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Regional Climate, Edaphic Conditions and Establishment Substrates Interact to Influence Initial Growth of Black Spruce and Jack Pine Planted in the Boreal Forest

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Abstract: In eastern Canada, spruces (*Picea* spp.) and pines (*Pinus* spp.) are among the main commercial species being logged for their lumber or wood fiber. Annually, about 175 million seedlings are planted in areas totaling ~100,000 ha. Appropriate microsite selection is essential during reforestation operations, given that it can improve the chances of survival and initial growth of the seedlings. In fir (*Abies* spp.) and spruce forests of eastern Canada, the optimal characteristics of establishment microsites have yet to be identified; these would be determined by different physical and climatic variables operating at several scales. Our study determined the influence of climatic (regional-scale), edaphic (stand-scale), local (microsite-scale) and planting conditions on the establishment substrate and initial growth of black spruce (*Picea mariana* Britton, Sterns and Poggenb.) and jack pine (*Pinus banksiana* Lamb.). Substrate characterization and growth monitoring (three growing seasons) for the two species were conducted on 29 planted cutblocks that were distributed over an east–west climatic gradient (precipitation and temperature) in the balsam fir and black spruce–feather moss forests of Quebec (Canada). Linear mixed models and multivariate analyses (PCAs) determined the effects of climatic, edaphic and micro-environmental variables and their interactions on the establishment substrate and seedling initial growth. The predictive models explained, respectively, 61% and 75% of the growth variability of black spruce and jack pine. Successful establishment of black spruce and jack pine depended upon regional conditions of precipitations and temperature, as well as on their interactions with stand-scale edaphic variables (surface deposit, drainage and slope) and local variables (micro-environmental) at the microsite-scale (establishment substrate types and substrate temperature). Mineral, organo-mineral and organic establishment substrates exerted mixed effects on seedling growth according to regional precipitation and temperature conditions, as well as their interactions with edaphic and local variables at the stand and microsite-scales, respectively.

Keywords: climate; spruce stands; fir stands; seedling growth; soil; establishment substrate; multi-scale

1. Introduction

The boreal forest of Eastern Canada remains a strong supplier of wood for both domestic and export markets. Indeed, the forest products industry is engaged in extensive harvesting and forest management activities across the region [1]. Softwoods, most notably spruces (*Picea* spp.) and pines (*Pinus* spp.), are among the main commercial species being logged for their lumber or wood fiber [2]. In Eastern Canada, reforestation operations complement natural regeneration to restore or maintain forest productivity, to ensure continuous wood production that meets local and global demands [3]. Annually, about 175 million trees are planted in eastern Canada, across an area totaling about 100 000 ha [4]. In Quebec (Canada), black spruce (*Picea mariana* Britton, Sterns and Poggenb.) and jack pine (*Pinus banksiana* Lamb.) represent 77% of the ~130 million seedlings planted in this province each year [5]. Although they can be found on similar sites in the boreal forest, jack pine is a shade-intolerant species with high potential rates of resource capture relative to black spruce, which is a shade tolerant species adapted to low-resource environments [6].

In the boreal forest, reforestation is generally preceded by mechanical soil preparation (MSP) to create favourable conditions for seedling establishment on suitable microsites [7–11]. Following site preparation, seedlings are to be planted in microsites that maximize their survival and initial growth. Suitable conditions are determined by climatic and physical variables at several scales [12]. These variables include regional climate (temperature, total precipitation and relative humidity), soil characteristics at the stand-scale (drainage, surface deposits and slope) and seedling microenvironment at the microsite-scale (establishment or rooting substrate, substrate temperature, planting position and humus thickness) [13]. Yet, microsites that promote seedling growth are likely to differ, depending upon geomorphological characteristics at the stand-scale, regional climatic conditions and the characteristics of the species being planted [14–20].

It is important to identify the interactions between regional climate variables, stand characteristics and local planting conditions so that practitioners can adapt reforestation practices to reflect their respective regional situations. Incorporating these interactions into site planning would further ensure successful plantation establishment in the context of ongoing global change that will have significant effects on temperature and precipitation patterns and, consequently, on the conditions for tree establishment [21–25]. The subsequent application of this knowledge would have immediate effects on silvicultural practices and the productivity of managed forest stands. Therefore, the overall objective of our study was to identify the role that environmental variables play at regional, stand and microsite scales in the growth of black spruce and jack pine plantations. More specifically, we determined the influence of climatic (regional scale), edaphic (stand scale), local (microsite scale) and planting conditions, both on the establishment substrate and on the initial growth of black spruce and jack pine. These plantations were established in the balsam fir (*Abies balsamea* (L.) Mill.) and spruce–moss bioclimatic domains of boreal Quebec (Canada). We tested the hypothesis that the effects of the establishment substrate leading to the highest growth rate depended on the interactions between the regional climate and the edaphic and planting conditions across boreal Quebec.

2. Materials and Methods

2.1. Study Area and Data Collection

We used data that were collected from 29 operational cutblocks (average area: 8.5 ha) that had been submitted to mechanical site preparation and planted. The selected planted cutblocks covered a wide moisture and temperature gradient from eastern to western Quebec; the plots were located in the balsam fir and black spruce–feather moss bioclimatic domains (Figure 1). The balsam fir domain is dominated by mixed stands of yellow birch (*Betula alleghaniensis* Britton), paper or white birch (*Betula papyrifera* Marshall) and softwoods such as balsam fir, white spruce (*Picea glauca* (Moench) Voss) and white cedar (*Thuja occidentalis* L.) [26]. The black spruce–feather moss domain is dominated by closed-canopy black spruce stands [26].

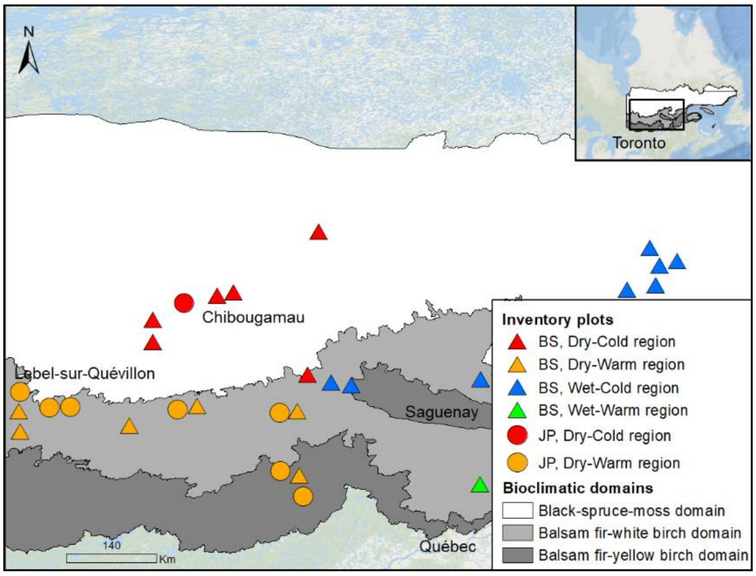

Figure 1. Location of permanent inventory plots distributed in cutblocks planted with black spruce (BS, filled triangles) and jack pine (JP, filled circles) in the balsam fir (grey areas) and spruce–moss (white area) bioclimatic domains of boreal Quebec, Canada [26]. Plots are located in four regions that were delineated based on their precipitation and temperature regimes (different coloured symbols). The regions are Dry–Cold, Dry–Warm, Wet–Cold and Wet–Warm.

Twenty-one cutblocks were reforested with black spruce between 2010 and 2016; eight cutblocks were reforested with jack pine between 2011 and 2016 (Figure 1). In all cases, containerized seedlings were derived from local seed sources and produced in governmental or contracted private nurseries over two years in 45-cavity containers (each with a volume of 110 cm^3). One to four weeks after cutblock reforestation, we established a 130 m transect and installed permanent sampling plots (8 m radius; 200 m^2, or about 40 seedlings per plot) every 50 m along the transect, to a maximum of five plots per cutblock. The transect was oriented east–west and located in the middle of the block. A total of 105 plots were established in sites that had been planted with black spruce and 40 plots in sites that were planted with jack pine. All seedlings were identified with a numbered metal tag to allow long-term monitoring at the seedling level. In each plot, we measured stem diameter at ground-level and seedling height at the end of three consecutive growing seasons following planting. A total of 4492 seedlings (2996 black spruce and 1496 jack pine) were identified and monitored.

During the first three growing seasons on each site, data were collected at the microsite-scale for each seedling (≤ 1 m^2): (1) Planting substrate, which was classified into one of five types (fibric organic matter, humic organic matter, intact forest litter, exposed mineral soil and an organo-mineral mixture [27]); (2) relative planting position (mound, shoulder of the scarifying furrow and scarifying furrow depression); and (3) humus thickness (cm). We measured soil temperature on an hourly basis using iButton probes (Alpha Mach iButton®, Bombardier, Ste-Julie, Quebec). Loggers were buried at a 10 cm depth next to a seedling that was located at each plot centre. The logged data were subsequently used to calculate monthly averages.

At the stand-level, we extracted surface deposit data, slope classes and drainage classes from the most recent ecoforestry map that was produced by the Government of Quebec [28]. The site slope was categorized as zero to low (<8%), gentle (<15%), moderate (<30%), strong (<40%) or steep (>41%). Soil drainage was rated as rapid, good, moderate, imperfect or poor. The inventoried cutblocks are found on one of five types of surface deposits: thick till, thin till, rock deposits, glaciolacustrine deposits or fluvio-glacial deposits.

At the regional level, extrapolated monthly data were extracted for temperature, total precipitation and relative humidity from NASA's Global Climate Data Platform (2 m resolution) (https://power.

larc.nasa.gov/data-access-viewer/, accessed on 10 April 2019). The climatic data were collected from May to September (growing season) during the first three growing seasons for each cutblocks; i.e., the climate data we used as the explaining variables corresponded to the 3-year growth periods specific to each plantation included in our dataset.

2.2. Statistical Analyses

We conducted all statistical analyses in R software (version 3.5.1, Vienna, Austria) [29]. We used seedling height and ground collar diameter data to calculate a volume index (V), based upon the volume of a cone [30], which was computed as follows:

$$V = \pi \times (D/2)^2 \times (H/3) \quad (1)$$

where V is volume in cm^3, D is stem diameter at ground level (cm) and H is height (cm). We then calculated relative volume growth (RGRV), following [12], according to the following formula:

$$RGRV = [\ln (V_3) - \ln (V_0)]/(t_3 - t_0) \quad (2)$$

where V_3 and V_0 represent tree volumes at time t_3 (i.e., after three growing seasons) and t_0 (at planting).

Ten environmental variables, together with their interactions, were incorporated into a linear mixed model as fixed effects explaining volume growth. The geographical distribution (longitude and latitude) of the plots were considered random effects in the model, which was fitted using the lme4 library [31]. ANOVA analysis was also used to evaluate the effect of the explanatory variables on volume growth. Explanatory variables were categorized into three groups: (1) The microsite scale, which included humus thickness, planting position, substrate type and monthly average substrate temperature; (2) the stand scale, which included surface deposit, slope class and drainage class; and (3) the regional scale, which was represented by the seasonal climate data (i.e., average monthly temperature, monthly total precipitation and average relative humidity). We considered effects to be significant at $\alpha = 0.05$.

Lastly, we used the medians of the mean monthly temperature (13.5 °C) and total monthly precipitation (95.9 mm) as boundaries to delineate four regional groups: the dry and cold region; wet and cold region; dry and warm region; and wet and warm region. The use of the median values of temperature and precipitation was more relevant than the mean values to delimit the four regions. Unlike the mean value, the median value is relatively insensitive to outliers and detects the break point that can subdivide the data into several groups [32–34]. This subdivision method of data has already been successfully applied in ecology in previous studies [35,36]. Table 1 summarizes the number of black spruce and jack pine seedlings in each delineated region.

Table 1. Number of jack pine and black spruce seedlings in the four regions, with their corresponding height and ground collar diameter at the end of their third growing season.

Species	Region	Number of Seedlings	Ground Collar Diameter (mm)	Height (cm)
Black spruce	Wet–Warm	1120	18.0 (±6.3)	89.7 (±26.8)
	Wet–Cold	1289	12.9 (±5.2)	61.8 (±27.0)
	Dry–Warm	239	9.6 (±4.6)	51.4 (±18.2)
	Dry–Cold	348	9.6 (±6.6)	47.1 (±21.9)
Jack pine	Dry–Warm	1034	15.2 (±6.7)	69.3 (±25.1)
	Dry–Cold	462	10.2 (±2.5)	44.1 (±9.6)

Note: Data are presented as the mean (±standard deviation).

We assigned the cutblocks and their plots to these distinct groups according to their temperature and precipitation regimes (Figure 1). Principal component analyses (PCAs) were then used for each group to assess the correlations among seedling growth, establishment substrates and environmental variables at the regional, stand and microsite levels. PCAs were produced using CANOCO software (version 5, Ithaca, NY, USA) [37,38].

3. Results

Our dataset comprised 4492 seedlings distributed across the two species and over the four regions (Table 1). After three growing seasons, black spruce seedling ground collar diameter and height ranged from 9.6 to 18 mm and from 47 to 90 cm, respectively, with the larger sizes observed in the wetter regions. Jack pine seedlings, which were only found in the dry regions, respectively ranged from 10.2 to 15.2 mm in ground collar diameter and from 44 to 69 cm in height.

3.1. Black Spruce

Our predictive model explained 61% of variation in the data (Table 2). Several individual environmental variables affected seedling growth at the stand and regional levels, including slope and monthly mean temperature. Significant interactions also were observed among environmental variables at microsite, stand and regional scales. These included two-way interactions between substrate type and total monthly precipitation, substrate type and surface deposit, soil temperature and surface deposit as well as drainage and surface deposit; significant three-way interactions were observed for substrate type, surface deposit and drainage, and for substrate type, drainage and slope (Table 2). No effects on seedling growth were reported for relative humidity, humus thickness and planting position (Table 2).

Table 2. ANOVA summary of the effect of the explanatory variables and their interactions at three spatial scales on the relative growth volume of black spruce and jack pine seedlings in the boreal forest of Quebec.

Explanatory Variables		Black Spruce (Model R^2 = 0.61)		Jack Pine (Model R^2 = 0.75)	
		F-Value	***p*-Value ***	**F-Value**	***p*-Value ***
Microsite scale	Humus thickness	0.944	0.331	0.790	0.374
	Planting position	1.055	0.384	0.357	0.840
	Substrate temperature (°C)	0.649	0.420	2.775	0.096
	Substrate type	1.429	0.199	1.661	0.127
Stand scale	Surface deposit	0.598	0.621	5.627	**0.001**
	Drainage class	1.608	0.206	0.291	0.884
	Slope class	3.928	**0.007**	2.773	**0.040**
Regional scale	Precipitation (mm)	0.103	0.748	1.953	0.162
	Temperature (°C)	8.067	**0.009**	1.425	0.233
	Relative humidity (%)	0.067	0.796	1.030	0.310

Table 2. *Cont.*

Explanatory Variables		Black Spruce (Model R^2 = 0.61)		Jack Pine (Model R^2 = 0.75)	
		F-Value	*p*-Value *	F-Value	*p*-Value *
Interactions	Substrate type × Substrate temperature	1.399	0.211	2.713	**0.008**
	Substrate type × Precipitation	3.742	**0.001**	4.385	**0.002**
	Substrate type × Relative humidity	1.604	0.142	1.954	0.070
	Substrate type × Planting position	0.889	0.633	1.544	0.055
	Substrate type × Surface deposit	2.031	**0.018**	3.205	**0.001**
	Substrate type × Drainage class	1.050	0.399	2.069	**0.006**
	Humus thickness × Surface deposit	1.170	0.320	0.414	0.661
	Planting position × Substrate temperature	1.307	0.258	0.968	0.436
	Planting position × Surface deposit	0.859	0.603	1.309	0.219
	Planting position × Drainage class	1.443	0.139	0.807	0.671
	Surface deposit × Substrate temperature	2.781	**0.043**	0.300	0.825
	Surface deposit × Drainage class	2.329	**0.034**	1.039	0.385
	Surface deposit × Slope class	0.580	0.679	1.355	0.255
	Drainage class × Slope class	1.977	0.101	2.334	0.072
	Substrate type × Substrate temperature × Surface deposit	0.750	0.690	2.222	**0.030**
	Substrate type × Planting position × Drainage class	1.169	0.241	1.241	0.206
	Substrate type × Surface deposit × Drainage class	2.134	**0.008**	0.934	0.505
	Substrate type × Drainage class × Slope class	2.522	**0.002**	0.827	0.578
	Planting position × Substrate type × Substrate temperature	1.402	0.096	0.810	0.676
	Planting position × Drainage class × Surface deposit	0.920	0.565	0.926	0.508
	Surface deposit × Drainage class × Slope class	0.563	0.573	0.042	0.839

* Values in boldface type are significant at $p = 0.05$.

In the Dry–Cold region (Figure 2a), seedling growth was favoured by mineral-type substrates and moderate slopes. However, seedling growth was negatively influenced by litter, organo-mineral, fibric and humic substrates, together with zero slopes. In the Wet–Cold region (Figure 2b), seedling growth was favoured by an increase in substrate temperature. Increased seedling growth also has been associated with the presence of litter and organo-mineral substrates, and sites with poor to imperfect drainage on rocky surface deposits. Seedling growth was negatively influenced by fibrous substrates, especially at sites with thick surface deposits (thick tills). In the Dry-Warm region (Figure 2c), seedling growth was favoured by fibrous substrates, but negatively affected by mineral substrates. Thick surface deposits, imperfect drainage and gentle slopes appeared to favour seedling growth. In the Wet–Warm region (Figure 2d), seedling growth was higher for seedlings that were planted in humic (poorly drained sites) and fibric (well-drained sites) substrates. Sites on thick surface deposits (thick tills), with moderate and extreme slope classes, favoured seedling growth. In addition, organo-mineral substrates, glaciolacustrine surface deposits and shallow slopes negatively affected seedling growth in this region.

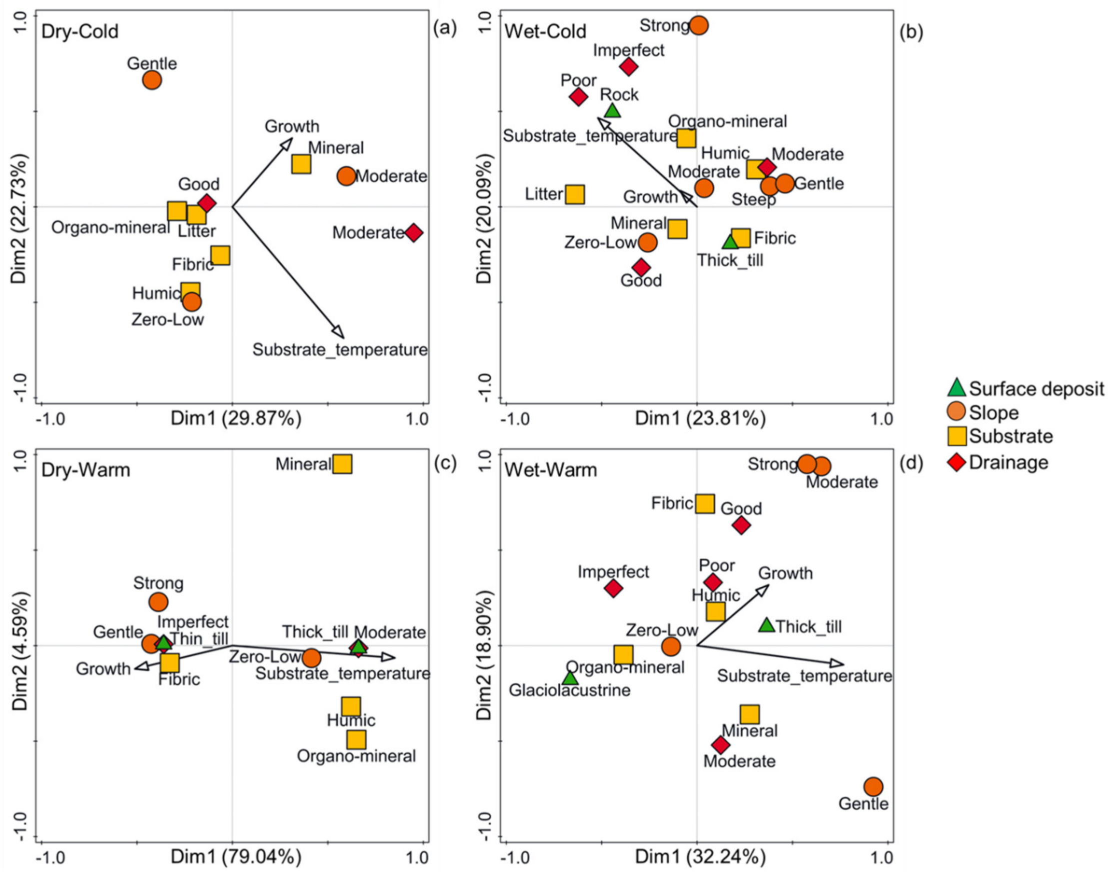

Figure 2. Principal component analysis (PCA) summary of black spruce growth responses to local variables at the microsite level and soil variables at the stand level, within four regions that are delineated by annual precipitation and average temperature: (**a**) Dry–Cold; (**b**) Wet–Cold; (**c**) Dry–Warm; and (**d**) Wet–Warm.

3.2. *Jack Pine*

The predictive model explained 75% of variation in the jack pine data (Table 2). There was a significant effect of slope (stand level) on seedling growth. Further, significant two- and three-way interactions were observed among environmental variables at the microsite, stand and regional scales. Interactions involved substrate type and ground temperature, substrate type and total monthly precipitation, substrate type and surface deposition and substrate type and drainage. As was the case with black spruce, we encountered no significant effects of relative humidity, humus thickness and planting position on jack pine seedling growth (Table 2).

The representative jack pine plots were located in the western portion of the study area, i.e., the driest areas of the gradient. In the Dry–Cold region (Figure 3a), seedling growth was favoured by humic substrates and sites with thin till and glaciolacustrine surface deposits, which has been characterized by imperfect to moderate drainage. Lower jack pine seedling growth was associated with well-drained sites. Slope classes did not influence jack pine seedling growth in these two regions. In the Dry–Warm region (Figure 3b), jack pine seedling growth was favoured by increased substrate temperature, together with fibrous, litter, humic (sites with till deposits) and organo-mineral substrates. In addition, seedling growth was negatively affected by mineral-type substrates, particularly on sites with thin surface deposits (thin tills) and rapid drainage.

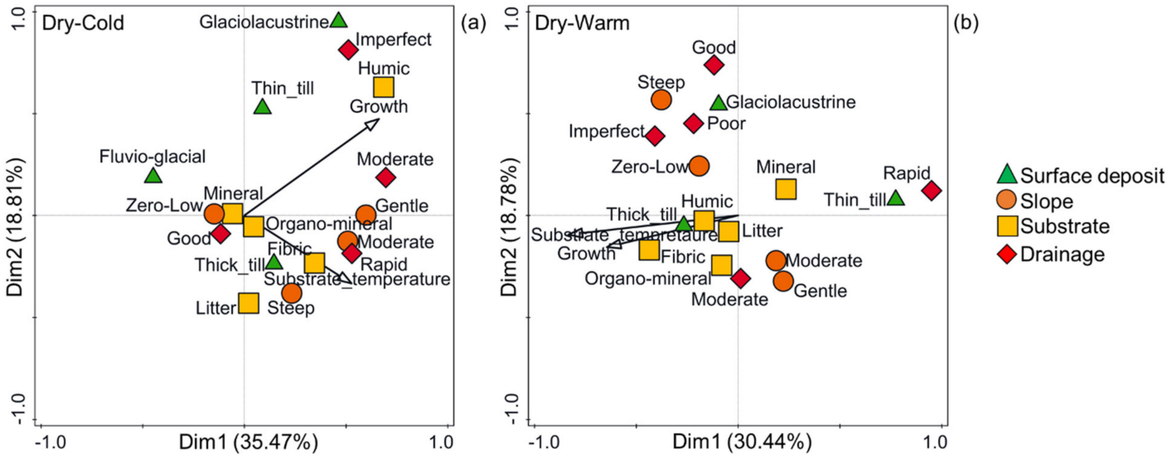

Figure 3. Principal component analysis (PCA) summary of jack pine growth responses to local variables at the microsite level and soil variables at the stand level, within four regions that are delineated by annual precipitation and average temperature: (**a**) Dry–Cold; and (**b**) Dry–Warm.

4. Discussion

We found that growth responses of black spruce and jack pine seedlings were closely associated with regional climate variables (temperature and precipitation), which allows a better understanding of both stand scale soil conditions effects (surface deposit types, drainage and slope) and local conditions effects at the microsite scale (types of establishment substrate and soil temperature) (Table 2). These responses are consistent with several previous studies [39–41].

4.1. Black Spruce

In the boreal forest, black spruce can establish on many types of surface deposits, with a preference for deep forest soils and deposits (e.g., thick tills) [42] due to high nutrient availability [43,44]. Nevertheless, growth of black spruce is sensitive to water availability in surface deposits and the overlaying soil. Indeed, the species is adversely affected by extreme water levels in the soil, including those causing water stress [45,46] or chronic flooding conditions [47–49]. Thus, moderately to well-drained sites are to be preferred for reforestation activities to increase the success of black spruce establishment [42]. At the microsite scale, reforestation on north-facing slopes should also be preferred, given that these locations are characterized by relatively favourable moisture conditions for seedling establishment [10,50].

In the dry regions (Figure 2a,c) of our study area, regardless of whether they are warm or cold, access to water is a limiting factor for conifer growth, especially during the establishment and juvenile stages [51]. Water availability in establishment substrates substantially influences seedling growth during these periods [52,53]. Organic and mineral substrates offer the best conditions for seedling growth, under conditions of both excess moisture (e.g., paludified sites) and moisture deficiency (e.g., clay substrates characterized by their high moisture retention capacity, even during dry periods) [10,11,52,53]. In Wet–Cold regions (Figure 2b), substrate temperature is considered an important factor limiting seedling growth [54,55], particularly when decomposition processes are slowed by low temperatures [56].

The growth of black spruce seedlings is positively related to increasing temperature [57–59], but only up to a certain limit above which physiological processes are negatively affected [60,61]. In Wet–Cold region, organo-mineral substrates are the best substrates for establishing seedlings [14,62,63]. When an optimal balance is attained between mineral and organic fractions, organo-mineral substrates are good thermal insulators (soil temperature conservation) [64] and are characterized by high moisture retention and natural drainage in the case of excess water [65]. In addition, organo-mineral substrates provide seedlings with direct access to nutrients, thereby stimulating expansion of initial roots and the appearance of adventitious roots [49,66–68].

In the Wet–Warm region (Figure 2d), seedling growth was favoured by fibrous and humic organic substrates yet constrained on mineral and organo-mineral substrates. Excess water naturally drains from organic substrates, owing to their porous texture, thereby reducing the risk of anaerobiosis when compared to fine-textured mineral substrates (e.g., predominantly clay). The latter pose high risks for root asphyxiation due to surface water stagnation and reduced gas exchange, particularly in depressions [17,69–71]. In addition, elevated temperature and moisture conditions can contribute to increased microbial activity in organic substrates. Increased microbial activity, in turn, increases the availability of nutrients, especially N, which has a positive effect on seedling growth [72,73].

4.2. Jack Pine

Jack pine is less sensitive to temperature variation than black spruce [60,74,75]. While moderate temperature increases favour the growth of jack pine seedlings, higher temperatures lead to slower growth [60,74–76]. Several studies have confirmed the influence of precipitation regime and soil conditions on jack pine establishment in the boreal forest [77–79]. Jack pine generally performs better than black spruce in dry conditions [25,80–82]. Well-drained surface deposits, including till, fluvio-glacial expanses and lacustrine and sandy deposits, promote jack pine growth [83–86]. Further, jack pine performance is better on dry, well-drained mineral and organic substrates, particularly sand, silty sand and humus, compared to poorly drained wet substrates [83,85,87]. In the dry regions of our study area (Figure 3a,b), we found that jack pine seedling growth was favoured by organic (fibric, humic and litter) and organo-mineral substrates. Organic microsites are characterized by high porosity, which permits very rapid drainage of water, thereby providing a relatively dry and favourable environment for seedling growth [84,88–90]. In well-drained dry environments, organo-mineral substrates allow natural moisture drainage and thus promote the establishment of jack pine seedlings [91].

5. Conclusions and Implications for Forest Management

Future climate change will directly affect tree growing conditions in the boreal forest zone [92]. In eastern Canada, tree species will be particularly vulnerable to temperature increases [25]. Our analyses allowed us to identify regional, stand and microsite variables that affect the growth of recently planted black spruce and jack pine seedlings. Our results thus make it possible to consider how plantation silviculture will have to be adapted to promote the success of seedling establishment in the face of climate change.

We demonstrated that black spruce and jack pine establishment in boreal Quebec depends upon regional climatic conditions. In turn, regional climate interacts with soil conditions at the stand level and local conditions at the microsite level. In the dry regions of our study area, black spruce seedling growth was favoured on microsites that were dominated by a fibric and mineral substrate and on moderate slopes. In the Wet–Cold regions under study, growth of black spruce seedlings was favoured by the increase in substrate temperature, the presence of microsites that are dominated by a litter and organo-mineral substrate and on rocky surface deposits with poor drainage. In the Wet–Warm regions of our study, the growth of black spruce seedlings was favoured by microsites that are dominated by a humic substrate on poorly drained sites and fibric on well-drained sites. Sites with thick till deposits, with moderate and extreme slope classes, appeared to favour the growth of black spruce seedlings. Growth of jack pine seedlings in the dry regions of our study area (the only sites that were sampled for this species) was favoured by microsites that were dominated by organic and organo-mineral substrates.

Some regions had fewer plots than others did, as the distribution of the plots was dependent on operational management planning and reforestation activities during the corresponding years, combined with constraints related to plot establishment in remote areas. Our study is ongoing, with new plots being added in new plantations across the entire study area to better balance the design. Further measurements and analyses that will include a larger set of plots will thus allow confirming the robustness of our first conclusions.

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