

OVERLAND TRANSPORT OF LEAVES IN TWO FOREST TYPES IN SOUTHERN VICTORIA, AUSTRALIA AND ITS IMPLICATIONS FOR PALAEOBOTANICAL STUDIES

DAVID C. STEART^{1,3}, PAUL I. BOON^{1*} & DAVID R. GREENWOOD²

¹ Institute for Sustainability and Innovation, Victoria University of Technology (St Albans campus), PO Box 14428, Melbourne City Mail Centre, VIC 8001 Australia

² Environmental Science, Brandon University, 270 18th Street, Brandon, MB, R7A 6A9 Canada

³ Current address: Department of Geology, Royal Holloway University of London, Egham, Surrey TW20 0EX United Kingdom

* to whom reprint requests should be addressed, Email: paul.boon@vu.edu.au

STEART, D. C., BOON, P. I. & GREENWOOD, D. R., 2006. Overland transport of leaves in two forest types in southern Victoria, Australia and its implications for palaeobotanical studies. *Proceedings of the Royal Society of Victoria* 118 (1): 65–74. ISSN 0035-9211.

The distance that leaves travel from their parent tree has important implications for palaeobotanical studies in which past vegetation types and climates are reconstructed. We quantified the distance moved overland by leaves of five tree species (*Acacia melanoxylon*, *Atherosperma moschatum*, *Eucalyptus regnans*, *Lomatia fraseri* and *Nothofagus cunninghamii*) in two contrasting, but contiguous, forest types in south-eastern Victoria: a) cool temperate rainforest dominated by Myrtle Beech, *Nothofagus cunninghamii*; and b) wet sclerophyll forest dominated by Mountain Ash, *Eucalyptus regnans*. Regardless of species, leaves generally remained close to their parent tree: 80 % of leaves moved less than 0.2 m over an observation period of six months and the greatest distance moved by any leaf was 3.4 m. Contrary to expectations, slope had little overall effect on leaf transport. We conclude that leaves from trees in these two forest types are transported less than one tree height from their parent tree during normal weather conditions. Greater transport may occur during extreme weather, which could promote extensive wind-borne leaf transport from the tree canopy.

Keywords: *Eucalyptus*, *Nothofagus*, palaeoclimate, taphonomic bias, wind transport, leaves

PLANT FOSSILS constitute a fundamental source of information on the evolutionary history of plant lineages, vegetation and climate change, however, taphonomic bias often complicates attempts to reconstruct palaeoclimates and past vegetation types. There are three main sources of preservational, or taphonomic, bias in the macrofossil record of plants (Spicer 1981, 1991; Ferguson 1985; Burnham 1989, 1993; Greenwood 1991; Burnham et al. 1992): a) differential production of plant parts (i.e., leaves, reproductive organs and woody parts); b) differential transport and sorting of plant organs among species once they have been shed from their parent plants; and c) differential decay and preservation of plant organs from different species.

In earlier papers we reported on differential production of plant parts (Stewart et al. 2005) and differential aqueous transport of leaf material within streams (Stewart et al. 2002). In this communication, we focus on differential overland transport of leaves belonging to tree species within two contrasting forest types. This aspect of taphonomic bias is important in palaeobotanical studies for two reasons. First,

the accuracy with which a fossil-leaf deposit represents the original flora depends partly upon how far the component leaves were transported before burial and preservation (Ferguson 1985; Greenwood 1991; Spicer 1989, 1991). If little or no overland transport occurs after abscission, the leaf fossil record will reflect more accurately the local tree species than if leaves were moved large distances from their parent plant, or leaves were imported from distant plant communities (Ferguson 1985; Spicer 1989, 1991).

Second, if leaves move little after falling to the ground, fossil leaf assemblages should consist mostly of riparian or wetland plant species since these habitats are most conducive to leaf preservation (Spicer 1989, 1991). The prediction is especially important in the Australian context because there is a general paucity of sclerophyll taxa, such as *Eucalyptus* and *Acacia*, in the leaf fossil record (Cookson 1954; Christophel 1989; Lange 1982; Hill 1982, 1992, 1994; Martin 1994; Hill et al. 1999; Greenwood et al. 2000; Macphail & Hill 2001). These genera are not commonly considered as riparian. The extent of overland transport of leaves in

Australian forests needs to be assessed to determine if sclerophyll taxa have been excluded from fossil-forming processes because of lack of overland transport from their parent trees, or alternatively whether they were genuinely absent from an ancient community.

The role played by overland transport in controlling the species membership of the fossil assemblage is also critical in determining the accuracy and fidelity of palaeoclimate reconstruction. Several studies have shown, for example, that whereas the relative proportion of woody plants with toothed leaves is correlated with mean annual temperature, and thus can act as a proxy for palaeotemperature (Greenwood et al. 2004), local floristic patterns may confound this relationship (Burnham et al. 2001; Kowalski & Dilcher 2003; Greenwood 2005).

The published data on overland transport indicates that leaves are not spread far from their parent plant, with most abscised leaves remaining within 10 to 20 metres of the bole of the parent (Spicer 1981, 1991; Ferguson 1985; Burnham et al. 1992; Greenwood 1991, 1992; Burnham 1994, 1997). Ferguson (1985) argued that, if leaves were relatively mobile after abscission, one would expect leaf litter on the forest floor to become increasingly well mixed with time. Several studies (e.g. Ferguson 1985; Burnham et al. 1992; Greenwood 1991, 1992; Burnham 1994, 1997) have shown that this does not happen. Indeed, the boundaries between the leaf halos of different tree species remain evident even after many months. Empirical studies undertaken outside of Australia also suggest that leaves move little from their parent plant once abscised. Ferguson (1985), for example, placed 500 spray-painted leaves of *Fagus sylvatica* in a closed woodland coppice of *Alnus glutinosa* and found that only one leaf had moved more than two metres after 98 days. In a later study, France (1995) found that coniferous pine needles and deciduous angiosperm leaves moved, on average, only ~0.3 m and ~0.5 m per year, respectively. In one of the few Australian studies, Carpenter and Horwitz (1988) reported limited overland transport of leaves in a Tasmanian rainforest, where the forest dominant species (*Eucalyptus obliqua*) was almost completely excluded from the detritus in a nearby stream, and by implication, the local macrofossil record. Furthermore, Greenwood (1991) found in tropical rainforest in northeastern Queensland that the large leaves (up to 15 x 1.5 cm) of the stenophyllous conifer *Prumnopitys amara* (Podocarpaceae) travelled further downslope (22 m) towards a stream than they travelled upslope (18 m), suggesting pref-

erential downslope overland transport of the leaves of this species.

Spicer (1981) and Ferguson (1985) examined the factors controlling the overland transport of leaves. They concluded that leaf size had little effect on overland transport, whereas leaf weight and wetness, as well as wind speed, were major determinants. An implication of the effect of wind speed on overland transport is that leaves could be expected to move further in open (windy) than closed (relatively quiescent) forests. Long-distance transport via wind is especially important during catastrophic atmospheric events, such as hurricanes and tornadoes (van der Burgh 1994). A number of other studies also provide anecdotal evidence that leaves travel overland primarily via by wind blow or water wash under storm conditions (e.g. Drake & Burrows 1980; Dudgeon 1982 and Greenwood 1992). These factors probably interact strongly. Dudgeon (1982), for example, noted that delicate leaves, such as those of *Liquidambar formosana*, were most easily moved by gusts of wind. The slope of the land is likely also to be an important factor in leaf movement, as there is a positive relationship between bank slope and overland transport into streams (Fisher and Likens 1973; Sedell et al. 1974; Fisher 1977; Greenwood 1991; France 1995).

In this paper we report on a series of observations designed to quantify the distance travelled by leaves from a range of common tree species in two contrasting forest types in south-eastern Australia. Specifically, we tested four hypotheses: a) leaves would not travel substantial distances (>5 m) from where they were placed on the forest floor; b) this pattern would be evident across different plant species; c) leaves would travel further in open forest rather than closed forest; and d) leaves would travel greater distances over steep than level ground.

MATERIALS AND METHODS

Field site

Field experiments were undertaken at Cumberland Creek, in the Central Highlands of Victoria, south-eastern Australia (145°52'40", 37°33'28"; Fig. 1). The site has been described in Steart et al. (2002, 2005). As shown in Fig. 1, two contrasting forest types are present at the site: a) cool temperate rainforest (CTRF); and b) wet sclerophyll forest (WSF). Cumberland Creek flows through a shallow (~5–6 m deep) valley through the middle of the site. Slopes along the creek vary from 10° to 60°. The site has a

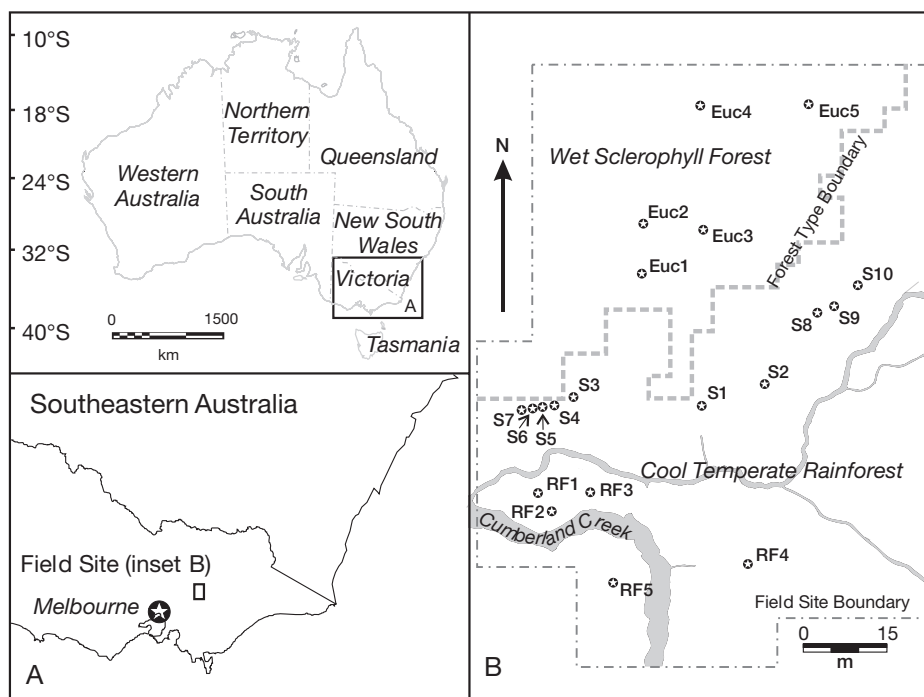


Fig. 1. Location of field site at Cumberland Creek in the Central Highlands of Victoria, south-eastern Australia. Fig. 1A shows the general location of the field site in southern Victoria; Fig. 1B shows a small-scale overview of the site, and shows the 20 locations where leaves were placed at the commencement of the experiment. These locations are cross-referenced to data in Table 3.

mean annual rainfall of ~1700 mm, and is subject to occasional winter snowfall.

Two tree species dominate the cool temperate rainforest: *Nothofagus cunninghamii* (Hook.) Oerst. and *Atherosperma moschatum* Labill. Some tall *Eucalyptus regnans* F.Muell. are scattered through the rainforest as emergent trees. In contrast, the wet sclerophyll forest surrounding the rainforest is dominated by *Eucalyptus regnans* with a subcanopy of *Acacia dealbata* Link. and *Acacia melanoxylon* R.Br. The shrub *Lomatia fraseri* R.Br. occurs occasionally across the site.

Leaf-transport protocols

Freshly abscised leaves from the five species of forest tree (Table 1) were collected in fibreglass-mesh nets suspended beneath the various species. After collection, 400 leaves from each species were air-dried (~50% relative humidity), weighed, then sprayed lightly with a bright pink fluorescent paint (White Knight Highlight Paint, Melbourne). Sprayed leaves were re-weighed to determine the

effect of colour-tagging on leaf density; the paint increased the density of the leaves by 10% to 55% (Table 1).

The field experiment commenced in January 1999. In total, 2000 color-tagged leaves were tracked over six months. Twenty sets of 100 leaves, each consisting of 20 color-tagged leaves from each of the five tree species, were prepared. Leaves from ten sets were placed in a small pile around stakes on level ground in the two contrasting forest types, five packs in the cool temperate rainforest and five in the wet sclerophyll forest. To maintain spatial independence, each leaf set was at least 5 m from its nearest neighbour. Leaves from five sets were placed on steep sections of the creek valley floor, and the remaining five were placed on medium-sloped sections of the creek valley. The gradients of the slopes were determined trigonometrically; steep slopes were classified as 45° to 50°, and medium slopes as 20° to 30°. The ground cover at the steep locations consisted of a dense and tangled mat of the ferns *Blechnum watsii* and *Polystichum proliferum*. Vegetation in three of the medium-slope sites consisted of dense *Blechnum watsii*, while two sites consisted of

Species	Density before painting (g m ⁻²)	Density after painting (g m ⁻²)	Change in leaf density (%)
<i>Acacia melanoxylon</i>	183	209	14
<i>Atherosperma moschatum</i>	94	147	56
<i>Eucalyptus regnans</i>	243	268	10
<i>Lomatia fraseri</i>	121	140	15
<i>Nothofagus cunninghamii</i>	101	151	46

Table 1. Effect on leaf density of colouring leaves with spray paint.

bare ground with no ground-level vegetative cover. Such areas were atypical along the valley sides, but allowed us to distinguish between the effects on leaf transport of slope and vegetation cover.

The distance each leaf had moved from its initial starting location at the marker stake was measured after six months. Areas up to 10 m away from the stake were thoroughly searched for painted leaves. When identifiable leaves were recovered, the distance travelled was measured from the stake to the leaf petiole. In those cases where the leaves had decomposed over the six-month observation period, the distance from the marker to the shell of paint (where clearly identifiable) was measured.

Statistical analysis

Data were transformed with a log_e transformation, then analysed with a 2-way Analysis of Variance. For the calculation of F ratios, the site factor was considered a random factor within each location category and the species factor was considered as fixed (Zar 1984). Multiple regression was used to determine the variables that most influenced differences in

transport among sites and species. The location variables tested were: a) forest type; b) density of the ground-level vegetation; c) flat versus steep slope; and d) medium versus flat and steep slope. The leaf variables tested were: a) leaf area; and b) average leaf weight (after painting). All statistical analyses were undertaken with Minitab 12 and the significant differences between the means determined with Tukey LSD post hoc tests.

RESULTS

Of the initial 400 leaves deployed for each species, the number of leaves recovered after six months varied from 314 for *Acacia melanoxylon* to 391 for *Lomatia fraseri* (Table 2). Of the leaves that were recovered, over 40 % stayed within 0.1 m of their original position at the marker stake and about 80 % remained within 0.2 m of their original position. The percentage of leaves that travelled less than 0.3 m over the six months ranged from 90 % (*Lomatia fraseri*) to 97 % (*Acacia melanoxylon*).

Table 3 shows the mean distance travelled by leaves of the five tree species at each of the 20 de-

Number of leaves recovered for each distance class	Distance class (cm)					
	0	0-9.9	10-19.9	20-29.9	30-39.9	> 40
<i>Acacia melanoxylon</i> (314)	38	127	100	40	5	4
<i>Atherosperma moschatum</i> (347)	31	129	113	51	11	12
<i>Eucalyptus regnans</i> (374)	34	121	131	52	20	11
<i>Lomatia fraseri</i> (391)	23	96	187	50	14	21
<i>Nothofagus cunninghamii</i> (337)	34	138	106	35	6	18

Table 2. Mean distances travelled by leaves as a function of tree species, pooled across all locations at the two forest types, shown for six different distance classes. Values in parentheses after species names refer to the number of leaves (of the original 400) recovered after six months.

Location	Forest Type	SC	VC	<i>Acacia melanoxylon</i>	<i>Atherosperma moschatum</i>	<i>Eucalyptus regnans</i>	<i>Lomatia fraseri</i>	<i>Nothofagus cunninghamii</i>
RF1	CTRF	F	B	0.06	0.09	0.13	0.11	0.09
RF2	CTRF	F	B	0.28	0.23	0.20	0.24	0.17
RF3	CTRF	F	B	0.07	0.11	0.12	0.09	0.11
RF4	CTRF	F	B	0.08	0.13	0.10	0.08	0.09
RF5	CTRF	F	B	0.26	0.21	0.37	0.46	0.43
Euc1	WSF	F	B	0.09	0.12	0.13	0.13	0.12
Euc2	WSF	F	B	0.09	0.07	0.09	0.13	0.04
Euc3	WSF	F	B	0.10	0.05	0.06	0.11	0.12
Euc4	WSF	F	B	0.18	0.20	0.40	0.27	0.17
Euc5	WSF	F	B	0.10	0.12	0.05	0.14	0.07
S1	CTRF	M	B	0.13	0.18	0.19	0.16	0.12
S2	CTRF	M	B	0.18	0.23	0.14	0.25	0.46
S8	CTRF	M	H	0.11	0.14	0.17	0.06	0.10
S9	CTRF	M	H	0.03	0.15	0.04	0.08	0.11
S10	CTRF	M	H	0.01	0.04	0.06	0.08	0.06
S3	CTRF	S	H	0.19	0.31	0.37	0.35	0.18
S4	CTRF	S	H	0.13	0.10	0.12	0.12	0.14
S5	CTRF	S	H	0.13	0.06	0.07	0.14	0.08
S6	CTRF	S	H	0.06	0.13	0.17	0.14	0.08
S7	CTRF	S	H	0.06	0.05	0.06	0.06	0.07

Table 3. Mean distances travelled by leaves as a function of tree species and deployment location at each of the two forest types. Abbreviations: CTRF = cool temperate rainforest; WSF = wet sclerophyll forest; RF = rainforest locations 1 to 5; Euc = wet sclerophyll forest locations 1 to 5; S = slope locations 1 to 10; SC = slope classification (F = flat, M = medium and S = steep); VC = Vegetation Coverage (B = bare ground and H = heavy ground cover). The positions of the 20 individual deployment locations used to quantify leaf transport are shown in Fig. 1C.

ployment locations at the field site; Fig. 2 shows the results of the 2-way ANOVA of these data. Analysed as a group, leaves of *Lomatia fraseri* at location RF5 and *Nothofagus cunninghamii* at location S2 in the cool temperate rainforest travelled the greatest distance (mean distances of 0.46 m). *Eucalyptus regnans* leaves in location S3, also in the cool temperate rainforest travelled the next greatest mean distance as a group, at 0.37 m. The greatest distance travelled by an individual leaf was 3.4 m; a single *Eucalyptus regnans* leaf from the wet sclerophyll rainforest at site Euc5. The ANOVA indicated that there was a significant difference ($P < 0.001$) in transport distances among sites (Fig. 2A). There was also a significant difference between tree species with respect to the dis-

tance travelled; *Lomatia fraseri* was significantly different from *Acacia melanoxylon*, but there were no significant differences in distance travelled among the other three species (Fig. 2B). This apparently contradictory result is probably a function of low statistical power of the post-hoc tests in comparison with ANOVA.

Eleven different regression models were tested, each including a different subset of variables (Table 4). The best fits ($r^2 = 0.226$ and $r^2_{adj} = 0.185$) were obtained with Model 9, which incorporated five of the six possible variables. (Leaf weight was not included in the regression equation because it was correlated with leaf area.) Only two of these five variables were significant: vegetation coverage ($t = 2.79$, $P = 0.006$), and b) medium versus flat/steep

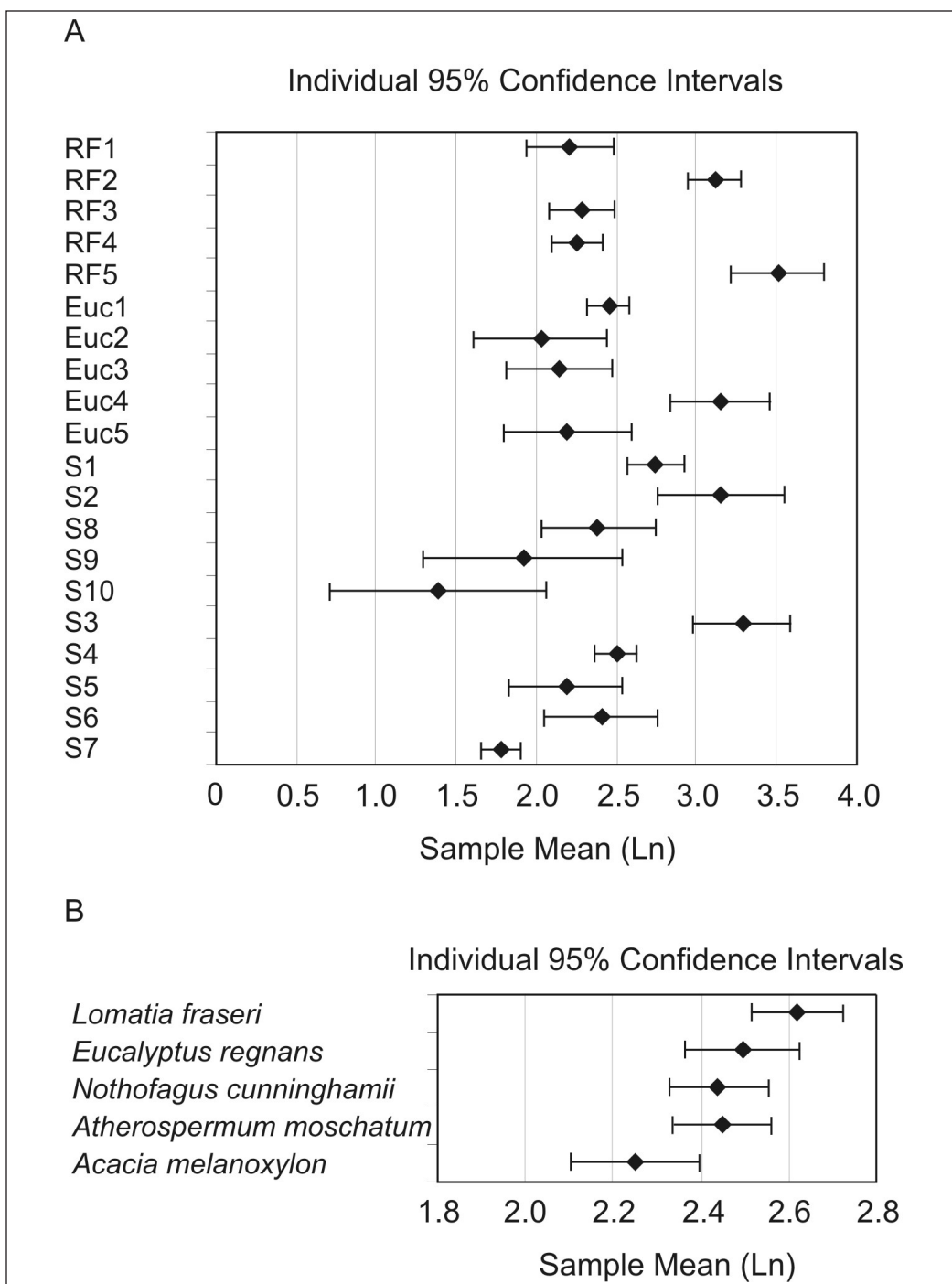


Fig. 2. Graphical representation of statistical analysis (2-way ANOVA) of the mean distances travelled by leaves as a function of tree species and location at each of the two forest types. Fig. 2A shows the analysis of mean distance travelled in terms of site comparisons; Fig. 2B shows the comparison across species. Distances were \log_e transformed prior to analysis. Error bars show the 95 % confidence limits.

Model	r^2	r^2_{adj}	Cp	SD	Variables included					
					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 4. Results for best-subset regressions for the mean transport data shown in Table 3. Abbreviations for statistical terms: 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 SD is the standard deviation. Abbreviations: LA = Leaf Area; LW = Leaf Weight; FT = Forest Type; VC = Vegetation Coverage; S1 = Flat versus Steep Slope; S2 = Medium versus Flat/Steep Slope. The X symbol in a cell indicates that the stated variable was included in the regression analysis.

slope ($t = -4.441$, $P < 0.001$). The best-fit regression equation (Model 9) was:

$$\begin{aligned} \text{Log (distance moved)} = & 2.92 + 0.00763 (\text{Leaf area}) \\ & - 0.2803 (\text{Forest type}) + \\ & 0.4033 (\text{Vegetation coverage}) - \\ & 0.0437 (\text{Flat versus steep slope}) - \\ & 1.0489 (\text{Medium versus flat/steep Slope}) \end{aligned}$$

We also tested the application of a full quadratic model to determine whether the addition of cross-product or squared terms would improve the regression model but it did not. 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; 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.

The regression analysis indicates that both the abundance of the ground vegetation and some aspects of slope (i.e. medium versus flat/steep slope only) were significant predictors of overland leaf transport. In other words, leaves of all tree species travelled greater distances on the medium-slope sites with no ground-level vegetation than they did on medium-slopes sites with abundant ground-level

vegetation. Conversely, the area of the leaves was not a significant factor, nor did forest type or flat versus steep slopes explain the extent of overland transport. It is possible that these results may be a function of the very small distances travelled in what is a rather closed environment with substantial hydrodynamic roughness and the consequent very low wind velocities.

DISCUSSION

We aimed to test four hypotheses in this field experiment: a) leaves would not travel substantial distances (>5 m) from where they were placed on the forest floor; b) this pattern would be evident across different plant species; c) leaves would travel further in open forest rather than closed forest; and d) leaves would travel greater distances over steep than level ground. In terms of the first prediction, we found that leaves of all species travelled little once they had fallen to the ground. The maximum distance travelled overland in six months by any leaf was 3.4 metres, and over 80 % of leaves moved less than 0.2 m. This finding, of negligible leaf transport, accords well with the reports of Spicer (1981), Ferguson (1985) and France (1995).

Our third hypothesis was that leaves would travel further in open forest rather than closed forest, related to likely differences in exposure and wind speed. In this case we found no statistically significant differences in mean transport distance between the two forest types, and conclude that the 'openness' of the wet sclerophyll forest in comparison with rainforest had little or no impact on the transport of leaves on the ground.

Our fourth hypothesis posited that leaves would travel greater distances over steep than level ground. There was increased leaf transport down the medium slopes in the cool temperate rainforest sites, but only where the slopes had no ground vegetation cover. The limited distances involved, however, indicate that the assertions made by Sedell et al. (1974) and Fisher and Likens (1973), of a strong positive relationship between slope and overland transport, must be questioned where leaves move over dense ground vegetation. The effect of slope on leaf transport distance was difficult to interpret and, in any case, quite small even if statistically significant (Table 3); here the maximum mean distances among sites are in the order of only tens of centimetres. The effect of the density of the ground vegetation was significant, with the ANOVA and the regression model both indicating a statistically significant effect. 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 could become captured. Seen overall, our results indicate that even for the steep sides in heavily vegetated valleys, overland transport is insignificant.

The small scale of movement in both the open vegetation of the wet sclerophyll forest and in the closed vegetation of the cool temperate rainforest suggests that the movement of leaves via wind-assisted lateral transfer is very low in these two forest types. It is probable that the high humidity and rainfall of both forest types played a role in this result; Spicer (1989) and Ferguson (1985) noted that moisture not only increased the weight per unit area of a leaf but causes leaf-to-leaf adherence, and the resultant leaf mass remains resistant to transport.

The ANOVA results indicate some differences in transport across species, and thus did not provide unequivocal support for our second hypothesis regarding among-species differences. There was a significant difference in mean transportation distances between *Lomatia fraseri* and *Acacia melanoxylon*, but not among the other species. This effect

raises the theoretical possibility of differential sorting between the various tree species, though the results of regression analysis suggest that this is not linked to leaf area. In practice, the effect in the forest systems examined would probably be very small, since once the leaves had fallen to the ground, no leaves travelled far enough for differential sorting to have a pronounced effect. The location in the forest most likely to present an opportunity for differential sorting is on the immediate banks of the stream. Here transport distances to an aquatic systems (and hence a potential site of deposition) are very short, and slight enrichment of one species over another are possible.

It is plausible that, in many forested streams, 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. Under these conditions any fossil deposits resulting from such communities would reflect the mesic riparian vegetation and not the surrounding sclerophyllous communities. This effect may partly explain the relative paucity of *Eucalyptus* and *Acacia* leaves in the Australian plant-fossil record. These taxa 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 these species grew mainly on ridges and areas not immediately adjacent to local watercourses, macrofossils would be rare since their leaves lack the ability to disperse over significant distances overland.

An additional outcome stemming from our observations is that the proportion of species with toothed leaf margins found in a fossil assemblage will reflect the leaf margin proportion of the riparian vegetation, and not that of the interior forest. The leaves of the forest interior are largely unable to be transported overland into the stream, thus explaining in part the discrepancy noted by Greenwood (2005) in the proportion of species with toothed leaf margins between samples collected from the streambed and those from the forest interior in Australian wet forests sites. This bias towards the riparian vegetation must be considered when reconstructing the species composition of the palaeovegetation or using the relative proportion of leaf margin type (or other

species attribute) to reconstruct climate, based on a fossil leaf assemblage.

ACKNOWLEDGEMENTS

We thank Dr Neil Diamond (formerly of the Department of Mathematics and Statistics, Victoria University) for statistical advice and Paul White, who helped with field work and associated tasks. David Steart was supported by a Victoria University post-graduate award. This research was partially supported by an ARC Discovery grant and a NSERC (Canada) Discovery Grant (311934-05), both awarded to David Greenwood.

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