Original article

Diversity of woody plant seedling banks under closed canopy in fragmented coppice forests

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Abstract –
• Seedling banks of woody species established under closed canopy have received little consideration in coppice forests despite their potential importance for natural regeneration.
• This study aimed to evaluate the influences of canopy composition and of distance from the nearest forest edge on the abundance and species richness of the seedling bank, for different ecological groups of seedlings (age, successional status and dispersal vector) in 68 fragmented coppice stands.
• Seedlings were found in 67 stands, with 19 species identified. Eight species present as older seedlings were lacking as first-year old seedlings, suggesting temporal variability of species recruitment. Seedling abundances of species with low-dispersal ability were positively correlated with the abundances of their conspecific adults. Seedling abundance of mid-successional species was negatively correlated with the distance from the nearest forest edge, while mid-to-late successional species seedling abundance presented the opposite pattern.
• Our results showed that woody species were able to establish frequently under closed canopy in these fragmented coppices and form a seedling bank which may be used for natural regeneration.

woody seedling bank / *Quercus* **spp. / forest edge / Southwest France / coppices**

Résumé – Une banque de semis diversifiée sous canopée fermée dans des taillis fragmentés.
• Peu d'études ont porté sur les banques de semis de ligneux installés sous canopée fermée dans des taillis, malgré leur importance potentielle pour la régénération naturelle.
• Nous avons exploré le lien entre l'abondance et la richesse des semis de ligneux, et la composition de la canopée et la distance à la lisière la plus proche, dans 68 peuplements gérés en taillis. Les semis ont été regroupés en fonction de leur âge, et les espèces en fonction de leur mode de dispersion et de leur place a priori dans la succession forestière.
• Nous avons trouvé des semis dans 67 peuplements, appartenant à 19 espèces distinctes. Huit espèces présentes sous forme de semis plus âgés, manquent sous forme de semis de l'année, suggérant une variabilité temporelle du recrutement des espèces. L'abondance des semis des espèces à dispersion limitée est corrélée à celle des adultes. L'abondance des semis des espèces post-pionnières nomades, capable de s'installer en pleine lumière, est négativement corrélée à la distance à la lisière, tandis que celle des semis des espèces post-pionnières, plus sciaphiles présente le patron opposé.
• Nos résultats indiquent que plusieurs espèces de plantes ligneuses sont capables de s'établir fréquemment sous canopée fermée dans ces taillis fragmentés, formant ainsi une banque de semis potentiellement utilisable pour la régénération naturelle de ces forêts.

banque de semis de plantes ligneuses / *Quercus* **spp. / lisière forestière / Sud-Ouest de la France / taillis**

1. INTRODUCTION

There is an increasing interest in using natural regeneration in temperate woodlands as a management strategy that may contribute to forest sustainability (Modry et al., 2004), since it makes it possible to produce mixed stands and to maintain natural genetic variability (Harmer et al., 1997). Tree species recruitment into the forest canopy after disturbance can come from the seed rain, the seed bank in the soil or from the seedlings already established before the disturbance, i.e., the "seedling bank" (Grime, 1979), which is a kind of "advance regeneration" (Frey et al., 2007). These seedlings have

established beneath a closed canopy and may survive in a suppressed state for several years (Streng et al., 1989). Seedling bank composition and species richness thus result from ecological processes that took place before the logging disturbance, under the influence of a closed canopy. These processes have received less attention than events after logging disturbances, despite their possible influence on the future adult tree community (Hodgson and Grime, 1990). Few studies, however, have considered the seedling bank and its determinants in coppice forests, a forest management system frequently found in Europe (Gracia et al., 2001; Le Duc and Havill, 1998).

Seedling presence depends both on seed availability and on the possibility of the species to establish and survive in a given site (Nakashizuka, 2001). For the seedling bank under closed

canopy, stand characteristics may partly determine seedling density and community composition by affecting seed availability through the proximity of conspecific adults (Frey et al., 2007). The dependence of seedling establishment on adult presence and/or abundance may vary between plant species according to their dispersal abilities (vector type and/or seed mass) (Grashof-Bokdam, 1997; Hewitt and Kellman, 2002; McEuen and Curran, 2004).

In fragmented woodlots, particular attention should be focused on forest edges since they may have a considerable impact on woodlots (Laurance and Yensen, 1991) by influencing fluxes of species, matter and energy (Cadenasso et al., 2003; Harper et al., 2005). This is an important intra-forest factor, which has been previously shown to influence the spatial pattern of seedlings and saplings in fragmented forests (Gehlhausen et al., 2000; Hewitt and Kellman, 2004; Matlack, 1993; Ranney et al., 1981). Opposed spatial patterns for successional groups according to the distance from the edge have been observed: "early successional species or disturbance-tolerant (shade-intolerant) species have higher seedling densities at the forest edge, while the seedling densities of "interior" species (shade-tolerant) abruptly diminish near the edge" (Marchand and Houle, 2006).

This study aims: (i) to identify which woody species were able to establish themselves under closed canopy of coppice forests; and (ii) to evaluate the influences of canopy composition and of distance to the nearest forest edge on the abundance and species richness of the seedling bank, according to different ecological groups of seedlings (age, successional status and dispersal vector).

2. MATERIALS AND METHODS

2.1. Study area

The study area was located in the LTER (Long Term Ecological Research) site "Vallées et Coteaux de Gascogne" in Southwestern France (Lat: 43° 13' N, Long: 0° 52' E) (Fig. 1). The dominant climatic influence is oceanic with 12.5 °C mean annual temperature and 750 mm mean total precipitation. This hilly region (200–400 m a.s.l.) is characterised by short and steep slopes along the river valleys descending from the Pyrenees Mountains. Forests have three types of soil: superficial limestone soils (rendosols or calcosols), brown acid soils (brunisols) and brown washed soils (neoluvisols) (Duchaufour, 1983). Forests cover 15% of the area with numerous small woodlots ranging in area from less than 1 ha to 50 ha, and a few larger forest tracks (600 ha) (Balent and Courtiade, 1992). The vegetation composition is the result of both Atlantic and Mediterranean influences on a Medio-European flora, with oaks (*Quercus robur, Q. pubescens, Q. petraea)* being the main tree species, often in combination with hornbeam (*Carpinus betulus*), cherry (*Prunus avium*), wild service tree (*Sorbus torminalis*), chestnut (*Castanea sativa*) and field maple (*Acer campestre*). The majority of the forests are composed of oak and hornbeam coppice stands, with 30–50 standard oak trees per ha retained to produce timber (Deconchat and Balent, 2001). Small stands (0.5–3 ha) of coppice are clear-cut every 30–50 years; the standard trees are cut approximately every 60 years. These standard trees are regenerated mostly from seeds, while coppice is regenerated
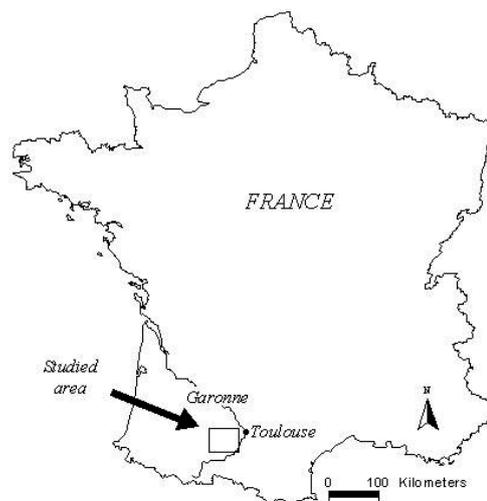

Figure 1. Location of the study area in France.

mainly by resprouting. The majority of these woodlots are owned or managed by farmers.

2.2. Sampling design

Forty-two woodlots were selected in the study area. The area of the selected woodlots in the sample ranged from 0.32 ha to 167 ha. Stands were defined as spatial units within the woodlots with visually homogeneous canopy composition, structure and age. Sixty-eight mature stands (age ranged from 12 years to 77 years since the coppice was last logged) were chosen to represent the diversity of composition and structure found in the region, ranging from pure oak coppice to beech timber forest, with a higher frequency of coppice-with-standards (60% of the plots). In each stand, we located a 20×20 m square plot in a place avoiding gaps where the canopy could be visually regarded as closed (median canopy openness = 14.6% measured from hemispherical photographs for a subset of 43 stands). The plots were selected so as to cover a wide range of distances from the edge: from 19 m to 459 m. Five 1-m^2 subplots were installed in each plot, in the centre and in the four corners of the 400 m^2 plot, to make an inventory of the seedlings.

2.3. Data collection

All seedlings less than 20 cm tall were identified during the summer of 2003 in the 1-m^2 subplots. As the threshold between seedling and sapling is not clearly stated from the literature, we decided to restrict our study to the seedlings < 20 cm (Hille Ris Lambers and Clark, 2003). The seedlings were separated into first-year and older-than-first-year age classes (> 1 year old) on the basis of cotyledon presence/absence and stem woodiness (Hille Ris Lambers and Clark, 2003). Hereafter, the older-than-first-year seedlings are referred to as "older seedlings". The older seedlings were suspected to be less than five years old (personal observations). This age partition enabled us to account for the effects of canopy composition and distance from the edge both on seedling establishment after germination (first-year seedlings), and on seedling growth and survival (older

Table I. Species recorded in the seedling census and their frequency (percentage of the plots where the species is present) as first-year and older seedlings. The successional status indicates their position in the vegetation succession: early successional species are associated with the beginning of the succession, produce many small seeds and are light demanding; mid-successional species are in the middle of the succession as mid-to-late successional species, but are more opportunist and able to establish themselves in open spaces; mid-to-late successional species are in the middle of the succession and have a greater longevity than early successional species; late successional species are associated with the end of the succession and produce fewer big seeds. The dispersal mode indicates the main dispersal vectors: "Wind" for anemochorous species, "Mammal, Bird" or both for zoochorous species. These data are taken from Rameau et al. (1989).

Species	Successional status	Dispersal mode	Total seedling number		Frequency	
			≤ 1 year	> 1 year	≤ 1 year	> 1 year
Acer campestre L.	Mid	Wind	10	121	7.35	23.53
Carpinus betulus L.	Mid-to-late	Wind	12	62	7.35	19.12
Castanea sativa Mill.	Mid-to-late	Mammal	1	20	1.47	2.94
Corylus avellana L.	Mid	Bird, mammal	0	4	0	4.41
Cornus sanguinea L.	Early	Bird	6	21	7.35	13.23
Crataegus monogyna Jacq.	Mid	Bird	9	53	10.29	38.23
Fagus sylvatica L.	Late	Bird, mammal	0	10	0	7.35
Fraxinus excelsior L.	Mid	Wind	3	17	1.47	4.41
Ilex aquifolium L.	Late	Bird	1	15	1.47	5.88
Mespilus germanica L.	Unknown	Mammal	0	2	0	1.47
Populus tremula L.	Early	Wind	0	2	0	1.47
Prunus avium L.	Mid-to-late	Bird	14	91	13.23	54.41
Prunus spinosa L.	Early	Bird	0	39	0	22.06
Quercus petraea Liebl.	Mid-to-late	Bird, mammal	141	231	25.00	26.47
Quercus pubescens Willd.	Mid	Bird, mammal	76	386	20.59	45.59
Quercus robur L.	Mid	Bird, mammal	47	191	19.12	39.70
Sorbus torminalis (L.) Crantz	Mid	Bird	8	34	5.88	17.65
Ulmus minor Mill.	Mid	Wind	0	13	0	10.29
Viburnum lantana L.	Unknown	Bird	0	3	0	4.41

seedlings) (Clark et al., 1999). Species were identified according to Rameau et al. (1989). When identification of an oak seedling was ambiguous at the species level because of high morphological variability and the ability of oak species to interbreed (Petit et al., 2004), the genus level (*Quercus* sp.) was used instead.

Species were grouped according to their dispersal mode (Tab. I), since dispersion is one of the key processes determining the spatial structure of plant population (Nathan and Muller-Landau, 2000). We also grouped species according to their successional status, because disturbance is an important force in forest communities that initiates secondary succession (Jentsch et al., 2002). Finally, we wanted to investigate if we could identify different regeneration patterns among the three oaks present in these stands, because of this genus' dominance in the forests studied.

The tree species of the dominant layers (taller than 7 m) of each 400 m^2 plot were identified and counted, and regarded as potential sources of seeds. We will use the expression "conspecific adults" to refer to these trees. The distance to the nearest forest edge was measured in the field from the centre of each 400 m^2 plot.

2.4. Data analyses

The data of the five 1-m^2 subplots (seedling counts and identification) were pooled for each plot (400 m^2), and seedling abundance and richness were then calculated for each plot and used as response variables in all the subsequent analyses. Species richness (without the *Quercus* sp. genus group) and abundance were calculated for the two age groups; abundance was calculated for the species groups based on dispersal vector and position in the forest succession. Oak

species abundances were also calculated, discarding the *Quercus* sp. seedlings.

These response variables were related to canopy composition and distance to the forest edge. Non-parametric tests were used since most of the data were not normally distributed, with $p \leq 0.05$ as a significance level criterion. The Wilcoxon signed-rank test was used for the comparison between the first-year and older-than-first-year seedling abundances. Spearman's rank correlation (r_s) was used to estimate the relationship of seedling abundance with conspecific adult abundance and with the distance to the nearest forest edge. Cross-tabulations were used to estimate the relationship between presences of seedlings and of conspecific adults. All statistical analyses were carried out using SYSTAT 9 (SYSTAT, 1999).

3. RESULTS

3.1. General seedling distribution

In 67 of the 68 stands inventoried, we found at least one seedling. We found first-year seedlings in 46 stands and older seedlings in 66 stands (Fig. 2). These seedlings belonged to 19 species, including 12 tree and seven shrub species (Tab. I). Total species richness was higher for the older seedling community than for that of the first-year (19 and 12 species, respectively). *Q. petraea* had the highest frequency of the first-year seedlings, and three other species had a frequency greater than or equal to 10% (Tab. I). Among the older seedlings, two species had frequencies of more
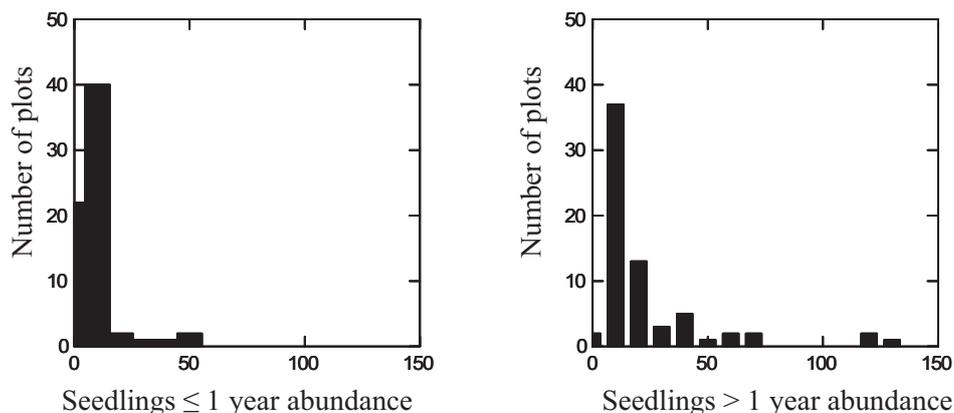
Figure 2. Histogram of seedling abundance (sum of the number of seedlings counted in the five 1 m² plots of each 400 m² plots), for first year seedlings (left) and older seedlings (right), on studied stands.

Table II. Descriptive statistics of total species richness and total or per group (see Tab. I for the definition of these groups) abundances (sum of the number of seedlings counted in the five 1 m² plots of each 400 m² plots), for first year and older seedlings.

Age of seedlings		All seedlings		Successional groups				Dispersal groups			
				Early	Mid	Mid-late	Late	Bird	Bird-Mammal	Mammal	Wind
		Species richness	Abundance	Abundance				Abundance			
≤ 1 year	Min	0	0	0	0	0	0	0	0	0	0
	Max	5	47	2	33	47	3	4	47	1	6
	Median	1	2	0	0	0	0	0	0	0	0
> 1 year	Min	0	0	0	0	0	0	0	0	0	0
	Max	8	128	25	118	116	9	41	118	17	103
	Median	3	8.5	0	4.5	2	0	2	4	0	0

* Only one plot had no seedlings.

than 40% (*P. avium* was the most frequent), and a further five lay between 20 and 40% (Tab. I). Species richness per plot of first-year seedling community was lower than that of the older seedling community (Tab. II). First-year seedling abundance was much lower than older seedling abundance (Wilcoxon signed-rank test: Z = −5.989; $p < 0.001$). Mid-to-late successional species were the most abundant successional group among the first-year seedlings (total of 168 seedlings compared with 150 seedlings for mid successional species) whereas, when considering older seedlings, it was the mid-successional species, followed by the mid-to-late successional species (Tab. II). The species dispersed by bird-mammal vectors were the most abundant group for both the first-year and older seedlings (Tab. II). Median values of zero for successional and dispersal groups in Table II, imply that there are none of these types at more than half of the sites in the first-year class.

man $r_s = 0.05$ $p > 0.05$ and $r_s = 0.172$ $p > 0.05$). The presence of bird-dispersed species seedlings showed no relationship with conspecific adult presence in the canopy, contrary to wind-dispersed species seedlings (Tab. III). Bird-mammal dispersed species were present as adult trees in almost all the plots, preventing us from studying their relationship with seedling abundance.

For first-year seedlings, the mid-to-late species group was the only one linked to adult abundance but not to their presence, indicating that a few plots with many seedlings and adults had a strong influence on this relationship (Tab. III). For the older seedlings, mid-to-late seedlings were linked to adult abundance but also to adult presence, just as in the case of the mid-successional species.

The presence of oak seedlings was significantly linked to the presence of conspecific adults in the canopy for first-year *Q. robur* and *Q. pubescens* seedlings (Tab. IV).

3.2. Relationship with conspecific adult

The species richness of first-year and older seedlings was not correlated with adult species richness (respectively: Spear-

3.3. Distance from the nearest forest edge

Species richness of older seedlings decreased with distance from the edge (Spearman $r_s = −0.261$; $p < 0.05$),

Table III. Spearman correlations (r_s), between stand variables and abundance of seedlings for the different groups (see Tab. I for the definition of these groups). Groups with no or too few individuals were discarded. Level of significance for r_s are ns = not significant; * $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$ and *** $p \leq 0.001$.

Age of seedlings	Group of species	Distance from the forest edge (m)	Presence of conspecific adults	Abundance of conspecific adults
≤ 1 year	Mid successional	ns	ns	ns
	Mid-late successional	**0.313****	ns	**0.399****
> 1 year	Mid successional	**−0.346***	**	**0.526*****
	Mid-late successional	**0.224***	***	**0.232***
≤ 1 year	Bird	**−0.247***	ns	ns
	Bird-Mammal	**0.428****	ns $	ns
	Wind	ns	*	**0.200***
> 1 year	Bird	**−0.332****	ns	ns
	Bird-Mammal	ns	ns $	ns
	Wind	ns	*	**0.267***

$ indicates that there are too few situations where there are no conspecific adults, so there is no significant result.

Table IV. Statistical parameters of relationships: (1) between abundance of oak seedlings and distance from the nearest edge (Spearman correlation test, p values); and (2) between density of oak seedlings and presence of the same adult species (Mann-Whitney independence test: ns = not significant; * $0.01 < p \leq 0.05$; ** $0.01 < p \leq 0.01$; *** $p \leq 0.001$).

Age of seedlings	*Quercus* species	Distance from forest edge (m)	Presence of conspecific adults
≤ 1 year	*Q. pubescens*	ns	***
	Q. robur	ns	ns
	Q. petraea	**0.540*****	***
> 1 year	*Q. pubescens*	ns	***
	Q. robur	ns	**
	Q. petraea	**0.451*****	***

whereas first-year seedling abundance increased with this distance (Spearman r_s = 0.245; p < 0.05). Seedling abundance of mid-to-late successional species was positively correlated with the distance from the edge both for first-year seedlings and to a lesser extent for older seedlings (Tab. III and Fig. 3). For mid-successional species, this correlation was negative and concerned only the older seedlings (Fig. 3). Bird-mammal dispersed species, contrary to bird-dispersed species, presented a positive correlation between abundance of first-year seedlings and distance from the edge. For older seedlings, the bird-dispersed species group was the only one negatively correlated with this distance. The higher abundance of *Q. petraea* seedlings was positively associated with distance from the edge (Tab. IV).

4. DISCUSSION

4.1. Seedling abundance and diversity

The total species richness of the seedling community (19 species) was a substantial proportion (round to 40%) of the total woody species richness recorded for adult trees at the sampling sites (48 species, data taken from the dominant layers), as well as of the regional species pool (66 species, data taken from National Forest Inventory). This is a level of diversity very similar to the levels found in other temperate forests (Harmer et al., 1997; Modry et al., 2004). Seedling establishment in the coppices studied was frequent. Indeed, several species had a relatively high seedling frequency (Tab. I) compared with the values obtained in other coppices dominated by *C. betulus* (Le Duc and Havill, 1998). Oak canopy produces less shade than that of *C. betulus* (Le Duc and Havill, 1998). This could explain the establishment of more species in our stands. Seedling density found in these coppices (median = 2 seedlings m^{-2}; see also Fig. 2) suggests that seedling recruitment does not seem to hamper natural regeneration of these forests (Harmer et al., 1997). The seedlings established for more than one year substantially contributed to the whole seedling bank (Tab. II), suggesting that these stands have a "seedling bank" sensu Grime (1979): i.e. plants < 50 cm tall which can survive in a suppressed state for many years (Streng et al., 1989). Indeed, not all the first-year seedlings could contribute to the persistent bank of seedlings, because they may survive shortly on seed reserves and die before the second year (Streng et al., 1989). However, saplings (> 20 cm tall) in these stands are frequent and abundant (unpublished data). This suggests that part of the older seedlings found here could grow to saplings. Some species present as older seedlings are missing in the first-year seedling communities (Tab. I). This may indicate some temporal fluctuations in species recruitment (Frey et al., 2007), perhaps due to the masting characteristic of species such as ash (Tapper, 1992). Oaks which dominate the seedling community (Tab. I) showed a high mortality (max: 73 dead seedlings/m^2). This could create the opportunity for other species to develop. Oaks are effectively less abundant as saplings, compared with other species such as *Carpinus betulus* or *Prunus avium* (unpublished data).
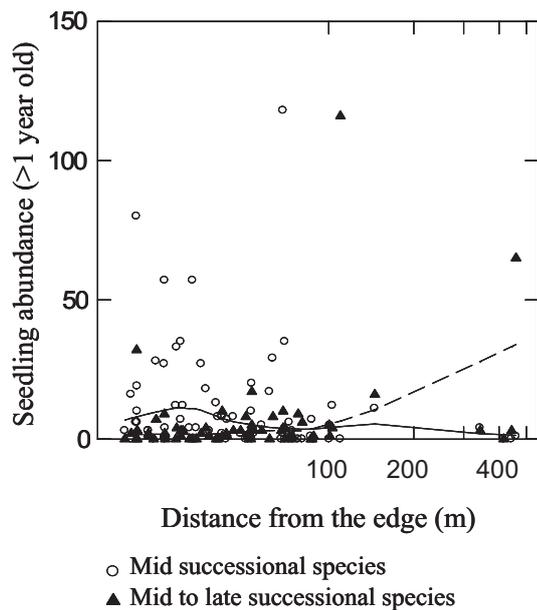
Figure 3. Abundance (sum of the number of seedlings counted in the five 1 m² plots of each 400 m² plots) of older seedlings according to distance from the forest edge (m) for mid-successional species (open circles, solid line) and mid-to-late successional species (bold triangles, dashed line) (see Tab. I for the definition of these groups). Distance from the edge is on a logarithmic scale. Relationships between seedling abundance of each group and distance from the edge are materialized by lines obtained by a lowess smoothing with a tension fixed to 0.5 (SYSTAT, 1999).

4.2. Relationship with conspecific adults

The presence of conspecific adults appeared to be of great importance for species with limited dispersal capacities (few big seeds, narrow range of dispersal distances) (Hille Ris Lambers and Clark, 2003), as we can see for the three oaks species (Tab. IV). This suggests that recruitment in these temperate forests could be limited by dispersal (McEuen and Curran, 2004). Harmer and Morgan (2007) also observed that since acorns are heavy, many fall directly beneath their parent trees, although they can be dispersed by birds and small mammals over several kilometres (Gomez, 2003). On the contrary, bird-dispersed species, with smaller seeds and with a broader range of dispersal distances, were independent of conspecific adult presence (Tab. III). Seed dispersal limitation of forest trees can emerge, indeed, at various spatial scales (e.g., from stand to landscape) (Clark et al., 1998; McEuen and Curran, 2004). For species with limited dispersal capacities (oaks in our case), recruitment limitation may occur at the stand scale, whereas for species with higher dispersal capacities such as bird-dispersed species (*P. avium*, for example), it may occur at the landscape scale (Grashof-Bokdam, 1997; Hewitt and Kellman, 2002). The dependency on adult presence found for wind-dispersed species was less expected. This group is commonly considered as having better dispersal abilities than zoochorous species (Johnson, 1988), although several studies

have also reported some dispersal limitations for this group (Grashof-Bokdam, 1997; Houle, 1994).

4.3. Spatial pattern according to the distance from the forest edge

Species richness increased near the forest edge, as found by Marchand and Houle (2006). First-year seedling density increased with distance from the edge, as has been found in other temperate forests (Goldblum and Beatty, 1999). But species are expected to respond differently to edge influence according to their shade tolerance (Harper et al., 2005), with abundance of seedlings of early successional (shade-intolerant) species decreasing and abundance of late-successional (shade-tolerant) species increasing with distance from the edge (Gehlhausen et al., 2000; Hewitt and Kellman, 2004; Matlack, 1993; Ranney et al., 1981). The patterns found here for mid and mid-to-late successional groups (Fig. 3), which showed opposite trends, are consistent with these results. However, Marchand and Houle (2006) have recently shown, for a shade tolerant species, how this pattern could be inverted for a closed edge. This observation underlines the crucial importance of edge structure on edge influence (Harper et al., 2005). Indeed, increased light intensity is commonly found at open edges, a feature that is reversed as edges mature (Ranney et al., 1981). Our results are consistent with this statement, as we suspect that our edges are "open edges", as they are more frequently logged than woodlot interiors (De Warnaffe et al., 2006). Bird-dispersed species had higher seedling abundances at forest edges, consistently with previous work reporting higher densities of bird-dispersed species at edges (Ranney et al. 1981). All in all, distance from the forest edge seems to play an important role for seedling bank diversity by providing different niches for species according to their physiological characteristics (Gehlhausen et al., 2000) and dispersal vectors.

5. CONCLUSION

Although the observations made in this study are only a glimpse of the regeneration of these coppices stands, we noticed that seedlings of several woody species were able to establish themselves and survive for several years under a closed canopy. These seedlings can promote stand sustainability since they are new genets, increasing response plasticity to environmental constraints (Espelta et al., 1995). Despite the observations made on seedling distribution patterns according to distance from the forest edge and conspecific adult presence, the spatio-temporal variability of seedling patterns prevents us from making definite predictions about the future of these seedlings (Houle, 1994). Substantial seedling establishment does not ensure the subsequent renewal of the species (Gracia et al., 2001) since sapling survival may be particularly dependent on an opening of the canopy for some species such as oak (Espelta et al., 1995). A long-term study of regeneration in these forests should provide some interesting supplementary information about the spatio-temporal dynamics of this seedling bank (Frey et al., 2007).

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