Population age structure and reproductive behavior of the monocarpic perennial Heracleum mantegazzianum (Apiaceae) in its native and invaded distribution ranges[1]

Jan Pergl,[2,5] Irena Perglová,[2] Petr Pyšek,[2,3] and Hansjörg Dietz[4]

[2]Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic; [3]Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 01 Praha 2, Czech Republic; and [4]Institute of Integrative Biology ETH, Universitätsstrasse 16, CH-8092 Zürich, Switzerland

Many invasive species are benign in their native region—are there interactions between their key traits and the new habitats that explain invasion success? The giant perennial herb *Heracleum mantegazzianum* is a problematic invader in Europe and is also naturalized in North America. We compared its population structure and reproductive behavior in the native (W. Caucasus) and invaded (Czech Republic) areas in managed (pastures) and unmanaged sites. The age structure of the populations and age at flowering were analyzed using herb-chronology, a method based on counting annual rings in the secondary xylem of roots. The species was strictly monocarpic; most plants in unmanaged sites in the invaded range flowered in the third and fourth yr (maximum 12 yr). In unmanaged habitats, plants from the native range flowered later than those from the invaded range. In both ranges, flowering was delayed in managed sites where the population density was higher and most plants flowered around the fifth year. Reproductive output of individual plants was neither related to population density nor to age at flowering. More favorable climatic conditions in the invaded region, together with increased chances for dispersal in a densely colonized central Europe, seemed to allow the massive invasion.

Key words: biogeography; Caucasus; Czech Republic; demography; habitat type; *Heracleum mantegazzianum*; herb-chronology; invasive alien plant.

Biological invasions, that is, the spread of introduced species into non-native areas, rank among the most important factors and consequences of global change, threatening native biodiversity (Dukes and Mooney, 1999). It is, therefore, imperative to gain a thorough understanding of the mechanisms underlying biological invasions and the key traits of invasive species for informed management decisions. A promising direction for studying the characteristics of invasive species (sensu Richardson et al., 2000; Pyšek et al., 2004) is to compare their behavior in the native and introduced ranges. This biogeographical approach is important for understanding the principles underlying plant invasions (for a review, see Hierro et al., 2005), yet it has been rarely used. For example, it has been suggested that alien species escape from their specialized herbivores and enemies, which may increase their performance in the new region (Keane and Crawley, 2002; Wolfe, 2002) or may even result in the evolution of increased competitive ability (Blossey and Nötzold, 1995; Blair and Wolfe, 2004; Rogers and Siemann, 2004). In their native

regions, several species have been reported to grow at lower population densities (Bastlová-Hanzélyová, 2001), produce fewer seeds (Noble, 1989; Rees and Paynter, 1997), have lower growth rates, and are smaller (Blossey and Nötzold, 1995; Bastlová-Hanzélyová, 2001; Siemann and Rogers, 2001; Jakobs et al., 2004), although these patterns are not always consistent (Thébaud and Simberloff, 2001; Agrawal and Kotanen, 2003; Hierro et al., 2005).

It is particularly important to investigate possible differences in the reproductive behavior of species between their native and introduced ranges because reproductive traits have often been identified as crucial for the invasion success of introduced plants (Baker, 1965; Noble, 1989; Roy, 1990; Saxena, 1991; Rejmánek, 1996; Rejmánek and Richardson, 1996; Pyšek, 1997). Invasive plants that are unable to reproduce vegetatively depend entirely on seed production (Pyšek, 1997; Moravcová et al., 2005). In these species, timing of flowering and life span are particularly important traits for successful naturalization and spread (Baker, 1965; Noble, 1989; Roy, 1990; Saxena, 1991; Rejmánek, 1996). Species that adopt a monocarpic strategy are convenient study subjects from an evolutionary point of view, as the 'decision' of when to flower involves a trade-off between flowering as early as possible vs. accumulating more resources leading to a higher seed set, but with an increased risk of dying before reproduction (Childs et al., 2003; Metcalf et al., 2003). The strategy thus depends on the balance between the risk of death and the profit from delayed reproduction and differs between distinct habitat conditions or management regimes (Bullock et al., 1994; Crawley, 1997). Hence, the time of reproduction in monocarpic plant species seems to be more closely related to developmental stage or plant size than to plant age (Harper, 1977; Gross, 1981; Kachi and Hirose, 1985; Lacey, 1986; Crawley, 1997).

However, the important question remains whether there are differences among habitats in the plant age at which sufficient

size for flowering is attained. Habitat conditions that are conducive to rapid growth and hence early attainment of the threshold size for flowering may be particularly important for the invasion process in introduced monocarpic perennials. The recently developed method of herb-chronology (analysis of annual rings in the secondary root xylem of perennial forbs) allows efficient age determination in perennial forbs that have annual rings in the permanent main roots (Dietz and Ullmann, 1997, 1998; Dietz, 2002; von Arx and Dietz, 2006). Therefore, the use of this method makes it possible to relate individual age directly to reproductive investment in invasive perennial forbs.

The present study provides the first information on the age at which the monocarpic invasive species *Heracleum mantegazzianum* flowers and sets seed in the native and invaded distribution ranges and compares reproductive output and other related population characteristics between both ranges. *Heracleum mantegazzianum* is one of the major plant invaders in Europe (Tiley et al., 1996). Despite an increasing number of studies that have helped to reconstruct its invasion history (Pyšek, 1991, 1994; Pyšek et al., 1998; Müllerová et al., 2005) and contributed to understanding its biology and ecology (Pyšek et al., 1998; Moravcová et al., 2005; Krinke et al., 2005), there is virtually no information about the biology and behavior of this species in its native range. The only exceptions are studies associated with the use of the *Heracleum* species as agricultural crops, without any relevance to invasion dynamics (Satsyperova, 1984). Although grazing has been recommended to control invasive populations of *H. mantegazzianum* (Nielsen et al., 2005), its effect on the life cycle and demography of this species remains unknown. The need for studying plant invasions in relation to grazing is further accentuated by the fact that the effect of grazing on alien species may vary and does not always lead to their suppression (Petryna et al., 2002; Kimball and Schiffman, 2003; Dorrough et al., 2004)

By studying the population structure and reproductive effort of *H. mantegazzianum* among distinct habitats in its native (Caucasus) and invaded (Czech Republic) distribution ranges, we aimed to answer the following questions: (1) Does the population age structure and the related age at flowering of *H. mantegazzianum* differ between the native and the invaded ranges? (2) Is reproductive output related to age at flowering? (3) How do these patterns vary between managed and unmanaged habitats in the two ranges?

MATERIALS AND METHODS

Study species—The monocarpic perennial *Heracleum mantegazzianum* Sommier et Levier (Apiaceae, Giant hogweed) is the tallest herbaceous species in Europe; it reaches 200 to 500 cm in height with leaves up to 300 cm long. The plant develops a thick but relatively soft, permanent taproot with an additional two to five parallel vertical roots, which usually develop in the following years and eventually give rise to a flowering stem that may reach up to 15 cm in diameter. The flowers (compound umbels of four orders; Moravcová et al., 2005) are insect-pollinated and protandrous, but self-fertilization within the same plant and the same umbel is possible (Perglová et al., 2006). *Heracleum mantegazzianum* produces a large number of fruits, which split into two-winged mericarps, each containing one seed (Moravcová et al., 2005). Estimates of seed production range from 5000 to more than 100 000 seeds per plant (Pyšek et al., 1995; Tiley et al., 1996), however, the values of 10 000–20 000 seem to be the most common average in Europe, with maxima occasionally reaching around 50 000 fruits (Perglová et al., 2006). *Heracleum mantegazzianum* reproduces exclusively by seed and forms a short-term persistent seed bank. A small proportion (less than 3%) of the seeds remain viable in the soil for at least 2 years (Krinke et al., 2005). Seeds released

from parent plants are morphophysiologically dormant; i.e., a period of embryo growth is required and dormancy is broken by wet and cold conditions over winter. After dormancy is broken, the germination rate is about 90% regardless of where on the parent plant the seeds were produced (Moravcová et al., 2005).

Heracleum mantegazzianum is native to meadows, clearings, and forest margins at higher altitudes in the western Caucasus (Russia, Georgia) (Mandenova, 1950) where it grows in species-rich, tall-herb mountain meadows up to the treeline (at ca. 2000 m). Due to its size and exotic appearance, it became popular as a garden ornamental and was introduced to many European countries. Now it is naturalized or invasive in many European countries and central Russia (Tiley et al., 1996; Nielsen et al., 2005). It is also naturalized in Canada and the United States (Morton, 1978; Ochsmann, 1996; Kartesz and Meacham, 1999). The first record in the Czech Republic dates back to 1862 (chateau in Lázně Kynžvart in W. Bohemia). In later years, it spread spontaneously across the country and became invasive (Pyšek, 1991; Pyšek and Pyšek, 1995; Pyšek et al., 2002; Müllerová et al., 2005). The species often develops large stands (Müllerová et al., 2005), dominates invaded sites, and replaces the native vegetation (Pyšek and Pyšek, 1995; Tiley et al., 1996). Besides threatening biodiversity and landscape management in the invaded area, its phytotoxic chemicals can harm humans and livestock (Drever and Hunter, 1970; Tiley et al., 1996). So far programs to control the spread of the species have only had limited success (Nielsen et al., 2005).

Study areas—The study was conducted in the Caucasus (native distribution range) and the Czech Republic (invaded distribution range). The study area in the Caucasus was located in the western part of the Russian territory (Fig. 1) between 570 and 1735 m a.s.l. (Table 1). Climatic data are only available for the localities in the Arkhyz area, but reasonably reflect the climate in the whole region; the January temperature varies between −36 and 16°C and the July temperature between −3 and 35°C. Total annual precipitation is 863 mm (30-yr average, Russian Hydrometeorological Institute). The study area in the Czech Republic was located in the Slavkovský les Protected Landscape Area, W. Bohemia (see Krinke et al., 2005 for details), in the vicinity of the first introduction of *H. mantegazzianum* to the country in 1862 (Pyšek, 1991). The altitudinal range of the study area is 370–980 m a.s.l. (Kos and Maršáková, 1997; Table 1). The climate is temperate with January temperatures between −5.1 and −0.2°C (min/max) and July temperatures between 10.5 and 21.5 °C. The total annual precipitation is 1094 mm (Mariánské Lázně meteorological station, 50-yr average). Strong invasion of the region by *H. mantegazzianum* started in the 1940s, following an 80-yr lag phase (Pyšek and Prach, 1993). Now extensive areas are heavily infested by the species (Müllerová et al., 2005).

In both study areas, populations of *H. mantegazzianum* were sampled in unmanaged and managed habitats. Unmanaged habitats in the Caucasus are mountain meadows or former clearings located between the altitudes of 900-1700 m a.s.l. and harboring tall-herb communities. To simplify comparisons between ranges, we use the term unmanaged for possibly natural sites of the species (Mandenova, 1950; Tiley et al., 1996) as well as for sites where humans created forest clearings and left them without further management. The species does not form dense stands in these habitats in Caucasus but rather populations of scattered plants in species-rich communities with *Angelica purpurascens*, *Cirsium* sp., *Dactylis glomerata*, *Petasites* sp., *Pulmonaria* sp., *Rumex alpinus*, and *Telekia speciosa* as dominant species (J. Pergl and I. Perglová, unpublished data). In submontane areas of the Caucasus, *H. mantegazianum* spreads into river valleys, abandoned fields, and pastures. Six pastures, located between 500-1300 m a.s.l., were included as managed habitats in the native range. At these sites, the cover of *H. mantegazzianum* was higher than at the unmanaged sites (Table 1). In each region, the study sites were distributed so as to cover the range of variation in environmental conditions and management. Within the Czech Republic, unmanaged sites were grasslands and abandoned settlements and their surroundings; these sites were located where populations have been developing undisturbed for several decades (Müllerová et al., 2005). In both areas studied, managed habitats were cattle and sheep pastures, but grazing was more intensive and regular in the Czech Republic (pastures are fenced and overgrazed three times a year) than in Caucasus where extensive grazing is traditionally applied (smaller droves of livestock or individual animals move freely in unfenced areas). In both managed and unmanaged habitats in the Czech Republic, *H. mantegazzianum* forms dense stands with a more or less closed canopy (Table 1).

Population sampling—Six sites (populations) were sampled for each combination of distribution range (native/invaded) and habitat type (managed/unmanaged) during 2003 and 2004 (Table 1). To cover a wider range of habitat
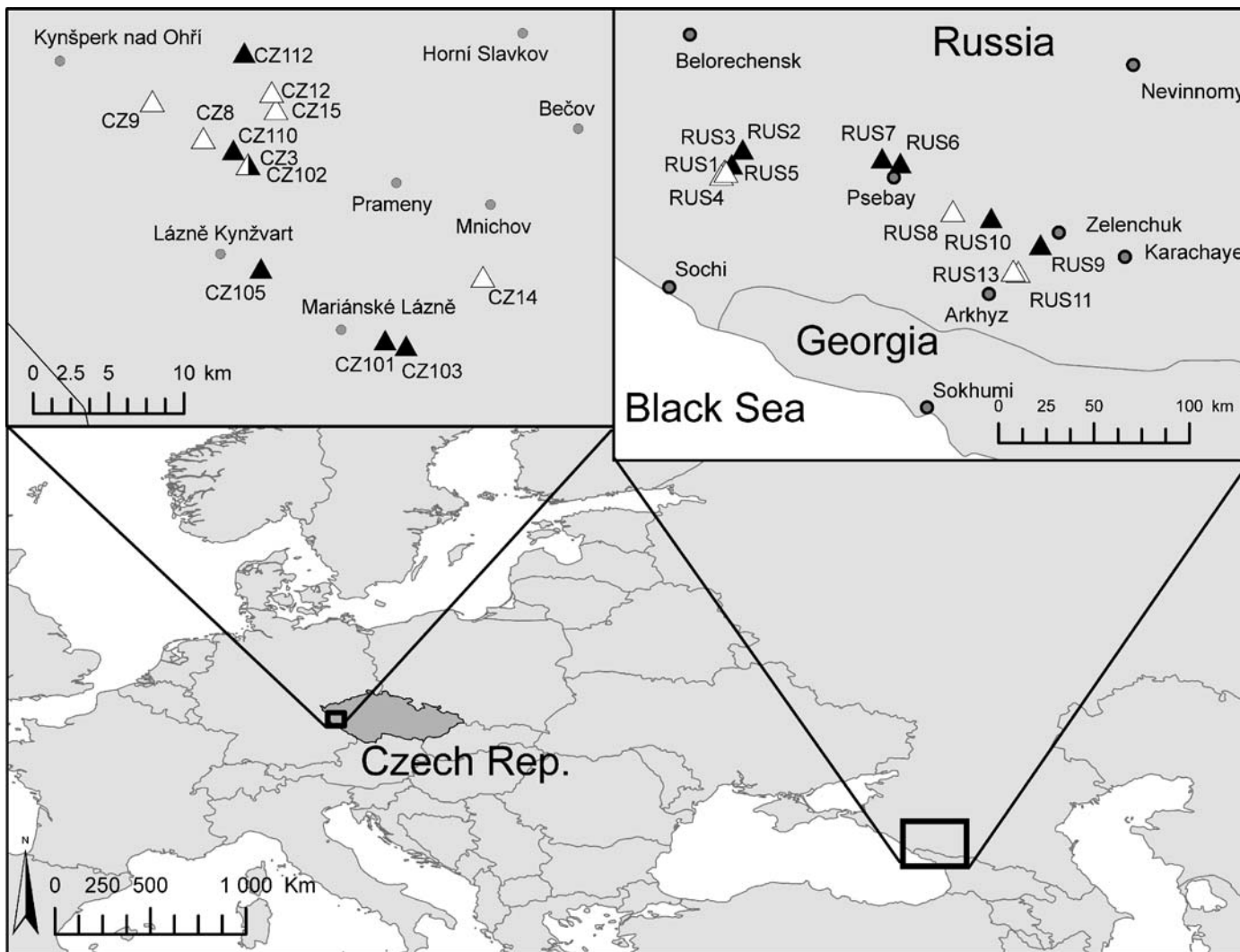
Fig. 1. Location of the study areas in the native (Caucasus) and invaded (Czech Republic, Central Europe) distribution ranges; ▲ managed, △ unmanaged habitats.

conditions in which the species occurs (Krinke et al., 2005; Moravcová et al., 2005; Pergl et al., 2006), an additional site was sampled in the Czech Republic, but not used in analyses because it was on extremely dry soil. Because soil properties have been reported to affect the age of flowering in some species (Crawley, 1997), representative soil samples were taken in each study site and analyzed using standard methods for pH_{H20}, pH_{KCl}, content of Mg, Ca, K, P, and percentage of N and C (Page et al., 1982; Moore and Chapman, 1986). Soil samples were collected at 10–20 cm depth, air-dried, sieved (2 mm mesh sieve), and stored in paper bags. Although the soil parameters varied largely among sites (data not shown), we did not find any significant relationships with the investigated population parameters of *H. mantegazzianum* and therefore did not use them in further analyses.

Whenever possible, we sampled the central part of the population at each site to minimize edge effects. The area used for sampling was small relative to the overall extent of the populations. Therefore, for low-density populations, there were no differences between the edge and inner parts, so that the bias due to possible edge effect could be avoided. We established a plot of a minimum size of 1 m^2 within which all plants with leaves larger than 5 cm were recorded. This size threshold was set to avoid collecting plants that had germinated in the year of sampling. The sampling area was gradually extended to 2, 4, 6, 9, 12, and 16 m^2, respectively, until at least 30 plants (vegetative or flowering) were included. To measure the density of vegetative and flowering plants in very sparse populations, the position of individual plants was mapped without plots, using tape and *x* and *y* coordinates. If the number of flowering plants within the

plots was below 10, we collected flowering individuals from the nearest neighborhood of the plot until the sample size of 10 individuals was reached. Only at the RUS 5 site was the number of plants too low to sample 30 individuals. In each population, we recorded the population density and determined the age, stage, and the reproductive score (vigor) of each sampled individual. Plants from the neighborhood were not considered in analyses related to the density and age structure of populations.

In late July and August, we determined individual age by means of herb-chronology, i.e., analysis of annual rings in the secondary root xylem of perennial forbs (Fig. 2; Dietz and Ullman, 1997; Dietz and Schweingruber, 2002). For this the primary (main) root of each sampled plant was obtained from at least 15 cm below the top of the root. Only the core (xylem) part of the root was collected, stored in a cold environment, and analyzed within the next 3 days. Thin cross-sections of the root xylem were cut 10 cm from the root crown. Annual rings were counted immediately after staining the cuttings with phloroglucinol-HCl (Dietz and Ullman, 1997). A minimum of two sections was analyzed for each plant. To verify the results from the field, annual rings were also analyzed in plants of known age that were grown from seedlings in the experimental garden of the Institute of Botany, Průhonice, since 2002. In these plants annual rings were reliably formed, confirming the annual nature of root rings in *H. mantegazzianum*.

For technical reasons, it was impossible to count the number of fruits of *H. mantegazzianum* in the field. We therefore developed an alternative approach to determine and compare the reproductive vigor of the plants. The complex

TABLE 1. Location and characteristics of study sites and population parameters for *Heracleum mantegazzianum* in its native (RUS, Caucasus) and invaded (CZ, Czech Republic) distribution ranges. Habitat type: man = managed, unm = unmanaged. Analyzed plants: Veg = vegetative, Flow = Flowering. na = not available.

Location	Region	Latitude (N)	Longitude (E)	Altitude (m a.s.l.)	Habitat type	Population density (plants/m²)	Median plant age (maximum)	No. analyzed plants		Mean reproductive score (±SD)
								Veg	Flow	
RUS2	Lago-Naki	44°14′	40°07′	877	man	3.7	5 (6)	20	13	—
RUS3	Lago-Naki	44°10′	40°04′	1285	man	4.2	5.5 (7)	20	10	—
RUS6	Psebay	44°10′	40°52′	572	man	8.5	4 (5)	29	13	—
RUS7	Psebay	44°11′	40°46′	672	man	2.9	3.5 (4)	28	10	—
RUS9	Arkhyz	43°47′	41°31′	1061	man	7.5	4 (5)	29	10	—
RUS10	Pregradna	43°55′	41°17′	943	man	3.2	4.5 (5)	20	12	—
RUS1	Lago-Naki	44°08′	40°02′	1431	unm	11.0	4 (6)	36	10	11.94 ± 1.87
RUS4	Lago-Naki	44°07′	40°01′	1465	unm	7.3	3 (4)	40	10	12.42 ± 1.75
RUS5	Lago-Naki	44°08′	40°02′	1455	unm	0.3	5 (7)	14	10	14.21 ± 2.54
RUS8	Pregradna	43°56′	41°07′	922	unm	5.5	3 (4)	21	10	10.65 ± 1.91
RUS11	Arkhyz	43°39′	41°25′	1735	unm	1.7	5 (6)	20	10	10.68 ± 1.13
RUS13	Arkhyz	43°04′	41°24′	1500	unm	0.6	4 (4)	23	10	15.43 ± 3.72
CZ102	Slavkovský les	50°40′	12°38′	790	man	12.3	5 (7)	61	10	—
CZ103	Slavkovský les	49°57′	12°44′	660	man	12.0	4 (5)	37	12	—
CZ105	Slavkovský les	50°00′	12°38′	630	man	9.0	5 (7)	48	13	—
CZ110	Slavkovský les	50°04′	12°37′	710	man	14.5	4 (5)	28	10	—
CZ111	Slavkovský les	50°04′	12°44′	778	man	12.0	5 (7)	48	10	—
CZ112	Slavkovský les	50°08′	12°37′	553	man	7.3	4 (5)	33	10	—
CZ3	Slavkovský les	50°04′	12°38′	788	unm	6.2	3 (4)	38	10	na
CZ8	Slavkovský les	50°05′	12°36′	643	unm	3.3	3 (4)	31	10	13.26 ± 2.04
CZ9	Slavkovský les	50°06′	12°34′	506	unm	6.5	3 (4)	28	10	13.14 ± 1.05
CZ12	Slavkovský les	50°06′	12°39′	596	unm	1.3	3 (3)	22	10	13.42 ± 1.51
CZ14	Slavkovský les	49°59′	12°46′	752	unm	3.8	3 (4)	34	10	13.23 ± 1.56
CZ15	Slavkovský les	50°06′	12°38′	596	unm	3.0	3 (4)	18	12	11.98 ± 1.44

Note: The reproductive score was not determined for plants in managed habitats because the levels of damage and regeneration of the aboveground plant mass varied. Codes for localities in the Czech Republic correspond to the numbering used in Moravcová et al. (2005) and Krinke et al. (2005).

flowering architecture of *H. mantegazzianum* (Tiley et al., 1996; Moravcová et al., 2005) results in each umbel contributing differently to the overall seed set. To estimate the reproductive output of individual plants, coefficients reflecting the relative importance of umbels of particular order were developed, based on seed production of umbels on 100 test plants studied in the field. The proportional contribution of the terminal umbel (first order), satellite and terminal umbels of branches (second order), and umbels of third order to overall seed set was 5 : 1 : 0.05 (I. Perglová, unpublished data). These co-efficients were summed for each plant yielding a reproductive score based on all umbels of all orders. The reproductive score was not determined for grazed plants on pastures because plants at different sites were in different stages of recovery from damage by grazing. This made it impossible to estimate the number of potential umbels and seeds produced.

Statistical analysis—All analyses were performed with S-PLUS (2001). We tested for differences in the age of flowering plants between distribution ranges and habitat types using factorial ANOVA with interactions. All six sites per range/habitat type combination were included in the analysis. Habitat type and distribution range were included as fixed factors. As sites in the native and invaded ranges as well as within habitat types differed in altitude (ANOVA; distribution range: $F_{1,20} = 5.687$, $P = 0.027$; habitat: $F_{1,20} = 24.422$, $P < 0.001$), its effect was filtered out from the model by replacing the age with residuals from a linear regression of the age on altitude ($F_{1,22} = 4.357$, $P = 0.048$). This approach was used due to the relatively small number of replicates within a group, compared to the number of tested factors. Preliminary analysis showed significant interactions between habitat types and sites nested within ranges that cannot be reasonably interpreted, so the age of flowering plants was averaged within sites to avoid the nested design. This allowed for simplifying the model without losing any important information. Means across sites were transformed by reciprocal transformation, which was checked for appropriateness by the Box-Cox method (Crawley, 2002) and by normal probability plots of the fitted values.

The effect of distribution range and habitat type on the proportion of flowering plants was tested using a two-way ANOVA. The proportion of flowering plants was calculated as their percentage of the total number of plants older than 1 year that were recorded within the sampling plot. Differences between frequency distributions of the ages at flowering were tested using multiple *G* tests with Bonferroni's correction (Zar, 1999).

Only unmanaged sites were used to analyze the reproductive score of flowering plants. Locality CZ3 was excluded from the analysis because of missing information on the number of umbels on plants. Data were analyzed using ANCOVA with site nested within distribution range and age of flowering plants included as a covariable. The minimal adequate model for the reproductive score was determined by using stepwise selection from the maximal model based on the Akaike information criterion (AIC). This method weighs the significance of a model by its complexity (Crawley, 2002).

For population density analyses, only individuals older than 1 year were used. Data were analyzed by two-way ANOVA with interactions, using the same set of populations as in the analysis on age at flowering. Distribution range and habitat type were included as fixed effects and the density of vegetative plants and number of flowering plants within a sample plot were used as response variables.

RESULTS

Population density—In most habitats in both ranges, the mean population density of *H. mantegazzianum* varied between 4 and 5 plants/m² (Table 2). In managed sites in the introduced range, the mean population density was significantly higher with 11 plants/m² (significant interaction between range and habitat type in their effect on population density; Table 3 and subsequent one-way ANOVA for each combination). The variation in density between unmanaged sites was remarkably high in the native area, ranging between 0.3 and 11 plants/m². Population density was not significantly related to altitude (regression on pooled data: $F_{1,22} = 2.07$, $P = 0.16$).
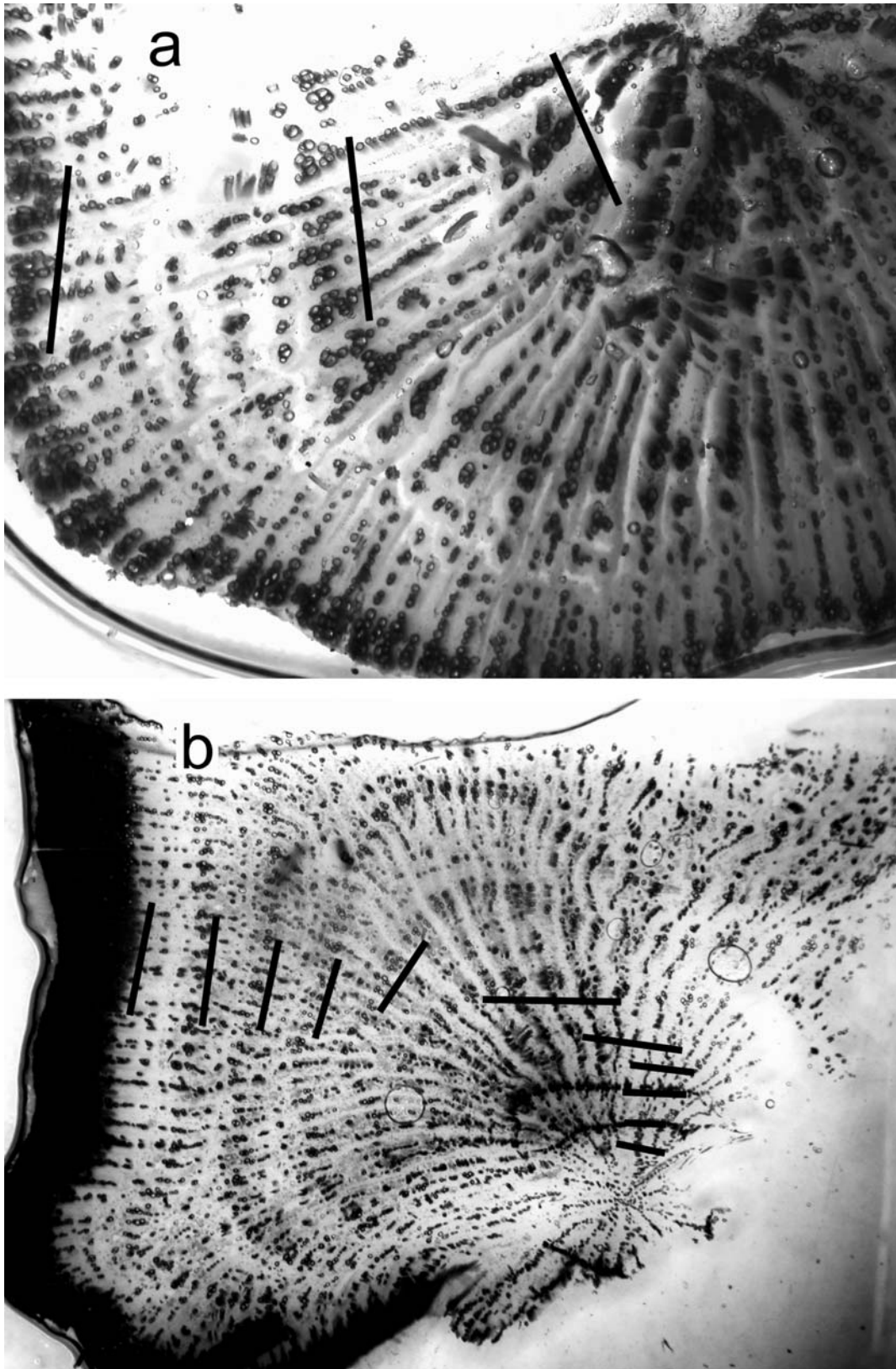
Fig. 2. Cross-sections of the root showing the annual rings in the secondary xylem of a (a) 4- and a (b) 12-yr-old individual. The markers indicate the transitions between latewood of the previous year and the earlywood of the following year.

TABLE 2.   Density of *Heracleum mantegazzianum* populations (individuals/m²) and age of flowering plants in different habitat types of the native and invaded distribution range. Population density includes both flowering and vegetative plants older than 1 year.

Distribution range	Habitat type	Population density (indiv/m²)		Age (yr)	
		Mean	SD	Median	Max
Native (Caucasus)	unmanaged	4.38	3.91	4	7
	managed	4.99	2.18	5	7
Invaded (Czech Republic)	unmanaged	4.58	1.86	3	4
	managed	11.17	2.37	5	7

Age of flowering plants—All 302 flowering plants of *H. mantegazzianum* that were aged were at least 3 years old. In unmanaged sites, the median age of flowering plants was 3 yr in the invaded and 4 yr in the native range, while in managed sites it was 5 yr, irrespective of the origin of the plants (Table 2). In unmanaged sites in both distribution ranges, relatively more plants flowered at the age of 3 yr than at any other age, and the number of flowering plants tailed off at increasingly higher ages. In managed sites, in contrast, the highest proportion of flowering plants was found among the 4- or 5-yr-old plants (Fig. 3). In unmanaged sites in the Czech Republic, the maximum age of flowering plants was 4 yr, while in managed sites in the Czech Republic as well as in both habitat types in Caucasus, it was 6 or 7 yr. The oldest flowering plant was 12 yr old, but it grew at the extremely dry, unmanaged locality in the Czech Republic (invaded range), which was not used in statistical analysis. The population in this site was clearly an outlier because the majority of plants flowered between the 5th and 8th year, in remarkable contrast to other unmanaged populations from the invaded range.

Because the interaction between habitats and ranges was significant (Table 3), the analysis was done separately for each habitat and range combination. Plants from unmanaged habitats in the native Caucasus region tended to flower at a later age than those growing in the corresponding habitats in the Czech Republic (subsequent one way ANOVA; $F_{1,10} = 8.74$, $P = 0.014$; Tables 2 and 3). Plants growing in the managed habitats in the invaded range lived longer, i.e., they flowered later than those in unmanaged habitats in the same range ($F_{1,10} = 24.06$, $P < 0.001$; Tables 2 and 3). There were no differences between unmanaged and managed habitats in the native distribution range ($F_{1,10} = 0.50$; $P = 0.50$), and managed habitats did not differ between ranges ($F_{1,10} = 0.0001$; $P = 0.99$). The difference in unmanaged habitats between distribution ranges was mediated through altitude because it disappeared once the altitude was filtered out. In this model, the habitat–range interaction became nonsignificant and so did distribution range ($P = 0.67$), while the significance level of habitat increased ($P = 0.001$; Table 3). This is an evidence for a strong effect of altitude on the age at flowering, although it was not possible to test this relationship directly because of a limited number of samples within groups (native sites are located at higher altitude and sites at comparable altitudes do not exist in the invaded range).

Age at flowering was not significantly related to population density as indicated by a regression ($F_{1,22} = 0.613$, $P = 0.442$).

The frequency distribution of age at flowering indicates that in managed sites the highest proportion of flowering plants occur at intermediate age (Fig. 3). In unmanaged sites, on the contrary, the proportion of flowering plants decreased with increasing age across the whole range of age classes. This holds for both distribution ranges, but the decrease is most profound in unmanaged sites of the invaded range. Proportions of flowering plants were significantly different among habitats within ranges as well as among ranges within habitats (all *G* tests were highly significant; $P < 0.001$). The proportion of flowering plants in the youngest age class in unmanaged sites in the Czech Republic and Caucasus was 89% and 31%, respectively.

Proportion of flowering plants—The percentage of flowering individuals among all individuals older than 1 year was rather similar across distribution ranges and habitats (Fig. 4). The mean values ranged from 16% in managed sites in the Czech Republic to 29% in managed sites in the Caucasus and were not significantly related to distribution range ($F_{1,20} = 0.118$), habitat type ($F_{1,20} = 0.434$), or their interaction ($F_{1,20} = 1.970$, $P = 0.176$).

The proportion of flowering plants in individual age classes (cohorts) increased with the age of the cohort (Fig. 4), and the pattern observed reflected the differences in the mean age at flowering, with postponed flowering of plants in the native range and managed habitats (Fig. 3). In the native range, nearly half of the plants in a population flowered in the 4th year, and this proportion increased to 62–75% and 88–100% in the subsequent age classes. The most remarkable difference between habitat types within the native range was in the 3rd year, with almost one third of plants in unmanaged sites flowering but with only 10% flowering in managed habitats. Managed sites in the invaded range harbored a consistently lower proportion of flowering plants up to the 7th year when the majority of plants in the population flowered. Unmanaged habitats in the invaded range had a pattern remarkably distinct from all other sites with flowering concentrated in the 3rd and 4th years when over a half of the plants flowered (Fig. 4).

TABLE 3.   Summary of ANOVA showing the effect of distribution range and habitat type on the density of populations and age of flowering plants of *Heracleum mantegazzianum*. The results for analysis of age cover the full model, and a model with altitude being held constant (see Materials and methods/Statistical analysis for details on statistical treatment).

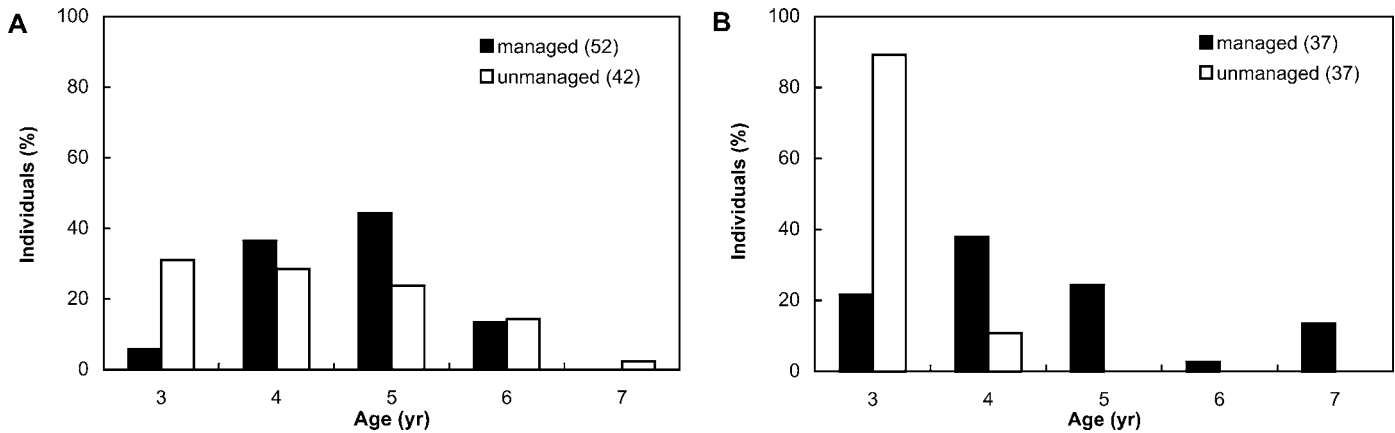| Source of variation	df	Population density			Age of flowering					
					Full model			Altitude held constant		
		MS	F	P	MS	F	P	MS	F	P
Habitat	1	90.13	10.37	0.004	0.0165	10.68	0.004	0.0262	23.06	<0.001
Range	1	50.79	5.84	0.025	0.0069	4.43	0.048	0.0002	0.16	0.670
Habitat × range	1	64.02	7.37	0.013	0.0067	4.35	0.050	0.0018	1.62	0.217
Error	20	8.69			0.0015			0.0011		

Fig. 3. Frequency distribution of age at flowering in managed and unmanaged habitats in the (A) native and the (B) invaded distribution range. Numbers in the key are sample sizes (number of individuals) at each site.

Variation in reproductive score with plant age—The reproductive scores of individual flowering plants in both distribution ranges varied between 9 and 15, corresponding to 10 000–25 000 seeds per plant. Selection toward the minimal adequate model (based on AIC) showed that reproductive score was not related to plant age. The reproductive scores differed significantly among sites within distribution ranges (ANOVA, $F_{9,94} = 4.81$, $P < 0.001$), but not between distribution ranges ($F_{1,9} = 0.26$, $P = 0.622$). The mean values ($\pm$ SD) were very similar in unmanaged habitats in the native range (12.6 ± 2.9, $N = 60$) and in the invaded range (13.0 ± 1.65, $N = 45$).

DISCUSSION

Our study is significant in the context of current research on plant invasions (e.g., Richardson and Pyšek, 2006) in that it compares the population ecology of a problematic invasive plant between the native and the introduced range to gain understanding of the mechanisms underlying the invasion success of the species (Hierro et al., 2005). For analysis of the age structure and especially timing of reproduction, which is a key trait of a nonclonal monocarpic species like *H. mantegazzianum*, we used the relatively recent approach of herb-chronological dating. The method allows direct access to this important parameter without the need to perform multiyear surveys. A population with individuals at a younger age at reproduction introduces more seeds to the system. Therefore, our approach allowed us to efficiently investigate whether there is early flowering in invasive populations, probably favoring invasion.

Population structure and patterns of reproduction in Heracleum mantegazzianum—Our results provide the first information on the age structure in populations of *H. mantegazzianum* in its native and invaded distribution ranges. In different habitats in both regions, the species had relatively broad age distributions for a monocarpic perennial forb. The shape of the age structure was determined by the age at flowering because each plant dies after seed production. Under favorable site conditions, many monocarpic perennial forbs can flower in the second year of growth (e.g., Reinartz, 1984; De Jong et al., 1986). However, in *H. mantegazzianum* all plants sampled in the field flowered at the age of 3 years or later.

Flowering in the second year was only observed in about one third of plants (22 out of 70) grown from seed under favorable conditions in a common garden (J. Pergl et al., unpublished data). Two-year-old flowering individuals were also reported from a common garden hybridization study on *H. mantegazzianum* and *H. sphondylium* in Scotland (Stewart and Grace, 1984). At the other end of the gradient, we found few individuals in this study and a previous pilot study that lived for more than 10 yr before entering the flowering stage. Such remarkable variation in the life span of *H. mantegazzianum* indicates rather high phenotypic plasticity in the timing of flowering in response to varying resource accumulation in distinct habitats (cf. Harper and White, 1974; Gross, 1981; De Jong et al., 1998).

There are reports on perennation of flowering individuals of *H. mantegazzianum* into the following year from both native and invaded distribution ranges (Tiley et al., 1996; Shumova, 1972; Morton, 1978; Tiley and Philp, 1997). However, surviving flowering plants were never observed in our study. Roots of flowering plants always died during mid summer, and by late summer their central parts were almost completely decayed. The strictly monocarpic life history of the species was further demonstrated in a common garden experiment in which none of the flowering plants survived into the following year, not even when all flowering umbels were removed before seed set (Pyšek et al., 2006). The reported survival of flowering plants into following years may be attributed to misinterpretation. Plants often grow in clumps, where a group of seedlings germinated in a safe site (sensu Harper, 1977), and vegetative plants that did not flower in the previous year sprout in close vicinity of the last year's dead stem. Without closer inspection, they may be considered as resprouting from the rootstock leading to the wrong conclusion that the species is polycarpic (Morton, 1978).

The general trend of flowering at a later age and a wider range of ages of flowering plants in the native Caucasus as compared to the Czech region in unmanaged sites can be related to the effect of altitude and associated differences in environmental conditions, in particular the length of the vegetation period, which is considerably shorter in the high mountains. However, in managed habitats, the age of flowering plants did not differ between distribution ranges, suggesting that management effects like pasturing are of greater
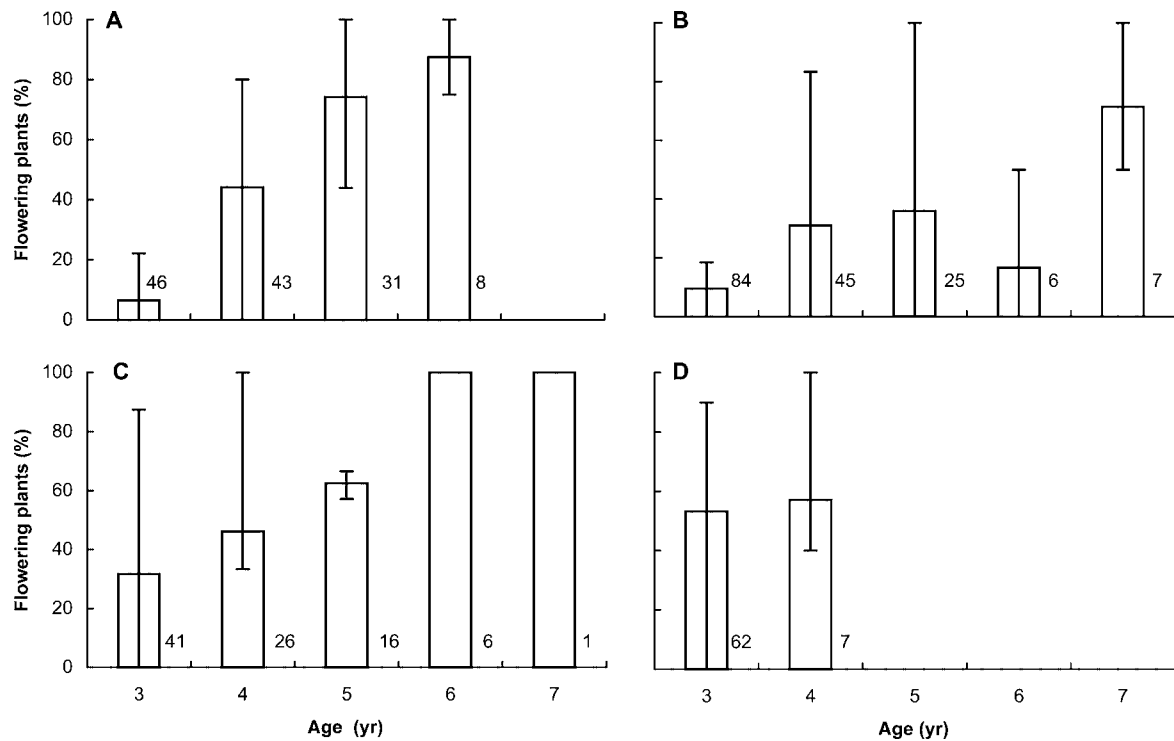
Fig. 4. The mean percentage of flowering plants of *Heracleum mantegazzianum* within individual age classes (cohorts), shown separately for different distribution range–habitat combinations (A) native/managed, (B) invaded/managed, (C) native/unmanaged and (D) invaded/unmanaged. For these combinations, the values were averaged across study sites. Minimum and maximum proportions are indicated by the length of vertical lines. Sample sizes are shown next to each column.

importance for population development of *H. mantegazzianum* than climatic differences. Across distribution ranges, we found clear evidence that flowering of *H. mantegazzianum* was postponed to later ages in managed habitats, and this pattern became even more pronounced when altitude was held constant. Plants growing in pastures probably need more time for sufficient resource accumulation to start flowering because of repeated biomass removal and trampling, which may not only injure the plants directly but may also impair growth by soil compaction. Similar results indicating that the age of plants at or above a threshold probability of flowering increases with the adversity of site conditions were found for other perennial forbs (e.g., Werner, 1975; Dietz and Ullmann, 1998). Interestingly, the oldest plants were not found in a pasture but in an unmanaged site in the invaded range. In the latter, strong constraints on resource accumulation imposed by low water availability appear to have resulted in a very extended vegetative growth phase (note that the chemical composition of the soil was similar across distribution ranges and habitat types). This contrasts with other unmanaged sites in the Czech region where almost all plants flowered early compared to managed habitats or the native area.

The proportions of flowering plants within individual cohorts indicate a similar population structure in the native distribution range, regardless of the type of management, and in managed sites in the Czech Republic. Grazing in the invaded range results in more evenly distributed flowering across age classes, an effect similar to relatively severe climatic conditions in the native range of Caucasus. Plants in unmanaged sites in the invaded range seem to be less affected by these constraints,

and favorable conditions appear to cause early flowering in the majority of individuals.

Reproductive output of *H. mantegazzianum* did not increase with the age of plants. This indicates the existence of a threshold in the amount of resources needed to trigger flowering as in other monocarpic species where age at flowering is a function of the rate of resource accumulation (e.g., Harper, 1977; Crawley, 1997). Our snapshot analyses of well- and long-established populations indicate that, independent of the presence or absence of habitat management or of position in the distribution range, the reproductive output of *H. mantegazzianum* populations appears to be maintained over time by a stable proportion of flowering plants. Correspondingly, in a previous study using longitudinal data from aerial photographs spanning 40 yr of invasion, the percentage of flowering individuals was rather stable since the beginning of the invasion of a site (Müllerová et al., 2005). *Heracleum mantegazzianum* thus appears to maintain high and stable reproductive output over both space and time in different environmental settings.

We have no indication that the range of population densities observed in our study affected the age at flowering or the reproductive vigor in *H. mantegazzianum*. Populations with the highest density were found in managed sites in the invaded range, probably due to higher grazing pressure compared to a more extensive grazing in the Caucasus (lower rate of number of cattle per unit of area). Dispersal of *H. mantegazzianum* seeds by the cattle, disturbances associated with grazing, and the regular removal of above-ground biomass minimizing

interspecific and intraspecific competition may have promoted seedling establishment at these sites.

Implications for invasion—The vigorous populations of *H. mantegazzianum* recorded in this study correspond to previous studies, which showed that the species was little constrained by the characteristics of the invaded environment (Moravcová et al., 2005; Müllerová et al., 2005). This broad ecological niche of the species and its high plasticity in the timing of flowering certainly adds to its high invasiveness. But are there clear differences in population parameters between the native and invaded ranges, and what can be inferred from these with regard to the remarkable success of *H. mantegazzianum* as an invader? The early flowering in unmanaged habitats and a high population density in managed habitats indicate more rapid population development in the invaded area than in the native area, which might have contributed to the accelerated spread of this species in the Czech region.

Climatic matching between the native and the introduced area, which is of primary importance for a species' ability to set seed in the new region (Pauchard et al., 2004; Liška and Soldán, 2004; Thuiller et al., 2005), is often crucial for successful invasion. Early flowering of *H. mantegazzianum* in the unmanaged sites in the Czech region may have been promoted by more favorable climatic conditions than exist in the high altitudinal belt of the native region of the Caucasus. The ability of the species to accelerate its life cycle under these conditions may have resulted in increased production of highly germinable seed (Moravcová et al., 2005), mainly in the early phases of habitat colonization.

At high population densities, plant individuals may have reduced seed set, the principle underlying the law of constant yield (Harper, 1977). However, across the range of densities observed in our study the reproductive score of *H. mantegazzianum* individuals did not decline with density. Hence, the high population densities observed in managed habitats in the invaded area translate into higher seed output per area. Interaction effects of this high seed production with the high level of human activity, transport of biomass, and increased regime of disturbances in managed habitats may have strongly promoted the efficient spread of the species in the Czech region.

It seems that the more favorable climatic conditions in the Czech region, together with increased chances for dispersal in a densely colonized Central European landscape, resulted in the massive invasion. Interestingly, we observed a similar phenomenon in habitats strongly influenced by humans at lower altitudes of the Caucasus where the species begins to form dense stands resembling those in the Czech Republic (J. Pergl and I. Perglová, personal observation). This suggests that species invasions in part may not be unique phenomena driven by specific conditions in the new area but may be paralleled by expansions of the same species in the native area as a result of global factors such as climate change or changing land use.

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