Journal of Ecology 2000, **88**, 436–446

Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe

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Summary

1 The geographical variation of seed production, predation and abortion was analysed in *Juniperus communis* for 31 populations in seven distinct regions throughout the species' distribution range in Europe, including both the northern and southern boundaries.

2 The number of seeds per cone and the number of filled seeds per cone varied significantly between geographical regions and among populations within regions. Populations from the Mediterranean mountains (south-east Spain) showed the highest values in the number of seeds per cone but the lowest values in the number of filled seeds per cone.

3 Losses due to predispersal seed predation varied significantly among populations within a region but not between regions, suggesting that predation incidence depends on local-scale factors. Seed abortion rates were higher in southern Iberian populations than in the other regions, and varied significantly among populations and regions. As a result of predation and abortion, seed production was lowest in the Iberian regions.

4 Seed abortion showed a significant quadratic relationship with latitude, with higher values of abortion at either end of the gradient, but particularly at the southern limit.

5 The production of filled seeds declined gradually towards both northern and southern distribution limits. In the Mediterranean mountains (southern limit), low seed production coincided with a marked limitation placed upon natural regeneration by summer drought, leading to a demographic bottleneck in populations. Although seed abortion levels were relatively high in the subarctic tundra (northern limit) populations, they were free from predispersal seed predators, suggesting that population viability here may be under less pressure.

Key-words: geographical patterns, *Juniperus communis*, predispersal seed predation, seed abortion, seed production, latitudinal gradients, distribution boundaries.

Journal of Ecology (2000) **88,** 436–446

Introduction

The geographical range of many plant species is determined by climate (Woodward & Williams 1987; Woodward 1990; Pigott 1992; Archibold 1995). In the northern hemisphere, low temperatures often limit the viability of plant populations at their northern boundary (e.g. Marshall 1978; Woodward 1990, 1997; Pigott 1992; Loik & Nobel 1993), while water availability is the main limiting factor at the southern boundary (e.g. Pigott & Pigott 1993; Gardner & Fisher 1996; García *et al.* 1999). These abiotic factors can have marked effects by increasing the mortality of individuals, especially those in juvenile stages, and by depressing reproductive capacity

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due to severe reduction in the production of fertile, filled seeds (Woodward 1990; Pigott 1992; and references therein).

Analysis of the production of healthy seeds throughout the distribution range of a plant species is thus crucial in order to determine population viability at a broad geographical scale. A reduction in reproductive ability would be expected due to increased genetic drift and inbreeding depression in those populations situated in marginal areas of the range, as these represent a genetically impoverished situation relative to populations in the centre of distribution (Brussard 1984; Hoffmann & Blows 1994; Kärkkäinen *et al.* 1996; Nantel & Gagnon 1999). Reduction in seed production for genetic reasons can also occur in small, fragmented populations (Ellstrand & Elam 1993; Aizen & Feisinger 1994; Fischer & Matthies 1997, 1998; Jules 1998). Seed set can also change in response to climatic and latitudinal gradients. It is known that seed production decreases dramatically in the northernmost populations of several tree species due to climatic stress (Pigott 1989, 1992; Pigott & Huntley 1981; Hofgaard 1993; Despland & Houle 1997). Reduction in seed fertility among populations in marginal, climatically stressful areas can lead to regeneration failure and, ultimately, extinction (Ward 1981, 1982; Pigott & Huntley 1981; Pigott 1989, 1992; Woodward 1990). Despite repeated evidence that the production of viable seeds is a limiting factor in populations at their northern limits (e.g. Pigott & Huntley 1981; Pigott 1989, 1992), no studies have compared seed viability at the northern and southern boundaries of a species' distribution. The relationship between reproductive capacity and the potential for population regeneration at distribution limits is therefore poorly understood.

Common juniper *Juniperus communis* L. (Cupressaceae) is among the most widely distributed gymnosperms in the Holarctic, ranging from circum-Mediterranean mountains up to subarctic tundra (Jalas & Suominen 1985; Polunin & Walters 1985). This species shows a continuous distribution in northern and central Europe, but populations become progressively more fragmented towards the Mediterranean Basin, where the species is located exclusively in high-mountain areas. These populations, such as those in the southern Iberian peninsula, are characterized by a very low regeneration ability under natural conditions (García *et al.* 1999). In addition, low seed production in juniper has frequently been associated with high levels of predispersal seed predation and extensive seed abortion (Chambers *et al.* 1999), with populations in southern Spain showing lower fertility than those at northern latitudes (e.g. Ward 1982; Houle & Babeux 1994; García 1998a). In the present paper, we analyse the geographical variation of total seed production in *J. communis*, and also consider seed losses due to predispersal seed predation and seed abortion. We carried out large-scale sampling throughout the species' latitudinal gradient in Europe, including populations from the centre as well as from the northern and southern boundaries of the distribution range. The main questions we address are: (i) how does production, abortion and predation of common juniper seed change at different spatial scales (both among populations within a region and between regions); (ii) is there any relationship between viable (filled) seed production and latitude; and (iii) is there a relationship between limited reproductive capacity (in terms of filled seed production) and population regeneration at its distribution boundaries?

NATURAL HISTORY

Juniperus communis is a typical shrub of poor soils and harsh environments. In central and northern Europe, it grows at low altitudes in pasture lands, abandoned fields, and clearcuts, as well as at high altitudes, in subalpine meadows above the treeline in Eurosiberian mountains and in dry shrublands in circum-Mediterranean mountains. It is also found in the taiga–tundra limit in northern Europe (e.g. Kallio *et al.* 1971; Falinski 1980; Ward 1981; Jalas & Suominen 1985; Polunin & Walters 1985; Franco 1986; Rosén 1988). Juniper populations in the southern Iberian Peninsula constitute the southernmost examples in Europe and can be considered to represent the southern geographical limit of the species (see also Jalas & Suominen 1985). Although several varieties or subspecies have been described, the genetic basis for different ecotypes is poorly documented (Kallio *et al.* 1971; Franco 1986).

This species is a dioecious and wind pollinated. Every spring, female individuals bear axillary cones which take more than 2 years to develop into fleshy spherical structures, called galbulae (Roques 1983; Chambers *et al.* 1999). Cones ripen fully in the autumn of the third year of development, becoming blue-grey coloured, *c.* 6.5 mm in diameter and containing 1–3, rarely 4, seeds per cone. Some seeds abort even within well-developed cones. Aborted seeds show an undeveloped embryo that does not fill the seed locule, whereas healthy (filled) seeds show a white, oily embryo and nucella that entirely fills the seed locule. Externally, aborted seeds are indistinguishable from filled seeds, since the seed coat develops normally irrespective of the embryo abortion.

Juniper seeds and cones are attacked by several insect species (see Ward 1981; Roques 1983), although the main predispersal seed predator is *Megastigmus bipunctatus* Swed. (Hymenoptera, Torymidae; see García 1998a). This chalcid, which is distributed throughout Europe and Central Asia (Vikberg 1966; Roques 1983; Roux & Roques 1996), is specific to *J. communis* and *J. sabina*, and its pre-

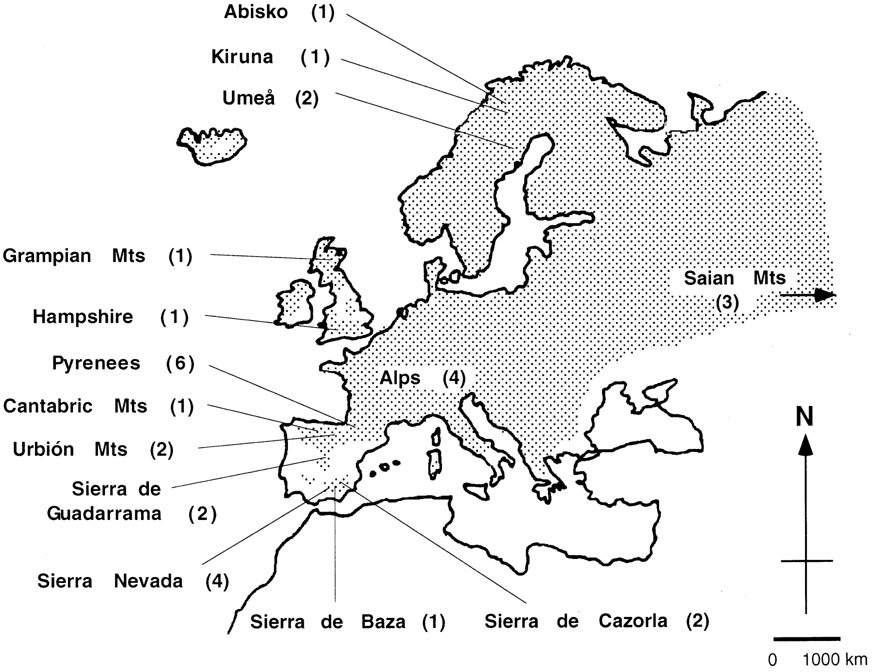

Fig. 1 Geographical areas and populations sampled for the study of seed production, predation and abortion in *Juniperus communis*. Figures in parentheses indicate the number of populations sampled for each area. The distribution of *J. communis* in Europe is represented by the dotted area (after Jalas & Suominen 1985).

dation is easily distinguishable from other predatory species (see Vikberg 1966; Roques 1983).

Methods

We collected 21 586 ripe cones from 572 *J. communis* plants in 31 populations sampled during the autumn of 1994, 1995 and 1996. Sites were grouped within seven geographical regions: southern Iberian Peninsula, central Iberian Peninsula, northern Iberian Peninsula, Alps, Great Britain, Saian Mountains and northern Scandinavia (see Fig. 1 and Table 1 for population descriptions and sample sizes). This geographical division was made according to the marked biogeographical differences among sites and in order to ensure an adequate sample size within each region.

Within each population, we selected female shrubs by walking along randomly located transects within local areas of 10–30 ha. Our aim was to sample a representative population of the reproductive shrubs belonging to a variety of plant sizes and cone crop sizes that were present in a given location and sampling period. Random samples of 30–70 ripe cones per plant were taken and bagged for later analysis. All cones were opened in the laboratory and the seeds examined individually. Each seed was assigned to one of the following categories: *predated*, showing signs of predation; *aborted*, having an undeveloped embryo; and *filled*, having an undamaged, well-developed embryo. Seed predation was invariably attributable to *M. bipunctatus* in all the sampled plants and populations. Only seeds in the filled category were considered to contain a living embryo (D. García, personal observation; see also Houle & Babeux 1994).

For each plant, we calculated: (i) the total number of seeds per cone, the number of depredated, aborted and filled seeds per cone, averaging all the sampled cones for each plant; and (ii) the proportion of predated, aborted and filled seeds, relative to the overall seed sample per plant.

STATISTICAL ANALYSIS

Geographical variation in seed production, predation and abortion was analysed using a nested ANOVA, considering as main factors 'region' and 'population' nested within region (random factors) for each one of the following dependent variables: mean numbers of total and filled seeds per cone (averaged within plants) and proportions of predated, aborted and filled seeds per plant. The variance components and significance for this model was estimated with GLM and VARCOMP procedures (SAS Institute Inc. 1997), considering the unbalanced design and using type III sum of squares (Ayres & Thomas 1990; Shaw & Mitchell-Olds 1993). To determine the difference in the proportion of aborted seeds per plant between populations in

Table 1 Characteristics of the 31 *Juniperus communis* populations sampled: geographical location, elevation, sampling date and sample sizes of plants, cones and seeds for each population

Region	Area	Population	Code	Co-ordinates	Elevation (m a.s.l.)	Date	No. of plants	No. of cones	Total no. of seeds
Southern Iberian Peninsula	Sierra Nevada, Granada, Spain	Campos de Otero	1	37°06′ N, 3°21′ W	2200	1995	75	2551	6240
	Sierra Nevada, Granada, Spain	Dornajo	2	37°06′ N, 3°21′ W	1900	1995	19	360	584
	Sierra Nevada, Granada, Spain	Trevenque	3	37°06′ N, 3°21′ W	1600	1995	20	608	1396
	Sierra Nevada, Granada, Spain	Maitena	4	37°06′ N, 3°21′ W	2100	1995	20	785	1868
	Sierra de Baza, Granada, Spain	Boleta	5	37°18′ N, 2°27′ W	2000	1995	20	654	1674
	Sierra de Cazorla, Jaén, Spain	Collado Cabañas	6	37°36′ N, 3°03′ W	2000	1995	20	655	1427
	Sierra de Cazorla, Jaén, Spain	Nava las Correhuelas	7	37°42′ N, 3°06′ W	1700	1994	12	182	451
Central Iberian Peninsula	Sierra de Guadarrama, Madrid, Spain	Puerto Navacerrada	8	40°29′ N, 3°33′ W	2200	1996	20	787	2085
	Sierra de Guadarrama, Madrid, Spain	Valdesquí	9	40°28′ N, 4°06′ W	1900	1996	20	646	1700
Northern Iberian Peninsula	Sierra Cebollera, Soria, Spain	Puerto Sta. Inés	10	42°02′ N, 2°21′ W	1650	1996	20	776	2161
	Sierra de Urbión, Soria, Spain	Puerto Piqueras	11	42°02′ N, 2°18′ W	1450	1996	20	730	1956
	Western Pyrenees, Navarra, Spain	Lakora N	12	42°34′ N, 0°33′ W	1500	1995	12	646	1505
	Western Pyrenees, Navarra, Spain	Lakora S	13	42°34′ N, 0°33′ W	1500	1995	9	454	954
	Western Pyrenees, Navarra, Spain	Belagoa	14	42°33′ N, 0°33′ W	1000	1995	11	582	1191
	Western Pyrenees, Navarra, Spain	Piedra S. Martín	15	42°33′ N, 0°32′ W	1750	1996	19	739	1896
	Western Pyrenees, Navarra, Spain	Orhy	16	42°35′ N, 1°01′ W	1450	1996	18	674	1864
	Central Pyrenees, Huesca, Spain	Hecho	17	42°24′ N, 0°25′ W	1700	1996	20	780	2202
	Cantabric Mountains, Asturias, Spain	Somiedo	18	43°05′ N, 6°09′ W	1000	1996	10	323	607
Alps	Swiss Alps, Uri, Switzerland	Andermatt	19	46°23′ N, 8°22′ E	1750	1995	5	510	1016
	Swiss Alps, Uri, Switzerland	Oberalppass	20	46°23′ N, 8°01′ E	1900	1995	13	1166	2842
	Swiss Alps, Oberland, Switzerland	Eigergletscher	21	46°20′ N, 8°11′ E	2100	1995	6	212	394
	Swiss Alps, Oberland, Switzerland	Grimselsee	22	46°20′ N, 8°20′ E	2200	1995	8	370	700
Great Britain	Hampshire, England, UK	Noar Hill	23	51°03′ N, 0°34′ W	200	1996	22	790	1556
	Grampian Mountains, Scotland, UK	Glen Gairn	24	57°03′ N, 3°06′ W	410	1996	6	129	260
Saian Mountains	Buriatia, Siberia, Russia	Arshan 1	25	51°33′ N, 99°32′ E	800	1995	13	912	1623
	Buriatia, Siberia, Russia	Arshan 2	26	51°33′ N, 99°32′ E	800	1995	24	1008	1389
	Buriatia, Siberia, Russia	Arshan 3	27	51°33′ N, 99°32′ E	800	1995	4	115	214
Northern Scandinavia	Umeå, Västerbottens, Sweden	Nydala 1	28	63°30′ N, 20°09′ E	100	1994	25	728	1689
	Umeå, Västerbottens, Sweden	Nydala 2	29	63°30′ N, 20°09′ E	100	1996	20	1078	2189
	Kiruna, Lapland, Sweden	Kiruna	30	67°32′ N, 20°09′ E	400	1996	23	519	844
	Kiruna, Lapland, Sweden	Abisko	31	68°13′ N, 18°30′ E	600	1996	38	1195	1881

the southern Iberian peninsula and each of the remaining regions, we fitted a posteriori contrasts (differences in the Minimum Square Mean) and pairwise comparisons for the above model.

The relationship between latitude and seed viability was assessed using regression models with latitude as the independent variable and the proportions of predated, aborted and filled seeds per plant as the dependent variables. We used simple and second-order regression models, choosing the latter only when it showed a higher R^2 and significance level (see Aizen & Woodcock 1992 for a similar procedure). As latitude was expressed in whole degrees, in order to avoid pseudoreplication we used the mean value of the dependent variables as a sample unit in the regression model for those populations sharing the same latitude degree (Hulbert 1984). We included in this analysis the data on the proportions of predated, aborted and filled seeds reported by Ward (1982) for several populations in southern England (Breck, Roche Court 1, Roche Court 2 and Blakes Firs, latitude = 51°).

Significance of the statistical analyses used in the present study were fixed to the standard level, $P < 0.05$ (Zar 1996). However, when analysing more than one related variable, to avoid an increase in Type I errors, we chose the sequential Bonferroni test for fitting the significance level (for $k > 3$, see Rice 1989). When necessary, variables were transformed for normality, homoscedasticity and linearity, using the arcsine transformation for data expressed as frequencies, and the log transformation for all others (Zar 1996).

Results

VARIATION IN SEED NUMBER PER CONE

The total number of seeds per cone was highly variable among regions. The highest values tended to be found in the three regions of the Iberian Peninsula, with the lowest means in the Saian Mountains (Fig. 2). Conversely, the number of filled seeds per cone showed the lowest values in the three regions of the Iberian Peninsula, and the highest values in the Saian Mountains (Fig. 2). The total number of seeds per cone showed a significant negative correlation with the number of filled seeds per cone ($r_s = -0.857$, $P = 0.014$, $n = 7$ regions, Spearman rank correlation) and a significant positive correlation with the number of aborted seeds per cone ($r_s = 0.928$, $P = 0.002$, $n = 7$ regions). The total number of seeds per cone varied significantly between both regions and populations, with region and population effects accounting for 58.7% of the variance in the number of seeds per cone (Table 2). Region and population also explained significant amounts of variation in the number of filled seeds per cone (Table 2).

VARIATION IN THE PROPORTION OF PREDATED, ABORTED AND FILLED SEEDS

The percentage of predated seeds varied significantly between populations for each of the regions considered, but not among regions (Table 2, Fig. 3). Seed predation was higher in the Iberian Peninsula, particularly in the central and northern regions, than in the other regions of Europe, although the highest

Table 2 Summary of nested ANOVAs with region and population within region as main factors and the number of seeds per cone, the number of filled seeds per cone and the percentages of predated, aborted and filled seeds per plant as dependent variables. The sums of squares (SS), *F*-ratio, the significance levels (* $P < 0.05$ with Bonferroni adjustment), and the percentages of variance explained by main factors are shown (d.f.: Region = 6, Population = 24, Residual = 541 for each model)

		SS	*F*	*P*	% variation
No. of seeds per cone	Region	1.03	5.14	0.0015 *	29.96
	Population [Region]	0.96	13.40	< 0.0001 *	28.72
	Residual	4.28			
No. of filled seeds per cone	Region	2.18	3.72	0.0089 *	21.44
	Population [Region]	2.81	12.44	< 0.0001 *	31.09
	Residual	5.08			
% of predated seeds per plant	Region	4.06	1.52	0.2128	5.86
	Population [Region]	12.86	17.52	< 0.0001 *	45.76
	Residual	16.55			
% of aborted seeds per plant	Region	17.74	7.86	< 0.0001 *	33.87
	Population [Region]	10.69	7.63	< 0.0001 *	18.20
	Residual	31.58			
% of filled seeds per plant	Region	27.88	9.74	< 0.0001 *	44.35
	Population [Region]	13.67	10.54	< 0.0001 *	19.65
	Residual	29.25			

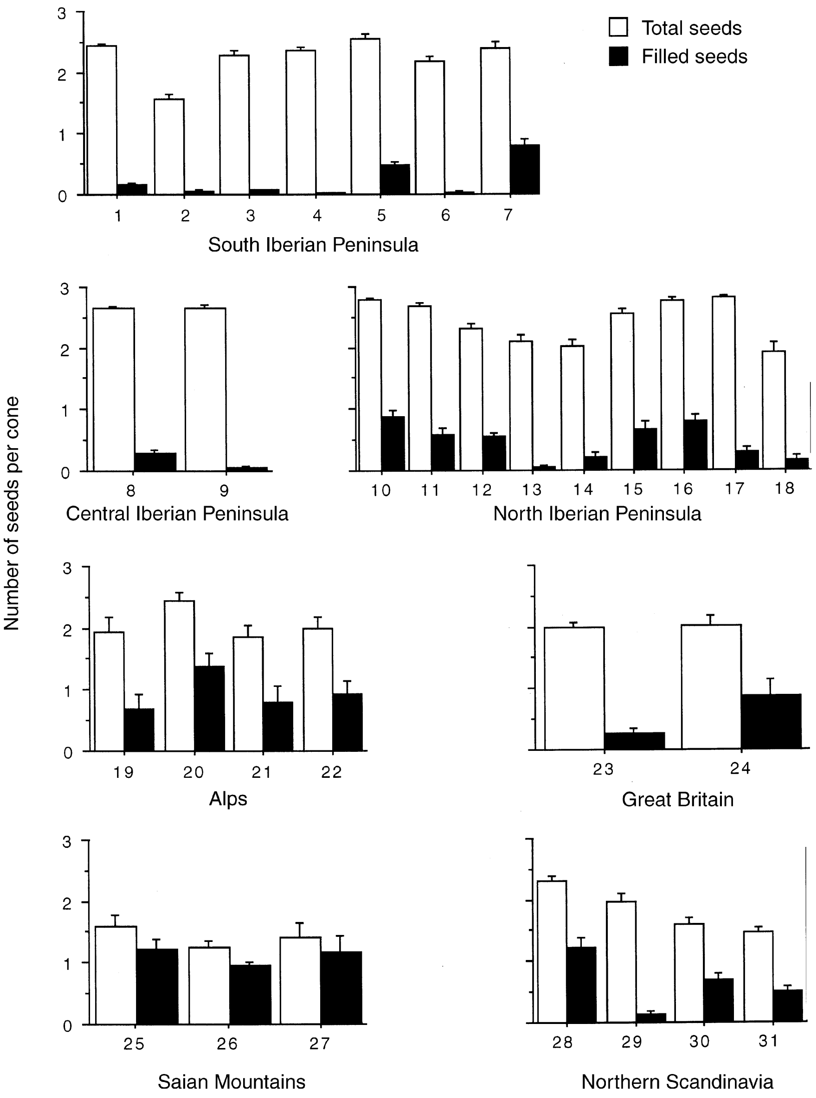

Fig. 2 Mean values (+ SE) of the total number of seeds per cone and the number of filled seeds per cone in different populations of *Juniperus communis*, located in different regions in Europe (see Table 1 for population codes and sample sizes).

percentage of predated seeds was recorded in Sweden (Fig. 3). Zero predation was recorded in two populations in the Alps, one in the Saian Mountains, and the populations above the Polar Circle in northern Scandinavia (Kiruna and Abisko).

Seed abortion was higher in the Iberian regions, with the highest values in the southern Iberian Peninsula (Fig. 3). In contrast, the percentage of aborted seeds per plant in the Saian Mountains' populations did not exceed 18%. Intermediate values were recorded in the Alps, Great Britain and northern Scandinavia (Fig. 3). Both population and region were significant factors affecting the percentage of aborted seeds per plant, with regional differences accounting for a higher percentage of variance than population differences (Table 2). The percentage of aborted seeds in the southern Iberian Peninsula was significantly higher than in other regions ($t > 2.37$, $P < 0.05$ after Bonferroni, d.f. = 1, for all pairwise contrasts between southern Iberian Peninsula and the other regions).

As a result of seed predation and seed abortion, the percentage of filled seeds in Iberian regions averaged less than 11%; the lowest value for populations in this area being 1.4% (Fig. 3). At the other extreme, most of seeds from Saian Mountains' populations were healthy. The remaining regions showed intermediate values in the percentage of filled seeds (Fig. 3). Region and population together accounted for 64% in the variation of the percentage of filled seeds, both factors being significant in the nested ANOVA model (Table 2).

Across regions, the number of seeds per cone correlated significantly with the percentage of aborted seeds per plant ($r_s = 0.857$, $P = 0.013$, $n = 7$ regions,

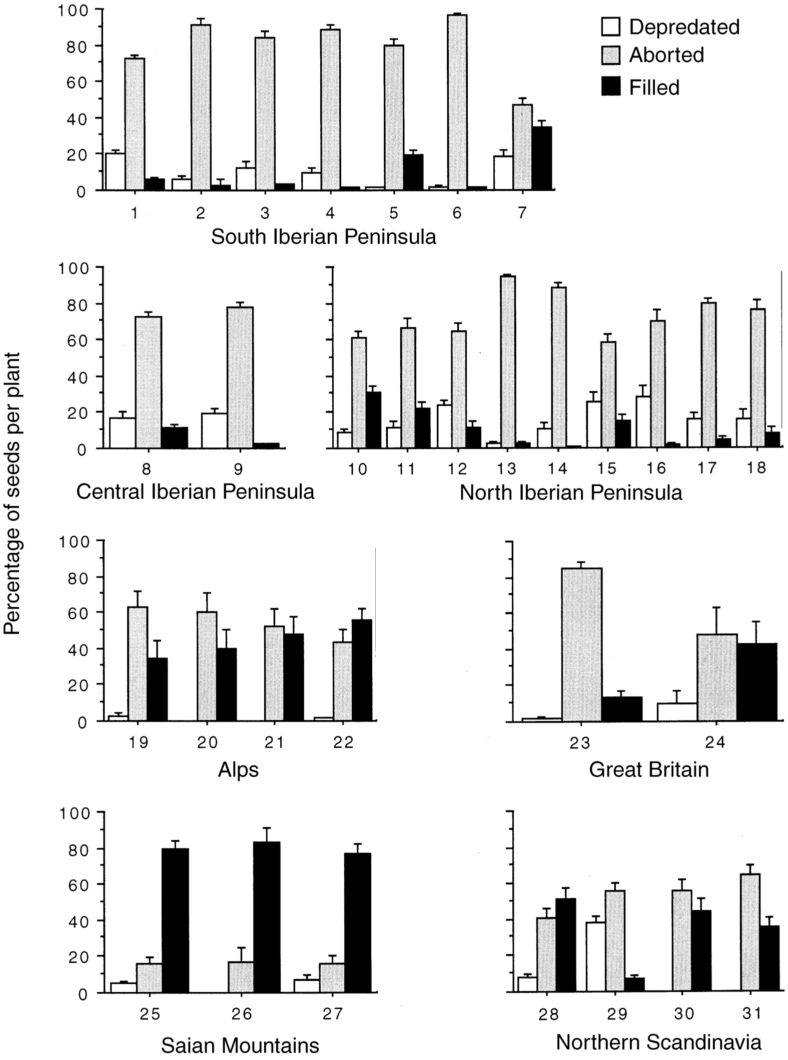

Fig. 3 Mean values (+SE) of the percentages of predated, aborted and filled seeds per plant in different populations of *Juniperus communis*, located in different regions in Europe (see Table 1 for population codes and sample sizes).

Spearman rank correlation) and, negatively, with the percentage of filled seeds per plant ($r_S = -0.821$, $P = 0.023$, $n = 7$ regions). The percentage of predated seeds in different regions was independent of the number of seeds per cone in these regions ($r_S = 0.643$, $P = 0.119$, $n = 7$ regions).

RELATIONSHIP BETWEEN LATITUDE AND SEED PRODUCTION, PREDATION AND ABORTION

Seed predation was independent of latitude ($y = 1.91 - 0.96x$; $R^2 = 0.26$, $F = 2.90$, $P = 0.126$, $n = 10$, simple regression analysis). However, the percentage of aborted seeds per plant showed a significant quadratic relationship with latitude (Fig. 4), with the highest values of seed abortion at the two extremes of the latitudinal gradient (especially in the southern limit, corresponding to populations in the southern Iberian Peninsula) and the lowest at central latitudes ($y = 43.56 - 49.09x + 14.08x^2$, $R^2 = 0.77$, $F = 11.74$, $P = 0.005$, $n = 10$, polynomial regression analysis). Consequently, the percentage of filled seeds tended to increase at central latitudes and decrease at the southern and northern latitudinal limits ($y = -44.02 + 50.78x - 14.41x^2$, $R^2 = 0.66$, $F = 6.71$, $P = 0.023$, $n = 10$, polynomial regression analysis).

Discussion

GEOGRAPHICAL VARIATION IN SEED PRODUCTION

Our results show a hierarchical pattern of spatial variation in seed production in *J. communis* over its

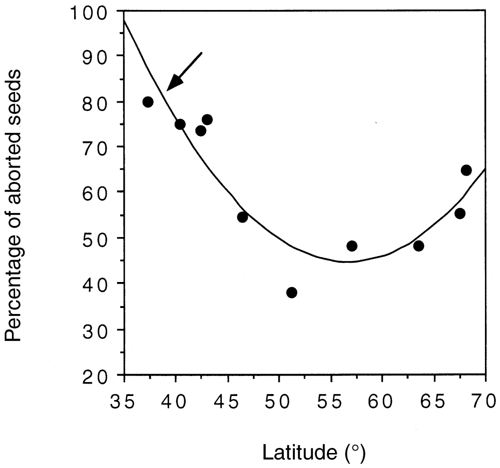

Fig. 4 Variation in the percentage of aborted *Juniperus communis* seeds per plant in relation to the latitude. Each point represents the mean values for both variables for those populations sharing the same degree of latitude. The arrow indicates the point corresponding to the southern Iberian Peninsula. The curve resulting from the regression analysis is also shown.

range in Europe. Despite among-population differences, most of the variation in the numbers of aborted and filled seeds per cone can be explained by regional differences; variation in the percentages of aborted and filled seeds per plant are also primarily accounted for by regional differences (Table 2 and Figs 2 & 3). However, filled seed production decreased significantly towards both northern and southern ends of the latitudinal gradient, with populations located in the Iberian Peninsula, especially those from the Mediterranean high-mountains, showing the lowest values of filled seed production.

The geographical variation in the percentage of aborted seeds paralleled the variation in the number of seeds per cone, with the regions showing more seeds per cone also having higher seed abortion rates. This trend could be considered a negative trade-off between seed number and seed fertility (producing less seeds per cone but filling more of them, Stephenson 1981; Lee 1988; see also Houle & Babeux 1994) and is expressed at a suprapopulation scale (Hiura *et al.* 1996). However, the increased number of seeds per cone involved not only a higher number of aborted seeds per cone but also a significant drop in both the number and proportion of filled seeds. Therefore, even compared to regions with a similar cone crop, the Iberian Peninsula was at a reproductive disadvantage, producing a smaller crop of filled seeds per plant.

The regional and latitudinal patterns of seed production reported here suggest that seed abortion in juniper is controlled by climatic factors that ultimately limit pollen availability and depress vegetative growth and reproductive output. Thus, juniper seed viability strongly declines towards regions having harsher environments, for example, the mountains of the Mediterranean Basin and the subarctic tundra of northern Sweden (see also Houle & Babeux 1994). These two contrasting regions are characterized by a long cold winter in the Arctic tundra (Wielgolaski 1997) and a cold winter coupled with a dry summer in the Mediterranean high mountains (Montávez *et al.* 1996), which result in a short period for vegetative growth and reproduction in both areas. This can negatively influence seed development in gymnosperms by diminishing pollination success and increasing ovule abortion and embryo losses after fertilization (Owens *et al.* 1982, 1991; Hofgaard 1993; Houle & Filion 1993; Despland & Houle 1997; and references therein). In addition, the negative consequences of adverse climate in terms of seed production would be exacerbated by the long developmental period of *J. communis* seeds and cones (3 years from cone set to ripening, see also Despland & Houle 1997; Chambers *et al.* 1999).

In addition to climatic effects, the geographical pattern in juniper seed production may also be related to genetic factors. This idea is supported by the relationship between regional separation and differences in seed abortion as well as by the fact that southern Iberian populations have been physically isolated from the continuous range in Europe since the last Ice Age (Jalas & Suominen 1985; Polunin & Walters 1985; García *et al.* 1999). Thus, the higher seed abortion rate in the southern Iberian Peninsula might also result from the accumulation of deleterious mutations in these relict populations (Levin 1984; Wiens *et al.* 1987; Charlesworth 1989; Owens *et al.* 1991; Husband & Schemske 1996), as inbreeding depression is expected to increase with population fragmentation, shrinking population size and long-term genetic isolation (Ellstrand & Elam 1993; Hauser & Loeschcke 1994; Lande 1994, 1995).

The seed losses due to predation by *M. bipunctatus* varied markedly among populations. These differences may be associated with local conditions, such as among-population variations in seed crop (Rappaport & Roques 1991; Turgeon *et al.* 1994; Jarry *et al.* 1997; García 1998b) or abundance of natural enemies (Kelly *et al.* 1992; Traveset 1991, 1992). However, the strong local differences within regions disappeared when different regions were considered. Thus, chalcid incidence did not appear to be associated with climatic factors operating at a regional scale. It is possible, however, that *M. bipunctatus* has a boreal distribution limit, given that damage by wasp was not observed within the Kiruna and Abisko populations of the Swedish tundra.

REPRODUCTIVE CAPACITY AT GEOGRAPHICAL LIMITS

This study shows a strong correlation between juniper seed production, population fragmentation, distance between populations, and climatic stress. Consequently, the production of filled seeds declines gradually towards the limits of plant distribution. In the case of the southern limit, represented by Mediterranean mountain populations, the lowest frequency of filled seeds (resulting from extreme values of seed abortion and predation) coincides with a serious limitation placed upon natural regeneration (García *et al.* 1999). Although this depressed regeneration appears to be related primarily to low seedling recruitment due to summer drought (García 1998b; García *et al.* 1999), the low percentage of filled seeds is clearly a prime factor adding to this demographic bottleneck. Thus, the regeneration ability of juniper in Mediterranean mountains is constrained not only by the limited availability of microsites suitable for recruitment, but also by greatly reduced seed viability due to seed abortion and predation (see also Eriksson & Ehrlén 1992). Furthermore, juniper recruitment is discouraged in these areas by disturbances such as fire and clearances (Zamora *et al.* 1996). This contrasts with the situation at the northern limit where subarctic populations appear to have fewer limiting factors, i.e. lower levels of seed abortion than at the southern limit and an absence of seed predators. In addition, these subarctic populations form a continuum with the northern part of juniper's distribution range.

In summary, more negative factors are currently acting synergistically to affect juniper population viability at the southern limit than at the northern one. The distribution limit of this species in the southern Iberian Peninsula is composed of remnant populations from a previous period with a milder climate that allowed effective regeneration (Eriksson 1996; García *et al.* 1999). As a result, the southern distribution limit of *J. communis* represents a receding front, while the northern limit appears to represent an advancing front during the current interglacial period (Kallio *et al.* 1971; García 1998b; García *et al.* 1999).

Acknowledgements

We are indebted to numerous people who collaborated with us either in cone sampling, the locating of populations or the provision of facilities for field work: Colin Ryall, Eva M. Iñesta, Encarni Tortosa, Jorge Castro, J. Ramón Obeso, Juan L. García-Castaño, Manuel Carrión, Myriam Márquez, Thomas and Peter Palo, and Olga P. Strezh. Dr Ian Woodward and two anonymous referees provided helpful comments on an earlier version of the manuscript. The Pedagogic Institute of Irkutsk and the University of Granada provided logistic support for our stay in Russia. The Consejería de Medio Ambiente (Junta de Andalucía) permitted our field work in the Natural Parks of Sierra Nevada, Sierra de Baza and Cazorla. David Nesbitt improved the English version of this text. This study has been supported by a grant PFPU-MEC to DG and projects CICYT PB90–0852 and AMB95–0479 (RZ), and PB91–0114 and PB96–0857 (PJ).

References

Aizen, M.A. & Woodcock, H. (1992) Latitudinal trends in acorn size in eastern North American species of *Quercus*. *Canadian Journal of Botany*, **70**, 1218–1222.

Aizen, M.A. & Feisinger, P. (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, **75**, 330–351.

Archibold, O.W. (1995). *Ecology of World Vegetation*. Chapman & Hall, London.

Ayres, M.P. & Thomas, D.L. (1990) Alternative formulations of the mixed-model ANOVA applied to quantitative genetics. *Evolution*, **44**, 221–226.

Brussard, P.F. (1984) Geographic patterns and environmental gradients: the central-marginal model in *Drosophila* revisited. *Annual Review of Ecology and Systematics*, **15**, 25–64.

Chambers, J.C., Vander Wall, S.B. & Schupp, E.W. (1999) Seed and seedling ecology of piñon and juniper species in the Pigmy Woodlands of western North America. *Botanical Review*, **65**, 1–38.

Charlesworth, D. (1989) Evolution of low female fertility in plants: pollen limitation, resource allocation and genetic load. *Trends in Ecology and Evolution*, **4**, 289–292.

Despland, E. & Houle, G. (1997) Climate influences on growth and reproduction of *Pinus banksiana* (Pinaceae) at the limit of the species distribution in eastern North America. *American Journal of Botany*, **84**, 928–937.

Ellstrand, N.C. & Elam, D.R. (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics*, **24**, 217–242.

Eriksson, O. (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, **77**, 248–258.

Eriksson, O. & Ehrlén, J. (1992) Seed and microsite limitation of recruitment in plant populations. *Oecologia*, **91**, 360–364.

Falinski, J.B. (1980) Vegetation dynamics and sex structure of the populations of pioneer dioecious woody species. *Vegetatio*, **43**, 23–38.

Fischer, M. & Matthies, D. (1997) Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). *American Journal of Botany*, **84**, 1685–1692.

Fischer, M. & Matthies, D. (1998) Effects of population size on performance in the rare plant *Gentianella germanica*. *Journal of Ecology*, **86**, 195–204.

Franco, J.A. (1986) Juniperus. *Flora Iberica*, **Vol. I**: Lycopodiaceae–Papaveraceae (eds S. Castroviejo, M. Laínz, G. López, P. Monserrat, F. Muñoz, J. Paiva & L. Villar), pp. 181–188. Real Jardín Botánico, Servicio de Publicaciones del CSIC, Madrid.

García, D. (1998a) Interaction between juniper *Juniperus communis* L. and its fruit pest insects: pest abundance, fruit characteristics and seed viability. *Acta Oecologica*, **19**, 517–525.

García, D. (1998b) *Regeneración natural del enebro* Juniperus communis *L. en áreas de alta montaña mediterránea: conectando la ecología reproductiva con el reclutamiento poblacional*. PhD Thesis, University of Granada, Granada, Spain.

García, D., Zamora, R., Hódar, J.A. & Gómez, J.M. (1999) Age structure of *Juniperus communis* L. in the Iberian peninsula: conservation of remnant populations in Mediterranean mountains. *Biological Conservation*, **87**, 215–220.

Gardner, A.S. & Fisher, M. (1996) The distribution and status of the montane juniper woodlands of Oman. *Journal of Biogeography*, **23**, 791–804.

Hauser, T.P. & Loeschcke, V. (1994) Inbreeding depression and mating-distance dependent offspring fitness in large and small populations of *Lychnis flos-cuculi* (Caryophyllaceae). *Journal of Evolutionary Biology*, **7**, 609–622.

Hiura, T., Koyama, H. & Igarashi, T. (1996) Negative trend between seed size and adult leaf size throught the geographical range of *Fagus crenata*. *Ecoscience*, **3**, 226–228.

Hoffmann, A.A. & Blows, M.W. (1994) Species borders: ecological and evolutionary perspectives. *Trends in Ecology and Evolution*, **9**, 223–227.

Hofgaard, A. (1993) Seed rain quantity and quality, 1984–1992, in a high altitude old-growth spruce forest, northern Sweden. *New Phytologist*, **125**, 635–640.

Houle, G. & Babeux, P. (1994) Variation in rooting ability of cuttings and in seed characteristics of five populations of *Juniperus communis* var. *depressa* from subartic Quebec. *Canadian Journal of Botany*, **72**, 493–498.

Houle, G. & Filion, L. (1993) Interannual variations in the seed production of *Pinus banksiana* at the limit of the species distribution in northern Québec, Canada. *American Journal of Botany*, **80**, 1242–1250.

Hulbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Husband, B.C. & Schemske, D.W. (1996) Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution*, **50**, 54–70.

Jalas, J. & Suominen, J. (1985) *Atlas Florae Europaea*, **Vol. 1**. Cambridge University Press, Cambridge, UK.

Jarry, M., Candau, J.-N., Roques, A. & Ycart, B. (1997) Impact of emigrating seed chalcid, *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), on seed production in a Douglas-fir seed orchard in France and modelling of orchard invasion. *Canadian Entomologist*, **129**, 7–19.

Jules, E.K. (1998) Habitat fragmentation and demographic change for a common plant: *Trillium* in old-growth forest. *Ecology*, **79**, 1645–1656.

Kallio, P., Laine, U. & Mäkinen, Y. (1971) Flora of Inari Lapland, 2. *Reports of the Kevo Subarctic Research Station*, **8**, 92–100.

Kärkkäinen, K., Koski, V. & Savolainen, O. (1996) Geographical variation in the inbreeding depression of Scots pine. *Evolution*, **50**, 111–119.

Kelly, D., McKone, M.J., Batchelor, K.J. & Spence, J.R. (1992) Mast seeding of *Chionochloa* (Poaceae) and predispersal seed predation by a specialist fly (*Diplotoxa*, Diptera: Chloropidae). *New Zealand Journal of Botany*, **30**, 125–133.

Lande, R. (1994) Risk of population extinction from fixation of new deleterious mutations. *Evolution*, **48**, 1460–1469.

Lande, R. (1995) Mutation and conservation. *Conservation Biology*, **9**, 782–791.

Lee, T.D. (1988) Patterns of fruit and seed production. *Plant Reproductive Ecology: Patterns and Strategies* (eds J. Lovett Doust & L. Lovett Doust), pp. 179–202. Oxford University Press, New York.

Levin, D.A. (1984) Inbreeding depression and proximity-dependent crossing success in *Phlox drummondii*. *Evolution*, **38**, 116–127.

Loik, M.E. & Nobel, P.S. (1993) Freezing tolerance and water relations of *Opuntia fragilis* from Canada and the United States. *Ecology*, **74**, 1722–1732.

Marshall, J.K. (1978) Factors limiting the survival of *Corynephorus canences* (L.) Beauv. in Great Britain at the northern edge of its distribution. *Oikos*, **19**, 206–216.

Montávez, J.P., Roldán, C., Rodríguez, A. & Jiménez, J.I. (1996) Primeros resultados de la climatología de Sierra Nevada. *Sierra Nevada: Conservación y Desarrollo Sostenible*, **Vol. I** (eds J. Chacón & J.L. Rosúa), pp. 87–99. University of Granada, Granada, Spain.

Nantel, P. & Gagnon, D. (1999) Variability in the dynamics of northern peripheral versus southern populations of two clonal plant species, *Helianthus divaricatus* and *Rhus aromatica*. *Journal of Ecology*, **87**, 1–14.

Owens, J.N., Simpson, S.J. & Molder, M. (1982) Sexual reproduction of *Pinus contorta* II. Postdormancy ovule, embryo, and seed development. *Canadian Journal of Botany*, **60**, 2071–2083.

Owens, J.N., Colangeli, A.M. & Morris, S.J. (1991) Factors affecting seed set in douglas-fir (*Pseudotsuga menziesii*). *Canadian Journal of Botany*, **69**, 229–38.

Pigott, C.D. (1989) Factors controlling the distribution of *Tilia cordata* Mill. at the northern limits of its geographical range. *New Phytologist*, **112**, 117–121.

Pigott, C.D. (1992) Are the distributions of species determined by failure to set seed? *Fruit and Seed Production: Aspects of Development, Enviromental Physiology and Ecology* (eds C. Marshall & J. Grace), pp. 203–216. Cambridge University Press, Cambridge, UK.

Pigott, C.D. & Huntley, J.P. (1981) Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and cause of seed sterility. *New Phytologist*, **87**, 817–839.

Pigott, C.D. & Pigott, S. (1993) Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. *Journal of Ecology*, **81**, 557–566.

Polunin, O. & Walters, M. (1985). *A Guide to the Vegetation of Britain and Europe*. Oxford University Press, Oxford, UK.

Rappaport, N. & Roques, A. (1991) Resource use and clonal differences in attack rate by the Douglas-fir seed chalcid, *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), in France. *Canadian Entomology*, **123**, 1219–1228.

Rice, W.R. (1989) Analysing tables of statistical tests. *Evolution*, **43**, 223–225.

Roques, A. (1983). *Les Insectes Ravageurs des Cônes et Graines de Conifères en France*. INRA, Paris.

Rosén, E. (1988) Development and seedling establishment within a *Juniperus communis* stand on Öland, Sweden. *Acta Botanica Neerlandica*, **37**, 193–201.

Roux, G. & Roques, A. (1996) Biochemical genetic differentiation among seed chalcid species of genus *Megastigmus* (Hymenoptera: Torymidae). *Experientia*, **52**, 522–530.

SAS Institute Inc. (1997) *SAS/STAT Software: changes and enhancements through release 6.12*. Cary, North Carolina, USA.

Shaw, R.G. & Mitchell-Olds, T. (1993) ANOVA for unbalanced data: an overview. *Ecology*, **74**, 1638–1645.

Stephenson, A.G. (1981) Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics*, **12**, 253–279.

Traveset, A. (1991) Pre-dispersal seed predation in Central American *Acacia farnesiana*: factors affecting the abundance of co-occurring bruchid beetles. *Oecologia*, **87**, 570–576.

Traveset, A. (1992) Effect of vertebrate frugivores on bruchid beetles that prey on *Acacia farnesiana* seeds. *Oikos*, **63**, 200–206.

Turgeon, J.J., Roques, A. & De Groot, P. (1994) Insect fauna of coniferous seed cones: diversity, host plant interactions and management. *Annual Review of Entomology*, **39**, 179–212.

Vikberg, V. (1966) Observations on some Finnish species of *Megastigmus* Dalman (Hym., Torymidae), including the biology of *Megastigmus bipunctatus* (Swederus). *Annual Entomologica Fennica*, **32**, 309–315.

Ward, L.K. (1981) The demography, fauna and conservation of *Juniperus communis* in Britain. *The Biological Aspect of Rare Plant Conservation* (ed. H. Synge), pp. 319–29. John Wiley & Sons Ltd, London.

Ward, L.K. (1982) The conservation of juniper: longevity and old age. *Journal of Applied Ecology*, **19**, 917–928.

Wiens, D., Calvin, C.L., Wilson, C.A., Davern, C.I., Frank, D. & Seavey, S.R. (1987) Reproductive success, spontaneous embryo abortion and genetic load in flowering plants. *Oecologia*, **71**, 501–509.

Wielgolaski, F.E. (1997) Fenoscandian Tundra. *Ecosystems of the World: Polar and Alpine Tundra* (ed. F.E. Wielgolaski), pp. 27–84. Elsevier, Amsterdam.

Woodward, F.I. (1990) The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society, Series B*, **326**, 585–593.

Woodward, F.I. (1997) Life at the edge: a 14-year study of *Verbena officinalis* population's interaction with climate. *Journal of Ecology*, **85**, 899–906.

Woodward, F.I. & Williams, B.G. (1987) Climate and plant distribution at global and local scales. *Vegetatio*, **69**, 189–197.

Zamora, R., Gómez, J.M., García, D. & Hódar, J.A. (1996) Ecología reproductiva y regeneración del matorral de la alta montaña de Sierra Nevada: capacidad de respuesta a las perturbaciones. *Sierra Nevada: Conservación y Desarrollo Sostenible*, **Vol. II** (eds J. Chacón & J.L. Rosúa), pp. 407–22. University of Granada, Granada, Spain.

Zar, J.H. (1996). *Biostatistical Analysis*. 3rd edn. Prentice Hall, New Jersey, USA.

Received 15 June 1999
revision accepted 23 November 1999