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8. Ecological needs, habitat preferences and plant communities invaded by *Heracleum mantegazzianum*

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8.1 Introduction

Heracleum mantegazzianum Sommier & Levier is a monocarpic, perennial tall forb of the *Apiaceae* family. In its native region in Western Greater Caucasus, it is distributed over a wide altitudinal range from the foothills (50 m a.s.l.) to the subalpine zone (2200 m a.s.l.). The main native habitat types are alluvial softwood forests of the foothills and valley bottoms, forests clearings and abandoned grasslands in the montane zone, and subalpine tall-herb vegetation (see Otte *et al.*, Chapter 2, this volume). In the 19th century, *H. mantegazzianum* was introduced to Europe and cultivated in botanic and private gardens (Pyšek, 1991). Since its introduction the species has repeatedly escaped from cultivation and invaded a variety of habitats (Ochsmann, 1996).

Several studies have investigated habitat preferences of *H. mantegazzianum* in its invaded range in Europe. The extent of invasion in European landscapes was studied by Pyšek and Pyšek (1995) in the Czech Republic, and by Schepker (1998) and Thiele and Otte (2006a) in Germany. These studies found that stands of *H. mantegazzianum* can sometimes cover a few hectares but are mostly constrained to small patches. Some information on invaded habitat types has been provided recently by Pyšek (1994), Pyšek and Pyšek (1995), Ochsmann (1996), Tiley *et al.* (1996), Wade *et al.* (1997), and Thiele and Otte (2006a). Ecological needs of *H. mantegazzianum* have been studied by Pyšek and Pyšek (1995) and Ochsmann (1996) in a number of sites based on Ellenberg indicator values of the invaded vegetation. Exact measurements of soil nutrients and other soil parameters are given by Clegg and Grace (1974), Neiland (1986), Tiley *et al.* (1996), Otte and Franke (1998) and Thiele and Otte (2006b). Plant communities that include *H. mantegazzianum* have been described by Weber (1976), Dierschke (1984), Klauk (1988), Kolbeck *et al.* (1994), Otte and Franke (1998), Sauerwein (2004) and Thiele and Otte (2006b).

This chapter describes the habitats, plant communities and ecological needs of *H. mantegazzianum* in its invaded range in Europe, based on literature and our field research (Thiele and Otte, 2006a, b). If not otherwise indicated, results presented in this chapter are based on our field studies carried out in 20 study areas in Germany in 2002-2003. Study areas were landscape sections of 1 km² chosen to represent the most heavily invaded areas in Germany. Mostly, the study areas were situated in the natural geographic

region ‘Western low mountain ranges’ and secondly in the region ‘Foothills of the Alps’ (Thiele and Otte, 2006a). For all stands of *H. mantegazzianum* in the study areas, we recorded the habitat type and stand area, and estimated the abundance of *H. mantegazzianum*. Vegetation relevés and site conditions were sampled from all stands larger than 25 m² (hereafter referred to as ‘extensive stands’), unless the stands were destroyed by management measures such as cutting or rotovating. The total sample size was 202. Each study area contained between three and 20 extensive stands of *H. mantegazzianum*.

8.2 Habitats invaded by *Heracleum mantegazzianum*

Heracleum mantegazzianum occurs in a variety of habitat types in its invaded range in Europe. Among the most common habitat types of *H. mantegazzianum* are linear structures along traffic routes (roadsides, railway margins) and flowing waters (Fig. 8.1; Pyšek and Pyšek, 1995; Thiele and Otte, 2006a). These habitats can be completely open or partly shaded by tree lines, single trees or shrubs. Furthermore, *H. mantegazzianum* can often be found at fringes and margins of woodlands and grasslands. In terms of area covered by stands of *H. mantegazzianum*, abandoned grasslands are the most represented habitat type, followed by tall-herb stands which can be found at long-abandoned former grassland sites or at other disused sites. Moreover, ruderal places, i.e. sites that recently have been severely disturbed by human activities, are suitable habitat (Neiland, 1986; Pyšek, 1994; Ochsmann, 1996). Examples are sand pits, building sites, and rubbish dumps. Closed tree canopies prevent invasion and growth of *H. mantegazzianum*, but it can occur beneath sparse canopies or in light gaps. Managed grasslands are a marginal habitat type for *H. mantegazzianum* in which the species sometimes can establish if there is a high pressure of *H. mantegazzianum* seeds from adjacent stands. However, regular mowing or grazing with adequate intensity (e.g. mowing twice a year) adversely affects the performance of *H. mantegazzianum* (lower growth height, prevention or reduction of fruit set, slower life cycle). As a result, occurrences of *H. mantegazzianum* in managed grasslands are not invasive as long as regular management is applied. In addition to rural habitat types, *H. mantegazzianum* also occurs in urban areas, gardens and parks (Pyšek, 1994; Pyšek and Pyšek, 1995).

Heracleum mantegazzianum develops stands of varying extent and density. In our field studies, we recognized point-like stands (smaller than 25 m²), linear stands (narrower than 1 m), and extensive stands (larger than 25 m²). Extensive stands were classified into dominant (with more than 50% cover of *H. mantegazzianum*) and open (with less than 50% cover). Of all extensive stands found during our field studies in Germany, 36% were dominant. The highest proportions of dominant stands (among extensive stands) were found in open roadsides where inadequate maintenance was applied, in abandoned grasslands, and in neglected grassland and field margins (Fig. 8.1). Particularly extensive invasions by *H. mantegazzianum* in abandoned pastures and former settlements are currently present in the Slavkovský les region, Czech Republic (see Pyšek *et al.*, Chapter 3, this volume; Pyšek and Pyšek, 1995; Müllerová *et al.*, 2005) and by *H. sosnowskyi* Manden. in abandoned agricultural land in Latvia (see Ravn *et al.*, Chapter 17, this volume).

8.3 Plant communities invaded by *Heracleum mantegazzianum*

An alternative and more detailed perspective on habitats of *H. mantegazzianum* is provided by phytosociological analysis of vegetation relevés. We made 202 vegetation relevés in the

20 study areas in Germany during 2002 and 2003. The size of relevé plots was 25 m². We recorded all vascular plant species in the plots and estimated their abundance based on the modified Braun-Blanquet scale (Braun-Blanquet, 1965; Wilmanns, 1989). The relevés were classified according to the Central European system of plant communities (Ellenberg, 1988; Oberdorfer 1993). Species names follow Wisskirchen and Haeupler (1998). The floristic composition, basic parameters of vegetation structure, and species numbers of plant communities with *H. mantegazzianum* are presented in Table 8.1.

Plant communities of *H. mantegazzianum* in its Central European invaded range predominantly belong to the vegetation classes of semi-natural grasslands and nitrophilous tall-herb communities (Kolbeck *et al.*, 1994; Ochsmann, 1996; Otte and Franke, 1998, Sauerwein, 2004; Thiele and Otte, 2006b). Woodlands with *H. mantegazzianum* belong partly to more or less natural alluvial forests (Kolbeck *et al.*, 1994; Sauerwein, 2004; Thiele and Otte, 2006b) but anthropogenic woodlands often do not match with the system of plant communities and, therefore, are not described in detail here. The same applies to some pioneer plant communities of *H. mantegazzianum* at severely disturbed sites, e.g. sand pits, and other anthropogenic vegetation types (Ochsmann, 1996; Thiele and Otte, 2006b). Klačuk (1988) classified the stands with dominant *H. mantegazzianum* as a separate association *Urtico-Heracleetum mantegazzianii*, but this proposal has been rejected by the majority of authors studying these plant communities (Schwabe and Kratochwil, 1991; Ochsmann, 1996; Otte and Franke, 1998; Sauerwein, 2004; Thiele and Otte, 2006b).

Within the class of semi-natural grasslands (Molinio-Arrhenatheretea) *H. mantegazzianum* is confined to communities of nutrient rich, mesic to moist sites. These belong to the order Arrhenatheretalia, which comprises oat grass meadows (Arrhenatherion) and rye grass-white clover pastures (Cynosurion). Principally, these communities are characterized by regular agricultural land use (mowing, pasturing). However, *H. mantegazzianum* is more prevalent in variants without regular land-use regimes. These are, on the one hand, ruderal grasslands maintained by rather irregular mowing or removal of shrubs, such as neglected road verges and grassland margins, and on the other hand, abandoned former agricultural grasslands.

Nitrophilous tall-herb communities of the class Galio-Urticetea which feature *H. mantegazzianum* are mainly terrestrial ground elder (*Aegopodium podagraria* L.) communities at mesic to moist sites (Aegopodion) and riparian tall-herb communities (Calystegion). In addition to these, *H. mantegazzianum* occasionally occurs in the alliance Alliarion, which comprises communities of shady fringes. Within the class Galio-Urticetea, *H. mantegazzianum* has the highest affinity to plant species that are especially typical or characteristic of Aegopodion communities. Apart from the name-giving species, ground elder, these are most frequently *Urtica dioica* L., *Galium aparine* L. and *Glechoma hederacea* L. In riparian tall-herb communities, *H. mantegazzianum* is usually confined to zones that are only inundated during floods but otherwise offer aerated top soils (Ochsmann, 1996; Thiele and Otte, 2006b). Therefore, from the phytosociological point of view, *H. mantegazzianum* is a species of terrestrial tall-herb communities of the alliance Aegopodion (Sauerwein, 2004; Thiele and Otte, 2006b).

According to Sauerwein (2004), *H. mantegazzianum* can also establish in ruderal annual communities of the alliance Sisymbriion (class Stellarietea mediae) in urban areas. However, a precondition for occurrences in annual communities is that frequent disturbances, essential for such vegetation types, have stopped.

Alluvial woodlands with *H. mantegazzianum* can partly be classified as alder-ash-gallery forests (Alnenion glutinoso-incanae, class Querco-Fagetea) along colline (100-200 m a.s.l.) to montane (500-900 m a.s.l.) rivers, or gray willow scrub (Salicion elaeagni, class

Salicetea purpureae) along montane to subalpine (-2000 m a.s.l.) rivers. These are the most natural vegetation types of *H. mantegazzianum* described from Central Europe. Other woodlands in which *H. mantegazzianum* occurs include young forestry plantings in river valleys and pioneer forests of, e.g., *Populus tremula* or *Salix caprea* (Sauerwein, 2004; Thiele and Otte, 2006b). It is noteworthy, that almost all woodlands with *H. mantegazzianum* that were found during our field studies had developed from abandoned grasslands during the last 50 years (see sections 8.4, 8.7). Generally, *H. mantegazzianum* in woodlands is restricted to sparse canopies, gaps, or margins where the species can benefit from increased light supply compared with closed canopies of forest interiors.

The frequencies of plant communities with *H. mantegazzianum* in the sites that we studied are presented in Fig. 8.2. *Heracleum mantegazzianum* occurs with about the same frequency in grasslands and tall-herb communities, which accounted for most of the relevés, while other open vegetation types and woodlands are less represented.

8.4 Types of disturbance and soil conditions in sites invaded by Heracleum mantegazzianum

Generally, sites invaded by *H. mantegazzianum* are not subject to regular land use except for marginal occurrences in managed grasslands. In our data set, 71% of relevé plots were disused and 17% were maintained by rather irregular mowing or removal of shrubs and trees, while only 12% of sites were under agricultural land use. The difference between the percentages of agricultural land use (12%) and the plant community type ‘managed grasslands’ (18%, Fig. 8.2) are due to some recently abandoned grasslands that were classified as ‘managed grasslands’ from a phytosociological perspective.

Disturbances apart from agricultural land use or maintenance mowing were detectable in 57% of extensive stands of *H. mantegazzianum*. Human-caused disturbances included clearing of trees or shrubs (10%), mechanical disturbing of the sward (7%), deposition of organic and inorganic waste (5%), and mining (5%). Furthermore, 34% of sites were disturbed by periodical flooding of rivers, which sometimes overlapped with human-caused disturbances.

The history of relevé plots during the last 50 years was reconstructed from longitudinal series of aerial photographs (see also Pyšek *et al.*, Chapter 3, this volume; Thiele and Otte, 2006b). Dates of the time series were the 1950s, 1970s, and approximately 2000. The prevalent change was abandonment of grassland management and arable land use (54% of plots). Another trend was severe disturbance or destruction of sites (18%) by, e.g., clearing of woodlands or open-cast mining (sand pit, rock quarry). The remaining sites were either under persistent management (agricultural land-use, maintenance) or derelict over the whole period. In general, sites preferred by *H. mantegazzianum* (i.e. sites without regular land use) are characterized by considerable habitat changes during recent decades.

Concerning soil texture, soils were mostly fairly deep (> 0.5 m) and had a medium or high capacity for soil moisture (available field capacity usually between 140 and 220 mm, Table 8.2). With respect to nutrient content (N, P, K, Mg, Ca), soils of *H. mantegazzianum* sites are variable but usually fair or rich, and the range of C/N ratios is markedly narrow (Table 8.2; Neiland, 1986; Tiley *et al.*, 1996; Thiele and Otte, 2006b). These site characteristics indicate that *H. mantegazzianum* needs fairly high nutrient and moisture levels for optimal growth. With respect to pH values, *H. mantegazzianum* was

found in a wide range of conditions from acidic to alkaline (Table 8.2). Extreme pH values were 4.0 (Thiele and Otte, 2006b) and 8.5 (Clegg and Grace, 1974).

In our field study, the light supply of relevé plots was estimated on a five-step ordinal scale ranging from deep shade to full light. Most plots were found at open sites with full light supply (78%), which shows that *H. mantegazzianum* needs high light levels. Average Ellenberg values of vegetation relevés indicate light to semi-shade situations (Ochsmann, 1996; Thiele and Otte, 2006b). Growth of the species in semi-shade is fairly good, but it cannot grow in full shade.

8.5 Population characteristics of *Heracleum mantegazzianum* in relation to plant communities and site conditions

Cover of *H. mantegazzianum* in the vegetation sampled during our field study varied between 1% and 95%. Low cover percentages were common, and about half of sampled plots had *H. mantegazzianum* cover of less than 20%. Nevertheless, in 31% of sampled plots ($n = 202$), and 36% of all encountered extensive stands ($n = 233$), *H. mantegazzianum* was dominant, with cover exceeding 50%.

There was no statistically significant relationship between soil characteristics and cover of *H. mantegazzianum*. However, in a few sites with low nutrient status and impeded drainage the cover and height of *H. mantegazzianum* was conspicuously low which suggests that poor nutrient supply and/or wetness constrain the species. With respect to plant communities, *H. mantegazzianum* cover could take on virtually any value in ruderal grasslands and tall-herb communities, whereas cover was constrained to moderate or low percentages in managed grasslands and woodlands due to regular land use and shading, respectively (Fig. 8.3).

Furthermore, regular land use and shading significantly reduced the abundance of flowering individuals of *H. mantegazzianum* in managed grasslands (median/maximum per 25 m²: 1.5/26, $n = 36$) and woodlands (0.0/5, $n = 19$) compared to ruderal grasslands (4.5/37, $n = 53$) and tall-herb communities (7.0/54, $n = 78$). In managed grasslands fruit set was also strongly reduced because of mowing or grazing of primary stems, whereas fruit set was generally abundant in any other vegetation type, even in woodlands when flowering occurred.

8.6 *Heracleum mantegazzianum* in secondary successional series

A gradient analysis (Correspondence Analysis) of our vegetation relevés with *H. mantegazzianum* revealed a main sequence of vegetation types from managed grassland to ruderal grasslands to tall-herb communities and, finally, to woodlands. Subordinately, a parallel sequence from severely disturbed sites to tall-herb stands to woodlands was found (Fig. 8.4; see Thiele and Otte, 2006b for details). These two parallel sequences represented the main gradient (first axis of the correspondence analysis) in the vegetation data. Towards the upper end of this gradient the age of abandoned or disturbed sites and the proportion of C-strategy (Grime *et al.*, 1988; Grime, 2001) among resident plant species increased whereas grassland management declined. Generally, these sequences of vegetation types with *H. mantegazzianum* can be interpreted as successional seres. Although some sites were actually in a stable state because of regular land-use or maintenance, the majority of sites with *H. mantegazzianum* were in the process of secondary succession following abandonment or severe disturbances. These secondary successions mostly started from grassland swards, but some were from bare ground after severe disturbance (e.g., sand pits, mining or clearing of forests). Both seres will,

ultimately, result in forests (Kahmen, 2004) unless land use is resumed or severe disturbances recur.

Along these successional seres, the cover of *H. mantegazzianum* showed a unimodal response (Fig. 8.5). In managed grasslands the cover of *H. mantegazzianum* was constrained by land use and in successional seres starting on bare ground plant cover was generally low due to recent disturbance. The highest cover of *H. mantegazzianum* was found in young stages of succession or in sites where succession was blocked by permanent ongoing low-intensity maintenance, such as neglected road verges and grassland margins. With increasing successional age, cover of *H. mantegazzianum* declined again, whereas that of native tall herbs steadily increased. Finally, when woody components took over, cover of *H. mantegazzianum* was more and more constrained by increasing shading.

Hence, it appears that declining cover of *H. mantegazzianum* with increasing successional age is attributable to inter-specific competition with other tall-herbs and woody species. However it should be borne in mind that the data were single records from different sites in different successional stages and not multitemporal observation of the same sites. Therefore, we do not have direct evidence for native species reducing *H. mantegazzianum* cover during succession at a particular site. The relationship between *H. mantegazzianum* cover and successional age could, on the one hand, be attributed to less successful invasion into old successional stages or, on the other hand, to successful invasion into young successional stages followed by declining *H. mantegazzianum* cover due to competition increasing with successional age.

8.7 Land-use changes as drivers of invasion

Comparison of current and historical aerial photographs of the 20 study areas in Germany indicated that landscapes with *H. mantegazzianum* have undergone considerable changes during the last 50 years (1950s to approx. 2000). The area covered by agricultural land (arable fields, managed grasslands) decreased dramatically over this period while that covered by forests increased (Fig. 8.6). Therefore, the predominant trend of land-cover changes in the study areas has been abandonment of agricultural land and development of woodlands, which were partly planted but mostly developed through natural colonisation and succession. Succession on former agricultural land determined the dynamics of habitats available for invasion by *H. mantegazzianum*.

To determine the long-term dynamics, habitats were ranked according to their vulnerability to invasion. The affinity of *H. mantegazzianum* to particular habitat types was evaluated using the electivity index E , used by Ivlev (1961) as a measure of selectivity in prey selection. The application of this formula (see Table 8.3) gives a range of values from +1.0 for a very high degree of selection to -1.0 for a complete avoidance. Thus, high values in our data indicate that *H. mantegazzianum* exhibits a strong affinity to a given habitat type, while low values indicate that it is rarely present in that habitat. The ranking of habitat types according to the electivity index showed that *H. mantegazzianum* has a high affinity to completely open (i.e. tree- and shrub-less) habitat types, such as abandoned grasslands and ruderal sites, but little affinity with woody habitat types (>10% cover of trees or shrubs).

Based on a conspicuous 'gap' in the electivity index values between completely open and woody habitats, we classified habitats with *H. mantegazzianum* into optimal and sub-optimal (Table 8.3). Dynamics of these two groups of habitats over the last 50 years were different. Sub-optimal habitat types accounted for the majority of the total area of habitats with *H. mantegazzianum* and exhibited a steady increase over the whole period,

while optimal habitats showed a unimodal trend. From the 1950s to the 1970s, the area of optimal habitats of *H. mantegazzianum* rose by 73.4%, but since then it has dropped back to approximately the same level as in the 1950s. In total, the cover of habitat types suitable for *H. mantegazzianum* in the study areas has been increasing, resulting in a 1.5-fold increase (Fig. 8.6).

A large proportion of optimal habitats of *H. mantegazzianum* in the 1970s (61%) and a substantial proportion of sub-optimal habitats (27%) originated from former agricultural land (Fig. 8.7A, B). From the 1970s to present, 35% of optimal habitats have become sub-optimal due to the establishment of woody plants in the course of succession (Fig. 8.7C). Further, 38% of sub-optimal habitats have developed into forests (Fig. 8.7D). These results show that the increase of optimal habitats of *H. mantegazzianum* from the 1950s to the 1970s is mainly due to abandonment of land whereas the subsequent decrease of optimal habitats is largely attributable to secondary succession. Decreasing land use has been a post war trend in isolated and poorer areas of Europe especially in mountainous areas (Baldock *et al.*, 1996; MacDonald *et al.*, 2000). Significantly, the study areas in Germany were mostly situated in mountainous areas where Bethe and Bolsius (1995) have recognized that agriculture is likely or very likely to be reduced.

8.8 Conclusions

Heracleum mantegazzianum invades a variety of habitat types in Europe. While roadsides, riverbanks, ruderal places, and woodland fringes have previously been documented as preferred habitats, results from our field study in Germany emphasize the importance of abandoned grasslands as habitats of *H. mantegazzianum* in European landscapes.

H. mantegazzianum can occur under a wide spectrum of environmental conditions. However, preferred habitats are rather similar, characterized by rich resource supply and disturbance but lack of regular management. Primary environmental factors constraining invasion of *H. mantegazzianum* are regular land use and shading by trees. Furthermore, it appears that low soil nutrient status and/or wetness constrain invasion.

From a phytosociological perspective, abandoned or neglected semi-natural grasslands are a major plant community type of *H. mantegazzianum* although the sociological centre of the species is on nitrophilous tall-herb communities. Plant communities with *H. mantegazzianum* form a successional gradient from grasslands, or subordinately severely disturbed sites, to tall-herb communities and woodlands. The successional age of the sites affects the cover of *H. mantegazzianum*. In old successional stages, cover is constrained by inter-specific competition from other tall herbs and woody species.

Habitats of *H. mantegazzianum* in German study areas have been very dynamic during the last 50 years. On the whole, the area available for invasion has increased considerably which is mainly due to abandonment of agricultural land use. However, optimal (i.e. open) habitats are characterized by a substantial turnover. Abandonment creates new habitat patches while secondary succession resulting in forests eliminates habitats. Altogether it appears that abandonment of land use is the primary driver of habitat dynamics and may well have enhanced invasion of *H. mantegazzianum* during recent decades.

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References

- Braun-Blanquet, J. (1965) *Plant Sociology: the Study of Plant Communities*, 1st edn. Hafner, London.
- Baldock, D., Beaufoy, G., Brouwer, F. and Godeschalk, F. (1996) *Farming at the Margins. Abandonment or Redeployment of Agricultural Land in Europe*. Institute for European Environmental Policy, London, The Hague.
- Bethe, F. and Bolsius, E.C.A. (1995) *Marginalisation of Agricultural Land in the Netherlands, Denmark and Germany*. National Spatial Planning Agency, The Hague.
- Clegg, L.M. and Grace, J. (1974) The distribution of *Heracleum mantegazzianum* (Somm. et Lev.) near Edinburgh. *Transactions of the Botanical Society Edinburgh* 42, 223-229.
- Dierschke, H. (1984) Ein *Heracleum mantegazzianum*-Bestand im NSG ‘Heiliger Hain’ bei Gifhorn (Nordwestdeutschland). *Tuexenia* 4, 251-254.
- Ellenberg, H. (1988) *Vegetation Ecology of Central Europe*, 4th edn. Cambridge University Press, Cambridge.
- Grime, J.P., Hodgson, J.G. and Hunt, R. (1988) *Comparative Plant Ecology: a Functional Approach to Common British species*. Unwin Hyman, London.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. J. Wiley and Sons, Chichester.
- Ivlev, V.S. (1961) *Experimental Ecology of the Feeding of Fishes*. Yale University Press, New Haven.
- Kahmen, S. (2004) Plant trait responses to grassland management and succession. *Dissertationes Botanicae* 382, 1-123.
- Klauck, E.J. (1988) Das Urtico-Heracleetum mantegazzianii. Eine neue Pflanzengesellschaft der nitrophytischen Stauden- und Saumgesellschaften. *Tuexenia* 8, 263-267.
- Kolbek, J., Lecjaksová, S. and Härtel, H. (1994) The integration of *Heracleum mantegazzianum* into the vegetation - an example from central Bohemia. *Biologia* 49, 41-51.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J. and Gibon, A. (2000) Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management* 59, 47-69.
- Müllerová, J., Pyšek, P., Jarošík, V. and Pergl, J. (2005) Aerial photographs as a tool for assessing the regional dynamics of the invasive plant species *Heracleum mantegazzianum*. *Journal of Applied Ecology* 42, 1042-1053.
- Neiland, M.R.M., Proctor, J. and Sexton, R. (1986) Giant hogweed (*Heracleum mantegazzianum* Somm. & Lev.) by the river Allan and part of the river Forth. *Forth Naturalist and Historian* 9, 51-56.
- Oberdofer, E. (1993) *Süddeutsche Pflanzengesellschaften III. Wirtschaftswiesen und Unkrautgesellschaften*, 3rd edn. Fischer, Jena.

- Ochsmann, J. (1996) *Heracleum mantegazzianum* Sommier & Levier (*Apiaceae*) in Deutschland - Untersuchungen zur Biologie, Verbreitung, Morphologie und Taxonomie. *Feddes Repertorium* 107, 557-595.
- Otte, A. and Franke, R. (1998) The ecology of the Caucasian herbaceous perennial *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in cultural ecosystems of Central Europe. *Phytocoenologia* 28, 205-232.
- Pyšek, P. (1991) *Heracleum mantegazzianum* in the Czech Republic: Dynamics of spreading from the historical perspective. *Folia Geobotanica & Phytotaxonomica* 26, 439-454.
- Pyšek, P. (1994) Ecological aspects of invasion by *Heracleum mantegazzianum* in the Czech Republic. In: de Waal, L.C., Child, L.E., Wade, P.M. and Brock, J.H. (eds.) *Ecology and Management of Invasive Riverside Plants*. J. Wiley and Sons, Chichester, pp. 45-54.
- Pyšek, P. and Pyšek, A. (1995) Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. *Journal of Vegetation Science* 6, 711-718.
- Sauerwein, B. (2004) *Heracleum mantegazzianum* Somm. et Lev., eine auffällige *Apiaceae* bracher Säume und Versaumungen. *Philippia* 11, 281-319.
- Schachtschabel, P. (1954) Das pflanzenverfügbare Magnesium im Boden und seine Bestimmung. *Zeitschrift für Pflanzenernährung, Düngung, Bodenkunde* 67, 9-23.
- Schepker, H. (1998) Wahrnehmung, Ausbreitung und Bewertung von Neophyten - Eine Analyse der problematischen nichteinheimischen Pflanzenarten in Niedersachsen. *Ibidem*, Stuttgart.
- Schwabe, A. and Kratochwil, A. (1991) Gewässer-begleitende Neophyten und ihre Beurteilung aus Naturschutz-Sicht unter besonderer Berücksichtigung Südwestdeutschlands. *NNA Berichte* 4, 14-27.
- Schüller, H. (1969) Die CAL-Methode, eine neue Methode zur Bestimmung des pflanzenverfügbaren Phosphates in Böden. *Zeitschrift für Pflanzenernährung und Bodenkunde* 123, 48-63.
- Thiele, J. and Otte, A. (2006a) Invasion patterns of *Heracleum mantegazzianum* in Germany on the regional and local scale: native biodiversity at risk? (submitted)
- Thiele, J. and Otte, A. (2006b) Analysis of habitats and communities invaded by *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in Germany. *Phytocoenologia* 36, 280-312.
- Tiley, G.E.D., Dodd, F.S. and Wade, P.M. (1996) *Heracleum mantegazzianum* Sommier & Levier. *Journal of Ecology* 84, 297-319.
- Wade, M., Darby, E.J., Courtney, A.D. and Caffrey, J.M. (1997) *Heracleum mantegazzianum*: A problem for river managers in the Republic of Ireland and the United Kingdom. In: Brock, J.H., Wade, M., Pyšek, P. and Green, D. (eds.): *Plant invasions: Studies from North America and Europe*. Backhuys Publishers, Leiden, pp. 139-151.
- Weber, R. (1976) Zum Vorkommen von *Heracleum mantegazzianum* Somm. et Levier im Elstergebirge und den angrenzenden Gebieten. *Mitteilungen zur floristischen Kartierung (Halle)* 2, 51-57.
- Wilmanns, O. (1989) *Ökologische Pflanzensoziologie*, 4th edn. Quelle and Meyer, Heidelberg.
- Wisskirchen, R. and Haeupler, H. (1998): *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart.

Table 8.1. Composition of plant communities with *Heracleum mantegazzianum* based on 202 vegetation relevés from 20 study areas in Germany. Constancy of plant species (% of the number of vegetation relevés in which they were recorded) is presented for the types of communities distinguished. Cover (%) and height of the vegetation layers were assessed separately for *H. mantegazzianum* and the remaining resident herbaceous plant species. Height refers to the main leaf canopy of the vegetation layers. FQ = total frequency of the species in the data set. Species are arranged according to their affinity to particular community types; those which did not exceed a constancy of 10% in at least one community type were omitted. Species names follow Wisskirchen and Haeupler (1998).

	Managed grasslands	Ruderal grasslands	Tall-herb communities	Woodlands	Other open vegetation	FQ
Number of relevés	36	53	78	19	16	
Average cover (%)						
Total	93.5	93.3	87.8	83.7	72.6	
<i>Heracleum mantegazzianum</i>	16.5	44.2	48.1	23.2	16.7	
Herb layer	88.5	73.1	52	39.6	64.3	
Tree layer	-	-	-	66.1	-	
Average height (m)						
<i>Heracleum mantegazzianum</i>	0.6	1.0	1.2	1.0	0.7	
Herb layer	0.4	0.6	0.7	0.5	0.6	
Tree layer	-	-	-	15.1	-	
Species number	24.5	22.1	14.3	16.8	22.1	
<i>Heracleum mantegazzianum</i>	100	100	100	100	100	202
Grasslands						
<i>Dactylis glomerata</i>	92	87	36	58	37	124
<i>Holcus lanatus</i>	78	68	12	16	32	81
<i>Arrhenatherum elatius</i>	58	75	22		19	81
<i>Alopecurus pratensis</i>	86	49	22		13	76
<i>Ranunculus repens</i>	75	47	19	21	43	78
<i>Galium mollugo</i> agg.	47	51	9	11	24	57
<i>Taraxacum officinale</i> agg.	69	30	8	5	19	51
<i>Festuca rubra</i> agg.	31	40	3	5	24	39
<i>Rumex acetosa</i>	42	32	3		24	38
<i>Anthriscus sylvestris</i>	36	36	13	11	6	45
<i>Phleum pratense</i>	47	23	4	5		33
<i>Veronica chamaedrys</i> s.l.	22	36	1	5		29
<i>Heracleum sphondylium</i>	39	19	4		6	28
<i>Achillea millefolium</i> agg.	39	19	3		6	27
<i>Agrostis stolonifera</i>	33	21	8	16	24	36
<i>Lathyrus pratensis</i>	33	19	6		24	31
<i>Festuca pratensis</i>	47	8				21
<i>Poa pratensis</i> s.str.	25	21	3	5		23
<i>Trifolium repens</i>	36	11		5		20
<i>Angelica sylvestris</i>	17	23	3		43	27
<i>Bistorta officinalis</i>	39	8	4		6	22
<i>Plantago lanceolata</i>	33	9	1			18
<i>Cirsium palustre</i>	14	21	5		32	25
<i>Agrostis capillaris</i>	33	8	8	5	37	29
<i>Vicia cracca</i>	14	19	3		19	20
<i>Cerastium holosteoides</i>	28	9				15
<i>Lolium perenne</i>	36	2	1		6	16
<i>Leucanthemum vulgare</i>	11	17			13	15
<i>Trisetum flavescens</i>	19	11	3		6	16
<i>Trifolium pratense</i>	25	6			6	13
<i>Myosotis nemorosa</i>	19	6		16	19	16
<i>Prunella vulgaris</i>	14	9	1		6	12
<i>Lotus pedunculatus</i>	11	11			32	15
<i>Ranunculus acris</i> agg.	17	6				9

<i>Anthoxanthum odoratum</i>	22	2				9
<i>Centaurea jacea</i>	19	4				9
Tall-herb communities						
<i>Urtica dioica dioica</i>	22	60	97	84	32	137
<i>Galium aparine</i> agg.	8	60	74	53	19	106
<i>Poa trivialis</i>	83	75	69	63	32	141
<i>Aegopodium podagraria</i>	39	19	51	37	6	72
<i>Glechoma hederacea</i>	22	30	42	42		65
<i>Impatiens glandulifera</i>	3	2	40	32		39
<i>Symphytum officinale</i>	11	2	37	16	6	38
<i>Stellaria nemorum</i>	6	4	32	21		33
<i>Alliaria petiolata</i>			31	11		26
<i>Calystegia sepium</i>	6	17	26	5	13	34
<i>Galeopsis tetrahit</i>	3	42	22	32	13	48
<i>Geum urbanum</i>	6	26	21	47	6	42
<i>Elymus repens</i>	47	45	17		19	57
<i>Solidago gigantea</i>		6	17	5		17
<i>Carduus crispus</i>		4	15			14
<i>Filipendula ulmaria</i>	22	21	14	5	13	33
<i>Petasites hybridus</i>	11	8	14			19
<i>Stachys sylvatica</i>	3	19	12	11		22
<i>Cirsium oleraceum</i>	14	6	12			17
<i>Humulus lupulus</i>		2	12		13	12
<i>Phalaris arundinacea</i>	3	11	10	26	13	22
<i>Poa nemoralis</i>		6	10	47		20
<i>Moehringia trinervia</i>		2	10	11	6	12
<i>Lamium album</i>	3	4	10			11
Woodlands						
<i>Acer pseudoplatanus</i>	3		6	32	19	15
<i>Fraxinus excelsior</i>	6	6	10	26		18
<i>Stellaria holostea</i>	3	11	6	21	6	17
<i>Alnus glutinosa</i>			5	21		8
<i>Festuca gigantea</i>	6		9	16		12
<i>Elymus caninus</i>		4	10	11		12
<i>Salix fragilis</i>			8	11		8
<i>Salix eleagnos</i>			1	11		3
<i>Alnus incana</i>				11		2
<i>Populus nigra</i>				11		2
Companion species						
<i>Cirsium arvense</i>	58	42	12		43	59
<i>Rubus fruticosus</i> agg.		25	18	37	32	39
<i>Deschampsia cespitosa</i>	17	19	9	26	43	35
<i>Hypericum perforatum</i>	19	28	3	5	32	30
<i>Rubus idaeus</i>	3	17	12	11	56	30
<i>Vicia sepium</i>	14	36	4	5	6	29

Table 8.2. Chemical characteristics of topsoil samples (five cores per plot, 25 cm depth) and available field capacity of the effective root zone (AFC) from 202 plots with *Heracleum mantegazzianum* in 20 study areas in Germany. Medians and the 10 and 90 percentiles are presented. The AFC gives the maximum amount of plant-available water in the soil in the effective root zone (i.e. up to approx. 1 m depth depending on soil density and texture). P and K were extracted with calcium-acetate-lactate solution using the CAL method (Schüller, 1969) while Mg was extracted with calcium chloride solution (Schachtschabel, 1954). N and C were analysed with a CN analyser. In 2002, the pH values of topsoil samples were measured in H₂O with a laboratory pH meter and additional drillings were conducted up to 1 m depth, if possible, to assess the AFC (n = 118). Data from Thiele and Otte (2006b).

Parameter	<i>n</i>	Median	10 perc.	90 perc.
P _{CAL} (mg/100g)	202	1.7	0.2	8.1
K _{CAL} (mg/100g)	202	8.3	4.2	21.6
N _t (% SDM)	202	0.3	0.2	0.4
Mg _{CACl₂} (mg/100g)	202	14.3	7.0	27.0
C _{org} (% SDM)	192	2.8	1.6	5.2
C/N ratio	192	9.8	8.2	16.3
pH _{H₂O}	118	5.6	4.9	6.4
AFC _{root zone} (mm)	118	168	140	220

Table 8.3. Habitat types for *Heracleum mantegazzianum* mapped from aerial photographs from 20 study areas in Germany. Affinity to particular habitat types was assessed using the electivity index $E = (r-p)/(r+p)$ (Ivlev, 1961), where r is the proportion of the habitat area covered by *H. mantegazzianum* and p is the proportion of the total area of the landscape sampled that is covered by that habitat. High values of E indicate that *H. mantegazzianum* exhibits a strong affinity to a given habitat type, while low values indicate that it tends to avoid that habitat. The value of zero indicates that *H. mantegazzianum* is present in a given habitat in the same proportion as the habitat is represented in the landscape. Based on E , habitats were ranked and classified into optimal and sub-optimal based on a conspicuous gap between completely open habitats and habitats containing woody components (>10% tree or shrub cover).

Habitat type	Electivity index
Optimal habitats:	
Overhead and buried cable routes	0.96
Abandoned grasslands, neglected grassland and field margins, and tall-herb stands	0.94
Open railwaysides	0.87
Open riverbanks	0.82
Ruderal areas	0.82
Open roadsides	0.69
Sub-optimal habitats:	
Afforestations	0.39
Copses	0.33
Shaded railway margins	0.33
Shaded riversides	0.32
Tree fallow	0.32
Shaded roadsides	-0.17
Partly-shaded railway margins	-0.52
Partly-shaded roadsides	-0.61
Forest margins	-0.74
Partly-shaded riversides	-0.76

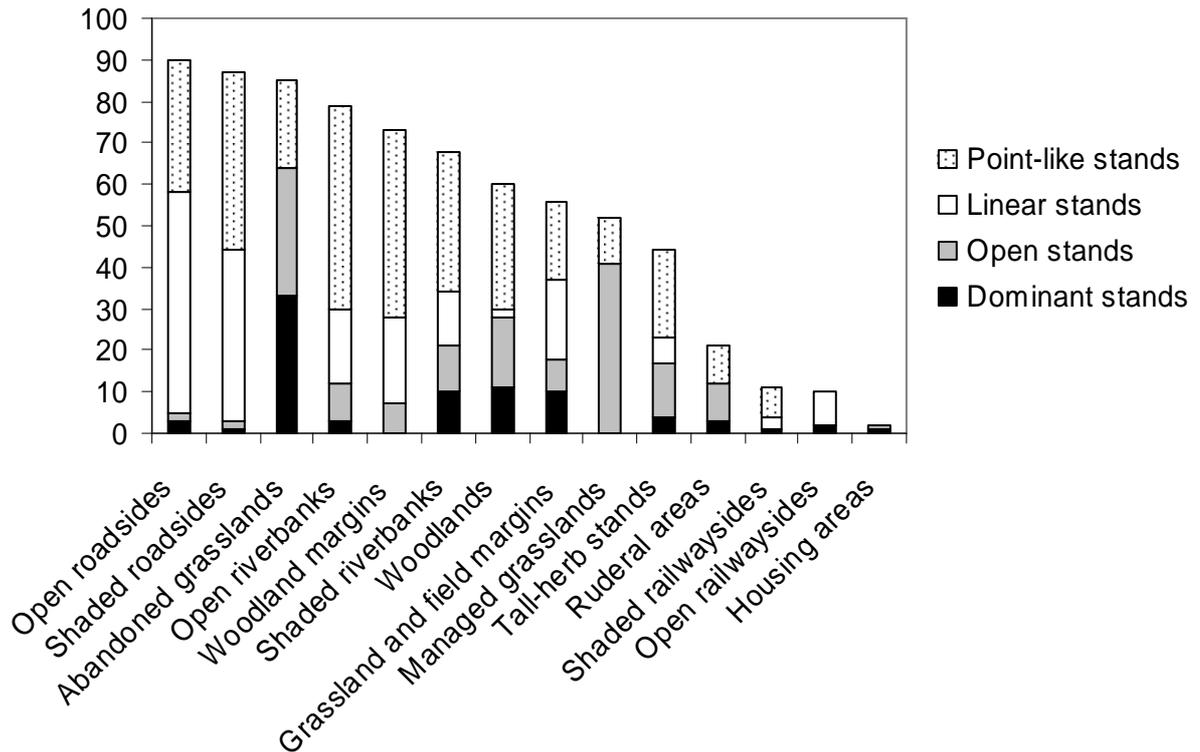


Fig. 8.1. Frequencies of habitat types invaded by *Heracleum mantegazzianum* in 20 study areas in Germany. Number of stands recorded in each habitat, based on 738 records from Germany, is shown and representation of different stand types within habitat types indicated. Stands exceeding 25 m² in size were classified into dominant (with more than 50% cover of *H. mantegazzianum*) and open (with less than 50% cover). Other categories distinguished are point-like (smaller than 25 m²) and linear (narrower than 1 m) stands. Data from Thiele and Otte (2006a). 'Open' habitat types are virtually treeless and shrubless while 'shaded' habitat types had more than 10% tree or shrub cover. 'Abandoned grasslands' are former agricultural grasslands which are currently disused. 'Woodland margins' are the outer 5 (-10) m of copses, forests, and shrubland. 'Woodlands' refers to the interior of copses and shrubland but not to forest interiors. 'Grassland and field margins' are marginal parts of grassland and arable fields, which are not used agriculturally. 'Tall-forb stands' can be found in long-abandoned sites of former agricultural grasslands or other long disused sites. 'Ruderal areas' are recently disturbed sites, such as sand pits, building ground and rubbish dumps, which are in an early stage of secondary succession.

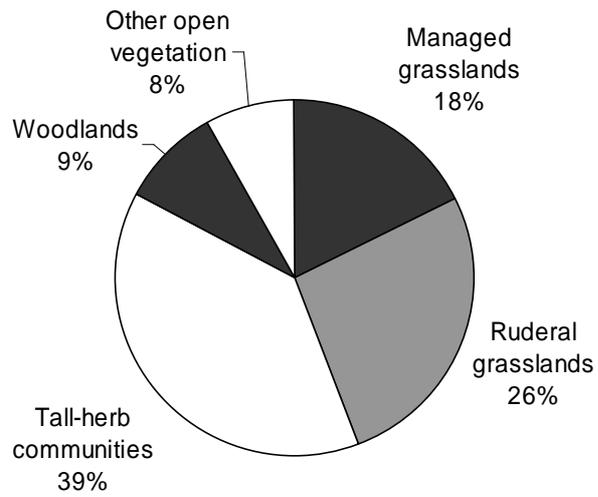


Fig. 8.2. Relative frequencies of plant communities with *Heracleum mantegazzianum* found at 202 sites in 20 study areas in Germany. Simplified from Thiele and Otte (2006b).

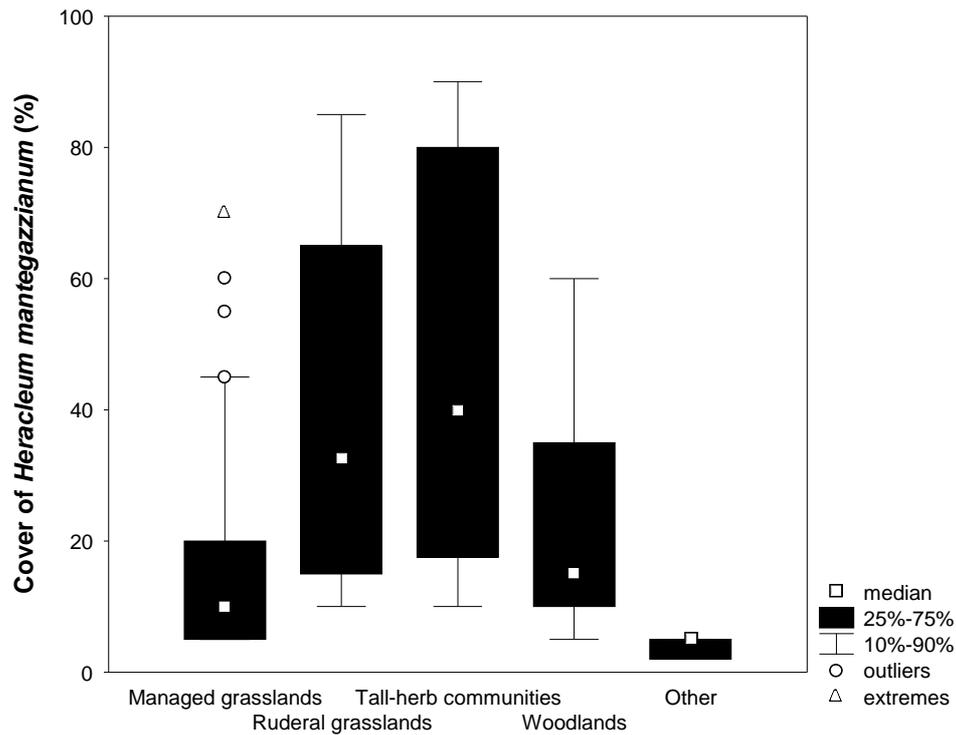


Fig. 8.3. Cover of *Heracleum mantegazzianum* (%) in different vegetation types. High cover percentages of *H. mantegazzianum* in the community type 'managed grasslands' are due to freshly abandoned grasslands classified as 'managed grasslands' from a phytosociological perspective. 'Other' community types mostly included severely disturbed sites, which generally had low plant cover and, therefore, also *H. mantegazzianum* cover was low. Data from Thiele and Otte (2006b). Outliers are further from the upper box level than $1.5 \times$ inter-quartile-range. For extremes the coefficient is 3. Sample sizes: managed grasslands = 36; ruderal grasslands = 53; tall-herb communities = 78; woodlands = 19; other = 16.

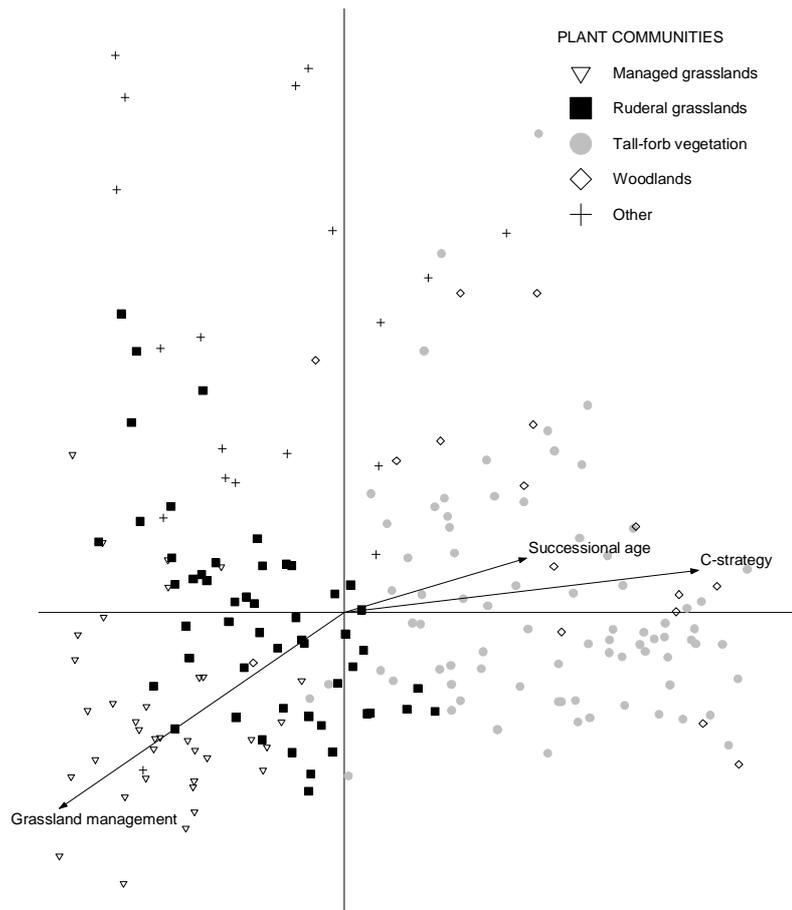


Fig. 8.4. Correspondence analysis (CA) of 202 vegetation relevés with *Heracleum mantegazzianum* from 20 study areas in Germany. The first (x) and second (y) axes of the CA are presented. The main gradient (axis 1) represented secondary successional seres after abandonment of grassland management or severe disturbance. For definition of plant communities see section 8.2. Arrows indicate trends in the environmental variables. 'Successional age' was derived from multitemporal series of aerial photographs and represents the time since abandonment of land use or severe disturbance events on a binary scale (before 1970s, after 1970s). 'C-strategy' refers to the classification of plant strategies according to Grime *et al.* (1988) and was calculated as the sum of proportions of c-strategy of plant species in the relevés. Data from Thiele and Otte (2006b).

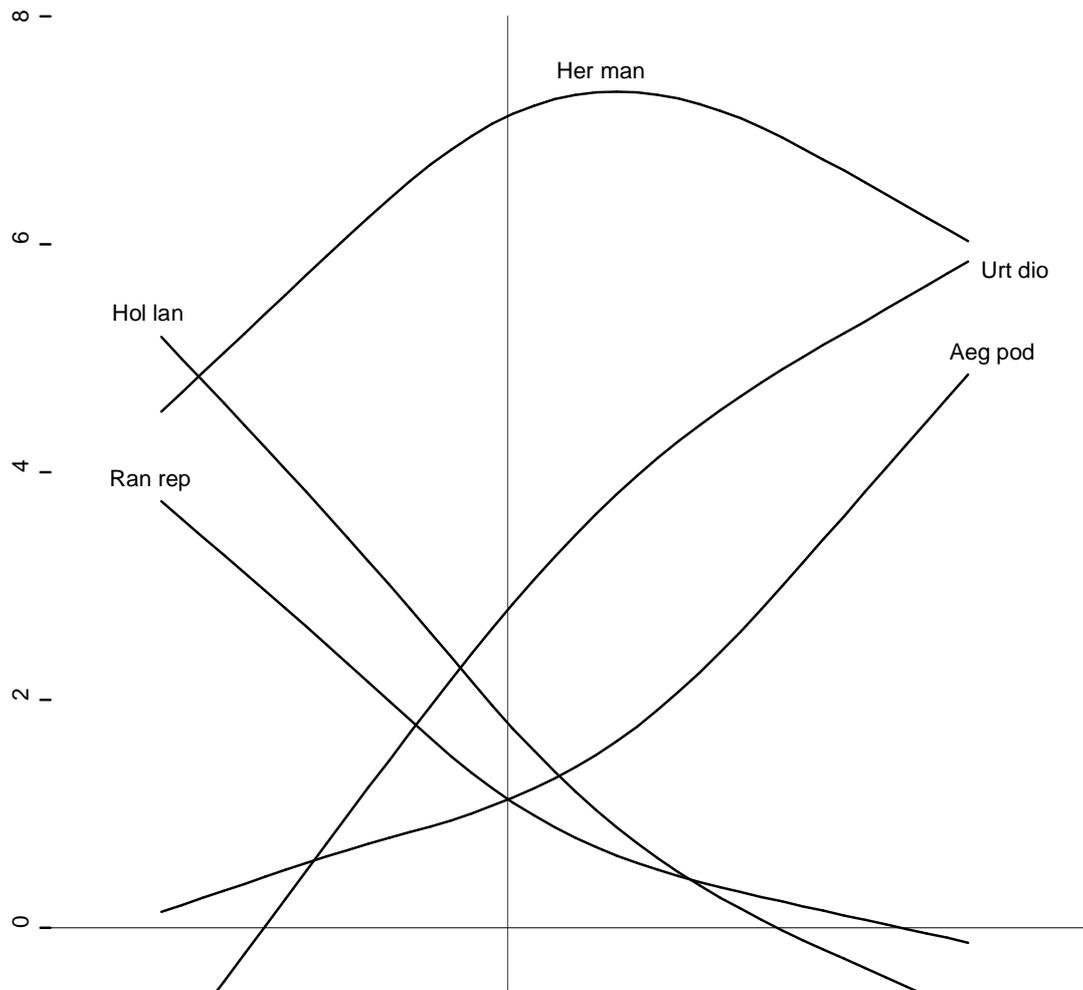


Fig. 8.5. Response curves of *Heracleum mantegazzianum* and selected resident species along the main gradient in 202 vegetation relevés from 20 study areas in Germany. Gradients were analysed by Correspondence analysis (CA). Response curves were calculated from cover-abundance estimates on the modified Braun-Blanquet scale by Generalized Additive Models in CANOCO. The x-axis depicts the first CA axis representing a successional gradient from managed grasslands to tall-herb stands and woodlands. Along this gradient grassland species declined and tall herbs increased. The y-axis depicts predicted cover-abundances classes of the species. The nine classes of the modified Braun-Blanquet scale were coded numerically (1-9). The maximum predicted cover-abundance class of *Heracleum mantegazzianum* Somm. et Lev. (Her man) of '7' corresponds to 25-50% cover. Abbreviations of species names: Aeg pod = *Aegopodium podagraria* L., Hol lan = *Holcus lanatus* L., Ran rep = *Ranunculus repens* L., Urt dio = *Urtica dioica* L. Modified from Thiele and Otte (2006b).

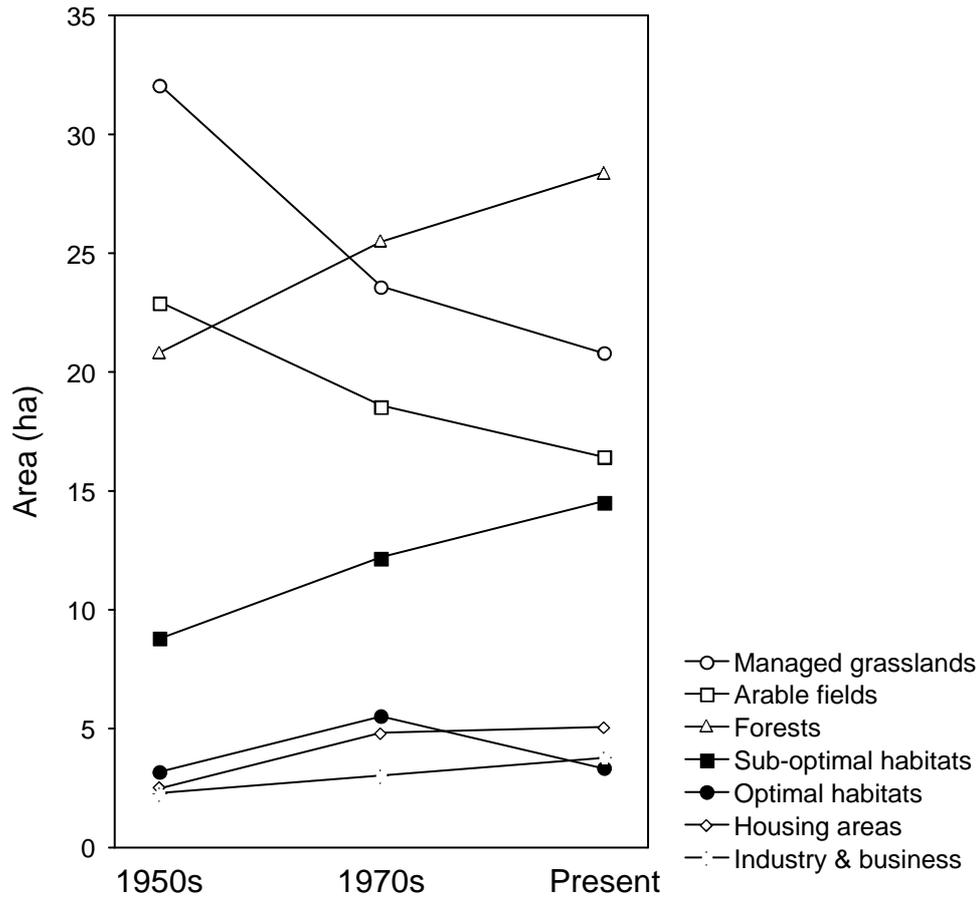
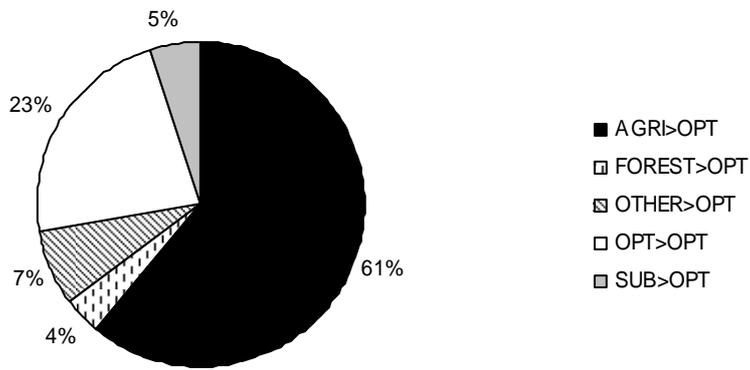
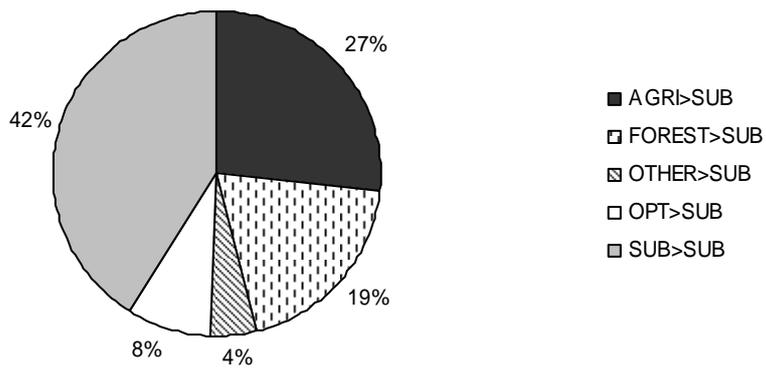


Fig. 8.6. Area covered by land-cover types and habitats of *H. mantegazzianum* averaged over 20 study areas of 100 ha in Germany for three dates: 1950s, 1970s, and approx. 2000. For classification of optimal and sub-optimal habitats see Table 8.3.

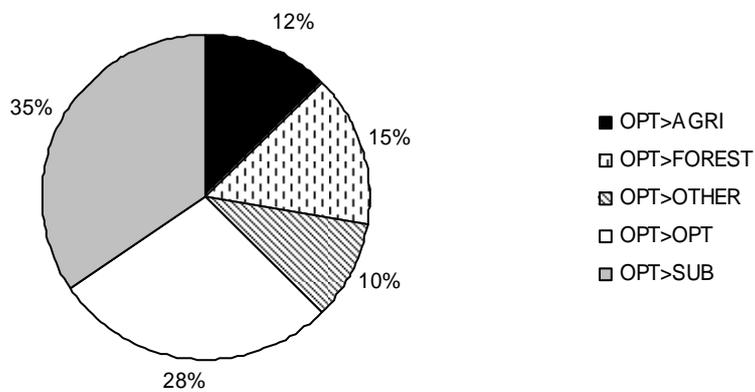
A. Origin of optimal habitats of the 1970s



B. Origin of sub-optimal habitats of the 1970s



C. Fate of optimal habitats of the 1970s



D. Fate of sub-optimal habitats of the 1970s

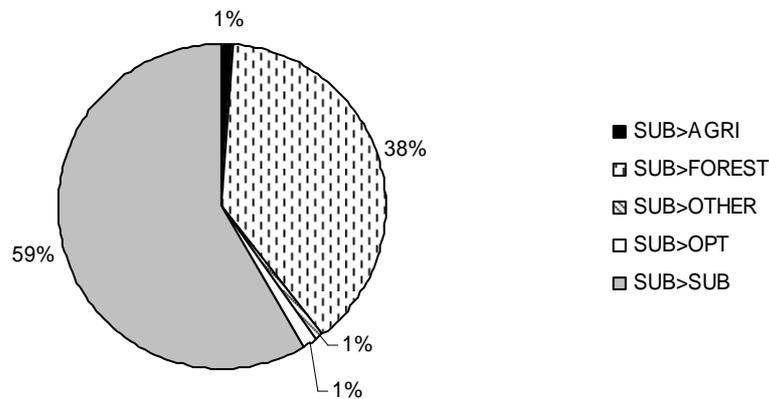


Fig. 8.7. Origin and fate of optimal and sub-optimal habitats of *Heracleum mantegazzianum* that existed in the 1970s in 20 study areas in Germany. Habitats were mapped from multitemporal time series of study areas for three dates: 1950s, 1970s, and approx. 2000. Habitats were classified into optimal and sub-optimal based on electivity indices (see table 8.3). Optimal habitats are open habitat types whereas sub-optimal habitats contain woody components (>10% tree or shrub cover). A and B: Origin of 1970s habitats, i.e. land-cover types from which they had developed since the 1950s. C and D: Fate of 1970s habitats, i.e. land-cover types into which they have developed until approximately 2000. Abbreviations of land-cover and habitat types: OPT = optimal habitats; SUB = sub-optimal habitats; AGRI = agricultural land (arable fields, managed grasslands); FOREST; OTHER = all other land-cover types which are not habitats of *H. mantegazzianum*.