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Nalini M. Nadkarni · Rodrigo Solano

Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach

Abstract Global climate change models predict reduced cloud water in tropical montane forests. To test the effects of reduced cloud water on epiphytes, plants that are tightly coupled to atmospheric inputs, we transplanted epiphytes and their arboreal soil from upper cloud forest trees to trees at slightly lower elevations that are naturally exposed to less cloud water. Control plants moved between trees within the upper site showed no transplantation effects, but experimental plants at lower sites had significantly higher leaf mortality, lower leaf production, and reduced longevity. After the epiphytes died, seedlings of terrestrial gap-colonizing tree species grew from the seed banks within the residual mats of arboreal soil. Greenhouse experiments confirmed that the death of epiphytes can result in radical compositional changes of canopy communities. Thus, tropical montane epiphyte communities constitute both a potentially powerful tool for detecting climate changes and a rich arena to study plant/soil/seed interactions under natural and manipulated conditions. This study also provides experimental evidence that the potential effects of global climate change on canopy and terrestrial communities can be significant for cloud forest biota. Results suggest there will be negative effects on the productivity and longevity of particular epiphytes and a subsequent emergence of an emerging terrestrial component into the canopy community from a previously suppressed seed bank.

Keywords Climate change · Epiphyte · Canopy · Tropical montane forest · Monteverde

N.M. Nadkarni (✉)
The Evergreen State College, Olympia, WA 98505, USA
e-mail: nadkarnn@evergreen.edu
Tel.: +1-360-8676621, Fax: +1-360-8666794

R. Solano
Monteverde, Apartado 5655, Puntarenas, Costa Rica

Introduction

The diverse assemblages of organisms in tropical montane forests face threats from deforestation, fragmentation, and habitat degradation, and are likely to encounter further challenges from impending changes in climate (Loope and Giambelluca 1998; Lawton et al. 2001). Lifting of the cloud bank caused by rising sea and land surface temperatures has been suggested to be linked to altered hydrological cycles as well as the population declines and extinctions of vertebrate species in tropical cloud forests (Crump et al. 1992; Donnelly and Crump 1998; Pounds et al. 1999). Empirical studies and global climate models (GCMs) for cloud forests indicate that even a slight rise in the concentration of greenhouse gases will increase the altitude at which clouds form in tropical mountains (ca. 200 m rise in cloud height during the northern hemisphere winter with a doubling of CO_2) (Benisten et al. 1997; Still et al. 1999). This hypothesis is built on evidence that rising sea surface temperatures have altered the climates of tropical mountains. Enhanced evaporation from warm ocean surfaces has generated large amounts of water vapor, and latent heat released as this moisture condenses has accelerated atmospheric warming. Because vertical thermal profiles have tended towards a moist adiabatic lapse rate, the decline in temperature with increasing elevation has diminished, amplifying the warming in the highlands relative to the lowlands. This "lifting cloud base" will alter regional hydrology by reducing the amount and frequency of critical dry season inputs of mist (low-intensity wind-blown precipitation) and cloud water (non-precipitating droplets deposited onto vegetation) (Bruijnzeel 1989; Clark et al. 1998a; Loope and Giambelluca 1998).

The decline of vagile organisms (reptiles, amphibians, and birds) attributed to these patterns has been based on population studies during unusual dry spells caused by El Niño events (Pounds and Crump 1994; Pounds et al. 1999). Little is known, however, about direct effects of predicted shifts in cloud bank levels on plants or sessile animals dwelling in cloud forests, many of whom depend

upon water and nutrients delivered in cloud water, and who cannot physically escape changes in climate by emigration (Bawa and Markham 1995).

Cloud forest epiphytes (canopy-dwelling plants with no vascular connections to the ground or host trees) are expected to be negatively affected by predicted climate changes because their dwelling-places are restricted to the atmospheric-terrestrial interface. Experimental studies that quantified the interception of host tree litter (Nadkarni and Matelson 1991) and other studies that partitioned atmospheric versus terrestrial nitrogen uptake with stable isotopes (Feild and Dawson 1998; Hietz et al. 1999) showed that epiphytes absorb and retain atmospheric water and nutrients directly. Epiphytes act as "capacitors" to regulate the seasonal release of precipitation, thereby providing flood and erosion control in the rainy season and water storage in the dry season (Still et al. 1999; Weathers 1999). They contribute substantially to the capture and retention of atmospheric nutrients, particularly nitrogen and marine aerosols. With healthy epiphytic communities, cloud forest ecosystems have the benefit of nutrient and organic matter fluxes originating at this interface. Without epiphytes, these inputs could be lost because clouds would pass through with minimized interception and retention, and the forests would become potentially less biologically active and resilient (Clark et al. 1998a, b).

In two concept papers (Lugo and Scatena 1992; Benzing 1998), epiphytes in tropical cloud forests were proposed as potentially superlative indicators of climate change. In addition to their tight coupling with atmospheric inputs, their "miniature" size, their high diversity of species and life forms, and their independence from the substrate make them conducive to manipulations that would be impossible with large terrestrial plants. Certain canopy-dwelling plants have long been used as indicators of atmospheric conditions, e.g., they provide empirical evidence for the connection of global air-sheds from their retention of fallout originating from nuclear explosions (Odum et al. 1970); they are used as indicators of heavy metal air pollution, especially in urban and industrial settings (Rao 1982). However, no experimental work has been done to directly test predicted effects of climate change on canopy-dwelling plants in tropical montane forests.

As part of a long-term study on the ecological roles of canopy biota (Nadkarni et al. 2000), we explored the sensitivity of epiphytes to the conditions that are predicted for future scenarios of atmospheric conditions that will lead to decreased cloud water input to the canopy. We carried out these transplant experiments along the existing gradient of cloud water input in the tropical montane landscape of Monteverde, Costa Rica, where changes in climate have been modeled (Pounds et al. 1999; Still et al. 1999).

Materials and methods

Site description

The study sites were located in the Monteverde Cloud Forest Reserve (MCFR), Puntarenas Province, Costa Rica (10° 18′ N,
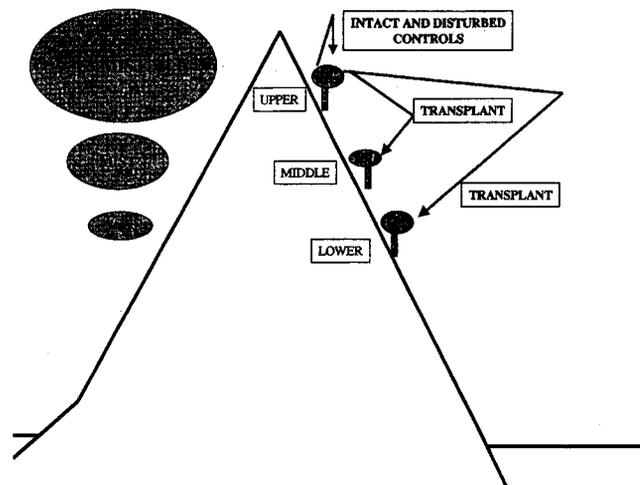
Fig. 1 Schematic of the field experiment design. The general approach was to move mats from the upper cloud forest to mid- and lower elevation sites where cloud water input is progressively less abundant, symbolized by the diminishing areas of circles. "Intact control" mats were marked with flagging, and were left undisturbed on trees at the upper cloud forest site (1,480 m). "Disturbed control" mats were cut from trees in the upper site, lowered to the ground, moved around, and then replaced in the same trees. Epiphyte mats used for transplants were cut from the upper site and moved to trees that were in the "mid-elevation" and "lower elevation" sites (1,410 and 1,330 m). Note that the vertical scale at the top of the mountain is expanded; the three sites are within 150 m in elevation and 1.5 km of each other

84° 48′ W). The landscape is a lower montane moist forest (sensu Holdridge 1967) adjacent to agricultural land. Total annual precipitation in the area is 2,000–2,400 mm (2,155 mm is the 33-year average for the official weather station, at 1,480 m, which is within 2 km of our sites) (Lawton and Campbell 1984; Clark et al. 2000). The canopy is exposed to frequent and intense wind and mist events throughout much of the year, especially during the windy-misty season (November-March) and the dry season (April-May) (Clark et al. 1998b). Details on the vegetation and climate of the area are in Lawton and Dryer (1980) and Clark et al (2000).

Research approach and measurements

Our approach was to move pieces of epiphyte mats from the upper cloud forest (where cloud water is frequent throughout the dry season) to trees that grow at a slightly lower elevation and are thus currently naturally exposed to less cloud water during the more protracted dry season – the very conditions predicted for tropical cloud forests by the GCMs under conditions of increasing CO_2. We established three sites along a short orographic gradient (<150 m in elevation and 1.5 km in distance). Although there are no long-term records that quantify this gradient in mist input, cloud water is observed to progressively decrease during the dry season as one moves from the upper end of the gradient ("upper site", 1,480 m) – to our two transplant sites – one located at the midpoint of the gradient ("mid-elevation", 1,410 m) and one located at the lower end ("lower elevation", 1,330 m) (Fig. 1).

The upper site is part of the Leeward Cove Forest (Lawton and Dryer 1980), within the Research Area of the MCFR. Mean diameter of trees (>10 cm diameter at breast height) is 65.5 cm; forest stature is 20–33 m, mean tree density is 154 individuals ha^{-1}, and forest species density is ca. 115 ha^{-1} (Nadkarni et al. 1995). Branch surfaces in the crown interior of nearly all mature trees support epiphytes (bryophytes, herbs, woody shrubs, and hemi-epiphytes) in interwoven root-humus mats up to 25 cm thick.

Mature trees of this upper forest support thick "epiphyte mats" on their inner branches, which consist of highly diverse vascular

Table 1 Results of control experiments to determine the effects of moving epiphyte mats on leaf production, mortality and plant 'longevity. "Intact" control mats were marked with flagging, and were left undisturbed on trees at the upper cloud forest site (1,480 m). "Disturbed" control mats were cut from trees in the upper site, lowered to the ground, driven around, and then replaced in the same trees. Leaf production and leaf mortality are expressed as the number of leaves that were produced and died as a proportion of the original number of leaves for each plant. Plant longevity is the number of months that plants remained alive over the 12-month monitoring interval. There were no significant differences between intact and disturbed plants for any of our measurements. Epiphyte mats were collected from four *Ficus tuerckheimii* trees

Taxon	No. of plants		Mean leaf production (%)		Mean leaf mortality (%)		Mean plant longevity (months)	
	Intact	Disturbed	Intact	Disturbed	Intact	Disturbed	Intact	Disturbed
Guzmania	6	11	9.0	8.8	9.7	9.8	11.7	11.8
Clusia	26	22	4.4	4.5	6.5	3.7	11.1	12.6
Elaphoglossom	24	22	2.5	6.7	3.5	6.2	11.5	12.6
Peperomia	15	12	6.2	4.3	7.6	4.1	10.6	11.2
Total	71	67						

and non-vascular plants (Ingram and Nadkarni 1993), and arboreal soil ("crown humus"). The dead organic matter is high in recalcitrant humic compounds, and is extremely acidic, and experiences greater frequencies of "drydowns", especially during the dry season, than the upper horizons of terrestrial soil (Bohlman et al. 1995). These mats can be peeled back and rolled up like a carpet, leaving the underlying bark substrate intact. Canopy soil supports the same major groups of invertebrates, but at reduced densities (Nadkarni and Longino 1990). Crown humus has equivalent amounts of microbial biomass C and N, fosters similar rates of net mineralization, but has much reduced rates of nitrification relative to forest floor soil (Vance and Nadkarni 1990).

A diverse seed bank comprising both terrestrial and epiphytic taxa is present in these arboreal mats, including terrestrial members of the Melastomataceae, Cecropiaceae, and Moraceae (N. Nadkarni and R. Solano, unpublished data). In 1998, seeds were extracted quantitatively from nine samples of canopy humus mats (10 cm circular cores taken from three *Ficus tuerckheimii* trees) at the upper site. Samples were air-dried, sieved through a 2 mm mesh screen, and sorted to species. Identifications were made with an existing Monteverde seed collection created by R. Solano and G.G. Murray. The five most common plant taxa represented in the seed bank of canopy-level included both terrestrial ("terr") families and obligate epiphytic ("epi") groups: *Cecropia* [Cecropiaceae (terr)]; *Phytolacca* [Phytolaccaceae (terr)]; *Lycianthes* [Solanaceae (epi)]; *Ficus* [Moraceae (terr)]; and *Oreopanax* [Araliaceae (epi)]. There were large numbers of terrestrial gap-colonizing early-successional species such as *Hampea appendiculata*, *Conostegia oerstediana*, and *Witheringia* spp. in the canopy mats (N. Nadkarni and R. Solano, unpublished data).

We climbed large, mature *Ficus tuerckheimii* (Moraceae, "strangler fig") trees with single-rope techniques (Perry 1978) to monitor the responses of four common epiphyte taxa in our experimental mats: *Guzmania pachystylis* (Bromeliaceae), a tank bromeliad; *Clusia* (Clusiaceae), a woody shrub; *Peperomia* sp. (Piperaceae), a scandent herb; and *Elaphoglossom* sp. (Lomariopsidaceae), a strap-leafed fern.

A critical question in this design is whether epiphytes can be moved from one tree to the other without effects on plant production or mortality. At the outset of the study, we tested this with a set of control experiments, comparing plants in undisturbed mats with mats we transplanted within the upper site. We established a set of "intact controls" (75-cm-long segments of epiphyte mats that we did not cut at all, but placed flagging around each end) and "disturbed controls", (similar-sized segments of epiphyte mats that we cut, lowered, drove around in our car, and then replaced in the same tree). We marked leaves of plants in our four taxa and measured the rates of leaf production, leaf mortality, and plant longevity at monthly intervals for 12 months. We marked each leaf of each plant with a small dot of paint, counted all leaves at the beginning of the experiment, and re-climbed trees and recounted all leaves at monthly intervals. Each month, new leaves were marked with paint.

Table 2 Number of trees, target plants, and leaves sampled for each plant taxon. Columns are for the number of trees, individual plants, original leaves (*orig lvs*), new leaves produced (*new lvs*), leaves that experienced mortality during the study (*dead lvs*), and the total number of leaves included (*orig lvs + new lvs*)

Taxon	Number of trees	Number of plants	Orig lvs	New lvs	Dead lvs	Total lvs
Guzmania	12	46	528	177	465	705
Clusia	11	82	783	273	461	1,056
Elaphoglossum	12	81	528	224	437	752
Peperomia	12	63	618	174	517	792
Total		272	2,457	848	1,880	3,305

We calculated leaf production as the number of new leaves produced during each sampling interval, and leaf mortality as the number of leaves missing from the former sampling interval. Because each plant started out with a different number of leaves, we expressed the data as percent leaf change: {[(number of new leaves-number of dead leaves)/number of original leaves]×100}. Plant longevity was the number of months the whole plant survived from the onset of the study. For the intact versus disturbed control experiments, a total of 138 plants were used from four trees (Table 1).

We later cut similar-sized experimental epiphyte mats from *Ficus tuerckheimii* trees in the upper site, and tied them to branches of 3–4 individuals of conspecific trees in each of the mid- and lower elevation sites. We marked plants as we had for the controls and measured them for 18 months after transplantation (Table 2). We carried out two sets of transplant experiments, one initiated during the dry season (January 1998), and another set during the wet season (June 1998). At the end of these monitoring periods, after epiphyte mortality in the lower sites occurred, we also documented the patterns of "revegetation" of the transplanted plots.

We also measured the amount of cloud water input and quantified the moisture content of the crown humus substrates of sample mats during the 4-month dry season at each of the three sites. Cloud water was collected with passive mist collectors (Falconer and Falconer 1980) within the canopy (18–23 m above the forest floor) in four trees at each of the three sites. Volume of input was recorded at 3–4 day intervals (36 collections total) for the 4-month dry season (13 February to 15 June 1999).

Gypsum blocks were used to detect relative moisture content of the mats (Delmhorst KS-D1 Digital Soil Moisture Tester). Although this method has been shown to be unreliable in some soils, they are useful for monitoring relative amounts of soil moisture (Campbell and Gee 1998). We were interested in the relative differences in the soil moisture among the sites, rather than the absolute moisture content of the soil mats, and so this method was warranted. Before installing the blocks, we carried out measure-

ments in which we placed blocks in 18 pieces of epiphytic mats in the laboratory for 24 h, and recorded the moisture content. We then oven-dried the mats and calculated the gravimetric water content. The r^2 for the two methods was 0.79.

Two gypsum blocks were buried in the arboreal soil mats of three branches per tree in each of three sample trees per site. The mat moisture levels were checked every 3–4 days from the ground, using wires that connected each sensor to the ground. Each time we climbed, we verified that the blocks were imbedded in the mats and that there was no apparent degradation of the gypsum blocks.

We carried out greenhouse studies to document the seed bank dynamics after epiphytes had died at the mid- and lower elevation sites. In June 1998, we collected 24 canopy mats (0.75×0.5 m) from four *F. tuerckheimii* trees in the upper forest. We clipped all of the "above-mat" stems of vascular epiphytes and pulled out all of the non-vascular plants from half the mats ("pruned"); the other half of the samples served as controls ("intact"). We placed them in a greenhouse (18×7 m, with translucent corrugated roofing sheets) that contained an automatically timed spraying system to deliver water. All mats were watered (misted 2 times per day for 5 min). The mean maximum and minimum temperatures measured weekly for 1 year were 25.2°C and 15.0°C. Conditions mimicked ambient conditions of the upper site.

Over a period 12 months, we identified each emerging individual seedling to genus or species, measured its height, and recorded the number of individuals of each taxon. Our greenhouse was located at 1,400 m. We were able to identify seedlings as young as 2 months old with our existing voucher seed collection and matched photographic collection of seedlings of over 80 species native to the MCFR.

Statistical analyses

We treated the individual plant as the independent sample unit (regardless of the mat or tree of origin), because a previous study in Monteverde on epiphyte survivorship showed that there was no effect of tree or mat on epiphyte longevity (Matelson et al. 1993). In that study, epiphyte longevity was normally distributed, and there was no effect of epiphyte attachment to particular mats (*t*-test, $P<0.35$), and no significant regressions of longevity on mat volume ($r^2=0.04$, $P<0.19$) or number of plants per mat ($r^2=0.01$, $P<0.64$). All statistical analyses were carried out with SYSTAT (1999).

Results

There were no significant differences in net rates of leaf production or leaf or plant mortality (*t*-tests) between intact and disturbed controls (Table 1), indicating that transplantation alone does not affect the viability or growth of epiphytes, so any differences in plant performance between the upper forest location and the two transplant sites should be due to the environmental differences rather than the impact of moving the mats.

In the upper elevation site, all of the taxa showed positive net leaf production and high longevity. However, we found striking and significant differences between plants in the upper forest versus mid- and lower elevation sites for net leaf change and plant longevity (Fig. 2). We used two-sample *t*-tests between each possible pair of sites, with Bonferroni correction for multiple comparisons. Effects were consistently more pronounced for transplants that were initiated in the dry season. For the dry season transplant, all four taxa showed significantly reduced net leaf production and longevity in the mid- and

lower elevation sites relative to the upper site. Differences in net leaf change ranged between –50 and –110% (Fig. 2A).
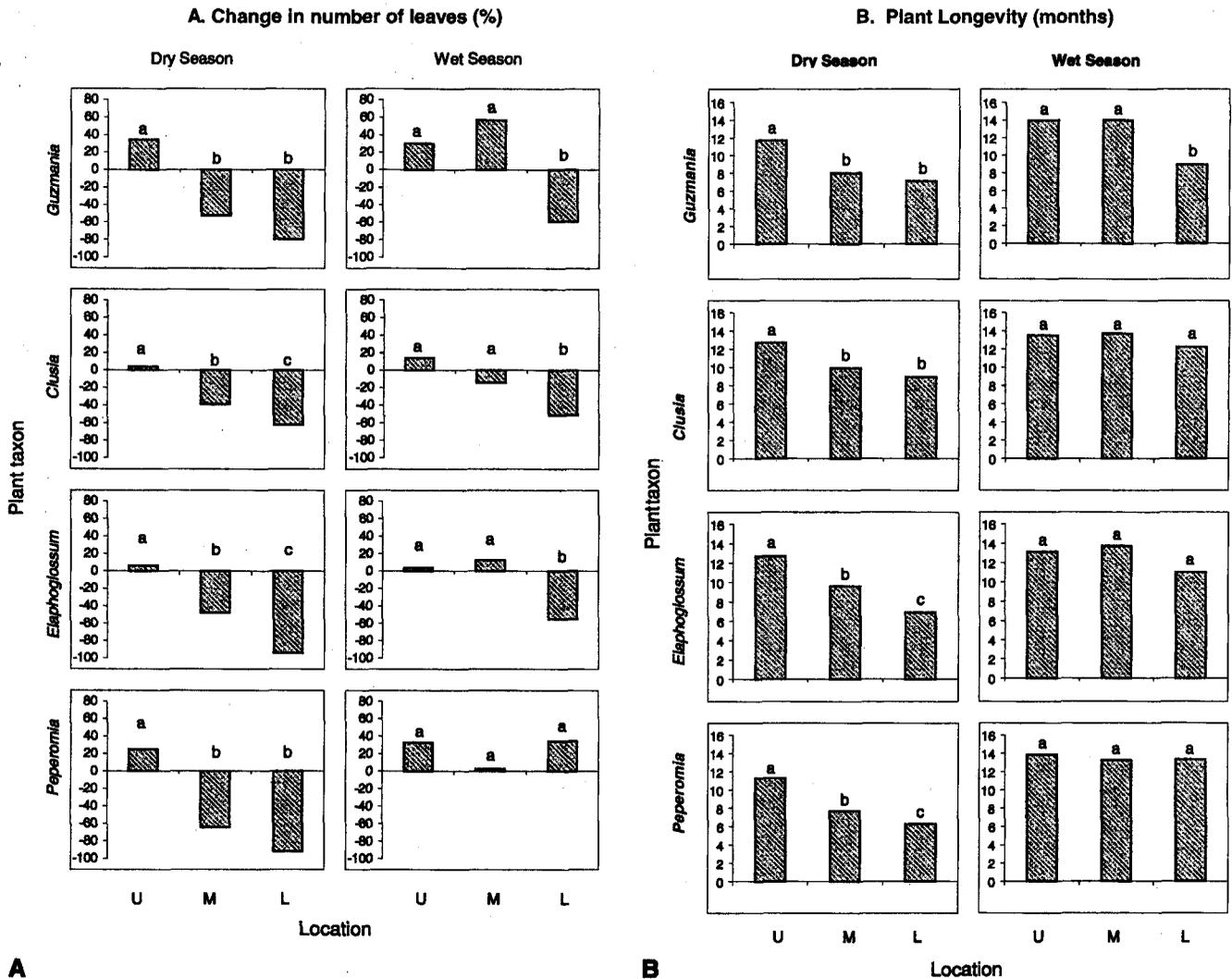
Different plant taxa showed different degrees of sensitivity. For *Clusia* and *Elaphoglossum*, leaf change was significantly more negative in the lower elevation than in the mid-elevation site, whereas the other two taxa did not show a significant difference between these two sites. We found significantly reduced longevity of *Elaphoglossum* and *Peperomia* (but not the other two taxa) at the lower elevation relative to the mid-elevation site.

Differences between the transplants and the controls were much less striking for the wet season transplants. Only one taxon (*Guzmania*) showed a significant reduction in plant longevity. Three of the four taxa (all but *Peperomia*) showed a significant reduction in net leaf change in the lower elevation site, compared to the upper elevation site (Fig. 2B).

Our measurements of canopy input and moisture confirmed that although the dynamics of cloud water followed similar general seasonal patterns, epiphyte mats received progressively smaller amounts of cloud water input (Fig. 3) and retained progressively smaller amounts of moisture (Fig. 4), from highest to lowest elevation sites. Over the collection period, cloud water collectors at the lower elevation site received a total of 660 mm, which was less than one-third of the cloud water collected at the upper site (1,840 mm), with intermediate amounts in the mid-elevation location (1,057 mm). The relative moisture content of the mats of crown humus also differed significantly, with a mean of 90.8, 61.7, and 35.3% for upper, middle, and lower mats, respectively (one-way ANOVA, $P<0.05$).

At the end of the 18-month experiment, following the death of nearly all of the epiphytes, we found startling and unexpected changes in composition of the canopy communities. We observed that numerous new seedlings had sprouted in the remaining mats of canopy humus that were still tied to the tree branches. These seedlings were neither re-sprouting epiphytes nor epiphyte seedlings, as we had expected, but rather, they were terrestrial seedlings that had grown out of the seed bank that existed in the residual arboreal soil. Although it was impossible to identify them to species at this young stage of their lives, we drew upon our previous experience to identify them to genus. The most numerous were gap-colonizing terrestrial species of the genera *Cecropia* (Moraceae), *Witheringia* (Solanaceae), and *Conostegia* (Melastomataceae). We have encountered these taxa as seedlings only extremely rarely in primary forest. They are virtually never seen in the canopy, but we have noted that they are occasionally present when epiphyte mats fall to the forest floor in canopy gaps that are large enough to receive direct light.

The greenhouse experiments mimicked what we found in the field. The abundance of seedlings was significantly greater in the pruned than the intact mats (1,531 and 326 seedlings, 127.6 per mat and 27.1 per mat, respectively; *t*-test, $P<0.01$). The number of taxa for

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A. Change in number of leaves (%)

Dry Season   Wet Season

(Plant taxon: Guzmania, Clusia, Elaphoglossum, Peperomia)

Location: U   M   L

B. Plant Longevity (months)

Dry Season   Wet Season

(Plant taxon: Guzmania, Clusia, Elaphoglossum, Peperomia)

Location: U   M   L

A   B

Fig. 2A, B Effects of experimental movement of epiphytic taxa from upper to mid- and lower elevation sites where they were exposed to progressively less cloud water. **A** Percent change of number of leaves was calculated as: {[(number of new leaves-number of dead leaves)/number of original leaves]×100}. **B** Plant longevity was recorded as the number of months from the outset of the study that the plant remained alive. The different letters indicate a significant difference at the 0.05 level with a Bonferroni correction factor for multiple comparisons. The number of plants and leaves is given in Table 2

all of the mats (taxon density) was also significantly higher in the pruned than the intact mats (37 vs 25 species). Individuals reached a mean height of 47 cm (±16.3 cm) with a maximum of 1.6 m.

The composition of individuals in the pruned mats was overwhelmingly dominated by terrestrial taxa (90.4%), whereas the intact mats had only a negligible number of terrestrial individuals (0.9%). The three most common taxa in the pruned mats (*Cecropia, Conostegia, Solanum*) were terrestrial gap-colonizing species, which appear in light gaps following tree falls, and exhibit early successional characteristics such as rapid growth and intolerance to shade (Haber 2000). This contrasted with the three most

common seedlings that appeared in the control mats (*Oreopanax, Neomirandea, Lysianthes*), which are obligate scandent epiphytic herbs or shrubs. Thus, the removal of an overtopping "epiphyte canopy" – whether by death due to desiccation (as in our field experiments) or by artificial removal from clipping (as in our greenhouse experiments) – appears to change the species composition of the epiphyte mats from epiphytic- to terrestrial-dominated.

Discussion

Our transplant experiments showed that exposure to environments with progressively less cloud water – conditions predicted as increasing for tropical montane forest by GCMs – had a generally negative effect on growth of epiphytic taxa, but the severity depended on the season of transplant and plant species. Our results predict that effects of climate change will not only result in decreased rates of epiphyte growth and leaf production and increased mortality, but may also radically alter the composition of canopy communities by releasing the seed bank of terrestrial plants within arboreal soils.
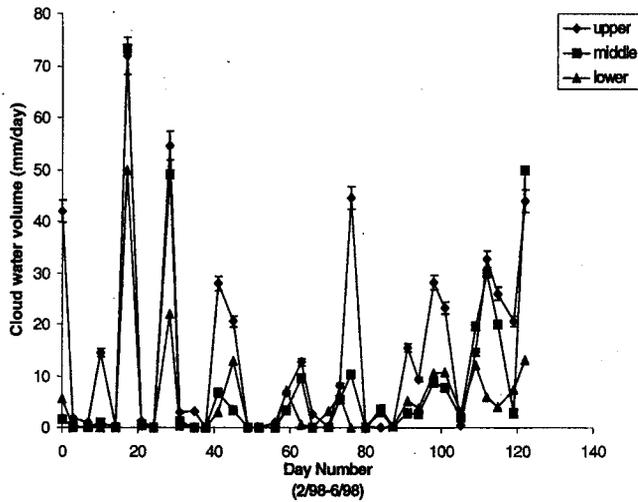
Fig. 3 Moisture input to the epiphyte mats. Volume of cloud water during 4 months of the dry season, measured every 3–4 days with passive cloud water collectors (29) in the canopy of four study trees at each of the three sites. Each point is the mean of four collectors; *bars* are standard errors
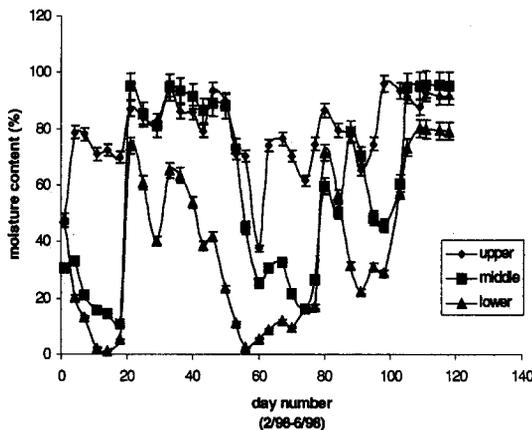
Fig. 4 Moisture retention by the epiphyte mats. Moisture content (%) of crown humus from experimental epiphyte mats at each of the three sites, measured with gypsum blocks every 3–5 days during 4 months of the dry season. Each point is the mean of eight gypsum blocks (two per tree for four trees); *bars* are standard errors

We envision the following scenario if GCM predictions for Monteverde are borne out: vascular and non-vascular epiphytes will decline, resulting from lack of cloud-derived water, which will then spur the germination and temporary occupation of the remaining crown humus by invading terrestrial plants from the seed bank. Over time, canopy-held soil will fall away and will not be replaced due to the lack of the nourishing cloud water that originally formed and maintained this material. Ultimately, the canopy of the upper cloud forest will become bare of crown humus and support only the most desiccation-resistant epiphytes (those with succulent or poikilohydric leaves, tank bromeliads), such as now exist in lower elevation forests.

Sufficient data exist to demonstrate the importance of epiphytes to ecosystem function and to show that they derive a significant fraction of their nutrition from atmospheric sources (Nadkarni and Matelson 1991; Clark et al. 1998a; Hietz et al. 1999). With epiphytes, the canopy can support a rich array of species and contribute to ecosystem biodiversity, productivity, and resiliency. Without epiphytes, environments in which they are prevalent could lose an important mechanism to capture and store nutrients and water. Thus, our results confirm the concerns that have been articulated about the future health of tropical montane forests (Bawa and Markham 1995; Benisten et al 1997; Loope and Giambelluca 1998).

Our study also indicates that epiphytes are potentially useful as indicator species for even subtle changes in climate characteristics. Optimal indicator species react quantitatively to relevant stress, respond within appropriate time scales, can be manipulated to calibrate responses, and occupy critical or "keystone" positions in the community. Thus, they would be more responsive than terrestrially rooted plants, which have access to the buffered pools of moisture and soil nutrients.

The unexpected emergence of the "suppressed" terrestrial seed bank from canopy mats is similar to the release of terrestrial seed banks after removal of herbs and bryophytes in other ecosystems, e.g., high arctic meadows (Sohlberg and Bliss 1987) and alvar grasslands (Zamfir 2000). Studies in various plant communities and greenhouse experiments have demonstrated that the germination and/or seedling emergence of vascular plants are affected by herbs, mosses, and lichens. The effects may be positive or negative; the latter has been related to their structure, allelopathy, water retention and/or shading effects that reduce light intensity or affect the red/far red ratio (During and van Tooren 1990). Understanding the mechanisms for the release of the latent seed bank in the crown humus of canopy-held mats that are also dominated by bryophytes, offers a rich area for future study of seed bank dynamics.

Canopy communities thus provide a unique combination for both single-species approaches and ecosystem approaches to study environmental change. Individual plants or plant parts can be monitored for changes in growth, nutrient status, or physiology. In addition, whole canopy communities – their arboreal soil, seed banks, invertebrates, vascular and non-vascular plants, and vertebrates – can also be monitored for emergent properties (e.g., net primary productivity, water retention capacity, species diversity) to provide insights beyond the reaction of individuals or particular taxa. If future research in other tropical cloud forest confirms the results reported here, then tropical montane forest canopy communities may become the world's best first biotic indicators of change.

References

Bawa KS, Markham A (1995) Climate change and tropical forests. Trends Ecol Evol 10:348–349

Benisten H, Diaz F, Bradley RS (1997) Climatic change at high elevation sites: an overview. Clim Change 36:233–251

Benzing DH (1998) Vulnerabilities of tropical forest to climate change: the significance of resident epiphytes. Clim Change 39:519–540

Bohlman S, Matelson TJ, Nadkarni NM (1995) Moisture and temperature patterns of canopy humus and forest floor soils of a montane cloud forest, Costa Rica. Biotropica 27:13–19

Bruijnzeel LA (1989) Deforestation and dry season flow in the tropics: a closer look. J Trop For Sci 1:229–243

Campbell GS, Gee GW (1986) Water potential: miscellaneous methods. In: Klute A (ed) Methods of soil analysis, part 1. Physical and mineralogical methods, 2nd edn. Agronomy 9. American Society of Agronomy, Madison, Wis. pp 619–633

Clark KL, Nadkarni NM, Schaefer DS, Gholz HL (1998a) Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. J Trop Ecol 14:27–45

Clark KL, Nadkarni NM, Schaefer DA, Gholz HL (1998b) Cloud water and precipitation chemistry in a tropical montane forest, Monteverde, Costa Rica. Atmos Environ 32:1595–1603

Clark KL, Lawton RO, Butler PR (2000) The physical environment In: Nadkarni NM, Wheelwright, NT (eds) Monteverde: Conservation and ecology of a tropical cloud forest. Oxford University Press, New York, pp 15–38

Crump ML, Hensley FR, Clark KL (1992) Apparent decline of the golden toad: underground or extinct? Copeia 1992:413–420

Donnelly MA, Crump ML (1998) Potential effects of climate change on two neotropical amphibian assemblages. Clim Change 39:541–561

During J, van Tooren BF (1990) Bryophyte interactions with other plants. Bot J Linn Soc 140:79–98

Falconer E, Falconer PD (1980) Determination of cloud water acidity at a mountain observatory in the Adirondack Mountains on New York State. J Geophys Res 85:7465–7470

Feild TS, Dawson TE (1998) Water sources used by *Didymopanax pittieri* at different life stages in a tropical cloud forest. Ecology 79:1448–1452

Haber WA (2000) Plants. In: Nadkarni NM, Wheelwright, NT (eds) Monteverde: conservation and ecology of a tropical cloud forest. Oxford University Press, New York, pp 39–94

Hietz P, Wanek W, Popp M (1999) Stable isotopic composition of carbon and nitrogen, and nitrogen content in vascular epiphytes along an altitudinal transect. Plant Cell Environ 22:1435–1443

Holdridge L (1967) Life zone ecology. Tropical Science Center, San José

Ingram SW, Nadkarni NM (1993) Composition and distribution of epiphytic organic matter in a neotropical cloud forest, Costa Rica. Biotropica 25:370–383

Lawton, RO, Campbell J (1984) Climate and vegetation of a neotropical montane forest. Bull Ecol Soc Am 65:59

Lawton RO, Dryer VL (1980) The vegetation of the Monteverde Cloud Forest Reserve. Brenesia 18:101–116

Lawton RO, Nair US, Pielke RA, Welch RM (2001) Climatic impact of tropical lowland deforestation on nearby montane cloud forests. Science 294:584–587

Loope LL, Giambelluca TW (1998) Vulnerability of island tropical montane forest to climate change, with special reference to East Maui, Hawaii. Clim Change 39:503–517

Lugo AE, Scatena F (1992) Epiphytes and climate change research in the Caribbean: a proposal. Selbyana 13:123–130

Matelson TJ, Nadkarni NM, Longino JT (1993) Survivorship of fallen epiphytes in a neotropical cloud forest, Monteverde, Costa Rica. Ecology 74:265–269

Nadkarni NM (1981) Canopy roots: convergent evolution in rainforest nutrient cycles. Science 213:1024–1025

Nadkarni NM, Longino JT (1990) Macroinvertebrate communities in canopy and forest floor organic matter in a montane cloud forest, Costa Rica. Biotropica 22:286–289

Nadkarni NM, Matelson, TJ (1991) Litter dynamics within the canopy of a neotropical cloud forest, Monteverde, Costa Rica. Ecology 72:2071–2082

Nadkarni NM, Matelson TJ, Haber WA (1995) Structural characteristics and floristic composition of a neotropical cloud forest, Monteverde, Costa Rica. J Trop Ecol 11:481–495

Nadkarni NM, Lawton RO, Clark KL, Matelson TL, Schaefer DA (2000) Ecosystem ecology and forest dynamics. In:Nadkarni, N, Wheelwright N (eds) Monteverde: ecology and conservation of a tropical cloud forest. Oxford University Press, New York, pp 303–350

Odum HT, Briscoe GA, Briscoe CB (1970) Fallout radioactivity and epiphytes. In: Odum HT, Pigeon RF (eds) A tropical rainforest, Chap H-23. National Technical Information Service, Springfield, Va.

Perry D (1978) A method of access into the crowns of emergent and canopy trees. Biotropica 10:155–157

Pounds JA, Crump ML (1994) Amphibian declines and climate disturbance: the case of the Golden Toad and the Harlequin Frog. Conserv Biol 8:72–85

Pounds JA Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. Nature 789:611–614

Rao DN (1982) Response of bryophytes to air pollution. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, London, pp 445–471

Sohlberg, H, Bliss LC (1987) Responses of *Ranunculus sabinei* and *Papaver radicatum* to removal of the moss layer in a high-arctic meadow. Can J Bot 65:1224–1228

Still CJ Foster PN, Schneider SH (1999) Simulating the effects of climate change on tropical montane cloud forests. Nature 789: 608–610

SYSTAT (1999) SPSS Science. Chicago, Ill.

Vance ED, Nadkarni NM (1990) Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. Soil Biol Biochem 22:677–684

Weathers KC (1999) The importance of cloud and fog in the maintenance of ecosystems. Trends Ecol Evol 14:214–215

Zamfir M (2000) Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. Oikos 88:603–611