

# Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood – white pine stands

Patricia Raymond, Alison D. Munson, Jean-Claude Ruel, and K. David Coates

**Abstract:** Large gaps (equivalent to twice the height of the trees, 1590 m<sup>2</sup>) originating from group selection cutting in mixed tolerant hardwood – eastern white pine (*Pinus strobus* L.) stands of Quebec were used for geostatistical analysis of the seasonal mean of daily percent photosynthetic photon flux density (%PPFD), soil temperature and moisture, regeneration density of white pine, yellow birch (*Betula alleghaniensis* Britt.), and paper birch (*Betula papyrifera* Marsh.), and growth of white pine. %PPFD, which measures the quantity of light above the shrub layer, varied according to the north–south axis, the maximum being located in the northern portion of gaps. Surficial soil (5 cm) temperature and moisture varied according to both north–south and east–west axes. The southwest sector offered favourable conditions for white pine, yellow birch, and paper birch establishment, with maximum soil moisture and minimum soil temperature encountered in this position. There was no evidence of gap partitioning at the early establishment stage, although asymmetry in the microclimate was observed. However, results indicate that spatial patterns could change in the future and a partition resulting from differential survival among species could occur. Finally, results outline a possible discordance between optimal regeneration and growth niches for white pine, since planted seedlings (>1 m) had the best growth in the central and northern section of gaps.

**Résumé :** Des grandes trouées (diamètre d'environ deux fois la hauteur des arbres, 1590 m<sup>2</sup>) issues d'une coupe de jardinage avec trouées dans les peuplements de feuillus tolérants et de pin blanc (*Pinus strobus* L.) du Québec ont été utilisées pour les analyses géostatistiques de la moyenne saisonnière du pourcentage de la densité du flux de photons photosynthétiques journalier (%PPFD), de la température et de l'humidité du sol, de la densité de régénération de pin blanc, du bouleau jaune (*Betula alleghaniensis* Britt.) et du bouleau à papier (*Betula papyrifera* Marsh.), et de la croissance du pin blanc. Le %PPFD, qui mesure la quantité de lumière au-dessus de la compétition, variait selon l'axe nord-sud, le maximum étant situé dans la portion nord des trouées. La température et l'humidité de la surface du sol (5 cm) variaient selon les deux axes nord-sud et est-ouest. Le secteur sud-ouest offrait des conditions favorables à l'établissement du pin blanc, du bouleau jaune et du bouleau à papier, avec une humidité du sol maximale et une température du sol minimale dans cette position. Il n'y avait pas de signe de partition des trouées au stade d'établissement initial, bien qu'une asymétrie dans le microclimat ait été observée. Cependant, les résultats indiquent que les patrons spatiaux pourraient changer dans le futur et qu'une partition résultant d'une survie différente parmi les espèces pourrait se produire. Enfin, les résultats montrent un désaccord possible entre les niches optimales de régénération et de croissance du pin blanc, car la croissance des semis plantés (>1 m) était meilleure au centre et au nord des trouées.

## Introduction

Gap-forming disturbance alters resource availability and physical conditions in forest understories (Minckler et al. 1973; Collins and Pickett 1988; Canham et al. 1990; Barik et al. 1992; Parsons et al. 1994). This, in turn, should affect tree regeneration success and growth of established seedlings (Bazzaz 1996; Coates 2000, 2002). In high-latitude

northern forests, where sun angles are much lower in the sky, optimal microclimates for different species should occur at different positions inside gaps as well as across a gradient of gap sizes (e.g., Canham et al. 1990). In northern tolerant hardwood forests, the spatial variation of vegetation within gaps has generally been studied in gaps originating from natural disturbance. Many of these studies have confronted the gap-partition hypothesis (Ricklefs 1977), where

Received 4 July 2005. Accepted 14 November 2005. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 10 March 2006.

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different species are expected to show preferences for certain sized gaps or positions within gaps because of resource heterogeneity (Poulson and Platt 1989; Wayne and Bazzaz 1993; Sipe and Bazzaz 1995; Barden 1996). However, few of these studies have demonstrated strong evidence of species partitioning within gaps and most of these experiments were conducted in small gaps ( $<0.5H$ , where  $H$  is stand height), the exceptions being Sipe and Bazzaz (1995) and Poulson and Platt (1989), who evaluated medium to relatively large gap sizes (respectively  $1H$  and  $1.5H$ ). One could argue that the gaps evaluated in previous experiments were too small to observe significant changes in microclimate that would provoke specialization in the gaps. Studies comparing gap sizes have demonstrated that solar radiation, together with soil and air temperature, increases with gap size (Philipps and Shure 1990) and that microclimate variation within gaps is greater in larger gap sizes ( $2H$ ) (Strong et al. 1997). In addition to gap size, latitude clearly influences the distribution of light resources within gaps (Canham et al. 1990). At higher latitudes the area receiving increased light does not necessarily coincide with the area of reduced competition for water and nutrients (Liefers et al. 1999).

Interestingly, few studies have examined microclimate and vegetation patterns in the same experiment. These types of data are needed as input for recently developed forest dynamics models, which can be used to predict the effects of silvicultural interventions in space and time (Coates et al. 2003). Spatially explicit models, such as SORTIE (Pacala et al. 1996; Coates et al. 2003), are based on submodels that predict local availability of resources, seedling recruitment, growth, and mortality. A better understanding of the processes underlying the submodels is critical to refine predictions after silvicultural treatments in managed forests. To our knowledge, this study in northern hardwood forests of Quebec is the first to compare spatial patterns of microclimate and regeneration from measures taken at the same points. We also use a geostatistical approach for interpolating between sampling points. This paper presents results of spatial variation within 45 m diameter ( $2H$ , circular) silvicultural gaps, created for regenerating mid-tolerant species in a tolerant hardwood – eastern white pine (*Pinus strobus* L.) stand. The objectives of our study were (i) to characterize spatial patterns of environmental resources (light, soil temperature, and soil moisture), natural regeneration (white pine, yellow birch (*Betula alleghaniensis* Britt.), and paper birch (*Betula papyrifera* Marsh.)), and growth of naturally regenerated and planted white pine seedlings; (ii) to understand how variability in environmental resources (light, soil microclimate) influences the patterns of regeneration and growth; and (iii) to evaluate the effectiveness of the  $2H$  gaps in creating adequate regeneration niches, considering the effect of high latitude on light availability.

## Materials and methods

### Study area

The study was conducted in the Forêt de l'Aigle ( $46^{\circ}16'N$ ,  $76^{\circ}17'W$ ), near Maniwaki, Quebec, Canada. It is located in the northern temperate deciduous forest, in the western Sugar Maple – Yellow Birch bioclimatic subdomain (MRNQ 2002) and in the Lac Dumont landscape unit (Robitaille and Saucier

1998). Mean annual temperature ranges from 2.5 to 5 °C, mean annual precipitation is 800–1000 mm, with 25% falling as snow, and the growing season is 170–180 days (Robitaille and Saucier 1998). The experiment was established in 1998, in a mixed northern hardwood – white pine stand. The stand was uneven aged ( $244 \text{ m}^3\cdot\text{ha}^{-1}$ ; dominant height 24 m). Tree species were white pine (24% of volume), sugar maple (*Acer saccharum* Marsh., 21%), red oak (*Quercus rubra* L., 12%), paper birch (10%), yellow birch (9%), red maple (*Acer rubrum* L., 5%), balsam fir (*Abies balsamea* L., 5%), American beech (*Fagus grandifolia* Ehrh., 4%), American basswood (*Tilia americana* L., 3%), white spruce (*Picea glauca* (Moench) Voss, 2%), and bigtooth aspen (*Populus grandidentata* Michx., 2%). Advanced regeneration ( $>10 \text{ cm}$ ) was composed of sugar maple ( $127\,800 \text{ stems}\cdot\text{ha}^{-1}$ ), red maple ( $14\,800 \text{ stems}\cdot\text{ha}^{-1}$ ), American beech ( $12\,400 \text{ stems}\cdot\text{ha}^{-1}$ ), red oak ( $10\,200 \text{ stems}\cdot\text{ha}^{-1}$ ), paper birch ( $3000 \text{ stems}\cdot\text{ha}^{-1}$ ), and balsam fir ( $2200 \text{ stems}\cdot\text{ha}^{-1}$ ), while yellow birch ( $500 \text{ stems}\cdot\text{ha}^{-1}$ ) and white pine ( $0 \text{ stems}\cdot\text{ha}^{-1}$ ) were scarce. Noncommercial species present in understory include *Acer spicatum* Lam., *Acer pensylvanicum* L., *Viburnum alnifolium* Marsh., *Sambucus* spp., *Corylus cornuta* Marsh., *Diervilla lonicera* Mill., *Pteridium aquilinum* L., *Aster acuminatus* Michx., *Aster puniceus* L., and *Solidago macrophylla* Pursh. The soil is a Dystric Brunisol (Soil Classification Working Group 1998) that developed on a thin glacial till and is characterized by a sandy loam to loamy sand texture. Sites were moderately well drained to imperfectly drained. Aspect varied southwest along a gentle slope ranging from 3% to 10%.

### Study design and data collection

The study used silvicultural openings (gaps) that were created by an operational logging prescription during fall 1998, which removed 35% of the basal area ( $\text{m}^2\cdot\text{ha}^{-1}$ ) from a 13.4 ha mixed tolerant hardwood – white pine stand (Raymond et al. 2003). In this stand, ten 45 m diameter ( $1590 \text{ m}^2$ ) gaps were produced by removing all trees and woody vegetation. Distance between gaps was  $\geq 75 \text{ m}$  (centre to centre). Single-tree selection between gaps removed another 25% of the standing trees to achieve the 35% basal area removal. Mineral soil was exposed by spot scarification, which was executed after the cut with the skidder blade. Each gap had 40 subplots (circular  $1 \text{ m}^2$ , 20 scarified and 20 nonscarified); their locations resulted from a random selection of angles and distances from gap centre. All subplots were positioned with an electronic theodolite (Wild TC100, Gais, Switzerland). The 10 gaps were used separately for spatial analysis of target species (eastern white pine, yellow birch, and paper birch) regeneration density (1999 germinants per hectare and 2001 total number of seedlings per hectare), and light availability. Regeneration abundance was monitored annually (1999–2001) in all subplots. Recruitment was very poor in 2000 and 2001 ( $<200 \text{ stems}\cdot\text{ha}^{-1}$ ).

Hemispherical photographs (Nikon Coolpix 950) were taken above the shrub layer (1.30 m) in all subplots in August 1999, to quantify light availability. Analysis of photographs (WinScanopy 2.3a, Regent Instruments, Sainte-Foy, Quebec) resulted in estimates of seasonal mean daily photosynthetic photon flux density (%PPFD). Five gaps of 10 were randomly selected (2, 4, 6, 8, 10) for monitoring and analysis of other variables, including planted and natu-

rally regenerated white pine cumulative diameter growth, soil temperature and moisture (growing season mean), light both over and under the shrub layer, and competition cover. One large-stock white pine seedling (container grown, 2 years old) was planted along the northern margin of each subplot in May 1999, for annual growth measurements (root-collar diameter for 1999–2001). Root-collar diameter was also recorded for the five tallest naturally regenerated white pine seedlings of each subplot in 2001.

Other variables were recorded in 20 randomly selected subplots (10 scarified, 10 nonscarified). Light availability over and under the shrub layer was quantified by a radiometer (August 2000, Decagon Devices Inc., Pullman, Washington) under overcast skies (Messier and Puttonen 1995). Averages were calculated as a mean of two perpendicular measures taken above the shrub layer (1.30 m) and four measures under the shrub layer (30 and 60 cm). Percent photosynthetically active radiation (%PAR) was calculated as the ratio of PAR measured in the gaps to PAR measured simultaneously in an adjacent open area (30 m logging road). Surficial soil temperature (probe, DigiSense, Vernon Hills, Illinois) and moisture (gravimetric method; Gardner 1986) at 5 cm depth were measured every 3 weeks during May–August of 1999 and 2000, at the centre of selected subplots (seasonal means were used in analysis). Depth of forest floor averaged 3 cm in the gaps. Competition cover was visually estimated after two growing seasons (August 2000).

### Statistical analysis

Spatial patterns were analysed using geostatistical techniques (Webster 1985; Robertson 1987; Isaaks and Srivastava 1989; Rossi et al. 1992) with GS+ software (version 5, Gamma Design Software, Plainwell, Michigan). Analysis was performed separately for each variable in each gap, with the objective to detect trends across gaps. The semivariogram is the principal tool used to characterize the degree of spatial autocorrelation present in the data and is fundamental to effectively estimate parameter values in unsampled areas (kriging). Nonstationarity of the variable may seriously distort the semivariogram (Worrall and Burt 1998). For this reason, data were detrended by using the residuals of the analysis of variance (ANOVA) (SAS version 8.1, SAS Institute Inc., Cary, North Carolina). This also had the advantage of extracting the effect of scarification present in the original data. Normality of residuals was checked and data were transformed when necessary, using log or square-root transformations. Semivariograms were then fitted to a spherical, exponential, or Gaussian function (Isaaks and Srivastava 1989), on the basis of the best reduced sums-of-squares fit. An anisotropic model was selected when anisotropy, a direction-dependent trend in the data (Robertson 2000), was present in the semivariogram. Spatial dependence was calculated as the proportion of sample variance (sill:  $C_0 + C$ ; Table 1) that was explained by structural variance ( $C$ ) (Robertson et al. 1993; Möttönen et al. 1999). For a given range of modelled separation distance, spatial dependence is high when the ratio  $C/(C_0 + C)$  approaches one and low when the ratio is near zero, indicating that spatial dependence occurs at scales smaller than the first lag interval (the shortest distance between sample points) or that measurement error is high (Robertson et al. 1993; Möttönen et al. 1999). In this study, semivariograms were

estimated on an active lag distance equal to 80% or less than the maximum distance between points (Robertson 2000) within a gap, and the first lag interval varied between 3.4 and 5.4 m.

We used kriging as an interpolation method for estimating values between sampled points within gaps. In this method, values are calculated from weights based on (i) the distance from nearby sample points and (ii) the degree of autocorrelation for those distances, as quantified previously in the semivariogram (Robertson 2000). Ordinary block kriging ( $2 \times 2$ ) using the 16 nearest neighbours and generation of contour plots were performed with GS+. Each contour plot was mapped with data that comes from kriging analysis. Finally, cross-validation analysis was used to evaluate the effectiveness of kriging parameters (Robertson 2000). In cross-validation analysis, each measured point in a spatial domain is individually removed from the data set and its value estimated by kriging as though it were never present. A plot then can be constructed of the estimated versus actual values for each sample location, with subsequent generation of regression statistics to evaluate the effectiveness of the interpolation.

## Results

### Spatial variation in light, soil temperature, and soil moisture

Spatial patterning was most consistently observed for %PPFD, with significant spatial patterns in all analysed gaps (Table 1). Spatial dependence was very strong in the estimated semivariograms, since 96%–100% of the total variance was explained by spatial structure, as expressed by the  $C/(C_0 + C)$  ratio (0.96–1.00). The interpolation by kriging was excellent as well ( $r^2 = 0.74$ –0.93 in cross-validation, Table 2). For %PPFD, the effective range of spatial dependence, that is, the maximum distance where values were autocorrelated, varied between 4 and 49 m. General trends emerged from contour plots of %PPFD, where maxima were observed more frequently in the northern portion and minima in the southern portion of gaps, with occasional specific minima in the southwest (Fig. 1a). %PAR under the shrub layer was less consistent across all gaps but exhibited moderate to strong spatial dependence (0.73–1.00). %PAR under the shrub layer was spatially dependent on a shorter distance (8–28 m) than %PPFD. Kriging interpolation  $r^2$  was good but significant patterns (three out of five) were variable across the gaps, probably due to the variability in the composition of the competing vegetation cover (Fig. 1b).

Semivariogram analysis showed that most gaps exhibited medium to strong spatial dependence for soil temperature, with the proportion of spatial structure ( $C/(C_0 + C)$ ) ranging from 0.49 to 1.00 in 1999 and from 0.66 to 1.00 in 2000. Gap 8 exhibited little spatial dependence in 1999. Spatial autocorrelation of soil temperature was estimated on distances ranging from 10 to 33 m in 1999 and from 8 to 106 m in 2000. Four gaps of five showed significant spatial patterns of soil temperature in 1999 and 2000. Patterns followed the same trends across years. Kriging resulted in more efficient interpolations in 1999 than in 2000, except for gap 8, which exhibited low  $r^2$  in 1999. Soil temperature varied along the north–south axis, with maxima in the north and minima in

**Table 1.** Semivariogram models calculated for kriging interpolation of light above (%PPFD) and below (%PAR) vegetation and mean soil temperature and water content (5 cm).

Gap	<i>n</i>	Model	Ani	Nug	Sill	Sdep	Range (effective range)	<i>r</i> <sup>2</sup>
<b>%PPFD above (1999)</b>								
2	40	G		1	512.9	1.00	$A_0 = 18.9$ (32.1)	0.99
4	40	G	104	0.5	450	1.00	$A_1 = 12$ (20.8), $A_2 = 2.6$ (4.4)	0.94
6	40	G		12	334.9	0.96	$A_0 = 20.9$ (35.4)	0.97
8	40	G	183	0.8	212.5	1.00	$A_1 = 28$ (48.5), $A_2 = 14$ (24.2)	1.00
10	40	G		1	512.9	1.00	$A_0 = 13.6$ (23.1)	1.00
<b>%PAR below (2000)</b>								
2	20	S		0.1	172	1.00	$A_0 = 16$ (16)	0.39
4	20	G		1	320	1.00	$A_0 = 8$ (13.6)	0.99
6	20	S		69.8	255	0.73	$A_0 = 12.4$ (12.4)	0.57
8	20	G		81	672.9	0.88	$A_0 = 16.4$ (27.9)	0.98
10	20	S	14	61	397.9	0.85	$A_1 = 26$ (26), $A_2 = 23.6$ (23.6)	0.99
<b>Soil temperature (1999)</b>								
2	20	S		0.0393	0.0973	0.60	$A_0 = 15.4$ (15.4)	1.00
4	19	S		0	0.21	1.00	$A_0 = 21$ (21)	0.74
6	20	E		1.016	3.014	0.66	$A_0 = 10.9$ (32.6)	0.99
8	20	S		0.36	0.7	0.49	$A_0 = 12$ (12)	0.91
10	20	G		0.28	1.7	0.73	$A_0 = 10$ (20.8)	0.74
<b>Soil temperature (2000)</b>								
2	20	E		0.08	0.235	0.66	$A_0 = 8$ (24)	0.91
4	20	G		0.0198	0.2329	0.92	$A_0 = 42.4$ (73.6)	0.96
6	20	G		0.095	1.098	0.91	$A_0 = 61$ (105.7)	0.85
8	20	S		0.001	0.951	1.00	$A_0 = 15.8$ (15.8)	0.86
10	20	S		0.02	0.105	0.81	$A_0 = 15$ (15)	0.93
<b>Soil water content (1999)</b>								
2	20	G		0.0001	0.06	1.00	$A_0 = 5$ (8.7)	0.53
4	20	E		0.001	0.0068	0.85	$A_0 = 5$ (15)	0.82
6	20	E	171	0.012	0.08	0.85	$A_1 = 14$ (42), $A_2 = 6$ (18)	0.29
8	20	E		0.052	0.122	0.57	$A_0 = 6$ (18)	0.91
10	20	S		0.0019	0.021	0.91	$A_0 = 17$ (17)	0.76
<b>Soil water content (2000)</b>								
2	19	E		0.00337	0.0248	0.86	$A_0 = 49.9$ (149.7)	0.99
4	20	S		0.0116	0.232	0.95	$A_0 = 15$ (15)	0.98
6	20	E		0.005	0.0405	0.88	$A_0 = 8$ (24)	0.23
8	20	G		0.001	0.029	0.97	$A_0 = 10$ (17.3)	0.82
10	19	S		0.014	0.0448	0.69	$A_0 = 18$ (18)	0.32

**Note:** *n*, number of sampling points in the gap; Model, model type: S, spherical; E, exponential; G, Gaussian; Ani, anisotropy axis (°). Semivariogram can be displayed as two-dimensional graph but given the great number of analyses, semivariogram parameters were summarized in tables. The nugget (Nug or  $C_0$ ) is the y-intercept of the graph, the sill ( $C_0 + C$ ) is the semivariogram value (y value) where each graph becomes a plateau (where points are no longer spatially correlated), the degree of spatial dependence (Sdep) is the ratio of structural to population variance ( $C + C_0/C$ ), and the range ( $A_0$ ) is the distance in metres (x value) where the plateau begins. In exponential and Gaussian models,  $A_0$  is not the range per se but rather a parameter used in the model to provide range. For these models, the effective range represents the separation distance at which the model will be within 5% of the asymptote and is estimated as  $3A_0$  for the exponential and  $1.7A_0$  for the Gaussian model. Same rules apply for the ranges of anisotropic models, the difference with isotropic (e.g., regular) models is that two ranges are included in the model:  $A_1$  is the range parameter for the major axis of variation and  $A_2$  is the range parameter for the minor axis (Robertson 2000).

the southern portion of the gaps. Temperature distribution peaked more specifically in the northwest in 1999 and 2000 (except for gap 10, which peaked in the northeast). The lowest soil temperature generally was found in the southwest

quadrant of the gaps. Examples of soil temperature variation in a gap are shown in Figs. 1c and 1d.

Soil water content also exhibited medium to strong spatial dependence (0.57–1.00) for both years, but overall model fit



**Table 2.** Kriging results and spatial patterns summary of light above (%PPFD) and below (%PAR) vegetation and mean soil moisture and temperature (5 cm).

Gap	Kriging			Spatial pattern			
	$r^2_{sv}$	RC	$r^2_{kr}$	Max.	Peak	Min.	Pit
<b>%PPFD above (1999)</b>							
2	0.99	0.97	0.86	N	N	S	SW, SE
4	0.94	0.95	0.93	N	N	S	S
6	0.97	1.05	0.80	N	NW	S	S
8	0.94	1.04	0.74	N, C	N	ed NE, SW	SW
10	0.99	0.99	0.89	N	N	S	SW, S
<b>%PAR below (2000)</b>							
2							
4	0.99	0.90	0.62	W	W	N, S	N
6							
8	0.98	0.91	0.47	N	N	S, W	SW
10	0.99	0.91	0.32	SE	SE	N, W	SW, NW
<b>Soil temperature (1999)</b>							
4	0.74	2.44	0.47	NW	NW	S	SW
6	0.99	1.21	0.32	NW	NW	S, E	SW
8	0.91	0.89	0.07	N, C	NW, C	SW, E	SW, SE, NE
10	0.74	1.08	0.59	N, E	NE	S, W	SW
<b>Soil temperature (2000)</b>							
4	0.96	2.47	0.38	N	NW	S	SW
6	0.85	3.17	0.20	W	NW	E	NE
8	0.86	0.86	0.27	NW, SE	NW, SE	SW, ed N	SW
10	0.93	2.26	0.14	NE	NE	ed W, S	SW
<b>Soil water content (1999)</b>							
2	0.53	0.99	0.14	NW	NW	E	SE, NE
4							
8	0.91	1.56	0.13	W	SW	E	SE, NE
10	0.76	0.70	0.16	N	N	W	NW, ed E
<b>Soil water content (2000)</b>							
2							
4	0.98	1.02	0.33	SW, E	SW	NW, C	NW
8	0.82	1.05	0.22	W, NE	SW	E, ed W	W, E
10							

**Note:**  $r^2_{sv}$ , proportion of variation explained by the semivariogram. RC and  $r^2_{kr}$  are statistics obtained in cross-validation analysis to evaluate the effectiveness of kriging: RC, regression coefficient of kriging (1.00 being perfect prediction);  $r^2_{kr}$ , proportion of variation explained by the best-fit line when kriging. Each spatial pattern is described at two levels: (i) general maximum and minimum zones (max. and min.) and (ii) specific peaks and pits in the distribution (see Fig. 1 for an example). The nonsignificant patterns are not shown. N, north; E, east; S, south; W, west; C, centre; ed, edges.

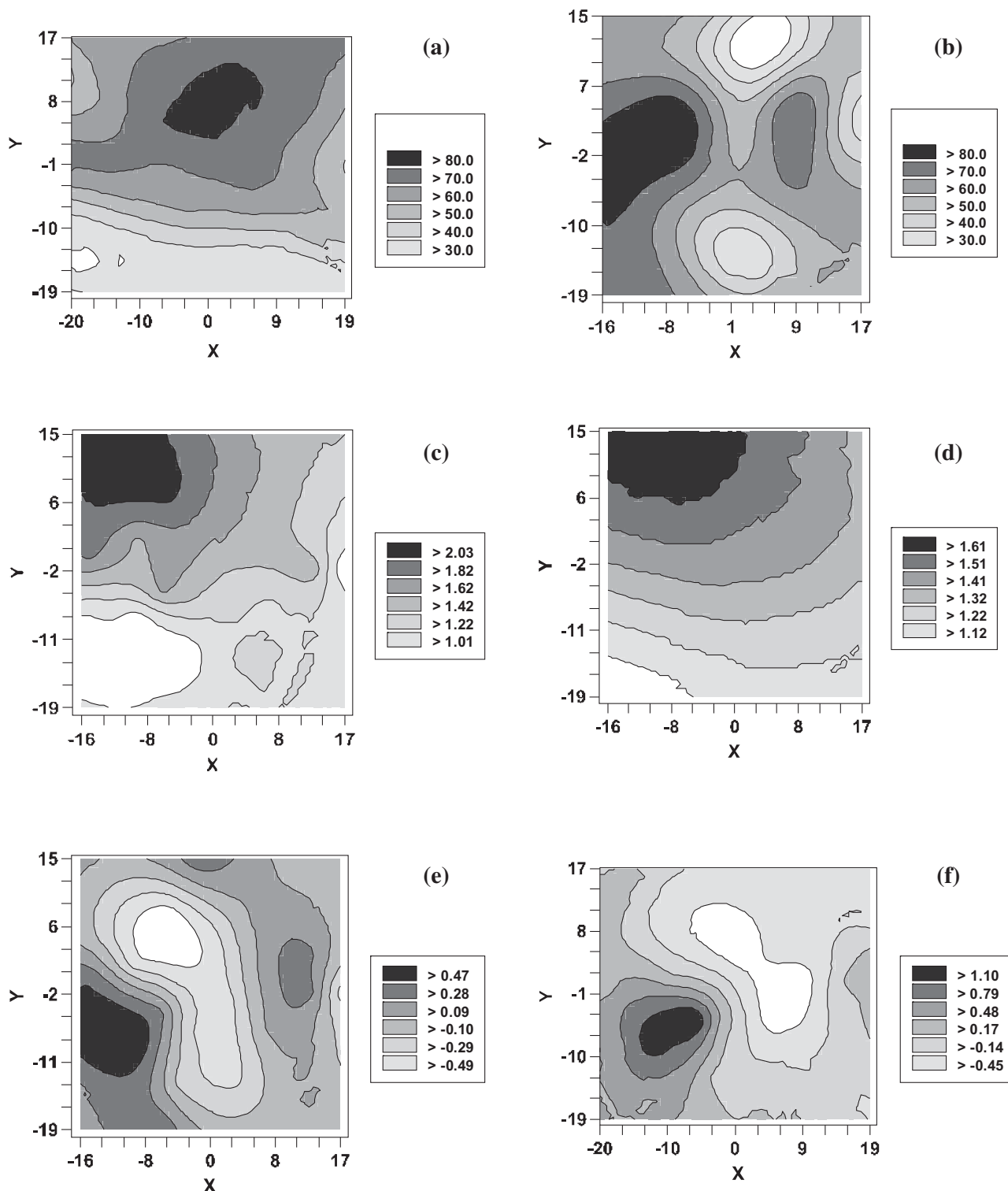
was not as good as the semivariograms estimated for soil temperature. Low  $r^2$  values were recorded for gap 6 (1999: 0.29, 2000: 0.23) and gap 10 (2000: 0.32). As with temperature, the spatial autocorrelation range of soil water content was more variable in 2000 (8–150 m) than in 1999 (5–42 m). Soil moisture was frequently more random than soil temperature, with three of five gaps presenting significant spatial patterns in 1999 and two gaps in 2000. Cross-validation  $r^2$  after kriging were generally lower for soil moisture than for soil temperature, especially in 1999. Soil moisture patterns were more complex and variable than temperature across gaps and years. Where a pattern was evident, soil moisture seemed to vary along both north–south and east–west axes. In 1999, soil moisture tended to be higher in the western and lower in the eastern sectors of gaps. In 2000, maximum

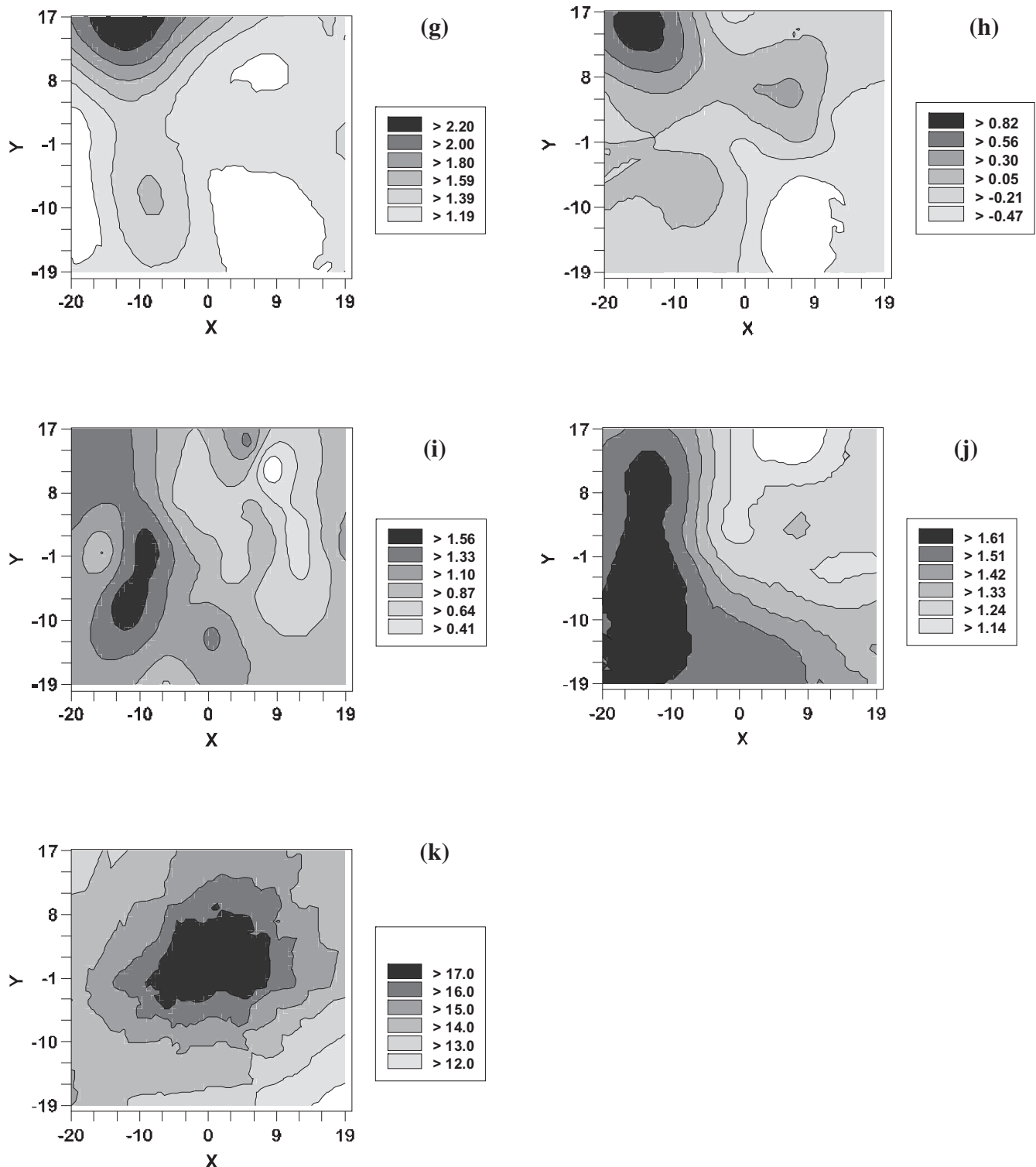
moisture was measured in the southwest sector and the minimum was not spatially consistent. In the example of gap 4 (2000, Fig. 1e), soil moisture was lowest in the northwest and central portion of the gap.

#### Spatial variation in naturally regenerated tree seedlings, shrubs, and herbs

White pine germinants were slightly less spatially dependent than those of yellow birch and paper birch. Half of the white pine semivariograms had low  $r^2$ , and spatial dependence was slightly lower for white pine (0.50–0.89) than for yellow birch (0.50–1.00) and paper birch (0.52–1.00) (Table 3). White pine germinant densities were autocorrelated over a shorter distance (4–22 m) than those of the established seedlings (3–104 m). Germinants and seedlings of

**Fig. 1.** Contour plots of significant spatial patterns in gap 4, which was selected for intensive vegetation and environmental monitoring: (a) seasonal percent photosynthetic photon flux density; (b) percent photosynthetically active radiation under the shrub layer; (c) 1999 soil temperature; (d) 2000 soil temperature; (e) 2000 soil moisture; (f) 1999 white pine germinants; (g) 1999 yellow birch germinants; (h) 2001 yellow birch seedlings; (i) 1999 paper birch germinants; (j) 2001 paper birch seedlings; (k) large stock seedlings cumulative diameter growth. Residuals of the ANOVA were used in spatial analysis of Figs. 1c–1j. Data in Figs. 1e, 1h, and 1g were either log or square-root transformed prior to semivariogram analysis. Axes *X* and *Y* represent the west–east and the north–south axes (metres), respectively.



**Fig. 1** (concluded).

yellow birch (4–95 m and 3–85 m) and paper birch (3–39 m and 3–19 m) were autocorrelated over similar distances.

The weaker spatial dependence of white pine occurrence was reflected in the kriging results, where the distribution was random in most of the gaps, with only 3 of 10 gaps having significant spatial patterns in 1999 and 2 in 2001 (Table 4). However, when significant, germinant patterns were

similar to those of the surviving seedlings 2 years later. Maximum white pine density was found along the gap margins or in the southwest quadrant. White pine density was minimum in the centre, north, or east (Fig. 1f). Yellow birch presence was more constant than white pine presence across the gaps and generally more abundant in the southwest and northwest quadrants than in the east. In gap 4, highest densi-

**Table 3.** Semivariogram models calculated for kriging interpolation of white pine, yellow birch and paper birch germinant density in 1999 and total number of seedlings in 2001 ( $n = 40$ ).

1999 germinant density							2001 seedling density							
Gap	Model	Ani	Nug	Sill	Sdep	Range (effective range)	r <sup>2</sup>	Model	Ani	Nug	Sill	Sdep	Range (effective range)	r <sup>2</sup>
White pine														
1	S		0.04	0.12	0.67	A <sub>0</sub> = 4.5 (4.5)	0.38	G		0.0329	0.1069	0.69	A <sub>0</sub> = 51 (86.7)	0.79
2	E	14	0.1	0.85	0.88	A <sub>1</sub> = 6 (18), A <sub>2</sub> = 5 (15)	0.42	S		0.045	0.118	0.62	A <sub>0</sub> = 16 (16)	0.83
3	G		2.82	6.708	0.58	A <sub>0</sub> = 9.9 (17.1)	0.98	S		0.18	0.6	0.70	A <sub>0</sub> = 8 (8)	0.96
4	S		0.53	1.09	0.51	A <sub>0</sub> = 19 (19)	0.98	G		0.02	0.035	0.43	A <sub>0</sub> = 18 (30.6)	0.75
5	E		0.0367	0.0735	0.50	A <sub>0</sub> = 7.2 (21.6)	0.77	E		0.001	0.345	1.00	A <sub>0</sub> = 4.2 (12.6)	0.79
6	S		0.27	0.642	0.58	A <sub>0</sub> = 9.8 (9.8)	0.98	R						
7	S		0.1	0.44	0.77	A <sub>0</sub> = 9 (9)	0.22	G		0	0.135	1.00	A <sub>0</sub> = 3 (5.1)	0.51
8	S		0.14	0.365	0.62	A <sub>0</sub> = 15 (15)	0.99	S		0.06	0.185	0.68	A <sub>0</sub> = 12 (12)	0.66
9	R							G		0.0174	0.0597	0.71	A <sub>0</sub> = 61 (103.7)	0.83
10	S		0.04	0.37	0.89	A <sub>0</sub> = 11 (11)	0.25	S		0.18	0.56	0.68	A <sub>0</sub> = 23 (23)	0.12
Yellow birch														
1	E		0	0.35	1.00	A <sub>0</sub> = 3.5 (10.5)	0.73	E		0	0.103	1.00	A <sub>0</sub> = 4 (12)	0.76
2	E		0.005	0.059	0.92	A <sub>0</sub> = 6 (18)	0.73	G		0.383	2.776	0.86	A <sub>0</sub> = 49.8 (84.6)	0.95
3	G		0.0893	0.2716	0.67	A <sub>0</sub> = 54.6 (94.6)	0.89	R						
4	G		0.03	0.12	0.75	A <sub>0</sub> = 10 (17.3)	0.94	S		0.1512	0.3614	0.58	A <sub>0</sub> = 16.6 (16.6)	0.99
5	S		0.2068	0.4146	0.50	A <sub>0</sub> = 61 (61)	0.75	S		0.02	0.088	0.77	A <sub>0</sub> = 9 (9)	0.79
6	H							H						
7	E		0	0.90	1.00	A <sub>0</sub> = 4 (12)	0.70	E		0.05	0.65	0.92	A <sub>0</sub> = 5 (15)	0.13
8	S		0.0215	0.137	0.84	A <sub>0</sub> = 7.3 (7.3)	0.37	E		0.026	0.07	0.63	A <sub>0</sub> = 7 (21)	0.20
9	S		0.10	0.77	0.87	A <sub>0</sub> = 9.6 (9.6)	0.14	R						
10	S		0	0.45	1.00	A <sub>0</sub> = 7 (7)	0.70	G		0.028	0.091	0.69	A <sub>0</sub> = 3.5 (6.1)	0.74
Paper birch														
1	S		0.40	1.55	0.74	A <sub>0</sub> = 6.5 (6.5)	0.60	E		0.4	1.7	0.77	A <sub>0</sub> = 3.0 (9.0)	0.28
2	G		0.0001	0.18	1.00	A <sub>0</sub> = 3.8 (6.5)	0.76	S		0.099	1.353	0.93	A <sub>0</sub> = 19.2 (19.2)	0.97
3	R							R						
4	E	0	0.001	0.30	1.00	A <sub>1</sub> = 30 (90), A <sub>2</sub> = 20 (60)	0.67	G		0.0282	0.0742	0.62	A <sub>0</sub> = 10.5 (17.9)	0.90
5	S		0.298	1.201	0.75	A <sub>0</sub> = 38.4 (38.4)	0.97	G		0.03	1.057	0.97	A <sub>0</sub> = 5.1 (8.7)	0.94
6	G		0.72	1.5	0.52	A <sub>0</sub> = 9 (15.3)	0.45	E		0	0.0265	1.00	A <sub>0</sub> = 3.6 (10.8)	0.50
7	S		0.20	0.75	0.73	A <sub>0</sub> = 18 (18)	0.87	S	55	0.01	0.1	0.90	A <sub>1</sub> = 18 (18), A <sub>2</sub> = 12 (12)	0.56
8	R							R						
9	R							S		0.4	1.2	0.67	A <sub>0</sub> = 9.5 (9.5)	0.70
10	S		0	0.58	1.00	A <sub>0</sub> = 8.5 (8.5)	0.88	R						

**Note:**  $n$ , number of sampling points in the gap; Model, model type; S, spherical; E, exponential; G, Gaussian; R, random data (no spatial structure); H, nonhomogeneous data; Ani, anisotropy axis ( $^\circ$ ). Semivariogram can be displayed as two-dimensional graph but given the great number of analyses, semivariogram parameters were summarized in tables. The nugget (Nug or  $C_0$ ) is the y-intercept of the graph, the sill ( $C_0 + C$ ) is the semivariogram value ( $y$  value) where each graph becomes a plateau (where points are no longer spatially correlated), the degree of spatial dependence (Sdep) is the ratio of structural to population variance ( $C + C_0/C$ ), and the range ( $A_0$ ) is the distance in metres ( $x$  value) where the plateau begins. In exponential and Gaussian models,  $A_0$  is not the range per se but rather a parameter used in the model to provide range. For these models, the effective range represents the separation distance at which the model will be within 5% of the asymptote and is estimated as  $3A_0$  for the exponential and  $1.7A_0$  for the Gaussian model. Same rules apply for the ranges of anisotropic models, the difference with isotropic (e.g., regular) models is that two ranges are included in the model:  $A_1$  is the range parameter for the major axis of variation and  $A_2$  is the range parameter for the minor axis (Robertson 2000).



**Table 4.** Kriging results and spatial patterns summary of white pine, yellow birch and paper birch germinant density in 1999 and total number of seedlings in 2001.

Gap	1999 germinant density							2001 seedling density						
	Kriging			Spatial pattern				Kriging			Spatial pattern			
	$r^2_{sv}$	RC	$r^2_{kr}$	Max.	Peak	Min.	Pit	$r^2_{sv}$	RC	$r^2_{kr}$	Max.	Peak	Min.	Pit
White pine														
2	0.42	0.81	0.12	ed N, W, S	N, SE, SW	E	E, C	0.83	1.54	0.13	ed N, S	N, SW	E	E, SE
4	0.98	0.78	0.15	SW	SW	N, E, C	N, C							
5	0.77	1.31	0.05	ed W, S, E	SW	N, C	N, C	0.79	0.55	0.04	ed W, S, E	SW, SE	N, C	C
Yellow birch														
1	0.73	0.86	0.22	S, W	SW	E, N	SE	0.76	1.71	0.11	W, N	NW	E	E
2	0.73	1.23	0.05	W	SW	E	E	0.95	0.82	0.19	W	SW	E	E
4	0.94	3.08	0.30	NW	NW	S, E	SW, SE	0.99	0.74	0.10	NW	NW	E	SE
7	0.7	0.63	0.10	W	SW	E	E							
Paper birch														
1	0.60	1.19	0.16	E	E	SW, NE	SW, NE	0.28	0.58	0.05	S	C	N	NW
2								0.97	0.66	0.14	ed W, S, E	S	C, N	C, N
4	0.67	1.96	0.24	W	NW, SW	E	NE	0.90	1.83	0.18	W, S	SW	NE	NE
5	0.97	0.94	0.28	W, S	SW	NE	NE	0.94	0.97	0.26	ed W, S, E	SW	C, N	C
6	0.45	0.74	0.12	N, SW	NE, SW	W, SE	W, SE							
7	0.87	0.88	0.33	SW	SW	N	NE	0.56	2.03	0.25	S	S	ed W, N, E	N
10	0.88	0.43	0.05	E	NW, E, SE	W	W, NE							

ties were measured in the northwest in 1999 and 2001 (Figs. 1g, 1h). A greater number of gaps were characterized by significant spatial patterns for paper birch than for either yellow birch or white pine. Paper birch emergence was often higher in the west, with peaks in the northwest or southwest (Fig. 1i). Lower emergence was found in the eastern part of the gaps, with pits in the northeastern sector. However, higher densities of the surviving seedlings were located in the south or at the edges of gaps, with peaks in the southern or southwestern sectors (Fig. 1j). Paper birch seedlings were often less abundant in the northern or central portion of gaps. Total competition cover of shrubs and herbs was generally random in the five analysed gaps, with only one gap having a significant, but weak ( $r^2 = 0.07$ ), spatial pattern (data not shown).

### Spatial variation in growth of naturally regenerated and planted white pine seedlings

Naturally regenerated white pine seedlings exhibited high spatial dependence in their cumulative diameter growth (0.97–1.00), while planted seedlings exhibited weak or no spatial dependence (0.38–0.70) (Table 5). Also, diameter growth of naturally regenerated seedlings was spatially dependent over a shorter and less variable distance (8–25 m) than that of planted seedlings (12–86 m). Kriging produced interpolated spatial patterns of diameter growth that differed between naturally regenerated and planted white pine. Three gaps of five had significant patterns for both seedling types. Naturally regenerated seedling diameter growth tended to be higher in the western part of the gaps and lower in the eastern part of the gaps. Planted large-stock seedlings had maximum cumulative diameter growth in the northern and central portion of gaps and minimum growth at the edges of gaps (Fig. 1k).

## Discussion

### Environmental variability in gaps

The percentage of full sunlight (%PPFD) under the tree canopy but above the shrub and herb layer was the most spatially dependent and consistent of the studied variables. The general north–south asymmetry in the distribution of sunlight was in line with light distributions in gaps described in the literature (Canham 1988; Poulson and Platt 1989; Canham et al. 1990; Wright et al. 1998; Lieffers et al. 2002). However, we found that light distribution was not entirely symmetrical on the east and west sides of the gaps, as it should be in theory (Canham 1988, Canham et al. 1990). Lower %PPFD on the east than on the west side could be explained by the location of gaps in the field: their aspect varied from south to west along an 8° slope and the east side could be slightly more shaded. Surficial soil temperature patterns along the north–south axis of gaps were quite consistent with light availability, but differed somewhat from light along the east–west axis. Our observations are consistent with literature regarding the asymmetry in soil temperature distribution along the north–south axis (Strong et al. 1997; Wright et al. 1998), but differ in the distribution along the east–west axis, which was rather more asymmetric than symmetric. Soil moisture patterns were harder to detect and seemed more complex than temperature patterns. Microsite characteristics such as microtopography, substrate type, and humus depth could add variability and blur spatial relationships. General trends in microclimate variation observed across gaps could be more influenced by the timing of solar radiation than by the total amount of light received during a day. The east and west sides receive the same relative amount of light during a given day (Canham 1988; Canham et al. 1990), but patches of sunshine occur earlier in the day on the west side than on the east side, which results in asym-

metry of microclimate conditions (Wayne and Bazzaz 1993). Finally, since local variation in slope and aspect can also influence the distribution of resources and potential vegetation patterns, the effect of these variables should be better understood and incorporated into spatially explicit models.

Differences in spatial relationships between 1999 and 2000 could be explained by changes in vegetation cover and annual variation of climate. In 1999, the first year after harvest, vegetation had only started to recolonize gaps and covered a small proportion of gap areas, but expanded greatly in 2000, with an average 55% cover (Raymond 2004). Thus, 1999 reflected microclimate patterns that were found with almost no vegetation on the ground. Gap recolonization by vegetation added variability and it was harder to model spatial relationships in semivariograms. Patterns were also less consistent across gaps. Furthermore, the monthly average growing season precipitation was lower in 1999 than in 2000 (90 vs. 118 mm, Mont-Laurier, Quebec, 46°34'N, 75°33'W), and spatial patterns may have been easier to detect under the drier conditions of 1999.

In this study, a few semivariograms had larger range values than the gap diameter values. The range is a parameter reported from a mathematical model representing the semivariogram and indicates where the plateau begins, that is, where the variable is no longer spatially autocorrelated. A larger range value than plot size is possible when the plateau is not reached before the maximum distance between points and indicates that spatial continuity is greater than overall sample variability (Rossi et al. 1992). In the present study, large ranges were noted for Gaussian and exponential functions, for which the sill never converges (Robertson 2000). In such functions, the effective range is estimated as the separation distance at which the model is within 5% of the asymptote (Robertson 2000). A larger range than gap diameter also means that the variable was spatially autocorrelated in all points of the gap, according to the relationship quantified in the semivariogram.

### Regeneration of tree seedlings

The central and northern sides of gaps can be less favourable to early establishment of white pine, given the higher susceptibility of white pine to late-spring frost and extreme high-temperature events (Strong et al. 1997). However, the lower spatial dependence of white pine may indicate that factors other than soil microclimate influenced the spatial distribution. Given that it has a larger seed size and more limited dispersal (30–60 m, Horton and Bedell 1960) than do the birches, white pine is probably more dependent on distance to parent trees and their position around the gap. Another component of the present study demonstrated that the number of white pine seeds in different positions of the gaps was highly correlated with inverse distance from parent trees (Nolet et al. 1999). Patterns of establishment might also be explained by the direction of prevailing winds, originating from the west (Nolet et al. 1999). Other studies assessed the importance of seed trees on white pine population structure (Palik and Pregitzer 1994) and mechanism of regeneration (Dovciak et al. 2001) in mixed stands. White pine seed trees are particularly important in mixed stands, where gap edges are composed of a mixture of white pine and other species. The variability in species composition of the

mixture from one gap to another may explain in part the variability in regeneration patterns across gaps. Seed predation likely added variability to germinant distribution (Palik and Pregitzer 1994; Raymond et al. 2003), since small mammals can remove seeds from where they fall to new seed caches (Abbott and Quink 1970; Vander Wall 1994). Therefore, when using gaps for naturally regenerating white pine in mixed stands, the silviculturist should avoid gaps larger than  $2H$ , while paying attention to location of parent trees relative to dominant winds, to improve white pine regeneration density and distribution.

Unlike white pine, the spatial pattern of yellow birch and paper birch seemed tied to microsite conditions found in gaps. Yellow birch and paper birch are not limited by seed dispersal, since their light-winged seeds can be wind dispersed over a long distance, especially on crusted snow (Greene and Johnson 1995, 1997). However, they are sensitive to drying of litter (Erdmann 1990). Favourable soil moisture conditions found in the western sector of gaps could explain the peak in yellow birch and paper birch germination (Perala and Alm 1989). Yellow birch and paper birch exhibited similar trends for emergence, but results indicated that future survival and growth patterns could differ from those of emergence. Paper birch tended to survive in greater numbers in the south or along gap edges, where soil temperature is lower (Strong et al. 1997) and where interspecific competition may be less intense. In British Columbia, Wright et al. (1998) observed a greater emergence and survival of forest tree species in the south than in the north of 600 m<sup>2</sup> gaps. In a shelterwood study conducted in paper birch stands, the best microsites for seedling recruitment and growth were shaded but not overtopped by canopy trees (Perala and Alm 1989).

White pine and yellow birch are both mid-tolerant species but responded differently to environmental variability of gaps. The importance of environmental factors such as distance and location of parent trees and microclimate vary according to species, which may influence the success of silvicultural treatments. Thus, we must be cautious when we want to extrapolate results from experiments aiming for yellow birch regeneration to white pine regeneration on the sole basis of similar shade tolerance.

### White pine seedling growth

Spatial patterns of white pine growth differed between naturally regenerated and planted seedling. The 3-year-old naturally regenerated seedlings were usually smaller than the surrounding vegetation and were still dependent on soil microclimate conditions, as reflected in higher growth in the moister western versus eastern side of the gaps. This result is in line with those of Barden (1996) and Wayne and Bazzaz (1993), who measured the best growth efficiency of plants in the western part of gaps. Soil moisture is particularly important during white pine early establishment, when the root system is not completely developed (Ahlgren and Ahlgren 1981; Elliott and Vose 1993; Wetzel and Burgess 1994). Our results suggest that this initial spatial pattern will change with time. Once root system development is completed, competition with vegetation and insufficient light become more limiting factors than water stress (Pacala et al. 1994; Elliott and Vose 1995). The spatial patterns of planted

**Table 5.** Semivariogram models, kriging results and spatial patterns summary of planted and naturally regenerated white pine cumulative diameter growth ratio (2001) and % competition cover (2000).

		Semivariogram							Kriging		Spatial pattern			
Gap	<i>n</i>	Model	Nug	Sill	Sdep	Range ( <i>A</i> <sub>0</sub> )	Effective range	<i>r</i> <sup>2</sup> <sub>sv</sub>	RC	<i>r</i> <sup>2</sup> <sub>kr</sub>	Max.	Peak	Min.	Pit
Planted white pine diameter growth														
2	39	E	0.04	0.12	0.67	4.0	12.0	0.60						
4	40	G	17.23	45.97	0.63	50.8	86.3	0.27	1.38	0.14	N, C	C	ed NW, S	SE
6	40	S	9	14.5	0.38	12.0	12.0	0.71						
8	40	E	19	32	0.41	16.0	48.0	0.91	0.94	0.09	N, C	N	ed W, E, S	W, NE
10	40	S	7	23.5	0.70	14.0	14.0	0.93	0.84	0.22	C, E	C, E	ed W, S, N	SW, NW
Naturally regenerated white pine diameter growth														
2	14	G	0.01	0.375	0.97	5.0	8.5	0.61	1.12	0.23	W	W, SW	E	NE
4	20	R												
6	14	G	0.001	0.44	1.00	7.0	11.9	0.48	0.95	0.29	N, SW, SE	SW, SE	E, W	E
8	7	G	0.0001	0.035	1.00	14.5	24.7	0.98	1.19	0.55	W	NW	E	NE
10	20	G	0.001	0.0385	0.97	7.0	11.9	0.70						
Competition cover														
2	20	R												
4	20	E	559	1118.1	0.50	41.3	123.8	0.50						
6	20	E	1	886.2	1.00	5.1	15.2	0.76						
8	20	R												
10	20	S	4.88	9.962	0.51	58.0	58.0	0.75						

seedlings showed the potential growth that white pine can have once it is established and is less suppressed by competition. At this stage, diameter growth followed spatial patterns similar to those of light (%PPFD), with maximum growth in the central and northern section of gaps. The gap centre is a zone where competition from canopy trees for above- and below-ground resources is reduced, which can favour white pine growth. In partial cuts, planted white pine growth seemed to be more sensitive to overstory than to understory competition (Saunders and Puettmann 1999). Long-term observations (18 years) made by Smith and Ashton (1993) in similar-sized gaps showed that best white pine growth occurred in the northern portion of gaps, beneath grey birch. Other field experiments (Poulson and Platt 1989; McClure and Lee 1993; Coates 2000) and model simulations (Ménard et al. 2002) have shown similar results for mid-tolerant species.

### Coincidence of regeneration and growth niches

Significant asymmetry in light, soil temperature, and soil moisture indicates that there was a potential for specialization and partitioning of species within gaps. Our study suggests that white pine, yellow birch, and paper birch had similar requirements for germination and early establishment. In our large 45 m diameter gaps, all three species were sensitive to seedbed desiccation, and as a consequence their regeneration niche overlapped, as they established preferably in the moister and cooler gap sectors. In this respect, there was no evidence of species partitioning within the gaps during early establishment. However, results indicated that spatial patterns could change in the future and segregation resulting from differences in survival could eventually occur. For example, Wright et al. (1998) and Coates (2002) found little evidence for partitioning during early establishment, but did

find trends indicating differential survival. In our study, longer term observations would be required to verify the gap-partitioning hypothesis through differential survival. In our 45 m diameter (equivalent to twice the height of the trees) gaps and at 46°N latitude, the area of maximum light was localized inside the gaps, in the northern and central portions. Thus, the coincidence of the area of increased light with the area of reduced competition for water and nutrients is theoretically possible (as noted by Lieffers et al. (1999)). Preferred establishment of white pine in the southwest and in the edges of gaps and best growth in the west indicate that the optimum areas for establishment and early growth can coincide. However, when seedlings were taller (>1 m) and in a better position with respect to competitors (planted seedlings), the best growth occurred under the area of maximum light availability (centre and north), and the poorest in the edges. From the perspective that the naturally regenerated seedlings tended to establish in the edges of large gaps, the optimum areas of establishment and growth will not necessarily coincide when seedlings are taller. Still, if naturally regenerated white pine seedlings survive in the central or northern section of gaps, this problem may not be as important. The situation of discordance of optimal regeneration and growth niches (Schupp 1995) was also underlined for other species by Wright et al. (1998) and Coates (2002).

### Conclusion

This study demonstrated that geostatistical analysis of 20–40 randomly distributed sampling points can detect subtle variation in spatial patterns of forest vegetation and microclimate in silvicultural gaps. Studies using only three or five sampling locations in the gaps are more limited in their interpretation, since variation between sampling points remains

unknown. Kriging was a useful tool for characterizing spatial patterns, because values between sampling points could be interpolated with selected semivariogram functions. However, for more variable data, such as soil moisture and competition cover, a greater number of points should be sampled to check if patterns could be detected over shorter distances. Low spatial dependence of white pine indicated that factors other than microclimate might influence its spatial distribution. Parent tree distance and position around the gap in relation to dominant winds might play a significant role in its distribution and should be taken into account during gap marking in group-selection cutting. Given the limited dispersal (30–60 m) and low tolerance to competition of white pine, gap sizes smaller than 45 m should be tested in tolerant hardwood – white pine stands. Smaller gaps should also be beneficial to yellow birch and paper birch establishment, since these species were sensitive to microclimate variation and smaller gaps could offer a more temperate microclimate to the seedlings. Seedlings could distribute more evenly in the gaps and increase the probability of coincidence of optimal regeneration and growth niches. The latter result would increase the probability of achieving the main silvicultural objective, which was to maintain the mixed composition of the stand by growing less shade-tolerant species such as white pine, yellow birch, and paper birch in silvicultural gaps.

## Acknowledgements

The authors would like to thank E. Thiffault, J. Langevin, A. Beaumont, S. Reynolds, P.D. Vlasia, S. Ostojic, and J. Deslandes for assistance in the field. Thanks to Catherine Périé, William Parsons, and two anonymous reviewers for helpful comments on this manuscript. Financial and technical support was provided by the Ministère des Ressources naturelles du Québec, the Natural Sciences and Engineering Research Council of Canada (NSERC) (to A.D. Munson), Scierie Davidson, Institut québécois d'aménagement de la forêt feuillue, Corporation de Gestion de la Forêt de l'Aigle, and Société Sylvicole Haute-Gatineau. P. Raymond benefitted from NSERC and Fonds pour la Formation des Chercheurs et l'Aide à la Recherche (FCAR, Quebec) Ph.D. grants.

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