

**Does local adaptation facilitate the success of plant invasions?  
A case study on *Buddleja davidii***

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*Buddleja davidii* Franch.  
Sommerflieder

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### General introduction

The worldwide exchange of species is considered as one of the greatest threats to global biodiversity (Sala *et al.* 2000). The number of species translocated by humans, either deliberately or by accident, has dramatically increased (Simberloff *et al.* 2005) as a result of the rapid expansion in international travel and trade (Elton 1958, Brandl *et al.* 2001). Thus, biological invasions may exceed natural dispersal processes in terms of dimension, speed, range and consequences on ecological, economic and social levels (Kowarik 2003). Biological invasions are defined as the overcoming of biogeographical barriers of species caused by humans and the subsequent spread beyond their native distribution area. In general the invasion process in the new range consists of three stages: introduction, naturalization and invasion per se (Lodge 1993, Richardson *et al.* 2000b). In this thesis, the term “invasive” is used to describe species that are not native to an ecosystem (i.e. nonindigenous), that reproduce consistently and sustain populations over many life cycles without direct intervention by humans. Depending on the region and environmental conditions, an invasive species can change an ecosystem and thereby alter its function (e.g. Gordon 1998), biodiversity (Richardson *et al.* 1996) and the regional gene pool (e.g. Ellstrand & Schierenbeck 2000, Vila *et al.* 2000). In addition, biological invasions may result in high economic costs. The cost of control of invasive species and the loss of native species in the United States amounts to \$ 137 billion annually (Pimentel *et al.* 2000). In Germany the management of just 20 problematic species costs approximately € 167 million per year (BMU 2003).

The effects of invasive species on global biodiversity were specifically addressed in the Convention of Biodiversity, an international treaty, adopted in Rio de Janeiro, Brazil in 1992 (CBD 2007). Governments from around the world have committed to prevent the introduction of invasive species and to control or eradicate them, if they

threaten ecosystems, habitats or native species (BMU 1992, CBD 2007). Consequently, a goal of prospective invasion biology should be to investigate mechanisms responsible for biological invasions with particular emphasis on how humans facilitate the invasive processes. Additionally, another aim should be the mitigation of the effects of already established species by prevention, eradication and control.

### *Mechanisms: Phenotypic plasticity and local adaptation*

A central question in invasion biology has been identifying the traits, that predispose a species to be invasive or not (Richardson & Pyšek 2006). The features which should characterize some plant species as “ideal weeds” (Baker 1974) have been also applied to the “ideal invader.” Successful invaders should have a wide ecological niche, a short life cycle, high growth rates and great longevity. Furthermore, they are self-compatible and able to reproduce vegetatively and sexually with high output of propagules or seeds that are easily dispersed. However, research has determined that there really is no consistency of life history and reproduction across all weeds or introduced plants (Williamson 1993, Williamson & Fitter 1996). A comparative review by Pyšek and Richardson (2007) revealed that height, vegetative growth, early and extended flowering and attractiveness to humans are those traits that are associated with invasiveness. Although these traits are obviously advantageous to an introduced species, their presence does not automatically imply the species will be a successful invader. It has rather been shown that the invasion process is stage- and habitat-specific (Pyšek & Richardson 2007). The tens rule (Williamson & Fitter 1996) predicts that 10% of all introduced species will escape to become casuals (i.e. species that reproduce but fail to sustain over a longer period) and that about 10% of the casuals become naturalized (i.e. successful reproduction and maintenance of population over a longer period). Only about 10% of the naturalized species will be able to become a problematic species (sensu Pyšek *et al.* 2004a). Even if we accept the more probable estimation of 5-20% of naturalized species (Pyšek *et al.* 2004a) that will become a pest, then mechanisms other than traits must be responsible for the success of invasive

species. In this context, it is often assumed that invasive species usually grow more vigorously and perform better than their conspecifics in the native range (Crawley 1986, Blossey & Nötzold 1995). Increased growth and fecundity, together with decreased levels of herbivory in the invaded range have been shown for e.g. *Solidago gigantea* (Jakobs *et al.* 2004) and *Senecio inaequidens* (Prati & Bossdorf 2004). However it is difficult to imagine that nonindigenous plants will perform better in an environment in which they have not evolved. How can this paradox be explained (Allendorf & Lundquist 2003)?

Plants have two options to achieve a higher fitness to successfully invade a new area: Either by phenotypic plasticity or by undergoing genetic differentiation resulting in local adaptation. Being able to alter the physiology or the morphology in response to environmental changes, i.e. to be phenotypically plastic (Schlichting 1986), should be advantageous for the invasion success of alien plants (Barrett 1992) which has been revealed in several species (e.g. Parker *et al.* 2003, Dybdahl & Kane 2005).

On the other hand, the time lag between the introduction and an extensive spread of plant species (Kowarik 1995, Mack *et al.* 2000, Mooney & Cleland 2001) which can last up to 200 years (Kowarik 1995) has led to the suggestion that invasiveness evolves after colonization due to altered selection pressure (Blossey & Nötzold 1995, Ellstrand & Schierenbeck 2000, Lee 2002, Müller-Schärer & Steinger 2004). These changes may produce locally adapted populations that would have a higher fitness in their local habitat than genotypes originating from other habitats. Thus, the ability for rapid evolution in invasive plant species is likely to facilitate their spread and establishment in new habitats and results in an expansion of area (Rice & Mack 1991b). Probably, evolutionary processes are crucial to whether an invasion will occur or not (Sakai *et al.* 2001). In this context, biological invasions represent 'natural experiments' that allow the study of rapid evolution in action.

Investigations on local adaptation in plant populations require a comparison of different genotypes under the same environmental conditions. This can be realized by common garden experiments that provide the opportunity to estimate whether phenotypic differences between populations result from environmental variation or

whether they are caused by genetic differentiation (Sakai *et al.* 2001, Kawecki & Ebert 2004). Ideally, genotypes should be reciprocally transplanted between the habitats from where the genotypes were collected (Kawecki & Ebert 2004).

One prerequisite for evolutionary adjustments is that the species or the population is genetically diverse (Carroll & Dingle 1996). The negative consequences associated with the loss of genetic variability are well documented in rare species (Matthies 2000, Fischer *et al.* 2000, Luijten *et al.* 2000, Durka 2000). Populations with only a few individuals may be affected by the loss of genetic diversity (e.g. founder effects), inbreeding depression and reduced evolutionary potential (Müller-Schärer *et al.* 2004). Hence, one would expect for invasive species that the establishment and adaptive evolution in a new area is impeded by genetic bottlenecks (Sakai *et al.* 2001). However, multiple introduction of a species from different geographic locations may counteract this genetic bottleneck (Müller-Schärer & Steinger 2004, Bossdorf *et al.* 2005). In addition, hybridisation, either interspecific or between previously isolated populations of the same species, can be an important stimulus for evolution of invasiveness (Ellstrand & Schierenbeck 2000). The study of genetic variation in invasive species is therefore important for their management (Barrett 1992).

Climate is a primary influence on plant fitness and, thus an important ecological filter limiting the distribution of plants. This was demonstrated, for example, by the clinal variations that occur with latitude in the invasive plant species *Solidago altissima* und *S. gigantea* in Europe (Weber 1997, Weber & Schmid 1998). However, next to abiotic filters (e.g. climate, nutrient availability, disturbance), adaptation to biotic conditions (e.g. competition, herbivory, pathogens) are also crucial for a species to expand into new geographic locations. For instance, the absence of herbivores and pathogens may also lead to evolutionary adaptation that may be expressed as increased competitive ability (EICA hypothesis; Blossey & Nötzold 1995, Joshi & Vrieling 2005). Moreover, invasive species may have impact on interactions between species within or between trophic levels in the new range (e.g. Richardson *et al.* 2000a). So, the invasive species may alter the succession process in new, unoccupied or disturbed habitats (Smale 1990) or influence existing plant pollinator-interactions



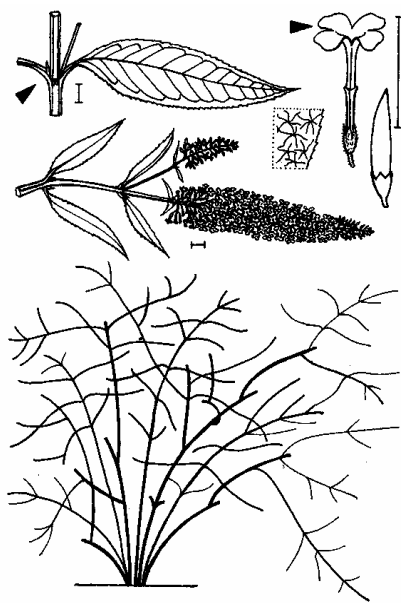
(Chittka & Schurkens 2001). So far, little is known about the evolutionary consequences of plant invasion and consequences to the native plant community. This thesis addresses the evolutionary processes associated with invasiveness using the invasive shrub *Buddleja davidii* as the model system.

*The study system: Buddleja davidii* Franch.

*Buddleja* is a cosmopolitan genus of the family Scrophulariaceae (Angiosperm Phylogeny Group II 2003) consisting of about 100 species in the tropical and temperate zones (Leeuwenberg 1979). Within the distribution centre of Asia, more than 90% of the *Buddleja* species are distributed in the Sino-Himalayan region (Leeuwenberg 1979).

One of these species is *Buddleja davidii*, commonly called butterfly bush. It is native to at least nine provinces in China (Lauener 1996) at altitudes between 800 m and 3000 m (Wu & Raven 1996). This multi-stemmed shrub reaches a height of 2 - 5 m (Lauener 1996). The deciduous or semi-evergreen plant (Owen & Whiteway 1980) is relatively short-lived up to an age of 30 years (Bellingham *et al.* 2005).

*Buddleja davidii* usually begins flowering and fruiting one year after germination, although some individuals may flower within the first year (Kreh 1952). Many fragrant



flowers appear at the terminal end of branches arranged in panicles that are up to 30 cm long (Figure 1). The hermaphroditic flowers produce nectar attracting mostly butterflies, but also bees and other insects are frequent. The shrub has a large annual seed production of up to several million seeds per plant (Kreh 1952, Campbell 1984). The fruit is a two-valved capsule that may release between 28 and 75 seeds (Kreh 1952, Brown 1990) that are 3 mm long with linear wings at both ends (Wu & Raven 1996) facilitating the dispersal by wind or even water (Campbell 1984).

**Figure 1.** *Buddleja davidii* Franch.  
(from: Rothmaler 2002).

*Buddleja davidii* was one of several plant species that was introduced from Asia to Europe in the 1890s for ornamental reasons. It is now one of the most popular woody species in gardens (Kay 2002), with more than 90 cultivars differing in growth form, flower colour and length of inflorescences as well as leaf shape and colour (Krüssmann 1976, Stuart 2006). *Buddleja davidii* can tolerate a wide range of soil conditions (Kreh 1952, Humphries & Guarino 1987, Webb *et al.* 1988). Although originally intended for cultivation, the species naturalized outside of gardens in the bombed, devastated areas of many cities (Kreh 1952, Kunick 1970, Owen & Whiteway 1980, Pfitzner 1983, Schmitz 1991). It rapidly colonizes bare, disturbed soils (Smale 1990) found on railroad embankments, quarries, roadsides and riparian areas (Randall & Marinelli 1996) and has also been found growing on walls and rock faces (Segal 1969).

*Buddleja davidii* has naturalized within sub-oceanic climates in the temperate and sub-mediterranean zones in most European countries as well as in Africa, New Zealand, Australia and in North America (Tutin 1972, Leeuwenberg 1979, Webb *et al.* 1988, Reichard & Hamilton 1997, Csurshes & Edwards 1998). It is listed on several countries' plant watch list because *B. davidii* may form dense stands that may displace native plant species. Due to the plants' popularity and its tolerance of a broad range of environmental conditions, high seed production and fast development to maturity, *B. davidii* has the potential to become a serious problem species in Europe as it has been reported in New Zealand (Kay & Smale 1990).

### *Aim and structure of this thesis*

Biological invasion can be considered as unintended experiments, providing the opportunity to investigate biogeographic, ecological and evolutionary mechanisms (Vermeij 1991, Lodge 1993, Sakai *et al.* 2001). There have been several studies that have explored the patterns of plant invasions, invasibility of communities, differences between phylogenetic groups and strategies of invasive plants and their control (Drake *et al.* 1989, Vitousek 1990, Pyšek 1995, Auge & Brandl 1997, Pyšek 1998, Alpert *et al.* 2000, Willis & Hulme 2002, Voitke & Dietz 2002). However, only a few studies have

attributed local adaptations as a reason for the success of plant invasions (e.g. Thompson 1998, Galloway & Fenster 2000, Parker *et al.* 2003). The aim of this thesis is to improve the understanding of how local adaptations contribute to the success of plant invasions using *Buddleja davidii* as the model system. The results of this research will contribute to the understanding of risks associated with the naturalization of *B. davidii* and development of best management strategies. This thesis specifically addresses different aspects of the potential rapid evolution in *Buddleja davidii*. First, it has to be determined whether plants differ in their performance between their native and invasive range. **Chapter 2** describes how the growth, reproduction and impact of herbivory differ among native and invasive populations of *B. davidii* in the field. This step is a prerequisite for testing different hypotheses (e.g. Enemy Release Hypothesis or Evolution of Increased Competitive Ability hypothesis) concerning the success of invasive plant species.

Chapters 3 and 4 test genetic differentiation between invasive *B. davidii* populations in the new range. Specifically, the adaptation of populations to climatic conditions is addressed in **Chapter 3**. For this purpose, common garden experiments were carried out and replicated in three central European regions, ranging from an oceanic to a sub-continental climate. The replication of common garden studies represents an approach that has been rarely realised. It allows both, investigations of genetic variation and local adaptation. For the latter, the integration of a reciprocal transplant experiment on populations originated from the three regions hosting the common gardens allowed to test for local adaptation. Genetic variation in response to different environments was investigated using various growth and fitness-related plant traits. Additionally, clipping treatments were used to simulate disturbance (Smale 1990) and frost damage to determine if there are differences among populations in re-sprouting ability and tolerance to damage.

**Chapter 4** further explores the local adaptation to frost in invasive *B. davidii* populations, specifically the physiological sensitivity to frost and response to frost damage. This study is based on the assumption that the geographic distribution of invasive *B. davidii* populations in Europe is restricted to the oceanic or sub-oceanic

climate due to sensitivity to frost. This research combines an eco-physiological approach and an ecological niche model to investigate whether evolutionary adjustments may exacerbate the prediction of spatial distribution of *B. davidii* and whether frost is actually limiting its further spread.

*Buddleja davidii* is an ecological specialist, able to colonise new coarse-textured, nitrogen-deficient surfaces (Humphries *et al.* 1982). In Europe railway embankments are typical habitats where large numbers of *B. davidii* have naturalized. There, plants have to be removed for safety reasons, mostly using the herbicide glyphosate. While the application of herbicides may exert a strong selection pressure on populations coincidentally, this may lead to evolution of herbicide resistance, which in turn, may hamper the management of weeds and invasive plants (Culliney 2005). **Chapter 5** investigates the susceptibility to the herbicide in populations of three different habitat types, that either has been treated with glyphosate or not. The potential for evolution of herbicide resistance will have far-reaching consequences for the successful and efficient management of invasive *Buddleja davidii* populations.

Overall, this thesis examines the genetic differences between invasive populations of *Buddleja davidii* in Europe with respect to different environmental influences and their importance for the invasion success of this species.

# The invasive shrub *Buddleja davidii* performs better in its introduced range

with Isabell Hensen & Harald Auge

Diversity & Distributions (2008), 14 (2): 225-233.

### Abstract

It is commonly assumed that invasive plants grow more vigorously in their introduced than in their native range, which is then attributed to release from natural enemies or to microevolutionary changes, or both. However, few studies have tested this assumption by comparing the performance of invasive species in their native versus introduced ranges. Here, we studied abundance, growth, reproduction and herbivory in ten native Chinese and ten invasive German populations of the invasive shrub *Buddleja davidii* (Scrophulariaceae; Butterfly Bush). We found strong evidence for increased plant vigour in the introduced range: plants in invasive populations were significantly taller, had thicker stems, larger inflorescences and heavier seeds than plants in native populations. These differences in plant performance could not be explained by a more benign climate in the introduced range. Since leaf herbivory was substantially reduced in invasive populations, our data rather suggest that escape from natural enemies, associated with increased plant growth and reproduction, contributes to the invasion success of *B. davidii* in Central Europe.

# Multiple common gardens suggest lack of local adaptation in a successful plant invader

with Jürg Stöcklin, Isabell Hensen & Harald Auge

### Abstract

Climatic conditions are widely recognized as important factors shaping distributional ranges of plant species, and driving genetic differentiation between populations resulting in local adaptation. Using the invasive shrub *Buddleja davidii* as study species, we performed a multiple common garden experiment in three central European regions, ranging from an oceanic to a sub-continental climate. Progeny from 20 invasive populations from central and west Europe were raised in each common garden to investigate genetic differentiation among these populations in response to the growing conditions of each garden. In addition, we incorporated a reciprocal transplantation experiment to test for local adaptation, by including one population from each of the three places harboring the common gardens. In contrast to our expectation, the results of our common garden experiments do not provide evidence for local adaptation of invasive *B. davidii* populations in Europe. All populations responded remarkably similar to the different environments, and trait values were not correlated to climatic conditions or the geographic coordinates of their home site. In addition, we did not detect a home-site advantage for the populations reciprocally transplanted between the common gardens, and did not detect differences in compensatory ability to mechanical damage. Assuming that invasive populations originate from cultivated individuals, we suggest that large-scale mixing of genotypes due to horticultural trade across Europe, and continuous gene flow from planted individuals, may have prevented local adaptation so far. Nevertheless, our data also indicate that large phenotypic plasticity enables invasive *B. davidii* populations to grow under various climatic and soil conditions, thus contributing to their geographic spread.

# Predicting the spread of an invasive plant: Combining experiments and ecological niche model

with Erik Welk, Harald Auge and Helge Bruelheide

Ecography, DOI: 10.1111/j.1600-0587.2008.05470.x

### Abstract

Rapid evolutionary adjustments to novel environments may contribute to the successful spread of invasive species, and can lead to niche shifts making range dynamics unpredictable. These effects might be intensified by artificial selection in the course of breeding efforts, since many successful plant invaders were deliberately introduced and cultivated as ornamentals. We hypothesized that the invasion success of *Buddleja davidii*, the ornamental Butterfly Bush, is facilitated by local adaptation to minimum temperatures and thus, exhibits unpredictable range dynamics. To assess the potential effects of adaptive evolution and artificial selection on the spread of *B. davidii*, we combined a common garden experiment investigating local adaptation to frost, with ecological niche modelling of the species' native and invasive ranges. We expected that populations naturalized in sub-continental climate are less susceptible to frost than populations from oceanic climate, and that the invasive range does not match predictions based on climatic data from the native range. Indeed, we revealed significant variation among invasive *B. davidii* populations in frost resistance. However, frost hardiness was not related to geographic location or climatic variables of the populations' home site, suggesting that invasive *B. davidii* populations are not locally adapted to minimum temperatures. This is in line with results of our ecological niche model that did not detect a niche shift between the species' native range in China, and its invasive range in Europe and North America. Furthermore, our niche model showed that the potential invasive range of *B. davidii* is still not completely occupied. Together with the frost resistance data obtained in our experiment, the results indicate that climatic conditions are currently not limiting the further spread of the species in Europe and North America.

# Herbicide tolerance in invasive Butterfly Bush (*Buddleja davidii*) populations in Europe

with Harald Auge

submitted to: The Ecology and Management of Alien Plant Invasions

### Abstract

In Europe, many invasive plant species grow in disturbed habitats like roadsides and railway tracks, where they have to be removed for safety reasons. Spraying chemical herbicides is the most commonly used technique for weed management along railway tracks. As a consequence of recurrent herbicide use plants can evolve resistance. This may in turn provoke either a higher frequency or an increased rate of herbicide application, causing additional environmental and economic costs. In Europe, invasive populations of introduced Butterfly Bush (*Buddleja davidii*) are spreading along railways although the herbicide glyphosate is used for weed management along railway tracks in most countries of Europe. Therefore, we asked to what extent *B. davidii* is susceptible to glyphosate, and whether populations invading railway tracks have evolved increased resistance compared with populations from other habitats. In order to investigate this, we carried out a greenhouse experiment using offspring of 12 *B. davidii* populations from three different habitat types: railway embankments, ruderal sites, and semi-natural habitats. After applying distilled water or four different concentrations of the herbicide glyphosate, we monitored plant survival. In contrast to our expectation, we found no evidence for glyphosate resistance in *B. davidii* because the recommended application rate of 30 mL/L resulted in 100% mortality. Furthermore, comparison of dose-response curves as well as LD<sub>50</sub> and LD<sub>90</sub> values revealed that populations from railway embankments have not evolved increased resistance to glyphosate so far.



### Synthesis

Human activity is one of the world's greatest evolutionary forces (Palumbi 2001) with impact on ecosystems in various ways: climatic change, alteration in land use, degradation, isolation and fragmentation of habitats (Vitousek 1990), and changes in biodiversity by deliberately or accidentally introducing non-indigenous species (Mooney & Cleland 2001, Lee 2002). Although a majority of the species that are introduced fail to survive, others thrive and become invasive (Williamson & Fitter 1996, Pyšek *et al.* 2004b). Such biological invasions are considered to be a major cause of extinction of native species throughout the world (Sala *et al.* 2000). Therefore, scientists focus on the prevention, eradication and control of invasive organisms. The understanding of biological invasions and the mechanisms associated with their success is an essential step in the development of meaningful control measures.

In plants the most conspicuous observation is the different performance of introduced plant species in the native compared to the invasive range, where they often grow more vigorously (e.g. Buckley *et al.* 2003, Prati & Bossdorf 2004, Jakobs *et al.* 2004). The increased vigour might be due to the absence of their natural enemies (Maron & Vila 2001, Keane & Crawley 2002). Alternatively, it might be possible that genetically fixed traits mirror the adaptations to the new environmental factors (Galloway & Fenster 2000). Such evolutionary changes can be rapid and may explain why some introduced species become invasive after a lag phase while others do not. The debate about adaptive evolution of invasive plant species as a possible explanation for their success has emerged during the last years. Evolution after introduction maybe caused either by genetic drift or by natural selection exerted by the novel biotic and abiotic environment (Mack *et al.* 2000, Leger & Rice 2003, Parker *et al.* 2003). Hence, differences in the performance between native and invasive range might be a result of rapid evolution expressed as increased competitive ability (EICA hypothesis, Blossey &

Nötzold 1995). Several studies have already revealed local adaptation in invasive plant species that are accounting for their invasion success, for example, in *Solidago canadensis* (Weber 1997) and *S. gigantea* (Weber & Schmid 1998) or *Impatiens glandulifera* (Kollmann & Banuelos 2004). In this thesis I studied the genetic differentiation and local adaptation of a perennial shrub, *Buddleja davidii* (butterfly bush) that is native to China yet invasive in West Europe, New Zealand and North America. Introduced to Europe as an ornamental in the late 1800's, it has been subject to artificial selection in its invasive range. Therefore comparisons between native and invasive populations of *B. davidii* offer excellent opportunities for examining invasion processes.

In the first study (chapter 2) it has turned out that the performance of *B. davidii* populations is enhanced in the new range, similar to observations on other species. Through a comparative approach we confirmed our hypothesis of a better growth and reproduction of *B. davidii* in the invasive range. Stems and inflorescences in European populations were 79% and 23% larger, respectively, in comparison with Chinese populations. The three subsequent experimental approaches (chapter 3-5) were conducted to determine reasons for the differences between the naturalized European (henceforth referred to as the invasive populations) and Chinese (henceforth referred to as the native populations) populations. On one hand leaf herbivory was substantially reduced in the invasive populations, which suggests that the escape from natural enemies may be responsible for increased vigour. On the other hand a more benign abiotic environment may positively influence the performance in the new range.

Climate is a primary driver of natural selection in plants (Kawecki & Ebert 2004), often explaining the distributional ranges of plant species (Woodward & Williams 1987). Adaptive divergence in relation to climatic conditions in the invaded range have been revealed in several plant species (e.g. Weber & Schmid 1998, Kollmann & Banuelos 2004, Jakobs *et al.* 2004). Climatic limitation of distributional ranges and its overcoming by genetic adaptation may be of particular importance for plant invasions. To study genetic differentiation with respect to climatic conditions among 20 invasive populations of *B. davidii* a common garden experiment was carried out (chapter 3). This

approach was replicated in three different climatic regions within the invasive range (Basel/Switzerland, Halle/Germany, Oldenburg/Germany). Although rarely implemented, replication across climatic regions studies reveal conclusions more accurately than a garden study conducted at a single location. We found high genetic variation in growth and reproduction traits among invasive populations of *B. davidii*, which may be either due to neutral forces such as founder effects or drift, or natural selection leading to local adaptation. Differentiation in plant traits did not correlate with geographic distances among populations, indicating that between-population variation is not likely due to isolation by distance. Plant fitness did not decrease with increasing geographic distance of the common garden to the respective home site of a population, and traits of growth and reproduction did not correlate with climatic characteristics of the populations' home site. These two latter results suggest that *B. davidii* populations are not locally adapted to their home environments. In addition to such correlative studies, local adaptation can also be investigated by reciprocal transplant experiments. Thus, a reciprocal transplantation was integrated into the common garden experiment: populations originating from the three cities harbouring the common gardens were included into the population subset. In contrast to our hypothesis, we found no significant genotype x environment interaction, again indicating a lack of local adaptation.

A second study dealing with genetic differentiation and local adaptation focused on frost as an important climatic factor limiting the distribution of plant species in the temperate zone (Woodward & Williams 1987). If *B. davidii* populations are locally adapted to minimum temperatures, one would expect that populations in sub-continental climate are less susceptible to frost than populations in oceanic climate. To test this hypothesis, we investigated frost resistance of plants growing in the common garden located in the sub-continental region (chapter 4). The study consisted of both, an experimental approach to local adaptation to minimum temperatures in the common garden and an ecological niche model to compare distribution of native and invasive populations of *B. davidii*. After all, we found significant differences in frost resistance among populations (population x frost interaction), but these differences

were not related to any climatic variable of their home site, indicating that populations are not genetically adapted to climatic conditions of their home site within the invasive range. However, the ecological niche model revealed that invasive *B. davidii* populations have not saturated their potential range suggesting that climatic conditions are not currently limiting the further spread of the species.

Neither the experiment nor the model confirmed Krivanek and Pyšek's (2006) assumption of that the current distribution border of *B. davidii* in Europe, running between the oceanic and sub-continental climate, is limited by the lack of frost tolerance.

Already established invasive plants must be managed to minimize their impact on the ecosystem. The most frequently used method to control plant populations is the chemical control by herbicides. However, recurrent herbicide application may lead to evolution of resistance in plants (Powles & Preston 2006). In Europe, *Buddleja davidii* often occurs along railways, where it is removed for safety reasons. Since the herbicide glyphosate is commonly used for this purpose, the question arises to what extent *B. davidii* may have evolved resistance to this herbicide. Specifically, we asked, if populations that invaded railway tracks show an increased resistance compared to populations from other habitats (chapter 5). We examined twelve *B. davidii* populations from three different habitat types: railway embankments, ruderal sites, and semi-natural habitats. Since the recommended application rate of 30 mL/L resulted in 100% mortality, it could be concluded that there is no evidence for glyphosate resistance in *B. davidii*. Furthermore, comparison of dose-response curves and LD<sub>50</sub> and LD<sub>90</sub> values revealed that populations from railway embankments have not evolved increased resistance to glyphosate so far. Therefore, glyphosate can be considered as an effective herbicide to be used to control the species.

A major conclusion that can be drawn from all three experimental studies of this thesis (chapter 3-5) is that we found no evidence for local adaptation in invasive *B. davidii* populations. This is in contrast to our expectation and may be due to a lack of genetic variation which is an important prerequisite for the response of a population to selection (Falconer & MacKay 1996). We speculate that the pattern of genetic

differentiation among *B. davidii* populations may rather reflect founder effects. Being a popular garden plant, the genetic variation of cultivated *B. davidii* may have been increased by plant breeding resulting in more than 90 cultivars (Stuart 2006). It is likely that the cultivars planted in the surrounding area were the seed source for the naturalized populations included in our studies.

Furthermore, trade and transport of cultivars across Europe may have led to a mixing of *B. davidii* genotypes and thus, have prevented local adaptation owing to gene-flow into invasive populations so far. Molecular studies are needed to determine the amount of genetic variation in invasive *B. davidii* populations, and the sources (i.e. which cultivars) that have particularly contributed to the gene pool of these populations.

The absence of adaptations may also be attributed to the relatively short period of time that has passed since the invasion of *B. davidii* in Europe began. Although it has been demonstrated that evolution in response to recent environmental conditions can occur within few generations (Davison & Reiling 1995, Thompson 1998, Bone & Farres 2001), the recentness of *B. davidii* invasion combined with founder effects and associated bottlenecks at each location has prevented the evolution of local adaptation thus far. However, the absence of evidence for local adaptation does not exclude rapid evolution in *B. davidii* in future. Furthermore, there remains the possible evolution of glyphosate resistance with the increasing use of herbicides (Powles & Preston 2006). Resistant populations will then serve as the sources of resistant alleles via gene flow through pollen or seeds.

Nevertheless, we could clearly demonstrate that the investigated populations of *B. davidii* that were included in this research show high phenotypic plasticity that enables the plants to grow and reproduce under different environmental conditions. Since other studies found a higher degree of plasticity in invasive than in native populations (see Bossdorf *et al.* 2005), the results support the suggestions, that high phenotypic plasticity is an important feature of successful invaders (Rice & Mack 1991b, Sexton *et al.* 2002).

In conclusion, *Buddleja davidii* is a highly invasive species that may cause serious problems in the invaded range due to its high growth rates, early maturity, high reproductive output of easily distributed seeds, and tolerance of a broad range of environmental conditions. The importance of plant breeding for invasion success of introduced plant species should be watched carefully, and should be considered in future studies on *B. davidii* in particular and on cultivated plants in general.

Overall, the next step should be a prospective monitoring of this plant species and to explore the effects of artificial selection on *B. davidii* invasiveness, realizing that, as the ecological niche model demonstrated, the invasion process is still on-going because the species has not saturated its potential distribution range.

### Zusammenfassung

Menschliche Aktivitäten haben einen enormen Einfluss auf ökologische und evolutionäre Prozesse. Diese Einflüsse vollziehen sich innerhalb und zwischen den Ökosystemen auf verschiedenen Ebenen und führen zu Änderungen des Klimas und der Landnutzung, zu Degradation und Fragmentierung von Habitaten und zu einer Veränderung der Biodiversität. Ein wichtiger Teilprozess der Änderung der biologischen Vielfalt ist die absichtliche Einführung oder unbeabsichtigte Einschleppung nicht-einheimischer Arten. Obwohl die meisten eingeführten Arten sich nicht etablieren, sind doch einige in der Lage im neuen Gebiet zu überleben und sich verstärkt auszubreiten, also invasiv zu werden. Solche biologischen Invasionen gelten weltweit als eine Hauptursache für das Aussterben einheimischer Arten. Deshalb liegt ein Schwerpunkt der Invasionsbiologie in der Erforschung gebietsfremder Arten, der Risikoabschätzung ihres Einflusses und der Verhinderung des Einschleppens bzw. der Beseitigung und der Kontrolle solcher Organismen. Zudem ist es erforderlich, biologische Invasionen und die damit verbundenen Mechanismen zu verstehen, um daraus sinnvolle Managementmaßnahmen ableiten zu können.

Eine auffällige Beobachtung bei pflanzlichen Invasionen ist das unterschiedliche Verhalten der Individuen im neuen Areal verglichen mit denen des Heimatareals. Im neuen Areal scheinen sie oft vitaler zu sein, schneller zu wachsen und eine höhere Reproduktionsrate aufzuweisen. Dies wird oft auf das Fehlen ihrer natürlichen Feinde – der Herbivoren und Pathogene, die häufig nicht mit in das neue Areal verschleppt werden – zurückgeführt (Enemy Release Hypothese). Andererseits ist es möglich, dass genetisch fixierte Merkmale eine Anpassung an die neuen Umweltbedingungen widerspiegeln. Solche evolutionären Veränderungen können rasch erfolgen und erklären, warum manche eingeführten Arten erst nach einer so genannten lag-Phase

invasiv werden und eine erhöhte Fitness aufweisen. Generell können evolutionäre Veränderungen bei invasiven Arten durch genetische Drift oder durch natürliche Selektion hervorgerufen werden. Im Verlauf der letzten Jahre wurde zunehmend über die adaptive Evolution als Ursache für den Invasionserfolg von Pflanzenarten diskutiert. So kann der Unterschied in der Pflanzenfitness zwischen dem neuen und dem ursprünglichen Verbreitungsgebiet das Ergebnis einer solcher schnellen evolutionären Veränderung sein, z.B. in Form der Evolution erhöhter Konkurrenzfähigkeit als Antwort auf das Fehlen der natürlichen Feinde (EICA-Hypothese). Verschiedene Studien haben bereits nachgewiesen, dass bei invasiven Pflanzenarten wie zum Beispiel *Solidago canadensis* (Weber 1997), *S. gigantea* (Weber & Schmid 1998) oder *Impatiens glandulifera* (Kollmann & Banuelos 2004), lokale Anpassung an die neue Umwelt zum Invasionserfolg beigetragen hat.

In meiner Dissertation habe ich die genetische Differenzierung und lokale Anpassung einer invasiven Art am Beispiel des Sommerflieder, *Buddleja davidii*, untersucht. Dieser aus China stammende Strauch ist in Westeuropa, Neuseeland und Nordamerika als invasive Art weit verbreitet. Er wurde als Kulturpflanze eingeführt und unterliegt seitdem züchterischen Veränderungen. Diese Art ist deshalb besonders geeignet, um Invasionsprozesse „in Aktion“ zu untersuchen.

Die erste, vergleichende Studie (Kapitel 2) zeigte, dass Populationen von *B. davidii* im neuen Areal (Deutschland) im Vergleich zu den Populationen im Heimatareal (China) vitaler sind und bestätigt somit dieses Phänomen auch für den Sommerflieder. Besonders bemerkenswert ist, dass in den europäischen Populationen die Sprosse um 79% und die Infloreszenzen um 23% länger waren als bei den chinesischen Populationen.

Die folgenden drei experimentellen Untersuchungen (Kapitel 3-5) beschäftigten sich mit möglichen Gründen dieser Unterschiede zwischen den beiden Kontinenten. Auf der einen Seite war die Blattherbivorie in den invasiven Populationen deutlich reduziert. Dieses Ergebnis deutet – in Übereinstimmung mit der Enemy-Release-Hypothese – darauf hin, dass der Verlust an natürlichen Feinden im neuen Areal für die erhöhte Vitalität der Art im neuen Areal verantwortlich ist. Auf der anderen Seite



können günstigere abiotische Umweltbedingungen das verbesserte Wachstum im neuen Areal verursacht haben. Das Klima ist eine der Haupttriebkkräfte natürlicher Selektion und begrenzt häufig die Verbreitungsgebiete von Pflanzenarten. Adaptive Divergenz in Bezug auf die klimatischen Bedingungen im invasiven Areal wurden bereits bei verschiedenen Pflanzenarten nachgewiesen. Das Überwinden klimatischer Grenzen mit Hilfe genetischer Anpassung ist vermutlich von großer Bedeutung für Pflanzeninvasionen.

Um zu überprüfen inwieweit dieser Aspekt auf invasive Populationen von *B. davidii* in Europa zutrifft, wurde ein so genanntes Common-Garden-Experiment durchgeführt (Kapitel 3). Dieser Ansatz wurde in drei klimatisch verschiedenen Regionen innerhalb des invasiven Areals wiederholt (Halle und Oldenburg in Deutschland und Basel in der Schweiz). Bisher wurde diese Form des Experimentes nur sehr selten durchgeführt, obwohl sie eine viel genauere Schlussfolgerung erlaubt als ein einzelnes Common-Garden-Experiment. Es stellte sich heraus, dass invasive Populationen von *B. davidii* genetisch variabel sind, was entweder auf neutrale Prozesse (wie Gründereffekte und Drift) oder auf natürliche Selektion zurückzuführen ist. Die Populationsunterschiede korrelierten nicht mit der geographischen Entfernung zwischen den Herkunftsorten der Populationen. Daraus lässt sich schlussfolgern, dass die Populationsdifferenzierung nicht allein auf genetische Isolation infolge räumlicher Distanz zurückzuführen ist. Außerdem korrelierte die Pflanzenfitness nicht mit der Entfernung des Versuchsgartens zum entsprechenden Herkunftsort, und die gemessenen Wachstums- und Reproduktionsmerkmale korrelierten nicht mit den klimatischen Merkmalen des Herkunftsortes. Beides deutet darauf hin, dass sich die Differenzierung zwischen den *B. davidii*-Populationen auch nicht auf einer lokalen Anpassung an ihre jeweilige Umwelt beruht.

Außer durch solche korrelative Ansätze kann lokale Anpassung mit Hilfe reziproker Verpflanzungsexperimente untersucht werden. Deshalb integrierten wir ein solches Verpflanzungsexperiment in das Common-Garden-Experiment, indem Nachkommen einer Population aus jeder der Common-Garden-Städte in die Populationsauswahl einbezogen wurde. Obwohl genetische Variation zwischen den

Populationen nachgewiesen wurde, gab es keine signifikante Genotyp x Umwelt-Interaktion, was als weiteres Indiz für das Fehlen lokaler Anpassung gewertet werden muss.

Eine zweite Studie untersuchte die genetische Differenzierung und die lokale Anpassung von *B. davidii* an Frost als einen wichtigen klimatischen Faktor, der die Verbreitung von Arten in der temperaten Klimazone beschränkt. Es galt zu klären, ob Populationen aus sub-kontinentalem Klima weniger frostempfindlich sind als Populationen aus ozeanischem Klima. Dazu wurde die Frostresistenz jener Pflanzen untersucht, die gemeinsam in dem im sub-kontinentalen Klima gelegenen Common-Garden (Halle) wuchsen (Kapitel 4). Diese Studie bestand zum einen aus einem experimentellen Ansatz, der lokale Anpassung an Minimumtemperaturen testete und zum anderen aus einem ökologischen Nischenmodell, um die Verbreitung von *B. davidii* im invasiven und nativen Areal zu vergleichen. Die Populationen wiesen zwar signifikante Unterschiede in ihrer Frostresistenz auf (Population x Frost Interaktion), diese korrelierten jedoch nicht mit den klimatischen Merkmalen des Herkunftsortes. Das weist darauf hin, dass die Populationen nicht genetisch an die klimatischen Bedingungen ihres Herkunftsgebietes innerhalb des invasiven Areals adaptiert sind. Jedoch zeigte das ökologische Nischenmodell, dass das potentielle Verbreitungsgebiet von *B. davidii* noch nicht vollständig ausgefüllt ist. Das legt die Vermutung nah, dass die zukünftige Verbreitung nicht durch die klimatischen Bedingungen begrenzt sein wird. Die Ergebnisse beider Untersuchungen konnten die Annahme von Krivanek and Pyšek (2006) nicht bestätigen: die gegenwärtige, zwischen dem ozeanischen und subkontinentalem Klima verlaufende Verbreitungsgrenze von *B. davidii* in Europa ist offensichtlich nicht auf mangelnde Frostresistenz zurückzuführen.

In vielen Fällen ist eine Bekämpfung bereits etablierter invasiver Arten oft notwendig, um ihre Einflüsse auf die Ökosysteme zu minimieren. In Europa wächst *B. davidii* hauptsächlich an Bahnstrecken, von denen sie aus Sicherheitsgründen entfernt werden muss. Am häufigsten werden dazu Herbizide, vor allem Glyphosat verwendet. Der Einsatz von Herbiziden kann allerdings zur Evolution von Resistenz führen. Aufgrund dieser Tatsache ergibt sich die Frage, ob sich bei *B. davidii* bereits

eine Herbizidresistenz entwickelt hat. Insbesondere galt es herausfinden, ob Individuen von *B. davidii*, die entlang von Bahngleisen wachsen, weniger empfindlicher auf das Herbizid reagieren als Individuen aus anderen Habitaten (Kapitel 5). Zu diesem Zweck wurden zwölf Populationen aus drei verschiedenen Habitattypen (Bahnanlagen, Ruderalstellen und halbnatürliche Habitate) in einem Gewächshausexperiment auf ihre Glyphosat-Resistenz untersucht. Eine 100% ige Mortalität bei der Anwendung der empfohlenen Dosis von 30 mL/L verdeutlichte das Fehlen der erwarteten Glyphosat-Resistenz. Des Weiteren zeigte ein Vergleich der Dosis-Antwort-Kurven und der LD<sub>50</sub>- sowie der LD<sub>90</sub>-Werte (d.h., der letalen Dosis, bei der 50% bzw. 90% der Pflanzen sterben), dass Populationen der Bahnanlagen keine erhöhte Resistenz entwickelt haben. Deshalb kann Glyphosat weiterhin als effektives Herbizid für die Kontrolle dieser Pflanzenart betrachtet werden.

Aus diesen drei experimentellen Untersuchungen kann zusammenfassend geschlussfolgert werden, dass es entgegen der ursprünglichen Erwartungen keine lokale Anpassung in invasiven Populationen von *B. davidii* gibt. Unzureichende genetische Variation, als grundlegende Voraussetzung für evolutionäre Veränderungen, könnte eine Ursache dafür sein. Es ist anzunehmen, dass das Muster genetischer Differenzierung zwischen den Populationen von *B. davidii* vielmehr Gründereffekte widerspiegelt.

Die Beliebtheit als Zierpflanze führte dazu, dass heute 70 verschiedene Kultivare von *B. davidii* im Handel sind. Es ist daher sehr wahrscheinlich, dass die Individuen der invasiven Populationen von denjenigen Kultivaren abstammen, die in der unmittelbaren Umgebung angepflanzt wurden. Ferner führten Handel und Transport dieser Kultivare zu einer Durchmischung der Genotypen von *B. davidii* quer durch Europa. Durch Genfluss von diesen kultivierten Beständen in die invasiven Populationen könnte eine Anpassung an lokale Bedingungen bisher verhindert worden sein. Zukünftige molekulare Studien sollten die genetische Variation in invasiven Populationen quantifizieren, und herausfinden, welche Kultivare besonders zum Genpool dieser Populationen beigetragen haben. Des Weiteren kann der kurze Zeitraum seit der ersten erfolgreichen Ausbreitung im neuen Areal das Fehlen von

Adaptationen begründen. Bei anderen Arten konnte bereits gezeigt werden, dass Anpassungen an bestehende Umweltbedingungen innerhalb weniger Generationen erfolgen können. Jedoch scheint der kurze Zeitraum im Zusammenspiel mit Gründereffekten und dem damit verbundenen genetischen Flaschenhals an jedem Standort eine lokale Anpassung bei *B. davidii* verhindert zu haben. Dennoch schließt die gegenwärtige Abwesenheit von lokalen Anpassungen, eine schnelle adaptive Evolution in Zukunft nicht aus. Außerdem besteht weiterhin das Risiko, dass *B. davidii* mit dem weiteren einseitigen Gebrauch von Glyphosat letztendlich doch Resistenzen entwickelt. Solche Populationen dienen dann als Quelle resistenter Gene, die sich durch Pollen oder Samen weiter verbreiten können.

Die im Rahmen meiner Dissertation durchgeführten Untersuchungen verdeutlichen, dass die invasiven Populationen von *B. davidii* eine hohe phänotypische Plastizität aufweisen. Dadurch wird es den Pflanzen offenbar ermöglicht, unter verschiedenen Umweltbedingungen zu wachsen und sich zu reproduzieren. Auch andere Studien belegten bereits ein erhöhtes Maß an phänotypischer Plastizität in invasiven Populationen im Vergleich zu nativen Populationen. Die Ergebnisse der vorliegenden Untersuchungen bestätigen, dass phänotypische Plastizität eine wichtige Eigenschaft eines erfolgreichen Eindringlings wie *B. davidii* ist.

*Buddleja davidii* bleibt aufgrund ihrer hohen Wachstumsrate, ihrer schnellen Entwicklung zur Fruchtreife, der hohen Samenproduktion und den geringen Ansprüchen an ihre Umweltbedingungen, eine Pflanzenart mit hohem Invasionspotenzial. Damit verbunden besteht auch weiterhin die Gefahr, einheimische Arten zu verdrängen bzw. Interaktionen zwischen den verschiedenen trophischen Stufen zu beeinflussen. Die Bedeutung der Pflanzenzucht für den Invasionserfolg eingeführter Pflanzenarten sollte nicht unterschätzt werden, sondern sorgfältig beobachtet und in zukünftigen Untersuchungen von *B. davidii* bzw. anderer kultivierter Pflanzenarten unbedingt berücksichtigt werden. Ein vorausblickendes Monitoring dieser Pflanzenart und weitere Untersuchungen zum Einfluss züchterischer Selektion auf die Invasibilität sind weitere wichtige Schritte zum Verständnis des Invasionsprozesses des Sommerfliederes. Da *B. davidii* ihr potentiell

klimatisches Verbreitungsgebiet innerhalb des neuen Areals noch nicht vollständig ausgefüllt hat, ist anzunehmen, dass der Invasionsprozess zukünftig fortschreiten wird.

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