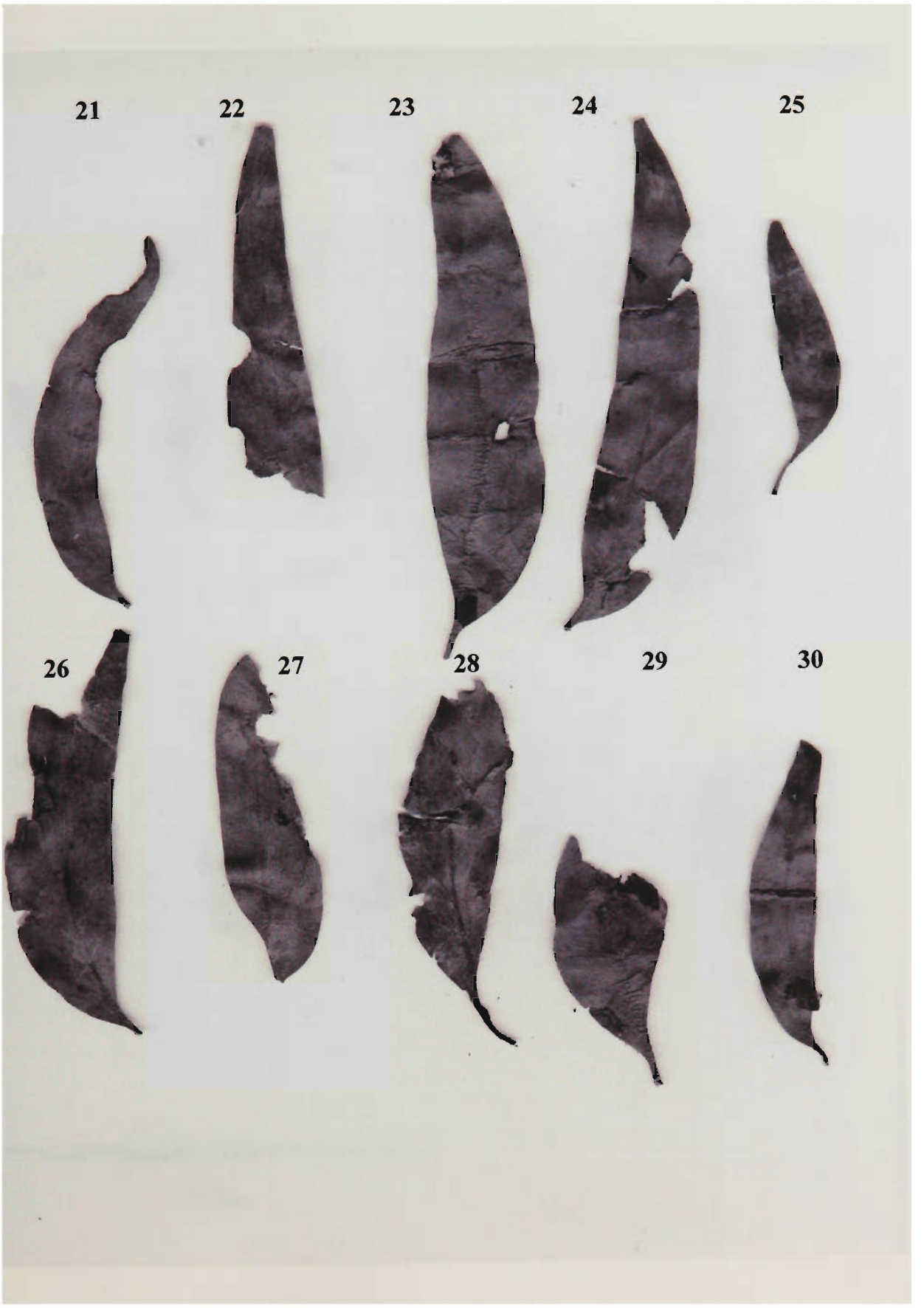
2 months



10 cm

Figure 5.6c(ii)

4 months



10 cm

Figure 5.6c(ii)

8 months

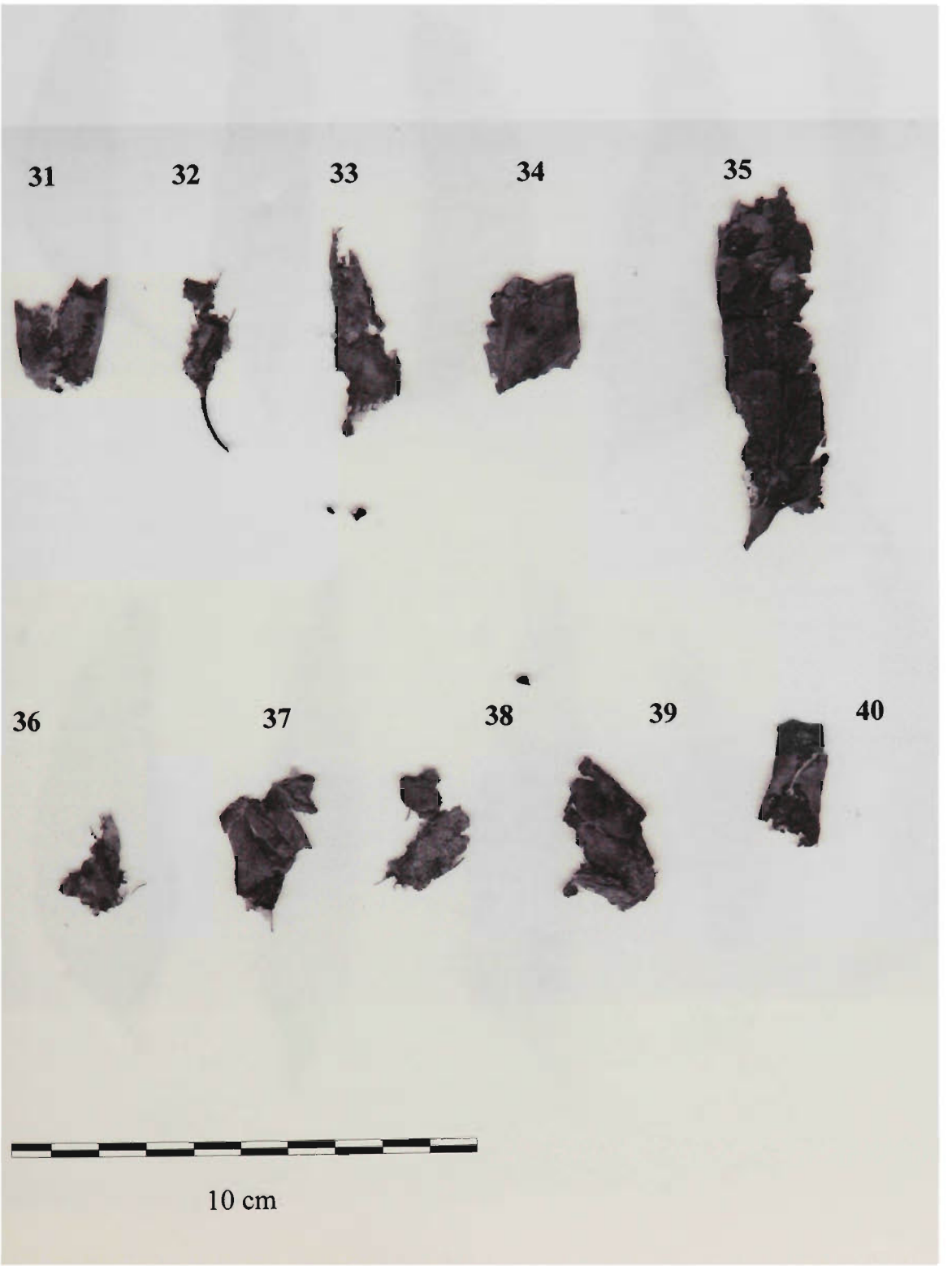


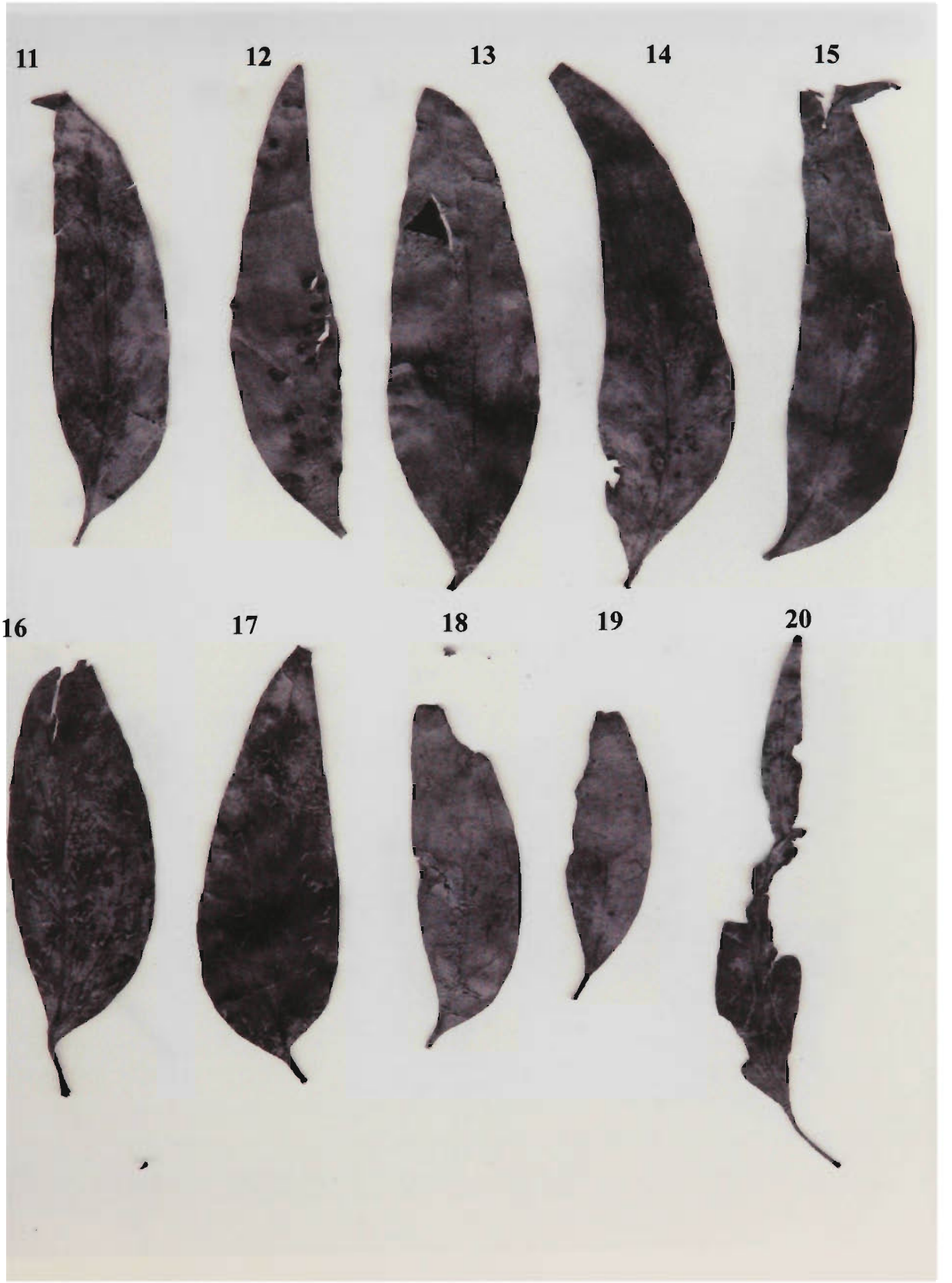
Figure 5.6c(iii)

1 month

10 cm

Figure 5.6c(iii)

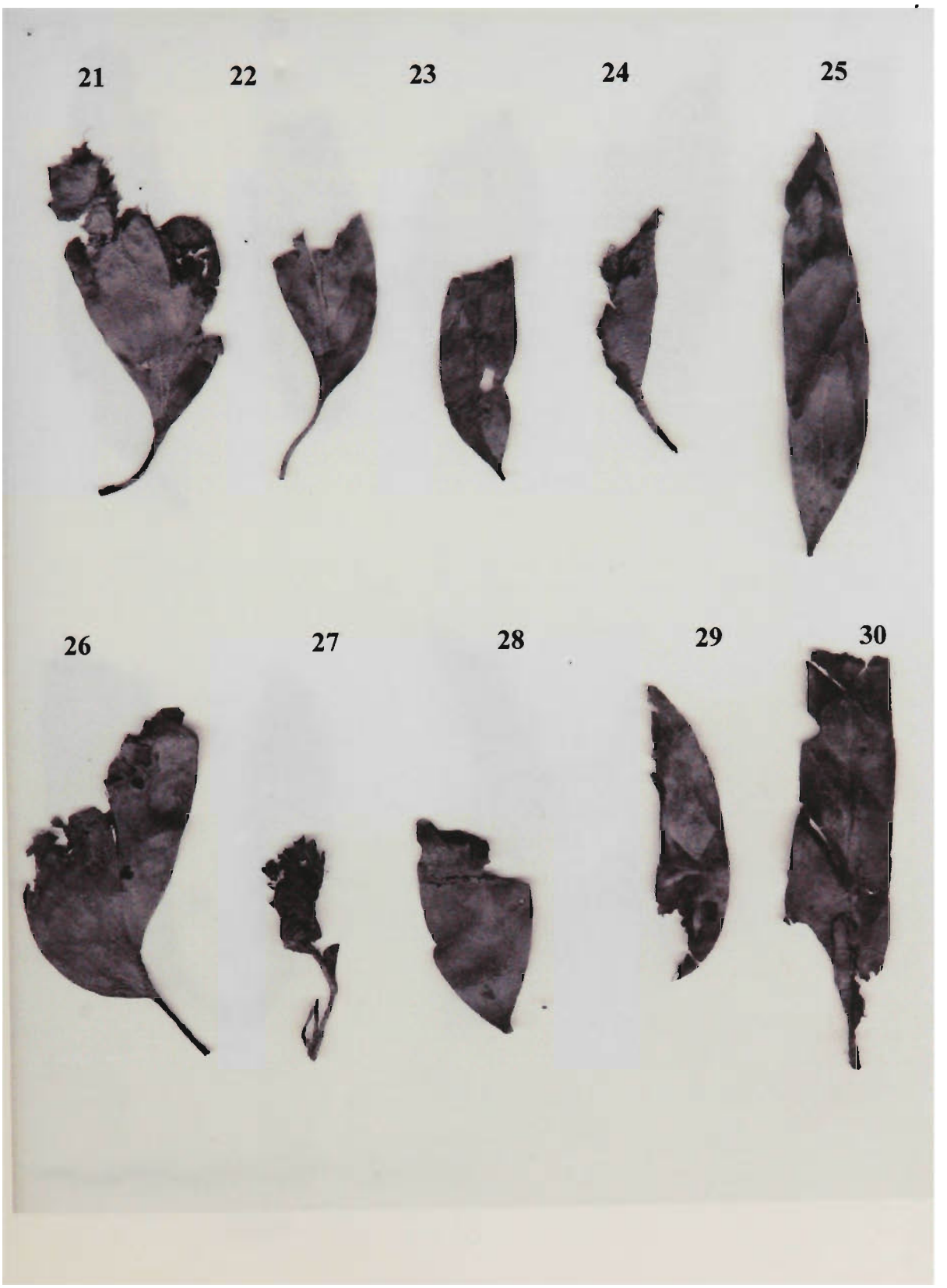
2 months



10 cm

Figure 5.6c(iii)

4 months



10 cm

Figure 5.6c(iii)

8 months

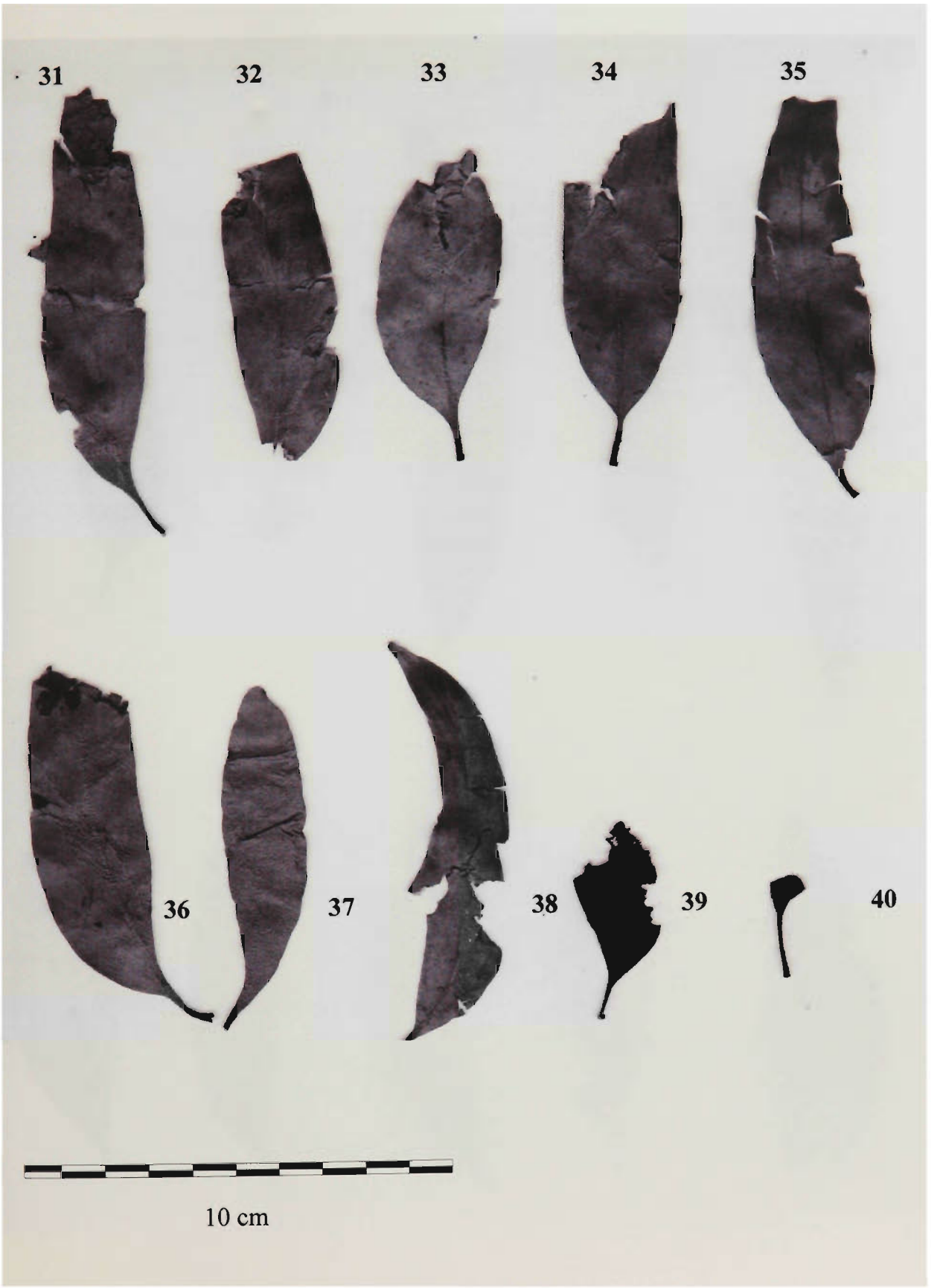


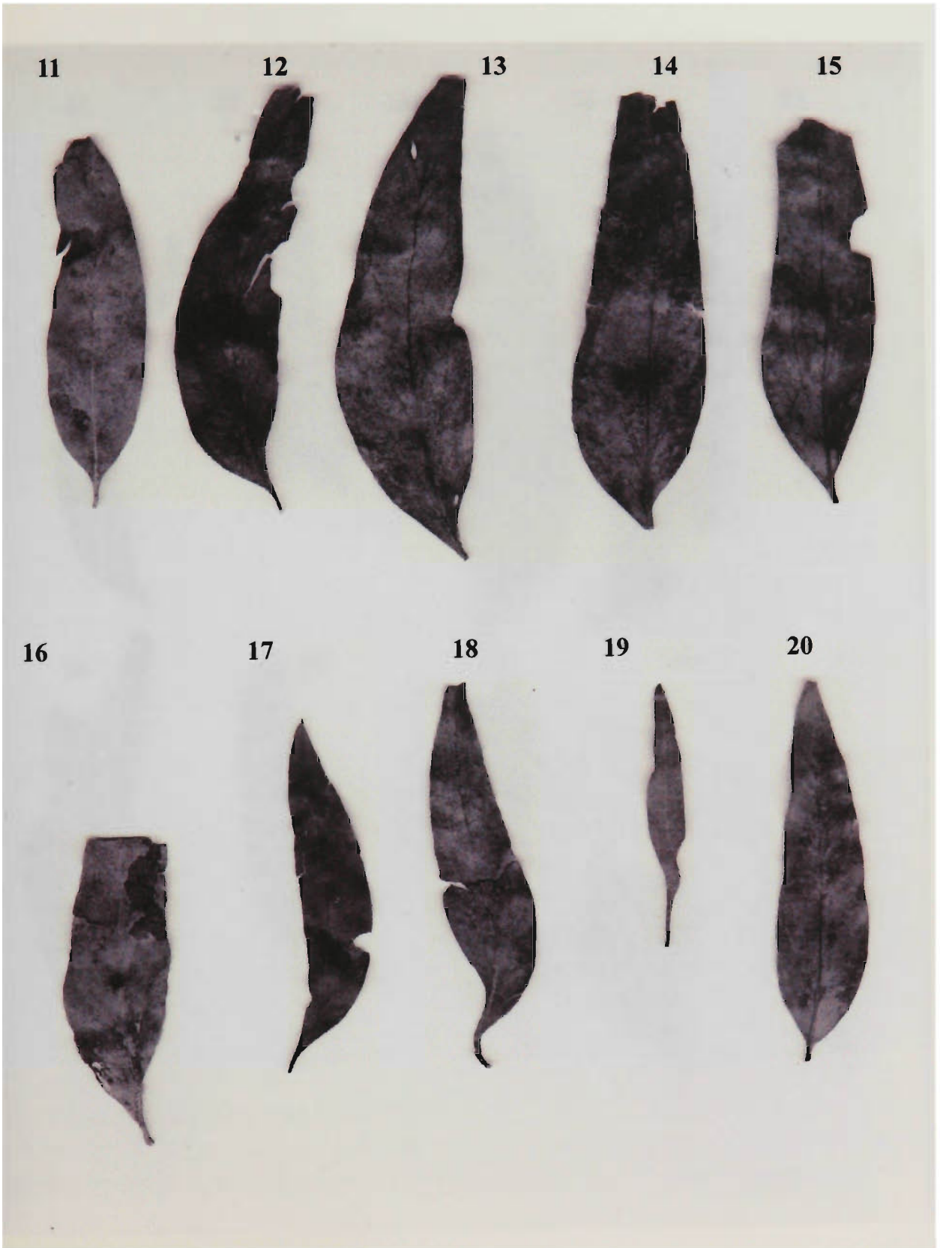
Figure 5.6c(iv)

1 month

10 cm

Figure 5.6c(iv)

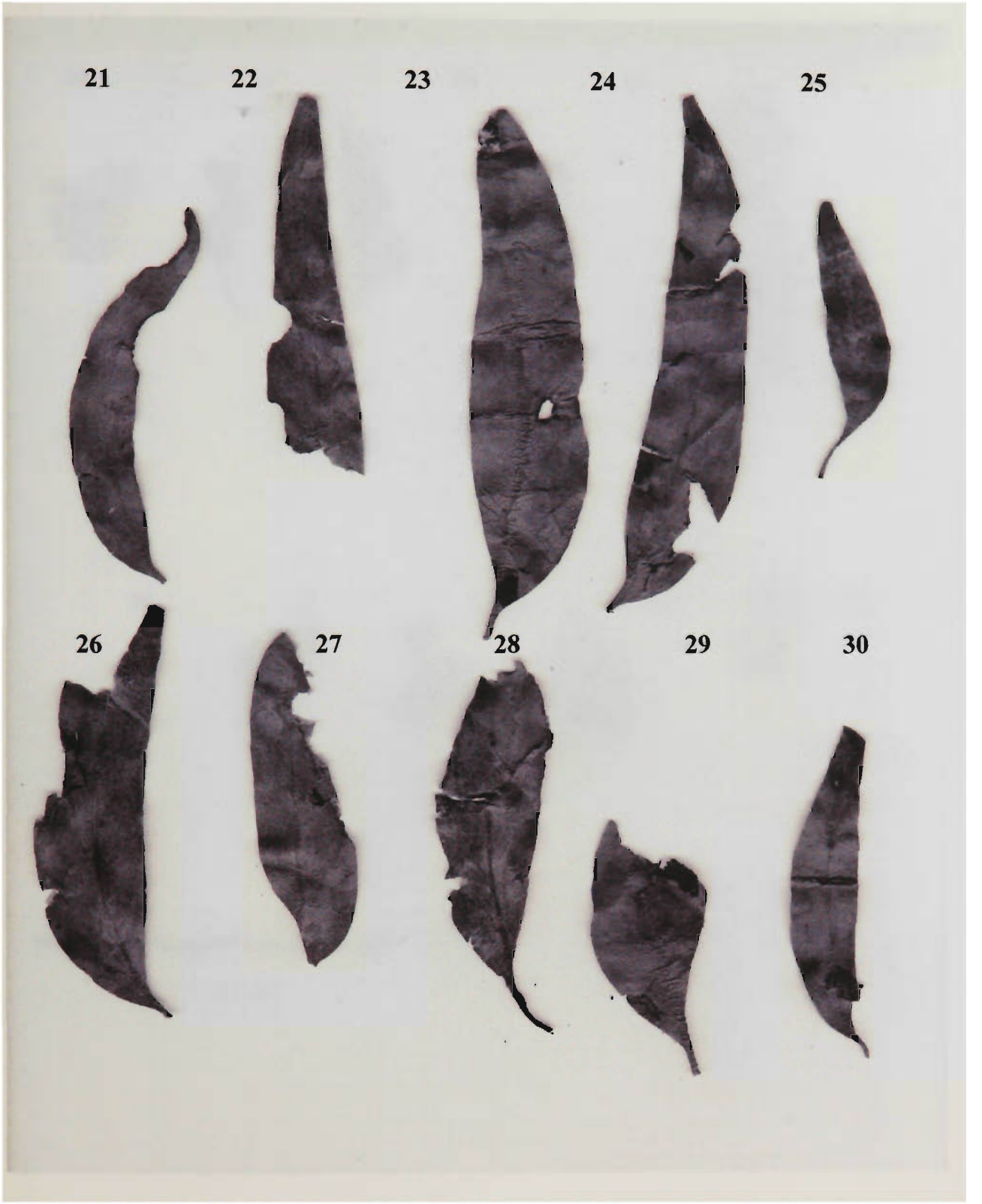
2 months



10 cm

Figure 5.6c(iv)

4 months



10 cm

Figure 5.6c(iv)

8 months

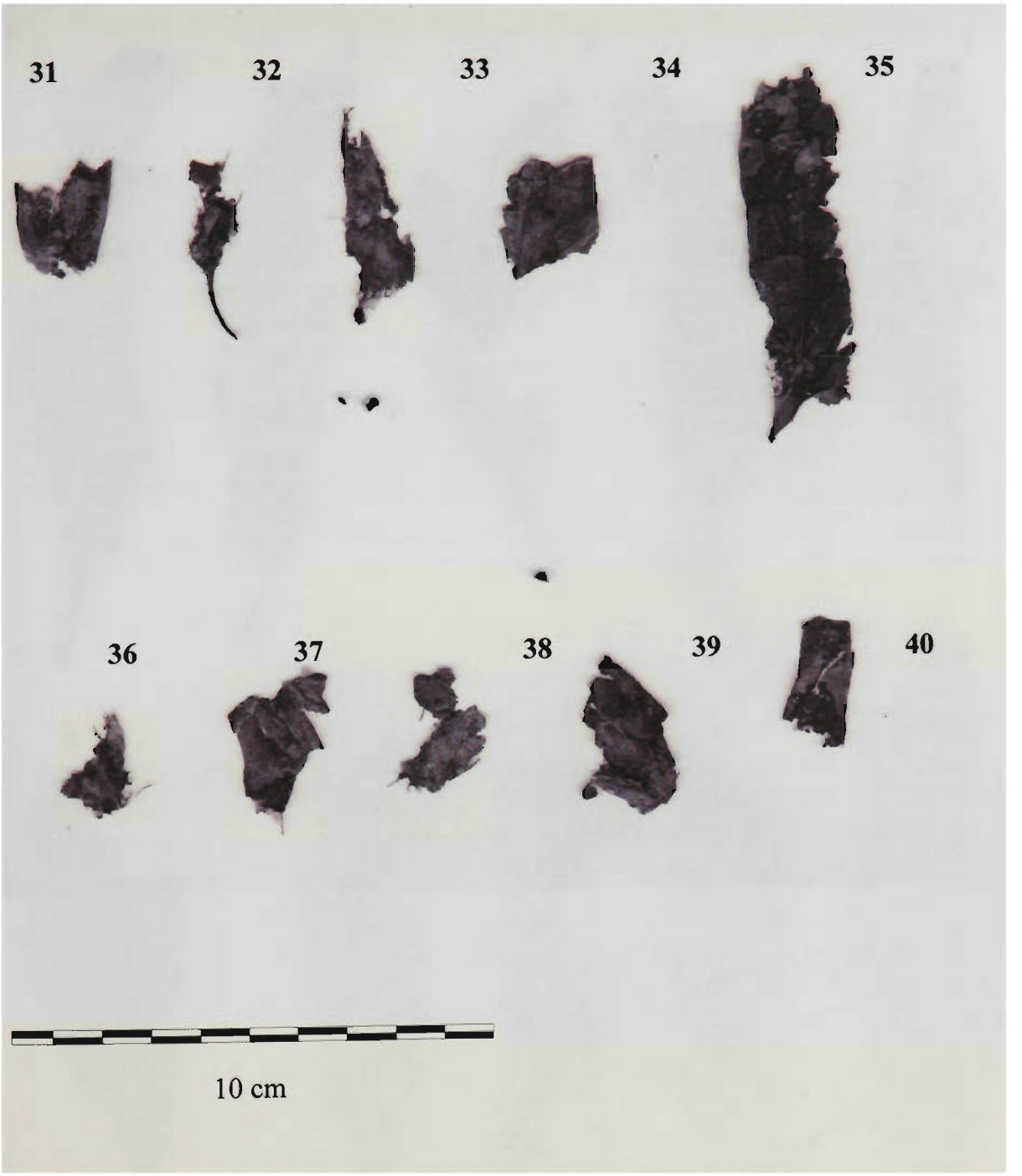


Figure 5.6d(i)

1 month

Figure 5.6d(i)

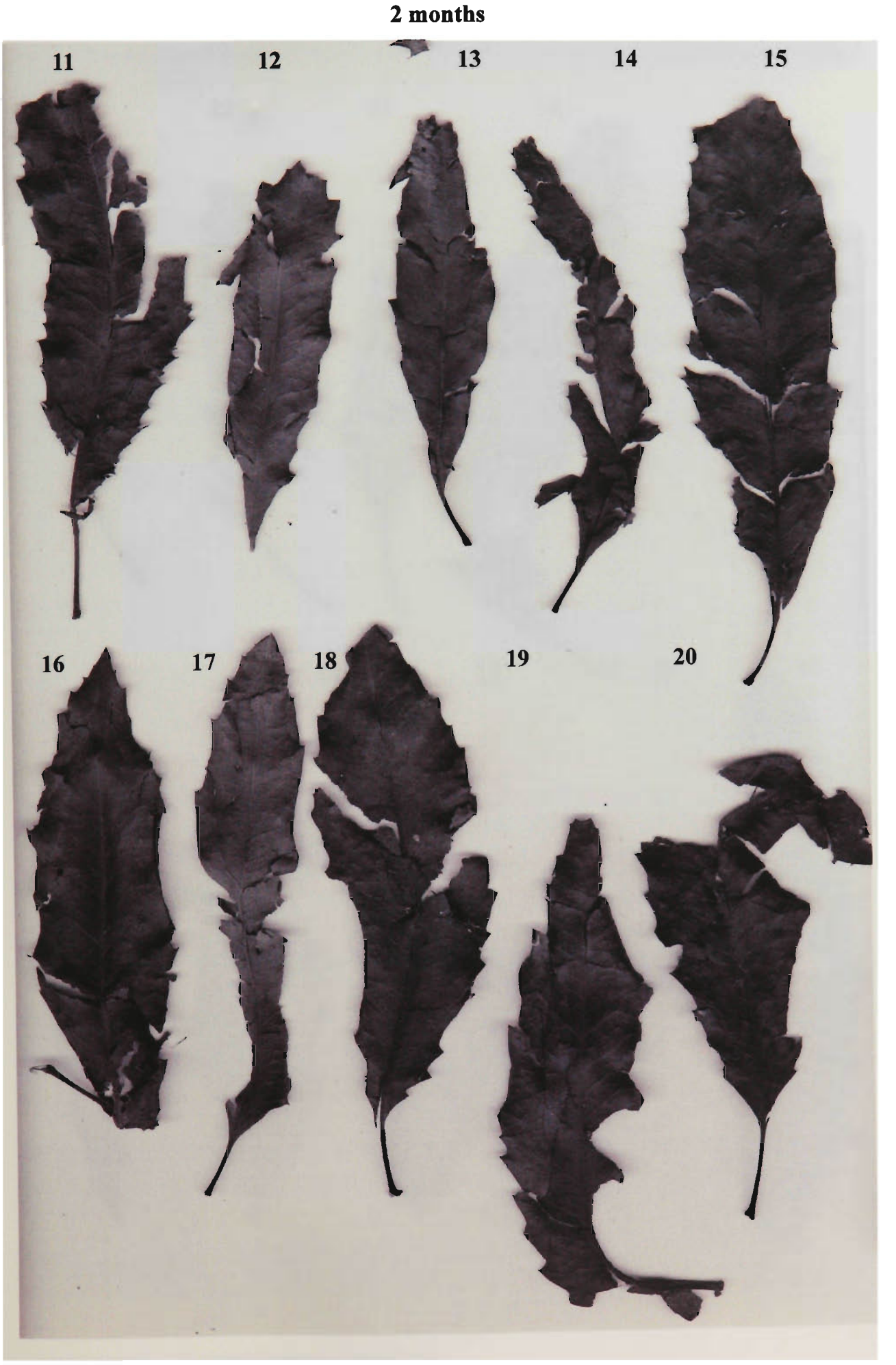


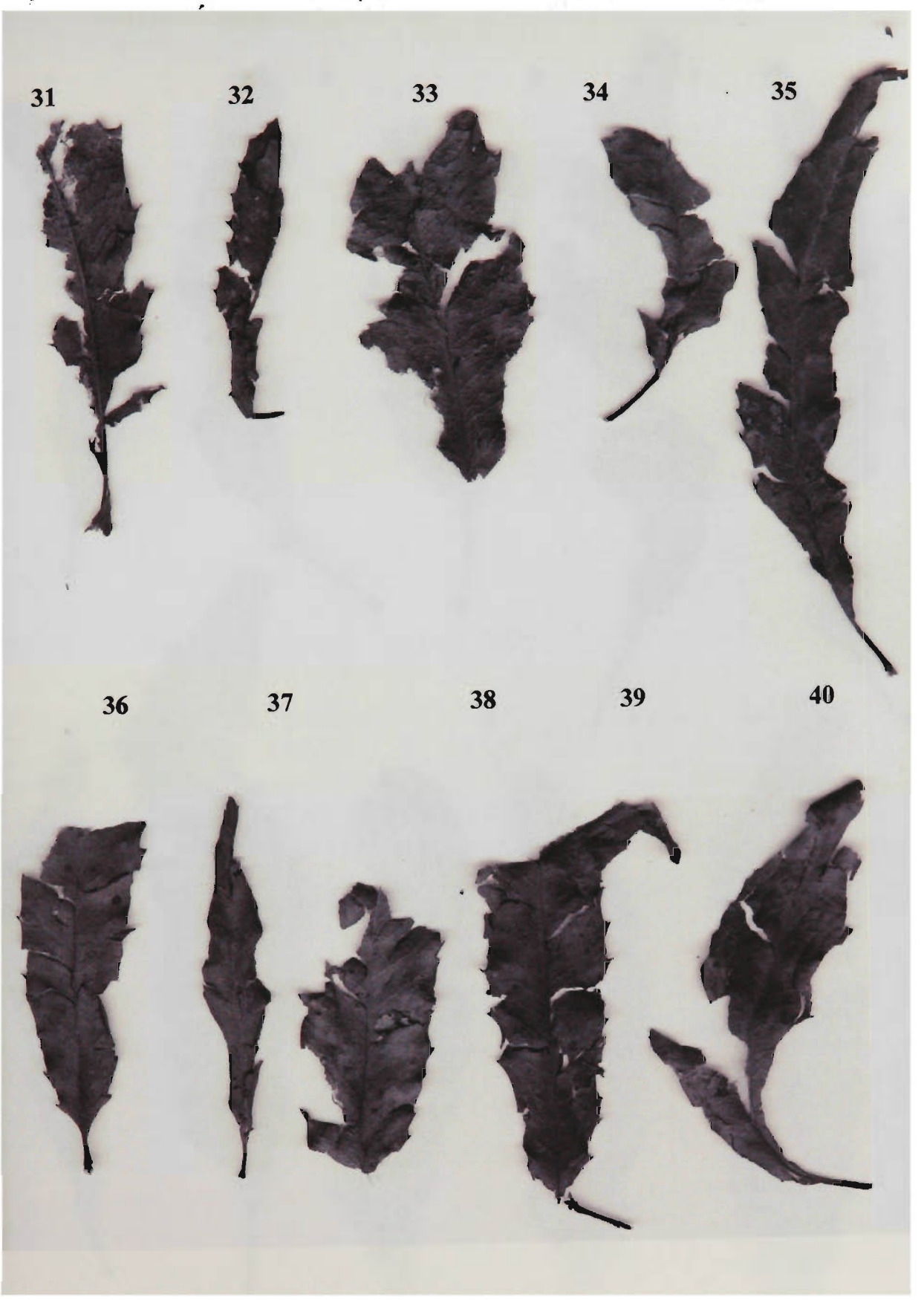
Figure 5.6d(i)

4 months

10 cm

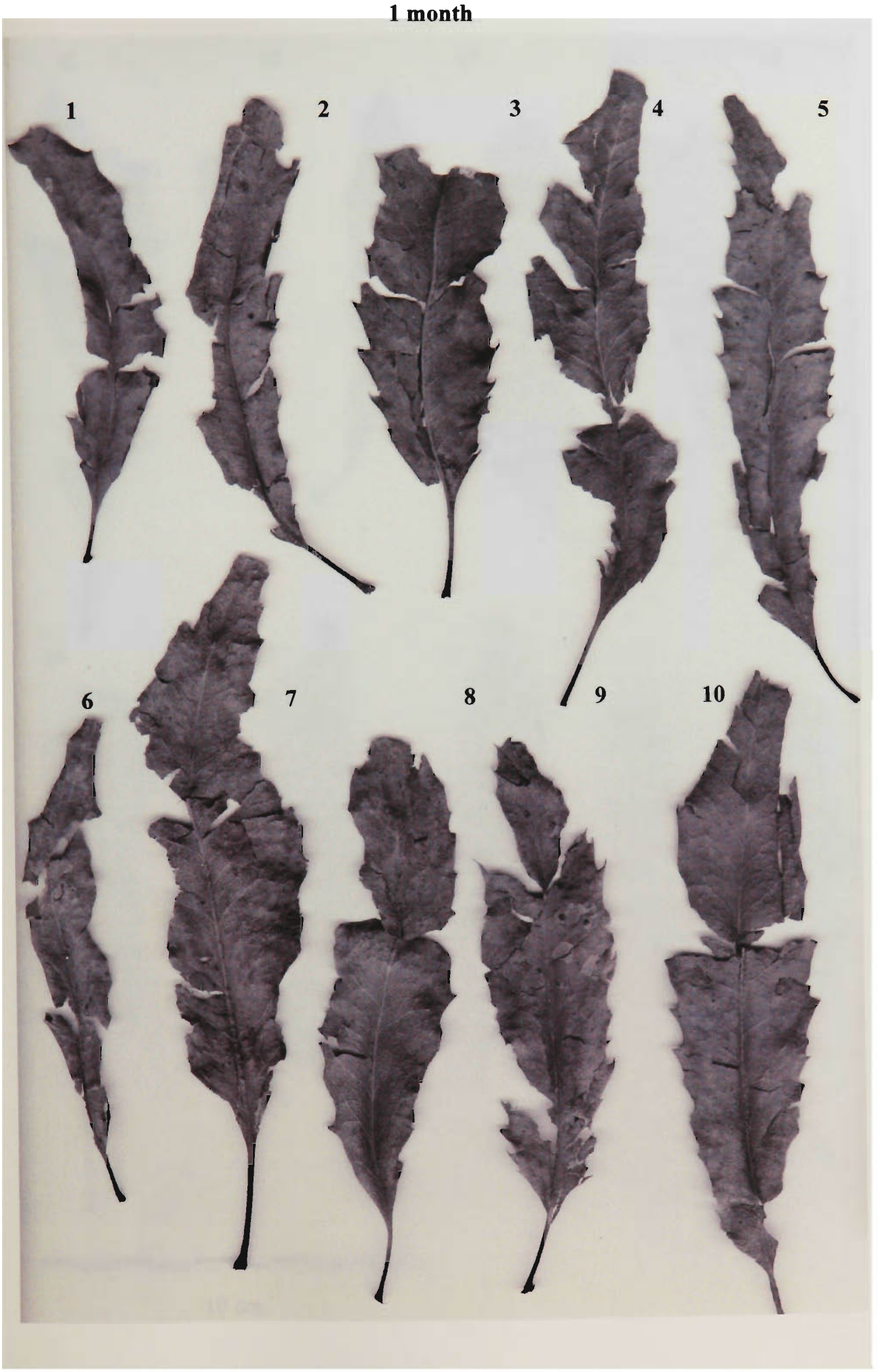
Figure 5.6d(i)

8 months



10 cm

Figure 5.6d(ii)



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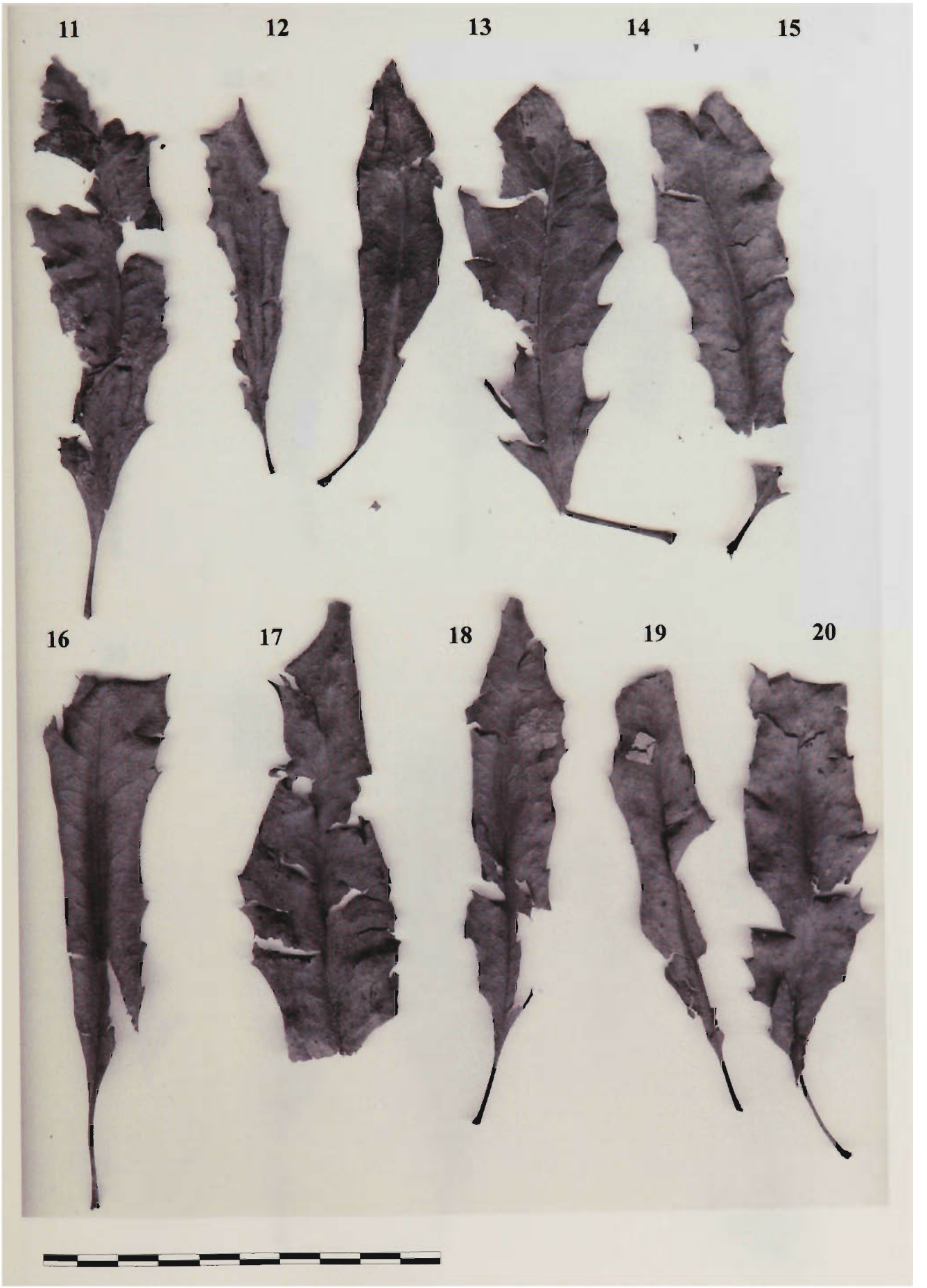


Figure 5.6d(ii)

4 months

10 cm

Figure 5.6d(ii)

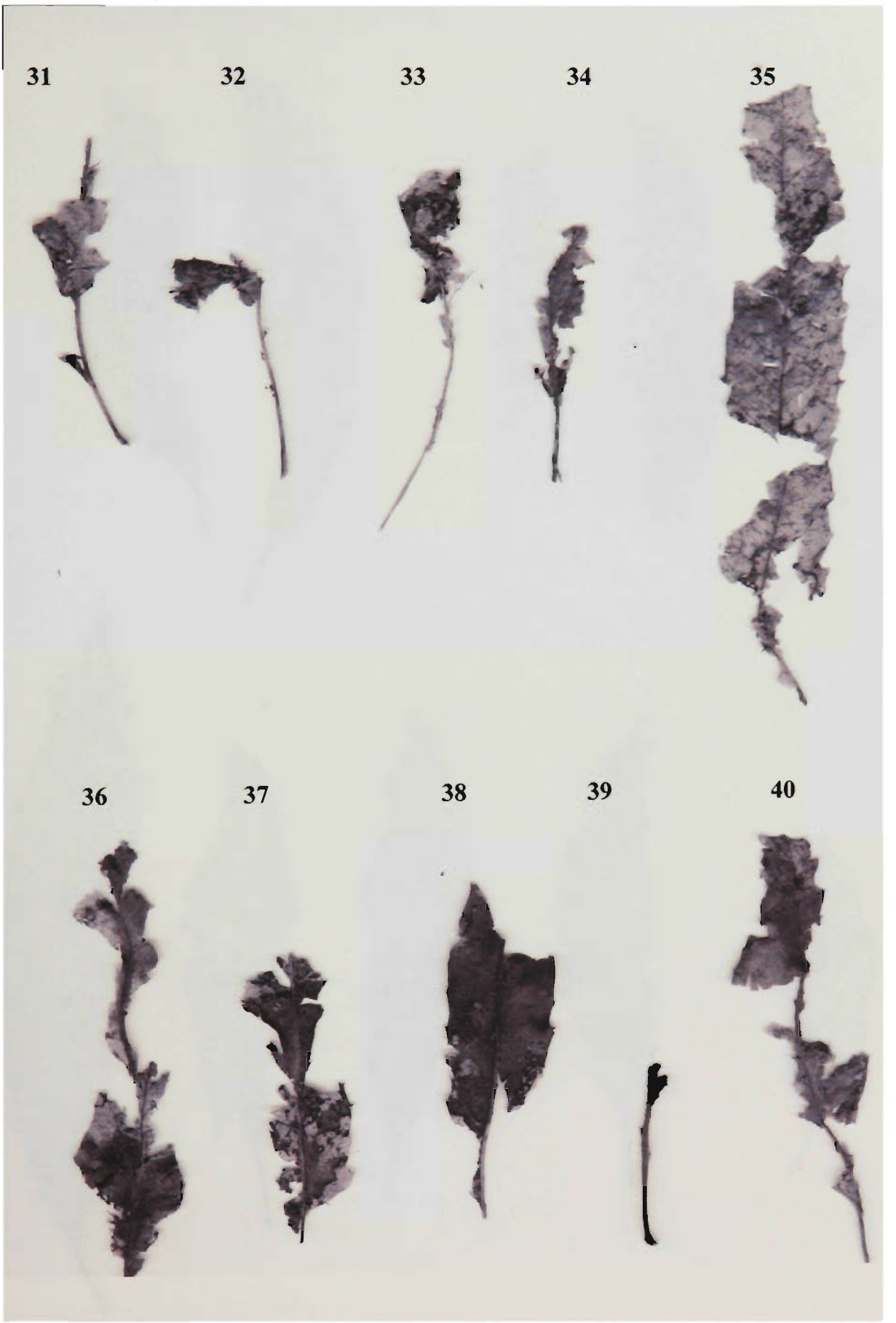


Figure 5.6d(iii)

1 month

10 cm

Figure 5.6d(iii)

Figure 5.6d(iii)

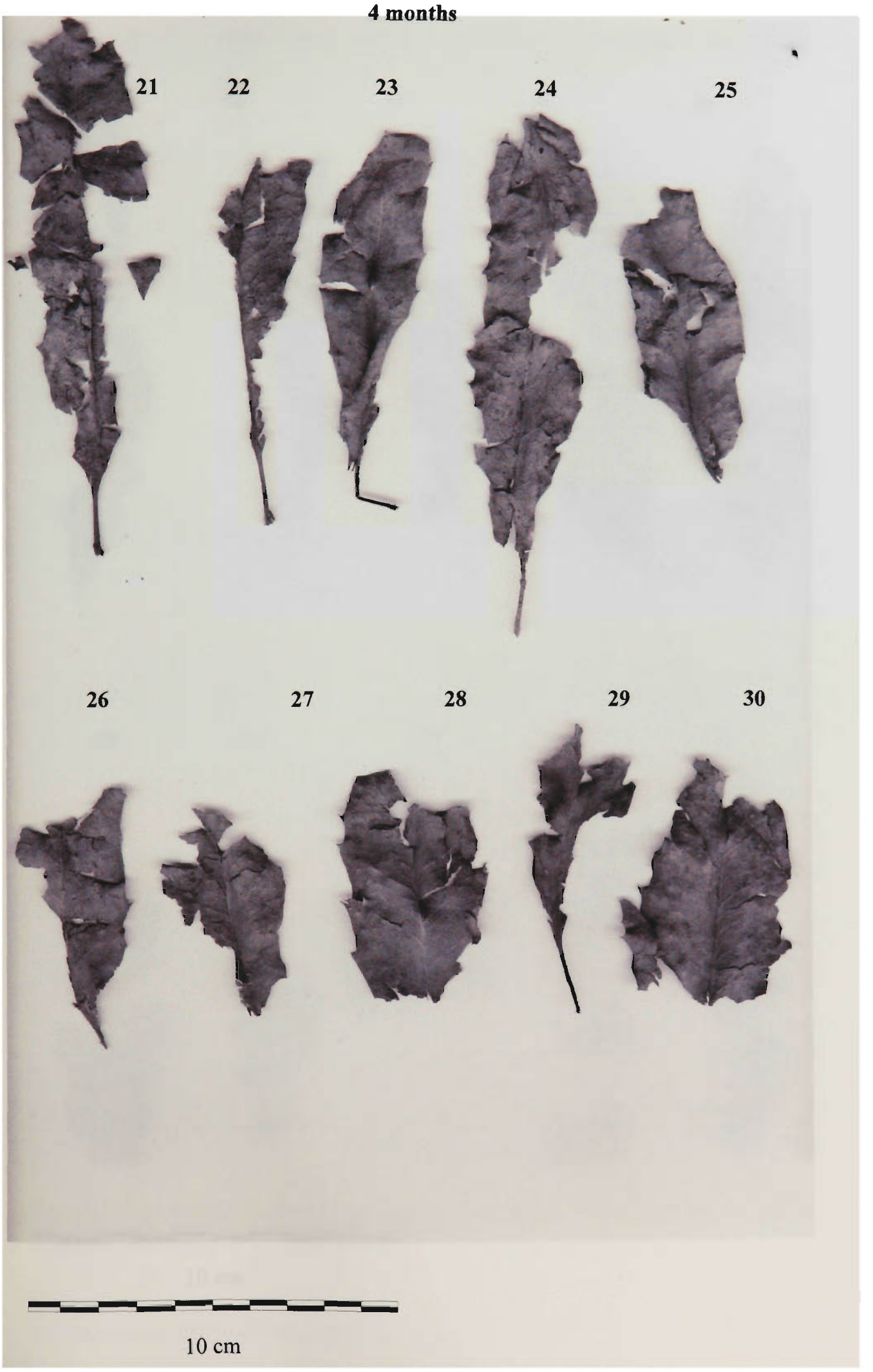
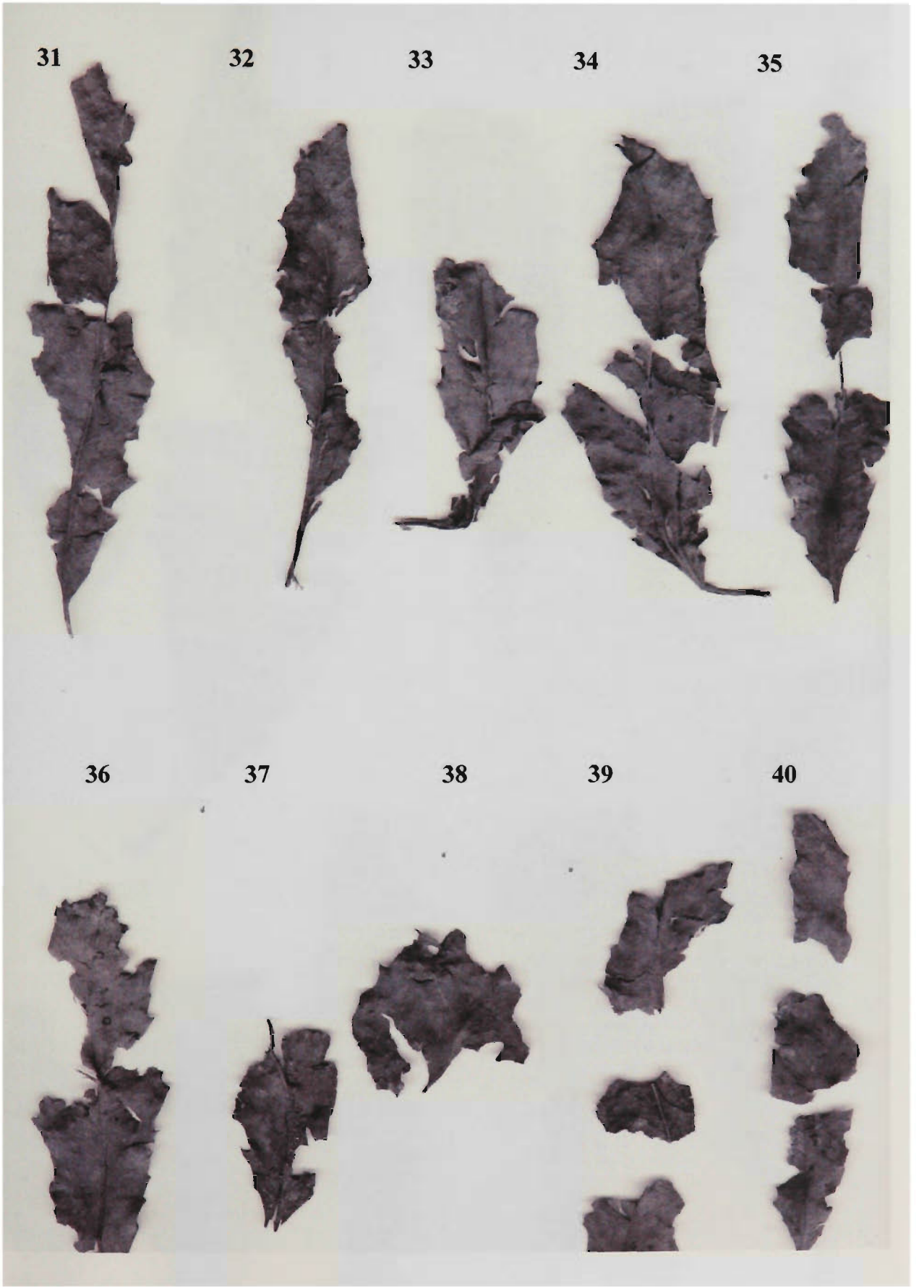


Figure 5.6d(iii)

8 months



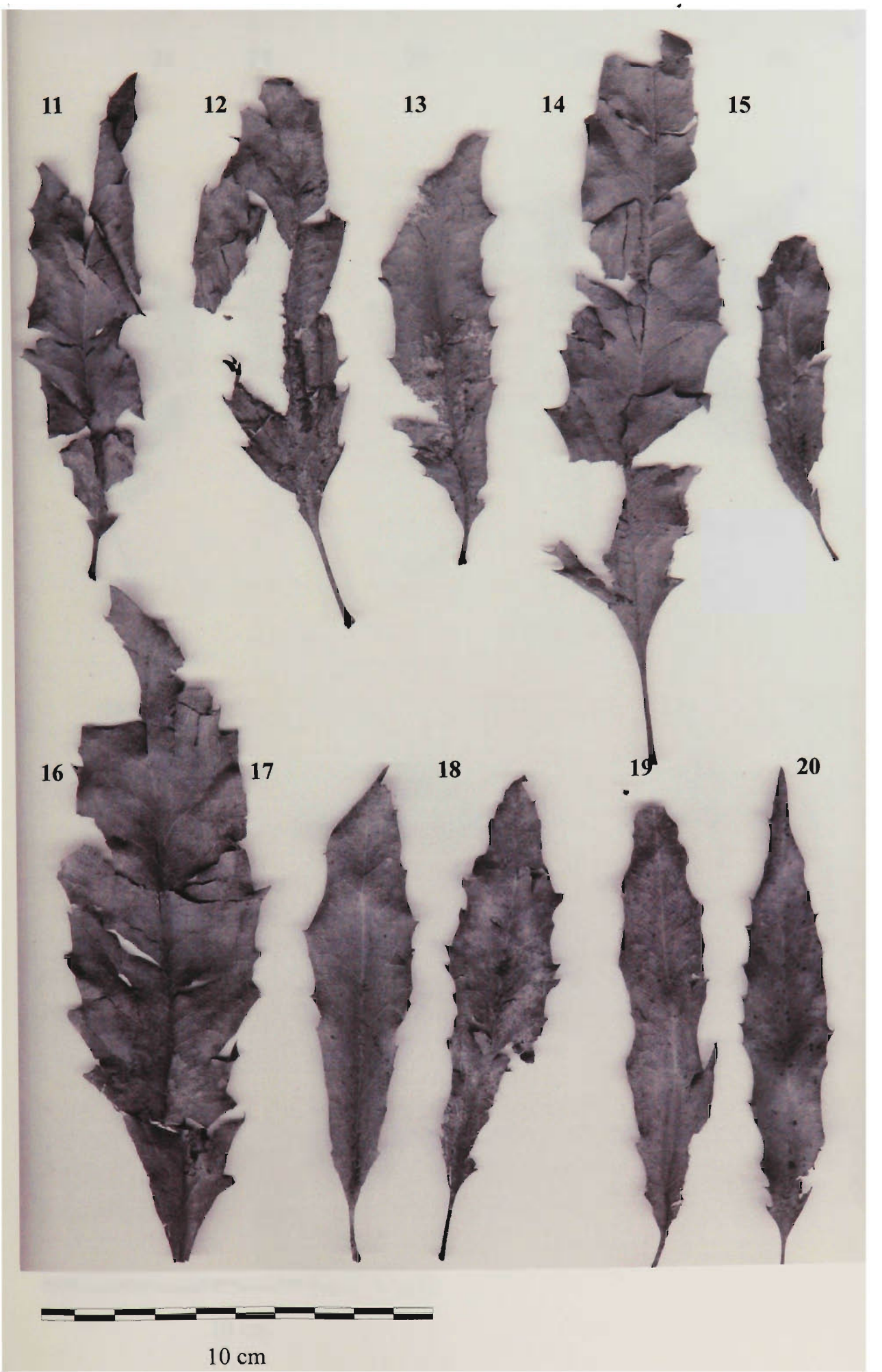
10 cm

Figure 5.6d(iv)

10 cm

Figure 5.6d(iv)

2 months



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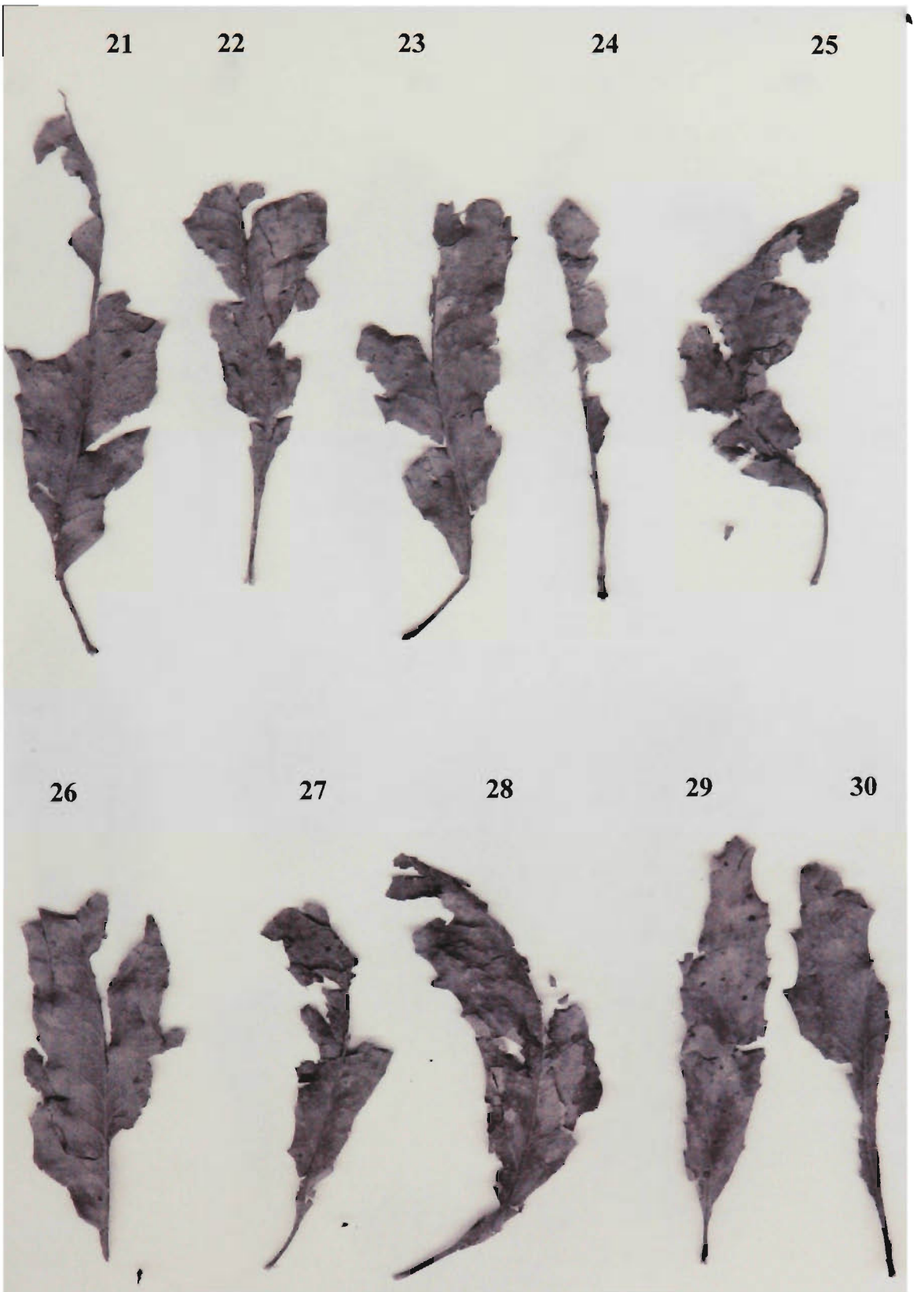
4 months



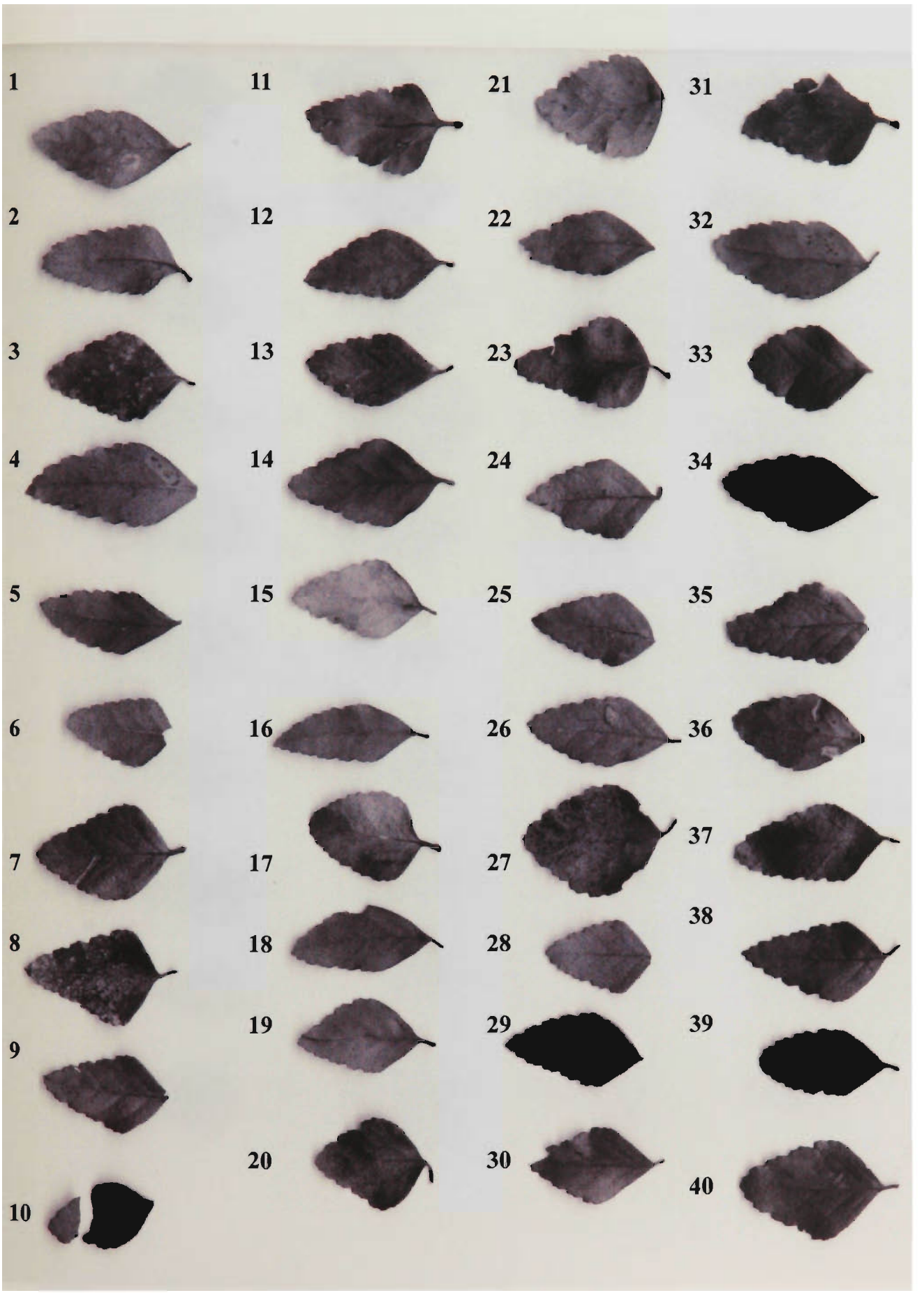
10 cm

Figure 5.6d(iv)

8 months

10 cm

Figure 5.6e(i)



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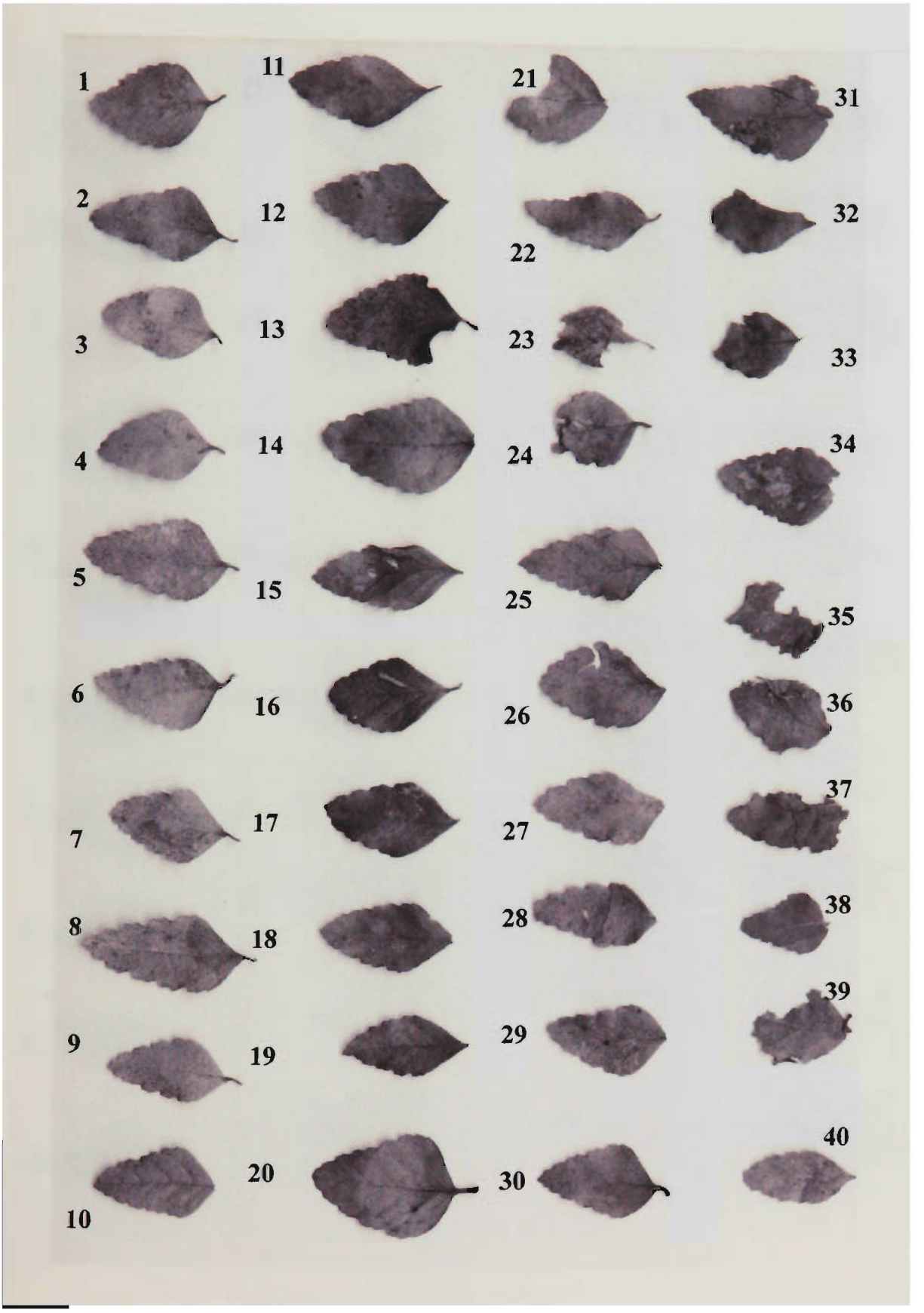

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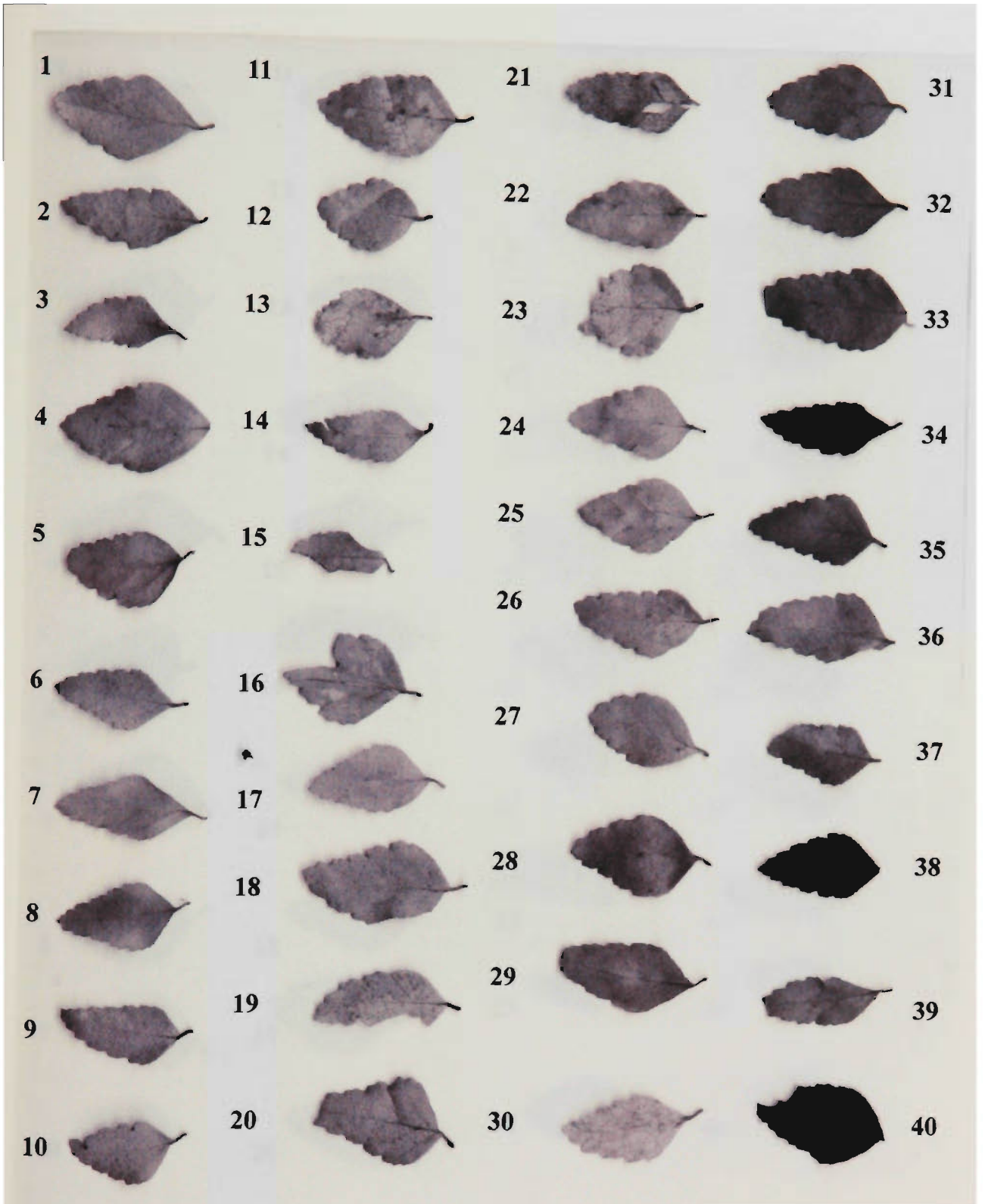

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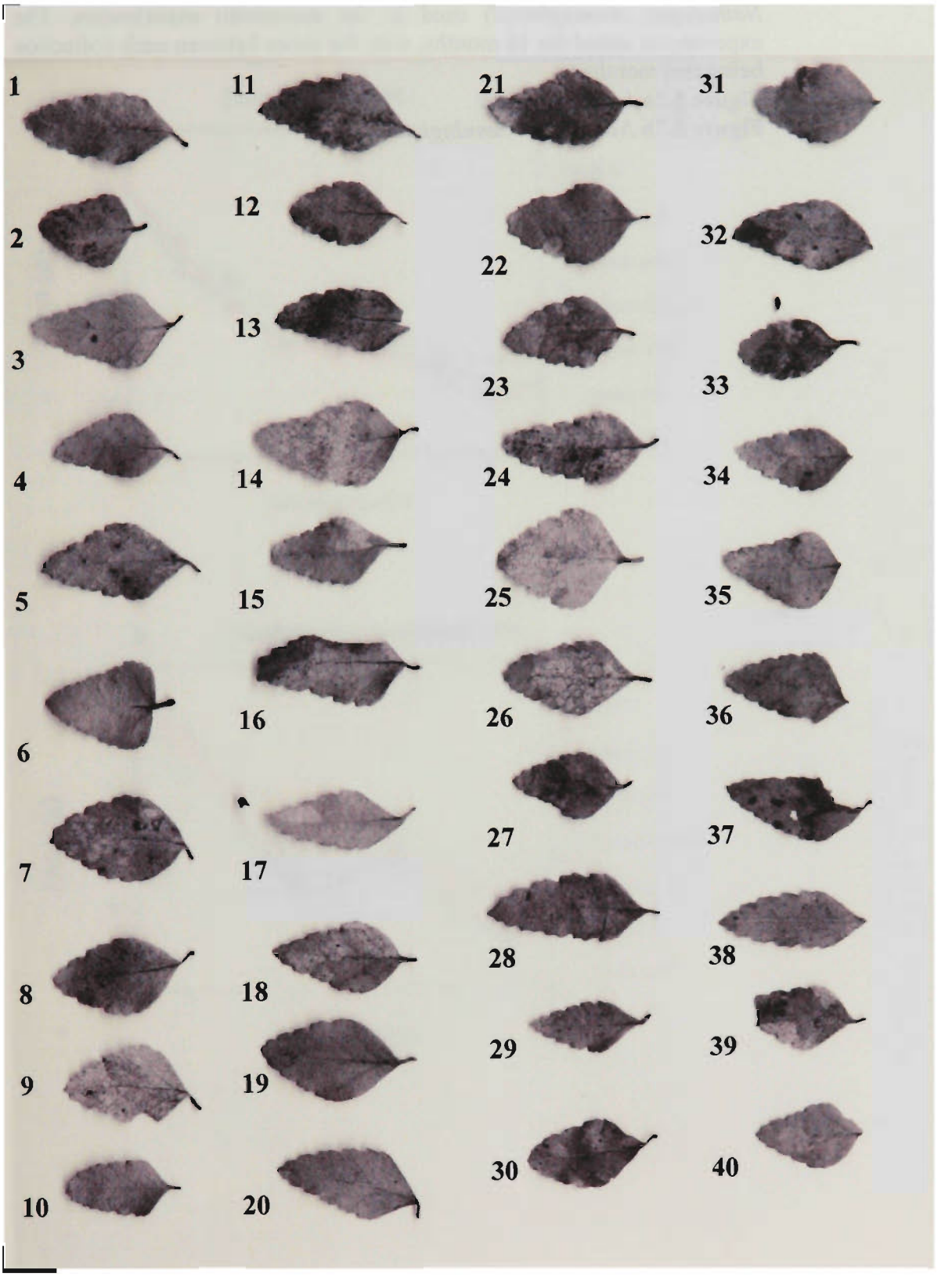
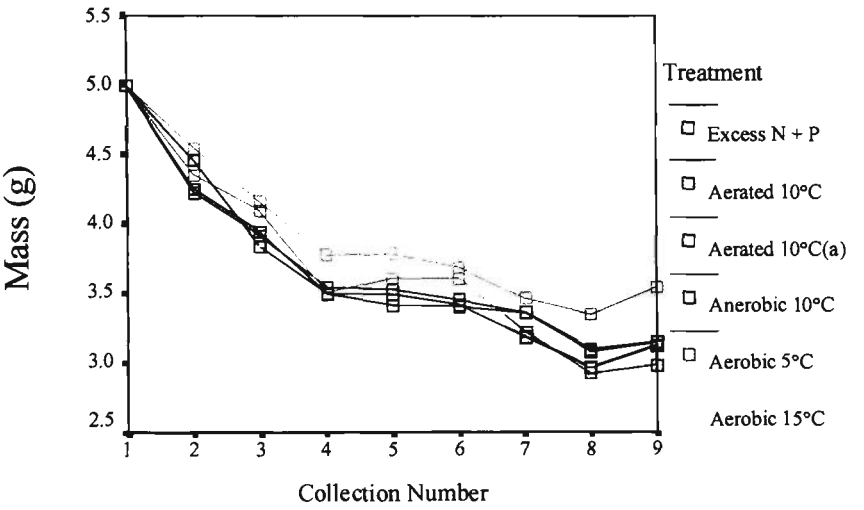
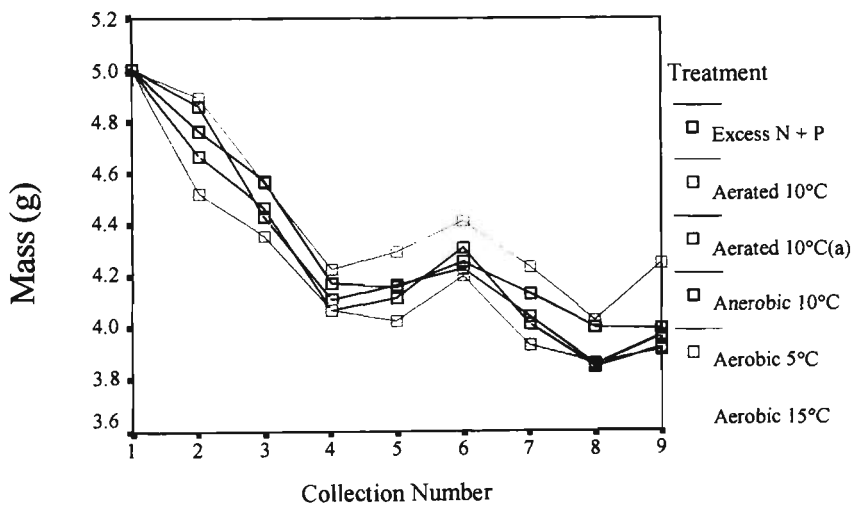


Figure 5.7 Mass loss versus time for the two species (*Lomatia fraseri* and *Nothofagus cunninghamii*) used in the mesocosm experiments. The experiments lasted for 16 months, with the times between each collection being two months.
Figure 5.7a *Lomatia fraseri*
Figure 5.7b *Nothofagus cunninghamii*

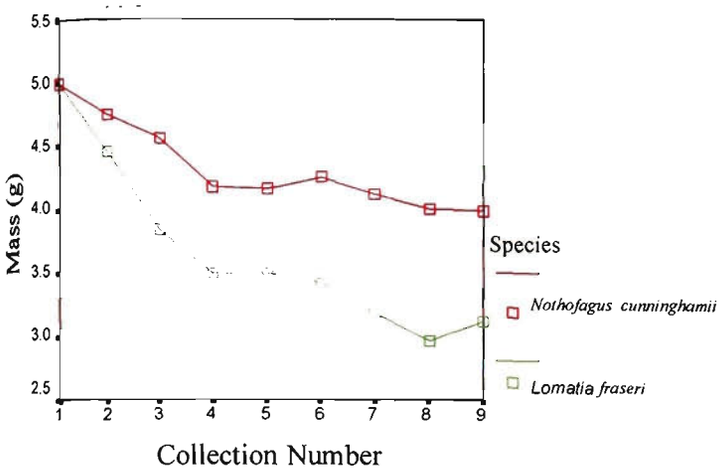
a *Lomatia fraserii*



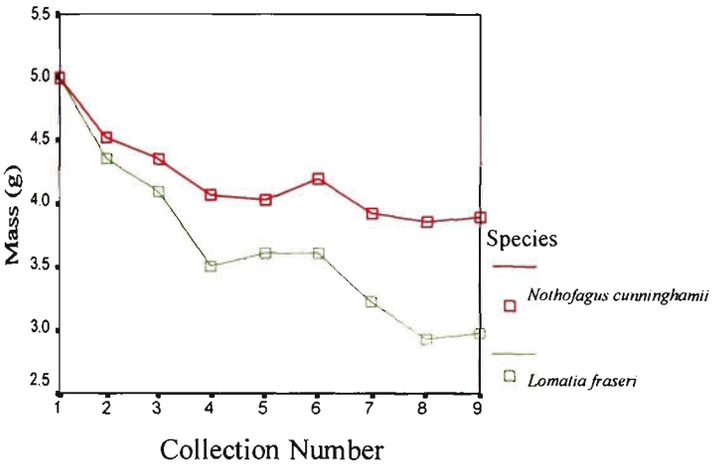
b *Nothofagus cunninghamii*



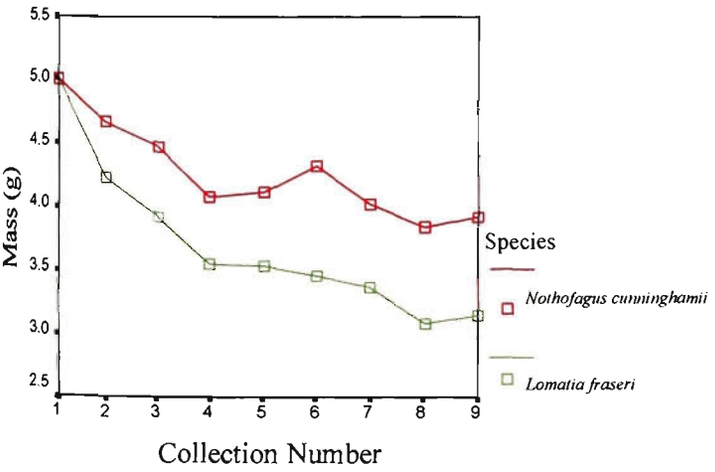
a Excess Nitrogen and Phosphorous



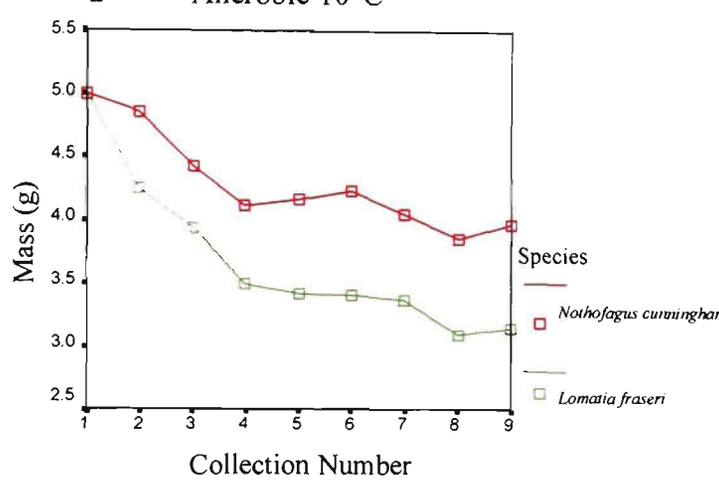
b Aerated 10°C



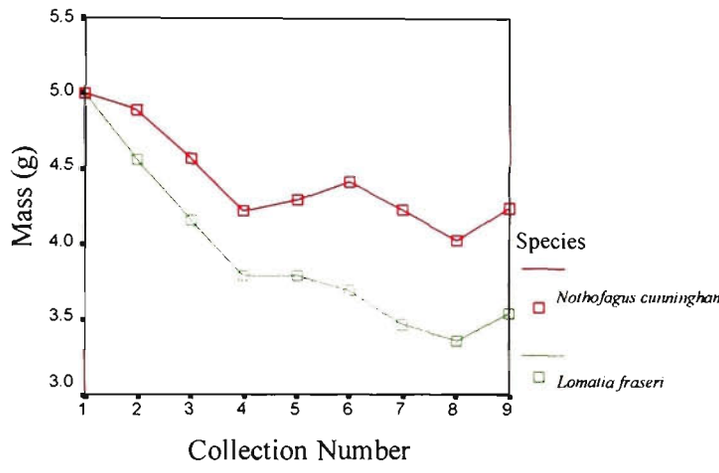
c Aerated 10°C(a)



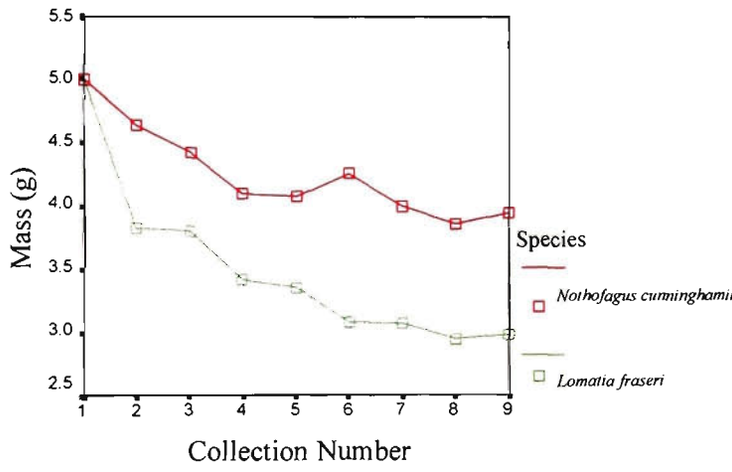
d Anerobic 10°C



e Aerobic 5°C



f Aerobic 15°C



Chapter 6

General Conclusions

The principal findings of this study indicate a) that the taphonomic bias is a significant part of the fossil forming process, b) that this bias can at least in part be quantified, and, (c) reconstructions of palaeoecosystems have the theoretical potential to be adjusted to correct for this bias. Few Australian (e.g. Hill & Gibson, 1986; Greenwood, 1991, 1992) or international (e.g. Spicer, 1981; Ferguson, 1985; Burnham *et al.*, 1992; France 1995) palaeobotanical studies have examined:

- the relationship between standing biomass rank order and abundance, and leaf number and leaf area rank order and abundance;
- how far leaf litter moved once it has fallen from a tree, (either overland or via stream transport); or
- the possible causative links between differing decay rates of leaves of different plant species, their leaf chemistry and the potential of these differences to bias the fossil record (e.g. Spicer, 1981, 1989; Ferguson 1985).

All of these areas have been examined in this study, and the findings of this study indicate that:

1. Determining the relative proportions of the leaf area of each species or taxon in either forest floor litter or in a potential plant fossil deposit can serve as a proxy indicator of the relative proportions of standing biomass in the source vegetation

(Figure 2.8). This agrees with previous research such as Burnham (1989) and Burnham *et al.* (1992), and partly redresses the paucity of data relating leaf area to basal area for Australian species.

There are some differences in the actual amount of leaf area produced by individual tree species, with species like *Eucalyptus regnans* producing less than the expected area of leaves and species like *Nothofagus cunninghamii* producing more (Figure 2.8). These differences between species in the production of leaf area per unit of basal area can alter the rank order abundance of the principal canopy species, but it preserves overall dominance patterns. The important species remain dominant.

2. Reliance on counting leaves as a proxy indicator of standing biomass may not be sufficient and is to be cautioned against particularly where there are substantial differences in sizes between the leaves found in a fossil flora or forest litter sample. Trees with small leaves like *N. cunninghamii* produce far larger numbers of leaves relative to their standing biomass than would trees with large leaves such as *E. regnans*, *Acacia melanoxylon*, and *Atherosperma moschatum*.

3. The litter taxon makeup will vary between locations (Chapter 2), and it is therefore imperative that the collection and analysis of fossil material occurs from multiple samples collected from multiple locations within a bedding plane.

Sampling that sums multiple bedding planes may lose important ecological information (Spicer 1988; Greenwood, 1991). Spicer (1988), suggests a number of strategies for collecting fossiliferous material which preserves this information. These strategies therefore allow the natural heterogeneity in the source vegetation to be recorded and accounted for and the variation in the source vegetation to be reconstructed both spatially and temporally.

4. This study clearly indicates that leaf material does not move great distances once it has come to rest, either after falling from a tree (Chapter 3) or upon entering high order streams (Chapter 4).

   The overland transport study indicated that no leaf material moved more than 3.4 metres during the six-month duration of the experiment and that 90% of all leaves remained within 0.3 m of where they had been placed.

5. Factors such as the slope of the land had little overall effect upon the transport distances of leaves once they have fallen from a tree. These results indicate that the assertions made by Fisher and Likens (1973) and Sedell *et al.* (1973) of a strong positive relationship between slope and overland transport distance are questionable in forests with heavy ground vegetation. The density of the ground vegetation is probably more significant than slope at determining the scale of overland transport. This agrees with Ferguson (1985) who indicated that as the number of obstacles around which leaf litter can become entrained increases, the transport distances decrease.

   The lack of significant overland transport distance observed at Cumberland Creek indicates that the heterogeneity of the source vegetation is likely to be preserved in forest floor leaf litter long after a leaf fall event. This again accords well with the research published by Ferguson (1985), and Burnham (1994, 1997; Burnham *et al.*, 1992). These results indicate that when a fossil deposit is being examined the natural spatial variations found in the source vegetation have a strong likelihood of showing up in the fossil record. This is particularly the case if the fossil deposit being examining consists of *in situ* forest floor litter and emphasises the need for careful stratigraphic controls when collecting plant macrofossils (Spicer,

1988; Burnham, 1989; Greenwood, 1991). The leaf litter in such a deposit will tend to reflect only those trees found growing in close proximity. The importance of collecting multiple samples from the same bedding plane and in a number of spatially separated locations in that bedding plane can not be over emphasised. The strategies employed require the careful, and exhaustive sampling and stratigraphic techniques as recommended by Spicer (1988).

6. Fossil deposits derived from leaf litter preserved *in situ* are therefore highly likely to represent the leaf litter of the nearby taxa only.

7. Leaf material entering streams is most likely to be derived from the local streamside vegetation and from leaves blown laterally during the initial abscission event and fall from the parent tree.

   The input of leaf material into streams via the overland transport and redistribution of leaf litter is predicted to be small. This has significant implications when reconstructing the vegetation of palaeolandscapes. Generally, the leaf litter entering streams will reflect the streamside vegetation, not the vegetation growing some distance from the streams. An exception to this general observation would be areas of high humidity, where riparian vegetation is able expand into neighbouring forest (Ferguson, 1999). In such a vegetaion formation the riparian flora could represent a wider regional flora.

8. For Cumberland Creek, a high order retentive waterway, no leaf travelled more than 100 m within a six hour period. Thus, these deposits can be used to characterise the local streamside source vegetation with confidence; where facies analysis indicates that a fossil deposit was produced by such a stream.

This finding is in accordance with a number of previous studies that indicate that long distance transport of leaf material in high order retentive streams is uncommon (e.g. Young et al., 1978; Ehrman & Lamberti, 1992; Jones & Smock, 1991). With the exception of Hill and Gibson (1986), little accurate data existed for Australian species.

9. The palaeobotanical assertion in point eight, that leaf deposits formed by high order streams can be used to reconstruct local streamside vegetation, does not apply to landscape-wide or regional characterisations of vegetation distribution. The relatively short distances leaves travel from their source tree during the initial abscission event (Ferguson 1985, 1995), and the negligible distances moved after the initial leaf fall under normal atmospheric conditions (this thesis; Ferguson, 1985; France, 1995), are so limited that landscape wide vegetation patterns would be difficult to reconstruct. The leaves of tree species growing more than two or three tree heights away from the stream would have little chance of entering it.

   For example, leaves of *Acacia dealbata*, one of the principal tree species found growing on the boundaries of the field site and which grew to a height of ~ 15 metres (Figure 2.6f), contributed no leaves at all to the stream side leaf litter traps even though they were growing just 30 to 35 metres from the nearest of the stream side litter traps. This species and its counterparts in that particular vegetation association would be excluded from the macrofossil record.

10. Spicer (1981, 1989) noted that powerful sorting effects were brought about by variation in leaf flotation times. These times were affected by factors such as whether both leaf surfaces were wetted, the degree of turbulence, and the extent of gas saturation of the water body. The prospect of differential stream transport

or sorting of the five plant taxa tested is significant at Cumberland Creek (Chapter 4).

In this study the likelihood of long distance transport was linked to size, weight per unit area, flexibility, flow rate and the number of obstructions in the stream; factors also found to be significant by Spicer (1981) and Ferguson (1985). Small leaves, like those of *Nothofagus cunninghamii*, have a much larger potential for transport than do large flexible ones, like those of *Eucalyptus regnans*. The large leaves of *E. regnans*can become rapidly entrapped on stream bed obstacles like stones, logs, twigs and overhanging vegetation, while the small *Nothofagus cunninghamii* leaves can flow around them. The rapid sinking of sclerophyllous taxa such as *Eucalyptus coccifera* and *Orites acicularis* reported by Hill & Gibson (1986) was also observed for the sclerophyllous taxa used in this study, *E. regnans* and *Acacia melanoxylon*. This suggests that in general Australian sclerophyllous taxa generally sink rapidly and have poor transport potential.

11. The stream flow rate is also important; as leaves subject to still or gently flowing conditions (Chapter 4) tend to remain afloat much longer than those subjected to rapidly flowing and turbulent waters. The longer flotation times of leaves in still or gently flowing conditions is probably of little consequence as the leaves are unlikely to be transported anywhere, although they may eventually settle to form an autochthonous organic debris dam.

    It should be noted that for high order streams such as Cumberland Creek, the prospect of differential sorting and transport between species is small. The transport distances in such streams are sufficiently small to ensure that long distance dispersal will be limited, and any resulting deposits will be representative of the local taxa. For large low order streams and rivers, the story could be quite

different. It is possible that leaf floras deposited by low order, slow flowing streams, with few obstacles disturbing the flow of surface waters, and little turbulence in the water column could reflect much larger stream side or regional floras. The leaves entering these rivers and streams have the potential to:

a) Be transported long distances, mostly intact. The actual distance that leaves of each species would be transported would be related to flotation times and the time intact leaves could be carried along by the river or stream suspended in the water column.

b) Be subject to differential sorting based on the above factors. The mean flotation times for brown or senesced leaves for *Nothofagus cunninghamii*, *Lomatia fraseri* and *Atherosperma moschatum* under low flow regimes is 18, 13 and 7 days respectively. In large rivers leaf materials could travel substantial distances in times as large as 13 – 18 days (Table 4.2). On the other hand, brown or senesced leaves of *Eucalyptus regnans* or *Acacia melanoxylon* would travel much shorter distances with mean flotation times of 2 days (Table 4.2)).

12. The differences in transportation potential demonstrated in this study mean that fossil deposits derived from large rivers and streams flowing through Australian landscapes, will most likely consist of locally derived taxa, and a larger regional flora consisting of those species that have good transport potential.

Taxa such a *Eucalyptus* and *Acacia* could sink, settle and be abraded by saltation along the river bed and destroyed long before reaching a site of deposition, while the other three species would have a much better chance of arriving at a site of deposition intact enough to be identified taxonomically. It is thus likely, that those taxa with poor transport potential such as *Acacia melanoxylon* and

Eucalyptus regnans will be under-represented or even absent in allochthonous fossil floras. Taxa with high transport potential such as *Nothofagus cunninghamii* and *Atherosperma moschatum* may be over-represented, distorting interpretations of species composition and relative abundance (Spicer, 1981, 1989, 1991; Spicer & Wolfe, 1987; Greenwood, 1991). The paucity of *Nothofagus* leaves in the Australian macrofossil record becomes especially intriguing in light of the above.

13. Reconstructions of source vegetation based upon fossil deposits derived from either slow flowing low order rivers and streams or turbulent high order streams need to take into account the transport and differential sorting potential's between these systems.

14. Between the five taxa studied, there is a strong decay rate bias between species. Species such as *Atherosperma moschatum* decay rapidly, regardless of how well they might be buried. This in itself helps explain the lack of a fossil record for the genus *Atherosperma*. Species such as *N. cunninghamii* have a high preservation potential under the right conditions.

15. The important indicator for decay rates is the lignin to nitrogen ratio rate (Berg & Matzner, 1997; Gallardo & Merino, 1999; Berg, 2000). The substantial literature on the lignin to nitrogen ratios in plant leaves, as well as published values for decay rate coefficients, potentially allows for the prediction of which species will decay rapidly and which will not. Species with high lignin to nitrogen ratios will have the lowest decay rates and the best chances of entering the fossil record.

    Literature and experimental based studies which compile lignin to nitrogen ratio data, can then be used to indicate which extant taxa have the potential to decay rapidly or slowly and under what conditions. These data sets can then be used to

predict which fossil taxa decay rapidly or slowly using the uniformitarian assumption. The resulting reconstructions of a fossil deposits source vegetation can be corrected for these and the other factors mentioned previously to give a more accurate model of what the palaeovegetation looked like and how it functioned.

16. The leaves of *N. cunninghamii* decay slowly if buried (Chapter 5), travel well (Chapter 4), and are over produced relative to basal area (Chapter 2). In combination these factors would suggest high preservation. A single species of *Nothofagus*, in the subgenus *Lophozonia* was examined in this study, and the dominant subgenus in the Paleogene to early Neogene record was *Brassospora*. Furthermore, *N. cunninghamii* is evergreen, and some species of *Nothofagus* (in subgenus *Fuscospora*) are deciduous. Therefore, caution must be exercised in applying the observation in this study across the genus. If the taphonomic factors that apply to *Nothofagus cunninghamii* were to apply to the genus as a whole (though this may not be tenable due to possible differences in ecology and leaf physiochemistry between the different subgenera), then paucity of Australian *Nothofagus* leaves in the Cenozoic fossil record is best explained by the trees being rare in the local riparian and lake-side vegetation, or growing in stands removed from water courses.

17. Leaves of *E. regnans* decay comparatively rapidly, on the ground or on the stream/sediment interface, transport poorly, and are underproduced relative to the standing biomass. They also decay comparatively slowly when buried. They thus have a low chance of being transported to a site of preservation, but once there have a high chance of preservation.

The trees would need to stand only a few tree heights away from the nearest watercourse to be largely excluded from the fossil forming process. The riparian vegetation would act as a filter limiting overland transport (as seen in Chapter 3) and entry to the stream. Hence, stands of eucalypts growing on ridges and drier sites associated with a mosaic of mesic vegetation and riparian gallery forests, similar to regions of northern Australia today (Groves, 1994), would have little chance of being seen in the plant macrofossil record. Such a suggestion for the palaeovegetation of Australia in the Oligocene - Miocene onwards might explain the occurrence of eucalypt pollen and the rarity of eucalypt leaves. Should this hold for the genus as a whole, then *Eucalyptus* leaves would be rare in the fossil record, as is the case.

18. The leaves of *Acacia melanoxylon* transported poorly and the trees produced numbers of leaves and a leaf area in proportions similar to their biomass (Chapter 2). The decay rates were variable (Chapter 5), but were generally slower for buried versus surface samples.

    It is probable that the paucity of *Acacia* leaves in the fossil record is due to the trees being uncommon in the landscape, or they grew in stands not immediately adjacent to watercourses. All of the leaves tested in chapter three have poor overland transport potential while *Acacia melanoxylon* leaves had poor stream transport potential and decayed slowly when buried. If the trees had been widespread in the palaeolandscape, it could be expected that more macrofossils would have been found, than have been found to date. The rarity of *Acacia* leaves in the Australian fossil record can not be explained by low leaf production compared to their standing biomass or decay rates when buried.

This study raises the possibility that the counting the numbers and areas of dispersed leaf cuticle in a fossil flora may reveal significant ecological information about the source vegetation. The preservation of cuticle is common throughout the Cenozoic fossil record and the floristic diversity of leaf cuticle floras is often higher than the associated macrofossil floras (Greenwood *et al.*, 2003). Should the amount of cuticle surviving the taphonomic process occur in proportions near those of the area of the leaves that produced them, then they could serve as a proxy indicator for leaf area. This could then allow for the reconstruction of structural and biomass makeup of fossil floras using leaf and cuticle floras alone. Unfortunately the proportions of leaf cuticle that survive the process of fossil formation are unknown, as is whether there is a species bias involved, so further work is required to quantify this.

Further Work

The lack of leaf physiochemical and taphonomic data for additional species of *Acacia, Eucalyptus* and *Nothofagus* (and in particular *Nothofagus* subgenus *Brassospora*), limit the generality of the conclusions of this study. However, the findings of this study also indicated that leaf physiochemical data, such as leaf lignin concentration and leaf lignin to nitrogen ratio have the potential to predict leaf decay rates. This discovery may be useful in estimating taphonomic bias if sufficient additional species for each genus can have their leaf physiochemistry determined.

It is therefore suggested that the lignin and lignin to nitrogrn ratios be determined for additional species of *Acacia, Eucalyptus* and *Nothofagus* (from all four subgenera, especially subgenus *Brassospora*). The leaf physiochemistry data from this study predicts that leaves high in lignin, with a high nitrogen to lignin ratio should decay slowly. If consistent patterns of lignin concentration and lignin to nitrogen ratios emerge across these three genera (and their subgenera), then lignin concentration and lignin to

nitrogen ratio can be used to predict decay rate bias for *Acacia, Eucalyptus* and *Nothofagus*. Subsequently, leaf samples from the additional species could be used in leaf decay rate experiments to ensure that the decay rate findings observed in chapter five of this study can be applied broardly for interpreting taphonomic assumptions for patterns in the fossil record.

Addition work needs also to be done on the relationship between standing biomass and the biomass of leaves produced for leaf mass, leaf area and leaf number. For example, the observation that *Eucalyptus regnans* is under-producing leaves and *Nothofagus cunninghamii* is over-producing leaves in terms leaf mass, number and area, needs further research before it can be applied to their respective genera as a whole. It is possible that these two species are exhibiting leaf production characteristics that are abnormal for their genera. It is thus suggested that areas of forest containing additional species of *Eucalyptus* and *Nothofagus* be mapped, the standing biomass of the canopy tree species determined, and the production (by species) of leaf mass, number and area measured. If this is done, and should the patterns of leaf under and over production observed for *Eucalyptus* and *Nothofagus* found in chapter two of this study hold across their respective genera, then a strong taphonomic bias in biomass production will have been found for the genus *Eucalyptus*. Such a bias could then be easily used to explain some of reasons why *Eucalyptus* leaves are rare in the Australian Tertiary fossil record.

Chapter 7

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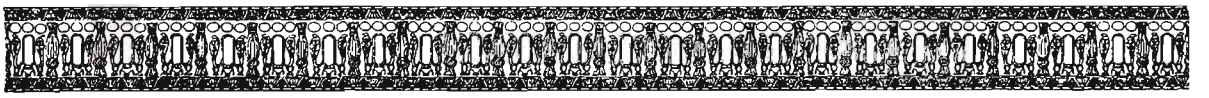
Chapter 8

Appendices



Note: All of the primary data sets used in this thesis are contained in the following two CD-ROMS. In all cases, numerial and text data is in either MS Excel™ or MS Word™ 97 format. All image files are in 'tif' format and were edited using Corel Photopaint™ 7.

Disk 1

Appendix 2
- Appendix 2.1 – Leaf litter trap data
- Appendix 2.2 – Marysville climate data (Rainfall 1905-1998)
  Marysville climate data (1997-1999)
- Appendix 2.3 – Tree data

Appendix 3
- Appendix 3.1 – Overland transport data

Appendix 4
- Appendix 4.1 – Leaf flotation data
- Appendix 4.2 – Stream transport data (Cumberland Creek)

Appendix 5
- Appendix 5.4 – Mesocosm data
- Appendix 5.4 – Mesocosm redox data

Disk 2

Appendix 5
- Appendix 5.1 – Decay data
- Appendix 5.2 – Zobbels solution
- Appendix 5.3 – Leaf cuticle images with cuticle thicknesses

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Chapter 9

Endpapers

9.1 Steart, D.C., Boon, P.I., Greenwood, D.R. & Diamond, N.T. (2002): Transport of leaf litter in upland streams of *Eucalyptus* and *Nothofagus* forests in south-eastern Australia. – Archiv für Hydrobiologie. **156**: 43-61.

9.2 Greenwood, D.R., Haines, P.W., & Steart, D.C. (2001): New Species of *Banksieaeformis* and *Banksia* 'Cone, (Proteaceae) from the Tertiary of Central Australia. – Aust. Syst. Bot. **14**: 871-890.

Arch. Hydrobiol. 156 1 43–61 Stuttgart, December 2002

Transport of leaf litter in upland streams of *Eucalyptus* and *Nothofagus* forests in south-eastern Australia

David C. Steart[1], Paul I. Boon[1]*, David R. Greenwood[1] and Neil T. Diamond[2]

With 3 figures and 3 tables

Abstract: Leaf transport – especially differences among species from diverse taxonomic groups – is generally less well understood than are the other phenomena that influence the fate of leaves in streams, such as conditioning by bacteria and fungi and fragmentation and consumption by invertebrates. To address this topic, we compared the transport behaviour of entire leaves from five indigenous species of tree in a naturally forested, upland stream in south-eastern Australia: two cool temperate rainforest taxa (*Nothofagus cunninghamii* (HOOK) OERST. and *Atherosperma moschatum* LABIL.), two sclerophyllous taxa (*Acacia melanoxylon* R. BR. and *Eucalyptus regnans* F. MUELL.) and one taxon from the ecotone between the two forest types (*Lomatia fraseri* R. BR.). Laboratory experiments indicated that, irrespective of flow regime, rainforest leaves sank markedly more slowly than did sclerophyllous leaves. *Eucalyptus regnans* leaves, for example, in moving water typically sank within 2 days of immersion, whereas *Nothofagus cunninghamii* leaves in moving water had a mean time before sinking of 8 to 67 days. These differences in flotation behaviour were reflected in field experiments that used marked leaves to quantify transport down a first-order stream in the study area. The field experiments showed the stream to be highly retentive, with leaves from no taxon travelling more than 100 m in six hours. Leaves from rainforest taxa, however, were transported longer distances in a given time than were sclerophyllous leaves, and in some of the latter cases (e.g., *Acacia melanoxylon*) retention commenced in distances as short as 5 m. There was some evidence that small leaves were transported greater distances than were large leaves; leaf texture and flexibility (a reflection of leaf morphology) also influenced transport distance, but the characteristics of the leaf margins seemingly did not. The ecological significance of these findings is that differential transport will influence the relative contribution made by

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various species to the pool of coarse particular leaf matter occurring in a given reach of a stream. It will also influence the amount of material available to downstream ecosystems and the formation of allochthonous fossil leaf assemblages.

Key words: Leaf transport, coarse POC, allochthonous input.

Introduction

Inputs of coarse particulate organic matter – largely derived from terrestrial vegetation – have long been recognised to dominate the inputs of organic matter to low-order, forested headwater streams (FISHER & LIKENS 1973, CUMMINS 1974, WINTERBOURN 1976, NEAVES 1978, BLACKBURN & PETR 1979, JOHNSON & COVICH 1997, BUNN 1986, CAMPELL et al. 1992 a, b, BENSON & PEARSON 1993, CAMPELL & FUCHSHUBER 1994). These inputs of leaves, wood and bark support an invertebrate community dominated by shredders and collectors. The detrital material is gradually broken down by physical forces and biological activity, both microbial and invertebrate, into finer particles (ANDERSON & SEDELL 1979, BENFIELD & WEBSTER 1985). The processed organic matter is either retained in situ or is translocated downstream where, supplemented by in-stream production by algae and submerged vascular plants, it supports an invertebrate community dominated by grazers and collectors. The storage and longitudinal translocation of detritus is thought to be so significant that the unused or partially processed organic material that is transported downstream contributes markedly to the "energy income" for animal communities in the lower reaches (VANNOTE et al. 1980).

The longitudinal transport of leaf material down streams is a key feature of the River Continuum Concept (VANNOTE et al. 1980, JOHNSON et al. 1995), and is of importance in understanding the formation of plant fossil deposits deposited in stream sediments (SPICER 1981, FERGUSON 1985, GREENWOOD 1991). A key topic for both limnology and palaeobotany would appear to the differential sorting of plant material upon transport. Leaves of different plant species vary widely in their anatomy and chemical composition, potentially influencing their buoyancy (and thus flotation time), and thus their retention within a stream reach and the distance travelled downstream in a given time (SPICER 1981). The differential transport of leaves of terrestrial taxa will be manifest in a biased contribution of various taxa among stream reaches and thus a biased leaf taxonomic composition in allochthonous leaf assemblages (SPICER 1981, GREENWOOD 1991). This topic has been relatively poorly addressed in the limnological literature even though the phenomenon was first reported over 100 years ago (SPICER 1981).

A relatively large number of studies has addressed the transport – or more specifically the retention – of allochthonous leaf material in streams (e.g.,

PROCHAZKA et al. 1991, NEWBOLD et al. 1982, SNADDON et al. 1992, SPEAKER et al. 1984, KING et al. 1987, KOETSIER & MCARTHUR 2000, GURTZ et al. 1988, SMOCK 1990, STEWART & DAVIES 1990, JONES & SMOCK 1991, WEBSTER et al. 1994, RACTLIFFE et al. 1995, WEBSTER & MEYER 1997, KOETSIER & MCARTHUR 2000, LARNED 2000). These studies have (in the main) shown the overwhelming importance of hydrology – especially stream velocity – in determining whether a leaf is translocated downstream or retained within a given stream section.

A considerably smaller number of studies has quantified the distance that individual leaves are translocated downstream. In one of the earliest reports, YOUNG et al. (1978) quantified the distances travelled by maple (*Acer rubrum*), beech (*Fagus grandifolia*) and oak (*Quercus rubra*) leaves in a woodland stream in Pennsylvania (USA) and found that the distances ranged markedly, from ~100 m to over 1 km. EHRMAN & LAMBERTI (1992) reported that the average distance travelled by *Ginkgo* leaves in a third-order woodland stream in Indiana (USA) ranged from 109 to 168 m; wooden dowels travelled 14 to 183 m. Other studies have indicated far more effective retention of leaves: JONES & SMOCK (1991), for example, reported that the mean transport distance of leaves in a first-order stream in Virginia (USA) could be as short as 1.6 m. WALLACE et al. (1995) concluded that the maximum downstream movement of surrogate "leaves" (plastic sheets) in headwater streams in North Carolina (USA) was ~42 m per year. In the first order Window Stream (South Africa) leaves could be retained within reaches over distances as short as 50 m (PROCHAZKA et al. 1991).

Relatively few ecological studies have addressed the topic of leaf sorting. The most detailed studies of leaf sorting have been reported in the palaeobotanical literature, largely because of the importance of being able to quantify the origins of fossil leaf material when analysing fossil leaf deposits and attempting reconstruction of the ecosystems that formed them (e.g., DRAKE & BURROWS 1980, SPICER 1981, FERGUSON 1985, SPICER & WOLFE 1987, CARPENTER & HORWITZ 1988, GREENWOOD 1992). SPICER (1981, 1989) noted that powerful sorting effects were brought about by variation in leaf flotation times, and that these times were affected by factors such as whether both leaf surfaces were wetted, the degree of turbulence, and the extent of gas saturation of the water body. With respect to leaf morphology, it has been shown that thin papery leaves of deciduous trees, such as *Alnus glutinosa* (L). GAERTN., sink within hours in aquaria, whereas the thick coriaceous leaves of the broad-leaved evergreen *Rhododendron* sp. float for several days (SPICER 1981, FERGUSON 1985). Variation in flotation times have been reported by HILL & GIBSON (1986), who found that leaves of the sclerophyllous taxa, *Eucalyptus coccifera* J. D. HOOK. and *Orites acicularis* R. BR., sank within two days, whereas the leaves of other taxa floated for several days. Anecdotal evidence

suggests also that large coriaceous leaves may be transported shorter distances in streams than small leaves within or between stands of tropical rainforest (GREENWOOD 1992).

The ability of leaves to remain buoyant and to be transported downstream clearly has significance for both limnology and palaeobotany. Only leaves of plant taxa that travel well downstream have the potential to contribute significant amounts of coarse particulate carbon (and thus energy) to the downstream ecosystems. In contrast, leaves of species that travel poorly will contribute coarse particulate detritus significantly only to the local ecosystems where they are entrained. (Note that downstream exports of fine particulate material dissolved organic matter may occur in the second case.) Differences in leaf retention among taxa will also contribute to discrepancies in taxonomic composition of fossil leaf assemblages (SPICER 1981, 1989, FERGUSON 1985, GREENWOOD 1991, 1992); taxa with poor transport potential will be under-represented or even absent in allochthonous fossil leaf assemblages, whereas taxa with high transport potential may be over-represented, distorting interpretations of species composition and relative abundance (SPICER 1981, 1989, 1991, SPICER & WOLFE 1987, GREENWOOD 1991).

In this study, we tested the hypothesis that leaves from plant taxa in different forest types would be transported different distances downstream. The field site chosen for our experiments – in the Central Highlands of Victoria, south-eastern Australia – is ideal to test this prediction. Temperate rainforest in south-eastern Australia is usually dominated by myrtle beech, *Nothofagus cunninghamii* (HOOK) OERST., and typically occurs as riparian stands (CONN 1993). In contrast, the surrounding areas are typically dominated by tall open forest dominated by one or more species of *Eucalyptus*, although individuals of the common species of both forest types may be found throughout the riparian and non-riparian areas. The leaves of the main woody taxa in these forests vary from chartaceous (e.g. some rainforest species) to markedly sclerophyllous (e.g. *Eucalyptus* spp.), offering marked differences in leaf anatomy by which to assess the influences of leaf anatomy on transport behaviour.

We were particularly interested in whether leaves of woody rainforest taxa and woody sclerophyllous taxa from the same small catchment differed in transport behaviour, and whether flow regime and leaf morphology played a significant role in determining leaf flotation, transport and retention. To this end, we used laboratory experiments to compare the flotation behaviour of five species of leaves (both green and brown) under three flow regimes, and complemented these laboratory studies with field observations, using marked leaves, to quantify the distances travelled downstream by the various leaf types.

Methods

Field site and leaf litter characteristics

Field experiments were undertaken at Cumberland Creek, in the Central Highlands of Victoria, south-eastern Australia (145° 53′, 37° 34′; Fig. 1). Cumberland Creek is a first order perennial stream, with a typical width of 1.2 to 1.8 m and a maximum depth of 0.8 m under typical baseflow conditions. The stream bed consists of coarse sand with occasional cobbles and large rocks. The underlaying geology is granitic. There are many large submerged logs of the mountain ash, *Eucalyptus regnans* F. MUELL, in and across the stream, together with smaller branches and twigs from a wider range of taxa embedded in the channel. The site is 880 m above sea level. It has a mean annual precipitation of ~1,700 mm (Fig. 1) and is subject to occasional snowfall in winter. Mean annual temperature is 9.6 °C.

The cool temperate rainforest vegetation of the Cumberland Creek catchment forms a broad riparian corridor, surrounded by open-canopied *Eucalyptus* forest (Fig. 1). The rainforest community is dominated by two tree species, *Nothofagus cunninghamii* and southern sassafras, *Atherosperma moschatum* LABIL., both of which grow to a height of ~35 m. A few large individuals of the principal sclerophyll species, *Eucalyptus regnans*, are also present within the rainforest area. The ground story vegetation of the rainforest zone is dominated by ferns, such as *Blechnum wattsii* TINDALE and *Polystichum proliferum* (R. BR.) PRESL. A shrub layer is virtually absent, except for numerous juveniles of the canopy trees and the occasional *Lomatia fraseri* R. BR. (a small tree or shrub, 2–5 m tall) near the fringes of the rainforest.

The tall open sclerophyllous forest surrounding the rainforest (Fig. 1) is dominated by submature *Eucalyptus regnans*, ~50 m tall, with an under-storey of *Acacia dealbata* LINK. and *Acacia melanoxylon* R. BR., which form a subcanopy of ~30 m height. This floristic pattern is typical for these forest types in the region (BLACKBURN & PETR 1979, CONN 1993).

The *Eucalyptus* and *Nothofagus* forests and streams of the nearby Cement Creek and Keppel Creek catchments in the Central Highlands region have been described by BLACKBURN & PETR (1979) and TREADWELL et al. (1997), respectively. Other relevant information has been presented in CAMPELL & FUCHSHUBER (1994, 1995). Total litter fall near Cement Creek is about 6 tonnes (dry weight) $ha^{-1}y^{-1}$, of which leaves constitute 25 % (*Eucalyptus regnans* leaves 11 % of total litter by weight; *Nothofagus cunninghamii* leaves 5 %; *Atherosperma moschatum*, leaves 6 %). Large amounts of wood and, to a lesser extent, leaf litter accumulate in the streams and form discrete aggregations. TREADWELL et al. (1997) reported that standing crop of wood (>1 mm size) in Keppel Creek was 3.9 kg/m^2, whereas coarse and fine benthic organic matter accounted for only 0.13 kg/m^2. The invertebrate taxa in the litter accumulations are principally stoneflies, a mayfly, two species of conoesucid caddis flies and chironomid larvae.

All the woody species in both the forest types of the study area are evergreen, but they show seasonal leaf shedding behaviour with a strong peak in litter fall in late spring, or October to November (BLACKBURN & PETR 1979, CAMPELL & FUCHSHUBER 1994; see also BUNN 1986). Heavy rain associated with summer thunderstorms

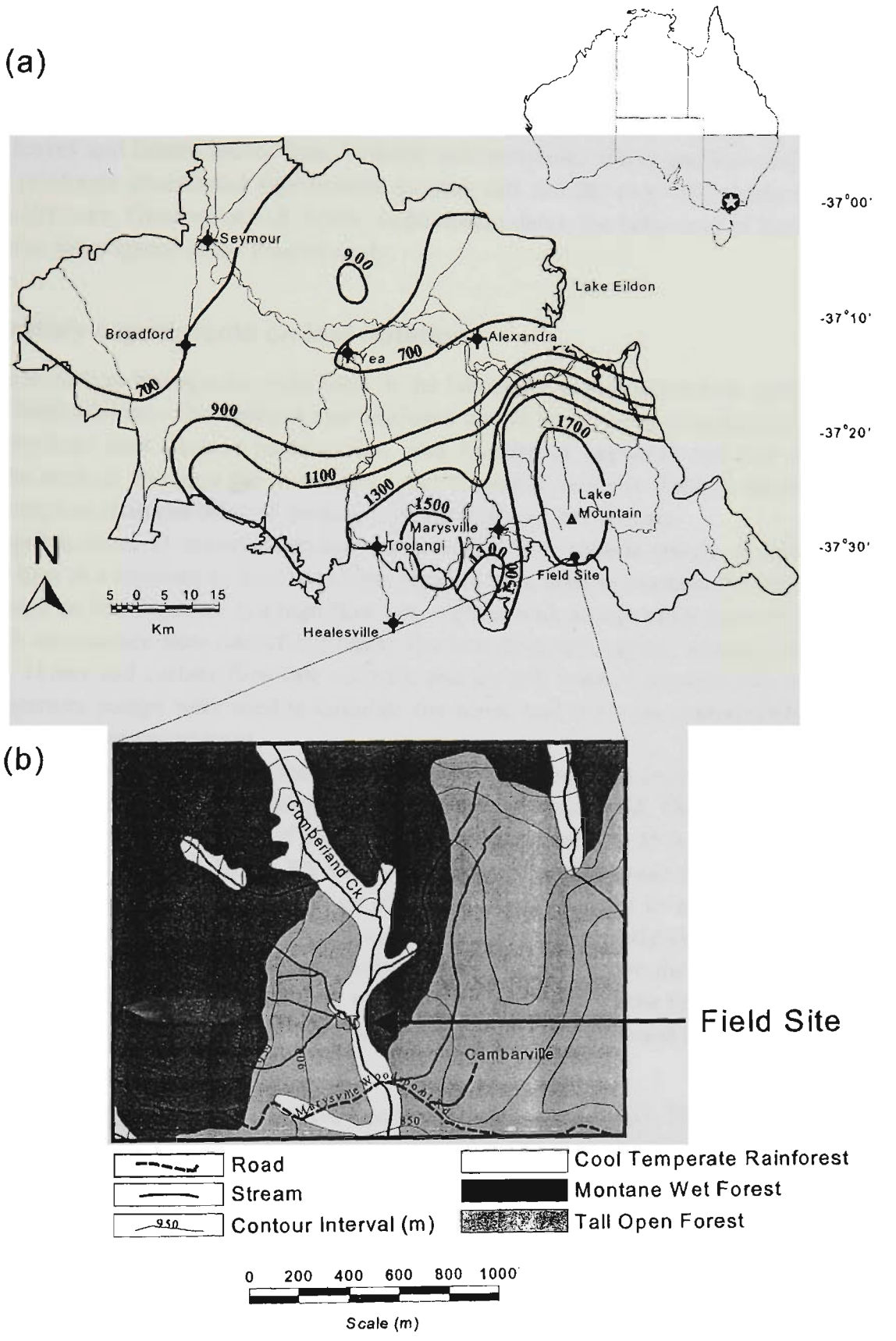

Fig. 1. Details of field site. **(a)** Map of the local region and location of Cumberland Creek, Central Highlands, Victoria, Australia. The map also shows the annual rainfall for the region (200 mm isohyets). **(b)** Detail of the field site area showing the areal distribution of the main forest types, topography (50 m contours), stream courses, and outline of the field site area.

may also wash detrital material, composed mainly of brown leaves, into the stream. Additionally, water stress over summer and periods of high winds strip green leaves from trees, which either contribute to the litter mass on the ground or, more typically in the case of the riparian zone, falls directly into the stream (see BUNN 1986). As green leaves and brown leaves from both the sclerophyllous forest and the cool temperate rainforest contributed significantly to litter fall and the crop of detritus in the stream (STEART, GREENWOOD & BOON, unpublished data), the behaviour of both leaf types was investigated in the present study.

Laboratory experiments on leaf flotation

Leaves from five tree species were used in the laboratory experiments: two cool temperate rainforest taxa (*Nothofagus cunninghamii* and *Atherosperma moschatum*), two sclerophyllous taxa (*Acacia melanoxylon*, and *Eucalyptus regnans*) and one taxon from the ecotone between the two forest types (*Lomatia fraserii*). Table 1 shows the morphological characteristics of the leaves of the different tree species.

Flotation times of leaves were determined using 90 L aquaria (60 cm × 30 cm × 45 cm) kept at a constant 10 °C. Three flow regimes were used to examine the effect of turbulence on leaf flotation: i) a high flow rate-regime, with an aquarium turnover time of 4 min and surface flow rate of ~25 cm/s; ii) a low flow-rate regime, with a turnover time of 11 min and surface flow rate ~5 cm/s; and iii) still water. Commercially available aquarium pumps were used to circulate the water, and were run continuously for the duration of the experiment.

Each aquarium contained either 100 brown or 100 green leaves of each species. The green leaves were freshly picked the day before they were used. The brown leaves consisted of recently abscised leaf litter, air dried at 20 °C and 45–55 % relative humidity for two weeks before usage. All leaves were placed carefully onto the surface water of the tank at the commencement of each experiment in order to avoid clumping and leaves sticking to the sides of the tank. The leaves subsequently circulated freely in a circular motion within the tank, without clumping or adhering to the sides.

The number of leaves that had sunk was recorded each day for the first 7 days, then at 5 and 10 day intervals until day 110. This counting strategy was used after a trial ex-

Table 1. Leaf characteristics of the five tree species used in this study. Values for average leaf areas and leaf densities were determined from data on 50 leaves per taxon.

Species	Size class	Average leaf area (cm^2)	Texture	Margin	Leaf density (g/m^2)
Nothofagus cunninghamii	Nanophyll	1.3	Papery	Toothed	101
Atherosperma moschatum	Microphyll	10.8	Papery	Toothed to rarely entire	94
Lomatia fraseri	Notophyll/ Macrophyll	36.2	Intermediate	Toothed	121
Eucalyptus regnans	Notophyll	17.2	Sclerophyll	Entire	243
Acacia melanoxylon	Microphyll	8.4	Sclerophyll	Entire	183

periment indicated that leaves tended to either sink in the first week of the experiment or remain buoyant over a period of months. The mean time before sinking (MTBS) was determined using Minitab Version 11 (Minitab for Windows, Release 11) and SPSS (SPSS for Windows Release 10.0.5). A log-normal distribution was chosen for curve fitting (where required) as it best described the patterns of sinking. More detailed statistical procedures are not warranted, since the experimental set up used only one aquarium per species/leaf colour/flow rate combination to calculate leaf settling periods. Thus the design offers only one replicate per experimental combination (i.e., it is pseudoreplicated). We examine the implications of this experimental design for interpretation of the results later in the Discussion.

Field experiments on leaf transport

Leaf transport was quantified in situ by measuring the distance leaves of the different taxa were transported downstream over a set time period. A gill net (mesh size: 4 mm) was deployed across Cumberland Creek, and marker stakes were placed upstream of the gill net at distances of 1, 2, 5, 10, 20, 50, 100 and 200 m. Twenty green and twenty (dried) brown leaves of each species were released at each marker stake, giving a total release for each species/leaf colour combination of 160 leaves. Before release, the leaves were given a unique mark, with small dots of Liquid Paper^{TM} (a water-insoluble typing correction fluid, Gillette Australia Pty. Ltd), that corresponded to the setting of each release point. The leaves were then dropped gently into the centre of the stream, and the time taken for each leaf (and the number of leaves in total) to reach the net were recorded. Data were collected either until all the leaves for a given distance had been accounted for, or the onset of evening ended each days' observations (corresponding to approximately 6 hours of transport time at this time of year).

The field experiments were undertaken in July to August 1999. Experimental days were chosen to reproduce as much as possible the same conditions, with the stream flow remaining about 1.5 m^3/s, and stream velocity (at the gill net) between 0.5 and 0.7 m/s.

Results

Laboratory experiments on leaf flotation

Figure 2 shows the patterns of leaf sinking for the five taxa, two leaf colours and three flow regimes used in the laboratory experiments. The mean time before sinking (MTBS) for each experimental combination, calculated from these data, is shown in Table 2. Figure 3 shows a complimentary approach to interpreting the data of Figure 2; the median time (in days, with Bonferroni-corrected 95 % confidence intervals) of the leaves remaining afloat. In this figure, the three morphological groups (rainforest leaves, sclerophyllous leaves, and the intermediate, ecotonic taxon) have been identified separately to ease taxonomic comparisons.

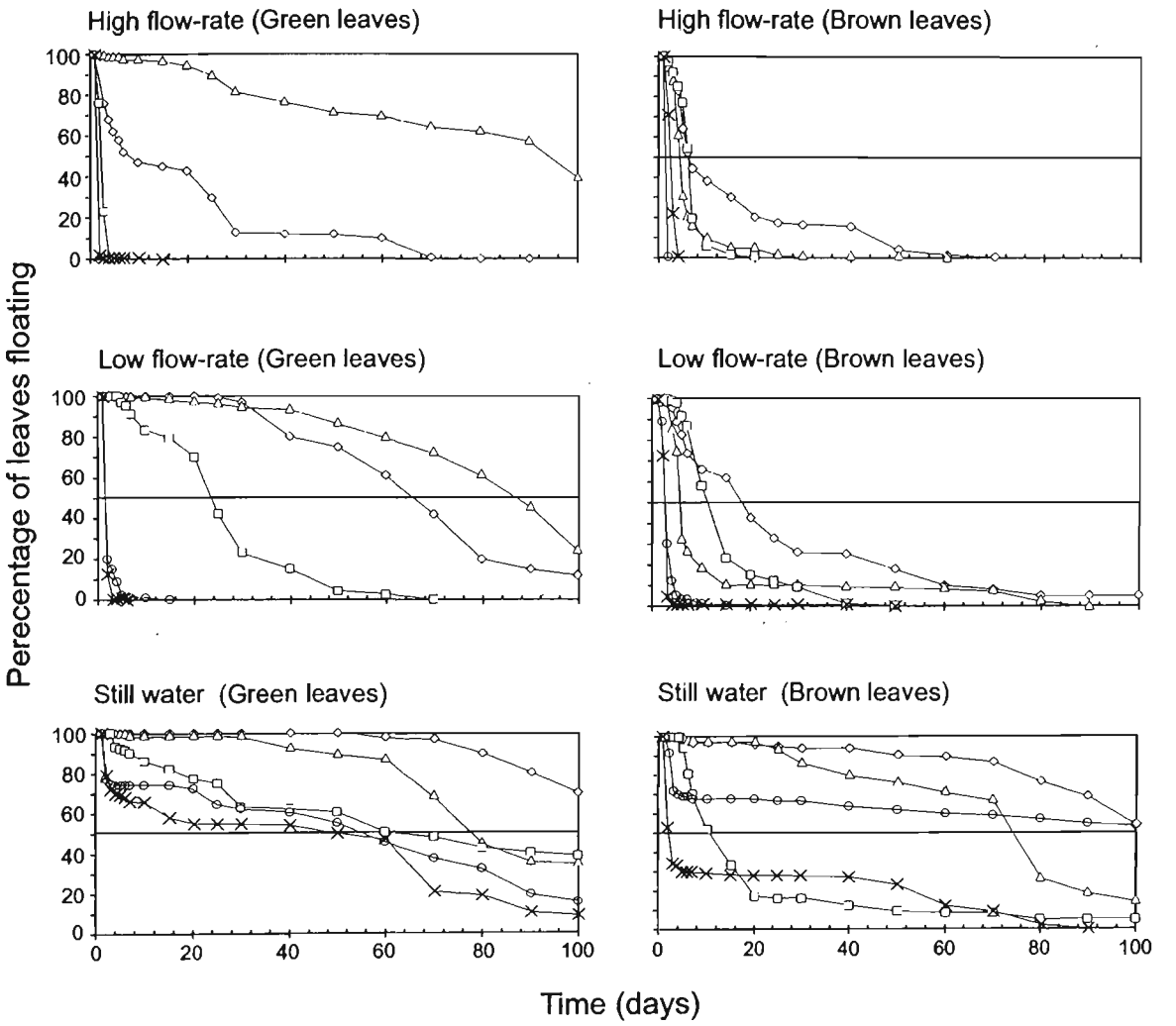

Fig. 2. Flotation behaviour of leaves of *Acacia melanoxylon, Atherosperma moschatum, Eucalyptus regnans, Lomatia fraseri* and *Nothofagus cunninghamii* under laboratory conditions. All six flow-rate versus leaf colour type combinations are shown for each of the five tree taxa. Key: *Nothofagus cunninghamii* ◇; *Atherosperma moschatum* △; *Lomatia fraseri* □; *Eucalyptus regnans* ○; *Acacia melanoxylon* ×.

The mean time before sinking (MTBS) varied from <1 day to >200 days (Table 2). Green leaves from the rainforest species, *Nothofagus cunninghamii* and *Atherosperma moschatum*, floated for the longest time, irrespective of flow regime (Fig. 2). Green leaves of *Nothofagus cunninghamii* and *Atherosperma moschatum* in still water, for example, had a MTBS of 132 and 88 days, respectively (Table 2). In contrast, sclerophyllous leaves tended to sink rapidly, with green *Eucalyptus regnans* and *Acacia melanoxylon* leaves in still water having a MTBF of 29 and 18 days, respectively. *Lomatia fraseri*, the ecotonal species, had a sinking behaviour that was intermediate between that of the rainforest and sclerophyllous taxa; the MTBS for green leaves of this species in still water was 64 days.

Flow rate also exerted a strong effect on sinking behaviour. With the exception of green *Atherosperma moschatum* leaves, the more vigorous the flow

Table 2. Leaf flotation times determined under laboratory conditions for combinations of each of five tree species, brown and green leaves, and three flow rates. MTBS = Mean Time Before Sinking.

Group	Species	Flow rate	Leaf colour	MTBS (days)
1	*Nothofagus cunninghamii*	Still Water	Green	132
2	*Nothofagus cunninghamii*	Low	Green	67
3	*Nothofagus cunninghamii*	High	Green	10
4	*Nothofagus cunninghamii*	Still Water	Brown	207
5	*Nothofagus cunninghamii*	Low	Brown	18
6	*Nothofagus cunninghamii*	High	Brown	8
13	*Atherosperma moschatum*	Still Water	Green	88
14	*Atherosperma moschatum*	Low	Green	97
15	*Atherosperma moschatum*	High	Green	129
16	*Atherosperma moschatum*	Still Water	Brown	70
17	*Atherosperma moschatum*	Low	Brown	7
18	*Atherosperma moschatum*	High	Brown	4
7	*Lomatia fraseri*	Still Water	Green	64
8	*Lomatia fraseri*	Low	Green	22
9	*Lomatia fraseri*	High	Green	2
10	*Lomatia fraseri*	Still Water	Brown	13
11	*Lomatia fraseri*	Low	Brown	13
12	*Lomatia fraseri*	High	Brown	5
25	*Eucalyptus regnans*	Still Water	Green	29
26	*Eucalyptus regnans*	Low	Green	1
27	*Eucalyptus regnans*	High	Green	<1
28	*Eucalyptus regnans*	Still Water	Brown	137
29	*Eucalyptus regnans*	Low	Brown	2
30	*Eucalyptus regnans*	High	Brown	<1
19	*Acacia melanoxylon*	Still Water	Green	18
20	*Acacia melanoxylon*	Low	Green	1
21	*Acacia melanoxylon*	High	Green	1
22	*Acacia melanoxylon*	Still Water	Brown	4
23	*Acacia melanoxylon*	Low	Brown	2
24	*Acacia melanoxylon*	High	Brown	2

the more rapidly the leaves sank. For example, the MTBS for green *Nothofagus cunninghamii* and brown *Eucalyptus regnans* leaves under still, slow and fast water flows were 132, 67 and 10 days and 137, 2 and <1 days, respectively (Table 2). In the case of green *Atherosperma moschatum* leaves, the MTBS under the three flow rates was 88, 97 and 129 days (Fig. 2) and these values are unlikely to be significantly different from each other (Fig. 3).

The effect of leaf colour on sinking behaviour was complex. Although green leaves generally sank more slowly than did brown leaves, differences in sinking behaviour across leaf colour were most evident in still water and became less apparent as flow rates increased (Table 2, Figs. 2, 3).

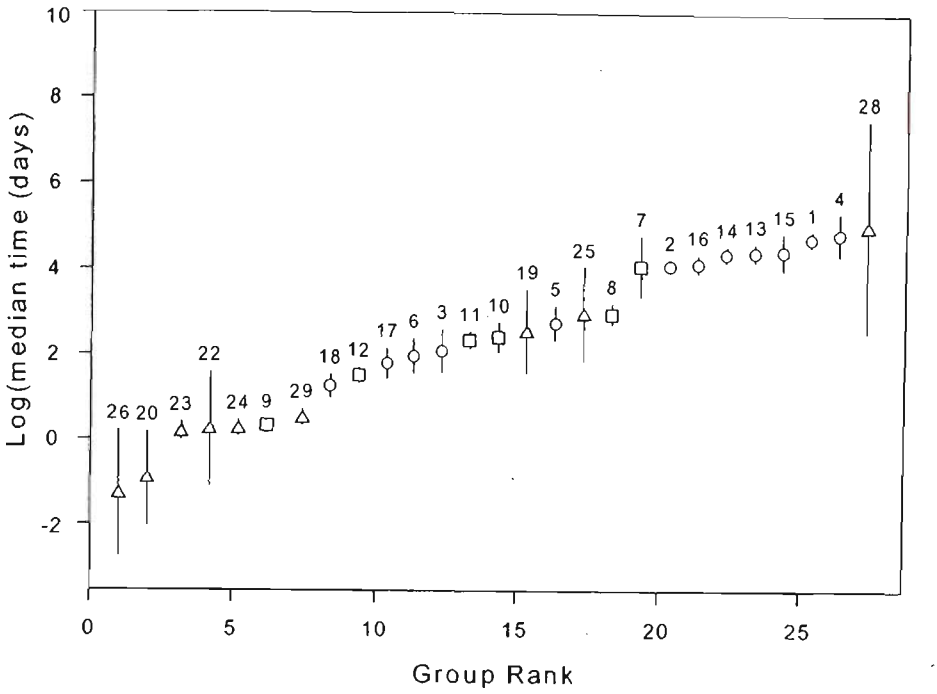

Fig. 3. Diagrammatic summary of flotation behaviour of leaves under laboratory conditions. The values shown are median times for leaves to remain floating; bars are joint 95 % Bonferroni confidence intervals for the median parameters. Groups 21, 27 and 30 have not been included (too few data points for reliable estimation). The coding of group numbers is the same as in Table 2. Key: Rainforest taxa ○; sclerophyllous taxa △; intermediate taxa □.

Field experiments on leaf transport

From the analysis of results on the sinking behaviour of the green and brown leaves of the five tree species under laboratory conditions (Figs. 2, 3, Table 2), predictions can be made about which leaf types are likely to travel the furthest distances under field conditions. Those species most likely to travel significant distances are *Nothofagus cunninghamii* leaves, followed by *Atherosperma moschatum* leaves, followed by the sclerophyllous taxa (with *Acacia melanoxylon* being the most likely to be transported any distance).

The in situ stream transport experiments showed differences in transport distance that largely matched these predictions (Table 3). After six hours, 20 % of the brown *Nothofagus cunninghamii* leaves, and 10 % each of the green *Nothofagus cunninghamii* and brown *Atherosperma moschatum* leaves had travelled 50 m. Green leaves of *Acacia melanoxylon*, a sclerophyllous species with the shortest overall flotation times, were the first to be filtered out. For this taxon, filtering became noticeable over distances of <5 m. The next species/leaf colour combination to be filtered out was brown *Acacia melanoxylon* leaves, followed by *Lomatia fraseri* leaves (green and brown), and *Eucalyptus regnans* (green and brown) leaves. Collectively, these three latter species were all filtered out to a significant degree over distances as short as 10 m, and none travelled more than 20 m in the six hour duration of the field experiments (Ta-

Table 3. Percentage recovery of leaves after six hours at various distances under field conditions. Values shown are percentage recoveries, n = 20 for each taxon and each leaf colour for each distance travelled.

Species	Leaf colour	Percentage recovery of leaves						
		Distance travelled (m)						
		1	2	5	10	20	50	100
Nothofagus cunninghamii	Green	100	100	100	100	25	10	0
	Brown	100	100	100	85	55	20	0
Atherosperma moschatum	Green	100	100	100	100	35	0	0
	Brown	100	100	100	75	60	10	0
Lomatia fraseri	Green	100	100	100	75	15	0	0
	Brown	100	100	100	100	40	0	0
Eucalyptus regnans	Green	100	100	100	75	15	0	0
	Brown	100	100	100	100	40	0	0
Acacia melanoxylon	Green	100	100	90	45	0	0	0
	Brown	100	100	100	70	40	0	0

ble 3). This result supports the contention that leaves of species that do not float well do not travel appreciable distances downstream.

Discussion

A number of conclusions can be drawn from the results presented in this paper. First, Cumberland Creek was highly retentive of coarse particulate detritus, and leaves of no taxon travelled downstream more than 100 m in six hours. Presumably this was a consequence of the tortuous nature of the stream, the large number of obstacles (often small snags entangled in large woody debris) in the stream channel, and the relatively low flow and discharge rates.

It is well known that discharge rate plays a major role in determining the retentiveness of stream ecosystems, and that leaf retention in headwater streams decreases dramatically as discharge increases (e.g., SPEAKER et al. 1984, CUFFNEY & WALLACE 1989, SNADDON et al. 1992). The effect of discharge on leaf retention was not determined, nor was it a primary aim, in our study. Nevertheless, some indication of the importance of discharge can be gauged by the influence of water turbulence in the laboratory experiments on leaf sinking times. These studies indicated that leaf sinking rates could increase by an order of magnitude if the flow rate were increased from still water to one of 25 cm/s. Note that the stream velocity at the gill net of Cumberland Creek during the field experiments was between 50 and 70 cm/s.

Second, the downstream transport of leaf material was highly selective, due to the very poor transport of leaves of sclerophyllous taxa, such as *Eucalyptus* and *Acacia*, and the markedly greater transport of leaves from the rain-

forest taxa, *Nothofagus* and *Atherosperma*. The primary difference between these taxonomic groupings is leaf morphology and chemistry; namely, the leathery texture, and thickened cuticles and cell walls (and concomittant richness in phenolic compounds) of the sclerophyllous taxa in comparison with the papery (chartaceous) character of the leaves of the rainforest species.

This result has clear limnological and palaeobotanical implications for the selective export of leaf material from forested catchments. A central plank of the River Continuum Concept for streams draining forested catchments is the downstream transport and ongoing processing of particulate organic matter into progressively finer particles (VANNOTE et al. 1980). Our results indicate that the export of leaves will occur to a greater extent from catchments vegetated with rainforest (or other riparian vegetation with chartaceous leaves) than with sclerophyllous vegetation. To date, neither of these vegetation types has featured prominently in studies of leaf transport and organic matter budgets (e.g., see papers following WEBSTER & MEYER 1997). Sclerophyllous shrublands and forests surrounding non-sclerophyllous riparian stands are a feature of Mediterranean type climates in South Africa (e.g. STEWART & DAVIES 1990, PROCHAZKA at al. 1991) and elsewhere. Furthermore, species of both *Eucalyptus* and *Acacia* are common plantation species and even woody weeds in California, Portugal, sub-Saharan Africa, India, parts of South America and some Pacific island nations (SAVILL & EVANS 1986, EVANS 1992). The present study therefore informs on the relative transport potential of the native and introduced sclerophyllous species, and riparian chartaceous species, to contribute to the organic budgets of streams in these areas. It thus also complements the comparative studies undertaken on litter accession and processing in forested and pasture-grass catchment on south-eastern Australia (CAMPELL et al. 1992b).

Clearly, leaves that have poor powers of dispersal have a high probability of becoming entrained, whereas leaves with good dispersal ability can travel appreciable distances downstream (SPICER 1981, 1989, FERGUSON 1985). This distinction may result in allochthonous leaf assemblages found in stream bed sediments reflecting differential transport in response to hydrodynamic sorting, rather than the ecological patterns that make up the local vegetation (SPICER 1989, GREENWOOD 1991). Importantly in an Australian setting, the transport of the dominant sclerophyllous canopy-tree taxon (*Eucalyptus*) and the dominant cool temperate rainforest canopy-tree taxon (*Nothofagus*) are significantly different. HILL & GIBSON (1986) suggested that the relative paucity of *Eucalyptus* leaves in the fossil record may be linked to their poor dispersive ability. Such a discrepancy in dispersive ability could be expressed in the leaf fossil record of the different taxa, although data on the behaviour of additional species of *Eucalyptus* and *Nothofagus* are required before generalisations can be made.

Third, the pattern of downstream transport observed in situ could be predicted quite accurately on the basis of median leaf flotation time, quantified in laboratory aquaria. In addition to the very clear distinction between leaves from rainforest taxa and sclerophyll taxa, there were a number of other relationships apparent between gross leaf characteristics and leaf buoyancy and transport distances in the field. There was evidence for the smallest leaves to be transported most easily and the largest leaves the least easily – *Nothofagus cunninghamii* and *Atherosperma moschatum* are nanophyllous and microphyllous, respectively, whereas both *Acacia melanoxylon* and *Eucalyptus regnans* are notophyllous and *Lomatia fraseri* is notophyllous-macrophyllous (Table 1). DANCE (1981) and GREENWOOD (1992) also indicated that small leaves travelled further in streams than did large ones.

PROCHAZKA et al. (1991) emphasised that flexibility was a significant factor in differential retention times between *Cunonia capensis* L. and *Brabejum stellatifolium* L., both of which are Afromontane elements of the fynbos biome, a sclerophyllous vegetation type. The leaves of *Cunonia capensis* are far more flexible than leaves of *Brabejum stellatifolium* and, as suggested by YOUNG et al. (1978), flexible leaves become easily entwined and wrapped abound twigs, sticks and other obstacles. This effect is mirrored in our own study, where the most flexible leaf types (green leaves of *Eucalyptus regnans* and *Acacia melanoxylon*) became entrained first, usually by becoming wrapped around twigs and branches embedded in the sides of the channel. Moreover, the less flexible brown leaves travelled a greater distance down the stream than did the more pliant green leaves, regardless of the leaves' taxonomic affiliations (Table 3).

SPICER (1981) clearly linked flotation time to the degree of turbulence of the surface water, and found that thin papery leaves such as *Alnus glutinosa* sank readily. We found the opposite pattern: the most papery leaves in our study were green leaves of *Atherosperma moschatum*, and these tended to float well regardless of the degree of turbulence in the laboratory experiments. A precautionary note is needed here though, as all the taxa in our study were evergreen, whereas a number of those in Spicer's studies were deciduous. SPICER (1981) noted that because of their thicker cuticles leaves from evergreen species are more resistant to water uptake and thus float longer than those from deciduous taxa. The clear difference between rainforest and sclerophyll taxa in both relative buoyancy and observed transport also could be a function largely of different cuticle thickness and composition, and thus of leaf wettability.

In contrast to the case with leaf flexibility, whether the leaf margins were entire or toothed was not a good predictor of in situ transport, even though it might have been anticipated a priori that toothed leaves would be caught more readily on surfaces of in-stream obstacles (cf. Tables 1 and 3).

Fourth, our results are in broad agreement with the few other published studies that have examined relative buoyancy and transport of sclerophyllous and rainforest leaves in Australian fresh waters. For example, HILL & GIBSON (1986), studying leaf flotation in Lake Dobson (Tasmania), reported that *Eucalypt coccifera* leaves sank very rapidly and were poorly dispersed. CARPENTER & HORWITZ (1988) reported that *Atherosperma moschatum* leaves readily floated in Tomalah Creek, a Tasmanian stream broadly similar to Cumberland Creek, and seemed to breakdown more quickly than did leaves of *Nothofagus cunninghamii*. Leaf material found drifting in Tomalah Creek was overwhelmingly *Nothofagus cunninghamii* (62 % of all whole leaves found), with a lesser representation of *Atherosperma moschatum*, and the virtual absence of *Eucalyptus obliqua* leaves. This pattern is consistent with our finding that *Nothofagus cunninghamii* leaves floated well under all but the most turbulent conditions, while *Eucalyptus regnans* sank rapidly. The organic-matter retentiveness of Cumberland Creek is also consistent with the finding that the nearby Keppel Creek accumulates organic matter at a rate of ~2.5 kg AFDW $m^{-2} y^{-1}$ (TREADWELL et al. 1997).

It is also interesting to compare the distances travelled by leaves in our study of Cumberland Creek (Table 3) with previously published transport distances. Although the comparison is rendered difficult by the different methods employed in the various studies, it would seem that the leaves were very rapidly entrained in Cumberland Creek in comparison with most other published studies (cf. texts cited in Introduction).

Finally, we should draw attention to two key limitations of our study. First, only one observational unit (aquarium) per taxon/leaf colour/flow rate combination was used in the laboratory experiments. The choice of this experimental design was one of pragmatism, in terms of space availability, temperature control, etc. Although the resultant pseudoreplication precluded most statistical procedures, we do not believe that it compromised the reliability of the data we obtained. Pseudoreplication evidently dogs many field ecological experiments (HURLBURT 1984), but it is far less likely to lead to incorrect findings in our case, mainly because the process we quantified (leaf sinking) was largely a physical phenomenon. The likely causes of error in the pseodoreplicated design (e.g., pump failure) were precluded, for example, by the daily observation of the aquaria. The risk of weak conclusions would have been far greater, for example, had a biological process been examined in which each observational unit could have developed its own ecological trajectory.

Second, our field study was concerned with the transport of entire leaves. Fine particulate and dissolved material also are centrally important in the ecology of headwater streams, and the transport and downstream contribution of these classes of material may differ markedly from the entire leaves that we examined.

Moreover, it is important to clarify that our field data refer specifically to the transport of leaves down the stream, and transport is only one of the number of processes that mediate organic-matter fluxes in lotic systems. The spiralling length for a given carbon atom derived from leaf litter will be contingent both on its transport rate and its processing rate; we quantified the former but not the latter. Although *Nothofagus cunninghamii* leaves were entrained far less effectively than were *Eucalyptus regnans* leaves, this difference alone does not indicate that *Nothofagus cunninghamii* leaves made a poorer contribution to carbon dynamics in that small reach of the stream. If *Nothofagus cunninghamii* leaves were, for example, processed more rapidly (e.g., colonised preferentially by aquatic fungi and then consumed more quickly by invertebrates), they would make a contribution to carbon dynamics that was disproportionate to their transport behaviour.

The elucidation of organic-matter fluxes, therefore, requires information on both transport and processing for the various taxa in the same stream, under the same environmental conditions. With one exception, there are insufficient data available on processing rates to achieve this for the taxa that we examined. BLACKBURN & PETR (1979), however, reported that *Nothofagus cunninghamii* leaves and *Eucalyptus regnans* leaves both fell into the "medium" processing category, with remarkably similar T_{50} values of 83 and 82 days, respectively. For a comparison across these taxa, the transport rate would yield a reliable first indication of local carbon input. In contrast, leaves of *Acacia melanoxylon* had T_{50} values of 88 to 239 days (BLACKBURN & PETR 1979). Thus *Acacia melanoxylon* leaves decay significantly more slowly than leaves of *Eucalyptus regnans*. As both these sclerophyllous taxa were rapidly entrained in Cumberland Creek, it would seem that the *Acacia* leaves would decay far more slowly than the *Eucalyptus* leaves in the resultant leaf packs. Speculation along these lines, where transport and processing phenomena are considered together, might generate significant advances in our understanding of the functioning of lotic systems that transverse divergent vegetation types across their catchment.

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New Species of *Banksieaeformis* and a *Banksia* 'Cone' (Proteaceae) from the Tertiary of Central Australia

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Abstract

Silicified leaf impressions attributed to the tribe Banksieae (Proteaceae) are reported from a new Tertiary macroflora from near Glen Helen, Northern Territory and from the Miocene Stuart Creek macroflora, northern South Australia. The fossil leaf material is described and placed in *Banksieaeformis* Hill & Christophel. *Banksieaeformis serratus* sp. nov. is very similar in gross morphology to the extant *Banksia baueri* R.Br. and *B. serrata* L.f. and is therefore representative of a leaf type in *Banksia* that is widespread geographically and climatically within Australia and that is unknown in *Dryandra* or other genera of the Banksieae. The leaf material from Stuart Creek and Woomera represents the lobed leaf form typical of Paleogene macrofloras from southern Australia, but one species, *B. langii* sp. nov., is closely similar in gross form to *Banksieaephyllum taylorii* R.J.Carpenter, G.J.Jordan & R.S.Hill *et al.* from the Late Paleocene of New South Wales and similarly may be sclerophyllous. Also reported are impressions of *Banksia* infructescences, or 'seed cones', in Neogene sediments near Marree and Woomera, South Australia. These fossils demonstrate the presence of Banksiinae in central Australia in the mid-Tertiary, potentially indicating the former existence of linking corridors between now widely separated populations of *Banksia*.

Introduction

The modern genus *Banksia* L.f. (Proteaceae, subtribe Banksiinae of Banksieae) is a common component of sclerophyllous heaths and other modern Australian sclerophyllous vegetation. *Banksia* has about 76 species and is generally restricted to oligotrophic soils but occurs over a wide climatic range, with annual rainfall from 300 to 2500 mm (Holliday and Watton 1990; Thiele and Ladiges 1996; George 1999*a*). *Banksia* has a disjunct east–west distribution, with major centres of diversity in south-western and south-eastern Australia. The centre of the continent and the Nullarbor Plain today do not support populations of *Banksia* or related taxa, most likely due to a lack of suitable climate in these areas. Few species of *Banksia* occur in northern Australia, with only *B. dentata* occurring outside of Australia on the island of New Guinea and the Aru Islands (George 1999*a*). However, even though the fossil record of the tribe Banksieae is extensive, only three fossil species of *Banksia s.s.* have been described (McNamara and Scott 1983; Jordan and Hill 1991; Hill *et al.* 1995; Greenwood *et al.* 2000). As *Banksia* and *Dryandra* cannot be distinguished solely on leaf architectural features, fossil leaves architecturally matching either genus are assigned to *Banksieaephyllum* Cookson and thus, by definition, are attributed to the Banksiinae (Blackburn 1981; Vadala and Drinnan 1998). However, some previously described *Banksieaephyllum* species have cuticular features that indicate affinity to the subtribe Musgraveinae, or do not indicate affinity to the Banksieae and/or Proteaceae (Carpenter and Jordan 1997).

Tertiary macrofloras within Australia are primarily known from near the coastal margin and particularly from the southern half of the continent and Tasmania (Greenwood 1994; Greenwood *et al.* 2000). Information on palaeovegetation, phytogeography and

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palaeoclimate for central Australia is therefore largely known from the microfloral record and geological features (Truswell and Harris 1982; Benbow *et al.* 1995). Palaeobotanical data have emphasised the presence of rainforest taxa in central Australia throughout much of the Cenozoic (Truswell and Harris 1982; Greenwood 1996; Barnes and Hill 1999). Limited macrofloral evidence suggests, however, that important evolutionary innovation within key Australian genera, such as *Banksia* and *Eucalyptus*, may have been occurring much earlier in central Australia than in the coastal fringes (Lange 1978, 1982, 1986; Greenwood *et al.* 1990; Greenwood 1994, 1996). Fossil evidence in the form of banksioid leaves (*Banksieaeformis* and *Banksieaephyllum* species), wood, pollen (*Banksieaeidites elongatus* Cookson) and *Banksia* fruiting cones are known from Paleocene to Pleistocene sediments throughout the modern range of *Banksia* (Redaway 1858; Smyth 1873, 1875; Cookson and Duigan 1950; Pike 1953; Patton 1957; Blackburn 1981; Hill and Macphail 1983; McNamara and Scott 1983; Hill 1988; Hill and Christophel 1988; Jordan and Hill 1991; Hill and Merrifield 1993; Carpenter *et al.* 1994; Vadala and Drinnan 1998), but have also been reported from central Australian localities (Chapman 1937; Greenwood *et al.* 1990; Greenwood 1996).

George (1981, 1999*a*) proposed an evolutionary series in *Banksia* based on cone and floral morphology and Hill and Christophel (1988) provided scenarios of inter-relationships between extant and fossil species of Banksiinae on the basis of leaf morphology. Hill and Christophel (1988) suggested that further records of fossil species over a wider geographic range were required to determine the ancestral leaf form and direction of evolution within the group. The present disjunct distribution of *Banksia* and the fossil record of Banksieae suggest that *Banksia* did occur in central Australia in the middle Tertiary. Hitherto the central Australian records of Banksiinae have not been discussed systematically. The classification of *Banksia* has recently been revised, incorporating leaf and infructescence morphological characters (Thiele and Ladiges 1996; George 1999*a*), some of which are referable to fossil material. Vadala and Drinnan (1998) provided a review of *Banksieaephyllum* and commented on the relationship of fossil Banksieae to the subtribe Banksiinae. This paper describes new records of Banksieae, including leaf impressions from Glen Helen near Alice Springs in the Northern Territory and Stuart Creek in northern South Australia and *Banksia* infructescences from Woomera and Poole Creek in northern South Australia. Where possible, these fossil taxa are incorporated within the infrageneric classification of *Banksia* provided by Thiele and Ladiges (1996).

Materials and Methods

The Fossil Sites

Glen Helen

The Glen Helen macrofloral locality consists of a small outcrop of flat-lying sediments situated 119 km west of Alice Springs and 5 km east of Glen Helen tourist camp in the southern part of the Northern Territory (23°S, 132°E; Fig. 1). It lies unconformable over an irregular basement of dipping Amadeus Basin sediments and similar outcrops extend from this site for about 95 km to the west–north-west, along a broad valley within the MacDonnell Ranges. The sequence was first mapped by Prichard and Quinlan (1962) who suggested a Cretaceous age on the basis of lithological correlations with subsurface sediments beneath the Burt Plain to the north. However, the dating of the Burt Plain sediments was later shown to be in error (Lloyd 1968) and the unit described here has been classified as Tertiary on all subsequent maps. Warren and Shaw (1995) consider these outcrops as a correlative of the Waite Formation, which contains an early Miocene vertebrate fauna in its type area 230 km to the north-east (Woodburne 1967). As there is no fossil evidence for this correlation and there are significant differences in lithology between the respective

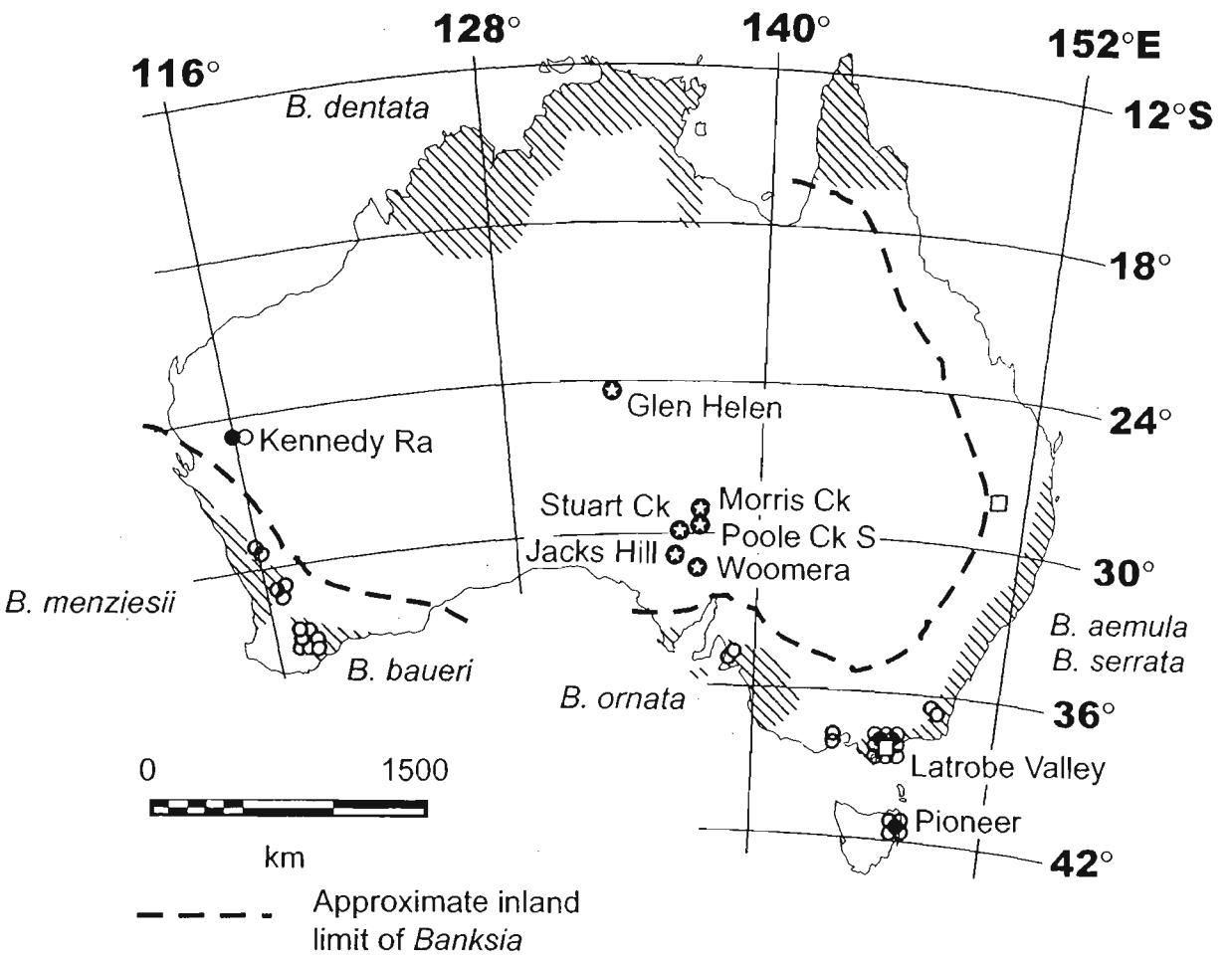

Fig. 1. Map of Australia showing distribution of selected species of *Banksia* today (shading) and location of the mid-Tertiary Glen Helen and Poole Creek macrofloral sites (✪) and other localities mentioned in the text. Tertiary fossil occurrences of *Banksia* cones (●), wood (□) and Banksieae leaves (○) are indicated. The total distribution of Banksiinae today is only slightly greater than that shown for the *Banksia* spp., but extending further up the east coast.

localities we regard the correlation as speculative and so only suggest a mid-Tertiary age for the Glen Helen flora. The outcrop near Glen Helen reaches about 15 m in thickness, mostly comprising weakly consolidated and poorly exposed gravel, sand and silt, apart from a 2–3-m capping of well-silicified sandstone (silcrete). Plant fossils are largely confined to the lower, somewhat ferruginised part of this silicified cap and dominated by moulds of wood fragments (rarely up to 0.5 m long), bark and twigs. Leaves are generally sparse or confined to local concentrations in single beds. The sediments were probably deposited fluvially and the predominance of detrital quartz, in comparison with modern alluvium in the area, suggests a warm, humid environment and deep weathering at the time of deposition.

Poole Creek

An impression of a *Banksia* infructescence or 'seed cone' was discovered in late November 1988 by one of us (D. R. G.), D. J. Barrett and B. Gare (at the time at Mines and Energy South Australia) *in situ* on a boulder in a creek-bed exposure of a silicified unit of the Miocene Etadunna Formation (29°37′S, 137°43′E), in the Southern Lake Eyre Basin near the Oodnadatta Track in the Poole Creek Palaeochannel (Greenwood *et al.* 1990; Greenwood 1996). The specimen remains *in situ* (Fig. 1). A mould of a *Banksia* infructescence collected near Woomera (see below) is considered conspecific with the Poole Creek specimen and is designated the holotype. The exposure of the silicified unit was sparsely fossiliferous, with

common poorly preserved cones of *Casuarina* (Fig. 1), coniferous shoots and small angiosperm leaves, including some that may be *Banksieaeformis*. Owing to the size of the boulders on which these impressions occurred, collection of the specimens was not possible.

The *Banksia*-cone mould preserved a three-dimensional impression of the external morphology of half of the structure, including the mature follicles (Figs 12 and 13). The mould was photographed in the field in natural light with 35-mm Ektachrome 100 ASA colour positive (slide) film. Black and white photographs were produced from these slides for the Figures here. The original slides are housed in the collection of the Mineral Resources Group of Primary Industry and Resources South Australia (PIRSA). As the *Banksia* specimen was not collectable, measurements were taken from photographs of the mature cone for comparison with infructesences from modern species of *Banksia* and fossil infructescences.

Stuart Creek, Jacks Hill, Woomera and Morris Creek

Material from Stuart Creek, Jacks Hill and Woomera represents collections made by various workers, including Tate (in Chapman 1937), Lange (1982, 1986) and Greenwood *et al.* (1990). Much of this material was collected from surface float of silicified Willalinchina Sandstone at the Willalinchina Hut locality near Stuart Creek Station homestead (29°45′S, 136°45′E), or at sites near this area in the Billa Kalina Basin. Specimens are also considered from Morris Creek in the southern Lake Eyre Basin (Greenwood *et al.* 1990; Greenwood 1996) and from South Australian Museum collections labelled 'Eyre Formation' from Koolymilka near Woomera (30°58′S, 136°33′E) and at several sites in the Stuart Range near Mt Eba Station, such as Jacks Hill (30°12′S, 135°42′E). The age of the Stuart Creek macrofloras and putative Eyre Formation at sites near Woomera and Jacks Hill are problematic and these floras have been assigned Eocene–Oligocene or Miocene ages (Ambrose *et al.* 1979; Wells and Callen 1986; Krieg *et al.* 1991; Callen *et al.* 1995). Sandstone from the Stuart Range and related sites was often formerly labelled 'Eyre Formation', but is now named Mount Sarah Sandstone, a rock unit potentially equivalent to the upper part of the Eyre Formation (and thus Eocene), but some outcrop of Mt Sarah Sandstone may be equivalent to the Oligocene–Miocene Etadunna or Doonbara formations (Callen *et al.* 1995). Biostratigraphic and lithological correlation of silcrete floras in the Billa Kalina Basin, however, indicates that the Willalinchina Sandstone, and thus the Stuart Creek flora, is Late Miocene (Callen *et al.* 1995). Specimen numbers for Stuart Creek material other than those in the South Australian Museum follow the PIRSA unique rock sample (RS) system, which ties each specimen to its collection locality according to 1 : 250 000 map sheets. Specimens from earlier collections (Chapman 1937; Lange 1982) were also examined, including material from additional sites (e.g. Morris Creek) for which little stratigraphic information is presently available. These are housed in the South Australian Museum (SAM) and are cited using SAM specimen numbers.

Modern Comparative Material

The cladistic analysis of *Banksia* by Thiele and Ladiges (1996) provides a useful starting point in the systematic analysis of the fossil material as these authors used leaf features, such as leaf margin and/or lobation type and mature infructescence characters, such as the gross shape of the axis and follicle shape. Several of their diagnostic characters can be observed on the fossils. Vadala and Drinnan (1998) provide a detailed compilation of leaf architectural and epidermal characters of extant Banksieae and *Banksieaephyllum–Banksieaeformis* species. While no attempt is made here to apply a cladistic analysis of the fossil material, the characters used by Thiele and Ladiges (1996) and by Vadala and Drinnan (1998) are used to compare the fossil species described here with previously described fossil species of Banksieae and to extant species of Banksiinae. Additional information on leaf and infructescence morphology is derived from Hill and Christophel (1988), Hill (1990), Holliday and Watton (1990), Jordan and Hill (1991) and George (1999*a*, 1999*b*) and from both field-collected modern material and herbarium material (MEL).

Leaf and infructescence material of *Banksia integrifolia*, *B. marginata*, *B. ornata*, *B. serrata* and *B. spinulosa*, was collected from natural populations in Victoria. This material was scored for morphometric characters of leaves and the infructescence to assess intra-specific and infra-specific level variation in these organs. In particular, the size and shape of leaves of similar form to the fossils and both infructescence and follicle size and shape and the number and position of follicles were assessed.

Systematic Palaeobotany

Family Proteaceae
Subfamily Grevilleoideae
Tribe Banksieae
Genus ***Banksieaeformis*** Hill & Christophel (1988)

Banksieaeformis serratus Greenwood, Haines & Steart, sp. nov. (Figs 2 and 3)

Diagnosis

Simple bilaterally symmetrical leaves; leaf base and apex unknown. Leaf greater than 9 cm long and 2.5 cm wide, margin serrate, teeth regular, apically directed and acute. Leaf rachis massive, venation pinnate, craspedodromous, more than 30 secondary veins, secondary veins *c.* 90–70° from the midvein, generally straight but diverging apically near the margin and a single vein entering each marginal tooth; secondary veins between teeth bifurcating prior to sinus.

Location: unnamed Tertiary unit (cf. Waite Formation) at Glen Helen, Northern Territory.

Holotype: P36575, stored in the South Australian Museum.

Collector: Peter W. Haines.

Etymology: the specific epithet is derived from the regular serrate margin.

Remarks

The leaf architecture (Figs 2 and 3) matches that of some extant species of *Banksia* (subtribe Banksiinae). According to Hill and Christophel (1988), fossil leaves with this morphology but lacking epidermal detail (i.e. lacking cuticle) should be placed in the organ-genus *Banksieaeformis*. These authors also considered that such leaves represent now extinct species within the tribe Banksieae of Proteaceae (which includes the modern subtribes, Musgraveinae (*Austromuellera* and *Musgravea*) and Banksiinae). The banksioid leaf type with a simple undivided lamina and dentate margins is common in *Banksia* (Table 1, Fig. 4), but is unknown in *Dryandra* and the Musgraveinae and so *B. serratus* is considered to represent Banksiinae, and probably *Banksia*.

Banksieaeformis serratus resembles *B. dentatus* Hill & Christophel, from the Tasmanian Oligocene Cethana macroflora, and to a lesser degree the organically preserved Middle–Late Eocene species, *Banksieaephyllum attenuatum* Hill & Christophel (1988) from Loch Aber in Tasmania and the Oligocene species, *B. fastigatum* (Deane) Cookson & Duigan (1950) from Yallourn in Victoria (Table 1). *Banksieaeformis serratus* differs from *B. dentatus* in the bifurcation of secondary veins prior to the sinus between the marginal teeth; the two species are otherwise very similar. Carpenter and Jordan (1997) suggested that *Banksieaephyllum attenuatum* may not represent Banksieae or perhaps may not even be a member of Proteaceae. The presence of epidermal information for *Banksieaephyllum attenuatum* and *B. fastigatum* and the lack of such detail for *Banksieaeformis serratus* restricts a complete comparison between these species; however, the secondary veins of *B. attenuatum* do not bifurcate at the sinus and this species is only superficially similar in general leaf form to *Banksieaeformis serratus*. *Banksieaephyllum longifolium* Hill & Merrifield (1993) from the Middle Eocene–Oligocene West Dale flora in Western Australia is entire-margined with brochidodromous venation and so is quite unlike the Glen Helen

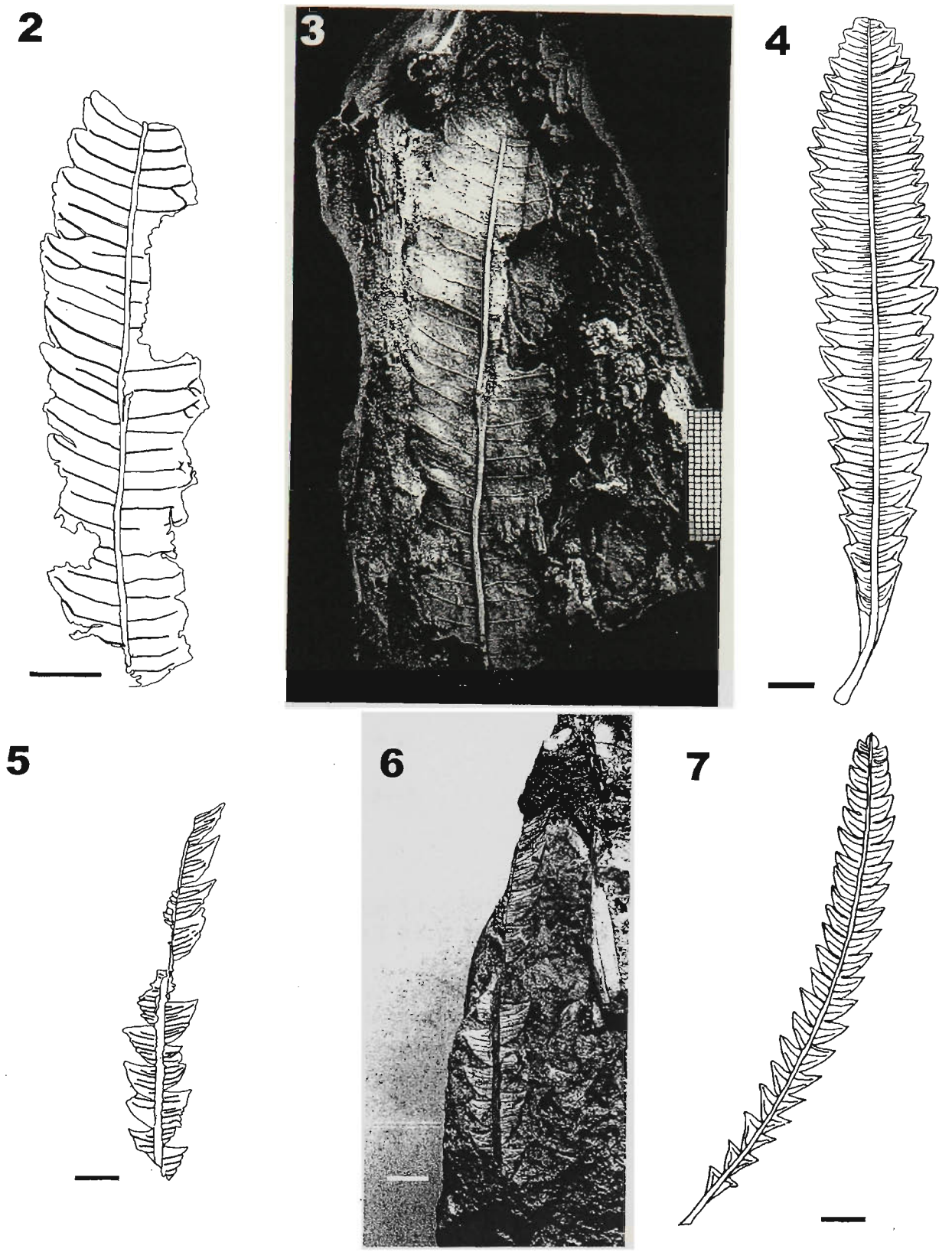

Fig. 2. Line drawing of *Banksieaeformis serratus* from the Glen Helen macroflora. Scale bar = 10 mm. (Drawing by A. Vadala from the photo by P. Haines.) **Fig. 3.** Photo of *Banksieaeformis serratus* from the Glen Helen macroflora. Scale bar = 10 mm. (Photo by P. Haines from a latex cast of the original specimen.) **Fig. 4.** Line drawing of extant *Banksia serrata* from field collected material. Scale bar = 10 mm. (Line drawing by A. Vadala.) **Fig. 5.** Line drawing of *Banksieaeformis langii* (6238 RS 122) from the Stuart Creek macroflora. Scale bar = 10 mm. (Drawing by A. Vadala from the PIRSA photo 39035.) **Fig. 6.** Photo of *Banksieaeformis langii* (6238 RS 122) from the Stuart Creek macroflora. Scale bar = 10 mm. (PIRSA photo 39035.) **Fig. 7.** Line drawing of extant *Dryandra formosa* by D. Steart from cultivated material. Scale bar = 10 mm.

Table 1. Gross leaf characteristics of some extant species of *Banksia* and *Dryandra* used for systematic analysis of fossils

Data for extant species from George (1981, 1999*a*, 1999*b*), Taylor and Hopper (1988), Holliday and Watton (1990), Thiele and Ladiges (1996) and specimens in MEL; data for fossil species from original descriptions of each taxon, as indicated in the text. Lobation incision is given as a 3-point scale where 0 = no lobes; 1 = <1/3 incision from margin to midrib; 2 = >1/3 incision; 3 = incision through to midrib (or apparently so). Where lobes are pungent or apiculate (i.e. with a sharp point), they are considered to represent 'teeth'

Species	Length (cm)	Width (cm)	L : W	Lobed	Incision	Teeth or apiculate lobes	Apex
Banksia subgenus *Banksia*							
Series Tetragonae							
B. lemanniana[A]	5–10	1.5–4	2–3	–	0	+	blunt
Series *Banksia*							
B. aemula[A]	8–22	1–2	8–11	–	0	+	round
B. menziesii[A]	15–30	2–4	7–8	–	0	+	round
B. ornata	5–8	2–3	2–3	–	0	+	round
B. serrata[A]	8–22	2–4	4–6	–	0	+	blunt
B. speciosa[B]	20–40	1.5–2.5		+	3	+	terminal lobe
Incertae sedis							
B. baueri[A]	7–13	1–2	6–7	–	0	+	round
Series *Salicinae*							
B. dentata[A]	10–25	2–8	3–5	–	0	+	Blunt or round
B. robur[A]	<30	<10	3	–	0	+	round
Series *Prostratae*							
B. chamaephyton[C]	20–50	4–15		+	3	±	terminal lobe
Series *Grandes*							
B. grandis	20–50	8–15		+	3	+	blunt
Series *Dryandroides*							
B. dryandroides[B]	5–15	1		+	3	+	blunt
Dryandra subgenus *Dryandra*							
D. formosa	7–16	0.6–1.1	>10	+	3	+	blunt
D. idiogenes	15–37	1.2–3.8	4–10	+	3	+	acute or blunt
Fossil species							
Banksieaeformis decurrens	*c.* 7	*c.* 1	*c.* 7	+	3	+	not known
B. dentatus	6	1	6	–	0	+	not known
B. langii	>8.5	1.2–1.6	5–7	+	3	+	acute
B. praegrandis	8–16+	2–8	2–4	+	3	±	acuminate
B. serratus	>9	*c.* 2.5	*c.* 4	–	0	+	not known
Kennedy Ra *Banksia* leaves		3		–	0	+	not known
Banksieaephyllum attenuatum	*c.* 6	≤ 1.5	*c.* 4	–	0	+	attenuate
B. cuneatum	>12	≤ 4	*c.* 3	+	3	+	not known
B. elongatum	>6	≤ 1	*c.* 6	+	3	+	not known
B. fastigatum	>3	1.5	>3	–	0	+	not known
B. longifolium	>7.5	1	7	–	0	–	?acute or blunt
B. regularis	*c.* 4	*c.* 0.8	*c.* 4	–	0/1	+	acute
B. taylorii		*c.* 2		+	3	+	acute
B. urniforme		≥0.6		+	3	–	not known
B. westdaliense		0.3		+	3	+	not known

[A]Species most similar to *Banksieaeformis serratus* sp. nov.

[B]Species most similar to *B. langii* sp. nov.

[C]Species most similar to *B. praegrandis*.

material. An undescribed *Banksieaeformis* from Western Australia matches *B. serratus* in most details, but has a bluntly denticulate margin (S. McLoughlin, pers. comm.; McLoughlin and Hill 1996), whereas *B. serratus* is serrate-margined. McNamara and Scott (1983) noted without illustration the presence of two poorly preserved *Banksia*-like leaves associated with *Banksia archaeocarpa*, commenting that these leaves matched in many respects those of the extant species *B. menziesii*.

Strap-like dentate- to serrate-margined leaves are found in several species of *Banksia*, most notably in Series *Banksia* and Series *Salicinae* (Table 1). The extant species, *B. aemula* R.Br., *B. baueri* R.Br., *B. menziesii* R.Br., *B. ornata* F.Muell. and *B. serrata* L.f. (Series *Banksia*) and *B. dentata* L.Fill., *B. oblongifolia* Cav. and *B. robur* Cav. (Series *Salicinae*), are comparable with *Banksieaeformis serratus*. Of these extant species, the morphology of the fossil leaf is closest to that of the leaves of *Banksia serrata* (Fig. 4). The teeth of *Banksia ornata* are quite prominent and apiculate, much more so than in *Banksieaeformis serratus*. The secondary veins in *Banksia robur* either terminate in marginal teeth or terminate within the blade; in *B. oblongifolia* and *B. dentata* intra-tooth secondary veins bifurcate at the sinus and loop back to fuse with the secondary vein terminating in the tooth; in *B. menziesii* and *B. serrata* the intra-tooth secondary veins bifurcate without fusing with the vein terminating in the tooth, as seen in *Banksieaeformis serratus*. The shape and prominence of the teeth in *Banksieaeformis serratus* are closer to those seen in *Banksia serrata* than those in *Banksia menziesii*.

Banksieaeformis langii Greenwood, Haines & Steart, sp. nov. (Figs 5 and 6)

Diagnosis

Leaves bilaterally symmetrical, pinnately lobed; lobes acute and apically directed. Apical side of lobe usually concave, rarely straight; basal side convex, sinuses acute; leaf base and apex unknown. Leaf length greater than 8.5 cm, width 1.2–1.6 cm; lobes typically with 4 veins, rarely 5, with a pronounced vein leading to the apex of the lobe and ramifying prominently. Leaf rachis massive.

Location: Willalinchina Sandstone, Stuart Ck and ?Eyre Formation (Mt Sarah Sandstone) near Woomera and at Jacks Hill, all in South Australia.

Holotype: 6238 RS 122, stored in the PIRSA Core Library.

Collector: unknown.

Other specimens: R368928 & 6238 RS 129, both specimens stored in the PIRSA Core Library; P17965B & P13568, stored in the South Australian Museum.

Etymology: the specific epithet recognises R. T. Lange, who played a significant role in the discovery and scientific exploration of the Stuart Creek site.

Remarks

Banksieaeformis langii corresponds to 'Banksieaeformis I' in Greenwood *et al.* (1990, fig. 3*B*) and was figured as a line drawing in Greenwood (1996, fig. 4*H*). The *Banksia*-like leaf type with arcuate lobes incised fully to the rachis is common in the Banksiinae, but is unknown in the Musgraveinae (Hill and Christophel 1988; Carpenter *et al.* 1994; George 1999*a*, 1999*b*). Specimens of *Banksieaeformis langii* have a massive rachis and the lobes appear quite thick and coriaceous, suggesting scleromorphy. Carpenter *et al.* (1994)

suggest that *Banksieaephyllum taylorii*, which has leaves with an architecture similar to *Banksieaeformis langii*, likely represents antecedents of the modern sclerophyllous Banksiinae and not the rainforest Musgraveinae and so *B. langii* is considered here to also represent Banksiinae. *Banksieaeformis langii* is locally common at some Stuart Creek sites (e.g. Willalinchina Hut) and has been collected in putative Eyre Formation sediments at Jacks Hill (P13568) and near Woomera (P17956B). The latter material is on display in the South Australian Museum.

Banksieaeformis langii resembles only superficially *B. decurrens* Hill & Christophel and the organically preserved species, *Banksieaephyllum cuneatum* Blackburn, both from the Eocene Maslin Bay flora (Blackburn 1981; Hill and Christophel 1988; Table 1). *Banksieaeformis langii* differs from both *Banksieaeformis decurrens* and *Banksieaephyllum cuneatum* in its much smaller size and more symmetrical individual leaf lobes and also in the presence of a well-developed cuneate base in both of the Maslin Bay species, a feature not observed on any of the Stuart creek material. Architecturally, there is a close resemblance between *Banksieaephyllum taylorii* Carpenter *et al.* (1994) from the Late Paleocene Lake Bungarby flora (NSW), *B. westdaliense* Hill & Merrifield (1993) from the Middle Eocene–Oligocene West Dale flora (WA) and *Banksieaeformis langii* (Table 1). Both *Banksieaephyllum taylorii* and *Banksieaeformis langii* lack a cuneate leaf base and these two species and *Banksieaephyllum westdaliense* have a similar lobe shape. The *Banksieaephyllum taylorii* and *B. westdaliense* leaves are smaller than those of *Banksieaeformis langii* and have three rather than four veins in each lobe, but these differences alone may not be of systematic importance as the two species of *Banksieaephyllum* are differentiated from each other primarily on the basis of cuticular characters. In the absence of cuticular information for the Stuart Creek material, *Banksieaeformis langii* is maintained as a separate species of *Banksieaeformis*. *Dryandra benthami* Ett. and *D. praeformosa* Ett., from Late Eocene florules of the Vegetable Creek macroflora (Ettingshausen 1888) have gross vegetative morphology that is closely comparable with *Banksieaeformis langii*. However, Cookson and Duigan (1950) and others (Hill 1988; Carpenter *et al.* 1994) consider that these species lack sufficient taxonomic information for comparison with other fossil species. The acute lobes of *B. langii* (Figs 5 and 6) differentiate it from the remaining lobed-leaved fossil Banksiinae, such as *Banksieaephyllum pinnatum* Cookson & Duigan and *B. urniforme* (Deane) Hill (Hill 1990), as the latter have rounded- or blunt-tipped lobes, respectively.

The modern species, *Banksia speciosa* R.Br., is comparable with *Banksieaeformis langii* (Table 1); however, the former differs from the fossil by having more-or-less symmetrical acute lobes, whereas *B. langii* has lobes that are apically directed. A closer affinity may be with the extant species, *Dryandra formosa* R.Br. (see fig. 44 in Hill and Christophel 1988; Fig. 7 herein), which strongly resembles *B. langii* (Figs 5 and 6). Carpenter *et al.* (1994) also considered that *Banksieaephyllum taylorii* was architecturally indistinguishable from *Dryandra formosa*, but noted marked differences in cuticular anatomy between these two species. The close similarity between the Stuart Creek (and both Woomera and Jacks Hill), Lake Bungarby and modern species, may therefore indicate a common lineage of proto-sclerophyllous Banksiinae across southern Australia in the Early Tertiary (see discussion in Carpenter *et al.* 1994). A *Banksia* infructescence on the same block (P17956) as *Banksieaeformis langii* may have come from a *B. langii* plant and so assignment of this taxon to *Banksia* may be appropriate. In the absence of attachment between these organs, assignment to *Banksieaeformis* is retained and assignment to *Banksia* must remain conjectural.

Banksieaeformis praegrandis (Tate) Greenwood, Haines & Steart, comb. nov. (Figs 8 and 9)

Synonymy: *Banksia praegrandis* Tate in Chapman, *Trans. Roy. Soc., South Austr.* 61: 1–16 (1937); *Banksieaeformis praegrandis* in Greenwood, *Aust. Syst. Bot.* 9: 95–112 (1996).

Emended Diagnosis

Leaves bilaterally symmetrical, pinnately lobed; lobes generally narrowly triangular with a narrowly rounded apex and apically directed. Apical side of the lobes straight to slightly concave, rarely strongly concave; basal side straight, but curving to produce a broad attachment to the rachis. Leaf base unknown, apex consisting of a terminally directed modified lobe (single specimen). Lobes opposite in some specimens, but becoming alternate further along the rachis in other specimens; some specimens fully alternate. Leaf length 8 to >16 cm, width across spread of lobes up to 8 cm (estimated), but may be as small as 2.0 cm. Individual lobes 0.8–2.7 cm wide at the midrib. Lobes typically with 2 prominent veins, rarely 1 or 3 or 4 on the one specimen, with a single vein leading to the lobe apex. Tertiary veins in a loose reticulate net. Leaf midrib massive.

Location: Eyre Formation at Morris Creek and Mt Alford and Willalinchina Sandstone at Stuart Creek and Elizabeth River, all in South Australia.

Holotype: P1198, stored in the South Australian Museum.

Other material: 6438 RS 534, RS 484; 6439 RS 150, RS 194, RS 039; 6238 RS 129, stored in the PIRSA Core Library.

Remarks

This leaf taxon has been previously described and illustrated by Chapman who used a name proposed by Tate; *Banksia praegrandis* Tate (Chapman 1937). The material viewed by Chapman (1937, figs 2 and 6) was collected near Elizabeth River, northern South Australia. *Banksieaeformis praegrandis* was illustrated and named by Greenwood (1996, fig. 4*H*) but not formally transferred to *Banksieaeformis* and corresponds to 'Banksieaeformis II' in Greenwood *et al.* (1990, fig. 3*A*). This species possesses the gross leaf morphology typical of modern members of the tribe Banksieae of the Proteaceae (e.g. Figs 8–10) and so this taxon is formally transferred to *Banksieaeformis*. The original material illustrated by Chapman (SA Museum, P1198) is conspecific with the specimens from Stuart Creek and Morris Creek. Material referrable to *B. praegrandis* has been collected from localities at Stuart Creek, Morris Ck, at Mt Alford and Woomera (Lange 1986; Greenwood 1996; SAM collections).

Banksieaeformis praegrandis differs from all previously described *Banksieaeformis* or *Banksieaephyllum* species by its long, narrow, widely spaced apiculate pinnae. The

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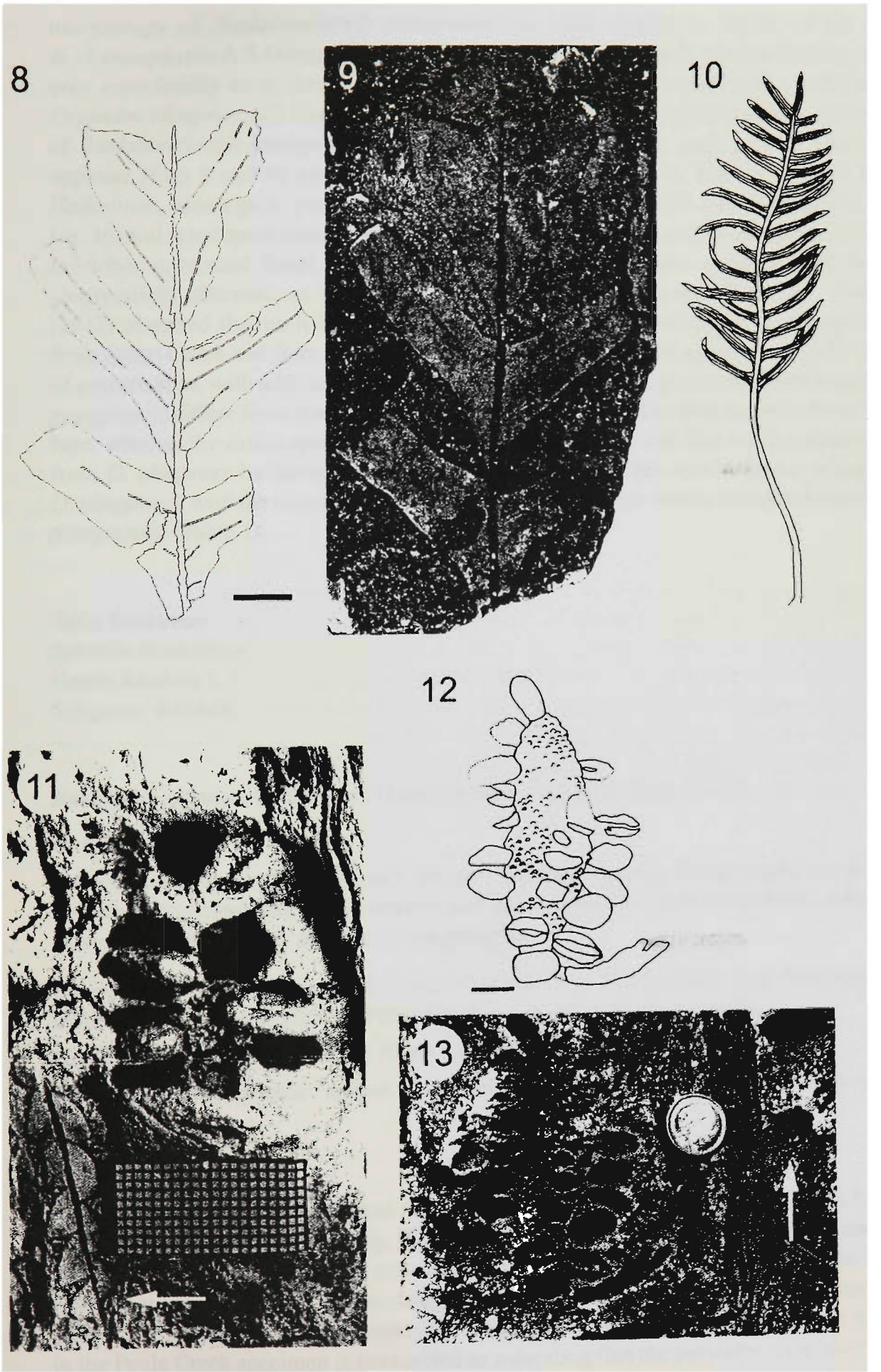
Fig. 8. Line drawing of *Banksieaeformis praegrandis* from the Stuart Creek macroflora. Scale bar = 10 mm. (Line drawing by A. Vadala from PIRSA photo 39034.) **Fig. 9.** Photo of *Banksieaeformis praegrandis* from the Stuart Creek macroflora. Scale bar = 10 mm. (PIRSA photo 39034.) **Fig. 10.** Line drawing of extant *Banksia chamaephyton* redrawn from Fig. 31*C* in George (1999*a*). **Fig. 11.** *Banksia longicarpa* infructescence impression (P17956a) from Koolymilka, near Woomera. Scale bar = 10 mm. *Banksieaeformis* cf. *B. langii* leaf (P17956b) arrowed. (Photo by P. Haines.) **Fig. 12.** Line drawing of *Banksia longicarpa* infructescence impression from Poole Creek south. Scale bar = 10 mm. (Line drawing by D. Steart from photo by D. Greenwood.) **Fig. 13.** Photo of *Banksia longicarpa* infructescence impression from Poole Creek south. Scale bar = 10 mm. A *Casuarina* infructescence mould is indicated by an arrow. (Photo by D. Greenwood.)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morphology of *Banksieaeformis praegrandis* is most similar to leaves of the extant *B. chamaephyton* A.S.George (Fig. 10) and *B. blechnifolia* F.Muell. (Series *Prostratae*) and only superficially so to *Banksia grandis* (Table 1). There is a superficial resemblance to *Dryandra idiogenes* A.S.George (George 1999*b*, fig. 49). The rounded apices of the lobes of *Banksieaeformis praegrandis* and the general tendency for each pair of lobes to be opposite (Figs 8 and 9) was noted by Chapman (1937, fig. 6). This is unusual for the Banksiinae, although is present in *Banksia grandis* Willd. (Hill and Christophel 1988, fig. 36) and some specimens of both *B. chamaephyton* (Fig. 10) and *D. idiogenes*. However, the lobes in several fossil specimens are not paired and show a tendency to become progressively alternate, as seen in modern leaves of *Banksia* and *Dryandra*. Chapman (1937) observed that each lobe in his specimen had six secondary veins, but specimens from Stuart Creek had from one to four prominent veins (Fig. 9), depending on the degree of preservation, with additional lesser veins present on some specimens. *Banksieaeformis praegrandis* differs from *Banksia chamaephyton* by having lobes that are quite broad at the base, whereas the extant species always has linear lobes (Fig. 10). The fossil species differs from *D. idiogenes* by having generally longer lobes (they are much shorter triangles in *D. idiogenes*), with the extant species also having much longer leaves than *Banksieaeformis praegrandis* (Table 1).

Tribe Banksieae
Subtribe Banksiinae
Genus ***Banksia*** L.f.
Subgenus ***Banksia***

Banksia longicarpa Greenwood, Haines & Steart, sp. nov. (Figs 11–13)

Diagnosis

Infructescence an elongate cylinder, abruptly tapering distally. Floral bracts not in rows. Follicles very prominent, few in number and concentrated in the lower portion of the axis; valves ovoid and robust; smooth; suture straight.

Location: ?Eyre Formation (Mt Sarah Sandstone) at Koolymilka, near Woomera and Etadunna Formation at BMR 3, Poole Creek south, all in South Australia.

Holotype: P17956a, stored in the South Australian Museum.

Etymology: The specific epithet is derived from the tall cylindrical form of the infructescence.

Remarks

The infructescence is elongate and the axis was probably cylindrical in life (Figs 11–13). The specimen from Woomera (Fig. 11) would appear to represent the top half of a cone, but as this specimen is curated in a museum it is designated the type. The mature bi-valved follicles are few in number and are irregularly arranged on both specimens and attached to a regularly textured massive cylinder (the woody axis). The regular patterning of the axis in the Poole Creek specimen is interpreted as indicating that the perianths were shed by the inflorescence at maturity, but may also reflect combustion of the perianths during a fire. Each element of the textured surface of the axis is an irregular polygon, similar to the

perianth base commonly persistent on *Banksia* infructesences, representing unfertilised individual flowers. Follicles are sparse, concentrated in the lower part of the axis, very prominent and broadly elliptic (defined here as 'domed').

The infructescences of *Banksia* and *Dryandra* R.Br. are similar in their common possession of woody bi-valved follicles attached to a central woody axis (George 1999*a*, 1999*b*). The infructesences of *Dryandra* typically have a very short axis with a low number of mature follicles. Infructesences with short axes are found in *Banksia* (subgenus *Isostylis*, e.g. *B. ilicifolia* R.Br.); however, the majority of modern species of *Banksia* have long axes sometimes bearing 10–20 mature follicles (Table 2). The specimens from Woomera and Poole Creek are clearly of the type found only in *Banksia* and so comparisons are restricted to species of that genus. Pike (1953) dismissed infructescence size as a diagnostic character for *Banksia*, basing her systematic analyses on cuticular characters. The Woomera and Poole Creek material are moulds and lack any epidermal detail. McNamara and Scott (1983) suggest that *Banksia* species can be distinguished on the basis of the overall shape of the inflorescence and follicle and bract form. Of the characters listed by Thiele and Ladiges (1996) for their analysis, seven characters of the infructescence may be preserved in fossil material. Comparisons between extant and fossil *Banksia* infructescences on the basis of gross morphological characters are presented in Table 2.

Thiele and Ladiges (1996) differentiated mature *Banksia* infructescences only as being spherical (subgenus *Isostylis*) or ovoid to elongate (subgenus *Banksia*). On this basis, *B. longicarpa* may be placed in subgenus *Banksia* (Table 2). Using the descriptions in George (1981, 1999*a*) and Holliday and Watton (1990) and herbarium collections, we differentiated five categories of infructescence shape (Table 2). Several extant species intergrade across more than one shape category, but none includes more than two categories. Intergradation may reflect imperfect development or in some cases phenotypic plasticity, or taxonomic imprecision in existing taxa. The shape of the mature follicles in plan view was considered by both McNamara and Scott (1983) and Thiele and Ladiges (1996) as a character in their analysis; follicle shape in longitudinal view was considered here morphometrically with length and width measurements on unopened follicles.

Infructescences of *Banksia* have been reported from Eldorado and Creswick in Neogene deep leads (Redaway 1858; Smyth 1873, 1875; Pike 1953), Miocene lignites of the Latrobe Valley (Cookson and Duigan 1950; Pike 1953), Victoria (summarised in Greenwood *et al.* 2000), Eocene sandstones from the Kennedy Range in Western Australia (McNamara and Scott 1983) and from both Oligocene and Pleistocene sediments from Tasmania (Hill and Macphail 1983; Jordan and Hill 1991; Fig. 1). All these fossil *Banksia* infructescences appear to represent subgenus *Banksia*, as all have dense condensed woody axes that are ovoid to elongate (Table 2). *Banksia longicarpa* and *B. archaeocarpa* McNamara & Scott have a similar number of follicles that are of similar size and shape, but *B. longicarpa* differs from *B. archaeocarpa* primarily in that the former possesses a tall cylindrical axis, whereas the Western Australian species has the form of an elongated ovoid. The un-named *Banksia* cones from Eldorado and Yallourn in Victoria (Cookson and Duigan 1950; Pike 1953) are squat and cylindrical in shape, with abundant fertile follicles and strongly flattened valves and so represent a separate species to *B. longicarpa*. A *Banksia* infructescence described from Melaleuca Inlet in Tasmania associated with *B. kingii* leaves (Jordan and Hill 1991) is of a similar size to *B. longicarpa* and has similar-shaped mature follicles, but is much stouter than the latter species and has more regularly spaced mature follicles.

Table 2. Infructescence characteristics of extant and fossil species of *Banksia*
Data from Holliday and Watton (1990), McNamara and Scott (1983), Thiele and Ladiges (1996) and specimens in MEL and NMV. Not all modern species are listed. Lengths and widths are ranges. 1, long cylinder; 2, short cylinder; 3, barrel to ovoid; 4, globular; 5, irregular

Species	Cone length (cm)	Cone width (cm)	Cone shape 1	2	3	4	5	Follicle
Subgenus *Isostylis*	1–2	2–4					X	flattened
Subgenus *Banksia*								
Series *Tetragonae*	7–16	7–12			X	X		domed
Series *Lindleyanae*	10–15	7–10			X			
Series *Banksia*	5–40	4–12	X	X	X	X	X	Domed or flattened
B. serrata	8–16	5–18	X					domed
Series *Prostratae*	6–20	5–8	X	X	X			domed or flattened
Series *Cyrtostylis*	7–30	5–10	X		X			domed or flattened
Series *Ochraceae*	7–13	6–10		X	X	X		flattened
Series *Grandes*	8–30	8–12	X		X			flattened
Series *Salicinae*	4–25	2–8	X	X	X			domed or flattened
B. integrifolia	7–15	4–8	X					flattened
B. marginata	4–10	4–6	X					flattened
Series *Spicigerae*	5–25	4–9	X	X				domed or flattened
B. spinulosa	5–20	4–9	X					domed
Series *Quercinae*	5–15	4–7	X					domed or flattened
Series *Dryandroides*	4–5	4			X	X		flattened
Series *Abietinae*	4–20	4–15	X	X	X	X		domed or flattened
Fossil species								
B. archaeocarpa	11	4			X			domed
B. lignitica	5.5	3		X				flattened
B. kingii	6.2	4.6		X				domed
B. 'eldorado'	4–7.5	2.5–3.5		X				flattened
B. 'pioneer'					X			
B. longicarpa	3–7	2–2.2	X					domed

Elongate infructescence axes are absent from Series *Tetragonae*, *Lindleyanae*, *Ochraceae*, *Dryandroides* and *Abietinae* of Genus *Banksia*, are rare in Series *Banksia* and *Grandes*, but they are typical of Series *Prostratae*, *Cyrtostylis*, *Salicinae*, *Spicigerae* and *Quercinae* (Table 2). Of the elongate taxa, small to moderate size similar to that of *B. longicarpa* is also seen in Series *Prostratae*, *Salicinae*, subseries *Occidentales* of Series *Spicigerae* and Series *Quercinae*. The small number of large, prominent, thick follicles in the fossil species is quite similar to those in *B. serrata* (Series *Banksia*), but unlike those in *B. integrifolia*, *B. marginata* (Series *Salicinae*) or *B. spinulosa* (Series *Spicigerae*) as the latter taxa have follicles that are quite flat and not domed into a substantial woody structure. The follicles of *B. longicarpa* (Figs 11–13) are smaller and less flattened dorsiventrally than

those in *B. serrata*, but otherwise similar. While placement of these fossils in Series *Banksia* is not suggested at this stage, it is likely that the closest match to *B. longicarpa* may be found by more detailed comparisons with taxa from Series *Banksia*.

Discussion

Banksia is an important and distinctive component of some sclerophyllous vegetation types in the modern Australian flora. The evolutionary history of *Banksia* is, however, poorly known despite the common presence of *Banksia*-like leaves (*Banksieaephyllum* and *Banksieaeformis*) in many Tertiary macrofloras (Fig. 1). This lack of insight into *Banksia* evolution from leaf fossils results in part from systematic uncertainty in the status of *Banksia*-like leaves (e.g. Carpenter and Jordan 1997, but see also Vadala and Drinnan 1998). The presence of *Musgraveinanthus* in the same sediments as *Banksieaephyllum* at Golden Grove in South Australia (and even within the same block of matrix; Barrett and Christophel 1990) prompted Christophel and Greenwood (1987) to suggest that in some Eocene macrofloras *Banksia*-like leaves may have represented the foliage organs of a plant from the related Subtribe Musgraveinae, rather than *Banksia* (Subtribe Banksiinae). Carpenter *et al.* (1994) concluded on the basis of cuticular information and the possession of cuneate bases, that these Eocene taxa had a greater affinity to *Musgravea* than to *Banksia*. However, Hill and Christophel (1988), Carpenter *et al.* (1994) and Vadala and Drinnan (1998) suggested that some members of *Banksieaephyllum* probably represented *Banksia* or a related taxon on the basis of more sclerophyllous epidermal features on these fossil leaves. On the basis of diagnostic epidermal features Carpenter and Jordan (1997) have also raised doubts that all *Banksia*-like Tertiary leaves are Proteaceae. The leaf material described here, however, lacks epidermal detail and matches closely with some modern species of *Banksia* (i.e. matches the diagnosis for *Banksieaeformis*) and so accordingly is assigned to *Banksieaeformis*. It is very likely that the fossil taxa *Banksieaeformis langii* and *B. serratus* represent *Banksia* specifically. In the absence of cuticular information, the affinity of *Banksieaeformis praegrandis* within the Banksieae remains speculative.

Reports of remains of *Banksia s.s.* from areas outside the main range of the extant genus are rare (Fig. 1), as most previous reports of *Banksia*-like leaves, *Banksia* cones and fossil wood attributed to *Banksia* are from Tertiary deposits in southern Australia and Tasmania (Cookson and Duigan 1950; Pike 1953; Patton 1957; Blackburn 1981; Hill and Macphail 1983; Hill 1988; Hill and Christophel 1988; Carpenter *et al.* 1994; Hill 1994; Vadala and Drinnan 1998; Greenwood *et al.* 2000). Previous reports of *Banksia*-like leaves and the tips of the fruiting spike of *Banksia* from silcrete near Lake Eyre South in South Australia lacked systematic precision or were anecdotal (Chapman 1937; Lange 1986; Greenwood *et al.* 1990; Greenwood 1996). The presence of *Banksia* cones at Poole Creek and near Woomera are therefore an indisputable record for the genus in northern South Australia and, together with the Kennedy Range fossils (McNamara and Scott 1983), provide a significant extension of the Tertiary geographical range of *Banksia*. *Banksia longicarpa* material lacks sufficient detail to allow a comprehensive systematic analysis, but matches most closely with members of Series *Banksia* and perhaps *B. serrata* most closely of all.

Each of the *Banksieaeformis* species described here, some species of *Banksieaeformis* and *Banksieaephyllum* from Oligocene sediments in Tasmania and Western Australia and the Paleocene *B. taylorii* from New South Wales, are very similar in architecture to extant species, whereas common *Banksia*-like leaves in Eocene–Miocene floras from south-eastern Australia appear to represent extinct lineages with cuneate bases that may be more

closely allied to the Musgraveinae than the Banksiinae (Hill and Christophel 1988; Carpenter *et al.* 1994; Vadala and Drinnan 1998). The presence of Tertiary *Banksia*-like leaves that may not represent Proteaceae (Carpenter and Jordan 1997) further emphasises the need for caution in interpreting phylogeny on the basis of single organs.

On the weight of available stratigraphic evidence, both *Banksieaeformis serratus* and *B. langii* are mid-Tertiary in age (Krieg *et al.* 1991; Callen *et al.* 1995; Warren and Shaw 1995), and thus their close similarity with extant species is perhaps to be expected. The remaining species, *Banksieaeformis praegrandis*, is known from both Eocene (Mt Sarah Ss. at Woomera and Eyre Formation at Mt Alford and Morris Creek) and Miocene sediments (Willalinchina Sandstone at Stuart Creek). The Woomera, Mt Alford and Morris Creek samples of *B. praegrandis* have broader, shorter lobes, but are otherwise indistinguishable from the Miocene examples from Stuart Creek and so were treated here as belonging to the same species. The significant temporal separation of these specimens is not considered problematic, as there appears to be no sound systematic reason for creating two separate taxa. The age difference may also be an artefact of current stratigraphic interpretation (Greenwood *et al.* 1990; Callen *et al.* 1995).

Palaeoecology

The use of individual fossil taxa as climatic indicators is problematic, as climatic tolerances evolve over time and taxonomic relationships based on single organs may underestimate phylogenetic distance. Nevertheless, the climatic envelopes of the nearest living relatives of fossil taxa may be informative, particularly in comparison with estimates derived from other sources. Greenwood (1996) estimated mean annual rainfall for the Lake Eyre Basin Middle Eocene Poole Creek and Nelly Creek macrofloras as 1100 and 1360 mm, respectively, but with large uncertainties attached to these estimates. He suggested that floristic and foliar physiognomic differences between the Poole and Nelly Creek floras (which contain a majority of broad-lamina taxa) and the Stuart Creek flora (which is dominated by stenophyllous forms) may reflect either a drier climate (through climate change over time) or perhaps poor soils in the Stuart Creek area promoting greater xerophylly and/or sclerophylly in the local flora there. It is likely that the Lake Eyre area was no wetter in the Late Miocene than in the Middle Eocene, and may even have been drier (Truswell and Harris 1982; Benbow *et al.* 1995). Most extant species of *Banksia* occur on sites where annual rainfall is between 500 and 1000 mm (all but *B. plagiocarpa* <1500 mm per year; based on 75 spp. for which rainfall values were provided in Taylor and Hopper 1988 and Holliday and Watton 1990). The extant saw tooth-lobed species most similar to *Banksieaeformis langii* (e.g. *Banksia speciosa* and *B. dryandroides*) are both found on sites with rainfall <800 mm per year and the extant species most similar to *Banksieaeformis praegrandis* (i.e. *Banksia chamaephyton*) occurs on sites <600 mm per year. This data suggests that the Stuart Creek flora grew under an annual rainfall of <1000 mm per year. The presence of *Banksieaeformis* spp. at Stuart Creek, Morris Creek and sites in the Stuart Range is therefore consistent with a lowering of annual rainfall between the Middle Eocene (1100–1360 mm $year^{-1}$) and Miocene for sites in the Lake Eyre area. However, at the lower range of uncertainty for the Middle Eocene rainfall estimates, or broadened tolerances in the past for the taxa (reflecting also taxonomic uncertainty), there is no or little change in rainfall indicated. Also the record of *Callicoma serratifolia* from the Stuart Creek flora (Barnes and Hill 1999) is inconsistent, with rainfall in the Late Miocene being much lower than 1000 mm per year, as this extant species is found in wet sclerophyll forest and warm temperate to subtropical rainforest along the east coast of Australia. Other taxa reported for

the Stuart Creek flora, such as Casuarinaceae aff. *Gymnostoma* and *Brachychiton*, are consistent with annual rainfall of about 1000 mm (Greenwood 1996).

McNamara and Scott (1983) speculated that damaged follicles on *B. archaeocarpa* may be evidence of insect attack and predation on these insects by birds (possibly parrots). Hill (1994) also suggested that other Tertiary Proteaceae inflorescences might demonstrate the development of animal pollination vectors. The development of a robust woody axis in *Banksia* inflorescences would seem to be an adaptation to mammalian pollination, but may also be a consequence of seroteny. The fossil record of honey possums (Tarsipedidae) is quite sparse; however, Miocene faunas in Etadunna Formation in the Lake Eyre area contain evidence of two possum families, the Phalangeroidea and Petauridae (Rich 1991), modern species of which are known to feed on *Banksia* inflorescences. It is therefore possible that *B. longicarpa* was pollinated by possums. The robust character of the follicles in *B. longicarpa* is possibly an adaptation to allow seeds to survive fire (serotiny), a common characteristic in modern species.

Conclusions

Without doubt, *Banksia* occurred formerly outside of its present range. The character, location and time frame of central Australian populations of *Banksia* may provide important insight into the phytogeography and evolution of this important genus of Australian plants. The fossil records presented here indicate that *Banksia* occurred in northern South Australia in the Miocene (*Banksia longicarpa*) and that Banksiinae, possibly *Banksia*, occurred near Alice Springs in the mid-Tertiary. The leaves of *Banksieaeformis serratus* from Glen Helen are quite similar to those of the species occurring in both south-western (*Banksia baueri* and *B. menziesii*, Series *Banksia*) and south-eastern Australia (*B. serrata* and *B. aemula*, Series *Banksia*) and also the sole Northern Territory species, *B. dentata* (Series *Salicinae*), whereas the northern South Australian *Banksieaeformis praegrandis* and *B. langii* reflect taxa restricted to Western Australia (e.g. *Banksia chamaephyton*, Series *Prostratae* and *B. speciosa*, Series *Banksia*, respectively), and in the case of *Banksieaeformis praegrandis* may not represent Banksiinae. The '*Banksia speciosa*' leaf type of *Banksieaeformis langii* is also known from the Paleocene of New South Wales (i.e. *Banksieaephyllum taylori*), indicating an ancient and widespread occurrence of this leaf type. This pattern of occurrence may reflect a former set of connected populations, or equally so, may reflect common leaf forms as adaptations to particular circumstances. Available fossil evidence suggests that a wide range of leaf morphologies were present early in the Tertiary, but that infructescences primarily represent subgenus *Banksia*; this supports suggestions of mosaic evolution within Banksiinae, with some leaf characters evolving independently of infructescence form in separate lineages. While estimates of rainfall presented here on the basis of taxa must be considered speculative, the *Banksieaeformis* species from the Lake Eyre region are consistent with a climatic drying between the Middle Eocene and the Miocene in this area, but do not conclusively indicate drying. Conversely, these taxa may indicate local vegetational mosaicism involving sclerophylly and/or fire (e.g. putative serotinous cone of *B. longicarpa*), as other taxa in the Stuart Creek macroflora (e.g. *Callicoma* and *Brachychiton*) at least are indicative of seasonally wet conditions.

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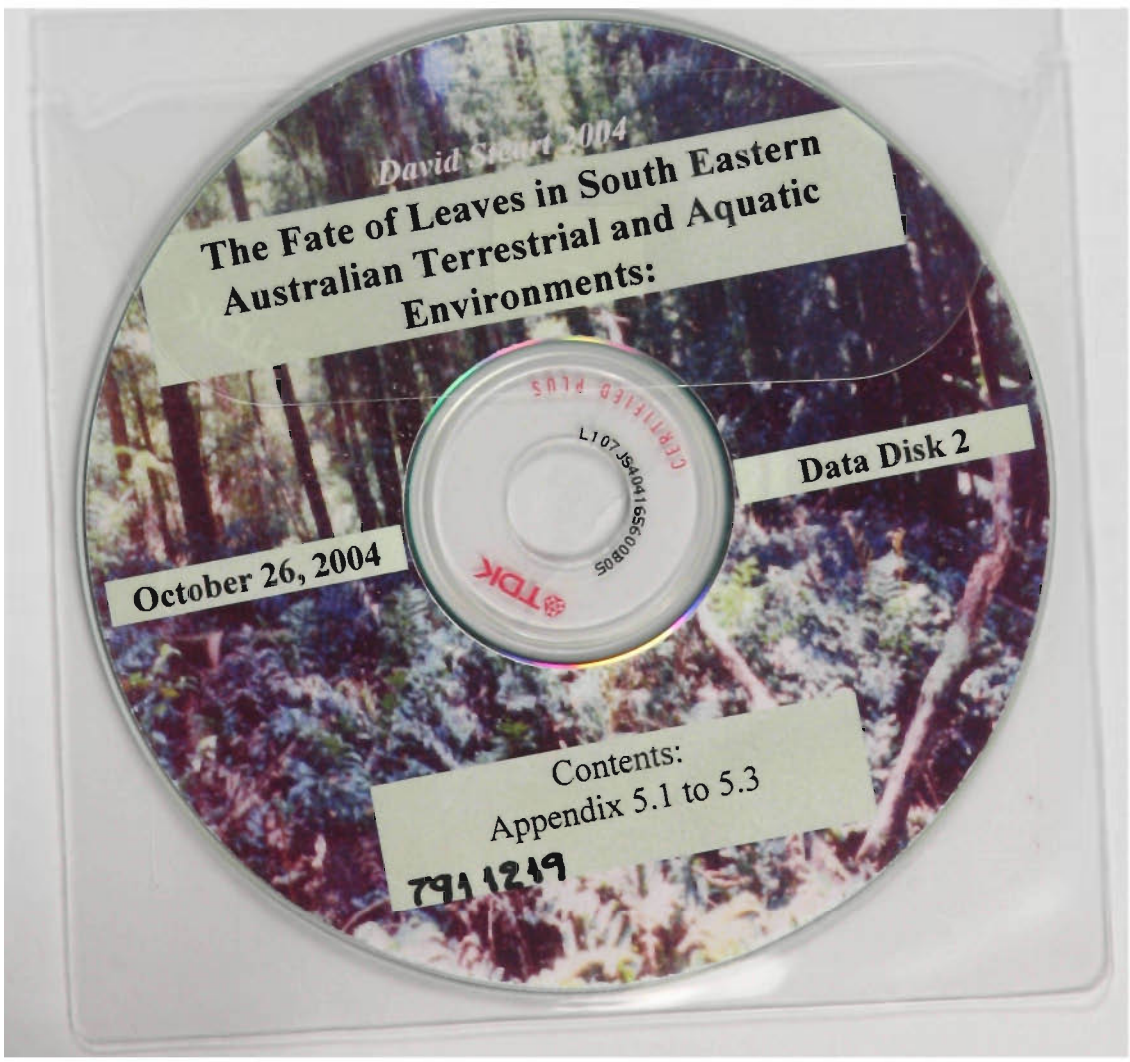
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Figure 5.8 Mass loss versus time for the two species (*Lomatia fraseri* and *Nothofagus cunninghamii*) versus treatment used in the mesocosm experiments. The experiments lasted for 16 months, with the times between each collection being two months.
Figure 5.8a Excess nitrogen and phosphorus,
Figure 5.8b Aerated water over the sediments at 10°C
Figure 5.8c Aerated water over the sediments at 10°C
Figure 5.8d Anaerobic sediments at 10°C,
Figure 5.8e Aerobic decay at 5°C,
Figure 5.8f Aerobic decay at 15°C.