

Invasive and native *Rhododendron ponticum* populations: is there evidence for genotypic differences in germination and growth?

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Previous studies have shown that the invasive spread of *Rhododendron ponticum* in the British Isles is influenced by the more favourable environmental conditions in the new territory than in the species' home range. In this study, we asked whether the species' invasion success might also involve a genotypic background for higher growth and germination rates in invasive populations. We tested the hypotheses that invasive populations have higher absolute germination rates, germinate faster and exhibit higher growth rates. We present data from greenhouse and climate chamber experiments with seed material and *Rhododendron* cuttings from six populations each of native Georgian, native Spanish and invasive Irish populations subjected to different temperature environments.

There were no differences in the maximum germination rate and optimum germination temperature between native and invasive origins. We found significant differences in germination velocity with the Irish seeds responding most rapidly to all germination treatments. Accordingly, in the growth experiment the invasive Irish origins had the highest relative growth rates in all environments tested.

Our results provide evidence for a genetic shift in invasive populations towards an increased investment in growth and towards a faster germination rate. Both traits would contribute to explaining this species' range expansion. The underlying evolutionary mechanisms for this shift are discussed, including the possibility of hybridisation or of an ecological release from hitherto experienced constraints in the native area.

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Many studies on the invasion biology of plant species have emphasised the promoting impact of favourable traits for a species' successful spatial expansion (Baker and Stebbins 1965, Baker 1974, Mack 1996, Williamson and Fitter 1996). In particular, characteristics associated with reproduction and rapid growth have been the focus of numerous studies (Rejmánek and Richardson 1996, Willis et al. 1999, Bastlová and Kvet 2002, Jakobs et al. 2004). In a recent review, Kolar and Lodge (2001) found that, primarily, high reproduction rates, vegetative

reproduction, early maturation, a short juvenile period and seed mass are positively linked to invasiveness.

In particular, many studies succeeded to attribute plant invasions to effective reproduction (Burke and Grime 1996, Radford and Cousens 2000, Grigulis et al. 2001). For example, in a study of 24 frequently cultivated pine species, Rejmánek and Richardson (1996) demonstrated that early and consistent reproduction and rapid population growth are positively correlated with successful invasions. For weedy species, Brändle et al. (2003)

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found a general relationship between the germination niche breadth and distributional range size. Apart from the absolute level of germination rates, a population's ability of rapid germination – as soon as the environment offers suitable conditions for germination – can also be favourable (Grime et al. 1981). In addition to between-species differences in germination patterns, differences in germination traits at the within-species level also exist. Without doubt, germination patterns are influenced by a multitude of interactions among seed characteristics and environmental variables. In this context, the genetic nature of seeds has to be considered. In their study on the genetic effects of germination timing and environment in the desert mustard *Lesquerella fendleri*, Cabin et al. (1997) provided evidence showing that the genetic constitution of seeds plays a significant role in regulating the timing and the success of germination. The authors found that allele frequencies varied significantly with both germination timing and environmental treatment. However, the adaptive value of differences in germination timing remains unclear in their study.

For many invasive plant species, rapid growth has similarly been shown to be of relevance by experimental approaches (Pattison et al. 1998). Grotkoop et al. (2002) found relative growth rates of pine species to be positively correlated with a calculated measure of invasiveness. In a 14-yr. common garden experiment, Siemann and Rogers (2001) were able to demonstrate a genetic basis for a more vigorous growth of invasive *Sapium sebiferum* genotypes than of native provenances from Asia.

Although there is no question that characteristics differ among genotypes, the study of the underlying mechanisms explaining how these genotypes evolved has resulted in two controversially discussed concepts (Parker et al. 2003): invasiveness as innate superiority due to previous evolution in competitive environments (Callaway and Aschehough 2000), or as adaptation resulting in the evolution of post-invasion genetic differences (Mack et al. 2000, Leger and Rice 2003), possibly as a consequence of the escape from enemies as posited by the EICA hypothesis (Blossey and Nötzold 1995, Maron and Vilà 2001, Keane and Crawley 2002). Leger and Rice (2003) pointed out that the distinction between environmentally induced phenotypic differences and a genetic change can be revealed by common garden experiments including both native and invasive individuals grown together in the same environment. Comparing size and fecundity of 20 native and invasive Californian poppies (*Eschscholzia californica*) populations, they found indications for a genetic shift in traits towards rapid growth and reproduction in different environments, and thus for an evolutionary context of loss of traits.

It is the intention of this study to assess the genotypic contribution to the invasiveness of *Rhododendron ponticum*. *Rhododendron ponticum* is an evergreen shrub of the Ericaceae family that is successfully spreading throughout Atlantic western Europe and today regarded as a common threat to natural ecosystems, especially in the British Isles (Cross 1981, Crawley 1987). Despite a clear evidence for a benign environment favouring the spread of *Rhododendron ponticum* (Erfmeier and Bruelheide unpubl.), there is reason to believe that specific genetic traits of germination and growth rates are involved in explaining the species' success in the British Isles. In a comparative field study of invasive Irish and native Spanish and Georgian populations, Erfmeier and Bruelheide (2004) found that germination and vegetative growth differed among the countries. With a median of 1.4 and 2.6 seedlings m² for the years 2000 and 2001, seedling establishment in both years was more successful in the new territory than in the native ones, where the median indicated no seedling occurrence in the field.

With the present study, we thus intend to provide evidence corroborating the theory that existing differences in germination pattern and growth rates between native and invasive *Rhododendron* populations in the field have a genetic background. By means of germination and growth experiments with *Rhododendron ponticum* seeds and cuttings exposed to different temperature treatments, we test the following hypotheses: 1) The invasive *Rhododendron* populations have higher absolute germination rates, thus explaining the observed pattern of more seedlings per unit area in Ireland. 2) In accordance with the assumption of rapid responses, we expected that seeds from the invasive populations would germinate faster. Analogously, 3) it is assumed that growth rates of the invasive *Rhododendron* reach higher values than plants from the native origins.

Material and methods

Study species

Rhododendron ponticum is an erect, evergreen Ericaceae shrub that reaches a height of 2–8 m (Tutin et al. 1972). In accordance with the species' disjunctive distribution (along the Black Sea coast, in Lebanon and on the Iberian Peninsula), two subspecies are currently recognised: plants in Turkey and in Georgia in the Caucasus area are typically attributed to the ssp. *ponticum*; whereas occurrences from southern Spain and Portugal are taxonomically assigned to ssp. *baeticum* (Tutin et al. 1972, Clapham et al. 1987, Castroviejo et al. 1993). In the Caucasus region, *R. ponticum* ssp. *ponticum* populations are associated with deciduous summergreen mixed and beech forest communities ranging from lowlands up to the timberline at 1900 m a.s.l.; whilst the Iberian occurrences are a component of Mediterranean scler-

ophyllous forests and can be found primarily along creeks, or as a scrubland element of humid mountain ranges (Mejías et al. 2002). Their altitudinal distribution ranges from 400 to 1200 m a.s.l.

The introduction of this species to the British Isles was reported for the year 1763 (Elton 1958). Since that time, the species has been repeatedly introduced to Great Britain and Ireland, where it has already invaded a large variety of natural communities, such as forests, heathlands and bogs, involving a huge economic impact due to costs of control and eradication (Dehnen-Schmutz et al. 2004).

Clonal spreading of *Rhododendron ponticum* is reported to be a successful mechanism of propagation (Mejías et al. 2002), but it appears to be of minor importance for local spreading in the British Isles (Cross 1975, Shaw 1984). In their new territory, in particular, sexual reproduction by means of numerous small wind-dispersed seeds is extremely effective (Erfmeier and Bruelheide 2004). Seed size differs according to taxonomical and geographical assignment: with 2 mm for plants of the ssp. *ponticum* (Davis 1978), 0.4–0.8 mm for Iberian seeds of the ssp. *baeticum* (Castroviejo et al. 1993), and with an intermediate length in British seed material (1.5 mm; Cross 1975). Germination in the new area occurs on many substrates, and light is essential for the germination of *Rhododendron ponticum* seeds (Cross 1975). Mature seeds, in general, do not need any further pre-treatment and will germinate immediately when exposed to appropriate environmental conditions. *Rhododendron ponticum* is classified as having a transient seed bank, i.e. its seeds persist in the soil for less than one year (Thompson et al. 1997). Optimum germination temperatures of closely related *Rhododendron* taxa are specified to be relatively high (e.g. 23°C for *R. ferrugineum* and 26/21°C for *R. maximum*; Baskin and Baskin 1998). Moreover, these species are described as non-dormant and thus do not require any cold stratification (Baskin and Baskin 1998).

Experimental material and sampling design

For both experiments we used plant material that was obtained from six native populations each in Georgia and in Spain, and from six invasive populations in Ireland. Populations were selected randomly across an area exhibiting maximum altitudinal and geographical habitat variability in each country. To ensure comparability between the countries, we chose only forest populations with a northern aspect and a slope of 10°–20°. For further details concerning selection modus, location and characteristics of the populations see Erfmeier and Bruelheide (2004).

Germination experiment

For each population of *Rhododendron ponticum*, freshly matured seeds of the three origins were collected in November 1999 in Georgia, in January 2000 in Spain and in February 2000 in Ireland by harvesting entire, naturally pollinated racemes from at least each 20 individuals per population. Seeds from all these plants were thoroughly mixed within a population's samples to minimise the effects of single individuals, and then stored in a dark, dry repository at 10°C for six months until use. In all germination experiments, pooled seeds of each population were divided into two size-dependent fractions to sort out the smaller ones. Only large size seeds were chosen at random for the experiments.

Germination tests for each population were carried out in petri dishes with 20 seeds from each of the 18 populations. Seeds were placed on filter paper discs having a diameter of 90 mm (Schleicher & Schüll) covering a layer of 80 ml of sterilised sand, which served as a water reservoir. All dishes were watered every second day with de-ionised water and sprayed with 50% ethanol solution once a week to avoid infection by mildew. The seeds were subjected to four different temperature treatments. Each population was replicated five times at each temperature level, and the dishes were arranged randomly in climate chambers. The dishes were placed in a controlled environment cabinet with a daily alternating temperature regime of 2/12°C, 9/19°C, 16/26°C and 23/33°C and a thermo- and photoperiod of 12 h. The temperatures were chosen to simulate mean daily maximum and minimum temperatures near the soil surface during the growing season both in the native and in the invaded areas. Referring to temperature data collected during the growing season 2000, we measured as a mean over six populations maximum temperatures of 34.8, 34.0 and 25.3°C in Georgia, Spain and Ireland, respectively. Mean minimum temperatures were highest in Spain (9.0°C), intermediate in Ireland (6.3°C) and coldest in Georgia (3.2°C). The environment cabinets were equipped with white light providing 40 $\mu\text{E m}^{-2} \text{s}^{-1}$ at seed level. Seeds were considered to have germinated when the first radicle emerged. The minimum duration of the test was 107 d, and the weekly census continued until no further germination was recorded for two weeks. Germination was monitored for a total of 24 weeks.

Growth experiment

In the autumn/winter of 1999/2000, cuttings of *Rhododendron* branches were collected randomly – and in parallel to the seed material – from different individuals in each of the six populations per country. Harvesting of 150 samples per population was performed by cutting branches with a length of 40 cm and at least three internode sections, which show the increase of the three

previous years and with evidence of lignification at the cut surfaces. All cuttings were brought into the greenhouse in Goettingen, Germany, where they were planted onto breeding boards into a 70:30% sand-peat substrate to re-grow roots.

In February 2001, these individuals were planted into 1.5 l pots and the best-developed individuals, i.e. those that had successfully developed roots, were chosen for the growth experiment. The plants were placed into controlled greenhouse cabinets subjected to a daily alternating temperature regime of either 7/13, 13/18 and 18/23°C and a thermo- and photoperiod of 8/16 (night/day) hours. The three temperature regimes were chosen to approximate the monthly mean temperatures during the growing season both in the native and the invaded areas (Erfmeier and Bruelheide unpubl.). Light intensity was adjusted to 200 $\mu\text{E m}^{-2} \text{s}^{-1}$ at plant level in all cabinets by artificial illumination. In addition, all plants received external light, which changed in the course of the experiment according to the ambient seasonal lengths of daylight periods. Cabinet humidity was set at constant 80% relative humidity. All pots were watered every second day and fertilised fortnightly during the growth period with a 0.05% NPK fertiliser.

Since rooting success was different depending on the plants' origins (with survivorship ratios of 38.3, 51.4 and 10.6% for Georgian, Spanish and Irish cuttings, respectively), the assignment of replicates to the temperature treatments was unequal across the three origins each yielding $n=6$ populations for the plants of Georgian and the Spanish origins, and $n=2$ for those of Irish origin.

The experiment was begun in April 2001 and monitored until September 2002. Measurements of growth parameters (increase in total shoot length and number of leaves), growth strategy traits (number of branches and internodes), as well as leaf morphology parameters (size and shape of leaves) were made in June, July, August and September 2001 and again in March, May, July and September 2002. For parameters of increase, we calculated both absolute (AGR) and relative (RGR) growth rates. Shape of leaves was defined as length from leaf base to greatest width divided by total leaf length.

Statistical analysis

Since most of the germination and growth parameters failed normal distribution (SAS, proc univariate, Shapiro-Wilk statistics; Anon. 2000), data required transformation prior to analysis. We used non-parametric statistics by transforming data into ranks (SAS, proc rank, Anon. 2000; for appropriateness of rank transformation see Brunner and Puri 2001). Analyses were performed by applying a two-factorial nested ANOVA design with the fixed factors "country" and "tempera-

ture" (temp). Populations were nested within countries (pop(country)) and treated as random (SAS, proc glm; Anon. 2000). Post-hoc tests were realised with Ryan-Einot-Gabriel-Welsh (REGWQ) multiple range tests.

To include the temporal development of germination patterns in the analyses, we fitted the data to a model using regression procedures. To compare time (days) elapsed to 10, 50 and 90% of maximum germination, the germination rates were related to the maximum percentage of seeds that germinated in a given population \times temperature combination for each dish. In consequence, the data exhibited values between 0 and 1 for each dish. The data were then fitted to a logistic regression model (SAS, proc nlin, Anon. 2000):

$$\text{RG} = \frac{e^{(a+b*t)}}{1 + e^{(a+b*t)}}$$

RG = Relative germination, i.e. absolute germination related to maximum germination; a, b = estimated constants; t = time [days].

Time (days) elapsed to 10, 50 and 90% of germination was calculated for each dish and subjected to a two-factorial nested ANOVA as described above. Illustration of modelled data for the Georgian origin at the lowest temperature level was rejected because >75% of the Georgian dishes still had not germinated at the end of the experiment. Nevertheless, non-parametric statistical analyses were realisable for Georgian samples by assigning the dishes with no germination to the respective highest ranks.

For analyses of growth parameters, the pre-experimental plant size was included as a covariate in the statistical models to correct for plant size differences. The covariate was only kept in the model if it demonstrated a significant covariate effect; otherwise, the model was implemented without including the covariate.

Results

Germination responses

After 14 weeks of treatment exposure, germination of *Rhododendron ponticum* seeds was strongly affected by temperature (main effect) (Table 1). With a median cumulative germination rate of 76.5, 70.0 and 76.0% for Georgian, Spanish and Irish populations, respectively, the rates were consistently highest at the temperature level of 16/26°C (Fig. 1). The magnitude of germination was high at a broad range of temperatures, but all temperature levels differed significantly from each other with lowest germination responses at the coldest level of 2/12°C.

Although germination rates of the invasive populations were consistently among the highest, we found no main effect difference between native and invasive

Table 1. Analysis of variance for germination rates of *Rhododendron ponticum* seeds after 14 weeks of temperature treatment. Data were transformed into ranks. ANOVA was performed with populations as random factor nested within country at five replicates per population (n = 360).

Source of variation	DF	Sum of squares	Mean squares	F	p
Temp	3	2293558	764519	258.64	<0.0001
Temp × country	6	73750	12292	4.16	0.0005
Pop (country)	15	425163	28344	9.59	<0.0001
Error	333	984312			
Country	2	91322	45661	1.61	0.2324
Error (pop(country))	15	425163			

origins in their response towards temperature treatment. Correspondingly, there was no significant difference among the origins in the demands on temperature for optimum germination. The median optimum temperature was 25.2, 24.3 and 24.9°C for the Georgian, the Spanish and the Irish origins, respectively ($F_{2,15} = 0.57$, $p = 0.5762$). There was a large variation among populations within country indicated by significant effects of populations nested within countries. This applies particularly for the Georgian origins with a large within-country variability.

In addition, we detected significant origin interactions with temperature (Table 1). The native Georgian origins responded more sensitively with higher germination losses at the highest temperature level (Fig. 1).

Analysis of variance revealed significant differences in germination speed (Fig. 2). Velocity of germination responses differed across the temperature levels (main effect) with fastest germination progression at 16/26°C and slowest response at the coldest temperatures. For the elapsed time to 10, 50 and 90% of maximum germination, we found significant differences among the origins (Table 2). The invasive populations required significantly less days to reach the 10 and 50% levels of germination than the native provenances. For the higher level of 90% of maximum germination, the native Spanish genotypes

managed to compensate for the Irish head start, but the difference to the slower Georgian origins still remained existent. For all investigated levels, we detected significant temperature-country interactions, i.e. the origins behaved differently depending on the temperature. This is primarily due to a clearly retarded germination of the native Georgian genotypes compared to the invasive Irish ones at the highest and lowest temperatures (Fig. 2D).

Growth responses

There were significant temperature effects with the highest growth responses at the highest temperature for most of the parameters (Table 3, Fig. 3). We additionally found significant differences for the main effect country: the absolute growth rates of both increase in shoot length and in number of leaves were significantly higher for the Spanish and Irish genotypes than for the Georgian ones (Fig. 3A, B). For relative growth rates of the shoot length, the response of the invasive Irish genotypes differed significantly from both the native Spanish and Georgian genotypes (Table 3). For RGR, we found a significant effect of the covariate, i.e. the pre-experimental plant size affected RGRs of the plants.

We detected significant interactions between the main factors temperature and country for the tested parameters AGR of shoot length, and both AGR and RGR of number of leaves. This pattern is primarily due to the strong response of the native Spanish genotypes and the weak response of the Georgian genotypes at the warmest temperature treatment; whereas the magnitude of the invasive Irish responses was consistently high at all temperature levels.

Traits of growth strategies were thus affected by temperature (Table 3): both number of branches and number of internodes increased with increasing temperature. For both parameters, the genotypes differed significantly with highest numbers of branches and internodes within the Spanish origins; whereas the Irish genotypes responded with a lower number (Fig. 4). Interactions between temperature and country were only detected for the branching behaviour, with a stronger

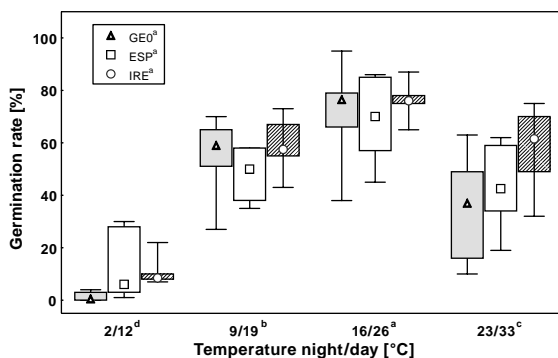


Fig. 1. Germination rates of *Rhododendron ponticum* seeds across four temperature regimes (n = 360). Medians, quartiles, minimum and maximum refer to population means (n = 5). Different letters indicate significant differences according to the REGWQ-test. $P < 0.0001$. For statistical details referring to rank transformed data see Table 1.

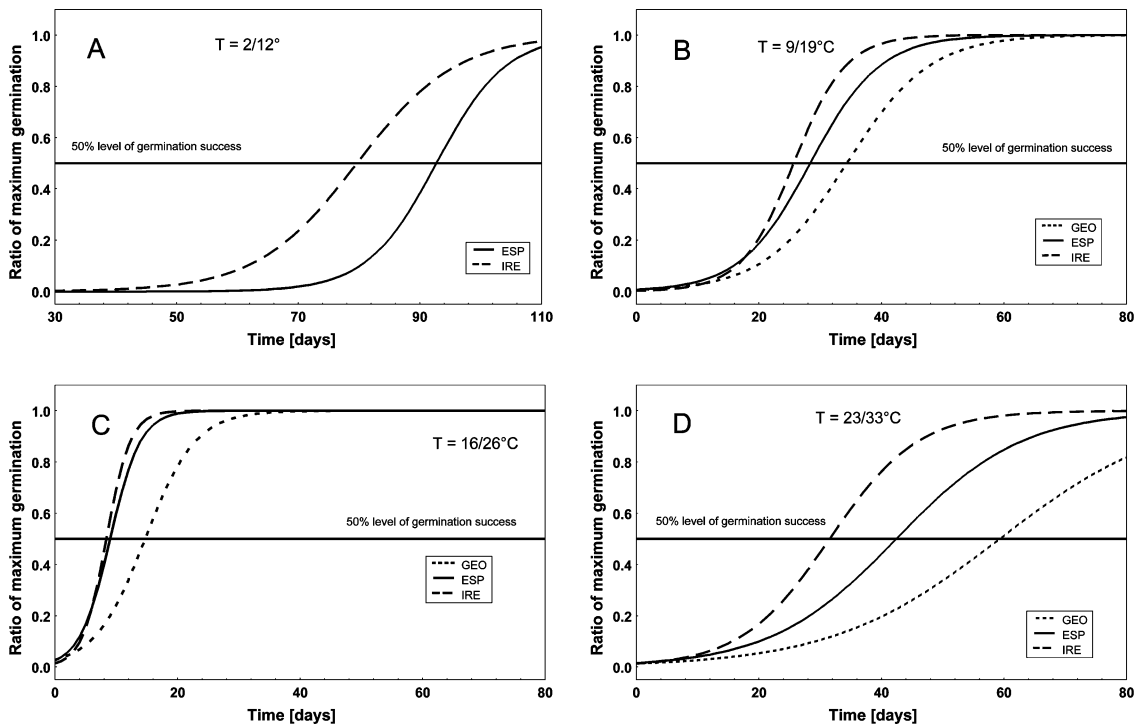


Fig. 2. Germination progress of *Rhododendron ponticum* seeds across four temperature regimes (each $n=90$): A) 2/12°C, B) 9/19°C, C) 16/26°C, D) 23/33°C. Germination development modelled by logistic regression (for details see Material and methods). $P < 0.0001$. For statistical details referring to rank transformed data see Table 2. GEO = Georgia, ESP = Spain, IRE = Ireland.

ramification of the Spanish genotypes at high temperatures.

For most of the leaf morphology parameters, we found no significant treatment effect. Length-width ratio and shape of leaves were the only traits that were affected by temperature and origin. Shape of leaves was sig-

nificantly larger at low temperatures and significantly larger for Georgian leaves (temp $F_{2,240}=4.04$, $p=0.0187$; country $F_{2,21.4}=8.47$, $p=0.002$). With decreasing temperatures the length of the leaves was larger in relation to the leaves' width, and the leaves of invasive genotypes had a higher length-width ratio than native

Table 2. Analysis of variance for the elapsed time to 10, 50 and 90% of final germination of *Rhododendron ponticum*. Data were transformed into ranks. ANOVA was performed with populations as random factor nested within country and five replicates each ($n=360$). G = Georgia, E = Spain, I = Ireland. Different letters indicate significant differences for the origin effects (country) according to the REGWQ-test.

Parameter	Source of variation	DF	Sum of squares	Mean squares	F	p	G	E	I
10% germination	Temp	3	3170009	1056670	790.82	<0.0001			
	Temp × country	6	83394	13899	10.4	<0.0001			
	Pop (country)	15	35489	2366	1.77	0.0375			
	Error	333	444947	1336					
	Country	2	142932	71466	30.21	<0.0001	a	b	c
	Error (pop(country))	15	35489	2366					
50% germination	Temp	3	3322183	1107394	1231.7	<0.0001			
	Temp × country	6	31271	5212	5.8	<0.0001			
	Pop (country)	15	68189	4546	5.06	<0.0001			
	Error	333	299393	899					
	Country	2	155736	77868	17.13	0.0001	a	b	c
	Error (pop(country))	15	68189	4546					
90% germination	Temp	3	3209986	1069995	870.69	<0.0001			
	Temp × country	6	18209	3035	2.47	0.0238			
	Pop (country)	15	88361	5891	4.79	<0.0001			
	Error	333	409224	1229					
	Country	2	150992	75496	12.82	0.0006	a	b	b
	Error (pop(country))	15	88361	5891					

Table 3. Analysis of variance for effects of temperature and origin on growth parameters of *Rhododendron ponticum*. The covariate (pre-treatment size of individuals) was only considered in the model if significant. Data were transformed into ranks. ANOVA was performed with populations seen as a random factor nested within country. G = Georgia, E = Spain, I = Ireland. Different letters indicate significant differences for the origin effects (country) according to the REGWQ-test.

Source of variation	Increase in shoot length AGR						Increase in no. of leaves AGR						No. of branches					
	DF	F	p	G	E	I	DF	F	p	G	E	I	DF	F	p	G	E	I
Temp	2	10.6	<0.0001				2	8.0	0.0004				2	3.7	0.0272			
Temp × country	4	4.3	0.0022				4	4.7	0.0011				4	3.9	0.0042			
Pop(country)	11	0.9	0.5871				11	2.3	0.0116				11	1.2	0.2643			
Error	254						254						254					
Country	2	98.8	<0.0001	b	a	a	2	53.4	<0.0001	b	a	a	2	12.2	0.0004	b	a	ab
Error (pop(country))	22.9						15.0						18.8					

Source of variation	Increase in shoot length RGR						Increase in no. of leaves RGR						No. of internodes					
	DF	F	p	G	E	I	DF	F	p	G	E	I	DF	F	p	G	E	I
Temp	2	5.6	0.0044				2	2.7	0.0684				2	7.3	0.0008			
Temp × country	4	2.1	0.0792				4	2.7	0.0332				4	0.1	0.9804			
Covar	1	27.7	<0.0001				1	19.8	<0.0001				1	4.0	0.0475			
Pop(country)	11	1.0	0.4131				11	1.6	0.1104				11	1.7	0.0813			
Error	253						252						252					
Country	2	48.2	<0.0001	c	b	a	2	7.9	0.0032	b	b	a	2	8.1	0.0028	a	a	a
Error (pop(country))	23.6						18.9						19.1					

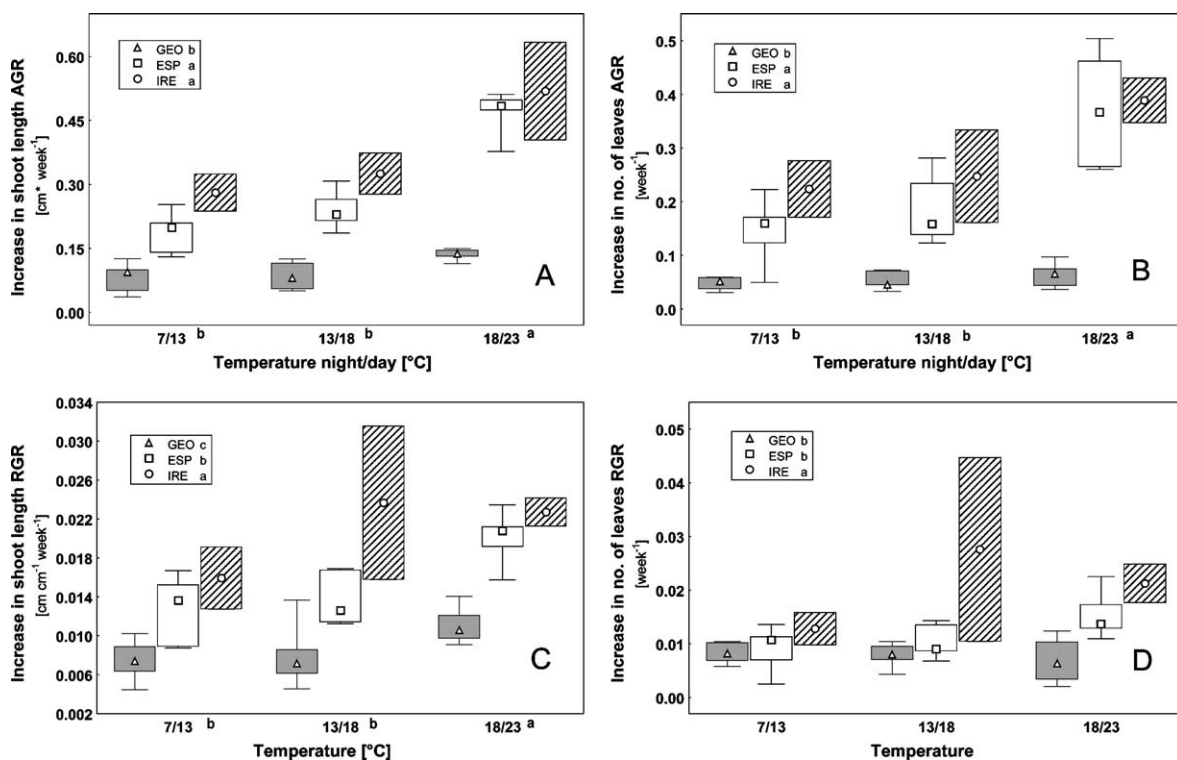


Fig. 3. Growth rates of *Rhododendron ponticum* across four temperature regimes: A) increase in shoot length – absolute growth rates (AGR), B) increase in no. of leaves – absolute growth rates (AGR), C) increase in shoot length – relative growth rates (RGR), D) increase in no. of leaves – relative growth rates (RGR). Medians, quartiles, minimum and maximum refer to population means ($n=6$ for Georgia and Spain, $n=2$ for Ireland). Different letters indicate significant differences according to the REGWQ-test. For statistical details referring to rank transformed data see Table 3.

Georgian genotypes (temp $F_{2,240}=9.86$, $p<0.0001$; country $F_{2,15,0}=3.94$, $p=0.0423$). For both leaf parameters, the covariate exerted no significant effect.

growth as a consistent pattern independent of the environments tested.

Discussion

The most striking result of this study was that the invasive *Rhododendron ponticum* populations were characterised by the ability of an immediate germination and

Germination

Although the germinability of invasive *R. ponticum*, in general, is high, it does not contribute to explaining the invasion success of Irish populations in contrast to the native ones. In many plant species, high germination rates have been identified to be associated with the

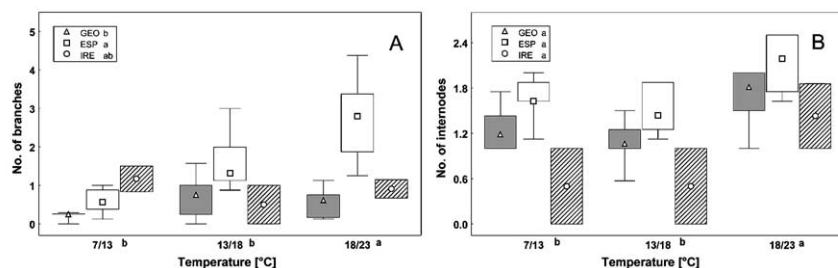


Fig. 4. A) Number of branches and B) number of internodes of *Rhododendron ponticum* across four temperature regimes: medians, quartiles, minimum and maximum refer to population means ($n=6$ for Georgia and Spain, $n=2$ for Ireland). Different letters indicate significant differences according to the REGWQ-test. For statistical details referring to rank transformed data see Table 3.

invasion success (Radford and Cousens 2000), but the contrary also applies. For example, the attempt to explain invasiveness in phylogenetically closely related species of the genus group *Atriplex* in terms of germination requirements was only partly successful: comparing two pairs each of invasive and non-invasive species of two sections of the genus, Mandák (2003) found that one species pair confirmed the hypothesis that germinability contributes to explaining the invasion success; while the other pair did not. In a comparison of eight perennial grass species, Milbau et al. (2003) searched for evident traits of invasiveness and invasibility, and found some "invasive" species to be characterised by high germination rates, whilst others were not.

However, the potential to yield high germination rates across a wide range of temperature regimes is given for *R. ponticum* – as we could demonstrate in this study – and can thus be assessed as a suitable precondition for effective reproduction and invasion in the sense of Baker's general purpose genotype (Baker 1974).

In fact, there is more reason to believe that genetic differences in the velocity of germination are involved in the invasion success of *Rhododendron ponticum*. The promoting impact of rapid responses has frequently been attributed to species' abundance (Grime et al. 1981) and successful plant invasion examples. In their two-year experimental study on grassland plant community invasibility in Derbyshire, United Kingdom, Burke and Grime (1996) concluded that, in particular, the combination of the ability to germinate at low temperatures at different light levels and the ability to germinate rapidly has to be considered as favourable. The authors assumed that early germination would be advantageous in a situation involving interspecific competition among seedlings. In any case, a repeated analysis after 5 yr. of continued experimental treatment did not confirm the persistence of any such effect (Thompson et al. 2001). Nevertheless, the advantage of occupying space to the exclusion of neighbouring plants can be a successful strategy in which early seedling emergence and establishment provide a head start effect in growth (Ross and Harper 1972, Miller et al. 1994, Thompson et al. 2001). This has been proven to apply similarly for woody species (Seiwa 2000).

The relevance of rapid germination for the invasion success of *Rhododendron ponticum* has to be evaluated in the context of the appropriate climatic conditions in the invaded area. In their comparative analysis of climatic and edaphic conditions of natural and invaded *Rhododendron* sites in Georgia, Spain and Ireland, Erfmeier and Bruelheide (unpubl.) presumed that the lower seasonal temperature amplitude and the absence of extreme temperature maxima in the summer in the invaded area decreased the probability and thus the risk of being affected by summer drought periods.

Consequently, it can be assumed that a selection towards precocious germination is less effective in the invasion area, but that it is of greater importance, e.g., in Spanish *rhododendron* populations that are at risk of being exposed to regular drought periods during the phase of seedling emergence (Mejias et al. 2002). It is plausible that the life strategy of Georgian *rhododendron* comprises a maximised distribution of risks over time including higher investment in persistence than in rapid responses. This is particularly reflected in these genotypes' delayed germination at cold temperatures. This precocious germination response at warmest and coldest temperature conditions can be interpreted as adaptation to an unreliable environment exhibiting sudden frost events or drought episodes (Thomas et al. 1994, Keller and Kollmann 1999), or, perhaps, to unfavourable nutrient conditions, as described for Georgian *rhododendron* sites (Erfmeier and Bruelheide unpubl.). Initially retarded germination does provide the possibility of opportunistic responses subsequent to disturbance events that have altered and temporarily ameliorated the site conditions (Grime 1979). This is very much in accordance with our findings of higher *Rhododendron ponticum* germination rates in Georgian pre-dispersal seed bank samples than in Spanish and Irish ones (unpubl.). The risk of experiencing severe losses, in contrast, is comparatively low for invasive genotypes in the new habitat, as the new site is characterised by low seasonal temperature variability and opportune edaphic conditions (Erfmeier and Bruelheide unpubl.).

Growth rates

Growth characteristics revealed clear genetic differences among the origins. High growth rates combined with the small number of internodes can be seen as an indication of selection for rapid growth of invasive Irish populations. Stem elongation is assumed to enhance fitness by improving the plant's competitive ability for light as a shade avoidance strategy (Weinig 2000) and an increase in shoot length is a frequently encountered trait of plant invaders (Williams et al. 1995, Reich et al. 1998, Baruch et al. 2000, Grotkoop et al. 2002). In their comparative and experimental study on growth pattern, biomass allocation and photosynthesis of invasive and native Hawaiian species, Pattison et al. (1998) found genotypic evidence for higher growth rates in the invasive species, particularly at low light conditions. The authors suggest that specific photosynthetic adaptations to capturing and utilizing light resources are effective in invasive plants. The inclusion of physiological parameters might be rewarding for *Rhododendron ponticum*. In a comparison of each one native and invasive *Rhododendron ponticum* population on leaf-level phenotypic variability, Niinemets et al. (2003) suggested an increased invest-

ment of foliar N in photosynthetic components to contribute to the species' invasive nature.

In any event, independently of the nature of the underlying driving mechanism, a variation in RGR is often associated with a shift in biomass allocation (Villar et al. 1998), resulting in changes in the root-shoot ratio of biomass. The present study provides no information on such a biomass allocation pattern, but additional growth experiments with *Rhododendron* seedlings indicate a shift towards increased shoot investment in individuals of invasive origin (unpubl.). A lower investment in root biomass compared to shoot investment in invasive populations supports the idea of a putative release from competitive stress. The resulting pattern of invasive and native *Rhododendron* origins differing in life strategies is very much in accordance with Grime's C-S-R-model of primary plant strategies (Grime 1979). Correspondingly, the invasive Irish genotypes in the new area could be attributed to be more ruderal (R) and competitive (C) and less stress tolerating (S) than native Spanish and Georgian plants are. The ability to translate enhanced resources, and compared to native *Rhododendron* sites in Georgia and Spain the invaded sites are characterised by elevated resource levels (Erfmeier and Bruelheide unpubl.), into rapid growth and early reproduction seems to have an adaptive value in a predictable environment.

Mechanisms involved

Parental environments can typically influence the phenotype of the offspring, including, in particular, germination patterns (Meyer and Allen 1999, Galloway 2001). Moreover, there is also a general trend of within-species variation along latitudinal gradients. For example, Murray et al. (2004), attributed larger seed mass at low latitudes for 34 perennial *Glycine* taxa to higher metabolic costs due to increased temperature and solar radiation.

We are aware that such circumstances limit the comparability of the different rhododendron origins to some extent and that a more precise distinction between parental environment and genotypic effects would have to refer to seed material derived from individuals grown under identical conditions (Baskin and Baskin 1998). Since the life-form of *Rhododendron ponticum* as a persistent woody plant prevents the species' fast experimental reproduction, satisfying this claim could not be realised in this project's time frame. Meanwhile, our experimental plants have reached the flowering stage, thus showing promise for future studies.

However, the attempt to assess involved mechanisms that have contributed to the encountered genetic differences between native and invasive populations needs to consider different explanation models that might apply.

Escape theories are currently often employed to explain a species' successful spread. Some recent approaches use the enemy release hypothesis, i.e. the escape from natural antagonists (Maron and Vilà 2001, Keane and Crawley 2002); whilst others include the release from co-evolved competitors in the home range (Callaway and Aschehough 2000, Reinhart et al. 2003). However, the general idea behind these assumptions is mostly the absence of the selection pressures that the invaders experienced in their home range. It is possible that similar regulative processes also apply to *Rhododendron*, for we found evidence of leaf herbivory in both the native and the invaded range, but this occurred to a lesser extent in the new area (unpubl.). A trade-off between reduced costs in enemy regulation and increased investment in vegetative growth, according to the EICA hypothesis (Blossey and Nötzold 1995), could then be a specific adaptation to the new environment.

Deviating properties of invasive populations in germination responses and growth rates could also be interpreted as altered ecological or morphological traits resulting from introgression. Hybridisation effects can thus be considered to explain new genotypes (Ellstrand and Schierenbeck 2000, Lee 2002). For *Rhododendron ponticum*, Milne and Abbott (2000) could demonstrate that hybridisation with closely related North American species that had similarly been introduced to Great Britain for horticultural purposes has probably occurred and might thus account for the detected differences. These conclusions are based on chloroplast and nuclear ribosomal DNA analysis. In any event, within our own AFLP analyses of native European and North-American populations of *Rhododendron ponticum*, *R. maximum*, *R. catawbiense* and of invasive Irish *Rhododendron* populations, we found no such evidence for introgression with North American material (unpubl.).

Similarly, the idea of preadapted introduced genotypes prior to introduction might apply. Natural selection in the new range might, thus, have favoured a specific genotype and subsequently led to the evolution of adapted ecotypes (Lambrinos 2004). The colonization of *Capsella bursa-pastoris* in North America is an example of successful spread without any significant genetic change since its repeated introduction from European sources as demonstrated by Neuffer and Hurka (1999). By isozyme analyses, the authors provided evidence for a similar variation pattern in both source origin and introduced range. It is possible, that the closer similarity between the Spanish and the invasive Irish rhododendron populations (Milne and Abbott 2000, Erfmeier and Bruelheide 2004) gives rise to the assumption that founder populations of Iberian origin have been well predisposed to being successful in the new range. As a result of a transplantation

experiment, Erfmeier and Bruelheide (unpubl.) concluded that the Iberian rhododendron individuals have the potential to be good invaders, too. However, the authors, furthermore, detected differences between invasive and Spanish populations that render preadaptation unlikely to be the sole explanation. Post-invasion adaptations, confirming the idea of a genetic shift, are thus likely to apply, too.

However, a deeper understanding of underlying selection mechanisms, which might include selection on numerous hybrid combinations (Lee 2002), is beyond the scope of this article and would have to be studied with appropriate methods of molecular genetics.

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