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Interception and retention of macroscopic bryophyte fragments by branch substrates in a tropical cloud forest: an experimental and demographic approach

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Abstract Although the significance of canopy plant communities to ecosystem function is well documented, the process by which such communities become established in trees remains poorly known. Colonization of tree surfaces by canopy-dwelling plants often begins with the establishment of bryophytes, so the conditions that affect the dispersal of bryophytes in the forest canopy merit study. We assessed success rates of one mechanism of bryophyte propagation, the aerial dispersal of macroscopic fragments, using an experimental approach. We quantified interception and retention of marked fragments released from a 36 cm×36 cm grid 50 cm above branches of saplings and mature trees of the species *Ocotea tonduzii* in a montane cloud forest in Costa Rica. Only 1% of bryophyte fragments dropped over sapling crowns in this manner were retained for the 6-month duration of the study, while branches in the forest canopy with intact epiphyte loads and branches that had been stripped of their epiphytes retained 24% and 5%, respectively. Our results suggest that larger-diameter branches and the presence of other epiphytes can both improve the retention of bryophyte fragments on canopy branches. Further work will be needed to address the relative roles of other dispersal mechanisms (spores, gemmae, microscopic bryophyte fragments) and the dynamics of growth and establishment of macroscopic bryophyte fragments following their interception.

Key words Bryophytes · Canopy studies · Monteverde · Plant demography · Succession

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Introduction

Neotropical montane cloud forests support higher diversity, structural complexity, and biomass of epiphytes than any other forest type (Madison 1977; Gentry and Dodson 1987; Ingram and Nadkarni 1993; Benzing 1995). Mature trees in mid-montane forests can support up to 44 kg ha⁻¹ of suspended organic matter (Hofstede et al. 1993), which consists of vascular and non-vascular epiphytes, lianas, mistletoes, hemi-epiphytes, and arboreal vertebrates and invertebrates (Nadkarni 1994), as well as arboreal soil from their decomposition in situ. This dead organic matter can reach a thickness of 30 cm on the upper sides of canopy branches (Nadkarni and Matelson 1991). Tropical cloud-forest canopy communities contribute to community- and ecosystem-level processes, including atmospheric water and nutrient interception and retention (Pócs 1980; Nadkarni 1981; Clark et al. 1998b), maintenance of biodiversity (Ingram and Nadkarni 1993), and provision of food and nesting resources for birds and arboreal mammals (Nadkarni and Matelson 1988).

Although some of the characteristics and potential functional roles of these cloud-forest canopy communities have been described (e.g., Vance and Nadkarni 1992; Matelson et al. 1993; Bohlman et al. 1995), very little is known about their founding and development. Colonization by non-vascular plants generally precedes the establishment of vascular epiphytes and the accumulation of crown humus (*sensu* Jenik 1973), in which most epiphytes and hemi-epiphytes become rooted (Dudgeon 1923; Van Oye 1924; Hosokawa et al. 1964; Nadkarni, *in press*). The focus of the present study is, therefore, on the dynamics of bryophyte colonization of tree surfaces.

Though the productivity of certain epiphytic bryophytes can be very high (up to 30–49% per year by dry mass; Clark et al. 1998a), rates of recolonization by epiphytic bryophytes (and other epiphytes) in mature canopy trees following disturbance can be extremely slow, and in the order of a decade or more (Nadkarni, *in press*). The constraints upon recolonization are not

known, but could be related to the failure of propagules to arrive at the sites of disturbance, low rates of retention of propagules at such sites, or physicochemical conditions that prevent plants' establishment and growth there. The relative importance of these three types of constraints – arrival, retention, and establishment – are unknown, but studies of both epiphytes and many terrestrial bryophyte systems have stressed the potential that limitation in dispersal can have for increasing randomness and co-existence of ecologically similar species (Düring and van Tooren 1986; Slack 1990; Kimmerer 1991; Wolf 1994; Benzing 1995).

Bryophytes employ a variety of dispersal mechanisms, including growth along the two-dimensional branch surfaces from existing plants at the edge of an epiphyte gap (herein, "encroachment"), and colonization by several types of aerial dispersal (propagation via gemmae or spores, dispersal of microscopic vegetative fragments, and macroscopic bryophyte fragments that fall through the canopy). A growing literature discusses the capabilities of bryophytes for aerial dispersal (reviewed in Düring and van Tooren 1986; also Slack 1990; Miles and Longton 1990; Longton 1994), but no experimental studies of bryophyte dispersal in forest canopies exist to date, and important differences may exist in the potential of dispersal strategies. Dispersal in the canopy implies both the arrival of propagules at the substrate and their persistence here long enough to allow establishment. Grime et al. (1990) suggested that epiphytic bryophytes might rely heavily on spore production for colony formation due to spores' mobility, but asexual diaspores may provide much greater effective dispersal distances in canopies because a short horizontal displacement off a branch may carry a gemma or fragment much further if it is taken by the wind. We begin our approach to the question of dispersal of bryophyte propagules in the forest canopy with a quantitative investigation of the dynamics of macroscopic vegetative fragments.

In this study, we quantified the rates of interception and retention of marked macroscopic bryophyte fragments on *Ocotea tonduzii* (Lauraceae) branches in a lower montane cloud forest in the Monteverde Cloud Forest Reserve (MCFR), Costa Rica. We compared two substrate types, branches of mature trees and of understory saplings, under two treatments, complete removal of epiphytes and a control where epiphytes in areas under study were left undisturbed. The two treatments were designed to address the possibility that pre-existing communities might affect subsequent colonization and succession rates (Kimmerer and Allen 1982; Frego 1996).

To analyze and interpret the data, we treated our results as would a plant demographer, and generated "cohort" or dynamic life-tables for each substrate type. We considered the "population" of bryophyte fragments from each release of fragments as a single cohort of individuals (i. e., a group of individuals "born" within the same short interval of time), and followed this cohort from birth to the "death" (i. e., disappearance from the sample area) of

the last survivor. This approach allowed us to estimate the natural interception and retention of one type of regenerative output of the bryophyte community (macroscopic vegetative fragments) and make estimates of the frequency of colonization events by this type of dispersal on branches of different diameters and epiphyte loads.

Materials and methods

Site description

Fieldwork was conducted from 12 June 1997 to 1 March 1998 in the MCFR, a lower montane moist forest in Costa Rica (10°18'N, 84°48'W). The 4-ha study area (1480 m elevation) is located in Leeward Cloud Forest (annual gross precipitation 2000–2500 mm) and encompasses a variety of slopes and areas of closed canopy and gaps. Mean diameter at breast height (dbh) for trees >10 cm dbh is 65.5 cm; mean tree density is 154 individuals ha⁻¹. Mean sapling density (trees <1–2 m in height) is 1510 stems ha⁻¹. The tree species studied, *O. tonduzii* (Lauraceae), is one of the most common under- and overstory trees in the study area (30% of the total basal area of trees >10 cm dbh, Nadkarni et al. 1995).

The epiphyte flora in the MCFR is extremely diverse and abundant (Nadkarni 1984; Ingram and Nadkarni 1993). Branch surfaces in the crown interior of nearly all of the mature trees support epiphytes (bryophytes, herbs, woody shrubs, and hemi-epiphytes) in interwoven root-humus mats up to 30 cm thick. Epiphytes fall from the canopy throughout the year at a mean rate of 50 g dry weight m⁻² year⁻¹ (Nadkarni and Matelson 1992a), exposing trunk and branch surfaces and creating epiphyte "gaps" on trees. Epiphytes fall in a variety of forms, including micro- and macroscopic fragments of bryophytes, individual plants and plant parts, and large mats that cover whole branches. The mean standing crop of fallen epiphytic material on the ground is 35 g m⁻² (Nadkarni and Matelson 1992a). The mean annual input of total terrestrial litterfall is 7 t ha⁻¹, of which 2% is macroscopic bryophyte fragments (Nadkarni and Matelson 1992b). Litterfall collected within the canopy (in arboreal litter collection traps) is nearly equivalent in biomass to litterfall collected on the forest floor and contains the same proportion of macroscopic bryophyte fragments (Nadkarni and Matelson 1991).

Sample trees

Eighteen randomly selected *O. tonduzii* saplings between 1 and 2 m in height were used for our understory substrate sample. We measured the height, diameter at 10 cm above ground, and stem (branch and trunk) length (Table 1). Experimental branches in saplings and adults were nearly horizontal, so branch angle was not measured. For 9 of the 18 sample saplings, all epiphytes (not including epiphylls on sapling leaves) were stripped from the entire sapling. All epiphytic bryophytes were oven-dried at 105°C for 24 h and weighed. The other nine trees served as controls, and their epiphytes were left undisturbed.

Eighteen canopy branches were chosen from a random subset of nine climbable mature *O. tonduzii* trees (>60 cm dbh) in the study area. Trees were rigged with climbing ropes following Perry (1978). Branches at least 20 m above the ground and strong enough to support the weight of researchers were chosen for sampling. For half of the selected branches, we removed all live epiphytes and crown humus from 33-cm sections (termed "cylindrats" because of their shape) of each branch, a disturbance that mimics natural mat-sloughing events on mature branches. Dry mass of the removed organic matter from the experimentally cleared cylindrats was determined after 5–7 days of oven-drying at 105°C. Equal-sized cylindrats on the other branches were demarcated with flagging tape and their epiphytes left undisturbed as controls. Diameters of all cylindrats were recorded (Table 1).

Table 1 Substrate dimensions (diameter and length in centimeters; standard deviation in *parentheses*) of canopy and understory branch substrates. Diameters of stripped canopy branches are without epiphytes

Canopy branches	Diameter
Stripped	24.4 (5.7)
Control	29.3 (18.6)
Overall	26.9 (13.6)
Understory sapling branches	Length
Stripped	82.3 (47.8)
Control	71.2 (38.7)
Overall	77.0 (43.6)

Data collection

We collected a wide variety of epiphytic bryophyte species that are representative of the forest canopy from the study area (including pendant-, fan-, mat-, weft-, and turf-forming, *sensu* Magdefrau 1982). These were air-dried and sprayed lightly with fluorescent paint so that we could monitor their presence over the study period. We separated them into uniform-sized bryophyte "fragments" which appeared similar in size to naturally occurring fragments that we found in litterfall traps in previous studies (Nadkarni and Matelson 1992a). We observed growth of our painted fragments after retention on branches in a few cases; the paint may have inhibited rhizoid growth in other cases, which would decrease retention (D. Norris, personal communication).

We constructed a device (the "Moss-tosser") to drop fragments uniformly over each sample area. This was modified from a small hanging clothes-drying apparatus to which we attached a rigid wire frame (6×6 mesh spaced 1 cm apart, 36 cm²), suspended horizontally by a hook above the branch substrates (Fig. 1). At each intersection of the grid, a clothes-pin was attached, holding a marked bryophyte fragment, selected for similar dry weights (mean dry weight=0.23 g; SD=0.03 g, ascertained using ten sets of unpainted fragments of the same size), but at random with respect to morphology, *i.e.*, fragments of all shapes were represented. Painted fragments weighed slightly more but appeared to perform similarly with respect to interception when dropped from the Moss-tosser. The frame was held from a uniform height (ca. 50 cm) over the branch substrates while the "loaded" clothes-pins were released individually. Bare substrates were always dry upon delivery, though mist and light rain occurred sporadically through the study period.

The number of fragments intercepted within each sample area was recorded immediately after the initial delivery. The marked bryophyte fragments were rechecked weekly for 25 and 22 weeks (saplings and canopy branches, respectively). The marking color remained visible for the length of the study. We carried out a new drop whenever all intercepted fragments at a particular sampling area were gone within the 6-month duration of the study. The experiment was repeated 38 times for saplings and 20 times for canopy branches.

Data analysis

We followed standard plant and animal demography methods to construct life-tables and survivorship curves to examine bryophyte fragment retention (*e.g.*, Leverich and Levin 1979). We constructed life-tables of the cohorts of dropped fragments following Begon *et al.* (1996). Based on our field observations and previous measurements of bryophyte production at the study site (Clark *et al.* 1998a), we partitioned the life-tables into four life-stages: (1) deposition (delivery of fragments by the Moss-tosser); (2) short-term interception (catching of fragments 0–7 days following deposition); (3) long-term retention (persistence of fragments on the sample area for 1 week to 6 months following deposition); and

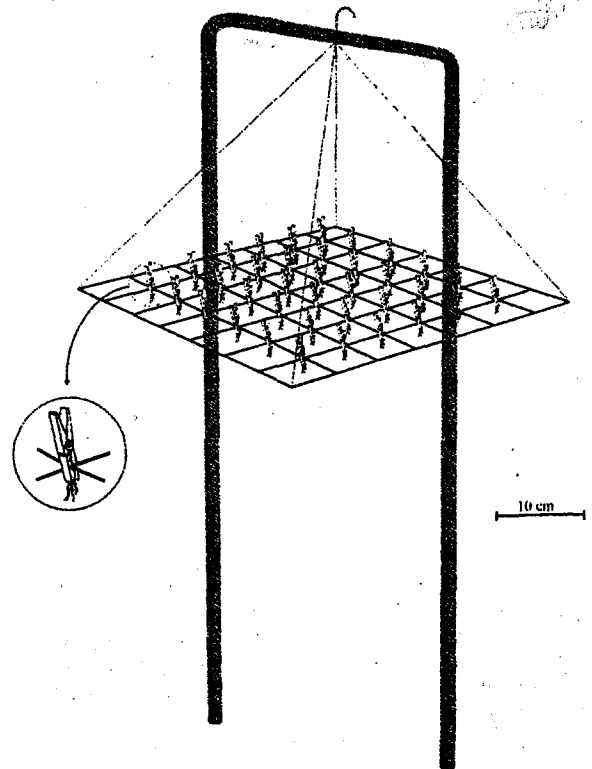


Fig. 1 Schematic of the "Moss-tosser", which was used to deliver experimental macroscopic bryophyte fragments from a uniform height to branch substrates in the field study

(4) "permanent" retention (persistence of fragments on the sample area for more than 6 months), which we considered long enough for bryophytes to establish themselves at the site. The amounts of interception in stripped and control branches and in saplings were compared with two-tailed *t*-tests and analysis of variance (ANOVA). Statistical analysis was done using Microsoft Excel.

Results

For saplings, there was no significant difference in the mean number of fragments intercepted per drop between the experimentally stripped saplings ($\bar{x}=10.7$, $SD=4.8$) and the control saplings ($\bar{x}=8.7$, $SD=7.5$) ($P>0.05$). Therefore, we combined the results of both treatments to generate life-tables and survivorship curves. In contrast, significantly more fragments were intercepted by the control branches (mean intercepted fragments per drop=24.4, $SD=3.0$) than by the experimentally stripped branches ($\bar{x}=14.9$, $SD=6.0$) ($P<0.001$), though mean branch diameter did not differ significantly between stripped and control branches (Table 1). We therefore carried out life-table and survivorship analysis on the control and experimentally stripped branches separately.

The proportion of fragments initially intercepted relative to the total number of fragments delivered to the sample areas varied significantly by substrate. The largest proportions were intercepted by intact canopy branches (70%), followed by stripped canopy branches

Table 2 Life-table of bryophyte fragments that were experimentally delivered and retained on sapling and control and stripped mature tree branch surfaces. Number of fragments and calculated proportions of fragments: A deposited by the Moss-tosser; B initially intercepted and retained in the short term (0–7 days) by the substrate; C retained in the long term (1 week to 6 months); and D retained “permanently” (>6 months). Terminology follows standard life-table definitions: a_x number of fragments observed at be-

ginning of stage; l_x proportion of cohort surviving to start of stage; d_x proportion of cohort dying during stage; q_x within-stage mortality rate, or intensity; k_x killing power of stage ($\log_{10} a_x - \log_{10} [a_{x+1}]$). Estimated annual retention on a horizontal meter-long section of branch was calculated using the estimated annual input rate of 0.22 fragments of the considered mass (0.23 g), based on a reported biomass input of 140 kg ha⁻¹ year⁻¹ (Nadkarni and Matelson 1992b)

Stage (x)	A	B	C	D	
	Deposition	Short-term interception and retention	Long-term retention	Permanent retention	Estimated permanent retention per meter branch per year
Understory sapling branches					
a_x	1330	403	58	18	
l_x	1.00	0.30*	0.04*	0.01*	0.007
d_x	0.70	0.26	0.03	0	
q_x	0.70	0.86	0.69	0	
k_x	0.52	0.84	0.51	0	
Stripped canopy branches					
a_x	385	164	40	18	
l_x	1.00	0.43*	0.10*	0.05*	0.033
d_x	0.57	0.32	0.06	0	
q_x	0.57	0.76	0.55	0	
k_x	0.37	0.61	0.35	0	
Control canopy branches					
a_x	315	220	95	76	
l_x	1.00	0.70*	0.30*	0.24*	0.159
d_x	0.30	0.40	0.06	0	
q_x	0.30	0.57	0.20	0	
k_x	0.16	0.36	0.10	0	

*Significantly different at the 0.001 level using ANOVA

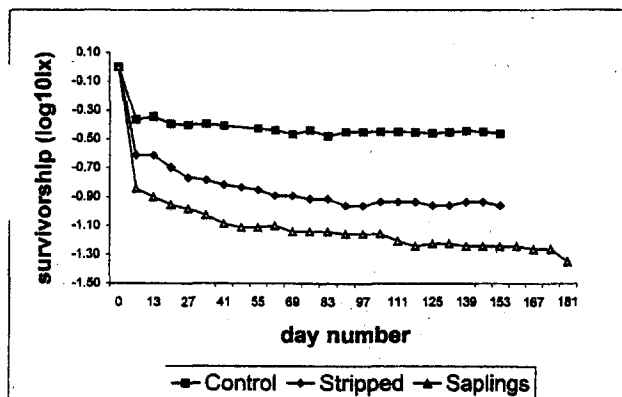


Fig. 2 Survivorship curves of experimental macroscopic bryophyte fragments on the three branch substrate types in our study of bryophyte establishment on *Ocotea tonduzii* trees. The control and stripped treatments are for large branches of mature canopy trees; the sapling treatment is for understory trees of the same species

(43%), and saplings (30%) ($P < 0.001$). The same sequence held for short-term retention (30%, 10%, and 4%, respectively), and long-term retention (24%, 5%, and 1%, respectively) (Table 2).

The survivorship curves for each of the substrate types (sapling, control branches, stripped branches) re-

flected a similar life-history pattern: high loss of fragments in the very early stages, with lower attrition during the later stages (Fig. 2). All three substrate types exhibit the “Type III” survivorship curve (Deevey 1947), which is typical for organisms that put forth many young, suffer a high early attrition rate, but survive for a long time if they survive past a certain point (i.e., probable longevity increases with age). The slopes of the lines at different life-stages were not significantly different, indicating that once a bryophyte fragment is intercepted, it will be retained in the same proportions, regardless of substrate type.

Discussion

We found no published data with which to directly compare our results, for no study of bryophyte reproductive ecology has considered retention of propagules of any kind in forest canopies. Total litterfall in the study site is ca. 7.0 t ha⁻¹ (Nadkarni and Matelson 1992b). Based on the composition of materials collected in litter traps, bryophyte fragments under natural conditions constitute 2.0% of that total (Nadkarni and Matelson 1992a), equivalent to an input of ca. 0.05 g over an area the size of the Moss-tosser in a single year. Such a calculation allows us to put our measured rates of retention into per-

spective. If we assume that natural macroscopic bryophyte litterfall is composed of fragments of the same average size we delivered, we can estimate that the probability of such a fragment falling on an area the size of the Moss-tosser in a year would be about 20%. Consequently, assuming a linear increase in retention with branch length, and knowing that each sample area consisted of a 33-cm-long section of branch, we can estimate annual probabilities of fragment retention per meter branch length of the three experimental groups: about 0.7% for a sapling branch, 3.3% for a canopy branch with no epiphytes, and 16% for a canopy branch with epiphytes (Table 2). The factors affecting these rates merit further study; fragment size and morphology might modify retention, while surface wetness might be especially significant for smaller fragments due to surface tension.

These small estimated probabilities suggest that successful colonization events by macroscopic bryophyte fragments are rare; there must be little dispersal of individuals or rearrangement of their biomass in canopy space by this method. How retention rates of spores, gemmae, and microscopic fragments compare with those of macropropagules in the forest canopy remains to be seen, and must be considered in conjunction with differences in establishment rates once a propagule is retained. Even a small number of colonization events could quickly generate the large observed biomass (ca. 120 kg ha⁻¹ on understory saplings and 3235 kg ha⁻¹ on mature trees; Nadkarni et al., in press) due to the very high productivity of bryophytes at this site (30–50% per year by biomass; Rieley et al. 1979; Bowden 1991; Clark et al. 1998a). In contrast to the large number of distinct, small colonies of twig epiphytes in the outer crown, bryophyte colonies in the inner crown tend to be largely contiguous, obscuring the minimum number of colonization events.

The presence of epiphytes clearly improved rates of retention of macropropagules; retention on undisturbed canopy branches was over twice that of their disturbed counterparts. This suggests that as a tree grows and its epiphyte load increases, its retention of epiphyte fragments also increases. Macroscopic fragment dispersal may consequently be an increasingly significant contributor of biomass and local diversity as epiphytic communities mature and develop. Just as the allocation of reproductive effort can change with age or population density in bryophyte communities (Düring 1979; Kimmerer 1991), success rates of reproductive efforts might also change. Mature plants might inhibit establishment of spores or gemmae (Mishler and Newton 1988), while improving rates of retention – and possibly of establishment and growth – of larger fragments (Økland and Økland 1996).

The dramatically lower rate of both initial interception and permanent retention on stripped branches suggests that much time may be necessary for colonization of exposed branches following natural and human-induced disturbances (e.g., moss or orchid harvesting for the horticultural industry, recreational tree-climbing,

canopy researcher activities) relative to the rapid growth of canopy communities once they are established. This corroborates results from long-term recolonization of experimentally stripped branches in the same study site (Nadkarni, in press); over a decade was needed before colonization by bryophytes occurred. The early colonizers grow up from the underside (ventral surface) of the branch, indicating that bryophyte fragment deposition is not important in the earliest stages of succession.

The dynamics of epiphyte community formation and maintenance are significant to our understanding of forest ecology in a variety of systems. Colonization by aerially delivered vegetative fragments appears to happen fairly rarely for saplings and stripped branches, but because of the high productivity of these bryophytes, may be important in maintaining the growth of epiphytes on mature and undisturbed canopy branches at the present site. A more complete understanding of epiphyte colonization and succession will require the exploration of the roles played by gemmae, spores, and microscopic bryophyte fragments in this forest type, as well as an examination of the effects of fragment size and morphology.

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