



An experimental assessment of the upper elevational limit of flowering plants in the western Himalayas

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Transplant experiments are a useful tool both for determining species' ranges and understanding their cause, yet such experiments have seldom been performed in areas where plants reach extremely high elevations. We examined the position of the upper elevational limits of vascular plants in E Ladakh, India, by transplanting individuals of 14 subnival species from 5800–5850 m elevation to a control site at the same elevation, as well as to edaphically suitable sites at 5960 m (subnival belt with sparse plant cover), to 6030 m (the highest elevation reached by vascular plants in the area) and to 6160 m elevation (no vascular plants observed). Two years later, transplants of 13 species survived at the control elevation, whereas 5 species survived at 5960 m, 2 species (*Waldheimia tridactylites*, *Poa attenuata*) at 6030 m, and none at 6160 m. The highest elevation at which transplanted flowering plants survived corresponds well to the observed elevational limit. Soil temperature data at the sites suggest that the growing season, defined as the period with mean daily soil temperature above zero, lasted nearly 3 months at 5960 m, ca 1.5 month at 6030 m, but <3 weeks at 6160 m, moreover interrupted at the highest elevation by several days with temperatures remaining below zero. The experiment confirmed the observed sharp limit of vegetation, set not by any physical barrier per se (e.g. not by the top of the massif), but instead by physiological constraints of the species. The result provides support for the assumptions of mid-domain effect models that domain limits are defined by shared organismal adaptations in relation to environmental gradients, in this case tolerance to freezing temperature.

Distributional areas of plants and animals are delimited by their edges, alternatively called boundaries, borders, margins or limits. Numerous factors have been suggested to determine the position of these limits (Gaston 2003), however, as the nature of the limits is usually complex, responsible factors are often uncertain and cannot be identified without adopting an experimental approach (Hobbie and Chapin 1998, Walther 2003, Angert and Schemske 2005). Among distributional limits, elevational limits are potentially easier to explain because fewer factors change along elevational gradients than along latitudinal gradients (Körner 2003). This holds especially true for the absolute upper elevational limit, i.e. the highest elevation reached by any individual belonging to the studied taxonomic group, because some of the factors complicating interpretation of distributional data, such as biotic interactions, play a negligible role at absolute limits. On the other hand, there are other severe limitations for putting up an experimental study at high elevations, such as logistic constraints.

The values of the upper elevational limits of vascular plants given in the literature vary considerably and have increased through time as new data have been uncovered. Thus, Webster (1961) considered Polunin's (1960) records from 5945 m in Nepal as the absolute maximum, while

later records increased this to 6130 m (Swan 1990), 6400 m (Miehe 1991), and 6700 m (Press 2000). As organisms generally become rare towards their elevational limits, we may infer that they are not well adapted to these marginal conditions. Their borders are therefore often fuzzy and difficult to estimate (Gaston 2003). Many records of vascular plants from the highest altitudes have been obtained accidentally, often by alpinists and geographers who focused on other topics than biologists, so that the number of errors and seriously biased estimates is quite high. Consequently, at present, there is little agreement on the position of upper boundaries of elevational distributions of many organisms, including vascular plants, and on the factors determining them. Moreover, biological interpretation of elevational limits is complicated by the fact that it is not clear to what extent the absence of individual species below and above their elevational limits reflects a lack of suitable habitats, their inability to cope with other abiotic and biotic factors, or dispersal limitation.

A number of fundamental ecological and evolutionary questions can be answered by studies focusing on elevational limits. These questions include the physiological limits of various processes at the upper elevational limits (Körner 2003), the role of colonisation and migration in

population dynamics (Griffith and Watson 2005, 2006), and genetic constraints preventing expansion of distributional limits (Herrera and Bazaga 2008). In addition, the position of the upper elevational limit is important in various theoretical studies in which the distribution of organisms is modelled within the area which they are potentially able to colonise (Grytnes and Vetaas 2002). For example, the outcome of mid-domain effect models, recently frequently utilised as null models of elevational distribution of species numbers, is very sensitive to the position of the distributional limits (Colwell and Lees 2000, Zapata et al. 2003, Hawkins et al. 2005). One of the issues debated is the cause of domain boundaries and their effectiveness (“hardness”) (Laurie and Silander 2002, Zapata et al. 2003, 2005, Colwell et al. 2004, 2005).

To find the position of the upper elevational limit of vascular plants in the western Himalayas and to contribute to the debate concerning the nature of the upper distributional limit of vascular plants, individuals of 14 subnival species were transplanted from 5800–5850 m to control sites at the elevation, as well as to edaphically suitable sites around the upper elevational limit close to 6000 m and above. Air and soil temperatures were measured throughout the year to assess whether temperature and the length of growing season are the factor limiting survival of plants along the elevational gradient. It is shown for the first time that the highest elevation at which transplanted flowering plants survived corresponds well to the observed elevational limit. This evidence is discussed in the context of MDE models of elevational distributions.

Material and methods

Study area

The study area is situated in eastern Ladakh, Jammu and Kashmir State, India. It belongs to the westernmost extension of the Tibetan plateau, and is associated with the Transhimalayan section of the western Himalayas (32°26′–33°36′N, 77°18′–78°30′E). A single climate station is available in the region, but is situated at the bottom of the Indus valley (Leh, 3500 m; Miede et al. 2001). Climate data from this station indicate arid conditions with an annual precipitation of 83 mm. The area is only rarely affected by monsoonal precipitation. At lower and middle elevations evaporation values are much higher than precipitation. At higher elevations above 5300 m, precipitation tend to increase (Miede et al. 2001)

At lower elevations much of the area is covered by desert and semi-desert. Steppe vegetation is found at middle elevations up to ca 5000–5400 m. Alpine grasslands form a narrow belt above the steppe vegetation and extend as narrow strips along rivers to middle elevations. Subnival vegetation (free solifluction belt) develops at the highest elevations. Trees and larger shrubs are generally limited to ca 4200 m a.s.l. Steppe and alpine turf vegetation is grazed by sheep, goats and yaks up to 5600 m (Jina 1995).

The snow line in the study area is situated at ca 6400 m, i.e. higher than the highest records of vascular plants. Permanent snow fields and glaciers therefore do not seriously limit elevational distribution of vascular plants.

The study area was small enough to be explored intensively. Uninhabitable steep rocky slopes are virtually absent, so that all parts of the area are relatively easily accessible. Due to a suitable geology (gneisses prevail), disintegration of rocks is fast and efficient in the study area. The prevailing plateaus, gentle slopes and dry climate prevent fast erosion. Due to the periglacial processes large soil patches are available at any elevation. Therefore, vascular plants in the study area do not seem to be limited by a lack of suitable substrat even at the highest subnival elevations.

Transplantation experiment

The transplantation experiment was carried out in the Luglung river valley, situated on the western slope of the Chalung mountains east of Lake Tso Moriri (33°05′N, 78°27′E; Fig. 1). The highest peaks in the surrounding area were 6400 m elevation. On 15 August 2001, 14 species from (5500–)5800–5850 m were transplanted to another site at the same elevation (5850 m; control; distance to the source site was ca 150 m), and to three localities situated 110, 180 and 310 m higher, i.e. 5960 m – corresponding to the elevation at which open subnival vegetation still occupies a considerable area, 6030 m – the highest elevation reached by vascular plants in the area, and 6160 m – the elevation at which no vascular plants have been observed. The target species belong to the most frequent subnival plants in the study area, and represent different growth and functional types (loose to compact cushion plants, rhizomatous plants, root-sprouters, rosette plants) (Table 1). The plant individuals, randomly selected in the source area, were carefully dug out; to minimise the disturbance, packed together with the soil attached to their roots and planted at the most suitable microlocalities at the selected elevation within the same day. In plants with a tap root, entire individuals were dug out, in rhizomatous and stoloniferous plants 3 to 5 inter-connected ramets were transplanted. The plants were randomly assigned to each altitude. The position of the transplanted plants was marked by coloured

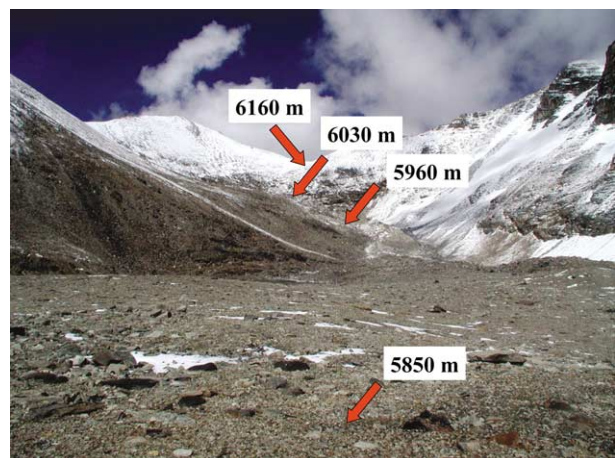


Figure 1. Location of the sites used for the transplantation experiment. Source area of the transplanted plants was at 5850 m. The plants were transplanted to all four sites indicated with arrows. Temperature was measured at the 5960, 6030 and 6160 m sites.

Table 1. Percentage of plants surviving 2 yr after transplantation from 5800–5850 (except for *Microgynoeceum* which originated from 5500 m) to the control site at the source elevation as well as to edaphically suitable sites at higher elevations, percentage of flowering individuals among transplanted plants (in brackets) and maximum elevation at which the species was recorded in the study area (max). All species, except for *Microgynoeceum* (annual) are polycarpic perennials.

| | Taxon | Family | Growth form (below-ground) | 5850 m | 5960 m | 6030 m | 6160 m | χ^2 | max |
|----|---|-----------------|--|----------|---------|--------|--------|----------|------|
| 1 | <i>Alyssum klimesii</i> Al-Shehbaz | Cruciferae | loose to compact cushion, tap root | 80 (70) | – | – | – | 24.0*** | 6010 |
| 2 | <i>Aphragmus oxycarpus</i> (Hook. f. & Thomson) Jafri | Cruciferae | compact cushion, tap root | 70 (30) | – | – | – | 21.0*** | 5900 |
| 3 | <i>Carex saganensis</i> Y.C. Yang | Cyperaceae | rhizomatous | 90 (20) | – | – | – | 27.0*** | 5810 |
| 4 | <i>Desideria pumila</i> (Kurz) Al-Shehbaz | Cruciferae | pleiocorm, tap root | 50 (0) | 10 (0) | – | – | 11.3* | 5950 |
| 5 | <i>Draba altaica</i> (C. A. Mey.) Bunge | Cruciferae | compact cushions, tap root | 80 (60) | – | – | – | 24.0*** | 5980 |
| 6 | <i>Draba oreades</i> Schrenk | Cruciferae | compact cushions, tap root | 90 (30) | – | – | – | 27.0*** | 6010 |
| 7 | <i>Eritrichium hemisphaericum</i> W.T. Wang | Boraginaceae | compact cushions, tap root | 60 (20) | – | – | – | 18.0*** | 5950 |
| 8 | <i>Microgynoeceum tibeticum</i> Hook. f. | Amaranthaceae | annual | – | – | – | – | – | 5570 |
| 9 | <i>Pegaeophyton scapiflorum</i> (Hook. f. & Thomson) Marq. & Shaw | Cruciferae | pleiocorm, tap root, rarely root-sprouting | 80 (40) | 10 (0) | – | – | 19.8*** | 5940 |
| 10 | <i>Poa attenuata</i> Trin. | Gramineae | tussock | 100 (80) | 80 (30) | 40 (0) | – | 10.7* | 5950 |
| 11 | <i>Saussurea hypsipeta</i> Diels | Compositae | usually single rosettes, tap root | 30 (20) | – | – | – | 9.00* | 6000 |
| 12 | <i>Saxifraga nanella</i> Engl. & Irmischer | Saxifragaceae | below-ground stolons | 90 (70) | – | – | – | 27.0*** | 5995 |
| 13 | <i>Stellaria depressa</i> E. Schmid | Caryophyllaceae | below-ground stolons | 80 (50) | 10 (0) | – | – | 19.8*** | 5950 |
| 14 | <i>Waldheimia tridactylites</i> Kar. & Kir. | Compositae | rhizomatous | 100 (40) | 70 (0) | 10 (0) | – | 15.3** | 6030 |

* $-p < 0.05$, ** $-p < 0.01$, *** $-p < 0.001$.

stones. No watering or fertilisation was applied. Due to the low temperatures restricting evaporation and large fields of melting snow in the surroundings of the localities, the plants did not suffer from water stress. The number of replications per site and per species was 10, so that altogether 560 plant individuals were transplanted. The locality was visited 12 months later, on 8 August 2002, to find that at 5800 and 5960 m many plants were alive. Transplanted plants could not be inspected at higher elevations due to a persisting layer of fresh snow. Therefore, the final assessment was carried out one year later, on 10 September 2003. The number of surviving plants was counted and flowering/fruitlet frequency was recorded. χ^2 was used to test the hypothesis that survival of individual species was the same at all elevations.

Temperature measurements

Three thermometers (HOBO Pro Temp/External Temp Data Logger, HOBO, Bourne, USA) were placed at the three localities used for transplantation (5960, 6030 and 6160 m), each with two sensors, recording soil temperature 5 cm below the soil surface and 10 cm above it at one-hour intervals. The thermometers were buried in the soil from 8 August 2002 to 10 September 2003, when they were collected. After they were transported to a laboratory, the stored data were downloaded into a computer. No obvious errors in temperature measurements were found in the data.

Results

Transplantation

Two years after the transplantation, plant survival at the elevation from which most plants originated (the control site at 5850 m) was relatively high, except for the only annual plant (*Microgynoeceum tibeticum*) which failed to establish from seeds produced in the year of transplantation (Table 1). The annual species, which originated at a lower elevation (5500 m) than the perennial species (5800–5850 m), failed to establish at the control site for perennials at 5850 m, which is 280 m above the maximum elevation at which the annual was recorded in the study area (5570 m, Table 1). Survival rate of almost all perennial species at the control site was $> 50\%$. In contrast, only 5 out of the 14 transplanted species survived at 5960 m. Moreover, in three of them only a single individual survived. Out of these five species, four remained sterile in 2002 and 2003 and only one flowered. At the 6030 m site two species survived, but they did not flower in the course of the first two years. Not a single plant survived at 6160 m, the highest elevation used in the experiment. All species (except the annual) have significantly different survival rates between the different elevations (Table 1).

Temperature measurements

While the growing season (defined here as the period with mean daily soil temperatures above zero) lasted nearly 3 months at 5960 m, at 6030 m it was shorter than

Table 2. Temperature regime at three sites along the elevational gradient in E Ladakh.

| Daily values | Elevation | Mean | Annual extremes | | Number of days with temperature | | |
|--------------|-----------|--------|-----------------|-------|---------------------------------|------|-------|
| | | | min | max | >0°C | >5°C | >10°C |
| Mean air | 5960 | -8.37 | -22.24 | 8.28 | 82 | 23 | 0 |
| | 6030 | -8.65 | -17.85 | 4.94 | 55 | 0 | 0 |
| | 6160 | -13.18 | -27.99 | 3.71 | 30 | 0 | 0 |
| Minimum air | 5960 | -12.23 | -28.05 | 1.60 | 63 | 0 | 0 |
| | 6030 | -9.78 | -18.05 | -0.16 | 0 | 0 | 0 |
| | 6160 | -16.59 | -31.30 | -0.16 | 0 | 0 | 0 |
| Mean soil | 5960 | -7.57 | -19.81 | 7.30 | 81 | 25 | 0 |
| | 6030 | -8.61 | -17.56 | 4.08 | 47 | 0 | 0 |
| | 6160 | -12.57 | -24.65 | 1.66 | 19 | 0 | 0 |
| Minimum soil | 5960 | -9.10 | -21.79 | 3.74 | 7 | 0 | 0 |
| | 6030 | -9.07 | -18.05 | 0.29 | 15 | 0 | 0 |
| | 6160 | -14.14 | -26.11 | -0.16 | 0 | 0 | 0 |

1.5 months. At the highest elevation (6160 m) the growing season was restricted to <3 weeks (Table 2); moreover it was interrupted by several days with temperatures remaining below zero (Fig. 2). Even in the beginning of August, when temperatures generally reached their highest values, air temperature regularly dropped below zero at all three sites, at the middle and higher sites repeatedly to ca -5°C. The sites differed mainly in the duration of the period with temperatures below zero in the course of 24-h cycles. While air temperature usually dropped below zero for <2–3 h at the lowest elevation, at the highest elevation freezing lasted between 8 and 16 h every day. Daily temperatures rose to 8–16°C at all three elevations, but for a much shorter time per day at higher elevations.

Freezing of the soil is more critical for vascular plants than frost above ground. At the lower elevation, soil temperatures never dropped below zero in the middle of the season (beginning of August). In contrast, at the middle elevation, soil temperatures dropped below zero every night, partly due to the freezing effect of the permafrost which is close to the soil surface at this elevation. At the highest elevation, soil temperatures rose to 2 to 4 degrees above zero every day, but for a few hours only.

At the end of August and in the beginning of September, when many plants still flowered and fruited at 5960 m, soil temperatures never rose above zero at the highest elevation, and at the middle elevation they dropped to zero every night for several hours. In contrast at the lowest elevation, soil temperatures still remained above zero, even during the night (Fig. 2).

Finally, at the end of September, soil temperatures always remained below zero at all three stations and slowly decreased to the steady -25°C measured in winter (data not shown).

Discussion

Position of the upper elevational limit

The values of upper elevational limits given in the literature vary considerably (as detailed in the Introduction). In the course of the past 200 yr the known position of the absolute elevational limit of vascular plants increased by ca 1600 m (von Humboldt 1807, Press 2000). Although a similar,

even if more recent, trend of increasing numbers of plants on the tops of mountains has been attributed to global climate change (Grabherr et al. 1994, Root et al. 2003, Walther et al. 2005), the apparent shift of the upper limit seems to be more plausibly explained by an increasing knowledge of mountain floras. It remains questionable how reliable the older records from extreme elevations are, due to the notorious difficulties with elevation estimation. According to our experience, errors in estimates traditionally based on the temperature of boiling water or on air pressure can amount to 300 m due to fluctuating air pressure. Imprecise location of sites may result in even more serious errors because the elevation of localities sometimes refers to neighbouring peaks. As estimation of elevation was often quite imprecise before GPS became available, an assumed error of +/-350 m for data from the literature data is not likely to be an overestimate. Some minor errors can be also caused by a conversion of feet to meters (e.g. 19 000 ft. to 5806 m).

A shift of distributional limits towards higher elevations in dry areas has been reported repeatedly (Hermes 1955) and is generally attributable to the higher levels of solar radiation that increase daily temperature maxima as well as to the low proportion of area covered by permanent snow and glaciers, as the lack of suitable habitats limits elevational distribution of vascular plants (Dickoré and Miede 2002). Due to the favourable geomorphology of the mountains in the study area, with gentle slopes up to the snow line, and due to the low precipitation, leaving most of the area unglaciated, there are suitable habitats (soil patches) for vascular plants up to ca 6400 m. Consequently, distribution of virtually all abundant vascular plants along the elevational gradient is more or less continuous, with breaks usually not broader than 50–100 elevational metres. Fast weathering of slates prevailing in the study area makes the occurrence of firm rocks with crevices suitable for colonisation of vascular plants extremely rare, especially at high elevations, so that there are no chasmophytic vascular plants above 5000 m in the study area (Klimeš 2003). This sharply contrasts with the situation in more glaciated mountains built from firm rocks where vascular plants may colonise microclimatically suitable habitats among rocks well above their continuous distribution (e.g. in the Alps and the main Himalayan range). Consequently, the observed upper elevational boundaries probably correspond well to the

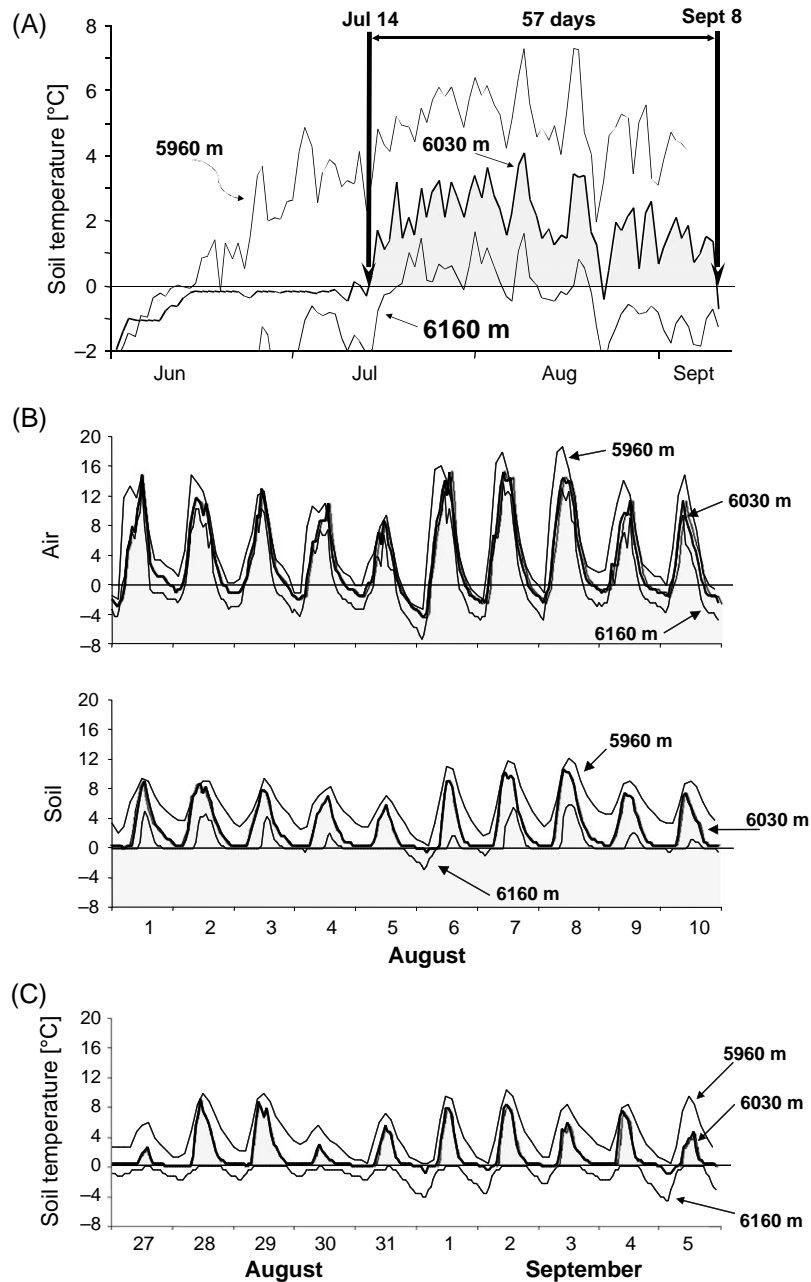


Figure 2. Air and soil temperatures measured in the Lunglung valley. (A) Mean daily soil temperatures; (B) daily course of air and soil temperatures in the beginning of August; (C) daily course of air and soil temperatures at the end of August and beginning of September.

ecophysiological limits of vascular plants in the study area and are relatively sharp.

Transplantation experiment and temperature measurements

Transplantation of adult plants out of their current distribution area provides a relatively simple and straightforward test on the limits of their current distribution (Bruehlheide 2003, Walther 2003). In spite of that, few experiments have been carried out with plants transplanted beyond their distribution range, namely above their distributional limit (Gaston 2003, Angert and Schemske 2005) and no study is known to us in which plants were

transplanted above the absolute upper elevational limits of vascular plants in a particular area. Larger experiments with transplanting vascular plants above their distributional limit were already being carried out in the 19th century (Kerner v. Marilaun 1888–1891, Bonnier 1895). Even if the design of these early experiments was not perfect, the results clearly demonstrated the difficulties that plants face when moved beyond from their elevational limits. Recent experiments showed that plants transplanted out of their distribution range display reduced growth and fitness (Angert and Schemske 2005, Geber and Eckhart 2005) and demonstrated how evolution of ecologically important traits enables them to reproduce above their current elevational limit (Griffith and Watson 2005, 2006). These reports

support the view of the upper elevational limit being an unstable, soft boundary.

In this experiment a relatively small increase in elevation from 5850 to 5960 m, i.e. 110 m, limited the survival of most transplanted plants. The adiabatic lapse rate of atmospheric temperature which in continental areas (such as the Transhimalaya in Ladakh) is ca 0.4 K per 100 m (Körner 2003), corresponds well to the difference between mean temperature at the 6030 and 5960 m sites (0.3 K) and indicates that the difference in temperature regime of the two sites was indeed small. On the other hand, the number of days with mean air and soil temperatures above 5°C, a measure frequently used to assess suitability of climatic conditions for vegetative growth of vascular plants (Kleidon and Mooney 2000), was zero at 6030 m but 23–25 at 5960 m. In contrast to the relatively small difference in temperatures between the lower two sites, the higher two sites, differing 130 m in elevation, showed contrasting temperature characteristics. This was likely caused by the proximity of the upper site to a pass, which lowered temperatures due to the openness of the site and due to strong winds (top phenomenon).

A further striking result of the transplantation experiment was that the proportion of flowering individuals declined more strongly than that of surviving plants. This suggests that the upper distributional limits of at least some of these plant species may not be determined by their vegetative physiological traits, but rather by their difficulty to reproduce. This also corresponds well with the lack of reproduction by the only annual species included in the experiment. Apparently, the perennial growth form, which is not dependent for successful reproduction each year, is more suitable for such extreme environments than an annual strategy.

Finally, it has been suggested that global climate change is already leading to an increase in the elevational distribution of alpine plant species (Grabherr et al. 1994, Walther et al. 2005), but that on the other hand dispersal limitation may delay the ability of species to track these climatic shifts (Körner 2003). Our study suggests that in the study area there is no such gap between the current upper distributional limit of the studied plant species and their climatically determined potential elevational distributions.

Implications for MDE models of elevational distributions

The upper elevational limit is important not only as an indicator of maximum severity of environmental conditions with which organisms must cope, but also as a variable used in null models predicting distribution of species numbers along elevational gradients (mid-domain effect models; MDE). The effectiveness of the domain boundaries is a characteristic that has been questioned (Laurie and Silander 2002, Zapata et al. 2003, 2005). In the study area, the absolute upper elevational boundary at ca 6000 m seems to be an effective distributional limit, above which plants cannot survive. The only two species that survived transplantation to 6030 m (*Waldbeimia tridactylites*, *Poa attenuata*) were the only two species naturally occurring at this elevation in the neighbourhood. Hence, the experiment

confirmed the observed limit of vegetation, set not by topography per se (not the top of the massif), but instead by physiological constraints of the species. A gradually diminishing species point to individualistic responses of what is likely a common ecological and physiological constraint (low temperatures). This result offers support for the contention of MDE proponents that domain limits are legitimately defined by shared organismal adaptations in relation to environmental gradients (Colwell et al. 2004, 2005), in this case tolerance to freezing temperatures. Field measurements showed that the number of days with soil temperatures above zero sharply dropped along the elevational gradient, a factor thus likely (together with solifluction) to limit expansion of flowering plant distributions to higher elevations. In the study area, where microsites with a special thermal regime are not available, the upper limit of vascular plant occurrence/growth is situated at ca 6030 m a.s.l., and is unexpectedly sharp, not broader than ca 100 m of elevation.

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