
19 Master of All Traits: Can We Successfully Fight Giant Hogweed?

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Giant Hogweed lives

(Genesis, 1971)

Introduction

The Caucasian *Apiaceae* giant hogweed, *Heracleum mantegazzianum* Sommier & Levier, has been with us in Europe for almost two centuries (see Jahodová *et al.*, Chapter 1, this volume), but as is the case with most invasive species, it has received serious attention only in recent decades. A need for practical solutions to the problems posed by ecological and economic impacts, and scientific appeal associated with one of the most spectacular plant invasions in Europe, were the main reasons for giant hogweed becoming the subject of the international GIANT ALIEN project, which included participants from various parts of Europe with a wide range of expertise (Nielsen *et al.*, 2005).

It is not surprising that during the work on the GIANT ALIEN project some myths were unmasked: the plant is almost never truly biennial in the field (Pergl *et al.*, Chapter 6, this volume); it does not produce over 100,000 fruits (Perglová *et al.*, Chapter 4, this volume); the seeds do not survive for 15 years in the soil (Moravcová *et al.*, Chapter 6, this volume); and it is not polycarpic (Pyšek *et al.*, Chapter 7, this volume). Surprisingly, the reputation of giant hogweed is even worse than it deserves – because of its attractiveness to the public it became a tabloid archetypal plant invader. It even attracted the attention of artists – long before scientists in Europe began to recognize the problem of this species, *H. mantegazzianum* was the subject of the song ‘The

Return of Giant Hogweed' by the rock group Genesis. The lyrics reproduced as mottos for chapters in this book indicate that the group made a good job in covering various aspects of the giant hogweed invasion.

The present chapter documents, by comparing with other plant invaders worldwide, why *H. mantegazzianum* is considered an aggressive invasive species and summarizes how the knowledge on the biology, ecology and distribution of *H. mantegazzianum* achieved during the GIANT ALIEN project can be interpreted in terms of the invasion potential of this species. From plant ecological and zoological perspectives, it highlights the features that allow *H. mantegazzianum* to be a successful invader, and what implications these circumstances have for its management and potential control.

What are the Attributes of an Aggressive Invader and How Does *Heracleum mantegazzianum* Compare with Other Invasive Species?

Extensive stands with a high cover

For any species, there are several assumptions that need to be met if it is to be viewed as an aggressive invader. The first assumption is the capability of creating large and dominant stands. Although in Central Europe two-thirds of *H. mantegazzianum* records relate to plants scattered in invaded vegetation without being dominant (see Thiele *et al.*, Chapter 8, this volume), it often forms dominant stands with a high cover (Fig. 19.1). Further, once suitable environmental conditions are met and the species starts to dominate the invaded vegetation, the stands can be very extensive. In the Slavkovský les study area, Czech Republic (see Perglová *et al.*, Chapter 4, this volume), on the basis of aerial photographs it is estimated that in ten 60-ha landscape sections, populations of *H. mantegazzianum* at present completely cover 41.9 ha (see Pyšek *et al.*, 2005; Chapter 3, this volume). This represents 7% of the total land in the region. These figures can be related to biomass, using the data from Tiley *et al.* (1996), who report a yield of 57 t/ha dry mass (including roots), based on measurements in the west of Scotland.

High rate of spread

Extensive populations can only result from a high rate of spread in the past, but these two measures, although closely related, do not necessarily indicate the same pattern of invasion. A species can be locally abundant and form extensive stands in a geographically limited region, yet it may not be widespread over a large region. Easy dispersal and rapid spread in the past also indicate a potential for the invasion to continue in the future, because they allow a species to spread over considerable distances from source populations and reach new areas. Quantitative information on the rate of *H. mantegazzianum* spread is available for the second half of the 20th century from the



Fig. 19.1. In the Slavkovský les study area, Czech Republic, populations of *H. mantegazzianum* cover approximately 7% of the landscape. Photo: P. Pyšek.

Czech Republic for both local and regional scales (Fig. 19.2). Interestingly, the pattern and rate of spread is similar at both scales; if the increase in the invaded area at local scale and in the number of squares at country scale is compared statistically, there is no difference in the slopes of both plots (for details, see Pyšek *et al.*, Chapter 3, this volume). This indicates that *H. mantegazzianum* spreads at the national scale at the same rate as locally in the region of its introduction to the country, and that the constraints imposed to its spread by landscape features and availability of suitable habitats are similar at both scales. That the invasion at the country scale is of a similarly high rate as that in the very suitable region of the Slavkovský les (Pyšek *et al.*, 2005; Chapter 3, this volume) indicates that the species seems to be little constrained by environmental settings. When suitable habitats are available, it spreads at a high and constant rate.

Comparing the rate of *Heracleum mantegazzianum* invasion with that of other species

Heracleum mantegazzianum regularly appears on global lists of the most invasive species (e.g. Cronk and Fuller, 1995; Weber, 2003) and is listed in the Global Invasive Species Database (Lowe *et al.*, 2000) among the 100 worst invasive alien species. What is its position among plant invaders of global significance expressed in quantitative terms? Exact data are unfortunately

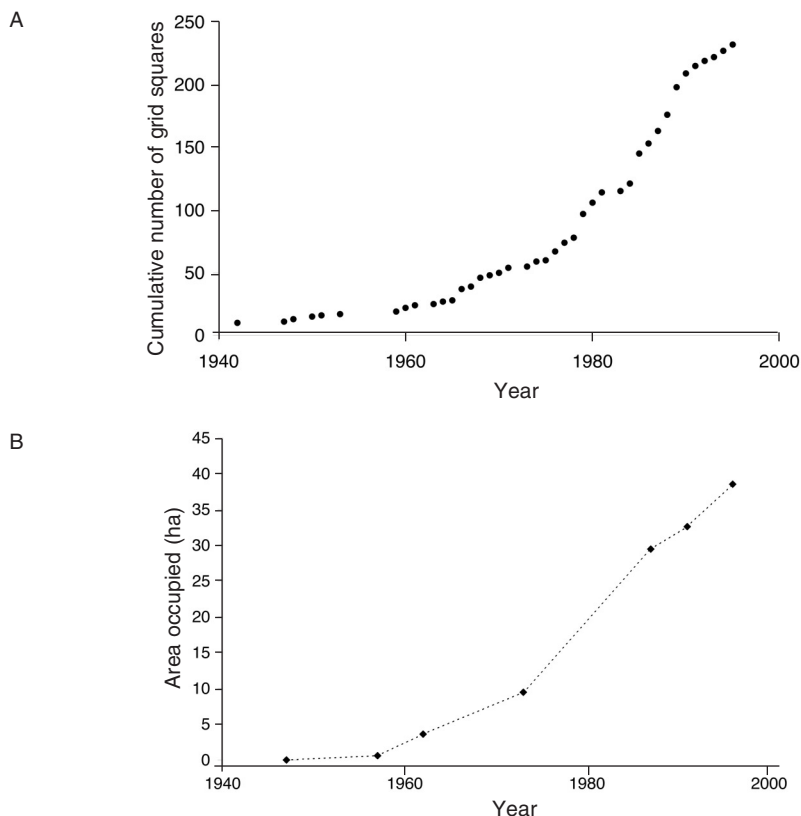


Fig. 19.2. *Heracleum mantegazzianum* spread was very fast at both national and local scales in the Czech Republic in the second half of the 20th century. (A) The pattern of increase in the cumulative number of squares ca. 11×12 km from which the species has been recorded up to the given time is similar to that in the actual population size in the Slavkovský les study area. (B) The population size is given in hectares, estimated as pooled value from ten sites of 60 ha each, monitored by using aerial photographs (Müllerová *et al.*, 2005; Pyšek *et al.*, Chapter 3, this volume). Thus, for example, 30 ha corresponds to 5% of the total landscape occupied.

limited, but recent reviews make it possible to compare the rate of invasion in the past.

The maximum rate of spread during the exponential phase of invasion was compared with that of other invasive neophytes in the Czech Republic (see Pyšek *et al.*, Chapter 3, this volume; Williamson *et al.*, 2005). On a regional scale and with global focus, there are two records of how fast the geographical distribution of *H. mantegazzianum* was increasing (Fig. 19.3). Using a simple measure of the number of grid squares divided by the period between initial and final mapping shows that the geographical range of major invasive species increases by hundreds to thousands of square kilometres a year (Pyšek and Hulme, 2005). The invasion of *H. mantegazzianum* in

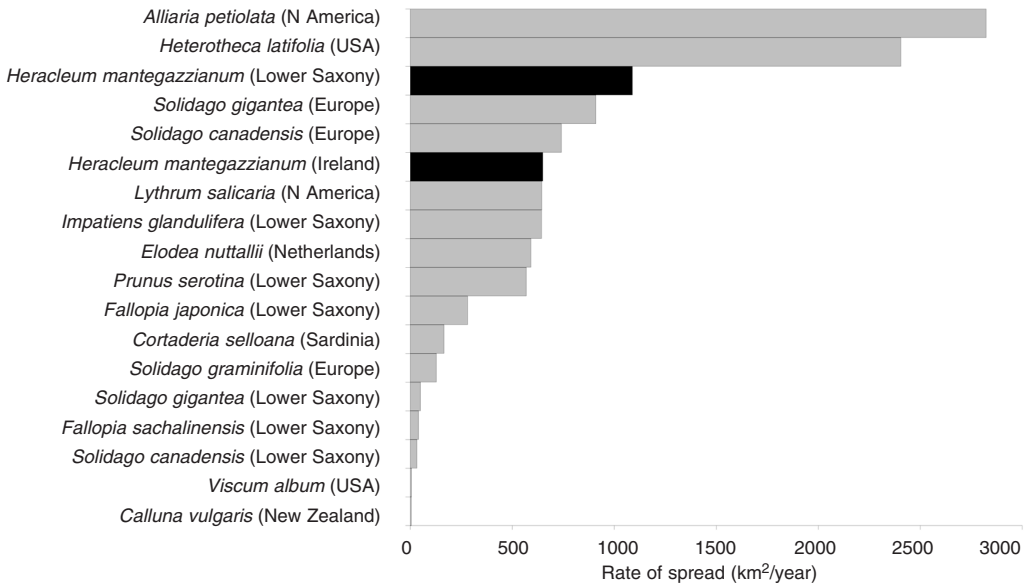


Fig. 19.3. The rate of increase in distribution of *H. mantegazzianum* at a regional scale compared to other species. The rate of spread in various regions is expressed as the number of grid squares divided by the length of the period over which the distribution was compared. For example, over the 16 years covered by the study of Schepker and Kowarik (1998), the distribution range in Lower Saxony, Germany, was increasing by 1089 km²/year. Based on data from Pyšek and Hulme (2005).

Europe is comparable with such spectacular invasions as that of *Alliaria petiolata* (Bieb.) Cavara & Grande (Weber, 1998) or *Heterotheca latifolia* Buckley (Plummer and Keever, 1963) in North America (Fig. 19.3).

In terms of the rate of increase in population size on a local scale, *H. mantegazzianum* spread by 1261 m²/year (see Müllerová *et al.*, 2005; Pyšek *et al.*, Chapter 3, this volume), which compares it to such prominent invasions as those of *Rhododendron ponticum* L. in the UK (Fuller and Boorman, 1977) or *Caulerpa taxifolia* (Vahl) C. Agandh in the Mediterranean Sea (Meyer *et al.*, 1998) (Table 19.1).

Rapid spread alone may not necessarily result in a dramatic invasion if the spread is not associated with the ability of invading populations to persist in invaded locations. Wade *et al.* (1997) surveyed *H. mantegazzianum* occurrence in Ireland and found that of the 96 historical sites, the species was still present at 43 in 1993. This represents 45% persistence and illustrates a remarkable ability of the species to thrive in the places once invaded. This value is lower than that reported for prominent clonally spreading invaders, such as *Fallopia* spp. (Pyšek *et al.*, 2001), but it needs to be noted that *H. mantegazzianum* was a target of control efforts in recent decades. It may be hypothesized that without locally successful eradications, the persistence would be higher.

Table 19.1. Comparison of the rate of invasion by *H. mantegazzianum* at a local scale with that of other species. The area covered by stands of the invading species was monitored over time or reconstructed from aerial photographs (see Pyšek *et al.*, Chapter 3). Data from Pyšek and Hulme (2005) – see references to primary sources therein.

| Species | Life form | Region | Habitat | Span of study (years) | Rate of spread (m ² /year) |
|-----------------------------------|-----------|----------------|---------------------|-----------------------|---------------------------------------|
| <i>Caulerpa taxifolia</i> | Alga | France | Sea bottom | 5 | 2000 |
| <i>Heracleum mantegazzianum</i> | Herb | Czech Republic | Pastures, disturbed | 45 | 1260 |
| <i>Rhododendron ponticum</i> | Shrub | UK | Forest, dunes | 20 | 1100 |
| <i>Spartina anglica</i> C.E. Hubb | Grass | New Zealand | Seashore | 9 | 22 |
| <i>Spartina anglica</i> | Grass | New Zealand | Seashore | 4 | 13 |
| <i>Spartina anglica</i> | Grass | New Zealand | Seashore | 41 | 1 |

Impact of *Heracleum mantegazzianum* on resident vegetation

Although impact is difficult to measure and includes various aspects (Williamson, 1998), that of *H. mantegazzianum* on resident vegetation is manifested through changes in vegetation structure, cover and species composition. It depends on the type of invaded plant communities and their successional status, being especially marked in ruderal grasslands and ruderal pioneer vegetation (see Thiele and Otte, Chapter 9, this volume). *H. mantegazzianum* excludes resident species or reduces their abundance, hence decreases the local species richness of invaded communities (Pyšek and Pyšek, 1995). Nevertheless, conflicts with nature conservation are unlikely as *H. mantegazzianum* was not reported to invade habitats of conservation concern, nor did the regional populations of common native species seem to be endangered, as documented for Germany (see Thiele and Otte, Chapter 9, this volume). As pointed out in Chapter 9, the impact of *H. mantegazzianum* on resident vegetation is driven by human-induced disturbances and some native species have similar effects on species richness of plant communities if they prevail in the course of succession.

The detailed analysis carried out in Chapter 9 seems to imply that the impact of giant hogweed is overestimated in the literature. However, even if the above-mentioned effects on resident vegetation are subtle, the fact that the species is able to cover up to 10% of the landscape with dense populations must be taken as clear evidence of a serious impact. Moreover, unpublished data are available from paired invaded and uninvaded plots in the Czech Republic to demonstrate that *H. mantegazzianum* exerts a rather severe effect on species diversity of invaded sites, reducing their species richness to about half of the state prior to invasion, which is comparable to the effect of *Fallopia* spp., but stronger than that of *Lupinus polyphyllus* Lindl. and *Impatiens glandulifera* Arn. (M. Hejda, unpublished data).

To summarize, *H. mantegazzianum* has all the attributes of a successful invasive species (Fig. 19.4). Extensive and often dominant stands associated

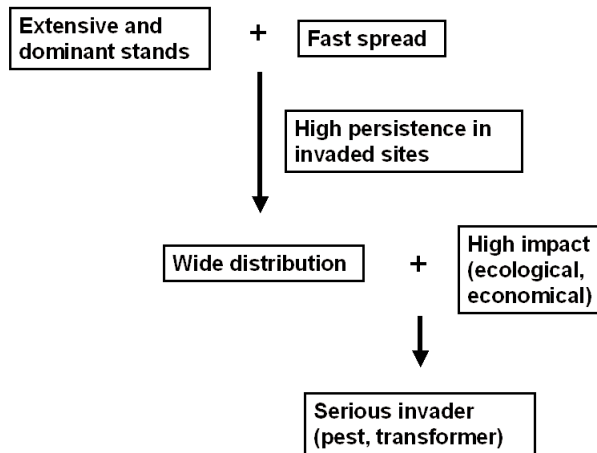


Fig. 19.4. A flow chart summarizing attributes of a successful plant invader. *Heracleum mantegazzianum* exhibits the attributes associated with a serious invader (see text for details).

with fast spread result in a wide distribution; this is possible because the persistence in localities once colonized is high. Consequently, any alien species with a wide distribution and marked impact is potentially a serious invader.

What Makes *Heracleum mantegazzianum* So Special: a Botanical Perspective

The GIANT ALIEN project produced detailed information on various aspects of the biology and ecology of *H. mantegazzianum* from both botanical and zoological perspectives. This makes it possible to highlight those species traits that contributed to such a successful and dramatic invasion. Before dealing with these traits, it needs to be noted that the size and attractiveness of this species as an ornamental led to its use in horticulture, and its early rapid dissemination between the countries of Europe via garden centres and botanical gardens. From this it follows that it was present in most countries before anyone was seriously concerned about its impact and spread as a naturalized, and later on invasive, species.

In the temperate conditions of Europe, *germination in early spring* provides the plants of *H. mantegazzianum* with the advantage of developing populations well ahead of the resident vegetation. Mean seedling density is usually around 500–700 seedlings/m², but extreme values can reach up to 3700. Relative growth rate of seedlings is higher than that of most native temperate herbs. Once seedlings get established after the period of self-thinning and reach the stage of juvenile plants and rosettes, their mortality is fairly low (see Pergl *et al.*, Chapter 6, this volume). Rapid growth of rosettes results in the *rapid formation of a dense cover*; placing the leaves above other species

provides the plants of *H. mantegazzianum* with advantage in the competition for light.

Later in the phenological development, it is important to note that there are *no constraints to flowering*. Many aliens introduced to the temperate zone of Europe fail due to constraints to flowering; the vegetation period is too short to complete the life cycle and bear fruits (Pyšek *et al.*, 2003). This limitation, however, concerns species introduced to warmer regions. *H. mantegazzianum* occurs naturally at higher altitudes of the Greater Caucasus where the flowering period is short. Therefore, an average plant completed flowering within 36 days at the study sites in the Czech Republic and bore ripe fruits ready to release approximately 2 months after the onset of flowering (see Perglová *et al.*, 2006 and Chapter 4, this volume). That is, the populations of *H. mantegazzianum* are not constrained by climate in most of Europe as far as flowering is concerned. This was confirmed by a historical study of invasion in the Slavkovský les area, which did not detect any year-to-year variation in the flowering intensity; the proportion of plants that flowered was very stable over 45 years of invasion (Müllerová *et al.*, 2005). Moreover, plants of *H. mantegazzianum* are able to postpone flowering for some years until sufficient reserves are stored, for example if they grow under stress from grazing or unfavourable site conditions (see Pergl *et al.*, 2006; Chapter 6, this volume).

Frequent overlaps between male and female flowering phases, both between- and within-umbels, allow for *self-pollination* and self-pollinated flowers give rise to viable seeds, a high percentage of which germinate. This has important implications for invasion: if a single plant or a few individuals arrive in a new locality or region, potential invasion is not constrained by the absence of a mating partner as would be the case in a strictly outcrossing species (see Perglová *et al.*, 2006; Chapter 4, this volume).

The *extremely high fecundity* of *H. mantegazzianum* has long been recognized and the ability of this species to produce enormous number of fruits is often exaggerated in the literature (see Perglová *et al.*, Chapter 4, this volume). Although reliable estimates based on a large number of plants and accounting for geographical variation yielded lower numbers, the average 20,500 fruits per plant still provides the species with enormous reproductive potential (see Perglová *et al.*, 2006; Chapter 4, this volume). The complex information on various phases of the life cycle, obtained during the GIANT ALIEN projects, allowed us to estimate the number of *H. mantegazzianum* fruits that enter the landscape. Taking the average fruit number and the mean density of flowering plants, which is very similar in study plots in the Czech Republic and Germany (0.7 and 0.8/m², respectively), the largest population in the Slavkovský les region (see Pyšek *et al.*, Chapter 3: Fig 3.4, this volume; Moravcová *et al.*, Chapter 5: Fig. 5.1, this volume), covering ca. 99,000 m² at the locality Žitný, is likely to produce about 1.4 billion seeds each year. To translate this figure to the whole landscape, it needs to be noted that 99,000 m² of *H. mantegazzianum* stands were recorded in a 60 ha section covered by aerial photographs (Müllerová *et al.*, 2005); the average fruit load would be ca. 2370 fruits of giant hogweed per m². Such extrapolations are prone to

estimation bias, but the value obtained clearly indicates that the fruit load is enormous.

This high fecundity is associated with very *high germination rates* once dormancy is broken; the percentage of seed that germinated reached 91% in laboratory conditions and germination does not depend on the position of the fruit on the plant (Moravcová *et al.*, 2005). These high percentages are probably not realized in the field and between-year fluctuations in seed quality are likely to occur (L. Moravcová *et al.*, unpublished), yet there is no doubt that the vast majority of seeds produced are viable, with potential to contribute to the population dynamics and further spread to new locations.

The majority of fruits do not disperse far from adult plants and form a *large seed bank*. Some macro-ecological implications can be drawn using the detailed information on seed bank obtained during the project. From the size of population in the Žitný locality and average seed-bank density (see Moravcová *et al.*, Chapter 5, this volume), it can be estimated that there are 380 million non-dormant seeds in the seed bank in spring. With germination percentage exceeding 90%, the number of seeds that can potentially produce new plants is only slightly lower: 3550/m², with a total of over 350 million estimated for the whole population.

The seed bank of *H. mantegazzianum* and its longevity became a kind of self-perpetuating myth; statements unsupported by data were taken from one source to another (for an account of this myth, see Moravcová *et al.*, Chapter 5, this volume). It is evident that reports on seeds surviving in the soil for 15 years, often cited in association with control strategies, are far from reality. An ongoing study monitoring seeds buried at different localities in the Czech Republic, selected in order to represent a range of climates and soil types, showed that on average 8.8% survived 1 year, 2.7% survived 2 years and 1.2% remained viable and dormant after 3 years of burial (see Moravcová *et al.*, Chapter 5, this volume). Relating these values to the seed-bank density in the autumn after the fruits are released (Krinke *et al.*, 2005), there are on average about 80 dormant seed/m² present in the soil after 3 years. The question of how long viable seeds are able to survive in the soil can only be answered conclusively when this experiment is finished (and possibly repeated in different climatic settings in other parts of Europe), but it seems unlikely that the longevity will be markedly longer than 3 years. Nevertheless, *H. mantegazzianum* has a *short-term persistent* seed bank which makes it possible to extend the germination period over time and respond to actual climate conditions in the site of introduction (Krinke *et al.*, 2005; Moravcová *et al.*, Chapter 5, this volume).

Last but not least, a *high regeneration ability*, especially in terms of fruit production (see Pyšek *et al.*, Chapter 7, this volume), is likely to contribute to the invasion of *H. mantegazzianum*. The species is one of the most prominent invaders in Europe, not only in terms of its invasion potential but also because of the attention it is paid by landscape managers and the public. Therefore, it is often targeted for control efforts (Nielsen *et al.*, 2005; Chapter 14, this volume; Buttenschön and Nielsen, Chapter 15, this volume). If control is mechanical, the ability to regenerate is crucial. The high regeneration ability

has been long recognized in a number of studies (for an overview, see Pyšek *et al.*, Chapter 7, this volume) and even umbels cut at late flowering or early fruiting are able to produce viable seeds (Pyšek *et al.*, 2007). It is important from the viewpoint of control strategies that, although regenerating plants produce much fewer fruits, the seeds are viable. Given the enormous fecundity, even if drastic reduction in fruit numbers is achieved, the resulting fruits are likely to ensure the renewal of targeted populations. A review of available studies conducted in different parts of Europe indicates that if plants are cut at ground level at peak flowering or beginning of fruit formation, regeneration ranges between 2.8% and 4.3% of the number of fruits produced by the control (see Pyšek *et al.*, Chapter 7: Table 7.2 and Fig. 7.2, this volume). Given the above-mentioned average fecundity exceeding 20,000 seeds per plant, the implications are obvious.

Landscape Features Set the Scene for Invasion

The role of plant traits needs to be assessed in the context of invaded communities and ecosystems. The above traits, however supportive in term of invasion success, would be hardly helpful if not realized in an environment vulnerable to invasion. Landscape characteristics are the scene upon which any invasion occurs and their importance has been repeatedly demonstrated in plant invasion literature (e.g. Campbell *et al.*, 2002; Wania *et al.*, 2006). In Europe, many invasions were shown to have accelerated in the second half of the 20th century, apparently because of landscape changes. Williamson *et al.* (2005), on the basis of the analysis of historical patterns of invasion of more than 60 species, suggested that the character of the landscape is more important than species' biological and ecological traits in determining the outcome of invasion.

For *H. mantegazzianum*, the suite of traits seems to be the main reason for invasiveness, but interactions with landscape features are also crucial. Data indicate that the species is less constrained by environmental settings than is the case in the majority of invasive alien plants (Müllerová *et al.*, 2005); it occurs under a wide spectrum of environmental conditions and successfully invades less-disturbed or semi-natural habitats. Nevertheless, habitats that suffer from massive invasion are almost always characterized by a rich resource supply, some degree of disturbance and the lack of regular management. Environmental factors constraining invasion of *H. mantegazzianum* are regular land use, shading by trees, low soil nutrient status and/or wetness (see Thiele *et al.*, Chapter 8, this volume). As for most invasions, it is also true for giant hogweed that the invasion is usually associated with poorly managed landscapes. This view is supported by the fact that in the Caucasus the species expands in disturbed habitats outside its natural ecological range (see Otte *et al.*, Chapter 2, this volume).

Herbivores and Pathogens: a Zoological Perspective

A large number of insect herbivores occur on *H. mantegazzianum* plants, but most of them occur only sporadically. Among common herbivores, specialization usually occurs mainly at family level (*Apiaceae*), sometimes on the level of a group of genera. Specialization on genus level is rare and species exclusively feeding on *H. mantegazzianum* do not seem to exist (see Hansen *et al.*, Chapter 11, this volume). During the rapid evolution of the large hogweed species, herbivores obviously did not follow with their own radiation (see Cock and Seier, Chapter 16, this volume). This results in more specialized herbivores being found beyond the native range of *H. mantegazzianum* because other *Heracleum* species occur there. A typical example is the aphid *Paramyzus heraclei* Börner, restricted to the genus *Heracleum*, occurring in both native and invaded areas. Comparably, most herbivores found in the native range of *H. mantegazzianum* were also present in the invaded part of Europe (see Hansen *et al.*, Chapter 11, this volume). A few species could not be evaluated sufficiently because they are rare or were only recently described as new species, thus the species-specific knowledge available is still poor. As a result of this, *H. mantegazzianum* has very similar herbivore populations in both native and invaded area, but the overall herbivore damage is slight. The considerable resistance to herbivory is probably due to very effective defence mechanisms (see Hattendorf *et al.*, Chapter 13, this volume), which permits *H. mantegazzianum* to establish the well-known tall plants.

Because *H. mantegazzianum* can store resources over a period of years before flowering, when it does flower, these resources are suddenly available for rapid utilization to grow a large, productive flowering structure. None of the associated herbivores and pathogens have sufficient impact at the population densities observed to significantly affect this flowering process. Thus, although it is possible that invertebrate herbivory may contribute to delaying the onset of flowering, once the flowering process starts, they are no longer significant. In this way, *H. mantegazzianum* also escapes its invertebrate herbivores.

Biological Control Perspective

In the GIANT ALIEN project, we specifically explored the scope for classical biological control, that is the introduction of host-specific natural enemies from the area of origin of *H. mantegazzianum* in the north-western Greater Caucasus. At the densities observed in the Greater Caucasus, none of the associated natural enemies caused sufficient damage to have a significant impact on *H. mantegazzianum* (see Seier and Evans, Chapter 12, this volume; Hattendorf *et al.*, Chapter 13, this volume). Furthermore, contrary to our expectation, we were unable to demonstrate that any of the insect or fungal natural enemies found in the Caucasus were specific to *H. mantegazzianum*, or safe enough to be introduced into Europe, all causing damage to other *Heracleum* spp. and most causing damage to parsnip, *Pastinaca sativa* L. (see Cock and Seier, Chapter

16, this volume). This result was unexpected, and in Chapter 16 we considered possible reasons for the lack of species-specific natural enemies. We hypothesized that this is because the co-evolution of *Heracleum* species and their natural enemies has been dynamic in the Caucasus region during the Quaternary. Periodic retreat into two small refugia during glacial periods, followed by expansion and mixing of populations during inter-glacial periods, has led to diversity and hybridization of the plant hosts, while containment of very small populations in the glacial refugia would not have selected for species-specificity on the part of associated natural enemies of *Heracleum* species. This hypothesis merits further examination and evaluation in the future.

Thus, the preferred biological control option by introducing exotic biological control agents is not possible. However, the alternative option of using indigenous natural enemies has not been adequately evaluated – in particular, the use of a laboratory-produced indigenous fungus as a mycoherbicide deserves study. Preliminary trials with a fungus known to attack many species in Europe have been made, but a more thorough programme, considering other species, particularly those more damaging to *H. mantegazzianum*, should be considered (see Seier and Evans, Chapter 12, this volume).

It also worth reiterating that current EU legislation would not facilitate the introduction of a weed biological control agent, and in the case of an exotic fungus, this option is more or less excluded by EU Directive 91/414 (1991) (see Cock and Seier, Chapter 16, this volume; Seier, 2005). It is important that the new EU Concerted Action Project, REBECA, starting in 2006, should address this issue, to facilitate weed biological control in Europe in the future. However, for *H. mantegazzianum*, we conclude that the introduction of exotic biological control agents is unlikely to be the solution, although it should be considered for other alien invasive plants in Europe (Sheppard *et al.*, 2006).

Conclusions: Master of all Traits

Plant ecological determinants of giant hogweed's invasiveness are simple and easy to determine. The species does not seem to possess any special characteristic/mechanism; extremely high fecundity, rapid growth, capability of self-pollination, extended germination period by means of short-term persistent seed bank, high germination, negligible impact of natural enemies – all these characteristics can be found in other plant invaders (Pyšek and Richardson, 2007).

A recent review of species traits associated with invasiveness identified, among others, fecundity, rapid growth and associated physiological measures, height, resistance to herbivory, early germination and flowering and persistent seed bank as important (Pyšek and Richardson, 2007). This volume illustrates that *H. mantegazzianum* has many such attributes (Fig. 19.5) and some of them compensate for the lack of some others typical of invasive species. For example, vigorous vegetative spatial growth is consistently recognized as an attribute of invasiveness (Callaway and Josselyn, 1992; Vila and D'Antonio, 1998; Larson, 2000; Morris *et al.*, 2002). However, the main advantage provided by this ability is efficient and rapid space pre-emption, which in

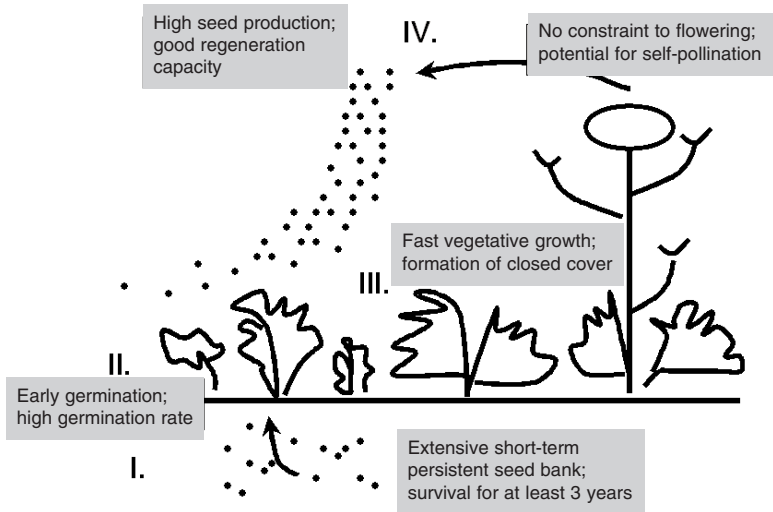


Fig. 19.5. Traits identified as contributing to the successful invasion by *H. mantegazzianum*, plotted on the scheme of the life cycle of a monocarpic plant: I – soil seed bank; II – stage of seedling recruitment; III – growth phase; IV – the terminal phase of seed production (stages according to Harper, 1977). Drawing: J. Pergl.

H. mantegazzianum is achieved by rapid growth of large leaves above the surrounding vegetation and the production of large numbers of vigorously growing offspring in the vicinity of fruiting plants.

Invasions by some plant species are facilitated by special mechanisms resulting from their specific biochemical features, e.g. substances resulting in a high flammability that changes the fire regime in invaded regions (D'Antonio and Vitousek, 1992). *H. mantegazzianum* has two different defence mechanisms: glandular trichomes and a phototoxic sap containing furanocoumarins that protect the plants against vertebrates, invertebrates, fungi, bacteria and viruses (Hattendorf *et al.*, Chapter 13, this volume). However, the role both mechanisms may play in facilitating the invasion by *H. mantegazzianum* in Europe is unclear. The resource-costly defence by glandular trichomes is less pronounced in the invaded area, thus releasing the plant from some defence costs. This would enable the invading plant populations to invest more in growth. The second defence mechanism by less costly qualitative toxic compounds did not change as suggested by the hypothesis of Blossey and Nötzold (1995). *H. mantegazzianum* showed higher levels in the invaded range of Europe even though no damaging specialized herbivores occur there. The plant appears to invest more in biochemical defence than necessary and the reason for this is not clear. However, we know that the levels and types of furanocoumarins in this species are variable, and this may reflect the original stock from which the introductions were made.

Therefore, it is a combination of superior traits associated with a single species and acting at different stages of the life cycle (Fig. 19.5) that provides

H. mantegazzianum with remarkable invasion potential and makes it a 'master-of-all-traits' of plant invasions. This has practical implications, as the species does not seem to have a weak link in its life cycle, on which the control measures could be most efficiently targeted. Appropriately conducted long-term mechanical and chemical control (Nielsen *et al.*, Chapter 14 and Pyšek *et al.*, Chapter 7, this volume) associated with suitable landscape management and revegetation schemes (Ravn *et al.*, Chapter 17, this volume) can be used, with reasonable success, to reduce the extent of invasion in heavily affected areas and prevent the species from further spread. It is unlikely, however, that the species can be completely eradicated by classical means of control. So the answer to the question raised in the title of this chapter is – yes, we can fight giant hogweed with some success but, for now ... giant hogweed lives.

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