DIFFERENCES IN MOSS MORPHOLOGY AND COMMUNITY COMPOSITION BETWEEN AN OPEN AND A FOREST UNDERSTORY HABITAT

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Abstract: Mosses are dependent on high water availability for survival and reproduction, and some moss morphologies can help reduce water loss. Water availability is presumably higher in the understory than in the open. We examined how moss morphology varied within and among understory and open habitats. We also investigated whether morphological differences across habitats were due to phenotypic plasticity of individuals or fixed morphological differentiation among species. We found that moss growth form and degree of "packing" of moss tissues were significantly related to habitat: mosses in open habitat tended to grow in a cushion form and be more packed. We also found differences in community composition across habitats, which reflected morphological differences. Thus morphological differences among species may represent adaptations to habitat conditions, such as water availability.

Key Words: moss, morphology, habitat, community

INTRODUCTION

Water availability limits the growth, survival and reproduction of many plants. This is especially true for mosses (Bryophyta), which, due to their non-vascular structure, are especially reliant on access to water. Nonetheless, some mosses grow in habitats exposed to relatively high sunlight and high evaporation rates. Morphological adaptations can reduce moss water loss in these conditions. Changes in leaf form and orientation, reduction in degree of leaf branching, and increased patch density can all slow the rate at which mosses lose water (Schofield, 2001).

These morphological differences can be driven by either phenotypic plasticity of individuals, or relatively fixed morphological differentiation among species. In the first case, individual mosses might modify their growth pattern in ways that match their local environment. In the second case, species may evolve different growth patterns that make them adapted to different environments.

If water availability influenced moss morphology across habitats, we would expect to see morphological differences between mosses located in a sun-exposed, open habitat, and in an understory habitat. Mosses growing in open areas would be thicker and denser, and have less branching (lower surface area: volume ratio) than mosses growing in understory areas. These morphological differences could be due to either phenotypic plasticity or species adaptations. If it were phenotypic plasticity, we would expect to see the same moss species, with different growth patterns, in each habitat. If it were species adaptations, we would expect to see communities composed of different species in each habitat.

METHODS

We conducted our study on 20-21 January 2006 in the area surrounding Estacion Biologica de Monteverde, Costa Rica. We randomly selected 25 trees in both the cloud forest understory and open areas around the station. Sampled trees were all greater than 16 cm in diameter at breast height (1.3 m), and supported moss communities covering at least 50% of the area of a 50 x 50 cm quadrat. The quadrat was divided into 100 equal subplots (5 x 5 cm). On each tree, we randomly chose three subplots within which we measured the thickness of moss, categorized the degree of branching (ordinal scale of 1-5), and estimated the degree of packing (ordinal scale of 1-5), defined as the three-dimensional packing of moss tissue within areas occupied by moss. We also categorized moss growth form as turf (clustered moss stems), mat (spreading moss stems), or cushion (round tufts) for both habitats. We compared moss thickness (log transformed), degree of packing, and degree of branching, using ANOVA in JMP 5.0.1. We compared growth form, by nesting trees within habitat and using contingency analyses and Pearson X^2 tests.

We investigated possible differences in community composition by randomly sampling ten additional trees from each area (understory and open). We recognized taxa (probably species or genera) based on morphotype and recorded the number of 5 x 5 cm squares in which each morphotype occurred in each sample. To compare communities occupying the two habitats, we used the morphotype abundance correlation matrix (Appendix 1) to perform a multivariate Principal Component Analysis (PCA), followed by an ANOVA, comparing habitats with respect to PCA 1 and PCA 2.

RESULTS

Neither moss patch thickness ($F_{1, 48}$ = 0.81, P = 0.37) nor degree of branching differed across habitats ($F_{1, 48}$ = 0.37, P = 0.55) (Table 1). We observed turf and mat growth formations in both habitats, but we only observed cushion growth formations in open habitats (X^2 = 47.84, df = 2, P < 0.001). Degree of packing was significantly higher in open habitats ($F_{1, 48}$ = 12.02, P < 0.0011).

TABLE 1. Morphological characteristics of moss in an open and understory habitats near Estacion Biologica de Monteverde, Costa Rica. Moss thickness, degree of branching, and degree of packing are reported as mean ± standard error (branching and degree of packing on a 1-5 scale, n = 25). Growth forms indicate percentage of samples that were predominantly cushion, mat, or turf in each habitat.

Habitat	Thickness (cm)	Branching	Degree of packing	Growth Form (% cushion : mat : turf)
Open	7.15 ± 1.32	1.95 ± 0.22	2.85 ± 0.16	41 : 29 : 29
Understory	8.83 ± 0.13	1.76 ± 0.22	2.08 ± 0.16	0 : 77 : 23

Samples of the moss community from open and understory habitats separated clearly along the 1st axis of the Principal Component Analysis ($F_{1,18}$ = 59.61, P < 0.0001; Fig. 1). Examination of the loading scores for PCA 1 (Table 2) revealed that morphotypes C and A (found in low-density, mat or turf growth forms) were strong indicators of the understory habitat, and morphotypes K and M (found in

aggregated, dense cushions) were strong indicators of the open habitat. We found only one morphotype (C) in both habitats, which occurred on one sampled tree in open habitat and eight trees in the understory.

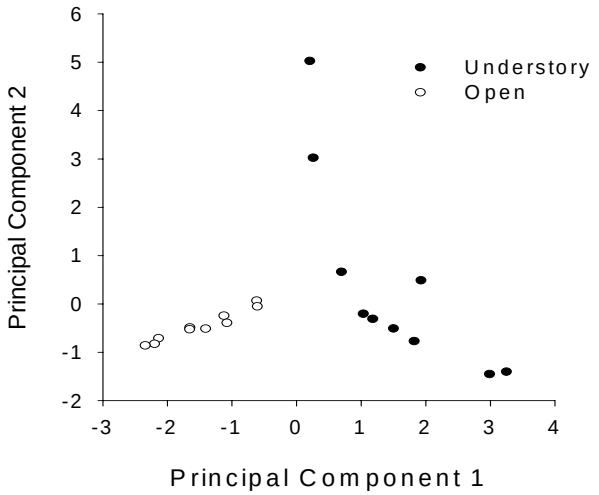

Figure 1. Moss community structure (on 20 sample trees) as represented by first two axes of Principal Component Analysis of moss morphotype abundance. Note separation of samples along PC 1 axis based on whether sample trees were in the understory or open habitat. Loading values for 16 moss morphotypes are in Table 1.

TABLE 2. Loading values from Principle Component Analysis of moss morphotypes (A-P) across 20 0.25 m^2 samples (1 sample on each of 10 trees in both open and understory habitats), near Estacion Biologica de Monteverde, Costa Rica.

PC 1		PC 2	
Moss morphotype	Loading	Moss morphotype	Loading
C	0.41	I	0.62
A	0.37	J	0.52
B	0.30	F	0.32
D	0.27	E	0.07
E	0.16	H	0.05
H	0.15	O	0.01
G	0.12	G	-0.04
F	0.04	P	-0.09
I	0.02	L	-0.10
J	0.02	N	-0.10
O	-0.05	B	-0.15
P	-0.18	K	-0.17
N	-0.22	D	-0.17
L	-0.26	M	-0.18
K	-0.39	A	-0.19
M	-0.39	C	-0.22

DISCUSSION

Some aspects of moss morphology were clearly related to habitat, and the patterns were partly interpretable with respect to differences in sunlight between habitats. In sun-exposed, open habitats, cushion growth and high percent cover can potentially reduce water loss by evaporation. However, moss patch thickness and degree of branching were not related to habitat. It is possible that microhabitats (within and among trees) influence moss patch thickness and degree of branching more than the coarse habitat (understory vs. open) conditions. For example, a patch of moss may grow better on a tree trunk with relatively high resource availability regardless of whether it is located in the open or the understory.

The clear separation between moss morphotypes across habitats suggests that differences between habitats in moss morphology mainly reflect community structure (species composition) rather than phenotypic plasticity within species. The general morphological characteristics associated with each habitat were well represented by two pairs of taxa. We were unable to test whether these morphological differences represent adaptations to different levels of sunlight and water availability, but it is plausible that open vs. understory habitats select different species from the local species pool, based partly on morphological attributes related to water retention.

LITERATURE CITED

Schofield, W.B. 2001. Physiology *in* Introduction to Bryology. The Blackburn Press: Caldwell, NJ. p. 290-304.

APPENDIX 1. Correlation matrix of moss morphotype (A-P) abundance across 20 0.25-m^2 samples (1 sample on each of 10 trees in both open and understory habitats).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
A	1.00	0.90	0.30	0.20	-0.06	-0.05	-0.15	-0.10	-0.14	-0.10	-0.32	-0.22	-0.29	-0.14	-0.10	-0.10
B		1.00	0.07	-0.11	-0.04	-0.11	-0.12	0.07	-0.12	-0.08	-0.26	-0.18	-0.23	-0.12	-0.08	-0.08
C			1.00	0.77	0.00	-0.18	0.34	0.05	-0.20	-0.14	-0.39	-0.30	-0.35	-0.20	-0.14	-0.14
D				1.00	-0.09	-0.09	-0.10	-0.07	-0.10	-0.07	-0.22	-0.15	-0.20	-0.10	-0.07	-0.07
E					1.00	0.03	-0.10	0.95	-0.09	-0.07	-0.21	-0.15	-0.19	-0.10	-0.07	-0.07
F						1.00	-0.10	-0.07	0.42	-0.07	-0.21	-0.15	-0.20	-0.10	-0.07	-0.07
G							1.00	-0.08	-0.11	-0.08	-0.23	-0.16	-0.21	-0.11	-0.08	-0.08
H								1.00	-0.07	-0.05	-0.16	-0.11	-0.15	-0.07	-0.05	-0.05
I									1.00	0.86	-0.23	-0.16	-0.21	-0.10	-0.07	-0.07
J										1.00	-0.16	-0.11	-0.15	-0.07	-0.05	-0.05
K											1.00	0.24	0.31	-0.05	0.10	0.50
L												1.00	0.20	0.00	-0.11	-0.11
M													1.00	0.60	-0.15	0.13
N														1.00	-0.07	-0.07
O															1.00	-0.05
P																1.00