RESEARCH ARTICLE

Germination performance of native and non-native *Ulmus pumila* populations

Heidi Hirsch[1], Catherina Wypior[1], Henrik von Wehrden[2],
Karsten Wesche[3], Daniel Renison[4], Isabell Hensen[1]

1 *Institute of Biology - Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle/Saale, Germany* **2** *Institute of Ecology, Faculty of Sustainability & Centre of Methods, Leuphana University, Scharnhorststraße 1, 21335 Lueneburg, Germany* **3** *Senckenberg Museum of Natural History Goerlitz, Am Museum 1, 02826 Goerlitz, Germany* **4** *Centro de Ecología y Resursos Naturales Renovables – Dr. Ricardo Luti (CERNAR), FCEFyN, UNC – CONICET, Av. Vélez Sarsfield 1611, X5016GCA Córdoba, Argentina*

Corresponding author: *Heidi Hirsch* (heidi.hirsch@botanik.uni-halle.de)

Abstract

Germination is a crucial step for invasive plants to extend their distribution under different environmental conditions in a new range. Therefore, information on germination characteristics of invasive plant species provides invaluable knowledge about the factors which might contribute to the invasion success. Moreover, intra-specific comparisons under controlled conditions will show if different responses between non-native and native populations are caused by evolutionary changes or by phenotypic plasticity towards different environmental influences.

This paper focuses on the germination of native and non-native *Ulmus pumila* populations. We expected that non-native populations would be characterized by their higher final germination percentage and enhanced germination rate, which might indicate an influence due to corresponding climatic conditions.

Germination experiments with a moderate and a warm temperature treatment did not reveal significant differences in final germination percentage. However, seeds from the North American non-native range germinated significantly faster than native seeds ($p < 0.001$). Additionally, mean time to germination in both ranges was significantly negatively correlated with annual precipitation ($p = 0.022$). At the same time, this relationship is stronger in the native range whereas mean time to germination in non-native populations seems to be less influenced by climatic conditions.

Different germination responses of the North American populations could be caused by a fast evolutionary change mediating a higher tolerance to current climatic conditions in the non-native range. However, our findings could also be caused by artificial selection during the introduction process and extensive

planting of *U. pumila* in its non-native range. Nevertheless, we assume that the faster germination rate of non-native populations is one potential explanation for the invasion success of *U. pumila* in its new range since it might provide a competitive advantage during colonization of new sites.

Keywords
Climatic influence, survival analysis, biological invasions, *Ulmus pumila*

Introduction

Introduced species often face different environmental conditions in their new range compared to their range of origin. Therefore, non-native species have to overcome several factors before they can become invasive (Heger and Trepl 2003). Moreover, even after becoming established in the new range, there are consistent characteristics which can alter the ongoing invasion spread. For example, germination is crucial for dispersal and to establish populations in new sites in order to expand in range (Theoharides and Dukes 2007, Donohue et al. 2010). Therefore, data about shifts in germination characteristics could provide valuable information to predict the success of an invading species.

Differing germination characteristics can be caused by evolutionary changes mediated by corresponding environmental conditions. For example, Eckhart et al. (2011) demonstrated that germination patterns in 20 populations of *Clarkia xantiana* along a climatic gradient were linked to the corresponding temperature, mean precipitation and variation in precipitation. Additionally, several studies have shown that plant species can exhibit differing germination responses which are related to differing habitats or biotic influences (e.g. Giménez-Benavides et al. 2007, Jorritsma-Wienk et al. 2007, Grondahl and Ehlers 2008). Similarly, shifts in the germination performance towards different environmental conditions can also be an important factor during range expansion in the course of invasion. Brändle et al. (2003) showed that for 31 weedy plant species the range size is influenced by the germination niche breadth. Furthermore, enhanced germination percentages and rates of invaders compared to their native congeners or competitors have been associated with increased colonization success of the invaders (Burke and Grime 1996, Muñoz and Ackerman 2011).

Intra-specific comparisons between native and non-native populations are important to understand the mechanisms of the invasion process (Hierro et al. 2005). Furthermore, it can be useful to compare native and non-native individuals under a common environment. Such experiments will allow to distinguish if differences between ranges are caused by phenotypic responses towards different environmental conditions or by genetic changes (Leger and Rice 2003, Kawecki and Ebert 2004, Erfmeier and Bruelheide 2005, van Kleunen et al. 2010). For example, Beckmann et al. (2011) found that non-native New Zealand populations of three grassland species show increased germination compared with the native European populations, which may indicate an adaptation to new climatic conditions in the non-native range. Several other comparative studies also reported differences in germination between native and non-native populations of the same species (e.g. Kudoh et al. 2007, Hierro et al. 2009).
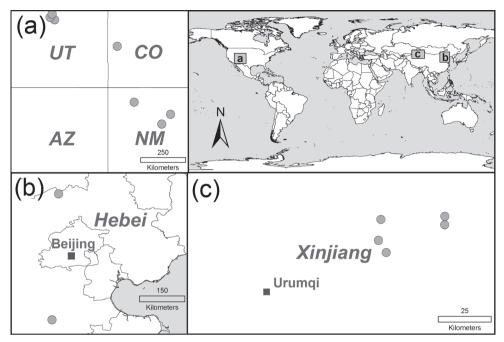
Although more than 300 tree species are classified as invasive, there are comparatively few studies on their invasion success (Lamarque et al. 2011, Richardson and Rejmánek 2011). Our study addresses the comparison of germination responses between native and non-native *Ulmus pumila* L. (Ulmaceae) populations. The Siberian elm is a native tree of temperate regions of East Asia, and occurs northwards up to the dry Gobi desert, where it is bound to water surplus sites and oases (Wesche et al. 2011). The flowering and fruit set production occur during the late winter to early spring (Wu et al. 2003). Each of the wind dispersed fruits (samaras) contains a single seed. The seeds lose their viability rapidly after maturity unless placed on suitable germination conditions or dried and placed at low temperatures (Baskin and Baskin 2000). *Ulmus pumila* can grow in a wide variety of habitats (e.g. slopes, valleys, plains), even with cold winters and long summer droughts (Wu et al. 2003, USDA and NRCS 2011). Since the Siberian elm performs better under harsh climatic conditions than most other trees, it has been planted in several regions outside its native range, e.g. in the semi-arid Southwestern United States as a fast growing windbreak or shade tree (Webb 1948, Leopold 1980). Furthermore, it is commonly used in elm breeding programs due to its high tolerance to the Dutch elm disease (Smalley and Guries 2000, Mittempergher and Santini 2004). Today, *U. pumila* is considered as naturalized or even invasive in 43 states of the U.S., as well as in Canada (Kartesz 2011, USDA and NRCS 2011), Mexico (Todzia and Panero 1998), Argentina (Mazia et al. 2001, Zalba and Villamil 2002), Spain (Cogolludo-Agustín et al. 2000), the European part of Russia, Estonia and Australia (NOBANIS 2012). Webb (1948) reported that different Chinese origins of the Siberian elm are characterized by differing frost hardiness. Therefore, it seems possible that specific adaptations towards local environmental conditions allow *U. pumila* to persist over such a wide distribution range. However, to our knowledge no information exists if early life cycle traits of *U. pumila* show such an adaptation and if this could contribute to the invasion success.

We focused our study on non-native populations in the Western U.S. and compared their germination performance under controlled conditions to the performance of populations from the native range in China. Thereby, we tested the following hypotheses: 1) Non-native populations will exhibit an increased percentage of germinated seeds. 2) Non-native populations are characterized by a faster germination. 3) Different germination responses might be influenced by different climatic conditions. In this context, we assume that populations located in regions with less stressful climatic conditions (e.g. higher annual precipitation) show enhanced germination characteristics.

Material and methods

Seed collection

We retrieved samaras (henceforth referred to as seeds) from seven populations from the native range (China) and seven populations from the non-native range (U.S.; Figure 1).

Figure 1. Sampled *Ulmus pumila* populations in the native range (**b, c**) and the non-native range (U.S.: **a**; **AZ** = Arizona, **CO** = Colorado, **NM** = New Mexico, **UT** = Utah). Populations are indicated by gray circles.

Seeds from China were collected in May and June 2009 and seeds from the U.S. in May and June 2010. We sampled at least 15 trees per population and pooled the seeds within populations. Where seeds had already been shed, they were collected from the ground. Material was stored in sealed plastic bags at 4°C following recommendations by Grover et al. (1963) to maintain seed viability.

Germination experiment

The germination experiment started in January, 2011 and was setup as a completely randomized design with eight replicates per population and treatment. Each replicate contained 20 seeds which were placed on filter paper in standard Petri dishes. In sum, we used 4480 seeds (14 populations × 2 temperature treatments × 8 replicates × 20 seeds per replicate) in our experiment. The dishes were filled with de-ionized water to keep the seeds permanently moist. Wings of the seeds were not removed due to their role in facilitating water uptake and in order to avoid seed damage (Rohmeder 1942, Namvar and Spethmann 1985). The experiment was performed in RUMED Light Thermostats germination chambers (Type 1301; Rubarth Apparate GmbH, Laatzen, Germany) under two temperature treatments (20°C/10°C and 32°C/20°C) with a photoperiod of 12 h cold white light (1200 Lux) and 12 h darkness. The two temperature treatments were used to account for the range of maximum temperatures during

the main germination period of *U. pumila* (see Appendix 1: Table A1). Germinated seeds (visible radicula) were reported and removed every second or third day. After two weeks, viability of non-germinated seeds was tested with triphenyl tetrazolium chloride (ISTA Tetrazolium Commitee 2008).

Statistics

All statistics were calculated with the software R (version 2.15.0; The R Development Core Team 2012). To test if the final germination percentage (logit transformed according to Warton and Hui 2011) differs between the accessions and temperature treatments, we used a linear mixed model with populations nested in ranges as random effect (package nlme, version 3.1-103; Pinheiro et al. 2012). The Akaike Information Criterion (AIC; Akaike 1974) was used for model selection. For visualization of the germination performance and to extract the restricted mean time to germination (henceforth referred to as mean time to germination) per population we used the Kaplan-Meyer estimates of the germination functions. To test if time to germination differs between the ranges and temperature treatments, we performed a survival analysis using an Accelerated Failure Time (AFT; Bradburn et al. 2003) regression following the recommendations of Onofri et al. (2010). We used a right censoring of non-germinated, but still viable seeds. Non-viable seeds were excluded from the analysis based on the assumption that these were already non-viable at the beginning of the experiment (Onofri et al. 2010). We used the AIC values to select the most appropriate distribution (exponential, loglogistic, lognormal or Weibull), since AFT models assume parametric distributions (Kleinbaum and Klein 2005). Population was added as a random effect to test if the model is affected by variation at the population level within the ranges. The Kaplan-Meyer statistics as well as the survival analysis were calculated with the package *survival* (version 2.36-12; Therneau and Lumley 2012).
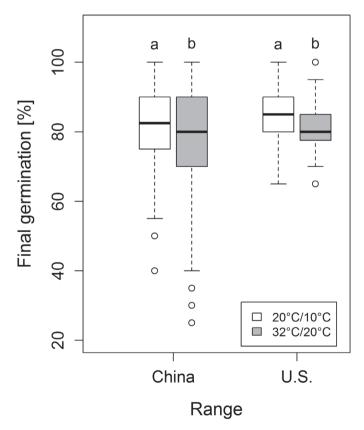
To test if the mean time to germination is adapted to different climate conditions between the native and the non-native range (see Appendix 2: Figure A1), we extracted climatic information per population (mean annual temperature and annual precipitation; see Appendix 1: Table A1) from the WORLDCLIM database (Hijmans et al. 2005). The effect of the climatic variables on germination was tested with a multiple linear regression. Additionally, we also included the effect of the population origin (native or non-native range) and the temperature treatment in our model. Selective model reduction was based on the AIC values.

Results

At the end of the germination experiment, 80.6 % of the tested seeds were germinated. From the non-germinated seeds were 2.1 % still viable (non-native origin: 1.3 %; native origin: 0.8 %).

The test for differences regarding the final germination percentage resulted in a final model containing only the temperature treatment as fixed effect. Consequently, no differences between the two ranges were detectable ($F_{1,12}$ = 0.416, p > 0.05, Figure 2). However, final germination percentages for both ranges were slightly lower under warm temperature conditions compared to a moderate temperature ($F_{1,209}$ = 6.513, p < 0.05; Figure 2).
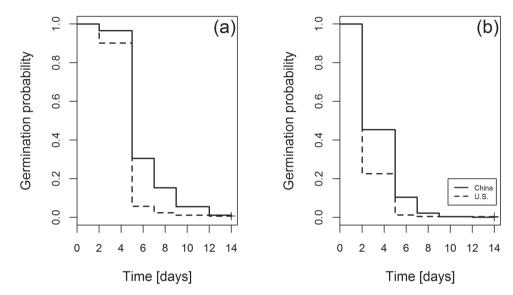
Investigation of the time to germination revealed that the most pronounced reduction of deviance was contributed by the temperature treatment (Table 1). Lower, but still significant effects were contributed by the random effect (population), the influence of the origin of the populations (range) as well as the interaction between range and temperature treatment. These results were obtained from a final AFT model with best fit for log-normal distribution showed including range as well as temperature as predictor variables and population as random effect. The enhanced germination rates under warmer temperatures as well as the differences between the two ranges are visualized in Figure 3.

Figure 2. Final germination (%) of *Ulmus pumila* seeds from native and the non-native ranges. No differences were found between the two ranges ($F_{1,12}$ = 0.416, p > 0.05). Germination percentage was significantly decreased under warmer temperature treatment ($F_{1,209}$ = 6.513, p < 0.05; significant differences are shown by different letters above the boxes).
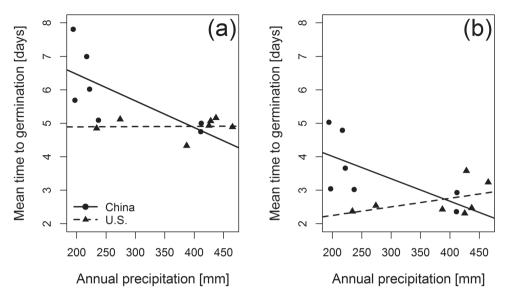
Table 1. Analysis of deviance results for the AFT model. The results show the differences in the time to germination of *Ulmus pumila* under consideration of range and temperature treatment (df = degrees of freedom).

Source	df	Deviance	Residual df	-2 × loglikelihood	p
Null model			3627	15151.90	
Range	1	165.75	3626	14986.25	<0.001
Temperature	1	1691.68	3625	13294.47	<0.001
Frailty (population in range)	12	673.16	3615	12621.30	<0.001
Range × temperature	1	6.34	3614	12614.96	0.012

Figure 3. Kaplan-Meyer curves of the germination functions for the non-native and native origins of *Ulmus pumila*. Curves are shown for the two temperature treatments (**a**: 20°C/10°C; **b**: 32°C/20°C). Censored data is symbolized by final crosses at the curves. The curves show the probability that seeds will germinate. Therefore, the germination probability has to be 1.0 at time = 0 because all seeds are non-germinated and have consequently the chance to germinate.

Considering the mean time to germination supports our result of the AFT model regarding a faster germination at higher temperatures ($F_{1,23}$ = 88.83, $p < 0.001$) and in the non-native range ($F_{1,23}$ = 14.48, p = 0.001). We also found a significant negative relation between mean time to germination and annual precipitation ($F_{1,23}$ = 5.98, p = 0.022) as well as a significant interaction between range and annual precipitation ($F_{1,23}$ = 9.46, p = 0.005). This interaction shows that native populations with less annual precipitation are characterized by increased mean times to germinate. In contrast, non-native populations show only weak response in their mean time to germination towards corresponding annual precipitation conditions (Figure 4). These results were obtained from the multiple regression model retaining population origin, temperature and annual precipitation as predictor variables after stepwise model selection (multiple R^2 = 0.84, $p < 0.001$).

Figure 4. Relationship between mean time to germination and annual precipitation per *Ulmus pumila* population (**a**: 20°C/10°C; **b**: 32°C/20°C). To emphasize the different responses between the two ranges (non-native range: triangles; native range: circles), trend lines per range are shown (non-native range: dashed line; native range: solid line).

Discussion

Our results revealed a slightly lower final germination of *U. pumila* seeds at higher temperatures. This could be caused by an earlier and stronger infestation by mold fungi at the 30°C/20°C temperature treatment (personal observation), because these warmer temperatures provide better growing conditions of mold fungi. For example, Barnett et al. (1999) showed for *Pinus palustris* that germination can be reduced by pathogenic fungi. However, we assume that these slightly differences show no relevant effects under natural conditions, because the final germination will be still high enough to support a colonization of *U. pumila* in regions with high temperature regimes, since seeds are produced in very high numbers. Furthermore, we found only a very low amount of non-germinated but still viable seeds. Consequently, we exclude that population growth and persistence of the Siberian elm might be supported by a generated seed bank, which would be also contrary to the already mentioned short life span of *U. pumila* seeds.

Contrary to our hypothesis, the invasion success of *U. pumila* in North America does not seem to be based on an enhanced final germination percentage. However, we have evidence for enhanced times to germination in non-native populations. We propose that the fast germination is one of the contributing drivers for the invasion success of *U. pumila* because it could provide advantages during inter-specific competition in the colonization processes (Donohue et al. 2010). This hypothesis is supported by results in other studies such as a grassland experiment by Milbau et al. (2003) which revealed that regenerative traits, like germination time, are correlated

with invasiveness. Furthermore, Seiwa (2000) showed that early-emerging seedlings of *Juglans ailanthifolia* are characterized by greater height than later-emerging seedlings due to a longer exposition to favorable light and temperature conditions before they are crowded by other species.

Additionally, we found that mean time to germination in both ranges seems to be influenced by climatic conditions such as annual precipitation (i.e. mean time to germination decreases with increasing annual precipitation). We assume that this relationship is based on less stressful germination conditions for the Siberian elm under climatic conditions with more rainfall since annual precipitation can be considered as a general measure of environmental quality (Philippi 1993, Hierro et al. 2009). However, the significant interaction between range and annual precipitation indicates that annual precipitation conditions show a stronger influence to the mean time to germination in native populations. In contrast, mean time to germination of non-native population seems to be less influenced by the annual precipitation conditions. Therefore, it might be possible that non-native populations are characterized by a higher tolerance towards different precipitation conditions compared to native populations. For example, evidence of germination rates related to different moisture regimes was shown for *Pinus ponderosa* in central Oregon (Weber and Sorensen 1992). Further, Maron et al. (2004) showed that such processes are also possible for introduced plants. In this context, it is often suggested that rapid evolutionary change is supported by standing genetic variance or genetic mixing (intra- or inter-specific; Lavergne and Molofsky 2007, Prentis et al. 2008, Dormontt et al. 2011). Genetic studies have also shown that non-native *U. pumila* populations in the Eastern and Central U.S. are characterized by genetic diversity levels which are comparable to native populations (Zalapa et al. 2009, 2010). Furthermore, it was demonstrated that a high proportion of these populations contain hybrids between *U. pumila* and *U. rubra* and that hybridization leads to a significant increase of genetic variability. As shown by Abbott et al. (2003), hybridization can lead to the introgression of traits which might affect the fitness of introgressants or their tolerance to novel habitats. For example, Rieseberg et al. (2007) were able to identify that introgression processes may supported range expansion of *Helianthus annuus*. However, genetic investigations are needed for our sampled populations of *U. pumila* in the Western U.S. to gain more detailed knowledge on the genetic diversity and eventually hybridization processes.

In contrast to natural evolutionary processes, the pattern of different germination reactions in our studied populations could also be caused by human-mediated selection of successful lineages during introduction (Donohue et al. 2010). For example, Chrobock et al. (2011) found evidence that cultivated non-native species germinate earlier and more successfully than related native species which indicates a human-mediated selection for these traits. Therefore, non-native species that escaped from cultivation and became invasive might be characterized by enhanced germination characteristics mediated by artificial selection. Such a type of selection could have influenced the germination performance of *U. pumila* due to selection during the intro-

duction process and extensive planting in the U.S. afterwards (Webb 1948, Leopold 1980, Mittempergher and Santini 2004). Consequently, further research approaches should also consider seeds or seedlings obtained from commercial suppliers to test for eventually human-mediated selection. Further, we are not able to exclude that the revealed differences between non-native and native populations are influenced by maternal effects. According to Moloney et al. (2009), a bias by maternal effects could be avoided by using second-generation offspring. However, long generation times render the implementation of this approach very difficult for woody plants. Therefore, we suggest that genetic investigations are needed to proof our assumption that the different germination patterns between non-native and native populations are caused by evolutionary change rather than maternal effects.

Additionally, it should be considered that our results could be biased by two methodical factors. First, differences between both ranges might be caused by different sampling years (seeds from the native range: 2009; seeds from the non-native range: 2010). We assume that this factor induced only a negligible influence to our results, because Grover et al. (1963) observed that Siberian elm seeds did not show any different viability during the first two years of the storage conditions used for our study. Nevertheless, we strongly recommend the usage of seeds from the same sampling year for further comparative germination experiments to provide uniform test conditions. Second, it could be argued that our replicates per population and treatment are just pseudoreplicates due to their spatially non-independence. However, we exclude that the observed differences in germination resulted significantly from technically differences among the used germination chambers, because both chambers are of the same model type produced by a high quality manufacturer, both chambers had the same basic conditions (e.g. same light equipment), and both chambers are frequently cleaned and fumigated. Nonetheless, a repeated switching of the temperature treatment and the corresponding replicates in further germination experiments as applied by Zuloaga-Aguilar et al. (2011) could help to improve the experimental design of such studies, and to reduce possible different test conditions.

It should also be mentioned that several other studies have shown that changed germination characteristics are often linked to changed post-germination traits as well (Donohue et al. 2010). Erfmeier and Bruelheide (2005) studied non-native *Rhododendron ponticum* populations and showed that genetic shifts influenced the germination and the growth performance. Therefore, colonization success of non-native *U. pumila* populations could be based on both an increased germination rate and a better growth performance than native populations. In order to accept this hypothesis, research on coevolution between germination and post-germination traits is needed.

Our work suggests that changed germination characteristics could be one of the drivers for the invasion success of *U. pumila*. However, further research (i.e. genetic analyses and growth experiments) is needed to find genetic evidence for our assumption and if the assumed evolutionary change of germination responses also influenced other early life cycle traits of non-native populations of the Siberian elm.

Acknowledgements

References

Abbott RJ, James JK, Milne RI, Gillies ACM (2003) Plant introductions, hybridization and gene flow. Philosophical Transactions of the Royal Society B 358: 1123–1132. doi: 10.1098/rstb.2003.1289

Akaike H (1974) A new look at statistical model identification. IEEE Transactions on Automatic Control AU-19: 716–722. doi: 10.1109/TAC.1974.1100705

Barnett JP, Pickens B, Karrfalt R (1999) Longleaf pine seed presowing treatments: effects on germination and nursery establishment. In: Landis TD, Barnett JP (Eds) National proceedings: forest and conservation nursery associations - 1998, General technical report SRS-25. USDA Forest Service (Asheville, NC): 43–46.

Baskin CC, Baskin JM (2000) Seeds. Ecology, biogeography, and evolution of dormancy and germination. Academic Press (San Diego): 666 pp.

Beckmann M, Bruelheide H, Erfmeier A (2011) Germination responses of three grassland species differ between native and invasive origins. Ecological Research 26: 763–771. doi: 10.1007/s11284-011-0834-3

Bradburn MJ, Clark TG, Love SB, Altman DG (2003) Survival Analysis Part II: Multivariate data analysis – an introduction to concepts and methods. British Journal of Cancer 89: 431–436. doi: 10.1038/sj.bjc.6601119

Brändle M, Stadler J, Klotz S, Brandl R (2003) Distributional range size of weedy plant species is correlated to germination patterns. Ecology 84: 136–144. doi: 10.1890/0012-9658

Burke MJW, Grime JP (1996) An experimental study of plant community invasibility. Ecology 77: 776–790. doi: 10.2307/2265501

Chrobock T, Kempel A, Fischer M, van Kleunen M (2011) Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland. Basic and Applied Ecology 12: 244–250. doi: 10.1016/j.baae.2011.03.001

Cogolludo-Agustín MÁ, Agúndez D, Gil L (2000) Identification of native and hybrid elms in Spain using isozyme gene markers. Heredity 85: 157–166. doi: 10.1046/j.1365-2540.2000.00740.x

Donohue K, Rubio de Casas R, Burghardt L, Kovach K, Willis CG (2010) Germination, postgermination adaptation and species ecological ranges. Annual Review of Ecology and Systematics 41: 293–319. doi: 10.1146/annurev-ecolsys-102209-144715

Dormontt EE, Lowe AJ, Prentis PJ (2011) Is rapid adaptive evolution important in successful invasions? In: Richardson D (Ed) Fifty years of invasion ecology: the legacy of Charles Elton. Wiley-Blackwell (Oxford, UK).

Eckhart V, Geber M, Morris W, Fabio E, Tiffin P, Moeller D (2011) The geography of demography: Long-term demographic studies and species distribution models reveal a species border limited by adaptation. The American Naturalist 178: S26-S43. doi: 10.1086/661782

Erfmeier A, Bruelheide H (2005) Invasive and native *Rhododendron ponticum* populations: is there evidence for genotypic differences in germination and growth? Ecography 28: 417–428. doi: 10.1111/j.0906-7590.2005.03967.x

Giménez-Benavides L, Escudero A, Iriondo J (2007) Local adaptation enhances seedling recruitment along an altitudinal gradient in a hight mountain Mediterranean plant. Annals of Botany 99: 723–734. doi: 10.1093/aob/mcm007

Grondahl E, Ehlers B (2008) Local adaptation to biotic factors: reciprocal transplants of four species associated with aromatic *Thymus pulegioides* and *T. serpyllum*. Journal of Ecology 96: 981–992. doi: 10.1111/j.1365-2745.2008.01407.x

Grover R, Martin EW, Lindquist CH (1963) Maturity and storage of Siberian elm seeds. Forest Science 9: 493–496. http://www.ingentaconnect.com/content/saf/fs/1963/00000009/00000004/art00019

Heger T, Trepl L (2003) Predicting biological invasions. Biological Invasions 5: 313–321. doi: 10.1023/B:BINV.0000005568.44154.12

Hierro JL, Eren Ö, Khetsuriani L, Diaconu A, Török K, Montesinos D, Andonian K, Kikodze D, Janoian L, Villarreal D, Estanga-Mollica ME, Callaway RM (2009) Germination responses of an invasive species in native and non-native ranges. Oikos 118: 529–538. doi: 10.1111/j.1600-0706.2008.17283.x

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. Journal of Ecology 93: 5–15. doi: 10.1111/j.1365-2745.2004.00953.x

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. doi: 10.1002/joc.1276

ISTA Tetrazolium Commitee (2008) Internationale Vorschriften für die Prüfung von Saatgut. Internationale Vorschriften für Saatgutprüfung (Bassersdorf).

Jorritsma-Wienk L, Ameloot E, Lenssen J, de Kroon H (2007) Differential responses of germination and seedling establishment in populations of *Tragopogon pratensis* (Asteraceae). Plant Biology 9: 109–115. doi: 10.1055/s-2006-924524

Kartesz JT (2011) North American Plant Atlas. http://www.bonap.org/MapSwitchboard.html [accessed 11.10.2011].

Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. Ecology Letters 7: 1225–1241. doi: 10.1111/j.1461-0248.2004.00684.x

Kleinbaum DG, Klein M (2005) Survival Analysis: A Self-Learning Text (Statistics for Biology and Health). Springer (New York): 590 pp.

Kudoh H, Nakayama M, Lihová J, Marhold K (2007) Does invasion involve alternation of germination requirements? A comparative study between native and introduced strains of an annual Brassicaceae, *Cardamine hirsuta*. Ecological Research 22: 869–875. doi: 10.1007/s11284-007-0417-5

Lamarque LJ, Delzon S, Lortie CJ (2011) Tree invasions: a comparative test of the dominant hypotheses and functional traits. Biological Invasions 13: 1969–1989. doi: 10.1007/s10530-011-0015-x

Lavergne S, Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. Proceedings of the National Academy of Sciences 104: 3883-3888. doi: 10.107/pnas.0607324104

Leger EA, Rice KJ (2003) Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. Ecology Letters 6: 257–264. doi: 10.1046/j.1461-0248.2003.00423.x

Leopold DJ (1980) Chinese and Siberian elms. Journal of Arboriculture 6: 175–179. http://joa.isa-arbor.com/request.asp?JournalID=1&ArticleID=1664&Type=2

Mazia CN, Chaneton EJ, Ghersa CM, Leon RJC (2001) Limits to tree species invasion in pampean grassland and forest plant communities. Oecologia 128: 594–602. doi: 10.1007/s004420100709

Milbau A, Nijs I, Van Peer L, Reheul D, De Cauweer B (2003) Disentangling invasiveness and invasibility during invasion in synthesized grassland communities. New Phytologist 159: 657–667. doi: 10.1046/j.1469-8137.2003.00833.x

Mittempergher L, Santini A (2004) The history of elm breeding. Investigación agraria: Sistemas y recursos forestales 13: 161–177. http://www.inia.es/gcontrec/pub/161-177-%2814%29-The_history_1161943529015.pdf

Moloney KA, Holzapfel C, Tielbörger K, Jeltsch F, Schurr FM (2009) Rethinking the common garden in invasion research. Perspectives in Plant Ecology, Evolution and Systematics 11: 311–320. doi: 10.1016/j.ppees.2009.05.002

Muñoz MC, Ackerman JD (2011) Spatial distribution and performance of native and invasive *Ardisia* (Myrsinaceae) species in Puerto Rico: the anatomy of an invasion. Biological Invasions 13: 1543–1558. doi: 10.1007/s10530-010-9912-7

Namvar K, Spethmann W (1985) Waldbaumarten aus der Gattung *Ulmus* (Ulme, Rüster). Allgemeine Forstzeitschrift 40: 1220–1225. http://www.baum.uni-hannover.de/publikation_single.html?&no_cache=1&tx_tkpublikationen_pi1 [showUid]=29

NOBANIS (2012) European Network on Invasive Alien Species. www.nobanis.org [accessed 10.07.2012].

Onofri A, Gresta F, Tei F (2010) A new method for the analysis of germination and emergence data of weed species. Weed Research 50: 187–198. doi: 10.1111/j.1365-3180.2010.00776.x

Philippi T (1993) Bet-hedging germination of desert annuals: variation among populations and maternal effects in *Lepidium lasiocarpum*. The American Naturalist 142: 488–507. http://www.jstor.org/stable/2462655, doi: 10.1086/285551

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2012) nlme: linear and nonlinear mixed effects models. R package version 3.1–103. http://cran.r-project.org/web/packages/nlme/index.html

Prentis PJ, Wilson JRU, Dormontt EE, Richardson D, Lowe AJ (2008) Adaptive evolution in invasive species. Trends in Plant Science 13: 288–294. doi: 10.1016/j.tplants.2008.03.004

Richardson D, Rejmánek M (2011) Trees and shrubs as invasive alien species - a global review. Diversity and Distributions 17: 788–809. doi: 10.1111/j.1472-4642.2011.00782.x

Rieseberg LH, Kim S-C, Randell RA, Whitney KD, Gross BL, Lexer C, Clay K (2007) Hybridization and the colonization of novel habitats by annual sunflowers. Genetica 129: 149–165. doi: 10.1007/s10709-006-9011-y

Rohmeder E (1942) Keimversuche mit *Ulmus montana* (With). Forstwissenschaftliches Centralblatt 64: 121–135. doi: 10.1007/BF01829274

Seiwa K (2000) Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. Oecologia 123: 208–215. doi: 10.1007/s004420051007

Smalley EB, Guries RP (2000) Asian elms: sources of disease and insect resistance. In: Dunn CP (Ed) The elms - breeding, conservation, and disease management. Kluwer Academic Publishers (Boston): 215–230.

The R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org.

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist 176: 256–273. doi: 10.1111/j.1469-8137.2007.02207.x

Therneau T, Lumley T (2012) survival: Survival analysis, including penalised likelihood. R package version 2.36–12. http://CRAN.R-project.org/package=survival

Todzia CA, Panero JL (1998) A new species of *Ulmus* (Ulmaceae) from southern Mexico and a synopsis of the species in Mexico. Brittonia 50: 343–347. doi: 10.2307/2807778

USDA, NRCS (2011) The PLANTS Database. National Plant Data Team, Greensboro, NC 27401–4901 USA. http://plants.usda.gov [accessed 05.10.2011].

van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecology Letters 13: 947–958.

Warton DI, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 92: 3–10. doi: 10.1890/10-0340.1

Webb WE (1948) A report on *Ulmus pumila* in the Great Plains region of the United States Journal of Forestry 46: 274–278. http://www.ingentaconnect.com/content/saf/jof/1948/00000046/00000004/art00011

Weber JC, Sorensen FC (1992) Geographic variation in speed of seed germination in central Oregon ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). Research Paper PNW-RP-444 Portland, OR: US Department of Agriculture, Forest Service, Pacific Nowthwest Research Station: 12 pages. http://www.treesearch.fs.fed.us/pubs/20559

Wesche K, Walther D, von Wehrden H, Hensen I (2011) Trees in the desert: Reproduction and genetic structure of fragmented *Ulmus pumila* forests in Mongolian drylands. Flora

- Morphology, Distribution, Functional Ecology of Plants 206: 91–99. doi: 10.1016/j. flora.2010.01.012

Wu ZY, Raven PH, Hong DY (Eds) (2003) Flora of China. Vol. 5 (Ulmaceae through Basellaceae). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis). http://www.efloras.org [accessed 20.11.2010].

Zalapa JE, Brunet J, Guries RP (2009) Patterns of hybridization and introgression between invasive *Ulmus pumila* (Ulmaceae) and native *U. rubra*. American Journal of Botany 96: 1116–1128. doi: 10.3732/ajb.0800334

Zalapa JE, Brunet J, Guries RP (2010) The extent of hybridization and its impact on the genetic diversity and population structure of an invasive tree, *Ulmus pumila* (Ulmaceae). Evolutionary Applications 3: 157–168. doi: 10.1111/j.1752-4571.2009.00106.x

Zalba SM, Villamil CB (2002) Woody plant invasion in relictual grasslands. Biological Invasions 4: 55–72. doi: 10.1023/A:1020532609792

Zuloaga-Aguilar S, Briones O, Orozco-Segovia A (2011) Seed germination of montane forest species in response to ash, smoke and heat shock in Mexico. Acta Oecologica 37: 256–262. doi: 10.1016/j.actao.2011.02.009

Appendix 1

Table A1: Location and climate information of the sampled *Ulmus pumila* populations. (doi: 10.3897/neobiota.15.4057.app1) File format: PDF.

Explanation note: Location and climate information of the sampled *Ulmus pumila* populations in China and the U.S. Maximum (max.) temperatures for the months May, June and July are provided to show the temperature range during the main germination period (lowest and highest values are italicized). Climatic information was extracted from the WORLDCLIM database (Hijmans et al. 2005).

Citation: Hirsch H, Wypior C, von Wehrden H, Wesche K, Renison D, Hensen I (2012) Germination performance of native and non-native *Ulmus pumila* populations. NeoBiota 15: 53–68. doi: 10.3897/neobiota.15.4057.app1

Appendix 2

Figure A1: Comparison of climatic conditions between the Chinese and North American locations of *Ulmus pumila*. (doi: 10.3897/neobiota.15.4057.app2) File format: PDF.

Explanation note: Comparison of climatic conditions (a: mean annual temperature; b: annual precipitation) between the Chinese and North American locations of *Ulmus pumila*. Wilcoxon rank sum tests were used to test for differences between both ranges. Mean annual temperatures are significantly higher for locations from the U.S. (W = 7, p < 0.05). Annual precipitation is marginal higher in the invasive populations compared to the native populations (W = 9, p = 0.05). Significant differences are symbolized by different lowercases above the boxes.

Citation: Hirsch H, Wypior C, von Wehrden H, Wesche K, Renison D, Hensen I (2012) Germination performance of native and non-native *Ulmus pumila* populations. NeoBiota 15: 53–68. doi: 10.3897/neobiota.15.4057.app2