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Life at the margins: the mating system of Mediterranean conifers

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Key words

Mixed mating, selfing, density, adaptive potential, *Abies alba*

Aims and introduction

Plant mating system involves processes related to the creation of new offspring, from flower and seed fecundity to mating barriers, the scale and shape of pollen and seed flow and the frequency of long distance dispersal. The mating system can be viewed as a force that contributes to the spread of genetic novelty or, on the contrary, to the accumulation of genetic load. Mixed mating, in which a single tree progeny results from a mixture of selfing and outbreeding, is widespread in conifers. It can be considered as an evolutionary advantage at ecological margins when mating partners become scarce (see review by Goodwillie et al. 2005). Here, we first analyze how the mating system responds to bioclimate and density variations. Second, we show how density affects the mating system of *Abies alba*, a European conifer that has numerous marginal populations under Mediterranean climate.

Material and Methods

We first conducted a survey of published data on the mating system of *Abies* and *Pinus* species where information on bioclimate and stand density was available. Second, we used isozymes to investigate the composition of individual progeny from a marginal *Abies alba* forest growing in Mediterranean France (Mont Ventoux, 44°10' N, 5°15' E) where low to high stand densities can be found. We then tested the adaptive potential of the different progeny by sowing them in controlled nursery conditions and measuring germination rate and seedling survival after 4 years

Results

Our survey showed that the proportion of selfed vs outbred progeny is not fixed within species. The highest variability in mating system was found where stand density was the most variable (Table 1). The few case studies reported for Mediterranean species and Mediterranean-type populations of non-Mediterranean species tended to have higher variability in their mating system (Table 1). Our isozyme analysis showed that the mean multi-locus outcrossing rate (t_m) of our Mont Ventoux population was 0.85, a value typical of that of mixed-mating conifers (Table 1). However, although trees were under the same meso-environment, individual outcrossing rates varied from 0.05 to 0.99, and were strongly correlated with stand type and density. Within the mature stand (tree density > 80/ha), t_m was 0.87. At the edge of this mature stand, t_m decreased to 0.71, with individual values from 0.45 to 0.99. At the margin of this stand (density < 20/ha), t_m was 0.43 (0.05 to 1.00). We found no difference in pollen pool genetic diversity between the different stand densities (H_e from 0.141 to 0.162). Significantly fewer seeds from the low density marginal stand were able to germinate (32% versus 53% in the high density stand). However, seedlings from the marginal stand had an overall better survival (81% than seedlings from the mature stand (63%) over a 4 year period, especially under low irrigation.

Discussion

For reasons ranging from tectonic to human-made constraints, species distribution areas are typically fragmented in the Mediterranean, and made of populations of highly contrasted sizes, densities and reproductive individual frequencies (Fady & Médail 2004; Blondel & Aronson 1999). For example, out of 9 *Abies* and 9 *Pinus* species in Europe, 13 are Mediterranean endemics, and an additional 3 find their "rear-edge" distribution in the Mediterranean. Thirteen of these species have patchy distribution areas under Mediterranean conditions. Hence, because it may be at an evolutionary advantage, a highly variable mating system may be expected in these Mediterranean conifers. Trees from low density stands may be at an evolutionary disadvantage because they produce more selfed progeny than trees from high density stands. However, selfed seeds may be purged early on (at the embryo stage) and the remaining seeds may produce seedlings with better fitness, possibly because of higher selective pressure in their local environment. However, the relationship between outcrossing rate and stand density may not be as straightforward as indicated from this investigation of a single reproductive event that happened during a high male and female fecundity year. First, in our investigation, we found a high variability in individual pollen pool genetic diversity (H_e from 0.014 to 0.224) regardless of mean stand density. Further, we found that individual full seed ratio was correlated to individual density within the stand, but that individual selfing rate was neither correlated to individual density nor to individual male fecundity. Since individual male and female fecundities were found to be highly variable from one year to the next, the spatial structure of selfing may also be modified over the years, and not directly predictable by just mean stand density. We suggest that further investigations on the role of ecological factors on the mating system should be carried out at individual level, over several years.

References

- Blondel J, Aranson J. 1999. Biology and wildlife of the Mediterranean region. Oxford Univ. Press, New York.
- Burczyk J, Adams WT, Shimizu JY. 1996. Mating patterns and pollen dispersal in a natural knobcone pine (*Pinus attenuata* Lemmon.) stand. *Heredity* 77: 251-260.
- Burczyk J. 1998. Mating system variation in a Scots pine clonal seed orchard. *Silvae Genet.* 47(2-3): 155-158.
- El-Kassaby YA, Dunsworth BG, Krakowski J. 2003. Genetic evaluation of alternative silvicultural systems in coastal montane forests: western hemlock and amabilis fir. *Theor. Appl. Genetics* 107(4): 598 – 610.
- Fady B, Médail F. 2004. Mediterranean Forest Ecosystems. In : J. Burley, J. Evans and J.A. Youngquist edit., *Encyclopedia of Forest Science*. Elsevier, Londres, 1403-1414.
- Fady B, Westfall RD. 1997. Mating system parameters in a natural population of *Abies borisii regis* Mattfeld. *Ann. Sci. Forest.*, 54: 643-647.
- Goodwillie C, Kalisz S, Eckert CG. 2007. The evolutionary enigma of mixed mating systems in plants: Occurrence, theoretical explanations, and empirical evidence. *Annual Review of Ecology Evolution and Systematics*, 36: 47-79.
- Gonzalez-Martinez SC, Gerber S, Cervera MT, Martinez-Zapater JM, Alia R, Gil L. 2003. Selfing and sibship structure in a two-cohort stand of maritime pine (*Pinus pinaster* Ait.) using nuclear SSR markers. *Ann. For. Sci* 60 (2): 115-121.
- Kaya N, Isik K, Adams WT. 2006. Mating system and pollen contamination in a *Pinus brutia* seed orchard. *New Forests* 31 (3): 409-416.
- Ledig FT, Conkle MT, Bermejo-Velasquez B, Eguluz-Piedra T, Hodgskiss PD, Johnson DR, Dvorak WS. 1999. Evidence for an extreme bottleneck in a rare Mexican pinyon: genetic diversity, disequilibrium and the mating system in *Pinus maximartinezii*. *Evolution*, 53(1), 91-99.
- Ledig FT. 1998. Genetic variation in *Pinus*. In: D.M. Richardson (edt): *Ecology and biogeography of Pinus*, Cambridge University Press, 251-280.
- Morgante M, Vendramin GG, Rossi P, Olivieri AM. 1993. Selection against inbreds in early life-cycle phases in *Pinus leucodermis* Ant. *Heredity* 70: 622-627.
- Neale DB, Adams WT. 1985. Allozyme and mating system variation in balsam fir (*Abies balsamea*) across a continuous elevational transect. *Can. J. Bot.* 63: 2448-2453.
- Rajora OP, Mosseler A, Major JE. 2002. Mating system and reproductive fitness traits of eastern white pine (*Pinus strobus*) in large, central versus small, isolated, marginal populations. *Canadian Journal of Botany* 80 (11): 1173-1184.
- Robledo-Arnuncio JJ, Alia R, Gil L. 2004. Increased selfing and correlated paternity in a small population of a predominantly outcrossing conifer, *Pinus sylvestris*. *Mol. Ecol.* (13): 2567-2577.
- Schroeder S. 1989. Outcrossing rates and seed characteristics in damaged natural populations of *Abies alba* Mill. *Silvae Genet.* 38(5-6): 185-189.
- Shea KL. 1987. Effects of population structure and cone production on outcrossing rates in Engelmann spruce and subalpine fir. *Evolution* 41: 124-136.
- Siegismund HR, Kjaer ED. 1997. Outcrossing rates in two stands of noble fir (*Abies procera* Rehd.) in Denmark. *Silvae Genet.* 46 (2-3): 144-146.

Table 1- Comparison of outcrossing rates (t_m) in *Abies* and *Pinus* species in relation to bioclimate and mean population densities. Values of t_m in parenthesis are population or individual extremes. M = Mediterranean, nM = non-Mediterranean, nM-R = “rear edge” Mediterranean distribution of a typically non-Mediterranean species.

Species	Bioclimate	Stand density	t_m	Reference (and geographic origin)
<i>Abies alba</i>	nM-R	Low to high	0.85 (0.05 – 0.99)	This study (Medit. France)
<i>P. maximartinezii</i>	nM	Low to high	0.82 (0.42-1.00)	Ledig et al 1999 (Mexico)
<i>Pinus engelmannii</i>	nM	Low to medium	0.72	in Ledig 1998 (Mexico)
<i>Pinus sylvestris</i>	nM-R	Low to high	0.75 (0.08 – 1.00)	Robledo et al 2004 (Spain)
<i>Abies alba</i>	nM	Medium to high	0.89 (0.68 – 1.00)	Schroeder 1989 (Bavarian Alps)
<i>Abies amabilis</i>	nM	Medium to high	0.81 (0.80 – 0.83)	El-Kassaby et al 2003 (Western Canada)
<i>Abies balsamea</i>	nM	Medium to high	0.89 (0.78 – 0.99)	Neale & Adams 1985 (Eastern USA)
<i>Abies lasiocarpa</i>	nM	Medium to high	0.89 (0.65 – 0.94)	Shea 1987 (Rockies, USA)
<i>Pinus leucodermis</i>	M	Medium to high	0.77 (0.72-0.82)	Morgante et al 1993 (Italy)
<i>Pinus strobus</i>	nM	Medium to high	0.93 (0.87 – 0.99)	Rajora et al 2002 (Canada)
<i>Abies borisii regis</i>	M	High	0.94 (0.91 - 0.96)	Fady & Westfall 1997 (Greece)
<i>Abies procera</i>	nM	High	0.94 (0.90 – 0.98)	Siegismund & Kjaer 1997 (Denmark)
<i>Pinus attenuata</i>	M	High	0.92 (0.89-0.98)	Burczyk et al 1996 (California, USA)
<i>Pinus banksiana</i>	nM	High	0.89 – 0.91	in Ledig 1998 (Canada – USA)
<i>Pinus brutia</i>	M	High	0.95	Kaya et al. 2006 (Turkey)
<i>Pinus contorta</i>	nM	High	0.95	in Ledig 1998 (Alberta, Canada)
<i>Pinus pinaster</i>	M	High	0.96	Gonzalez et al 2003 (Spain)
<i>Pinus ponderosa</i>	nM	High	0.96	in Ledig 1998 (Colorado, USA)
<i>Pinus sylvestris</i>	nM	High	0.98 (0.96 – 0.99)	Burczyk 1998 (Poland)