

Performance of seedlings of four coniferous species planted in two boreal lichen woodlands with contrasting soil fertility

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ABSTRACT

Lichen woodlands (LWs) are persistent unproductive areas of the Canadian boreal forests whose afforestation may potentially remove significant amounts of anthropogenic C from the atmosphere. The choice of species to be planted is nevertheless uncertain given the particular pedoclimatic conditions prevailing in this habitat as well as the rapidly changing climate at northern latitudes. In this study, we assessed the survival and the growth rates of four boreal coniferous species in two LWs with contrasting soil fertility. Five years after afforestation, survival rate was high for all species at both sites, ranging from 60 to 100 %. Tree height and diameter at stump height (DSH) were up to 60 % and 97 % higher at the LW with higher soil fertility, respectively. The height of jack pine (*Pinus banksiana* Lamb.; JP) trees was on average 15 %, 56 % and 68 % higher than that of tamarack (*Larix laricina* [DuRoi] K. Koch; TK), black spruce (*Picea mariana* [Mill.] BSP; BS) and white spruce (*Picea glauca* [Mill.] B.S.P.; WS), respectively. There was a significant species \times soil fertility interaction, reflecting a much higher growth difference between the two sites for JP than for the other species. Annual apical growth increased from one year to the other in JP, suggesting its ability to expand its root system and to acquire resources from the mineral soil rapidly after planting. The much larger photosynthetic biomass at the more fertile site was driven by a higher number of needles produced annually rather than by a higher mass of individual needles, which did not vary between sites. The photosynthetic biomass / woody biomass ratio was not significantly impacted by soil fertility. Overall, these results suggest that JP and TK may be good candidates for the afforestation of boreal LWs and that site selection is of crucial importance to optimize plantation productivity in the mid-term. Further studies must be conducted to assess the survival and the C sequestration potential of these species in the long-term.

1. Introduction

In Canada, forests cover 347 million hectares (about 35 % of terrestrial land area), of which about 68 % is dominated by coniferous trees (Natural Resources Canada, 2019). The Canadian boreal forest comprises significant surface areas covered by persistent unproductive lichen woodlands (LWs) resulting from successive wildfires and other perturbations (Jasinski and Payette, 2005; Girard et al., 2009; Payette and Delwaide, 2018). These LWs cover about 2 million hectares in Canada (Johnson and Miyanishi, 1999) and 1.6 million hectares in the province of Québec only, representing approximately 7 % of the black spruce feather moss domain of the boreal forest (Girard et al., 2008). There is an increasing recognition that the forestry sector can play a significant role in climate change mitigation, especially through afforestation of unproductive sites (Beauregard et al., 2019; IPCC, 2019).

Therefore, the afforestation of these LWs may create a significant net carbon sink at the scale of the country. Using carbon dynamics and budget models, and accounting for carbon emissions throughout the value chain, it was estimated that afforested LWs may create net carbon sinks of at least 77 t C ha⁻¹ over a period of 70 years and could sequester up to 8 % of industrial carbon emissions of the Province of Québec if implemented on a large scale (Gaboury et al., 2009; Boucher et al., 2012). The rare field trials have shown that afforestation of LWs is successful provided that appropriate site preparation using disk scarification is conducted (Hébert et al., 2013). Therefore, LWs of the eastern Canadian boreal forest may represent potential sites to host part of the 2 billion trees the Canadian government has recently committed to plant across its territory in the next decade to mitigate climate change (<https://www.canada.ca/en/campaign/2-billion-trees.html>).

Reforestation operations conducted by the forest industry are

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generally guided by wood demand and market needs, and designed and managed to create a more predictable production system (Puettmann et al., 2009). Hence, they rely on a few tree species, often planted in monospecific stands. Reforestation or afforestation operations with no commercial purpose offer the opportunity to introduce a variety of species that would otherwise not be planted, in order to increase biodiversity and possibly ecosystem services, including carbon sequestration. For instance, *Larix laricina* (DuRoi) K. Koch naturally occurs in eastern Canada boreal forests but represents only about 1 % of conifer seedlings produced annually in Québec's public and private tree nurseries for reforestation programs (Delisle, 2021), although it has high productivity rates in the first decades following establishment (Poulin, 2013). In addition, its deciduous foliage may reduce the impact of plantations on the albedo and thus maximize the cooling effect of carbon capture by the trees. However, this species is more prevalent on poorly-drained soils and in boreal peatlands (Eyre, 1980; Islam and Macdonald, 2004) and its survival and growth potential in afforested boreal LWs, which can experience water stress in the summer, has to our knowledge never been assessed.

The thickness and the quality of the soil vary between LWs, which results in large differences in tree growth from one plantation to the other (Fradette et al., 2021). Soil conditions, particularly N availability, can also affect bud phenology in conifers (De Barba et al., 2016; Deslauriers and Rossi, 2019; Marty et al., 2020), which may ultimately impact the survival and growth of planted species. However, LW soil fertility (e.g., organic horizon thickness, soil compaction, N availability) may not impact the growth of all species with the same magnitude. For instance, *Pinus banksiana* Lamb. (jack pine; thereafter JP) has a very strong ability to uptake N from N-depleted mineral soil horizons (Houle et al., 2014), which likely explains its much higher growth rate in LWs (Fradette et al., 2021). This species may therefore be less sensitive than others to organic soil characteristics. Therefore, edaphic factors should also be accounted for to optimize the choice of species to be planted at specific sites. The interaction between soil fertility and species, i.e. the relative response of species to a change in soil fertility, has to our knowledge never been investigated in boreal LWs.

In this study, we assessed the survival rate and the growth of four coniferous species of the eastern Canadian boreal forest – *Picea mariana* (Mill.) BSP (black spruce; thereafter BS), *Picea glauca* (Moench) Voss (white spruce; thereafter WS), *Pinus banksiana* Lamb. (jack pine; thereafter JP) and *Larix laricina* (DuRoi) K. Koch (tamarack; thereafter TK) – five years after afforestation in two boreal LWs with similar climatic conditions but contrasting soil fertility. Altogether these species represent > 95 % of seedlings produced in Quebec's public and private tree nurseries for reforestation (Delisle, 2021). A subsample of 54 trees of BS, WS and JP – the three dominant and of greatest economic importance species in the study region – were harvested from both sites to assess differences in aboveground biomass traits between sites, especially aboveground biomass partitioning between photosynthetic and woody tissues. Our goals were to test the potential of these four species for LW afforestation operations conducted above 50°N of latitude on soils with thin or no humus layer. Our second objective was to study whether there is an interaction between species and soil fertility, that is, whether the relative performance of the four species varies depending on site quality in boreal LWs. In addition, the variation in aboveground biomass traits in response to soil fertility has to our knowledge not been investigated for these species, especially the photosynthetic / woody biomass ratio. This trait may be plastic to environmental conditions - particularly to soil nutrient availability - as photosynthetic tissues also represent a reserve of N in evergreen species that can be used to support N demand for annual growth through effective resorption (Escudero and Del Arco, 1992; Escudero et al., 1992; Warren and Adams, 2004). Lower soil N availability can induce leaf shedding during early growing season to increase N translocation towards growing shoots and thus reduce the average leaf longevity of the tree (Pasche et al., 2002; Lamaze et al., 2003; Marty et al., 2009, 2010). Hence, a lower photosynthetic / woody

biomass ratio might be observed at the site with lower soil fertility.

2. Material and methods

2.1. Study area and site preparation

The two study sites – B25 (50°42'45" N; 72°40'26" W) and B27 (50°15'23" N; 72°03'38" W) – are part of an experimental plantation network within LWs of Québec's central black spruce-feather moss boreal forest, located 170–220 km north of the Lac St-Jean (Québec, Canada) (Fig. 1). Forested soils in the region are typical podzols which have developed from Precambrian charnockitic gneiss covered by thick undifferentiated till and are generally well drained. However, both sites experienced successive wildfires, the latter of which occurred in 1996 and 2005 at B25 and B27, respectively. These successive perturbations have turned the original forests into LWs with a typical thin organic soil layer and short vegetation mainly composed of ericaceous species including *Rhododendron groenlandicum* L., *Kalmia angustifolia* L. and *Vaccinium angustifolium* L., and various terricolous lichens of the *Cladonia* genus (Payette and Delwaide, 2018). The mechanisms involved in the transition from closed forests to LWs have been well described by Girard et al. (2009) and Payette and Delwaide (2018). A photograph of a mature LW before scarification can be seen in the [supplementary materials](#) (Fig. S1).

Prior to planting, a soil disk scarification was performed, using a TTS disk trencher. Disk scarification is a widely used soil preparation technique that creates furrows or patches of exposed mineral soil (Fig. S1), which has been shown to be a suitable substrate for several conifer species, including black spruce (Vioreck and Johnston, 1990; Prévost, 1992; Houle and Filion, 2003; Wang and Kemball, 2005; Kemball et al., 2006).

The two sites are characterized by similar climatic conditions (due to their proximity and similar altitude) but contrasting soil fertility. Mean annual air temperature averaged -1.5 °C during the study period (2014–2019) at the Environment and Climate Change Canada's closest weather station (Bonnard; 50°43'44.000" N; 71°00'47.000" W; 498 m a. s.l.), the year 2019 being the coldest (-2.16 °C) and the year 2016 the warmest (-0.79 °C) (Fig. S2). No reliable data was found for annual precipitation during the study period but it averaged 969 mm between 1981 and 2010.

Eight soil cores (15 cm deep and 8 cm diameter) were collected from each site on two diagonal transects, put in plastic bags, brought back to the laboratory and kept in the refrigerator until further treatment. Soils were then air-dried for a few days in a drying room, then sieved ($\phi = 2$ mm). For each site, the < 2 mm fractions of each soil core were pooled and mixed together, resulting in two mixed soil samples. Then, 350 g of each of these two pooled samples were sent to the inorganic and organic chemistry laboratory of the Direction de la Recherche Forestière (Québec, Canada) for chemical analyses (Ouimet et al., 2015). The results of the analyses are shown in Table 1. The B27 site clearly showed signs of lower fertility, including thinner organic (LFH) and Ae horizons, lower organic carbon concentration, a higher stoniness in the top soil, and 2 to 3 times lower NH_4^+ , Ca, K and Mg concentrations (Table 1).

2.2. Tree material and planting design

Both sites were afforested with containerized two-year old BS, WS, JP and TK seedlings in 19 randomly distributed monospecific contiguous plots at each site (Fig. 2). A total of 19 seedlots (eight for BS, five for WS, four for JP and 2 for TK) originating from various private and public tree nurseries were included in the tree material to be representative of the genetic diversity of the species used in Quebec's reforestation programs (Table S1). The unequal number of seedlots per species reflects the share of the species in Quebec's production and plantation programs, BS being the most widely produced and planted conifer species (56 % of the total number of seedlings produced every year), followed by WS (19.5 %), JP

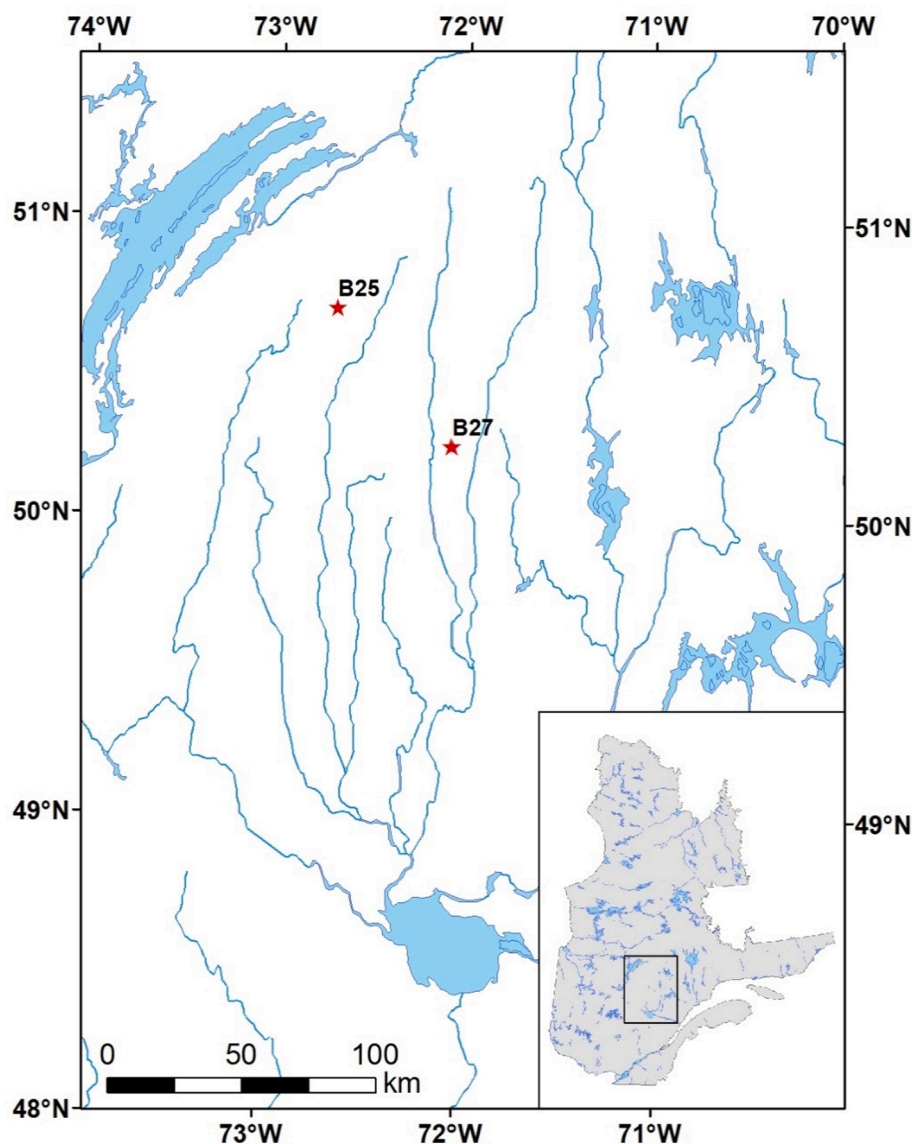


Fig. 1. Location of the two plantation sites (B25 and B27) in Québec, Canada.

Table 1

Soil characteristics and mean height at planting time (cm) of the four tree species in the B25 and B27 experimental sites.

		B25	B27
Soil characteristics	Stoniness (%)	45	30
	Stone repartition	Deep	Surface
	LFH thickness (cm)	4	3
	Ae thickness (cm)	5	2
	B-horizon texture	Sandy clay loam	Sandy loam
	C total (g kg ⁻¹)	46	17
	pH (CaCl ₂)	3.6	3.8
	NH ₄ ⁺ (mg kg ⁻¹)	4	2
	NO ₃ ⁻ (mg kg ⁻¹)	<1	<1
	P (mg kg ⁻¹)	13	15
	K (mg kg ⁻¹)	71	21
	Ca (mg kg ⁻¹)	126	53
	Mg (mg kg ⁻¹)	25	9
	Seedlings height (cm)	Black spruce	26.9 ± 6.4
White spruce		26.6 ± 7.9	27.4 ± 8.8
Jack pine		26.1 ± 7.7	23.1 ± 6.7
Tamarack		35.4 ± 4.7	34.4 ± 6.2

(18.5 %) and TK (1 %) (Delisle, 2021). The average height of the seedlings at planting was about 25 % higher for TK than for the other species across sites (Table 1). It averaged 34.6 ± 5.5 cm, 27.0 ± 8.3 cm, 27.0 ± 6.0 cm and 24.6 ± 7.4 cm for TK, WS, BS and JP, respectively.

The two sites were afforested in 2014 after soil scarification with a disk trencher. This method has been shown to be the most effective soil preparation technique in LWs (Hébert et al., 2013; Prévost, 1992). The two-year old seedlings were planted about 2 m apart in rows distant of ~ 2 m from each other, to obtain a density of ~ 2000–2500 trees ha⁻¹ (Fig. 2).

2.3. Survival rate and growth

In June 2019, i.e. five years after planting, the number of trees still alive was counted in rows (about 20 m long) of 10 trees that were previously geo-localized. Trees were qualified as dead when they could not be found or when they were seriously damaged and had not produced annual shoots at the sampling time. For each row, the survival rate was calculated as the ratio of the number of alive trees to the number of trees that had been planted. The survival rate was calculated on five rows per plot and per site for a total of 190 rows and 1900 trees (5

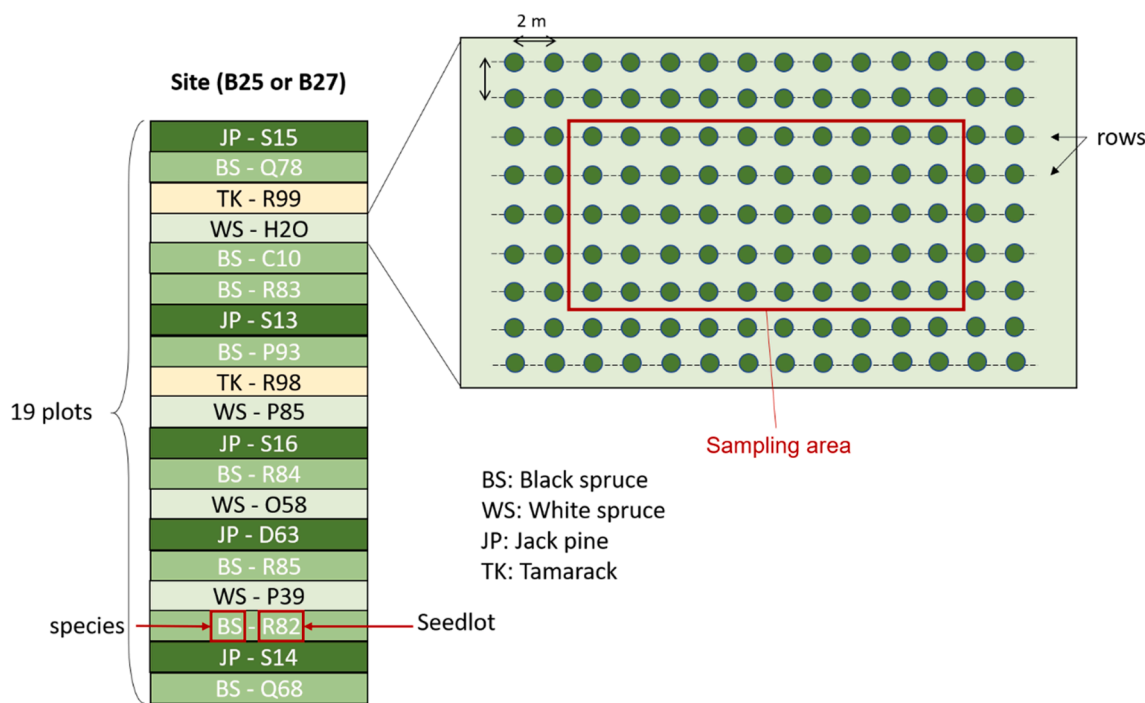


Fig. 2. Schematic representation of the experimental design. At each site (B25 or B27), 19 plots were afforested with a single species' seedlot. Trees were planted in rows at a distance of about 2 m from each other (~2000–2500 trees ha⁻¹). A sampling area including 5 rows of 10 trees was delimited within each plot.

rows × 10 trees × 19 plots × 2 sites = 1900 trees). The diameter at stump height (DSH) (15 cm above the soil surface) and the height of two randomly selected trees per row were also measured (5 rows × 2 trees × 19 plots × 2 sites = 380 trees).

2.4. Aboveground biomass characteristics

In late July 2019, we uprooted 27 trees from each site (3 seedlots × 3 species × 3 trees × 2 sites = 54 trees) and put them in individual ~ 8 dm³ pots with their root balls for further aboveground biomass characterization in the lab. We collected only BS, WS and JP trees (no TK) because of their similar leaf habit (persistent needles) and because they represent the most planted species in the afforested LWs network. The trees were then brought back to the university campus and left outside for three days. Their DSH and height were measured prior to being cut off at the collar. The length of the last four annual apical shoots was measured and the number of needles on the one-year old apical shoot (2018 growth season) was counted.

For each tree, the different shoot age classes were separated, put in individual paper bags and dried for 72 h at 55 °C. Once dry, the stem and needles of each shoot were separated and weighted. A sample of 30 one-year-old needles per tree, all located on first-order branches, was used to estimate the average mass of needles of each tree.

2.5. Calculations and statistical analyses

Mixed-effect models with site and species as fixed effects and seedlots as random effect were used to assess the impacts of these variables on survival rate, height and DSH of the trees measured in the field and on aboveground biomass characteristics (aboveground biomass, photosynthetic/wood biomass ratio, annual production of needles on the apical shoot and average needle mass) on the subset of 54 seedlings harvested from the field. Analyses were performed in R (R Development Core Team, 2019) with the *lmer* function in the *lme4* package (Bates et al., 2015). The package *emmeans*, which is an updated version of the *lsmeans* package (Lenth et al., 2018) was used to estimate marginal means and to conduct a post-hoc pairwise comparisons of least-square

means among factors' levels (Tukey's method). Differences were considered statistically significant at P-values < 0.05.

3. Results

3.1. Survival rates

Survival rate was very high, ranging from 0.6 to 1 across the 190 sampled rows. There was only a site effect on tree survival rate (Table 2), which was slightly higher at B27 (0.98 ± 0.06) than at B25 (0.95 ± 0.06) (Fig. 3A).

3.2. Height and DSH

There was a significant effect of both site and species on tree height

Table 2

Results of the mixed-effect model analysis (type III analysis of variance) on tree survival rate, height (cm) and diameter at stump height (DSH; mm). * indicates significant effects (P < 0.05).

Dependent variable	Fixed effects	Df	Sum sq.	Mean sq.	F-value	P-value
Survival rate	Site	1	0.0194	0.0194	5.42	0.02 *
	Species	3	0.0217	0.0072	2.01	0.15
	Site × Species	3	0.178	0.0059	1.65	0.18
Tree height	Site	1	20927.2	20927.2	139.63	< 2.2 10 ⁻¹⁶ ***
	Species	3	8225.9	2742.0	18.29	2.8 10 ⁻⁵ ***
	Site × Species	3	4741.0	1580.3	10.54	1.17 10 ⁻⁶ ***
DSH	Site	1	10.8472	10.8472	119.48	< 2.2 10 ⁻¹⁶ ***
	Species	3	9.4329	3.1443	34.63	5.4 10 ⁻⁷ ***
	Site × Species	3	4.3559	1.4520	15.99	9.0 10 ⁻¹⁰ ***

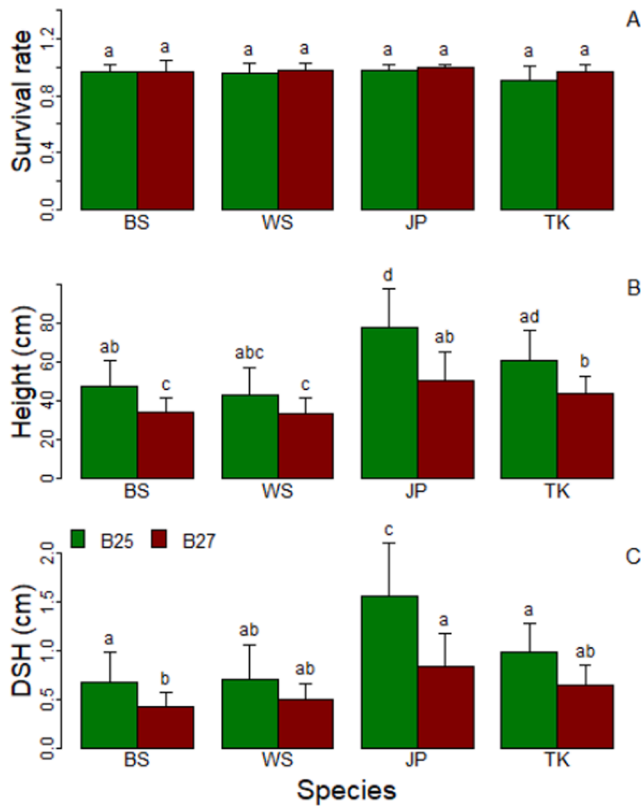


Fig. 3. (A) Survival rate, (B) tree height and (C) diameter at stump height (DSH) for black spruce (BS), white spruce (WS), jack pine (JP) and tamarack (TK) at the B25 and B27 sites, 5 years after afforestation. Values are means \pm SD. Values not sharing the same letter are significantly different across sites and species (Tukey method for comparing mean estimates; $P < 0.05$).

(Table 2). The height was significantly higher in JP (64 ± 17 cm) than in BS (41 ± 8 cm) and WS (38 ± 9 cm, respectively), whereas TK had an intermediate height (53 ± 11 cm). Tree height was higher at B25 than at B27 for all species by on average 42 % (Fig. 3B). The significant interaction between site and species (Table 2) reflected the much higher difference between B25 and B27 for JP (59 ± 30 %) than for the other species (30 ± 17 % for WS, 38 ± 11 % for BS, 38 ± 2 % for TK) (Fig. 3B). In five years, the height of the trees increased by on average 60 % for WS, 70 % for TK, 75 % for BS and 200 % for JP at B25 relative to their initial height shown in Table 1. At the B27 site, this relative increase was smaller averaging about 20 % for WS and BS, 30 % for TK and 110 % for JP.

There was also a site, a species and a site \times species interaction effect on DSH (Table 2), which was higher at B25 than at B27 for all species (by on average 63 %) and significantly higher for JP (1.2 ± 0.57 cm) than for the other species (0.55 ± 0.26 , 0.60 ± 0.30 and 0.81 ± 0.30 cm for BS, WS and TK, respectively) (Fig. 3C). As observed for tree height, the difference between B25 and B27 was much higher for JP (97 ± 63 %) than for the other species (41 ± 25 %, 55 ± 16 % and 58 ± 16 % for WS, TK and BS, respectively).

3.3. Aboveground biomass and apical growth dynamics

The aboveground biomass of the 54 seedlings harvested from the field for aboveground biomass traits analysis corroborated tree height and DSH values measured in the field. Aboveground biomass of harvested trees was higher i) at the B25 than at the B27 site; and ii) in JP than in BS and WS (Fig. 4). There was also a site \times species interaction reflecting the higher difference between B25 and B27 for BS (+300 %) and JP (+250 %) than for WS (+120 %).

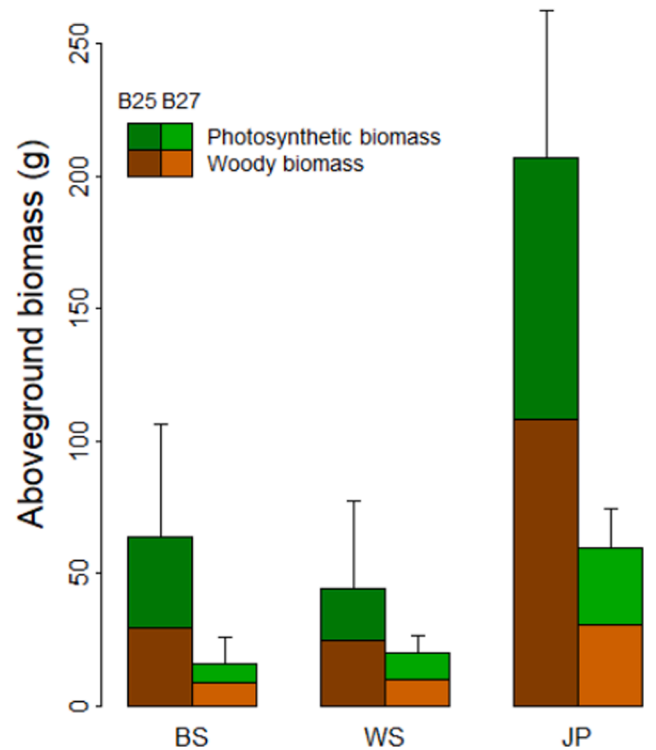


Fig. 4. Aboveground biomass partitioning between photosynthetic and woody biomass for black spruce (BS), white spruce (WS) and jack pine (JP) seedlings at the B25 and B27 sites. Each value is the mean \pm SD ($n = 9$).

Annual apical growth of JP trees increased by on average 92 % from 2016 (13 cm) to 2019 (25 cm) at the B25 site (Fig. 5). The increase was smaller (+30 %) and not significant at B27. In contrast, annual apical growth in BS and WS tended to slightly decrease over time at both sites.

3.4. Photosynthetic/woody biomass ratio

The photosynthetic/woody biomass ratio did not significantly vary among species and sites but there was a significant site \times species interaction (Table 3). The ratio was higher at B25 than at B27 for BS (1.32 ± 0.41 vs. 1.00 ± 0.36), whereas it was higher at B27 than at B25 for WS (1.18 ± 0.49 vs. 0.95 ± 0.30) and similar at both sites for JP (0.92 ± 0.22 vs. 0.92 ± 0.22) (Fig. 6 A).

3.5. Number and mass of needles

The site had a significant effect on the number of needles produced on the 2018 apical shoot (Table 3). The number of needles was higher at the B25 than at the B27 site for all species (Fig. 6 B). It averaged 116 ± 51 at B25 vs. 80 ± 32 at B27 across species. There was a significant species effect on individual needle mass but no site effect (Table 3; Fig. 6 C). The average mass of individual needles was much higher in JP (9.1 ± 2.4 mg) than in both spruce species (1.6 ± 0.4 mg and 0.9 ± 0.2 mg in WS and BS, respectively).

4. Discussion

4.1. Species survival and growth in boreal LWs

The high survival rates measured for the four species (>85 % on average) are in the range of those reported in other plantations throughout Québec after 4–10 years (Gagnon, 2016; Otis Prud'Homme et al., 2018). Surprisingly, the survival rate was slightly but significantly higher at B27 - the site with lower soil fertility - showing

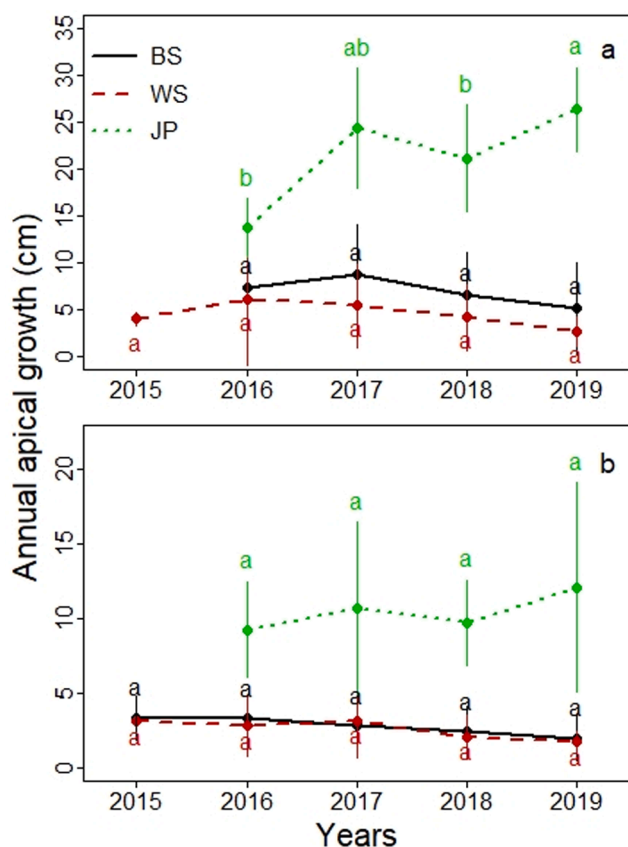


Fig. 5. Annual apical growth (cm) dynamics for white spruce (WS), black spruce (BS) and jack pine (JP) at (a) the B25 and (b) the B27 sites. Each value is the mean (\pm SD) annual apical growth of three trees. Values not sharing the same letter within each species are significantly different (one-way ANOVA followed by Tukey HSD test; $P < 0.05$).

Table 3

Results of the mixed-effect model analysis (type III analysis of variance) for aboveground biomass, photosynthetic/woody biomass ratio, number of needles on the 2018 apical shoot and average individual needle mass. * indicates a significant effect.

Dependent variable	Source of variation	Df	Sum sq.	Mean sq.	F-value	P-value
Aboveground biomass	Site	1	65,940	65,940	79.0	1.2 10^{-11} ***
	Species	2	66,630	33,315	39.9	0.0002 ***
	Site \times Species	2	32,453	16,227	19.4	7.3 10^{-7} ***
Photosynthetic / woody biomass ratio	Site	1	0.002	0.002	0.027	0.87
	Species	2	0.228	0.114	1.37	0.29
	Site \times Species	2	0.708	0.354	4.25	0.02*
Number of needles on the apical shoot	Site	1	14,411	14,411	9.66	0.003 **
	Species	2	868	434	0.29	0.75
	Site \times Species	2	1217	608	0.41	0.67
Average needle mass	Site	1	0.17	0.17	0.08	0.78
	Species	2	639.24	319.62	183.45	< 2 10^{-16} ***
	Site \times Species	2	1.65	0.83	0.47	0.66

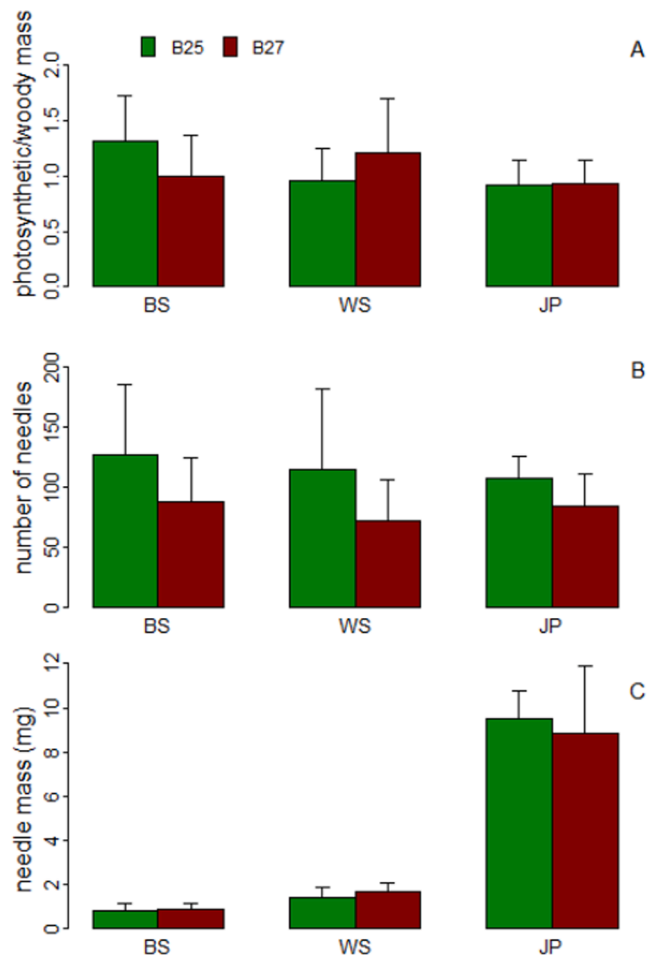


Fig. 6. Mean A) photosynthetic/woody biomass ratio, B) number of needles per apical shoot (year 2018) and C) individual needle mass (mg) for black spruce (BS), white spruce (WS) and jack pine (JP) at the B25 and B27 sites.

that although soil fertility impacts tree growth it does not necessarily decrease survival rate, at least within the first five years. The establishment phase is crucial for seedling survival in tree plantations as they are particularly sensitive to different environmental stresses (Lamhammedi and Bernier, 1994; Grossnickle, 2000). Therefore, the present results are encouraging and support the possibility of using a variety of species for boreal LW afforestation. Nevertheless, survival rate survey must be pursued on a longer time scale to capture the potential effects of extreme climate events, which may decrease survival rate of the tested species. The central and northern parts of Quebec are indeed expected to be particularly affected by climate change in the next five decades (Ouranos, 2015), which may induce increased water stress in the summer as well as late fall and early spring frost damage due to phenological maladaptation. The relative performance of each species may thus shift in the future.

Our data clearly show a much higher growth at the B25 than at the B27 site for all species, with tree height and DSH higher by on average 42 % and 63 % across species, respectively. The aboveground biomass of the 54 trees harvested from the field confirmed this difference, being on average three times higher at B25 than at B27 (Fig. 4). This difference was due to better soil fertility (Table 1) rather than to a milder climate since the B25 site is located at the same altitude but further north relative to B27 (Fig. 1). Although the discrepancy between the two sites may shrink over time, this clearly indicates that site selection may be as important as species selection for LW afforestation to create rapid carbon sinks, and that soil fertility is a crucial factor for modeling C sequestration dynamics in LW afforestation projects. In addition, our

data revealed that the magnitude of growth difference between the two sites differed among species, as shown by the significant species \times site interaction term for both height and DSH (Table 2). On average, JP benefited more from better soil fertility than the other species (59 % and 97 % higher height and DSH at B25 than at B27, respectively vs. 30–38 % and 41–58 % for the other species), pointing toward a higher growth limitation for JP than for the other species. This is opposite to what we hypothesized as this species' ability to uptake N from the highly N-depleted mineral soil has been reported (Visser, 1995; Houle et al., 2014). Hence, we expected a lower sensitivity of JP to soil fertility compared to the other species. This, however, corroborates *in situ* N fertilization experiments which have shown that JP benefits from N fertilization regardless of site quality, whereas N-based fertilization increases BS's short-term productivity only in good and excellent quality sites (Newton and Amponsah, 2006). Another study, conducted in controlled conditions, showed that TK's productivity was more responsive to N fertilization than that BS, but that its growth declined more dramatically than that of BS in poor or deteriorating conditions, reflecting BS's more conservative growth strategy (Islam and Macdonald, 2005).

Our data also clearly indicate a much higher relative elongation rate for JP than for TK and the spruce species in boreal LWs within five years following afforestation. The height of JP tripled at B25 and doubled at B27 between the planting date and 2019. This relative elongation rate was much lower in the other species (ranging from 60 to 75 % at B25 and 20–30 % at B27), especially in WS. This corroborates the higher biomass and C accumulation of JP than in BS in other afforested boreal LWs in the region (Hébert et al., 2006; Fradette et al., 2021). Such a high growth rate for JP is commonly reported in the first 15–20 years after establishment but tends to decline with time afterwards (Rudolph and Laidly, 1990). The main reason for JP's higher growth rate at the study sites, where the organic horizon is thin, may be its abovementioned very strong ability to uptake N from N-depleted mineral soil horizons (Houle et al., 2014). This species also has a good tolerance to water stress and drought (Hébert et al., 2006) and low sensitivity to growing season precipitation (Dietrich et al., 2016), a high N use efficiency (Robinson et al., 2001) and a great rate of mycorrhizal colonization with various ectomycorrhizal fungal species (Visser, 1995). Some of these characteristics, particularly its deeper root system and possibly its higher mycorrhization rate, may explain its growth dynamics following afforestation. In JP, the length of the annual apical shoot almost consistently increased from one year to the other, particularly at the B25 site (Fig. 5a), indicating JP's ability to obtain nutrients and water from the soil rapidly after planting. In contrast, the apical growth of BS and WS remained constant or tended to decrease almost consistently following afforestation, indicating a comparatively lower ability of these species to uptake nutrients from their new environment. The declining growth rate with time in spruce species suggests that trees first relied on nutrient reserves from the nutrient-rich soil cores they were planted with or on internal recycling to support their annual growth, and then had difficulty to access soil resources in the following years. Slow expansion of the root system outside the soil cores following planting has been suggested by $\delta^{15}\text{N}$ analyses for balsam fir trees in nearby boreal forests (Marty et al., 2020). Overall, these results show that JP is a very well-suited species for LW afforestation, where the organic soil is very thin or where the trees are planted in the mineral soil (i.e., in the furrow created by soil scarification). The good survival and growth performances of TK are also noticeable as it generally occurs in boreal peatlands (Eyre, 1980) and is well adapted to prolonged soil flooding (Islam and Macdonald, 2004). However, TK has been shown to tolerate a large range of soil conditions, including mineral soils with a shallow surface of organic layer (Johnston, 1990), and to be resistant to harsh conditions such as those occurring at treelines. In the past decades, both vertical and radial growth of TK as well as TK stand densification have been observed at the northeastern Quebec treeline in response to regional warming, contrasting with the inertia of black spruce (Dufour-Tremblay

et al., 2012). This observation suggests that TK may actually thrive in the future in LWs, where climate and soil conditions are harsh. The high performance and rapid growth of larch species have also been documented in plantations of northern and eastern Europe (Godvod et al., 2018; Cukor et al., 2020; Dubenok et al., 2020; Zeidler et al., 2022). In addition, planting TK offers other advantages in a context of global change. Its deciduous foliage may not reduce albedo to the same extent as other conifer species at least in winter and early spring. The reduction of albedo following afforestation at high latitude is a matter of concern as it produces a positive radiative forcing, which may in some circumstances offset the cooling effect of C sequestration (Betts, 2000; Bala et al., 2007; Bernier et al., 2011). The comparatively lower growth of spruce species is in good agreement with their well known intrinsic low relative growth rate in the first years following establishment (Nienstaedt and Zasada, 1990; Lamhamedi and Bernier, 1994). Black spruce is also more susceptible to water stress than other boreal conifers of Eastern Canada, which can reduce initial growth after planting (Bernier, 1993; Lamhamedi and Bernier, 1994).

4.2. Aboveground biomass characteristics

The differences in height and DSH among species and sites resulted in large differences in aboveground biomass. In the 54 randomly harvested seedlings it was on average i) 4 times, 3.5 and 2.5 higher at B25 than at B27 for BS, JP and WS, respectively; and ii) \sim 4 times higher in JP than in BS and WS, confirming the previously observed higher growth rate of JP in boreal LWs (Fradette et al., 2021). The variation in photosynthetic biomass between the two sites (Fig. 4) did not result from higher mass of individual needles but rather from a higher number of needles per shoot (Table 3; Fig. 5). The mass of individual needles was indeed surprisingly constant between sites, despite large differences in aboveground biomass, suggesting that the size of needles is strictly constrained by developmental factors.

Interestingly, the photosynthetic / woody biomass ratio did not significantly vary among sites and species despite large variation in aboveground biomass (Table 3). Whereas the variation in aboveground / belowground biomass ratio among species and biomes is well documented (Qi et al., 2019), much less is known about aboveground biomass partitioning between photosynthetic and woody biomass among conifer species and in response to soil fertility. In evergreen species, the photosynthetic / woody biomass ratio is theoretically influenced by the number, the mass and the longevity of needles annually produced per stem segment, as well as by wood properties (e.g., density, radial vs. longitudinal growth). We therefore expected a large variability in this ratio among species and sites. Although there was a large range in the photosynthetic / woody biomass ratio among the 54 seedlings (0.49–1.88), the site appeared to have no effect on this variation (Table 3). In addition, the ratio was on average surprisingly similar among species, needles accounting for about 50 % of aboveground biomass in the three species ($52 \pm 9\%$, $50 \pm 10\%$ and $47 \pm 6\%$ for BS, WS and JP, respectively). However, this ratio responded differently to soil conditions depending on the species (site \times species interaction; Table 3). The photosynthetic / woody biomass ratio was higher at B25 than at B27 for BS, whereas the contrary was observed for WS and no difference was found for JP (Fig. 5). Hence, our hypothesis that a higher ratio would be observed at the more fertile site was supported only for BS. The slightly lower ratio at B25 for WS occurred despite a higher needle production and similar individual needle mass at this site (Fig. 6B), suggesting that needle longevity may have been lower at the more fertile site (B25), which contrasts with what has been observed in other evergreen species (Marty et al., 2009, 2010). The lower annual biomass production at B27 likely reduced N demand from older needle cohorts relative to the B25 site, which can result in longer leaf longevity in some species (Pornon et al., 2011).

5. Conclusion

Our data show that survival rate in these afforested boreal open woodlands was high for all the tested species, regardless of soil fertility. This result is encouraging as the first years following planting are crucial for seedling establishment due to their sensitivity to environmental stresses during this period. Soil fertility markedly impacted seedling growth in the four species, although JP benefited more from better soil quality than the other species. Interestingly, the photosynthetic / woody biomass was similar across species and did not vary with site, despite large variations in aboveground biomasses. In addition, variations in photosynthetic biomass was driven by the number of needles rather than by their individual mass, which was constant between sites. Overall, our study indicates that soil fertility is an important factor to consider for plantation site selection and which should be accounted for when modeling C accumulation dynamics in plantations. Our data also confirms the higher growth rate of JP relative to spruce species – likely due to its rapid access to soil nutrient resources – and hence its potential for afforestation of open woodlands aimed at producing C offsets. Surprisingly, TK also performed well although this species is more associated to waterlogged conditions. The study must however be prolonged to validate whether these observations persist over time and assess the impact of extreme climate events on both the survival and the growth of trees in the long term.

CRedit authorship contribution statement

Charles Marty: Conceptualization, Methodology, Data curation, Writing – original draft. **Olivier Fradette:** Conceptualization, Methodology, Project administration, Writing - review & editing. **Claude Villeneuve:** Supervision, Project administration, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120601>.

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