Determining and projecting realised genetic gains: Results from early-stage spruce improvement programmes in New Brunswick, Canada

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Abstract

Two series of realised genetic gain tests of large plots, one for black spruce (*Picea mariana* (Mill.) B.S.P.) and one for white spruce (*Picea glauca* [Moench] Voss), were established in the early 1990s in New Brunswick, Canada, to investigate realised gains from planting improved seedlots representing early-stage tree improvement activities. Individual-tree growth was recorded up to age 15 (one-quarter of their rotation age). Four improved seedlots were included in the black spruce gain test. Planting the superior stand seedlot (CAN101) could obtain moderate gain (7.0% in volume/tree and 3.5% in volume/ha at age 15). Growth improvement for the seedlot (UNROG) collected from a seedling seed orchard (FRA_SSO) established using phenotypically selected plus trees was negligible but genetic roguing improved the FRA_SSO seedlot's growth, resulting in 3.3 and 2.1% increase in 15-yr volume per tree and per hectare, respectively. The highest gain was observed by deploying the elite half-sib family (01-15), which resulted in a gain of 27.6% in 15-yr volume/ha. Three improved seedlots were included in the white spruce realised-gain test. The seedlot (OVSSO) collected from a provenance seedling seed orchard had 9.2% more volume/ha at age 15 years. Much higher gains were observed in the seedlots collected from an unrogued clonal seed orchard (DNR_CSO). Mixed cone collections from the DNR_CSO achieved 25.6% more volume/ha at age 15 than the unimproved seedlot. Practicing supplemental mass pollination with unimproved pollen in the DNR_CSO greatly reduced its seedlot gains, i.e. 12.9% in 15-yr volume/ha. In both tests, the gain varied with age or site index. Realised gains in this study differed greatly from those observed in the corresponding genetic tests using small-plots. This suggests that using a small plot size for trials could greatly bias the actual gains possible on a plantation-scale, particularly when using seedlots obtained from orchards.

Keywords: black spruce; white spruce; large-plot gain test; seed orchard.

Introduction

For justifying and future planning of tree breeding programmes, and for predicting forest outturns, demonstrating and quantifying realised genetic gain can be extremely important, yet challenging to achieve. While genetic gain has often been demonstrated (e.g. Eldridge, 1982; Dhakal et al., 1996; Carson et al., 1999a; Lambeth, 2000; Li et al., 2001; Andersson et al., 2003; Chmura et al., 2003; McInnis & Tosh, 2004; St Clair et al., 2004; Vergara et al., 2004; McKeand et al., 2006; Weng et al., 2008b), quantifying realised gain (e.g. Dhakal et al., 1996; Carson et al., 1999a; Lambeth 2000; St Clair et al., 2004; Vergara et al., 2004) is typically tentative, especially in respect of final crop performance. Here, we report preliminary estimates of realised genetic gains from selective breeding of two species of spruce (*Picea*). Black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* [Moench] Voss) are the most important commercial species planted in New

Brunswick (NB), Canada, where approximately 30 and 15 million seedlings, respectively, are being planted annually. Due to their economic importance, the New Brunswick Tree Improvement Council (NBTIC) started improvement activities for both species in mid-late 1970s. Similar to other important commercial species elsewhere, the program started with finding superior stand- and/or provenance sources through extensive stand- and/or provenance tests (NBTIC, 1977; 1978). Following that, 1233 black spruce and 414 white spruce plus trees were phenotypically selected across NB to start the first-generation breeding programs (Simpson & Tosh, 1997). Based on a combination of available information at the time and species biology, two different strategies were adopted (Fowler, 1986). For black spruce, a strategy called seedling seed orchard (SSO) paired with family tests was used. This was done by collecting seed from the plus trees, followed by establishing SSO and family tests concurrently. The orchards usually included a large number of families planted at narrow spacing (1 x 2 m) so that they could be intensively rogued. Overall, 80 ha of SSO were established from 1978 to 1986. For white spruce, a strategy employing clonal seed orchards (CSO) and control-pollinated progeny tests was adopted. This was implemented by grafting the plus trees into the CSO and breeding gardens. Polycross pollinations were done on the clones in the breeding gardens using pollen collected from unrelated trees, and the resulting seed was used to establish progeny tests. A total of 41 ha of CSO was set up from 1985 to 1990 in NB. The black spruce SSO started producing seed crops steadily in 1987, followed by the white spruce CSO in 1991(Simpson & Tosh, 1997).

Over the last 30 years, almost all spruce plantations in NB Crown Lands were established using seedlots of various improvement levels. In order to develop intensive and sustainable management plans for these plantations, quantifying realised genetic gains (ΔG_R) from these seedlots is important. A demonstration of ΔG_R of improved seedlots requires planting improved and unimproved commercial seedlots under controlled environments of operational conditions. Often, tree breeders compare seedlot performance in small-plot (i.e. single-tree or row-plot) genetic tests to minimise any environmental effects (Talbert et al., 1985; Dhakal et al., 1996; Li. et al., 1998; McInnis & Tosh, 2004). These ΔG_R estimates, however, may be biased, as small plots do not closely resemble the plantation conditions. Accurate prediction of ΔG_R requires establishing large-plot gain tests to mimic operational conditions (Weng et al., 2008b). Since large-plot gain tests are expensive to establish and maintain, only a few studies have utilised this design to explore ΔG_R from operational tree improvement activities. Information from large-plot gain tests is only available in pine species, including radiata pine (*P. radiata* D. Don) (Eldridge, 1982; Carson et al., 1990a, b), slash pine (*P. elliottii* Englem var. *elliottii*) (Tankersley et al.,

1983; Vergara et al., 2004), Scots pine (*P. sylvestris* L.) (Chmura et al., 2003), loblolly pine (*P. taeda* L.) (Lowerts, 1987), and jack pine (*P. banksianna* Lamb.) (Weng et al., 2008b). So far, ΔG_R from tree improvement activities for other species, such as black or white spruce, are limited. Furthermore, comparisons of ΔG_R observed in large plots and small plots of the same seedlot have rarely been reported.

In order to explore both growth trajectories and productivity of genetically improved plantations, long-term, large-plot gain tests for the important commercial species were established in NB by the NBTIC in the early 1990s. This article reports the results of two of these tests, one for black spruce and one for white spruce. The objectives of this paper were: (1) to quantify ΔG_R in growth traits up to one-quarter of their rotation ages (about 60 years) from early-stage tree improvement activities; and (2) to compare these ΔG_R to those observed in small plot genetic tests. These results will provide valuable insights for breeding strategy development, forest management planning, and incorporating tree improvement effects into growth and yield modelling.

Materials and Methods

1991 black spruce gain test (BSRGT)

Black spruce seedlots

In 1991, a gain test was established to quantify actual ΔG_R in black spruce early-stage improvement activities. In total, five seedlots were included in the test: two stand seedlots (CAN101 and TAYBRK), two orchard seedlots (UNROG and 1STROG), and one half-sib family seedlot (01-15). CAN101 represents an elite-stand seedlot from a site at 46° 10' N and 65° 09' E, while the TAYBRK is an average-performing stand seedlot from a site at 47° 20' N and 66° 05' E (NBTIC, 1977). TAYBRK seed is consistently planted in all NBTIC genetic tests as a checklot and it was used also for that purpose in this study. The UNROG and 1STROG seedlots were both collected from the same site, the Fraser seedling seed orchard (FRA_SSO). The FRA_SSO is located at 46° 87' N and 67° 43' E near Plaster Rock and was established in 1979. The FRA_SSO was originally 4 ha in area and included 184 families, derived from plus trees selected for height growth across NB. An associated family test for the FRA_SSO was established across NB at six sites in 1979 (NBTIC, 1979). Based on the 10-year height growth results from this family test, the whole orchard was genetically rogued in early 1989. This procedure removed 60% of the original families (NBTIC, 1979). Both the UNROG and 1STROG seedlots represent samples of bulk mixed cone collection from the FRA_SSO: the UNROG seed was collected in 1988 before the FRA_SSO was rogued, while the 1STROG seed was collected in 1989 after the FRA_SSO was rogued.
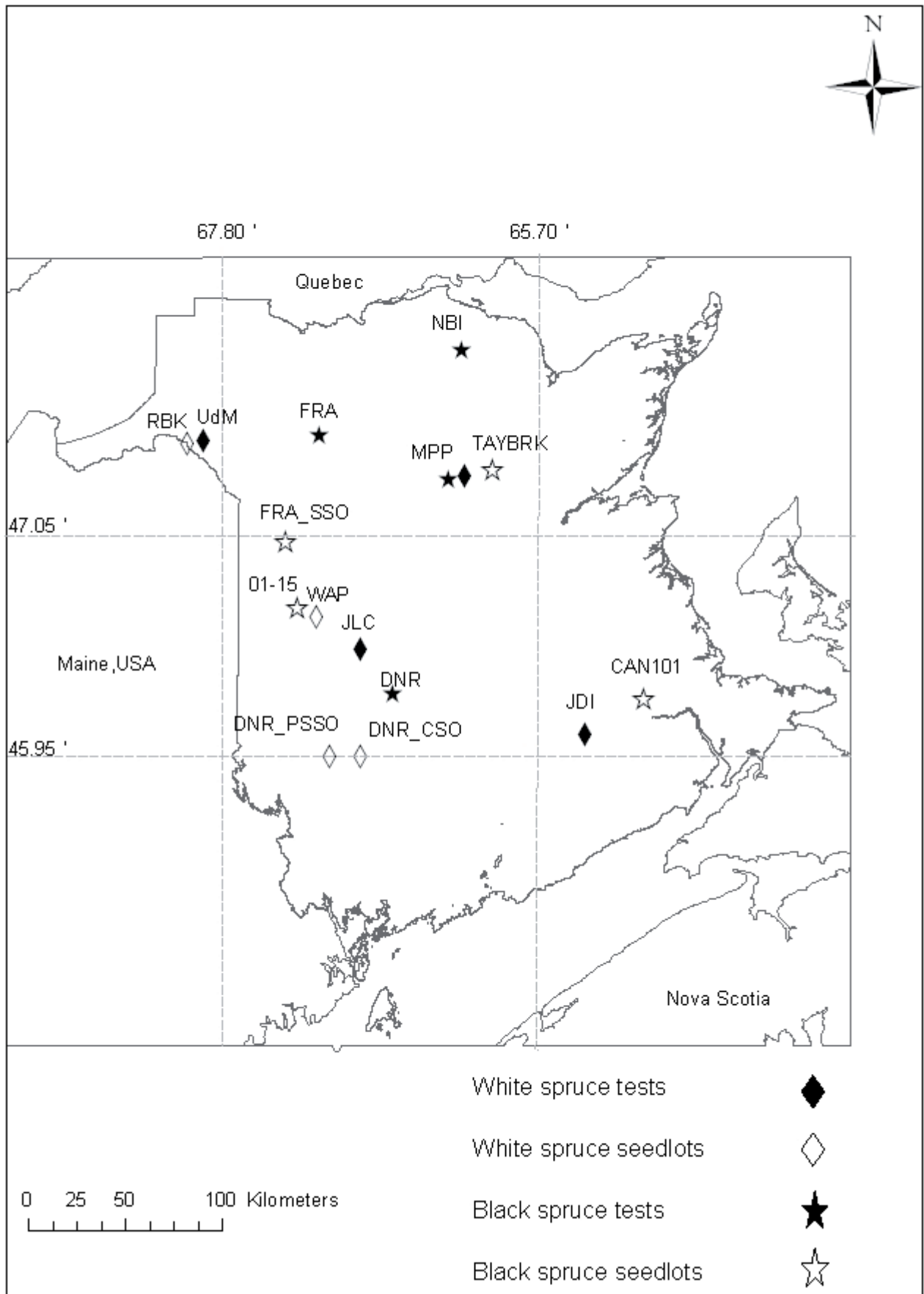
FIGURE 1: Geographic locations for seedlots and testing sites in the black spruce and white spruce realised gain tests.

The elite half-sib family seedlot (01-15) was identified on the basis of superior height growth at 10 years in the FRA_SSO family test (NBTIC, 1979). Note that seed of 01-15 in this study was collected from its parent tree in its natural stand at 46° 48'N and 67° 33'E, not from the FRA_SSO (where it is also planted). The relative geographic location of each seedlot can be found in Figure 1.

Black spruce seedling production

The seedlings of all seedlots were grown at the Kingsclear tree improvement greenhouse. The seed were sown in Feb., 1991 in Can Am #3 containers using a 3:1 peat : vermiculite growing medium. The greenhouse was maintained at 21 °C during the daytime and 15 °C at night. A soluble fertiliser schedule was applied to the growing medium. When the seedlings were 18 weeks old, they were moved out to a shaded area. The test was then planted in July, when the seedlings were 6 months old.

Black spruce test sites

The BSRGT was established at four test sites: DNR; FRA; MPP; and NBI. The geographical location of each of these sites is shown in Figure 1. Table 1 contains details of summer rainfall and the annual number of days with a temperature above 5 °C at each site. These test sites are located within one breeding zone and represent the main deployment region for seed from the FRA_SSO. All the test sites were scarified

with chains, and slash was removed before planting (NBTIC, 1991). The conditions for each test site were expressed as 'site index at age 50' (SI50), which was calculated using the estimated average height of the top 20 trees (roughly analogous to the 250 tallest trees per ha) of the TAYBRK checklot (Ker et al., 1983). The SI50 was lowest for the MPP site, but the SI50 values of the three other sites were comparable (Table 1). A randomised complete block design of four blocks and large plots was used at each site. Each plot consisted of 64 trees of a seedlot planted in an 8 row x 8 column design at a spacing of 2 x 2 m. As no border trees were planted around plots, only the inside 36 trees (6 row x 6 column) were measured, to reduce effects of competition between seedlots. Available data included tree heights at ages 5, 10 and 15 years (HT_5, HT_{10} and HT_{15}), and DBH at age 15 (DBH_{15}). Individual-tree volume data at age 15 (VOL_{15}/tree) was computed using a volume equation [1] for black spruce derived by Honer et al., (1983):

$$VOL_{15}/tree = \frac{0.0043891 * DBH_{15}^2 * (1-0.04365*a_1)^2}{a_2 + (0.3048*a_3/HT_{15})} \quad [1]$$

where a_1 (=0.164), a_2 (=1.588) and a_3 (=333.364) are regression coefficients. These data are shown in Table 1. Volume per hectare at age 15 years (VOL_{15}/ha) was calculated by adding individual tree volumes scaled by a tree factor of 69.44 which approximates a plot size of 144 m².

TABLE 1: Site information for realised genetic gain tests in New Brunswick.

Site	Rainfall (mm)[a]	GDD (5 °C)[b]	SI50 (m)[c]	VOL_{15}/tree (m³)
Black spruce gain test				
DNR	400-450	1600-1800	17.0	0.0202
FRA	450-500	1200-1400	16.5	0.0224
MPP	500-550	1400-1600	15.0	0.0138
NBI	450-500	1400-1600	16.2	0.0174
White spruce gain test				
JDI	400-450	1600-1800	19.2	0.0243
JLC	450-500	1400-1600	17.8	0.0202
MPP	450-500	1400-1600	15.8	0.0067
UdM	450-500	1400-1600	16.9	0.0145

[a] May to September rainfall;
[b] Annual growing degree days above 5 °C;
[c] Estimated Site Index at age 50 years old.

1993 white spruce realised gain test (WSRGT)

White spruce seedlots

Five seedlots were included in this test, CSO1, CSO2, OVSSO, RBK and WAP. The CSO1 and CSO2 seedlots were both collected from the DNR clonal seed orchard (DNR_CSO) situated at 45° 89' N and 66° 95' E near Lower Queensbury. The DNR_CSO was established in 1985 using 50 white spruce clones. These clones were grafted from plus trees selected based on height growth, stem straightness and crown form across NB. Supplemental mass pollination was done on the clones in this orchard in 1991. A mixture of pollen was used which had been collected from 20 unrelated natural-stand trees located either at Woodlasstook Park or Acadia Forest Research Station in 1990. The CSO2 seedlot represented a mixed cone collection following the supplemental mass pollination in 1991, while the CSO1 seedlot represented a mixed cone collection from 1992. Thus, both the CSO1 and CSO2 seedlots come from the same orchard stock but represent different pollen qualities. The third seedlot, OVSSO, was a mixed cone collection in 1992 from the DNR white spruce provenance seedling seed orchard (DNR_PSSO) at Pokiok (45° 87' N and 67° 11' E). The DNR_PSSO was established in 1978 using seed collected from average trees grown in the Ottawa Valley area of Ontario (latitude ranging from 44° 55' to 45° 56' N and longitude ranging from 77° 20' to 78° 05' E). The Ottawa Valley provenance has been demonstrated to be one of the best provenances in terms of height growth in NB (Fowler & Coles, 1977). The DNR_PSSO had been genetically rogued initially in 1988 based on its associated family test, also planted in NB, leaving 36 of the original 72 families. Two stand seedlots, RBK (47° 31' N and 68° 13' E) and WAP (46° 53' N and 67° 22' E), were planted for comparison. These two stand seedlots were demonstrated to have average performance in height growth in stand tests, and are consistently planted in all NBTIC genetic tests as checklots. The data from these two seedlots was averaged to provide one set of checklot data. The relative geographic location of each seedlot is shown in Figure 1.

White spruce seedling production

The greenhouse and corresponding procedure for the seedling production were the same as those for the BSRGT. The seed was sown on January, 1993.

White spruce test sites

The WSRGT was established at four sites: JDI; JLC; MPP; and UdM. The geographical location of each of these sites is shown in Figure 1. Table 1 contains details of summer rainfall and the annual number of days with a temperature above 5 °C at each site. These sites belong to same breeding zone and represent the main reforestation area for white spruce in NB. The SI50, calculated using the average HT_{15} of the 20 tallest trees from each of the RBK and WAP checklots per site, ranged from 15.8 (MPP) to 19.2 m (JDI). The site preparation, test establishment, experimental design and tree measurement were the same as those for the BSRGT. The VOL_{15}/tree and VOL_{15}/ha were calculated using the same formulae as black spruce, but with different coefficients of a_1 (=0.176), a_2 (=1.440) and a_3 (=342.175).

Data analysis for both tests

The validity of the growth data was first inspected using the SAS univariate procedure (SAS Institute Inc., 1990). Overall, less than 0.2% of the observations were detected as outliers (those located outside three interquartile ranges) and removed from further analyses. By species and trait, the cleaned data was subjected to analysis of variance (ANOVA) with the following linear model:

$$y_{ijkl} = \mu + I_i + b_{j(i)} + S_k + ls_{ik} + bs_{jk(i)} + e_{ijkl}$$

where y_{ijkl} is the lth tree observation of the kth seedlot planted in the jth block within the ith site, μ the overall mean, I_i the random ith site effect, $b_{j(i)}$ the random jth block within ith site effect, S_k the fixed kth seedlot effect, ls_{ik} the random interaction effect between site and seedlot, $bs_{jk(i)}$ the random interaction effect between block and seedlot, and e_{ijkl} the random error. Analyses of individual sites were also carried out using the same model but without site and its interaction with the seedlot. The ANOVA on survival was done based on the plot survival, using the same model but without block and its interaction with the seedlot. The SAS PROC GLM and PROC MIXED (Littell et al., 2002) were used for the analyses of variance and to calculate the least-squares means of seedlot. The CONTRAST option was used to compare significance levels of differences between improved and checklot seedlots, which was only done for those traits showing significant seedlot differences. Note that here and elsewhere in the text, except where otherwise indicated, the term significant refers to $p < 0.05$.

The TAYBRK seedlot was used as the checklot for the BSRGT while the average performance of the RBK and WAP seedlots were used as the checklot for the WSRGT in this study. The ΔG_R were calculated as differences between the improved and checklot seedlots; the difference was subsequently expressed as a percentage of the checklot on both an individual-tree and a per-hectare basis. Due to limited data points, the patterns of ΔG_R following SI50 or age were simply investigated using the SAS PLOT procedure (SAS Institute Inc., 1990).

Results

Survival

The 15-year survival was 84%, down 2% from year 10 and 7% from year 5 for the BSRGT, and was 85%, down 1% from year 10 and 9% from year 5 for the WSRGT. The survival varied significantly ($p<0.01$) from site to site, i.e. ranging from 79% (FRA) to 92% (DNR) for the BSRGT and from 70% (UdM) to 92% (MPP) for the WSRGT at age 15 years. There was no significant difference in survival among seedlots for both tests, with ranges of 79% (UNROG) to 86% (01-15) for the BSRGT and 83% (OVSSO) to 86% (CSO2) for the WSRGT at age 15 years. Overall, these survivals were high enough to ensure an accurate comparison between improved seedlots and checklots.

Analyses of variance for growth traits

Results of the ANOVA are listed in Table 2. For the BSRGT, the variance due to site effects differed significantly ($p<0.01$) from zero, with site means (data not shown) ranging from 537 (MPP) to 640 cm (DNR) in HT_{15} and from 0.0138 (MPP) to 0.0224 m^3

(FRA) in VOL_{15}/tree. The differences among seedlots were significant ($p<0.01$) for all traits, with 01-15 always being the best seedlot, followed by CAN101, 1STROG, the TAYBRK checklot and UNROG (Table 2). The seedlot ranking was not significantly changed from site to site as evidenced by non-significant site x seedlot interaction (Table 2). The significant block and block x seedlot interaction effects were detected in most traits (Table 2), but they only explained a small portion (<5%) of the total phenotypic variation. The differences with the TAYBRK checklot were significant in all traits for the 01-15 seedlot, in HT_5 and HT_{10} for the CAN101 seedlot, but not for all other cases (Table 2). Compared to the analysis across sites, detecting statistically significant differences among seedlots was more difficult at each individual site (details not shown). For example, the among-seedlot differences in VOL_{15}/tree were significant at two better sites (DNR and FRA), but not at the poorer sites (MPP and NBI).

Similar ANOVA results to the BSRGT were also found in the WSRGT. The site effects were even stronger, with site means ranging from 420 (MPP) to 612 cm (JDI) in HT_{15} and from 0.0067 (MPP) to 0.0243 m^3 (JDI) in VOL_{15}/tree (Table 1). All improved seedlots

TABLE 2: *F*-value[1] and significance level[2] of analyses of variance on height at age 5, 10 and 15 years (HT_5, HT_{10} and HT_{15}), DBH, and volume at age 15 years (DBH_{15} and VOL_{15}/tree) for the black spruce and white spruce realised gain tests.

Source	d.f.	HT_5	HT_{10}	HT_{15}	DBH_{15}	VOL_{15}/tree
Black spruce gain test						
Site (S)	3	58.78**	97.12**	45.04**	32.56**	56.10**
Block(S)(B)	12	3.67**	2.34*	1.83	1.38	1.12
Seedlot	4	8.53**	9.52**	5.95**	5.49**	6.72**
01-15[3]	1	11.69**	23.84**	18.36**	9.13*	18.13**
1STROG[3]	1	0.46	1.59	2.95	0.33	0.27
CAN101[3]	1	11.71**	6.01*	3.27	0.06	1.03
UNROG[3]	1	1.39	0.46	0.01	1.99	0.14
S x Seedlot	12	1.49	1.49	1.97	1.08	1.82
B x Seedlot	48	3.38**	3.37**	2.90**	2.61**	2.56**
White spruce gain test						
Site (S)	3	52.88**	88.99**	72.95**	31.54**	59.77**
Block(S)(B)	12	1.89*	2.02*	3.28**	3.04**	3.28**
Seedlot	4	5.62**	5.35**	8.71**	8.95*	8.50**
CSO1[3]	1	12.46**	19.27**	27.92**	32.10**	29.62**
CSO2[3]	1	8.09*	3.74	3.79	3.21	4.56
OVSSO[3]	1	10.97**	2.88	4.33	9.20*	7.77*
S x Seedlot	12	1.00	0.16	0.78	0.92	0.78
B x Seedlot	48	4.06**	2.92**	2.61**	1.99**	2.61*

[1] The denominators of the *F* test were a pseudo-error term for S (provided in type3 option in PROC Mixed), B x seedlot for B, S x Seedlot for Seedlot, B x Seedlot for S x Seedlot, and error for B x Seedlot;
[2] * at α=0.05 and ** at α=0.01;
[3] Testing against the checklot TAYBRK for black spruce and the average of RBK and WAP for white spruce.

TABLE 3: Realised genetic gains (ΔG_R) in percentage by across sites and single site (ranges) for height at age 5 (HT_5), 10 (HT_{10}), and 15 (HT_{15}), DBH at age 15 (DBH_{15}) and volume at ages 15 and 50 (VOL_{15} and VOL_{50}) in the 1991 black spruce and 1993 white spruce tests relative to the relevant checklot.

Seedlot	ΔG_R													
	HT_5		HT_{10}		HT_{15}		DBH_{15}		VOL_{15}/tree		VOL_{15}/ha		VOL_{50}/ha*
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
Black spruce gain test													
01-15	9.3	4.0~13.8	11.7	9.6~15.7	9.9	4.9~14.7	5.9	3.9 ~ 6.9	25.3	15.1~28.9	27.6	3.2~41.0	3.8
CAN101	9.1	2.9~13.9	5.8	-2.5 ~ 9.3	4.9	-0.8 ~ 7.5	0.7	-4.7 ~ 2.4	7.0	-7.3~13.9	3.5	-20.7~16.1	0.2
1STROG	1.8	-1.1 ~ 3.2	2.9	0.4 ~ 4.2	3.6	2.1 ~ 5.9	-1.0	-4.5 ~ 0.2	3.3	-2.8 ~ 7.9	2.1	-13.0 ~ 6.5	0.3
UNROG	-3.3	-8.1~ 0.6	-1.4	-8.4 ~ 1.7	-0.2	-5.5 ~ 5.8	-2.2	-6.7 ~ 0.7	-1.3	-10.1 ~ 7.4	-6.1	-28.2~11.5	-10.6
White spruce gain test													
CSO1	7.9	3.9~17.6	8.5	1.4~23.5	7.4	3.1~13.6	9.4	5.6~15.6	21.8	14.5~39.0	25.6	10.2~50.4	3.0
CSO2	6.4	-7.2~11.3	3.5	-5.5 ~ 7.1	2.3	-1.1 ~ 4.8	2.6	-3.4 ~ 4.3	7.8	-3.7~10.1	12.9	-1.9~34.2	1.8
OVSSO	7.3	1.9~13.6	3.5	0.4 ~ 6.8	2.7	1.3 ~ 6.3	5.1	-1.1~11.7	11.0	-4.3~24.9	9.2	-0.9~17.6	0.9

* Volume at age 50 was predicted using the STAMAN package

grew significantly faster and larger than the RBK/WAP checklot at all ages, with CSO1 being the best seedlot while the OVSSO and CSO2 seedlots were comparable (Table 3). Significant differences with the RBK/WAP checklot were detected in all traits for the CSO1 seedlot, in HT_5, DBH_{15} and VOL_{15}/tree for the OVSSO seedlot and only in HT_5 for the CSO2 seedlot (Table 2). Single-site analyses found that detecting significant differences among seedlots was easier at the poorer sites (data not shown). For example, the significant among-seedlot differences in VOL_{15}/tree were found at the MPP and UdM sites, but not at the JDI and JLC sites.

Realised genetic gain (ΔG_R)

The ΔG_R for both species are listed in Table 3. For the BSRGT, the ΔG_R in HT_{15} were positive for all improved seedlots but the UNROG. The selection for height resulted in a moderate increase in DBH_{15} for the 01-15 seedlot (mean 5.9%), but had negligible or even negative effects for the CAN101 seedlot (mean 0.7%) and for the two FRA_SSO seedlots (1STROG and UNROG; means $\leq$ -1.0%). Correspondingly, the ΔG_R in VOL_{15}/tree was high for 01-15 (mean 25.3%), moderate to low for CAN101 (mean 7.0%) and 1STROG (mean 3.3%), but negative for UNROG (mean -1.3%). The respective ΔG_R in VOL_{15}/ha were 27.6, 3.5, 2.1, and -6.1%. Similarly, all improved white spruce seedlots enhanced height growth and, as expected, the CSO1 had the largest ΔG_R, followed by OVSSO and CSO2. Even if the selection was primarily on height growth, each seedlot had a slightly higher improvement in DBH_{15} than in the respective HT_{15}. Correspondingly, the respective ΔG_R in VOL_{15} was high, being 21.8, 11.0 and 7.8% on an individual-tree basis and 25.6, 9.2 and 12.9% on a per-hectare basis.

The ΔG_R in height also varied with age (Table 3). For both species, the trend of decreasing ΔG_R with age was found for most of the seedlots, although those of the highest ΔG_R (01-15 and CSO1) started to decline only at later ages. The exceptions to this were the FRA_SSO seedlots (UNROG and 1STROG) which showed a reversal pattern. No matter which pattern happens, the absolute differences between the improved and checklot seedlots increased with age. For example, despite a decreasing trend in ΔG_R with age, the absolute differences were 10 cm in HT_5 and increased to 19 cm in HT_{10} and 24 cm in HT_{15} for the CAN101 seedlot.

The ΔG_R fluctuated considerably with SI50 for both species (Figure 2). Overall, no consistent SI50-related trend stood out. While some seedlots showed an increasing ΔG_R with SI50 up to a certain point but then decreased as the SI50 increased further, others showed either a consistent increase with SI50 or a random pattern. In general, the better seedlots had higher ΔG_R at all sites than poorer seedlots. This was
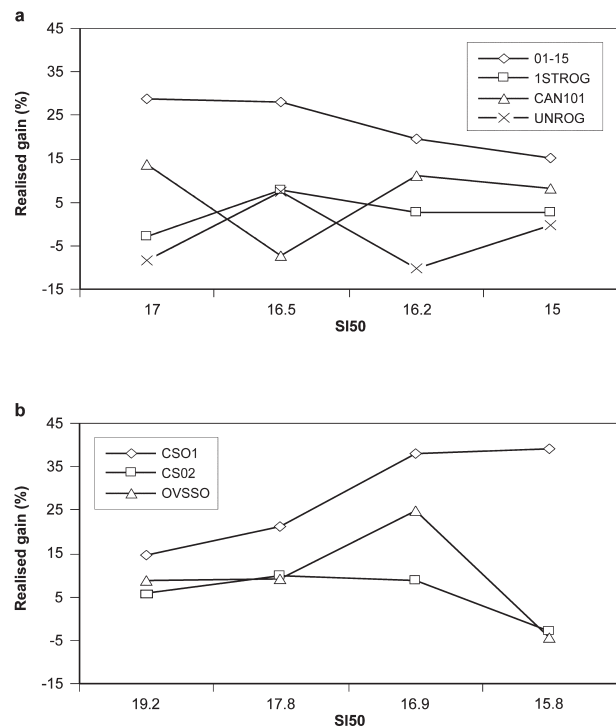

FIGURE 2: Realised gains in individual tree volume at age 15 under various site index at age 50 (SI50) observed in (a) the black spruce realised gain test and (b) the white spruce realised gain test.

particularly true for the best seedlots (01-15 for black spruce and CSO1 for white spruce).

Comparison in realised gain (ΔG_R) between small and large plots

The three checklots used in this study were also planted in corresponding small-plot genetic tests. Data from all these tests provides an opportunity to compare differences in ΔG_R between the two plot sizes used. As shown in Table 4, the differences in ΔG_R between the two plot sizes were large and varied with species, trait and seedlot. Overall, the HT_{15} ΔG_R values for the small-plots were greater than those for the corresponding large-plots for both species, with one exception (01-15). In contrast, the DBH_{15} and VOL_{15} ΔG_R values for the small-plot tests were smaller than those for the large-plot test in the case of black spruce but greater than the corresponding large-plot tests for white spruce. It can also be seen from Table 4 that, for black spruce, these discrepancies were generally larger, in relative terms, for the orchard seedlots (1STROG and UNROG) compared to the other two seedlots (CAN101 and 01-15). For CAN101, the two plot sizes showed similar gains.

TABLE 4: Comparisons in realised genetic gain in height, DBH and volume at age 15 between genetic tests of small–plots and the realised gain trials of large–plots.

Species	Seedlot	Trait	Realised gain (%)	
			Large plot	Small plot[1]
Black spruce	01-15	HT_{15}	9.9	4.1
		DBH_{15}	5.9	4.5
		VOL_{15}/tree	25.3	18.3
	CAN101	HT_{15}	4.9	6.8
		DBH_{15}	0.7	0.3
		VOL_{15}/tree	7.0	4.5
	UNROG	HT_{15}	-0.2	2.3
		DBH_{15}	-2.2	-3.8
		VOL_{15}/tree	-1.3	-6.1
	1STROG	HT_{15}	3.6	8.0
		DBH_{15}	-1.0	-1.7
		VOL_{15}/tree	3.3	-2.8
White spruce	OVSSO	HT_{15}	2.7	6.8
		DBH_{15}	5.1	9.6
		VOL_{15}/tree	11.0	24.3
	CSO2	HT_{15}	2.3	4.6
		DBH_{15}	2.6	6.9
		VOL_{15}/tree	7.8	14.5

[1]01-15, family test of single-tree plots; CAN101, stand test of 16-tree square plots; UNROG and 1STROG, family test of single-tree plots; OVSSO, family test of 2-tree plots; CSO2, progeny test of 2-tree plots.

Discussion

Realised genetic gains (ΔG_R)

This study provides the first ΔG_R estimates from the early-stage improvement activities for two important spruce species in NB. Results indicate that growth improvement through selection and/or breeding is readily achievable for both species. As expected, the ΔG_R, in general, increased with improvement level with few exceptions. Deploying elite-stand seedlots of black spruce (i.e. CAN101) could achieve low to moderate gains, although these were achieved at very low cost. Deploying the elite family (i.e. 01-15) could lead to seven times more ΔG_R for 15-yr volume per hectare than planting CAN101 seedlot. The trend of increasing ΔG_R with improvement level was more obvious for the white spruce. The biological significance of improved seedlots compared to the relevant checklot might be greater than is statistically evident due to the limited replicate numbers (only four per site) (St. Clair et al., 2004). However, the ΔG_R values observed in this study were still reasonably high (Table 3). Our overall results suggest that the early-stage tree improvement activities have a substantial impact on forest productivity and could be an economically worthwhile endeavour for both species. A 2 to 5% improvement in volume gain over unimproved stock would be sufficient to justify a tree improvement program (Davis, 1967; Zobel & Talbert, 1984).

Currently, the seed-orchard system is the main deployment strategy in NB. Thus, the ΔG_R values observed in the orchard seedlots have particular interest for tree breeders. The most surprising finding was that the ΔG_R values for volume for the FRA_SSO seedlots of black spruce were negative or only slightly positive, even after genetic roguing (Table 3). This is because: (1) phenotypic selection of plus trees for height growth under such a low selection intensity seldom resulted in much gain in the progeny simply because the environmental variation is so high that it masks true genetic differences; and (2) selection for height growth did not significantly improve diameter at breast height (DBH) growth. Similar results were also observed in a previous black spruce genetic test (NBTIC, 1999), where a seedlot collected from an unrogued seedling seed orchard was 1.7% taller in

height but 6.0% smaller in DBH and 11.2% smaller in volume at age 10 than the checklot (also TAYBRK). However, as demonstrated by seedlot 01-15 in this study, the volume gains for the FRA_SSO could be greatly improved through selective harvest of cones from only the best subset of families in the orchard. Thus, the low volume gains for the black spruce orchard seedlots do not devalue the seed orchard strategy. Instead, they emphasise the importance of increasing selection precision. Diameter at Breast Height growth should also be incorporated into selection procedures for black spruce, given that volume growth is the target for improvement. In contrast to black spruce, selection for white spruce height growth resulted in high positive ΔG_R not only in height but also in DBH, resulting in moderate to high positive ΔG_R in volume of the orchard seedlots. Establishing a seed orchard using seed collected from average trees in an elite provenance (i.e. the DNR_PSSO) is controversial, at least in theory. Even if the provenance effect is large, it is very unlikely that genetic variance among provenances is completely additive and, thus, may not be captured by such a seed-orchard strategy. Despite this theoretical disadvantage there is a case for applying such a strategy to white spruce. Planting the OVSSO seedlot (collected from the DNR_PSSO) could obtain over 9% more VOL_{15}/ha relative to the RBK/WAP checklot. Better still, three times more ΔG_R in VOL_{15}/ha could be obtained by planting the unrogued DNR_CSO seedlot (CSO1) than the OVSSO seedlot. These results suggest that phenotypic plus tree selection for height growth coupled with a seed orchard approach could be very effective in improving volume growth for white spruce. It is important to mention that, for white spruce, some ΔG_R observed in the orchard seedlots may be due to the reduced inbreeding resulting from breaking up the family structure of natural stands of trees (Coles & Fowler, 1976).

The timing of gain assessment was important as the ΔG_R varied with age. While some studies have shown that ΔG_R in growth traits are constant over age (Talbert et al., 1985), most studies have shown that ΔG_R expressed as a percentage tend to decline with age (Talbert, 1981; Carson et al., 1999a, b; McInnis & Tosh, 2004; Weng et al., 2008b). Such a trend was generally true in this study, although the seedlots of higher ΔG_R started to decline at older ages. The significant exceptions were the orchard seedlots (1STROG and UNROG) of black spruce (Table 3). The reason for this is not readily evident. Surprisingly, a similar trend was also found for the seedlot collected from a jack pine seedling seed orchard (Weng et al., 2008b). No matter which trend happens, the absolute gains (the difference between improved and checklot seedlots) increased with age, at least within the ages measured. Genetic gain at rotation age is always the objective for tree breeders. Since strong tree-to-tree competition has developed by age 15 years for both species, differences observed here at 15 years can be expected

to be good indicators throughout the rotation. Based on NB experience for both species, 15-year data can provide a reliable projection in volume at age 50 using the STAMAN v.5.5 software package (Dick, A., New Brunswick Growth and Yield Unit, personal communication, September 1, 2009). The STAMAN (New Brunswick Growth and Yield Unit (NBGYU), 2005) is a distance-independent individual-tree growth model which forecasts stand development with periodic DBH growth and survivorship functions and is utilised in NB for Crown land forest management. For both species, the projected realised volume gains per hectare diminished at later ages (details not shown). At age 50, however, the predicted volume gains per hectare ranged from -10.6% to 3.8% for black spruce and from 0.9% to 3.0% for white spruce (Table 3). These simulated gains were likely to be very conservative. In the STAMAN package, tree height is forecasted indirectly *via* non-linear equations of height with DBH, which are developed from data collected from unimproved stands. It is reasonable to expect the heights of the improved seedlots are underestimated based on these equations (Weng et al., 2008a).

The above discussion was based on across-site performance of the seedlots. Genetic differences in tree growth may be poorly expressed on very poor sites, and better expressed as site quality improves. Once site quality improves beyond a certain point, however, growth conditions become somewhat 'luxurious' and genetic differences again become obscured (Dhakal et al., 1996). Also, selections (i.e. seed orchard roguing) are usually based on breeding values, which are always predicted under an assumption of an average environment across multiple testing sites. Thus, it seems logical to expect a maximum gain for a particular improved seedlot at a site of 'moderate' conditions. This was true in some seedlots (1STROG for black spruce and CSO2 and OVSSO for white spruce) but not for others in our results (Figure 2). Mixed results have also been reported in literature; some studies have found ΔG_R to be either independent of site fertility (Andersson et al.,, 2003; Vergara et al., 2004) or actually higher on poorer sites (Eldridge, 1982), whereas others reported an increasing trend in ΔG_R with better sites (Dhakal et al., 1996; Matziris, 2000; Carson et al., 1999b; McKeand et al., 2006; Weng et al., 2008b). These results indicate that each seedlot or species may have its own 'moderate' site requirement for growth. Despite substantial site to site variation in ΔG_R, no seedlot and site interaction was found (Table 2) and the better seedlots in general had higher gain at all sites (Figure 2). This finding is not surprising given that all the sites are located within one breeding zone. Similar results were also reported in loblolly pine (Lambeth, 2000), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (St. Clair et al., 2004) and jack pine (Weng et al., 2008b).

Comparisons with other large-plot tests of realised genetic gains

Relatively few tests have utilised large plots to estimate ΔG_R from plantations of improved seedlots, although the advantages of this approach are well recognised (Zobel & Talbert, 1984). Among the few studies which have applied a large-plot design to demonstrate ΔG_R from the first-generation programmes, Carson et al. (1999a) reported a 4.5% increase in height at mid-rotation from the unrogued clonal seed orchards of radiata pine in New Zealand, a programme in which parents had been selected for full crown dominance and very superior tree form (Burdon et al., 2008). Eldridge (1982) reported a 20% increase in volume per hectare at 12 years from unrogued clonal seed orchards in Australia. Vergara et al., (2004) reported a 7.7% and 10.2% increase in individual-tree volume and stand volume, respectively, for slash pine from unrogued or slightly rogued seed orchards. However, other studies have found no improvement in various ΔG_R values for unrogued clonal seed orchards (i.e. for 4-year height for Scots pine (Chmura et al., 2003), 4- to 8-year volume for loblolly pine (Lowerts, 1987), or 15-year volume for slash pine (Tankersley et al., 1983)). Although direct comparisons between our study and the above-cited ones cannot be made due to differences in species, selection intensities etc., overall results suggest that it is important to be critical and analytical of any gains that are reported and that are being considered for application.

Comparison of test plot size

The small number of large-plot gain tests means information from them is scarce. Consequently, realised gains obtained from genetic tests using small plots are often incorporated into measures used to adjust tree improvement effects in growth and yield prediction. However, realised gains from tests using small-plot and large-plot gain tests may differ for several reasons. Firstly, trees of pure genotypes growing in small plots may have a different competition situation compared to those of mixed genotypes growing in large plots. This difference may become larger if dominant phenotypes gain earlier competitive advantages in small-plot genetic tests (Cannell, 1982). Secondly, compared to genetic tests using small plots, gain tests that involve large plots which mimic operational conditions often have greater error variances due to the increased variation within replicates and less intensive silviculture activities. Thirdly, small-plot genetic testing sites may not be representative of large-plot gain tests. The bias becomes larger when stronger site effects and/or site-by-genotype interaction appear in either test. Finally, ΔG_R of seed orchard seedlots in large-plot gain tests are greatly affected by factors such as foreign pollen contamination or inbreeding compared with small-plot tests based on controlled pollination. This lack of control over pollination is especially a problem while orchard

trees are young and produce limited pollen (Burdon et al., 2008). Even with foreign pollen contamination, it is not unusual to have a 10 to 15% reduction between the growth rates from the test of small plots compared to plantings made under operational conditions (Zobel & Talbert, 1984).

Results from this study showed that the small-plot genetic tests bias ΔG_R relative to large-plot gain tests for most seedlots. For traits that are directly selected, i.e. height in this study, small-plot tests may overestimate the actual gains obtainable from large-plot tests, likely a result of the difference in competition between the two test plot sizes, foreign pollen contamination and/or inbreeding occurring within the orchards. For traits that are indirectly selected, i.e. DBH_{15} and VOL_{15} in this study, the bias could be significant and in both directions, depending on tree species. For white spruce, the upward biases were obviously larger for DBH and volume than for height. This is probably because height is less sensitive to competition than diameter and volume. However, such a phenomenon was not evident for black spruce, in which the small-plot tests underestimated the DBH and volume gains in the large-plot gain test. The reason for this is not known. One possible explanation, although speculative, is that competition effects on DBH growth in the small-plot genetic tests were weaker for the checklot than for other tested genotypes. Our results also show that plot size may have an effect on bias. When two tests have similar plot size, the bias would be small. For example, the gains for the CAN101 seedlot in a genetic test (NBTIC, 1977) of similar plot size (16-tree square plots) and genotype mixture as the large-plot gain test in this study were relatively comparable. Overall, published results provide evidence that ΔG_R observed from small-plot genetic tests should be used with caution to predict ΔG_R in operational plantations. Other studies have compared ΔG_R in large plots with the respective theoretical gains predicted by quantitative genetic theory based on small-plot genetic tests (St. Clair et al., 2004; Vergara et al., 2004; Weng et al., 2008b). These results generally suggest that theoretical gains can closely predict ΔG_R in large plots for a single genotype (i.e. a single family) but overestimate ΔG_R of orchard seedlots.

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