

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

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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 particulate 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, CAMPPELL et al. 1992 a, b, BENSON & PEARSON 1993, CAMPPELL & 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 be 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

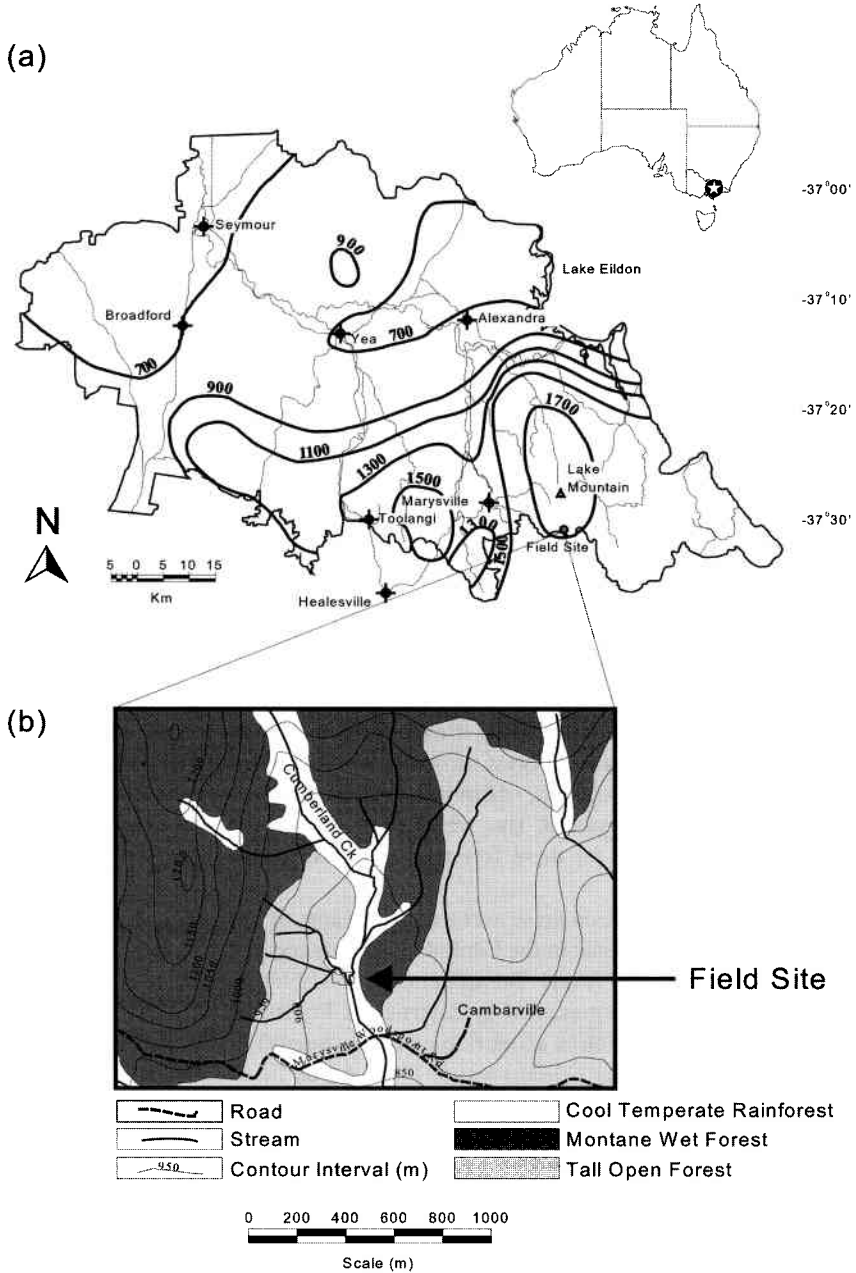
Field experiments were undertaken at Cumberland Creek, in the Central Highlands of Victoria, south-eastern Australia (145° 53', 37° 34'; Fig. 1). Cumberland Creek is a first order perennial stream, with a typical width of 1.2 to 1.8 m and a maximum depth of 0.8 m under typical baseflow conditions. The stream bed consists of coarse sand with occasional cobbles and large rocks. The underlying 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 watsii* 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 CAMPBELL & FUCHSHUBER (1994, 1995). Total litter fall near Cement Creek is about 6 tonnes (dry weight) ha<sup>-1</sup> y<sup>-1</sup>, 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<sup>2</sup>, whereas coarse and fine benthic organic matter accounted for only 0.13 kg/m<sup>2</sup>. 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, CAMPBELL & 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 <sup>2</sup> ) | Texture      | Margin                   | Leaf density (g/m <sup>2</sup> ) |
|--------------------------------|----------------------|--------------------------------------|--------------|--------------------------|----------------------------------|
| <i>Nothofagus cunninghamii</i> | Nanophyll            | 1.3                                  | Papery       | Toothed                  | 101                              |
| <i>Atherosperma moschatum</i>  | Microphyll           | 10.8                                 | Papery       | Toothed to rarely entire | 94                               |
| <i>Lomatia fraserii</i>        | Notophyll/Macrophyll | 36.2                                 | Intermediate | Toothed                  | 121                              |
| <i>Eucalyptus regnans</i>      | Notophyll            | 17.2                                 | Sclerophyll  | Entire                   | 243                              |
| <i>Acacia melanoxylon</i>      | 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<sup>TM</sup> (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).

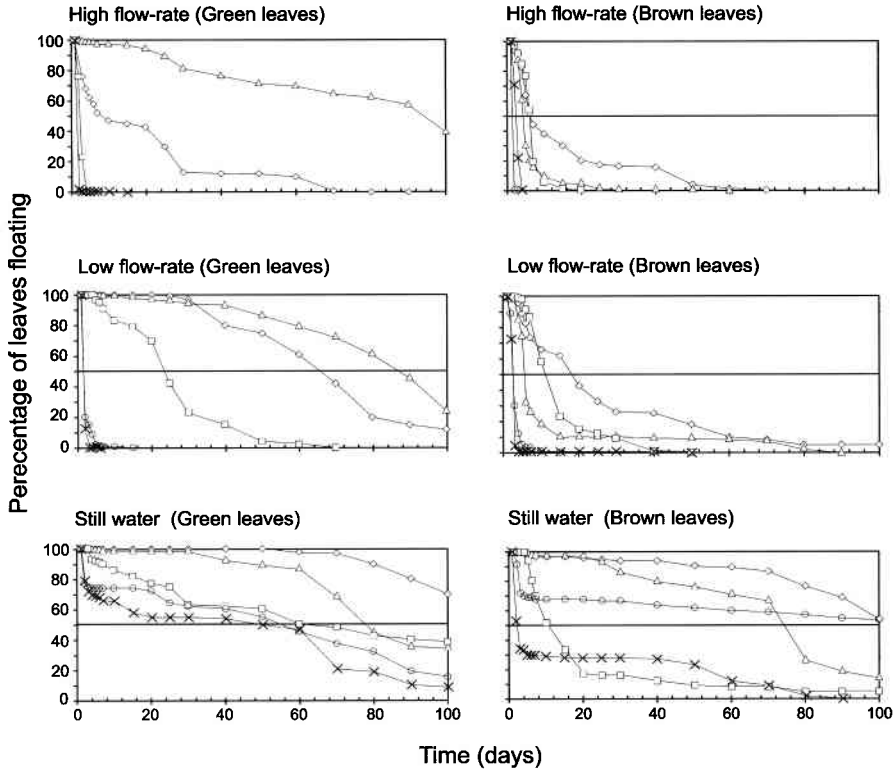
The field experiments were undertaken in July to August 1999. Experimental days were chosen to reproduce as much as possible the same conditions, with the stream flow remaining about 1.5 m<sup>3</sup>/s, and stream velocity (at the gill net) between 0.5 and 0.7 m/s.

## **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 MTBS 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.

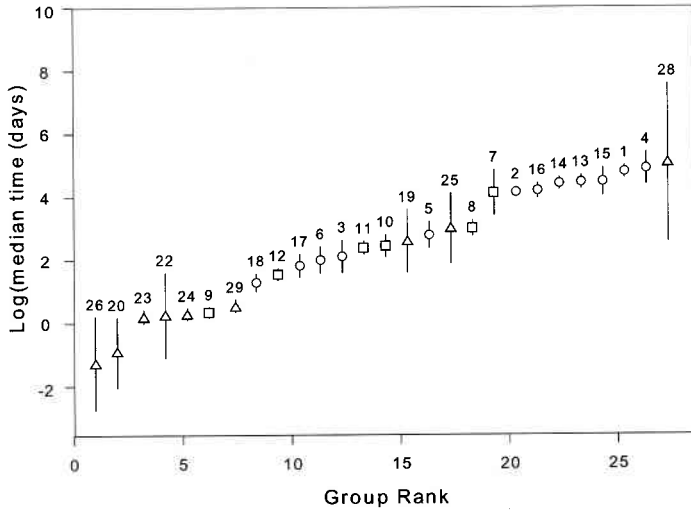
Flow rate also exerted a strong effect on sinking behaviour. With the exception of green *Atherosperma moschatum* leaves, the more vigorous the flow

**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     | <i>Nothofagus cunninghamii</i> | Still Water | Green       | 132         |
| 2     | <i>Nothofagus cunninghamii</i> | Low         | Green       | 67          |
| 3     | <i>Nothofagus cunninghamii</i> | High        | Green       | 10          |
| 4     | <i>Nothofagus cunninghamii</i> | Still Water | Brown       | 207         |
| 5     | <i>Nothofagus cunninghamii</i> | Low         | Brown       | 18          |
| 6     | <i>Nothofagus cunninghamii</i> | High        | Brown       | 8           |
| 13    | <i>Atherosperma moschatum</i>  | Still Water | Green       | 88          |
| 14    | <i>Atherosperma moschatum</i>  | Low         | Green       | 97          |
| 15    | <i>Atherosperma moschatum</i>  | High        | Green       | 129         |
| 16    | <i>Atherosperma moschatum</i>  | Still Water | Brown       | 70          |
| 17    | <i>Atherosperma moschatum</i>  | Low         | Brown       | 7           |
| 18    | <i>Atherosperma moschatum</i>  | High        | Brown       | 4           |
| 7     | <i>Lomatia fraseri</i>         | Still Water | Green       | 64          |
| 8     | <i>Lomatia fraseri</i>         | Low         | Green       | 22          |
| 9     | <i>Lomatia fraseri</i>         | High        | Green       | 2           |
| 10    | <i>Lomatia fraseri</i>         | Still Water | Brown       | 13          |
| 11    | <i>Lomatia fraseri</i>         | Low         | Brown       | 13          |
| 12    | <i>Lomatia fraseri</i>         | High        | Brown       | 5           |
| 25    | <i>Eucalyptus regnans</i>      | Still Water | Green       | 29          |
| 26    | <i>Eucalyptus regnans</i>      | Low         | Green       | 1           |
| 27    | <i>Eucalyptus regnans</i>      | High        | Green       | <1          |
| 28    | <i>Eucalyptus regnans</i>      | Still Water | Brown       | 137         |
| 29    | <i>Eucalyptus regnans</i>      | Low         | Brown       | 2           |
| 30    | <i>Eucalyptus regnans</i>      | High        | Brown       | <1          |
| 19    | <i>Acacia melanoxylon</i>      | Still Water | Green       | 18          |
| 20    | <i>Acacia melanoxylon</i>      | Low         | Green       | 1           |
| 21    | <i>Acacia melanoxylon</i>      | High        | Green       | 1           |
| 22    | <i>Acacia melanoxylon</i>      | Still Water | Brown       | 4           |
| 23    | <i>Acacia melanoxylon</i>      | Low         | Brown       | 2           |
| 24    | <i>Acacia melanoxylon</i>      | 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 |
| <i>Nothofagus cunninghamii</i> | Green       | 100                           | 100 | 100 | 100 | 25 | 10 | 0   |
|                                | Brown       | 100                           | 100 | 100 | 85  | 55 | 20 | 0   |
| <i>Atherosperma moschatum</i>  | Green       | 100                           | 100 | 100 | 100 | 35 | 0  | 0   |
|                                | Brown       | 100                           | 100 | 100 | 75  | 60 | 10 | 0   |
| <i>Lomatia fraseri</i>         | Green       | 100                           | 100 | 100 | 75  | 15 | 0  | 0   |
|                                | Brown       | 100                           | 100 | 100 | 100 | 40 | 0  | 0   |
| <i>Eucalyptus regnans</i>      | Green       | 100                           | 100 | 100 | 75  | 15 | 0  | 0   |
|                                | Brown       | 100                           | 100 | 100 | 100 | 40 | 0  | 0   |
| <i>Acacia melanoxylon</i>      | 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 concomitant 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 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. 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. 1992 b).

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 around 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 coccoifera* 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  $\sim 2.5 \text{ kg AFDW m}^{-2} \text{ y}^{-1}$  (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 pseudoreplicated 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.

### Acknowledgements

Funding for this research was provided by a postgraduate scholarship from the School of Life Sciences & Technology (Victoria University) to DCS, and the Australian Research Council from grants to DRG (SGS 40/96 & A39802019). We would also like to thank the Victorian Department of Natural Resources & Environment for logistical support and for permission to undertake the study in a reserve under their control. DCS particularly thanks National Parks Ranger MILES STEWART-HOWE for his assistance and advice, and PAUL WHITE and other volunteers who gave of their time and labour for the field work. Two anonymous referees provided excellent and constructive comments that led to a marked improvement in the final manuscript.



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Submitted: 10 May 2001; accepted: 14 August 2002.