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Analysis of habitats and communities invaded by Heracleum mantegazzianum Somm. et Lev. (Giant Hogweed) in Germany

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with 6 figures and 5 tables

Abstract. The aim of the present study was to analyse *Heracleum mantegazzianum*'s habitat preference and to identify recipient communities in its invasive range in Central Europe with regard to the species' effects on resident vegetation and potential implications for nature conservation. Field investigations were carried out in 20 study areas (each 1×1 km^2) in Germany. In all encountered stands of *H. mantegazzianum* the vegetation composition and various site parameters were sampled. Additionally, time series of aerial photographs of study areas were analysed to reconstruct the history of invaded sites.

H. mantegazzianum occurs in a variety of different habitat types, such as grasslands, roadsides, riverbanks, woodland margins etc. Stand densities of the species vary widely from scattered individuals to dominant stands. Primary constraining factors for *H. mantegazzianum* densities are land use, shading and low-productive site conditions. Site conditions of preferred habitats are more or less uniform, and are characterised by high productivity in combination with lack of land use and recent or historic disturbances or habitat changes. *H. mantegazzianum* is a successful invader and a potentially dominant species only if these particular habitat requirements are met. However, even then most stands of the species are not dominant.

The majority of invaded sites have been subject to human caused habitat changes within the last 50 years which have enabled or facilitated invasion. The most important process here is land-use decline, especially abandonment of grasslands.

The prevailing vegetation types with *H. mantegazzianum* are ruderal Arrhenatherion grasslands and Galio-Urticetea tall-forb stands which represent stages of secondary successions from grasslands to woodlands after abandonment of land use. Successional age seems to play a role with respect to stand densities of *H. mantegazzianum* as maximum densities occur prevalently at sites which represent young successional stages.

The results of the present study suggest that high densities of *H. mantegazzianum* can decrease native diversity of invaded stands, especially in abandoned grasslands. However, a loss in diversity is a typical effect of the processes that facilitate the invasion of *H. mantegazzianum*, i.e. abandonment of grassland management and severe disturbances or even habitat destruction (e.g. due to mining), and can be brought about by native species, such as *Urtica dioica*, as well. From this point of view *H. mantegazzianum* can be seen rather as a symptom of diversity loss than the cause of it.

Further, the results suggest that *H. mantegazzianum* does not seriously threaten to conflict with nature conservation as preferred habitats and plant communities are very common today and habitats which are of special conservation interest present no favourable conditions for this species.

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1 Introduction

1.1 Motivations and objectives

The study species, *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) is a monocarpic, plurennial mega forb of the Apiaceae family (Ochsmann 1996) native to the Northwestern Great Caucasus where it occurs in meadows, clearings and at forest margins at altitudes between 800 and 2200 m a.s.l. (Mandenova 1950). It was introduced to Europe as an ornamental plant in the 19th century and after repeated escapes from cultivation a massive spread was observed in several European countries (e.g. Great Britain, Czech Republic, Germany) during the second half of the 20th century (cf. Pyšek 1991, 1994, Ochsmann 1996, Tiley et al. 1996, Wade et al. 1997).

H. mantegazzianum is reported to reduce native biodiversity of invaded vegetation (Lundström 1984, Pyšek & Pyšek 1995). Moreover, a survey addressed to the nature conservation authorities of German districts in 2001 brought up reports of the species to occur in nature reserves and sometimes even in protected habitat types (Thiele & Otte, submitted). Yet hitherto invasion of habitats and plant communities of special conservation interest has never been scientifically confirmed. Also research on the species' habitat preferences and its effect on local native biodiversity has to date been restricted to rather few localities or single regions.

Therefore, the objectives of the present study were:

(1) To analyse the species' habitat preference over a possibly wide geographical range in Germany,
(2) to identify invaded plant communities,
(3) to assess effects on recipient communities and, finally,
(4) to evaluate risks imposed by the species on nature conservation.

1.2 Overview of previous knowledge

On national level, information on the distribution of vascular plant species is provided by the floristic mapping project of Germany ('Floristische Kartierung') based on the grid of the topographic map of Germany 1:25.000 (cell size ca. 11 × 11 km^2). In 2002, *H. mantegazzianum* was reported for 57% of grid cells (considering all records observed or confirmed after 1980). But this is probably an underestimate as data from two German states (Schleswig-Holstein, Hesse) were virtually missing. The present distribution of *H. mantegazzianum* is biased towards western and northwestern Germany and the southernmost parts of eastern Germany (Saxony, Thuringia) where the species is present in the vast majority of cells, whereas the remaining parts of eastern Germany exhibit only sparse records and southern Germany shows intermediate frequency (German national floristic database, 'Datenbank Gefäßpflanzen'; www.floraweb.de).

The extent of *H. mantegazzianum* stands in invaded landscapes was studied by PYŠEK & PYŠEK (1995) in the Czech Republic, as well as by SCHEPKER (1998), and by THIELE & OTTE (submitted) in Germany. Some basic information on invaded habitats has been provided recently by listings (e.g. WADE et al. 1997) or quantitative accounts of broad habitat categories (PYŠEK 1994, PYŠEK & PYŠEK 1995, OCHSMANN 1996). Characterisations of site conditions based on Ellenberg indicator values of Central European plant species (ELLENBERG et al. 1992) were given by PYŠEK & PYŠEK (1995) from western Bohemia (50 sites) and OCHSMANN (1996) from the Göttingen area in Germany (57 sites). Specific measurements of site parameters have to date been limited to small numbers of plots. Data on soil nutrients, pH values, and soil organic matter were presented by NEILAND (1986) and TILEY et al. (1996) from a total of 20 sites in Scotland and by OTTE & FRANKE (1998) from two sites in Germany. CLEGG & GRACE (1974) reported data on pH values and organic matter in the soil from the region of Edinburgh (18 sites). Finally, a preliminary overview of the invasion and ecology of *H. mantegazzianum* can be found in KOWARIK (2003, pp. 207).

Previous descriptions of plant communities with *H. mantegazzianum* have been based on comparatively small numbers of relevés and restricted to single localities or regions. The first published vegetation relevés of *H. mantegazzianum* stands were reported from the Czech part of the Ore Mountains by WEBER (1976). DIERSCHKE (1984) described a similar stand from the eastern part of Lower Saxony (Germany) which he classified as Heracleum mantegazzianum – Galio-Urticenea-community, i.e. a rankless community of the (sub-)class of nitrophilous herb communities of fresh to moist habitats (Galio-Urticenea (Passarge 1967) Th. Müller in Oberd. 1983, syn. Galio-Urticetea Passarge ex Kopecky 1969). On the basis of 18 relevés from Schleswig-Holstein (northern Germany) and Saarland (south-western Germany) KLAUCK (1988) introduced a new association, Urtico-Heracleetum mantegazzianii, which he categorised under the alliance Aegopodion Tx. 1967. The notion of a separate association of *H. mantegazzianum* was accepted by KOLBECK et al. (1994) who reported 40 relevés from Central Bohemia pointing out that this community occurs in a variety of mesophilous to hygrophilous habitats, such as forest fringes, field edges, ditches, moist grassy slopes and ruderalised areas. They also reported three relevés from forest vegetation which corresponded to human-influenced forms of Stellario-Alnetum Lohm. 1957 forests (sub-alliance of Alder-Ash-Forests, Alnenion glutinoso-incanae Oberd. 1953, within the alliance Alno-Ulmion Br.-Bl. et Tx. 1943). Next to predominant occurrences of *H. mantegazzianum* in Galio-Urticetea and Aegopodion communities, OCHSMANN (1996) also found the species in grassland communities and, though only vegetatively, in beech forests of the Göttingen area (Lower Saxony, Germany). In accordance with SCHWABE & KRATOCHWIL (1991) he advocated the rejection of a separate association of *H. mantegazzianum* (Urtico-Heracleetum Klauck 1988).

This view was supported by Otte & Franke (1998) who conducted eight relevés in Hesse (Germany) in derelict sites (grasslands and gardens) and in riverbank sites which they subsumed to the orders Glechometalia Tx. in Tx. et Brun-Hool 1975 and Calystegietalia (Convolvuletalia) Tx. 1950, respectively, and by Sauerwein (2004) who presented a study of *H. mantegazzianum* communities in northern Hesse.

2 Study areas

For field investigations, study areas were defined as landscape sections of 1 by 1 km² which had to meet the criterion of containing at least three stands of *H. mantegazzianum*. This criterion was set in order to (i) avoid marginally infested landscapes containing only isolated and 'accidental' stands, (ii) to objectify the sampling procedure (all encountered areas meeting the requirements were surveyed), and (iii) enable efficient data ascertainment.

In 2001, a survey on *H. mantegazzianum* was conducted by addressing questionnaires to the nature conservation authorities of all of 440 German districts ('Landkreise') including cities independent from a district administration ('kreisfreie Städte'). The received data were used to create a ranking of districts by invasion intensity (Thiele & Otte, submitted) in order to identify districts most likely to contain suitable study areas.

The 35 most heavily invaded districts, according to the estimates based on the survey, were chosen as potential study regions and their nature conservation authorities were asked to send copies of topographic maps (1 : 10.000 – 1 : 25.000) depicting known *H. mantegazzianum* stands. Maps were received by 33 districts and on examination 22 seemed to have suitable investigation areas. Altogether, 30 potential study areas were scrutinized on field excursions and, finally, 20 study areas proved to meet the requirements defined above. These study areas, distributed over 14 districts in seven German states (North Rhine-Westphalia, Rhineland-Palatinate, Hesse, Bavaria, Lower Saxony, Thuringia and Saarland), were surveyed in the summer seasons of 2002 or 2003. Grid coordinates and altitudes of study areas are given in Table 1.

3 Materials and methods

3.1 Establishment of plots

In all extensive stands except for some stands of which the vegetation cover had been completely destroyed recently, e. g. by ploughing or rotovating, plots of 25 m² were established in order to investigate site conditions and record plant communities. Locations of plots were chosen to be representative of the stand as a whole and their position was mapped with GPS. If two patches of conspicuously different densities of *H. mantegazzianum* were located inside one homogenous habitat, both patches were sampled separately. Altogether, 202 plots were studied in 2002 or 2003.

Table 1. State, district, grid coordinates and altitudes of study areas. Coordinates represent the south-western corner of each study area (1×1 km²) according to the German geodetic system ('Gauß-Krüger'). If the altitudinal range of plots in a study area was less than 20 m, average values are supplied, otherwise the lowest and highest value of investigated plots.

No.	State	District ('Landkreis')	Grid east	Grid north	Altitude (m a. s. l.)
1	Rhineland-Palatinate	Altenkirchen	3410.500	5623.000	160
2	Rhineland-Palatinate	Ahrweiler	2588.300	5594.500	135–175
3	North Rhine-Westphalia	Ennepe-Ruhr-Kreis	2593.800	5696.400	85
4	North Rhine-Westphalia	Euskirchen	2545.800	5595.000	470–490
5	North Rhine-Westphalia	Euskirchen	2535.500	5589.000	590
6	Bavaria	Freising	4465.500	5362.500	480–500
7	Bavaria	Garmisch-Partenkirchen	4430.200	5270.000	865
8	Bavaria	Garmisch-Partenkirchen	4443.500	5253.500	930
9	Lower Saxony	Göttingen	3552.500	5710.500	235
10	North Rhine-Westphalia	Hagen	3396.700	5687.000	145–195
11	North Rhine-Westphalia	Hagen	2600.100	5695.500	90
12	North Rhine-Westphalia	Hagen	3397.000	5689.800	260–290
13	Hesse	Kassel	3529.200	5684.000	270–305
14	Hesse	Lahn-Dill-Kreis	3467.000	5595.500	260
15	North Rhine-Westphalia	Olpe	3421.500	5664.500	255–275
16	Thuringia	Wartburgkreis	3569.500	5620.500	325–350
17	Hesse	Waldeck-Frankenberg	3488.300	5668.500	260
18	Hesse	Waldeck-Frankenberg	3477.800	5655.500	325–345
19	Hesse	Waldeck-Frankenberg	3487.500	5661.200	260–310
20	Saarland	St. Wendel	2589.000	5482.100	360–395

3.2 Reconstruction of site history

Time series of aerial photographs (1950s, 1970s, approx. 2000) were acquired for study areas and overlain with the coordinates of plots in ArcView GIS 3.2 (© Environmental Systems Research Institute, Inc.). Aerial photographs were interpreted by eye and plots were assigned to a particular land-cover type for every point of the time series. On the whole, 11 different land-cover types, e. g. 'arable land', 'grassland', 'shrub' could be discerned. The different combinations of land-cover types along the time series were classified 'by hand' into groups of similar site histories.

3.3 Sampling of site conditions

Soil samples were collected in October of the respective year using a soil corer of 3 cm diameter. In each plot, five cores of 25 cm depth were taken at random locations after removing litter and dead plant material from the soil surface. Samples were air-dried, sieved (< 2 mm) and extracted with both calcium-acetate-lactate for the determination of plant-available phosphorus and potassium (Schüller 1969), and $CaCl_2$ solution for the determination of magnesium (Schachtschabel 1954). Total nitrogen and total carbon content were analysed with a CN-analyser.

In 2002, also the pH values of topsoil samples were measured in H_2O with a laboratory pH meter (WTW '325-A/Set 1 Electrode SenTix 97T') and additional drillings were conducted up to 1 m depth, if possible, to characterise soil morphology, especially with regard to water supply (n = 118). The drill cores were investigated for signs of soil wetness and, where applicable, soil wetness or impeded drainage was classified on an ordinal scale according to AG Boden (1982). Bulk density was estimated (low, medium, high) and soil material was taken from the drill core beneath the a-horizon to determine the soil character. Values of available field capacity were derived from soil character and bulk density with corrections for lateral inflow or outflow of water depending on topology (AG Boden 1982).

Light availability was estimated using an ordinal scale, which comprised five levels (dark shade, shade, semi-shade, light, full light). Land use of the study sites as identified in the field was assigned to three categories, 'none' (including fallow and derelict land), 'maintenance' (e.g. irregularly mown fringes or road verges), and 'grassland' (regularly used meadows and pastures). Where applicable, disturbances of sites were recorded, which in the context of this study include all externally caused changes to the structure of the vegetation apart from land-use practices, e.g. deposition of waste material or removal of shrubs and trees.

3.4 Sampling of vegetation

Vegetation sampling was done following the method of Braun-Blanquet (1964) using the modified cover abundance scale as proposed by Wilmanns (1989). Height and cover of the different vegetation layers and cover percentages of litter and bare soil surface were estimated for each plot as parameters of vegetation structure. In addition to tree, shrub, herb and moss layers, the vegetation structure parameters were separately estimated for *H. mantegazzianum.* All vascular plant species within a plot were recorded. Nomenclature follows Wisskirchen & Haeupler (1998).

The assignment of species as character or differential species was adopted from Ellenberg et al. (1992), Oberdorfer (1993), Dengler (1997), Dierschke (1997), and Dierschke (2004). Nomenclature of plant communities below the (sub-) class level follows Oberdorfer (1993) if not otherwise indicated.

3.5 Parameters derived from the floristic composition of vegetation samples

Unweighted averages of the indicator values for light, moisture, soil reaction and nutrients given by Ellenberg et al. (1992) and calibrated C-S-R strategy types by Grime et al. (1988) were calculated for each sample to supplement the set of recorded site parameters. To avoid bias due to the selection of plots under the premise of *H. mantegazzianum* occurrence, this species was omitted in the calculations. The calibration of unbalanced C-S-R radii for species was performed in the manner demonstrated by Ejrnæs & Bruun (2000) and Ecke & Rydin (2000). Only species categorised by Grime et al. (1988) were included in this analysis. These comprised about 70 % of the entire species pool of the data set and 98 % of species with relative frequencies greater than 10 %. Furthermore, the cover sum of nanophanerophytes and woody chamaephytes pooled together was calculated by summing up mean values of cover-abundance classes of the modified Braun-Blanquet scale.

3.6 Data analysis

Major gradients in the vegetation data set were explored by correspondence analysis (CA, Hill 1973), a method of indirect gradient analysis (Lepš & Šmilauer 2003), using the program package CANOCO for Windows 4.5 (© Biometris). For gradient analysis the cover-abundance of species was transformed to the numeric values 1 to 9 representing the levels of the modified cover-abundance scale. A detrended correspondence analysis with detrending by segments revealed a gradient length on the first axis of 2.8 and thus indicated predominant linear response of species along the first ordination axis. Therefore, CA was setup with biplot scaling (ter Braak & Šmilauer 1998). Furthermore, scaling was chosen to focus on inter-sample distances and downweighting of rare species was selected. In addition, response curves of selected species along the first ordination axis were produced using Generalized Additive Models (GAM) in CANOCO.

Calculations of descriptive statistics and correlation coefficients were performed with Statistica 6.0 package (© StatSoft, Inc.). Medians and percentiles were calculated instead of means and standard deviations as distributions of soil nutrient concentrations and average indicator values for soil reaction deviated considerably from normal distribution. Classification of medians was done according to content classes of P, K and Mg for arable fields (Landesanstalt für Landwirtschaftliche Chemie 2002) or rather according to AG Boden (1994) for organic carbon, pH and available field capacity.

Sorting of vegetation samples and assignment to known syntaxa was done ‘by hand’ on the basis of characteristic and differential species.

4 Results

4.1 Habitat preference

4.1.1 Land use and disturbance

H. mantegazzianum prevalently occurred at sites without a regular land-use regime, like abandoned grasslands or other derelict land (71 % of plots). 17 % of sites were subject to rather irregular management (e. g. maintenance

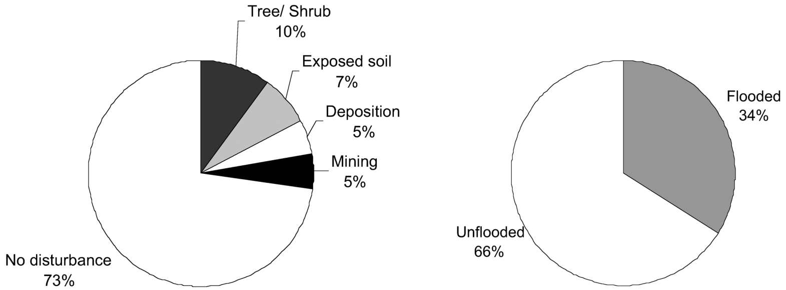

Fig. 1. Relative frequencies of disturbances in investigated plots. (A) Mechanical disturbances (predominantly human caused) and (B) disturbance due to flooding. Short cuts for disturbance categories: (A) Tree/ Shrub = Removal of single trees or shrubs in the open landscape or along fringes, Exposed soil = mechanical disturbances of the sward leading to patches of exposed soil, Deposition = deposition of organic material, e. g. garden waste, Mining = recently abandoned open cast mining (former sand pit or rock quarry), No disturbance = no obvious signs of disturbance found in the field; (B) Flooded = site located inside the inundation area of a river and, thus, subject to periodic or episodic flooding, Unflooded = site located outside inundation areas.

cut) and 12 % were regularly mown or grazed. Notably, when regular management was applied *H. mantegazzianum* was constrained to low densities, while lack of land use or irregular maintenance allowed for high densities of the species.

Recent mechanical disturbances of the vegetation were found in 27 % of plots altogether (Fig. 1A) and were predominantly human caused. The encountered kinds of disturbances generally cause open patches in the vegetation. 34 % of plots were situated inside the inundation area of rivers and, thus, were subject to episodic or periodic disturbance due to flooding (Fig. 1B) which sometimes overlapped with anthropogenic disturbances. All disturbances combined accounted for 57 % of plots.

4.1.2 Site history

During the period covered by the time series of aerial photographs (1950s to approx. 2000), the majority of sites with *H. mantegazzianum* showed changes which are attributable to land-use decline (53.5 %, Table 2). The most prominent process was abandonment of managed grasslands leading to herbaceous successional stages which accounted for 27.7 % of all sites. Prevalently, the abandonment occurred between the 1950s and the 1970s (33 sites) and, secondarily, between the 1970s and today (23 sites). In another 14.9 % of sites cessation of grassland management before the 1970s or, exceptionally, between the 1970s and today led to development into woodlands or forests. Furthermore, conversion of margins of managed grasslands and, subordinately, arable fields into disused but probably occa-

Table 2. Frequencies (absolute and relative) of categories of site history for investigated plots. Individual site histories were grouped on two levels: (i) broad groups of site history representing similar processes (given in bold) and (ii) subdivisions of the former comprising very similar or identical site histories.

Site history category	Frequency	
	abs.	rel. [%]
Abandonment of agricultural land use	**108**	**53.5**
Abandonment of grasslands	56	27.7
Natural or human assisted afforestation of former grasslands	30	14.9
Conversion of grassland margins to (irregularly maintained) fringes	16	7.9
Abandonment of arable land use	6	3
Persistent agricultural land use	**36**	**17.9**
Persistently managed grasslands	26	12.9
Rotation of land use (arable ↔ grassland)	10	5
Persistent maintenance	**9**	**4.5**
(Irregularly) maintained margins and fringes	9	4.5
Removal of forest, woodland, scrubland	**19**	**9.4**
Recent deforestation (natural (windfall) or anthropogenic)	14	6.9
Recent clearing of scrubland	5	2.5
Mining / habitat destruction	**17**	**8.4**
Succession after abandonment of sand pits or rock quarries	14	6.9
Succession after habitat destruction	3	1.5
Persistent disuse	**22**	**6.5**
Disused terrestrial herbaceous sites	6	3
Disused riverbanks	5	2.5
Forest (margins)	2	1

sionally maintained herbaceous fringes occurred alongside boundary lines, like e.g. paths, tracks, ditches, and small rivers (7.9 %) and, rather rarely, recent abandonment of arable fields was observed (3 %).

Sites subject to continuous agricultural land use over the whole period were found with a frequency of 17.9 %. Predominantly, these sites were persistently managed grasslands and, secondarily, former arable land which was converted to managed grasslands prior to approx. 2000. However, 25 % of these sites showed signs of declining use or abandonment during the time span between the most recent aerial photograph (approx. 2000) and the field survey (2002, 2003). Other constant habitats were maintained grassland-like fringes which persisted since the 1950s at 4.5 % of sites.

Processes putting afforested sites and scrubland back to herbaceous stages were found at 9.4 % of sites. These included felling of forest trees on supply line routes, windbreak (during a 1990 hurricane), removal of extensive scrub by land machinery, and removal of single bushes or trees along field margins and railway embankments.

Habitat destruction by opencast mining (rock quarry, sand pit) or other (unknown) means inducing subsequent secondary successions on bare soil occurred at 8.4 % of sites. Termination of mining had, throughout, taken place after the 1970s, while other kinds of habitat destruction were found before the 1970s, between the 1970s and today, or in both time spans.

Constant habitats which were never subject to any kind of land management within the surveyed time period were observed at 6.5 % of sites in the form of forests, quasi-natural herbaceous riverbanks or disused terrestrial herbaceous vegetation.

To summarize, by far the majority of sites had undergone considerable habitat alterations due to change or abandonment of land use, or severe disturbances (71.3 %). Constantly managed or maintained sites (22.4 %) and, on the other hand, long-term disused sites (6.5 %) accounted for much lesser proportions.

4.1.3 Soil texture and water balance

Concerning soil texture, loamy soils prevailed (63 %), followed by silty or loamy sands (19 %), silty or loamy clay (14 %) and loamy silt (4 %). Pure sand was found only once at a riverbank site and pure clay soils did not occur. Estimates of available field capacity showed a median of 168 mm and the 10–90 percentile range was 140 to 220 mm which can be classified (from an agricultural perspective) as medium capacity for soil moisture (Table 3). Some sites showed signs of impeded drainage which was classified as ‘very modest’ or ‘modest’ in 19 % and ‘medium’ in 2.5 % of sites. Periods of wetness did not extend into the summer. On the whole, soils offered favourable conditions, were generally well aerated, at least during the growing season, and provided for a good water supply.

Table 3. Chemical characteristics and available field capacity of the effective root zone (AFC) of soils sampled from investigated plots (median, minimum, 10 and 90 percentile, maximum and evaluation of the medians where applicable). Nutrient content classes B, C and D refer to suboptimal, optimal, and more than optimal supply of the respective nutrients in arable fields.

Parameter	n	median	min.	10 perc.	90 perc.	max.	evaluation of median
P_{CAL} [mg/100g]	202	1.7	0.00	0.2	8.1	31.4	content class B
K_{CAL} [mg/100g]	202	8.3	0.75	4.2	21.6	77.8	content class C
N_t [% SDM]	202	0.3	0.04	0.2	0.4	1.0	n/a
Mg_{CACl2} [mg/100g]	202	14.3	2.96	7.0	27.0	50.1	content class (C–)D
C_{org} [% SDM]	192	2.8	0.36	1.6	5.2	9.0	medium humic
C/N ratio	192	9.8	6.40	8.2	16.3	28.3	narrow
pH_{H2O}	118	5.6	4.0	4.9	6.4	7.3	medium acidic
$AFC_{root\ zone}$ [mm]	118	168	30	140	220	275	medium

4.1.4 Chemical soil conditions

Median values of phosphorus, potassium and magnesium (Table 3) could be classified as fair or rich, according to the classification of nutrient contents of arable soils (classes B, C, (C–)D, respectively). Also total nitrogen content suggested good supply of this resource. Notwithstanding wide-ranging variance and occasional low values, measured soil nutrient concentrations indicated a generally high trophic level of investigated plots.

Total carbon content was exceedingly high in 10 samples altogether, which was due to a noticeable lime content in 9 samples and high content of organic carbon in one sample from an anthropogenically disturbed soil. These samples were left out when calculating statistics for carbon given in Table 3. In the remaining 192 samples total carbon content was equivalent to organic carbon (humus). The median value was 2.8 % which indicates medium humic soils.

C/N ratios were markedly narrow with a median of 9.8 and values only exceptionally exceeding 20. These values make a reference to fast nutrient cycling and underpin a good nutrient balance of sites.

PH values varied widely and the limiting values of the 10–90 percentile range (4.9–6.4) corresponded to strongly acidic and moderately acidic soil reaction while the median of 5.6 could be classified as medium acidic. This shows that the species is quasi indifferent to soil reaction and can colonise, with respect to pH values, all soils except for extremely calcareous or acidic ones.

4.1.5 Light supply

H. mantegazzianum was prevalently found at open sites whose light supply was classified as ‘full light’ (46 %) or ‘light’ (32 %) while ‘semi-shade’ (15 %) and, in particular, ‘shade’ (7 %) made up only minor proportions. The median value was in the class ‘light’. Results show a clear preference of the species for sites with high light supply although growth of the plant is still fair in semi-shaded situations. No occurrences, however, were found in dark shade of a closed tree canopy.

4.1.6 Ellenberg indicator values

Ellenberg indicator values are presented here (Table 4) to supplement the results of site parameters measured or estimated in the field. Mean light supply numbers underpinned the preference for open sites with a tolerance for moderate shading. Also moisture values which indicated water supply in the range of fresh to moist conditions were in good agreement with the field records. Average nutrient values suggested moderate to pronounced nutrient richness which again fitted the field data well.

The median of average soil reaction numbers was 6.5 which corresponded to near neutral pH values and, for comparison, plants assigned to the value 7 are not able to colonise strongly acidic soils. Only very few

Table 4. Unweighted mean Ellenberg indicator values of vegetation relevés from investigated plots (median, minimum, 10 and 90 percentile, maximum and evaluation of median). Evaluations of medians follow the definitions of the indicator scales in ELLENBERG et al. (1992).

Indicator scale	n	median	min.	10 perc.	90 perc.	max.	evaluation of median
Light	202	6.6	4.8	5.6	7.0	7.4	semi-light (– semi-shade)
Moisture	202	6.0	4.8	5.2	6.8	7.5	fresh – moist
Reaction	202	6.5	4.1	5.6	7.0	7.7	circum-neutral – lightly acidic
Nutrients	202	6.4	4.0	5.3	7.5	8.3	moderately rich – rich

outliers were in a range that is indicative of soil reaction intermediate between moderately acidic and acidic conditions. Thus, Ellenberg values for soil reaction seemed to indicate slightly higher pH values than actually measured in the soil samples.

Altogether, Ellenberg values corresponded well to measured and estimated parameters of abiotic site conditions.

4.2 Plant communities invaded by H. mantegazzianum (Table 5)

4.2.1 Overview

H. mantegazzianum occurred primarily in two main vegetation classes: (1) semi-natural grasslands (Molinio-Arrhenatheretea) and (2) nitrophilous tall-forb communities (Galio-Urticetea). Some occurrences were also found in alluvial woodlands (Alnenion glutinoso-incanae, Salicion elaeagni), pioneer tree stands, plantations and former orchards. In such tree-dominated communities *H. mantegazzianum* was, however, restricted to margins and gaps. Singular occurrences of *H. mantegazzianum* could be observed in herbaceous pioneer vegetation at strongly disturbed site such as former quarries and a brownfield.

4.2.2 Grasslands (Molinio-Arrhenatheretea)

Within the class Molinio-Arrhenatheretea *H. mantegazzianum* was confined to eutrophic grassland communities with mesic water balance, i. e. freely-draining soils with favourable water supply, namely the alliances Arrhenatherion and Cynosurion (Table 5, 1.1 and 1.2). Only twice *H. mantegazzianum* was found in wet-grassland communities of the alliance Calthion.

The stands belonging to the alliances Arrhenatherion and Cynosurion share frequent records for the full range of Molinio-Arrhenatheretea and Arrhenatheretalia species. Cynosurion stands additionally show preferential occurrences of species characteristic of pastures and meadows with high mowing frequency, namely *Lolium perenne*, *Phleum* *pratense*, *Trifolium repens* and *Plantago major*, while the Arrhenatherion stands are characterised by consistent records of *Arrhenatherum elatius* and generally slightly higher frequencies and abundances of other tall grasses, such as *Alopecurus pratensis* and *Trisetum flavescens*.

Cynosurion-grasslands colonised by *H. mantegazzianum* were found in horse paddocks and mown pastures representing the typical sub-community of the Cynosuro-Lolietum Br.-Bl. et De Leeuw 1936. Species typical of poor or dry subtypes (e.g. C.-L. luzuletosum, C.-L. ranunculetosum bulbosi; cf. Dierschke 1997), such as *Luzula campestris* agg., *Hieracium pilosella*, *Viola canina* or *Ranunculus bulbosus*, were completely absent whereas differential species of moist sub-communities (C.-L. lotetosum uliginosi), such as *Lotus pedunculatus* (syn. *Lotus uliginosus*), *Achillea ptarmica* and *Carex hirta* occurred at least in some of the relevés in moderate quantity. Notably, tall forbs characteristic of the alliance Filipendulion (*Filipendula ulmaria*, *Lythrum salicaria*) and of nitrophilous herb communities of the class Galio-Urticetea (*Urtica dioica*, *Aegopodium podagraria*), had fairly high constancies indicating low land-use intensity.

The observed Arrhenatherion communities comprised (managed) meadows (Table 5, 1.2.1 and 1.2.2) and ruderal grasslands (1.2.3 and 1.2.4). Meadows with *H. mantegazzianum* mostly belonged to the Arrhenatheretum elatioris Koch 1926 although some stands were missing the characteristic species *Arrhenatherum elatius* and *Galium mollugo* agg. Most of the stands were used for haymaking, however, some meadow-like stands without agricultural land use were included too. These were road verges and green areas apparently subject to regular maintenance mowing and also former agricultural meadows, which have been abandoned only recently prior to sampling. The meadows and meadow-like stands could predominantly be allocated to the typical sub-community group of the Arrhenatheretum elatioris (Table 5, 1.2.1) which is characterised by the lack of differential species (Dierschke 1997). Some relevés contained species indicating fairly moist conditions, such as *Angelica sylvestris*, *Cirsium palustre* and *Lotus pedunculatus*, and therefore belonged to the sub-community group of *Silene* (= *Lychnis*) *flos-cuculi* (Table 5, 1.2.2) which is transitional to Molinietalia wet grasslands. As with Cynosurion stands, species indicative of nutrient poor or dry subtypes (sub-community group of *Briza media*, cf. Dierschke 1997) could not be found.

The ruderal grasslands (Table 5, 1.2.3 and 1.2.4) comprised abandoned or neglected stands of agricultural origin and rather irregularly managed swards on road verges, field margins, embankments and ditches. They could be distinguished from the meadows by species characteristic of Artemisietea and, especially, Galio-Urticetea communities supplementing the stock of common grassland plants and sometimes reaching fairly high abundances. On the other hand, ruderal grasslands are, by definition, distinct from tall-forb communities in the preponderance of grassland monocots and herbs (Fischer 1985). The most constant and typical ruderal species of the ruderal grasslands with *H. mantegazzianum* were *Urtica dio-*

Table 5. Constancy table of vegetation types with *Heracleum mantegazzianum* found in study areas. All relevés that could be assigned to specific syntaxa or at least compiled to a group of similar vegetation stands (anthropogenic floodplain forests) were included into the constancy table (n = 179) while singular relevés not assignable to a specific syntaxon were omitted and are referred to in the text only (n = 23). The symbols representing constancy classes follow common convention (cf. e.g. Dierschke 1994, p. 192). If the number of relevés in a column is less than five, absolute frequencies are presented (col-

1 Arrhenatheretalia
1.1 Cynosurion
1.2 Arrhenatherion
1.2.1 Managed Arrhenatherion meadows
1.2.2 Managed Arrhenatherion meadows, wet sub-com.
1.2.3 Ruderal Arrhenatherion grasslands
1.2.4 Ruderal Arrhenatherion grasslands, wet sub-com.

		1				
		1.1	1.2			
			1.2.1	1.2.2	1.2.3	1.2.4
	Number of relevés	7	24	5	43	10
	Average height of layers [m]					
	Tree layer				13 $^{0-20}$	10 $^{0-10}$
	Shrub layer				5 $^{0-5}$	3,3 $^{0-5}$
	Field layer	0,2 $^{0.15-0.3}$	0,4 $^{0.2-0.8}$	0,5 $^{0.4-0.7}$	0,6 $^{0.1-1.2}$	0,6 $^{0.3-1}$
	Heracleum mantegazzianum	0,4 $^{0.25-0.6}$	0,6 $^{0.3-1}$	0,8 $^{0.6-1.1}$	0,9 $^{0.35-1.7}$	1,0 $^{0.8-1.7}$
	Average cover of layers [%]					
	Total	93 $^{80-98}$	93 $^{60-100}$	97 $^{90-100}$	94 $^{80-100}$	89 $^{50-98}$
	Tree layer				42 $^{0-90}$	38 $^{0-50}$
	Shrub layer				5 $^{0-5}$	3 $^{0-5}$
	Field layer	88 $^{80-95}$	88 $^{60-99}$	93 $^{85-95}$	72 $^{20-95}$	79 $^{30-95}$
	Heracleum mantegazzianum	15 $^{2-60}$	17 $^{1-70}$	15 $^{10-20}$	46 $^{5-90}$	35 $^{10-80}$
	Litter	5 $^{1-10}$	19 $^{0-60}$	15 $^{1-60}$	19 $^{0-70}$	11 $^{1-20}$
	Mosses	1 $^{0-2}$	2 $^{0-10}$	2 $^{0-5}$	12 $^{0-45}$	18 $^{0-75}$
	Soil	15 $^{2-60}$	12 $^{0-50}$	3 $^{0-10}$	18 $^{0-60}$	5 $^{0-20}$
	Average species number	31,57 $^{15-46}$	21,92 $^{8-35}$	27 $^{21-32}$	20,47 $^{6-47}$	28,9 $^{17-40}$
	Heracleum mantegazzianum	V $^{+-4}$	V $^{+-4}$	V $^{a-b}$	V $^{a-5}$	V $^{a-5}$
	Cynosurion					
	Phleum pratense	**V** $^{1-a}$	IV $^{+-b}$	I ^{a}	II $^{1-b}$	I ^{1}
	Trifolium repens	**V** $^{1-a}$	II $^{1-a}$	.	I $^{+-m}$	+ ^{m}
	Lolium perenne	**V** $^{1-b}$	II $^{1-b}$	.	r ^{1}	.
D	Plantago major major	**V** $^{+-1}$	.	.	r $^{+}$	.
	Arrhenatherion					
	Arrhenatherum elatius	.	**IV** $^{1-4}$	**III** ^{a}	**IV** $^{1-4}$	**IV** $^{1-a}$
	Galium mollugo agg.	III $^{+-1}$	**IV** $^{+-1}$	**IV** $^{1-m}$	**III** $^{+-a}$	**III** $^{+-a}$
d	Angelica sylvestris	.	r $^{+}$	**V** $^{+-a}$	+ $^{r-+}$	**IV** $^{+-1}$
d	Cirsium palustre	.	r $^{+}$	**IV** $^{+-1}$	r $^{r-+}$	**V** $^{r-+}$
d	Lotus pedunculatus	I ^{1}	.	**III** $^{+-m}$	.	**III** $^{1-m}$
	Arrhenatheretalia					
	Dactylis glomerata	V $^{1-b}$	V $^{1-3}$	IV $^{+-b}$	V $^{1-3}$	IV $^{1-3}$
D	Anthriscus sylvestris sylvestris	III $^{+-1}$	IV $^{+-1}$	.	III $^{r-a}$	+ ^{r}
D	Veronica chamaedrys s.l.	.	II $^{+-m}$	I ^{a}	II $^{+-m}$	III $^{+-m}$
D	Heracleum sphondylium	I ^{1}	III $^{r-a}$	.	II $^{r-1}$	.
	Trisetum flavescens flavescens	.	II $^{1-a}$	.	I $^{+-m}$	+ ^{1}
	Leucanthemum vulgare	I ^{1}	I $^{1-m}$	.	+ $^{+-1}$	III $^{+-1}$
	Crepis biennis	II $^{+}$	I $^{+}$	.	r $^{+}$	.
	Mol.-Arrhenatheretea					
	Holcus lanatus	IV $^{1-b}$	IV $^{1-4}$	V $^{1-b}$	IV $^{+-3}$	V $^{1-b}$
	Ranunculus repens	V $^{1-b}$	IV $^{+-a}$	IV ^{1}	III $^{r-a}$	IV $^{1-a}$
	Alopecurus pratensis	IV $^{1-a}$	V $^{1-4}$	IV $^{a-3}$	III $^{1-3}$	II $^{a-4}$

umns 2.2, 3.1, 3.2, 4). Companion species that never exceeded frequency class 'I' in any column and had no more than a single occurrence in a column with less than five relevés are listed in the table footer. Differential species of associations and higher syntaxa are marked with 'D' while differential species of sub-communities are marked with 'd'. Differential species of the class Galio-Urticetea differentiate against Artemisietea s.str. and vice versa. Differential species listed under Calystegion or Alliarion each differentiate against the other alliances within Galio-Urticetea (cf. DENGLER 1997).

2 Galio-Urticetea
  2.1 Galio-Urticetea basal communitiy
  2.2 Galio-Alliarion
  2.3 Aegopodion
    2.3.1 Aegopodion, typical sub-communities
    2.3.2 Aegopodion, Calystegia sub-communities
  2.4 Calystegion, Aegopodium sub-communities

3 Alno-Ulmion
  3.1 Stellario-Alnetum
  3.2 Alnetum incanae
4 Salicion elaeagni
5 Anthropogenic floodplain forests

2					3		4	5
2.1	2.2	2.3		2.4	3.1	3.2		
		2.3.1	2.3.2					
21	3	10	13	31	3	2	2	5
16 $^{0-30}$	14 $^{10-18}$	19 $^{0-20}$	12 $^{0-18}$	15 $^{0-20}$	19 $^{17-20}$	9 $^{8-10}$	14 $^{12-15}$	17 $^{12-20}$
2 $^{0-2.3}$	2,8 $^{0-3}$	0,8 $^{0-0.8}$	7 $^{0-7}$	1,8 $^{0-2.2}$		1,5 $^{0-1.5}$	4,3 $^{2.6-6}$	2,5 $^{0-2.5}$
0,6 $^{0.1-1.4}$	0,4 $^{0.3-0.5}$	0,5 $^{0.2-1.1}$	0,7 $^{0.3-1.2}$	0,8 $^{0.3-1.7}$	0,4 $^{0.35-0.45}$	0,8 $^{0.8-0.8}$	0,8 $^{0.4-1.2}$	0,6 $^{0.3-1.1}$
1,4 $^{0.6-2.4}$	1,2 $^{1-1.3}$	1,2 $^{0.4-1.8}$	1,2 $^{0.8-1.8}$	1,0 $^{0.4-1.7}$	1,0 $^{0.8-1.1}$	1,1 $^{0.8-1.3}$	1,3 $^{1.3-1.3}$	0,9 $^{0.6-1.1}$
90 $^{45-95}$	90 $^{90-90}$	82 $^{15-100}$	89 $^{70-98}$	88 $^{45-98}$	87 $^{80-90}$	75 $^{60-90}$	75 $^{65-85}$	86 $^{80-90}$
33 $^{0-50}$	52 $^{30-65}$	20 $^{0-30}$	22 $^{0-45}$	33 $^{0-60}$	80 $^{70-85}$	28 $^{15-40}$	48 $^{30-65}$	73 $^{60-80}$
5 $^{0-5}$	3,5 $^{0-5}$	2 $^{0-2}$	80 $^{0-80}$	1,5 $^{0-2}$		5 $^{0-5}$	5,5 $^{1-10}$	3 $^{0-3}$
35 $^{1-90}$	45 $^{20-65}$	38 $^{5-98}$	58 $^{20-80}$	66 $^{20-95}$	30 $^{25-40}$	48 $^{15-80}$	25 $^{25-25}$	44 $^{25-80}$
67 $^{5-95}$	57 $^{10-80}$	52 $^{5-95}$	47 $^{10-85}$	34 $^{5-90}$	13 $^{5-20}$	15 $^{10-20}$	40 $^{35-45}$	16 $^{5-30}$
18 $^{5-60}$	9 $^{2-15}$	23 $^{5-60}$	24 $^{1-60}$	23 $^{5-60}$	52 $^{35-60}$	5 $^{5-5}$	23 $^{20-25}$	26 $^{1-60}$
15 $^{0-70}$	30 $^{5-50}$	14 $^{2-60}$	10 $^{0-60}$	8 $^{0-60}$	1 $^{1-2}$	3 $^{1-5}$	15 $^{5-25}$	12 $^{5-30}$
47 $^{0-90}$	33 $^{20-50}$	42 $^{1-85}$	32 $^{0-70}$	41 $^{0-95}$	27 $^{20-30}$	50 $^{20-80}$	43 $^{25-60}$	28 $^{0-80}$
11,05 $^{4-23}$	22,33 $^{22-23}$	10,8 $^{6-17}$	19 $^{12-29}$	14,97 $^{4-26}$	14,33 $^{11-18}$	23 $^{16-30}$	19 $^{12-26}$	16,8 $^{11-22}$
V $^{a-5}$	3 $^{a-5}$	V $^{a-5}$	V $^{a-5}$	V $^{a-5}$	3 $^{a-b}$	2 $^{a-b}$	2 ^{3}	V $^{a-3}$
+ $^{1-a}$	.	.	+ ^{1}	.	.	1 ^{1}	.	.
.	.	.	.	.	.	.	.	.
r ^{1}	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
I $^{1-a}$	.	II $^{1-m}$	II ^{1}	II $^{1-a}$	.	.	.	.
.	.	I $^{1-a}$	I ^{1}	+ ^{1}	.	1 $^{+}$	.	.
.	.	.	.	+ $^{r-+}$	.	.	.	.
I $^{r-+}$	.	.	+ $^{+}$	.	.	.	.	.
.	.	.	.	.	.	.	.	.
III $^{+-b}$	1 ^{1}	I ^{1}	IV $^{+-a}$	I $^{1-a}$	1 $^{+}$	.	1 ^{r}	IV $^{+-m}$
r ^{a}	.	+ ^{1}	II $^{r-+}$	I $^{r-a}$	.	.	.	I ^{r}
.	.	.	+ ^{m}	.	.	.	.	I ^{m}
r ^{r}	.	+ ^{1}	+ ^{r}	.	.	.	.	.
r ^{1}	.	.	+ ^{1}	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
I $^{1-a}$	.	.	I $^{1-b}$	+ $^{+-a}$	.	.	.	.
II $^{+-1}$	2 ^{1}	.	II $^{+-m}$	+ $^{+-1}$	1 $^{+}$	1 $^{+}$	.	I ^{1}
r ^{a}	.	I $^{1-b}$	III $^{1-a}$	II $^{1-m}$	.	.	.	.

Table 5. (cont.)

	Festuca rubra agg.	I^{a}	II^{1-b}	IV^{m}	II$^{1-3}$	IV^{1-a}
	Rumex acetosa	I^{+}	III^{+-m}	II^{1}	II^{r-1}	III^{r-1}
	Agrostis stolonifera	III^{a-b}	II$^{1-3}$	I^{3}	I^{1-a}	II$^{1-3}$
	Lathyrus pratensis	III^{+-1}	II^{+-1}	II^{1}	II^{+-a}	+$^{+}$
	Achillea millefolium agg.	III^{1-m}	II^{+-b}	I^{1}	I^{+-1}	I^{+-m}
	Poa pratensis s.str.	III^{+-a}	II^{+-a}	.	I^{1-a}	III^{1}
	Bistorta officinalis	V^{+-1}	I^{+-m}	IV^{1-a}	r^{1}	I^{1}
	Festuca pratensis	III^{1-b}	III^{+-b}	II^{1-m}	r^{1}	I^{1-a}
	Cardamine pratensis pratensis	I^{r}	II^{+-1}	III^{+-1}	r^{+-1}	I^{1}
	Vicia cracca	I^{1}	+$^{+-1}$	II^{+-m}	I^{1-a}	II^{+-1}
	Plantago lanceolata	I^{1}	III^{+-m}	.	+$^{+}$	I^{+}
	Cerastium holosteoides	III^{+-1}	II^{+-m}	.	I^{+-1}	.
	Ajuga reptans	.	r^{+}	I^{+}	r^{1}	III^{+-1}
	Trifolium pratense	I^{1}	II^{+-a}	I^{+}	+$^{+-1}$	.
	Prunella vulgaris	III^{1-m}	r^{+}	.	.	III^{r-1}
	Sanguisorba officinalis	II^{1}	+$^{+-1}$	III^{+-1}	.	+^{1}
	Centaurea jacea	III^{+-1}	+$^{+-1}$	II^{1-m}	r^{r-+}	.
	Ranunculus acris agg.	III^{+}	+$^{+-1}$	I^{1}	r^{1}	+^{1}
	Bellis perennis	III^{+-1}	r^{+}	.	.	.
	Colchicum autumnale	.	.	I^{+}	.	.
Galio-Urticetea						
D	Poa trivialis	V$^{1-3}$	IV^{1-b}	IV^{m-a}	IV^{+-4}	III^{1-b}
	Urtica dioica dioica	III^{+-1}	II^{+-a}	.	**IV**$^{1-3}$	**II**^{1}
D	Galium aparine	.	I^{+}	.	**IV**$^{+-a}$	**II**$^{+-1}$
D	Galeopsis tetrahit	.	r^{+}	.	**II**$^{r-1}$	**III**$^{+-1}$
	Glechoma hederacea	III^{+-1}	II^{+-m}	.	**II**$^{1-m}$	**+**$^{+}$
	Geum urbanum	II^{+}	.	.	**II**$^{+-m}$	.
	Rumex obtusifolius	III^{+}	II^{r-1}	.	**I**$^{r-+}$	**+**$^{+}$
	Chelidonium majus	.	.	.	.	.
Artemisietea s. l.						
	Solidago gigantea	.	.	.	+$^{+-1}$	.
	Artemisia vulgaris	I^{1}	.	.	r^{+}	+$^{+}$
	Arctium minus	III^{+-a}	.	.	r^{+}	.
Artemisietea s.str.						
	Elymus repens	III^{1-a}	IV^{+-3}	III$^{1-3}$	III^{+-4}	I^{1-a}
	Tanacetum vulgare	II^{+}	r^{a}	.	I^{r-a}	.
D	Agrimonia eupatoria	.	.	I^{1}	I^{+}	+^{1}
D	Cirsium vulgare	.	.	.	.	I^{r-+}
D	Convolvulus arvensis	.	r^{1}	.	+$^{r-1}$	.
	Pastinaca sativa	.	r^{+}	.	r^{+}	.
	Linaria vulgaris	.	r^{r}	.	.	.
	Melilotus albus	.	.	.	r^{r}	.
	Melilotus officinalis	.	.	.	.	+$^{+}$
	Picris hieracioides s.l.	.	r^{+}	.	.	.
Alliarion						
	Alliaria petiolata	.	.	.	.	.
D	Stachys sylvatica	.	r^{+}	.	II^{+-1}	.
	Geranium robertianum	I^{r}	.	.	.	.
D	Moehringia trinervia	.	.	.	r^{+}	.
D	Poa nemoralis	.	.	.	+$^{+-1}$	.
D	Brachypodium sylvaticum	.	.	.	.	.
D	Scrophularia nodosa	.	.	.	.	.
D	Epilobium montanum	.	r^{+}	.	.	I^{+-1}

r^{m}	.	+^{1}	.	.	.	.	.	.
.	.	.	+^{r}	r^{r}	.	.	.	.
r^{a}	.	+^{m}	I^{1}	+^{1}	.	2^{a-b}	1^{1}	.
r^{+}	.	+$^{+}$	+$^{+}$	+$^{+-1}$	.	.	.	.
r^{1}	.	+^{r}	.	.	.	.	.	.
r^{1}	.	.	+^{1}	.	.	.	.	.
.	.	+^{1}	.	+$^{+}$	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	+$^{+}$	+$^{+}$	.	.	.	.
.	.	.	+$^{+}$	r^{1}	.	.	.	.
r^{r}	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
r^{1}	.	.	.	r^{+}	.	.	.	.
.	.	.	.	.	.	.	.	.
r^{r}	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
III$^{1-4}$	3^{+-1}	IV$^{1-4}$	IV$^{1-3}$	IV$^{1-3}$	3^{1}	2^{m}	1^{1}	III^{a-b}
V^{+-5}	3^{m-b}	V^{+-3}	V$^{1-3}$	V$^{1-5}$	3^{1}	2^{+}	2^{1-b}	V^{1-a}
III^{+-a}	3^{1}	IV^{+-a}	IV^{+-a}	V^{+-a}	1^{+}	.	2^{+}	IV^{1}
I^{r-1}	.	II^{r-1}	.	II^{+-1}	.	.	2^{r-+}	I^{1}
I^{1-m}	2$^{1-3}$	III^{1-b}	IV^{+-a}	II^{+-a}	.	.	1^{1}	IV^{1-a}
I^{+-1}	2^{+-1}	I^{+-1}	III^{+-1}	+^{1}	.	.	1^{r}	IV^{+-a}
+$^{+}$	1^{1}	.	+$^{+}$	+$^{r-1}$	.	1^{r}	1^{r}	.
.	.	.	+$^{+}$	.	.	.	.	.
I^{+-1}	2^{+}	.	+$^{+}$	I$^{1-4}$	.	.	.	I^{1}
.	.	.	+^{r}	+$^{r-+}$	.	.	.	.
.	.	.	.	r^{+}	.	.	.	.
I^{1-a}	.	.	II^{1-m}	I^{+-a}	.	.	.	.
.	.	+$^{+}$	.	+^{r}	.	.	.	.
r^{r}	.	.	.	.	.	.	.	I^{r}
.	.	.	.	+$^{+}$	.	.	.	.
r^{r}	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
r^{1}	**3**$^{1-a}$	II^{+-1}	II^{+-1}	II^{r-m}	1^{1}	.	.	I^{1}
r^{+}	**2**$^{r-1}$	+^{1}	I^{+}	+$^{r-1}$	1^{+}	.	.	I^{+}
+$^{+-1}$	**2**$^{+-1}$	.	.	r^{1}	.	1^{+}	1^{1}	II^{+-1}
I^{+-1}	**1**^{1}	+^{1}	I^{+-1}	r^{1}	.	.	.	II^{1-m}
+^{1}	**1**^{a}	.	+^{a}	I^{1-m}	1^{1}	.	1^{1}	III^{1-a}
.	**1**^{1}	.	+^{1}	.	.	1^{1}	.	.
.	**1**^{1}	.	.	r^{r}	.	.	.	.
I^{+-1}	.	.	+^{1}	.	.	.	.	.

Table 5. (cont.)

	Chaerophyllum temulum	.	r ^{1}	.	+ $^{+-1}$	.
D	Lapsana communis	.	r ^{1}	.	r $^{+-1}$	.
D	Lamiastrum galeobdolon	.	.	.	.	.
Aegopodion						
	Aegopodium podagraria	III ^{a}	II $^{+-a}$	II ^{a}	II $^{+-a}$	.
	Petasites hybridus	II $^{+-a}$	+ $^{+-1}$	.	+ $^{+-a}$	.
	Lamium maculatum	.	.	.	r ^{1}	.
	Silene dioica	.	.	.	.	.
	Lamium album	.	r ^{1}	.	r $^{+}$	.
	Cruciata laevipes	.	r ^{1}	.	.	.
	Chaerophyllum bulbosum	.	.	.	r $^{+}$	.
	Chaerophyllum aureum	.	I $^{+-1}$	.	r $^{+}$	.
Calystegion						
	Impatiens glandulifera	I $^{+}$	.	.	r ^{r}	.
D	Symphytum officinale	I ^{1}	I $^{r-+}$	.	r ^{3}	.
	Calystegia sepium	I ^{1}	r $^{+}$	.	I $^{+-1}$	+ ^{1}
	Carduus crispus	.	.	.	r $^{r-+}$	.
	Humulus lupulus	.	.	.	r $^{+}$	.
D	Filipendula ulmaria	III ^{1}	+ $^{+-1}$	III $^{+-1}$	II $^{+-1}$	+ $^{+}$
D	Phalaris arundinacea	.	.	I ^{b}	I $^{+-1}$	.
D	Cirsium oleraceum	I $^{+}$	I $^{r-+}$	.	+ $^{+-1}$	.
D	Stachys palustris	I ^{1}	.	I ^{1}	r ^{1}	.
D	Lythrum salicaria	III $^{+}$	.	.	r ^{r}	.
D	Eupatorium cannabinum	.	.	.	+ $^{+-1}$	.
D	Poa palustris	.	.	.	r ^{1}	.
	Cuscuta europaea	.	.	.	.	.
D	Rubus caesius	.	.	.	.	.
	Myosoton aquaticum	.	.	.	.	.
	Epilobium hirsutum	.	.	.	r ^{r}	.
D	Mentha longifolia	.	.	.	+ ^{1}	.
Stellario-Alnetum						
D	Stellaria nemorum	II $^{+-1}$	.	.	r ^{1}	.
D	Alnus glutinosa	.	.	.	.	.
D	Salix fragilis	.	.	.	.	.
Alnetum incanae						
	Alnus incana	.	.	.	.	.
Alno-Ulmion - Fagetalia						
	Elymus caninus	.	.	.	r $^{1-a}$	.
	Festuca gigantea	II ^{1}	.	.	.	.
	Stellaria holostea	.	.	I ^{1}	I $^{+-1}$	+ ^{1}
	Circaea lutetiana	.	.	.	.	.
	Impatiens noli-tangere	.	.	.	.	.
	Arum maculatum	.	.	.	.	.
	Rumex sanguineus	I $^{+}$	.	.	r $^{r-1}$	+ $^{+}$
Salicion elaeagni						
	Salix eleagnos	.	.	.	.	.
Anthropogenic floodplain forests						
	Fraxinus excelsior	.	+ $^{+}$	.	+ $^{+-a}$	.
	Acer pseudoplatanus	.	r ^{r}	.	.	.
	Populus nigra	.	.	.	.	.
	Salix alba	.	.	.	.	.
Companions						
	Cirsium arvense	V $^{+-a}$	IV $^{r-1}$	V $^{+-1}$	II $^{+-a}$	III $^{+-b}$

.	.	+^{1}	+$^{+}$	.	.	.	.	.
r^{r}	.	.	.	r^{+}	.	.	.	.
r^{b}	.	.	.	+$^{+-1}$	.	.	.	.
.	1^{3}	**V**$^{+-3}$	**IV**$^{1-4}$	**IV**$^{+-b}$	3^{a-3}	.	1^{1}	III$^{1-3}$
.	.	**I**$^{+-5}$	**II**$^{1-3}$	**I**$^{+-a}$	.	.	.	.
.	.	**+**^{1}	**II**$^{+-1}$	**+**^{1}	.	.	.	.
.	.	.	**II**$^{+-1}$	**+**$^{+-1}$	1^{+}	.	.	.
.	1^{1}	.	**I**$^{+}$	**I**$^{+-1}$	.	.	.	.
.	.	.	**I**^{1}	.	.	.	.	.
.	.	.	**+**^{r}	.	.	.	.	.
.	.	.	.	.	.	.	.	.
I^{1-b}	3^{+-1}	.	**II**$^{+-a}$	**IV**$^{r-3}$	2^{+-1}	1^{1}	2^{+-a}	I^{1}
r^{a}	3^{+-a}	+$^{+}$	**III**$^{+-b}$	**III**$^{r-4}$	.	.	.	III^{1-a}
I^{+-1}	.	.	**II**$^{+-3}$	**III**$^{+-a}$	1^{+}	.	.	.
.	1^{r}	+$^{+}$	**I**$^{r-1}$	**II**$^{+-1}$	.	.	.	.
.	1^{+}	.	**+**$^{+}$	**II**$^{+-a}$	.	.	.	.
r^{a}	.	+$^{+}$	**II**$^{+-1}$	**I**$^{+-b}$	.	.	.	.
.	.	.	**I**^{1}	**I**$^{+-a}$	2^{+-1}	2^{1-a}	.	I^{+}
+$^{r-1}$	.	.	**I**$^{r-+}$	**I**$^{+-a}$	.	.	.	.
.	.	.	**II**$^{+-1}$	**r**^{1}	.	.	.	.
.	.	.	.	**+**$^{r-1}$	.	.	.	.
.	.	.	.	**+**$^{+-1}$	.	.	.	.
.	.	.	**+**^{1}	**+**^{1}	1^{+}	.	.	.
.	.	.	.	**+**$^{+-m}$	.	.	.	.
.	.	.	**+**$^{+}$	**r**$^{+}$	.	.	.	I^{+}
.	.	.	.	**r**^{1}	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	**+**$^{+}$	.	.	1^{+}	.	.
.	.	I^{a}	IV^{1-a}	III^{+-3}	**3**$^{+-a}$	.	.	I^{a}
.	2$^{3-4}$	+^{3}	+^{3}	.	**3**$^{4-5}$	.	.	I^{4}
.	.	+^{a}	+^{a}	I^{a-4}	**1**^{a}	1^{a}	.	.
.	.	.	.	.	.	**2**^{a}	.	.
.	.	.	I^{+-1}	I^{+-a}	**2**^{1}	.	.	.
.	.	.	I^{+}	I^{+-1}	**2**^{1}	1^{+}	.	.
+$^{1-m}$	.	.	I^{+-1}	r^{1}	**1**^{a}	.	.	II^{m}
r^{1}	.	.	.	.	**1**^{1}	.	.	.
.	.	.	+^{r}	.	**1**^{1}	.	.	.
.	.	.	.	.	**1**$^{+}$	.	.	.
r^{+}	.	+$^{+}$	+^{1}	.	.	1^{+}	.	.
r^{b}	.	.	.	.	.	.	**2**$^{3-4}$	.
I^{+}	1^{+}	+$^{+}$	.	+$^{r-+}$	.	.	1^{+}	III^{+-4}
+$^{r-+}$	2^{1-a}	.	.	r^{a}	.	1^{+}	.	IV^{+-5}
.	.	.	.	.	.	.	.	II^{b-4}
.	.	.	.	.	.	.	.	I^{4}
+$^{r-a}$	.	+^{1}	.	I^{+-a}	.	.	.	.

Table 5. (cont.)

Taraxacum officinale agg.	V^{+-b}	IV^{+-a}	.	II^{+-1}	I^{+-1}
Rubus fruticosus agg.	.	.	.	II^{+-a}	+$^{+}$
Deschampsia cespitosa	I^{+}	+$^{+-1}$	III^{a-b}	+$^{+-1}$	III^{+-a}
Vicia sepium	III^{+}	r^{+}	I^{1}	II^{+-m}	I^{1}
Hypericum perforatum	.	II^{+-a}	I^{1}	II^{1}	III^{+-1}
Agrostis capillaris	III$^{1-3}$	II^{1-b}	I^{1}	r^{1-a}	I^{a-b}
Rubus idaeus	.	r^{1}	.	I^{+-a}	II^{+-a}
Epilobium sp.	.	r^{+}	.	+$^{r-1}$	III^{+-1}
Stellaria graminea	III^{+-m}	II^{+-m}	I^{+}	+$^{+-a}$	III^{+-1}
Bromus hordeaceus agg.	III^{+-m}	II^{+-1}	.	I^{+-1}	.
Myosotis nemorosa	II^{+}	r^{+}	IV^{+-1}	.	II^{+}
Alchemilla sp.	II^{+}	II^{+-1}	.	r^{+}	+$^{+}$
Senecio fuchsii	.	.	.	r^{r-+}	II^{+-1}
Holcus mollis	I^{a}	r^{b}	II^{1-b}	r^{b}	III^{1-b}
Vicia hirsuta	.	II^{+-1}	.	I^{+-1}	.
Sambucus nigra	.	.	.	.	.
Anthoxanthum odoratum	.	II^{1-a}	II^{+-1}	.	+^{1}
Cardamine flexuosa	.	.	.	.	.
Stellaria media agg.	III^{+-1}	.	.	r^{1}	.
Veronica hederifolia	.	.	.	r^{1}	.
Chaerophyllum hirsutum hirsutum	.	.	.	+$^{+-a}$	.
Geranium sylvaticum	.	r^{1}	IV^{1}	.	+$^{+}$
Valeriana officinalis agg.	.	.	II^{1}	+$^{r-+}$	.
Achillea ptarmica	II^{1}	.	II^{1-m}	.	.
Caltha palustris	.	.	III^{+-a}	.	.
Epilobium angustifolium	.	.	.	.	II^{r-a}
Epilobium palustre	.	.	II^{+-1}	.	+^{1}
Juncus inflexus	.	.	III^{1-m}	.	+^{1}
Mentha arvensis	II^{1}	.	I^{1}	.	+$^{+}$
Potentilla erecta	.	.	I^{1}	.	II^{1}
Trifolium medium	.	r^{1}	.	.	II^{1-m}
Senecio alpinus	.	.	.	.	.
Tussilago farfara	.	.	.	.	+^{r}
Veronica beccabunga	.	.	.	.	.

ica, *Galium aparine* and *Galeopsis tetrahit*. Additional ruderal species of fresh to moist tall-forb communities (Alliarion, Aegopodion, Calystegion) as well as other species with low mowing and grazing compatibility, such as *Lupinus polyphyllos*, *Senecio fuchsii*, *Epilobium angustifolium*, *Rubus* sp., and *Rosa* sp.) had rather scattered and infrequent occurrences.

Due to constant occurrences of *Arrhenatherum elatius* and *Galium mollugo* agg. it was possible to integrate the ruderal grasslands colonised by *H. mantegazzianum* into the alliance Arrhenatherion, yet a more detailed assignment to associations or rankless communities known from literature was not feasible. Vegetation types described as, e.g., Artemisia-Arrhenatherum community (Dierschke 1997, Bornkamm 1974) or Tanaceto-Arrhenatheretum (Fischer 1985) typically contain species characteristic of Artemisietea communities, the most frequent being *Artemisia vulgaris* and *Tanacetum vulgare* among others. As Fischer (1985)

I^{r-+}	1^{+}	.	$+^{+}$	.	.	1^{+}	.	.
II^{r-b}	2^{+-1}	.	II^{+}	$+^{1}$	1^{+}	1^{a}	.	I^{+}
$+^{+-1}$	1^{+}	I^{+-1}	$+^{+}$	r^{+}	.	2^{1-a}	1^{1}	II^{+-b}
r^{+}	.	.	$+^{+}$	r^{+}	.	.	.	.
.	.	$+^{+}$	.	r^{1}	.	.	.	.
I^{1-b}	.	$+^{1}$	$+^{1}$	r^{m}	.	.	.	.
I^{+-b}	1^{+}	$+^{1}$	$+^{r}$	$+^{+-b}$	.	.	.	.
$+^{r-+}$	.	$+^{+}$	$+^{+}$	r^{+}	.	1^{1}	1^{1}	.
.	.	.	.	.	.	.	.	.
r^{1}	.	.	.	.	.	.	.	.
.	.	.	.	.	.	2^{1}	1^{1}	.
.	.	.	.	r^{+}	.	.	.	.
$+^{1}$	1^{+}	.	$+^{+}$	$+^{+-1}$	.	.	.	.
r^{1}	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
r^{r}	3^{r-+}	.	$+^{+}$	$+^{r}$	.	.	2^{r-a}	.
.	.	.	.	.	.	.	.	.
r^{1}	1^{1}	.	II^{1-a}	.	.	1^{1}	1^{a}	I^{a}
.	.	.	$+^{1}$	$+^{1}$	.	.	.	.
.	1^{+}	.	.	I^{+-a}	.	.	.	II^{+-1}
.	.	.	$+^{a}$	r^{1}	.	.	2^{r-+}	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	I^{1}
.	.	.	.	.	.	.	.	.
.	.	.	.	r^{+}	.	.	.	.
r^{+}	.	.	.	.	.	.	.	.
.	.	.	$+^{1}$	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
r^{r}	.	.	.	.	.	2^{+-1}	.	.
.	.	.	.	.	.	2^{+-a}	.	.
.	.	.	.	.	.	2^{1}	.	.

points out, the Tanaceto-Arrhenatheretum (Artemisia-Arrhenatherum-community) is transitional between Arrhenatheretum and Tanaceto-Artemisietum Sissingh 1950 of the alliance Dauco-Melilotion, which belongs to the drought-resistant and thermophilic branch (Onopordetalia) of the Artemisietea s.l. In contrast, the ruderal grasslands colonised by *H. mantegazzianum* contained several species of the Galio-Urticetea but rarely Artemisietea species. Consequently they are transitional to Glechometalia or Calystegietalia, which represent tall-forb communities of permanently fresh or moist sites.

By analogy with the meadows, the ruderal grasslands colonised by *H. mantegazzianum* could be split up into fresh (Table 5, 1.2.3) and moist sub-communities (1.2.4).

In two relevés from abandoned grassland sites that could vaguely be connected with Calthion wet-grassland communities *H. mantegazzia-*

Table 5. (cont.) Infrequent companions.

1.1: Capsella bursa-pastoris l, Carex hirta l, Festuca arundinacea l, Galinsoga ciliata l, Persicaria maculosa l, Potentilla anserina l, Rumex crispus l, Trifolium dubium l, Veronica arvensis l, Veronica serpyllifolia l, Vicia angustifolia l, Vicia sp. l.

1.2.1: Bromus inermis r, Bromus sterilis r, Calamagrostis epigeios r, Campanula rapunculus r, Capsella bursa-pastoris r, Centaurea cyanus r, Chenopodium album agg. r, Crepis capillaris +, Cynosurus cristatus +, Daucus carota r, Echinops sphaerocephalus r, Epilobium obscurum, Epilobium tetragonum, Festuca arundinacea r, Galinsoga ciliata r, Galium verum agg. r, Geranium palustre l, Hieracium sabaudum r, Hypochoeris radicata r, Leontodon autumnalis l, Lupinus polyphyllus +, Lysimachia nummularia +, Persicaria maculosa r, Pimpinella saxifraga +, Polygonum aviculare s.l. r, Prunus avium r, Prunus spinosa r, Rumex crispus +, Silene flos-cuculi r, Sinapis arvensis r, Thlaspi arvense r, Tragopogon pratensis +, Trifolium dubium +, Trifolium hybridum r, Tripleurospermum perforatum +, Veronica arvensis l, Veronica opaca r, Veronica serpyllifolia r, Vicia angustifolia r, Vicia tetrasperma l.

1.2.2: Carex hirta l, Galium palustre s.l. l, Galium verum agg. l, Juncus articulatus l, Mentha sp. l, Ranunculus flammula l, Scirpus sylvaticus l, Silene flos-cuculi l.

1.2.3: Agrostis gigantea r, Anemone nemorosa r, Ballota nigra r, Bromus inermis r, Bromus sterilis r, Calamagrostis epigejos r, Campanula rapunculus r, Carduus personata +, Carex disticha r, Carex hirta r, Carex sp. r, Carpinus betulus r, Carum carvi r, Clematis vitalba r, Clinopodium vulgare +, Cornus sanguinea sanguinea r, Crepis capillaris r, Cynosurus cristatus r, Epilobium ciliatum +, Epilobium obscurum r, Equisetum arvense l, Euphrasia off. rostkoviana r, Fagus sylvatica r, Fallopia japonica r, Festuca arundinacea r, Geranium dissectum r, Geranium sp. r, Hordeum vulgare r, Hypericum maculatum agg. r, Juglans regia r, Juncus effusus r, Knautia arvensis r, Lamium purpureum r, Lotus corniculatus r, Lupinus polyphyllus l, Luzula campestris et multif. r, Malus domestica r, Malva moschata r, Medicago lupulina +, Mentha sp. r, Myosotis ramosissima r, Myosotis sp. r, Orobanche flava r, Persicaria maculosa r, Picea abies r, Pimpinella saxifraga +, Plantago major intermedia r, Potentilla anserina r, Potentilla reptans r, Prunus avium r, Prunus spinosa r, Quercus robur r, Ranunculus auricomus agg. r, Rosa sp. +, Salix sp. r, Sonchus oleraceus r, Stellaria alsine r, Torilis japonica r, Tragopogon pratensis r, Trifolium campestre r, Trifolium hybridum +, Tripleurospermum perforatum r, Triticum aestivum r, Veratrum album r, Veronica arvensis r, Veronica filiformis +, Veronica persica r, Veronica sp. r, Vicia angustifolia r, Vicia sativa r, Vicia tetrasperma +.

1.2.4: Aesculus hippocastanum l, Calamagrostis epigejos l, Carex disticha +, Carex hirta l, Centaurea nigra +, Clinopodium vulgare +, Cytisus scoparius scoparius +, Epilobium ciliatum +, Equisetum sylvaticum l, Galium palustre s.l. +, Geranium dissectum +, Glyceria fluitans +, Hypericum pulchrum +, Juncus acutiflorus +, Juncus conglomeratus +, Juncus effusus l, Lupinus polyphyllus l, Lysimachia nummularia +, Malus domestica +, Mentha sp. l, Molinia caerulea +, Myosotis scorpioides agg. +, Phyteuma spicatum +, Pimpinella major +, Potentilla anserina +, Prunus serotina +, Prunus spinosa +, Quercus robur +, Rumex crispus l, Salix aurita +, Salix sp. +, Solidago virgaurea l, Sorbus aucuparia +, Succisa pratensis +, Teucrium scorodonia +, Vicia sp. l, Vicia tetrasperma +, Vicia villosa +, Viola reichenbachiana +, Viola riviniana l.

2.1: Bromus sterilis +, Calamagrostis epigejos +, Carex sylvatica r, Conyza canadensis r, Crataegus monogyna agg. r, Dryopteris carth. et dilat. +, Dryopteris filix-mas +, Epilobium ciliatum r, Epilobium obscurum r, Equisetum arvense +, Euonymus europaea r, Fragaria vesca l, Hypericum pulchrum r, Lolium multiflorum r, Lonicera xylosteum r, Lysimachia nemorum r, Malus domestica r, Myosotis sp. r, Plantago major intermedia r, Populus tremula r, Potentilla reptans +, Rosa sp. l, Rubus sp. r, Salix caprea r, Scirpus sylvaticus r, Scutellaria galericulata r, Solidago canadensis r, Veronica filiformis r, Veronica montana r.

2.2: Acer campestre campestre 1, Betula pendula 1, Carex remota 1, Corylus avellana 1, Dryopteris filix-mas 1, Ranunculus ficaria 1, Scirpus sylvaticus 1, Veronica montana 1.

2.3.1: Acer platanoides +, Arctium sp. +, Carex hirta +, Chrysosplenium alternifolium l, Cornus sanguinea sanguinea +, Equisetum arvense l, Equisetum palustre +, Leonurus cardiaca +, Origanum vulgare +, Quercus robur +.

2.3.2: Acer campestre campestre +, Aethusa cynapium agg. l, Arctium sp. +, Athyrium filix-femina +, Clinopodium vulgare +, Corylus avellana +, Dryopteris carth. et dilat. +, Dryopteris filix-mas +, Galium palustre s.l. +, Geranium palustre l, Hesperis matronalis +, Lysimachia nemorum +, Myosotis sp. +, Persicaria maculosa +, Populus tremula +, Prunus spinosa +, Quercus robur +, Rubus sp. +, Rumex conglomeratus +, Salix caprea +, Sonchus oleraceus +, Stellaria alsine +, Veronica filiformis +, Veronica montana +, Vicia sp. +.

2.4: Aster sp. r, Betula pendula r, Bromus inermis r, Bromus sterilis +, Carex hirta r, Carex sp. r, Chrysosplenium oppositifolium r, Clinopodium vulgare r, Corylus avellana r, Crataegus monogyna agg. +, Dryopteris filix-mas +, Echinops sphaerocephalus r, Epilobium ciliatum r, Epilobium obscurum r, Equisetum fluviatile r, Fallopia japonica r, Galium palustre s.l. r, Geranium palustre r, Hesperis matronalis r, Hypericum maculatum agg. r, Hypericum sp. r, Iris pseudacorus r, Juncus articulatus r, Juncus effusus r, Lycopus europaeus r, Persicaria amphibia r, Persicaria maculosa +, Prunus avium r, Quercus robur r, Ranunculus ficaria +, Scirpus sylvaticus r, Stellaria alsine r, Vicia sp. r.

3.1: Myosotis sp. 1, Polygonum sp. 1.

3.2: Barbarea vulgaris 1, Carex flacca 1, Equisetum arvense 1, Lonicera xylosteum 1, Potentilla anserina 1, Salix appendiculata 1, Salix sp. 1.

4: Equisetum arvense 1, Lonicera xylosteum 1, Myosotis sylvatica 1, Phyteuma orbiculare 1, Prunus padus 1, Salix appendiculata 1, Solanum dulcamara 1.

5: Acer campestre campestre l, Calamagrostis arundinacea l, Cardaminopsis arenosa l, Carex remota l, Clinopodium vulgare l, Crataegus monogyna agg. l, Dryopteris filix-mas l, Fallopia japonica l, Picea abies l, Prunus avium l, Ranunculus ficaria l, Rosa sp. l.

num co-occurred with wetland species such as *Angelica sylvestris*, *Cirsium palustre*, *Lotus pedunculatus*, *Juncus effusus*, *Galium palustre*, *Juncus inflexus*, *Silene flos-cuculi* and *Juncus articulatus*. As these relevés did not exactly match Calthion communities but differed considerably from the Arrhenatheretalia communities they were grouped as 'other' vegetation types in the gradient analysis (ch. 4.3) and not included into the frequency table.

4.2.3 Nitrophilous tall-forb communities (Galio-Urticetea)

Relevés of tall-forb communities with *H. mantegazzianum* showed consistent records of species characteristic or typical of the class Galio-Urticetea of which the most constant and abundant were *Urtica dioica*, *Poa trivialis* and *Galium aparine* (Table 5, 2). On the basis of presence-absence and proportions of diagnostic species groups the stands could mostly be assigned to the alliances Aegopodion, Calystegion and, subordinately, Alliarion, but some stands almost completely lacking character species of syntaxa below the class level had to be classified as a basal community of the class. Altogether, five types of tall-forb communities with *H. mantegazzianum* were distinguished: (1) Galio-Urticetea basal community, (2) Alliarion, (3) Aegopodion, typical sub-communities, (4) Aegopodion, *Calystegia* sub-communities, and (5) Calystegion, *Aegopodium* sub-communities.

Galio-Urticetea basal community was quite ubiquitous in its range of habitats and found at a variety of man-made sites without regular management, such as roadsides, railway embankments, former horticultural land, abandoned meadows, an abandoned sand pit, and forest clearings. Apart from the typical species of Galio-Urticetea mentioned in the previous paragraph, *Dactylis glomerata* was the only constant (Table 5, 2.1). Various other grassland, tall-forb, and sometimes woodland species co-occurred but usually with low frequency and abundance, and the stands were generally species poor. *H. mantegazzianum* was mostly the dominant species (i.e. cover > 50 %), sometimes with co-dominant *Urtica dioica* which occasionally was dominant as well.

Alliarion stands with *H. mantegazzianum* were rare exceptions (3 relevés) and occurred in more shaded situations along fringes or in gaps of tree rows. Characteristic species were *Alliaria petiolata* and *Geranium robertianum*, accompanied by some woodland species such as *Stachys sylvatica*, *Poa nemoralis* and *Brachypodium sylvaticum* among others (Table 5, 2.2).

Aegopodion and Calystegion communities made up the majority (70 %) of tall-forb stands with *H. mantegazzianum* found in the present study. The two alliances are quite closely related not only by sharing a full set of class character species, but also Calystegion character species may spread to Aegopodion stands, and vice versa (Table 5, 2.3 and 2.4) with an increase of Calystegion species with flooding frequency.

Typical Aegopodion sub-communities are fully terrestrial and differentiated from the remaining by the lack of Calystegion species (Table 5, 2.3.1). The stands were characterised by constant co-occurrences of *Urtica dioica* and *Aegopodium podagraria*. The latter is, in fact, rather a characteristic species of the class (Dengler 1997) but also commonly regarded as an Aegopodion character species (Ellenberg 1992, Oberdorfer 1993). Further character species of the alliance Aegopodion were widely lacking in the given set of relevés except for few records of *Petasites hybridus* and *Lamium maculatum*. Basically, this community type corresponded to the Urtico-Aegopodietum podagrariae (R.Tx. 1963) Oberdorfer 1964 in Görs 1968 in its typical sub-association although floristically noticeably impoverished in character species of the alliance and typical companions. Habitats colonised by this community type were mostly abandoned grassland sites and sometimes disturbed forest margins and small clearings in (floodplain) forests.

Aegopodion sub-communities with *Calystegia sepium* differed floristically from Calystegion sub-communities with *Aegopodium* only in the number and cover-abundance sum of the character and differential species of the respective alliances and orders (Table 5, 2.3.2 and 2.4). The only constant Aegopodion species was again *Aegopodium podagraria*. Other species characteristic of Aegopodion (or the order Artemisietalia sensu Dengler 1997) were *Petasites hybridus*, *Lamium maculatum*, *Silene dioica*, *Lamium album*, *Cruciata laevipes* and *Chaerophyllum bulbosum* which, however, were limited in frequency to class II (max. 40%) or lower classes. Recorded character species of Calystegion (or Calystegietalia, respectively) were *Impatiens glandulifera*, *Calystegia sepium*, *Carduus crispus*, *Humulus lupulus* and, rarely, *Cuscuta europaea*, *Myosoton aquaticum* and *Epilobium hirsutum*. These were supplemented by a set of moisture-tolerant plants, most prominently *Symphytum officinale*, serving as differential species for the order Calystegietalia (cf. e.g. Dengler 1997).

Aegopodion sub-communities with *Calystegia* mostly corresponded to the Urtico-Aegopodietum convolvuletosum (cf. Oberdorfer 1993) except for two relevés which could best be affiliated with the Phalarido-Petasitetum hybridi Schwick 1933. Calystegion communities with *H. mantegazzianum* resembled most closely the Urtica-Convolvulus sepium community Lohmeyer 1975, which is typical of the banks of small rivers in (sub-) montane regions (cf. Oberdorfer 1993).

These two vegetation types were found in a variety of different habitats, partly natural, like small clearings in alluvial Alder-Willow forests or riverbanks with tall-forb vegetation, but mostly in semi-natural or anthropogenic habitats like artificial river embankments, railway embankments, abandoned (alluvial) grasslands, understorey of planted tree rows along rivers, abandoned horticultural land, and at ruderalised forest fringes in river valleys.

4.2.4 Woodlands

Some relevés with *H. mantegazzianum* could be affiliated to specific woodland communities of the (sub-) alliances of Alder-Ash-gallery forests (Alnenion glutinoso-incanae, class: Querco-Fagetea) and Gray Willow scrub (Salicion elaeagni, class: Salicetea pupureae). Other woodland relevés that originated from afforestations of alluvial grasslands or man-made sites in river valleys could not be allotted to any specific syntaxa but were included into Table 5 as a group of substitutes of Alnenion communities (anthropogenic floodplain forests). Finally, *H. mantegazzianum* was singularly found in *Salix caprea* and *Populus tremula* pioneer stands, an Oak copse and beneath an Oak-Wild Cherry tree row. Altogether, occurrences of *H. mantegazzianum* in woodlands were rather scarce and restricted to gaps, sparse canopies or fringe areas where the species could benefit from increased light levels compared with closed forest stands. Noteworthy, all but two woodlands had developed from grasslands or similar vegetation after the 1950s (cf. chapter 4.1.2).

Within Alnenion glutinoso-incanae, *H. mantegazzianum* was found to occur in two associations of Alder-Ash-gallery forests that grow in the inundation area of small rivers in the (sub-)montane and colline zones. These are, by name, Stellario-Alnetum glutinosae and Alnetum incanae (Table 5, 3.1 and 3.2). The ecological distinction of these communities coincides with the preferences of the characteristic alder species – *Alnus glutinosa* on loamy soils of submontane and colline riversides and *Alnus incana* on calcareous sands and shingle banks of montane rivers. Both associations share common species of moist and rich woodlands such as, e.g., *Festuca gigantea* and *Circaea* sp. (cf. Oberdorfer 1993). Among the companions were some species typical of Galio-Urticetea tall-forb communities like *Urtica dioica*, *Galium aparine* and *Impatiens glandulifera*.

In Stellario-Alnetum stands also *Aegpodium podagraria* and *Stellaria nemorum* were consistent and conspicuous elements of the field layer and the relevés all belonged to the typical sub-community. Concerning ecosociological subtypes of Alnetum incanae the relevés were more or less intermediate between typical and wetter sub-associations (A. i. typicum and A. i. phragmitetosum, respectively) and differential species of the summer-dry subtype (A. i. caricetosum albae) were lacking completely.

Salicion elaeagni comprises Gray Willow scrubs on base-rich shingles and sandbanks in the montane zone of alpine rivers. Stands with *H. mantegazzianum* were found in older, more consolidated stages of fresh variants of Salicion elaeagni communities which build up forest-like stands with a generally more or less closed canopy and an understorey of quite demanding plants (cf. Oberdorfer 1993), which are represented in the relevés by *Urtica dioica*, *Galium aparine*, *Galeopsis tetrahit* and *Impatiens glandulifera* among others (Table 5, 4). The investigated stands resembled quite closely a Salicetum elaeagni (Hag. 1916) Jenik 1955 phalaridetosum although differential and accompanying species did not perfectly match species lists known from literature. Oberdorfer (1993) points out that this sub-community type is transitional to Alnetum incanae.

Habitats of Salicion elaeagni and Alnenion glutinoso-incanae stands were more or less natural gallery forests that had developed from open riverbank habitats after the 1950s probably subsequent to abandonment of cattle grazing. Incidentally, seedlings of *H. mantegazzianum* were also found at open river sandbanks close to Salicion elaeagni stands but were not able to survive a summer flooding event.

As mentioned above *H. mantegazzianum* sometimes occurred in anthropogenic floodplain forests which did not match known syntaxa. These featured *Fraxinus excelsior*, *Acer pseudoplatanus*, *Populus nigra* and *Salix fragilis* among the dominant woody components and may be viewed as substitutes of the drier branch of Alnenion glutinoso-incanae forests. (Table 5, 5).

4.2.5 Other vegetation types with H. mantegazzianum

Next to the plant communities described above which accounted for the majority of relevés *H. mantegazzianum* occurred in various other types of open vegetation which could not be affiliated with known syntaxa. These types stood out from the former primarily on account of severe disturbances of the sites and, in few cases, also due to comparatively unfavourable site conditions. To give an impression of the spectrum of these vegetation types some examples shall be briefly mentioned.

At a former military site and in former quarries some stands were found in young successional stages dominated by *Calamagrostis epigeios*. Companions were *Cirsium arvense*, *Urtica dioica*, *Rubus* sp., few other unspecific grassland species, and a variety of ruderal species of open habitats. Furthermore, singular occurrences of *H. mantegazzianum* were found on a recently abandoned arable field, in a former scrub which had been cleared by rotovating, and an abandoned orchard. Finally, two relevés were recorded from a windbreak site where *H. mantegazzianum* grew together with Molinietalia wet grassland species, like *Angelica sylvestris*, *Cirsium palustre*, *Molinia caerulea*, small sedges and rushes, interspersed with few tall forbs of the order Atropetalia, like *Senecio fuchsii* and *Epilobium angustifolium*.

4.2.6 Relative frequencies of vegetation types with H. mantegazzianum

Grasslands accounted for 45 % of all relevés (Fig. 2). Of these, the ruderal Arrhenatherion grasslands made up the largest proportion (27 % of the total) followed by managed Arrhenatherion meadows (15 %). Typical Arrhenatherion sub-communities prevailed by far over the moist subtypes. Tall-forb communities were slightly less frequent than the grasslands (39 %) with more or less even shares of Aegopodion, Calystegion, and Galio-Urticetea basal communities while Alliarion communities were notably rare with only about 1 % of all relevés. Alongside the gradient from typical Aegopodion sub-communities through *Calystegia* sub-communities of Aegopodion to Calystegion communities frequencies increased (5 %, 6 %, 15 %, respectively). Woodlands (Alnenion glutinoso-incanae, Salicion elaeagni, anthropogenic floodplain forests)

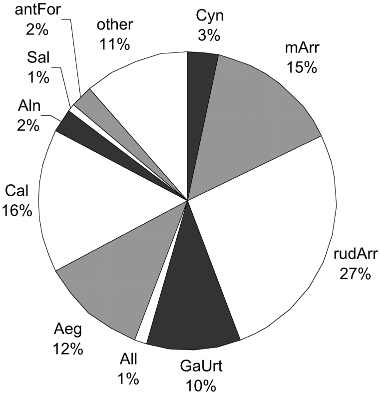

Fig. 2. Relative frequencies of vegetation types with *Heracleum mantegazzianum* found in study areas. Percentages were rounded up or down to amount to 100 %, exactly. Short cuts of vegetation types: Cyn = Cynosurion; mArr = managed Arrhenatherion; rudArr = ruderal Arrhenatherion; GaUrt = Galio-Urticetea basal community; All = Alliarion; Aeg = Aegopodion; Cal = Calystegion; Aln = Alnenion glutinoso-incanae; Sal = Salicion elaeagni; antFor = anthropogenic floodplain forest; other = all remaining relevés not assigned to specific syntaxa.

made up merely 6 %, altogether. Other vegetation types contributed 11 % of relevés.

4.2.7 Red list status of species and communities

According to national and regional red data lists for plant communities and vascular plant species in Germany (e. g. www.floraweb.de) the communities colonised by *H. mantegazzianum* are throughout listed as 'not endangered' and co-occurring indigenous plant species are also virtually absent from the red data lists. Single occurrences in man-made habitats of *Leonurus cardiaca* and *Orobanche flava*, both nationally and regionally listed as 'endangered', were the only exceptions.

4.3 Gradient analysis

The first axis of CA ordination of relevés mainly represented a gradient from managed grasslands – prevalently hay meadows and subordinately (mown) pastures – over young stages of abandoned or neglected grasslands (ruderal grasslands) to tall-forb stands with increasing proportions of woody components and, finally, woodlands (Fig. 3). Environmental variables significantly correlated with the ordination axes are presented in Fig. 4. Along the main gradient (axis 1) the intensity of land use declined from regular grassland management, via irregular maintenance to abandonment or disuse, and the time span since abandonment of sites increased. While light supply declined due to increasing cover of trees at the upper end of

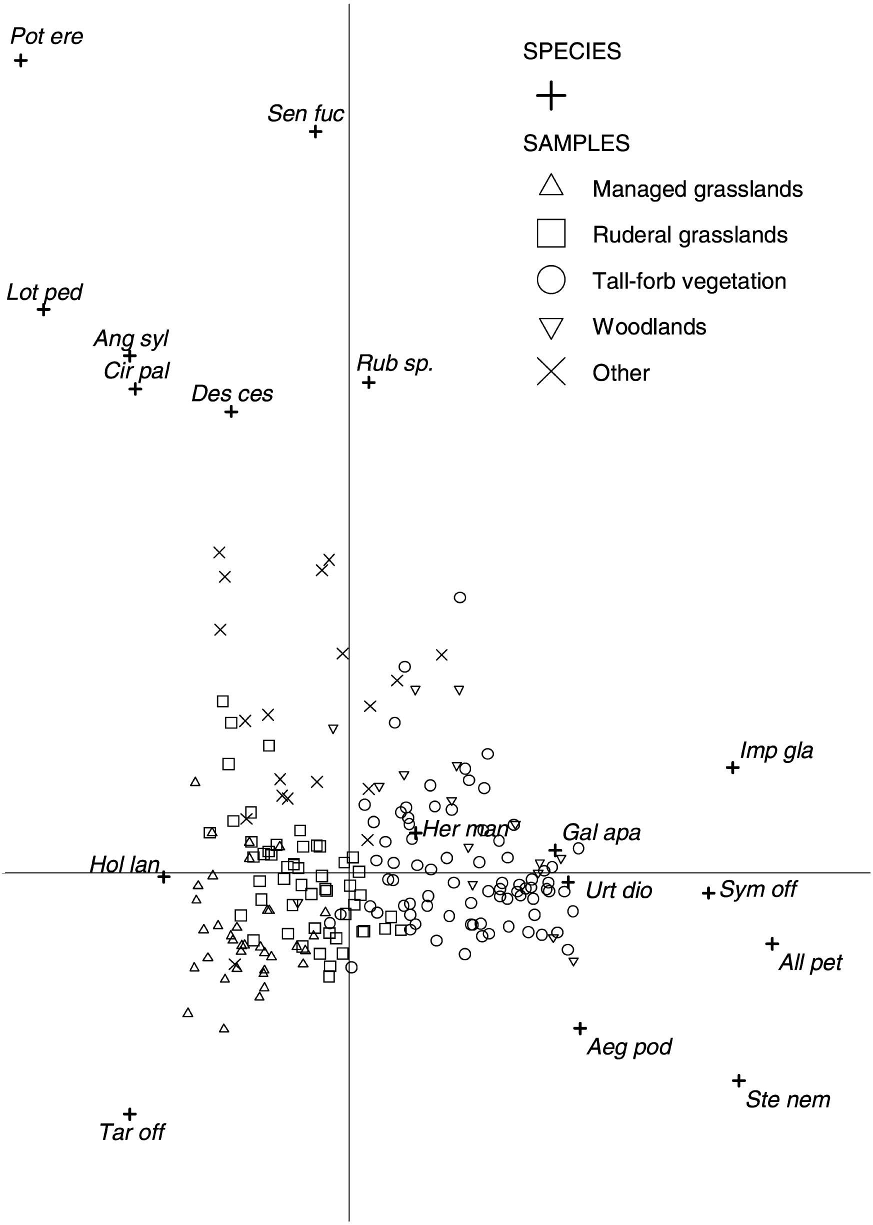

Fig. 3. CA ordination biplot of sites and species. Axis 1 (x) and axis 2 (y) are presented. All of 202 investigated plots were included in the analysis and plotted in the diagram. The first CA axis mainly represented a successional series from grasslands to tall-forb stands and woodlands. Only species above a predefined cut-off value of fit on the first two axes were plotted. Short cuts of species names: Aeg pod = *Aegopodium podagraria*, All pet = *Alliaria petiolata*, Ang syl = *Angelica sylvestris*, Cir pal = *Cirsium palustre*, Des ces = *Deschampsia cespitosa*, Gal apa = *Galium aparine* agg., Her man = *Heracleum mantegazzianum*, Hol lan = *Holcus lanatus*, Imp gla = *Impatiens glandulifera*, Lot ped = *Lotus pedunculatus* (syn. *uligi-*

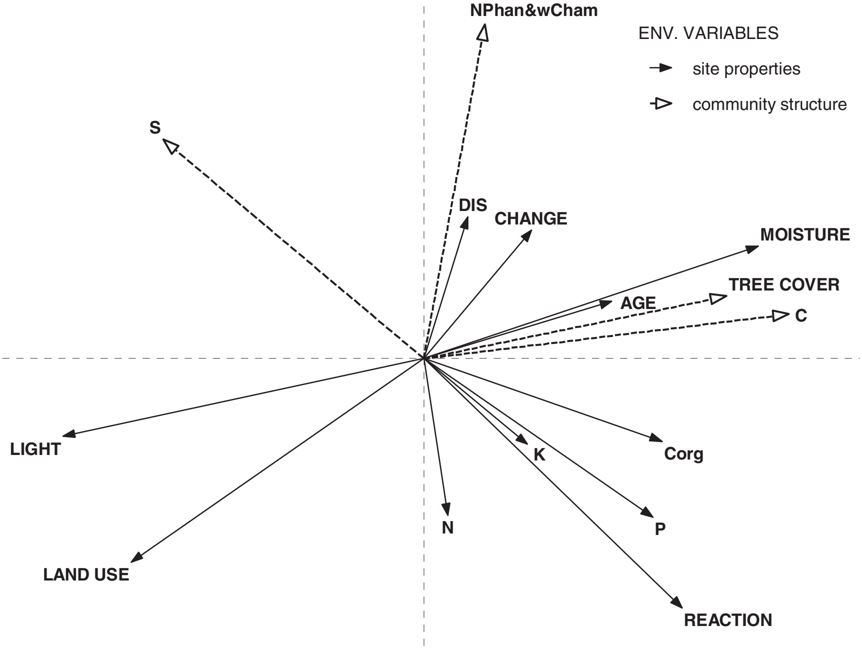

Fig. 4. CA ordination diagram of environmental variables. Axis 1 (x) and axis 2 (y) are presented. The first CA axis mainly represented a successional series from grasslands to tall-forb stands and woodlands. Only environmental variables with a t-value of 1.96 or greater were plotted. Classification of environmental variables: 'site properties' include all variables actually measured or estimated in the field as well as average Ellenberg indicator values; 'community structure' comprises all parameters of the structure of the vegetation stands (strategy types, layers). Short cuts of variable names: AGE = habitat change before the 1970s (yes, no), C = proportion of C-strategy (Grime et al. 1988), CHANGE = habitat change in the last fifty years (yes, no), Corg = organic carbon content of soils; DIS = disturbance (yes, no), K = plant-available potassium content of soils, LAND USE = regular management regime (yes, no), LIGHT = estimated light supply, MOISTURE = average Ellenberg indicator values for moisture supply, N = total nitrogen content of soils, NPhan&wCham = pooled cover abundance of nanophanerophytes and woody chamaephytes, P = plant-available phosphorus content of soils, REACTION = average Ellenberg indicator values for soil reaction, S = proportion of S-strategy (Grime), TREE COVER = cover percentage of the tree layer (if present).

Fig. 3. (cont.)
nosus), Pot ere = *Potentilla erecta*, Rub sp. = *Rubus fructicosus* agg. & *Rubus idaeus*, Sen fuc = *Senecio fuchsii*, Ste nem = *Stellaria nemorum*, Sym off = *Symphytum officinale*, Tar off = *Taraxacum officinale* agg., Urt dio = *Urtica dioica*. Classification of sites: 'Managed grasslands' comprise managed Arrhenatherion and Cynosurion communities, 'Ruderal grasslands' refers to abandoned or irregularly maintained Arrhenatherion grasslands, 'Tall-forb vegetation' includes all communities of the class Galio-Urticetea (basal community, Alliarion, Aegopodion, Calystegion), 'Woodlands' comprises all woodland relevés whether assigned to known syntaxa (Alnenion glutinoso-incanae, Salicion elaeagni,) or not, and 'Other' catches the remainder of relevés which could not be grouped or assigned to specific syntaxa.

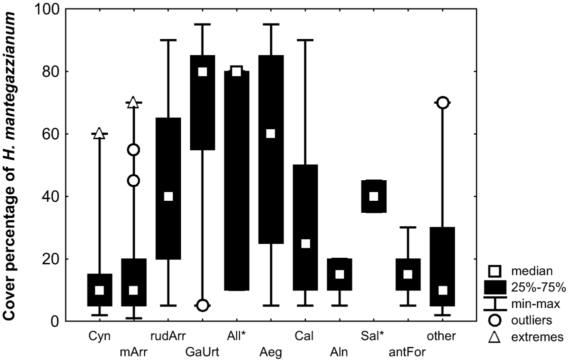

Fig. 5. Cover percentages of *H. mantegazzianum* with respect to vegetation types (medians, quartiles and min-max ranges). Outliers are further from the upper box level than 1.5*interquartile-range. For extremes the coefficient is 3. Key to vegetation types: Cyn = Cynosurion; mArr = managed Arrhenatherion; rudArr = ruderal Arrhenatherion; GaUrt = Galio-Urticetea basal community; All = Alliarion; Aeg = Aegopodion; Cal = Calystegion; Aln = Alnenion glutinoso-incanae; Sal = Salicion elaeagni; antFor = anthropogenic floodplain forests; other = all relevés not assigned to specific syntaxa.
* Few observations: All = 3, Sal = 2.

the gradient, the supply of moisture and soil nutrients, particularly phosphorus and potassium, increased. With regard to plant strategies, there was an increase in competition (C-strategy) while stress-tolerance (S-strategy) decreased.

The second axis separated (former) agricultural sites, i. e. managed grasslands or sites developed therefrom after abandonment, in the lower part of this axis from a smaller group of sites that never were subject to agricultural land use in the upper part (Fig. 3). Most relevés of the latter group could neither be assigned to specific plant communities nor grouped in homogenous vegetation types and therefore were categorised as 'Other' in the ordination plot (see ch. 4.2.5). Consequently, land use also declined along the second axis and likewise did the soil nutrient status, particularly nitrogen. In reverse, the proportion of disturbed sites increased and, especially, heavy disturbances, such as mining and windbreak, were found in the upper array of the second axis. With respect to vegetation texture, there was a marked increase in the pooled cover abundance of nanophanerophytes and woody chamaephytes which was prevalently attributable to *Rubus* and *Salix* sp. Furthermore, an increase in stress-tolerance (S-strategy) could be observed along the second axis.

4.4 Cover abundance of H. mantegazzianum in relation to recipient community, gradient analysis and species numbers

Cover values of *H. mantegazzianum* varied in a wide range between 1 % and 95 % and showed an uneven distribution with 47 % of values in the class '1–20 %', 17 % in the class '20–40 %' and 12 % each in the higher classes (40–60 %, 60–80 %, 80–100 %). The pattern of medians of cover values with regard to community type exhibited low values for managed grasslands (Cynosurion, Arrhenatherion meadows) and shady woodland habitats (Alnenion glutinoso-incanae, anthropogenic floodplain forests), while ruderal grasslands and tall-forb communities comprised the whole range of cover values (ruderal Arrhenatherion, Galio-Urticetea basal community, Alliarion, Aegopodion, Calystegion; Fig. 5). Exceptional high cover percentages in managed grasslands were due to massive recruitment of *H. mantegazzianum* seedlings in disturbed swards but the specimens did not manage to grow to normal height due to mowing or grazing.

Dominant stands (cover of *H. mantegazzianum* > 50 %) made up the largest proportion in Galio-Urticetea basal community (85 %) and Aegopodion (52 %). Two out of three stands in Alliarion were dominant, but due to the small number of observations this ratio is vague. From these terrestrial tall-forb communities towards riparian ones (Calystegion) there was a conspicuous decrease in median cover values (Fig. 5).

Regular mowing or grazing, and shading reduced the abundance of flowering individuals of *H. mantegazzianum* in managed grasslands (median/maximum: 1.5/26 generative individuals/25 m^2) and woodlands (0/5) compared to ruderal grasslands (4.5/37) and tall-forb stands (7/54). Fruit set was strongly reduced by cutting or biting off of the primary stems in managed grasslands, while in the remaining vegetation types fruit set was generally abundant, even in woodlands where flowering individuals occurred.

As indicated by the gradient length of 2.8 measured by DCA most species showed linear response along the first ordination axis. Grassland species, such as *Holcus lanatus*, *Ranunculus repens*, *Taraxacum officinale* agg. and *Rumex acetosa* declined whereas tall-forbs and herbs typical of tall-forb vegetation, such as *Urtica dioica* and *Aegopodium podagraria*, increased (Fig. 6). In contrast to the majority of species, *H. mantegazzianum* showed a unimodal response along the first ordination axis with a maximum predicted cover-abundance class of '3' (cover percentage 25–50 %) in the central part of axis 1 according to the fitted GAM. Also along the second axis the response of *H. mantegazzianum* was unimodal.

Cover values of *H. mantegazzianum* were negatively correlated with the number of vascular plant species of relevés. When all relevés were included into correlation analysis the Pearson correlation coefficient was $r = -0.29$ ($p < 0.001$; Spearman's $R = -0.28$, $p < 0.001$). However, managed grasslands in which *H. mantegazzianum* cover values were low, had generally higher species numbers compared to the tall-forb communities. Leaving out managed grasslands, there was still a negative correlation but with a lower correlation coefficient of $r = -0.24$ ($p = 0.002$; Spearman's $R = -0.23$, $p = 0.003$).

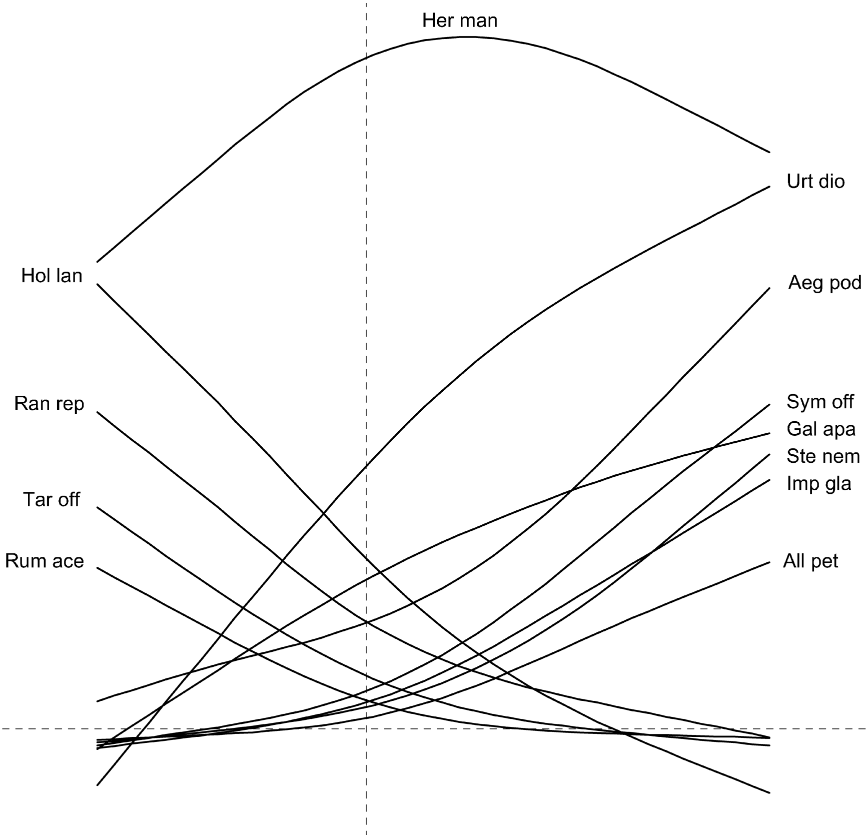

Fig. 6. Response curves of selected species along the first axis of CA ordination. The first CA axis (x) mainly represented a successional series from grasslands to tall-forb stands and woodlands. The vertical dashed line indicates the zero point (i. e. center) of the first CA axis. The y-axis depicts predicted cover abundances of the species. The horizontal dashed line indicates the zero point of predicted cover abundances. The maximum predicted cover abundance class of *Heracleum mantegazzianum* (Her man) was in class '3' (i. e. 25–50 % cover). Only species above a predefined cut-off value of fit on the first axis and *Heracleum mantegazzianum* were plotted. Curves were calculated by Generalized Additive Model in CANOCO using default settings. Short cuts of species names: Aeg pod = *Aegopodium podagraria*, All pet = *Alliaria petiolata*, Gal apa = *Galium aparine* agg., Her man = *Heracleum mantegazzianum*, Hol lan = *Holcus lanatus*, Imp gla = *Impatiens glandulifera*, Ran rep = *Ranunculus repens*, Rum ace = *Rumex acetosa*, Ste nem = *Stellaria nemorum*, Sym off = *Symphytum officinale*, Tar off = *Taraxacum officinale* agg., Urt dio = *Urtica dioica*.

5 Discussion

5.1 Habitats

5.1.1 Spectrum of habitats and site conditions

From a broad perspective *H. mantegazzianum* colonises a variety of different habitats such as abandoned or neglected grasslands, roadsides, riverbanks, railway embankments, forest and scrubland fringes, ruderal areas and even managed grasslands or woodlands (NEILAND 1987, PYŠEK 1994, PYŠEK & PYŠEK 1995, OCHSMANN 1996, TILEY et al. 1996, THIELE & OTTE, submitted) which has lead to the assumption that the species is generally superior over indigenous ones and quality of the recipient habitat is rather unimportant (PYŠEK 1991, PYŠEK & PYŠEK 1995).

However, closer examination of habitat characteristics reveals that the preferred habitats are more or less uniform. Abiotic sites conditions are generally characterised by high trophic level, fast nutrient cycling, favourable soil reaction and favourable water balance offering good water supply as well as good aeration of soils which altogether is in good agreement with other studies on chemical soil characteristics (e.g. TILEY et al. 1996, OTTE & FRANKE 1998) or Ellenberg indicator values (PYŠEK & PYŠEK 1995, OCHSMANN 1996) of *H. mantegazzianum* sites. Furthermore, preferred habitats have in common that they are disused or neglected and it seems that they are also regularly characterised by episodic disturbances providing particularly suitable conditions for recruitment.

The factors differing most conspicuously among different habitats and communities colonised by *H. mantegazzianum* are land use and light supply. These act as constraining factors on *H. mantegazzianum* at the lower or upper end of the major gradient in the vegetation data, respectively.

To further delimit the optimal range of abiotic site conditions it is interesting to consider *H. mantegazzianum* stands in more detail that grow under apparently pessimal conditions with regard to nutrient status and water balance. The sites in question are two abandoned wet grasslands (ch. 4.2.2) and a windbreak area colonised primarily by Molinietalia wet grassland species (ch. 4.2.5). All of these sites were open, disused and at least the latter was severely disturbed recently. Furthermore, *H. mantegazzianum* stands have been present in the immediate vicinity since about 10 years before the study which in combination should offer good possibilities for invasion of *H. mantegazzianum*. Nevertheless *H. mantegazzianum* abundances were low (cover values < 10 %) and the smaller than normal specimens rarely managed to flower. In contrast to the remaining sites, nutrient status was moderate to poor (P ~ 0.1 mg/100 g; N ~ 0.2 g/100 g) and drainage was noticeably impeded. Therefore, it seems likely that the species' abundance and growth is limited by poor and wet conditions. Obviously, *H. mantegazzianum* is also hampered by low water supply as it was never found in habitats characterised by dry soils.

Summarising, it can be concluded that the quality of recipient habitats is crucial for the invasion of *H. mantegazzianum*. Although its ecological niche is fairly wide the species is an invader, in the sense of attaining high densities and having great impact on the resident vegetation (cf. Davis & Thompson 2000) only if particular habitat requirements are met.

5.1.2 Creation of suitable habitats by changing land-use regimes

Generally, sites of *H. mantegazzianum* are well suited to agricultural land use. Analysis of site history revealed that more than 50 % of sites had still been used agriculturally, predominantly as meadows or pastures, before the 1970s or even thereafter (Table 2) but have been abandoned or partly turned into rather irregularly maintained grasslands fringes or margins alongside rivers, roads, and forests. This shows that a major proportion of favourable sites has been newly created within the last 50 years in the course of declining grassland management in the invaded landscapes.

The timing of abandonment or de-intensification of invaded grasslands coincides, temporally, with the phase of exponential increase of *H. mantegazzianum* distribution from the 1960s onwards, which suggests that the massive spread and increase of the species was enhanced considerably by changes in land management.

5.2 Plant communities and vegetation dynamics

Correspondence analysis shows that the main gradient in the set of relevés is attributable to secondary successions on, primarily, abandoned grasslands and, secondarily, ruderal sites (Fig. 3). Along this successional gradient *H. mantegazzianum* shows a unimodal response with the highest predicted stand densities in the array of recently abandoned or ruderalised sites. This suggests that successional age plays a role with respect to densities of *H. mantegazzianum* stands and possibly also to the invasion success of the species as hypothesized by Pyšek & Pyšek (1995).

At the older end of the successional gradient shading by woody components of the vegetation is an obvious constraining factor. But as only comparatively few plots featured a largely closed tree canopy and were consequently classified as woodlands, it appears that in older successional stages also competition by other herbaceous species, particularly tall forbs, restricts *H. mantegazzianum*.

Concerning the structure of the vegetation stands, it is striking that a shrub layer is either completely absent or very sparsely developed (max. 10 % cover). Obviously, shrubs are, once successfully established, strong competitors to *H. mantegazzianum* and capable to suppress seedlings and adult plants with their shade.

Plant communities with *H. mantegazzianum* reflect site conditions and dynamics of the habitats which are characterised by high productivity and, in the majority, considerable historical or recent alterations in management regimes (cessation or de-intensification of land use) or severe disturbance events (e.g. mining, removal of tree or shrub layer, mechanical damaging of the sward). Floristically, this is expressed in high constancies of a set of more or less nutrient demanding and ruderal species regularly co-occurring with *H. mantegazzianum* in ruderal grasslands, tall-forb vegetation and woodlands. These are *Poa trivialis*, *Urtica dioica*, *Galium aparine* and *Glechoma hederacea* which act as baseline species of virtually all communities with *H. mantegazzianum* except for managed grasslands and indicate its preference for Galio-Urticetea communities. At the level of alliances *H. mantegazzianum* centers on Aegopodion which can be seen from its concordance with the characteristic or differential species of Aegopodion along the gradient from terrestrial to riparian communities of Calystegion. Notwithstanding, a considerable part of relevés belongs into the latter alliance. This centring on Aegopodion communities was also reported by other authors (e.g. Sauerwein 2004).

The findings of the present study support the view that it is not advisable to keep up a separate association of *H. mantegazzianum* (Urtico-Heracleetum Klauck 1988) within the alliance Aegopodion. Firstly, the Aegopodion communities with *H. mantegazzianum* are not ecologically different from other communities of this alliance (cf. Otte 1994, 1996) and consequently lack own character or differential species apart from *H. mantegazzianum* itself. Secondly, *H. mantegazzianum* would perform rather poorly as a character species as it frequently occurs in vegetation types belonging to different alliances or even different classes.

While the spectrum of tall-forb communities found in the present study is in good agreement with findings of other authors, occurrences of *H. mantegazzianum* in managed grassland communities (Arrhenatherion, Cynosurion) and their early stages of succession after abandonment have been more or less neglected and never described in detail hitherto. However, the large proportion of ruderal grasslands found colonised by *H. mantegazzianum* in the present study emphasises the importance of abandoned or neglected grasslands for this species.

5.3 Assessment of impacts on the diversity of communities

Assessment of impacts of *H. mantegazzianum* on recipient communities should take into account the particular effects of the species but also its relationship to potential indigenous competitors and their effects on communities in comparable situations. Therefore, relevant questions concerning the role played by *H. mantegazzianum* are whether the species (i) affects community composition and α-diversity, (ii) is generally superior to competing indigenous species, and (iii) exerts different effects on resident communities as compared to indigenous species.

H. mantegazzianum can attain high cover values of up to 95 % of the stand's surface area. A possible effect of raised cover values of one species should be reduction in cover or even complete displacement of resident species. The negative correlation of *H. mantegazzianum* cover values with species-richness of relevés suggests that the species causes a decrease in α-diversity, which is consistent with assumptions of other authors (Lundström 1994, Pyšek & Pyšek 1995). Yet, it has to be considered that a higher species number at a given site before the species' invasion is hypothetical. It would also be conceivable that the species diversity was already low prior to the arrival of *H. mantegazzianum*, possibly due to disturbances or other historical factors which in turn could be a driving factor of *H. mantegazzianum* invasion (Woods 1997 in Meiners et al. 2001). Thus, a secure estimation of the species' effects on α-diversity could only be brought about by long-term observations starting prior to invasion.

Despite the difficulties to assess causal effects from the correlation between species numbers and cover values, it is quite plausible that light-demanding herbs will decrease and possibly disappear when a tall-forb builds up a closed canopy of leaves. Therefore, it is reasonable to assume that high densities of *H. mantegazzianum* cause a decrease in species numbers of swards consisting of light-demanding and rather low-growing species, which applies especially to abandoned grasslands.

Cover values of *H. mantegazzianum* were often rather low and only about a third of the surveyed stands had cover values greater than 40 %. It has to be taken into account that populations of *H. mantegazzianum* and the abundances of the species are not necessarily in equilibrium with their environment. Populations with low abundances might be in an early stage of invasion and further increase but, on the other hand, dense stands might decrease under competition by other tall forbs, shrubs or trees. Nevertheless, the distribution of cover values suggests that the species does not always have the potential for becoming dominant. The most frequent native tall forb in relevés with *H. mantegazzianum* was *Urtica dioica* which is itself a strong and high-growing competitor (C-strategist according to Grime et al. 1988). Inferring from the observations of the present study it appears that neither species is generally competitively superior to the other one as they co-occur in virtually every possible mixing ratio.

Habitat changes as found for the majority of sites (abandonment of grasslands, severe disturbances) provoke secondary successions starting from herbaceous swards or bare soils and, thus, naturally involve colonisation by species formerly excluded or removed from the sites through land use, shading, or severe disturbances. Obviously, *H. mantegazzianum* can benefit from dynamics as described above in generally suitable habitats and under favourable site conditions. But this is also the case with some indigenous plant species. The most frequent and competitive is without doubt again *Urtica dioica*. With regard to the third question, it can be stated that *Urtica dioica* as well as *H. mantegazzianum* are occasionally able to build up dominant stands and decrease species numbers in the course of successions. In this respect, their impacts are comparable.

Concludingly, *H. mantegazzianum* is in fact a successful coloniser and sometimes invader (sensu Davis & Thompson 2000) but it is not generally superior to indigenous species and does not have more negative impacts on the vegetation than some natives or other non-natives do under the same circumstances. With regard to the processes forming the habitats of the species (abandonment, disturbance) which can often lead to a decrease in species numbers due to non-native as well as native colonisers (Schmidt

1981, Neuhäusl & Neuhäuslova-Novotna 1985, Meiners et al. 2001), it can be stated that *H. mantegazzianum* is rather a symptom of biodiversity loss than the cause of it.

5.4 Evaluation of risks for nature conservation

According to a survey *H. mantegazzianum* has invaded nature reserves in approximately a third of all districts of Germany and it colonises protected habitat types in almost as many. Among the mentioned habitat types were, e.g., wet grasslands, alluvial (softwood) forests, alder swamp forest, lakeshores, calcareous and acidic marshes, terrestrial reed stands, and poor (chalk) grasslands (Thiele & Otte, submitted). This suggests that the species might be in conflict with aims of nature conservation.

However, within study areas virtually no habitat types or plant communities of interest for nature conservation were found to be invaded apart from exceptional open stands in slightly wet abandoned grasslands (Calthion-like stands) and some occurrences in alluvial (softwood) forests (Alnenion, Salicion). This might primarily be attributable to the habitat spectrum of the study areas that generally contained few habitats of interest for nature conservation. But site conditions supporting protected communities and rare species are often characterised by stress factors such as nutrient deficiency, drought, excessive wetness etc., and in the case of semi-natural habitats (e.g. grasslands) they also depend on suitable management. Starting from the observed habitat requirements of *H. mantegazzianum* it can be assumed that the species is not able to invade rare and endangered communities, as long as appropriate low productive site conditions and management are still prevailing. Only at the extreme margins of its ecological niche it could interfere with rare species and communities but there *H. mantegazzianum* is struggling itself and is constrained to low abundances. In conclusion, the assumption that *H. mantegazzianum* is in conflict with aims of nature conservation can be largely refuted by our findings.

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