

Foliar N and P dynamics of *Heracleum platytaenium* (Apiaceae) in relation to edaphic characteristics along an elevation gradient in northern Turkey

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Heracleum platytaenium (Apiaceae) is an endemic species in the Central Black Sea region, in the north of Turkey. Its foliar N and P dynamics and absolute and proportional N and P resorptions along an elevation gradient were investigated. The foliar N and P concentrations varied along the elevation gradient and during the growing season in basal leaves. N and P concentrations of stem leaves did not change significantly during the growing season, although significant changes were observed along the topographic gradient. N and P concentrations of basal leaves declined during May and June, and increased through July. Absolute and proportional resorptions were usually higher in slope positions in both basal and stem leaves, except for N resorption in stem leaves. N and P resorptions were more effective in the slopes between the upper and lower parts of the gradient. Absolute and proportional N and P resorptions in basal and stem leaves were significantly correlated with foliar N and P concentrations. Soil fertility varied significantly along the elevation gradient, but no consistent pattern was found between soil fertility and resorption. Foliar resorption was significantly correlated with soil moisture, and nutrient resorption probably reflected topographic differences in soil moisture rather than in soil fertility. Root/shoot ratio was comparatively low at the beginning of the growing season and increased towards the end of the growing season.

Key words: absolute N and P resorption, *Heracleum platytaenium*, monocarpic plants, plant ecophysiology, proportional N and P resorption, root/shoot ratio

Introduction

Concentrations of nutrients in mature leaves can indicate the nutritional status of a plant. For this reason, foliar analysis is a classic tool for diagnosing nutrient use efficiencies and it has long

been applied to forest trees, shrubs and herbs, which retranslocate sizeable proportions of the nutrient content of leaves before leaf abscission. Resorption increases the control of the individual plant over the nutrient resources and allows the plant to reutilize them (Tamm 1964,

Mayor & Roda 1992). One of the most important methods of measuring nutrient use efficiency in plants is to determine foliar resorption, the process of nutrient translocation from the leaves into storage tissues during senescence (Killingbeck 1986, Killingbeck & Costigan 1988). It has been reported that individuals growing in less fertile sites may use nutrients more efficiently than those growing in more fertile sites. However, several other studies have shown that the relationship between resorption and soil fertility is not present in all cases (Chapin 1980, Chapin & Kedrowski 1983, Ralhan & Singh 1987, del Arco et al. 1991, De Mars & Boerner 1997, Knops & Koenig 1997).

Some stress factors such as low soil moisture may reduce resorption, especially of nitrogen. Several studies examining foliar nutrient resorption among temperate deciduous stands support these hypotheses for nitrogen and phosphorus (Boerner 1984, Kost & Boerner 1985, De Mars & Boerner 1997).

Kutbay and Ok (2001) stated that nutrients and moisture vary with topographic position within an ecosystem. Examination of nutrient dynamics along interstand topographic gradients may be used to examine hypotheses relating soil fertility to plant nutrient content and resorption.

Heracleum platytaenium (Apiaceae) is a tall (1–2.5 m), coarse herb with a thick stem and rootstock. The basal leaves are ternate and trisect, whereas the stem leaves are broad, inflated truncate to retuse, with dentate sheaths. Flowers are white. It is an endemic species belonging to the Euxine phytogeographic region (Davis 1972). It usually occurs in forest clearings — especially in *Fagus orientalis* forests — and on streambanks. *Heracleum* can grow up to a height of 2.5 m between April and June, so it has a high relative growth rate and is a typical representative of the CR (competitive/ruderal) strategy type and adapted to circumstances with a low impact of stress (Burrows 1990, Pyšek & Pyšek 1995). *Heracleum platytaenium* was chosen for study of nutrient dynamics and nutrient resorption during the growing season because it occurs along the entire topographic gradient and is an endemic species.

In this study, nutrient dynamics and nitrogen and phosphorus resorption in basal and stem

leaves and the root/shoot ratio of *Heracleum platytaenium* along an elevation gradient were investigated. This study addressed two main objectives: (1) to investigate whether foliar N and P concentrations change during the growing season and along the elevation gradient, and (2) to assess the relationships between foliar N and P concentrations and absolute and proportional resorption. The interactions between soil nutrient availability and soil moisture and resorption were also examined.

Material and methods

Heracleum platytaenium specimens were collected from the vicinity of Samsun city, which is situated in the northern part of Turkey (36°10'E, 41°22'N) along an elevation gradient from 30 to 900 m. Mean minimum temperature is 6.9 °C and mean maximum temperature is 23.3 °C at 30 m. Mean minimum temperature values at our study plots at 300, 600 and 900 m were 0.8 °C, –1 °C and –2.8 °C respectively, and the corresponding mean maximum temperature values were 20.2 °C, 19.2 °C and 18.3 °C. Mean annual precipitation at 30, 300, 600 and 900 m was 732.06, 862.74, 1024.74 and 1087.92 mm, respectively (Ministry of Agriculture 1994).

Four topographic positions were sampled over the elevation range (30 m, 300 m, 600 m and 900 m). Plant individuals were located within a single plot at each elevation. 20 × 20-m plots were sampled along the elevation gradient. Plots were in homogeneous stands of vegetation on northwest facing slopes. From each topographic position and each plot five *Heracleum platytaenium* individuals (≥ 1.5 m tall) were randomly selected. Plant specimens were selected ≥ 1.5 m from the stems of neighboring plants to avoid potential microsite variation (Boerner & Koslowsky 1989). Plant individuals were obtained from April to July. Five individuals were sampled per elevation from each plot in each sampling date and they were flagged and the same individuals were sampled from April to July. Five foliage samples were pooled to create one value per individual.

All of the basal leaves were senesced in July. However, stem leaves were senesced in June.

Five fresh leaves from each of the individual plants were taken during mid-growing season (in the first half of May 1998). Freshly abscised leaves (five leaves) were also collected from each individual during the second half of July 1998 (basal leaves) and during the second half of June 1998 (stem leaves) to calculate the absolute and proportional resorption. Root and shoot samples were taken along the elevation gradient during the growing season and they were dried at 60 °C to constant weight.

Leaf samples were dried at 60 °C to constant weight, ground, and sieved. Nitrogen content was determined by the micro Kjeldahl method with a Kjeltex Auto 1030 Analyser (Tecator, Sweden) after digesting the samples in concentrated H₂SO₄ with a selenium catalyst. Sieved leaf samples were digested in a mixture of nitric and perchloric acids prior to P analysis. Concentration of P was determined with the stannous chloride method by using a Jenway spectrophotometer (Allen *et al.* 1986).

Leaf area of basal and stem leaves was measured with a leaf-area meter (LI-3000, LICOR-USA). Leaves were then oven-dried at 60 °C over at least three days. Specific leaf mass (SLM) was calculated as the leaf dry mass per unit leaf area (Kutbay 2001).

Absolute resorption was calculated as the difference between the mid-growing season foliar concentration for each individual and the freshly abscised foliar concentration. Proportional resorption was determined by dividing the absolute resorption by the nutrient concentration in mature leaves. The proportional resorption is thus the proportion of nutrient concentration in a mature leaf that is removed from the leaf before it is shed.

Five soil cores were taken from under the plant specimens according to fixed spatial arrangement

with a soil corer to a depth of 80 cm during the growing season. *Heracleum platytaenium* has a rather thick tap root and rooting depth mostly exceeded 90 cm, so soil samples were obtained to 80 cm, which is the effective root zone for this species. On each sampling date, plant and soil samples were obtained simultaneously. Soil samples were air-dried and sieved through a 2-mm mesh prior to analysis. Soil texture was determined by the Bouyoucus hydrometer method. Soil nitrogen was determined by the micro Kjeldahl method. Soil phosphorus was determined spectrophotometrically following extraction with ammonium acetate (Bayraklı 1987). Because soil nitrogen and phosphorus concentrations and soil moisture changed very little during the growing season, soil data were determined from pooled April–July samples. For the determination of soil moisture about 250–300 g samples were placed in soil pans, weighed fresh, dried at 105 °C for 48 h, then weighed dry. Soil moisture was then calculated on a volume basis (Boerner 1985).

One and two-way ANOVA tests were carried out and Pearson correlation coefficients calculated with MINITAB (Schaeffer & Anderson 1989, Anon. 1998). Tukey's honestly significant difference (HSD) test was used to rank means following ANOVA (SPSS: Anon. 1998).

Results

There were no significant differences in SLM between mid-growing season and senesced leaf samples in either basal or stem leaves (Table 1).

N and P concentrations in basal leaves of *Heracleum platytaenium* exhibited significant differences among topographic positions and over the growing season. There were no significant differences in stem leaves during the

Table 1. Comparison of SLM values (± 1 S.E.) during mid-growing season and after abscission in basal and stem leaves by one-way ANOVA. NS = not significant.

Leaf type	SLM (g m ⁻²)	F	P
Mid-growing season basal leaves	90.74 \pm 4.95	0.340	0.563 NS
Abscised basal leaves	86.75 \pm 4.71		
Mid-growing season stem leaves	31.18 \pm 2.15	0.219	0.643 NS
Abscised stem leaves	29.88 \pm 1.74		

growing season, although significant differences were observed in stem leaves along the elevation gradient (Table 2).

Absolute N resorption of basal leaves varied significantly along the elevation gradient and was 1.3–3 times greater in slope topographic positions (300 and 600 m) than in the lower or upper positions (Table 3). Except for this, absolute P and proportional N and P resorptions in basal leaves and absolute and proportional N and P resorptions of stem leaves did not change significantly along the elevation gradient. N and P absolute and proportional resorptions were usually greater in the slope or upper topographic positions, especially at 300 and 600 m, as compared to lower topographic positions (Table 3).

There were significant differences between basal and stem leaves in respect to resorption

(Table 4). N and P concentrations of basal leaves declined during May, then further decreased in June and increased through July. Basal and stem leaves followed different patterns during the growing season in respect to N and P concentrations (Figs. 1–4). *Heracleum platytaenium* grows on sandy-loamy soils. Soil N and P concentrations were usually high and soil N concentrations were quite high in slope topographic position (300 m), but low in lowland positions, and soil P concentrations were low especially in upland positions. There were significant differences along the elevation gradient in soil N, P and soil moisture and soil N and P concentrations at slope topographic positions were different from upper and lower topographic positions according to Tukey's HSD test (Table 5).

Root/shoot ratio did not vary significantly along the elevation gradient. However, sig-

Table 2. Variance analysis on the basis of N and P concentrations (mg g^{-1}) of basal and stem leaves by two-way ANOVA; df = degrees of freedom; ** = $P < 0.01$; NS = not significant.

Leaf type	Nutrient (mg g^{-1})	Source	df	F	P
Basal	N	Elevation	3	4.17	0.009 **
Basal	N	Growing season	3	16.40	0.000 **
Basal	N	Error	73	–	–
Stem	N	Elevation	3	4.79	0.007 **
Stem	N	Growing season	1	2.05	0.161 NS
Stem	N	Error	15	–	–
Basal	P	Elevation	3	7.65	0.000 **
Basal	P	Growing season	3	11.47	0.000 **
Basal	P	Error	73	–	–
Stem	P	Elevation	3	12.85	0.000 **
Stem	P	Growing season	1	0.569	0.569 NS
Stem	P	Error	35	–	–

Table 3. Absolute (mg g^{-1}) and proportional (%) resorption along the elevation gradient in basal and stem leaves. Standard errors are given in parentheses. Means followed by the same letter are not significantly different at the 0.05 level when tested with Tukey's HSD test. * = $P < 0.05$; NS = not significant.

Leaf type	Nutrient	Resorption type	Lowland (30 m)	Slope (300 m)	Slope (600 m)	Upland (900 m)	F	P
Basal	N (mg g^{-1})	Absolute	0.54 (0.21) b	1.71 (0.28) a	1.09 (0.33) ab	0.80 (0.20) b	3.583	0.037 *
Basal	P (mg g^{-1})	Absolute	1.16×10^{-2} (3.29×10^{-3}) a	3.48×10^{-2} (9.63×10^{-3}) a	1.56×10^{-2} (5.42×10^{-3}) a	1.68×10^{-2} (7.90×10^{-3}) a	2.175	0.131 NS
Stem	N (mg g^{-1})	Absolute	0.55 (0.14) a	0.39 (0.11) a	0.44 (0.25) a	0.22 (0.10) a	0.702	0.565 NS
Stem	P (mg g^{-1})	Absolute	9.80×10^{-3} (1.98×10^{-3}) a	1.64×10^{-2} (9.19×10^{-3}) a	1.08×10^{-2} (3.83×10^{-3}) a	8.20×10^{-3} (2.47×10^{-3}) a	0.465	0.711 NS
Basal	N (%)	Proportional	28.97 (7.29) a	54.10 (6.72) a	48.83 (12.19) a	32.12 (6.82) a	2.072	0.144 NS
Basal	P (%)	Proportional	37.68 (7.39) a	56.69 (8.80) a	32.05 (9.81) a	34.73 (13.17) a	1.242	0.327 NS
Stem	N (%)	Proportional	26.22 (6.27) a	16.71 (4.67) a	20.71 (11.52) a	11.73 (5.75) a	0.664	0.586 NS
Stem	P (%)	Proportional	23.85 (4.79) a	24.18 (13.10) a	27.58 (8.31) a	22.37 (6.89) a	0.062	0.979 NS

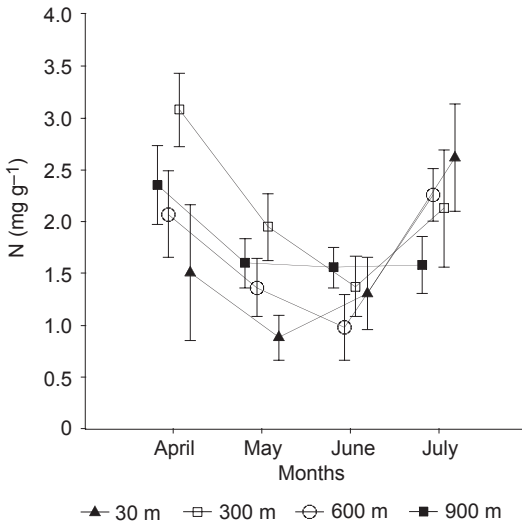


Fig. 1. Changes in nitrogen concentrations of basal leaves during growing season (mean \pm 2 SE, $n = 5$).

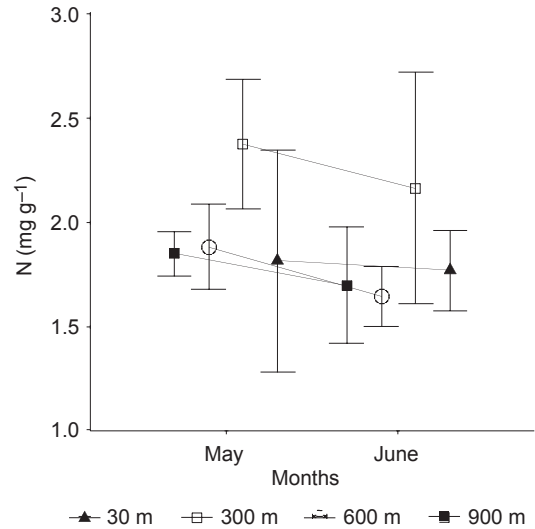


Fig. 2. Changes in nitrogen concentrations of stem leaves during growing season (mean \pm 2 SE, $n = 5$).

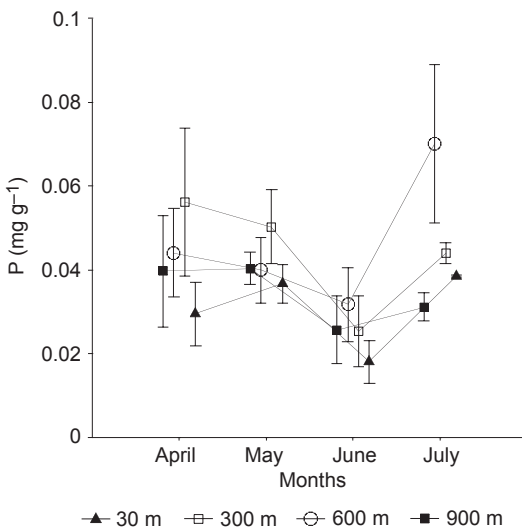


Fig. 3. Changes in phosphorus concentrations of basal leaves during the growing season (mean \pm 2 SE, $n = 5$).

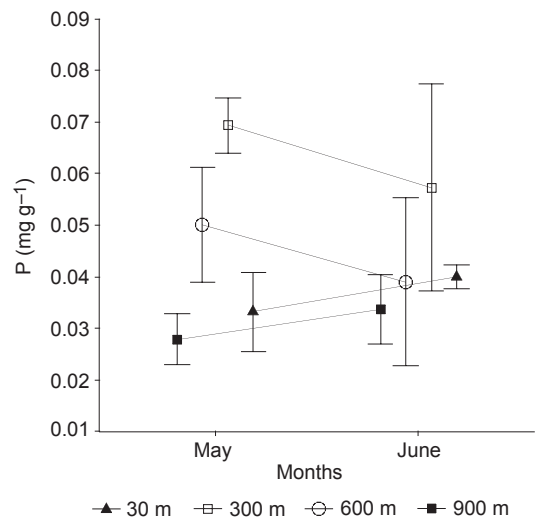


Fig. 4. Changes in phosphorus concentrations of stem leaves during the growing season (mean \pm 2 SE, $n = 5$).

nificant differences were observed during the growing season (Table 6). Root/shoot ratio was comparatively low at the beginning of the growing season and increased towards the end of the growing season (Fig. 5). Significant correlations were observed among N concentration in basal and stem leaves, absolute and proportional resorption, and soil moisture (Table 7 and 8).

Table 4. Comparison of basal and stem leaves on the basis of foliar resorption. NS = not significant; * = $P < 0.05$; ** = $P < 0.01$.

Nutrient	<i>F</i>	<i>P</i>
Absolute N	12.374	0.001 **
Proportional N	14.076	0.001 **
Absolute P	3.402	0.073 NS
Proportional P	5.844	0.021 *

Discussion

Significant differences were observed in basal and stem leaves with respect to foliar N and P concentrations along the elevation gradient. Our results agree with previous studies (Boerner 1984, Kost & Boerner 1985) that have shown higher foliar N concentrations in more fertile sites. High foliar N concentration was found in slope topographic positions (300 m) where soil N was higher. We also found significant differences in N and P concentrations in basal leaves during the growing season, although foliar N and P concentrations did not vary significantly during the growing season in stem leaves. The lack of significant differences in N and P concentrations during the growing season in stem leaves may be due to the short life span (two months) of stem leaves. At the beginning of June fruits appeared and stem leaves shrivelled up, so both N and P concentrations rapidly decreased in June in stem leaves. N and P concentrations decreased during June and increased again in July in basal leaves. The increasing N and P concentrations in basal leaves may be due to the shrivelling up of stem leaves in June and transferring of nutrients to the basal leaves in July. Similar results have been found for other *Heracleum* species (Pyšek & Pyšek 1995, Otte & Franke 1998).

It has been reported that mean proportional resorption rates for deciduous shrub and herb species are 54% for N and 52% for P (Aerts 1996). Proportional resorption rates in stem leaves were lower than those mean rates. However, proportional resorption rates in basal leaves especially in slope positions were within the ranges reported for deciduous shrubs and herbs.

Del Arco *et al.* (1991) reported that lowered moisture may reduce resorption, especially of nitrogen. In the present study absolute and proportional N resorption in basal and stem leaves is lower in upper topographic positions where moisture was lower as compared to lowland and slope positions.

De Mars and Boerner (1997) showed that low soil P availability in lowland sites may necessitate greater P conservation and hence higher resorption of P in herbaceous understory plants. However, in the present study P resorption in lowland positions was usually low because soil P availability was comparatively high.

Absolute N resorption in basal leaves was different at 300 m as compared with that at 30, 600 and 900 m, respectively. However, absolute P resorption, proportional N and P resorptions in basal leaves, and both absolute and proportional N and P resorptions in stem leaves were not statistically different among elevations. The lack of significant differences in N and P resorption may simply result from inefficient resorption of N and P in the upland and lowland topographic positions, as compared to slope positions.

Absolute and proportional P resorptions in basal and stem leaves were usually greater at 300 m where soil moisture was higher than in upland positions. Hocking (1982), Kost and Boerner (1985), and del Arco *et al.* (1991) stated that soil moisture is higher in slope topographic positions. There were significant correlations between absolute and proportional foliar resorptions and soil moisture, similar to those reported in other studies (Hocking 1982, Kost & Boerner 1985, del Arco *et al.* 1991).

Strong positive correlations were found between foliar N and P concentrations and abso-

Table 5. Mean values for soil parameters along the elevation gradient and comparison of soil parameters by one-way ANOVA test. Standard errors are given in parentheses. Means followed by the same letter are not significantly different at the 0.05 level when tested with Tukey's HSD test. ** = $P < 0.01$.

Soil parameter	Lowland (30 m)	Slope (300 m)	Slope (600 m)	Upland (900 m)	F	P
N (mg g ⁻¹)	0.27 (2.85 × 10 ⁻²) c	0.59 (9.48 × 10 ⁻³) a	0.46 (1.40 × 10 ⁻²) b	0.55 (2.44 × 10 ⁻³) a	73.553	0.001 **
P (mg g ⁻¹)	4.00 × 10 ⁻² (8.36 × 10 ⁻⁴) b	5.66 × 10 ⁻² (2.83 × 10 ⁻³) a	3.70 × 10 ⁻² (8.36 × 10 ⁻⁴) b	2.48 × 10 ⁻² (1.90 × 10 ⁻³) c	52.413	0.003 **
Moisture (cm ³ H ₂ O/ 100 cm ³ soil)	67.00 (2.14) a	61.80 (1.71) a	54.40 (0.24) b	54.40 (0.24) b	19.760	0.001 **

lute N and P resorptions. Chapin and Kedrowski (1983) found a positive correlation between the N concentration of mature leaves and N resorption. However, they did not find a correlation between P resorption and leaf P concentration. They suggested that leaf N concentration may partially control leaf N resorption, but that P resorption was not controlled by leaf P concentration. Several other authors have arrived at conflicting conclusions, in both intraspecific (Turner & Olson 1976, Shaver & Mellilo 1984) and interspecific comparisons (Chapin & Kedrowski 1983, Ralhan & Singh 1987, del Arco *et al.* 1991). Clearly, further investigation in this area is needed.

Individuals growing on nutrient-rich sites may have larger absolute and proportional resorptions of foliar nutrients, since their mature leaves are likely to have higher concentrations of nutrients, of which a greater proportion is in hydrolyzable form (Mayor & Roda 1992). However, we did not find a consistent pattern in this respect. For example, absolute and proportional N resorptions in stem leaves were higher at lowland positions where soil nitrogen concentration was quite low, while absolute and proportional N resorptions in basal leaves were higher in slope positions (300 m) where soil N was high. Our data on soil P and absolute and proportional P resorptions also support that hypothesis. Soil P concentrations in upland positions were rather low in the present study, although P concentrations can be high in lowland and slope positions. High absolute and proportional P resorptions were observed in slope positions (especially at 300 m) in stem and basal leaves where soil P concentrations were high. Several other studies

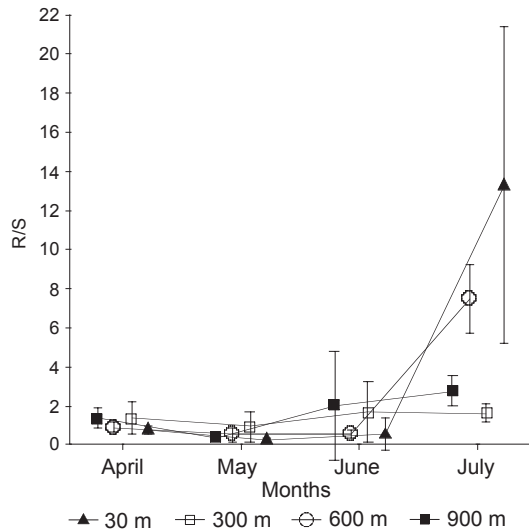


Fig. 5. Changes in root/shoot ratio during the growing season (mean \pm 2 SE, $n = 5$).

have shown that a relationship between resorption and soil fertility is not consistently present (Chapin 1980, Chapin & Kedrowski 1983, Ralhan & Singh 1987, del Arco *et al.* 1991, De Mars & Boerner 1997, Knops & Koenig 1997) and nutrient resorption probably reflected topographic differences in moisture rather than in

Table 6. Variance analysis on the basis of root/shoot ratio by two-way ANOVA; df = degrees of freedom; NS = not significant; ** $P < 0.01$.

Source	df	F	P
Elevation	3	2.02	0.118 NS
Growing season	3	13.57	0.002 **
Error	73	—	—

Table 7. Pearson correlation coefficients between foliar N and P concentrations (mg g^{-1}) and foliar resorption. ** $P < 0.01$.

Parameter	Correlation coefficient
N concentration in basal leaves and absolute N resorption in basal leaves	-0.680 **
N concentration in basal leaves and proportional N resorption in basal leaves	0.805 **
N concentration in stem leaves and absolute N resorption in stem leaves	-0.920 **
N concentration in stem leaves and proportional N resorption in stem leaves	0.596 **
P concentration in basal leaves and absolute P resorption in basal leaves	-0.591 **
P concentration in basal leaves and proportional P resorption in basal leaves	0.788 **
P concentration in stem leaves and absolute P resorption in stem leaves	0.817 **
P concentration in stem leaves and proportional P resorption in stem leaves	-0.698 **

fertility. Soil moisture varied significantly along the elevation gradient in the present study, and there were significant relationships between soil moisture and absolute and proportional N and P resorptions in basal and stem leaves.

In view of complexity of the interactions among various factors, the relationship of nutrient resorption from the senescing leaves to factors such as species adaptation to soil fertility are likely to be rather weak and uncertain.

There is a general tendency both between and within species to maintain a characteristic relationship between root and shoot dry weights, e.g. graminaceous species \geq trees (Marschner 1995). At the beginning of the growing season root/shoot ratio was comparatively low in *Heracleum platytaenium*. Low root/shoot ratio is believed to maximize growth in light-limited habitat and thus confer shade tolerance (De Lucia et al. 1998). *Heracleum* species usually inhabit light-limited habitats (Otte & Franke 1998).

However, root/shoot ratio increased towards the end of the growing season and this may be due to the allocation of photosynthates to below-ground parts like in other monocarpic plants (Marschner 1995). *Heracleum platytaenium* shows monocarpic senescence, in which the death of the vegetative plant parts is closely linked to fruit maturation and nutrients can be exported from senescing organs and translocated

to sinks (e.g. vegetative storage organs, developing leaves or fruits) and this redistribution is highly important for the economical use of nutrients (Feller & Fischer 1994).

N and P concentrations of basal leaves increased during July. In other words, accretion was observed in basal leaves of *Heracleum platytaenium* on the basis of seasonal patterns of N and P. In monocarpic *Heracleum* species senescence is caused by the depletion of nutrient and energy reserves, the vegetative organs competing with the generative organs for the remaining nutrients (Otte & Franke 1998). At the beginning of July the fruits of *H. platytaenium* were mature and basal leaves may have accumulated nutrients from the generative parts.

Chapin and Kedrowski (1983) also hypothesized that important interspecific differences were observed in retranslocation of forest understory species and accretion may also occur in forest understory species due to some factors, namely soil moisture levels. Boerner (1985) found that foliar P concentrations in *Hamamelis virginiana* increased until the onset of litter fall. In the present study high correlation coefficients were observed between resorption and soil moisture. For three populations of understory plants, growth and nitrogen dynamics were strongly correlated with soil moisture levels (Boerner 1985). Accretion may also be explained on the basis that the soil N and P are not limiting factors for the studied species, thus, root/shoot ratio increased towards the end of the growing season in *H. platytaenium*.

N and P are translocated from senescing stem leaves to basal leaves and remain there until abscission. Soil N and P concentrations were usually high; low N concentrations were observed in lowland plots and low P concentrations in upland plots. Soil moisture may also play a regulating or modifying role in seasonal nutrient patterns and nutrient use efficiency (Boerner 1985).

A negative correlation was found between soil N concentration in July and root/shoot ratio in July ($r = -0.566$). Marschner (1995) hypothesized that root/shoot ratio increases in wild plants as soil fertility decreases.

In summary, foliar resorption was usually higher in slope topographic positions and it was not significantly changed along the elevation gradient, except for absolute N resorption in

Table 8. Pearson correlation coefficients between absolute and proportional resorption and soil moisture. ** $P < 0.01$.

Parameter	r
Absolute N resorption in basal leaves and soil moisture	0.989 **
Proportional N resorption in basal leaves and soil moisture	-0.525 **
Absolute N resorption in stem leaves and soil moisture	0.989 **
Proportional N resorption in stem leaves and soil moisture	0.862 **
Absolute P resorption in basal leaves and soil moisture	-0.990 **
Proportional P resorption in basal leaves and soil moisture	-0.503 **
Absolute P resorption in stem leaves and soil moisture	0.990 **
Proportional P resorption in stem leaves and soil moisture	0.795 **

basal leaves. Soil fertility significantly varied along the elevation gradient. We did not find a consistent pattern between foliar resorption and soil fertility, and thus our study does not support the hypotheses that individuals growing on nutrient-rich sites may have larger absolute and proportional resorption of foliar nutrients. Instead, there was a clear relationship between foliar resorption and foliar N and P concentrations and soil moisture. Foliar resorption values in basal leaves were similar to the values previously reported for deciduous shrubs and herbs, but the resorption values in stem leaves were lower.

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