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Germination responses of three grassland species differ between native and invasive origins

Abstract The germination stage is critical in plant life-history and is also a key process during the expansion of species' ranges into new environments. In this study we investigated the germination patterns of three plant species (*Achillea millefolium*, *Hieracium pilosella* and *Hypericum perforatum*) that are invasive to New Zealand (NZ) and native to Central Europe. We asked whether the species show differences in germination temperature requirements, germination speed and maximum germination rates, and thus, whether they display evidence of adaptation to different conditions in the invasive range. Seeds from three populations per species and region were subjected to three different temperature regimes to compare germination rates among origins and across temperature conditions. For *Achillea millefolium* and *Hypericum perforatum*, germination rates were significantly higher for invasive NZ provenances than for native German ones. Seeds from invasive populations of all three species displayed increased maximum germination at medium temperature conditions when compared to native populations, which indicates altered germination strategies in the invaded range. Changes in temporal development patterns were most conspicuous for invasive *Hieracium pilosella* and *Hypericum perforatum* populations. These findings imply that adaptation in germination patterns towards different climatic conditions in invasive populations has occurred. Our study emphasises the importance of the germination stage during plant invasion and its role in explaining range expansion of these species.

Keywords Biological invasion · Germination rates · Germination velocity · *Achillea millefolium* · *Hieracium pilosella* · *Hypericum perforatum*

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Introduction

Invasive plant species are widely recognised to be a serious threat to native species diversity and community structure (Meyerson and Mooney 2007; Pimentel 2009). In many parts of the world, large numbers of non-native species have been introduced during the last centuries, and a considerable number of them have succeeded to persist in the wild. New Zealand (NZ) alone, for example, has been exposed to more than 25,000 non-native plant species, of which more than 2,200 have been estimated to have successfully established populations in the wild (Williams and Cameron 2006). One of the most prominent tasks in invasion ecology research is to find an answer to the question why some species become invasive while others do not (Rejmánek et al. 2005). In recent years, attempts to detect general patterns focused on identifying common traits among invasive plant species (e.g., Pyšek and Richardson 2007; Küster et al. 2008, 2009; Pyšek et al. 2009). A common conclusion, if applicable at all, seems to be that there are no 'invasive traits' per se that explain plant species invasion (Hulme 2008; van Kleunen et al. 2010). Nevertheless, a general feature seems to be that plant traits associated with reproduction are of vital importance for successful plant invasions (Mandák 2003; Erfmeier and Bruelheide 2005; Mihulka et al. 2006; Abraham et al. 2008).

The ability of a species to germinate rapidly under a wide set of environmental conditions has been regarded as an important trait for invasive species since Baker (1974). For example, Perglová et al. (2009) showed that two invasive species of *Impatiens* germinated faster and had a higher total germination rate when compared to the native *I. noli-tangere*. Comparisons of native and invasive populations provided further evidence for shifts in reproductive traits during range expansion. Thereby, several studies found increased sexual or clonal reproduction in invasive populations (e.g. Noble 1989; Brown and Eckert 2005; Buschmann et al. 2005; Meyer and Hull-Sanders 2008; Beckmann et al. 2009).

Research focusing on shifts in germination patterns in invasive species may increase our knowledge of genetic differentiation between native and invasive populations as suggested by Bossdorf et al. (2005), in particular as germination characteristics are not only environmentally triggered, but also under genetic control (Huang et al. 2010). However, only a few studies have investigated seed germination patterns between native and invasive populations. As one example, Kudoh et al. (2007) found seed dormancy to be higher in invasive, Japanese populations of *Cardamine hirsuta* when compared to seeds from native European populations. The authors suggested that this change in germination patterns might help to explain the rapid invasion of *C. hirsuta* in Japan during the last decades because it enhances germination in autumn and enables longer transportation of dormant seeds. In their germination experiment, Erfmeier and Bruelheide (2005) found no differences in maximum germination rates or temperature optima between native and invasive origins of *Rhododendron ponticum*. They revealed, however, that invasive seeds germinated earlier than those of native provenances, thus contributing to rapid range expansion. In a series of common garden experiments, Hierro et al. (2009) recently demonstrated genetic differentiation between native and invasive populations of *Centaurea solstitialis*. The authors suggested that 'the degree of risk experienced at early developmental stages could exert an important control over the germination strategy of *C. solstitialis* populations. Thus, rapid adaptations in germination strategies might contribute to the success of other invaders. However, examples supporting this idea mostly refer to single species studies, and, so far, no across-species comparisons have been carried out for species that grow in similar habitats.

The present study addresses germination patterns of *Hieracium pilosella*, *Achillea millefolium* and *Hypericum perforatum* between native and invasive origins of the seeds. We compared seeds of populations from NZ, where the species have been introduced in the nineteenth century and from their native provenances in Germany. Although germination ecology of these species has been studied before (e.g. Oomes and Elberse 1976; Bishop et al. 1978; Campbell 1985), a direct comparison of the germination performance between native and invasive populations has not been the subject of research so far.

In this comparative experimental approach, we aimed to determine differences in (1) germination temperature requirements, (2) germination speed and (3) maximum germination rates of seeds from native populations in Germany and from invasive populations in NZ of *Hieracium pilosella*, *Achillea millefolium* and *Hypericum perforatum*. In particular, we hypothesised that germination speed and germination rates were higher in invasive populations. Our goal was to investigate whether shifts in germination characteristics during range expansion might help explain exotic species' invasion success.

Methods

Study species

Achillea millefolium (Common yarrow) is a rhizomatous *Asteraceae* species that is widespread in the northern hemisphere. It is a perennial herb that grows in dry grasslands, along waysides and in pastures (Rothmaler and Werner 2005). *A. millefolium* was introduced to NZ in the mid-nineteenth century. First records date back to 1867 (Webb et al. 1988). Currently, it can be found throughout the country, but it is more common in drier areas of the South Island where the species particularly grows in disturbed areas such as roadsides, lawns and pastures. *A. millefolium* seeds are not dormant and germinate under a large variety of soil, temperature and light conditions. The germination process is known to be relatively insensitive to drought (Oomes and Elberse 1976; Robocker 1977).

The facultative apomict *Hieracium pilosella* (Mouse-ear hawkweed; *Asteraceae*) is native to Europe and northern Asia where it frequently occurs in dry grasslands, heathlands, open pine forests and along waysides. It is a major invasive weed in NZ as it infests tussock grasslands and reduces species richness in local communities (Scott 1993). *Hieracium pilosella* was first recorded in NZ in 1878 (Webb et al. 1988). The species can be found throughout the entire South Island where it is particularly frequent in eastern, dryer areas of the Southern Alps. *Hieracium pilosella* seeds show no dormancy and germinate quickly under suitable conditions (Koltunow et al. 1998). However, seedling survival in natural populations is relatively low with about 1% (Bishop et al. 1978).

Hypericum perforatum (St. John's Wort) is an erect, herbaceous plant of the *Hypericaceae* family. It is native to Eurasia and Northern Africa where it grows in dry grasslands, heathlands and in dry to fresh ruderal sites (Rothmaler and Werner 2005). *H. perforatum* was introduced to NZ in 1869 (Webb et al. 1988) and is today distributed widely over both islands. *Hypericum perforatum* seeds have shown to germinate preferably under relatively warm conditions (Campbell 1985).

Germination experiment

We collected mature seeds in three populations of every species in each country, leading to seed samples from 18 populations (Table 1). Seeds were sampled in February/March (NZ) and July/August (Germany) 2006 across multiple individuals and pooled for each population. Seed material was kept dry at approximately 15°C until the beginning of the germination experiment, which took place in autumn 2006 at the Institute of Biology/Geobotany and Botanical Garden, Halle. Three different temperature conditions were applied in germination

Table 1 Locations of sampled populations in New Zealand and Germany

Range	Species	Latitude	Longitude	Location	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Temperature seasonality (standard deviation × 100)
GER	*Achillea millefolium*	51.28876°	11.26469°	Oberheldrungen	16.60	0.30	634.50
GER	*Achillea millefolium*	51.42243°	11.06866°	Kyffhäuser	16.60	0.30	636.50
GER	*Achillea millefolium*	51.28926°	10.53344°	Menteroda	15.50	0.20	631.10
NZ	*Achillea millefolium*	−43.28337°	171.53615°	Rakaia	5.80	12.80	376.30
NZ	*Achillea millefolium*	−44.20826°	170.07684°	Ohau-Pukaki-Canal	7.10	12.80	433.60
NZ	*Achillea millefolium*	−44.64558°	168.93137°	Treble Cone Skifield	7.00	14.60	432.30
GER	*Hieracium pilosella*	51.52677°	11.30211°	Grillenberg	16.20	0.70	633.30
GER	*Hieracium pilosella*	51.65257°	11.75753°	Rothenburg	17.10	1.50	644.00
GER	*Hieracium pilosella*	52.72566°	12.12735°	Rehberger Berge	17.20	1.30	653.30
NZ	*Hieracium pilosella*	−44.01337°	170.50053°	Lake Tekapo	6.20	12.10	437.80
NZ	*Hieracium pilosella*	−44.18848°	170.22020°	Lake Pukaki	6.90	12.70	433.30
NZ	*Hieracium pilosella*	−44.58540°	169.65372°	Lindis Pass	4.30	0.70	446.70
GER	*Hypericum perforatum*	51.53070°	11.89119°	Lunzberge	17.40	1.60	646.80
GER	*Hypericum perforatum*	51.65086°	11.75768°	Rothenburg	17.10	1.50	644.00
GER	*Hypericum perforatum*	51.27164°	11.22357°	Heldrungen	16.80	0.40	637.00
NZ	*Hypericum perforatum*	−44.66327°	170.36404°	Lake Aviemore Dam	15.00	4.40	417.00
NZ	*Hypericum perforatum*	−44.25984°	169.99175°	Lake Ohau Dam	7.10	12.80	433.50
NZ	*Hypericum perforatum*	−44.73373°	169.28222°	Tasman Valley	10.70	15.70	443.00

Seeds were collected at these sites during Summer 2006 in both countries. Latitude and longitude are presented as decimal degrees. Mean temperature of wettest quarter, mean temperature of driest quarter and temperature seasonality values are long-term means and were extrapolated from the climate model provided by Hijmans et al. (2005)
GER Germany, *NZ* New Zealand

cabinets with a night/day cycle of 4/8°C, 10/20°C and 20/32°C, and a photo- and thermoperiod of 12 h. From each population, 30 randomly chosen seeds were placed in petri dishes on filter paper. Three replicates of each population were exposed to each temperature regime resulting in a total of 162 dishes. The dishes were watered every week or more often where necessary. Germination was monitored regularly, and germinated seeds were removed from the dishes. After 40 days, germination tests were stopped. Cumulative germination rates were calculated and used for statistical analysis.

Statistical analysis

Since germination rates lacked normal distribution, we used rank transformed data for subsequent analyses (as recommended by Quinn and Keough 2002). All analyses were done with SAS 8.2 (SAS Institute, Cary, NC). Maximum germination rates were analysed separately for each species using a two-factorial nested ANOVA design. 'Temperature' and 'country' were introduced as fixed factors (3×2 levels) and with random factor 'populations' nested within 'country' into a generalised linear mixed model (SAS proc glm). Ryan-Einot-Gabriel-Welsh post-hoc tests were performed in order to indicate the direction of differences between categories of each factor.

The results of the germination experiment were analysed for temporal development patterns using a logistic regression model (SAS proc nlin) following Erfmeier and Bruelheide (2005). We calculated the times when 10, 50 and 90% of the maximum germination occurred for every species and population separately, and analysed these variables using the same nested ANOVA design as described above. All figures were generated using R 2.10 (The R Core Development Team 2009).

Results

All species displayed significantly different germination patterns at the different temperature levels applied, with low germination at cold temperatures and highly increased germination at warmer temperatures (Table 2). Maximum germination rates differed between the species, with *Achillea millefolium* and *Hypericum perforatum* reaching significantly higher germination rates with a median of 80% and 90%, respectively (Fig. 1 a, b, e, f), compared to *Hieracium pilosella* with a median germination rate of 7% (Fig. 1c, d).

Maximum germination of *Achillea millefolium* was significantly higher for invasive NZ populations than for native German populations as indicated by a significant country effect (Table 2; Fig. 1). Maximum germination was also higher at warm and medium temperatures when compared to cold temperature (Table 2). A significant

Table 2 ANOVA results for the analysis of maximum germination rates

Source of variation	Achillea millefolium					Hieracium pilosella					Hypericum perforatum				
	df	Type III SS	F	P	Post-hoc	df	Type III SS	F	P	Post-hoc	df	Type III SS	F	P	Post-hoc
Temperature	2	35018.69	74.66	**<0.001**	w, m > c	2	6408.12	10.71	**<0.001**	w, m > c	2	141687.79	293.56	**<0.001**	w, m > c
Country	1	6424.46	27.39	**<0.001**	NZ > DE	1	966.89	3.23	0.079	n.s.	1	1520.04	6.3	**0.016**	NZ > DE
Temp × country	2	5450.29	11.62	**<0.001**		2	348.45	0.58	0.563		2	852.69	1.77	0.183	
Population (temp × country)	4	3305.48	3.52	**0.014**		4	12445.18	10.4	**<0.001**		4	487.93	0.51	0.732	
Residual	53	60517.83				53	33329.47				53	155166.86			

Bold numbers indicate significant effects ($P < 0.05$). Analysis was performed separately for the three species. Bold numbers indicate significant country and temperature effects or interactions ($P < 0.05$). Results of the Ryan-Einot-Gabriel-Welsh post-hoc tests indicate the direction of significant differences between categories of each factor

SS sum of squares, *df* degrees of freedom, *NZ* New Zealand, *DE* Germany, *w* warm (20/32°C), *m* medium (10/20°C), *c* cold (4/8°C)
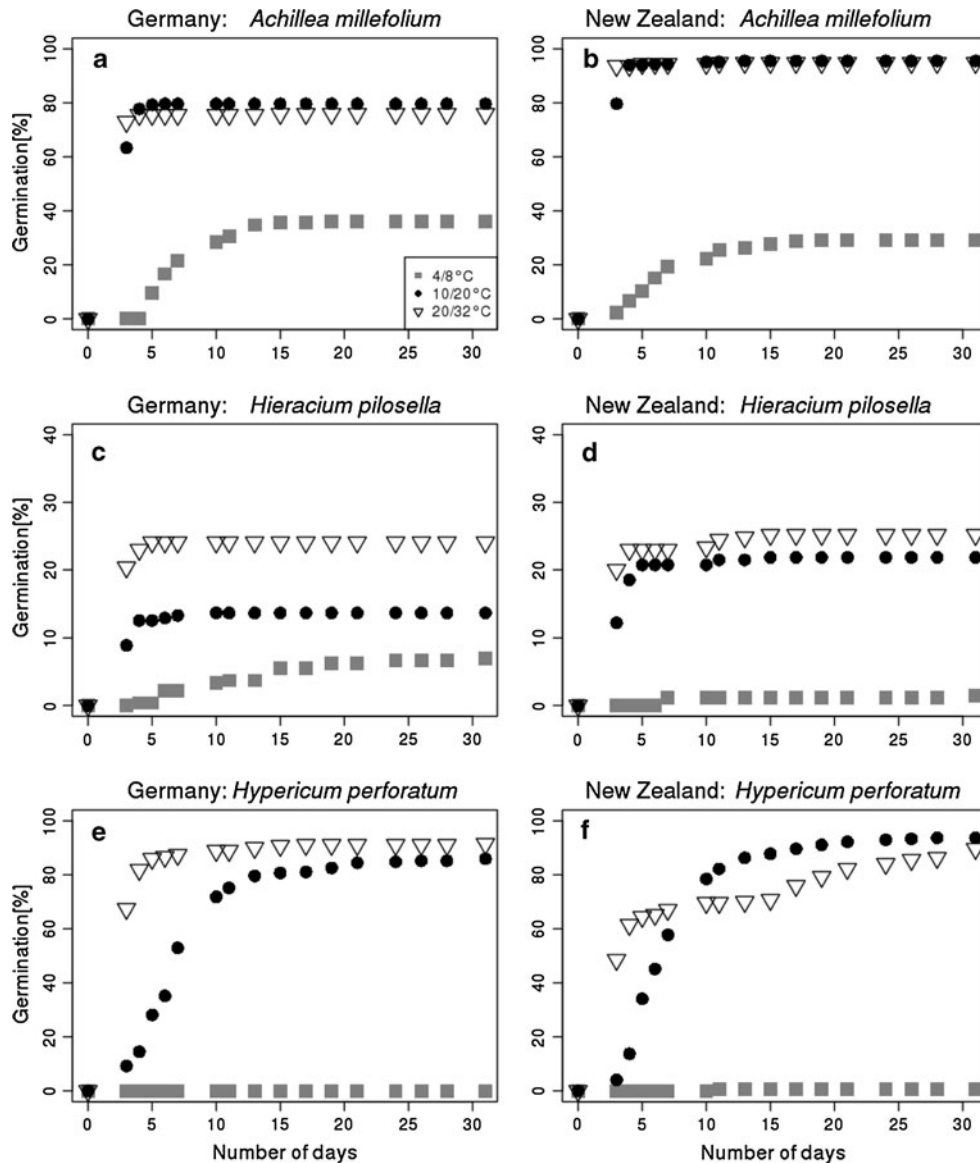
Fig. 1 Mean germination rates of *Achillea millefolium* (**a**, **b**), *Hieracium pilosella* (**c**, **d**) and *Hypericum perforatum* (**e**, **f**) seeds from Germany (*left*) and New Zealand (*right*) across three different temperature regimes with the time. For statistical details see Tables 2 and 3

interaction between temperature and country displayed that seeds from NZ germinated better in the warm and medium temperature environments than those from native German populations (Table 2; Fig. 1). Temporal development patterns of *Achillea millefolium* were affected by the temperature levels but displayed no effects of interaction with the country (Table 3).

Maximum germination rates of *Hieracium pilosella* were very similar under all three temperature regimes when compared between regions, yet differed significantly between temperatures (Table 2). NZ seeds reached 10% of maximum germination at the medium temperature earlier than German seeds, but showed no such differences between countries at cold and warm temperatures, which resulted in a significant coun-

try × temperature interaction effect (Table 3). For later stages of germination (i.e. 50 and 90% of maximum germination) no differences in germination speed were detected.

Maximum germination rates of *Hypericum perforatum* were found to be marginally significantly different between countries (Table 2). For native populations, the highest maximum germination was detected under warm conditions, whereas for invasive populations it was under medium temperature conditions (Fig. 1 e, f). Analysis of temporal development patterns revealed that NZ seeds reached 50 and 90% of maximum germination later than German seeds as indicated by a significant effect of country and significant country × temperature interactions (Table 3).

Table 3 ANOVA results for the time elapsed to 10, 50 and 90 percent of maximum germination

Source of variation	Achillea millefolium					Hieracium pilosella					Hypericum perforatum				
	df	Type III SS	F	P	Post-hoc	df	Type III SS	F	P	Post-hoc	df	Type III SS	F	P	Post-hoc
10.00%															
Temperature	2	32255.79	44.78	**<0.001**	w > m > c	2	22441.07	28.27	**<0.001**	w > m > c	2	24232.11	29	**<0.001**	w > m
Country	1	462.22	1.28	0.264	n.s.	1	293.6	0.74	0.376	n.s.	1	821.78	0.98	0.330	n.s.
Temp × country	2	309.46	0.43	0.654		2	3202.79	4.03	**0.030**		2	841	1.01	0.324	
Population (temp × country)	4	1112.45	0.77	0.549		3	5511.98	4.63	**0.010**		4	4504.22	1.35	0.277	
Residual	52	49654.30				34	52951.47				35	53794.00			
50.00%															
Temperature	2	52949.68	131.96	**<0.001**	w > m > c	2	20571.85	19.27	**<0.001**	w > m > c	2	15047.11	51.11	**<0.001**	w > m
Country	1	205.55	1.02	0.317	n.s.	1	305.41	0.57	0.456	n.s.	1	1067.11	3.62	0.067	n.s.
Temp × country	2	589.51	1.47	0.241		2	604.45	0.57	0.575		2	1272.11	4.32	**0.047**	
Population (temp × country)	4	1306.76	1.63	0.1845		3	1930.19	1.21	0.327		4	7399.44	6.28	**0.001**	
Residual	52	63749.25				34	54237.67				35	33028.56			
90.00%															
Temperature	2	58464.42	244.06	**<0.001**	w > m > c	2	14191.43	19.13	**<0.001**	w > m > c	2	5801.36	31.81	**<0.001**	w > m
Country	1	21.67	0.18	0.673	n.s.	1	138.45	0.37	0.547	n.s.	1	1013.36	5.56	**0.026**	n.s.
Temp × country	2	80.8	0.34	0.716		2	398.17	0.54	0.591		2	812.25	4.45	**0.044**	
Population (temp × country)	4	494.54	1.03	0.402		3	6266.38	5.63	**0.004**		4	687.44	9.33	**<0.001**	
Residual	52	64163.19				34	50876.79				35	19540.31			

Analysis was performed separately for the three species. Bold numbers indicate significant effects or interactions ($P < 0.05$). Results of the Ryan-Einot-Gabriel-Welsh post-hoc tests indicate the direction of significant differences between categories of each factor

SS sum of squares, *df* degrees of freedom, *NZ* New Zealand, *DE* Germany, *w* warm (20/32°C), *m* medium (10/20°C), *c* cold (4/8°C)

Discussion

With this study we found evidence for differences in seed germination temperature requirements between German and NZ populations for *Achillea millefolium* and *Hypericum perforatum*, confirming our general hypothesis for these species. For the third study species, *Hieracium pilosella*, a similar, yet not statistically significant trend could be observed (Table 3). Differences in germination in invasive populations were also found by Kudoh et al. (2007), who described suppressed germination at higher temperatures for invasive, Japanese populations of *Cardamine hirsuta* compared to native European populations. The authors linked these differences in seed dormancy to an adaptation to climatic conditions in Japan. In another recent common garden experiment, Hierro et al. (2009) found that germination patterns of *Centaurea solstitialis* varied between two climatically different regions of introduction. They explained these results with the degree of risk *C. solstitialis* experiences at early developmental stages and suggested that rapid adaptations in germination strategies contribute to the success of invasive species.

Differences in germination temperature requirements, as we detected in the present study, might be interpreted as an adaptation to climatic conditions in both regions and to the potential risk the seedlings have to take under these conditions. Compared to native German populations, seeds from invasive NZ populations benefited from medium temperature conditions (10/20°C), which corresponds well with the mean temperature of the wettest quarter of the year in NZ when germination can be expected to occur (Table 1). This would, consequently, result in greater establishment rates in invasive populations at such temperatures. While the assumption of genotypic differentiation between native and invasive populations is justified according to this finding, it cannot be validated with the data at hand. A thorough test of this assumption would require reciprocal field trials with more than one generation. Nevertheless, a genetic shift in invasive populations has been demonstrated previously (e.g. Willis et al. 1999; Siemann and Rogers 2003). Other studies have proven genetic differences in invasive plant species with respect to different climatic patterns, such as oceanic or continental conditions or altitudinal (e.g. Alexander et al. 2009) and latitudinal clines (e.g. Maron et al. 2007). Regional genetic variation has been addressed within non-native regions (Meyer and Allen 1999; Erfmeier et al. 2010; see Bossdorf et al. 2005 for review) as well as between native and non-native regions (Maron et al. 2007; Leger and Rice 2007). In the case of our study, the question as to whether the differences between regions reflect genetic differences, effects of the parental environment or maternal effects (or combinations of these factors) cannot be resolved and needs to be addressed in future studies. Furthermore, it cannot be excluded that the observed differences result from stochastic events (see Keller and Taylor 2008) as only three populations per species and country were incorporated in our study. A greater number of populations sampled within a wider climatic range would be advisable in order to overcome these shortcomings.

Temporal development of germination has rarely been addressed in previous studies on invasive plant species. It has been proven, however, to be significantly different between native and invasive regions at least in one case. Erfmeier and Bruelheide (2005) showed that invasive populations of *Rhododendron ponticum* germinated earlier and faster than native ones. In the present study, germination speed did also differ between regions for *Hieracium pilosella* and *Hypericum perforatum*. The slightly increased germination speed of NZ seeds of *Hieracium pilosella* was only relevant in the beginning at medium temperature, but might contribute to a 'head start' in establishment for this species under beneficial temperatures. Nevertheless, the investigation of temporal development patterns may provide contrasting results for other species and at different temperatures. Thus, both effects of temporal dynamics in germination and of environmental variation should be taken into account in future studies.

In general, invasion success has been ascribed to high germination rates (Radford and Cousens 2000; McAlpine et al. 2008). Accordingly, high germination rates do apply for *Achillea millefolium* and *Hypericum perforatum*. In contrast, for clonal growing species it has been suggested that they do not have to rely exclusively on the production of seeds in order to successfully invade new areas (Olesen et al. 2004). Nevertheless, in a related field study, we found that *Hieracium pilosella* benefits more from increased sexual reproduction in its invaded range, even though its overall germination rates are comparatively low (Beckmann et al. 2009). That germination is under genetic control has recently been demonstrated by Huang et al. (2010) who showed that germination phenology of *Arabidopsis thaliana* is linked to particular regions on chromosomes by performing a quantitative trait-loci analysis. Additionally, maternal effects and the parental environment are known to influence seed germination patterns (Galloway 2001; Donohue et al. 2005). For minimising these effects, F1 or later generation seeds from plants grown under identical conditions would be necessary (Baskin and Baskin 2001).

Despite our knowledge on seed germination being an important stage in plant life-history, comparative studies between native and invasive populations remain the exception. Future studies should enable more precise conclusions about the importance of shifts in germination patterns in the invasion success of invasive plant species. As already suggested by Hierro et al. (2009), we, therefore, recommend testing for differences in germination patterns, particularly in invasive species that have expanded into different regions with contrasting environmental conditions.

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