

Population life-cycle and stand structure in dense and open stands of the introduced tall herb *Heracleum mantegazzianum*

Jörg Hüls · Annette Otte · R. Lutz Eckstein

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Abstract Populations of the introduced *Heracleum mantegazzianum* consist of dense central stands, which gradually give way to open stands towards the margins. To analyse whether open stands are due to unsuitable conditions or represent the invading front for further spread, we studied life-cycle, population dynamics, stand structure and soil conditions of open and dense stands over two transition periods. Populations decreased during the first interval but increased after the extremely dry and warm summer of 2003 during the second interval. Open stands had shorter generation times, lower height, smaller proportions of small individuals and were less in equilibrium with the environment than dense stands. In open stands, growth to higher stages was most important, while in dense stands delayed development (self-loops) had a strong effect on population growth; stasis and fecundity contributed most to the difference in λ between stand types. By petiole extension *H. mantegazzianum* may raise its leaves just above the resident vegetation. Therefore, younger stages develop faster in open stands, whereas strong competition

by conspecific adults leads to longer generation times and a higher proportion of small individuals in dense stands. Disturbance due to extreme climatic conditions in summer 2003 equalised population dynamics of both stand types. Life-cycle variation between stand types makes it difficult to infer simple management rules. However, our data suggest that small and/or open stands of *H. mantegazzianum* may eventually serve as initials for further spread after land-use changes, whereas dense stands are stable and may represent sources of propagules.

Keywords Apiaceae · Elasticity · Intraspecific competition · Life table response experiment (LTRE) · Loop analysis · Management · Matrix models · Vital rates

Introduction

As a consequence of the large magnitude of transnational and trans-continental trade and exchange an increasing number of terrestrial plant species are being accidentally or deliberately introduced outside their natural ranges (Mooney and Hobbs 2000; Kowarik 2002; Levine and D'Antonio 2003; Taylor and Irwin 2004). Most of them are not adapted to the prevailing environmental conditions and probably go extinct soon after introduction (Crawley 1986; Williamson

J. Hüls · A. Otte · R. L. Eckstein (✉)
Department of Landscape Ecology and Resource
Management, Interdisciplinary Research Centre,
Justus-Liebig-University Giessen, Heinrich-Buff-Ring
26-32, 35392 Giessen, Germany
e-mail: Lutz.Eckstein@agrar.uni-giessen.de

and Fitter 1996; Sukopp 2001). However, some of the introduced species establish viable populations and even spread more or less rapidly within their new habitats (e.g. Elton 1958; Pyšek 1991; Williamson and Fitter 1996; Otte and Maul 2005). Introduced invasive species are considered a major threat to biodiversity (Elton 1958; Sala et al. 2000; but see Davis 2003). They will gain dominance if they possess the ability to change compositional, structural and functional components of the diversity of the invaded habitat (Noss 1990; Kolbek et al. 1994; Tappeiner and Cernusca 1996; Biermann and Daniëls 1997; Otte and Maul 2005).

If introduced species cannot be eradicated during initial dispersal and foundation of populations, their management and control will have to deal with populations and individuals of different ages and stages of development. Since establishment of populations and seed production for further spread are local processes, the study of invasive plants must ultimately address the dynamics and variation of local populations. Although detailed information on the population biology, i.e. analysis of the life-cycle, will help to understand the dynamics of establishment, reproduction and spread and may facilitate the development of management strategies, few comprehensive studies have focused on the species life-cycle (Crawley 1986; McEvoy and Coombs 1999; Parker 2000; Sakai et al. 2001; Walker et al. 2003; Koop and Horvitz 2005; Hyatt and Araki 2006).

Heracleum mantegazzianum Somm. et Lev. (Pyšek 1991; Tiley et al. 1996), a giant Hogweed native to the North-western Great Caucasus is successfully introduced in large parts of Europe during the last decades (e.g. Müllerová et al. 2005; Nielsen et al. 2005) and occurs as both open stands and dense (dominant) stands in a range of different habitats (Tiley et al. 1996; Thiele and Otte 2006). Owing to its phototoxic compounds (furanocoumarins: Pira et al. 1989) and its potential negative effects on local phytodiversity, *H. mantegazzianum* belongs to a group of the most important invasive plants species in Germany and is one of a few adventitious plant species outside crop fields that are selectively managed (Schepker and Kowarik 2002).

Although inconspicuous small ('nascent foci', Moody and Mack 1988) populations but also scattered individuals at the edge of stands may be important for the spread of introduced species (Parker 2000), it is not clear whether there is variation in the life-cycle between dense and open stands of *H. mantegazzianum* and whether open stands are a consequence of sub-optimal environmental conditions, i.e. sink populations that depend on support by source stands, or represent the invading front for further spread. Current management of *H. mantegazzianum* primarily focuses on dominant stands (Caffrey 1999; Nielsen et al. 2005). Therefore the aims of the present study were to analyse variation of the life-cycle between dense and open stands using matrix models, and to identify morphological traits and environmental conditions related to life-cycle variation. The following questions were addressed:

1. Is there significant variation in the life-cycle and population stage structure of dense and open stands of *H. mantegazzianum*?
2. Do open stands represent the invasive population front (high-population growth rate, λ) or are they a consequence of unsuitable environmental conditions (low λ)?
3. Are there significant differences in morphology and environmental conditions (soil nutrients) between dense and open stands that could explain variation in stand structure and population growth rate?

Material and methods

Study species

Detailed information on *H. mantegazzianum* can be found in, e.g. Ochsmann (1996), Tiley et al. (1996), Otte and Franke (1998), Nielsen et al. (2005) and Hüls (2005). In short: *H. mantegazzianum* is a monocarpic herbaceous perennial semirosette-hemicryptophyte of the Apiaceae family. Flowering plants can reach a height of 2–5 m (Tiley et al. 1996; Otte and Franke 1998) and produce on average about 40,000 seeds (Hüls 2005). The hermaphrodite flowers are

insect-pollinated, protandrous and are arranged in umbels of up to 80 cm diameter (Tiley et al. 1996; Moravcová et al. 2005). After maturation seeds are primarily released from the mother plant by passive autochory (Otte and Franke 1998). As in other family members (Stokes 1952), shed seeds show morpho-physiological dormancy (Moravcová et al. 2005). The species builds up a transient seed bank only (Krinke et al. 2005). *H. mantegazzianum* was introduced to Europe as an ornamental in the early 19th century and was widely distributed across Europe before 1900 (Nielsen et al. 2005). The exponential spread of this novel invasive coloniser (sensu Davis and Thompson 2000) started after the Second World War (e.g. Pyšek 1991; Müllerová et al. 2005). *H. mantegazzianum* occurs across a range of different habitat types such as open grasslands, roadsides, riverbanks and woodland margins (Thiele and Otte 2006). Stand densities of the species vary widely from scattered individuals to dominant stands. The majority of occupied sites have been subject to anthropogenic habitat changes within the last few decades, the most important process being land-use decline, especially abandonment of fertilised or nutrient rich open grasslands (Thiele and Otte 2006).

Data collection

Permanent plots

Five study sites were selected to represent some of the variation in environmental conditions of *H. mantegazzianum* stands in the western low-mountainous regions (Table 1), which is one of the most heavily infested areas in Germany

(Thiele and Otte, unpublished data). Depending on population size, we established two to ten permanent plots of 1 × 2.5 m in paired dense and open stands within each site. In open stands, *H. mantegazzianum* grew intermixed with the surrounding vegetation and covered < 10% of the ground, whereas in dense dominant stands the cover of *H. mantegazzianum* was almost 100%.

One site had to be omitted from the matrix analyses because most plants in the permanent plots were cut in 2002 before measurements could be taken. However, in 2003 plants from all sites were used to analyse vertical stand structure (see below). All individuals of *H. mantegazzianum* in the remaining sites were permanently marked in 2002. Their position, height, number of leaves, and size of leaves, stalks and stems were recorded to define the following stage classes used in the matrix models (cf. Fig. 1, Table 2):

- stage 1: small vegetative individuals; width of lamina 3.5–20 cm, height < 50 cm;
- stage 2: medium vegetative individuals; height > 50 but not reaching canopy, width of lamina 20–50 cm;
- stage 3: large vegetative individuals; reach ± canopy height (i.e. height of not more than 30 cm below average canopy height) or diameter of largest rosette leaf petiole > 1.8 cm. Width of lamina > 50 cm;
- stage 4: flowering individuals.

This classification resulted in stage classes characterised by different mortalities (Hüls 2005), based on characters that were relatively easy to measure in the field but still accommo-

Table 1 Geographic position of the five study sites, elevation, area covered by dense *Heracleum mantegazzianum* stands, and number of permanent plots established in the open and the dense stand

Site	Position °N latitude/°E longitude	Elevation m a.s.l.	Area m ²	Number of plots Open/dense stand
Allendorf*	8°38'09"/50°33'01"	155	600	8/8
Burgwald	8°45'03"/51°01'37"	330	600	8/8
Dönche	9°25'21.5"/51°17'49.5"	290	4,500	10/8
Druselstal	9°24'49"/51°18'15"	335	30	2/8
Viermünden	8°49'41"/51°05'28"	315	1,400	8/8

* This sites was omitted from the demographic analyses because most plants in the permanent plots were cut in 2002

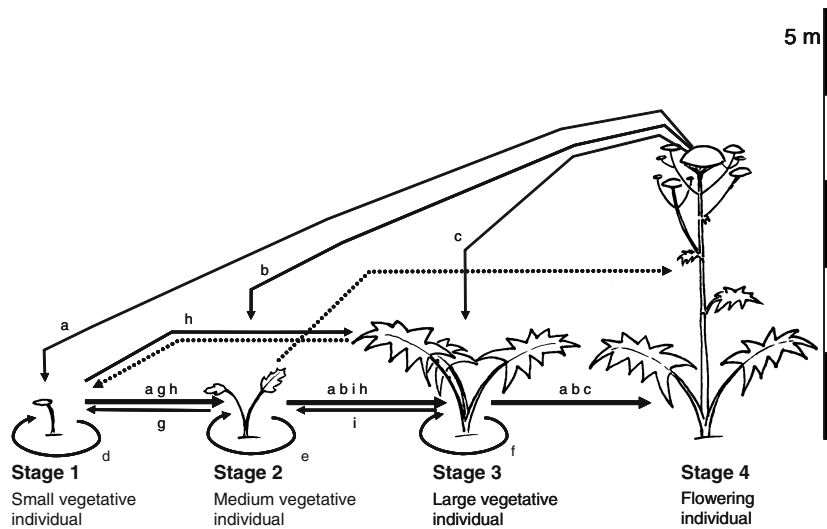


Fig. 1 Life-cycle of *Heracleum mantegazzianum* with observed transitions between four stages, i.e. (1) small, (2) medium and (3) large vegetative plants and (4) flowering plants. Stages were defined by the height of individual plants and the size of rosette leaves (see Material and methods). Since *Heracleum mantegazzianum* is a

monocarpic species, there is no stasis of flowering individuals. The transitions of the tree (edges; Wardle 1998) are shown in bold and each of the other lines represents the unique transition of one of the nine life-cycle loops denoted by different letters (a–i). Dotted lines represent rare transitions that were ignored in loop analysis

dated the morphological plasticity of the species at different sites. Since *Heracleum mantegazzianum* is a monocarpic species, there is no stasis of stage 4. Individuals with a lamina width < 3.5 cm (**stage 0**) were omitted from this study for several reasons: (1) their density in spring was so high that they could not be individually marked, (2) their mortality at census date reached almost 100%, (3) their extreme variation in numbers within days would make a comparison of different sites censused at different dates impossible and (4) due to their habit to develop a second leaf only after total senescence of the first leaf, they are partially leafless and as such impossible to track. Therefore, inclusion of these individuals would have introduced considerable sources of error in the matrix models. However, to estimate the error though omission of this stage, we used one of the study site where we estimated the fate of stage 0 without individually marking plants, in ten 0.1 m² plots. Using these data we compared a four-stage with a five-stage matrix for this site. Fecundity of flowering plants was higher in the five-stage matrix but since stage 0 plants almost completely

died and hence did not contribute to higher stage classes, we found hardly any differences with respect to the intrinsic matrix parameters. Therefore, all results in the following refer to four-stage matrices and fecundity is defined as the number of offspring reaching the threshold size of at least stage 1 individuals.

Additional censuses were carried out in 2003 and 2004, so that two life-cycle transitions could be modelled (intervals: 2002–2003, 2003–2004). The first interval represents population dynamics after years with ‘normal’ weather conditions (i.e. no extreme years), whereas the second interval represents the population dynamics after the extremely warm and dry summer in 2003 (cf. Ciaï et al. 2005). In total, this study was based on observations on 1,768 individuals (1,467 in dense and 301 in open stands) from 60 permanent plots in four sites.

Soil analyses

Soil samples were taken adjacent to permanent plots in dense and open stands of *H. mantegazzianum* in 2002. Using a soil corer (3 cm diameter), five soil samples (to 25 cm depth) per plot were

Table 2 Levkovich matrices of dense and open stands of *Heracleum mantegazzianum* for the transitions 2002–2003 and 2003–2004

				2002			
Dense stands	2003	Stage	N	1	2	3	4
		1	93	0.32	0.14	0.01	0.51
		2	112	0.19	0.40	0.04	0.33
		3	101	0.06	0.21	0.35	0.08
		4	75	0	0.01	0.46	0
				2002			
Open stands	2003	Stage	N	1	2	3	4
		1	3	0.13	0	0	0.15
		2	8	0.38	0.07	0	0.23
		3	32	0.13	0.69	0.17	0.23
		4	37	0	0.03	0.77	0
				2003			
Dense stands	2004	Stage	N	1	2	3	4
		1	760	0.25	0.04	0	9.77
		2	276	0.55	0.43	0.01	2.35
		3	123	0.05	0.44	0.65	0.04
		4	26	0	0	0.26	0
				2003			
Open stands	2004	Stage	N	1	2	3	4
		1	147	0	0	0	3.97
		2	27	0.67	0.25	0.03	0.59
		3	31	0.33	0.75	0.75	0
		4	6	0	0	0.19	0

Stage classes: small (1), medium (2) and large vegetative plants (3) and flowering plants (4). *N* denotes the number of individuals in each stage class and year. Matrices contain data on the fate of individuals from four study sites. Column values for stage 4 represent fecundity, whereas all other values are transition probabilities

pooled, dried at 40°C and sieved through a 2 mm screen. Soil analyses for plant available phosphorus (P), potassium (K), magnesium (Mg) and pH (in 0.01 mol/l CaCl₂) were carried out according to the protocols of VDLUFA (Hoffmann 1991). Nitrogen (N) and carbon (C) were analysed with a CNS analyser (vario MAX, Elementar Analyse-systeme, Hanau, Germany).

Calculations and Statistics

Life-cycle analyses

We constructed a life-cycle (Fig. 1) and a Levkovich matrix (Caswell 2001) based on the four

defined stage classes. Since open stands contain only few individuals, chance events may have a strong influence on the estimated transition probabilities. Therefore, we integrated the life-cycle information from the four study sites into one robust, pooled matrix for dense and one for open stands of *H. mantegazzianum* for the intervals 2002–2003 and 2003–2004, i.e. four matrices (Table 2). The programme PopTools Version 2.6.7 (Hood 2005) was used to obtain population growth rate (λ), per capita growth rate (r) and stable stage structure (SS_s). We estimated 95% confidence intervals of λ for open and dense stands using a bootstrap procedure (Manly 1991; Dixon 1993). Matrix elements representing transition probabilities were replaced by a binomial random distribution and matrix elements representing fecundity by an exponential random function for resampling. We then resampled 5,000 new values for λ and calculated the bootstrap mean (λ_b) and the accelerated 95% confidence interval (Dixon 1993) using PopTools. After decomposing the matrix into one matrix containing only transition probabilities and another containing only fecundity, we calculated the expected number of replacements (R_0) and the generation time (T) as described in Caswell (2001, p 126ff).

We analysed matrix elasticity (e), which is a prospective sensitivity analysis and expresses the effect of a relative change in each matrix cell for λ , keeping all other transitions constant (de Kroon et al. 1986). Since transitions are not independent of each other, we used loop analysis (van Groenendael et al. 1994; Wardle 1998; Caswell 2001) to quantify the contribution of different loops to population growth. Loops represent the potential paths through the life-cycle followed by individuals of the population. We selected a *tree* (a spanning sub-graph containing no loops and consisting of $n-1$ transitions, where n is the number of life-cycle stages) and identified the unique transitions (*chords*) that produced the nine loops corresponding to our transition matrix following the approach in Wardle (1998). To reduce the number of loops and negative contributions, we first set two very rare transitions (a_{31} , a_{42} , transition probability < 3%) to zero. Since loop h did not represent a unidirectional path (the direction

of the unique transition is in the opposite direction than the tree transitions) it had a negative elasticity (Wardle 1998) and could not be interpreted biologically. However, further reducing the matrix by removal of transition a_{31} did not have any large effect on the results of the loop analysis.

Additionally, we carried out a life table response experiment (LTRE; Caswell 1996, 2001; Parker 2000; Hyatt and Araki 2006). This retrospective analysis uses actually observed differences between the elements of two matrices multiplied by the respective sensitivity of λ to each matrix element 'midway' between the compared matrices to obtain the contribution of each matrix element to population growth. We used LTRE to compare the contribution of different transitions to λ in dense and open stands for the intervals 2002–2003 and 2003–2004.

SS_s was compared with the observed stage structure (SS_o) by means of Keyfitz's Δ (Caswell 2001, p 101) to analyse how close the actual stage distribution (SS_o) was to the equilibrium distribution (SS_s).

Stand structure

We used the product of number of rosette leaves, length and width of the largest rosette leaf of vegetative plants (stage 1–3) from permanent plots as an indicator of leaf area. We obtained the vertical distribution of leaf area of vegetative plants in dense and open stands of *H. mantegazzianum* by classifying the height of each individual in 25 cm increments. Additionally, the percentage of plants that reached a certain height class was calculated for the whole data set.

Soil analyses

Differences in soil nutrients and pH between dense and open stands were analysed by a paired *t*-test (Zar 1999) using the programme Statistica (Version 6.0, Stasoft Inc., Tulsa, USA).

Results

Life-cycle analyses

Dense and open stands of *H. mantegazzianum* were characterised by population growth rates (λ) significantly < 1 during 2002–2003 (Table 3). Consequently, plant numbers were decreasing in both stand types ($r < 0$, and $R_0 < 1$). Generation time was considerably lower in open than in dense stands. In contrast, from 2003 to 2004 populations of both stand types showed population growth rates > 1 (but $\lambda = 1$ was still within the confidence intervals), and increasing numbers of individuals ($r > 0$, $R_0 > 1$). Generation times were more or less similar in both stand types.

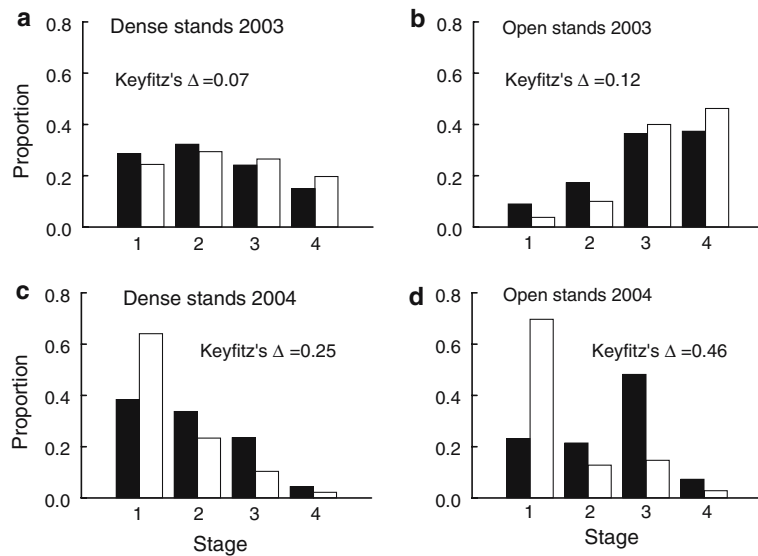
During the first study period both stable (SS_s) and observed stage structures (SS_o) of dense stands were characterised by equivalent proportions of small (0.286), medium (0.323) and large (0.241) vegetative individuals and slightly fewer flowering plants (0.150) (Fig. 2). SS_s and SS_o were very similar (Keyfitz's $\Delta = 0.07$), indicating that these stands were almost in equilibrium with the environment conditions. In contrast, open stands contained more large vegetative (0.364) and flowering (0.373) plants than dense stands, and relatively few small (0.090) and medium (0.172) vegetative individuals. Under projected equilibrium conditions there should be more small and medium vegetative and fewer large vegetative

Table 3 Intrinsic rate of population growth (λ), bootstrap estimate of λ (λ_b), lower and upper 95% confidence interval (CI-, CI+), per capita growth rate (r), expected

numbers of replacements (R_0) and generation time (T) of dense and open stands of *Heracleum mantegazzianum* for the intervals 2002–2003 and 2003–2004

Interval	Stand	λ	λ_b	CI-	CI+	r	R_0	T
2002–2003	Dense	0.75	0.74	0.56	0.87	–0.28	0.24	5.10
	Open	0.76	0.73	0.39	0.99	–0.27	0.45	2.99
2003–2004	Dense	1.38	1.31	0.79	1.63	0.32	6.45	5.79
	Open	1.24	1.07	0.72	1.40	0.22	3.94	6.23

Fig. 2 Stable stage distribution (*black bars*) and observed stage distribution (*open bars*) of dense and open stands of *Heracleum mantegazzianum* in 2003 **a, b** and 2004 **c, d**. Keyfitz's Δ is a measure for the distance between stable and observed distributions



and flowering plants than observed (Keyfitz's Δ : 0.12). During the second interval, small vegetative individuals dominated SS_0 of both stand types (Fig. 2). Deviations from SS_s were considerably larger than during the first interval and mainly caused by much less small vegetative individuals and large vegetative plants (in open stands) under equilibrium conditions.

Elasticity analysis revealed that from 2002–2003 survival within the same stage class and growth made the largest contribution to population growth rate of dense stands (Fig. 3), whereas growth and fecundity were most important in open stands, whereas during the second interval, the elasticities of vital rates between dense and open stands were very similar.

This was confirmed by analysis of alternative pathways through the life-cycle by means of loop analysis (Table 4). During the first interval, the developmental path across all stages (loop a) or a 'shortcut' jumping over stage 1 (loop b) contributed 47.2 and 64.3% to population growth in dense and open stands, respectively. Self-loops, i.e. delay within a certain stage (loops d–f) contributed 41% to growth in dense stands, but only 12.4% in open stands. In contrast, during the second interval the growth path across all stages (loop a) and survival in stage 3 (loop f) were most important for growth in both stand types.

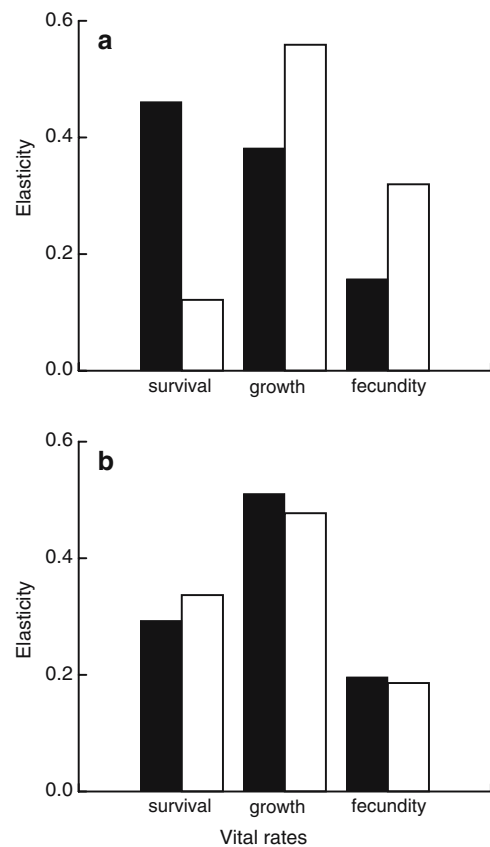


Fig. 3 Elasticity of survival, growth and fecundity of dense (*black bars*) and open stands (*open bars*) of *Heracleum mantegazzianum* for the intervals 2002–2003 **a** and 2003–2004 **b**

Table 4 Demographic loop characteristics of dense and open stands of *Heracleum mantegazzianum* for the transition intervals 2002–2003 and 2003–2004

	Dense stands					Open stands		
	Loop	Unique transition	Path	Elasticity of unique transition	Loop elasticity	Loop	Elasticity of unique transition	Loop elasticity
2002–2003	a	a ₄₁	1-2-3-4-1	6.6	26.4	a	6.6	26.6
	b	a ₄₂	2-3-4-2	6.9	20.8	b	12.6	37.7
	c	a ₄₃	3-4-3	2.1	4.2	c	12.6	25.1
	d	a ₁₁	1-1	7.9	7.9	d	1.4	1.4
	e	a ₂₂	2-2	18.2	18.2	e	1.8	1.8
	f	a ₃₃	3-3	14.9	14.9	f	9.2	9.2
	g	a ₂₁	1-2-1	3.9	7.9	g	0.0	0.0
	h	a ₁₃	1-2-3-1	3.0	-3.0	h	1.7	-1.7
	i	a ₃₂	2-3-2	1.4	2.7	i	0.0	0.0
2003–2004	a	a ₄₁	1-2-3-4-1	13.7	54.9	a	15.9	63.8
	b	a ₄₂	2-3-4-2	5.7	17.1	b	2.7	8.0
	c	a ₄₃	3-4-3	0.2	0.4	c	0.0	0.0
	d	a ₁₁	1-1	3.1	3.1	d	0.0	0.0
	e	a ₂₂	2-2	8.0	8.0	e	3.3	3.3
	f	a ₃₃	3-3	17.6	17.6	f	29.5	29.5
	g	a ₂₁	1-2-1	0.4	0.9	g	0.0	0.0
	h	a ₁₃	1-2-3-1	2.3	-2.3	h	6.3	-6.3
	i	a ₃₂	2-3-2	0.1	0.3	i	0.9	1.8

For the loops (a–i) depicted in Fig. 1, the unique transition (*chord*), the life-cycle path (*stage sequence*), elasticity of the unique transition (%) and the loop elasticity (%) are given. Loop h has negative loop elasticity and cannot be interpreted biologically (cf. Wardle 1998)

LTRE of differences in matrix elements actually observed between stand types revealed that the difference in λ can be explained by higher contribution of growth transitions in open stands and higher contribution of fecundity and survival in dense stands during both intervals (Fig. 4). Despite a higher elasticity of λ to fecundity in open stands during the first interval (Fig. 3a.), fecundity was actually higher in dense than in open stands. Hence, its contribution to the difference in λ was also higher in the former (Fig. 4).

Stand structure

Dense stands of *H. mantegazzianum* developed a thick leaf canopy at a height of between 75 and 200 cm with a peak between 75 and 150 cm (Fig. 5). In open stands most leaf area was found between 75 and 150 cm with a single peak between 75 and 100 cm. However, while about half of the population (46.3%) contributed to this main single leaf canopy layer in open stands and only 31.7% of the population was found below

the canopy, more than half of the population of dense stands (52.8%) was growing below the dense thick leaf canopy (Fig. 5).

Soil analyses

The soil below dense stands of *H. mantegazzianum* was characterised by higher pH and, on average, higher concentrations of soil nutrients and carbon (Table 5). Owing to relatively strong variation between sites, only pH differed significantly between dense and open stands after correcting for multiple testing.

Discussion

Open stands of *H. mantegazzianum* did not show higher intrinsic population growth rates than dense stands (Table 3). This is in contrast to the dynamics of *Cytisus scoparius*, where plots at the outer margin of the population (edge) and plots behind the front (intermediate) showed signifi-

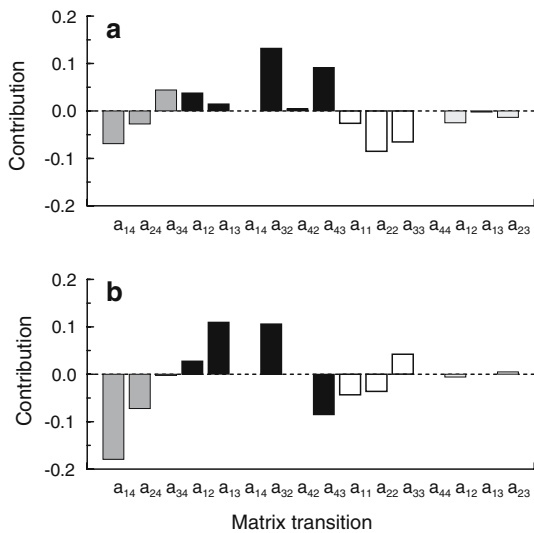


Fig. 4 Results of a life table response experiment (LTRE) for the comparison of open versus dense stands for the intervals 2002–2003 **a** and 2003–2004 **b**. Bars indicate the contribution of various life-cycle transitions (a_{ij} , i.e. transition from stage j in one year to stage i in the next year) to the difference between stand types in population growth rate. Transitions: fecundity (dark grey), growth (black), stasis (white) and regression (light grey). Bars > 0 denote higher contribution in open stands, bars < 0 higher contribution in dense stands

cantly higher growth rates than the population centre in Prairie sites (Parker 2000); however, in urban field sites differences in population growth rate between stand types were much smaller.

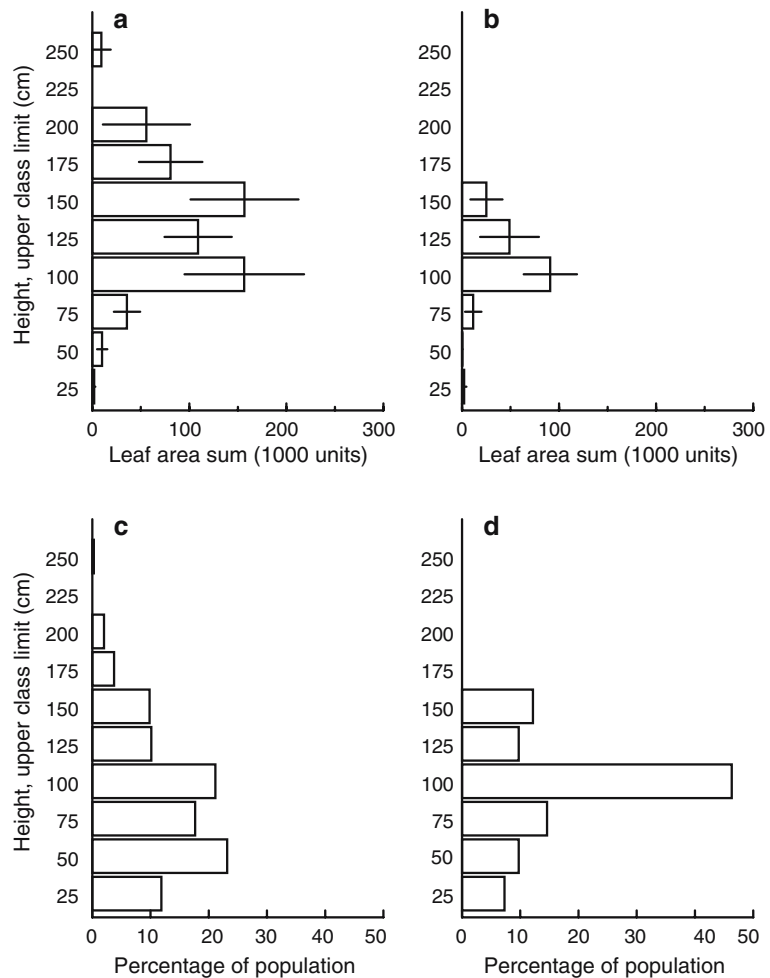
Dense stands of *H. mantegazzianum* were declining during the first interval (Table 3). Stable or declining populations ($\lambda \leq 1$) were also found in dominant stands of *H. mantegazzianum* in Czechia (Pergl et al. 2007), for central plots of populations of the invasive shrub *C. scoparius* (Parker 2000) and in populations of the annual invasive weed *Polygonum perfoliatum* (Hyatt and Araki 2006), both in North America. Likewise, in the invasive, nonnative shrub *Ardisia elliptica* simulations suggest that higher than present population growth rates were necessary to produce population sizes currently observed in the introduced range (Koop and Horvitz 2005). An average density of 7.7 plants per m^2 (range: 1.3–31.2) in dense stands of *H. mantegazzianum* in the present study suggests that populations were saturated. It is very probable that negative intraspecific interactions through large individuals (see below)

slowed down the development of small plants, leading to (1) a high contribution of self-loops to population growth (Table 4), (2) a longer generation time (Table 3) and (3) an accumulation of young stages in dense stands (Fig. 2). Saturation of local carrying capacity has been proposed as one reason for stable populations of *H. mantegazzianum* in Czechia (Nehrbass et al. 2006). Population growth of dense stands had a high-elasticity towards transitions related to stasis, a pattern typical of polycarpic perennials that recently was confirmed for an invasive, nonnative shrub (Koop and Horvitz 2005), whereas in open stands growth transitions were much more important (Figs. 4, 5).

Can low-population growth rates of open stands (edge plots) in *H. mantegazzianum* be explained by unsuitable abiotic site conditions? Our analyses suggest that differences in pH, soil nutrient and carbon contents between stand types were insignificant or small (Table 5), which was confirmed by an analysis of a large sample of dense and open *H. mantegazzianum* stands across Germany ($n = 202$, Thiele, unpublished data).

Since local abiotic conditions are probably not responsible for the weak population growth in open stands, an alternative explanation could be that these stands are kept open through biotic disturbance (mowing, grazing). Thiele and Otte (2006) showed that the main gradient in vegetation relevés of *H. mantegazzianum*, represented by the series *managed grasslands—ruderal grasslands—tall-herb communities—woodlands*, corresponded with increasing age of abandoned sites. Along this successional series, cover of *H. mantegazzianum* showed a unimodal response; highest cover was achieved in ruderal grasslands and tall herb communities. It is therefore not unlikely that low population growth rates in open stands are a consequence of at least irregular mowing or grazing by livestock or deer. However, this also means that, if management is abandoned, open stands may grow, out-compete the surrounding vegetation and become denser. In the course of further succession of invaded grassland to scrub and/or forest systems, *H. mantegazzianum* will disappear owing to its sensitivity to shade (e.g. Nielsen et al. 2005; Thiele and Otte 2006).

Fig. 5 Vertical distribution of leaf area in dense **a** and open **b** stands of *Heracleum mantegazzianum* and percentage of the population that contributes to certain height classes in dense **c** and open **d** stands. An index of leaf area was estimated as the product of number of rosette leaves, and length and width of the largest rosette leaf. Data in **a** and **b** are means \pm SE



Our data from two seasonal transitions suggested that population dynamics and differences between stand types may be strongly influenced by extreme climatic conditions. The extremely hot and dry conditions during summer 2003, which caused Europe-wide reduction in primary productivity (Ciais et al. 2005), led to gaps in the *Heracleum* populations owing to increased mortality of individuals (Hüls 2005). Both dense and open stands responded to this massive disturbance through increased fecundity and recruitment of new plants to fill these gaps. Consequently, both stand types showed similar population dynamics during this phase (Fig. 3b) also indicated by large deviations between observed and expected stage structure in 2004 (Fig. 2c, d). This response of *H. mantegazzianum* indicates its ability for rapid resilience after

massive disturbance. However, it appears reasonable to conclude that the first transition interval reflects the typical life-cycle differences between stand types, because populations had developed more or less undisturbed after years with normal climatic conditions. In this situation, large differences in population stage structure (Fig. 2a, b), population dynamics and generation time were present (Table 3, Figs. 3, 4).

The results of our soil analyses and morphometric measurements may shed some more light on the ecological processes that control life-cycle variation of this introduced herb: in open stands *H. mantegazzianum* exerted a strong interspecific competitive effect on the surrounding vegetation. By elongation of its petiole the species was able to place its leaf area just above the resident vegetation (Hüls 2005). This appears to be a

Table 5. pH and concentrations of plant available soil phosphorus (P, mg 100 g⁻¹ soil), potassium (K, mg 100 g⁻¹ soil), and magnesium (Mg, mg 100 g⁻¹ soil), total nitrogen(N_t, %) and carbon (C_t, %) and the C_t: N_t ratio of dense and open stands of *Heracleum mantegazzianum*

Stand	Population	pH	P	K	Mg	N _t	C _t	C _t :N _t
Dense	Allendorf	5.77	3.91	15.63	18.13	0.24	2.49	10.33
	Burgwald	5.57	1.86	17.47	10.39	0.22	2.67	11.80
	Dönche	5.21	0.90	13.14	36.06	0.32	3.40	10.63
	Druseltal	5.40	0.75	25.60	63.20	0.38	5.07	13.30
	Viermünden	5.47	1.20	9.61	28.10	0.36	3.39	9.34
	Mean	5.48	1.72	16.29	31.18	0.30	3.40	11.08
	SD	0.21	1.29	5.98	20.38	0.07	1.02	1.52
Open	Allendorf	4.90	0.86	4.54	13.70	0.20	1.78	8.80
	Burgwald	4.98	1.19	11.53	9.43	0.21	2.23	10.78
	Dönche	4.98	0.47	7.61	27.81	0.27	2.97	11.16
	Druseltal	4.89	0.86	14.40	61.20	0.39	5.57	14.30
	Viermünden	4.68	1.25	8.30	19.05	0.34	3.25	9.46
	Mean	4.89	0.93	9.27	26.24	0.28	3.16	10.90
	SD	0.12	0.31	3.79	20.71	0.08	1.47	2.13
<i>T</i>		5.305	1.370	3.75	3.045	2.158	1.180	0.379
<i>P</i>		0.0061	0.2426	0.0200	0.0382	0.0971	0.3032	0.7240

T and *P* give the *t*-value and the error probability of a paired *t*-test for differences between dense and open stands (*df* = 4). Significant differences after sequential Bonferroni correction for seven tests (*p* < 0.0071) in bold

cost-efficient way in terms of carbon and nutrients to monopolise the resource 'light' (Tappeiner and Cernusca 1996). Because a large proportion of *H. mantegazzianum* individuals, i.e. also younger stages, participated in the build-up of this leaf canopy, their individual development was accelerated and generation time was low (Table 3), while shade-intolerant grassland species disappeared (Kolbek et al. 1994; Gibson et al. 1995; Thiele and Otte 2006). This successful competitive growth strategy, which is amplified by an early phenological development of *H. mantegazzianum* (Otte and Franke 1998), changes the structure and composition of the invaded communities and gradually leads to species-poor or monospecific dense stands. However, in the course of this development, stand height and petiole length, but not leaf area, increased significantly (Hüls 2005). As a consequence, the intensity of intraspecific competition increased and only a small fraction of the population reached the closed leaf canopy (Fig. 5). The development of small individuals in the shade of this canopy was retarded, which led to (1) a higher generation time (Table 3), (2) a population stage structure with high proportions of small and medium size plants (Fig. 2) and (3)

high-mortality, especially of the smallest individuals. Since competition for light is strongly asymmetric among plants, size differences will lead to competitive hierarchies at the community level (Keddy 2001). The competitive growth strategy of this tall herb leading to closed canopies, together with early germination (Tiley et al. 1996; Otte and Franke 1998) and fast initial growth will enable the species to occupy gaps after disturbance. The latter are two traits of successful plant invaders (Newsome and Noble 1986) and probably two of the most important species traits responsible for the establishment success of *H. mantegazzianum* (Nielsen et al. 2005).

Owing to relatively large variation in life-cycle between stand types and years in *H. mantegazzianum* (Fig. 2, 3; Table 4) it is difficult to suggest simple management and control measures. Additionally, matrix elements are not independent of each other (Caswell 2001) and, consequently, a certain management regime is unlikely to affect only a single matrix entry. Nevertheless, generally low elasticities of population growth rates towards fecundity (Fig. 3) suggest that the commonly practised cutting of umbels in dense stands may not have strong effects on local

population viability (Caffrey 1999). Additionally, the management of fecundity in dense stands is time consuming and involves a health risk for untrained personnel, and after-ripening of the seeds and resprouting of basal umbels after treatment will further jeopardise the success of this management (Nielsen et al. 2005). On the other hand, it is one possibility to reduce the capacity of otherwise stable stands to act as source populations for seed dispersal and invasion of further habitats (Caffrey 1999; Moravcová et al. 2005, Nielsen et al. 2005). An integrated weed management strategy that considers stand area, density and accessibility and involves a combination of control mechanisms (cutting, grazing, uprooting) will be most effective (Nielsen et al. 2005). However, controlled demographic experiments on the effects of different management scenarios on population viability and extinction probabilities are needed (Shea and Kelly 1998; McEvoy and Coombs 1999).

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