Survival and reproductive fitness of two species of Pleurothallid orchids along a changing climatic gradient

Kerry Kemp

Dept. of Ecology and Evolutionary Biology, University of Colorado-Boulder

ABSTRACT

Increasing periods of consecutive dry days, upward altitudinal shifts in orographic cloud formation, and increasing minimum daily temperatures occurring due to global climate change are rapidly changing the climatic parameters of cloud forests in Monteverde, Costa Rica, where hundreds of diminutive orchids thrive. In order to analyze the affect of changing microclimate on orchid fitness, two species of Pleurothallid orchids, *Lepanthes eximia* (Range: 1100-2050 m) and *Lepanthes monteverdensis* (Range: 1400-1550 m) were transplanted to plots at 1530 m, 1645 m, 1800 m. They were monitored daily for leaf, flower, and fruit production and leaf thickness. The microclimatic conditions at each site were significantly affected by elevation (ANOVA with block design; min. temp vs. elevation: F = 8.43, p = 0.001; max temp. vs. elevation: F = 0.88, p = 0.45; precipitation vs. elevation: F = 8.16, p = 0.002). *Lepanthes monteverdensis* responded to this changing climatic gradient with significantly higher leaf thickness (ANOVA; F = 11.67, p < 0.0001) and a positive change in plant size (ANCOVA; F = 5.71, p = 0.001). Flowering in *L. monteverdensis* directly mirrored days with measurable precipitation as well, with these displays of increased fitness most prevalent at the mid-elevation site. A trend towards increasing mortality in *L. eximia* was predominant at lower elevation sites. Both species responded to microclimatic variables, suggesting that these factors are important in their survival and reproduction. With changing climatic conditions, higher elevations may now serve as a climate refuge for Pleurothallid species.

RESUMEN

Los períodos crecientes de días secos consecutivos, hacia arriba a nivel altitudinal cambia en la formación de las nubes, y en el incremento eb la mínima temperatura diaria que ocurren debido al cambio global del clima, lo que cambia rápidamente los parámetros climáticos de bosques de nuboso en Monteverde, Costa Rica, donde centenares de orquídeas diminutas prosperan. Para analizar el afecto de microclima cambiante en la salud de la orquídea, dos especie de orquídeas de Pleurothallid, *Lepanthes eximia* (la Gama: 1100-2050 m) y *Lepanthes monteverdensis* (la Gama: 1400-1550 m) fueron trasplantados a parce las a 1530 m, 1645 m, 1800 m. Ellos fueron controlados en la proucción de hojas, flores, y en la producción de fruta y el espesor de hoja. La microclima en cada sitio fue afectado apreciablemente por la elevación (ANOVA con el diseño del bloque; temporero de min. vs. la elevación: F = 8,43, P = 0,001; temporero máx. vs. la elevación: F = 0,88, P = 0,45; la precipitación vs. la elevación: F = 8,16, P = 0,002). *Lepanthes monteverdensis* respondió a este cambio el declive climático con mas espesor de hoja (ANOVA; F = 11,67, P <0,0001) y un cambio positivo en el tamaño de planta (ANCOVA; F = 5,71, P = 0,001). La produccion de flores en *L. monteverdensis* se reflejó directamente en lost días con precipitación mensurable, hay despliegues de incremento en la salud muy predominante en el sitio de elevación medio. Una tendencia hacia la mortalidad creciente en *L. eximia* fue predominante en sitios más bajos de elevación. Ambas especie respondieron a variables de microclima, sugiriendo que estos factores son importantes en su sobrevivencia y la reproducción. Con condiciones climáticas cambiantes, las elevaciones más altas ahora pueden servir como un refugio de clima para la especie de Pleurothallid.

INTRODUCTION

Tropical montane cloud forests are unique ecosystems where consistent abiotic conditions result in high species richness and endemism (Küper et al. 2004). These forests exist in areas of low orographic cloud formation over mountaintops (Stills et al. 1999). In Monteverde, Costa Rica these orographic clouds form when the trade winds from the Caribbean coast encounter the continental divide of the Cordillera de Tilarán mountain range and are forced upward (Pounds et al. 1999, Still et al. 1999, Clark et al. 2000). This forced ascension causes adiabatic cooling and condensation of water particles (Barros and Lettenmaier 1994), forming the mists characteristic of this forest (Pounds et al. 1999, Still et al. 1999). However, as the mists collide with the warm, dry air from the Pacific slope, they quickly dissipate, resulting in localized warming and drying as altitude decreases (Barros and Lettenmaier 1994), creating a distinct climatic gradient moving down the Pacific slope from the continental divide.

The result of this adiabatic cooling is a reduction in air temperature and increased precipitation with increasing altitude, creating conditions where horizontal precipitation (mist) and reduced evapotranspiration contribute significantly to cloud forest precipitation (Clark et al. 2000, León-Vargas et al. 2006). Precipitation may also vary spatially with exposure to the trade winds (Clark et al. 2000). The interacting components of topographic position, exposure to trade winds, and precipitation levels play a major role in controlling microclimate conditions in Monteverde (Clark et al. 2000).

Global climate change is shifting the abiotic conditions in these forests, increasingly compromising their borders. In Monteverde, reductions in mist frequency with the upward elevational movement of orographic cloud formation (Pounds et al. 1999, Still et al. 1999) is consistent with observed large-scale climate trends and greenhouse warming occurring in the tropics (Graham 1995, Pounds et al. 2006). During the dry season, the trade winds drive the formation of orographic clouds between 1400 and 1700 m, influencing precipitation patterns, cloud water deposition, and mist formation (Clark et al. 2000). Global warming trends are likely to shift this relative humidity surface upwards by several hundred meters during the dry season, greatly changing the microclimatic conditions for epiphytes (Still et al. 1999), and possibly exposing them to desiccation (León-Vargas et al. 2006). Pendulous epiphytes are highly dependent on atmospheric moisture and cloud water deposition from mists, surviving better when relative humidity is high (Still et al. 1999); therefore, daily microclimatic patterns may be important (Benzing 1998, León-Vargas et al. 2006). In the dry season, rainfall is more sporadic and microclimatic variability is greatest (Clark and Nadkarni 2000), these factors become especially important to the survival and fitness of epiphytes (Benzing 1998, Still et al. 1999, Haber 2000). In addition, species may undergo a shift in elevational distribution in response to changes in temperature and precipitation levels within their original range (Root et al. 2003, Parmesan 2006).

Orchids (Orchidaceae) contribute to a large portion of epiphytic diversity in tropical montane cloud forests (Küper et al. 2004) and are the richest epiphyte family in the Monteverde cloud forest (Atwood 2000, Haber 2000). Many endemic species of orchids are also found in these forests, where climatic conditions determined by orographic cloud formation make conditions ideal for their growth (Küper et al. 2004).

Microclimatic conditions and weather are important factors affecting the reproductive capability of orchid species (Pfeifer et al. 2006). Consequently, changes in abiotic conditions in response to global warming, such as rising orographic cloud formation, increasing frequency of consecutive dry days, and reduction of relative humidity (Pounds et al. 2006), have caused abiotic conditions important to the survival and reproduction of cloud forest orchids (Pfeifer et al. 2006) to consistently exist only at higher elevation sites (Still et al. 1999).

Two species orchids, *Lepanthes monteverdensis* and *Lepanthes eximia* were chosen for this study. *Lepanthes monteverdensis* is endemic to the Pacific slope of the Monteverde cloud forest, with a range from of 1400-1550 m in elevation (Hammel et al. 2003). *Lepanthes eximia* is more widely ranging, with a documented distribution from 1100-2050 m (Hammel et al. 2003). Although many orchids display mechanisms for water storage, these orchids-- of the subtribe Pleurothallidinae-- are characterized by diminutive size and the lack of pseudobulbs (water-storing stems) (Zuchowski 2005). This may increase their vulnerability to microclimate variability and localized drying.

This study sought to examine the growth and reproductive response of both orchid species to microclimatic conditions along an elevational gradient. Because conditions on the lower edge of their distribution are becoming unfavorable, higher elevations may provide a climate refuge for these species (Parmesan 2006). Therefore, it was expected that individuals of both species would respond differently to microclimates at low and high elevations. Because *L. eximia* is a more widely distributed species, it should display increased fitness, and hence increased growth and reproduction, at higher elevations where there is consistent horizontal precipitation throughout the dry season. *Lepanthes monteverdensis,* with a much more limited distribution, will have a more complex response to microclimate on an elevational gradient, only increasing its fitness up to elevations where conditions approach the climatic parameters under which it evolved.

MATERIALS AND METHODS

Study Sites

Three study plots were established on the property of the Monteverde Biological Station, situated on the Pacific slope of the Tilarán mountain range, which bisects Costa Rica and separates the Atlantic and Pacific slopes. Study areas were situated in lower montane wet forest and pre-montane wet forest, at elevations of 1530 m, 1645 m and 1800 m (on the Continental Divide). Average annual temperature at Monteverde is 18.5 °C, with a mean annual precipitation of 2519 mm (Clark et al. 2000). All sites were north-northeast facing to intercept moisture-laden trade winds. The relative percentages of canopy opening, as measured by a canopy densiometer, were 11.44%, 13.78%, and 26.26% at the low, mid and high elevation plots, respectively.

Experimental Methods

The study was conducted during late-April and early-May, at the end of the dry season. At each of the three study sites described above, 20 *L. eximia* specimens and 12 *L. monteverdensis* specimens were collected and transplanted from naturally occurring

populations from a single location (for *L. eximia*), or from a combination of nearby or lower elevation sources (for *L. monteverdensis*). Individuals were arranged on north-northeast facing branches and trunks of varying sizes at each site. Mist collectors and min-max thermometers were hung centrally within plots to monitor daily precipitation and daily minimum and maximum temperature values. For days on which data were not collected, temperature and precipitation levels from a nearby site were drawn upon to infer missing data. Each individual was monitored every other day for new leaf, flower, or fruit production. In contrast, observations of flower or bud development were made daily to estimate the exact time at which flowers were produced. Additionally, leaf thickness was measured with calipers to determine water storage ability of individual plants at each elevation. The single largest leaf of each individual plant was marked with indelible ink and measured it consistently throughout the data collection period. New growth was also marked with indelible ink to prevent double counting on subsequent observation periods. Plant mortality was recorded and net change in plant size was determined by subtracting the final from the initial numbers of leaves.

Statistical Analyses

A one-way test of variance with a block design, with days being blocked, was used to characterize the effect of elevation and starting size on plant fitness. Leaf thickness was contrasted at different elevations using a 1-way ANOVA. For both species, the relationship between elevation and fitness was investigated using a one-way ANCOVA (a one-way analysis of co-variance), where starting size and elevation were the co-variants and total production of leaves, flowers, or fruits were the dependent variables. Mortality in *L. eximia* was tested at varying elevations using a Chi- Squared One Sample Test for Goodness of Fit (Ambrose et al. 2002).

RESULTS

The microclimate of each study site was characterized by combined rainfall and horizontal precipitation, in addition to minimum and maximum daily temperatures (*Figure 1*). The microclimate varied between each habitat along an altitudinal gradient, although maximum temperatures did not significantly vary at the sites (One-way analysis of variance with block design; min. temp vs. elevation: $F = 8.43$, $p = 0.001$; max temp. vs. elevation: $F = 0.88$, $p = 0.45$; precipitation vs. elevation: $F = 8.16$, $p = 0.002$). Climatic conditions were additionally impacted on a daily basis, with some days having significantly different precipitation or temperatures than others (One-way analysis of variance with block design, blocked by day; max. temp vs. day: $F = 7.16$, $p < 0.0001$; min temp. vs. day: $F = 2.89$, $p = 0.001$; precip. vs. day: $F = 3.07$, $p = 0.004$).
  Average leaf thickness of individual plants differed at each elevation in *L. monteverdensis* (ANOVA; $F = 11.67$, $p < 0.0001$), but not in *L. eximia* (ANOVA; $F = 0.45$, $p = 0.0955$; *Figure 2*). Net change in plant size and numbers of flowers produced were additionally tested for responses to elevation, starting plant size, or both (One way analysis of covariance; x = elevation; co-variant = starting plant size). In *L. monteverdensis*, flower production was unrelated to elevation or starting size (F-value = 0.88, $p = 0.51$); however, change in plant size varied significantly across the climatic
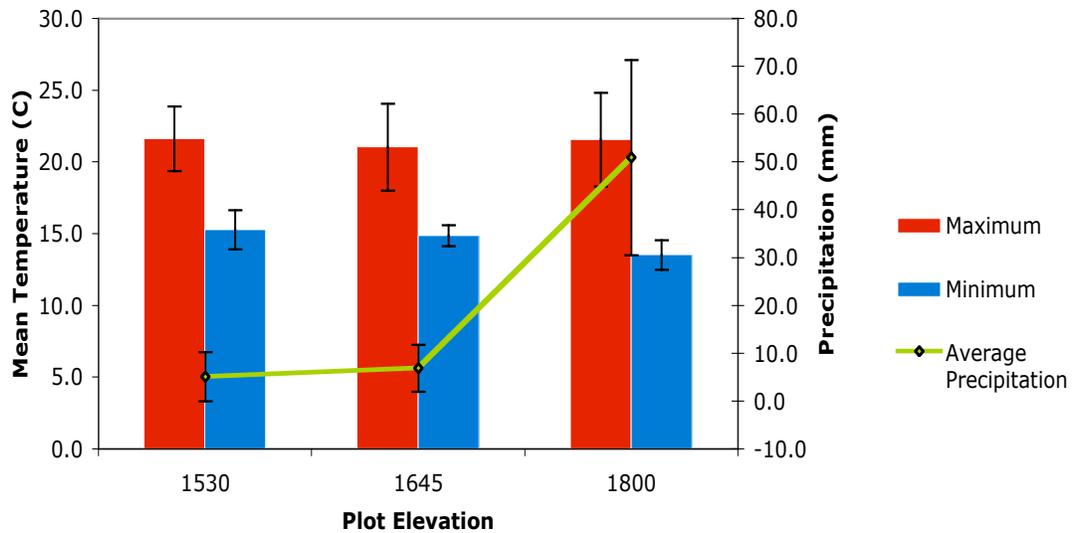
Figure 1: Mean minimum and maximum temperatures and average precipitation vary with elevation in the cloud forest of Monteverde, Costa Rica. Values for temperature and precipitation vary on the y-axes. The low elevation plot (1530 m) had a higher mean minimum temperature value (Min = 15.3 ± 0.32°C) and lower mean precipitation amount (precip = 5.1 ± 5.13 mm). Both the high elevation plot and the low elevation plot had the same mean maximum temperature (Max_{1550} = 21.6 ± 0.52°C; Max_{1800} = 21.6 ± 0.75°C). Although the daily minimum temperature varied only slightly between sites at 1530 and 1645 m (Min_{1530} = 15.3 ± 0.32°C, Min_{1645} = 14.9 ± 0.17°C), the site located at 1800 m was significantly colder (Min_{1800} = 13.5 ± 0.23°C). Precipitation at 1800 m was also significantly higher than at both lower elevation sites ($precip_{1800}$ = 51.0 ± 20.41 mL; $precip_{1645}$ = 6.9 ± 4.90 mL; $precip_{1530}$ = 5.1 ± 5.13 mL).
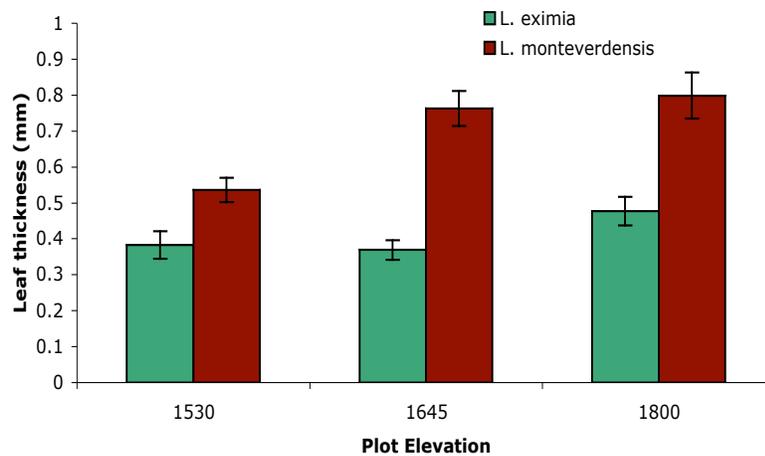

Figure 2: Mean leaf thickness of *L. monteverdensis* (red) in the dry season at three sites along an elevational gradient (Mean leaf thickness; 1530 m: 0.54 mm ± 0.03 mm, 1645 m: 0.76 ± 0.05 m, 1800 m: 0.80 mm ± 0.06 mm). Mean leaf thickness of *L. eximia* (green) was not significantly different over the change in elevation (Mean leaf thickness; 1530 m: 0.38 ± 0.04 mm, 1645 m: 0.37 ± 0.03 mm, 1800 m: 0.48 ± 0.04 mm).
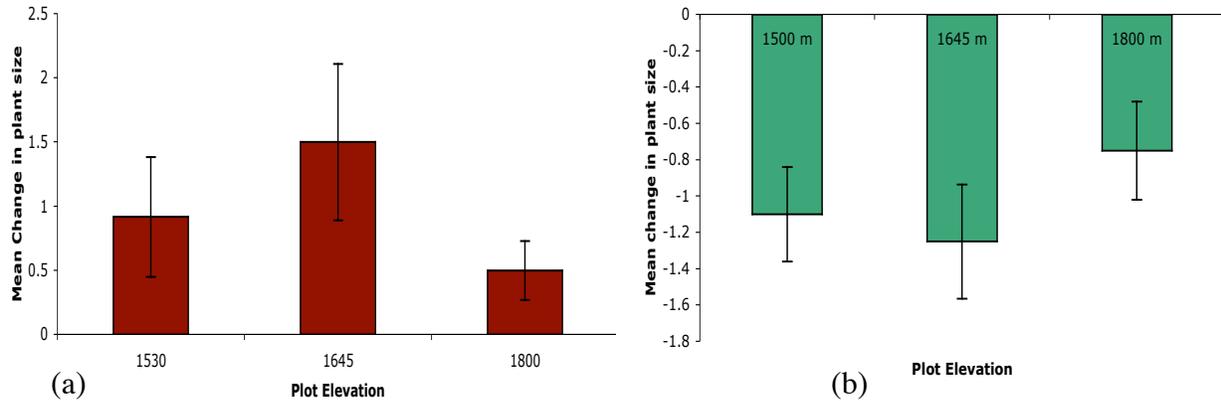
(a)　(b)

Figure 3: Mean change in plant size is (a) significantly effected by elevation in *L. monteverdensis* (1500 m: 0.92 ± 0.47, 1645 m: 1.5 ± 0.61, 1800 m: 0.5 ± 0.23) but (b) unrelated for *L. eximia* (1500 m: -1.1 ± 0.26, 1645 m: -1.25 ± 0.31, 1800 m: -0.75 ± 0.27). *L. eximia* shows leaf loss at all elevations, with the least change at 1800 m.

gradient (F = 5.71, p = 0.001; *Figure 3*), with elevation strongly determining final plant size (Elevation: F = 3.93, p = 0.03, Starting number of leaves: F = 3.16, p = 0.086, Elevation x starting number of leaves: F = 8.09, p = 0.002; *Figure 4c & 4d*). Although flower production showed no response (F = 0.46, p = 0.80), change in plant size in *L. eximia (Figure 4b)* was affected by the climatic gradient and starting size (F = 3.02, p = 0.018), with the strongest effect being starting plant size (Elevation: F = 0.15, p = 0.86; Starting number of leaves: F = 9.20, p = 0.004; Elevation x starting number of leaves: F = 4.02, p = 0.02; *Figure 4a & 4b*).

Mortality was observed in *L. eximia*, with 8 of 20 specimens dying at 1530 m, 7 of 20 specimens dying at 1645 m, and 2 of 20 dying at 1800 m. Although there was no significant difference in exhibited mortality levels at each site (Chi- Squared One Sample Test for Goodness of Fit: χ^2 = 3.65, d.f. = 2, p > 0.05), there seems to be a trend towards increased mortality at lower elevations. No mortality was observed among *L. monteverdensis* at any elevation.

The flowering of *L. monteverdensis* plants shows a temporal pattern in relation to precipitation, mirroring precipitation levels from the previous day. At the mid-elevation site, flowers were found to directly correspond with peaks in precipitation from the prior day (*Figure 5b*). Although this same trend is apparent at the 1800 and 1530 m sites, the correspondence is not as strong at these elevations (*Figure 5a and 5c*). Flowering phenology of *L. monteverdensis* was also plotted against minimum and maximum daily temperatures. Patterns of flowering showed a slight trend towards mirroring previous high nighttime minimum temperatures (*Figure 6*); this trend is greatest at the low elevation site (*Figure 6a*), with the mid-elevation site showing a similar trend (*Figure 6e*). The high elevation site displays less correspondence (*Figure 6c*). Flowering of *L. monteverdensis* did not have any graphical correspondence with maximum daily temperatures at any elevation (*Figures 6b* [1530 m], *6d* [1645 m], & *6f* [1800 m]).
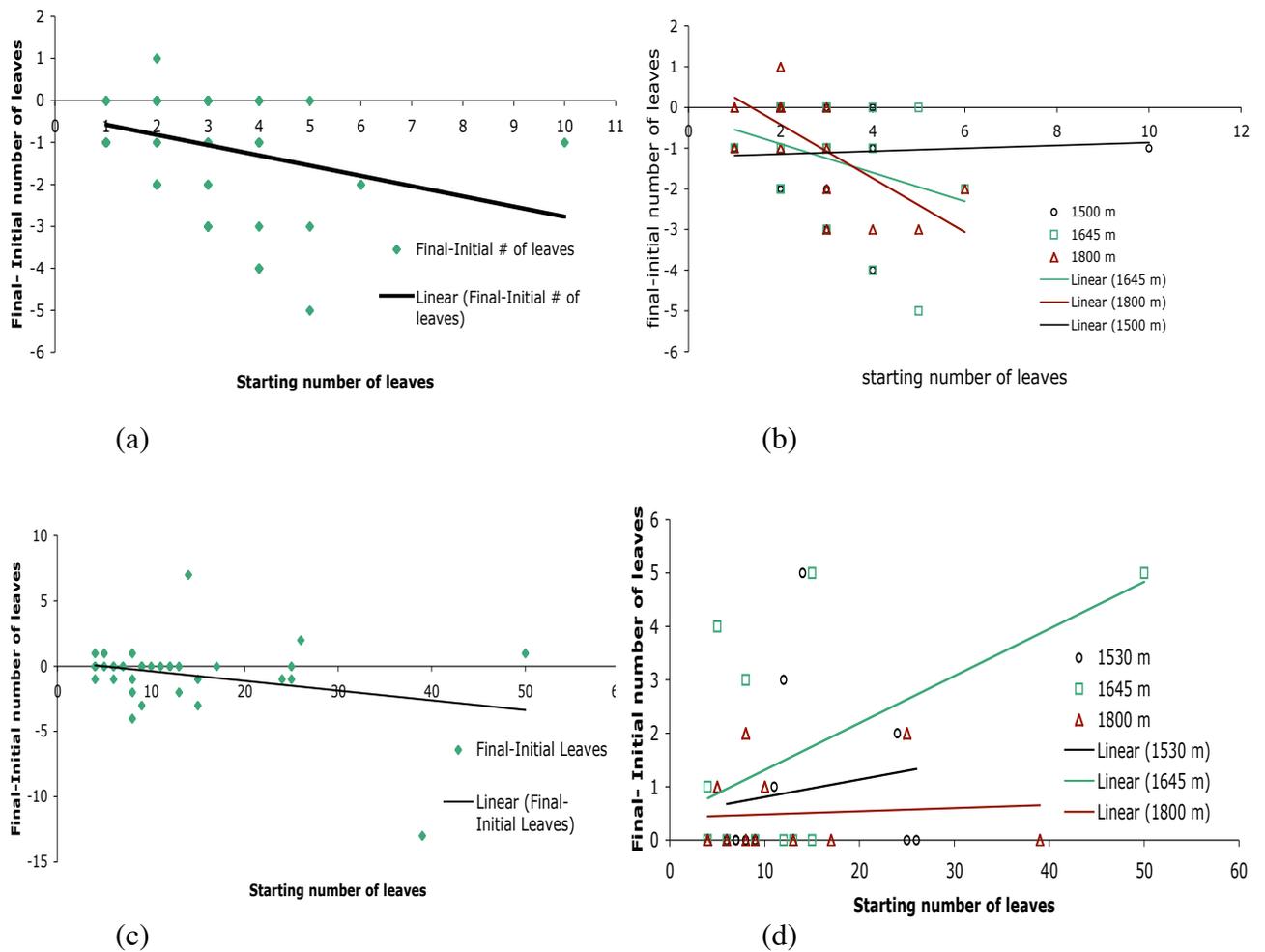
(a)

(b)

(c)

(d)

Figure 4: The change in plant size (as measured by change in number of leaves from start to finish) for *L. eximia* was (a) related to starting size, with larger individuals on average losing more leaves (though small plants only can lose a certain number of leaves before dying) and (b) elevation; there is, however, no strong trend at the lowest elevation site (black line), likely because plants of all sizes experienced mortality, and therefore lost all of their leaves. *L. monteverdensis* showed (c) no significant trend between initial size and leaf loss; individuals are not prone to more leaf loss if their starting size is smaller; conversely, (d) a strong relationship linked the interacting factors of elevation and starting size with positive leaf production, with the *L. monteverdensis* specimens at the mid-elevation site (1645 m; green line) showing the greatest growth.
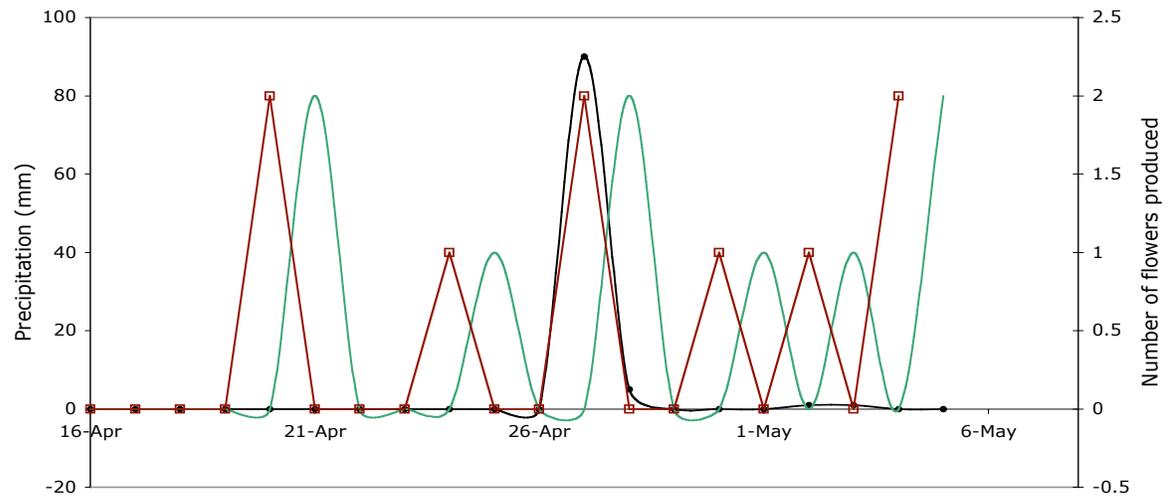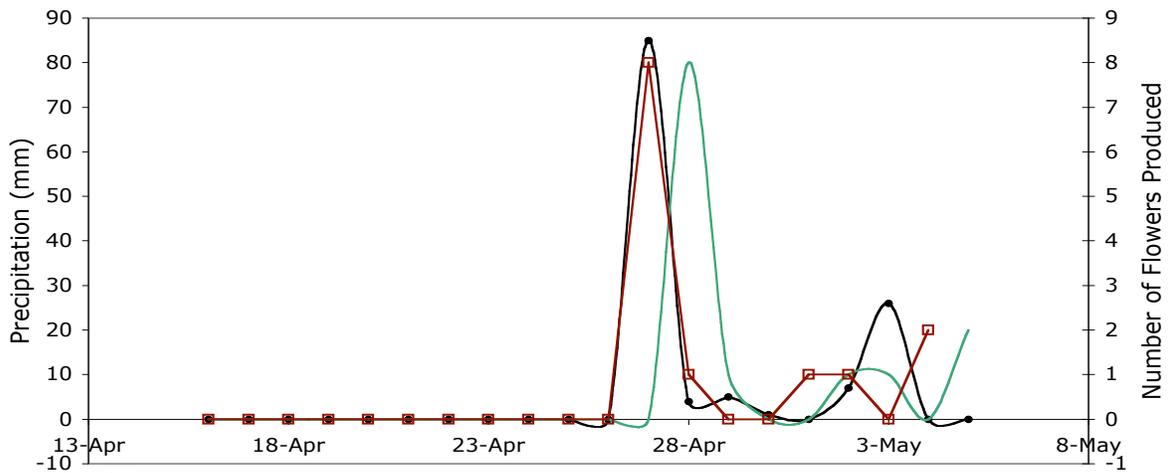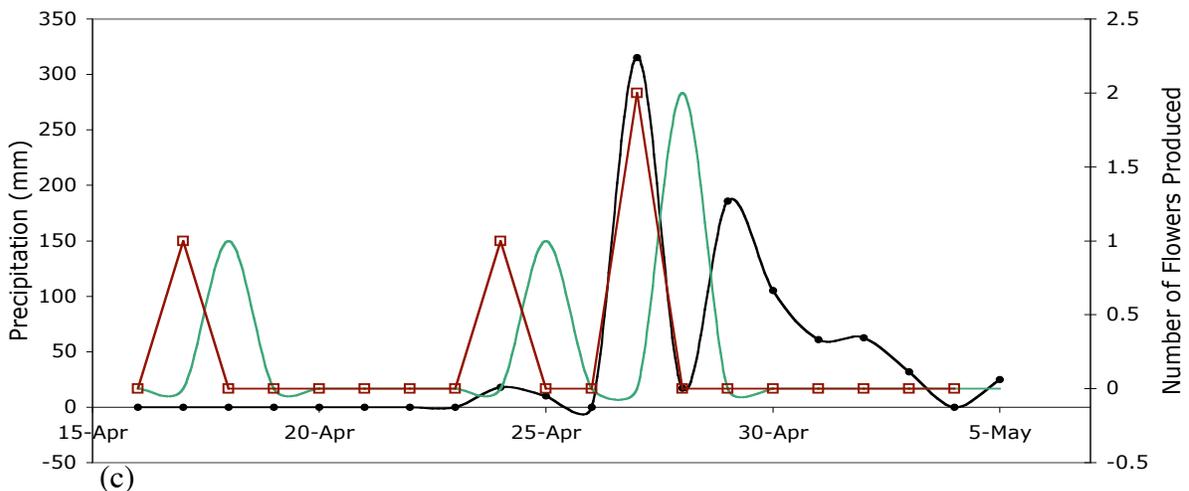
Figure 5: Flowering date minus 1-day (red line) corresponds with precipitation values (black line) for that day at (a) 1530 m, (b) 1645 m, and (c) 1800 m. The strongest pattern lies at the mid-elevation site [(b)]. Green lines show actual flower production by day. Values on both y-axes vary for each elevation.
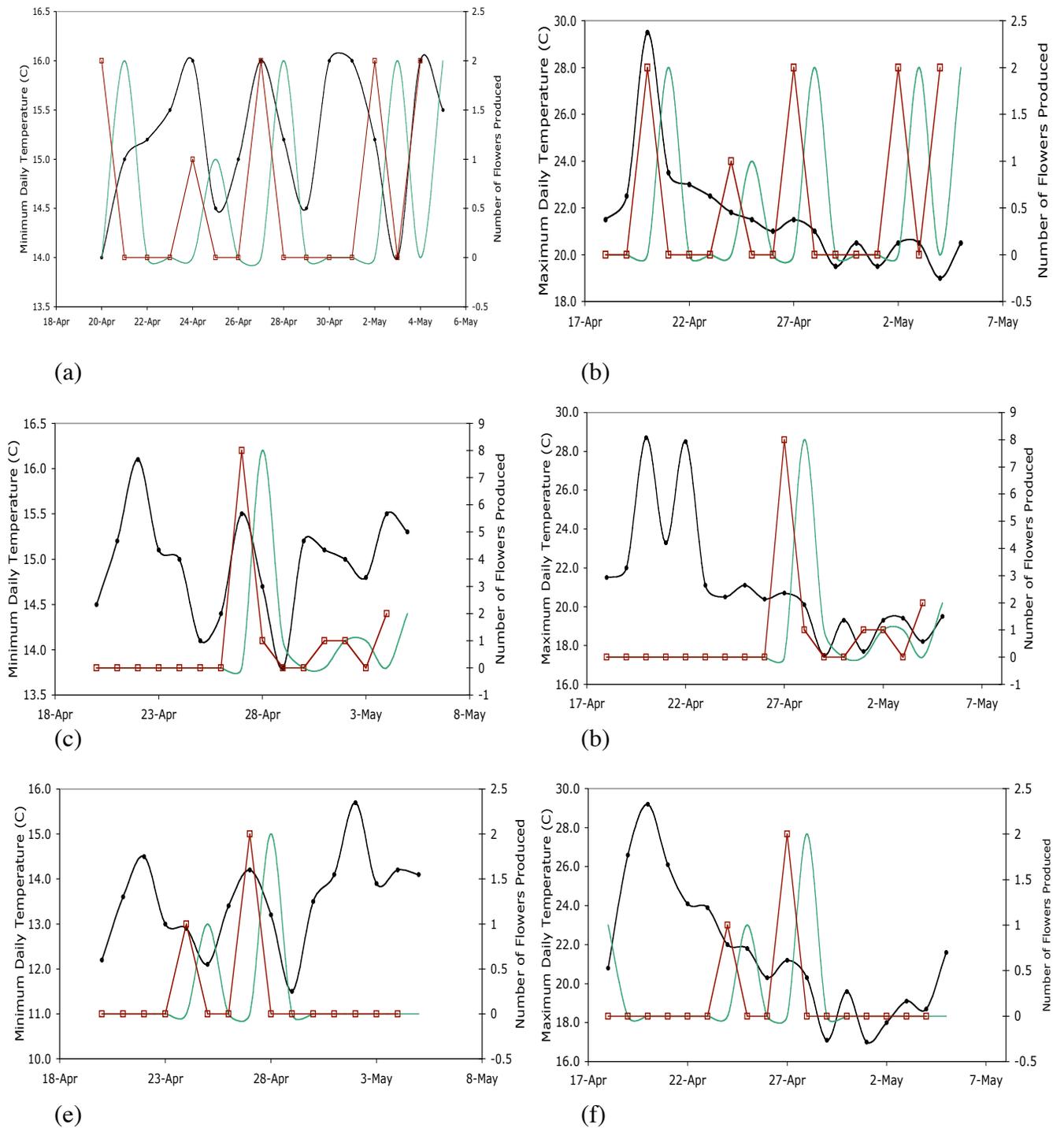
Figure 6: Days with higher minimum temperatures at (a) 1500 m, (c) 1645 m, and (e) 1800 m, are more likely to be followed by subsequent production of flowers in *L. monteverdensis*. Daily maximum temperatures [(b) 1500 m, (d) 1645 m and (e) 1800 m] do not correspond to flower production at any elevation. Black lines show daily minimum (left graphs) or maximum (right graphs) temperatures, green lines display flower production per day, and red lines show flowering date minus one day.

DISCUSSION

Microclimate varied along an elevational gradient due to orographic clouds formation at higher elevations (Pounds et al. 1999, Clark et al. 2000). These clouds significantly affect precipitation and temperature levels. Precipitation levels were greater at 1800 m, probably in part because of exposure to the moisture-laden trade winds from the Atlantic slope and adiabatic cooling of air particles at this elevation (Barros and Lettenmaier 1994). This exposure could have also resulted in higher average maximum daily temperatures than expected. Generally, temperatures were lower at night and more variable overall, with precipitation more consistent. Even though the mid-elevation and low elevation sites had north-northeastern exposure to trade winds, they were in the forest understory; therefore, experiencing fewer temperature extremes and moderated amounts of precipitation. While there is an overall difference in the mean precipitation and temperature of the three study sites, there is great day-to-day variability in these parameters. Variation may be linked to the El Niño-Southern Oscillation, which is the primary driver of temperature and precipitation fluctuations in tropical Central America (Malhi and Wright 2004). Hence, microclimatic conditions are impacted by daily variations in temperature and precipitation, as well as by elevation.

While leaf thickness of *L. monteverdensis* changed with increasing precipitation levels, *L. eximia* did not show this response. The relative size of the two species may explain this difference, with *L. monteverdensis* having larger, more succulent leaves than *L. eximia*. Thus, *L. eximia* may be unable to store extra water in its leaves, making it more susceptible to desiccation and changing climatic conditions. Also, perhaps after reaching a certain threshold (in this case, 10 days without measurable precipitation), these orchids were unable to recover from desiccation. Indeed, *L. eximia* suffered from high mortality at the low and mid-elevation plots, while *L. monteverdensis* had no mortality. Although the mortality experienced by *L. eximia* was not significantly affected by elevation, it was evident that *L. eximia* not experiencing desiccation stress and water deprivation were unlikely to experience mortality.

Plant size is significantly affected by climatic parameters in other species of orchids (Carey and Farrell 2002). It is not surprising, therefore, that both *Lepanthes* species studied here responded to the microclimate by either a positive or negative net change in number of leaves. *Lepanthes monteverdensis* had a net average gain of leaves at each site, with microclimate along an elevational gradient being the most important factor in its growth. Its performance was highest at 1645 m, indicating that conditions at this elevation were most optimal for its growth. *Lepanthes eximia*, the smaller of the two, experienced net leaf loss at each site related to its initial size, suggesting that small size can lead to leaf loss and subsequent mortality. Microclimate may be an additional factor that compounds stress for smaller plants, making them more susceptible to mortality. However, microclimate is not the primary determinant of relative fitness for *L. eximia*.

Lepanthes monteverdensis phenologically responded to precipitation, with flowering following a dry period punctuated by one or more rainy days. This pattern was most evident at the 1645 m, where a large pulse of flowering activity initially occurred within a day of the first heavy rain in at least ten days. The orchid's fitness was such that they were poised and able to respond immediately to this change in microclimate with a burst of reproductive activity. At 1530 m, *L. monteverdensis* produced small numbers of

flowers fairly consistently during the duration of data collection, with only slight pulses after heavy rainfall, perhaps as much in response to stress. *Lepanthes monteverdensis* at the higher elevation were less likely overall to produce flowers, possibly because they were not adapted to survive in the more exposed and cooler conditions found at the higher elevation plot. Rainfall during the vegetative growing season has been shown to significantly increase flower production in other orchid species as well (Carey and Farrell 2002).

In addition, the timing of flowering in *L. monteverdensis* also seemed to correspond with temperature fluctuations, following peaks in minimum nighttime temperatures. High minimum temperatures may be correlated to days with measurable precipitation, which are warmer due to radiant heating (Pounds et al. 1999, Pounds et al. 2006). Therefore, these two interacting components cannot be totally separated and caution is advised in applying these observed trends to other studies, especially because a longer time frame for study would likely define this trend and its affect on *L. monteverdensis* fitness better.   However, it can be inferred that *L. monteverdensis* responds more directly and is affected more strongly by minimum nighttime temperatures, which may be one of the limiting factors in its documented range. This has been documented for a native orchid species of Europe, whose northern distribution was limited by low temperatures (Carey and Farrell 2002).

Lepanthes monteverdensis, an endemic of the Monteverde cloud forest, responded most strongly to microclimate at a location above its previously documented upper elevational limit. Conditions at this elevation may be more optimal for its growth and reproduction, now more closely resembling the conditions under which this species evolved. In addition, *L. monteverdensis* was found naturally occurring at 1730 m, far above its documented range. Although this may be related to incomplete knowledge of its range, it suggests that *L. monteverdensis* may already be showing a biological response to microclimatic changes by changing its natural distribution.

This study suggests that *Lepanthes* fitness is affected by microclimatic conditions, especially precipitation, which may become less frequent on the lower edge of its distribution due to global climate changes (Pounds et al. 1999, Still et al. 1999). Mean daily minimum temperature increases in Monteverde, correlated with global warming trends, are resulting in favorable habitats at higher elevations to which some organisms were formally limited (Parmesan 2006, Pounds et al. 2006). Thus, if Pleurothallids' ability to disperse is not limited and their pollinators occur over the range, these altitudes may serve as a climate refuge in the future. However, the top of the mountain limits upward movement (Parmesan 2006) and endemic species, like *L. monteverdensis*, are unlikely to expand outside the range of conditions under which they are naturally adapted. In order to understand more thoroughly how these orchid species are effected by microclimate and future microclimatic changes, experimental and field studies of longer duration and larger sample sizes need to be undertaken.

ACKNOWLEDGMENTS

LITERATURE CITED

Ambrose, H.W., K.P. Ambrose, D.J. Emlen, K.L. Bright. 2002. A Handbook of Biological Investigation, 6th Ed. Hunter Textbooks Inc., North Carolina, pp. 96-98.

Atwood, J.T. Orchids. 2000. In: Monteverde: Ecology and Conservation of a Tropical Cloud Forest. N.M. Nadkarni and N.T. Wheelwright. Oxford University Press, Oxford, pp. 74-75.

Barros, A.P. and D.P. Lettenmaier. 1994. Dynamic modeling of orographically induced precipitation. Reviews of Geophysics 32(3): 265-284.

Benzing, D.H. 1998. Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. Climatic Change 39: 519-540.

Carey, P.D. and L. Farrell. 2002. *Himantoglossum hircinum* (L.) Sprengel. Journal of Ecology 641(1):206-218.

Clark, K.L., R.O. Lawton and P.R. Butler. 2000. The Physical Environment. In: Monteverde: Ecology and Conservation of a Tropical Cloud Forest. N.M. Nadkarni and N.T. Wheelwright. Oxford University Press, Oxford, pp. 15-20.

Clark, K.L. and N.M. Nadkarni. Mircoclimate Variability. In: Monteverde: Ecology and Conservation of a Tropical Cloud Forest. N.M. Nadkarni and N.T. Wheelwright. Oxford University Press, Oxford, pp. 33.

Graham, N.E. 1995. Simulation of Recent Global Temperature Trends. Science 267: 666-671.

Haber, B. 2000. Plants and Vegetation. In: Monteverde: Ecology and Conservation of a Tropical Cloud Forest. N.M. Nadkarni and N.T. Wheelwright, ed. Oxford University Press, Oxford, pp. 42-43, 55.

Hammel, B.E., M.T. Grayum, C. Herrera and N. Zamora, ed. 2003. Manual de Plantas de Costa Rica, Vol. III. Missouri Botanical Garden Press, St. Louis, pp. 235, 246.

Küper, W., H. Kreft, J. Nieder, N. Köster and W. Barthlott. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. Journal of Biogeography 31: 1477-1487.

León-Vargas, Y., S. Engwald, and M.C.F. Proctor. 2006. Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. Journal of Biogeography 33: 901-913.

Malhi Y. and J Wright. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. Phil. Trans. R. Soc. Lond. B 359: 311-329.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology and Systematics 37: 637-669.

Pfeifer, M., W. Heinrich, and G. Jetschke. 2006. Climate, size and flowering history determine flowering pattern of an orchid. Botanical Journal of the Linnean Society 151: 511-526.

Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N. Foster, E. La Marca, K.L. Masters, A. Merino-Viteri, R. Puschendorf, S.R. Ron, G.A. Sánchez-Azofeifa, C.J. Still and B.E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161-167.

Pounds, J.A., M.P.L. Fogden, and J.H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398: 611-615.

Root, T.L., J. T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421: 57-60.

Still, C.J., P.N. Foster, and S.H. Schneider. 1999. Simulating the effects of climate change on tropical montane cloud forests. Nature 398: 608-610.

Zuchowski W. 2005. Miniature Orchids. In: A Guide to Tropical Plants of Costa Rica. Zona Tropical Publication, Miami, pp. 425-427