

Spatio-temporal variation in population traits of *Hepatica nobilis* ssp. *nobilis*

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Manuscript received in June 2002

Abstract

In the NE Iberian Peninsula, the herb *Hepatica nobilis* commonly occurs in the understory of deciduous forests. I report data on spatio-temporal variation in performance of patchily distributed populations in a beech forest at Montseny Natural Park (NE Spain). During three years, I studied the spatial (between populations and between patches within populations) and temporal (between years) variation in plant size, growth, fecundity, and sexual and vegetative propagation of 16 patches in two *H. nobilis* populations. Plant size and growth varied greatly at all spatial and temporal scales, while fecundity showed more spatial than temporal variation. None of the plant attributes studied were related to plant density or canopy openness, except the number of ovules per flower that did show density dependence effects. In general, both populations experienced a generalized decrease in size and reproductive output over the three years of study. During the study period, only two seedlings were recruited in one of the populations and all ramets that emerged each year disappeared the next one. Overall, these results show that *H. nobilis* performance depend on small-scale patch characteristics and illustrate the species' remnant population dynamics characterized by very low recruitments rates.

Key words: Deciduous forests, fecundity, patch-specific characteristics, Mediterranean mountains, plant size, recruitment, vegetative propagation.

Resumen. *Variación espacio-temporal en características poblacionales de Hepatica nobilis: una planta herbácea de sotobosque con distribución parcheada*

En el NE de la Península Ibérica, la planta herbácea *Hepatica nobilis* ocurre en el sotobosque de bosques caducifolios. En este artículo se presentan datos sobre la variación espacio-temporal de las características poblacionales de la especie. Durante tres años, estudié la variación espacial (entre poblaciones y entre parches dentro de poblaciones) y temporal (entre años) en el tamaño, crecimiento, fecundidad, y propagación sexual y vegetativa de 16 parches en dos poblaciones de *H. nobilis*. El tamaño y el crecimiento variaron notablemente en todas las escalas temporales y espaciales, mientras que la fecundidad mostró más variación a escala espacial que temporal. Ninguna de las variables estudiadas

estuvo relacionada con la densidad poblacional o la cubierta del bosque, excepto el número de óvulos por flor que sí se mostró afectado por la densidad poblacional. En general, ambas poblaciones experimentaron un declive generalizado en tamaño y éxito reproductivo a lo largo de los tres años de estudio. Durante este periodo, sólo dos plántulas fueron reclutadas en una de las poblaciones y todos los brotes vegetativos que emergieron un año desaparecieron al siguiente. En general, estos resultados muestran, por una parte, que el desarrollo de *H. nobilis* depende de las características específicas de cada parche, y por otra, la dinámica de tipo remanente de la especie.

Palabras clave: Bosques caducifolios, características específicas del parche, fecundidad, montañas mediterráneas, propagación vegetativa, reclutamiento, tamaño.

Introduction

Phenological traits of deciduous woodland herbaceous species represent a clear adaptation to the short period of time in which resources (e.g. light and nutrients) are available between the end of the winter and canopy closure and the beginning of the summer (Muller, 1978). For instance, the annual photosynthetic phase is limited to only a few weeks, which determines final annual productivity (Nault & Gagnon, 1993), and successful recruitment of new individuals may depend strongly on the opening of canopy gaps, as seems to be the case for many woodland herbs (Bierzuchudek, 1982; Barkham, 1992; Watkinson & Powell, 1993; Damman & Cain, 1998; Jules, 1998; Bosch et al. 1998; Valverde & Silvertown, 1998). Woodland herbs show particular life-history traits, such as very slow individual growth rates, low seed production rates, and frequently the ability for vegetative propagation (e.g. bulbs, stolons or rhizomes), determining altogether their population performance and dynamics. Hence, populations can be patchily distributed due to heterogeneity in resource availability (Hutchings, 1998), and largely dominated by adult plants, as recruitment generally tends to be very low (Eriksson, 1993).

Quantifying the spatio-temporal variation in population attributes (e.g. survival, growth, and reproduction) and in the ecological factors that produce such variation is of paramount importance to understand the general trends in the demography of plants (e.g. Horvitz & Schemske, 1995; Silvertown et al., 1996; Colas et al., 2001). Significant spatio-temporal variation in several population attributes has been reported for woodland herbs by several studies (Inghe & Tamm, 1985; Nault & Gagnon, 1993; Damman & Cain, 1998; Valverde & Silvertown, 1998). This information becomes crucial for the conservation and restoration of woodland herbaceous populations, in particular when forests are managed, given the negative direct or indirect effects of logging on distribution, structure, and fate of woodland herbs (e.g. Barkham, 1992; Meier et al., 1995).

Hepatica nobilis Mill. (Ranunculaceae) is a clonal, woodland herb widely distributed throughout Europe. In the NE Iberian Peninsula, this plant may be found most frequently in the understory of oak and beech forests (Bolòs et al., 1993). In the beech forests of the Montseny Natural Park (NE Spain), *H. nobilis* popu-

lations generally consist of rather isolated clumps of a few plants or even single plants. Large populations formed by many individuals distributed in patches of different sizes and densities can also be found. However, these patchily distributed large populations tend to be rare, perhaps as a result of logging traditionally applied to beech forests in the area. In this 3-yr study, I analyze the spatio-temporal variation in population parameters of *H. nobilis*, such as individual plant traits, reproductive output, and sexual and vegetative regeneration in two large, patchily distributed populations growing in a beech forest at Montseny Natural Park. I address the following questions: (1) what is the spatial (between population and between patches within populations) and temporal (between years) variation in plant size, growth, and fecundity of *H. nobilis* plants? (2) What is the effect of plant density and light availability on plant performance? (3) What is the sexual and vegetative regeneration capacity of populations? And (4) what are the implications of points 1, 2 and 3 for the persistence of *H. nobilis* populations in beech forests?

Material and methods

Plant species and study site

Hepatica nobilis is a perennial herb that grows through the production of ever-green 3-lobed leaves from a short stem. Every year, this slow-growing plant may produce 3-4 new leaves. It has a short, thick rhizome that presents a very low clonal growth rate (Inghe & Tamm, 1985). In the understory of beech forests, the flowering season of *H. nobilis* may last from late March to May. *H. nobilis* produces 1-6 bluish-violet, white, or pinkish flowers (1.5-2.5 cm diameter) growing singly on leafless stalks (5-10 cm height). Flowers are hermaphroditic, self-compatible and highly self-fertile (F.X. Picó, unpublished data). The fruit contains 5-25 dry achenes (0.5 cm length) that have an elaiosome at the base. Fruit ripening and shedding takes place from May to June.

The study was conducted in 1998-2000 in a deciduous forest (41°45'N, 3°50'E; 1.100 m a.s.l.) in Montseny Natural Park (NE Spain), with beech (*Fagus sylvatica* L.) forming the canopy, and holly (*Ilex aquifolium* L.) as the dominant shrub. The herbaceous community is basically dominated by *H. nobilis*, with some patches of *Anemone nemorosa* L., *Primula veris* L. and some sparse individuals of *Helleborus foetidus* L. and *Daphne laureola* L. The climate is of Euro-Siberian type but with a strong influence from the Mediterranean Sea (13 km away from Montseny Natural Park). Mean annual precipitation is 1050 mm year⁻¹ with a maximum in spring and autumn, and mean annual temperature is 8°C with cold snowy winters and mild summers (Institut Cartogràfic de Catalunya, 1996). Selection coppicing (i.e. the partial removal of standing trees and biomass) is traditionally practiced in these beech forests, with coppice cycles of approximately 30 years (Diputació de Barcelona, 1984).

The only two large populations of *H. nobilis* found at the study forest are in Santa Fe and Sant Marçal (denoted as SF and SM hereafter). The populations are

separated by about 6 km with a continuous managed beech forest in between. Both SF and SM correspond to forest stands that have been remained unmanaged for a long time. No other large populations, but a few sparse, small groups or isolated plants, between SF and SM were found within an area of approximately 50 ha. The SF population contained 11 patches of *H. nobilis* whereas the SM population contained 5 patches (Table 1). Distances between adjacent patches ranged between 10 and 20 m in both populations. The total area occupied by SF and SM populations were approximately 1 and 0.5 ha, respectively.

Population sampling

In summer 1999, I measured the canopy cover over each population with a spherical densiometer (Spherical Densiometer Model-C, R.E. Lemon, USA) that gives the proportion of canopy openness at a given point (Table 1). At each patch, I recorded the canopy openness with the spherical densiometer at 20 points covering the whole patch area. I repeated the sampling just beside patches (20 points per patch) to compare canopy openness inside and outside patches.

Table 1 Characteristics of the SF (Santa Fe; 11 patches) and SM (Sant Marçal; 5 patches) *Hepatica nobilis* populations sampled: area occupied per patch (m²), total number of plants per patch (N), density per patch (plants m⁻²), mean proportion of canopy openness over each patch (%), and final number of plants included in the analyses and monitored during the three years of study.

Population	Patch code	Area	N	Density	Canopy	No. plants
SF	1	52.6	96	1.8	4.5	35
	2	8.3	39	4.7	7.1	25
	3	79.5	57	0.7	6.2	34
	4	50.9	107	2.1	4.9	37
	5	55.6	40	0.7	5.6	24
	6	84.1	508	6.0	7.9	51
	7	452.4	1492	3.3	4.3	26
	8	44.1	119	2.7	5.5	26
	9	9.4	30	3.2	3.8	21
	10	28.3	35	1.2	7.3	18
	11	21.6	34	1.6	3.6	24
SM	12	60.5	33	0.9	3.1	21
	13	57.2	182	3.2	3.9	42
	14	46.2	55	1.2	6.2	23
	15	35.3	28	0.8	5.3	17
	16	19.4	26	1.3	5.9	21

Given the capacity for clonal growth in *H. nobilis*, I checked whether two adjacent rosettes were anatomically connected or not. Thus, prior to sampling, I dug out 10 pairs of rosettes (separated by about 10-20 cm), and in no case rosettes were found to be connected through a rhizome. Because I do not know whether rosettes were genets (recruited from seed) or ramets (recruited from clonal propagation), I will refer to them simply as "plants" hereafter.

In May 1998, I randomly laid out two quadrats (1 m² area) per patch and tagged all plants within the quadrats. In addition, 2-3 transects (5 m each) were laid out across each patch, and all plants within these transects were also tagged to increase the sample size. All new plants that appeared inside the quadrats at each annual census were also tagged and monitored over time. I checked whether new plants were aerial shoots that emerged from a rhizome or seedlings by removing the leaf litter to seek for rhizome connections or cotyledons.

Plant measurements

At each annual census (in May), the number of leaves per plant and the longest diameter of five leaves per individual were recorded to obtain two estimates of plant size: the number of leaves and total leaf area. I estimated the area per leaf with the following equation: leaf area = 0.18 + 0.02 longest diameter (N = 100, R² = 0.93, F = 1237.1, P < 0.0001; linear regression), obtained from leaves from non-sampled plants. The total leaf area per plant was obtained as the product of the mean leaf area and the number of leaves. Plant growth was evaluated by using the relative growth rate of leaf area per plant (RGRa) for two growth periods (1998-1999 and 1999-2000) as $[\ln(S_{t+1}) - \ln(S_t)] / \Delta t$, where S_t is leaf area at time t .

At each census, I also counted the number of flowers produced per plant and the number of filled achenes per flower. Aborted achenes were easily recognizable due to their undeveloped appearance. The filled/total achene ratio was used to calculate the seed set, given that each achene contains a single ovule in *H. nobilis*. I calculated the proportion of flowers that escaped from predation, as snails can destroy the whole flower. The final reproductive output per plant was estimated by summing all filled achenes from all flowers.

In May 1999, I randomly chose 100 non-sampled *H. nobilis* plants from six different patches in the SF population to investigate the effect of density on plant performance. For each plant, I recorded all size and fecundity variables described above. All *H. nobilis* plants within a circle (40 cm radius) around each selected plant were counted, and their size and the distance to the target plant measured.

Statistical analyses

The spatio-temporal variation in plant performance and fecundity in the studied *H. nobilis* populations was analyzed by using three-way repeated measures ANOVA models. Year (repeated measures), population, and patch nested within population were the explanatory factors, while the response variables were the

number of leaves, leaf area, RGRa, flower production, number of ovules per flower, proportion of non-predated flowers, seed set, and total number of achenes produced. Because variables concerning fecundity are usually size dependent in plants, I first carried out linear regressions between these variables and leaf area, including all plants from all patches and populations for each of the years of study. Whenever these regressions were significant, ANOVAs were carried out on the residuals. The effects of density and canopy openness on the variables listed above were tested using linear regression models. When necessary, variables were arcsin- (for proportions) or log-transformed for normality, homocedasticity and linearity.

Results

Spatio-temporal variation in plant size and growth

The number of leaves produced per plant showed great temporal as well as spatial variation, both between populations and between patches within populations (Table 2). In addition, both year x population and year x patch interactions had significant effects on the number of leaves produced per plant, indicating that the year effect varied between populations and between patches within populations. Mean values per patch and year for the number of leaves sharply decreased over time (Fig. 1a). This pattern was also observed for total leaf area per plant (Fig. 1b), which is related to the shrinkage of plant size over time in both *H. nobilis* populations. Total leaf area per plant also showed a high temporal variability, and significant spatial differences were found only between patches within populations (Table 2). However, all interactions were also significant, indicating that

Table 2 Three-way repeated measures ANOVA for the effects of year (1998, 1999, and 2000), or growth period (1998-1999 and 1999-2000), population (SF and SM), and patch nested within population (11 and 5 patches for SF and SM populations, respectively) on the number of leaves per plant, the total leaf area per plant, and the relative growth rate of the total leaf area per plant (RGRa) in *Hepatica nobilis*. Significance: ns = nonsignificant, *P < 0.05, **P < 0.01, ***P < 0.0001.

Source	No. leaves		Leaf area		RGRa	
	df	F	df	F	df	F
Year	2	267.36 ***	2	337.38 ***	1	34.91 ***
Year x Pop.	2	7.39 **	2	16.13 ***	1	9.20 **
Year x Patch(Pop.)	28	4.47 ***	28	5.93 ***	14	2.03 *
Error	858		858		429	
Pop.	1	7.52 **	1	0.43 ns	1	21.77 ***
Patch(Pop.)	14	6.41 ***	14	6.67 ***	14	9.10 ***
Error	429		429		429	

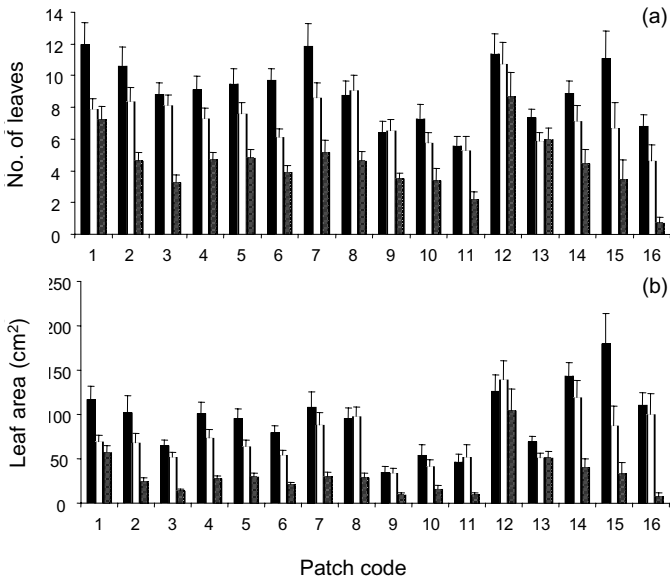


Figure 1 Means (+SE) per patch and year for (a) the number of leaves per plant, and (b) the total leaf area (cm²) per plant. Years: 1998 (filled bars), 1999 (hollow bars), and 2000 (hatched bars). Patch codes as in Table 1.

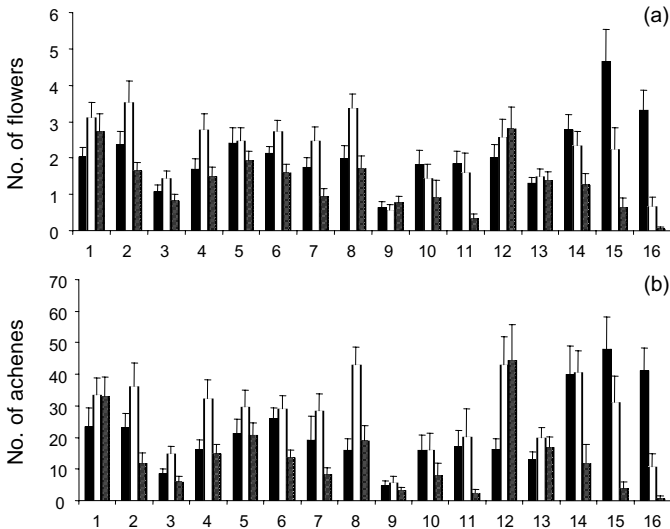


Figure 2 Means (+SE) per patch and year for (a) the number of flowers per plant, and (b) the final number of achenes produced per plant. Years as in Figure 1. Patch codes as in Table 1.

the population and patch effect strongly depended on the year. Finally, growth period, population, and patch effects, and growth period x population and growth period x patch interactions, all had significant effects on RGRa (Table 2). RGRa values were negative for all patches in both growth periods (range of means \pm SE over patches and growth periods = -0.1 ± 0.1 and -2.4 ± 0.5).

Spatio-temporal variation in fecundity

The number of flowers produced per plant significantly increased with total leaf area in all three years ($N = 445$, $R^2 > 0.29$, $F > 184.9$, $P < 0.0001$ for all three years; linear regression), as did the number of ovules per flower ($N > 221$, $R^2 > 0.21$, $F > 57.6$, $P < 0.0001$ for all three years; linear regression) and the number of achenes produced per plant ($N = 445$, $R^2 > 0.34$, $F > 137.2$, $P < 0.0001$ for all three years; linear regression). In contrast, neither the proportion of non-predated flowers nor seed set were significantly correlated to plant size ($P > 0.05$ in all three years for both variables; linear regression).

After removing the plant size effects, the number of flowers per plant showed significant variation from year to year as well as significant spatial variation at all scales (Table 3). In contrast, the number of achenes produced per plant only showed a significant patch effect and a significant year x patch interaction (Table 3). During the three years of study, the reproductive output experienced a decrease over time even though flower and achene production reached a maximum in 1999 in many of the studied patches (Fig. 2). The different temporal patterns of flower and achene production among patches at both populations explain the above significant interactions (Fig. 2).

The proportion of non-predated flowers was high (range of means \pm SE over patches and years = $79.9 \pm 6.7 - 100.0 \pm 0.0\%$), and only a slight between-population difference and a significant year x patch interaction were found (Table 3). The number of ovules per flower (range of means \pm SE over patches and years = $6.6 \pm 1.1 - 19.7 \pm 2.1$) also showed more spatial than temporal variation, although the year x patch interaction was significant (Table 3). Finally, seed set was highly variable, both between years and patches but not between populations (Table 3), and reached very high values over the whole 3-yr study (range of means \pm SE over patches and years = $70.2 \pm 5.1 - 100.0 \pm 1.0\%$).

Canopy openness and density effects on plant performance

There were no significant differences between canopy openness inside and outside patches ($F_{1,144} = 0.35$, $P = 0.55$; two-way ANOVA), which implies that the forest was very homogeneous in canopy structure. There were, however, significant differences between patches in canopy openness ($F_{7,144} = 4.56$, $P < 0.0001$; two-way ANOVA), but not in the interaction between patch and inside/outside position ($F_{15,144} = 0.64$, $P = 0.73$; two-way ANOVA). However, between-patch differences in the canopy openness were not too marked (see Table 1), and no significant effects of canopy openness on any variable in any year of study were

Table 3 Three-way repeated measures ANOVA for the effects of year (1998, 1999, and 2000), population (SF and SM), and patch nested within population (11 and 5 patches for SF and SM populations, respectively) on the initial flower production per plant, the proportion of flowers that survived predation per plant, the number of ovules per flower, the seed set, and the final number of achenes produced per plant in *Hepatica nobilis*. Significance: ns = nonsignificant, *P < 0.05, **P < 0.01, ***P < 0.0001.

Source	No. flowers		Flower surv.		Ovules/flower		Seed set		No. achenes	
	df	F	df	F	df	F	df	F	df	F
Year	2	11.48 ***	2	0.69 ns	2	0.38 ns	2	16.39 ***	2	0.42 ns
Year x Pop.	2	28.75 ***	2	0.41 ns	2	0.02 ns	2	4.58 *	2	1.78 ns
Year x Patch (Pop.)	28	4.12 ***	28	1.94 **	28	1.90 **	28	2.07 **	28	2.11 **
Error	858		332		268		268		858	
Pop.	1	27.48 ***	1	4.70 *	1	9.68 **	1	0.99 ns	1	0.01 ns
Patch (Pop.)	4	3.63 ***	14	1.02 ns	14	2.31 **	14	2.43 **	14	3.64 ***
Error	429		106		134		134		429	

found ($P > 0.05$ for all linear regressions including all patches from both populations).

I found significant density effects on the number of ovules per flower, which was significantly positively correlated ($N = 61$, $R^2 = 0.19$, $F = 6.20$, $P < 0.004$; multiple linear regression) with the total leaf area of the nearest plant ($r = 0.39$) and the distance to the largest plant ($r = 0.33$). Regressions were carried out on residuals of a previous significant regression between the number of ovules per flower and total leaf area ($N = 61$, $R^2 = 0.11$, $F = 7.07$, $P < 0.01$; linear regression). For the rest of the variables analyzed, I found no significant density effects ($P > 0.05$ for all multiple linear regressions). Moreover, I found no significant density effects for any variable studied when mean density values per patch (see Table 1) were regressed against mean values per patch and year ($P > 0.05$ for all linear regressions including patches from both populations).

Seedling recruitment and ramet dynamics

During this 3-yr study, I found no seedlings in any of the patches in SF population and only two seedlings in one patch in SM population (Table 4). In contrast,

Table 4 Number of seedlings and ramets of *Hepatica nobilis* that appeared in each quadrat during the three years of sampling (1998-2000) in the SF and SM populations.

Population	Patch code	Seedlings	Ramets
SF	1	0	6
	2	0	7
	3	0	4
	4	0	4
	5	0	3
	6	0	3
	7	0	0
	8	0	0
	9	0	2
	10	0	5
	11	0	0
SM	12	0	0
	13	2	0
	14	0	0
	15	0	0
	16	0	0
Total		2	34

I found a total of 34 new ramets in SF and none in SM (Table 4). However, none of them was found at the next census. In addition to this total lack of recruitment of new individuals or ramets to the population, 45-90% of the plants per patch tagged in 1998 lost their aboveground parts during the three years of study. I cannot confirm that these plants were dead, since a few tagged plants that had lost their aboveground parts in 1999 produced new leaves and flowers in 2000.

Discussion

Although it is generally assumed that the understory of late successional deciduous forests is a relatively stable environment (Damman & Cain, 1998), there is a degree of temporal and spatial variation in habitat characteristics that affect plant performance of woodland herbs (Inghe & Tamm, 1985; Nault & Gagnon, 1993; Damman & Cain, 1998; Valverde & Silvertown, 1998). This is also the case of the patchily distributed populations of *H. nobilis* presented in this paper. Plant size and individual growth rates of *H. nobilis* varied greatly between populations, patches, and years (Table 2). In contrast, although flower production also varied at all spatial and temporal scales, final achene production varied significantly only between patches within populations and the interaction year \times patch was also significant (Table 3). These results suggest that patch-specific characteristics plus the interaction with year-to-year variation in environmental conditions, chiefly determine the performance of *H. nobilis* patches.

As a result, plants in some patches performed better than plants in others during the three years of study (Figures 1 and 2). Nevertheless, no relationship between mean plant parameters and patch characteristics, in terms of total plant density or canopy openness above each patch, was found. In fact, current plant densities per patch were low and canopy openness records indicated that all patches analyzed were under a relatively closed canopy cover (Table 1). At a smaller scale, complex density effects were detected affecting *H. nobilis* performance. In particular, the number of ovules per flower increased with the distance to the largest plant, indicating that growing nearby large plants did decrease potential fecundity. However, the number of ovules per flower also increased with the leaf area of the nearest plant, reflecting perhaps a better habitat quality at those microsites. These results indicate that fecundity of *H. nobilis* plants is affected by small-scale habitat characteristics within patches. Such small-scale dynamics have been reported for many other plant species in which microhabitat can affect several plant and population parameters, such as recruitment rates, total plant biomass, and population structure (Guo, 1998; Menges & Hawkes, 1998; Ne'eman & Izhaki, 1999), which in turn may have a major impact on plant microevolutionary events (Stanton & Galen, 1997; Albert et al., 2001).

Apart from patch-specific differences in *H. nobilis* performance, a generalized decrease in plant size and fecundity was observed at both populations (Fig. 1 and 2). This pattern could be attributed to general weather conditions affecting *H. nobilis* performance. In fact, other studies clearly indicated the adverse effect of harsh environmental conditions (e.g. summer droughts) on survival and flow-

ering in *H. nobilis* (Inghe & Tamm, 1985). In my case, however, the relationship between general population performance and weather conditions (total annual precipitation and mean annual or monthly temperatures) was not straightforward. Low seedling recruitment is a typical trait of long-lived, clonal woodland herbs (Eriksson, 1989), but the case of the two *H. nobilis* populations presented in this study seems to be extreme: only two seedlings were observed in one patch during the three years of study (Table 4). This could be a specific trait of *H. nobilis*, as prolonged periods (up to seven years) of very low seedling recruitment have also been observed for this species (Inghe & Tamm, 1985).

Recruitment limitation in *H. nobilis* might be related to particular germination requirements (e.g. light), as seed losses due to flower predation or ovule abortion were not a limiting factor in this case. It must be emphasized that *H. nobilis* seeds might have strong dormancy mechanisms, since all germination experiments carried out in the laboratory failed. Unfortunately, I have no data on the importance and extent of soil seed bank for *H. nobilis* recruitment. On the contrary, ramet dynamics appeared to be more active in one of the studied populations (Table 4) even though none of them survived to the following year, perhaps because they were also affected by the same environmental conditions that negatively affected adult plants. As many other long-lived plants, these recruitment patterns indicate that the dynamics of *H. nobilis* populations is of the remnant type (*sensu* Eriksson, 1996; 2000). That is, plant populations are maintained due to the long-life spans of adult plants in combination with episodic but successful recruitment events when environmental conditions become appropriate. Hence, although single-site estimates of population dynamics, including several years, may indicate that populations are declining due to the lack of recruitment and some mortality events, they could have means of enduring from decades up to hundreds of years even under adverse environmental conditions (see examples in Eriksson, 1996; García et al., 1998; 2000; Picó & Riba, 2002).

The pattern of population performance reported for *H. nobilis* in this study does not differ substantially from that of many other woodland herbs (Inghe & Tamm, 1985; Eriksson, 1989; Nault & Gagnon, 1993; Watkinson & Powell, 1993; Eriksson & Froborg, 1996; Damman & Cain, 1998; Valverde & Silvertown, 1998). However, patchily distributed populations of *H. nobilis* are rare in the beech forest studied. The fact that the occurrence of *H. nobilis* in managed stands of beech forest is restricted to small clumps composed of a few plants might indicate that logging negatively affect *H. nobilis* persistence, as reported for many other woodland herbs (Meier et al., 1995). Unfortunately, a comparison between managed and unmanaged stands has not been possible given the lack of plants in managed stands. Further studies on *H. nobilis* seed germination and seedling recruitment requirements, the so-called "windows of opportunity" for recruitment in clonal plants (Eriksson & Froborg, 1996), and patch characteristics (e.g. nutrient and light availability) that enhance plant performance, are needed to better understand the possibilities of population recovery after logging.

Acknowledgements

I want to thank P. Cortés, C. Biel, M. Riba and S. Gili for field assistance. I am grateful to J. Retana, H. Berk, and Ø. Totland who provided exceptionally helpful comments on different drafts of this manuscript. I thank the Director of the Montseny Natural Park for granting me permission to work in the park. This research was partially supported by the Comissionat per a Universitats i Recerca de la Generalitat de Catalunya, grant 1997FI-00854.

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