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Morphological plasticity of *Primula nutans* to hummock-and-hollow microsites in an alpine wetland

Received: August 23, 2005 / Accepted: January 16, 2006 / Published online: March 29, 2006

Abstract Hummock-and-hollow microtopography is common in wetlands of the Qinghai–Tibetan Plateau. The physical environment of hummocks contrasts strongly with that of hollows. To address how *Primula nutans* Georgi, a herbaceous species broadly distributed on the plateau, can inhabit both hummocks and hollows, we investigated the plasticity of its morphology and biomass growth in relation to the environmental variables during the growing season. The results are as follows: (1) total daily photosynthetic photon flux density, maximum soil temperature, and diurnal soil temperature range were significantly larger on the hummocks than in the hollows; (2) individual ramets had smaller leaves, higher leaf mass per unit area, and shorter petiole and peduncle length on the hummocks, but leaf and root dry weights per ramet differed little between microsites; (3) *P. nutans* allocated most of its dry mass to peduncles and flowers and the proportion of reproductive mass was significantly higher for plants in the hollows than on the hummocks; (4) the coefficients of variation of most morphological and biometric parameters was higher on hummocks than in hollows. The results suggest that *P. nutans* favors hummocks but can tolerate hollows through morphological adjustments in that the mass investment to peduncles and flowers is much larger in plants in the hollows than hummocks.

Key words Alpine plants · Biomass · Grassland · Microtopography · Spatial heterogeneity

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Introduction

The genus *Primula* contains 425 herbaceous species, of which 75% are found in the Himalayan Mountains and western China (Richards 2003). Within the genus, *P. nutans* is the most widespread species. It is found around much of the Arctic and in the mountains of central Asia (Richards 2003). Not only distributed across a broad geographical area, the species can also survive in a variety of habitats, ranging from open, sandy river valleys to moist meadows and grassy wetlands (Richards 2003; Herzsuh et al. 2005).

Wetlands are widely developed on the Qinghai–Tibetan Plateau (Zhao 1999). Most of these wetland are hummocky, i.e., the topography is characterized by elevated mounds (hummocks) alternating with flatter and wetter hollows. The hummocks are often randomly distributed and oval in shade. Their size ranges in height from several centimeters to about one meter, and in diameter from several decimeters to meters. Such microtopography can also be found in many other wetlands around the world (Nungesser 2003). The mature topography of these wetlands seems very stable and is able to remain unchanged for centuries or even millennia (e.g., Belyea and Clymo 2001; Nungesser 2003; McMullen et al. 2004). The physical environment contrasts markedly between the hummocks and hollows (e.g., Vivian-Smith 1997; Nungesser 2003). Hummock microsites often have a higher light availability, higher temperature, and lower soil moisture content than in the hollow microsites. Little detailed information is, however, available on the nature of this difference in alpine wetlands, in particular in the wetlands on the Qinghai–Tibetan Plateau. Understanding the environmental characteristics of this topography and their heterogeneity at an appropriate scale is indispensable if we are to assess the adaptive responses of individual species to this heterogeneous environment.

Little is known about how the plants respond to environmental heterogeneity at such small spatial scales (Bell and Lechowicz 1994; Kephart and Paladino 1997), in particular to the hummock-and-hollow microtopography and what the mechanism involved is. It is proposed that some common

species can grow both on hummocks and in hollows, whereas rare species tend to favor hummock microhabitats (Vivian-Smith 1997). We hypothesized thus that *P. nutans* can exploit both contrasting microsites as habitats, since the species has an ability to acclimate to contrasting microhabitats in hummock-and-hollow microtopography.

The aim of the present study was to test the hypothesis through (1) clarifying the characteristics of the physical environments of hummocks and hollows in the typical alpine wetland habitat of *P. nutans*, one of the most common species on the Qinghai–Tibetan Plateau, and (2) evaluating the morphological responses of *P. nutans* to the hummock and hollow microtopography.

Materials and methods

Plant materials

Primula nutans is a perennial herb with circumpolar distribution from North America to Europe and Asia. It grows in seashore meadows, alpine meadows, and wetlands. The annual ramets of *P. nutans* expand their leaves in early spring. On the Qinghai–Tibetan Plateau, the above ground parts of *P. nutans* emerge by late April and leaves fully expand by early May. Flowering occurs immediately after leaf expansion in midspring, that is, in early June. We focused on *P. nutans* because it may be used as a potential indicator species for the monitoring of global warming in alpine ecosystems due to its early phenology and the high sensitivity of the genus to temperature elevation (Sparks and Manning 2000; Bisgrove and Hadley 2002). The rosette-form ramet has two to five leaves. The leaves defoliate in September, and the parent ramet dies; only the below-ground gemmae survive from autumn through the winter to produce new ramets at the start of the following growing season.

Study site

The study site is located in the Luanhaizi wetland (37°36'N, 101°21'E, 3,250 m a.s.l.) at the northeastern edge

of the Qinghai–Tibetan Plateau (Fig. 1). The annual mean temperature is -2°C , and the annual rainfall averages 500 mm (Gu et al. 2003). The wetland lies on the north-western side of a small lake, where the ground is either flat or has very gentle slopes (Fig. 1). The relatively sparse vegetation is dominated by *Carex allivescens* and *Kobresia tibetica* and *P. nutans*. The area has been subjected to grazing by livestock (sheep, yaks, and dairy cattle), but the grazing intensity has generally been low from May to August because of the seasonal rotation of grazing that is practiced in the region; the majority of the livestock graze in higher and cooler pastures throughout the growing season. Other details on the study site are described elsewhere (Hirota et al. 2004).

The mean individual area of hummocks is 1,632 cm² ranging from 163 to 15,700 cm². In the study site, hummocks took 27% of the total area (a measurement in March 2005). The vegetation on the hummocks is often lower in height than in the hollows.

Assessments of microsite environment

In early spring 2004, we randomly established four plots (each 1 × 1 m, including both hummock and hollow microsites) in the wetland to permit long-term measurement of environmental parameters. In each plot, we installed two quantum sensors (GaAsP Photodiode G1118, Hamamatsu Ltd., Hamamatsu City, Japan) 5 cm above the ground surface, and one temperature sensor (a copper-constantan thermocouple) and one soil moisture sensor (ECH₂O, Decagon Devices, Inc., Pullman, WA, USA) at a depth of 5 cm in the soil of the hummock and hollow microsites, respectively. All quantum sensors were calibrated under sunlight and artificial shade against a standard quantum sensor (Li-Cor Model 190S, Li-Cor, Lincoln, NE, USA; Tang and Washitani 1995). We recorded photosynthetic photon flux density (PPFD) and soil temperatures at 1-min intervals using a datalogger (Thermic 2300A, Eto Denki Ltd., Tokyo, Japan). We measured soil moisture every 15 min with a different datalogger (Em5, Decagon Devices, Inc.) during the period from 1 June 2004 to 31 August 2004.

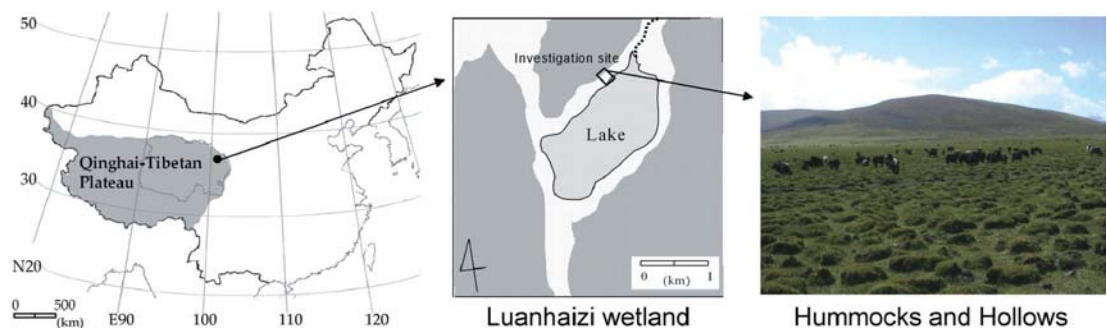


Fig. 1. Location of the study site (the Luanhaizi wetland of the Qinghai–Tibetan Plateau) and a photograph of the topography, showing typical hummock and hollow microsites. The left two maps were derived and modified from Hirota et al. (2004)

Morphological parameters

During the period from June to August, we periodically harvested 20–30 flowering ramets from every microsite each month and measured their dry weights and the following morphological parameters: petiole length, leaf size, and peduncle length. We measured leaf size using a CI-202 Portable Leaf Area Meter (CID, Inc., Vancouver, WA, USA). We divided each sampled ramet into roots, leaves, and peduncles, then oven-dried these materials at 80 °C for 24 h and measured their dry weights. Based on the measured leaf area and dry weight, we calculated the following parameters (on an individual ramet base, except for leaf mass per unit area, which was based on individual leaves):

- Leaf Mass Ratio (g g^{-1}) = leaf dry weight/total ramet dry weight
- Reproductive Mass Ratio (g g^{-1}) = dry weight of flower and peduncle/total ramet dry weight
- Root Mass Ratio (g g^{-1}) = root dry weight/total ramet dry weight
- Leaf Mass per unit Area (LMA, g m^{-2}) = leaf dry weight/leaf area
- Leaf Area Ratio (LAR, $\text{cm}^2 \text{g}^{-1}$) = leaf area per individual/total ramet dry weight
- Coefficient of Variations (CV) = $100 \times \text{SD}/\text{M}$

where, SD is the standard deviation of means and M is the grand mean.

We used the Student *t*-test for the comparison of the quality of two means between different months or between microsites. All analyzes were performed using the Kaleida-Graph for Windows (Synergy Software, Inc., PA, USA) software, and the results are expressed as means and their standard deviations (SD).

Results

Differences in light and temperature between hummocks and hollows

The averaged total daily PPFD was significantly higher on the hummocks than in the hollows consistently throughout the mid growing season from June to August (Table 1), and tended to be more variable during the day in the hollows, in particular on clear days (Fig. 2). As vegetation grew higher, the mean daily PPFD at the height of 5 cm above the ground decreased remarkably from July.

Mean daytime soil temperature at the depth of 5 cm was similar between the microsites in June but significantly higher on the hummocks in July and August (Table 1). Mean nighttime soil temperature however was always higher in the hollows. The diurnal range of soil temperature was therefore much larger on the hummocks in the late growing season, but only 1.7°C in the hollow in August (Table 1). Mean soil moisture content was consistently higher in the hollows than on the hummocks (Table 1).

Morphological, biomass and allometric responses

In a typical portion of the landscape with distinct hummocks and hollows, we found that the ramet density of *P. nutans* was markedly higher on the hummocks than in the hollows (Fig. 3).

In June, morphological and biomass growth were considerably similar on the hummocks and hollows, but we recorded significantly higher LMA, smaller leaves, and shorter petiole lengths for ramets growing on hummocks in August (Table 2). The mean August LMA values were 63

Table 1. Means \pm SD (standard deviations) of environmental variables for the hummock and hollow microsites

	June		July		August	
	Hummock	Hollow	Hummock	Hollow	Hummock	Hollow
Total daily PPFD ($\text{mol m}^{-2} \text{day}^{-1}$)	39.40 \pm 1.04 ^{Aa}	30.02 \pm 6.87 ^{Ba}	30.85 \pm 2.84 ^{Ab}	15.68 \pm 5.07 ^{Bb}	18.52 \pm 3.41 ^{Ac}	9.77 \pm 5.30 ^{Bc}
Air temperature (°C)						
Daytime mean		12.27 \pm 2.22 ^a		13.14 \pm 3.01 ^a		21.0 \pm 2.5 ^b
Nighttime mean		5.89 \pm 2.94 ^a		5.10 \pm 3.91 ^a		12.8 \pm 3.8 ^b
Diurnal range		6.38 \pm 2.48 ^a		8.04 \pm 3.60 ^a		8.3 \pm 5.1 ^b
Soil temperature (°C)						
Daytime mean	15.49 \pm 0.57 ^{Aa}	15.37 \pm 0.84 ^{Aa}	16.78 \pm 1.27 ^{Aa}	15.25 \pm 2.04 ^{Ba}	17.2 \pm 0.5 ^{Aa}	15.7 \pm 1.8 ^{Ba}
Nighttime mean	7.68 \pm 0.58 ^{Aa}	8.28 \pm 0.01 ^{Ba}	9.79 \pm 0.17 ^{Ab}	10.95 \pm 0.35 ^{Bb}	13.1 \pm 0.4 ^{Ac}	14.0 \pm 0.6 ^{Bc}
Diurnal range	7.81 \pm 1.15 ^{Aa}	7.09 \pm 0.86 ^{Ba}	6.98 \pm 1.44 ^{Aa}	4.29 \pm 2.38 ^{Bb}	4.2 \pm 0.9 ^{Ab}	1.7 \pm 2.4 ^{Bb}
Daytime maximum	25.84 \pm 3.33 ^{Aa}	24.84 \pm 4.2 ^{Ba}	26.65 \pm 4.17 ^{Aa}	21.43 \pm 4.50 ^{Bb}	23.7 \pm 2.0 ^{Aa}	18.9 \pm 4.2 ^{Bc}
Daytime minimum	3.54 \pm 0.59 ^{Aa}	5.00 \pm 0.14 ^{Ba}	5.80 \pm 0.31 ^{Ab}	8.32 \pm 0.62 ^{Bb}	10.2 \pm 0.4 ^{Ac}	12.3 \pm 0.9 ^{Bc}
Mean soil moisture content (%)	30.2 \pm 5.1 ^{Aa}	36.6 \pm 2.3 ^{Ba}	34.5 \pm 1.3 ^{Ab}	37.6 \pm 3.4 ^{Ba}	34.0 \pm 0.0 ^{Ab}	37.5 \pm 1.3 ^{Ba}

PPFD was measured with eight sensors set 5 cm above ground on the hummocks and another eight sensors set 5 cm above ground in the hollows. Data were recorded every 1 min during a 24-h period, but the PPFD data were analyzed only from 06:00 to 21:00 Beijing time. Air and soil temperatures were measured every 5 min, and soil moisture was measured every 15 min. Soil temperature and soil moisture sensors were installed at a depth of 5 cm at four points each for the hummock and hollow microsites. Different superscripts on the SD indicate significant difference between hummocks and hollows in the same month indicated by upper-case letters, and unpaired comparison of the quality of two means among months in the same microtopography are indicated by lower-case letters ($P < 0.05$, Student *t*-test for comparison of the quality of two means)

Fig. 2. An example of the diurnal change in PPFD (a, b) and temperature (c, d) on a typical hummock (HU, dashed line) and its neighboring hollow (HO, solid line) on an overcast day (a, c) and a clear day (b, d) in July 2004. AIR represents the temperature about 5 cm above the surface of vegetation, and S represents the temperature at a depth of 5 cm in the soil

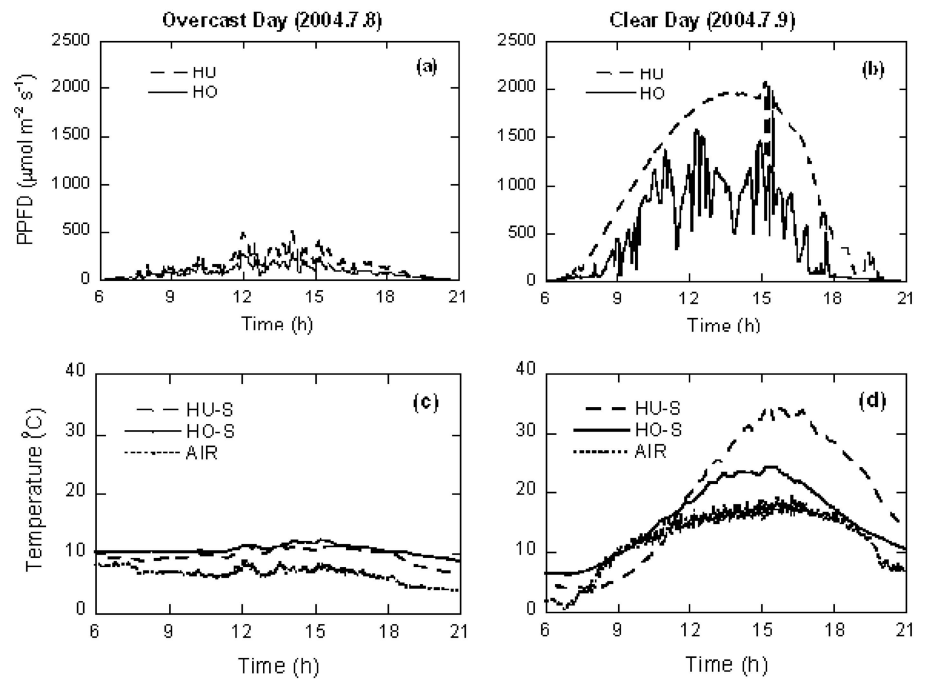
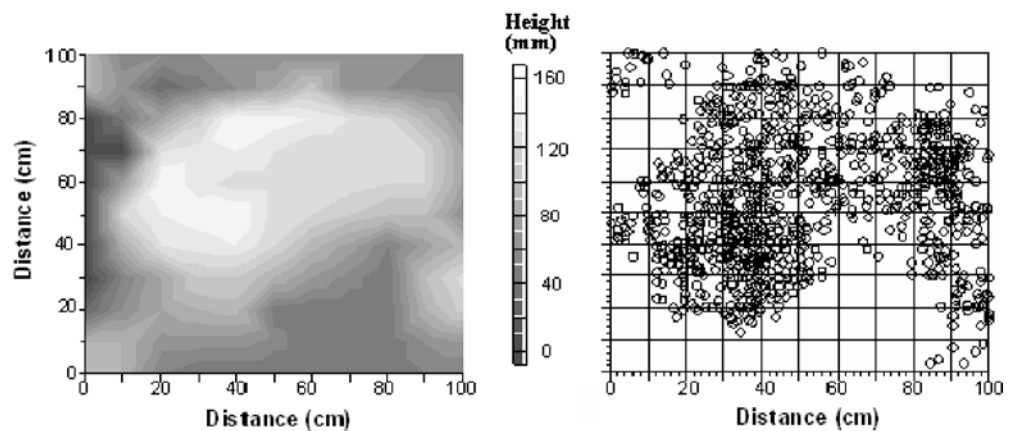


Fig. 3. Left: contour map indicating the height relative to the lowest point in the hollow. Right: the spatial distribution of *Primula nutans*. All measurements were made in June 2004. Height: mm relative to the mean bottom of the surrounding hollows



and 50 g m^{-2} in the hummocks and hollows, respectively. However, biomass allocation to leaves and roots, total leaf area per ramet did not differ significantly between microsites (Table 2).

In August, peduncles accounted for the greatest proportion of total ramet biomass: 59% in the hummock plants and 69% for those in the hollows (Fig. 4). The peduncles were significantly longer for the plants growing in the hollows (Table 2). The average peduncle length of the plants from the hollows was about 178 mm, which was about 60 mm longer than that of the plants growing on the hummocks (Table 2), the difference was significant.

Environmental heterogeneity and phenotypic plasticity

Coefficient of variations (CV) was used to index the environmental heterogeneity or phenotypic plasticity (Table 3). In most cases, CVs of the environmental variables were higher for the hollows than hummocks. PPFD showed the

highest CV among all the environmental variables except for nighttime air temperature in June and July.

Coefficient of variations of most phenotypic parameters, however, were higher for plants from the hummocks than hollows in August, but it was similar between the two microtopography sites in June (Table 3). Moreover, CVs of most parameters showed higher value in August than June. Among the morphological and mass parameters, those relevant to leaf trait showed higher CV than other parameters.

Discussion

Heterogeneity of PPFD and soil temperature in hummock-and-hollow microtopography

Hummock and hollow microtopography has long been appreciated in plant ecology (Tansley 1939). Depending on the history of development, the hummocks and hollows can

Table 2. Morphological and allometric parameters in *Primula nutans* growing on hummocks and in hollow microsities

	June (<i>N</i> = 20, <i>n</i> = 35)		July (<i>N</i> = 20, <i>n</i> = 51)		August (<i>N</i> = 25, <i>n</i> = 54)	
	Hummock	Hollow	Hummock	Hollow	Hummock	Hollow
Morphological parameters						
Petiole length (mm)	6.20 ± 2.49 ^{Aa}	9.56 ± 2.32 ^{Ba}	8.24 ± 2.40 ^{Ab}	10.65 ± 3.86 ^{Ba}	10.60 ± 3.62 ^{Ac}	15.92 ± 4.09 ^{Bb}
Leaf size (cm ²)	0.72 ± 0.26 ^{Aa}	0.87 ± 0.26 ^{Ba}	0.63 ± 0.34 ^{Ac}	0.73 ± 0.29 ^{Ba}	0.63 ± 0.33 ^{Ac}	1.62 ± 0.70 ^{Ba}
Total ramet leaf area (cm ²)	2.25 ± 0.49 ^{Aa}	2.54 ± 0.75 ^{Aa}	1.60 ± 1.06 ^{Ac}	1.52 ± 0.42 ^{Ba}	2.13 ± 1.01 ^{Ac}	2.72 ± 1.20 ^{Ba}
Peduncle length (cm) ^d	7.62 ± 0.81 ^{Aa}	7.54 ± 1.94 ^{Aa}	13.31 ± 2.39 ^{Ab}	15.72 ± 3.20 ^{Bb}	12.04 ± 4.19 ^{Ab}	17.82 ± 4.28 ^{Bb}
Mass parameters						
Leaf dry weight (mg)	14.9 ± 5.0 ^{Aa}	13.7 ± 4.92 ^{Aa}	– ^c	–	10.3 ± 7.5 ^{Ab}	12.9 ± 5.1 ^{Aa}
Reproductive mass (mg) ^f	25.2 ± 4.8 ^{Aa}	20.4 ± 6.38 ^{Ba}	37.4 ± 15.2 ^{Ab}	37.4 ± 14.5 ^{Ab}	37.3 ± 17.4 ^{Ab}	68.6 ± 28.7 ^{Bc}
Root dry weight (mg)	14.3 ± 5.6 ^{Aa}	14.5 ± 2.80 ^{Aa}	–	–	15.6 ± 7.5 ^{Aa}	18.6 ± 5.9 ^{Ab}
Total dry weight (mg)	54.4 ± 10.2 ^{Aa}	48.6 ± 9.43 ^{Aa}	–	–	63.2 ± 28.6 ^{Aa}	100.1 ± 30.4 ^{Bb}
Allometric and allocation parameters						
Leaf mass area (g m ⁻²)	61.17 ± 15.14 ^{Aa}	49.98 ± 9.88 ^{Ba}	–	–	62.96 ± 19.66 ^{Ac}	50.42 ± 8.22 ^{Ba}
Leaf area ratio (cm ² g ⁻¹)	51.22 ± 4.99 ^{Aa}	51.46 ± 8.13 ^{Aa}	–	–	24.93 ± 6.51 ^{Ab}	25.00 ± 10.68 ^{Ab}

Values represent mean ± SD for measurements of flowering individuals. Different superscripts on the SD indicate significant difference between hummocks and hollows in the same month indicated by upper-case letters, and among months in the same microtopography indicated by lower-case letters ($P < 0.05$, Student *t*-test for comparison of the quality of two means, sample number *N* for ramets and *n* for leaves, respectively)

^dPeduncle length includes the average length of flowers

^cData are not available

^fReproductive mass includes the mass of peduncle and flower

Table 3. Coefficients of variation for environmental variables measured for the hummocks and hollows, and those for the morphological and allometric parameters in *Primula nutans* (flowering ramet) growing on hummocks and in hollow microsities (see details in Tables 1 and 2)

	June			July			August		
	Hummock	Hollow	Both	Hummock	Hollow	Both	Hummock	Hollow	Both
Environmental parameters									
Total daily PPFD	2.6	22.9	17.2	9.2	32.3	36.3	18.4	54.2	41.0
Mean daytime air temperature			15.2			22.9			11.9
Mean nighttime air temperature			49.9			76.7			29.7
Mean daytime soil temperature	3.7	5.5	3.8	7.6	13.4	10.2	2.9	11.5	8.6
Mean nighttime soil temperature	7.6	0.1	6.0	1.7	3.2	6.8	3.1	4.3	5.2
Mean soil moisture content	16.9	6.3	14.6	3.8	9.0	7.7	0.0	3.5	5.9
Morphological parameters									
Petiole length	40.2	24.3	37.5	29.1	36.2	36.1	34.2	25.7	36.0
Leaf size	36.1	29.9	34.2	54.0	39.7	44.9	52.4	43.2	66.7
Total ramet leaf area	21.8	29.5	26.7	27.6	66.3	60.8	47.4	44.1	46.2
Peduncle length ^a	10.6	25.7	19.4	18.0	20.4	20.9	34.8	24.0	34.2
Mass parameters									
Leaf dry weight	33.6	35.9	43.8	– ^b	–	–	72.8	39.5	50.0
Reproductive mass ^c	19.0	31.3	48.0	40.6	38.8	40.5	46.6	41.8	52.8
Root dry weight	39.2	19.3	37.5	–	–	–	48.1	31.6	41.2
Total dry weight	18.8	19.4	21.6	–	–	–	45.3	30.4	42.7
Allometric and allocation parameters									
Leaf mass ratio	22.2	32.1	44.2	–	–	–	43.8	41.4	43.8
Reproductive mass ratio	23.4	25.0	15.2	–	–	–	15.3	16.5	16.9
Root mass ratio	26.9	21.9	27.2	–	–	–	24.0	39.0	34.1
Leaf mass area	24.8	19.8	25.0	–	–	–	31.2	16.3	29.2
Leaf area ratio	9.7	15.8	13.5	–	–	–	26.1	42.7	38.7

^aPeduncle length includes the average length of flowers

^bData are not available

^cReproductive mass includes the mass of peduncle and flower

be different in their size and morphology (Ivanov 1981; Glaser 1992 via Weltzin et al. 2001). These differences are influenced by various physical and biological factors (Ehrenfeld 1995; Karofeld 1998; Nungesser 2003). For example, the change of ground water level is the major environmental driver of the “growth” of hummocks

(Couwenberg 2005), while soil characteristics, frozen degree and the accumulation of peat can all result in the formation of hummocks (Mark 1994; Tallis and Livett 1994; Tallis 1994; Karofeld 1998). However, no data is available for detailed comparisons of environments between hummocks and hollows. The current study provides some

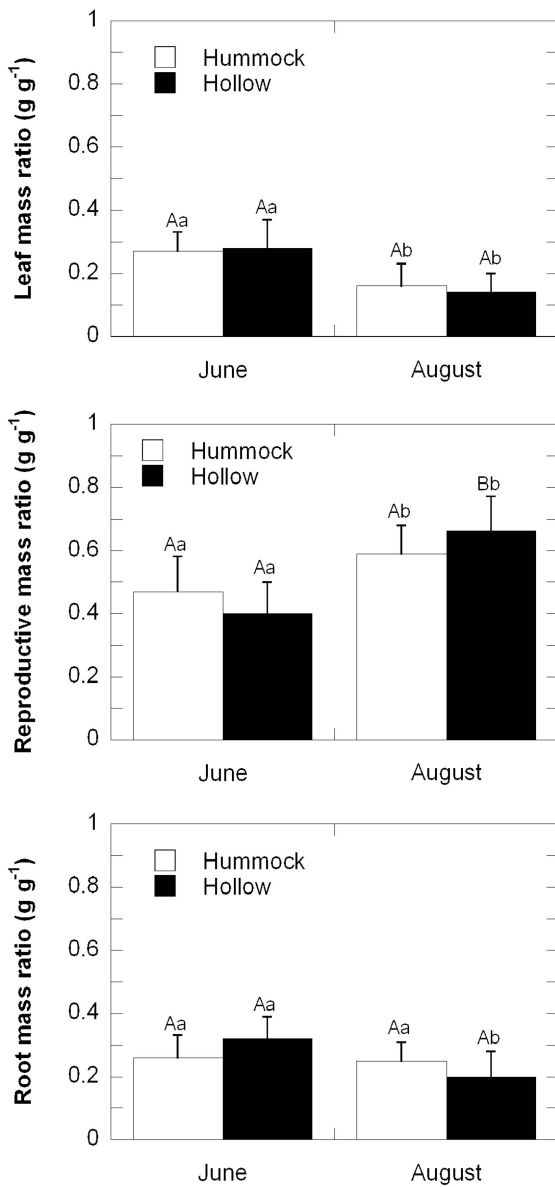


Fig. 4. Leaf mass ratio (*top*), reproductive mass ratio (*middle*) and root mass ratio (*bottom*) for *Primula nutans* growing on the hummocks and in the hollows. Vertical bars indicate SD. Different superscripts indicate significant difference between hummocks and hollows in the same month indicated by uppercase letters, and among months in the same microtopography indicated by lowercase letters ($P < 0.05$, Student *t*-test for comparison of the quality of two means, $N = 20$ in June and $N = 25$ in August)

insights into the spatial environmental heterogeneity of the hummock-and-hollow microtopography in the wetland on the Qinghai–Tibetan Plateau.

Photosynthetic photon flux density (PPFD) incident on a microsite is of primary importance since radiation drives other environmental variables such as soil temperature and soil moisture. In temperate lowland grassland, PPFD is spatially heterogeneous (Tang et al. 1988). The current study indicates that PPFD was also highly variable in space in the wetland. The significantly higher PPFD on the hummocks (Fig. 2) may have resulted from their more-exposed surface

and the shorter vegetation (Table 1). The short height on the hummocks can be due to low height growth and/or grazing pressure, which sometimes enhances the spatial heterogeneity of the vegetation (e.g., review by Adler et al. 2001). However, grazing was not a major factor in this study since the study site had been fenced to exclude cattle in the growing season. The shading by the hummocks at low solar elevations may be responsible for the low total daily PPFD recorded in the hollows, but the microtopography is not likely to be the major factor resulting in the PPFD difference, since PPFD was less different between June and August (Table 1). Sunshine duration might be also a factor affecting PPFD environment if a hollow is very small and deep.

The difference in PPFD should further result in the difference in the observed soil temperature and moisture content (Fig. 2; Table 1). However, our measurements showed no significant difference between the microsites in mean daytime or nighttime soil temperatures. One major reason may be that most heat exchange occurs at the surface of the soil or vegetation. This interpretation is supported by the large difference in temperature at certain times of day (Fig. 2), with a significantly higher maximum soil temperature on the hummocks than in the hollows (Table 1). Dense shading of the soil surface by the high leaf area index (LAI) approximating three on the hummocks might reduce the insolation and thus the difference in soil temperature between the hummocks and hollows. In general, the hollows in wetlands often retain a higher amount of soil moisture than the hummocks, but the average soil moisture content did not differ significantly between the microsites in June and July (Table 1).

Leaf morphological response to microsite characteristics

Alpine plants commonly produce less area per unit leaf mass, i.e., their LMA is higher but specific leaf area (SLA) is lower than plants from lowland (Körner 2003). SLA ranges between 1.4 and 2.6 dm² g⁻¹, i.e., between 38.5 and 71.4 g m⁻² in LMA for herbaceous plants from high altitudes (Körner et al. 1989). *P. nutans* thus exhibited relatively high LMA in the study. The environmental driver of the SLA changes with elevation is likely to be temperature but no conclusive evidence seems to exist for dicots (Körner 2003).

The higher LMA of *P. nutans* on the hummocks than in the hollows might be due to the difference of PPFD environment in the contrasting microsite. PPFD was significantly higher on the hummocks than in the hollows (Fig. 2; Table 1). Plants on the hummocks should develop “sun leaves” with smaller leaf size, higher LMA and shorter petioles, whereas those in the hollows should develop “shade leaves” (Larcher 2003). Moreover, the hummock microsites might experience stronger wind and lower humidity than the hollow microsites, which could also contribute to the small sized and thicker leaves, as well as shorter petioles observed on the hummock microsites. A reduction in the leaf area and/or petiole length will probably reduce the susceptibility of plants to wind-induced mechanical damage

because of the decrease of drag forces (Niklas 1996). In addition, the late snow melt in the hollows may also play an important role. Kudo (1996) reported that alpine plants in temperate zones have higher SLA at late snow melt sites than early snow melt sites.

Despite the wide distribution of hummocky microtopography in wetlands around the world, to our knowledge there has been no report on the morphological acclimation of plants to hummocky environments, though some evidence suggested the importance of polymorphism in the survival of plants in harsh but spatially heterogeneous environments, e.g., *Dryas octopetala* in Alaska (Max et al. 1999), *Saxifraga oppositifolia* in the high Arctic (Crawford 1997; Kume et al. 2003). The leaf morphological plasticity revealed by *P. nutans* is likely to contribute to the adaptation of the species to exploit a wide range of microsites and habitats. It is suggested that phenotypic plasticity could be critical for the same genotype to match environmental heterogeneity (Schlichting 1986).

It is interesting to notice that the total biomass production of *P. nutans* was higher in the hollows than on the hummocks in August, even though it had similar biomass in June. Rather stressful conditions on the hummock such as the high radiation and drought environment in mid summer might suppress biomass accumulation. For example, photo-inhibition often limits biomass production in the alpine grassland (Cui et al. 2003; Zhang and Tang 2005). To draw firm conclusions, however, further measurements of in situ assimilation rate and daily patterns are needed in the future.

Bloor and Grubb (2004) recently quantified morphological plasticity using CVs and found that the plasticity of different plant traits could be ranked as follows: stem form > crown traits > root form > leaf form > biomass allocation. In our study, leaf traits showed larger plasticity than peduncles from the analysis of CV (Table 3). Moreover, CV for most plant traits was higher for plants growing on the hummocks than in the hollows, which may be related to heterogeneity of certain environmental factors such as the large variation in PPFd.

Peduncle height and its potential significance to seed dispersal of plants in hollows

A comparison between 30 alpine species and 20 lowland species demonstrated that the alpine plants allocated three times more of their above-ground biomass to floral structures than lowland species (Fabbro and Körner 2004), which suggests that alpine plants increase their effort to attract pollinators to compensate for the assumed pollinator scarcity at high altitude. *P. nutans* invested about 50% of the aboveground biomass to the floral mass including peduncle and flower biomass. The reproductive mass ratio was similar between the hummock and hollow microsites in June, but was significantly higher in plants in the hollows than on the hummocks in August. The increase of reproductive investment in *P. nutans* in the hollows resulted from the high peduncle, which may compensate the lower ground level in the hollows to hold up the flowers higher to attract pollina-

tors. Moreover, a slight increase in the peduncle height means greater extension of seed dispersal distance, as the importance of the initial release height of seeds (diaspores) has been intensively discussed recently (Oliver et al. 2003; Soons et al. 2004; Soons and Ozinga 2005). On a meadow close to our study site, the wind velocity increased by a value of about 1.7 m s^{-1} (estimated from Fig. 5 in the citation) from 0 to 1 m aboveground at 20:00 when the wind velocity was often the highest during the day (Li et al. 2000). The vertical wind-profile could be larger at a higher wind speed. We therefore expected that the increase of peduncle height in *P. nutans* would be potentially advantageous for seed dispersal.

Acknowledgments This study was supported by the 21st Century COE Program of the University of Tokyo, "Biodiversity and Ecosystem Restoration," sponsored by the Japan Society for the Promotion of Science, and by the Global Environment Research Program S1-I(2) grant from the Ministry of the Environment of Japan. The authors thank Dr. Aayako Shimono (National Institute for Environmental studies, Japan) for her advice and assistance with the fieldwork. We thank Dr. Mingyuan Du for his kind permission to use the photograph in Fig. 1. We also thank Drs. Xiaoyong Cui (Graduate University of Chinese Academy of Sciences, China), Hiroyuki Muraoka (Gifu University, Japan), Hibiki Noda (Tokyo University, Japan), Mitsuru Hirota (National Institute for Environmental studies, Japan), and Song Gu, Yingnian Li, Xinquan Zhao (Northwest Institute of Plateau Biology, Chinese Academy of Sciences, China) for their assistance in our study.

References

- Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128:465–479
- Bell G, Lechowicz MJ (1994) Spatial heterogeneity at small scales and how plants respond to it. In: Caldwell MM, Pearcy RW (eds) Exploitation of environmental heterogeneity by plants. Academic Press, New York, pp 391–414
- Belyea LR, Clymo RS (2001) Feedback control of the rate of peat formation. *Proc R Soc Lond B* 268:1315–1321
- Biggrove R, Hadley P (2002) Gardening in the global greenhouse: the impacts of climate change on gardens in the UK. Technical Report. The UK Climate Impacts Program, Oxford, UK
- Bloor J, Grubb P (2004) Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. *Funct Ecol* 18(3):337–348
- Couwenberg J (2005) A simulation model of mire patterning revisited. *Ecography* 28:653–661
- Crawford RMM (1997) Habitat fragility as an aid to long-term survival in arctic vegetation. In: Woodin SJ, Marquiss M (eds) Ecology of arctic environments. British Ecological Society Special Publication No. 13, Blackwell Scientific, Oxford, pp 113–136
- Cui X, Tang Y, Gu S, Nishimura S, Shi S, Zhao X (2003) Photosynthetic depression in relation to plant architecture in two alpine herbaceous species. *Environ Exp Bot* 50:125–135
- Ehrenfeld JG (1995) Microsite differences in surface substrate characteristics in *Chamaecyparis* swamps of the New Jersey Pinelands. *Wetlands* 15:183–189
- Fabbro T, Körner C (2004) Altitudinal differences in flower traits and reproductive allocation. *Flora* 199(1):70–81
- Glaser (1992) Ecological development of patterned peatlands. In: Wright HE Jr, Coffin BA, Aaseng NE (eds) The patterned peatlands of Minnesota. University of Minnesota Press, Minneapolis, pp 27–42
- Gu S, Tang Y, Du M, Kato T, Li Y, Cui X, Zhao X (2003) Short-term term variation of CO₂ flux in relation to environmental controls in an alpine meadow on the Qinghai–Tibetan Plateau. *J Geophys Res* 108:1–9, DOI 10.1029/2003JD003584

- Herzschuh U, Zhang C, Mischke S, Herzschuh R, Mohammadi F, Mingram B, Kürschner H, Riedel F (2005) A late quaternary lake record from the Qilian Mountains (NW China): evolution of the primary production and the water depth reconstructed from macrofossil, pollen, biomarker, and isotope data. *Global Planet Change* 46:361–379
- Hirota M, Tang Y, Hu Q, Hirata S, Kato T, Mo W, Cao G, Mariko S (2004) Methane emissions from different vegetation zones in a Qinghai–Tibetan Plateau wetland. *Soil Biol Biochem* 36:737–748
- Ivanov KE (1981) *Water movement in mirelands*. Academic Press, London
- Karofeld E (1998) The dynamics of the formation and development of hollows in raised bogs in Estonia. *Holocene* 8:697–704
- Kephart SR, Paladino C (1997) Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var *oraria* (Caryophyllaceae). *Am J Bot* 84:179–189
- Körner C (2003) *Alpine plant life, functional plant ecology of high mountain ecosystems* 2nd edn. Springer, Berlin Heidelberg New York
- Körner C, Neumayer M, Menendez-Riedl S, Seets-Scheel A (1989) Functional morphology of mountain plants. *Flora* 182:353–383
- Kudo G (1996) Intraspecific variation of leaf traits in several deciduous species in relation to length of growing season. *Ecoscience* 3:483–489
- Kume A, Bekku YS, Hanba YT, Kanda H (2003) Carbon isotope discrimination in diverging growth forms of *Saxifraga oppositifolia* in different successional stages in a high Arctic glacier foreland. *Arct Antarct Alp Res* 35:377–383
- Larcher W (2003) *Physiological plant ecology* 4th edn. Springer, Berlin Heidelberg New York
- Li YN, Shi SB, Cao GM, Yang YG, Shen ZX (2000) The observational studies on characteristics of microclimate in Haibei alpine meadow regions of Qi-Lian Mountain (in Chinese with English abstract). *Plateau Meteorology* 19(4):512–519
- Mark AF (1994) Patterned-ground activity in a southern New Zealand high-alpine cushionfield. *Arct Alp Res* 26:270–280
- Max KN, Mouchaty SK, Schwaegerle KE (1999) Allozyme and morphological variation in two subspecies of *Dryas octopetala* (Rosaceae) in Alaska. *Am J Bot* 86:1637–1644
- McMullen JA, Barber KE, Johnson B (2004) A paleoecological perspective of vegetation succession on raised bog microforms. *Ecol Monogr* 74:45–77
- Niklas KJ (1996) Differences between *Acer saccharum* leaves from open and wind-protected sites. *Ann Bot* 78:61–66
- Nungesser MK (2003) Modeling microtopography in boreal peatland: hummocks and hollows. *Ecol Model* 165:175–207
- Oliver T, Peter P, Susanne B (2003) Assessment of wind dispersal potential in plant species. *Ecol Monogr* 73(2):191–205
- Richards J (2003) *Primula*. Timber Press, Portland, OR
- Schlichting CD (1986) The evolution of phenotypic plasticity in plants. *Annu Rev Ecol Syst* 17:667–693
- Soons MB, Ozinga WA (2005) How important is long-distance seed dispersal for the regional survival of plant species? *Divers Distrib* 11:165–172
- Soons MB, Heil GW, Nathan R, Katul GG (2004) Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* 85(11):3056–3068
- Sparks TH, Manning M (2000) Recent phenological changes in Norfolk. *Trans Norfolk Norwich Nat Soc* 33:105–110
- Tallis JH (1994) Pool-and-hummock patterning in a southern pennine blanket mire II. The formation and erosion of the pool system. *J Ecol* 82:789–803
- Tallis JH, Livett EA (1994) Pool-and-hummock patterning in a southern pennine blanket mire I. Stratigraphic profiles for the last 2800 years. *J Ecol* 82:775–788
- Tang Y, Washitani I (1995) Characteristics of small-scale heterogeneity in light availability within a *Miscanthus sinensis* canopy. *Ecol Res* 10:189–197
- Tang Y, Washitani I, Tsuchiya T (1988) Fluctuation of photosynthetic photon flux density within a *Miscanthus sinensis* Canopy. *Ecol Res* 3:253–266
- Tansley AG (1939) *The British islands and their vegetation*. Cambridge University Press, London
- Vivian-Smith G (1997) Microtopographic heterogeneity and floristic diversity in experimental wetland communities. *J Ecol* 85:71–82
- Weltzin JF, Harth C, Bridgham SD, Pastor J, Vonderharr M (2001) Production and microtopography of bog bryophytes: response to warming and water-table manipulations. *Oecologia* 128:557–565
- Zhang Y, Tang Y (2005) Inclusion of photoinhibition in simulation of carbon dynamics of an alpine meadow on the Qinghai–Tibetan Plateau. *J Geophys Res* 110:G01007, DOI:10.1029/2005JG000021
- Zhao K (1999) *Lakes and marshes in China* (in Chinese). Publisher of Science, Beijing