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Population structure of a fleshy-fruited species at its range edge – the case of *Prunus mahaleb* L. in northern Switzerland

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Abstract

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Little is known about age structure and reproduction in small populations of woody species at their range edge. Here, we report on the demographic structure of the fleshy-fruited *Prunus mahaleb* at the margin of its distributional range in northern Switzerland. The aim of the study was to investigate distribution patterns, age structure and plant performance as affected by population size and isolation, altitude and climate. Fifteen small populations were chosen in the Swiss and French Jura, where the species is rare and restricted to exposed cliffs and scree slopes, which are surrounded by beech and oak forests. Plant distribution within populations was often clumped or linear. Irregular recruitment was indicated by uneven age structures with a low number of young plants and missing age classes in some populations. Mean plant age per population ranged from 14 to 42 years. Plant age, stem length and diameter, photosynthetically active crown volume and annual growth increment all differed significantly among populations albeit without correlation to population size or altitude. However, recruitment was highest at altitudes between 500 and 600 m, and recruitment and mean plant age were negatively correlated with precipitation during the vegetation period. Plant size was negatively correlated with distance to the nearest population, and positively correlated with nearest neighbour distance. As a conservation tool, forest tree removal may reduce shading and thus increase both vegetative and sexual recruitment in *P. mahaleb*.

Key words: Age structure, distribution pattern, plant performance, rare tree species, recruitment.

Introduction

Plant performance in small and isolated populations is a central topic of current ecological research (Oostermeijer et al. 1994; Colas et al. 1997; Fischer and Matthies 1998a,b; Kahmen and Poschlod 2000; Kollmann and Pflugshaupt 2001; Pluess and Stöcklin 2004). Small population size and isolation have both natural and anthropogenic causes, with natural isolation more often occurring at the edge of a species range (Gaston 2003). Population size and isolation may affect biotic interactions and components of plant fitness such as the transition between age stages and the demographic population structure (Menges 1991; Ellstrand and Elam 1993; Widén 1993; Fischer et al. 2000a, b; Hegland et al. 2001; Lienert et al. 2002).

Perennial species with long periods until first reproduction should, at least in the short term, be less vulnerable to the negative effects of habitat isolation. Thus, populations of these species would have to be isolated for several generations to suffer from inbreeding depression or genetic drift (Colas et al. 1997; Allphin and Windham 2002). Species with historically isolated populations are called 'old rare species' (Huenneke 1991). Their isolation is often the result of environmental change such as the climate cooling that followed the warmest time of the post-glacial period (Burga and Perret 1998). This is also the case in *Prunus mahaleb*, a fleshy-fruited woody species that reaches its northern range edge in Switzerland, where it occurs in small and spatially isolated populations. Thus, this species offers the opportunity to study the consequences of long-term isolation in small populations of a long-lived plant. Woody species with annual rings have the advantage that a precise age structure can be reconstructed (Bergeron and Gagnon 1987; Schweingruber and Nogler 2003).

Flowering, fruiting and seed dispersal of *P. mahaleb* have been intensively studied in Spain and Switzerland (Gutián 1993, 1994; Gutiérrez et al. 1993; Jordano 1993; Kollmann and Pflugshaupt 2001; Pflugshaupt et al. 2002). Swiss plants proved to be smaller than Spanish ones; they often have a more prostrate growth form and produce fewer flowers and fruits (Kollmann and Pflugshaupt 2001). The small size and low reproductive success of Swiss populations might have implications for their demographic structure, i.e. plant distribution, age structure and plant performance (Silvertown and Charlesworth 2001). In the present contribution, we examine this possibility by investigating the following questions: (1) Is the spatial distribution of plants within populations of *P. mahaleb* regular, random or clumped? (2) Are there population-specific patterns in age structure? (3) Are there differences in plant performance among populations? (4) Are potential differences in population structure and plant performance correlated with density, population size, population isolation, altitude or precipitation?

Materials and Methods

Study species

Prunus mahaleb L. (Rosaceae) is a shade-intolerant tall-shrub or small tree growing along forest edges or in sparse forests. Plants flower during approximately one week in late April or May (Gutián 1994; K. Pflugshaupt, pers. observ.). Flower and fruit production are highly variable among years, and rates of fruit abortion are high (Gutián 1993; Pflugshaupt et al. 2002). The main pollinators are flies and bees (Westrich 1989; Jordano 1993), whereas seeds are dispersed by frugivorous birds (Herrera and Jordano 1981; Jordano 1994; Jordano and Schupp 2000).

The species mainly occurs in the submediterranean zone of southern and south-eastern Europe, but its distribution extends northwards to central Europe (Müller 1986; Ellenberg 1988; Scholz and Scholz 1995). In southern Switzerland, some large continuous populations (>1000 individuals) can be found in the Valais, whereas in northern Switzerland most populations are isolated and rather small (10–100 individuals; Kollmann and Pflugshaupt 2001). This pattern of distribution is interpreted as a relict of a warm period after the last glaciation (7500–4500 years BP), when the species was probably more widespread (Burga and Perret 1998). Like other submediterranean plants, *P. mahaleb* has survived subsequent cooler periods at natural forest borders along cliffs and scree slopes with southern exposure (Kollmann 1997). At such sites, the soil is too shallow and dry for most forest trees to grow (Moor 1979; Müller 1986). The minimum distance between most populations in northern Switzerland is 3–30 km (Table 1), suggesting that the probability of pollen and seed dispersal among populations is low (Waddington 1983; Slatkin 1985; Godoy and Jordano 2001; Kreyer et al. 2004).

Study populations

The selection of study populations was based on published sources, herbarium records and personal observations in northern Switzerland and neighbouring areas in eastern France (Moor 1962, 1979; Welten and Sutter 1982; Köppler 1995; Kollmann and Pflugshaupt 2001). Fifteen populations were chosen with no recent human disturbance but sufficient accessibility. These populations covered a wide range in population size and were evenly distributed in the Swiss and French Jura and around Lake Walensee (Fig. 1, Table 1).

Demographic survey

The population structure of the 15 populations was investigated in winter 1999/2000. First, the total area of all populations was recorded, after which all individuals >0.2 m height (total 330 plants) were mapped with a GPS (Global Positioning System; Trimble Navigation Limited, Sunnyvale, CA); accuracy ± 0.5 m. Sampling was not complete in the populations HO, LN, MH, OL, RA and WS due to inaccessibility of some plants on steep cliffs. To analyse plant distribution patterns, the distance to the three nearest neighbour plants (>0.2 m height) was measured. In spring 1999 and 2000, all young individuals (<10 years, <0.2 m height) were recorded in each population (in total 113 plants) to assess recruitment, and the number of flowering individuals was counted as estimate of effective population size. The number of mapped individuals was not correlated with population size (Pearson correlation; $r=0.021$, $P=0.94$), because the proportion of flowering plants varied strongly among populations.

As indicators of plant size and growth, stem length, crown diameter (in two orthogonal directions) and stem diameter at 0.5 m from the stem basis were measured for all 330 individuals, and the proportion of photosynthetically active canopy (indicated by leaf buds) was estimated in 10% classes. Canopy volume was approximated as an ellipsoid based on three orthogonal axes. Growth form was described as 'vertical', 'horizontal' or 'creeping'. For individuals with >10 cm stem diameter, two wood cores were taken through the central pith: The cores were sanded, annual rings counted under a binocular microscope and the average annual growth increment calculated following Schweingruber (1996). Some cores with decayed centre or ambiguous rings had to be eliminated. The age of smaller plants was estimated based on branching and the annual extension growth of the main axis. These values were significantly correlated with tree-ring age in those individuals where both methods could be applied (linear log-log

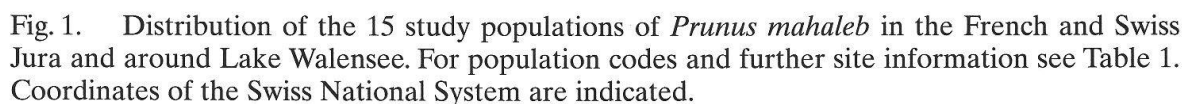
Tab. 1. Site characteristics and code of the 15 populations of *Prunus mahaleb* studied in the Swiss and French Jura and around Lake Walensee. Rank order of the populations follows effective population size (number of flowering individuals). Degree of isolation is derived from the distance to the nearest population; precipitation means are based on records for 1931–1970 (Kirchhofer 2000). Coordinates of populations in France according to the French national scale.

Nearest village, site name	Code	Coordinates	Altitude (m a.s.l.)	Precipitation Apr–Oct (mm)	Isolation (km)	Individuals flowering
Remigen, Rütifels	RE	656.050/264.025	590	765	9	7
Thalheim, Staffelegg	TH	648.325/254.600	680	765	3.5	15
Chassagne, St. Denis	CS	886.000/2237.925	530	830	4	20
Vorberg, Biel	BO	587.750/223.350	520	615	6	20
Mouthier, Hte-Pierre	MH	900.450/2232.700	670	830	9	20
Weesen, Power station	WE	728.725/222.175	480	945	13	20
Rotenflue, Oberrüti	RO	599.100/248.225	590	615	1.25	20
Liesberg, Gravel pit	LI	599.500/249.750	530	615	0.75	20
Hofstetten, Chöpfli	HO	605.000/259.250	500	735	7	24
Montgesoye, Forest gap	MG	893.300/2238.750	480	830	1.5	25
Osterfingen, Steinmüri	OS	679.625/278.575	520	705	28	25
Weesen, Lake shore	WS	728.500/222.175	420	945	13	30
La Neuveville, Forest gap	LN	573.875/213.350	620	615	5.5	50
Olten, Säliflue	OL	635.875/243.050	550	675	12	50
Ravellenfluh, Oensingen	RA	620.750/238.175	620	615	0.75	100

regression; $r^2 = 0.360$, $P < 0.05$, $n = 38$). The age of all other trees was estimated based on the resulting calibration line.

Climatic data and altitude

Several climatic data and altitude were investigated as potential explanatory variables for the observed demographic patterns. Precipitation during the vegetation period (April–October; Table 1) was chosen because the shallow substrates of all study sites had limited abilities to store water, and summer drought was considerable in several sites and correlated with flower and fruit characteristics in a previous study (Kollmann and Pflugshaupt 2001). Mean annual temperature was not included since it was



Statistical analyses

A Kolmogorov-Smirnov test was used to detect deviation of age distribution of the individual populations compared with the total of 443 individuals. As *P. mahaleb* starts reproduction at about 10 years, intervals of 10 years were used to describe the age

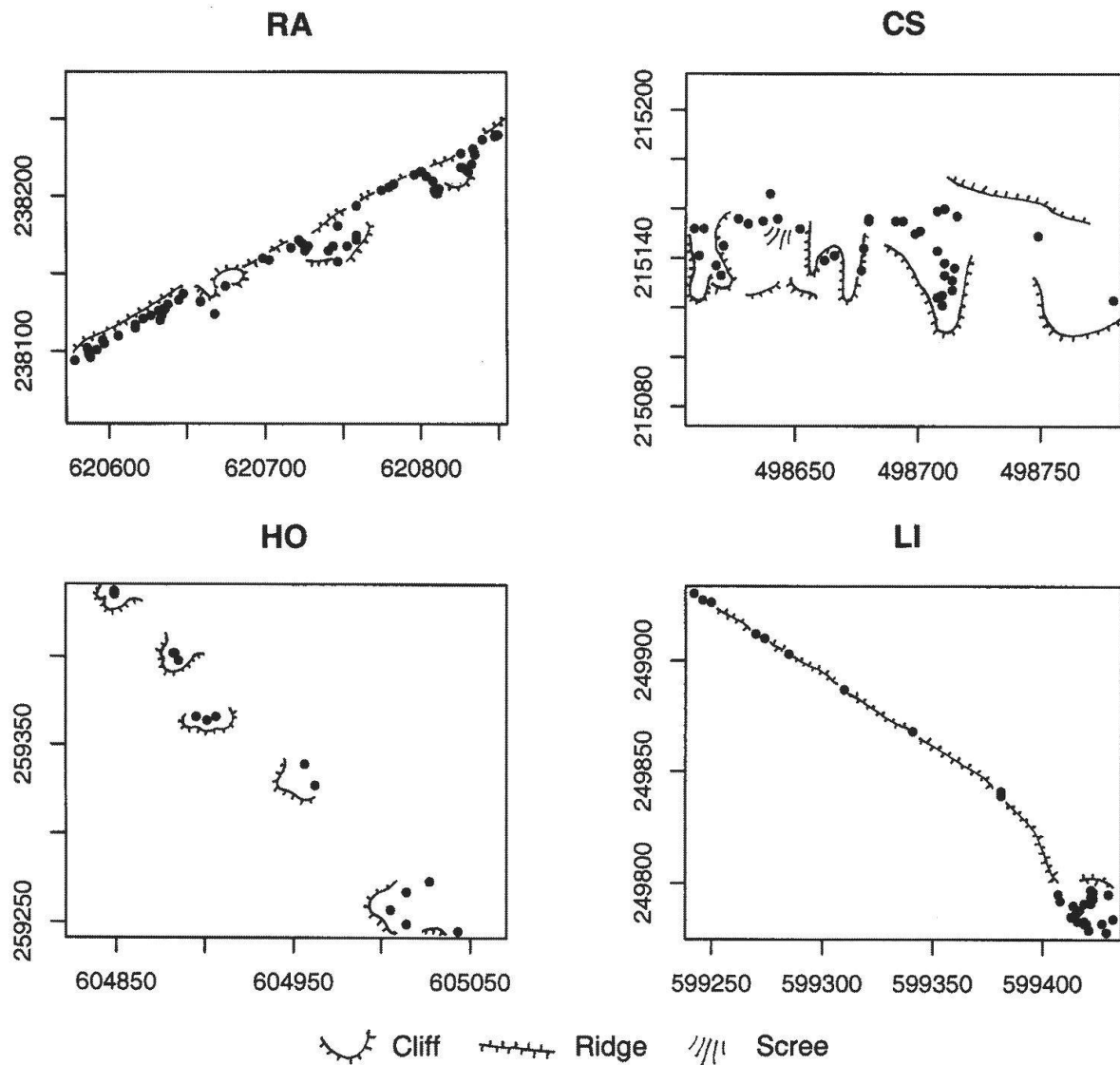


Fig. 2. Examples of the distribution of *Prunus mahaleb* individuals >0.2 m height in four representative populations (RA, CS, HO, LI), including coordinates of the Swiss National System. For population codes and site information see Table 1.

structure of populations. One-way ANOVA followed by Tukey-HSD multiple tests were used to investigate differences in plant size and growth among populations.

Results

Plant distribution patterns

All populations of *P. mahaleb* covered rather small areas (about 200–7500 m²), and the distribution of the individual plants was strongly determined by local topography (Fig. 2). Most populations exhibited more or less linear patterns following steep cliffs, ridges or scree slopes, where forest cover was reduced. The plants also grew along natural forest edges in between sparse rock vegetation and beech (*Fagus sylvatica* L.) or

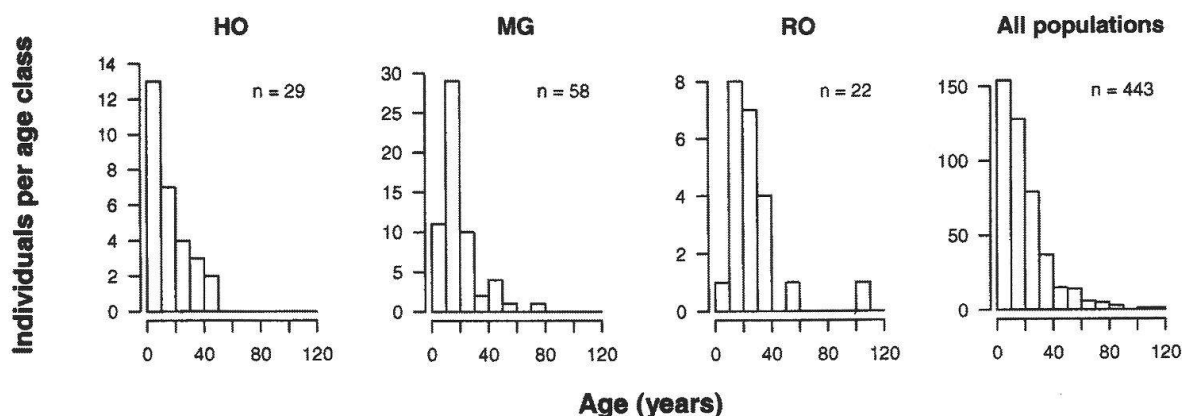


Fig. 3. Age distribution in three populations of *Prunus mahaleb* (10-year classes), and cumulated age structure of all 15 study populations. The three selected populations are examples for continuous L-shaped distribution (HO), relative low number of young plants (MG), and gaps in the age distribution (RO).

mixed oak forests (*Quercus pubescens* Willd., *Q. petraea* (Mattuschka) Liebl.) on deeper soils. Few individuals were observed in the centre of exposed cliffs or scree slopes, and in some sites relatively old individuals with clear signs of senescence were found half overgrown by advancing forest trees.

Average plant distance within populations was less than 10 m. The analyses of plant distribution patterns with Ripley's *K* function indicated significant clumping at nine study sites (BO, HO, LI, LN, MH, OS, RA, RE, WS); individuals were randomly distributed in six populations (CS, MG, OL, RO, TH, WE). Regular plant distribution occurred in none of the populations. Clumping was observed at a distance of 5–20 m in five populations, in the populations BO, LI and RA clumping occurred at 5–70 m, and in OS at 5–40 m.

Population age structure and recruitment

The age structure in ten of the 15 study populations deviated from the distribution of the total sample of 443 individuals (Kolmogorov-Smirnov test, $P < 0.05$). Nine populations showed relatively low recruitment as indicated by a relatively low number of plants younger than 10 years (CS, LN, MG, MH, OL, RO, TH, WE, WS; Fig. 3). Seedlings and/or vegetative sprouts were common in some populations (BO, OS) but almost missing in others (TH, WE). Young plants were found under some of the oldest trees with relatively high fruit production. Missing age classes were observed in populations BO, CS, LN, MG, MH, OS, RE, RO and TH. Most populations had an L-shaped age distribution with a maximum age < 80 years, and only in five populations some old individuals of 80–120 years were found (OS, RE, RO, TH, WS). Mean tree age in all populations varied from 14 to 42 years, and there were significant differences between populations (ANOVA; $F_{14, 315} = 4.1$, $P < 0.001$), with markedly higher age in the populations TH, WS and MH (Table 2).

Plant size and growth

Average plant height (measured as stem length) was 1.8–4.2 m with considerable variation among populations (ANOVA; $F_{14, 315} = 5.2$, $P < 0.001$; Table 2). Most individuals were tall shrubs or small trees with a vertical growth form, whereas on scree slopes

Tab. 2. Plant age, size and growth in 15 populations of *Prunus mahaleb*. The rank order of the populations follows mean age. Means ($\pm SE$) are given plus the results of a one-way ANOVA and Tukey-HSD multiple test at $P < 0.05$. Populations without common superscript letters are significantly different. For population codes see Table 1.

Code	Plant age (years)	Stem diameter (cm)	Stem length (m)	Photosynthetically active crown volume (m ³)	Annual growth increment (mm yr ⁻¹)
TH	42.3 \pm 4.5 ^a	5.1 \pm 0.8 ^{abcd}	4.2 \pm 0.3 ^a	8.9 \pm 2.3 ^{ab}	1.7 \pm 0.4 ^{bc}
WS	39.4 \pm 4.5 ^{ab}	8.6 \pm 0.8 ^a	3.6 \pm 0.3 ^{ab}	11.9 \pm 2.3 ^a	2.9 \pm 0.4 ^{abc}
MH	35.6 \pm 5.4 ^{abc}	5.0 \pm 1.0 ^{abcd}	2.9 \pm 0.4 ^{abcd}	7.5 \pm 2.7 ^{ab}	1.7 \pm 0.5 ^{abc}
RO	29.4 \pm 3.6 ^{abcd}	4.0 \pm 0.6 ^{bcd}	2.5 \pm 0.2 ^{bcd}	5.1 \pm 1.8 ^{ab}	1.6 \pm 0.3 ^{bc}
OL	26.3 \pm 4.7 ^{abcd}	7.2 \pm 0.8 ^{ab}	2.7 \pm 0.3 ^{abcd}	6.6 \pm 2.4 ^{ab}	3.3 \pm 0.4 ^{ab}
CS	24.5 \pm 2.7 ^{abcd}	3.6 \pm 0.5 ^{cd}	2.5 \pm 0.2 ^{bcd}	4.0 \pm 1.4 ^{ab}	1.7 \pm 0.2 ^{bc}
WE	21.8 \pm 4.9 ^{abcd}	5.8 \pm 0.9 ^{abcd}	2.8 \pm 0.4 ^{abcd}	10.0 \pm 2.5 ^{ab}	2.8 \pm 0.4 ^{abc}
OS	21.8 \pm 3.0 ^{bcd}	5.6 \pm 0.5 ^{abc}	3.2 \pm 0.2 ^{abc}	10.2 \pm 1.5 ^a	2.6 \pm 0.3 ^{abc}
RE	20.6 \pm 4.2 ^{abcd}	5.4 \pm 0.7 ^{abcd}	2.4 \pm 0.3 ^{bcd}	6.7 \pm 2.1 ^{ab}	3.1 \pm 0.4 ^{ab}
HO	21.2 \pm 4.2 ^{bcd}	4.7 \pm 0.7 ^{bcd}	2.5 \pm 0.3 ^{bcd}	5.0 \pm 2.1 ^{ab}	2.4 \pm 0.4 ^{abc}
LN	21.0 \pm 3.1 ^{bcd}	3.4 \pm 0.6 ^{cd}	2.3 \pm 0.2 ^{cd}	7.0 \pm 1.6 ^{ab}	2.1 \pm 0.3 ^{bc}
MG	21.0 \pm 2.5 ^{cd}	2.8 \pm 0.4 ^d	1.8 \pm 0.2 ^d	1.9 \pm 1.3 ^b	1.5 \pm 0.2 ^c
LI	17.4 \pm 2.8 ^{cd}	3.8 \pm 0.5 ^{cd}	2.1 \pm 0.2 ^d	2.5 \pm 1.4 ^b	2.2 \pm 0.2 ^{bc}
RA	17.2 \pm 3.5 ^{cd}	4.9 \pm 0.6 ^{bcd}	2.0 \pm 0.2 ^d	3.0 \pm 1.8 ^{ab}	3.0 \pm 0.3 ^{ab}
BO	14.4 \pm 2.9 ^d	4.0 \pm 0.5 ^{bcd}	2.4 \pm 0.2 ^{bcd}	4.3 \pm 1.5 ^{ab}	3.6 \pm 0.3 ^a
<i>F</i> (<i>P</i>)	4.1 (<0.001)	5.1 (<0.001)	5.2 (<0.001)	3.0 (<0.001)	5.0 (<0.001)

horizontal or creeping plants prevailed, for example in population TH. Average stem diameter varied between 2.8 and 8.6 cm, with significant differences between populations ($F_{14, 315} = 5.1$, $P < 0.001$). Plant length and stem diameter were positively correlated (Pearson correlation; $r = 0.612$, $P = 0.02$). Thus, stem diameter was preferred as a measure of plant size in the following analyses, because of the variation in growth form which interfered with measurements of stem length (Table 2).

There were also significant differences between populations in photosynthetically active crown volume ($F_{14, 316} = 3.0$, $P < 0.001$), with high values in the populations WS, OS and WE. The average proportion of photosynthetically active canopy per plant crown volume was 70–93%, but some populations had markedly lower values (OS, 54%; RE, 45%). Average annual growth increment was 1.5–3.6 mm ($F_{14, 315} = 5.0$, $P < 0.001$) with highest values in the population BO and lowest in MG.

Explanatory factors

Although plant size and growth varied considerably among populations, few significant correlations were found with population size, degree of isolation or altitude (Table 3). Degree of isolation was negatively correlated with stem diameter and proportion of active crown volume.

There was a quadratic relationship between the proportion of plants younger than 10 years and altitude (Fig. 4). Recruitment was highest at mid altitude between 500 and 600 m. Moreover, recruitment was negatively correlated with precipitation during the vegetation period (Table 3), whereas precipitation showed a negative linear

Tab. 3. Pearson product-moment correlation (r) between plant traits (capital letters; population means) and population or site characteristics (small letters; population or site means; $n = 15$) in *Prunus mahaleb*. AGE, plant age; STEM, stem diameter; CROWN, photosynthetically active crown volume; GROWTH, annual growth increment; RECR, proportion plants <10 yr; Bonferroni corrections were not applied following Moran (2003) (^{ns}, $P > 0.10$; (*), $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; significant correlations are given in bold).

	AGE	STEM	CROWN	GROWTH	RECR
Nearest neighbour distance	0.170 ^{ns}	0.746**	0.709**	0.574*	0.126 ^{ns}
log Population size	0.241 ^{ns}	0.084 ^{ns}	0.148 ^{ns}	0.279 ^{ns}	0.045 ^{ns}
log Isolation	0.214 ^{ns}	-0.555*	-0.538*	0.326 ^{ns}	0.176 ^{ns}
Altitude	0.226 ^{ns}	0.322 ^{ns}	0.155 ^{ns}	0.359 ^{ns}	0.126 ^{ns}
Precipitation Apr–Oct	-0.473(*)	0.416 ^{ns}	0.516*	0.138 ^{ns}	-0.512*

correlation with altitude ($r^2 = 0.307$, $P = 0.032$). Nearest neighbour distance was positively correlated with stem diameter, photosynthetically active crown volume and growth increment (Table 3).

Discussion

Population structure and regeneration

Prunus mahaleb in northern Switzerland and eastern France shows population structures, which might be explained by deviating site conditions at the range edge, as described for *Pinus resinosa* in Quebec (Bergeron and Gagnon 1987) and *Pinus banksiana* in Maine (Conkey et al. 1995). The spatial distribution of individuals within the study populations of *P. mahaleb* was often clumped or linear, reflecting the distribution of growth sites. Indeed, the species is restricted to a small zone between deciduous forests and treeless rocky outcrops in Switzerland, whereas it is common in sparse Mediterranean forests (Scholz and Scholz 1995). A clumped distribution might also be promoted by root sprouting, which seems to be the dominant mode of recruitment in many tree species under adverse site conditions (Bellingham and Sparrow 2000).

The populations showed missing age classes which may indicate failure of recruitment in some years. However, the missing age classes can also be explained by stochastic mortality of old individuals at least in very small populations. Populations with episodic lack of recruitment and gaps in the age structure have been found in several woody species, for example, in cliff stands of the conifer *Thuja occidentalis* (Kelly and Larson 1997). However, these authors argue that cliffs or rock outcrops offer relatively constant site conditions even when neighbouring forests experience large-scale disturbance. For the *P. mahaleb* sites in northern Switzerland, drought and rock fall might nowadays be the only significant sources of disturbance, whereas fires are rare. No distinct recruitment cohorts were observed, which might correlate with an apparent lack of catastrophic disturbance events. In contrast, in similar studies on American tree species, distinct periods of enhanced recruitment were found after such events (Bergeron and Gagnon 1987; Frelich and Graumlich 1994; Conkey et al. 1995; Cuevas 2002).

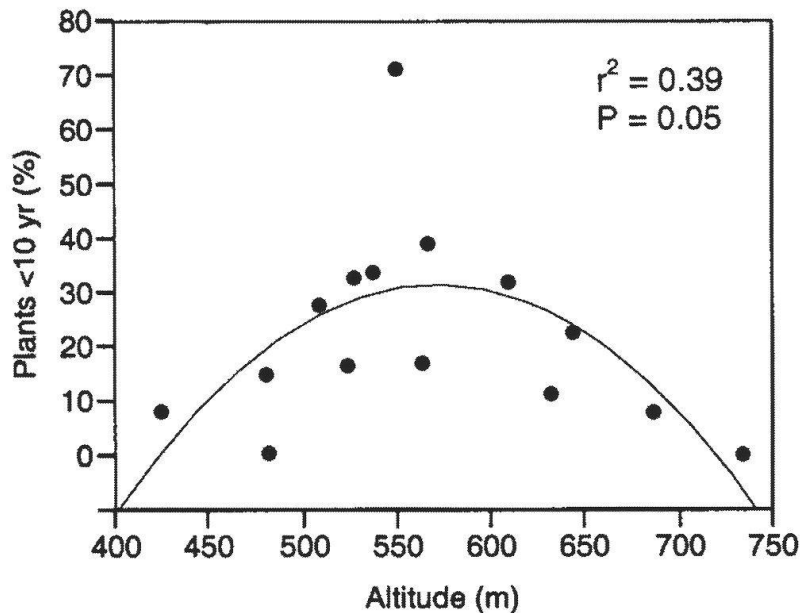


Fig. 4. Quadratic relationship between recruitment, i.e. the proportion of plants younger than 10 years, and altitude in 15 populations of *Prunus mahaleb* ($r^2 = 0.391$, $P = 0.051$).

Fruit abortion is high in woody Rosaceae (Guitián 1994; Rasmussen and Kollmann 2004), and in *P. mahaleb* complete failure to produce fruits has been observed in a number of populations, particularly in dry years (Pflugshaupt et al. 2002). This is in contrast to the negative correlation between precipitation and recruitment found in the present study. An explanation might be light limitation of sexual or vegetative recruitment if higher precipitation results in more closed canopies. Recruitment was highest at mid altitude between 500 and 600 m. This result may be at least partly explained by the lower and upper growth limit of the species in northern Switzerland. The lower distribution limit might reflect the lack of suitable habitats in the Swiss lowlands, whereas the upper growth limit is likely due to decreasing temperature, which determines the montane distribution margin in many woody species (Gaston 2003).

Effects of population size and isolation

This study and previous observations on flowering, pollination and fruit production of *P. mahaleb* in northern Switzerland (Kollmann and Pflugshaupt 2001; Pflugshaupt et al. 2002) revealed, at best, limited evidence for negative effects of population size and isolation. However, smaller populations had a more irregular age structure, and less isolated populations showed higher average values for stem diameter and photosynthetically active crown volume. So far, we have no causal explanation for the latter. Maybe small populations of 'old rare species' have managed to avoid negative effects of inbreeding and genetic drift (Colas et al. 1997; Allphin and Windham 2002), which have been observed in 'young rare species' (Oostermeijer et al. 1994; Fischer and Matthies 1998a,b; Lienert et al. 2002; Pluess and Stöcklin 2004). However, in the present study all populations were rather small, and some markedly larger populations of *P. mahaleb* would be needed to rigorously test the effects of population size and isolation.

Conservation perspectives

Although the relict populations of *P. mahaleb* in northern Switzerland have been restricted to half-open habitats along steep cliffs or scree slopes for some time, we found little evidence for negative effects of population size and isolation. However, there seems to be increasing competition due to advancing forest canopies. Climate change and/or atmospheric nutrient input may promote these successional processes contributing to local extinction of *P. mahaleb* and other associated rare plant species. To reverse these negative trends occasional cutting of competing forest trees imitating the former coppicing management is recommended. This would also benefit the associated rock and grassland vegetation, which is negatively affected by rock-climbing, hiking, grazing and climate change (Witschel 1998; Muller et al. 2004; Rusterholz et al. 2004).

Zusammenfassung

Populationen der Felsenkirsche (*Prunus mahaleb*) wurden am nördlichen Rande des Verbreitungsgebietes untersucht um festzustellen, inwieweit räumliche Verteilungsmuster, Altersstruktur und Wuchsleistung der Pflanzen von der Populationsgrösse, der Isolation, der Meereshöhe oder dem Klima abhängen. Betrachtet wurden 15 Populationen, die im Schweizer oder französischen Jura an natürlichen Waldgrenzen (Felsen und Schutthängen) vorkommen. Die Pflanzen wuchsen oft in geklumpfter oder linearer Anordnung. Ungleichmässige Altersstrukturen mit wenigen Jungpflanzen wiesen auf unregelmässige Fortpflanzung hin. Das mittlere Alter der Pflanzen einer Population lag zwischen 14 und 42 Jahren. Das Alter, die Grösse und der jährliche Zuwachs der Pflanzen unterschieden sich zwischen den Populationen, korrelierten jedoch nicht mit der Populationsgrösse oder der Meereshöhe. Die Verjüngung war zwischen 500 und 600 m ü.M. am intensivsten. Verjüngung und mittleres Pflanzenalter korrelierten zudem negativ mit der Niederschlagsmenge während der Vegetationszeit. Die Pflanzengrösse korrelierte negativ mit dem Abstand zur nächsten Population und positiv mit dem Abstand zwischen benachbarten Bäumen. Die Beseitigung von benachbarten Waldbäumen kann möglicherweise zur Erhaltung der Bestände beitragen, indem geringere Beschattung die vegetative und sexuelle Vermehrung der Art verbessert.

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