Species Interactions and Substrate Specificity among Log-Inhabiting Bryophyte Species

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SPECIES INTERACTIONS AND SUBSTRATE SPECIFICITY AMONG LOG-INHABITING BRYOPHYTE SPECIES[1]

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Abstract. Fallen logs in temperate deciduous forests are a transient substrate on which a dozen or more bryophyte species can co-occur. This study aimed to assess whether establishment capabilities and species interactions determine the habitat specificity of these species. I performed a modified Dewit replacement series experiment on three moss species (*Anomodon rostratus*, typical on bark of hardwood logs; *Leucobryum albidum*, characteristic of *Pinus* logs; and *Platygyrium repens*, a generalist species) in order to evaluate their competitive interactions. The species were grown from leaf fragments sown on four substrates: *Pinus* bark and wood, and *Quercus* bark and wood. Substrate had a significant effect on establishment for all three species. However, only on *Pinus* bark was the frequency dependent on the species sown. Randomization test analogs of analysis of variance indicated that the biomass of *Anomodon* and *Platygyrium* grown in monoculture differed significantly across substrates, while that of *Leucobryum* did not. There was considerable variability in performance within bryophyte species and there was no evidence for significant interactions between pairs of species.

Key words: Anomodon; *bryophytes; competition; establishment;* Leucobryum; *logs; moss;* Pinus; Platygyrium; Quercus; *randomization tests; replacement series analysis.*

INTRODUCTION

Although it is widely believed that competition occurs in nearly all plant communities, the role of competition in determining species composition continues to be debated (Pianka 1981, Connell 1983, Schoener 1983, Diamond and Case 1986, Walter 1988, Begon et al. 1990, Goldberg and Barton 1992, Bengtsson et al. 1994). If community structure is strongly determined by species interactions, existing species distributions should be predictable from the study of these interactions. However, if other factors, such as disturbance or short duration of the habitat (White 1979, Watson 1980*b*, Slack 1982, 1990) act to decrease the impact of species interactions, the outcome of such studies will not sufficiently explain present species distributions (Connell 1975, Pickett 1980). In this paper I will use the word "competition" in the sense of Harper (1977), that is, a negative impact of one plant upon another. "Interaction" will be used in a broader sense to include both positive and negative influences.

The amount and intensity of competition among bryophytes is generally assumed to be low (Smith 1982, Schuster 1984, Schofield 1985, During and van Tooren 1987, 1990). This assumption stems from two sources: (1) a number of life history strategy theories predict a low importance of competitive interactions in disturbed habitats—mosses often grow in such places (Gadgil and Solbrig 1972, Grime 1974, During 1979); and (2) studies of microhabitat occupation indicate that niche breadths tend to be broad and overlapping (Slack 1977, Watson 1980*a*, 1981*a*, Vitt and Slack 1984, Rydin 1986, 1987, Glime and Vitt 1987).

Studies of the effect of differing environmental conditions on species interactions among bryophytes have shown that the outcome, either positive or negative, can be influenced by water table depth (Hayward and Clymo, 1983, Rydin 1986, 1993), moisture conditions (Li et al. 1992), water chemistry and successional status (Kooijman and Kanne 1993), nitrogen deposition levels (Twenhöven 1992), and irradiance levels (Hayward and Clymo 1983). In a design similar to that used in this study, Scandrett and Gimingham (1989) studied growth in relation to species interactions among three bryophyte species found in *Calluna* heathlands. Using replacement-series methodology, they found that performance of certain species was inhibited when grown in mixture; the results were significantly affected by light and moisture treatments and the identity of the second species. Several authors (e.g., Söderström 1987, Slack 1982, 1990) propose that because of the temporary nature of decomposing logs, competition plays little role in structuring bryophyte communities on logs. The role of interactions among bryophyte species in determining habitat specificity on temporary substrates such as fallen logs has yet to be assessed.

The establishment phase is a crucial step in determining the species composition of a site, both for vascular plants (Harper 1977) and for bryophytes (Rydin 1986, Li and Vitt 1994). Schuster (1957) stated that establishment of hepatics on fallen logs was governed primarily by stochastic factors and that this led to the observed variability in species composition. Establish-

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ment of bryophytes on logs is also limited by the dispersal capabilities of these organisms, particularly in fragmented forests with few fallen logs, or with logs in only a few stages of decay (Söderström 1987, 1988*b*, Andersson and Hytteborn 1991).

My experiment addresses four main questions: (1) Is there an effect of substrate on species establishment and performance? (2) Do these effects depend on the species? (3) Do the species interact? (4) Are the results consistent with field observations?

MATERIALS AND METHODS

Study system

Cryptogam species composition on decaying logs in the Duke Forest (North Carolina, USA; 36° N, 79° W) appears to be strongly related to the species of the log and to the presence or absence of bark (S. McAlister, *in press*). The greatest differences in composition are observed among communities on hardwood bark, decorticated hardwood logs, and pine wood and bark. These patterns are similar to those found by Nakamura (1987), Söderström (1988*a*), Harmon (1989), and Andersson and Hytteborn (1991), and also to patterns on live trees in the Duke Forest (Palmer 1986) and in other areas in eastern North America. In an experiment examining the establishment of mosses and liverworts on wood substrates in the forest, establishment rates from leaf fragments were very low, but differed among the bryophyte species and the substrate type (S. McAlister, *unpublished manuscript*). The present study was conducted in a greenhouse because of these low establishment rates. While greenhouse conditions do not exactly reproduce the forest environment, such experiments can help elucidate the factors that influence a species' performance.

Experimental species

I used three species for this experiment: *Anomodon rostratus* (Hedw.) Schimp., *Leucobryum albidum* (Brid.) Lindb., and *Platygyrium repens* (Brid.) BSG. *A. rostratus* occurs on bark at tree bases, on boulders, and on soil banks (Crum and Anderson 1981), but among logs it occurs almost exclusively on bark of newly fallen hardwood logs (S. McAlister, *in press*). In the Duke Forest, *L. albidum* is most frequent on pine logs (S. McAlister, *in press*), particularly pine bark; it is one of the few moss species that grows on pine bark (Crum and Anderson 1981, Palmer 1986). *P. repens* is typical of "logs, stumps and the trunks or bases of trees" (Crum and Anderson 1981). I found it on logs of many types, but it was most abundant on decorticated hardwood logs. *Anomodon* and *Platygyrium* are pleurocarpous species; they produce sporophytes laterally, and the plants are prostrate and branch freely. *Leucobryum* is an acrocarp; sporophytes terminate the apical growth, and the plants grow upright in clumps and are sparsely branched (Crum and Anderson 1981).

Experimental procedures

In order to obtain substrates for this experiment, I collected wood and bark from logs in Durham Divisions 60 and 75 of the Duke Forest, Durham County, North Carolina, during late October and early November 1988. The logs were subjectively chosen to have as consistent a stage of decay and surface texture as possible, as these are two of the most important determinants of species composition (Söderström 1988*a*). Exterior portions of the logs were cut into 6 × 6 × 1 cm blocks. The blocks were steam-sterilized after all visible plant pieces were removed.

Sporophyte-free clumps of mosses were collected in the same localities as the substrates. The clumps were carefully sorted (while viewing under a dissecting microscope) into pure collections of the three species. The plants were then blended for ≈3 min in a Waring blender (methods similar to Bayfield 1976, Shaw 1986, Mishler and Newton 1988). I weighed the appropriate amounts of the resulting fragments to the nearest milligram. Fragments of each species in the mixtures were weighed separately and then combined.

The three species, *Anomodon rostratus* (A), *Leucobryum albidum* (L) and *Platygyrium repens* (P) were sown on four substrates: *Pinus* bark (PB), *Pinus* wood (PW), *Quercus* bark (QB), and *Quercus* wood (QW). Each of the species was planted at two monoculture densities: 25 mg/25 cm^2 and 50 mg/25 cm^2, and three two-species combinations were sown at component densities of 25 mg/25 cm^2 each. Although the initial planting quantity was measured in grams, I use the term "density" to be consistent with the replacement-series literature. There were five replicates of each treatment, except for the high-density monocultures that had 10 replicates. The experiment was a completely randomized design.

I sowed the experiment on 21 November 1988. The mosses were evenly sprinkled onto the central 5 × 5 cm area on each of the moistened substrate blocks. These blocks were placed onto ≈5 cm of fine vermiculite in 7-cm (3-inch) pots so that the top of each block was ≈1 cm below the level of the pot rim. The 252 pots were randomly arranged in seven flats (the seventh had a number of "filler" pots with only vermiculite).

The flats were covered with one layer of shade cloth (suspended ≈3 cm above the substrate blocks) so that irradiance more closely approximated that on the forest floor. Photosynthetically active radiation (PAR) (measured under the shade cloth using a LI-COR PAR sensor) varied from 100–550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on a sunny day in November, to 30–60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on a cloudy day in February, to 300–900 $\mu mol \cdot m^{2} \cdot s^{-1}$ on a sunny day in May just before the harvest.

The pots were watered by filling the flats to about 1 cm below the level of the substrate blocks because in a pilot experiment misting from above washed the fragments off the substrate blocks. This approximate level was maintained consistently through the winter and early spring; thereafter the flats were allowed to dry out between waterings in order to control the growth of contaminating blue-green algae, predominantly *Nostoc*.

I harvested this experiment from 25 through 27 May 1989. I estimated the cover of each species by viewing the blocks through a transparent grid of squares with the aid of a magnifying lens illuminated with a fluorescent ring. The cover of each species was estimated with the aid of the grid. I then allowed the mosses to air-dry completely, pulled off all the live biomass of each species from each block, and determined the air-dried biomass of each species to the nearest 0.1 mg.

I thus obtained three different measures of species performance: frequency, or the number of blocks on which a species grew, cover estimates, and biomass measurements. The differences in results between analyses of presence/absence and quantitative data are often quite informative (Palmer 1990). For example, results may show that plants are able to establish frequently, but have poor growth, or that they establish infrequently, but grow well. Patterns of abundance may obscure relationships of environmental factors to species presence or absence, and differences in growth form among the species under consideration could differentially affect estimates of species abundance.

Data analyses

I analyzed data from the mixtures twice in order to determine the effects of one species on another (associate effects): once with species "A" as the "target" species, comparing its performance in monoculture with that in mixture with the "associate" species "B", and once with B as target and A as associate.

I used *G* tests for independence of frequency (with Williams' correction) to test hypotheses concerning differences in frequencies. *G* tests are appropriate when the variable under consideration is a function solely of the experimental treatments and is not constrained by one or the other of the two factors whose influence is being investigated, i.e., the marginal totals are not fixed (Sokal and Rohlf 1981).

To test for associate effects within substrates, I compared the frequency of each species when grown in monoculture with that when grown in each of the two mixtures for each of the four substrates (twelve 2 × 2 frequency tables for each species). *G* tests were also used to determine if the frequency of each of the three species in both the monoculture densities was independent of substrate (two 2 × 4 frequency tables for each species). I also compared the frequency of the three species grown in the high-density monocultures on each of the four substrates (four 1 × 3 tables).

Replacement-series methods (de Wit 1960) and randomization-test analogues of analysis of variance (Edgington 1987) were used to determine whether species interactions occurred.

Replacement-series diagrams are used to show two species' performance as a function of their proportion in mixture (e.g., Fig. 1). Analysis of such data can be complex, and numerous ratios and indices of one sort or another have been proposed to concisely present the relationship of species' competitive abilities (de Wit 1960, de Wit and van den Bergh 1965, McGilchrist and Trenbath 1971, Wiley and Rao 1980). I have chosen to use the relative yield total (RYT), which is straightforward and robust (Connolly 1986). This index is designed to answer the question "does the mixture yield any more or less than predicted from monocultures at the same [total] density?" (Aarssen 1985) and is a measure of niche overlap (Harper 1977, Aarssen 1985, Taylor and Aarssen 1990). It is calculated by summing the ratio of the yield of species A in mixture at component density *N*/2 to its monoculture yield at density *N*, with the analogous ratio for species B (Harper 1977). This assumes that, if there is no interference between plants, the yield of each species is proportional to its density (de Wit 1960, de Wit and van den Bergh 1965, Joliffe et al. 1984, Firbank and Watkinson 1985:504). However, in bryophytes the effects of increases in density are not as clearcut as in vascular plants. Bates (1988) found that increasing total density may result in better growth of the individual shoots, possibly due to decreases in water loss (During and van Tooren 1990, Økland 1994) in the more compact clumps.

Statistical analysis of RYT and replacement-series diagrams are complex and ambiguous at best. A more powerful comparison can be used to test whether competition did occur in the two-species mixtures: comparing the yield of a species in mixture with its yield in monoculture when the sowing density of the monoculture is equal to the component densities of the mixtures.

The classical choice with a factorial design such as this (two treatments—monoculture and mixture, and four substrates—PB,PW,QB,QW) is an analysis of variance (ANOVA). However, the data I collected violated several assumptions underlying parametric tests

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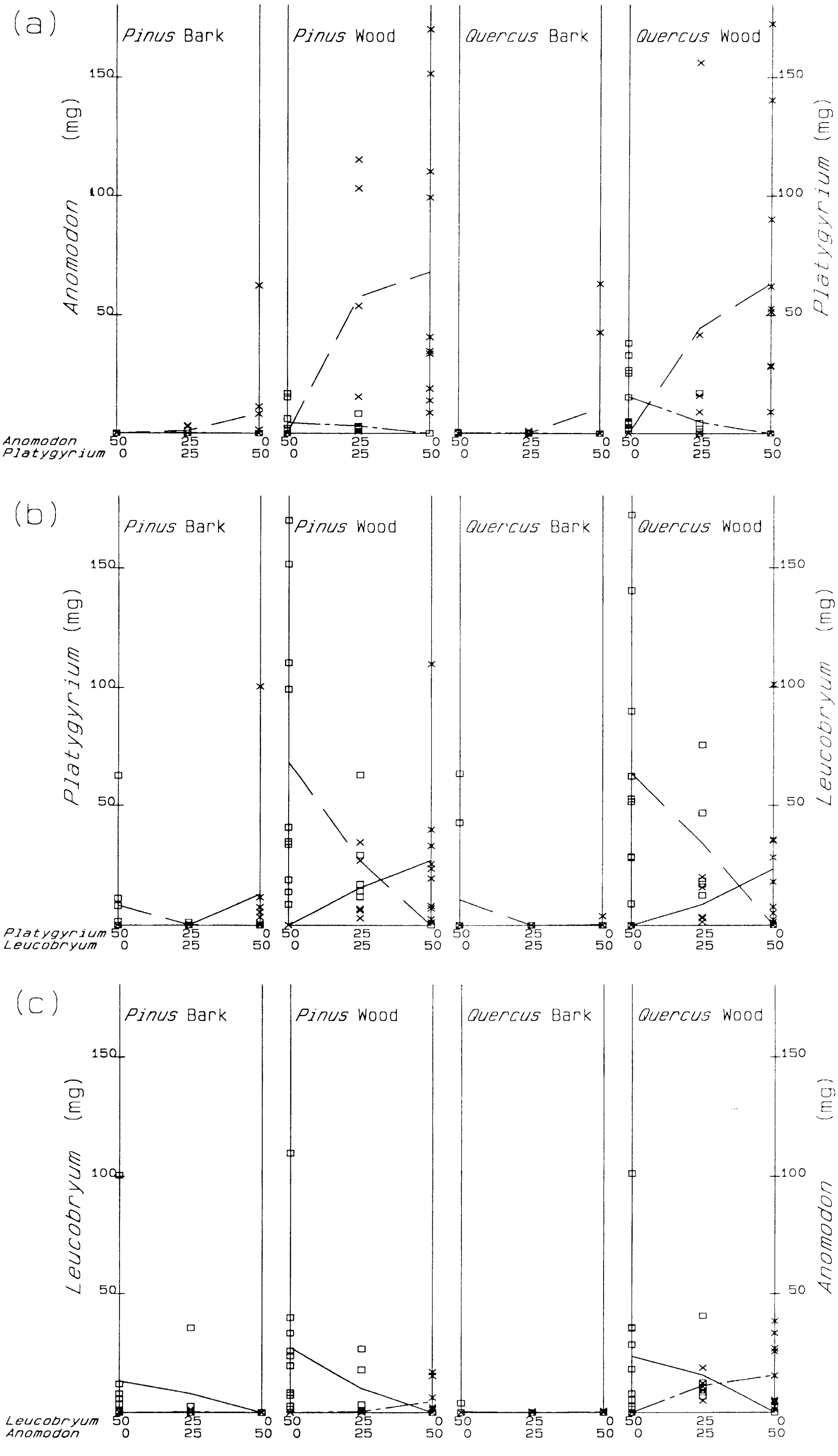
FIG. 1. Replacement-series diagrams for the three two-species bryophyte mixtures on the four log substrates. All twelve panels are on the same scale. Sowing densities for the two species are shown across the bottom of each panel. Biomass values for each species from individual pots are indicated by ☐ (for species name on the left of each panel) or by × (for species name on the right of each panel). Lines are drawn through the mean air-dried biomass values at the three sowing densities for each bryophyte species. — — — represents *Anomodon* in (a) and (c); - - - represents *Platygyrium* in (a) and (b); ——— represents *Leucobryum* in (b) and (c).


(a)
Pinus Bark
Pinus Wood
Quercus Bark
Quercus Wood
Anomodon (mg)
Platygyrium (mg)
150
100
50
Anomodon 50 25 0
Platygyrium 0 25 50
(b)
Pinus Bark
Pinus Wood
Quercus Bark
Quercus Wood
Platygyrium (mg)
Leucobryum (mg)
150
100
50
Platygyrium 50 25 0
Leucobryum 0 25 50
(c)
Pinus Bark
Pinus Wood
Quercus Bark
Quercus Wood
Leucobryum (mg)
Anomodon (mg)
150
100
50
Leucobryum 50 25 0
Anomodon 0 25 50
Sowing density (mg)

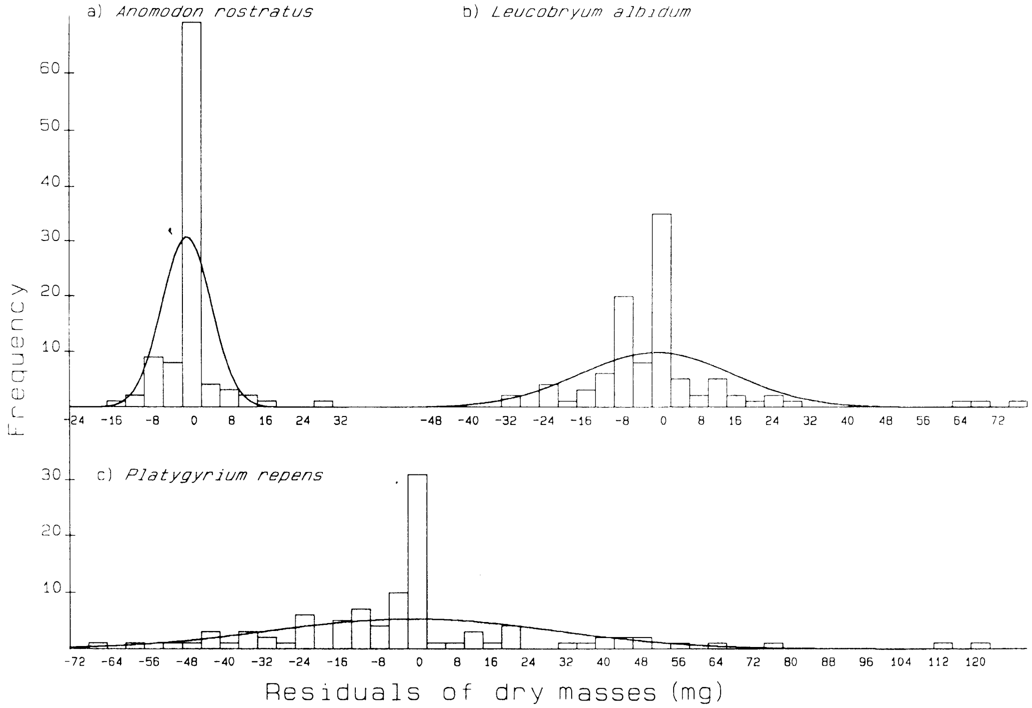


FIG. 2. Distribution of residuals of air-dried biomass of the three bryophyte species. Total number of observations = 240; histogram is in units of 50 observations. For each panel a normal curve with the same mean and variance as the data is shown by a thick line.

and ANOVA in particular (Fig. 2). These assumptions include a normal distribution of residuals and equality of within-cell variances (Sokal and Rohlf 1981, Edgington 1987). Nonparametric tests (such as the Kruskall-Wallis) are often proposed when such assumptions are violated. However, the ranking involved in these tests results in the loss of much of the information in a quantitative data set and the method is not robust when there are a large number of ties in data (Noether 1971), which is the case in this study. I thus decided to use randomization tests.

A randomization test is a statistical method that computes the significance of experimental results by comparison with random permutions of the data (Edgington 1987). The general algorithm is as follows: The appropriate test statistic (in this case an F statistic) is calculated for the observed data. The data are then randomly permuted subject to constraints depending on the null hypothesis (in this case, $H1_0=$ A species' performance is independent of the presence of another species, and $H2_0=$ A species' performance is independent of the substrate on which it is sown), and a new test statistic is calculated for this configuration of the data. The test statistics derived from a large number of such permutations of the data are then compared to the test statistic from the original configuration of the data. The proportion of these that are greater than or equal to the observed test statistic indicates the significance level (e.g., Fig. 3).

RESULTS

At the time of harvest, bryophyte species were found growing in over half of the pots, with *Leucobryum* and *Platygyrium* having slightly higher establishment frequencies (61% each) than *Anomodon* (51%). Total frequency of establishment for the three species was 33% on *Pinus* bark, 93% on *Pinus* wood, 13% on *Quercus* bark, and 91% on *Quercus* wood. There was high variability within both substrates and species.

The average percentage frequency for the three species on the four substrates is shown in Table 1. For nearly all combinations of species and substrate, the results of G tests for independence of frequency were nonsignificant. The exception to this was that *Leucobryum* seemed to have a negative effect on the presence of *Anomodon* ($P < 0.05$). However, when multiple comparisons are taken into account, this is also nonsignificant. There is thus no evidence that one species affects the establishment of another when both are sown at the same time. This failure to reject the null hypothesis may be due to the small sample size.

The frequencies of all three species in monoculture were each highly significantly dependent on the substrate (Table 1). Frequency of establishment was 100% on *Pinus* wood for both *Platygyrium* and *Leucobryum*; *Anomodon* averaged 87%. The establishment rate was somewhat lower for all species on *Quercus* wood. Bark of both types appeared to be an inhospitable substrate for establishment in the greenhouse.

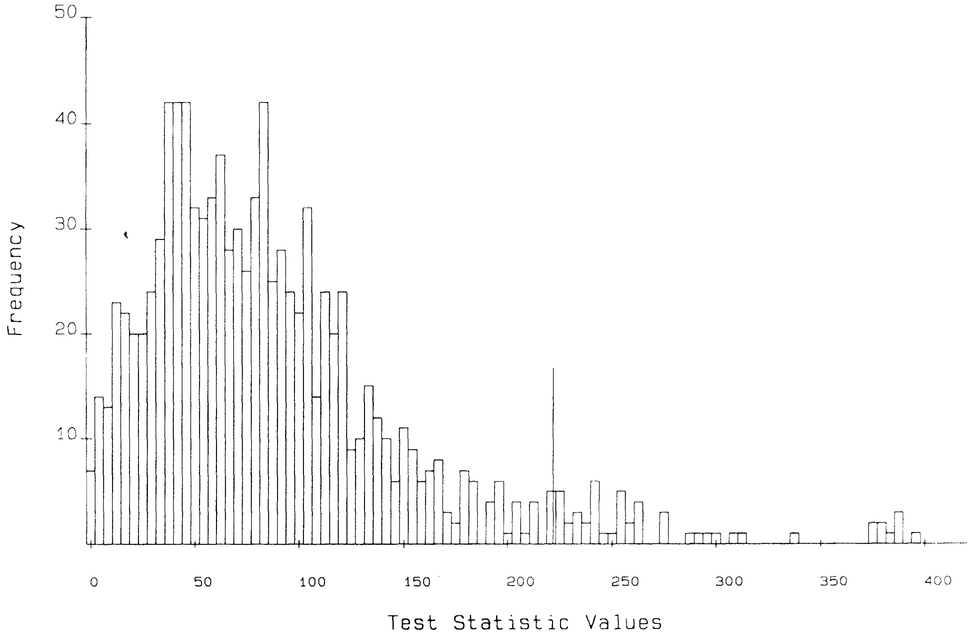


FIG. 3. Distribution of the test statistic (F) generated from 1000 random permutations of the data used in one of the comparisons. The histogram is in units of 10 observations. The vertical line indicates the observed test statistic. The proportion of generated test statistics greater than or equal to the observed test statistic is 0.049.

TABLE 1. Average percentage frequency for the three bryophyte species on the four log substrates. Abbreviations: A = *Anomodon*, L = *Leucobryum*, P = *Platygyrium*; subscripts indicate treatment type: $_{25}$ = low density monoculture (25 mg/25 cm^2), $_A$ = grown with *Anomodon*, $_L$ = grown with *Leucobryum*, $_P$ = grown with *Platygyrium*, $_{50}$ = high-density monoculture (50 mg/25 cm^2). (N = 10 for high-density monoculture, N = 5 for other treatments). Boldfacing indicates direction of significant comparisons (all possible such comparisons were made). Boldface italics indicates the one species effect that was significant ($P <$ 0.05) (but see *Results*).

Substrate	Bryophyte frequency (%)			
	Anomodon			
Treatment:	A_{25}	A_L	A_P	A_{50}
Pinus bark	**20**†	20	20	**0*****
Pinus wood	***100***†	***40****	100	**80*****
Quercus bark	**0**†	20	40	**30*****
Quercus wood	**80**†	100	80	**100*****
	Leucobryum			
Treatment:	L_{25}	L_A	L_P	L_{50}
Pinus bark	**40****	60	20	**70*****
Pinus wood	**100****	100	100	**100*****
Quercus bark	**0****	0	0	**10*****
Quercus wood	**60****	100	100	**90*****
	Platygyrium			
Treatment:	P_{25}	P_A	P_L	P_{50}
Pinus bark	**40****	40	20	**40*****
Pinus wood	**100****	100	100	**100*****
Quercus bark	**20****	20	0	**20*****
Quercus wood	**100****	80	100	**90*****

* $P < 0.05$, ** $P < 0.01$, † $P < 0.005$, *** $P < 0.001$. Level of significance was determined from G test for independence of frequencies.

Analyses comparing the frequency of the three species grown in the high-density monocultures on each of the four log substrates indicate that species appear to establish relatively consistently within three of the four substrates; only on *Pinus* bark was the frequency dependent on the species sown. This effect seems to be due to the higher establishment rate for *Leucobryum* (70%(L) vs. 0%(A) and 40%(P)) on *Pinus* bark.

Leucobryum and *Platygyrium*, species with the highest overall frequency, also achieved higher cover and biomass on average than did *Anomodon* (Table 2). This holds true whether values are averaged over all substrate blocks, or are obtained by only considering substrates where growth occurred. When only those substrates where growth occurred are considered, *Platygyrium* grew over ≈29% of the available substrate, *Leucobryum* ≈22%, and *Anomodon* ≈10%. The average percentage cover and dry biomass for the three species on the four substrates are shown in Tables 3 and 4. Comparing these results to those presented in Table 1, it is clear that species that established frequently on a substrate generally had high cover and biomass as well. Substrates on which species did not have a high frequency of establishment also were inhospitable to growth. Correlation between biomass and cover values (square-root transformed cover data with only non-zero values included) was highest for *Anomodon* (r^2 = 0.844), followed by that for *Platygyrium* (r^2 = 0.774) and for *Leucobryum* (r^2 = 0.707). The

TABLE 2. Dry biomass and percentage cover averaged over all substrates for the three bryophyte species. Along the diagonal are the values from the low-density monocultures, off the diagonal are values of the target species when grown with the associate species. Values in parentheses are obtained by considering only substrates where growth occurred. $N = 20$ for the first entry in a column, and is variable for the entries in parentheses.

	Associate species		
Target species	*Anomodon*	*Leucobryum*	*Platygyrium*
Anomodon			
Dry biomass (mg)	3.03 (6.08)	2.92 (6.51)	2.15 (3.61)
Cover (%)	5.90 (11.80)	4.62 (10.34)	5.50 (9.14)
Leucobryum			
Dry biomass (mg)	8.25 (12.67)	5.55 (11.09)	9.95 (11.11)
Cover (%)	12.25 (18.86)	12.92 (25.83)	10.90 (19.82)
Platygyrium			
Dry biomass (mg)	25.92 (43.26)	15.35 (27.92)	19.62 (30.19)
Cover (%)	17.60 (27.08)	16.68 (30.30)	20.90 (29.86)

appearance of all three species was quite similar to wild-grown plants. However, the strands of *Anomodon* were slightly thinner and paler in color than is usual (S. McAlister, *personal observation*), which may have been due to nutrient shortage due to the absence of water from above (Furness and Grime 1982).

Replacement-series analyses

Fig. 1 depicts replacement-series diagrams for the three species pairs on each of the four substrates. For all three species pairs the effect of substrate on biomass is evident. Species differences are also evident: in mixture on the two wood substrates, *Platygyrium* reached nearly 2 times the biomass of *Leucobryum* and 4 times that of *Anomodon*.

The yield of each species in the high-density monocultures was not significantly different from the yield in the low-density monocultures (using randomization tests similar to those discussed in *Results: Intraspecific effects*, below), thus the hypothesis of constant final yield was not rejected. These results are in accordance with the design suggestions of Taylor and Aarsen (1990) to control for the possible dependence of interpretations from replacement-series experiments on the resource supply/demand ratio (density dependence).

Although several of the mean biomass curves discussed below appear curvilinear, the subsequent statistical analyses do not support this. In general, extreme variability makes the following interpretations only

TABLE 3. Average percentage cover for the three bryophyte species on the four substrates. Abbreviations and subscripts as in Table 1. Values in parentheses are as in Table 2. Lines indicate direction of analysis using randomization tests for associate effects; lines end under the values being compared.

Substrate	Bryophyte cover (%)			
		Anomodon		
Treatment:	A_{25}	A_L	A_P	A_{50}
Pinus bark	0.3 (1.4)	0.4 (2.1)	1.0 (4.9)	0.0 (0)
Pinus wood	5.1 (5.1)	1.1 (2.8)	11.0 (11.0)	7.5 (9.4)
Quercus bark	0.0 (0)	0.1 (0.7)	0.6 (1.4)	0.3 (0.9)
Quercus wood	18.2 (22.7)	16.9 (16.9)	9.4 (11.8)	20.2 (20.2)
	—— $P = 0.527$ ——			
	——————	$P = 0.710$ ——————		
		Leucobryum		
Treatment:	L_{25}	L_A	L_P	L_{50}
Pinus bark	6.7 (16.7)	6.8 (11.3)	0.6 (2.8)	14.0 (19.4)
Pinus wood	32.1 (32.1)	20.3 (20.3)	24.7 (24.7)	39.8 (39.8)
Quercus bark	0.0 (0)	0.0 (0)	0.0 (0)	0.4 (4.2)
Quercus wood	12.9 (21.5)	21.9 (21.9)	18.3 (18.3)	28.6 (31.8)
	—— $P = 0.904$ ——			
	——————	$P = 0.670$ ——————		
		Platygyrium		
Treatment:	P_{25}	P_A	P_L	P_{50}
Pinus bark	4.3 (7.2)	4.0 (10.1)	1.7 (8.3)	6.0 (20.1)
Pinus wood	48.8 (48.8)	43.9 (43.9)	34.2 (34.2)	52.2 (52.2)
Quercus bark	0.1 (0.7)	0.6 (1.4)	0.0 (0)	5.9 (29.5)
Quercus wood	30.4 (30.4)	21.9 (27.4)	30.8 (30.8)	34.8 (38.7)
	—— $P = 0.450$ ——			
	——————	$P = 0.500$ ——————		

TABLE 4. Average dry biomass for the three bryophyte species on the four substrates. Abbreviations and subscripts are as in Table 1; values in parentheses are as in Table 2. Boldfacing indicates direction of analysis using randomization tests for substrate effects. Lines indicate direction of analysis using randomization tests for associate effects; lines end under the values being compared.

Substrate	Bryophyte biomass (mg)			
		Anomodon		
Treatment:	A_{25}	A_L	A_P	A_{50}
Pinus bark	<0.01 (0.1)	0.2 (1.2)	0.2 (1.2)	**0.0**‡ (0)
Pinus wood	1.7 (1.7)	0.3 (0.8)	3.3 (3.3)	**4.5**‡ (5.7)
Quercus bark	0.0 (0)	0.1 (0.4)	0.2 (0.6)	**0.15**‡ (0.6)
Quercus wood	10.4 (13.0)	11.1 (11.1)	4.9 (6.1)	**15.6**‡ (15.6)
	——— $P = 0.942$ ———			
	———————— $P = 0.612$ ————————			
		Leucobryum		
Treatment:	L_{25}	L_A	L_P	L_{50}
Pinus bark	7.3 (18.2)	7.6 (12.6)	0.1 (0.7)	13.0 (18.5)
Pinus wood	11.0 (11.0)	9.8 (9.8)	15.5 (15.5)	27.0 (27.0)
Quercus bark	0.0 (0)	0.0 (0)	0.0 (0)	0.4 (3.9)
Quercus wood	3.9 (6.5)	15.6 (15.6)	8.8 (8.8)	23.5 (26.1)
	——— $P = 0.441$ ———			
	———————— $P = 0.844$ ————————			
		Platygyrium		
Treatment:	P_{25}	P_A	P_L	P_{50}
Pinus bark	5.1 (12.6)	1.2 (3.0)	0.3 (1.3)	**8.4**† (20.8)
Pinus wood	46.5 (46.5)	57.7 (57.7)	27.0 (27.0)	**68.2**† (68.2)
Quercus bark	0.3 (1.7)	0.2 (1.2)	0.0 (0)	**10.6**† (53.0)
Quercus wood	26.6 (26.6)	44.6 (55.8)	34.1 (34.1)	**63.5**† (70.6)
	——— $P = 0.567$ ———			
	———————— $P = 0.477$ ————————			

† $P < 0.018$, ‡ $P < 0.009$.

cautious at best. Due to poor growth, no patterns are discernable on the bark substrates for any of the species pairs. When growing with *Anomodon* the generally convex mean biomass curves of *Platygyrium* on wood substrates (Fig. 1a) indicate that the effect of interspecific interactions on the growth of *Platygyrium* appeared to be less than the intraspecies effects. The essentially straight curves (Fig. 1a) indicate that inter- and intraspecies interactions appear equal for *Anomodon* when sown with *Platygyrium* and with *Leucobryum* (Fig. 1c). The nature of inter- and intraspecies interactions appeared to change with substrate for *Leucobryum* when grown with both *Anomodon* (Fig. 1c) and *Platygyrium* (Fig. 1b). Being on its "own" substrate does not seem to lessen the effect of interspecific interactions for any of the three species.

Various patterns of mixture productivity and resource use are suggested from the relative yield totals (RYT) for the three species pairs (Table 5). For *Anomodon* growing with *Platygyrium*, RYT values are all >1, indicating that together the species produce more biomass than would be expected based on their individual performances. Harper (1977) calls such overyielding "mutualism or avoidance." RYT values are just under 1 (≈0.9) for *Leucobryum* growing with *Platygyrium* on wood substrates, indicating that these species achieve about the same biomass in mixture as with an equivalent monoculture density; this result has been interpreted to mean the species have similar resource requirements (Harper 1977, Firbank and Watkinson 1985). On *Pinus* bark these species together produce less biomass (RYT = 0.043); this could be considered "antagonism" (Harper 1977), but is likely a function of an inhospitable substrate. The mixture of *Anomodon* and *Leucobryum* on *Pinus* wood produced less biomass, but the two perform better than expected (RYT = 1.37) on *Quercus* wood.

TABLE 5. Relative yield totals for the bryophyte two-species mixtures. A = *Anomodon rostratus*, L = *Leucobryum albidum*, P = *Platygyrium repens*.

Substrate	A–P	L–P	A–L
Pinus bark	…*	0.04	…
Pinus wood	1.58	0.97	0.43
Quercus bark	1.35	0	…
Quercus wood	1.02	0.91	1.37

* Ellipses indicate calculation unable to be made because of lack of growth.

The lack of distinctive patterns of species interactions is likely due to the extreme variability in the performance of the three species among and within the substrates. There was a 350-fold range in dry biomass values for *Leucobryum* in the high-density monocultures across all substrates, a 100-fold range for *Platygyrium*, and a 40-fold range for *Anomodon*. Variability in biomass values in the low-density monocultures and mixtures was also high. This variability in performance is likely due to the inherent variability of substrate characteristics, particularly surface texture, despite the fact that substrate blocks were chosen to be as homogeneous as possible.

Associate effects

The comparison of a species performance in mixture to that in monoculture at the same component density is a strong test of the occurrence of interspecific competition. Also, unlike the interpretation of the replacement-series diagrams above, this comparison can be tested statistically.

Randomization tests comparing the biomass and percentage cover of each species grown in monoculture on all four substrates to the performance of the same species when grown in each of the two mixtures (a 2 × 4 factorial design—Tables 3 and 4) reveal that none of the "associate" effects are significant: none of the *P* values are less than ≈0.5. Under these conditions then, none of these bryophyte species significantly affect the growth of another species.

Intraspecific effects

In the absence of intraspecific competition, doubling the input biomass would be expected to produce twice the output biomass. To test for the occurrence of intraspecific competition, I used another 2 × 4 design, comparing the biomass of each species when grown in low-density monoculture with 0.5 times the biomass of the species when grown in high-density monoculture. All three comparisons were nonsignificant ($P < 0.696$, 0.474, and 0.881 for *Anomodon, Leucobryum,* and *Platygyrium,* respectively). Thus, at these densities there is no evidence for intraspecific competition between any of the three species.

Substrate effects

I tested the hypothesis of substrate effects in two ways. First, I used a randomization test analogue of a one-way ANOVA—testing for substrate effects within the high-density monocultures of the three species. As is indicated by the boldface entries in the fourth column in Table 4, substrate had a strong effect on the biomass of *Anomodon* and *Platygyrium* when grown in high-density monoculture. However, the biomass of *Leucobryum* did not differ significantly across substrates.

Second, substrate effects were tested in a two-way ANOVA analogue (Table 6). Results from this second method are similar to, albeit more complex than, results from the first method. Growth of *Leucobryum* in mixture with *Platygyrium* did differ significantly among the four substrates, but the biomass in mixture with *Anomodon* was not related to substrate type (Table 6: column ECS). Growth of both *Platygyrium* and *Anomodon* in all mixtures was strongly dependent on substrate (Table 6).

Growth following establishment

The results in the previous three subsections are from analyses treating zero biomass as data, in essence looking at the combined effects on establishment and growth. I also repeated the analyses while treating zero biomass or cover as missing values, thus looking at growth after any effects on establishment had occurred. The sample size was markedly decreased in these analyses, and thus the power of discrimination lowered considerably, so that results must be interpreted cautiously.

TABLE 6. Significance levels from randomization tests for substrate effects in a factorial design with two treatments: low-density bryophyte monoculture and mixture (treatments indicated as in Table 1) and four substrates (not indicated). Comparison of analyses treating zero biomass or cover as a value of zero, thus having equal cell sizes (ECS), and as missing values removed (MVR; i.e., no zeroes). Zeroes were removed to analyze growth only where establishment actually occurred. (See *Results: Growth following establishment.*)

Bryophyte species	Dry biomass		Cover	
	ECS	MVR	ECS	MVR
Anomodon				
A and A_L	0.001	0.020	0.001	0.001
A and A_P	0.001	0.064	0.001	0.025
Leucobyrum				
L and L_A	0.118	0.813	0.001	0.379
L and L_P	0.012	0.600	0.003	0.391
Platygyrium				
P and P_A	0.001	0.165	0.001	0.001
P and P_L	0.001	0.196	0.001	0.009

Substrate did not have a significant effect on the biomass or cover of *Leucobryum* when establishment rates were factored out (Table 6: MVR columns). Biomass of *Platygyrium* was also not significantly affected. Substrate did have a significant effect on the cover of *Platygyrium* and on both the biomass and cover of *Anomodon.*

Results from tests for "associate" effects were very similar to those discussed above: growing with an "associate" did not significantly affect the performance of these three species.

To summarize, substrate does appear to be an important factor in establishment from fragments for all three bryophyte species studied. It appears to be less important for growth once establishment is taken into account, except for *Anomodon,* the species with the most restricted distribution on logs in the forest. Once *Leucobryum* and *Platygyrium* found favorable microsites (i.e., cracks in the bark where water availability was higher), they grew reasonably well in all substrates (except *Leucobryum* on *Quercus* bark), whereas *Anomodon* seemed less able to grow on three of the four substrates. These bryophyte species did not significantly affect the establishment or growth of one another.

DISCUSSION

The identity of the substrate appears to be an important factor in establishment from fragments for all three bryophyte species studied. However, under experimental conditions some species could establish on substrates where they did not naturally occur, suggesting that distributional patterns in the forest may not be determined soley by ability to establish.

Platygyrium repens had a high establishment frequency and abundance on all substrates in this experiment, which is consistent with its previously observed distribution on many substrate types (S. McAlister, *in press*). Its abundance in the forest thus appears to be related to an ability to establish from fragments and to grow on a variety of substrates. *Platygyrium* produces abundant brood branches in nature, and these vegetative propagules undoubtedly contribute to its prevalence and its success in this experiment.

In this experiment, *Leucobryum albidum* achieved the highest frequency and abundance on *Pinus* wood, not *Pinus* bark, and was both more frequent and abundant on *Quercus* wood than on *Pinus* bark. This contrasts with its observed high frequency and abundance on *Pinus* bark in the forest. These inconsistencies are likely due to several factors. (1) *Pinus* bark seemed to be an even less hospitable substrate in the greenhouse than in the forest. I believe this is due to its poor water-absorptive capacity; the bark blocks seemed unable to absorb moisture from below. Except for deep cracks, the bark blocks never became moist enough for fragments to establish. (2) *Quercus* wood blocks absorbed water well and remained more consistently moist than in the forest, which may account for the good growth of *Leucobryum* on *Quercus* wood. It is also possible that the steam sterilization altered chemical constituents in the wood.

The growth and establishment of *Anomodon rostratus* in the greenhouse was particularly distinct from its forest distribution. There are several possible explanations for these differences. The lack of growth on *Quercus* bark can be attributed to two factors. (1) Like *Pinus* bark, *Quercus* bark did not absorb water well in this experimental setup, thus providing little opportunity for fragments to initiate growth. (2) On horizontal logs, or blocks, there is no stem flow. *Anomodon rostratus* growing on the bark of newly fallen logs is essentially a relict from communities on upright trees; it established on the bark at the tree bases (in the presence of stem flow) before the trees fell. Indeed, the vigor of *Anomodon* on the horizontal bark of fallen logs appears to diminish with time since treefall (S. McAlister, *personal observation*). Abundant moisture allowed *Anomodon* fragments to initiate growth on *Pinus* wood; however, the plants did not flourish: cover and biomass on *Pinus* wood were on average about one third of that on *Quercus* wood. The sole occurrence of *Anomodon* establishment on *Pinus* bark was one small fragment deep in a crack. The excellent growth of *Anomodon* on *Quercus* wood suggests that this substrate is not inherently unfavorable. *Anomodon* has a very low light compensation point ($\approx 6\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Larry Giles, *personal communication*), and many forest mosses are inhibited by even moderately high irradiance levels (Richardson 1981, Proctor 1982). The high irradiance in gaps such as those created by the fall of a large hardwood tree may restrict its growth on this substrate in the forest (depending on how long it takes for the gap to close).

In this study there were no significant negative or positive interactions between the species in any of the combinations studied. Relative yield total (RYT) values were generally close to unity, indicating utilization of the same resources (niche overlap). Growth in mixtures was not different than growth in monoculture for any of the species among substrates. This is in contrast to Scandrett and Gimingham (1989), who did find inhibition of growth in mixtures, especially by *Hypnum*. This might be in part because their species were very similar ecologically—all soil-dwelling, weft-forming pleurocarps, whereas the species used in this study were all rather different ecologically and in growth form.

As predicted from its widespread distribution and abundance on logs in the forest, growth of *Platygyrium repens* was the least negatively affected in mixture. However, *Leucobryum* and *Anomodon* did not appear to have a negative effect on other species when on their "own" substrates.

Mixtures of either pleurocarp and the acrocarp *Leucobryum* generally had lower biomass than expected from monoculture results. Competitive interactions can be mediated through growth form (Mägdefrau 1982, During and van Tooren 1987, 1990, Økland 1990, Rydin 1993). The pleurocarpous species *Anomodon* and *Platygyrium* thus could have usurped a majority of the substrate by growing across it, preventing the acrocarpous species (*Leucobryum*) from spreading once it established. Alternatively, the pleurocarps could grow over *Leucobryum*, restricting its photosynthesis.

Growth form has also been postulated to lead to positive interactions: intermingling of their strands may create a network that would decrease water loss by both pleurocarpous species (Mägdefrau 1982, Schofield 1985, Scandrett and Gimingham 1989, Økland 1994), thus increasing their photosynthetic potential. Further filling of air spaces by the combination of *Leucobryum* and either *Anomodon* or *Platygyrium* may create a similar benefit to both. There was some support from the replacement-series analyses for the hypothesis that a mixture of two pleurocarps would outperform monocultures. However, the lack of evidence for significant interactions supports the view held by many that in disturbed habitats, or in habitats of limited duration, the influence of competition on bryophyte species composition is low.

The inconsistencies in the present study between observed species distributions and their ability to establish in an experimental setting suggest that chemical factors (which presumably remained reasonably similar in the experiments to those of the forest logs) are less important than physical factors such as substrate texture (ability to lodge) and water retention, which were more favorable in the greenhouse. Differences in the stages of decay between field and greenhouse substrates may also have contributed to the distinctions. Different physiological tolerances of the bryophytes to extremes in these factors may affect continued growth. The observation of inconsistencies between greenhouse and field results runs counter to Scandrett and Gimingham's (1989) study of *Hypnum, Hylocomnium,* and *Pleurozium,* wherein experimental results paralleled knowledge of the species' physiology and dominance patterns on heathland.

The structure of bryophyte communities on fallen logs is a function of the combination of all the above factors. The considerable variability in performance within species and substrates found in the present study, while it may have obscured the ability to detect patterns in establishment and growth, has pointed out that no one factor can dominate species composition. I believe this variability is an unavoidable, and indeed integral, part of the ecology of bryophyte communities on fallen logs.

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