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Fine-scale spatial patterns of recruitment in red oak (*Quercus rubra*): What matters most, abiotic or biotic factors?[1]

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Abstract: Seedling recruitment in temperate oaks is expected to depend mostly on biotic filters, given the relative independence from resource limitation conferred by large seed size. We investigated the magnitude and fine-scale spatial pattern of red oak (*Quercus rubra*) recruitment in a mature forest in southern Québec. We compared the scale of operation of experimentally assessed seed and seedling predation to that of several abiotic factors. We sought to interpret concordance or discordance between seed rain and seedling recruitment in terms of spatial heterogeneity in these environmental filters. Most of the demographic variables (adult leaf area index [LAI] and seed rain, newly emerged seedling, and recruited seedling densities) were highly heterogeneous and structured at fine spatial scales. Topography, soil moisture, and light, but not litter thickness, also showed significant spatial autocorrelation at fine spatial scales. However, most of the biotic filters (*e.g.,* seed removal, seed germination, and seedling mortality) were not spatially structured, except for clipping by voles, which was significantly autocorrelated at small distance classes. Failure to detect autocorrelation in most of the biotic filters suggests that they may operate at scales different from that studied, *e.g.,* at a coarser scale for seed predation, but at a finer scale for insect folivory. A path analysis revealed that a large proportion of the variance in seedling recruitment was the result of direct links between the demographic variables studied. Another path analysis, accounting for the effects of biotic filters, highlighted the critical role played by seed predators on recruitment. However, restricted seed dispersal was the major factor influencing the spatial distribution of recruits: indeed, spatial concordance between seed rain and recruit density suggested that even when they are heterogeneous at the same spatial scale, environmental filters are not strong enough to disrupt the patterns generated by primary seed dispersal. Hoarding by rodents accounted for a significant proportion of the spatially homogeneous seed removal; it also reduced potential recruitment limitation associated with microsite availability, thereby increasing the proportion of variation in the spatial pattern of recruitment accounted for by primary seed dispersal.

Keywords: environmental filters, seed predation, seedling predation, seedling recruitment, spatial autocorrelation, spatial concordance, spatial heterogeneity.

Résumé : Le recrutement de plantules chez les chênes des régions tempérées dépendrait principalement de filtres biotiques, les réserves importantes accumulées dans les graines procurant aux nouvelles plantules une certaine indépendance face à la disponibilité locale des ressources. Pour vérifier cette hypothèse, nous avons étudié le patron spatial de recrutement chez le chêne rouge (*Quercus rubra*) dans une forêt mature du sud du Québec. Nous avons comparé l'échelle spatiale à laquelle s'opère la prédation sur les graines et sur les plantules à celle de plusieurs facteurs abiotiques connus pour leur influence sur le recrutement de plantules. Notre but était d'interpréter la concordance ou la discordance entre la pluie de graines et le recrutement de plantules en termes d'hétérogénéité spatiale de différents filtres environnementaux. La plupart des variables démographiques (indice de surface foliaire des adultes; densité de la pluie de graines, des plantules récemment émergées et des plantules établies) étaient hétérogènes et fortement structurées à une échelle spatiale relativement fine. La topographie, l'humidité du sol et la disponibilité de la lumière étaient également autocorrélées à une échelle spatiale relativement fine. Par contre, l'épaisseur de la litière n'était pas fortement structurée. La plupart des filtres biotiques (dont la dissémination secondaire et la germination des graines, ainsi que la mortalité des plantules) n'étaient pas autocorrélés, à l'exception de la prédation sur les plantules exercée par les petits rongeurs qui elle était significativement structurée à une échelle spatiale fine. L'absence d'autocorrélation spatiale pour la plupart des filtres biotiques suggère que ceux-ci opèrent à des échelles différentes de celle que nous avons étudiée, soit à une échelle plus grossière pour ce qui est de la prédation sur les graines et à une échelle plus fine pour ce qui est de l'herbivorisme. Une analyse de pistes a démontré qu'une bonne proportion de la variance associée au recrutement était le résultat de liens directs entre les variables démographiques étudiées. Une seconde analyse, tenant compte des effets cumulatifs des filtres biotiques, a mis en évidence le rôle critique joué par les prédateurs dans le recrutement. Cependant, le faible potentiel de dissémination des graines semble être l'élément influençant le plus la distribution locale des plantules. En effet, la concordance spatiale entre la pluie de graines et les plantules établies suggère que même lorsqu'ils sont hétérogènes à une même échelle spatiale, les filtres environnementaux ne sont pas suffisamment forts pour modifier le patron généré par la dissémination primaire. La dissémination secondaire par les petits rongeurs contribue à réduire l'effet limitatif de la disponibilité des micro-sites sur le recrutement et renforce l'influence de la dissémination primaire sur le patron d'établissement des plantules.

Mots clé : autocorrélation spatiale, concordance spatiale, filtres environnementaux, hétérogénéité spatiale, prédation sur les graines, prédation sur les plantules, recrutement de plantules.

Nomenclature: Marie-Victorin, 1995.

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Introduction

The magnitude and spatial patterns of plant recruitment depend on how different factors affecting survival (*e.g.,* seed and seedling predation and constraints to seed germination and seedling establishment) behave spatially in relation to seed dispersal patterns (Jordano & Herrera, 1995; Schupp & Fuentes, 1995; Clark, Macklin & Wood, 1998; Nathan & Müller-Landau, 2000). Because the spatial distribution of these environmental filters usually differs (spatial uncoupling: Herrera *et al.,* 1994; Houle, 1995; Jordano & Herrera, 1995), the initial template established by seed dispersal is frequently disrupted, the pattern of recruitment being spatially unpredictable from that of the seed rain (spatial discordance: Houle, 1995; Jordano & Herrera, 1995; Schupp & Fuentes, 1995). Furthermore, processes constraining recruitment frequently operate at spatial scales different from that of seed dispersal. For example, some abiotic factors affecting seed germination and seedling emergence, such as soil moisture and nutrient availability, mostly vary at fine spatial scales and are often associated with microtopography (Molofsky & Augspurger, 1992; Farley & Fitter, 1999; Ferrari, 1999; Kollmann, 2000). Conversely, seed and seedling predation usually occurs at much coarser scales (Curran & Webb, 2000; Kollmann, 2000; Rey *et al.,* 2002). Consequently, identifying the specific scales at which major recruitment filters operate is essential in order to interpret spatial uncoupling: indeed, processes may appear homogeneous when acting at a coarser or a finer scale than that of dispersal, and spatial discordance between seeds and recruits may be expected only when environmental filters operate at the same spatial scale as that of dispersal (Schupp & Fuentes, 1995).

Seedling recruitment is a major bottleneck in the population dynamics of most temperate forest trees (Houle, 1992; Clark, Macklin & Wood, 1998; Clark *et al.,* 1998; LePage *et al.,* 2000). Abiotic conditions and resources, as well as biotic factors, have been found to determine the magnitude and spatial distribution of recruits within stands (George & Bazzaz, 1999a,b; Beckage & Clark, 2003). However, the relative importance of abiotic and biotic constraints should be related to seed size: indeed, large-seeded species should be less influenced by abiotic conditions as reserves accumulated in the seed should make establishment relatively independent of heterogeneity in soil moisture, nutrients, and light (Grime & Jeffrey, 1965; Seiwa & Kikuzawa, 1996). This has been suggested for temperate oaks (*Quercus* spp.), whose reserve-rich acorns make germination and first-year seedling survival rather insensitive to heterogeneity in abiotic factors (Kolb *et al.,* 1990; Crow, 1992; Ashton & Larson, 1996; Walters & Reich, 1996; George & Bazzaz, 1999b). However, acorns and large seedlings are conspicuous rewards for herbivores, making seed and seedling predation significant constraints to recruitment (Ostfeld & Canham, 1993; Crawley & Long, 1995; Kollmann & Schill, 1996; George & Bazzaz, 1999a,b). Nevertheless, the true role of acorn predators, such as rodents, squirrels, and jays, remains ambiguous, given that their hoarding activity after seed removal may result in secondary dispersal and not just in seed predation (Sork, 1984; Vander Wall, 1990; Kollmann & Schill, 1996).

In this paper, we analyze the magnitude and fine-scale spatial structure of red oak (*Quercus rubra*) recruitment in a mature forest in southern Québec. Losses in recruitment and in performance due to herbivores, such as seed predators and folivorous insects, have been described over the entire geographic distribution of the species, but abiotic factors may be particularly significant at the northern limit of the species' range (Crow, 1992; Byington, Gottschalk & McGraw, 1994; George & Bazzaz, 1999a,b; García, Bañuelos & Houle, 2002). We thus evaluated the relative impact on red oak recruitment of several biotic and abiotic factors and determined the scale(s) at which these factors operate, using observational and experimental approaches. We sought to interpret concordance or discordance between seeds and recruits in terms of the spatial behaviour of these environmental filters.

Methods

The study site was located on Île-aux-Grues (47° 02' N, 70° 33' W), an island of the Montmagny archipelago in the St. Lawrence River (Québec, Canada). The island (*ca* 6.5 × 1.5 km; maximum altitude: 20 m a.s.l.) was deforested 300 y ago for agriculture, except for its southwestern tip, which is still covered by a mixed hardwood forest (*ca* 75 ha). Once managed for sugar maple sap extraction, the forest has remained unexploited for the last 50 y. Forest soils are dystric brunisols, with scattered bedrock outcrops. The bedrock is mostly sandstone, slate, and shale. Mean annual temperature at a nearby weather station (Montmagny) is 4.4 °C and annual precipitation totals 1,087 mm, of which 23% falls as snow (Atmospheric Environment Service, 1993). The frost-free period lasts *ca* 146 d (Atmospheric Environment Service, 1982).

A 50- × 50-m area (0.25 ha) was delimited in the forest of the southwestern section of the island. The stand was dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and white ash (*Fraxinus americana*) both in terms of stem density (respectively 440, 152, and 128 individuals$\cdot$ha^{-1} with DBH $\geq$ 5 cm) and basal area (respectively 5.98, 6.87, and 6.19 m$^2\cdot$ha^{-1}). Adult individuals of red oak were scattered over the entire plot (100 individuals$\cdot$ha^{-1} with DBH $\geq$ 5 cm; basal area of 5.51 m$^2\cdot$ha^{-1}). This stand might be considered to comprise a red oak population at the northern limit of the species' distribution (Sander, 1990). The 50- × 50-m plot was subdivided into 100 5- × 5-m quadrats. We chose 50 of these quadrats, in a checkerboard pattern, as stations, in which we studied the following variables.

DEMOGRAPHIC VARIABLES

At the end of August 1999, a litter trap (0.5 m tall and 0.38 m diameter, made of polyethylene) was placed in the centre of each sampling quadrat. Leaves were collected fortnightly until the end of November, when the traps were removed. Red oak leaves were weighed after drying in an oven at 80 °C for 24 h. For each sample, leaf surface was estimated from the following formula:

$$\text{Leaf surface} = (164.18 \times \text{dry mass}) - 2.91$$

(from a regression model with $R^2 = 0.851$, $F_{1,\,72} = 410.0$, $P < 0.0001$).

We used the ratio "cumulated leaf surface ÷ trap surface" (leaf area index, LAI, $m^2 \cdot m^{-2}$) as an index of adult canopy density and as an estimate of tree fecundity (Clark, Macklin & Wood, 1998). Besides simultaneously representing adult presence and fecundity, this index provided a frequency of zeros in the sampled quadrats much lower than adult basal area or density and was thus a more suitable variable for our spatial analyses (see below; Legendre & Fortin, 1989).

Litter traps were also used to estimate seed rain density, since predators did not have access to acorns in the traps (no removal was recorded over a period of several weeks from 10 traps placed near the sampling area and to which 10 acorns each had been added). Seeds were collected from traps fortnightly, and their viability was determined by a tetrazolium test. Seed rain density was calculated for each quadrat as the cumulated number of viable acorns$\cdot m^{-2}$.

In each corner of each sampling quadrat, we established one 1- × 1-m sub-quadrat in which every month, from May to September 2000, we counted the number of newly emerged seedlings. Every seedling was individually labelled and its survival was recorded at each survey. We also noted whether seedlings emerged from acorns lying on the surface (above or under litter) or buried in the soil (1-2 cm under litter), considering buried acorns to be cached by animals (for a similar procedure see Gómez, 2003) and counting the number of seedlings per cache. We calculated, for each sampling quadrat, the cumulated number of emerged seedlings as well as the number of recruits (seedlings surviving to the end of the season), by averaging over the four 1- × 1-m sub-quadrats.

ABIOTIC CONDITIONS

We determined the spatial structure of some abiotic conditions believed to affect seed and seedling mortality through desiccation and freezing, two important factors for oak recruitment in the study area (García, Bañuelos & Houle, 2002). Elevation (topography) was measured at 121 points regularly positioned over the 50- × 50-m area with a Pentax AL-M5C level and standardized so that the lowest point on the area corresponded to 0 m. To measure soil moisture (gravimetrically), one soil core of *ca* 150 mL (to 9 cm deep) was taken in each 1- × 1-m sub-quadrat in April 2000, after several days without rain. We expected this measure to be representative of the spatial pattern of soil humidity after melting, in a season of high water availability. It has been suggested that leaf litter protects acorns against desiccation (García, Bañuelos & Houle, 2002). Thus, mean litter thickness was calculated from five measurements per 1- × 1-m sub-quadrat after leaf fall, at the end of October: a pin was inserted through the litter and the number of leaves transpierced was counted. We additionally measured light availability in order to relate resource abundance to seedling performance. Photosynthetic photon flux density (PPFD) was measured with a radiometer (model 189, Li-Cor, Inc., Lincoln, Nebraska, USA) at 25 cm from the ground in the centre of each 1- × 1-m sub-quadrat in June 2000, between 1000 and 1200, under uniform cloudy conditions. All variables were averaged (four measures) over each sampled quadrat.

RECRUITMENT LOSS AND SEEDLING PERFORMANCE

SEED REMOVAL BY PREDATORS

In early September 1999, in each sampling quadrat, three 50- × 50-cm surfaces were covered with nylon net to prevent seed arrival. At the end of the seed dispersal season (mid-October), the nets were removed and one group of five acorns, glued on a plastic strip nailed to the soil, was placed on each surface (n = 750 acorns). Glue (epoxy) prevented seed movement from the strips by rain, snow, or wind, but allowed removal by predators. Acorns had previously been collected from under *ca* 10 trees near the study area. All the seeds used in this experiment were sound seeds, soundness having been tested by a floating method (95% of sunk acorns proved to be sound and 99% of sound seeds were viable after a tetrazolium test). One group of acorns was protected from predation by a metal wire cage (1 cm mesh) of 50 × 50 × 15 cm, another group was covered by a half-cage consisting of a metal wire top of 50 × 50 cm held by four 15-cm poles, and another group (unprotected) served as a control. We considered the half-cage as a procedural control, accounting for the cage-cover effect but allowing predators to access the seeds. Seeds were surveyed fortnightly, from fall 1999 to spring 2000 when the area was free of snow, counting the number of seeds remaining on the strips and the number of seeds removed by predators or preyed upon *in situ*. As shown by field observations (direct diurnal observations of seed consumption, faeces occurring in seed depots) and the type of seed remains left by predators, removal was most probably due to rodents (squirrels, *Tamiasciurus hudsonicus*, and deer mice, *Peromyscus maniculatus*). Although present in the area, no blue jay (*Cyanocitta cristata*) was detected within the plot over the study period.

Percent seed removal per quadrat was calculated after pooling the acorns from both the controls and the half-cages, since no differences in removal rate were found between these two treatments (repeated-measures ANOVA with block [quadrat] effect: $F_{1,\,147} = 2.39$, $P = 0.128$; no removal was recorded on caged acorns).

SEED GERMINATION

Germination (percent germinated seeds per sampling quadrat) was studied by recording radicle protrusion in early May 2000 on seeds protected by the full cages in the seed predation experiment (see above).

SEEDLING SURVIVAL, PERFORMANCE, AND DAMAGE

Seedling survival and damage by herbivores (or other factors) were studied on transplanted seedlings. Acorns (from the seed pool described above) were stratified in the dark, at 5 °C, for 4 months. Emerged seedlings were transplanted in 200-mL pots filled with potting soil, placed in a greenhouse, and individually labelled and measured (stem length, number of leaves, and length of each leaf). Total leaf area was calculated by the sum of individual leaf surfaces, estimated from the following formula:

$$\text{Leaf surface} = (4.86 \times \text{leaf length}) + 1.29$$

(from a regression model with $R^2 = 0.811$, $F_{1,\,49} = 205.5$, $P < 0.0001$).

In May 2000, three groups of four seedlings each were transplanted with their soil core in the 50 quadrats ($n = 600$ seedlings). One group of seedlings was protected from vertebrate predators by a metal wire cage (1 cm mesh) of 50 × 50 × 30 cm, another group was covered by a half-cage consisting of a metal wire top of 50 × 50 cm held by four 30-cm poles, and another group (unprotected) served as a control. Seedlings were checked every 15-20 d during the spring and summer for damage and survival. We considered two types of damage: leaf damage (partial or complete loss of leaves to drought, transplanting stress, or herbivores, mostly larvae of Lepidoptera) and stem clipping by vertebrates (meadow voles, *Microtus pennsylvanicus*, which characteristically kill tree seedlings by clipping the stem near the ground level, leaving a noticeable diagonal edge; Ostfeld & Canham, 1993). Resprouting after clipping was also noted. Photosynthetic activity (net carbon assimilation rate) was measured on July 3, 2000 (a sunny day) between 1000 and 1400 on one seedling of the caged group in each of the 50 quadrats with an infra-red gas analyzer (LCA-4, ADC, Ltd., Hoddesdon, UK).

In mid-September 2000, we collected the aerial part of the seedlings to take the following measurements: survival status (plants that had lost all of their leaves or were clipped with no resprouting were considered dead if the cross-section of the stem at the root collar was completely dry), clipping, resprouting, number of leaves, total leaf area (CI-202 leaf area meter, CID, Inc., Vancouver, Washington, USA), and percent leaf damage by folivores, drought, or stress (visual estimation, with an accuracy of 5%).

Percent seedling survival and clipping frequency (the main cause of mortality, see Results below) were calculated exclusively from control seedlings, half-cage seedlings having a significantly lower probability of clipping (ANOVA with block [quadrat] effect: $F_{1,\,49} = 5.77$, $P = 0.02$; no clipped seedlings were found under the full cages). No differences among the three treatments were found for folivory (ANOVA with block [quadrat] effect: $F_{1,\,522} = 0.53$, $P = 0.586$), and thus all seedlings (except those that had been clipped) were used to estimate percent leaf loss to folivores.

Statistical analyses

Spatial autocorrelation

We studied the spatial structure of the different variables first by analyzing their distribution over the study area (with contour plots) and by testing for autocorrelation with Moran's I (Legendre & Legendre, 1998). This index typically varies between -1 (repulsion) and + 1 (contagion), with non-significant values close to zero. Moran's I can be calculated for different distance classes (d) and represented in a correlogram (Legendre & Fortin, 1989). Before testing for the significance of individual I-values, the correlogram must be globally significant, *i.e.,* one value must be significant at $P \leq 0.05/k$, with k representing the number of distance classes (Bonferroni criterion). The shape of the correlogram and the significance of each value of I were used, along with the contour plots, to interpret the spatial structure of the variables. We considered nine distance classes of 7.1 m each for all of the variables, using the centroid of each sampling station as coordinates.

Partial Mantel tests

We tested for the relation between different variables and the abundance of red oak recruits with partial Mantel tests (Smouse, Long & Sokal, 1986; Legendre & Fortin, 1989). A partial Mantel statistic is similar to a partial correlation coefficient (with a value from -1 to + 1) and can account for the spatial position of sampling points. The test establishes the intensity of the relationship between a matrix of the residuals of the linear regression of two variables (in fact, of two distance matrices, one for each variable) and a distance matrix of geographical locations (Oden, 1992). We thus calculated this coefficient between recruit density and, respectively, adult LAI, seed rain density, topography, soil moisture, litter thickness, and PPFD. We also correlated the actual number of recruits with the number of recruits estimated by multiplying a randomly generated seed rain by experimentally determined survival probabilities (a synthetic measure of the final effect of various filters on recruitment, evaluated by multiplying the experimental probabilities of acorn survival and germination, and of seedling survival). A positive, significant relationship between these two measures of recruitment would mean that the environmental filters acted as homogeneous spatial sieves. Finally, we estimated how seedling photosynthetic rate was related to spatial variations in PPFD. P-levels for the partial Mantel tests were determined by a permutation procedure (from 1,000 permutations).

Path analyses

We used causal modelling to explain spatial variations in the density of recruits in terms of density of previous stages (Mitchell, 1992; Jordano & Herrera, 1995). This model included both direct and indirect links. We built a first model with the actual data of adult LAI (an estimate of fecundity), seed rain density, and the density of emerged seedlings and of recruits. We used the results of this model to interpret the importance of the different stages in the final spatial pattern of recruitment. We also built a similar, but experimentally based model in which we started with a randomly generated seed rain (values from 0 to 100 acorns$\cdot$m^{-2}) and estimated the number of units (seeds or seedlings) in successive stages with experimentally assessed probabilities: seed removal by predators, germination probability, and seedling survival probability (see above). The aim of this second model was to discern the relative importance of different processes in generating a particular spatial pattern of recruitment from a given seed rain.

Statistical analyses were performed with the Autocor, Mantel, and Piste modules from R 4.0 statistical software (Casgrain, Legendre & Vaudor, 1997).

Results

Spatial structure of recruitment, abiotic conditions, and filtering processes

Adult LAI showed a spatially autocorrelated structure characterized by two peaks in opposite corners of the study area (upper left and lower right) and low values in between (Figure 1). The correlogram for this variable was globally significant, with positive and significant values at 7-14 m and again at 49-57 m and significant negative values at 28-35 m, a pattern suggesting 14-m patches separated by *ca* 35 m (Figure 1). Only 14% of the sampling stations received viable seeds. Considering only seed-containing traps and those occurring in quadrats where adults were present, we estimated a seed production of 13.2 ± 4.5 acorns$\cdot$m^{-2} of crown area (mean ± SE). Seed rain was highly heterogeneous in space, as revealed by the high CV value (Table I) and the patchy structure depicted by the contour plot (Figure 1). However, no significant spatial autocorrelation was detected for this variable (Figure 1). A small fraction (only 4.1%) of these acorns emerged as seedlings in the following spring and summer (Table I). Most of these seedlings (92.3%, $n = 26$) were from buried acorns, the number of seedlings per hoard averaging 2.8 ± 0.7 (min - max = 1 - 8). The number of emerged seedlings was also very heterogeneous in space, with two small patches in opposite corners of the study area (Table I; Figure 1). This variable was spatially structured, with a significant positive value of Moran's *I* at the smallest distance class (*ca* 7 m) and a significant negative value at 35 m (Figure 1). A very similar spatial structure was found for the number of recruits (Table I; Figure 1), since a large proportion of the emerged seedlings survived to the end of the season (88.5%, $n = 26$).

The CV of abiotic conditions ranged from 12% (soil moisture) to 65% (topography; Table I). All of the abiotic variables except litter thickness showed significant spatial autocorrelation (Table I; Figure 2). Topography had significant positive values of Moran's *I* from 7 to 21 m and significant negative values from 35 to 49 m, suggesting the dominance of a gradient from high values at the lower right corner of the study to low values at the upper right corner (Figure 2). Soil moisture and PPFD contour plots and their associated correlograms revealed small-scale patchiness, with significant positive values of Moran's *I* at 7-14 m (Figure 2). The lack of global significance for the correlogram of litter thickness suggests a rather homogeneous and random distribution for this variable.

Unlike abiotic conditions, no significant spatial autocorrelation was detected for seed removal, seed germination, and seedling mortality (Table I; Figure 3). Percent seed removal was high and rather homogeneous in space (≥ 90% in a large portion of the study area), with only two small patches in the upper and central right sections of the study area, where values decreased to 40-60% (Figure 3). Similarly, percent seed germination was greater than 60% on most of the area, with an apparently random spatial distribution (Figure 3). However, none of the germinated seeds produced an emerged seedling, because all died of early spring frosts. Clipping by voles affected *ca* 20% of the transplanted seedlings (control treatment, $n = 200$) and was the only variable showing significant spatial autocorrelation, with two patches of 7-14 m in diameter (Table I; Figure 3). Folivory by insects affected 77.1% of the transplanted seedlings ($n = 600$), with leaf area losses averaging 16%. The contour plot and low CV value of this variable suggest a random, relatively homogeneous distribution (Figure 3). Only 25 of the 600 transplanted seedlings died during the study period, most of them (56%) because of clipping by voles. Seedling mortality was strongly heterogeneous (high CV-value, Table I), with mortality reaching values of 35% in some parts of the study area (Figure 3). As a result of the cumulated probability of post-dispersal seed loss, seed germination failure, and seedling mortality, only 6% of the experimental seeds produced an established seedling (Table I). This cumulated survival probability was highly heterogeneous, although not significantly autocorrelated in space (Figure 3). Net photosynthetic rate was very low, with a large portion of the area showing values < 0.25 µmol $CO_2\cdot m^{-2}\cdot s^{-1}$ and only a few small patches of seedlings with values > 0.75 µmol $CO_2\cdot m^{-2}\cdot s^{-1}$ (Table I; Figure 3).

VARIABLES CORRELATED WITH RECRUITMENT AND PERFORMANCE

Adult LAI was correlated to recruit density, but not significantly so after the Bonferroni correction. Seed rain density was significantly and positively correlated to recruit density, independently of spatial location (partial Mantel test, Table II). Estimated recruit density (calculated from a randomly generated seed rain and the experimentally assessed recruitment probabilities) and actual recruit density were positively correlated, independently of space (Table II). A partial Mantel test also showed a positive and significant relationship between adult LAI and seed rain density ($r = 0.206$, $P = 0.039$). Seedling net photosynthetic rate was independent of PPFD (partial Mantel test, $r = -0.042$, $P = 0.358$).

RECRUITMENT CAUSAL MODELS

The model considering the effects of adult LAI and of seed rain and emerged seedling densities accounted for a high percentage of the variation in the actual number of red oak recruits (Figure 4). Model significance was essentially related to linear, direct effects between variables through the regeneration sequence, especially in the transition from seed rain to emerged seedlings and from emerged seedlings to recruits (Figure 4). A similar pattern of dominance of linear, direct effects emerged from the model based on the experimentally assessed recruitment (Figure 4). There, the model explained almost 100% of the variance in the estimated number of recruits, this effect being mostly due to the transition from seeds after removal to emerged seedlings.

Discussion

MAGNITUDE AND SPATIAL STRUCTURE OF ABIOTIC CONDITIONS AND BIOTIC FILTERS

Our results revealed a significant spatial structure for most of the abiotic variables considered, with only litter thickness having a random distribution pattern: indeed, topography, soil moisture, and PPFD all showed positive autocorrelation at small distance classes, suggesting gradient or patchy distributions with a small grain size (Farley & Fitter, 1999; Nicotra, Chazdon & Iriarte, 1999). Such fine-scale variations would make the forest floor a rela-

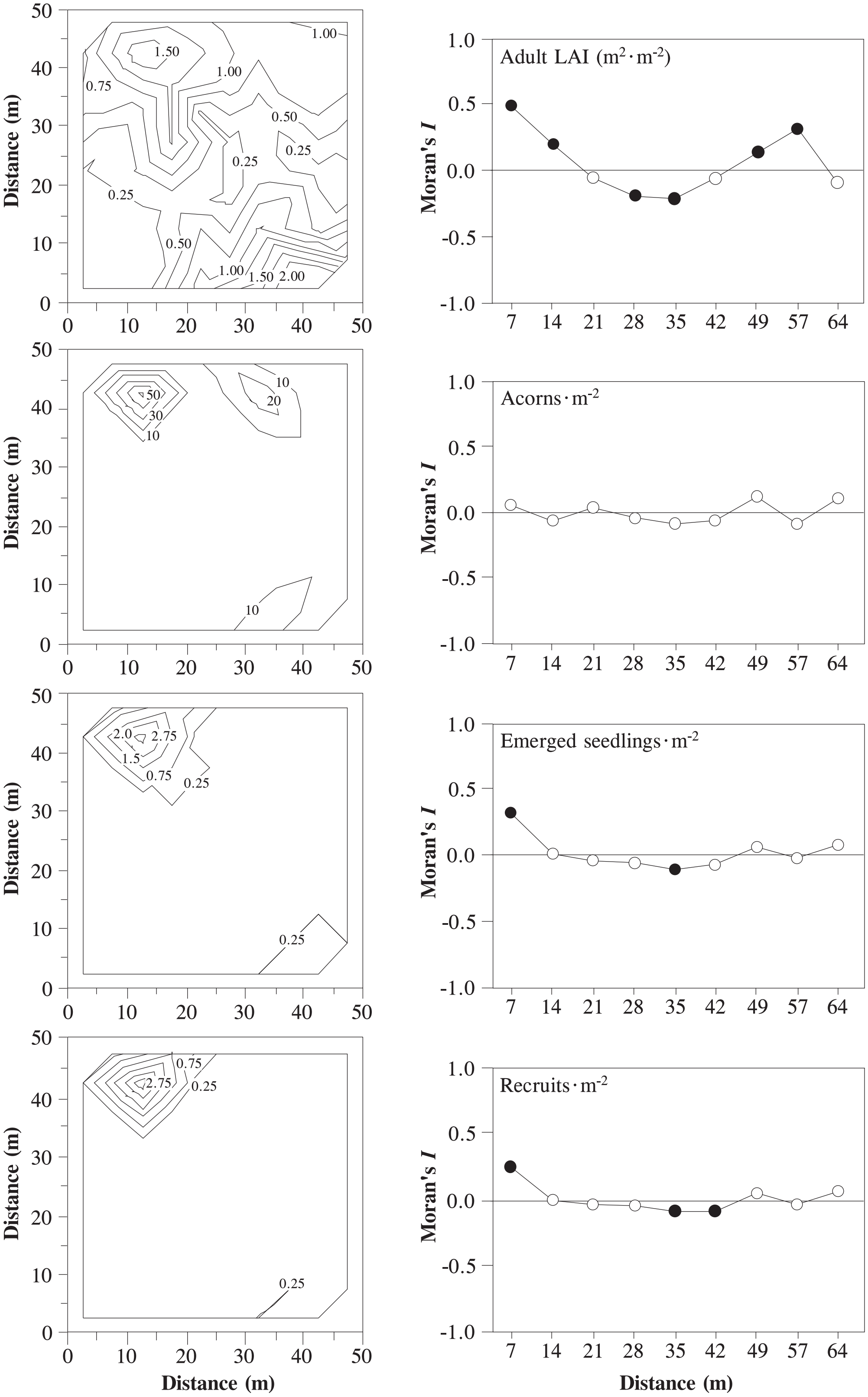


FIGURE 1. Spatial patterns of *Quercus rubra* demographic variables at Île-aux-Grues, Québec, Canada. Left: interpolation maps from 50 data points dispersed in a checkerboard pattern over the 50- 50-m sampled surface. Right: spatial correlograms, with filled circles indicating significant values of Moran's *I* (for globally significant correlograms). From top to bottom: leaf area index (LAI) of adult trees; seed rain density; density of emerged seedlings; density of recruited seedlings.

tively heterogeneous template for red oak regeneration, assuming these abiotic factors actually have the potential to affect recruitment probabilities (Houle, 1992; LePage *et al.,* 2000; García, Bañuelos & Houle, 2002).

TABLE I. Demographic variables, abiotic conditions, and biotic processes evaluated for red oak (*Quercus rubra*) at Île-aux-Grues, Québec, Canada. The coefficient of variation (CV: SD/mean × 100) is presented as a measure of spatial heterogeneity. Spatial autocorrelation, evaluated by global significance of the correlogram, is shown for each variable.

Variable	Mean ± SE	CV (%)	Spatial autocorrelation
Adult leaf area index ($m^2 \cdot m^{-2}$)	0.73 ± 0.08	78.19	yes
Seed rain density ($acorns \cdot m^{-2}$)	3.16 ± 1.32	295.68	no
Emerged seedlings ($seedlings \cdot m^{-2}$)	0.13 ± 0.07	358.70	yes
Recruits ($seedlings \cdot m^{-2}$)	0.11 ± 0.06	398.21	yes
Topography (m)	0.93 ± 0.09	65.88	yes
Soil moisture (%)	40.49 ± 0.71	12.42	yes
Litter thickness (leaf layers)	2.79 ± 0.12	31.06	no
PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	6.85 ± 0.56	58.06	yes
Seed removal (%)	91.40 ± 2.27	17.55	no
Seed germination (%)	72.00 ± 3.08	30.22	no
Seedling mortality (%)	6.00 ± 1.96	231.45	no
Cumulated survival probability	0.06 ± 0.02	221.62	no
Clipping (%)	19.50 ± 5.06	183.68	yes
Folivory (%)	16.49 ± 1.11	47.53	no
Photosynthetic rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	0.34 ± 0.05	111.01	no

In sharp contrast, we found little evidence of spatial structure for the experimentally estimated biotic variables. Seed removal by squirrels and mice was high and rather homogeneous over the study area, leaving only a few small-sized patches with moderate seed survival. High rates of acorn removal are typical in oak species, given the high profitability of their seeds for predatory rodents (Sork, 1984; Crawley & Long, 1995; Kollmann & Schill, 1996; George & Bazzaz, 1999a). Furthermore, rodent activity is usually homogeneous at small spatial extent, especially when rodent densities are high and structural gradients such as those imposed by the presence of understory, canopy gaps, or forest edges are absent (Kollmann & Schill, 1996; Ostfeld, Manson & Canham, 1997; George & Bazzaz, 1999a,b). Like seed removal, germination failure was random and relatively homogeneous. This pattern was also probably related to the "soft" gradient imposed by our experimental design, *i.e.,* acorns unburied and uncovered by litter, exposed to forest floor conditions, in a light/temperature/soil moisture regime apparently insufficient to affect germination (Ashton & Larson, 1996; García, Bañuelos & Houle, 2002). Clipping on seedlings by voles was the only experimental variable showing a significant spatial structure, with a low average value and fine-scale patchiness probably determined by the low population density of meadow voles within the forest (Ostfeld & Canham, 1993; Ostfeld, Manson & Canham, 1997). On the other hand, transplanted first-year seedlings showed a high rate of survival during the season, as has been shown for this species in other temperate forests of North America (Good & Good, 1972; Crow, 1992; Beckage & Clark, 2003). Despite the importance of clipping as a cause of seedling mortality and the rather similar patchiness of clipping frequency and seedling mortality rate (see contour plots), no spatial autocorrelation was detected for percent seedling mortality. This result could be partially conditioned by the high frequency of zeros in the sampled quadrats (Legendre & Fortin, 1989). As a result of the quantitative (net losses) and qualitative (spatial pattern) distribution of recruitment limitation (post-dispersal stages), the cumulated probability of seedling recruitment was rather homogeneous and spatially unstructured, at least at the spatial scale considered here. Finally, variables related to seedling performance were also randomly dispersed. A high proportion of seedlings were affected by insect folivory, but the total leaf area loss per seedling was rather low, probably not affecting growth and survival in the short term (Byington, Gottschalk & McGraw, 1994). Seedling photosynthetic activity was low, as has been found in deep shade under closed forest canopies (Walters & Reich, 1996; Cavender-Bares & Bazzaz, 2000).

In short, our spatial analyses showed that different environmental filters potentially affecting red oak recruitment have different scales of operation. Our study, which combined a grain size of *ca* 7 m and a spatial extent of 0.25 ha, allowed us to detect the fine-scale patchiness of some abiotic conditions and biotic processes. However, failure to detect autocorrelation was also informative, since it suggested a different spatial scale of operation for the other conditions and processes: sometimes coarser, as in the case of seed predation (given the large home range of mice populations; Ostfeld, Manson & Canham, 1997; Manson, Ostfeld & Canham, 1998), and sometimes finer, as for insect folivory (probably determined at the level of the individual seedling; Byington, Gottschalk & McGraw, 1994; Stowe *et al.,* 1994).

MAGNITUDE AND SPATIAL STRUCTURE OF RECRUITMENT: CONCORDANCE BETWEEN STAGES

The seed rain described at our study site might be considered to result from an event of moderate-to-high acorn production, comparing our values of acorns per m^2 of crown area to those obtained in other temperate forests in New England (7.41 ± 2.98 $acorns \cdot m^{-2}$, 11-y average; Healy, Lewis & Boose, 1999). Contrary to what could be expected for a population at the limit of the species' range (Pigott, 1992; García *et al.,* 2000), we found a proportion of establishment one order of magnitude higher than what has been described for the species in the Appalachian Mountains (*ca* 0.005 seedlings per dispersed seed; Clark, Macklin & Wood, 1998). However, given the high interannual variability in acorn production typical for this species (Healy, Lewis & Boose, 1999) and the narrow temporal scope of our sampling, the consequences of these magnitudes of recruitment must be carefully interpreted.

Fine-scale patchiness in the seed rain was associated with the presence of adult canopy, as suggested by similarity in the contour plots of adult LAI and seed rain density and the significant correlation between these two variables. However, our analyses failed to detect any spatial structure in seed rain, probably because of the high number of stations with zeros (Legendre & Fortin, 1989).

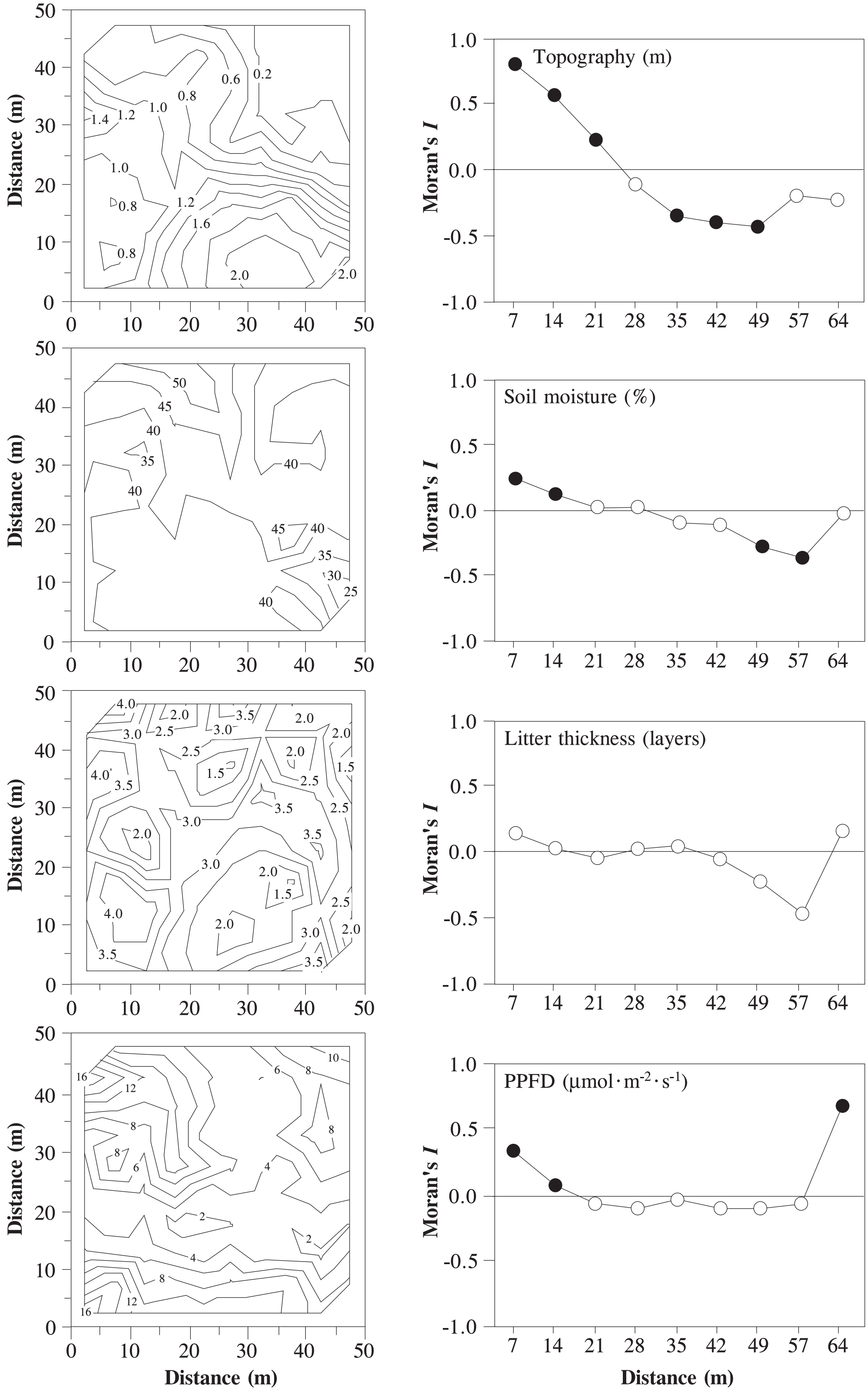


FIGURE 2. Spatial patterns of abiotic conditions potentially affecting *Quercus rubra* recruitment at Île-aux-Grues, Québec, Canada. Left: interpolation maps from 50 data points dispersed in a checkerboard pattern over the 50- 50-m sampled surface. Right: spatial correlograms, with filled circles indicating significant values of Moran's *I* (for globally significant correlograms). From top to bottom: topography; percent soil moisture; litter thickness; photosythetic photon flux density (PPFD).

Nevertheless, fine-scale patchiness was maintained through the post-dispersal stages, as both emergence and recruitment were spatially autocorrelated at small distances. Therefore, seed rain and seedling recruitment are

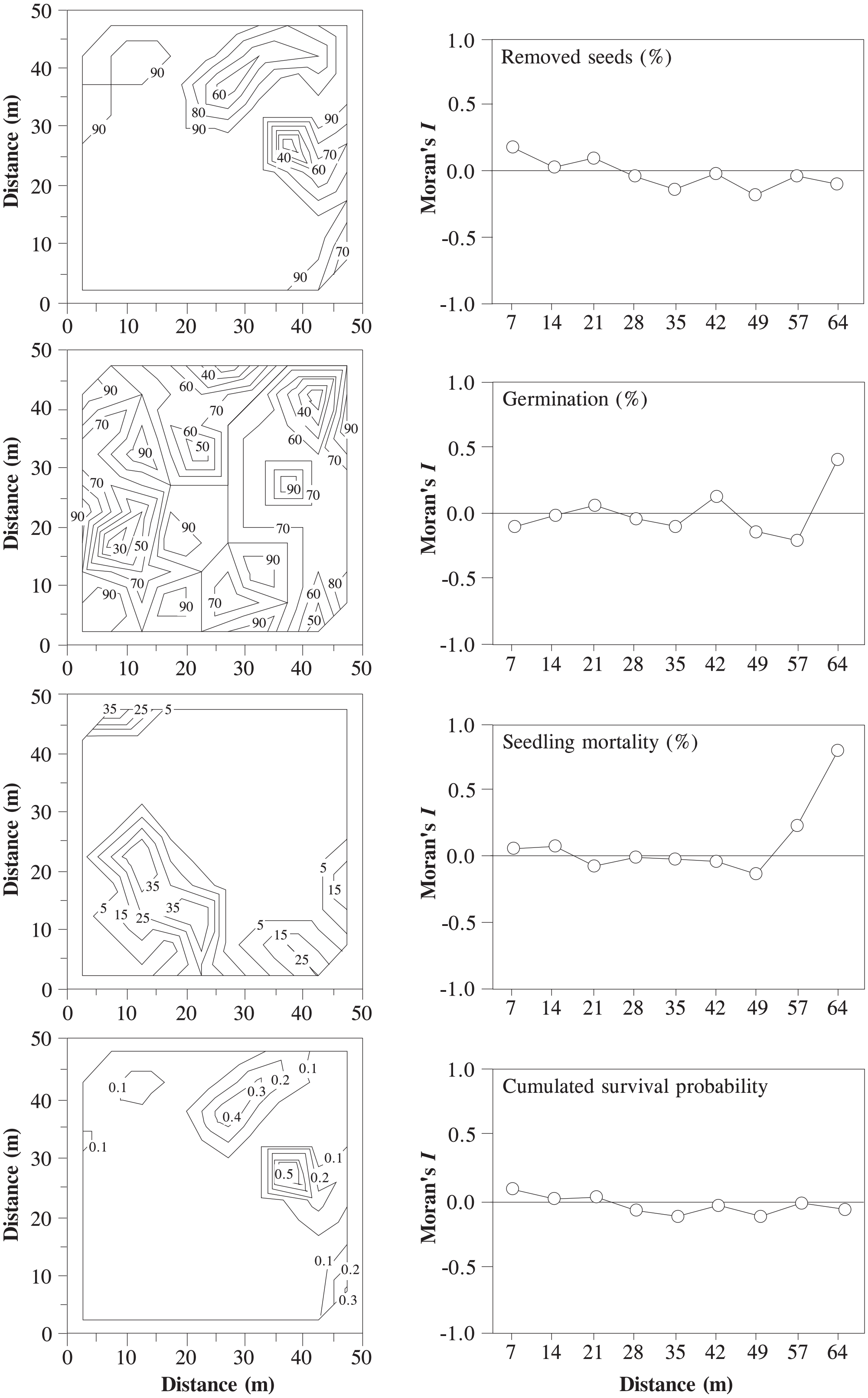


FIGURE 3. Spatial patterns of biotic processes potentially affecting the recruitment and performance of *Quercus rubra* seedlings at Île-aux-Grues, Québec, Canada. Left: interpolation maps from 50 data points dispersed in a checkerboard pattern over the 50- 50-m sampled surface. Right: spatial correlograms, with filled circles indicating significant values of Moran's *I* (for globally significant correlograms). From top to bottom, this page: percent seed removal; percent seed germination; percent seedling mortality; cumulated survival probabilit. From top to bottom, next page: percent clipped seedlings; percent losses to folivores; seedling photosynthetic rate.

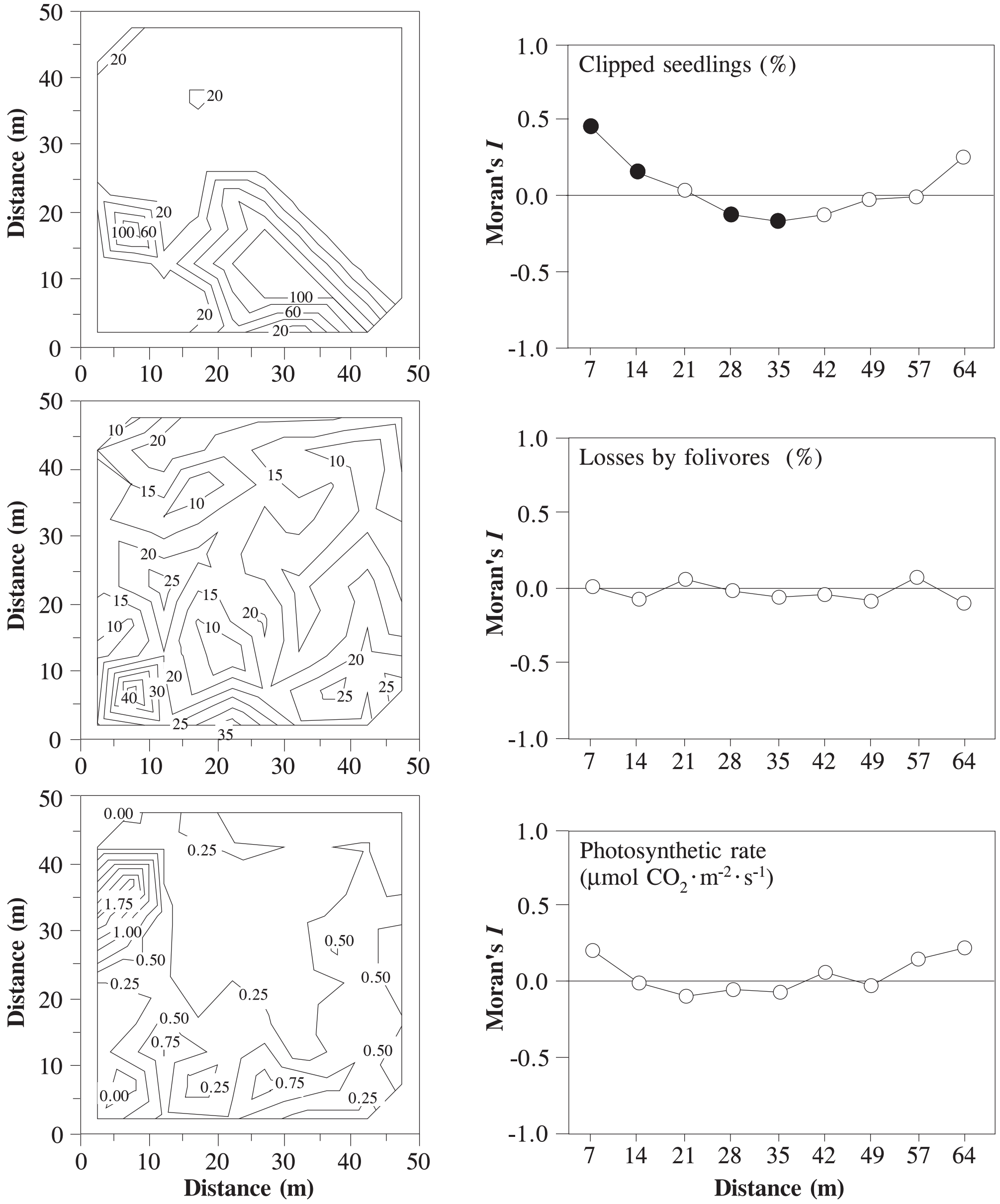


FIGURE 3. Continued.

spatially concordant (Houle, 1992; 1998). This was evidenced by our partial Mantel tests, in which recruit density was significantly related to seed rain density. In addition, our path analysis on actual recruitment suggested a succession of effects determining the spatial pattern of recruitment, from adult LAI to emerged seedlings. Thus, the final spatial distribution of recruits is the result of contagious seed dispersal close to conspecific adults (Ribbens, Silander & Pacala, 1994).

Such spatial concordance means that heterogeneity imposed by environmental filters is not strong enough to disrupt the spatial gradients generated by seed dispersal (Houle, 1995; Schupp & Fuentes, 1995). The positive, marginally significant relationship between the actual and the experimentally estimated recruitment suggests that the series of biotic factors we considered acted as a random filter. Some processes seemed to occur at the same scale as seed rain (clipping, seedling mortality), but their disruptive effect was overwhelmed by the apparent coarse-scale homogeneity of seed removal. In fact, as shown by the path analysis on the experimentally estimated recruitment, seed removal was the most important stage determining the spatial distribution of post-dispersal probabilities (Good & Good, 1972; George & Bazzaz, 1999a,b), accounting for most of the homogeneity. On the other hand, our analyses also failed to show any effect of the abiotic conditions on recruitment. Although heterogeneous, light availability had probably negligible effects in terms of survival during the first year, as suggested by the low and light-independent values of photosynthesis (Walters & Reich, 1996; but see George & Bazzaz, 1999a,b; Beckage & Clark, 2003, for the effect of light heterogeneity on older seedlings). Similarly, the spatial variability of both topography and soil moisture seemed to be insufficient to uncouple recruitment from the seed rain, as suggested above for germination. However, abiotic factors may be acting at a coarser scale, as demonstrated by the massive death of germinating acorns in our experiment due to early spring frosts (Kollmann & Schill, 1996; García, Bañuelos & Houle, 2002).

A likely explanation of the inconsistency between our experimentally assessed emergence and emergence in natural conditions is hoarding by acorn predators. In fact, almost all of the naturally emerging seedlings established from cached acorns. Burial seems to have protected seeds and newly emerged seedlings from desiccation and frost (Ovington & McRae, 1960; Kollmann & Schill, 1996; García, Bañuelos & Houle, 2002), probably causing recruitment to be more independent from fine-scale heterogeneity in abiotic conditions. Nevertheless, hoarding activity had a spatial component correlated to the pattern of seed removal (Kollmann & Schill, 1996). In fact, it is known that some of the acorns removed by small mammals like mice and squirrels are hoarded *in situ* or at very short distances from acorn sources (Sork, 1984; Jensen & Nielsen, 1986; Miyaki & Kikuzawa, 1988; Kollmann & Schill, 1996; but see Nakashizuka *et al.,* 1995). Thus, recruitment seems to depend on the post-dispersal seed shadow (*sensu* Janzen, 1971; Sork, 1984) generated by hoarding rodents that is, in fact, a spatial correlate of the seed rain. In other words, in our system, secondary dispersal by scatter-hoarding rodents (squirrels and mice) reinforced primary seed dispersal, a result that contrasts with the well-demonstrated disrupting effect of "predator" rodents (Russell & Schupp, 1998; Curran & Webb, 2000; Rey *et al.,* 2002). The effect of the animal dispersers on microsite amelioration might thus be determinant for recruitment in areas at the limit of the species' range, as shown by the complete lack of establishment from surface-germinated seeds in our experiment and from the low proportion of natural seedlings establishing from unburied acorns (García, Bañuelos & Houle, 2002).

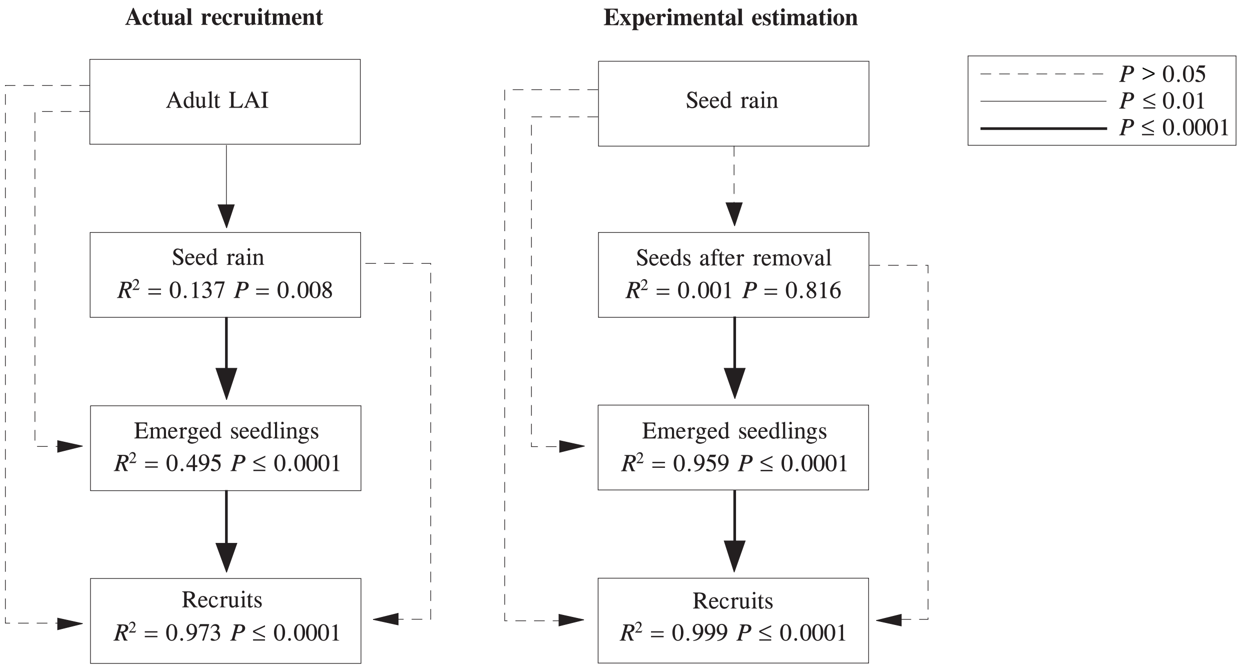
TABLE II. Coefficient of correlation (r) and associated P-value between red oak recruit density and different variables at Île-aux-Grues, Québec, Canada. Correlations were calculated by means of partial Mantel tests, accounting for the effect of spatial location.

Variable	r	P
Adult leaf area index	0.204	0.045
Seed rain density	0.708	0.006 [1]
Topography	-0.086	0.178
Soil moisture	0.075	0.199
Litter thickness	-0.049	0.387
Photosynthetic photon flux density	0.077	0.122
Estimated number of recruits[2]	0.614	0.038

[1] Significant after Bonferroni correction (P ″ 0.05/7).

[2] Seed rain density probability of cumulated survival (experimentally determined).

As a concluding, summarizing remark, we propose a hierarchical, scale-dependent effect of scatter-hoarding animals on red oak recruitment (Gómez, 2003). Birds like jays, because of their great mobility and large home range, are capable of inducing both microsite-amelioration and distance effects on recruitment, even long-distance dispersal effects that may have contributed to the rapid post-glacial expansion of red oak in North America (Johnson & Webb, 1989; Clark *et al.,* 1998). However, fine-scale rodent dispersal appears to be spatially neutral since it does not greatly modify the distances at which acorns are primarily dispersed from the parent plant. At our study site, many parts of the stand that represented


Actual recruitment

Experimental estimation

FIGURE 4. Path analysis models relating *Quercus rubra* seedling recruitment to various demographic stages. Left: model based on actual data from adult leaf area index (LAI, a measure of fecundity), seed rain density, and density of emerged seedlings and of recruits. Right: experimentally based model, from a randomly generated seed rain and experimentally estimated probabilities of survival.

appropriate recruitment sites for red oak did not receive viable seeds (Ribbens, Silander & Pacala, 1994; Clark, Macklin & Wood, 1998). Since burial contributed significantly to reducing microsite limitation for recruitment, hoarding increased the proportion of variation in the spatial pattern of recruitment accounted for by seed dispersal, making recruitment even more dispersal-limited.

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