

Spatial Variability of Substrate Water Content and Growth of White Spruce Seedlings

Mohammed S. Lamhamedi,* Louise Labbé, Hank A. Margolis, Debra C. Stowe, Louis Blais, and Mario Renaud

ABSTRACT

Irrigation by jet-type sprinklers contributes to the spatial variability of substrate water content and growth of containerized white spruce [*Picea glauca* (Moench) Voss.] seedlings grown outdoors during their second growing season. Geostatistical analyses were used to identify the spatial structure of this variability throughout the growing season and to help develop a sampling strategy to facilitate irrigation management. Boundary line analysis confirmed that the heterogeneity of height growth is related to seasonal variations in substrate water content and that maximum height growth and seedling biomass is attained when average seasonal substrate water content is approximately 40% (v/v). Parameters estimated from semi-variograms, most notably the range (a) and total variance ($C_0 + C_1$) of substrate water content, can be used to define sampling strategies specific to irrigation management and morphophysiological evaluation of seedlings. The relationship between leaching and substrate water content can be used, in conjunction with kriged maps, to estimate potential losses of mineral nutrients and to quantify water use for the production of white spruce seedlings during their second growing season in a forest nursery. More than 15% of the seedlings in the crop used in the present study were rejected at delivery. Knowledge of the spatial variability within a crop enables forest nurserymen to modify sampling techniques and cultural practices, produce more uniform seedlings and reduce the quantity of seedlings that fail to meet morphophysiological criteria.

SPATIAL VARIABILITY of environmental resources in outdoor forest nurseries can make it difficult to produce homogenous lots of forest tree seedlings that meet the 28 strict government criteria for planting stock in the province of Quebec. These include height, diameter, root architecture and development, plug cohesion, and shoot N concentration (Direction de la production des semences et des plants, 2005). On a provincial scale, 21% of the large white spruce seedlings grown in 25–350A containers (IPL, Saint-Damien-de-Buckland, Quebec, Canada) were rejected during the autumn inspections of 2002, 2003, and 2004 because of insufficient height and/or root development. These black plastic containers (35 cm by 37 cm) have 25 square cavities; each with a volume of 350 cm³. Considerable attention has been devoted to developing standard soil substrates that enable seedling producers to control the availability of water and nutrients in the rhizosphere (Landis et al., 1989; Lemaire et al., 1989; Landis, 1990). Mixtures of peat and vermicu-

lite are common in northern nurseries for containerized seedling production (Landis, 1990), while forest nurseries in tropical and Mediterranean environments have now begun to use standardized compost materials (Miller and Jones, 1995; Lamhamedi et al., 2000a). In recent years, fertilization regimes have been improved to more closely match the nutritional needs of tree species to their stage of development (Landis et al., 1989; Girard et al., 2001; Salifu and Timmer, 2003). Despite these advances in substrate composition and fertility, rhizosphere water content and irrigation scheduling in forest nurseries are often based on random tactile or gravimetric tests. The substrate is often intentionally oversaturated to ensure that there are no “dry spots” (Lamhamedi et al., 2002, 2003; Bilderback, 2002). Without precise control, surplus irrigation can induce nutrient leaching from container cavities, thus increasing the risk of local groundwater contamination. Sprinkler-jet systems, which are commonly used for irrigation in forest nurseries, may also introduce considerable spatial variability in the amount of water applied to different parts of the nursery bed. This, in turn, may subsequently affect seedling growth (Juntunen et al., 2002; Lamhamedi et al., 2003).

A variety of indices have been devised to monitor irrigation uniformity of sprinkler systems. The Christiansen coefficient of uniformity (CUCs), one of the oldest and most widely accepted uniformity coefficients (CU) in use, was originally developed to describe water distribution from a single sprinkler head (Christiansen, 1942). Although it has been routinely used to assess the uniformity and efficiency of water delivery in irrigation systems, CUCs can only identify the presence or absence of spatial variability. To calculate the coefficient, a large array of measurements must be reduced to an average condition. The sum of the absolute deviations from the mean is scaled as an index ranging from 0 to 100%, where 100% is the most equitable delivery of water to each plant.

Geostatistical methods are based on the theory of regionalized variables (Matheron, 1963), and make explicit use of the spatial information content of a data set. The technique of kriging optimizes spatial distribution by predicting and interpolating values for neighboring nonsampled points. It has been successfully applied to several different fields of research (Trangmar et al., 1985; Robertson et al., 1988; Vieira, 1999; Taboada et al., 2002; Wallerman et al., 2002). However, to our knowledge, no studies have yet investigated the spatial variability of sprinkler irrigation in containerized seedling nurseries. There is also a lack of information on the effect that variability in rhizosphere moisture content has on subsequent seedling growth.

The objectives of this study were (i) to use geostatistical

M.S. Lamhamedi, L. Blais, and M. Renaud, Direction de la recherche forestière, Ministère des Ressources naturelles et de la Faune, 2700, rue Einstein, Sainte-Foy, QC, G1P 3W8, Canada; L. Labbé, H.A. Margolis, and D.C. Stowe, Faculté de foresterie et de géomatique, Pavillon Abitibi-Price, Université Laval, Sainte-Foy, QC, G1K 7P4, Canada. Received 5 Apr. 2005. *Corresponding author (mohammed.lamhamedi@mrnf.gouv.qc.ca).

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Abbreviations: CU, uniformity coefficient; CUCs, Christiansen coefficient of uniformity.

Table 1. Morphophysiological characteristics of air-slit containerized (25–350A) white spruce seedlings at the end of their first (1+0) and second (2+0) growing season, when they were grown under tunnel conditions and outside, respectively.

Variables	White spruce (1+0)		White spruce (2+0)	
	Shoot	Root	Shoot	Root
Height, cm	7.11 (0.22)†		29.7 (31.62)§	
Root collar diameter, mm	2.07 (201.54)		6.60 (21.19)	
Dry biomass, g	0.81 (17.45)	0.30 (94.28)	6.50 (52.24)	1.9 (52.57)
Tissue concentration, g kg ⁻¹				
N	22.67 (1.97)‡	23.20 (4.34)	30.28 (9.52)¶	ND#
P	3.00 (2.24)	3.49 (4.48)	3.22 (10.74)	ND
K	8.43 (8.49)	7.21 (7.44)	10.02 (11.51)	ND
Ca	1.97 (6.81)	1.89 (5.92)	2.81 (12.31)	ND
Mg	1.19 (3.76)	1.58 (15.57)	1.30 (17.74)	ND
Quantity of fertilizer applied, mg plant ⁻¹ ††				
N		78.01		398.85
P		28.88		177.79
K		48.74		265.64

† Average (% CV) of the fifty seedlings used to determine height, root collar diameter and dry biomass of white spruce seedlings (1+0).

‡ Average (% CV) of the five composite samples used to determine the concentration of mineral nutrients in white spruce seedlings (1+0), each composite sample was composed of ten seedlings.

§ Average (% CV) of 399 seedlings used to determine the height, root collar diameter and dry biomass of white spruce seedlings (2+0).

¶ Average (% CV) of 133 composite samples used to determine the concentration of mineral nutrients in white spruce seedlings (2+0), each composite sample was composed of three seedlings.

The mineral concentrations of the root tissue were not determined.

†† Compilation of the fertilizers applied during the white spruce seedlings' first two growing seasons (1+0) and (2+0).

tical analysis to evaluate the spatial heterogeneity of seedling growth and substrate water content generated by sprinkler irrigation; (ii) to determine the effects of substrate water content during the growing season on the leaching of mineral nutrients from containerized white spruce seedlings (2+0); and (iii) to define a sampling strategy, based on the results of the geostatistical analysis, which would facilitate more objective irrigation management and seedling quality evaluation.

MATERIALS AND METHODS

Production of Experimental Material

The study was conducted at Pampev Inc., a private forest nursery located in Saint-Louis-de-Blandford, Quebec, Canada (46°25' N lat., 72°00' W long.). Open pollinated white spruce seeds were obtained from a single seed orchard (WEV; Drummond, Quebec, Canada 45°59' N, 72°30' W). The seeds were sown into air-slit containers (IPL 25–350A, IPL, Saint-Damien-de-Buckland, Quebec, Canada) containing a peat/vermiculite growing medium (3/1, v/v; bulk density of 0.084 g cm⁻³) during the third week of May 2000. Substrate uniformity was closely monitored during potting and seeding. Once an hour (after filling 780–800 containers) a container was removed from the production line for verification of substrate density.

As is the practice in Quebec, the seedlings were cultivated under an unheated polyethylene tunnel during their first growing season (1+0 seedlings), and outside during their second year of growth (2+0 seedlings) (Margolis, 1987). While grown under the tunnel, the seedlings were irrigated and fertilized by a mobile boom system (Aquaboom, Industries Harnois, Saint-Thomas-de-Joliette, Quebec, Canada). In early November 2000, the seedling containers were moved out of the tunnel and placed directly on the ground surface, where they remained until the following spring. Seedlings exhibited little variability in morphological characteristics and foliar nutrient levels at the end of the first growing season (Table 1).

At the end of April 2001, the seedling containers were raised to a height of 12 cm above the ground to facilitate air circulation around the root plugs during the second growing season. An irrigation line containing nine sprinklers (model Vyr-35, VYRSA, Burgos, Spain) ran down the center of the nursery bed.

Each rotary sprinkler head had two nozzles and emitted a jet of water, with a theoretical diameter of action of 30.2 m, at a pressure of 344.7 kPa and a flow rate of 25.7 L min⁻¹. Fertilizers were applied with a Vicon agricultural sprayer (Model LS1910T, Cambridge, ON, Canada) equipped with a 1910-L reservoir and two eight-nozzle irrigation rails (Model SS6520, Spraying Systems Co., Wheaton, IL). The sprayer was pulled by a 45 kW (60 HP) tractor that advanced at a speed of 1.6 km h⁻¹. The fertilizer was released at a rate of 7.90 L min⁻¹ and a pressure of 300 kPa. Irrigation was scheduled in response to random evaluations of gravimetric substrate water content and seedling growth as is common practice in many forest seedling nurseries (Landis et al., 1989). The fertilization regime was adapted to the seedlings' phenological stage and relied heavily on the expertise of the seedling production manager to meet the established quality and growth standards for white spruce (2+0) planting stock. The quantities of the different mineral elements applied during the second growing season are listed in Table 1.

Experimental Layout

The experimental layout, covering the irrigation pattern of two adjacent sprinklers and encompassing an area of about 248 m², was installed on 10 May 2001. The sampling area was situated in the middle of a nursery bed and was contiguous to the rest of the crop on its northern and southern boundary. The eastern and western edges of the experimental area were separated from the adjacent seedling beds by narrow alleys. The experimental design consisted of 1820 containers (26 containers wide × 70 containers long) (Fig. 1). A distance of 12.6 m separated adjacent irrigation lines and sprinklers on the same line were placed 12.0 m apart, permitting the sprinklers to cover 57.6 and 59.6% of their diameters of action, respectively. At this sprinkler spacing, the CU specified by the sprinkler manufacturer is 89% (VYRSA, 2005). Before beginning the present study, the new sprinkler heads were installed. They were adjusted and aligned to optimize the pressure (50 psi/345 KPa) and water distribution.

Monitoring Rhizosphere Water Content

Substrate water content in the rhizosphere was measured by time domain reflectometry (TDR) using a portable moisture

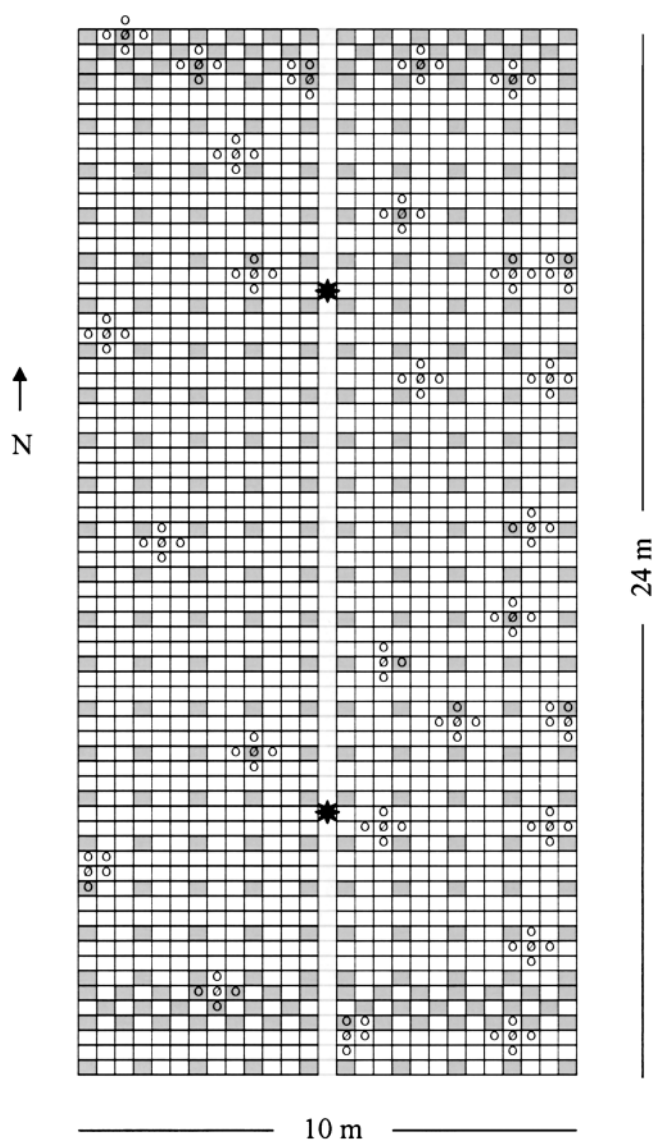


Fig. 1. Schematic of the experimental layout covering the area irrigated by two adjacent sprinklers and a total of 1820 air-slit containers (25–350A). *: Sprinklers □: Air-slit containers that were not sampled ■: Air-slit containers (25–350A) that were sampled. Substrate moisture content was monitored by inserting double diode probes through the five central cavities of the container. The height and root collar diameter of the seedlings growing in these cavities were also measured on each of the sampling days. ○ and ○: Containers that were sampled at the end of the growing season (27 Sept. 2001) for measurement of root and shoot dry mass and nutrient content analyses (3 plants/container). Ø: Containers that were sampled to quantify the amount of leachate.

monitoring system (MP-917, Environmental Sensors Inc, Victoria, BC, Canada) equipped with a double-diode probe. Each probe consisted of two parallel stainless steel waveguides (3.17 mm diam., 407 mm long, spaced 10 mm apart), which were inserted through the middle of the root plugs in the five central cavities of the container. These probes were designed specifically for use with air-slit containers (Lamhamedi et al., 2000c, 2001, 2002, 2003; Stowe et al., 2001). The measured substrate water content represented the average volumetric water content in the five central cavities in each of the sampled containers (five rows of five cavities/container). The calibration parameters, necessary to convert the TDR signal to volumetric water content ($\text{cm}^3 \text{H}_2\text{O cm}^{-3}$ substrate) in 3/1 peat/

vermiculite growing medium, were developed for the MP-917 by Lambany et al. (1996, 1997).

Five sampling dates were chosen to illustrate the degree of spatial variability in substrate moisture content over the growing season: June 12, several hours after a short period of irrigation; June 27, immediately following an irrigation session; July 11, after a week of cloudy and rainy weather; August 11, after irrigation and 10 Sept. 2001, after a long period of dry weather and no irrigation. Three hundred and thirty-six containers (18.5% of the total number of containers in the experimental area) were systematically sampled on the first sampling date (June 12). At this time, every third row (24 rows in total) was selected, and every second container was sampled in each of these rows (14 of 26 containers per row). Geostatistical analysis of the data from the first sampling date permitted us to quantify the spatial variability of the substrate water contents in the containers and decrease the sampling intensity to 16.5% of the experimental area, or 300 containers (i.e., every fourth row, and every third container per row) for the subsequent sampling dates (June 27, July 11, August 11, and September 10). To obtain a precise estimate of the variance between two closely spaced samples, every second container was sampled in the three rows located at both ends of the experimental area (Fig. 1).

The CUCs of rhizosphere water content was calculated to account for the combined effects of sprinklers, microclimate variability, shoot architecture and substrate physical properties on the spatial distribution of substrate moisture. The coefficient was calculated as follows:

$$\text{CUCs} = 100 \left(1.0 - \frac{\sum_{i=1}^n |\theta - \theta_i|}{\sum_{i=1}^n \theta_i} \right)$$

where θ is the average volumetric water content of the substrate at each sampling date; θ_i is the volumetric water content of each sampling point (container); and n is the number of sampling points, which varied from 294 to 335.

Seedling Growth and Nutritional Status

For each sampling date, seedling height and substrate water content were measured simultaneously. The height and diameter of the five (2+0) seedlings in the cavities through which the MP-917 probes were inserted were measured, for a total of 995–1680 seedlings per date. The average height and root collar diameter of the five seedlings in each container were used for geostatistical analyses.

Seedlings were destructively sampled near the end of the growing season (27 Sept. 2001), for determination of root collar diameter, shoot height and oven-dry mass of shoot, and root tissues. The sample grid was stratified into two groups, as a function of average seasonal moisture content and geostatistical analyses of data collected during the preliminary intensive sampling (June 12). Substrate moisture classes were selected in accordance with morphophysiological responses of white spruce seedlings during their first growing season (Lamhamedi et al., 2000c, 2001) and from the observations we made in the current study regarding the variations in substrate water content in the rhizosphere of the (2+0) seedlings. Twenty-seven seedling containers were randomly selected from the two strata. Thirteen containers had average seasonal substrate water contents between 25 and 38% (v/v), while the remaining 14 containers averaged between 38 and 45% (v/v). The four containers adjacent to each of the previously mentioned 27

containers were also sampled, for a total of 133 containers (Fig. 1). Three seedlings were randomly selected from each container for morphological measurements (height, diameter). The seedlings were then oven-dried (65°C for 48 h), weighed, and composited for nutrient analysis.

Fertilization

To verify the homogeneity of the distribution of fertilizer solution intercepted by the seedling canopy, we systematically arranged 108 cups over the experimental area (Li and Rao, 2000). The quantity and nutrient concentration of the solution falling into each cup was determined and geostatistical analysis was performed on the data to verify the pattern of fertilizer distribution.

Leaching

The volume and nutrient concentration (NH_4^+ , NO_3^- , H_2PO_4^- , K^+ , Ca^{2+} , Mg^{2+}) of the solution leached from the 27 randomly selected containers (Fig. 1) were measured on 7 Aug. 2001. The containers were chosen to be representative of the spatial variability of substrate water content observed during the preliminarily sampling on 12 June 2001. The leachate was captured in plastic containers that had been placed under the airslit containers before a routine fertilization session (Gagnon and Girard, 2001; Lamhamedi et al., 2001). The leachate volume and the water content of the substrate in each of the sampled containers were measured simultaneously. The mineral nutrient concentration of the leachate solution was analyzed according to the procedure described in Lamhamedi et al. (2001).

Microclimate

A meteorological station was installed approximately 15 m south of the experimental area to measure air temperature, relative humidity (HMP-35C probe, Campbell Scientific, Edmonton, AB, Canada), and precipitation (Rain gauge model TE525M, Texas Instruments, Dallas, TX). A second rain gauge was installed near the center of the experimental area to monitor the total quantity of water received by the plants (precipitation and irrigation). Temperatures at the substrate surface and within the rhizosphere were monitored by temperature probes (Model 107B, Campbell Scientific, Edmonton, AB, Canada) placed in a single seedling container near the center of the seedling bed. Environmental data were recorded with a data logger (CR10X, Campbell Scientific, Edmonton, AB, Canada).

Statistical Analyses

The distribution and extent of spatial heterogeneity of substrate water contents and growth variables (height and root collar diameter) of white spruce (2+0) seedlings were quantified with geostatistical analysis. Geostatistical methods are used to estimate the degree of autocorrelation between variables measured at each sampling point. Values for locations between the measured points were interpolated and mapped using kriging (Vieira et al., 1983; Trangmar et al., 1985). Interpolation was performed using semi-variance estimates (γ), which are described by following equation:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_{i+h})]^2$$

where $N(h)$ is the number of paired observations $[z(x_i), z(x_{i+h})]$ separated by a lag distance h . Empirical semi-variograms of substrate water content, seedling height and root collar diame-

ter were adjusted for each of the sampling dates. Plots of semi-variance versus increasing lag distance were fitted to three types of theoretical models: exponential, spherical, and Gaussian. The exponential model is defined as:

$$\gamma(h) = C_0 + C_1 \left[1 - e^{-\frac{h}{a}} \right]$$

The spherical model is defined as:

$$\gamma(h) = \begin{cases} C_0 + (C_1 - C_0) \left[1.5 \frac{h}{a} - 0.5 \left(\frac{h}{a} \right)^3 \right] & \text{if } 0 < h < a \\ C_1 & \text{if } h \geq a \end{cases}$$

and the Gaussian model is defined as:

$$\gamma(h) = C_0 + C_1 \left\{ 1 - e^{-\left[\frac{3(h/a)^2}{a} \right]} \right\}$$

where $C_0 + C_1$ corresponds to the sill; h is the distance separating points; and a is the range. The sill, or total semi-variance ($C_0 + C_1$), the nugget effect (C_0), and the range (a) were estimated from each semi-variogram. The strength of spatial dependency in the semi-variance or covariance estimates (C_1) can be defined by the range, that is, the maximum radius within which points are spatially autocorrelated and the sample points are dependent. The degree of spatial dependency usually is expressed in terms of the ratio $C_1/(C_0 + C_1)$. At distances greater than the range, the semi-variance plateaus at a value equal to the sample variance (s^2), thus implying spatial independence (Trangmar et al., 1985). The nugget effect represents the unexplained or random variability, which usually can be attributed to measurement error or to variability below the scale of sampling. The selection of the best model that fit the data was based on cross-validation of the predicted and observed values. The geostatistical approach that was used in the present study is described in greater detail by Royle et al. (1980) and Isaaks and Srivastava (1989).

Modeling and preparation of the semi-variograms was performed using VARIOWIN v.2.2 (Pannatier, 1996), while ordinary kriging, cross-validation and mapping were done with both GS+ version 5.3a (Gamma Design Software 2002, Plainwell, MI) and VARIOWIN v.2.2. Unlike GS+, VARIOWIN corrects the variance at each distance h by weighting each estimate by the number of paired points that are used. This adjustment minimizes the importance of low variances resulting from a small number of paired points.

The integral of the substrate water content during the growing season (θI) ($\text{cm}^3 \text{ water cm}^{-3} \text{ substrate} \times \text{day}$) was calculated for each of the 294 containers using the data collected on June 27, July 11, August 11, and September 10. This integral was calculated as:

$$\theta I = \sum_{i=1}^{i=n} \frac{\theta_i + \theta_{i+1}}{2} (t_{i+1} - t_i)$$

where θ_i is the substrate water content in the rhizosphere on sampling date t_i . The integral of substrate water content represents the area under the curve of the variations in measured substrate water content over the entire sampling period. This approach has been proven to be an effective tool in seedling physiology research (Grossnickle and Major, 1994; Myers, 1988).

To determine the number of samples (n) required for an accurate estimate of substrate water content in the experimental area, or the number of seedlings (n) that should be sampled to assess plant quality, we used the total sample variance ($C_0 + C_1$) for each of the variables, as determined from their respective semi-variograms. Sample points with a variance ($C_0 + C_1$) were

spaced at an interval greater than the range and were therefore independent and randomly distributed. The number of samples (n) that were needed was determined using the following formula:

$$n = \frac{t_{1-\alpha/2}^2 s^2}{d_r^2}$$

where $t_{1-\alpha/2}$ represents the critical value of t from the Student distribution associated with a 95% confidence interval and $(n - 1)$ degrees of freedom; s^2 is the total sample variance when there is independence among samples and d_r^2 is the relative acceptable error, which was fixed at $\pm 5\%$.

RESULTS

Microclimate

During the period of shoot growth (June to September 2001), the maximum daily air temperatures, 2 m above the ground, at the substrate surface and in the rhizosphere were 33.9, 37.3 and 25.3°C, respectively; while minimum daily temperatures were -1.5 , -1.4 , and 0.9°C , respectively (Fig. 2a-c). For the same period, average daily relative humidity varied between 63 and 99% (Fig. 2d).

Cumulative amounts of precipitation and irrigation, registered by rain gauges between June and September 2001, were 410.8 and 265.2 mm, respectively (Fig. 3). Sprinkler irrigation represented almost 40% of the total water (676 mm) received by the seedlings. In general, more irrigation water was applied to the seedlings at the beginning of the growing season (June and July, 177.5 mm) than at the end of the growing season (August and September, 87.7 mm). However, there was more precipitation during the second half of the growing season (June-July: 185 mm; August-September: 225.8 mm). The amount of irrigation water applied to the crop in a given sampling interval varied between 17.9 and 106.6 mm, while the amount of precipitation varied between 47.6 and 147.7 mm (Fig. 3).

Spatial Variability of Substrate Water Content and Uniformity Coefficient

Both the spherical and exponential models of the omnidirectional semi-variograms for substrate water content showed the presence of spatial structure for each of the sampling dates (Fig. 4). As shown by the nugget (C_0) and sill ($C_0 + C_1$) semi-variances, this spatial structure changed over the course of the growing season. The highest total sample variances ($C_0 + C_1$) were observed for July 11 and August 11. The degree of spatial dependence in substrate water content, as indicated by the range, also fluctuated over time (Fig. 4). The greatest values for the range were observed on June 27 (9.02 m) and July 11 (10.78 m). On the other sampling dates (June 12, August 11, and September 10), the range varied between 3.52 and 3.99 m. The percentage of the total variance attributed to spatial structure [$C_1/(C_0 + C_1)$] varied between 63% (June 12) and 79% (June 27) for the different models. On the last sampling date, a substantial decrease was observed in

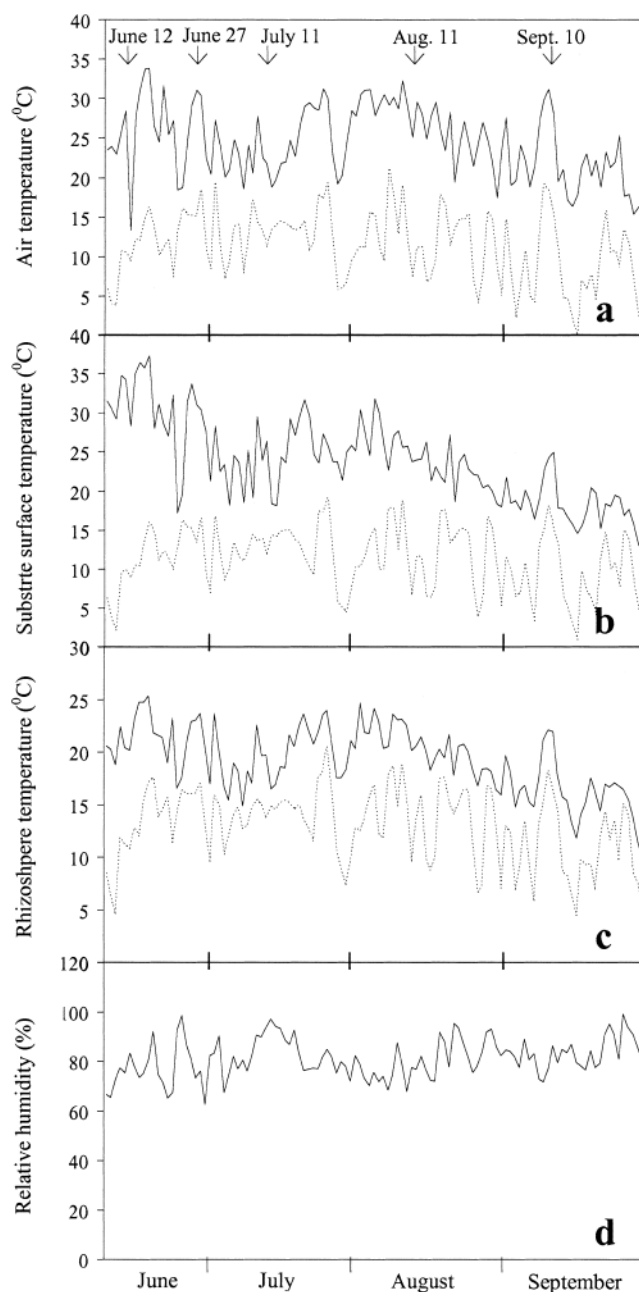


Fig. 2. Variation (a) of maximum and minimum daily air temperatures 2 m above the ground, (b) at the substrate surface and (c) in the rhizosphere, as well as the fluctuations in (d) relative humidity during the second growing season of air-slit containerized white spruce seedlings at Pampev Inc., a private forest nursery located in Saint-Louis-de-Blandford, QC, Canada ($46^\circ 25' \text{ N}$, $72^\circ 00' \text{ W}$).

the total variance of the substrate water content, spatial dependence ratio, and range (Fig. 4).

The observed cross-validation values (R^2) for substrate water content confirm the strength (robustness) of the adjusted models (Fig. 4). Using the measured substrate water content values of the sampled points, kriging can be used to predict and map values of neighboring non-sampled points (Fig. 5). From one sampling date to another the distribution of zones of similar substrate water content was extremely variable (Fig. 5). For example, the distribution appears to be less uniform on August 11

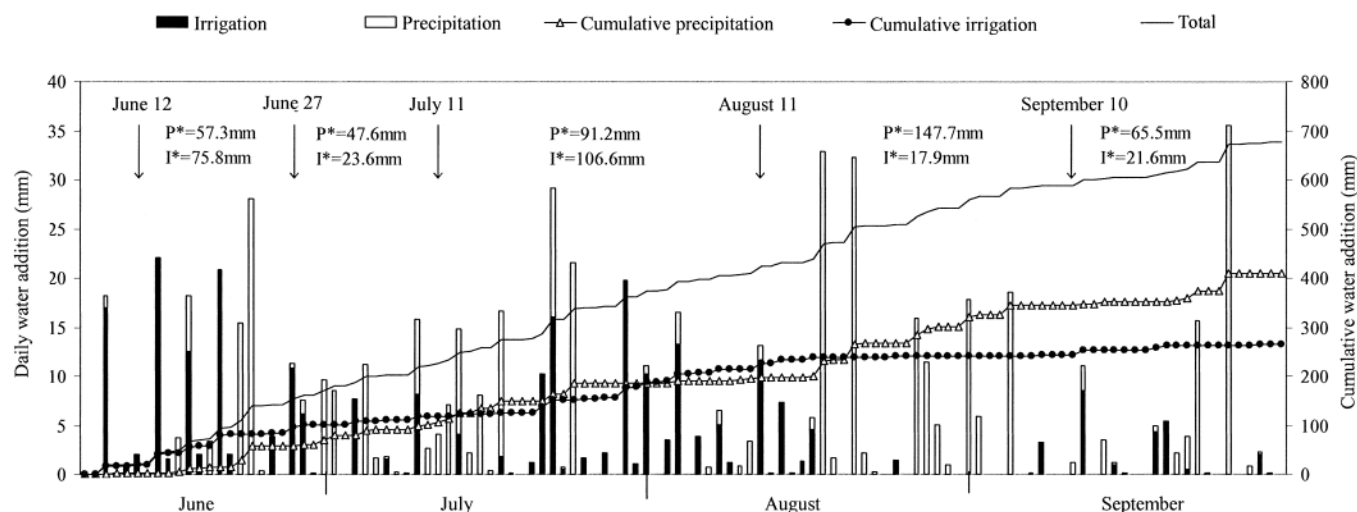


Fig. 3. Daily and cumulative quantities of water received by the (2+0) white spruce seedlings in the form of precipitation (P) and irrigation (I). The arrows indicate the different sampling dates on which the substrate water content, seedling height and root collar diameter were measured. P* and I* indicate the total quantities of water received between two consecutive sampling dates, as precipitation and irrigation, respectively.

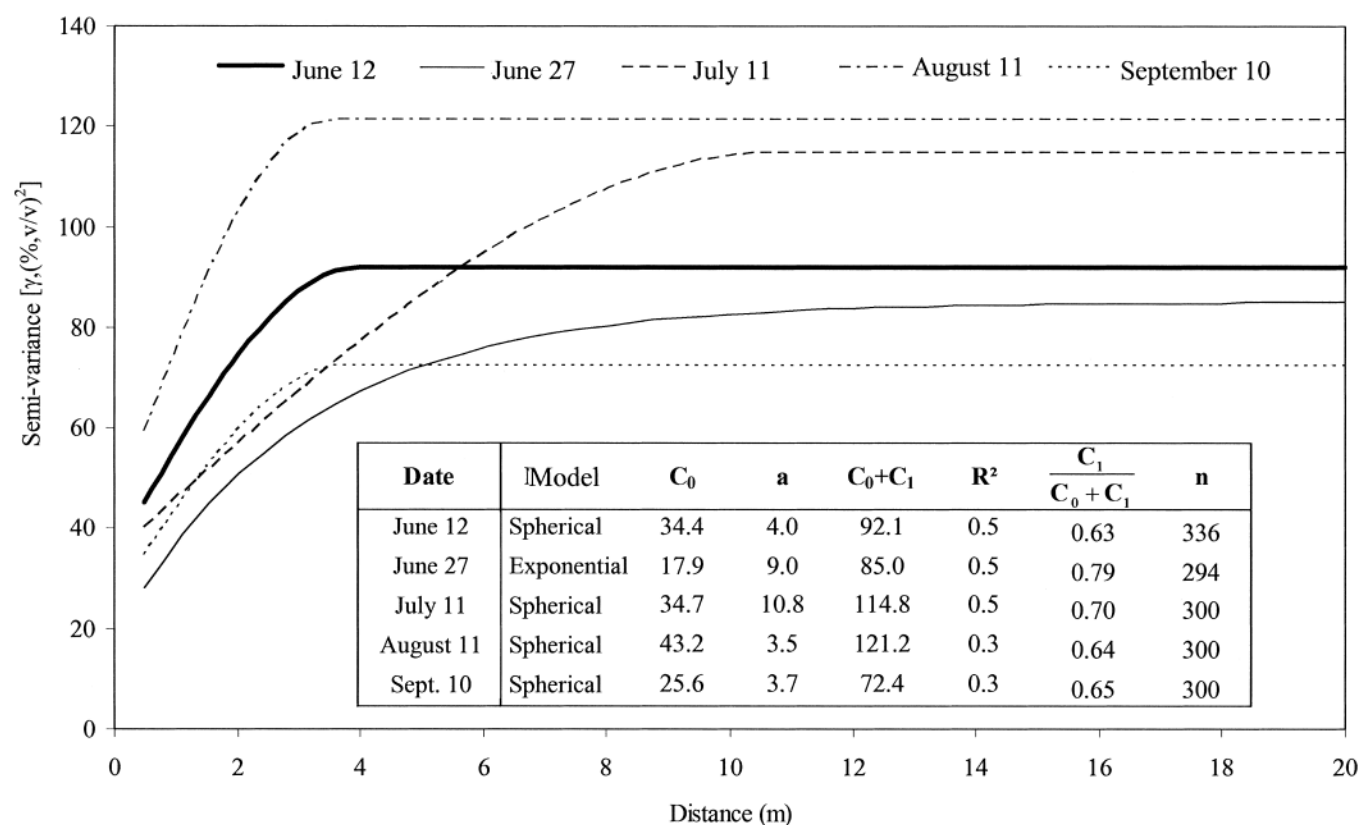


Fig. 4. Omnidirectional semi-variograms of the substrate water content in the rhizosphere of the (2+0) white spruce seedlings. The table includes the estimated theoretical model parameters for each of the sampling days (a : range; C_0 : nugget effect; $C_0 + C_1$: total variance; R^2 : cross-validation; $C_1/(C_0 + C_1)$: spatial dependence; n : number of containers sampled). For each container sampled, the data represent the average substrate water content in the five central cavities through which the MP-917 probes were inserted.

and September 10 (short range, low spatial dependence). This is reflected in a more scattered distribution of substrate water contents within the experimental area (Fig. 5d, e). These variations in substrate water contents are important, given the quantity of water received by the seedlings, in the form of precipitation and irrigation, before each sampling date (Fig. 3). For a given sampling date, there was also a large variation in substrate water content from one

region of the experimental area to another (17–53% v/v on August 11 and 7–41% v/v on September 10). Substrate humidity is influenced by microenvironmental factors such as air temperature, precipitation, humidity, wind, and radiation. Seedlings along the western border of the experimental area were more exposed to dominant winds and less sheltered from incoming solar heating of their black plastic containers. Consequently, these

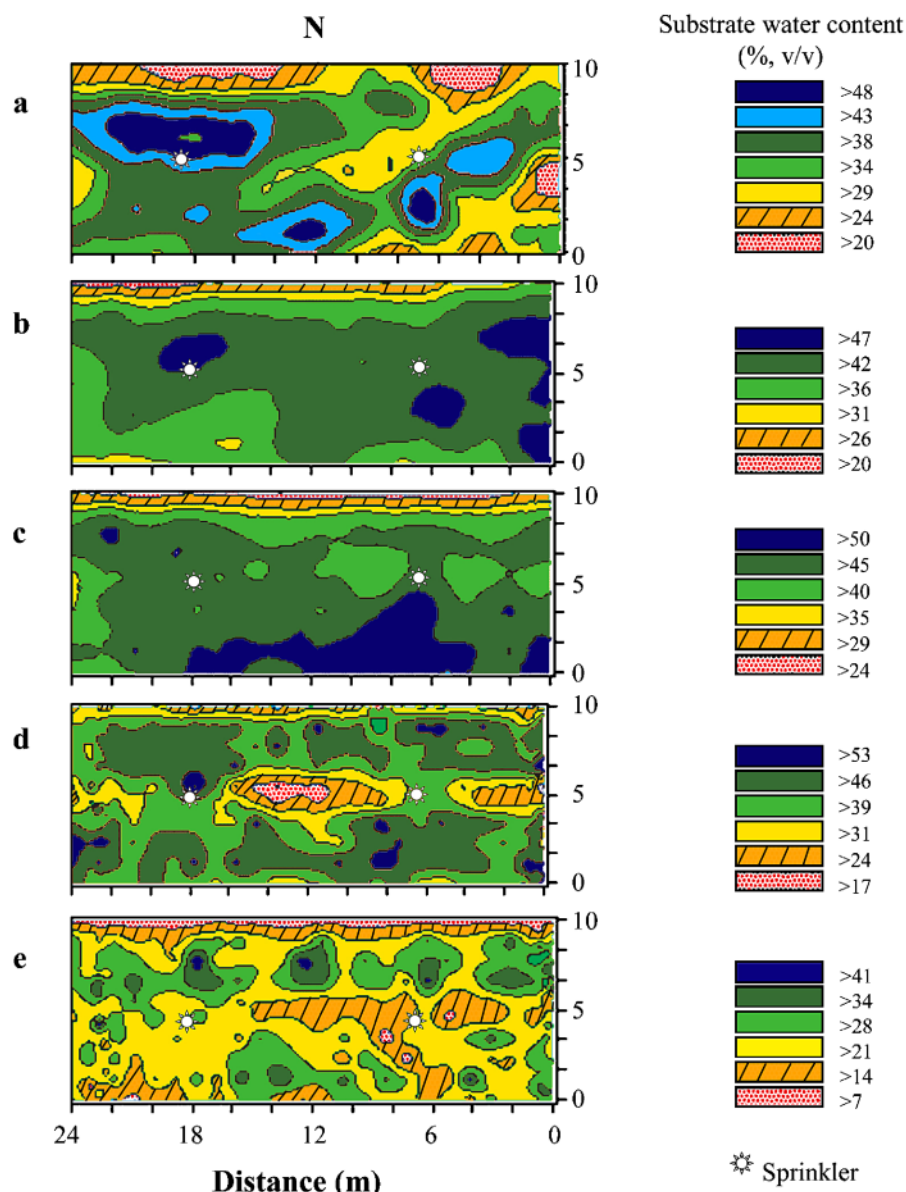


Fig. 5. Mapped representations of the substrate water contents. The interpolated values were determined for each of the sampling dates by kriging: (a) June 12, (b) June 27, (c) July 11, (d) August 11 and (e) 10 Sept. 2001.

plants exhibited low substrate water contents throughout the growing season (Fig. 5).

Substrate water content spatial variability was confirmed through calculation of the rhizosphere CUCs. The CUCs values of the sprinkler-irrigated crop were 79, 84, 84, 78, and 73% for June 12, June 27, July 11, August 11, and September 10, respectively. Increasing uniformity of substrate water content, as indicated by higher CUCs values, reflects more spatial dependence in the data. This dependence is estimated by α , the range, (Spearman's rank correlation: $r_s = 0.90$, $p < 0.05$, $n = 5$).

The Relationship between Growth and Substrate Water Content

Height growth of white spruce seedlings displayed increasing spatial dependence as the growing season progressed. The total variance ($C_0 + C_1$) of the theoretical

geostatistical models increased from 6 to 23 cm^2 between the first and final sampling dates, respectively (Fig. 6). The percentage of variance attributed to the spatial structure [$C_1/(C_0 + C_1)$] varied from 38 to 56%, while R^2 cross-validation values varied from 21 to 30%. The range remained relatively constant (3.4–3.6 m) throughout the growing season, with the exception of the July 11 sampling date, when the range was relatively low (2.0 m).

Diameter growth showed spatial variability on July 11 sampling. This variability fit an exponential model, with a range of 7 m and a total variability ($C_0 + C_1$) of 0.53 mm^2 (Fig. 7). Forty percent of the variance was explained by the spatial structure [$C_1/(C_0 + C_1)$].

The omnidirectional semi-variogram for the water content integral was best described by an exponential model ($C_0 = 13.90$, $C_0 + C = 46.30$, $a = 3.58$ and $n = 294$) with a cross validation value $R^2 = 0.47$ (Fig. 8a,

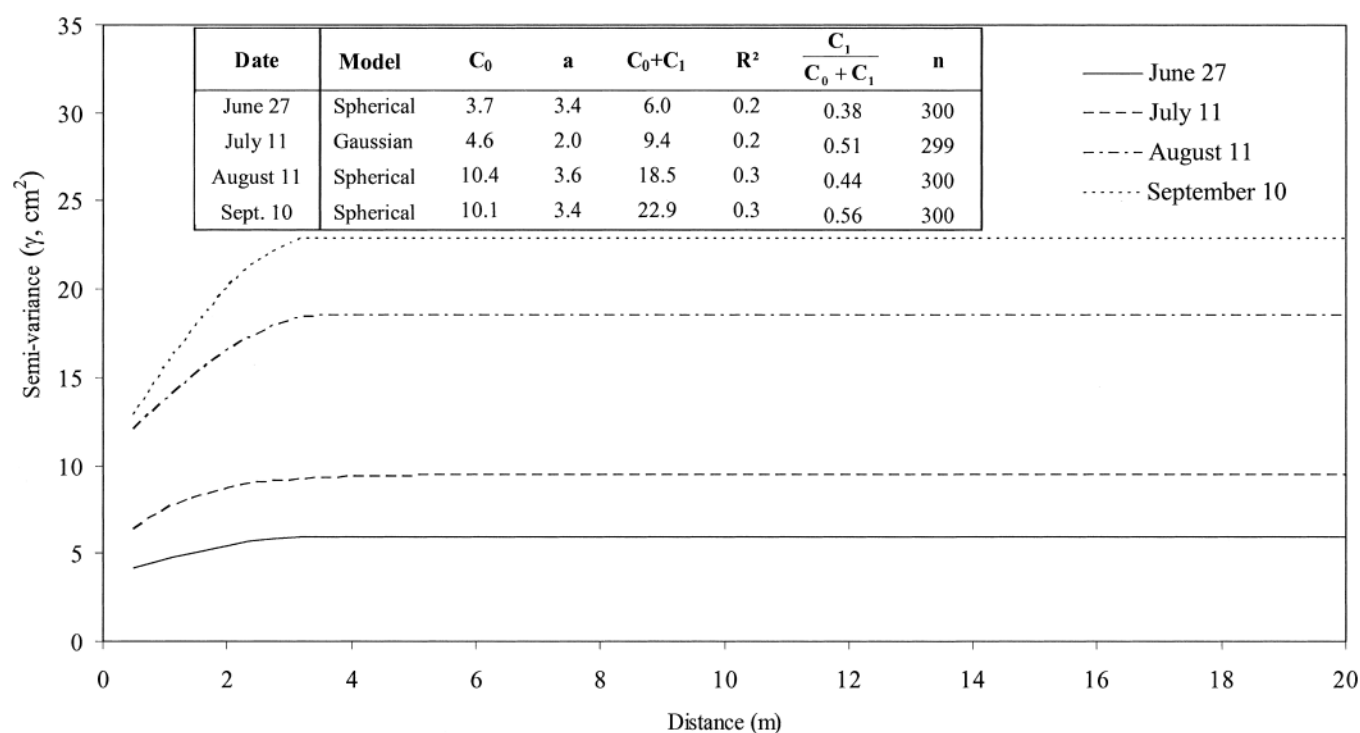


Fig. 6. Omnidirectional semi-variograms of the height of the (2+0) white spruce seedlings. The table indicates the estimated theoretical model parameters for each of the sampling days (a : range; C_0 : nugget effect; $C_0 + C_1$: total variance; R^2 : cross-validation; $C_1/(C_0 + C_1)$: spatial dependence; n : number of containers sampled). For each container sampled, the data represent the average height of the seedlings in the five central cavities through which the MP-917 probes were inserted.

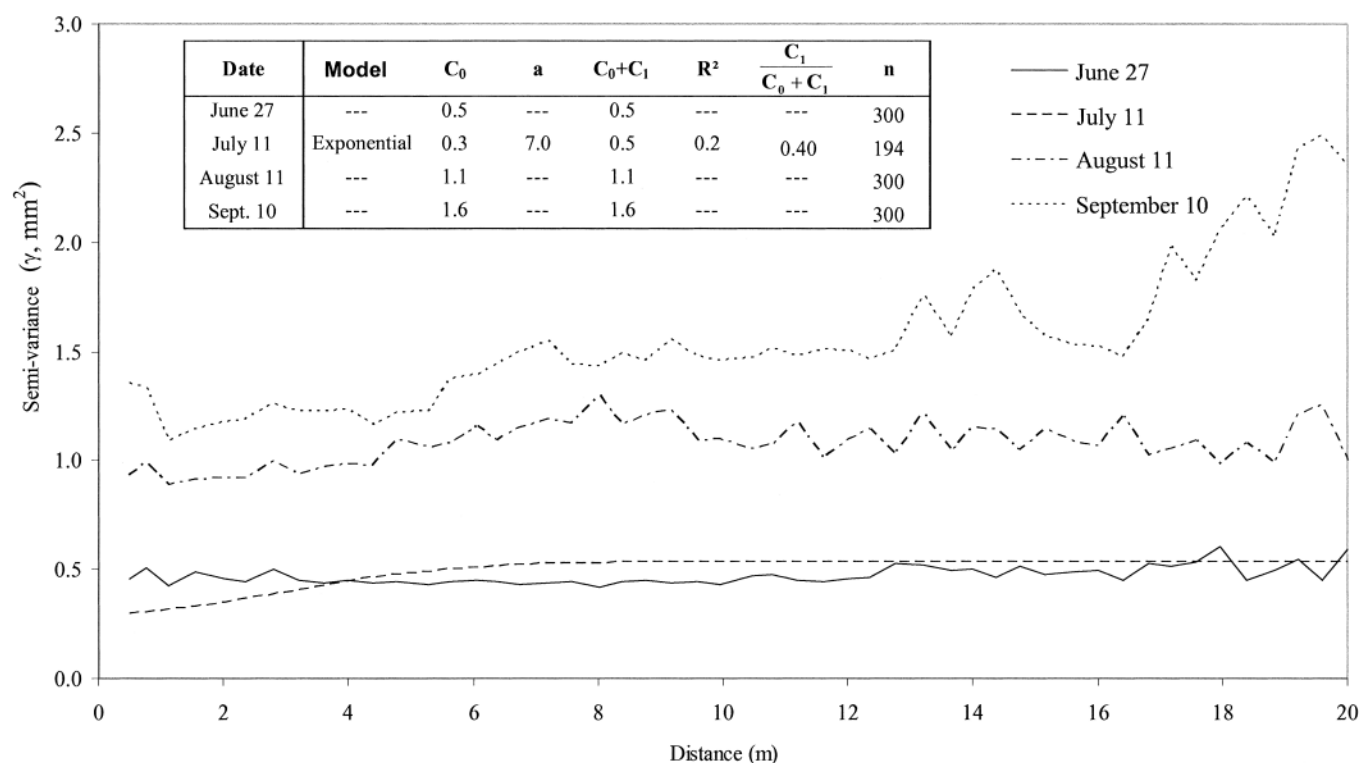


Fig. 7. Omnidirectional semi-variograms of the root collar diameter of the (2+0) white spruce seedlings. The table indicates the estimated theoretical model parameters for each of the sampling days (a : range; C_0 : nugget effect; $C_0 + C_1$: total variance; R^2 : cross-validation; $C_1/(C_0 + C_1)$: spatial dependence; n : number of containers sampled). For each container sampled, the data represent the average root collar diameter of the seedlings in the five central cavities through which the MP-917 probes were inserted.

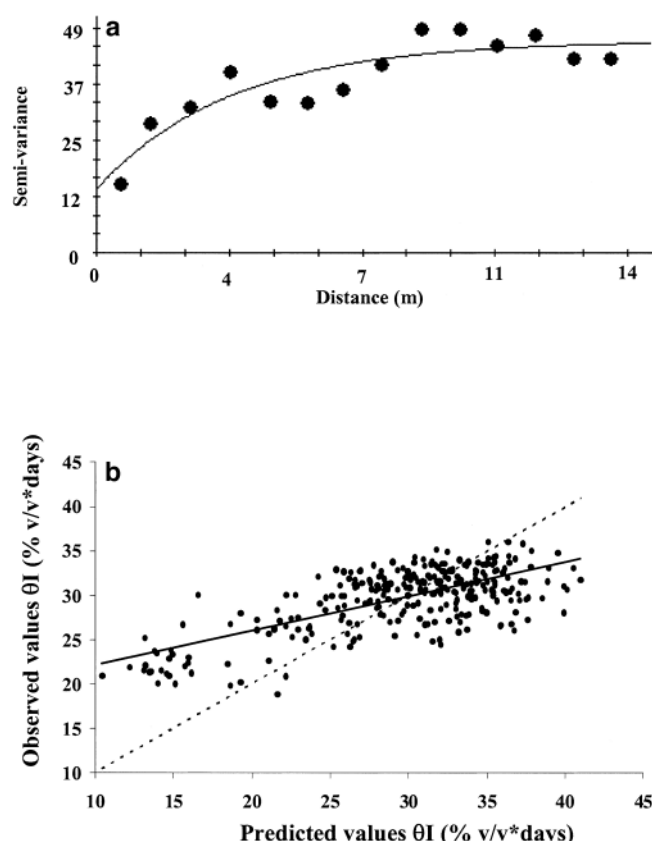


Fig. 8. Omnidirectional semi-variogram of (a) substrate water content integral fitted to the exponential model ($C_0 = 13.90$, $C_0 + C_1 = 46.30$, $a = 3.58$, $R^2 = 0.80$), as well as (b) its cross-validation between the observed and predicted values.

b). In contrast to a theoretical model, the observed semi-variogram revealed a periodic pattern in the total variance. This was due to the sprinkler spacing. The overlap in the water distribution by the sprinklers (3–4 m) is reflected in the repeated undulating pattern (4–5 m) of the sill of the semi-variance curve (Fig. 8a). This periodicity was observed in the water content semi-variograms for different sampling dates (results not shown). The regions of the experimental area that had lower substrate water contents during the growing season were generally associated with poorer height growth (Fig. 9a, b).

Fertilizer Solution, Leaching, and Electric Conductivity

Geostatistical analysis confirmed that the fertilizer solution was uniformly distributed by the agricultural sprayer. The volume of solution leached from an individual seedling container was positively correlated to the water content of the substrate in the container (θ) by the following relationship: Volume of leachate (mL) = $11.902\theta - 424.31$, $r^2 = 0.38$, ($P < 0.001$). At substrate water contents above 55% (v/v) leaching was more pronounced, but quantities were more difficult to predict. The quantity of leachate varied from 3 to 765 mL for containers with substrate water contents of 28.3 and 61.4% (v/v), respectively. Leaching of different mineral nutrients (N: NH_4^+ and NO_3^- , P, K, Ca, and Mg) followed the

Table 2. The optimal number of containers that should be sampled in the region between two consecutive sprinklers to determine substrate water content and seedling height.

Date	Variance	Optimal number of samples†
Substrate water contents		
June 12	92.07% ²	14
June 27	85.02% ²	12
July 11	114.84% ²	15
August 11	121.20% ²	19
September 10	72.42% ²	11
Seedling height		
June 27	5.96 cm ²	1
July 11	9.37 cm ²	1
August 11	18.54 cm ²	3
September 10	22.88 cm ²	4

† The optimal number of samples was calculated with a 95% confidence level, $\alpha = 5\%$.

relationship: Mineral quantity (g) = $ae^{b\theta}$, increasing exponentially with substrate water content (θ : %, v/v). Coefficients of determination and probability values for nutrients in the leachate varied from 0.20 to 0.30 and from 0.01 to 0.05, respectively.

An evaluation of the electrical conductivity of the substrate collected on 27 Sept. 2001, near the end of the growing season, indicated that mean substrate salinity, regardless of substrate water content class, was $193 \mu\text{S cm}^{-1}$, with a coefficient of variation of 28.8%.

Optimal Number of Sampling Points

To enable nursery personnel to assess the substrate water content variability and facilitate irrigation decision making, 11 to 19 containers should be sampled in the region between two consecutive sprinklers. Depending on the extent of spatial heterogeneity, one to four containers should be sampled to properly evaluate seedling height growth (Table 2).

DISCUSSION

Spatial Variability of Substrate Water Content, Seedling Growth, and Uniformity of Water Distribution

Geostatistical analyses demonstrated the presence of spatial variability in substrate water content and height growth of sprinkler-irrigated white spruce seedlings during their second growing season in a forest nursery. The size and distribution of the homogenous zones of similar substrate water contents varied from one sampling date to another (Fig. 5). Using time domain reflectometry, and geostatistical analysis, Long et al. (2002) illustrated the presence of extensive spatial variability in the water content of the soil in a wheat field. This variability results from the heterogeneity of water dispersion by sprinklers (Beeson and Knox, 1991; Ascough and Kiker, 2002) and is influenced by the microclimate in which the plants are grown, most notably wind, water pressure, temperature, and relative humidity. The quality of the irrigation equipment used and the manner in which it is employed (Landis et al., 1989; Fare et al., 1992) are important as well. Under forest nursery conditions, variations in substrate water content can be caused by differences in evapo-

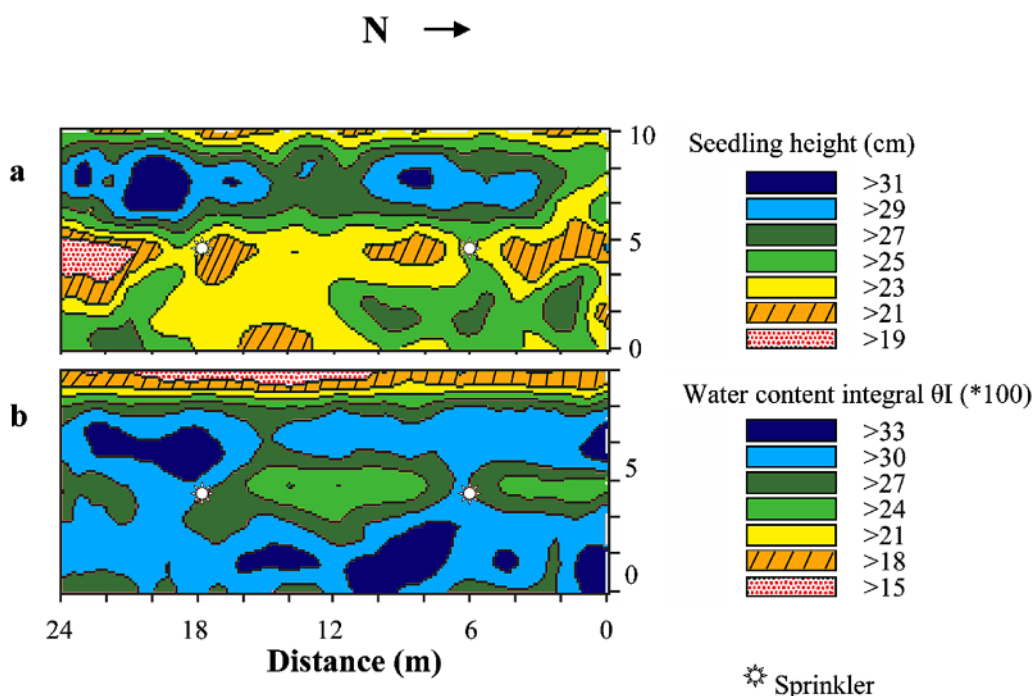


Fig. 9. Kriged maps of (a) the height of the (2+0) white spruce seedlings on 10 Sept. 2001 (spherical model) and (b) substrate water content integral (θI) (omnidirectional model).

transpiration and the interception of water droplets by foliage. These characteristics are governed by the genotype of each seedling, including its shoot architecture (orientation and number of branches, branching angle, needle length, and leaf area) and have been shown to be especially variable in white spruce (Lamhamed et al., 2000b).

For certain sampling dates, we found very pronounced variations in substrate water content across the experimental area (Fig. 5, 6). Spatial variability of growth and nutritional status of white spruce seedlings may be due to the sensitivity of white spruce to low substrate water contents (Lamhamed et al., 2001, 2002; Stowe et al., 2001). Shoot and root growth of tunnel-grown white spruce seedlings are known to be negatively affected by the prolonged maintenance of a low (15% v/v) substrate water content (Lamhamed et al., 2001) during the first growing season. Other research in Quebec forest nurseries has suggested that the substrate water content of containerized white spruce seedlings should be maintained at 40% during the active growing phase and 25% during the hardening phase during the second growing season (Labbé 2004). In a more extensive report of the present study (Labbé 2004), boundary line analysis (Chambers et al., 1985) was used to demonstrate that maximum height growth and seedling biomass were attained when the integral of variation in substrate water content for the 2001 growing season was approximately $3000 \text{ cm}^3 \text{ water} \times \text{cm}^{-3} \text{ substrate} \times \text{day}$. This corresponds to an average seasonal substrate water content of >40% (v/v).

We found that height growth of the seedlings grown outside, under unsheltered conditions, was not linearly correlated to substrate water content. This indicates that growth was related to interactions of several factors such

as plant genotype, shoot architecture, substrate fertility, and substrate water content. The gradual increase in total variance ($C_0 + C_1$) of seedling height from one sampling date to another (Fig. 6) indicates that the heterogeneity of height growth of (2+0) white spruce seedlings was intimately linked to extreme fluctuations in substrate water content over the course of the growing season.

The use of a mechanized boom provides homogenous irrigation and fertilization regimes ($\text{CU} > 95\%$) during the seedlings' first year of growth under tunnel conditions and is likely responsible for the low spatial heterogeneity and total variance in height growth in (1+0) seedlings. Unfortunately, the high maintenance and infrastructure costs associated with the operation of boom-irrigation systems outdoors in northern climates is prohibitive for private forest nurseries, which function with extremely low profit margins. Unsheltered seedling production outdoors during their second growing season exposes the plants to precipitation, wind, and temperature variations. These elements amplify spatial variability of sprinkler water distribution and substrate water content in the experimental area, which, in turn, leads to heterogeneous seedling height growth. Factors other than substrate water content may also contribute to this heterogeneity of growth in spruce seedlings. Studies have detected an early variability in root and shoot architecture of spruce seedlings and the efficiency with which they utilize mineral nutrients and allocate photosynthetic products between root and shoot tissues (Grossnickle, 2000; Lamhamed et al., 2000b, 2001).

The presence of a spatial structure for root collar diameter growth was only evident on July 11 (Fig. 7), which coincides with the beginning of the diameter growth phase of nursery-grown conifer seedlings (Mexal and Landis,

1990; Landis et al., 1999). However, the large range (7 m) and small spatial dependence ratio (0.4) suggests a relative homogeneity of seedling root collar diameter and a spatial dependence that is shorter than the range.

The observed CUCs values, which ranged from 73 to 84%, were lower than the values specified by the manufacturer (89%) for 12 m $\times$ 12 m sprinkler spacing under optimal conditions (VYRSA, 2005). Environmental conditions (wind, temperature), and the interception of water droplets by the seedling canopy affect the amount of water reaching the substrate surface. Movement of water from the surface through the rhizosphere, where measurements of substrate moisture are made, may also be affected by the hydrophobic nature of the peat growing medium if the water content of the substrate is low.

Rhizospheric Conditions and Nutrient Leaching

Variations in substrate water content can affect not only leaching and substrate fertility, but also the absorption capacity and initiation of new white roots and the efficiency with which individual seedlings use mineral nutrients (Lamhamedi et al., 2003). Despite the absence of spatial variability in the distribution of fertilizer solution, Labbé (2004) showed that the nutritional status of the seedlings for any given mineral (N, P, K, Ca, Mg) at the end of the second growing season is related to seasonal variations of substrate water content. Morvant et al. (1997) found that the choice of irrigation system has an effect on root distribution, the accumulation of soluble salts and N, and substrate pH.

In dry areas, where substrate water contents are low (7–25%, v/v), the wettability of peat/vermiculite substrate (3/1, v/v) is very slow due to the hydrophobic properties of the material (Bernier and Gonzalez, 1995; Heiskanen, 1999). This could result in heterogeneity of substrate water content among cavities in the same seedling container. Relatively prolonged episodes of drought may increase the proportion of lignified roots (Pallardy et al., 1995), thus negatively affecting the absorption capacity and viability of the root system as well as the resistance to water flow at the root-soil interface (Faiz and Weatherley, 1982; Passioura, 1988; Lamhamedi et al., 1992). Compared with other growing media, peat substrates have high capillary capacity (Caron et al., 2005). Due to their fine texture, peat particles exhibit a high cohesion and consequently, the substrate at the base of the seedling cavity remains saturated with water. Excess water reduces the amount of oxygen in the rhizosphere, affecting gas exchange and the absorption of water and mineral nutrients. High substrate water contents cause plants to accumulate ethylene and abscisic acid (ABA), modifying stomatal function and foliar architecture (Kozłowski, 1997; Hopmans and Bristow, 2002; Islam et al., 2003). Meanwhile, despite variations in substrate water content, average monthly temperatures in the rhizosphere varied little during the growing season (13.3–17.4°C). Temperatures in this range do not limit the absorption of mineral elements or fine root growth in boreal conifer species (Lamhamedi and Bernier, 1994; Domisch et al., 2001).

Low substrate water contents and the absence of

leaching may lead to the accumulation of salts in the substrate and have a subsequent negative effect on seedling growth as a result of ionic toxicity or severe water deficits (Landis et al., 1989; Niknam and McComb, 2000). In the current study, the average salt accumulation at the end of the growing season remained very low (193 $\mu\text{S cm}^{-1}$) relative to critical salinity values (>1800–2000 $\mu\text{S cm}^{-1}$) for non-halophytic plants in forest nurseries (Timmer and Parton, 1984; Landis et al., 1989).

Sampling Strategy

The parameters determined from the semi-variogram, notably the range and the total variance ($C_0 + C_1$) of substrate water content and seedling height, could be used to improve sampling strategies specific to irrigation management and morphophysiological assessments of forest seedling lots (i.e., number, location and distance between sampling points). Accounting for the overlap in the wetting patterns of the sprinklers (3–4 m), the sampling locations should be selected as a function of the number of consecutive sprinkler pairs, rather than the dimension of the area allocated to the production of the seedling crop. Range values can be used to determine the optimal distance between two sampling points, given that samples taken at an interval exceeding the range, are independent of each other. The total variance values ($C_0 + C_1$) associated with each variable could be used to determine the maximum number of seedlings and containers to use for quality assessment of a seedling lot or to determine the average substrate water contents that are specific to irrigation decision making for each section of the nursery (Table 2). The optimum number of samples is a function of the level of precision established by the nursery staff. When used in conjunction with the kriging maps, the relationship between leaching and substrate water content can be used as a guide to estimate the potential losses of mineral nutrients and quantify water use for the production of white spruce seedlings (2+0) on an operational scale in a forest nursery.

CONCLUSIONS

Research Needs

The current study illustrated the presence of spatial variability in substrate water content over the course of the second growing season of containerized white spruce seedlings. This variability likely accentuated the heterogeneity of height growth of white spruce seedlings (2+0). More than 15% of the seedlings in the crop used in this study (*Picea glauca* provenance WEV, Pampev Inc.) were rejected for morphological problems in the spring of 2002, before their delivery for planting.

The parameters estimated from the semi-variograms, most notably the range and total variance ($C_0 + C_1$) of substrate water content, can be used to define sampling strategies specific to irrigation management and morphophysiological evaluation of seedling lots. This further suggests that three components are essential to the production of homogeneous lots of white spruce seedlings (2+0): (i) a fertilization schedule that is specific to sec-

ond year white spruce seedlings when they are grown outside, (ii) the maintenance of average substrate water contents at approximately 40% (v/v), and (iii) a sampling strategy that takes into consideration the spatial variability of substrate water content when scheduling irrigation of containerized forest seedling crops.

In light of the results of this study and our previous work (Lamhamedi et al., 2001; Stowe et al., 2001), it was evident that the presence of vertical slits in the walls of the air-slit container cavities encourage rapid substrate drying, which could subsequently have a negative effect on the physiology and growth of white spruce seedlings, which are known to be sensitive to substrate water content variations. This is one of the reasons that white spruce seedlings are no longer produced in air-slit containers in private forest nurseries in the province of Québec. From our results of this and previous studies (Lamhamedi et al., 2001; Stowe et al., 2001), to produce homogenous seedling lots of white spruce and significantly decrease the number of plants rejected at delivery we suggest the improvement of several cultural practices. For example, seedlings should be produced in closed-walled containers (volume of each cavity $\leq 320 \text{ cm}^3$). Improving cultural conditions by growing the seedlings under shelters with retractable roofs that can be closed in the case of rain or under tunnels covered in material that maximizes light intensity and quality (red/infrared ratio) will allow nursery managers to diminish the effects of environmental factors and better control substrate moisture and fertility with precision irrigation systems ($\text{CU} \geq 95\%$). This should make seedling height growth more homogenous and improve root development. If the number of seedlings rejected during morphophysiological assessment at delivery can be reduced, producing quality seedlings will be more profitable.

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