Factors controlling the lower elevational limits in tropical montane plants in the Andes and their implications under the current climatic change

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Chapter 1

General introduction: Factors controlling the lower elevational limits and the current climatic change

INTRODUCTION

Investigations on the factors that limit the distribution of plant species have a long history. Already Darwin (1859) proposed that both climatic factors and interspecific competition could determine them. This hypothesis was specified later by Dobzhanky (1950) and MacArthur (1972), who postulated that along an uniform ecological gradient, that leads from favorable to unfavorable physical conditions, the distribution limits where the abiotic stress is high are determined by the species autoecological adaptability, whereas where the conditions are less physically stressfull by biotic factors. According to this hypothesis it would be expected that upper elevational limits awere principally defined by low temperatures and air pressure, and/or high UV-irradiation, while the lower limit are determined by biotic factors such as interspecific competition, predation, and/or pathogenes. To date, this theory has received support from investigations in temperate mountains (Friend & Woodward, 1992; Körner, 1999), however it is still unclear which specific mechanisms determine the distribution limits. For the lower elevational limits it has been possible to identify some mechanisms:

a) Autoecological limitation: In this case, the species are limited by their own physiology without an interaction with other organisms (Krebs, 1994). This autoecological limitation has been reported for *Meum athamanticum* (Apiaceae) in the Harz mountains in Germany (Bruelheide & Lieberum, 2001), and *Pacelia secunda* (Hydrophyllaceae) in the south Andes in Chile (Cavieres & Arroyo, 2000). For both species it was established that the physiological and phenological adaptability restrict the species to grow at lower elevations. This mechanisms represent an exception to the overall pattern described above.

The following three mechanisms are based on biotic interactions. For these mechanisms, the realized elevational niches of the species do not correspond to their potential elevational niches.

b) Interspecific competition: According to this hypothesis, a species, due to its ecological adaptability, could be present at lower elevation, outside its real elevational limit. However it is excluded from these elevations by other species that use the resourses more effectively. This hypothesis is based on the assumption that the adaptation to adverse ecological conditions affects the growth rates and fitness of a plant (Tilman, 1982, 1990; Keddy, 1990; Begon *et al*., 2000). Althought for plant ecologist competition is an important factor determinig the distribution limits (e.g. Ellenberg, 1953; Jäger, 1990), to the date there are only few studies that have tested the efects of competition on the elevational distributions of plants (Bruelheide & Lieberum, 2001, Choler *et al*., 2001). From investigation along the elevational gradient it has been established that plants in alpine communities can compete for light (Grytnes, 2000; Onipchenko et al., 2001), water (Rochow, 1970), or for available space for establishment (Kikvidze *et al*., 2005; Scheidel *et al*., 2003).

c) Herbivory: The lower elevational limits can be determined by herbivory on seeds or on germinated plants. Herbivory can affects plants in two ways, firstly by leading to a total or to a partial lost of photosynthetic area or roots that can affect the plant fitness (Marquis, 1984; Brown & Gange, 1990; Strauss, 1991), and secondly by increasing the seedling mortality during the establishment (Crawley, 1983; Louda, 1989). An example of this is the herbivory by slugs that determines the lower elevational limit of *Arnica montana* (Asteraceae) in the Harz mountain in Germany (Bruelheide & Scheidel, 1999, see also Galen, 1990).

d) Pathogens: Based on sharp elevational limits of plants it has been suggested that phytopathogens may be an important factor determining the elevational limits of plants (Burger, 1992; 1995). In this way, if seeds or spores of a plant are dispersed in an area occupied by a pathogen, they cannot establish there. To the date, there are no examples of limitation by pathogens along the elevational gradient, but from agroecosystems and temperate forest it has been observed that pathogens are an important factor determining the distribution and diversity of the ecosystems (Cook, 1979; Auspurger, 1988; Schroth & Hancock, 1982; Packer & Clay, 2000)

In spite of the concrete and relevant information on the mechanisms that determine the lower elevational limits of plants, the questions remain if there are additional mechanisms, which mechanisms are more frequent, and whether this frequency is subjected to regular variations, under different geographic or ecological conditions and for different plant groups.

A further problem is that all previous experimental approaches have been carried out in temperate mountains, and the information obtained from these studies can not be direct applied to tropical mountain communities. In fact, the high diversity and disperse distribution patterns of tropical communities (Gentry, 1982) could dimish the effect of interspecific interactions (Hubbell & Foster, 1986). Futhermore, in temperate mountains it is possible to define vegetational belts along the elevational gradient, whereas in tropical mountains the high diversity and the low dominance of the species in the communities make the definition of vegetational belts more difficult, since each species has different and independent elevational distributions (Kessler, 2000). Therefore, it could be expected that the relative importance of the above cited mechanisms differ between tropical and temperate mountain communities.

The establishment of the actual mechanisms that determine the lower elevational limits of tropical montane plants is not only important at scientific level, but also relevant under the current ecosystem problematic, since the reaction of the plants to global warming will depend on the factors that determine their distribution ranges (Woodward & Williams, 1987; Woodward, 1990; Pigott, 1992; Archibold, 1995; Still *et al*., 1999; Hughes, 2000). In case of a rapid increase in temperatures mechanisms such as autoecological limitation (a), herbivory (c) and pathogens (d) could lead to abrupt local extinctions. Competition (d), opposite to the previous three mechanisms, will conduce to slow elevational shifts of the species, not neccesary implying species losses (Dukes & Mooney, 1999).

The determination of the factors that limits the elevational distribution of tropical plants is also relevant because, due to the present anthropogenen destruction and fragmentation the natural ecosystems, the migration and expansion chances of the species under the current climatic changes will be limited (Kappelle *et al*., 1999; Bush, 2002). In contrast to natural climatic changes in the past, e.g. Pleistocene warming, two factors stand out that make current climatic change different: first, the higher speed and intensity of the current changes in the tempeartures, and second, that the effects of human land use may prevent species from responding in a natural migration (Bush, 2002). According to this, it is possible that species that overcame past climatic change events would not suvived the current one. In this way, investigations on the reaction of plants to climate change are a key issue in ecology (Sternberg *et al*., 1994; Schlesinger *et al*., 2001).

Research objectives

As the worldwide first experimental approach on the elevational limits of tropical plants, it was the central goal of this investigation to elucidate the factors that determine the lower elevational limits in tropical mountains plants. To develope this goal, we set up two central questions for this investigation:

1) Which specific mechanisms limit the distribution towards lower elevations in tropical plants?
2) Since the current global warming will principally affects lower elevational limits, how will it affect the elevational distributions of tropical plants?

To answer these questions we carried out investigations on tropical mountain plants with the following objetives:

- to establish the spatial variability of the lower and upper elevational limits and correlate this variability with biotic and abiotic factors (chapter 2.).
- to describe the effect of litterfall on the elevational distribution of two stoloniferous understory herb species of tropical montane forest with different elevational distribution under field conditions (chapter 3).
- to test wheter or not there is a changing pressure of vegetation on the distribution and occupation patterns of puna plants (chapter 4).
- to document how a change in the elevational distribution affect the biomass allocation patterns of seedlings of two high-Andean plant species (chapter 5).
- to describe the response of tropical non-vascular epiphyte communities to a simulted warmer and dryer climatic scenario, by translocating them to lower elevations (chapter 6).

Outline of chapters

In Chapter two we assess the importance of biotic and abiotic factors in the determination of the elevational limits of tropical ferns, by observing the elevational variability of these limits. We expected that species range limits were spatially more regular when they were determined by abiotic than by biotic factors. Based on previous information from species lists, herbaria, and altitudinal transects we obtained the elevational distribution of 224 ferns of montane forests of Bolivia. We observed the symmetry of the distributions for each species calculating the skewness and assumed that if the distribution limits were not related to a particular type of factor the elevational distribution of the species should be relative symmetric, whereas abiotic factors should determine truncated and biotic factors attenuated limits. Most of the species were asymmetric distributed and showed truncated upper limits and attenuated lower limits.

The results of this chapter are consistent with the observation that upper elevational limits are determined mainly by climatic factors while lower elevational limits are determined by biotic interactions.

In chapter three we analyzed the effects of litterfall on two understory species of tropical montane forest by observing their growth at different elevations. One species was restricted to high elevations whereas the other had a wide elevational distribution range. After two years, we found that the species restricted to higher elevation was more sensitive to damage by litterfall than the wideranging species. Based on these results, it can be suggested that litterfall may be playing an important roll in the determination of the lower elevational limits in plants of tropical montane forests, and that the elevational distribution reflect the species plasticity and resiliance to litterfall disturbs.

Our interest in chapter four was to examine the role of surrounding vegetation on the elevational distribution and occupation patterns of five high Anden geophyte species along an elevational gradient of 3800-4400 m. Studying the structure of vegetation and the abundance of the geophyte species we found that structural changes in the vegetation appeared to determine the presence/absence and abundance of the geophyte species along the gradient. These results reinforce the idea that biotic interactions, either competitive or facilitative, are important in the determination of the distribution ranges of high Andean plants.

In chapter five we describe the changes in the allocation patterns for seedlings of two puna species when growing outside their natural elevational ranges. We cultivated two species of *Lepidium* (Brassicaceae) at two elevations, simulating for one species the invasion of colder and for the other the growth in warmer environments. According to our results, the ability or inability to change the resource allocation patterns of these species appear to be playing an important role in the present elevational distribution, and could be key factor in the reaction of these species to climate change.

In chapter 6 an experiment was set up to assess the effect of a warmer and more seasonal environment on non-vascular epiphyte communities. For that we translocated complete non-vascular epiphyte communities from 3000 m to 2700 m and 2500 m. After two years, epiphyte communities translocated to lower elevations did not differ in total bryophyte cover from those left at 3000 m, but they were more dynamic, with higher cover changes of species composition. Over-saturated communities, with high total cover and with no available space bteween bryophyte individuals were more resistant to cover changes than unsaturated communities. The response of epiphytes to the translocation was distinctly species-specific, ranging from increases to decreases with elevation. At the structural level, the assemblages translocated to lower elevations turned to a more equitative species abundance pattern. The results of these chapter suggest that community structure and species composition will change markedly as a result of future temperature increases, but that communities will not collapse.

Conclusions and perspectives

From the five experimental approaches to the elevational limits we could establish:

1) a differential spatial variability of the upper and lower elevational limits of Andean plants. Species show truncated upper limits and attenuated lower limits. This suggests not only that upper and lower elevational limits are determined by different environmental factors (upper-abiotic, lower-biotic) but also that under climate change, Andean species can migrate at different rates at their lower and upper limits. It implies that the prediction of plants distributions exclusively by climate envelope models could be flawn since biotic factors, which could principally affect lower elevational limits, are not taken into account.
2) That not only particular variables, e.g., herbivory or pathogens, could determine the lower elevational limits of andean plants. Also ecosystem characteristics such as productivity and seasonality, particularly litterfall in montane forests and above-ground biomass and grass cover in puna ecosytems seem to play an important role in the limitation at lower elevations. Since climate change in tropical mountains could lead to increased ecosystem productivity and seasonality due to incresead CO_2 input, temperature and changes in the hydric regimes, it could be expected that species elevational ranges become affected.
3) That the growth under moderated temperatures, could conduce in puna species to changes in the resourse allocation patterns, i.e. root:shoot ratios, in seedlings which could affect the plants resistance to frost and drought events specially during the winter season. That means that climate change in puna ecosystems could not only affect plants at the lower elevational limits but also plants located at the range center.
4) That epiphyte communities of montane forests react rapidly to moderated temperature increases and changes in the hydric regimes. The response of the community implies

changes at community structure and composition, but not an overall biomass loss. According to this it could be postulated not only that epiphyte communities may be already reacting to climate change but also that communities will not necessary collapse under the new climatic scenaria, and that ecosystem functions mediated by epiphytes, such as nutrient cycling and water retention may only experince limited changes.

Despite these interesting results it is necessary to indicate that many factors, such as germination, dispersal limitation, and the direct effect of herbivory and pathogens could not be included in this investigation. In this way a complete perspective of the factors that determine the lower elevational limits of tropical montane plants and the effect of the climatic change on them is still incomplete. Only knowing the importance of these factors will permit to establish the true effect of the climatic change in these areas and to predict in an adequate way the response of the vegetation to this scenario.

Chapter

2

Differential spatial variability of the upper and lower elevational range limits of pteridophytes in the Bolivian Andes

J Jácome, M Kessler, AR Smith

ABSTRACT

Aim To establish the importance of biotic and abiotic factors in the determination of the elevational limits of tropical ferns, based on Kaufmann's hypothesis (1998) that species range limits are spatially more regular when they are determined by abiotic than by biotic factors.

Location Bolivian Andes

Methods Using information from species lists, herbariums and altitudinal transects, we obtained the elevational distribution of 224 fern. We observe the symmetry of the distributions calculating the skewness. We assumed that if the distribution limits were not related to a particular type of factor the elevational distribution of the species should be relative symmetric, while abiotic factors should determine truncated- and biotic factors attenuate-limits.

Results The species presented different distribution patterns, which ranged from symmetric- to asymmetric-distributions. However most of the species were asymmetric distributed and showed truncated upper limits and attenuated lower limits.

Conclusions Our results supports Kaufmann's hypothesis and is consistent with the observation that upper elevational limits are determined mainly by climatic factors (low temperatures, frost) while lower elevational limits are determined by biotic interactions (interspecific competition, herbivory, pathogens, etc.). In this way we think that upper and lower elevational limits are likely to shift with different intensity and speed in response to climatic changes, and that upper limits are more informative for studies of the elevational zonation of taxa than lower limits.

INTRODUCTION

Recent studies have documented that species are responding to climate change by altering their distribution ranges (Parmesan & Yohe, 2003; Root *et al*., 2003). This response seems to be determined by the species' migration rates and by factors determining their range margins (Parmesan *et al*., 1999; Pearson & Dawson, 2003), i.e., historical (Gaston & Chown, 1999), abiotic (Woodward, 1996; Cox & Moore, 2000), and biotic factors (MacArthur, 1972; Woodward & Williams, 1987). Dobzhansky (1950) and MacArthur (1972) proposed that across strong environmental gradients of, e.g., nutrient availability or temperature, the range margins of species are determined towards the more unsuitable extremes of these abiotic factors by the factors themselves, whereas towards the more suitable environmental conditions by biotic factors, such as competitors, predators or pathogens. For example, the northward range limits of North American tree species are determined by adaptations to low winter temperatures (Loehle, 1998). However, these adaptations also limit their growth rate and thus their competitive abilities at their southern range limits (Loehle, 1998). Similar situations have been documented for some temperate montane plants, where the upper limits are usually determined by abiotic factors such as low temperatures or quantity of snowfall while at lower altitudes the limits are associated with competition, predation, herbivory and pathogens (Loehle & LeBlanc, 1996; Bruelheide & Lieberum, 2001; Bruelheide & Scheidel, 1999; Rochow, 1970; Vetaas, 2002). For example, Vetaas (2002), compared the natural and ex-situ niches of four Rododendron species along an elevational gradient in the central Himalayas and found that without the influence of biotic factors the species were able to grow under higher, but not under lower temperatures than when observed growing under natural conditions.

While the above patterns are thus well documented, little thought has been given to how they affect the actual spatial distribution of species range limits. Kaufman (1998) proposed that abiotic factors such as low temperatures or increasing aridity should generate spatially fairly even range limits because of the relatively consistent, regular distribution of these abiotic factors in space. Biotic factors such as competitors or pathogens, on the other hand, are more patchily distributed (Hughes, 1990) and as a result generate more irregular range margins. Kaufmann (1998) was able to support these predictions studying the spatial variation of the latitudinal range limits of Neotropical mammals: the range limits of individual species were smoother, i.e., geographically more regular, towards the poles than towards the equator.

The aim of the present study is to establish if the pattern detected by Kaufmann (1998) could be also observed in other groups of organisms such as plants, in this case ferns, as well as to other ecological gradients such as the elevational gradient.

METHODS

Our investigation relies on information obtained from species list and from an exhaustive herbarium revision carried out for the elaboration of the Pteridophyte section of the Catalogue of the Vascular Plants of Bolivia (Kessler & Smith, in press).

For this study we took only into account species of Andean ferns distributed in the Yungas biogeographical region, north from the parallel 18° S; where a clear climatic discontinuity determines a transition from tropical to subtropical montane forests (Navarro & Maldonado, 2002; Kessler, 2004). Species with registers below 500 m a.s.l were excluded of the analysis because it was considered that they might naturally be distributed beyond this elevation, occurring also in lowland forests, being in this way not possible to determine for them the lower range margins. Species with less than 15 registers were also excluded, trying to avoid inaccurate and unreliable distributions. According to these criteria, we obtained the elevational distribution for 224 fern species.

We observe for these species the distribution asymmetry, calculating the skewness ($g1$), which represent how much one tail of the distribution curve is drawn out more than the other (Sokal & Rohlf, 1995). For our case if the distribution for one species show a truncated upper range margin the skewness value would be negative and on the contrary if the species shows a truncated lower limit the skewness value would be positive. We assumed that abiotic factors, because of their relatively spatial consistent, should determine truncated- and biotic factors; because their patchy distribution, attenuate-limits.

To observe if the species distribution present a general pattern of asymmetry, we compare the observed frequencies of species with negative and positive skewness, and determine if the skewness values for the species fit a normal distribution. We expected that if the biotic and abiotic factors were not related to a particular limit, the observed frequencies should not depart from the expected values obtained from a Chi-square distribution and the skewness values should be normal distributed. For these purpose we carried out a Chi-square (Fowler *et al.*, 1998) and Shapiro-Wilk test (Conover, 1999).

RESULTS

From the 224 analyzed species of Andean ferns 139 were negative and 85 positive skewed. According to these values the frequency of species with negative skewness is greater than the expected if the biotic and abiotic factors were not related to a particular range margin ($X^2_{1,2}$= 13.01, $P<0.0001$). The distribution of the skewness values of these species departs from the normality (W_{224}=0.95551, $P<0.0001$), showing also a strong asymmetry to negative values, indicating a tendency of the species to present truncated upper and a attenuated lower limits (**Fig. 2.1**).

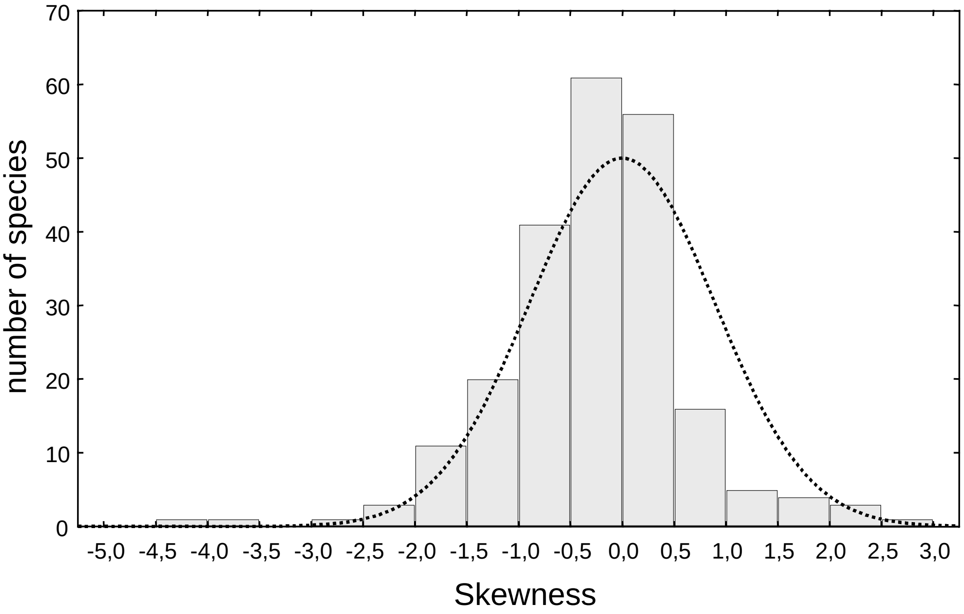

Fig. 2.1 Comparison of the observed frequency distribution of skewness values on species of Andean Pteridophytes and its expected normal distribution.

Observing in detail the altitudinal distribution of the 6 most frequent species (**Fig. 2.2**), it is possible to observe not only species with negative skewed distributions but also with positive and quite symmetrical distributions. Negative skewness could be not only consequence of clear truncated distributions at the upper limits like in *Hymenophyllum axilare* but also of very drawn out distribution at the lower limits like in *Woodsia montevidensis*.

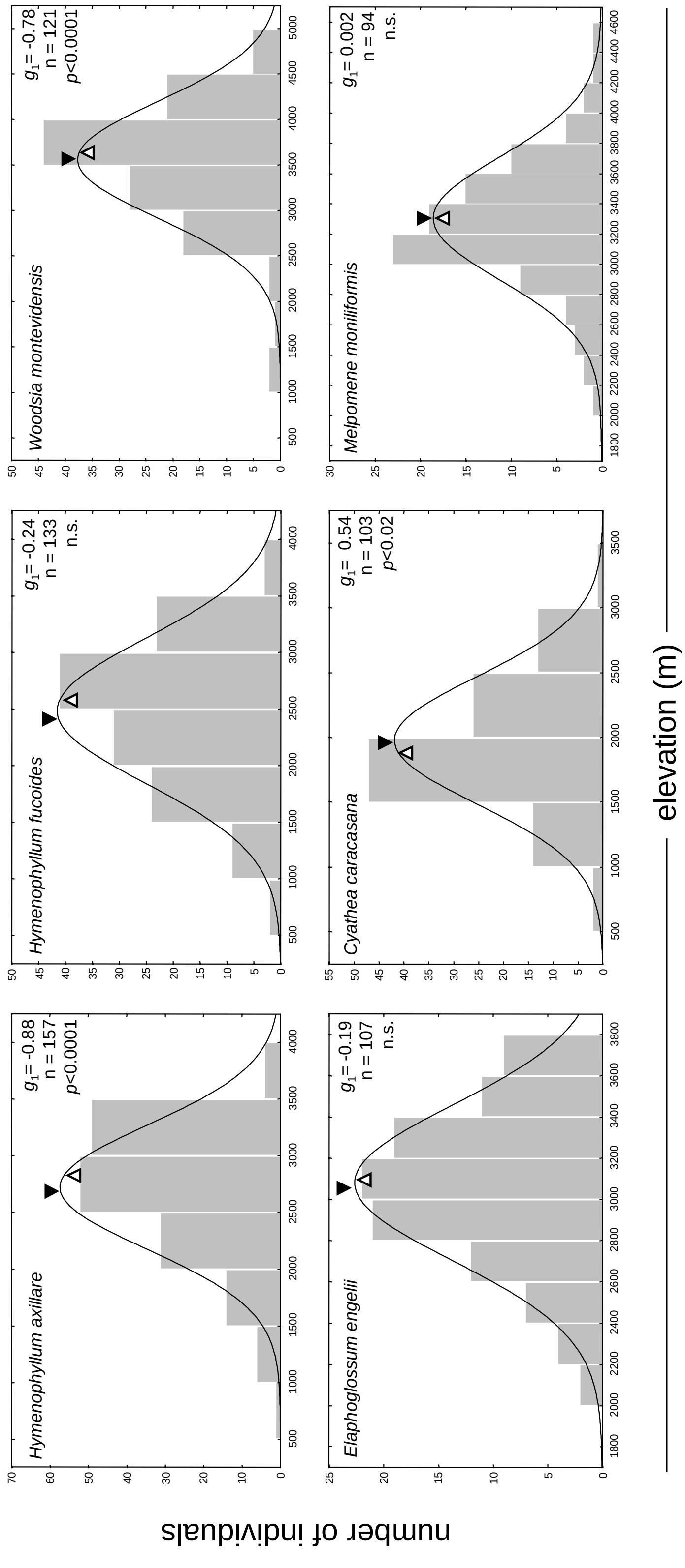

Fig. 2.2 Comparison of the observed frequency distribution of register along the altitudinal gradient for the six most important species of pteridophytes in the Yungas forests and their expected normal distribution. White triangles represent the median an the black triangles the mean value. At the right upper corner for each species he skewness value ($g1$), number of registers (n) and the significance departure from the normality are provided (P, for significant; n.s. non significant).

DISCUSSION

Our results show that the upper elevational limits of ferns in the Bolivian Andes are in general somewhat abrupt, in contrast to lower limits which are more attenuate or gradual. This is consistent with the hypothesis of Kaufman (1998) concerning the shape of species range limits and the possible differential effect of abiotic and biotic factors as postulated by Dobzhansky (1950) and MacArthur (1972).

The more spatially regular and defined upper range limits of Andean ferns suggests that they are primarily determined by abiotic factors related to climate, e.g., frost frequency or the location of condensation belts (Webster, 1995). Within a given geographical region these factors are closely dependent on elevation and therefore show limited spatial variation. Opposed to this, biotic conditions, e.g., the occurrence of potential competitors or pathogens, are known to be frequently patchily distributed (Hughes, 1990; Gaston & Blackburn, 2000). This irregular distribution of biotic interactors could explain the variability of the lower elevational limits among the studied Andean ferns. The greater importance of biotic factors at lower elevations is likely to be the result of both more benevolent abiotic conditions (i.e., higher temperatures, better nutrient cycling, etc.), and increase in the number of species that can act as competitors, herbivores, parasites, or pathogens (Burger, 1992; Bruelheide & Lieberum, 2001; Vetaas, 2002).

This differentiation of determinant factors at upper and lower range limits does not imply that each type of factor exclusively determines each of these distribution limits. Unsuitable abiotic conditions at the upper limits can render plants more vulnerable to, e.g., herbivores, while the strength of biotic interactions at the lower elevational limits may well be influenced by occasional stressful climatic events, e.g., droughts (Roy *et al.*, 2004). As a result, the elevational distribution of species is likely to be a response of the plants to the influence of multiple factors (Gaston & Blackburn, 2000). Nevertheless, our results are consistent with the observed differences in the relative importance of abiotic and biotic factors at the upper and lower range limits.

The results of this and related studies have a number of important implications for biogeography and conservation. First, they suggest that species may respond to climatic changes with different intensity and speed at their upper and lower elevational limits (Vetaas, 2002; Pearson & Dawson, 2003). The upper elevational limit of a plant species is likely to closely follow the shift of climatic conditions with a time lag imposed by the dispersal ability and generation time of that species. The situation at the lower limit is quite different and more complex. For example, competing plant species may take a long time to invade the elevational range of another species and eventually displace it. Opposed to this, once the climatic conditions allow pathogens or herbivores to establish themselves, these may very quickly destroy populations of a given plant species (Loehle & LeBlanc, 1996). Upper and lower elevational limits may thus shift with different speed and as a result species elevational ranges may contract or expand. Overall, biotic communities are unlikely to be displaced elevationally as fixed entities but will rather be scrambled up in an unpredictable way. Palynological studies of Andean forests have documented plant communities during Pleistocene times that lack present-day equivalents and thus provide evidence for the individualistic response of species to climatic changes (e.g., Van't Veer & Hooghiemstra 2000).

Second, the higher consistency of the upper elevational limits of plants suggest that schemes of the elevational zonation of montane plant communities are more reliably constructed based on upper than on lower elevational distributions of taxa. A similar argument can be applied to gradients of latitude, humidity or nutrient availability. In all those cases, the species limits towards the less favourable conditions for overall plant growth, i.e., towards colder, dryer or nutrient-deficient sites, are more likely to be consistent at different locations than the limits towards the more favourable conditions.

Chapter

3

Differential responses to litterfall damage among two understory herbs of a tropical montane forest determine their elevational distributions

J Jácome, M Kessler

ABSTRACT

In order to assess the hypothesis that understory species of lower elevations in tropical forest are more resilient to damage caused by litterfall than species of higher elevations, we measured litterfall amount and studied the its effect on the cover, number of shoots, and distance between shoots of two stoloniferous understory herb species with different elevational distribution (*Pilea strigosa*, 2900-3300 m; *Viola boliviana*, 2000-3300 m). We translocated plants of both species from forests located at 3000 m to 2700 and 2500 m. During the first year the litterfall on each plant was removed, whereas in the second year it was left to accumulate. Litterfall amount decreased significantly with elevation. In the first year, both study species showed no mortality and in general the plants increased in cover, number of shoots at all three elevations, and enhanced the distance between patches, especially at lower elevations. In the second year, plants of *P. strigosa* suffered a greater mortality than plants of *V. boliviana*, and showed a reduction in cover and in the number of shoots at 2500 m and 2700 m. *Viola boliviana* showed no changes in the general pattern of increase in cover and number of shoots, and the presence/absence of litter did not seem to affect a general increase in cover and number of shoots during the two years. These results suggest that litterfall amount plays an important roll in the determination of the lower elevational limits in plants of tropical montane, and that the elevational distribution reflect the species plasticity and resiliance to litterfall disturbances. Changes of forest phenology in response to global climatic change may accordingly influence the elevational distribution of understory herb species.

INTRODUCTION

The question of what determines the elevational limits of plant species is a crucial one for ecologists under the present climatic change scenaria (Pearson & Dawson, 2003), and has been the subject of numerous investigations. Factors that affect the distribution of species along the elevational gradient are mainly temperature and precipitation at the upper limits (Friend & Woodward, 1992; Körner, 1999), and interspecific competition (Bruelheide & Lieberum, 2001), herbivory (Galen, 1990; Reader, 1992; Bruelheide & Scheidel, 1999; Scheidel *et al*., 2003), and pathogens (Rochow, 1970; Burger, 1992, 1995) at the the lower limits.

One of the ways in which plants within a forest ecosystem interact is litterfall, which is an important cause of damage and mortality for many herbaceous species and tree seedlings in tropical forests (Nuñez-Farfan & Dirzo, 1988; Clark & Clark, 1991; Drake & Pratt, 2001). At higher elevations in tropical montane forests the amount of litterfall decreases, since productivity and seasonality decrease, due to the low temperatures and continuous water supply by mist events (Borchert, 1998; Tanner *et al*., 1998). In spite of this pattern, to date no studies have focussed on the effect of litterfall on the elevational distribution of tropical plants.

Many understory herb species in tropical montane forest are characterized by vegetative spread by stolons or rhizomes. The ability of these plants to survive and recover from litterfall disturbs is likely to differ between species due to distinct growth patterns. Bell & Tomlinson (1980) described that among species with rhizomes or stolones it is possible the define two different growth models, one with predetermined branching and another with a more flexible pattern. In this way, species suitable to cope with damage by litterfall should have the capacity to reiterate and regain biomass after litterfall disturbance (Gillman *et al*., 2003). Accordingly, it can be postulated that the prevalence of montane species at a particular elevation should be an indication of how adaptable they are to litterfall disturbance.

In this paper we describe the effect of litterfall on two stoloniferous understory herb species in a tropical montane forest with different elevational distributions. One species is restricted to elevation above 2900 m whereas the other has a wide elevational range, being present from 2000 m to about 3300 m.

METHODS

Study site and species

We conducted the study from February 2003 to February 2005 in a humid montane cloud forest at 2500 m to 3000 m in the department of La Paz, Bolivia (16°16-17'S, 67°48-53'W). The study site was located in a buffer zone adjacent to the Cotapata National Park, along the road that connects the city of La Paz and the municipality of Coroico. The climate is per-humid with frequent precipitation events exceeding 3000 mm per year, and mist events that are constant all year round, especially above 2700 m. The average annual temperatures range from 12°C to 20°C. In most of the region a diffuse seasonality dominates, with the drier periods occurring from August to October, but it is not possible to clearly define a dry season, since nocturnal mist events, which supply a great amount of water, are also present during the dry months (Ribera, 1995; Navarro & Maldonado, 2002; Bach, 2004). Due to the extremely steep topography of the area, that impedes its use for agriculture, the vegetation is still mainly constituted by pristine tropical montane rain forest (sensu Holdridge, 1967). Below 2700 m, slightly decreasing humidity causes the forest to become more seasonal (Ribera, 1995; Navarro & Maldonado, 2002).

The study species *Viola boliviana* W. Becker (Violaceae) and *Pilea strigosa* Wedd. (Urticaceae) are understory herbs of tropical montane forests, with stoloniferous-rhizomatous growth habit, that occur locally in dominant patches. The species have different elevational distributions: *V. boliviana* (2000-3300 m) and *P. strigosa* (2900-3300 m) (based on vouchers deposited in the Herbario Nacional de Bolivia). In the study area both species are principally observed in rather flat and poor drained soils, and in forest areas with canopy discontinuities or small gaps. *P. strigosa* and *V. boliviana* do not grow higher than 20 cm and their rhizomes can grow on or in the soil (**Fig. 4.1**).

Experimental set-up

We carefully extracted 30 plants of each species from natural populations at 3000 m. Since both species grow in patches we considered a plant a ramet with one to two shoots, separated by no more than 1 cm. Ten of these plants were replanted at the original elevation, whereas ten each were moved to 2700 m and 2500 m, respectively. Thus *P. strigosa* was translocated outsite its elevational ranges, whereas *V. boliviana* remained within its range. The transplantation to lower elevations implied elevational differences of 300 m and 500 m, a temperature increase of about 1.5°C and 2.5°C, and a reduction of about 1300 mm mean annual precipitation (Bach, 2004), and in this way a more marked seasonality at lower elevations, as has been described by Ribera (1995). The temperature increases due to the transplantation to lower elevations correspond to the range of predicted climate change for the next 50-100 years in tropical forests (Pounds *et al*., 1999).

At each elevation the plants were planted inside natural forest habitats, trying to simulate their original growth conditions of irradiation, to diminish the influence of microenvironmental differences that could affect them. The plants were monitored for cover, number of shoots and distance between shoots at ca. 3 months intervals during the two years.

Half of the plants of each species at the three elevations were planted in plastic pots of 25 cm diameter filled with soil from the source elevation, to establish if soil differences affected the results. The plant were located in pairs, by species and by treatment (one in a pot and the other growing directly in the soil), to control litterfall microsite heterogeneity (Gillman & Ogden, 2005). Beside each pair of plants a circular litterfall trap of 0.5 square metres, that corresponded to the area of the plastic pot, were established to measure the amount of litterfall on the plant between the monitoring dates. During the first year the plants were monitored for changes in the studied variables and the litterfall removed. In the second year we evaluated the changes without removing the litterfall.

Data analysis

First, we evaluated if there were differences in the litterfall among the three localities comparing dry weight of the litterfall trapped during the two years. For this analysis we carried out an one-way ANOVA (Zar, 1999). Data on litterfall were log-transformed to adjust them to normal distribution and to increase homogeneity of variance.

To search for trends in cover and in the number of shoots with the litterfal dry weight we conducted lineal regressions for each species. Survivorship at each monitoring date was registered. The principal criteria for survival was the presence of branches and leaves growing above the leaf litter.

Data on cover, number of shoots, and distance between shoots were tested, separately for each species, for differences between elevations and treatments (pot or direct in soil) through repeated measurements ANOVA (Zar, 1999). For the statistical tests we used the program Statistica 6 (Statsoft, 2003).

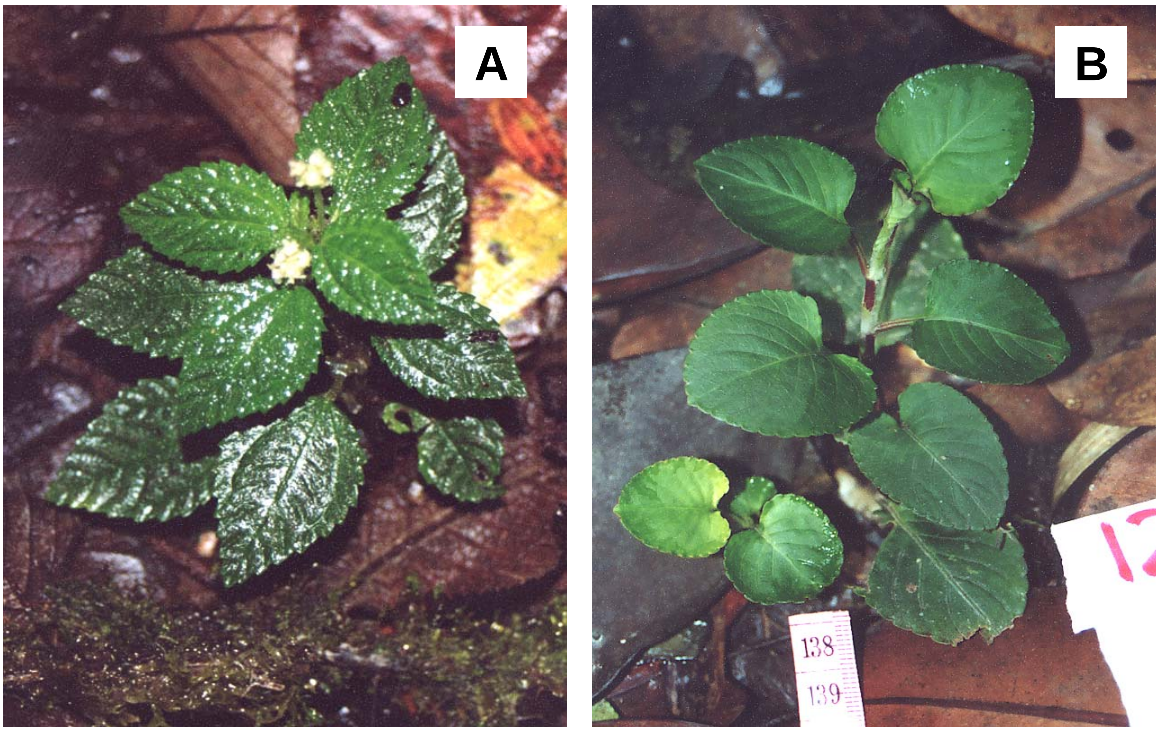

Fig. 3.1 *Pilea strigosa* Wedd. (Urticaceae) (**A**) and *Viola boliviana* W. Becker (Violaceae) (**B**).

RESULTS

The amount of litterfall during the two years decreased significantly with increasing elevation ($F_{(2,166)}$=19.44, p<0.00001) (**Fig. 3.2**). The change in the amount of litterfall is specially notorious from 2700 m to 3000 m (Tukey HSD test, MQ=0.48, p<0.00003), whereas the was no significant difference between 2500 m and 2700 m.

After two years, the suvivorship of the study plants varied according to elevation and species. The highest plant mortality for both species was recorded at 2500 m, where 50% of the plants of *P. strigosa* and 30% of *V. boliviana* died. At 2700 m and 3000 m the mortality of *P. strigosa* decreased to 20% whereas for *V. boliviana* no mortality was registered at these elevations.

In *P. strigosa* and *V. boliviana* there were no significant differences in both number of shoots or cover between plants planted in soil from the source elevation and plants in soil of a particular elevation, indicating that soil differences alone do not affect the measured variables (ANOVA. *P. strigosa,* No. shoots F(12,144)=0.19, p=0.98, Cover F(12,144)=0.91, p=0.53. *V. boliviana*, No. shoots F(12,144)=1.57, p=0.11, Cover F(12,144)=1.16, p=0.31). Accordingly, we excluded the type of soil as factors from the remaining analyses.

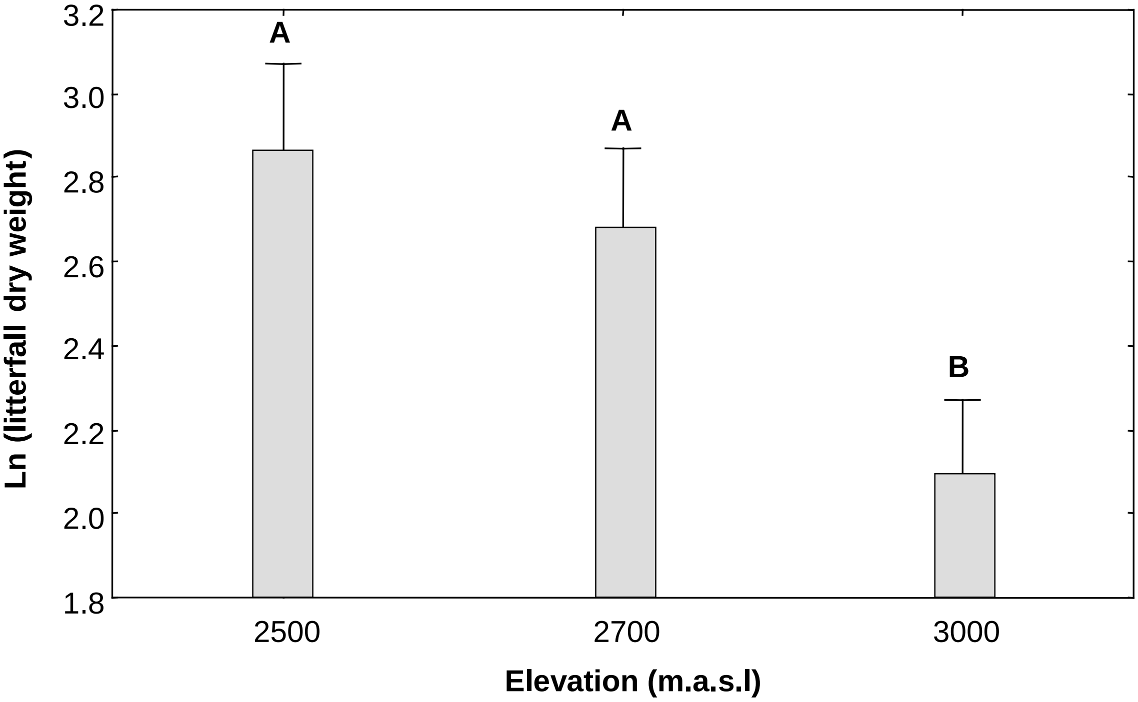

Fig. 3.2 Annual litterfall amount in 30 traps of 0.5 cm^2 at three elevations. Values are the mean + standard deviation. Different letters indicate significant differences between the means (ANOVA test).

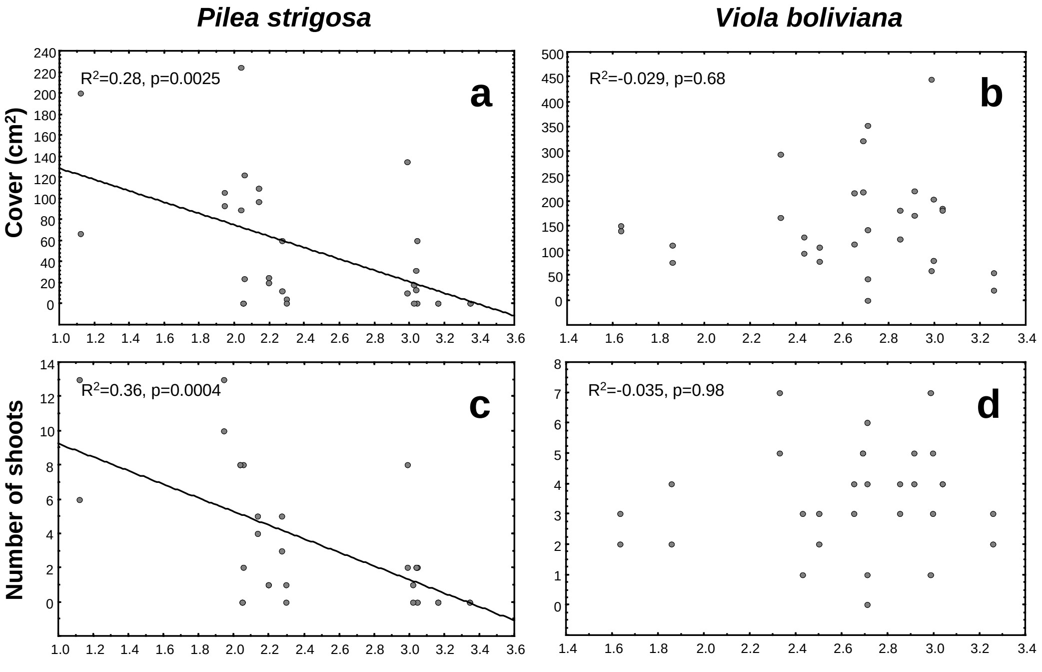

Fig. 3.3 Changes on cover (a and b) and number of shoots (c and d) for *Pilea strigosa* and *Viola boliviana* in relation to litterfall.

The amount of litterfall affected the number of shoots and the cover in *P. strigosa* after two years, with a greater quantity of litter corresponding to a diminution in the number of shoots and decreased cover (**Fig 3.3a, c**). In contrast, *V. boliviana* did not seem to be affected by litterfall after two years (**Fig 3.3b, d**).

During the first year when the litter was removed every three months, the plants of *P. strigosa* presented a marked increase in the number of shoots and in cover at all three elevations. However, in the second year when the litterfall was not removed, differences in the study variables were observed between elevations (**Fig. 3.4a, c, e**). For *V. boliviana*, the retention or remotion of litterfall did not affect cover and number of shoots during the two years (**Fig. 3.4b, d, f**). For *P. strigosa*, control plants tranlocated to their original elevation at 3000 m increased the cover significantly more than plants translocated to 2500 m and 2700 m (ANOVA, F(12,144)=3.21, p=0.00042). At 2500 m, the plants showed almost the same cover that they had at the beginning of the experiment (**Fig. 3.4a**). In *V. boliviana*, the move to lower elevations did not affect the cover increases (**Fig. 3.4b**), in that the plants at all three elevations had relatively similar cover after two years (ANOVA, F(12,144)=1.16, p=0.31). For cover, we found similar trends, with plants of *P. strigosa* at 3000 m having more shoots than plants moved to 2500 m and 2700 m (ANOVA, F(12,144)=3.5, p=0.0001) (**Fig. 3.4c**). For *V. boliviana*, the number of shoots increased at all three elevation. However, it is interesting to observe that during the second year the increase in the number of shoots was much more marked at 2500 m and 2700 m. This determined that at the end of the experiment plants at 2500 m and 2700 m had more shoots than control plants at 3000 m (ANOVA, F(12,144)=1.91, p=0.036) (**Fig. 3.4d**).

In the first year, when the litter was removed, plants of *P. strigosa* moved to 2500 m increased the distance between patches, in contrast to plants at 2700 m and 3000 m. However, this pattern changed in the second year, when the litterfall was not removed, determining that at the end of the experiment no differences in the distance between shoots were observed among plants located at different elevations (ANOVA, F(2,5)=1.15, p=0.38) (**Fig. 3.4e**). It is interesting to observe that *V. boliviana* did not show any changes in the distance between patches until the last monitoring, when strong differences were registered (ANOVA, F(2,18)=4.18, p=0.032). The distance between patches after two years were greater for plants moved to 2500 m and 2700 m than for the control plants at 3000 m (**Fig. 3.4f**).

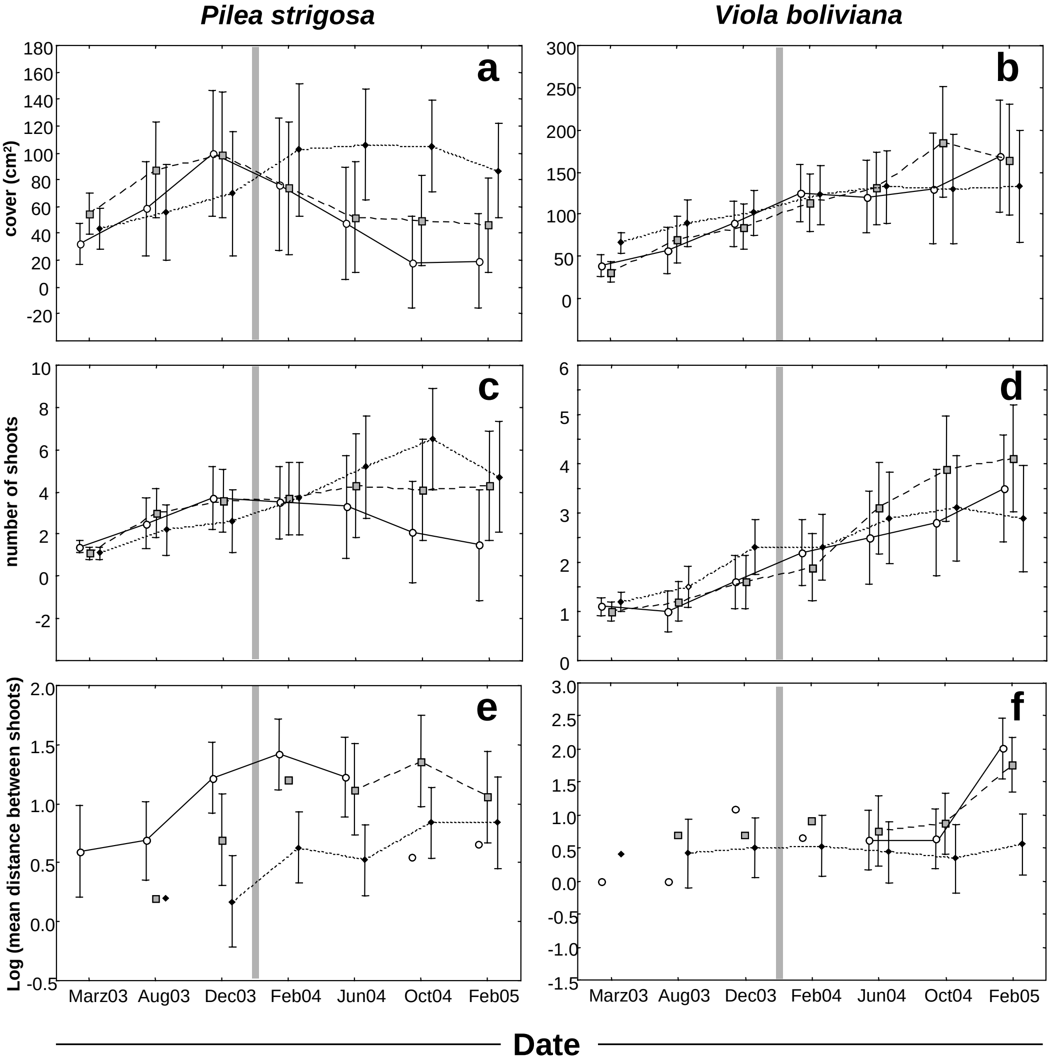

Fig. 3.4 Changes in cover, number of shoots, and distance between shoots for *Pilea strigosa* (**a**, **c** and **e**) and *Viola boliviana* (**b**, **d** and **f**) at three different elevations (2500 m ○; 2700 m ■ ; 3000 m ◆). The values are the mean± 0.95 confidence interval. The gray line indicates the date from which the litterfall was left to accumulate.

DISCUSSION

Studies on tropical forests have shown that temperature and seasonal variations in the hydric regimes determine higher productivity rates and phenological changes respectively, which may lead to an increase in the amount of litterfall in the ecosystems (Borchert, 1994; 1998; Tanner *et al*., 1998). We found that even small elevational changes, in this case 300 m and 500 m, imply significant differences in litterfall amount (**Fig. 3.2**).

Althought the study species have the same growth habit, litterfall had different effects on them, causing in *P. strigosa* a diminution in the cover area and in the number of leaves with increasing litterfall, whereas in *V. boliviana* a litterfall increase had no effects on the plants (**Fig. 3.3**). These different responses are likely a result of the different growth strategies of the species. Differential effects of litterfall on plants species with similar growth habits or growth stages have previously been observed in tropical plants and seem to be determined by reiteration and grow rates of the species after the litterfall disturbance (Guariguata, 1998). Bell & Tomlinson (1980) described that among species with rizomatous or stoloniferous growth habits there are species with precise branching patterns while others have opportunistic or adaptable patterns. Adaptative reiteration is important in the productivity of stoloniferous plants since it permits them to cope with microenvironmental heterogeneity (Bell & Tomlinson, 1980). Stoloniferous species of the genus *Viola*, including our study species *V. boliviana*, present this adaptable branching pattern as well as stolons with indetermined elongation distance (Schellner *et al*., 1982; Griffith, 1996, 1998). Accordingly, they can cope well with damage and cover by litter. In contrast to this, *P. strigosa* was unable to flexibly cope with an increase of litterfall because its branching pattern is fixed (**Fig. 3.4a, c**). Gillman & Ogden (2001) described a similar pattern for seedlings in temperate forests, and postulated that some plants that initially survive literfall damages eventually die by smothering from further accumulation of litter. In this way a greater susceptibility in *P. strigosa* to damage by litterfall accumulation could restrict its establishment and maintainance to sites where the amount and frequency of litterfall are low. Another possibility to cope with litterfall damage, especially for plants with stoloniferous or rhizomatous growth habits, is to produce spaced shoots (Mark, 1998; Gillman & Ogden, 2005). Nevertheless *P. strigosa* apparently did not space the shoots far enough, since in the second year, when the litter was not removed, the plants showed strong reductions in cover and number of shoots (**Fig. 3.4e**).

These relationships to litterfall amount correspond well with the elevational distributions of the species. *Pilea strigosa*, which is sensitive to high levels of litterfall disturbances and litterfall amount, is naturally limited to elevations above 2900 m. The cover and number of shoots in this species was also greater at upper than at lower elevations (**Fig. 3.4a, b**). For *V. boliviana*, naturally distributed from 2000 m to 3300 m, the variation in frequency or amount of litterfall did not determine considerable changes in the plant growth and mortality at the studied elevations (**Fig. 3.4b, d**). In contrast to *P. strigosa*, *V. boliviana* seemed to space the shoots enough to secure an increased survival after two years even under high litterfall at

2500 m (**Fig. 3.4f**). These increased distance between shoots could be favouring the establishment of *V. boliviana* in sites under great risk of litterfall damages.

Our results suggest that litterfall may be playing an important roll in determining the lower elevational limits in plants of tropical montane forest. Species resilient to litterfall disturbances should present wider elevational distributions, whereas species susceptible to this factor should be restricted to higher elevations. This elevational limitation would not necessarily imply a sharp distribution limit, because microsite heterogeneity in litterfall risk (Gillman & Ogden, 2005) could permit the establishment of litterfall-sensitive species at elevations where the average quantity of litterfall would otherwise smother the plants.

In Neotropical montane forests, climate change is expected to alter temperatures and hydric regimes by a shift of the relative humidity surface by hundreds of metres, especially during the dry season (Still *et al*., 1999; Vuille *et al*., 2003). Since temperature and precipitation controls the growth and phenology of plants it is expected that climate change would lead to an increased productivity and to a synchronization of the leaf exchange in tropical forests (Borchert, 1998; Prance, 1990; Condit et al., 1996), increasing the amount of litterfall and affecting the distribution of litterfall sensitive forest understory species.

Chapter

4

Effects of the vegetation structure on the elevational distribution of high-Andean geophytic plants

J Jácome, M Kessler

ABSTRACT

We examine the role of surrounding vegetation on the elevational distribution and occupation patterns of five high Anden geophyte species along an elevational gradient (3800-4400 m.a.s.l.). For that we characterized the vegetation along transects at each 200 m of elevation, according to the canopy height, the above and below ground biomass and the grass cover, and compared our observations with elevational distributions and occupation patterns of the studied species along these transects. We found that at lower elevations (3800 and 4000 m) there is a clear increase in the above ground biomass, the grass cover and the canopy height. These structural changes in the vegetation appeared to determine the presence-absence and abundance of the geophyte species along the gradient. The elevational distribution of the species along the studied transect could be a consequence of the adaptabilty to changes in the vegetation and to the restriction to particular habitats.

INTRODUCTION

Tropical high Anden plant communities correspond to the vegetation located above the natural elevation limit of contiguous, closed-canopy forest. In dry areas of the central Andes the main vegetation at high elevation is the puna (Kessler, 1995), which correspond to grasslands or steppes distributed from about 3900 m to 4700 m (Navarro & Maldonado, 2002). In these areas there is a great seasonal variation in rainfall and cloud cover, with clear dry periods with higher daytime maximum temperatures and lower nighttime minimum temperatures than in wet periods. Freezing temperatures are common in the night but they persist seldom throughout the day (Smith & Young, 1987; Kessler, 1995). This pattern described by Smith & Young (1987) as "summer every day, winter every night" at higher elevations in the tropics implies for many species a physiological barrier for the distribution and determines for many species upper distribution limits (Sarmiento, 1986; Sakai & Larcher, 1987). Plants of such stress dominated, cold habitats allocate a high proportion of the biomass to below-ground structures (Grime, 1979), to avoid damages by frost or irradiation (Körner, 1999).

In contrast to the rather obvious causes for the upper elevational limits of puna species, little is known about the factors determining the lower limits of these species. The available information about lower limits and the factors that detemine them is exclusively from studies carried out in temperate regions (Friend & Woodward, 1992; Körner, 1999). These studies show that biotic interactions with surrounding vegetation at the lower elevational limits have negative effects on alpine plants (Choler *et al.*, 2001; Callaway *et al.*, 2002; Klanderud & Totland, 2005). This is due to the low competition ability of high mountain plants which seems to be limited by their low acclimation plasticity because of their low metabolic rates which are normally genetically fixed (Criddle *et al.*, 1996; Körner, 1999). Thus, interspecific competition appears to restrict species from higher elevations from moving downward along the elevational gradient. It should be expected that surrounding vegetation will affect species in high Andean regions in the same way. However, because the high diversity and rather disperse distribution of species in tropical communities (Gentry, 1982), interspecific competition is more diffuse and thus observations obtained from temperate regions cannot be directly extrapoled to tropical areas.

In the present study we analyzed if the surrounding vegetation, especially grass cover, has a negative effect on the distribution patterns of five geophytic puna plants at their lower elevation limits along an elevational gradient from 3800m to 4400 m. To assess how adaptable puna species are to changes in the vegetation we also described the biomass allocation patterns of the five species.

METHODS

Study area

The study was conducted in the department of La Paz, Bolivia, on the north-eastern slope of the Huayna Potosí peak (16°45´ S, 68° 9´W) along the Zongo valley, from dense grasslands at 3800 m to open puna steppes at 4400 m. The climate in the region is characterized by a distinct seasonality of precipitation, with 90% of the annual precipitation amount (668mm) falling during the austral summer; from October to April, and more than 50% within the three main wet season months, from December to February (Francou *et al.*, 2003). The average annual temperature is about 5°C, with a high incidence of frost events especially at higher elevations in the autral winter (Montes de Oca, 1997). At upper elevations, in the steppes, there is a great abundance of geophytic species (sensu Raunkier, 1934) such as *Geranium sessiliflorum* Cav., *Hypochaeris echegarayi* Hieron., *Oxalis oreocharis* Diels., *Nototriche longirostris* (Wedd.) A.W. Hill., and *Myrosmodes paludosum* (Rchb. f.) P. Ortiz. (**Fig. 4.1**) These species have relative narrow elevational ranges of about 600 m, and some are rare below 4000 m (elevational data from herbaria MO and LPB).

Field sampling

The field work was conducted in February of 2005. We recorded the presence and abundance of *G. sessiliflorum*, *H. echengarayi*, *O. oreocharis*, *N. longirostris* and *M. paludosum* on 120 plots of 0.1 m^2 at four elevations (3800 m, 4000 m, 4200 m, and 4400 m). At each elevation 30 plots were located along 3 transects of 50 m (ten plots per transect). The transects were located along well drained and flat to slightly sloping areas that correspond to the conditions where these species are usually observed. Additionally, we recorded in each plot vegetation height and the cover percentage of grasses. We also arbitrarily selected and extracted three entire plots on each transect, to obtain the above- and below-ground dry biomass of the vegetation. Above-ground biomass was completely extracted from the plots, whereas for the below-ground dry weight we took 3 samples of soil of 125 cm^3 from the first 10 cm depth.

From these plots we also collected the individuals of the study species to register their dry weight and the biomass allocated to shoots and roots.

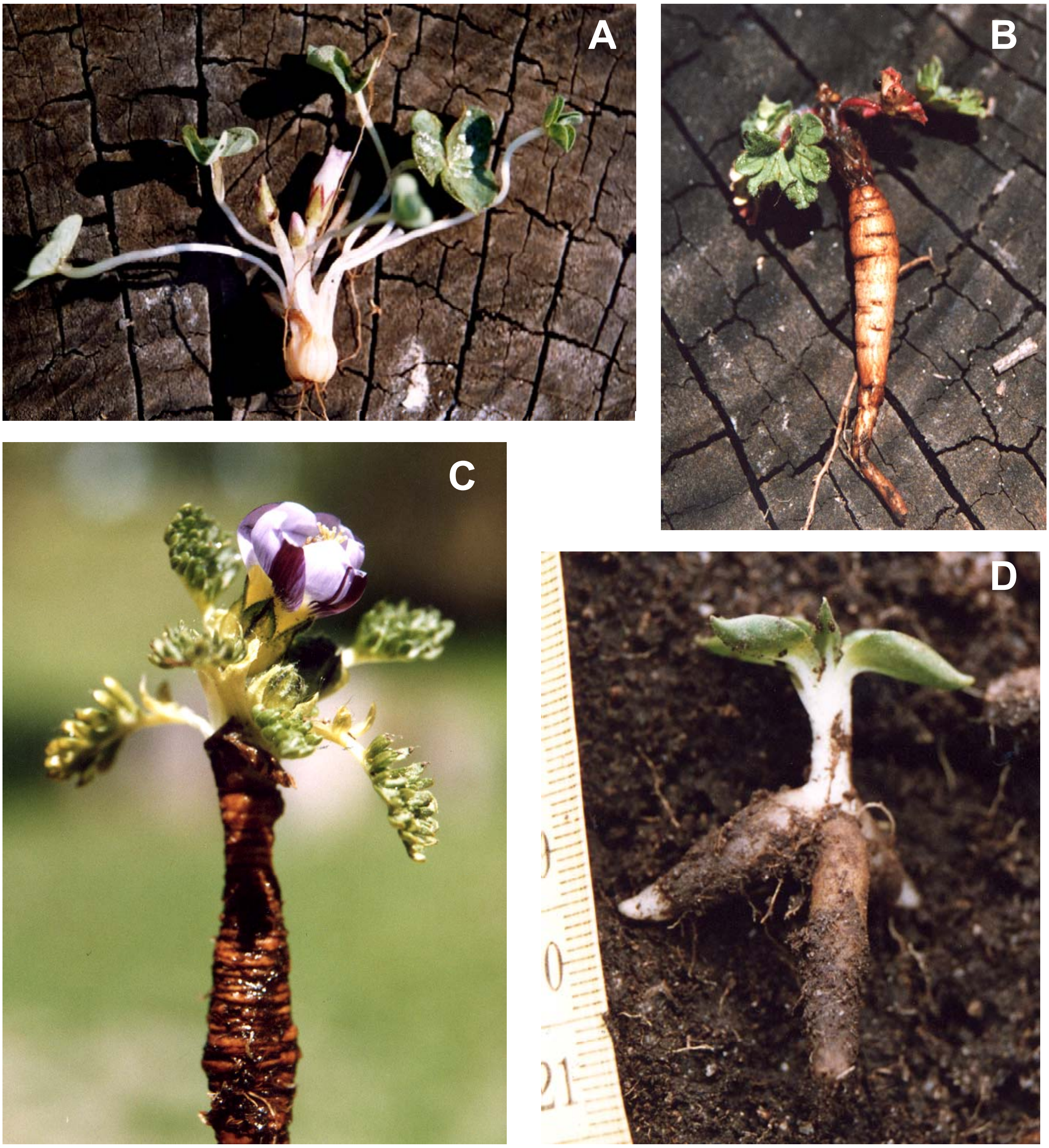

Fig. 4.1 *Oxalis oreocharis* (**A**), *Geranium sessiliflorum* (**B**), *Nototriche aristata* (**C**) and *Myrosmodes paludosum* (**D**).

Data analysis

To assess if there were differences in vegetation structure among the studied elevations we compared the vegetation height, the grass cover percentage, and the above- and below-ground biomass between elevations with a Kruskal-Wallis test for each factor (Fowler *et al.*, 1998). Since the most important structural component in the vegetation in this area are grasses we characterized the vegetation in detail by observing the frequency of plots at each elevation according to the grass cover. To observe if the presence of each geophyte species was associated with particular conditions of the studied variables, we evaluated if there were any differences in the height and biomass of plots with and without geophytes regarding the elevation. Since the factor for this analysis has two stages, presence or absence of a particular geophyte species, we carried out separte Kruskal-Wallis tests for each species and studied variables (Fowler *et al*., 1998). We also examined if the presence of each geophyte species was associated with a particular grass cover by observing the frequency of plots, arranged by cover classes of 10 %, where the species were registered. To test if the number of plots where the geophytes species were recorded was different between elevations, we compared the observed frequencies at the upper elevation with the frequencies at lower elevations with a Chi-square test (Zar, 1999). With the purpose to determine how adaptable the geophyte species are to changes in the vegetation along the elevational gradient we observed if the proportion of the biomass allocated to roots changed with increases in the above-ground biomass of the plots. For this analysis we carried out a Spearman correlation (Fowler *et al.*, 1998).

For the statistical tests we used the program Statistica 6 (Statsoft, 2003).

RESULTS

Along the studied gradient we observed important changes in the vegetation structure. Grasslands at 3800 m had taller vegetation than the grasslands at upper elevations (*Kruskal-Wallis test*, H(3,36)=10.12, p=0.017). The height difference was especially strong from 3800 m to 4000 m, where the vegetation height was strongly reduced. From 4000 m upwards there was a gradual reduction in the vegetation height, with the grassland height at 4400 m being lower than 10 cm (**Fig. 4.2a**). The grass cover also changed with elevation, with grasses occupying almost 50% of the plots at 3800 m and 4000 m, whereas from 4000 m upwards this was only about 20% (*Kruskal-Wallis test*, H(3,120)=40.43, p<0.0001) (**Fig. 4.2b**). The productivity of the grasslands, measured by the above-ground biomass, also decreased with elevation, particularly above 4200 m (*Kruskal-Wallis test*, H(3,36)=20.54, p=0.0001) (**Fig. 4.2c**). Although it was possible to observe an increase of below-ground biomass at lower elevations, there was no overall differentiation with the below-ground biomass at upper elevations (*Kruskal-Wallis test*, H(3,36)=20.54, p=0.0001) (**Fig. 4.2d**).

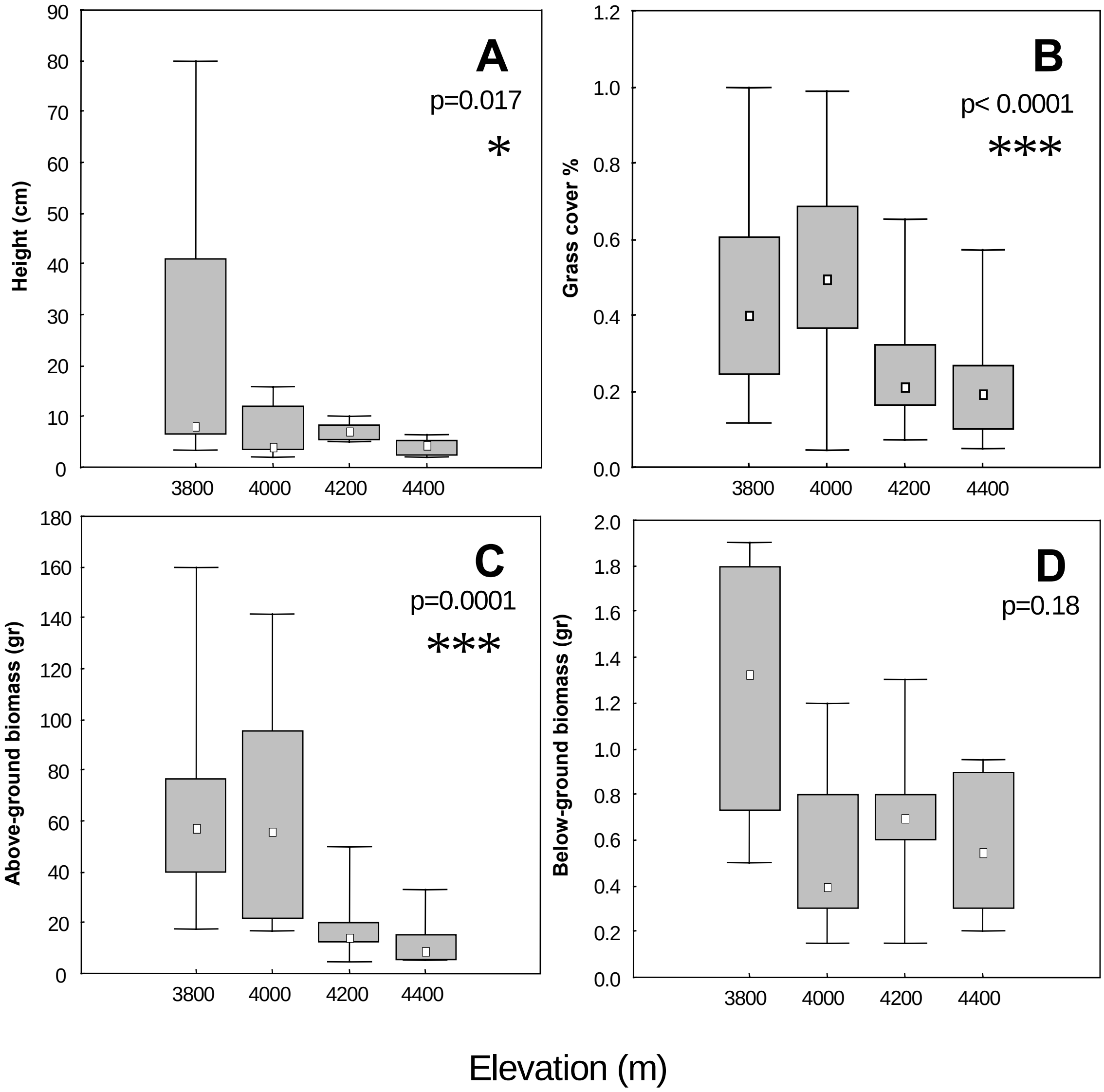

Fig. 4.2 Changes in the vegetation structure (A- height, B- grass cover, C- aboveground-, and D- below-ground biomass) along the elevational gradient in Zongo Valley, Bolivia. Values are median, quartiles (25 - 75%), maximum, and minimum of the variables. Significance levels from *Kruskal-Wallis tests* are indicated as * (<0.05), **(<0.01) and *** (<0.001).

Characterizing in detail the grass cover on the plots at the different elevations, we observed that at lower elevations, 3800 m and 4000 m, more than 50% of the plots are cover by grasses whereas at upper elevations, 4200 m and 4400 m, grasses occupy less than 40 % of the plot (**Fig 4.3**).

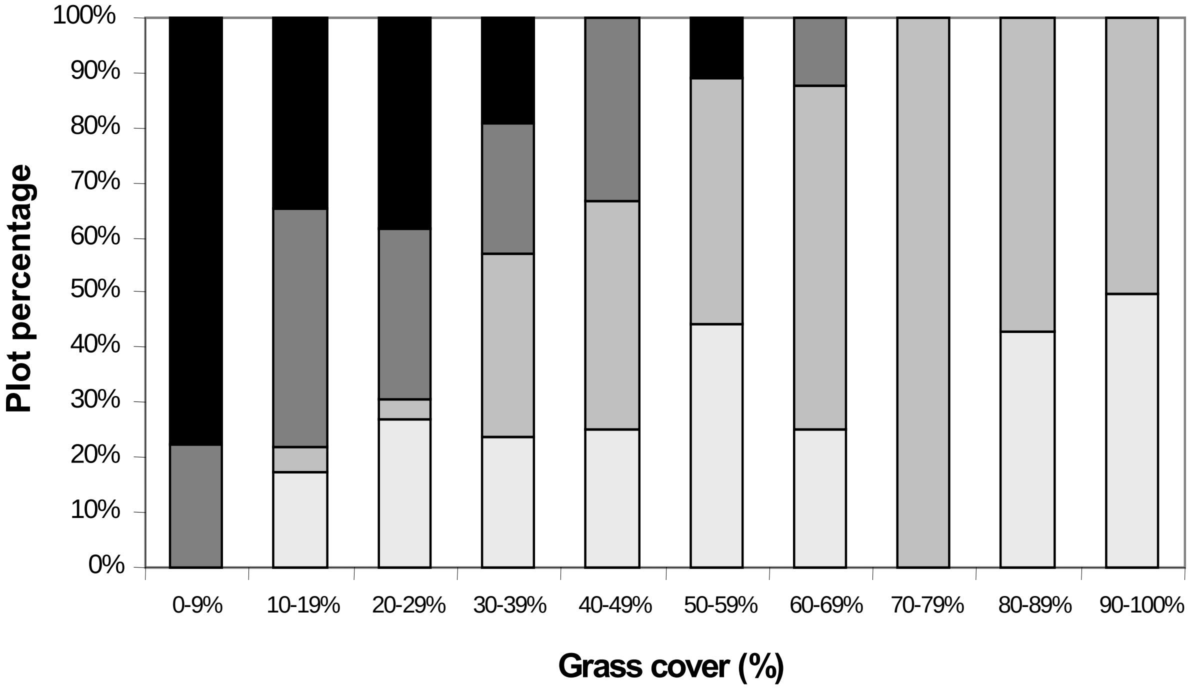

Fig. 4.3 Plot percentage by elevation in relation to grass cover percentage in Zongo Valley, Bolivia. In black values for plots at 4400 m, in dark gray for 4200 m, in intermediate gray for 4000 mand in light gray for 3800 m.

There was a clear habitat preference among the geophyte species studied. Species were principally recorded in habitats with reduced above-ground biomass (**Fig. 4.4**). *Myrosmodes paludosum* appeared to be also associated with reduced below-ground biomass. Only two species, *N. aristata* and *M. paludosum* showed strong preferences for habitats with lower vegetation height. Contrary to the other geophyte species studied, *O. oreocharis* did not show clear habitat preferences.

The grass cover did not seem to affect in general the establishment of geophyte species, however observing in detail the effect of grass cover on each species it is possible to postulate that grass cover diferentially affects each species (**Fig. 4.5**). *Nototriche aristata*, *M. paludosum* and *H. echegarayi* appered to be restricted to plots with grass cover under 50 %, while for *O. oreocharis* and *G. sessiliflorum* the establishment did not seem to be affected by the grass cover.

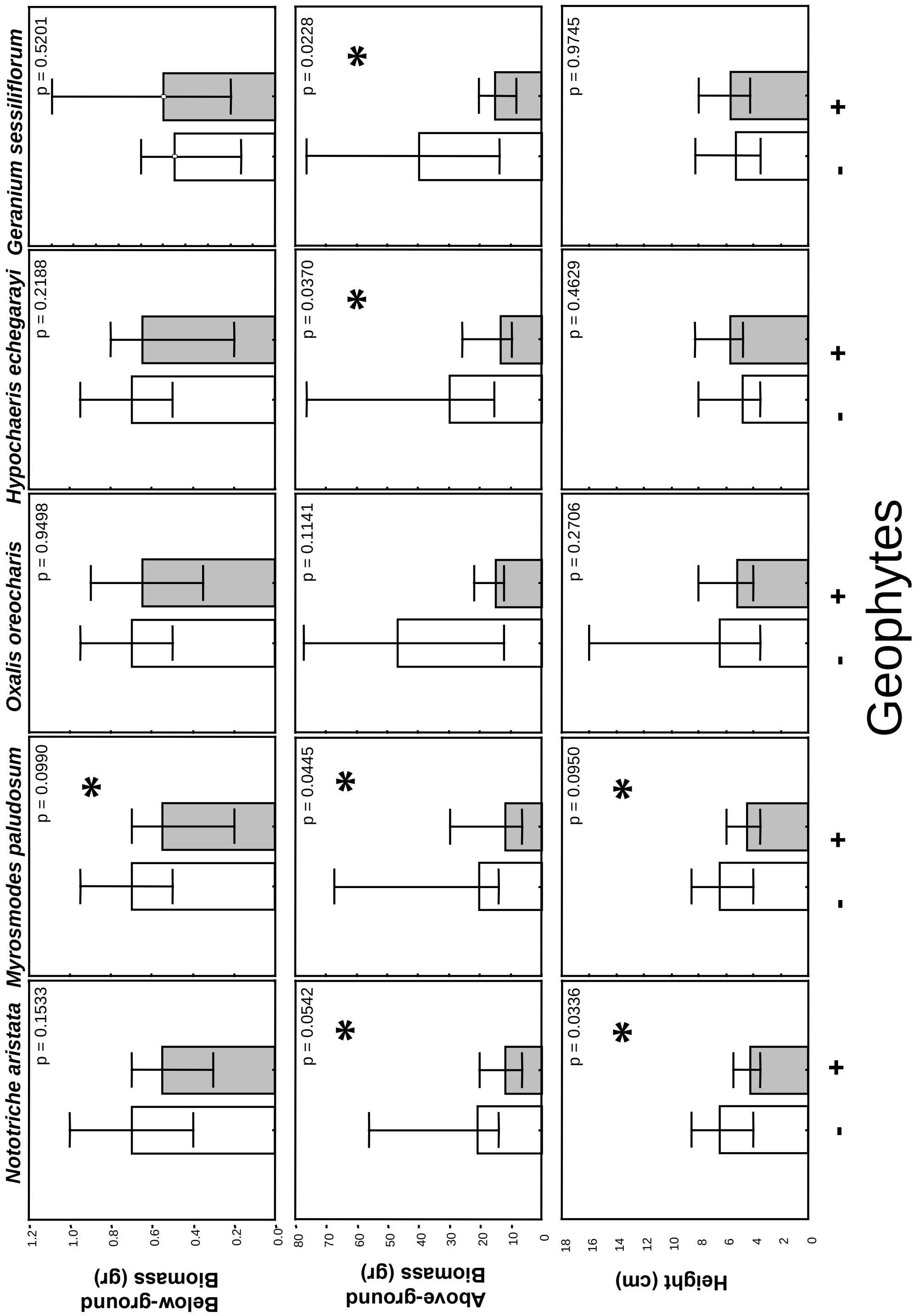

Fig. 4.4 Vegetation structure (height, aboveground, and belowground biomass) of plots with and without (in gray and white, respectively) the geophyte species studied. Values are median, and quartiles (25 – 75%) of the variables. Significance levels from *Kruskal-Wallis tests* are indicated as * (<0.1).

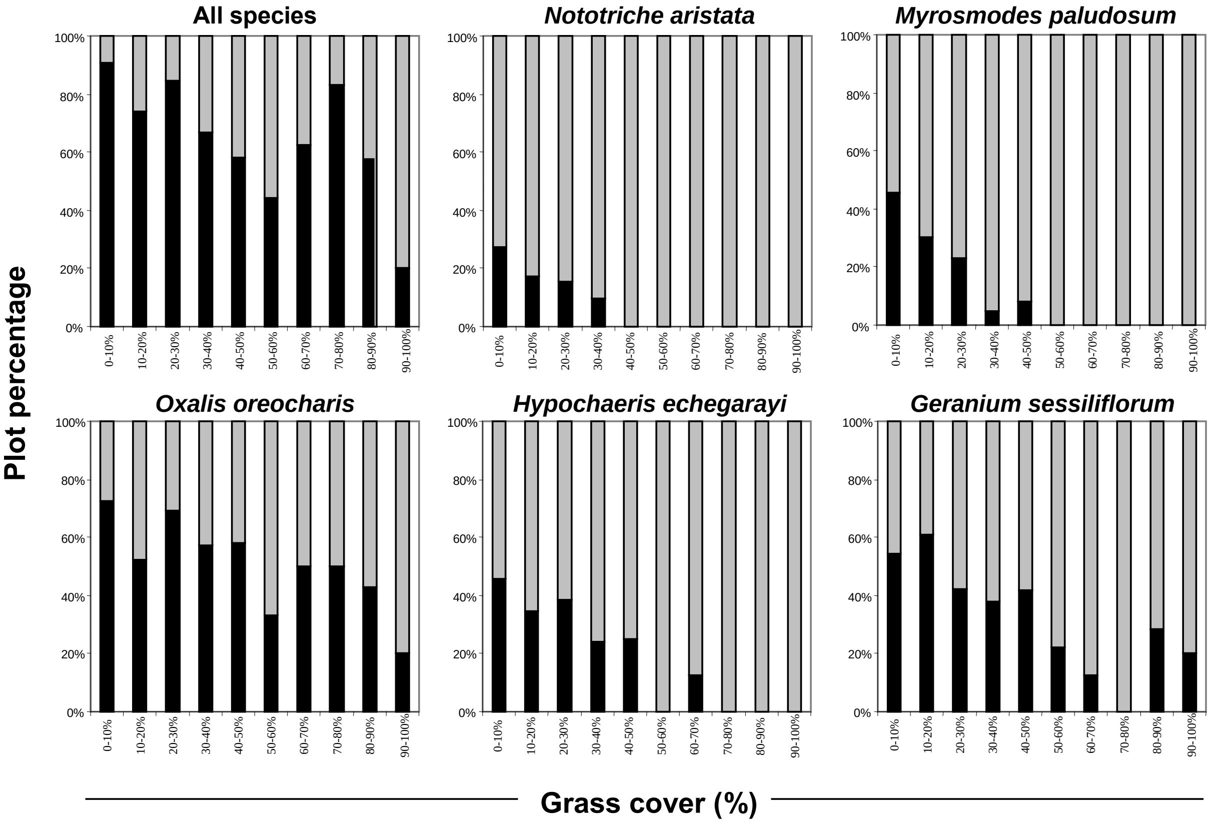

Fig. 4.5 Plot percentage with indivuduals of the geophyte species studied (in black) for different grass cover percentage in Zongo Valley, Bolivia.

The percentage of plots in which geophyte species were recorded differed between the elevations (*Chi-square tests*, 3800 m vs. 4400 m χ^2=42.27, d.f.=4, p<0.0001; 4000 m vs. 4400 m χ^2=42.88, d.f.=4, p<0.0001; 4200 m vs. 4400 m χ^2=26.67, d.f.=4, p<0.0001). Optimal habitat occupation where found for *O. oreocharis* and *H. echegarayi* at 4200 m whereas for the other species, *G. sessiliflorum*, *N. longirostris* and *M. paludosum*, it was found at 4400 m (**Fig. 4.6**).

The percentage of biomass allocated to the roots was not correlated to the above-ground biomass of the plots (*Spearman correlation*, 4000 m r= -0.24, p=0.14; 4200 m r=0,11, p=0.39; 4400 m r=0,029, p=0.68), in this way changes in the above-ground biomass did not lead to any changes in the resouce allocation of the geophytes species studied. It was interesting to observe that changes in the petiole length in *O. oreocharis* were correlated to the above ground biomass of the plots (*Spearman correlation*, r=0.29, p=0.0017). This correlation could not be tested in the other species since most of them have sessile leaves.

DISCUSSION

Our results show that changes in the vegetation structure affect the the abundance and frequency of geophyte species in high Andean ecosystems. A greater abundance of geophytes was associated with lower above-ground biomass and vegetation height, and decreased grass cover, whereas an increase in these factors determined a strong disminution of the number of geophytes.

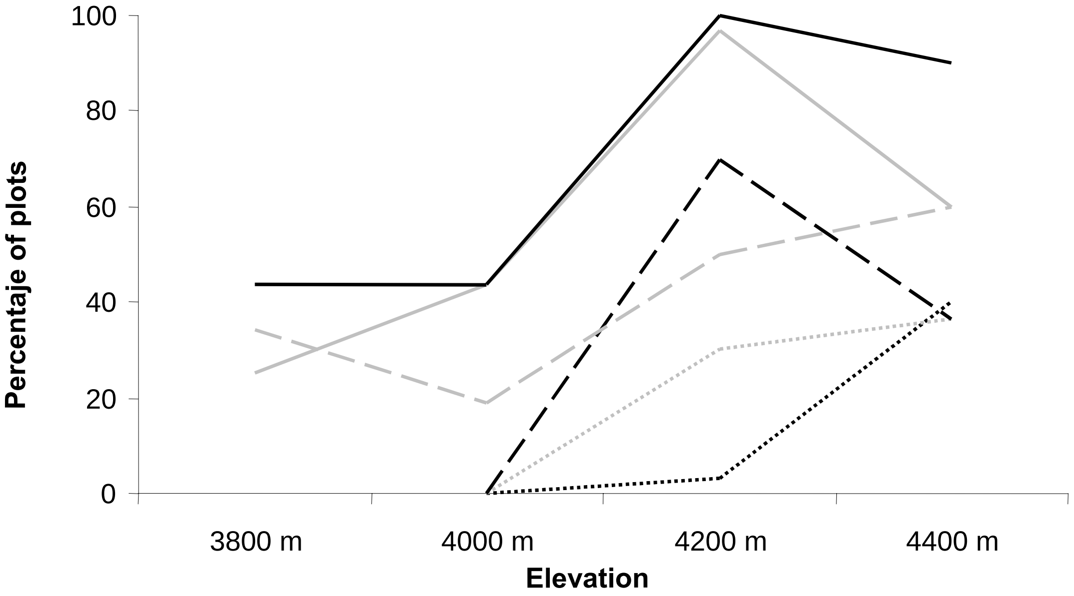

Fig. 4.6 Registration frequency in percentage of plots of all geophytes studied (—), *Oxalis oreocharis* (—), *Hypochaeris echegarayi* (−−), *Geranium sessiliflorum* (−−), *Myrosmodes paludosum* (····) and *Nototriche aristata* (····) along the elevational gradient in Zongo valley, Bolivia.

Apparently, vegetation with higher primary production limits the establishment and abundance of geophytes, suggesting an increase in the competitive interactions between the studied species and the surrounding vegetation. Previous studies in alpine communities have indicated that sorrounding vegetation can lead to increased competitive interaction for light (Grytnes, 2000; Onipchenko *et al*., 2001), water (Rochow, 1970) or for available space for establishment (Kikvidze *et al*., 2005; Scheidel *et al*., 2003). Some studies in high montane vegetation have indicated that the less physical stressful conditions of lower elevations, which promotes higher vegetation development, also intensify the competitive interactions among species (Callaway *et al*., 2002; Kammer & Mohl, 2002). However, it is important to indicate that in spite of being competition the factor that seems to excludes to the species from lower elevations, the competitiveness of the species could be determined by their plasticity to adapt to varying environmental conditions (Billings *et al*., 1971; Bruelheide & Lieberum, 2001). In this way, if a species cannot take enough advantage of more favourable conditions of lower elevation it will be excluded by species that can use the conditions better (Woodward, 1975; Woodward & Pigott, 1975). In general, the species of geophyte studied did not show any difference in their resource allocation patterns, investing the same proportion of biomass to roots without regarding changes in the vegetation from closed grassland at lower elevations to steppes at upper elevations. This suggests a low acclimation plasticity of the species to warmer conditions of lower elevations. Low acclimation plasticity has also been reported for other alpine and high montane plants (Graves & Taylor, 1986; Bruelheide & Lieberum, 2001). It has been postulated that plants submitted to large daily temperature fluctuations such as the conditions of high montane areas in the tropics, generaly exhibit low changes in the metabolic rates with increasing temperatures, since metabolic rates in these plants are genetically fixed (Criddle *et al*., 1996; Körner, 1999).

Nevertheless, it is important to note that not all of our study species reacted in the same way or with the same intensity to structural changes of the vegetation. *Oxalis oreocharis* in particular did not seem to be affected by the changes in the structure of the vegetation. Plastic morphological characteristics of *O. oreocharis,* such as petiole length may be buffering the effects of the surrounding vegetation on this species. In this way, we observed that individuals of *O. oreocharis* growing in plots with high above-ground biomass, tend to elongate the petioles, and to allocate more to above-ground structures. This morphological plasticity in could be contributing to its greater plot occupation at lower elevations, in contrast to the other geophyte species studied.

As the structure and composition of high montane communities is primarily determined by temperature (Coe, 1967; Hedberg, 1951), a moderation of temperature-related stress factors, as consequence of global warming, may cause a shift of the equilibrium between stress and competition (Kammer & Mohl, 2002; Klanderud & Totland, 2005). Accordingly, climate change in these areas could lead to changes in the dominance patterns and to species invasions from adjacent areas, especially of grasses. Competition with grasses has been already postulated to be a critical factor in the distribution of plants at high elevations (Rochow, 1970), since it has been established that above-ground biomass of grasses responds rapidly to warmer conditions (Zhang & Welker, 1996).

Chapter

5

Effects of simulated climate change on biomass allocation patterns of seedlings of two Andean *Lepidium* species (Brassicaceae) with different elevational distributions

J Jácome, M Kessler

In: Ecotropica (2005) in press.

ABSTRACT

The current climatic change has made temperatures rise, affecting plant growth, and probably even more deeper in extreme and restricted environments at high altitudes such as those in the Andean region. In order to address the question on how climate change would alter plant growth in high Andean ecosystems we cultivated two species of *Lepidium* (Brassicaceae) (*L. meyenii*: natural distribution 4050-4600 m; *L. bipinnatifidum*: 3100-3900 m) at two sites (3100 m, 4100 m), simulating the invasion of colder and the growth in warmer environments. Biomass production of both species did not differ due to changes in elevation during the establishment phase, but *L. meyenii* shifted its resource allocation from predominantly below-ground at high elevation to mostly above-ground at lower elevations, while resource allocation in *L. bipinnatifidum* remained constant. The elevational distribution of both species is thus not limited by mean temperatures but by their ability to shift resource allocation patterns, determining their ability to cope with extreme climatic events (frost, drought). As such climatic extremes may be more common in the future, the response of plant species to global change will therefore not be a simple shift of elevational ranges, but likely result in an overall reduction of range sizes.

INTRODUCTION

In tropical mountains, global climate change is expected to lead to increasing temperatures and lifting of cloud condensation layers, possibly also establishing new biotic interactions. These events are likely to force species to either migrate upwards or to adapt to changed environmental conditions (Pounds *et al*., 1999). It is likely that the migratory response of some species will not be fast enough to encompass climate change (Bush, 2002), and will be hampered by habitat loss and fragmentation, or simply by the maximum height of mountain ranges, increasing the number of species in danger of extinction (Thomas *et al*., 2004). Even species able to migrate are unlikely to encounter identical climatic conditions at higher elevations, because climate change does not simply imply an increase of temperatures but also shifts in precipitation regimes, cloudiness, and especially the frequency of extreme environmental conditions such as droughts and frost (Vuille *et al*., 2003). It is therefore likely that all species will be forced to some degree to adjust their autoecological behavior. Optimal partioning models and theories suggest that plants respond to variation in the environment by allocating biomass among plant organs to optimize the capture of nutrients, light, water and CO_2 in a manner that maximizes plant growth rates (Bazzaz, 1996; McConnaughay & Coleman, 1999). Thus the study of the biomass allocation patterns of plant species of tropical mountains at different elevations can indicate how adaptable the species will be to climate change. Little is known about the responses of tropical montane plants to climatic change under field conditions. To date, only one field study has been done to test the predicted effects of climate change on tropical montane epiphyte plant communities (Nadkari & Solano, 2002), and comparable studies for other life forms or in other high mountain ecosystems such as puna and páramo are completely lacking.

The purpose of the present study was to document how the biomass allocation patterns of seedlings of two high-Andean plant species react to a simulated global warming under field condition. For one species we simulated the move to higher elevations, for the other the shift was to lower elevations. We concentrated on the establishment and juvenile stages due their relevance in the establishment and maintenance of populations (Harper, 1977) and susceptibility to environmental stress (Larcher, 1994).

METHODS

We selected two species of Lepidium (Brassicaceae) because some of the Andean taxa occur at very high elevations and are thus most likely to be affected by climate changes, and because some species of *Lepidium* are of local economic and nutritional value. We chose two species with different elevational distributions: *L. meyenii* Walp. (4050-4600 m) and *L. bipinnatifidum* Dom. Sm. (3100-3900 m). The elevational distributions of the species were obtained from vouchers deposited in the Herbario Nacional de Bolivia (LPB).

The study was conducted in Bolivia, near the city of La Paz. Plants were cultivated at two localities of different elevation: El Alto (4100 m; 16º28’ S, 68º15’W) and Mallasa (3100 m; 16º32’S, 68º08’W). Thus each species was cultivated at one site within its natural elevational distribution and one outside of it. Seeds of each species were collected from a population located within their distribution ranges.

Seeds of each species were planted in 40 plastic pots of 25 cm diameter filled with soil from the upper locality. Half of the pots were located at 4100 m and the other half at 3100 m, under natural conditions of solar irradiation and temperature. The plants were watered regularly to avoid water deficit. Soil elevational translocation was not expected to change soil properties in the short term during the experiment, due to the low organic matter content characteristic of dry puna soils, and homogeneous watering, since organic matter and water content are reported to induce changes in soil properties (Scheffer & Schachschabel, 2002). Thus by using the same soil and by watering we limited the differences between both sites to climatic conditions (temperature, irradiation, air humidity, etc.).

After two months the plants were collected and the root:shoot ratios were calculated, dividing the root dry weight by the shoot dry weight. A Krukal-Wallis sum of ranks tests (Fowler *et al.*, 1998) were used to test for differences in the weight of below-ground and above-ground structures, and root:shoot ratios between localities for each species. For the test the significance level was $\alpha=0.05$.

RESULTS

In the case of the higher elevation species *L. meyenii*, transplantation to a lower elevation led to a greater biomass production by the seedlings in contrast to seedlings growing within their natural elevational ranges (Kruskal-Wallis-Test: H (1, N=20)=6.60, p=0.0102) (**Fig. 5.1**).

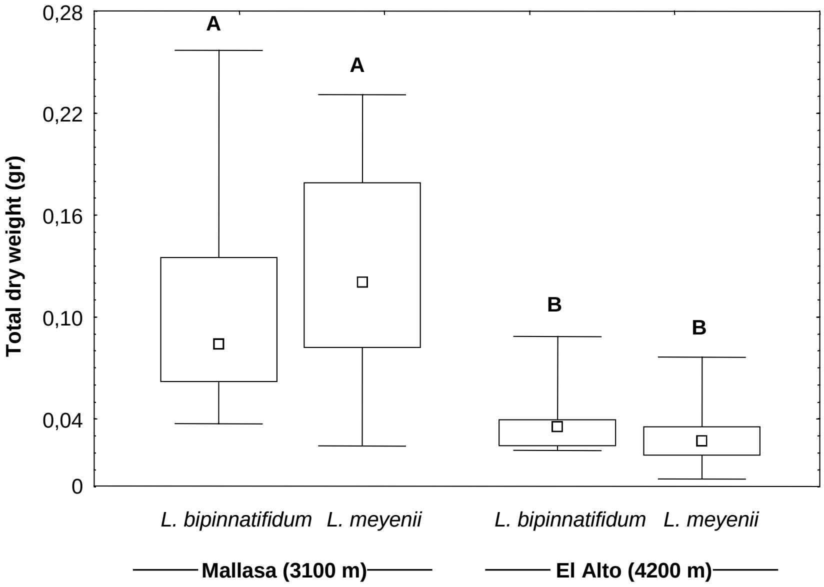

Fig. 5.1 Median, quartiles, maximum, and minimum dry weight of seedlings of *Lepidium meyenii* and *Lepidium bipinnatifidum* after two months at the localities of El Alto and Mallasa. Different letters indicate significant differences between the medians (Kruskal-Wallis test).

The seedlings located at the upper site invested nearly 70% of their dry weight in roots and about 30% in above-ground biomass, while those at the lower site showed the opposite pattern, allocating 30% and 70% of the total dry biomass to below- and above-ground structures respectively (Kruskal-Wallis-Test: H (1, N=20)=11.57, p=0.0007) (**Fig. 5.2**).

For the lower elevation species *L. bipinnatifidum*, cultivation at higher elevations reduced the biomass (Kruskal-Wallis-Test: H(1, N=20)=10.08, p=0.0015) (Figure 1), but did not change the allocation pattern, which was about 50% to roots and shoots in both localities (Kruskal-Wallis-Test: H (1, N=20)=0.82, p=0.36) (**Fig. 5.2**).

Comparing the two species, there was no statistical difference in the dry weight at each of the two cultivation sites nor in biomass allocation patterns at 3100 m, but *L. meyenii* had significantly more below-ground biomass at 4100 m than *L. bipinnatifidum* (Kruskal-Wallis-Test: H (1, N=20)=14.28, p=0.0002).

DISCUSSION

The greater productivity of the seedlings of both species at the lower site likely reflects stronger growth in warmer environments as a result of increased metabolic rates (Precht *et al.*, 1978), which leads also to the overall plant size pattern along the elevational gradient (Körner *et al.*, 1989).

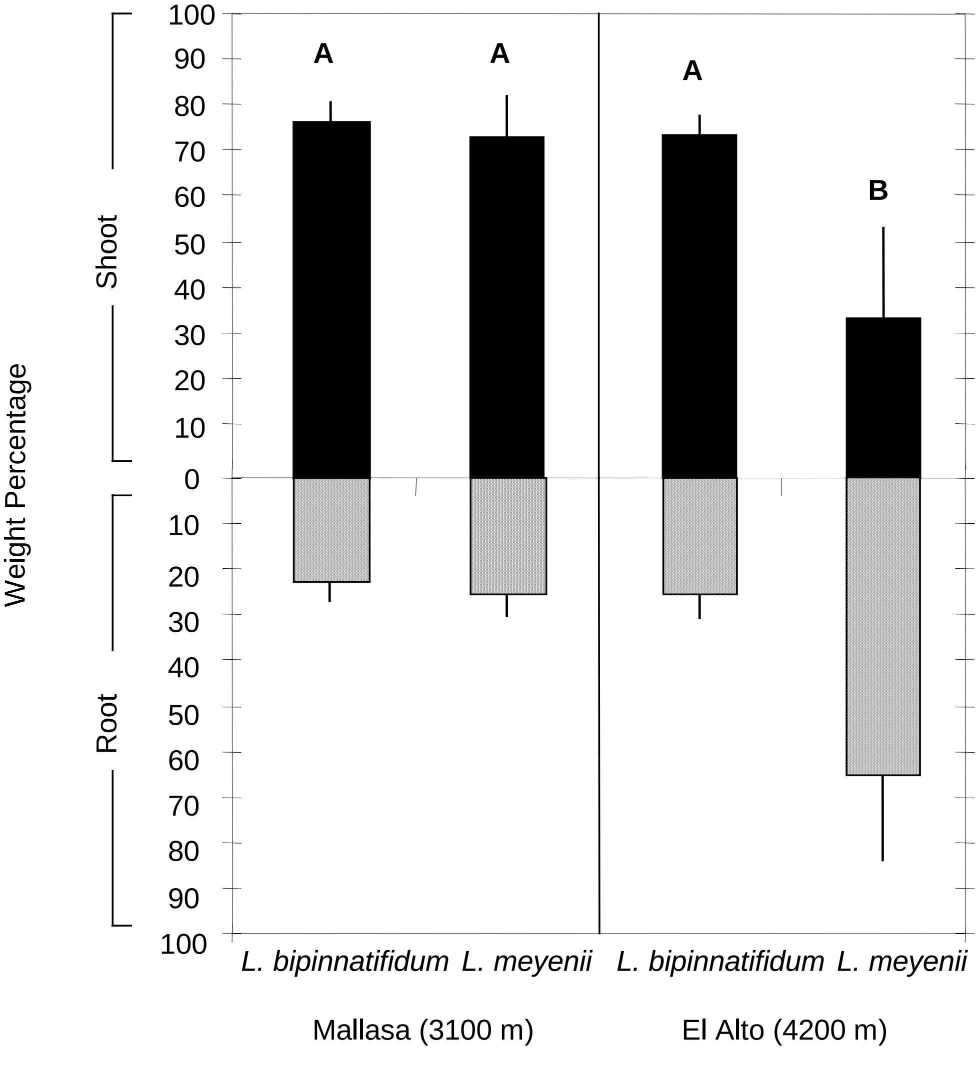

Fig. 5.2 Biomass allocation in aerial parts and roots in seedlings of *Lepidium meyenii* and *Lepidium bipinnatifidum* after two months at the localities of El Alto and Mallasa. The values are medians ± quatile of the percentage of the total dry weight in aerial parts and roots.

It is striking that *L. meyenii* had the same growth as *L. bipinnatifidum* about 1000 m below its natural lower elevation limit, indicating that its elevational distribution is unlikely to be limited by temperatures. Possible limiting factors could include higher water stress at the lower site under natural conditions, since precipitation in the study area does not increase significantly at lower elevations, or biotic interactions such as competition or herbivory (Loehle & LeBlanc, 1996; Schenk, 1996; Vetaas, 2002). This suggests that *L. meyenii* may at least be initially favored by increasing temperatures as a consequence of climate change, with phenomena such as interspecific competition becoming important limiting factors. However, it is important to consider the marked change in the allocation pattern in *L. meyenii* growing in warmer environments, with most of the biomass located in above-ground structures. This could make the seedlings of *L. meyenii* more sensitive to the drought and frost events that occur in the austral winter in the region, since plant morphology is one of the main determinants of drought and frost resistance (Larcher, 1994). The possible risk of increasing frost damage under elevated temperatures has also been outlined for boreal ecosystems, and has been suggested as one of the main detrimental effects of global warming on plants of cold environments (Kellomaki *et al*., 1995). Strong drought events in the central Andes in the last decades due to climate change are believed to have led to significant losses of biodiversity and decreases in plant growth rates (Halloy, 2002). The example of *L. meyenii* in our study shows how a greater susceptibility to climatic extremes may be induced by changes in the biomass allocation as a reaction to growing under warmer environmental conditions. However, warmer conditions imply not only increasing temperatures but also changes in the cloud cover, affecting the irradiation and nutrient availability, factors which have also been documented to lead to changes in the root:shoot ratios (Körner & Renhardt, 1987; McConnaughay & Coleman, 1999). In this way clarifying the role of each of these factors could help us to understand and predict how high-Andean plants will react to climate change.

The inability to adapt biomass allocation may limit the elevational distribution of potential invasive species in the study area, as has been shown in *L. bipinnatifidum*. While our study does not allow a determination of the cause of a growth response under higher temperatures, it enables us to develop an idea of the factors limiting the upper elevational distribution of the species. At the upper site, *L. bipinnatifidum* grew about as well as *L. meyenii*, but failed to shift its biomass allocation to an increased production of below-ground biomass. During our experimental period no extreme frost events occurred, but based on similar studies elsewhere (Precht *et al*., 1978; Floistad & Kohmann, 2003) we suspect that a single strong frost event could have severely damaged the above-ground parts of *L. bipinnatifidum* seedlings, which would then have had fewer resources in their roots to compensate for the damage compared with *L. meyenii*. Thus our study shows that the elevational distribution of the two species of

Lepidium cannot be explained by mean temperatures alone, but is likely to be more strongly limited by extreme climatic events and biotic factors in their interaction with the adaptability of the individual plant species, particularly with the biomass allocation patterns.

If the relationship of mean temperatures to climatic extremes remains constant in the future, then temperature increases will simply lead to an elevational shift in the distribution of species niches. However, global climate change not only implies changes in temperature but also in CO_2 concentration, precipitation regimes, and irradiation (Root *et al*., 2003). Recent observations from the Bolivian Andes suggest that precipitation and cloudiness are likely to change more strongly than temperatures (Vuille *et al*., 2003). Whereas temperatures show only a moderate increase in this region, precipitation and cloudiness are markedly decreasing, especially in the dry season (austral winter). This implies a higher frequency of extreme climatic events such as frost and drought. This could lead to drastic reductions in the niche area available to plant species as a result of new constraints at both upper and lower elevational limits, and stresses the importance of the adaptability of species to these new conditions. Nevertheless, it is important to note that adaptability via biomass allocation may result from true adjustments or as a consequence of ontogenetic development (Coleman *et al*., 1994). In this way the adaptability of high-Andean species to future climatic scenarios could vary according to species and growing stage.

Chapter

6

Responses of tropical non-vascular epiphytic communities to a simulated climate change: short-term changes

J Jácome, M Kessler

ABSTRACT

In order to address the question on how climate change might alter epiphyte communities, and to describe if this response will principally take place at community or specific level, we translocated complete non-vascular epiphyte communities along an elevational gradient in the Bolivian Andes.We cut 60 branches with their intact communities at 3000 m and hung 20 of them into trees at each 3000 m (control), 2700 m (simulated temperature increase 1.5ºC), and 2500 m (2.5ºC). On each branch we recorded the cover of each species at the beginning of the experiment and after one and two years. After two years epiphytes communities translocated to lower elevations did not differ in total bryophyte cover from those left at 3000 m, but they were more dynamic, with higher cover changes by species. Saturated communities, with high total cover and with no available space bteween bryophyte individuals were more resistant to cover changes than unsaturated communities. The response of epiphytes to the translocation was distinctly species-specific, ranging from increases to decreases across elevation. At the structural level, the assemblages translocated to lower elevations turned to a more equitative species abundance pattern. We infer that community structure and species composition will change markedly as a result of future temperature increases of at least up to 2.5°C, but that communities will not collapse and that overall cover and ecosystem functions such as nutrient cycling and water retention will only experience limited changes.

INTRODUCTION

Biological responses to climate change are already observed in many ecosystems, involving changes in the phenology and physiology of organisms, in the distribution of species, in the composition and interactions within the communities, and in the structure and dynamics of ecosystems (Walther *et al*., 2002). Climate change will pressure and induce responses principally on species populations at the distribution margins, especially those located at the warmer edges such as lower latitude and lower elevation range margins (Hughes, 2000; Walther *et al*., 2002). Factors that establish the current lower elevational or latitudinal limits of the species could become crucial in the determination of the type and rate of the responses to climate change. A series of studies have experimentally established that lower latitudinal and elevational limits appear to be principally associated with biotic factor such as competition, predation, or pathogens (e.g., Rochow, 1970; Loehle, 1998; Bruelheide & Scheidel, 1999; Bruelheide & Lieberum, 2001). However, it is still unclear which specific mechanisms determine the range margins, and therefore how species will respond to climatic change along latitudinal and elevational gradients.

One of the principal concerns about climate change is how it will affect community composition and ecosystem functioning (Hunt & Wall, 2002; van der Putten *et al*., 2004). It has been suggested that climate change might lead to strong, abrupt changes of species diversity and community composition which will alter ecological processes and thus the community maintainance (Zabaleta *et al*., 2003; Welker *et al*., 2005). Such community collapses would have unforseeable consequences for ecosystem functioning. Whether these critical scenaria are realistic is uncertain, however, in partly due to methodological problems, because transplantation experiments of plants to different environments are usually conducted with one or few selected species whose relevance to the entire communities is uncertain (e.g., Nadkarni & Solano, 2002), or by manipulation of environmental conditions such as temperatures, CO_2-concentration, or temperatures at the community level, in which case the experimental design cannot properly simulate the full range of environmental changes and may influence the observed responses (e.g., Jónsdóttir *et al*., 2005). To date, no experimental transplantation of entire communities have been conducted. Further, predictions on the response of species and ecosystems to climate change are based principally on studies from temperate ecosystems, with few studies from tropical areas, especially montane regions which are expected to be particularly susceptibel to climate change (Pounds *et al*., 1999; Still *et al*., 1999).

Tropical mountain cloud forests are mainly determined by orographic clouds, continuous mist, and frequent rainfall (Still *et al.*, 1999). These climatic conditions favour high species diversity and the development of an exuberant non-vascular epiphytic flora (Wolf, 1994; Kessler, 2001), which is responsible for important ecological processes in these forests, such as water interception and nutrient cycling (Coxson & Nadkani, 1995; Cavelier *et al.*, 1996; Benzing, 1998). Global climate models predict profound changes in the hydric regimes for tropical mountain cloud forests, principally implying an upward shift of the cloud condensation surface during the winter season by hundreds of meters, leading to a reduction in the cloud cover and to increased evapotranspiration (Still *et al.*, 1999; Foster, 2001; Chen *et al.*, 2002; Vuille *et al.*, 2003). Non-vascular epiphytes are good indicators of changes in hydric regimes since they do not have water-transporting root systems and cannot obtain water from the soil (Gignac, 2001). Therefore, cloud forest epiphytes are expected to become strongly negatively affected by a climatic change. Nadkarni & Solano (2002), in a first experimental approach on the effects of climate change on canopy communities of a tropical cloud forest in Costa Rica, observed decreased productivity and longevity of several vascular epiphytes and the invasion of terrestrial species into the canopy community. Their results were principally based on the individualistic response of epiphyte species to simulated climatic change, and information about the reaction of tropical montane epiphytes at the community level is completely lacking.

Studies on climate change effects on temperate vegetation have shown different community responses that include species specific (Weltzin *et al.*, 2003) and functional group responses (Price & Waser, 2000; Weltzin *et al.*, 2003). For tropical epiphyte communities it would be reasonable to expect specific responses since communities are constituted by species with different microclimatic requirements, stress tolerances and geographical distributions; however the role of community structure, composition and productivity on these individual changes and in the community functioning remains unknown.

The objetive of this study was to describe the response of tropical non-vascular epiphyte communities to a simulted warmer and dryer climatic scenario by translocating them to lower elevations. This experimental approach, previously applied by Nadkani & Solano (2002), permits a good approximation to the effects of the climatic change on tropical montane plant communities, since communities are maintained under natural abiotic conditions but also because they are exposed to changing biotic interctions.

METHODS

Study site

The study was carried out from February 2003 to Februar 2005 in the department of La Paz, Bolivia, between the the localities of Chuspipata and Yolosa (16°16-17'S, 67°48-53'W) along the road that connects the cities of La Paz and Coroico. This area is mainly covered by tropical montane rain forest (sensu Holdridge 1967). The climate is humid, with precipitation exceeding 2000 mm per year and average annual temperatures ranging from 12 °C to 20 °C (Bach, 2004; Schawe, in prep). In the immediate study region, above ca. 2700 m climatic conditions are more humid, whereas below this elevation dry spells occur regularly, principally during the dry season (June-October). Details on vegetation and climate of the study area can be found in Navarro & Maldonado (2002).

Simulated climate change

For our experiment we cut 60 branches of one meter length each with non-vascular epiphyte communities from 10 trees located at 3000 m. We selected branches growing at intermediate conditions of irradiation from the lower part of the tree crowns, corresponding to zone 3 according to Johannson's tree zonation (Johansson, 1974; ter Steege & Cornelissen, 1989)

The branches were hung the same day from other trees, trying to simulate their original growth conditions of irradiation and exposition, to diminish the influence of microenvironmental differences that could cause changes in the community composition (Gradstein *et al.*, 2001). Twenty of these branches were hung up at the original elevation whereas 20 each were moved to 2700 m and 2500 m, respectively. These elevational differences of 300 m and 500 m imply a temperature increase of about 1.5°C and 2.5°C and a reduction of about 25% mean annual precipitation (Bach, 2004), which is within the range of predicted climate changes for the next 50-100 years (Woodward 1992, Pounds *et al.*, 1999). With this experimental design we therefore did not only simulate a warmer but also dryer conditions.

On each branch we recorded the cover of each bryophyte species at the beginning of the experiment and after one and two years, measuring the maximum and minimum diameter for each species patch. Since we could not carry out a destructive inventory of the branches, only the species distinguishable direct in field with a magnifying glass of 20x were recorded separately.

Data analysis

We compared the initial total bryophyte cover on each branch with the cover after one and two years and tested for differences in the bryophyte cover between elevations. Differences in the total bryophyte cover between dates and elevation were statistically tested carrying out a repeated measurements ANOVA (Zar, 1999). Data on bryophyte cover were log-transformed to adjust them to normality and to increase homogeneity of variance.

We evaluted the effect of the translocation to lower elevations on community structure in two ways, first by observing changes in the community similarity, and second by comparing the rank-cover pattern of the community during the two years. To observe changes in the community similarity we calculated Bray-Curtis dissimilarity indices (Magurran, 1988) for each branch between the initial community composition and the composition after one and two years, respectively. The dissimilarity values were calculated with the cover data of the ten most important species on each brach, since the Bray-Curtis similarity index tends to overweight the importance of rare species (Legendre & Legendre, 1998) and because our data on these rare species that were often difficult to identify were less reliable. Because changes in the communities could be affected by interspecific interactions, we also calculated the bryophyte saturation of the branches as the total cover of all bryophyte species present on the branch, divided by the branch area (length*diameter). As bryophyte patch overlap occurred, saturation values could exceed one. We tested if there was a difference in the similarity values between elevations after one and two years carrying out an ANCOVA (Zar, 1999), after logaritmic or arcsin square root transformation on the data to improve normality and variance homogeneity.

To compare the rank-cover patterns of the community between elevations we selected at each elevation the twelve most important species according to their cover on all branches at a particular elevation. Then we ranked these species by cover and obtained for each rank the cover change after one and two years. Cover change was calculated as the absolute difference of the final and initial relative cover at each elevation. Then, we performed pairwise comparisons between ranks at different elevations, examining for differences in cover change between elevation. For this analysis we used a pairwise t-test (Fowler *et al*., 1998).

We also observed how elevation affected the community dynamic, measuring the cover change for each branch. For this, cover data of all bryophyte species present on a branch were first relativized to the total bryophyte cover on the branch. The relativization of the cover was necessary since in some cases it was difficult to establish clear limits of the bryophyte patches, leading to over- or sub-estimation of the species cover in different years. Taking the relativized cover we determined the cover change for each species on a branch as i) the absolute and ii) as the real difference between consecutive years. With the absolute difference it was possible to establish differences in the magnitude of the cover changes, whereas with the real differences a general pattern of cover increase or decrease could be determined. Since interspecific interactions could also affect the cover changes, we also included in this analysis the bryophyte saturation of the branch as covariable. With these data we carried out a GLIM (general lineal model) (Crawley, 2002), with elevation as main factor, branch as random factor, bryophyte saturation as covariable and cover change as response variable. Data on cover change were log-transformed to adjust normality and homogeneity of variance. A critical point in our experimental design was whether the wood degradation would originate changes in the bryophyte community per se, obscuring the translocation effects. To assess this bias we analyzed separately the cover changes in the first and in the second year. In this way we expected that changes caused by wood degradation would obscure the effects of elevation during the first but not during the second year. For the statistical tests we use the program Statistica 6 (Statsoft, 2003).

To account for differences in cover change by elevation for the most important bryophyte species in the studied communities, we did a descriptive comparison of their cover changes during the two years, since sample size was too low for species specific quantitative analyses.

RESULTS

Epiphyte cover

Total bryophyte cover we did not show differences between epiphyte communities at different elvations during the two years ($F_{(2,56)}=1.446$; $P=0.24$). However, it was interesting to observe that epiphyte communities at 3000 m and 2700 m appeared to slightly increase in biomass in the second year, whereas at 2500 m biomass remained relatively constant.

Community structure

After two years, epiphyte communities of branches translocated to 2500 m had changed more strongly than control communities left at 3000 m (ANOVA , $F_{(2,51)}=3.69$, $P=0.031$). The differentiation between communities appeared to change gradually with the elevation, since dissimilarity values after two years of communities translocated at 2700 m did not differ significantly from those of communities at both 2500 m and 3000m (**Fig. 6.1**).

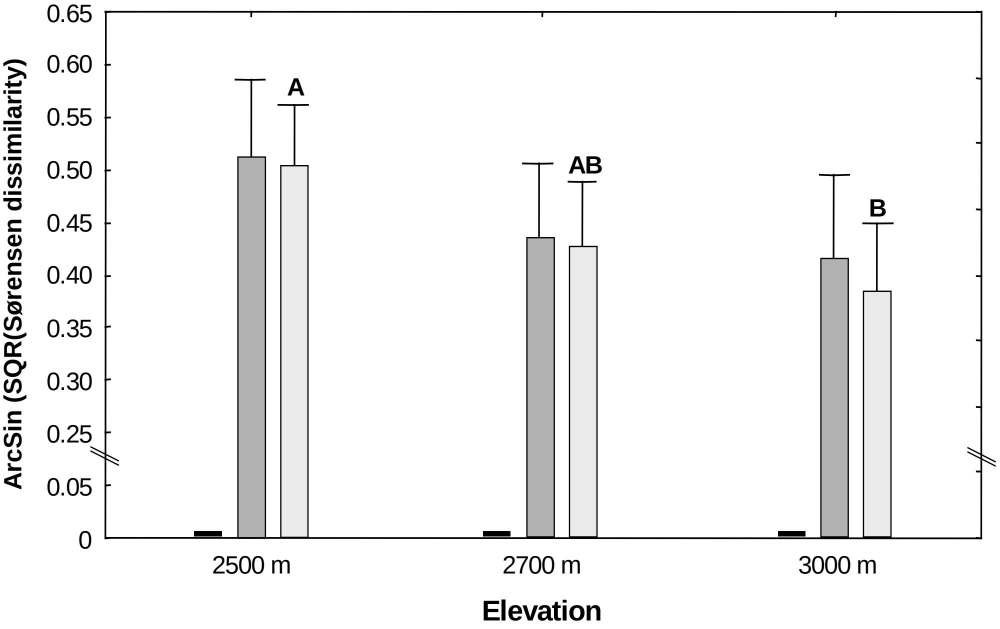

Fig. 6.1 Effect of experimetal translocation of non-vascular epiphyte communities from upper (3000 m) to mid-(2700 m) and lower-(2500 m) elevations. In black dissimilarity values at the beginning, dark grey after one year and light grey after two years. Different letters indicate significant differences between the means (ANOVA test).

Community saturation affected the similarity changes, with saturated communities after two years more similar to the original communities than unsaturated communities (R^2=0.063, F($_{1,53}$)=3.57, P=0.064) (**Fig. 6.2**).

According to the rank-cover analysis, communities from branches translocated to 2500 m had a tendency for greater cover change than communities from branches established at 3000 m (t=1.84; p=0.094). These changes in community structure also occurred gradually with elevation, with communities at 2700 m not differing significantly in cover changes from communities at 2500 m and 3000m (2500 m t=0.94; p=0.94; 3000 m t=0.11; p=0.91). It is also important to observe that the dominance pattern, where a few species represent most of the bryophyte biomass on the branches, was maintained in communities at 2700 m and 3000 m but not at 2500 m **(Fig. 6.3)**.

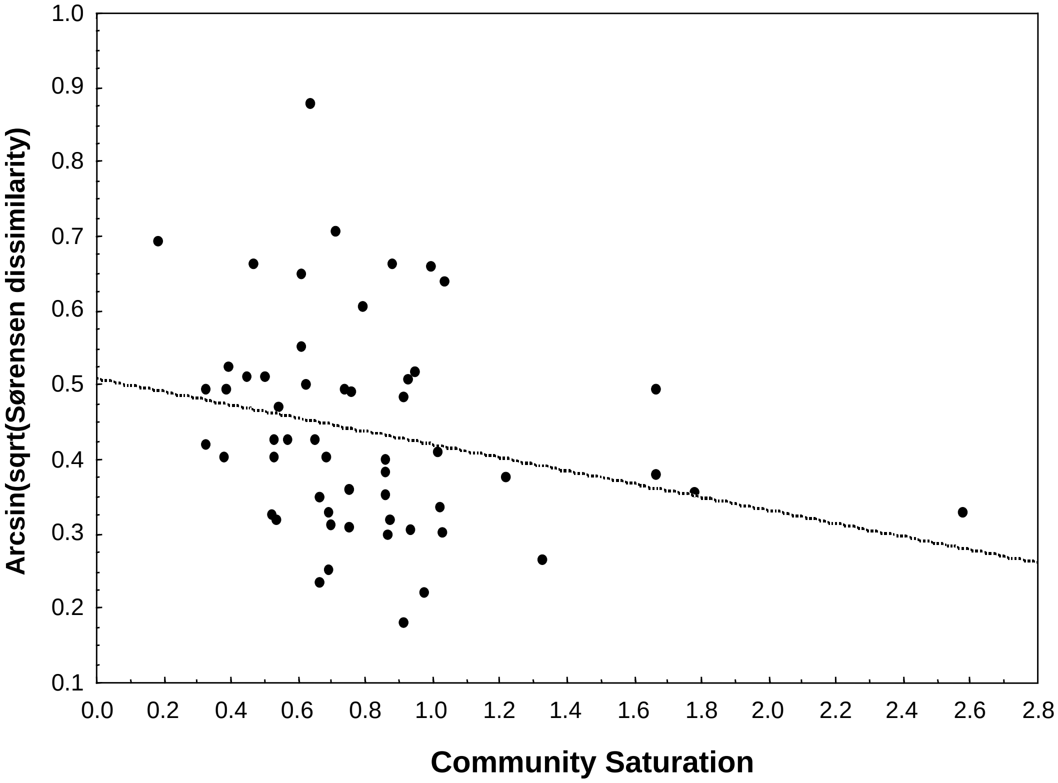

Fig. 6.2 The relationship between community dissimilarity after two years (Bray-Curtis Index), and space saturation in the community. Each point represents a a community and the line is a least-square linear regression.

Community dynamics

Analyzing the community dynamics at different elevations by comparing cover changes, we observed during the first year no significant differences in the cover changes ($F(_{2,325})=1.22$; $p=0.29$). After the second year, the cover of bryophyte communities on branches at 2700 m and 2500 m changed more strongly than bryophyte community branches left at at their original elevation ($F(_{2,54})=3.58$; $p=0.034$) **(Fig. 6.4)**. These changes, however, did not show a general pattern of increase or decrease with the elevation ($F(_{2,54})=0.88$;$p=0.41$), with cover increases and decreases at all three elevations. Community saturation affected the cover changes in the second year, especially in saturated communities ($R^2=0.013$, $F(_{1,331})=4.58$, $P=0.03$). Thus, communities with little available space showed lower cover changes than unsaturated communities**.**

Pattern of cover change with elevation varied among species. For species such as *Plagiochila bifaria* (Sw.) Lindenb., *P. gymnocalycina* (Lehm. & Lindenb.) Lindenb. and *Hypotrachyna* sp. the translocation to lower elevations determined a decrease in the cover, whereas for

Campylopus anderssonii (Müll. Hal.) Jaeger., *Usnea* sp. and *Plagiochila* aff. *stricta* Lindenb. cover increased. Species such as *Lepicolea pruinosa* (Tayl.) Spruce., *Herbertus acanthelius* Spruce. and *Syzingiella anomala* (Lindenb. & Gott.) Steph. seemed to be not affected by the change of elevation **(Fig. 6.5).**

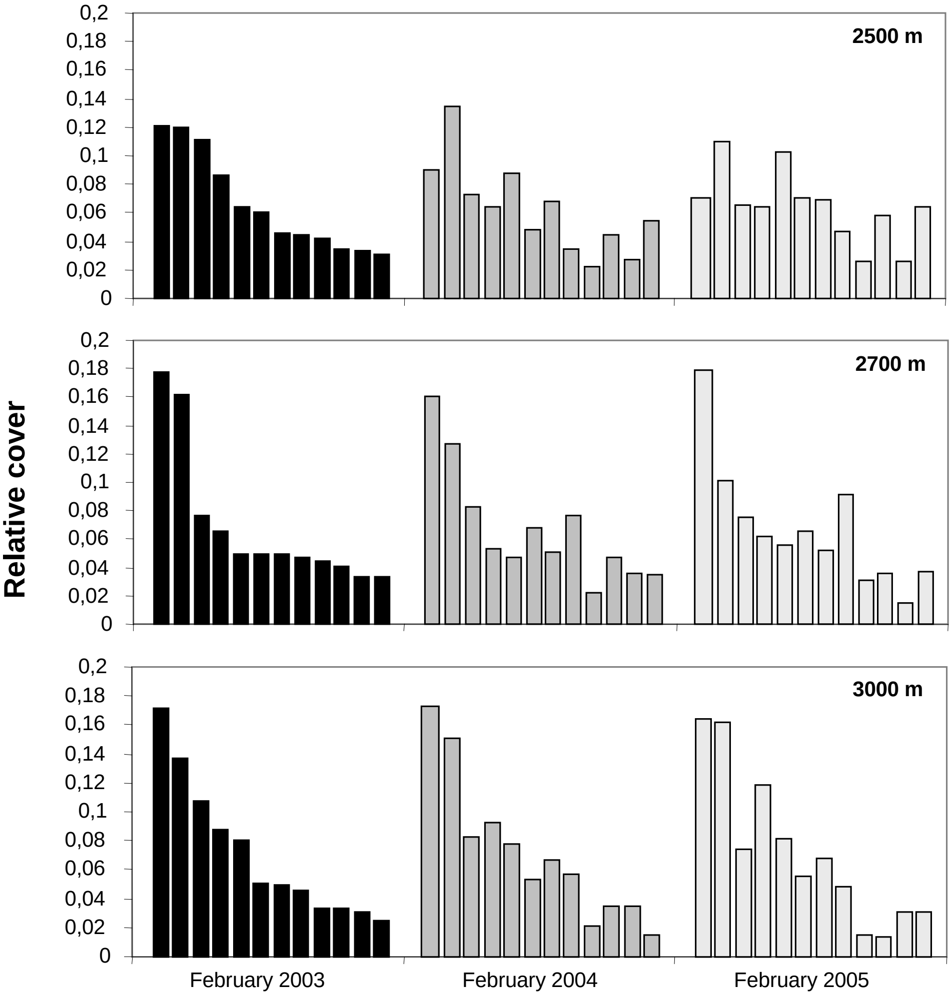

Fig. 6.3 Rank-cover patters by elevation at the beginning, and after one and two years. Species at each elevation ware arranged according to cover at the beginning of the experiment, and this order was maintained in the illustrations after one and two years.

DISCUSSION

This is the first study to transplant entire plant communities to lower elevations in an effort to simulate predicted future climate changes. The translocation represented a elevational difference of 300-500 m and an increase in temperatures of about 1.5-2.5°C, as well as changes in the hydric regime during the dry season (austral winter), especially in a greater amplitude of the daily relative humidity range and the lower frequency of precipitation and mist events (Schawe, in prep).

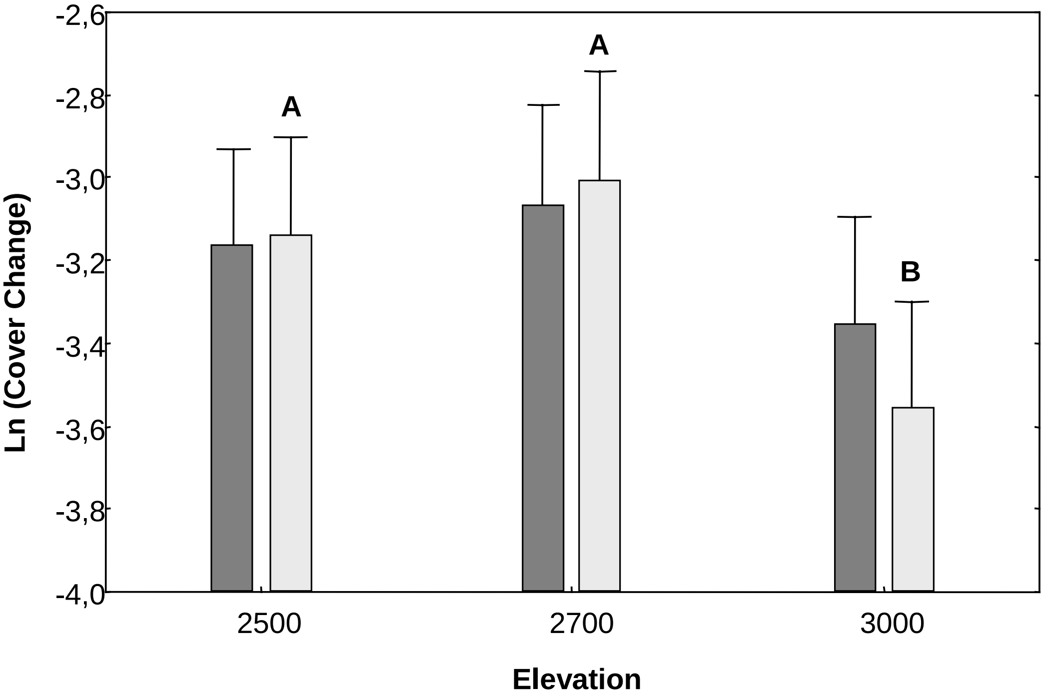

Fig. 6.4 Effect of experimetal translocation of non-vascular epiphyte communities from upper (3000 m) to mid-(2700 m) and lower-(2500 m) elevations on cover changes. In light grey and black cover change for the non-vascular epiphyte communities after one and two years respectively. ifferent letters indicate significant differences between the means (ANOVA test).

Observing that the tolerance to temperature changes in non-vascular plants is largely mediated by water relations (Gignac, 2001), it is possible to establish that the changes on the studied non-vascular epiphytic community should be associated with the differences in the hydric regimes of the elevational belts, and that the effect of increased temperature on epiphyte communities could be promoted or downgraded according the water regimes.

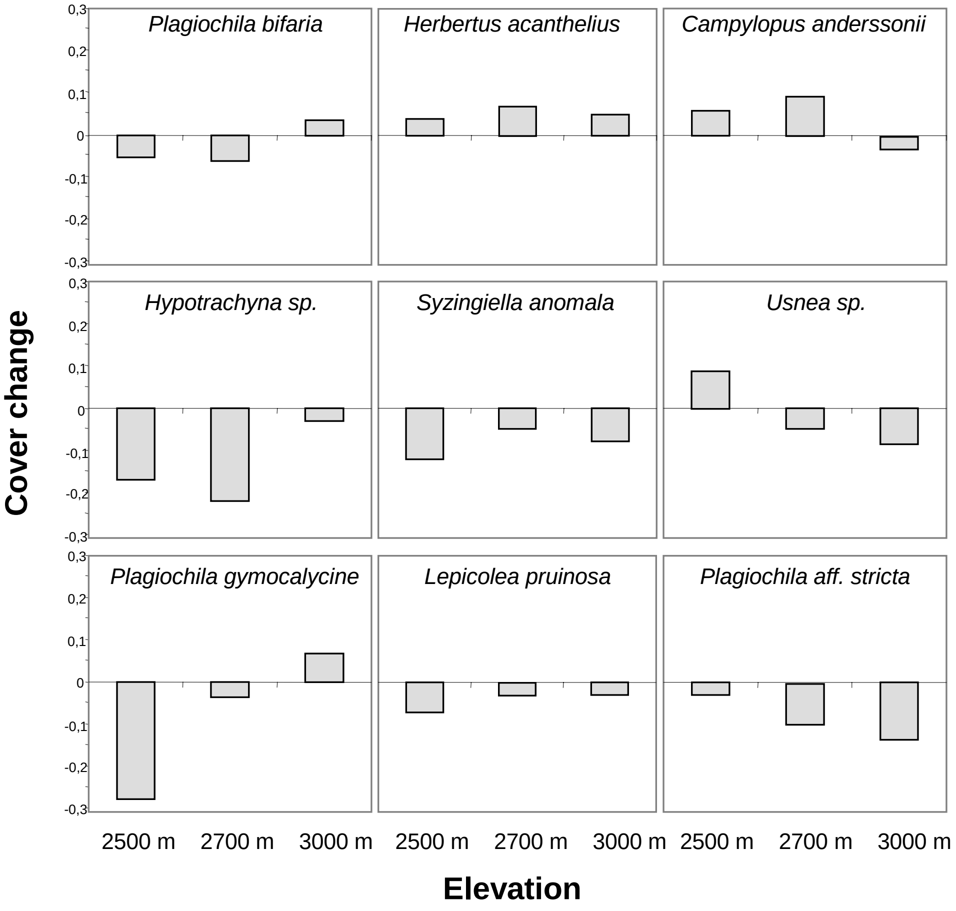

Fig. 6.5 Effects of experimetal translocation of epiphyte communities from upper (3000 m) to mid-(2700 m) and lower-(2500 m) elevations on the cover of non-vascular epiphyte species.

The changes in the non-vascular epiphyte community translocated by us to lower elevations did not imply severe changes in the total bryophyte cover, but rather changes in the structure and dynamics of the communities. The maintainance of bryophyte cover suggest that communities that are already established will not collapse in the short term as a result of climatic changes in the range of those simulated here. Apparently, the transition towards the new communities adapted to the changed climatic conditions will be gradual as species replace each other, rather than abrupt through the dieback of existing species and the new colonization of the then empty habitats by new species. This suggest that ecological processes, such as nutrient cycling and water retention, mediated by non-vascular epiphyte communities (Nadkarni, 1984; Coxson, 1991; Hofstede *et al.*, 1993; Benzing, 1998), would not be strongly affected. However, great care must be taken when predicting long term responses to climate change from short term observations, since some responses detected over short time periods may be transitional and may thus not well reflect long term community responses (Hollister *et al.*, 2005; Jónsdóttir *et al.*, 2005).

At the structural level, the community translocated to lower elevation turned to a more equitative pattern, with a decreased dominance. This structural change could indicate a resetting in the community, probably after a cover reduction of the heat- and drought-sensitive species and cover increase of heat- and drough-resistant species. Changes in the community structure translocated to lower elevations are expected, since bryophytes are particularily reactive to climatic changes due to their narrow responses on critical resource gradients (e.g., light and humidity) and small niche volumes (Bazzaz, 1998; Gignac, 2001). Changes in community structure associated with changes in hydric regimes caused by climatic changes have been described by Buckland *et al.* (1997) and McLaughlin *et al.* (2002). The structural change could also suggest a return to succesional stages since succesional species, which could becoming more important, have been reported to have broader niches and in this way may be more resistant to changes in temperature and humidity (Bazzaz, 1998). We expect that the long term outcome of the translocation experiment will ultimately result in a community abundance structure broadly similar to the orginal one, but with different dominant species.

The greater dynamics of the non-vascular epiphyte community at lower elevations do not imply a general increase or decrease in the species cover. This result is not unexpected since the translocated communities were constituted by different taxonomic groups that included bryophytes and lichens and by different species with different climatic requirements and geographical distributions. Patterns of cover increase for some species and decrease for other, as product of changes in temperature and humidity, has been previously described by Bates *et al.* (2005) for bryophyte communities in temperate grasslands, who also determined that the responses depend on the particular microclimatic requirements of each species. This species individualistic reaction is a well known pattern of response to climatic changes (Huntley, 1991; Shugart, 1998; Lawton, 2001), and represent one of the greatest barriers to predict how biodiversity will response to a global warming. It also suggest that communities will not migrate or react as a package (Lawton, 2001). On the other hand, this individuality will also affect the interspecific interactions, conducting to a community recomposition (Walther *et al.*, 2002; Heegaard & Vandvik, 2004; Kladerud & Totland, 2005). In spite of our expectations the species response to translocation did not correspond to their elevational distribution (data from Gradstein *et al.* (2003) and from the herbaria GOET and MO-W^{3}MOST). Thus, species with wide or restricted elevational ranges were positive as well as negative affected at lower elevations, with out reveling any particular pattern. Similar complex reactions to have been already described in previuos studies and constitute one of the points of critique to the validity of bioclimatic modells for predicting the outcome of climate change on the vegetation (Pearson & Dawson, 2003), since many factors other than climate (e.g., competition, community composition, succesional stage) play an important role in determining species ditribution and the dynamics of distribution changes (Davis *et al*., 1998).

The cover change of the communities was not only affected by the elevation but also by the cover itself. Saturated communities with no available space were more resistant to cover changes than unsaturated communities. This could either be due to facilitative shelter of the communities or simply a consequence of the reduced space available to react. Kladerud & Totland (2005), observing communities of alpine plants, postulated that vegetation may have a facilitative shelter effect on other species, buffering the effect of climatic changes on the community. In this way it is possible that saturated non-vascular epiphyte communities could maintain adequate microclimatic conditions (e.g., humidity and nutrient quantities)(Benzing, 1998; Hofstede *et al*., 1993), and prevent the establishment of invasive species (Pitelka *et al*., 1997; Buckland *et al*., 1997).

Being aware that saturation is closely related with dominance it can be also establish that the response to abiotic changes will also depent on it. Effects of dominance on the response to climatic changes has been previously observed by Grime (1997), Grime *et al*. (2000), Epstein *et al*. (2000), Zabaleta *et al*. (2003), and Kladerud & Totland (2005). They described that many ecological processes are crucially dependant of the functional characteristics of dominant plants. Ecological processes in tropical montane forests that are mediated by epiphytes include nutrient circulation and water retention (Nadkarni, 1984; Coxson, 1991; Hofstede *et al*., 1993; Benzing, 1998), and thesen could be affected by dominance changes in the epiphytic communities.

The detection of short term changes without extreme variation in elevation suggests that tropical montane forest communities may already be responding to the slight variations in temperature and hydric regimes. In fact, Loope & Giambelluca (1998) and Pounds *et al*. (2004) have observed population decreases and local extinctions for plants and animals of tropical montane forests.

In conclusion we can establish that non-vascular epiphyte communities reacted rapidly to climatic changes and that the individualistic responses in the communities may in the future result in a decoupling of present day ecological interactions, with the formation of new relationships, and leading to changes in structure and composition of the communities

(Hughes, 2000; Andrew & Hughes, 2005). Since the adaptation to new climatic conditions for epiphyte communities seem to occur gradually, ecological processes mediated by epiphytes should be maintained.

Fast responses to climatic changes in tropical mountains have been previously observed in paleaecological studies and in vascular epiphytes (Nadkarni & Solano, 2002; Bush, 2002, 2004). These investigations as our study involved communities of elevational transitions or ecotones. Communities of ecotones determined by climate such as elevational ecotones are especially sensitive to temperature and humidity changes, reacting in this way faster to climate changes than non-ecotones communities (Foster, 2001; Bush, 2002).

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Summary

To date all experimental approaches on the mechanisms that determine the lower elevational limits of plants have been carried out in temperate regions. Despite of the concrete and relevant information from these studies it is uncertain that these information could be applied to tropical mountain communities since diversity and community structure in these areas are different. Through a series of experimental approaches we examine the importance of some factors on the lower elevational limits of tropical plants. Since the current global warming will principally affect lower elevational limits, we also evaluated how climate change could affect the distribution of tropical montane plants. In the first approach we assess the importance of biotic and abiotic factors in the determination of the elevational limits of tropical ferns by observing the symmetry of the distributions for each species calculating the skewness. We assumed that abiotic factors should determine truncated and biotic factors attenuated limits, and that species range limits were spatially more regular when they were determined by abiotic than by biotic factors. The species presented different distribution patterns, which ranged from symmetric- to asymmetric-distributions. However most of the species were asymmetricaly distributed and showed truncated upper limits and attenuated lower limits. This is consistent with the observation that upper elevational limits are determined mainly by climatic factors while lower elevational limits are determined by biotic interactions. In a second experimental approach we analyzed the effects of litterfall on two understory species of tropical montane forest by observing their growth at different elevations. After two years, we found that the species restricted to higher elevation were more sensitive to damage by litterfall than the wideranging species. Based on these results, it can be suggested that litterfall may be playing an important role in the determination of the lower elevational limits in plants of tropical montane forests, and that the elevational distribution reflect the species plasticity and resiliance to litterfall disturbs. In the third approach we examined the role of surrounding vegetation on the elevational distribution and occupation patterns of five high Andean geophyte species. Studying the structure of vegetation and the abundance of the geophyte species we found that structural changes in the vegetation appeared to determine the presence/absence and abundance of the geophyte species along the elevational gradient. In the fourth experiment we described the changes in the biomass

allocation patterns for seedlings of two puna species when growing outside their natural elevational ranges. According to our results, the ability or inability to change the resource allocation patterns of these species appear to be playing an important role in the present elevational distribution, and could be key factor in the reaction of these species to climate change. In the last experimental approach we assess the effect of a warmer and more seasonal environment on non-vascular epiphyte communities. For that we translocated complete non-vascular epiphyte communities from 3000 m to 2700 m and 2500 m. After two years, epiphyte communities translocated to lower elevations did not differ in total bryophyte cover from those left at 3000 m, but they were more dynamic, with higher cover changes of species composition. The response of epiphytes to the translocation was distinctly species-specific. According to this it could be postulated not only that epiphyte communities may be already reacting to climate change but also that communities will not necessary collapse under the new climatic scenaria, and that ecosystem functions mediated by epiphytes, such as nutrient cycling and water retention may only experience limited changes.

With this worldwide first experimental approach on the elevational limits of tropical plants, it has been possible to determine some relevant factors for the elevational distribution of plants in the Andes, and how climate change could affect them. However it is necessary to indicate that many factors, such as germination, dispersal limitation, and the direct effect of herbivory and pathogens could not be included in this investigation. In this way a complete perspective of the factors that determine the lower elevational limits of tropical montane plants and the effect of the climatic change on them is still incomplete. Only knowing the importance of these factors will permit to establish the true effect of the climatic change on these areas and to predict in an adequate way the response of the vegetation to this scenario.

Zusammenfassung

Über die Ursachen der unteren Höhengrenzen von Pflanzenarten in tropischen Gebirgen ist nur wenig bekannt. In Frage kommen vier Faktorenkomplexe: Autökologische Eigenschaften der Arten, interspezifische Konkurrenz, Herbivorie/Prädation und Pathogene. Die Reaktion von Pflanzenarten und Vegetationseinheiten auf zukünftige Klimaveränderungen kann sehr unterschiedlich ausfallen, je nachdem welche dieser Faktoren ausschlaggebend sind. Mit einer Reihe von Experimenten untersuchten wir die Relevanz von einigen Faktoren für die Lage der unteren Höhengrenzen von Pflanzenarten in tropischen Gebirgen. Da die Reaktion von Pflanzenarten auf globale Klimaveränderungen teilweise von den arealbegrenzenden Faktoren abhängt, bewerteten wir auch, wie Klimaveränderungen die Verbreitung von Pflanzen in tropischen Gebirgen betreffen könnten.

Im ersten Experiment untersuchten wir die Relevanz von biotischen und abiotischen Faktoren für die Festlegung von Höhengrenzen von tropischen Farnen, indem wir die Symmetrie und Schiefe des Verbreitungsmusters für jede Art beobachten. Wir nahmen an, dass abiotische Faktoren scharfe Verbreitungsgrenzen und biotische Faktoren fließende Verbreitungsgrenzen bestimmen sollten, und dass die Verbreitungsgrenzen räumlich regelmäßiger sind, wenn sie von abiotischen Faktoren bestimmt worden sind. Die Farnarten hatten verschiedene Verbreitungsmuster, die von symmetrischer bis zu asymmetrischer Verteilung reichten. Jedoch waren die meisten Arten asymmetrisch verteilt und zeigten abgeschnittene obere Höhengrenzen und fließende untere Höhengrenzen. Dieses Muster passt zur Hypothese, wonach obere Höhengrenzen hauptsächlich durch klimatische Faktoren, untere Höhengrenzen hingegen durch biotische Interaktionen bestimmt sind. In einem zweiten Experiment untersuchten wir den Effekt von Streufall auf zwei Unterwuchsarten des tropisch-montanen Waldes, indem wir ihr Wachstum auf drei verschiedenen Höhen beobachteten. Nach zwei Jahren fanden wir, dass die auf höheren Stufen verbreiteten Arten empfindlicher gegenüber Streufall waren als Arten mit größerer Höhenamplitude. Diese Ergebnisse lassen vermuten, dass der Streufall einen wichtigen Einfluss auf die Lage der unteren Höhengrenzen von Unterwuchsarten der tropisch-montanen Wäldern spielt, und dass die Höhenamplitude teilweise die Widerstandfähigkeit der Arten gegenüber Bedeckung durch Streufall widerspiegelt. Im dritten Versuch untersuchten wir den Einfluss der umgebenden Vegetation

auf die Verbreitung und räumliche Verteilung von fünf hochandinen Geophyten. Wir fanden, dass Unterschiede in der Vegetationsstruktur Strukturänderungen in der Vegetation die Anwesenheit/Abwesenheit und Abundanz von geophytischen Arten entlang des Höhengradienten zu bestimmen schienen. Im vierten Experiment beobachteten wir die Veränderungen in den Biomasseverteilung zwischen Wurzel und Spross in Keimlingen von zwei Puna-Arten, die wir außerhalb ihrer natürlichen Höhenverbreitung wachsen ließen. Unsere Ergebnissen zeigen, dass die Fähigkeit oder Unfähigkeit dieser Arten die Biomassezuteilungsmuster zu ändern, einen wichtigen Einfluss auf ihre gegenwärtigen Verbreitungsmuster haben, ein Schlüsselfaktor in der Reaktion dieser Arten auf die Klimaveränderung sein könnten. Im letzten Experiment bewerteten wir die Wirkung von wärmeren und trockeneren Umweltbedingungen auf Epiphytengemeinschaften. Dafür verpflanzten wir ganze Epiphytengemeinschaften von 3000 m auf 2700 und 2500 m Höhe. Nach zwei Jahren gab es keine Unterschiede in der Bryophyten-Gesamtdeckung zwischen Gemeinschaften auf verschiedenen Höhen, aber auf Artniveau waren die Deckungsänderungen in Gemeinschaften auf 3000 m dynamischer, mit größeren Veränderungen in die Artenzusammensetzung. Die Reaktion der Epiphytengemeinschaften auf Verpflanzung war ausgesprochen artenspezifisch. Dementsprechend kann nicht nur postuliert werden, dass Epiphytengemeinschaften bereits jetzt auf die Klimaveränderung reagieren, sondern auch dass Gemeinschaften unter den neuen klimatischen Bedingungen nicht zusammenbrechen werden, und dass die Ökosystem-Funktionen, die die Epiphyten erfüllen, nur beschränkte Änderungen erfahren werden.

Mit diesen Experimenten war es möglich, einige relevante Faktoren für die Verbreitungsmuster von Pflanzenarten in den Anden zu bestimmen, und wie Klimaveränderungen sie betreffen könnten. Jedoch ist es notwendig anzumerken, dass viele Faktoren, wie Keimung, eingeschränkte Ausbreitung (dispersal limitation) und die direkte Wirkung von Herbivoren und Pathogenen in dieser Untersuchung nicht berücksichtigt werden konnten. In diesem Sinne ist das Gesamtbild der Faktoren noch unvollständig. Nur die Bestimmung der Relevanz aller Faktoren wird erlauben, die tatsächlichen Auswirkungen des Klimawandels auf die Vegetation in diesen Gebieten vorauszusagen.

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