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Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions

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Summary

The objective of this paper is to identify the factors that promote the invasiveness of *Rhododendron ponticum* L. by the means of comparative field observations. *Rhododendron ponticum* (Ericaceae) is an evergreen shrub with a natural distribution in the Mediterranean and Black Sea area and was introduced to the British Isles in 1763. Thenceforward, the species has been considered as a major threat to natural ecosystems there.

We compared native and invasive populations of *Rhododendron ponticum* with respect to trait patterns that are associated with invasiveness. Six populations each in the natural part of its range, in Georgia (Caucasus) and Spain as well as six invasive ones in Ireland were examined with regard to biometrical, morphological and ecological characteristics.

Invasive Irish populations differed from non-invasive ones mainly in growth patterns and showed much higher rates of annual shoot growth in the field and higher rates of seedling recruitment. In contrast, native Spanish populations were discriminated by their shape and age; whereas native Georgian rhododendron, above all, showed distinctive leaf characteristics. In general, the relationship between Irish and Spanish populations was closer than to the Georgian ones. Our results suggest that both genotype and environment account for the trait pattern found in Irish populations. Differences in genetically fixed traits had a greater effect in morphological differences to Georgian provenances. In contrast, the invasive Irish rhododendron were favoured by a more benign environment than the Spanish populations.

Key words: clonality, growth rate, invasiveness, leaf characteristics, seedling recruitment

Introduction

In recent years, biological invasions by non-native species have become a focus of ecological research mainly because of their profound impact on ecosystems (Mooney & Drake 1986; Williamson 1996; Parker et al. 1999; Lonsdale 1999). Invasiveness matters, in particular, since many invasive species have been reported to exert high reproduction pressure on the community invaded (Noble 1989) or to be highly productive and to attain a larger size in their new area (Crawley 1987; Blossey & Nötzold 1995). In this context, especially high relative growth rates (RGRs), that can be ascribed to specific leaf attributes of the invading plants, have been regarded as a responsible component role in invasion processes (Cornelissen et al. 1998; Grotkopp et al. 2002). However, there is no straight forward way to detect crucial life history traits of an invasive species, since ecological, physiological, morphological and genetic characters or a specific combination of them have to be considered (Baker & Stebbins 1965; Baker 1974; Williamson 1996). Moreover, the success of a species in a new habitat is mainly due to how the species' characteristics interact with the new environment (Lodge 1993).

In studies on invasion ecology, we consider a multistage approach useful: 1) observation of the invasion event in the new area 2) comparison of native and inva-

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sive populations in the field and then 3) experimental demonstration of the impact of putative key factors.

The obvious first step is to study a species' spread in the new habitat (Sukopp & Starfinger 1995; Wade et al. 1997) and to compare these observations with other invasion patterns (Lodge 1993). In this way, e.g., Kowarik (1995) was able to reconstruct introduction and spreading dynamics of woody species in Germany and, thus, reveal the relevance of a lag phase between a species' introduction and the initiation of its invasion process. Although such observational studies offer useful hints on possible key factors promoting invasiveness, they cannot answer questions as to whether these factors are actually the crucial ones. To assess the strength of the effects of these factors, experimental approaches are necessary (Bruelheide 1999; Lavorel et al. 1999). Consequently, there are many studies that immediately focus on phase 3, thus, comparing specific traits experimentally (Thébaud et al. 1996; Weber & D'Antonio 1999; Siemann & Rogers 2001).

However, at this point, there is no evidence that these traits are also operative in the species' native habitat, which should be analysed in the second step. Surprisingly, there are only few studies that take native and invasive ranges into account. In any case, these comprehensive approaches are laborious and difficult to realise. Nevertheless, in this manner, Grigulis et al. (2001), e.g., were able to demonstrate that for *Echium plantagineum* the rates of seedling establishment from the seed bank and the rate of incorporation into the seed bank were higher in the invaded area in Australia than in native Mediterranean populations. Investigations in native and exotic populations of *Cytisus scoparius* in Europe and Australia have shown that absolute seedling mortality is higher in the introduced range (Paynter et al. 1998; Sheppard et al. 2002 and references therein). In any case, a higher variability in seedbank patterns and in the transition from seedbank to seedling due to habitat specific differences more than compensates for this loss (Sheppard et al. 2002). Providing a systematically quantifying comparison of an invasive species both in its native and invasive range can, therefore, narrow down the spectrum of possible key factors.

The objective of this study is to apply this procedure to *Rhododendron ponticum*. This paper is the first of a consecutive series of studies that intend to elucidate the connection of both the ecological and the genetic background of this species' invasion success.

Rhododendron ponticum L. is a suitable system for studying an invader's ecology both in its new and native habitats. Since its introduction to the British Isles in the 18th century the species has spread into natural ecosystems with massive invasions. It is currently regarded as one of the 'top twenty' British alien plant species (Crawley 1987).

Rhododendron ponticum has a disjunct distribution. Formerly widely spread in Europe during the Tertiary and Pleistocene (Jessen et al. 1959; Mitchell & Watts 1970; Meusel et al. 1978), the species presently occurs in the Western Caucasus region, Asia-Minor, in the eastern part of the Balkans, as well as in an outpost on the southern part of the Iberian peninsula (Fig. 1). Although range expansion in Western Europe is still in progress, native *Rhododendron* stands are described differently, either as having stable populations in specific habitats (e.g. in Georgia) or as declining populations of a severely endangered species, e.g. in Southern Spain, (Blanca et al. 2000). The origin of invasive *Rhododendron* populations is still being discussed. Milne & Abbott (2000) recently used restriction fragment length polymorphisms of chloroplast DNA to show the existence of a mostly Spanish provenance for this species.

A few studies have focused on the population biology of *Rhododendron ponticum*, to date. In particular, invasive British and Irish populations have been the focus of numerous scientific investigations (Cox & Hutchinson 1963; Cross 1975; Cox 1979; Shaw 1984; Tabbush & Williamson 1987). Recent studies dealt with the ecology and control of *Rhododendron ponticum* in Turkey (Esen 2000). The basic parameters of reproductive biology and critical life stages in Spain were studied by Mejías et al. (2002), and plasticity parameters were analysed in a Spanish and a Belgian population (Niinemets et al. 2003). Thus, no research project has taken the total range into consideration, although this has been clearly recognized as necessity (Mejías et al. 2002).

The objectives of this study are to make a general comparison of *Rhododendron ponticum's* native and introduced range, with a special focus on patterns of

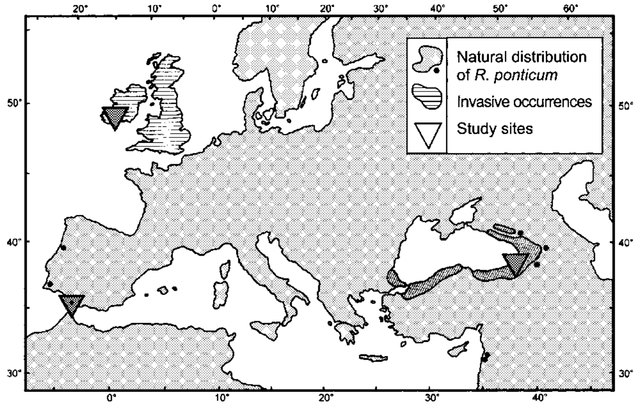

Fig. 1. Native distribution and invaded areas of *Rhododendron ponticum* (after Cross 1975) and location of study sites. Each symbol comprises six study sites.

growth and morphology. We hypothesize, in particular (i) that invasive Irish populations show higher growth rates in the field than native occurrences, and (ii) that reproduction is more successful in the new area. Finally, our aim is to point out the most possible key factors promoting invasiveness that should be tested in subsequent experiments.

Material and methods

Study object

Rhododendron ponticum L. (Ericaceae) is an erect, evergreen shrub attaining a height of 2–8 m (Tutin et al. 1972). Taxonomical differentiation exists between plants of the Black Sea area (ssp. *ponticum*) and Iberian occurrences (ssp. *baeticum*) based on distinctive traits in leaf morphology: individuals assigned to the ssp. *baeticum* in general have smaller leaves and a larger length-width-ratio than individuals of ssp. *ponticum* (Tutin et al. 1972; Davis 1978; Castroviejo et al. 1993). *R. ponticum* ssp. *ponticum* is an element of deciduous summergreen mixed forest and beech forest communities in the pontic lowlands and extends up to the subalpine level. In Southern Spain and Portugal *Rhododendron ponticum* ssp. *baeticum* is either associated with mediterranean sclerophyllous forests under maritime influence, mainly along creeks, or a scrubland element of humid mountain ranges (Mejías et al. 2002). Iberian populations can be found between 400 and 1200 m a.s.l.

Introduction to the British Isles dates back to the year 1763 (Elton 1958). Since that time, the species has extended its range in Western Europe, where it exerts a major impact on natural communities. Particularly in Great Britain and Ireland *Rhododendron ponticum* has invaded oak-dominated *Quercus petraea*- and mixed forests as well as heaths and bogs. The present invasion tendency appears to be eastward with actual occurrences in the Netherlands and Belgium as well as in Northwest Germany (Niinemets et al. 2003; personal observations).

The species propagates by producing numerous small seeds. Vegetative growth occurs by layering branches on the ground. Cover with litter can lead to rooting, subsequent separation of branches from the parental plant and finally result in independent ramets that seem to have no obvious connection to each other. Nevertheless, in Britain, vegetative spread is very limited, *Rhododendron ponticum* is not able to sucker (Shaw 1984). Cross (1975) pointed out that Irish *Rhododendron* axes lack mechanical strength so that the plant extends rather laterally than vertically.

Table 1. Names, locations and vegetation characteristics of the studied populations.

Country	Pop.	Location	Elevation	Latitude	Longitude	Aspect	Slope	Cover *R.p.* shrub layer	Cover *R.p.* herb layer	Canopy cover
			[m.a.s.l.]			[°]	[°]	[%]	[%]	[%]
Geo	A	Banis-Khevi	980	N 41°53.020’	E 043°21.188’	336	22	70	30	75
Geo	B	Keda-Akutsa	500	N 41°35.557’	E 041°57.107’	320	15	60	4	100
Geo	C	Dandalo	910	N 41°38.035’	E 042°07.588’	10	18	60	10	65
Geo	D	Botanical Garden, Batumi	85	N 41°41.975’	E 041°43.219’	37	14	60	20	80
Geo	E	Djarnali	175	N 41°33.165’	E 041°36.611’	340	15	50	10	74
Geo	F	Mtirala	960	N 41°39.119’	E 041°47.184’	360	30	50	10	55
Esp	G	Garganta de Puerto Oscuro	790	N 36°30.919’	W 005°37.416’	105	8	80	4	85
Esp	H	Garganta de Passada Llana	760	N 36°30.403’	W 005°35.960’	122	7	60	10	65
Esp	I	Arroyo del Montero	660	N 36°29.650’	W 005°35.962’	229	4	80	10	80
Esp	K	Garganta de Enmedio	445	N 36°32.085’	W 005°38.222’	357	5	60	10	70
Esp	L	Llanos del Juncal	740	N 36°06.334’	W 005°32.468’	32	10	60	4	70
Esp	M	Rio de la Miel	430	N 36°06.486’	W 005°31.306’	67	10	70	10	80
Ire	N	National Park Killarney, Torc Mnts.	60	N 52°00.161’	W 009°30.301’	350	15	40	10	65
Ire	O	National Park Killarney, Ladies View	35	N 51°58.394’	W 009°35.494’	14	12	40	20	60
Ire	P	Glengariff	35	N 51°45.388’	W 009°33.820’	297	18	60	10	55
Ire	Q	Galtee Mnts.	180	N 52°22.452’	W 007°58.744’	179	15	80	10	70
Ire	R	Knockmealdown Mnts.	220	N 52°15.535’	W 007°57.065’	353	22	80	10	50
Ire	S	Greenan,Wicklow Mnts.	120	N 52°55.945’	W 006°18.555’	31	10	80	80	65

Study sites and sampling design

Study areas were chosen across the species' entire range; thus, including the species' central range in the Black Sea area, on the Iberian peninsula and its invasive occurrences in the British Isles. In Georgia, Spain and Ireland six populations each were studied (Table 1). All study sites were confined to forests because these are the typical habitats in Georgia and Spain. In addition, the focus on forests provided also comparable growth conditions among all sites. Selection of study sites was performed by covering the altitudinal and geographical range within each country including different forest types with the intention of sampling the span of possible occurrences. All study sites faced north and had a similar slope of 10 to 20°. A single Georgian site (F) had to be located along a steeper inclination due to a lack of alternatives, whereas Spanish sites, in general, were less steep. In Georgia and Ireland, study sites were located along a transect of a length of 150 km and 250 km, respectively. The transect followed a west to east gradient of decreasing annual precipitation. Due to sparse Iberian occurrences, the Spanish populations of *Rhododendron ponticum* had shorter distances between them (maximum 50 km). The Spanish sites can be assigned to two groups: four sites located in humid forests of the Aljibe Mountains in small river valleys ('canutos') and two further locations near the Strait of Gibraltar with a more maritime influence, partially under cloud forest conditions.

The sampling survey within a population was carried out systematically. At each site, a square of 16m*16m was set up in a homogenous *Rhododendron* population and divided into a grid with a 4-m mesh size. Since the grid was laid out from an arbitrary point and strictly orientated towards north, the exact position of the 16 grid points was random. In five Spanish populations plots with a length of 32 m and a width of 4 m were established along both sides of a creek. Each plot covered a total area of 256 m^2.

Biometrical parameters

At each site, 16 individuals were selected for biometrical measurements. The individual with a minimum height of 50 cm that was nearest to the grid point was chosen for biometrical survey and permanently marked for consecutive recording. Study sites were established and investigated from November 1999 to February 2000 and populations were repeatedly measured in summer 2000 (July to September) and 2001 (August to October).

In the winter of 1999/2000 the biometrical parameters height, extension and basal diameter of each individual were measured. For each marked individual the highest sprout with a terminal vegetative bud was chosen, and the number of shoots and leaves were recorded with reference to the previous year's internode. Internode elongation of the preceding vegetation period was regarded as the annual increase in shoot length and recorded as growth parameter. Measurements of growth parameters were repeated in summer 2000 and 2001. Each time the increase in shoot length and basal diameter, the incidence and the number of new branches and the number of leaves were recorded. Leaf morphology was described in 1999 by length, width and shape. Shape was defined as length from leaf base to widest width divided by length. In total, we measured 2673 leaves.

Population parameters

To analyse population structure, a density survey was conducted along a transect of 1m*1m subplots diagonally aligned within the study square. Within a total of 16 subplots per population, all detected *Rhododendron* individuals were recorded. We counted seedlings, saplings and individuals of different height classes. For each individual the basal diameter at soil surface was measured in two directions.

The proportion of clonality within a population was assessed in the transect survey by classifying each encountered individual as derived from either sexual or vegetative reproduction. Identification of ramets in the populations followed recognition of layerings combined with simultaneous adventitious rooting.

Fruit set

The number of both generative buds and racemes was counted for each of the 16 target individuals marked per site in 1999. Transition from buds to racemes was determined by repeated counting in 2000. In 2000, we collected 10 racemes each from individuals with sufficient fruits. Successful maturing was then quantified by counting the proportion of capsules containing seeds on the total capsule set within a raceme. We calculated fruit set as the ratio of mature fruits to total fruits per individual.

The impact of self-fertilisation was tested by the use of gauze bags in the winter of 1999/2000. Within each population, eight generative buds of different individuals were chosen and bagged with gauze bags of a mesh width of 2 mm to exclude insect mediated pollination. In the summer of 2000, the bagged fruits were gathered to analyse fruit set. The next adjacent non-bagged raceme was collected as a reference for fruit set.

Age determination

Age determination of *Rhododendron* individuals referred to ramets. Due to vegetative reproduction the genet might be much older. Within each population ten randomly chosen individuals were cut for counting growth rings. The associated diameters were measured to generate a population specific linear regression model. Age of target individuals and of transect individuals was then estimated referring to the particular basal diameters.

Statistical analyses

Survival of leaves

The survival rate of leaves was defined by calculating the transition probabilities for encountered leaves in 1999 and 2000 to the year 2001. Furthermore, in 2001 all existing leaves were counted and dated back to the year of their apparent emergence with reference to the respective internode. For Irish individuals, we encountered the incidence of several internodes per year in 2000 and 2001. In these cases, survival rate of leaves was then adjusted to the correct age of internode.

Data analysis

All calculated parameters were tested for normal distribution (proc univariate, Shapiro-Wilk-statistics, SAS Institute 2000). Since most of the parameters were not normally distributed, the data were transformed into ranks. We then employed a nested ANOVA model, with main factor 'country' (fixed) and 'population' (random) nested within country (proc glm; SAS Institute 2000). Post-hoc tests were performed using Ryan-Einot-Gabriel-Welsch (REGWQ) multiple range tests. If not stated otherwise, significance levels for all tests were set at $\alpha = 0.05$. In all figures, data are presented as median values with quartiles and the range between minimum and maximum.

Simple regression analysis was used to examine pairwise relationships between selected traits (proc corr; SAS Institute 2000) to clarify interactions. These results refer to Spearman rank correlations (r_s) due to the parameters' non-normal distribution.

The relationship among all traits was analysed by a Prinicipal Component Analysis (PCA), an unconstrained linear approach. Ordination of individuals was performed with SAS procedures (proc factor and proc princomp) using a data matrix at the population level to elucidate the assignment of provenances to their particular key variables and their potential divergence.

In the PCA, we considered all recorded traits of growth, reproduction and morphology that were also analysed by univariate statistics with the exception of 'Number of racemes 2000', 'p transition bud 1999-fruit 2000', 'Proportion of mature fruits' due to missing values, and variables that are transferable into one another. Thus, the matrix consisted of 36 variables and 18 populations. The resulting coordinates of traits were scaled by a factor of 4 for plotting.

Results

Biometrical data

Growth

Over the total investigation period the invasive Irish populations showed highest values in all growth parameters in all years (Table 2). Increase of shoot length was significantly the largest in Ireland. For example, in 2001 the increase in Ireland was 19.6 cm compared to 7.1 cm and 4.6 cm in Georgia and Spain, respectively. Thus, the increase in shoot length of invasive popula-

Table 2. Growth parameters and leaf morphology. Values are medians of population means (n = 6), i.e. the mean of all sampled individuals in a population; p values refer to ANOVA, * $\alpha = 0.05$; ** $\alpha = 0.01$, *** $\alpha = 0.001$, n.s. = not significant; n = 6 for each provenance. Different letters indicate significant differences according to the REGWQ-test. No. refers to labelling of parameters in Fig. 11.

No.	Variable	d.f.	F	p	GEO	ESP	IRE
1	Increase in shoot length 1999 [cm]	2	7.52	0.0055^{**}	9.82^{b}	9.84^{b}	17.1^{a}
2	Increase in shoot length 2000 [cm]	2	25.28	$<0.0001^{***}$	6.12^{b}	6.61^{b}	20.69^{a}
3	Increase in shoot length 2001 [cm]	2	27.00	$<0.0001^{***}$	7.14^{b}	4.58^{b}	19.64^{a}
4	Sum of total increase in shoot length 1999–2001 [cm]	2	14.50	0.0003^{***}	30.65^{b}	38.89^{b}	124.68^{a}
5	Number of branchings 2000	2	8.77	0.0030^{**}	0.19^{b}	0.34^{b}	1.47^{a}
6	Number of branchings 2001	2	7.30	0.0061^{**}	0.47^{b}	0.38^{b}	1.19^{a}
7	Number of internodes	2	6.28	0.0104^{*}	1.00^{b}	1.00^{b}	1.27^{a}
8	Leaf number 1999	2	37.57	$<0.0001^{***}$	7.19^{c}	8.72^{b}	11.81^{a}
9	Leaf number 2000	2	51.08	$<0.0001^{***}$	6.38^{c}	7.75^{b}	15.25^{a}
10	Leaf number 2001	2	30.52	$<0.0001^{***}$	6.55^{b}	5.79^{b}	14.13^{a}
11	Sum of leaf number 1999–2001	2	21.16	$<0.0001^{***}$	23.75^{b}	30.37^{b}	73.78^{a}
	RGR Increase in basal diameter [mm year^{-1} mm^{-1}]	2	11.59	0.0009^{***}	0.04^{b}	0.02^{c}	0.08^{a}
12	Increase in basal diameter [mm^{2} year^{-1}]	2	12.64	0.0006^{***}	1.73^{b}	1.43^{b}	6.19^{a}
13	p leaf transition 1999–2001	2	3.67	0.0503n.s.	0.83	0.50	0.55
14	p leaf transition 2000–2001	2	3.18	0.0707n.s.	0.97	0.89	0.91
15	Maximum age of leaves [years]	2	1.48	0.2596n.s.	2.13	1.89	1.87
16	Length of leaf [cm]	2	21.29	$<0.0001^{***}$	19.94^{a}	15.36^{b}	14.99^{b}
17	Width of leaf [cm]	2	38.18	$<0.0001^{***}$	5.51^{a}	3.92^{b}	3.86^{b}
18	Shape of leaf [cm cm^{-1}]	2	12.39	0.0007^{***}	0.66^{a}	0.63^{b}	0.64^{b}
19	Leaf area [cm^{2}]	2	36.07	$<0.0001^{***}$	90.94^{a}	51.16^{b}	48.84^{b}
20	Length-width ratio [cm cm^{-1}]	2	4.29	0.0336^{*}	3.69^{b}	3.96^{ab}	4.05^{a}
21	Maximum leaf area [cm^{2}]	2	50.02	$<0.0001^{***}$	122.29^{a}	67.27^{b}	71.47^{b}
22	Maximum length of leaf [cm]	2	39.31	$<0.0001^{***}$	22.90^{a}	17.57^{b}	17.99^{b}
23	Maximum width of leaf [cm]	2	41.19	$<0.0001^{***}$	6.65^{a}	4.83^{b}	4.86^{b}

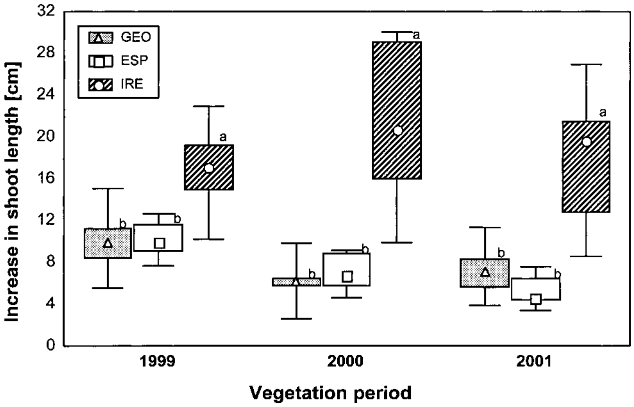

Fig. 2. Absolute increase in shoot length during vegetation periods 1999, 2000, 2001. Medians, quartiles, minimum and maximum refer to population medians (n = 6), i.e. the mean of 16 individuals in a population. Different letters indicate significant differences according to the REGWQ-test.

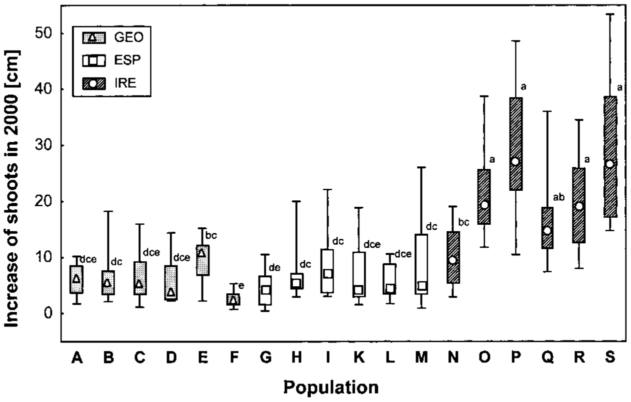

Fig. 3. Absolute increase in shoot length in 2000 on the population level. Values are medians, quartiles, minimum and maximum (n = 16). Different letters indicate significant differences according to the REGWQ-test.

tions was two to four times higher than in native populations (Fig. 2). Variability within the countries was different: growth values of Spanish populations were consistently low; whereas Georgian increases in shoot length in 2000 ranged from population medians 2.6 cm to 9.8 cm and the Irish ones from 9.9 cm to 30.0 cm. Significant differences between populations were especially found within Irish provenances (Fig. 3). Although the increase in shoot length of most of the Irish populations with a median of 9.6 cm was significantly higher than that of Spanish and Georgian populations, the Irish population N did not differ significantly from native populations in 2000. This trend was also observed for population N in 1999 and 2001.

With a median leaf number of 12.0, 15.1 and 14.3 for the subsequent years, the Irish populations produced significantly more leaves than the Spanish and Georgian ones (Fig. 4). Variability was highest within the Irish populations, especially in 2000 and 2001 (minimum and maximum 10.1–19.0 and 9.1–19.0). Significant differences were encountered for all recorded growth parameters: with a median of 1.5 branches per sprout in 2000 and 1.2 in 2001 branching occurred more often in Irish populations (Table 2). In a similar manner, the number of internodes per year was significantly higher in the same periods. The median increase in basal diameter over two years was 6.2 cm in the Irish populations; whereas the native ones reached less than a third of this value.

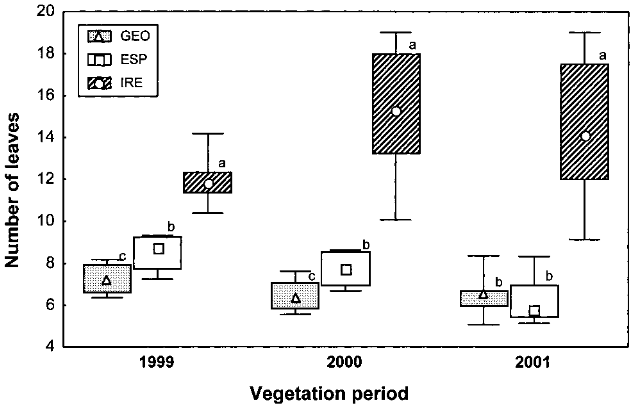

Fig. 4. Absolute increase in number of leaves during vegetation period 1999, 2000, 2001. Medians, quartiles, minimum and maximum refer to population medians (n = 6), i.e. the mean of 16 individuals in a population. Different letters indicate significant differences according to the REGWQ-test.

Life span of leaves showed no significant differences between countries (Table 2), although the probability of leaf transition from 1999 to 2001 just barely failed to be significant: with a median transition probability of 0.8 Georgian leaves tended to have a longer persistency than Irish (0.6) and Spanish (0.5) leaves.

Morphology

Data on leaf morphology revealed clear differences between the Georgian populations and those of other origin (Table 2, Fig. 5): leaves from Georgian rhododendrons reached a median length of 19.9 cm; whereas individuals from Spain and Ireland had significantly shorter leaves with 15.4 cm and 15.0 cm, respectively. Analogously, Georgian *Rhododendron* leaves were widest and had both highest median leaf area of 90.9 cm^2 and maximum leaf area of 122.3 cm^2, based on population medians of the largest leaf of each of the 16 sampled target individuals in a population. Purely morphological traits such as length-width ratio and shape of leaves revealed highly significant differences between

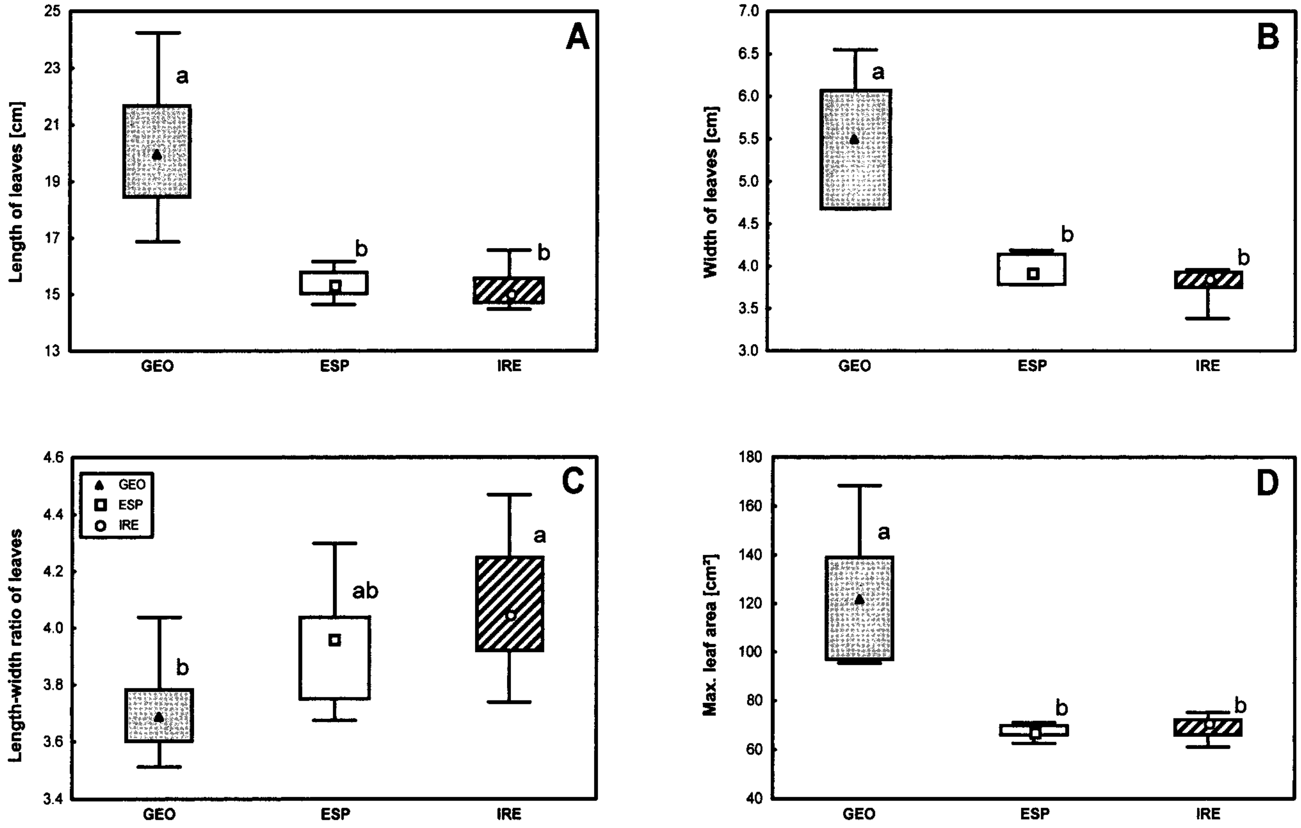

Fig. 5. Leaf characteristics of Georgian, Spanish and Irish populations. A) Absolute length of leaves, B) Absolute width of leaves, C) Length-width ratio of leaves D) Maximum leaf area. Medians, quartiles, minimum and maximum refer to population medians (n = 6), i.e. the mean of 16 individuals in a population. Different letters indicate significant differences according to the REGWQ-test.

Georgian provenances on the one hand, and Spanish and Irish ones on the other hand. The Irish and Spanish *Rhododendron* leaves were more narrow and straighter. Similarly, the parameter shape, defined as length from leaf base to widest width divided by width, showed a significantly different expression for Georgian leaves compared to Spanish and Irish ones.

Population parameters

Population structure

The distribution of all target individuals in height classes (Fig. 6) reveals that Spanish populations were dominated by high individuals. The majority of studied Spanish individuals was found to have a height of 2–3 m; whereas most of the Irish individuals belonged to the 1–2 m class. The majority of Georgian individuals were even smaller with highest frequencies in the class up to 1 m. Data on volume and extension of the investigated individuals showed similar trends (Table 3). The calculated mean age of the target individuals was highest in the Spanish populations, where it reached a median of 53 years (minimum 25 years and maximum 85 years). Georgian and Irish target individuals were significantly younger with a median of 22 and 23 years, respectively (Fig. 7). Density of populations, which was calculated from all individuals > 20 cm, showed no significant dif-

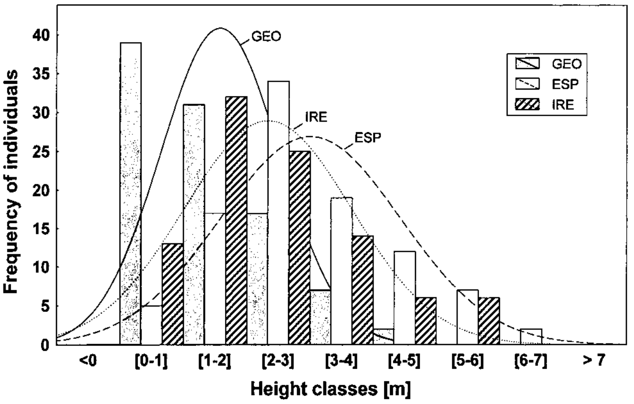

Fig. 6. Frequency distribution of individuals within each country. Values are absolute numbers of individuals in each class (n = 96 for each country).

Table 3. Reproduction characteristics and population traits. Values are medians of population means (n = 6), i.e. the mean of all sampled individuals in a population; p values refer to ANOVA (variable indices 1 = referring to target individuals, 2 = referring to additional individuals, 3 = referring to transect squares); * $\alpha = 0.05$, ** $\alpha = 0.01$, *** $\alpha = 0.001$, n.s. = not significant. Different letters indicate significant differences according to the REGWQ-test. No. refers to labelling of parameters in Fig. 11.

No.	Variable	d.f.	F	p	GEO	ESP	IRE
24	Number of generative buds 1999^1	2	1.55	0.2435n.s.	1.37	1.63	5.94
25	Number of racemes 1999^1	2	0.16	0.8503n.s.	0.78	0.72	1.31
	Number of racemes 2000^1	2	1.86	0.2474n.s.	1.14	1.78	4.23
	p transition bud 1999-fruit 2000^1	2	0.14	0.8726n.s.	0.87	0.90	0.92
	Proportion of mature fruits^1	2	0.08	< 0.9221n.s.	0.89	0.89	0.89
26	Ratio p gauze/p reference^2	2	1.40	0.2781n.s.	0.09	0.07	0.05
27	Proportion of clonality [%]^1	2	22.74	$< 0.0001^{***}$	56.35^a	5.28^c	12.95^b
28	Seedlings 2000 [m^{-2}]^1	2	7.36	0.0059^{**}	0.00^b	0.00^b	1.38^a
29	Saplings 2000 [m^{-2}]^1	2	0.69	0.5189n.s.	0.09	0.00	0.09
30	Seedling 2001 [m^{-2}]^1	2	19.66	$< 0.0001^{***}$	0.00^b	0.00^b	2.59^a
	Age transect individual [years]^1	2	6.52	0.0092^{**}	12.14^b	23.34^a	16.01^{ab}
31	Density of individuals > 20cm [m^{-2}]^1	2	0.70	0.5123n.s.	2.34	1.56	1.84
32	Extension in direction 1 [m]^3	2	8.64	0.0032^{**}	1.38^b	2.97^a	2.14^a
33	Extension in direction 2 [m]^3	2	9.81	0.0019^{**}	1.26^b	2.26^a	1.83^a
34	Height of target individuals [m]^3	2	12.75	0.0006^{***}	1.61^c	2.93^a	2.16^b
35	Volume of target individuals [m]^3	2	10.8	0.0012^{**}	2.01^b	20.83^a	6.48^a
36	Age target individuals [years]^3	2	15.52	0.0002^{***}	21.84^b	53.09^a	23.08^b

ferences between the countries (Table 3). Although maximum values (5.5 individuals per m^2) were much higher in Georgian populations, they did not differ significantly from Spanish or from Irish populations.

Reproduction

Regeneration studies showed significant differences in reproduction success with a consistent pattern in both observation periods (Fig. 8). There was no seedling establishment in any of the Georgian populations: whereas rare establishment events were encountered in Spain only in populations K and M in the year 2000 (with a median of 2.9 and 0.2 seedlings per m^2) and in population K and L in 2001 (with a median of 2.5 and 0.1 seedlings per m^2). In contrast, seedling density was much higher in Ireland, with a median of 1.4 and 2.6 seedlings per m^2 in 2000 and 2001. Population N was the only Irish site in 2000 where no seedlings were encountered. In 2001, the maximum of seedling density

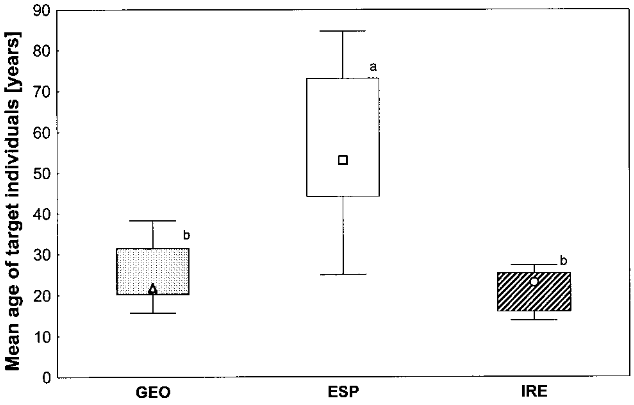

Fig. 7. Calculated mean age of Georgian, Spanish and Irish individuals. Medians, quartiles, minimum and maximum refer to population medians (n = 6), i.e. the mean of 16 individuals in a population. Different letters indicate significant differences according to the REGWQ-test.

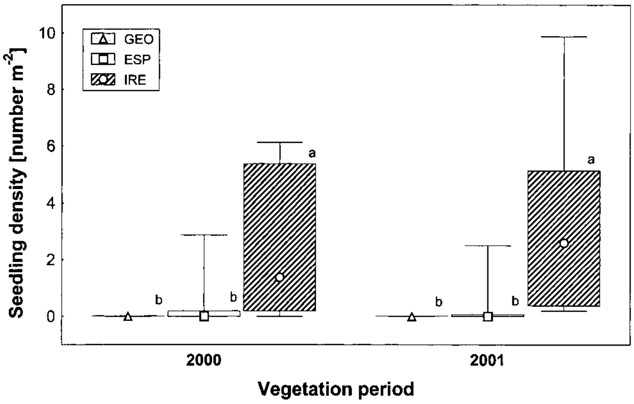

Fig. 8. Seedling density in Georgian, Spanish and Irish populations in 2000 and 2001. Medians, quartiles, minimum and maximum refer to population medians (n = 6), i.e. the mean of 16 transect squares in a population. Different letters indicate significant differences according to the REGWQ-test.

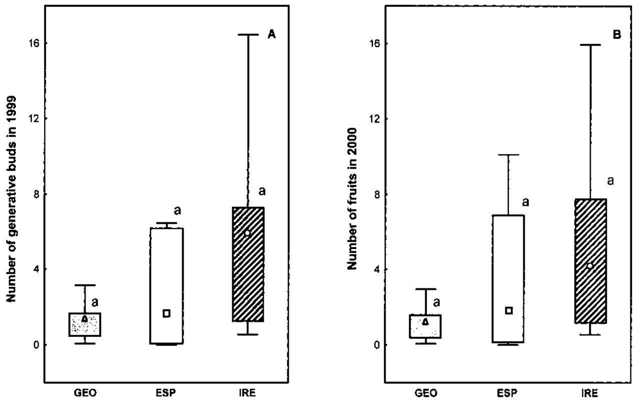

Fig. 9. Absolute numbers of generative buds in 1999 (A) and numbers of succeeding fruits in 2000 (B). Medians, quartiles, minimum and maximum refer to population medians (n = 6), i.e. the mean of 16 individuals in a population. Different letters indicate significant differences according to the REGWQ-test.

was observed in the Irish population O, with a mean value of 9.9 seedlings per m^2.

We found no significant difference in the number of generative buds in 1999 between the three countries (Fig. 9a, Table 3). However, although not significant, the Irish individuals displayed a trend toward a higher flowering rate. Variability among Irish populations was much higher than in Georgian and Spanish populations with a minimum number of 0.1 buds per individual in population N and a maximum of 16.5 buds in population Q. The transition probability from buds 1999 to fruits 2000 was the same in all countries (Table 3). In addition, the provenances showed no significant difference in fruit set. Nevertheless, the median number of racemes per individual was higher in Irish populations with a median of 4.2 racemes (and a maximum of 15.9 racemes in population Q) compared to a median of 1.1 and 1.8 racemes per individual in Georgia and Spain (Fig. 9b). The proportion of mature fruits as a measure of fecundity of fruit set was the same in all countries. A median percentage of 89% of all capsules reached maturity (Table 3).

Gauze bag treatment reduced fruit set to less than 10% compared to non-bagged fruits (Table 3). The treatment effect was high in all countries, but did not differ significantly between them.

The proportion of clonality was significantly different between the countries (Fig. 10): Georgian *Rhododendron* populations reached a median proportion of clonality of 56%, while only 5% of the Spanish individuals and 13% of the Irish individuals showed clonal spread.

Intercorrelation

PCA revealed a clear pattern for all examined traits (Fig. 11). The first axis explained about 37.2% of the total variation of the data set and showed a strongly positive correlation with most of the growth traits, such as increase in shoot length (nos.1–4 in Fig. 10), number of leaves (nos. 8–11), number of branching (nos. 5–6) and number of internodes (no. 7). The traits of leaf morphology (nos. 16–23) and leaf age (nos. 13–15) were negatively correlated with axis 1. The second axis explained about 24.6% of total variance and was closely correlated with size traits. A third axis still explained a further 10.9% of the total variance and was related to traits of reproduction, such as numbers of buds, fruits, seedlings and saplings (nos. 24–26, 28–30). The populations of all origins were clearly assigned to specific key factors. Georgian populations were closely associated with leaf traits; whereas discrimination of Irish populations was mainly due to their growth rates. The Spanish and also the Irish populations N and Q were characterised by size traits. The latter two Irish populations deviated from the rest; i.e. they were more closely correlated with Spanish populations than with Irish ones.

Leaf age was positively related to population density when based on the pooled data of the three countries (Fig. 12). Leaf persistence increased significantly with density of individuals above 20 cm. The correlation was also significant when based only on Georgian ($r_s = 0.841$, $p = 0.036$) and Spanish ($r_s = 0.829$, $p = 0.0416$) populations, but was not for Irish ones ($r_s = 0.787$, $p = 0.1429$). Leaf area and number of leaves were negatively correlated in the pooled data set (Fig. 13a). However, this relationship was due to differences between countries. Georgian plants had few lea-

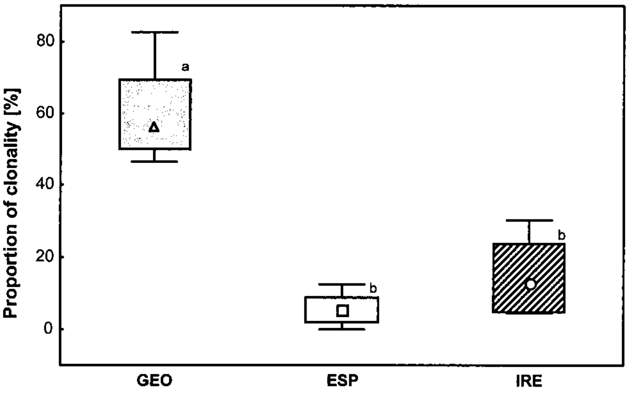

Fig. 10. Proportion of clonality within the countries. Medians, quartiles, minimum and maximum refer to population medians (n = 6), i.e. the mean of 16 transect squares in a population. Different letters indicate significant differences according to the REGWQ-test.

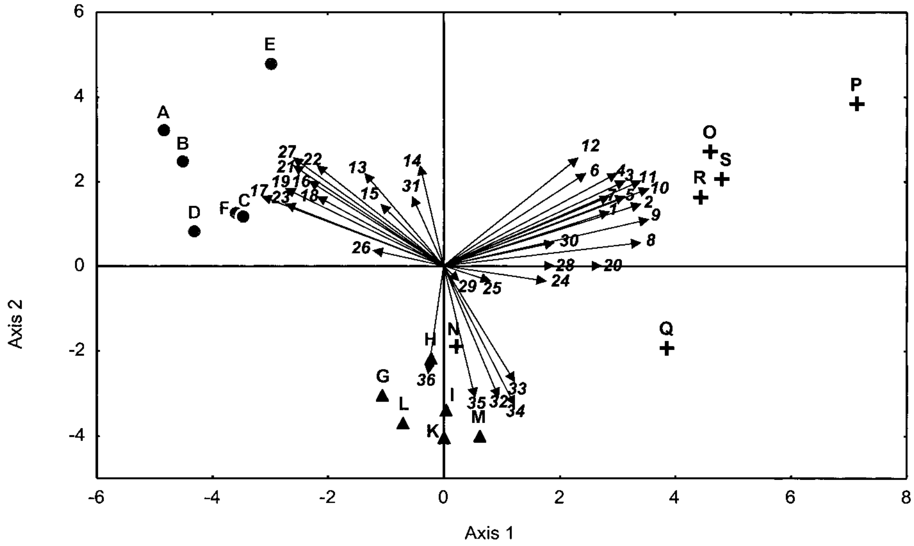

Fig. 11. PCA ordination diagram of 1st and 2nd axis. Letters refer to population indices (A–F: Georgian populations, G–M: Spanish populations, N–S: Irish populations). Numbers and arrows refer to recorded variables.

ves but at the same time large specific leaf areas. In contrast, the median leaf area was smaller in the Spanish and Irish populations; whereas the number of leaves was higher. Total leaf area per marked shoot in 1999 was positively correlated with the number of leaves in Georgian and Spanish populations but not in the Irish ones (Fig. 13b). Although Irish and Spanish rhododendrons did not differ from each other in median leaf area (Table 2), the Irish plants had a larger total leaf area per marked shoot (Fig. 13b). This larger leaf area was attained by a larger number of leaves per shoot. Neither the Irish nor the Spanish individuals achieved full compensation for smaller leaf areas compared to Georgian individuals, but compared to Spanish rhododendrons, the Irish ones managed to make up for losses to a higher degree.

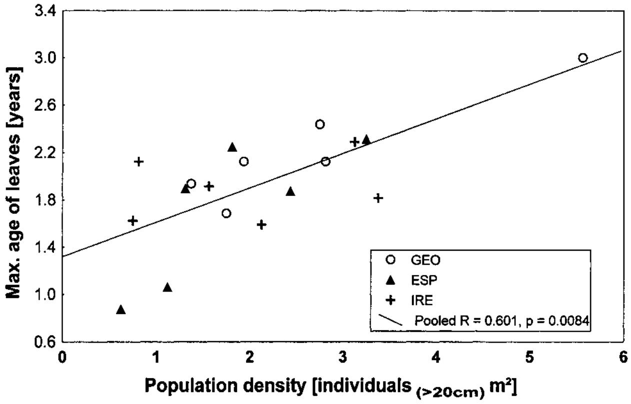

Fig. 12. The relationship between age of leaves based on the mean of 16 individuals in a population and population density assessed by 16 transect squares in a population.

Discussion

The three provenances of *Rhododendron ponticum* were clearly differentiated with respect to morphological and plant ecological characteristics. According to Baker (1974), rapid growth, high seed production, vigorous vegetative reproduction and competitiveness, in particular, can be expected to be of importance for an invasive species. At first glance, these assumptions seem to apply for *Rhododendron ponticum* in general. However, we clearly showed that some factor groups of invasive traits were explicitly connected to Irish *Rhododendron*, whereas others were not.

A larger size, which is often mentioned as an attribute of invaders (Blossey & Nötzold 1995; Crawley 1987), was associated with Spanish rhododendron, rather than with the invasive Irish ones. Spanish populations are striking for their high fraction of king-sized and comparably old individuals. Thus, the generalisation that more species are larger as aliens than as natives (Crawley 1987) cannot be confirmed. Recent studies contend that these summarising observations do not comply with essential requirements of comparability and, thus, reject any generalisation for reasons of sampling bias (Simons 2003). Thébaud & Simberloff (2001) also refused any generalised assumption of increased height in invasive plants in their introduced range. They utilised the Flora Europaea data, as did Crawley (1987), supplemented by California and Carolina records to perform reciprocal comparisons. The former authors compared floras of native and introduced range and looked for tendencies of plants to be taller in some particular region, no matter what their origin, and demonstrated that, apart from an origin effect, an effect of destination, i.e. of habitat, applied, too. It is

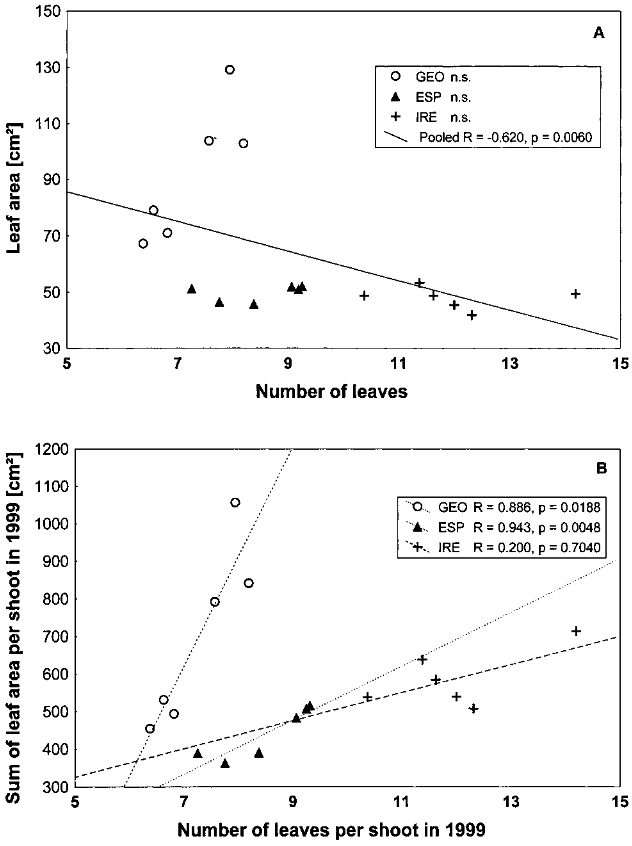

Fig. 13. The relationship between A) leaf area and number of leaves and B) sum of leaf area per shoot in 1999 and number of leaves in 1999. Each value is based on the mean of 16 individuals in a population.

possible that, in the present study, the restriction to populations at forest sites in all countries might have influenced the results of plant size, since many rhododendron in Ireland can be found in open areas, where they attain larger sizes than those recorded in the present study. Ultimately, this matter can only be answered by reciprocal transplant experiments (Bruelheide 1999; Willis et al. 2000).

Another factor associated with invasiveness is clonal spreading. However, this characteristic was typical for Georgian rather than Irish populations. Pornon et al. (2000) could demonstrate that layering is only weakly developed or absent in younger populations but extensively developed in closed and mature ones in *Rhododendron ferrugineum*. Although we did not find high proportions of clonality for Spanish populations, Mejías et al. (2002) reported that in many cases excavation revealed a layering origin from a bigger plant. These authors discuss the meaning of a variable balance between sexual reproduction and vegetative multiplication depending on environmental condition. However, although vegetative propagation was encountered in single Irish populations, clonality does not seem to be a prominent factor in invasiveness of *Rhododendron ponticum* in Ireland.

The results confirmed our first hypothesis that Irish populations show higher growth rates than native ones. Since the high growth rates are the most prominent feature of the Irish populations, they are quite probably the decisive factor to explaining the invasion success of *Rhododendron ponticum*. They might be genetically or environmentally determined. For example, in greenhouse experiments *Lythrum salicaria* shows a better growth in introduced populations from North America than in native ones from Europe and Asia (Bastlová & Kvet 2002). Willis et al. (1999) documented higher plant growth for non-indigenous genotypes of *Lythrum salicaria* from Australia and the USA compared to indigenous ones, although these differences were not significant. Greenhouse experiments with different *R. ponticum* origins also confirmed highest growth rates for the Irish populations (unpublished data). In contrast, a common garden experiment with native and invasive provenances of *Carduus nutans*, *Digitalis purpurea*, *Echium vulgare* and *Senecio jacobaea* provided only little support for a genetically determined trait, but supported the hypothesis of a response to benign environmental conditions in the new area of introduction (Willis et al. 2000).

It is probable that both concepts apply for *Rhododendron ponticum*. Depending on whether invasive Irish and Georgian or Irish and Spanish populations are compared, the differences seem to have either a genetical or an environmental explanation. With respect to, most probably, genetically fixed traits, i.e. of leaf morphology, the Irish individuals differ from Georgian ones, but show high similarity to Spanish rhododendrons. These results agree with the finding that invasive British populations have mainly originated from Spanish populations (Milne & Abbott 2000). Thus, the differences in leaf morphology, which ascribe large and persistent leaves to Georgian populations, are probably due to taxonomical separation of the two subspecies.

Shorter-lived leaves might be associated with lower construction costs in Irish rhododendron. Nagel & Griffin (2001) reported lower area-based leaf construction cost values for invasive *Lythrum salicaria* plants compared to five co-occurring herbaceous plants and shrubs. They suggested that the production of more photosynthetic leaf surface area with lower energy expense, resulting from either lower requirements or higher energy efficiency, would help to outcompete neighbouring native species. These results agree with those obtained in the study of Baruch & Goldstein (1999). In a comparative investigation between native and invasive species in Hawaii, the authors showed that invasive plants had a higher specific leaf area and lower construction cost than native ones. The authors ascribe this to a generally more efficient use of resources combined with higher growth rates of invasive species. Nevertheless, a less costly leaf construction compared to Georgian individuals applies similarly to Spanish ones and, thus, does not explain why Spanish rhododendron are less invasive than Irish ones. The obvious answer can only be that Spanish populations are climatically constrained. The fact that Irish rhododendron have profited from a release from climatic restrictions is expressed, on the one hand, by rapid and high growth, and on the other hand by only brief interruption during winter periods as seen by the recorded numbers of internodes in Irish populations. For Irish sites in general, two to three periods of stem elongation are mentioned, in May-June and July-August, a third period may occur in September and a few buds might already open in February (Cross 1975). The pattern of range expansion also supports this view since the spread of invasive rhododendron in their new range mainly concentrates on the West coasts of Ireland and Britain, thus, apparently profiting from climatically suitable conditions (Usher 1986). Additionally, the hypothesis that a release from climatic constraints is effective was also supported by own observations: Spanish rhododendron individuals once transplanted to an Irish forest site developed well under local conditions (unpublished data).

Environmental conditions, in general, also seem to be of vital importance for the second key factor of Irish populations, i.e. reproduction. Sexual reproduction was limited in both native origins but was high in Ireland, this confirming our second hypothesis. Reduced fruit set seems to be less important in a natural setting. Similarly, reduced germination capacity is also of little import, as laboratory experiments have shown (personal observations). In contrast, failure of seedling establishment seems to be crucial. These findings agree with the results of Mejías et al. (2002), who studied population structure and reproduction patterns in 20 sampled *Rhododendron* populations in Southern Spain. Some of their populations are identical to our own study sites (G, H, K, L). Mejías et al. (2002) concluded that in spite of relatively high fruiting rates, recruitment in Spanish populations is low and depends on the availability of safe sites. Cross (1975) found similar requirements for successful recruitment in Ireland, but Irish sites offer a higher number of suitable sites that shield seedlings from drought. The occurrence of safe sites in Spain is closely restricted to the contact zone of the rivers, where humid soils and bryophyte carpets can be found (Mejías et al. 2002). We can also confirm this by additional observations in two Spanish populations (I and K) along the waterline, where seedling densities of 0.1 and 7.1 seedlings per m^2 were encountered in 2000 (personal observation). Mejías et al. (2002), thus, hypothesized, that the main invasion process in invaded Western European areas occurs by effective seedling recruitment. The actual findings are in accordance with the results of Grigulis et al. (2001). The authors studied demographic parameters in the life cycle of *Echium plantagineum* both in its native area in Mediterranean Europe as well as in invaded ranges in Australia. They found seedling establishment in Australia that is five times greater than in native habitats; whereas the proportion of seed bank loss during the germination period was similar between both sites, thus, indicating a lower number of safe sites for seedling establishment in the species' native range.

Despite the findings of a clear trait complex promoting invasiveness in Irish populations, the large variation in these traits among Irish populations should not be ignored. In the area of introduction, the performance of individuals (and populations) with respect to growth and seedling establishment varied to a much higher degree than in the species' native area. Not all Irish populations showed the observed key factors to the same degree, i.e. some were more similar to Spanish populations. Whether these circumstances are caused by a corresponding variability of habitat specifics or whether they are the result of different genotypes cannot be assessed by observational studies. Growth experiments with populations from all provenances under controlled conditions and profound analyses of site conditions to correlate seedling establishment with environmental characteristics are necessary to distinguish between specific invasive traits and a pure habitat effect or even genotype-environment interactions.

In any case, we can draw the conclusion that growth rates and seedling recruitment, in particular, affect the invasion success of *Rhododendron ponticum* in the British Isles, and that both, genotype and environment, have a strong impact on this process.

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