SUCCESSIONAL TRUNK COLONIZATION: DO VINES FACILITATE COLONIZATION BY VASCULAR EPIPHYTES?

MATTHEW J. UNGERER AND REESA C. YALE

Abstract. Vines and epiphytic plants are prominent members of Neotropical forests that utilize tree trunks for structural support. We hypothesized that vines would colonize younger trees and facilitate subsequent colonization by vascular epiphytes. Most vascular epiphytes used vines or moss as a substrate for colonization and very few were attached to the trunk directly. We found that vines can be found unattached to epiphytes, but that epiphytes are not often found without vines or moss. However, the proportion of vascular epiphytes to total trunk colonizers did not increase with tree age as predicted, perhaps because our sampling did not include very young and very old trees.

Key Words: Bromeliad, climber, fern, liana, Monteverde, orchid, palm

INTRODUCTION

The abundance of vascular epiphytes is a distinguishing feature of many Neotropical forests. Vines are among the first colonizers in areas of disturbance while vascular epiphytes are typically late-successional species (Kricher 1989). We observed that: (1) the trunks of smaller trees without vascular epiphytes were often colonized by vines, (2) the trunks of larger trees had an abundance of both vines and vascular epiphytes, and (3) vascular epiphytes were usually not directly attached to the tree trunk. We hypothesized a succession of tree trunk colonizers, with vines colonizing the trunk first and facilitating colonization by vascular epiphytes. We predicted that younger trees would have a lower proportion of vascular epiphytes to total colonizers (vascular epiphytes plus vines) than older trees, and that there would be more vascular epiphytes attached to vines than attached directly to the trunk.

METHODS

Data were collected during the dry season in the premontane tropical moist forest at the Monteverde Biological Reserve, Costa Rica. Measurements were taken at 15 sites, > 20 m apart, for trees in each of four diameter (dbh) classes: 5-10 cm, 15-20 cm, 25-30 cm and 35-40 cm. The diameter classes were assumed to approximately correspond to age classes. Within each site, we sampled the closest tree in each of the four age classes with a monocormic base and a relatively straight, unbranched trunk. To control for the effects of sunlight on epiphyte load, we only sampled the lower 8 m of the trunk. For each tree, we recorded diameter, number of vines, and number of epiphytes in four categories (bromeliads, orchids, palms, and other epiphytes). Each epiphyte was classified as attached to a vine, moss or directly to the tree trunk. Vines were defined as any vascular plants that wound around or were attached to the trunk. Epiphytes were defined as vascular, non-parasitic, aerial canopy plants.

The data for each category epiphyte taxonomic group were pooled for analysis (see Appendix for epiphyte category means for each tree size class). We compared the proportion of epiphytes to total colonizers (epiphytes plus vines) between age classes using a one-way ANOVA. One-tailed paired t-tests were used to compare the number of vine-attached epiphytes and moss-attached epiphytes to the number of unattached epiphytes. We used a Chi-Square to compare the proportions of epiphytes and vines attached to the trunk and attached to each other.

RESULTS

The proportion of epiphytes to total colonizers did not vary with diameter class ($F_{3, 49} = 0.68$, $P = 0.57$). However, epiphytes usually exploited vines and moss as substrates in their attachment to the tree trunk (Fig. 1). We found more epiphytes using vines as a substrate than attached directly to the tree trunk ($t_{59} = 1.71$, $P = .046$). We also found many more epiphytes attached to patches of moss than attached directly to the tree trunk ($t_{59} = 4.84$, $P < .0001$).

Vines occurred more often without epiphytes (84% of 212 vines) than epiphytes occurred without vines (74% of 256 epiphytes; Table 1).

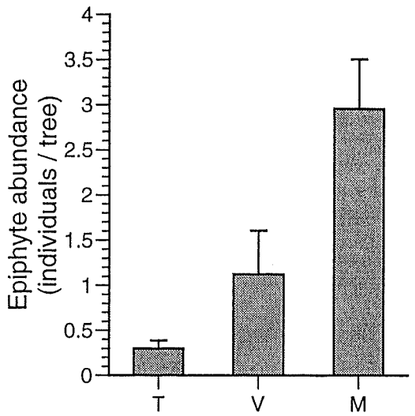

FIG. 1. Mean number of epiphytes (± 1 SE) attached to the trunk, vines and moss.

TABLE 1. Chi-square analysis comparing vines and epiphytes with the null hypothesis that epiphytes occur with vines vs. without vines in the same proportion as vines occur with epiphytes vs. without epiphytes (X^2 = 7.04, P < 0.01, expected values in parenthesis).

Plant type	Together	Apart	TOTAL
Vine	34 (45.7)	178 (166.2)	212
Epiphyte	67 (55.2)	189 (200.8)	256
TOTAL	101	367	-

DISCUSSION

Epiphytes seem to use either vines or moss as a substrate in their attachment to tree trunks, and are only rarely attached directly to tree trunks. In contrast, vines occur frequently without epiphytes. This implies that vines facilitate colonization by epiphytes more than epiphytes facilitate colonization by vines. However, the proportion of epiphytes to total colonizers did not increase with tree age as predicted by this model of tree trunk succession.

Our interpretation would have been improved if we had quantified presence of moss cover on tree trunks. Both vines and moss provide nooks and crevices for the attachment of epiphytes and a substrate for nutrient and water acquisition by epiphyte roots. This seemed especially important on trees with smooth bark. Moss appeared to be an early colonizer of tree trunks and vascular epiphytes were often attached to moss. The first epiphytes to colonize a tree trunk may be more likely to attach to moss than to vines, because vines grow up the trunk from the ground, but mosses can grow at any location on the trunk. At this stage, epiphytes can access more sunlight by growing on patches of moss located further from the ground than they could by attaching to vines near the base of the trunk. Once the vines have reached a height of several meters from the ground, epiphytes begin to attach to the vines as well.

Our sampling methods may have limited our ability to detect changes in the proportion of epiphytes with tree age. Very large trees (> 50 cm in dbh) seemed to contain a higher number of vascular epiphytes to vines on their trunks. However, these trees were omitted from our study because they were covered in a tangled mass of moss, vines, and epiphytes, that were difficult to quantify. Furthermore, trees that were smaller than our smallest age class appeared to often have moss and vines, but rarely epiphytes. Had we been able to sample younger and older trees, a change in the proportion of epiphytes may have been more apparent. It would also be beneficial to control for some of the variance between trees, perhaps by concentrating on trees within the same family.

LITERATURE CITED

Benzing, David H. 198?. Epiphytic vegetation: a profile and suggestion for future inquiries. Pp. 155-61.

Kricher, John C. 1989. *A Neotropical Companion*. Princeton University Press, Princeton, New Jersey.

APPENDIX. Mean number of vascular epiphytes per tree (± 1 SE) by dbh class.

dbh	Ferns	Bromeliads	Palms	Orchids	Other
5-10 cm	0.13 ± 0.13	1.87 ± 0.74	0.13 ± 0.13	0.13 ± 0.091	0
15-20 cm	0.47 ± 0.29	1.07 ± 0.34	0	0.067 ± 0.67	0.67 ± 0.25
25-30 cm	1.4 ± 0.72	2.2 ± 0.80	0.27 ± 0.27	0.4 ± 0.27	0.47 ± 0.24
35-40 cm	3.2 ± 1.19	3.13 ± 1.31	0.27 ± 0.18	0.87 ± 0.36	0.73 ± 0.27

SOIL DECOMPOSITION RATES ALONG AN ELEVATION GRADIENT IN A TROPICAL CLOUD FOREST

KENNETH C. DEEM, DANIELLE L. POULIN, AND ANA I. BAPTISTA

Abstract. We examined the decomposition rates of soils at different elevations within the tropical montane forest at La Estacion Biologica Monteverde. We hypothesized that the cooler high elevation sites would have lower rates of decomposition and greater accumulation of organic matter than low elevation sites. As predicted, temperatures were significantly lower and litter depth and total soil organic matter were significantly greater at the high elevation site. Soil respiration rates measured at a common temperature (29-30°C) were very similar across elevations, but may have declined with temperature if measured at natural temperatures. Alternative explanations for greater total organic layer in high elevations include increased litter fall with elevation, greater litter recalcitrance in higher elevations, reduced activity of soil macro invertebrates at higher elevation, and differences in the species composition and physiological attributes of microbial communities.

Key Words: A-horizon, leaf litter, Monteverde Biological Reserve, O-horizon, respiration rate, soil organic matter, temperature

INTRODUCTION

Climatic conditions within montane cloud forests vary across a short elevational gradient, leading to the development of distinctly stratified vegetation life-zones. Microbial decomposition of organic matter may also vary along this gradient. Litter decomposition and soil respiration rates are microbially-mediated processes and increase with increasing temperature (Jordan 1985). Because temperature typically decreases with increasing elevation, soil microbial activity should decrease with increasing elevation. Higher decomposition rates should result in more rapid recycling of leaf litter and organic matter, whereas slower decomposition rates should result in greater pools of leaf litter and organic matter. Past studies have shown that tropical montane forests accumulate large amounts of organic matter on the forest floor because of slowed microbial activity (Grubb 1977). We hypothesized that higher elevation soils in the Monteverde Cloud Forest should have lower decomposition rates than lower elevation soils. We predicted that soil respiration rates and temperature would be lower at higher elevations, and that the O and A soil horizons, that contain leaf litter and organic matter, would be deeper at higher elevations.

METHODS

We selected three elevations (1520, 1650, and 1760 m) in the cloud forest at the Estacíon Biologica Monteverde, Costa Rica. At each elevation, we chose three 1-m^2 subplots at least 15 m apart. To control for the effects of slope, we chose relatively flat subplots at each elevation. We collected all standing leaf litter from a 0.1 m^2 area within each subplot and recorded wet mass. We placed a leaf litter trap (laundry basket) in that same area for 24 h to measure litter fall mass and calculate input rates. We measured leaf litter depth at three points in each subplot. We recorded three measurements of soil temperature in the O-horizon for each subplot using a Barnant 90 Digital Thermometer. We took soil cores (2.5 cm x 40 cm) at three points in each subplot to determine O- and A-horizon depths. The O-horizon was distinguished as the top layer of dark, brown, fibrous soil. The A-horizon, directly below the O-horizon, had a lighter brown color and a clay-like texture. The A-horizon was bounded underneath by a reddish clay-textured B-horizon. We collected three O-horizon soil samples from each plot for soil respiration rate measurements, and measured soil moisture at three points in each subplot using the Demetra System Soil Tester. Soil respiration rates were measured using volumetric respirometers. Respiration flasks (containing a bottom layer of soda lime, middle layer of cotton and top layer of soil) were capped with a rubber stopper with an inserted plastic pipette. Flasks were placed in a 29-30°C water bath and the change in water volume was recorded over 30 min. Soil samples were then dried overnight and weighed.