Structure and dynamics of trembling aspen – white spruce mixed stands near Fort Nelson, B.C.[1]

Richard Kabzems and Oscar García

Abstract: The trembling aspen (*Populus tremuloides* Michx.) – white spruce (*Picea glauca* (Moench) Voss) mixedwoods near Fort Nelson are distinguished by the large size of individual trees, longevity, and the low occurrence of internal decay in trembling aspen. The development of these forest ecosystems has had limited documentation and may be significantly different than those described in other portions of the boreal forest. At five study stands, stem analysis techniques were used to examine the patterns of height and radial growth over time according to species and structure type. There were two patterns of species establishment that were consistent with the stand structure. In codominant stands, recruitment periods for trembling aspen and white spruce overlapped. The stratified stands were consistently associated with a 29- to 58-year lag in white spruce recruitment. Spruce that were codominant with aspen at the time of sampling had sustained periods of rapid height and diameter growth. White spruce that were later to establish on site had slower rates of height and diameter growth. White spruce ages indicated that a dominant recruitment episode was more common than continuous recruitment. Height and diameter growth of trembling aspen were similar in both stand types. The differences in trembling aspen growth patterns between stands were due to site quality. The white spruce in codominant stands did not appear to go through a period of suppression and then release associated with stand-level trembling aspen mortality, as commonly described for other boreal mixedwoods. The vigor and longevity of trembling aspen in Fort Nelson appear to prolong the period of trembling aspen domination of mixed stands well beyond the time periods observed in other boreal ecosystems.

Résumé : Les peuplements mélangés de peuplier faux-tremble (*Populus tremuloides* Michx.) et d'épinette blanche (*Picea glauca* (Moench) Voss) situés près de Fort Nelson se distinguent par la forte dimension et la longévité des arbres ainsi que la faible présence de carie de cœur chez le peuplier faux-tremble. Le développement de ces écosystèmes forestiers est peu documenté et pourrait être très différent de ceux qui ont été décrits dans d'autres parties de la forêt boréale. L'analyse de tiges a été utilisée pour étudier l'évolution de la croissance radiale et en hauteur dans le temps dans cinq peuplements, en fonction de l'espèce et du type de structure. Deux patrons d'établissement des espèces consistants avec la structure du peuplement ont été observés. Dans les peuplements où ils sont codominants, les périodes de recrutement du peuplier faux-tremble et de l'épinette blanche se recoupent. Les peuplements stratifiés sont toujours associés à un délai de 29 à 58 ans dans le recrutement de l'épinette blanche. Les épinettes blanches qui étaient codominantes avec le peuplier au moment de l'échantillonnage ont connu des périodes de croissance rapide en hauteur et en diamètre. Les épinettes blanches qui se sont établies plus tard sur le site ont un taux de croissance en hauteur et en diamètre plus faible. L'âge des épinettes blanches indique que le recrutement des tiges dominantes a été épisodique plutôt que continu. La croissance en hauteur et en diamètre du peuplier faux-tremble est semblable dans les deux types de peuplements. Les différences dans les patrons de croissance du peuplier faux-tremble entre les peuplements sont dues à la qualité de station. Dans les peuplements codominants, l'épinette blanche n'a pas semblé passer par une période de suppression suivie d'une période de dégagement associée à la mortalité du peuplier faux-tremble à l'échelle du peuplement, tel que généralement décrit pour les autres forêts boréales mixtes. La vigueur et la longévité du peuplier faux-tremble de Fort Nelson semblent prolonger la période de domination de cette espèce dans les peuplements mélangés bien au-delà des périodes de temps observées dans d'autres écosystèmes boréaux.

[Traduit par la Rédaction]

Introduction

A distinctive feature of western Canadian boreal forests are mixed stands of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx.), often referred to as mixedwoods (e.g., Kabzems et al. 1976). The variety of stand structures and species proportions found in trembling aspen – spruce mixedwoods reflect the

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type of harvesting or natural disturbance that initiated the new stand, the more rapid height growth of young trembling aspen, the ability of white spruce to establish and grow under trembling aspen, the greater shade tolerance of spruce, variation in the time of establishment, and other ecological factors (Lieffers et al. 1996).

Ecosystem-based management initiatives have been proposed to address the combination of economic, social, and environmental values found in boreal forests (e.g., Veeman et al. 1999). These initiatives often seek to emulate features of natural disturbances (e.g., Song et al. 2002). A fundamental information need for boreal ecosystem management is the study of patterns of response to natural disturbances.

The examination of the different strategies of germination and growth for each tree species can be used to explain and predict the composition and structural features of boreal forests (Dix and Swan 1971). A more complete understanding of the successional dynamics for the structure and composition of boreal forest ecosystems will enable forest managers to develop innovative silviculture systems that continue to provide the multiple benefits, which we receive from boreal mixedwoods.

Previous studies in the boreal forest commonly describe a classic successional sequence after a severe disturbance from a broadleaf-dominated to a conifer-dominated phase (e.g., Rowe 1956; Foote 1983; Cogbill 1985). By considering seed source and the type of seedbed created by wildfire, this general successional model was expanded to four successional pathways for spruce-dominated boreal mixedwood stands near Fort Nelson by Parminter (1983). Chen and Popadiuk (2002) describe potential stand development pathways for a mesic boreal mixedwood site in eastern Canada, giving examples of cyclic, convergent, divergent, parallel, and individualistic models of stand development. Depending on seed sources, the type and severity of disturbance, and stochastic variables, a wide variety of stand structures and compositions are possible. These can be broadly grouped into (*i*) single- and multiple-cohort broadleaves, (*ii*) single-cohort mixtures of broadleaves and conifers, with or without a stratified structure, (*iii*) multiple-cohort mixtures of broadleaves and conifers, with or without a stratified structure, (*iv*) single-cohort conifers, and (*v*) multiple–cohort mixed conifers (Chen and Popadiouk 2002).

More recently there has been debate regarding the timing of the initiation of the spruce cohort within these mixed species stands. Using careful ageing and dendrochonology techniques, perceptions of apparently delayed or intermittent spruce recruitment have been demonstrated to be growth differences between two species that actually recruited together in a short time period, immediately after the most recent disturbance (e.g., Gutsell and Johnson 1999; Peters et al. 2002).

Similar to other boreal ecosystems, stand-replacing wildfire has been identified as a key influence on ecosystem structure and dynamics in the Fort Nelson area (Annas 1977; Parminter 1983). The estimated average fire return intervals for mixed broadleaf–conifer forests are between 100 and 150 years and 150–200 years for coniferous types (Parminter 1992). Far less common in the western Canadian boreal forest are the large size of individual trees, longevity, and the low occurrence of internal decay in trembling aspen, which characterize the trembling aspen – white spruce mixedwoods around Fort Nelson. Trembling aspen stands with average heights greater than 30 m, merchantable volumes over 350 m^3/ha, and ages in excess of 120 years are common in the Fort Nelson area (S. Joyce, B.C. Ministry of Forests, Fort Nelson, personal communication). The development of these forest ecosystems has had limited documentation (Annas 1977; Parminter 1983) and may be significantly different from those described in other portions of the boreal forest (e.g., Dix and Swan 1971; Youngblood 1995).

The perceived differences between trembling aspen – white spruce mixedwoods near Fort Nelson with similar ecosystems in other jurisdictions has contributed to the uncertainty regarding mixedwood dynamics in both natural and managed conditions (B.C. Ministry of Forests 2000). Do stands that currently express a codominant trembling aspen and white spruce structure represent a later temporal stage of mixedwood succession, or do they have a different developmental pathway than stands that currently express a stratified structure? This uncertainty is a critical issue for timber supply analysis in an area where spruce–deciduous and trembling aspen – coniferous inventory types make up 18.0% and 12.4%, respectively, of the total timber harvesting land base of 925 000 ha (B.C. Ministry of Forests 2000).

The objective of this study was to document the dynamics of mixed trembling aspen – white spruce stands in the boreal forests of northeastern British Columbia. In particular, we wanted to relate the current structure types to stand origin and past development for evidence of successional changes in species composition as described in other boreal trembling aspen – white spruce stands.

Materials and methods

Study area

The study area is within the Fort Nelson Forest District of northeastern British Columbia, near the community of Fort Nelson (58°50′N, 122°45′W). The area is classified as the moist warm subzone of the Boreal White and Black Spruce biogeoclimatic zone (BWBSmw2; DeLong et al. 1990). Annual precipitation averages between 330 and 570 mm, with 35%–55% of this falling as snow. Mean annual temperature is –0.6 °C. The mean frost-free period is 105 days (DeLong et al. 1990).

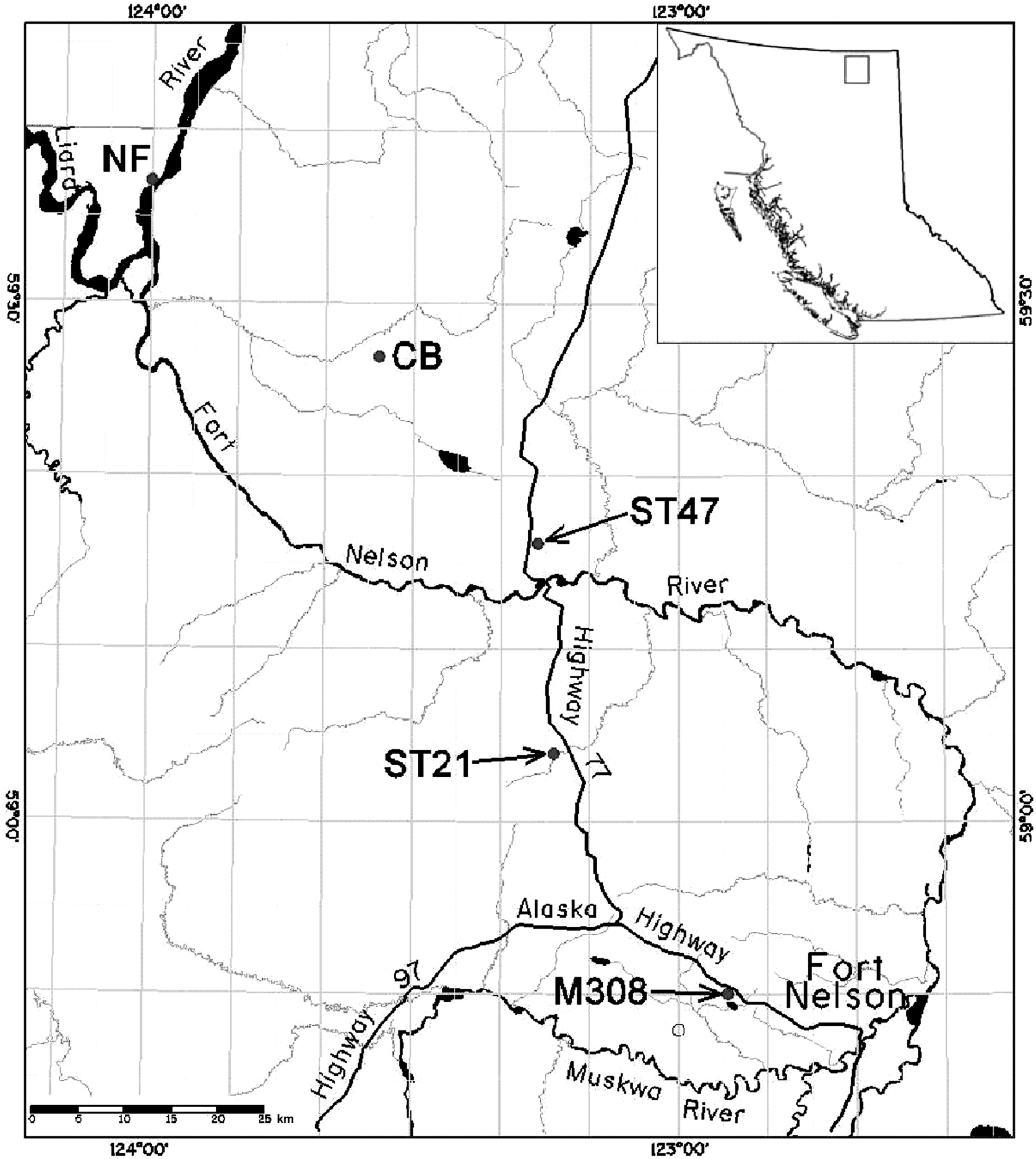
Sampling design

Five stands were selected from proposed harvesting areas within the Fort Nelson Forest District (Fig. 1). Each study stand was composed of mixed forest types dominated by trembling aspen with a site index (breast height age 50) of at least 18 m. The total stand merchantable volumes were over 300 m^3/ha. These stands represent forest types that are the focus of commercial harvest in the Fort Nelson area. The stands were identified as Mile 308 (M308), Simpson Trail km 21 (ST21), Simpson Trail km 47 (ST47), Capot Blanc (CB), and Nelson Forks (NF). Five fixed area replicate plots (500 m^2, 0.05 ha) were established within each sample stand in 1999. The plots were uniform in site characteristics, and all were classified as having fresh moisture regimes and rich nutrient regimes (DeLong 2002).

Sampling

Total heights of trees and length of live green crown were

Fig. 1. Location of study sites in the Fort Nelson area. Study stands were NF, Nelson Forks; CB, Capot Blanc; ST47, Simpson Trail km 47; ST21, Simpson Trail km 21; and M308, Mile 308 of the Alaska Highway.



measured with a Criterion laser sighting device. Diameter at breast height (1.3 m, DBH) was measured with a diameter measuring tape. Regeneration less than 4 cm in diameter was assessed in a concentric 100-m^2 (0.01 ha) subplot.

Diameter and height distributions from all 25 sample plots were compared within and among the five study sites. The within-stand plots were more similar to each other than the five stands using Kolmogorov–Smirnov two sample tests

Table 1. Structural characteristics of the destructively sampled Fort Nelson plots.

Location	Tree species	Density (stems/ha)	Basal area (m^2/ha)	Quadratic mean DBH (cm)	Average height (m)	Average crown length (m)
Capot Blanc	Aspen	560	49.8	33.7	31.2	6.9
	White spruce	580	3.9	9.3	6.8	4.7
	Subalpine fir	20	0.7	20.9	14.1	11.3
Mile 308	Aspen	1000	40.0	22.6	26.3	5.4
	White spruce	1080	6.9	9.0	7.8	4.8
	Paper birch	40	0.4	12.0	10.4	7.3
ST21[a]	Aspen	400	37.8	34.7	30.5	9.4
	White spruce	1500	7.0	7.7	5.9	4.1
ST47[b]	Aspen	200	17.1	33.0	28.9	7.8
	White spruce	500	24.5	25.0	18.2	11.8
	Paper birch	40	0.5	12.4	8.4	4.9
	Black spruce	20	0.2	11.4	9.3	7.4
Nelson Forks	Aspen	260	33.0	40.2	33.9	8.1
	White spruce	440	22.7	25.7	22.6	10.1
	Subalpine fir	380	2.4	7.2	7.2	2.9

[a]Simpson Trail km 21.
[b]Simpson Trail km 47.

(Sokal and Rohlf 1995). Available resources limited destructive sampling to one of the five replicate plots within each stand, which was randomly selected.

In the second year of the study (2000), trees within one randomly selected plot within each candidate stand were destructively sampled for stem analyses. A minimum of 10 trembling aspen and 20 white spruce were sampled from each plot. Roughly proportional allocation was used to select sample trees in strata defined by 5-cm DBH classes. Because of the large size of trembling aspen individuals within the study and the limitations of helicopter access at the Capot Blanc and NF sites, stem discs for trembling aspen were cut at 0.3 m above ground level, 0.8, 1.3, 1.8, 3.0 m, and then every 3.5 m up the stem. All white spruce less than 8 m tall, at all locations, were sampled at 0.1, 0.3, 1.3, 1.8, and 2.3 m, and then at regular intervals every 1.0 m for the remainder of the stem. Spruce stems taller than 8 m in height at helicopter access locations (Capot Blanc, NF) and at ST47 (because of the large size of some individual spruce) were sampled every 2.0 m above the 2.3-m mark. White spruce stems taller than 8 m in height at ground access locations (Mile 308, ST21) were sampled every 1.0 m above the 2.3-m mark.

Within the destructively sampled plot, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), paper birch (*Betula papyrifera* Marsh.), and white spruce that were not sampled for stem analysis were felled and had one basal disc (0.1 m above the ground) removed for ageing. At the Mile 308 site, 18 white spruce stumps were excavated and discs cut to compare stump age (0.1 m) with age at the point of germination.

To derive unbiased estimates corresponding to live trees present at the time of sampling on a per hectare basis, we calculated expansion factors based on the stratified sampling and plot size for each tree. The expansion factors were obtained by dividing the plot number of trees in each DBH stratum by the number of subsample trees in the stratum and dividing the result by the corresponding plot size (0.01 ha for DBH < 4 cm and 0.05 ha for DBH ≥ 4 cm).

Stem analysis

Discs were sanded with increasingly finer grades of sandpaper. Growth rings were measured along two radii on the cross-sectional discs. Ring widths were measured and recorded using Windendro™. The trembling aspen discs that had advanced rot or decay, which prevented accurate age determinations, were documented and excluded from analysis. Past height development for the stem analysis trees was reconstructed from the ring counts at each stem disc height. Current tree age was estimated from stump-height ring counts. Past DBH development was determined from the ring measurements on the breast-height (1.3 m) disc.

Trembling aspen site index (dominant height in m at 50 years breast height) was estimated for each site using the stem analysis data. The site index values were estimated as 22, 19, 25, 21, and 23 for Capot Blanc, Mile 308, ST21, ST47, and NF, respectively.

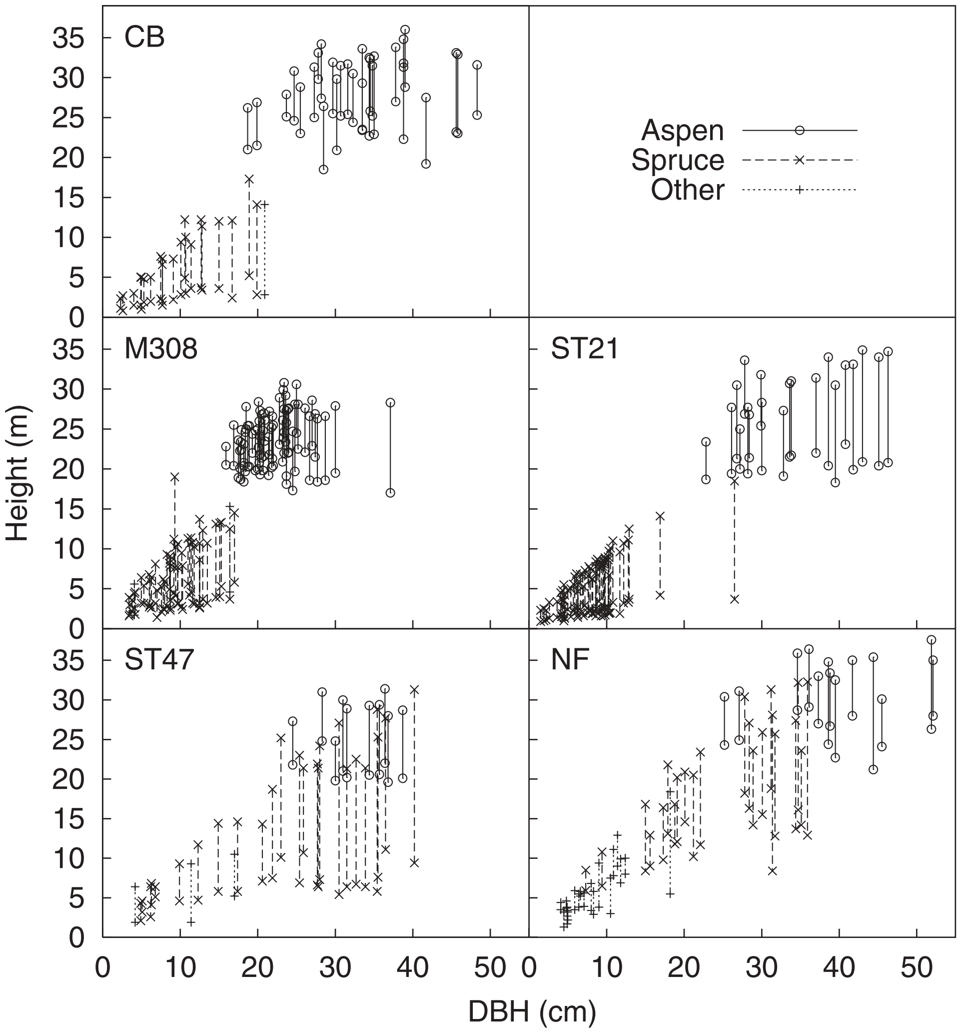
Results

Current stand structure

Two general types of mixedwood stands occurred within the areas planned for harvest (Table 1). The Capot Blanc, Mile 308, and ST21 stands were stratified mixedwoods. Mature trembling aspen with average heights of 27–30 m dominated the overstory layer. There was a clear and consistent separation between the upper trembling aspen layer and the lower layer of white spruce or subalpine fir (Fig. 2). Trembling aspen diameters were greater than spruce diameters in all three of these stands. Live crowns on trembling aspen varied from 5.4 to 9.4 m, which was 20%–31% of the bole length (Table 1). On white spruce, live crown lengths of 4.1–4.8 m were all over 61% of the bole length.

The NF and ST47 sites had a codominant structure (Fig. 2). On both of these sites, some white spruce were present in the dominant canopy layer with trembling aspen. Average diameters were greater for trembling aspen compared with white spruce at the NF site, but not very different

Fig. 2. Stand structure variables (diameter at breast height (DBH), height, and green crown level) for the destructively sampled subplot in each of the five study sites: CB, Capot Blanc; M308, Mile 308 of the Alaska Highway; ST47, Simpson Trail km 47; ST21, Simpson Trail km 21; and NF, Nelson Forks. The length of the live green crown is displayed by the vertical range on the height axis.



between species at the ST47 site (Table 1 and Fig. 2). The live crowns of trembling aspen were 7.8–8.1 m, which was 24%–27% of the bole length in the codominant stands. White spruce had live crown lengths of 10.1–11.8 m, which was 45%–65% of the bole over the range of diameters sampled (Fig. 2).

Species composition

Trembling aspen and white spruce dominated all study stands (Table 1). Subalpine fir was only found at the Capot Blanc and NF sites. Minor amounts of paper birch and black spruce (*Picea mariana* (Mill.) BSP) were present (Table 1).

Height growth

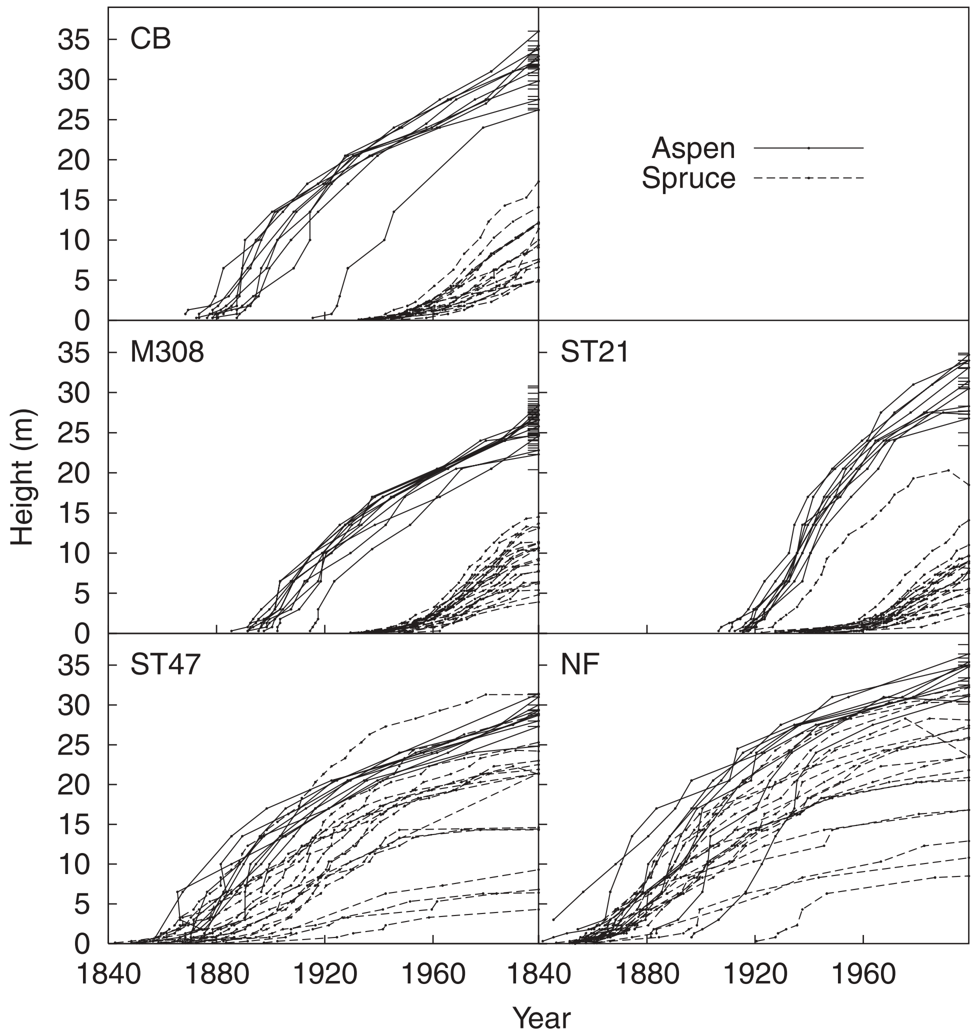
The height trajectories for the sampled trees are illustrated in Fig. 3. Trees that died before 1999 are not represented in the graphs, so that for early ages mostly larger trees are represented. Nevertheless, vertical cross sections of the graphs give a good picture of how canopy structure has developed over time. Establishment times indicated by the curve origins are examined in more detail below.

It is clear that Capot Blanc and Mile 308 always had a two-storied structure, resulting from a delay in the spruce establishment relative to the trembling aspen. In ST47 and NF, on the other hand, the timing and conditions of establishment allowed some spruce to share the upper canopy with the trembling aspen, although spruce still dominated the lower canopy positions. Canopy stratification is also clear in ST21, but a regeneration delay is less clear. Instead, there is prolonged suppression of early spruce growth. Early spruce height growth is shown in more detail in Fig. 4 and Table 2.

Age structure

Stump age was estimated from basal ring counts at 30 cm height in trembling aspen and 10 cm in other species. Both full stem analysis trees and trees with only basal discs were included. Dramatic differences between stump and total age have been found in conifers (e.g., DesRochers and Gagnon 1997; Peters et al. 2002). To assess differences in this instance, we excavated 18 white spruce stumps from Mile 308. The large size of spruce stumps or requirements for helicopter access prevented additional sites from being assessed for this feature. The average count difference between the 10-cm stump height and the germination point was 8.1 years (standard deviation of 4.6 years), with a maximum of 16 years

Fig. 3. Height development of stem analysis trees in each of the five study sites: CB, Capot Blanc; M308, Mile 308 of the Alaska Highway; ST47, Simpson Trail km 47; ST21, Simpson Trail km 21; and NF, Nelson Forks. For reference, short line segments on the right hand axis show the aspen height distribution in the sample plot at the time of sampling.



(Fig. 5). No similar comparison was done for trembling aspen, as it was assumed that sampling at 0.3 m height would include the first year's growth of trembling aspen stems.

In the stratified stands and the NF codominant site, the majority of spruce recruitment occurred as a relatively short pulse, illustrated by the rapid change in the number of stems per hectare over a period of about 20 years (Fig. 6). In contrast, the ST47 site had no such identifiable pulse of spruce recruitment, but rather spruce recruitment was ongoing over a period of 50+ years (Fig. 6).

The Capot Blanc, Mile 308, and ST21 stands had mostly nonoverlapping age distributions for each species (Fig. 6). The average ages of the trembling aspen ranged from 29 to 58 years older than white spruce ages in these three stands (Table 3). The occurrence of other species in these stands was sporadic. In the ST47 and NF sites, the species age distributions overlapped. At ST47, the average age of the spruce was 136 years, with a range of 55 years (Table 3). Trembling aspen ages averaged 138 years, with only a 9-year age range. At NF, the white spruce averaged 143 years, with only a 15-year range in ages (Table 3). The trembling aspen at NF had an average age of 138 years, with a 54-year range in ages (Table 3). There was a substantial younger subalpine fir component in NF, which had an average age of 99 years, which was 44 years less than the average age of the white spruce component (Table 3). The measures of age variation (range and standard deviation, Table 3) were greatest for subalpine fir when compared with trembling aspen or white spruce at any other location in the study.

The age pattern of the limited number of paper birch in the study stands (Table 3) indicated that birch had regenerated with the initial disturbance (Mile 308) and at some later time within the mature stand (ST47, Mile 308). Where paper birch was present, decayed birch stems and coppice centres indicated that greater numbers of birch had been present at earlier stages of stand development (unpublished data).

Diameter growth

The trends for DBH growth were obtained from radial increments measured on the discs (Fig. 7). The patterns were similar to those of height growth (Fig. 3), confirming the relationships between current structure and development history. Curves were smoother than those for height because

Fig. 4. Early height development for white spruce stem analysis trees in the five study sites: CB, Capot Blanc; M308, Mile 308 of the Alaska Highway; ST47, Simpson Trail km 47; ST21, Simpson Trail km 21; and NF, Nelson Forks. Year 0 was set to the earliest date in each site data.

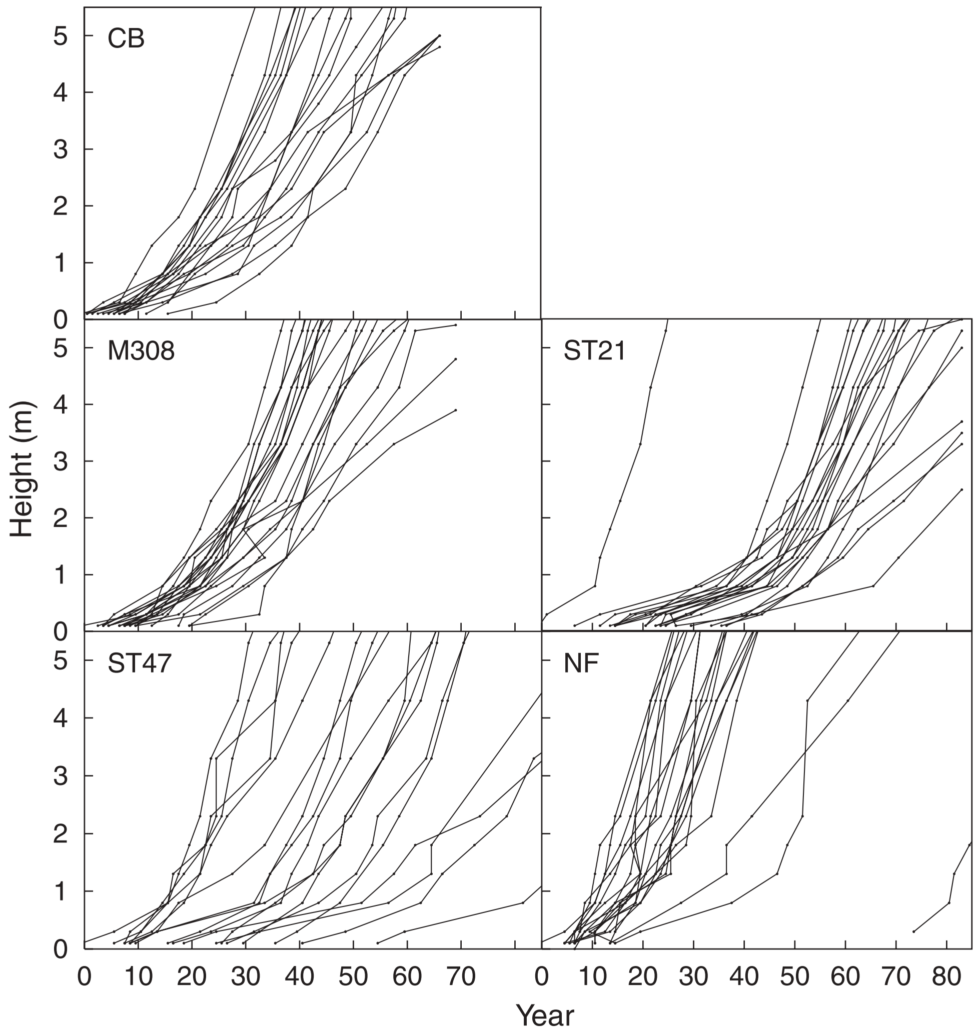


Table 2. Median years for white spruce to grow from 10 cm to 1.3, 2.3, or 5.3 m for the stem analysis trees (quartiles in parenthesis).

	Years to:		
Location	1.3 m	2.3 m	5.3 m
Capot Blanc	18 (15, 23)	27 (21, 34)	42 (37, 53)
Mile 308	18 (16, 21)	26 (22, 29)	40 (37, 45)
ST21[a]	27 (25, 31)	35 (31, 37)	47 (44, 64)
ST47[b]	20 (14, 26)	27 (20, 36)	43 (32, 53)
Nelson Forks	13 (7, 17)	16 (12, 21)	26 (22, 35)

[a]Simpson Trail km 21.
[b]Simpson Trail km 47.

values were available for every year. The wider spread of diameter values was to be expected from the typically larger variance of diameter distributions and the higher sensitivity of diameter increment to growing space. The early DBH growth rates showed no major differences across sites. Sites differed mainly in the time to reach breast height.

Discussion

The five stands examined in this study are not an adequate sample to quantify age and structure patterns over the 8.2×10^6 hectares of the Fort Nelson Forest District. While recognizing the limitations of the small sample size, this study provides an initial comparison of successional patterns near Fort Nelson with other areas in the boreal forest.

There were two general patterns of species establishment that corresponded to stand structure. Ages of trembling aspen and white spruce either overlapped (codominant stands) or they did not (stratified stands). The stratified stands were consistently associated with a 29- to 58-year lag in white spruce recruitment, creating a multiple cohort mixture of trembling aspen and conifers with a stratified structure. If the 8-year average difference between white spruce stump height age and age of origin was included, the recruitment lag would still range from 21 to 50 years.

While the recruitment periods of trembling aspen and white spruce overlapped in the codominant stands, there were interesting variations in the pattern of regeneration be-

Fig. 5. Comparison of white spruce ages at stump height (10 cm) and at the point of origin for 18 sample trees at the Mile 308 site.

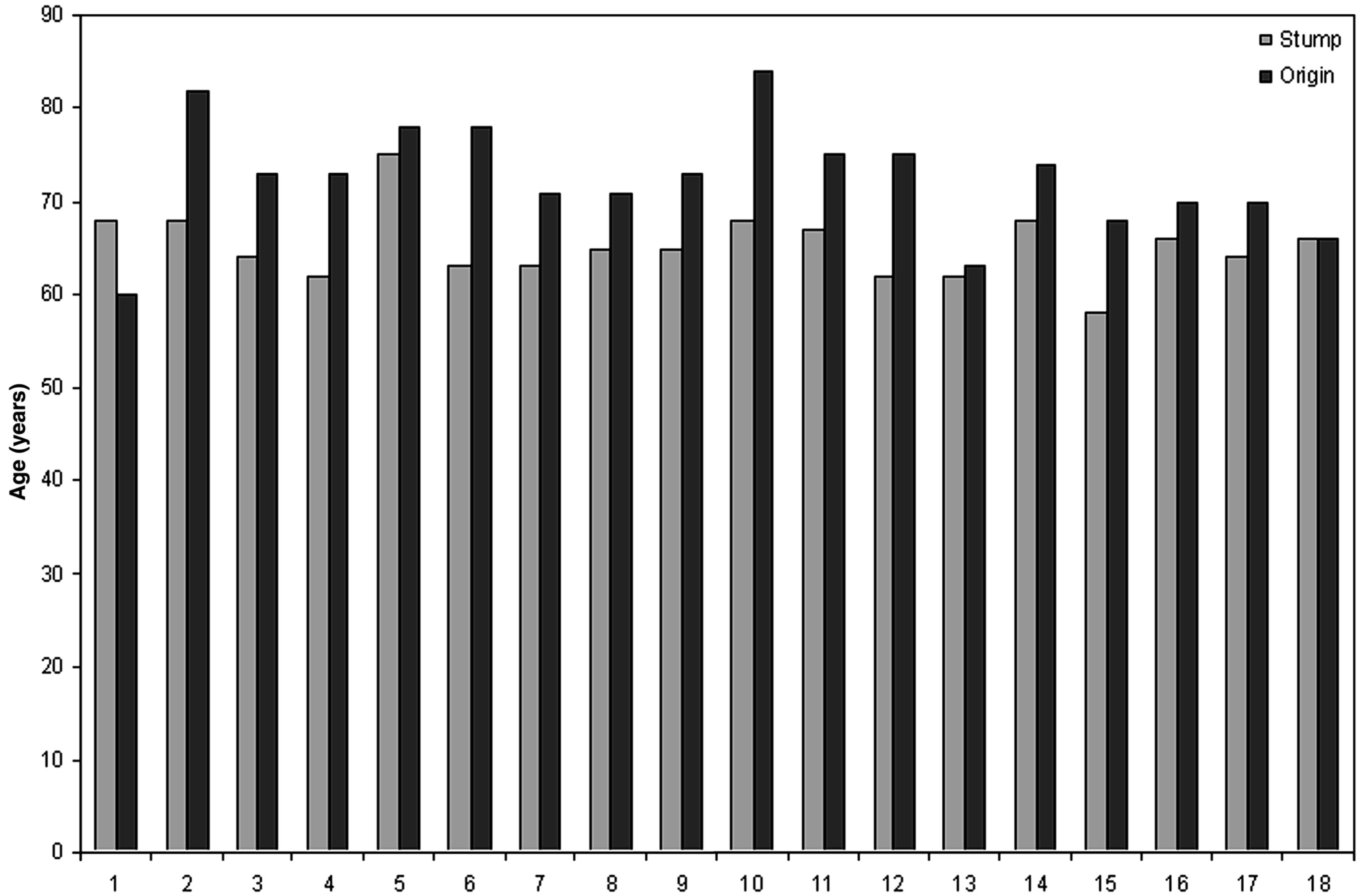


Table 3. Basal ring counts in the destructively sampled Fort Nelson plots.

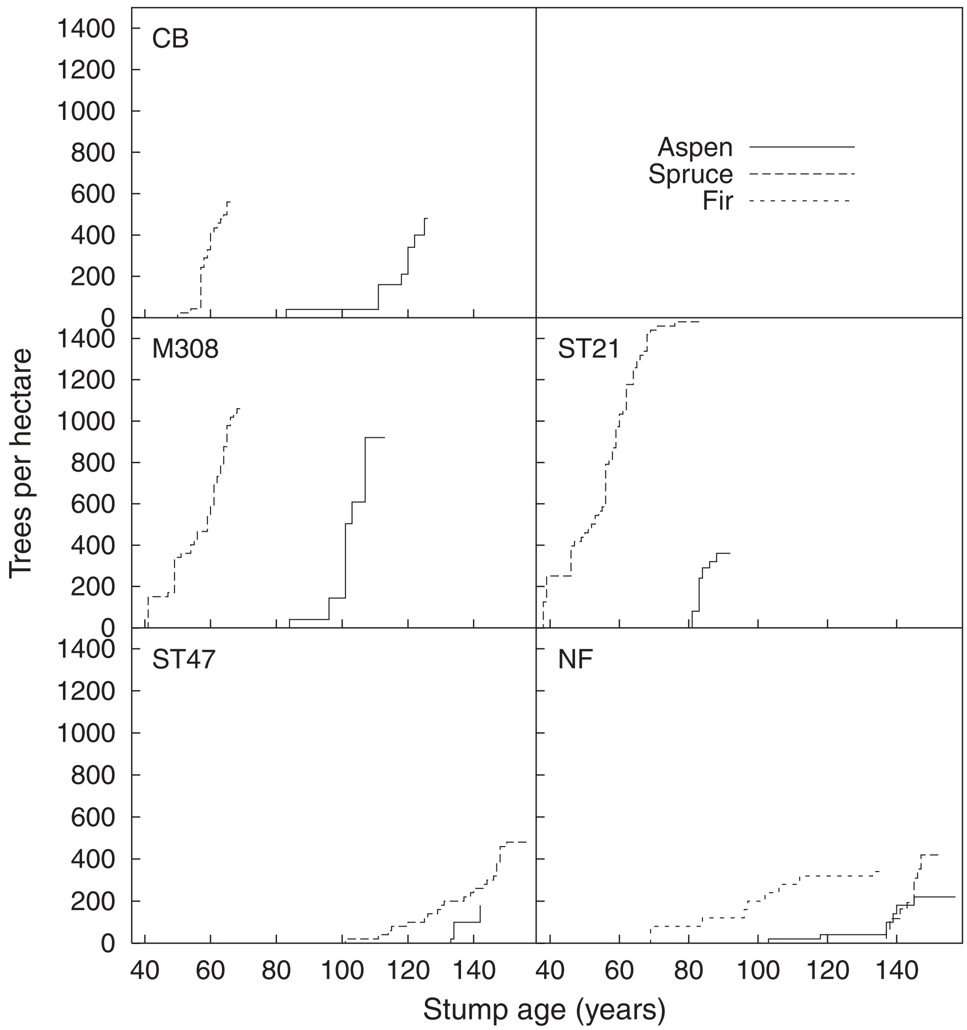
Location	Tree species	Sample size	Age (mean±SD, years)	Range (years)
Capot Blanc	Aspen	8	117±11	83–126
	White spruce	19	59±4	50–66
	Subalpine fir	1	65	—
Mile 308	Aspen	8	103±6	84–113
	White spruce	40	56±9	41–69
	Paper birch	2	—	19–111
ST21[a]	Aspen	10	84±3	81–92
	White spruce	53	55±10	38–83
ST47[b]	Aspen	4	138±4	133–142
	White spruce	25	136±14	101–156
	Paper birch	2	—	33–87
	Black spruce	1	71	—
Nelson Forks	Aspen	7	138±14	103–157
	White spruce	18	143±4	137–152
	Subalpine fir	10	99±21	69–135

[a]Simpson Trail km 21.
[b]Simpson Trail km 47.

tween the two locations. At the NF site, an aspen was the oldest tree on site at 157 years (Table 3). However, aspen regeneration apparently ranged over a 54-year period. White spruce regeneration at the NF site ranged over a 15-year period. Assuming an 8-year difference between stump age and origin (based on the excavations at the M308 site), the maximum age of white spruce would be 160 years. The difference between 157-year-old aspen and 160-year-old white spruce is small and could be interpreted as representing the same stand-initiating disturbance. The range in aspen regeneration ages suggests some subsequent disturbances may have occurred. At ST47, the white spruce age range of 55 years is much greater than 9 years for trembling aspen. The oldest white spruce on site was 156 years, 14 years older than the oldest aspen age recorded at ST47 (Table 3). The ST47 age structure suggests that white spruce established first, and a cohort of aspen recruited after the first spruce.

With the possible exception of ST47, trembling aspen was a pioneer species in this study, consistent with its general characterization (e.g., Dix and Swan 1971). Most trembling aspen stands are a single cohort and originate within 2–4 years of disturbance (Dix and Swan 1971; Cogbill 1985; Peterson and Peterson 1992). This study provided examples of trembling aspen age structures that suggested more than one cohort was recruited. The greatest variation in trembling aspen ages was found at the NF site, with a range of 54 years between the youngest and oldest sampled trembling aspen (Table 3). Late recruitment of one aspen individual also appeared to occur at the Capot Blanc site. Growth ring

Fig. 6. Estimated trees per hectare not older than each age. These are empirical distribution functions, calculated by weighting each frequency according to the respective tree expansion factor. CB, Capot Blanc; M308, Mile 308 of the Alaska Highway; ST47, Simpson Trail km 47; ST21, Simpson Trail km 21; and NF, Nelson Forks.



patterns were consistent across discs in each tree, so most of the variation did not appear to be attributable to inaccurate aging. Disturbances such as windthrow, which created canopy gaps after the initial tree recruitment, may have allowed some trembling aspen regeneration to occur after the main cohort on these sites. A third possible explanation for the range in trembling aspen ages is the regeneration of trembling aspen from seed (Peterson and Peterson 1992). Trembling aspen seedlings were observed in recent ash beds during field work in Fort Nelson (unpublished data) and may have been the dominant trembling aspen regeneration mechanism after disturbance at the NF site.

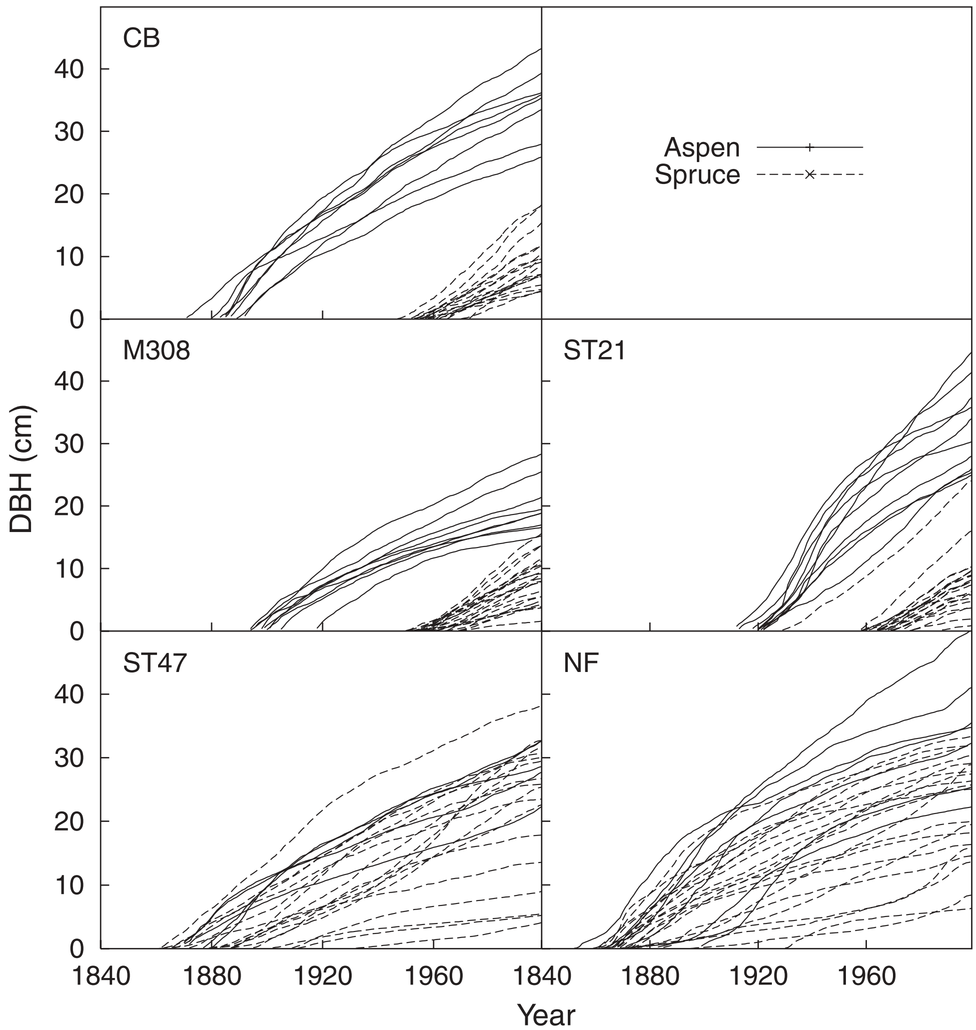
Eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) populations are currently at high levels in the Fort Nelson area. Dendrochronologic examinations have indicated periodic outbreaks with an interval of approximately 26 years (Burleigh et al. 2002). Budworm cycles have contributed to multicohort stand structures in eastern Canadian boreal forests (Cogbill 1985). The greater variation in white spruce ages at the ST47 site and the random regeneration pattern of subalpine fir at the NF site may be partially due to periodic eastern spruce budworm outbreaks.

The combination of factors that could explain the 29- to 58-year delay in spruce establishment cannot be definitively determined in this study. These factors are likely to include available seedbed (suitably decomposed coarse woody debris), existence of a seed source (adjacent seed-bearing spruce), mast years for seed production, and microenvironmental conditions that enhance initial survival of the spruce germinants (Stewart et al. 2001).

After reaching 1.3 m in height, white spruce height growth rates were similar across all sites (Fig. 4 and Table 2). The time to reach the 1.3-m threshold was the shortest for the NF site, with a median age of 13 years. The longest time was 27 years for ST21 white spruce. These are similar to the results of Lieffers et al. (1996), which indicated that rates of white spruce height growth were more rapid after reaching a threshold height of 2.3 m. In addition to light competition from overstory trembling aspen, the shrub and herb layers may also reduce available light for white spruce under 2 m in height (Constabel and Lieffers 1996).

The combination of a highly productive trembling aspen stand and the shortest regeneration lag for white spruce re-

Fig. 7. Diameter at breast height (DBH) development of stem analysis trees in each of the five study sites: CB, Capot Blanc; M308, Mile 308 of the Alaska Highway; ST47, Simpson Trail km 47; ST21, Simpson Trail km 21; and NF, Nelson Forks.



cruitment may explain the longer time to reach the 1.3-m threshold at ST21. The white spruce at ST21 appear to have been able to recruit under a younger trembling aspen stand, but height growth was suppressed (Fig. 4). Greater leaf area is found on younger trembling aspen stands (Pinno et al. 2001) and also with more productive trembling aspen stands. The individual spruce, which apparently recruited first at ST21 (Fig. 4), had the shortest time to the 1.3-m threshold and showed rapid initial height growth. Similarly at ST47, the earliest white spruce to establish on site had more rapid initial height growth than later recruits (Fig. 4). The slower growth rates for white spruce that established later on in stand development could also be partially attributed to the competition from established spruce.

In the codominant stands, the dominant white spruce showed little or no evidence of suppression of early height growth. Some white spruce would have been in the upper canopy 40–60 years after stand initiation (Fig. 3). In Alaska, Youngblood (1995) reported white spruce that established at the same time as trembling aspen, maintaining similar height growth to the trembling aspen and sometimes emerging through the broadleaf canopy. The Fort Nelson codominant stands do not show an obvious release of white spruce later in stand development, which could be attributed to mortality of dominant trembling aspen (Fig. 3).

For similar sites currently dominated by white spruce, it should be possible to examine whether trembling aspen or white birch had dominated the stand at earlier stages of development. Given the size and longevity of trembling aspen in Fort Nelson, there should be an obvious legacy of snags, coarse woody debris, or trembling aspen woody material in the forest floor if trembling aspen was part of the original stand. Timber cruises and other surveys of spruce-dominated stands in the Fort Nelson area do not identify a legacy that indicates a period of trembling aspen domination (S. Sawin, Slocan Forest Products, Fort Nelson, personal communication). These observations support the evidence from this study that stratified stands may not represent the only pathway in the successional development of older, white spruce-dominated stands in the Fort Nelson area.

The initial density and distribution of the two species in the codominant stands cannot be determined in this type of study. Similarly, rates of mortality during stand development are unknown. These questions can only be addressed from analysis of long-term, permanent sample plots. The within-stand variation for white spruce of the same age indicates

Table 4. Comparison of aspen component in mixed aspen–spruce stands between Fort Nelson and other locations in western Canada.

Location	Average age (years)	Density (stems/ha)	Basal area (m^2/ha)	Quadratic mean DBH (cm)	Average height (m)	Aspen total volume (m^3/ha)
Capot Blanc, SI 22 m @ 50 years	117	560	49.8	33.7	31.2	508.2
Mile 308, SI 19 m @ 50 years	103	1000	40.0	22.6	26.3	441.6
ST21, SI 25 m @ 50 years	84	400	37.8	34.7	30.5	478.1
Nelson Forks, SI 23 m @ 50 years	138	260	33.0	40.2	33.9	320.7
ST47, SI 21 m @ 50 years	138	200	17.1	33.0	28.9	269.1
Manitoba[a]	138	44	5.8	40.8[d]	21.3	101
Saskatchewan[b]	110[e]	na	27.5[e]	23.1[de]	>24[e]	195.7
Alberta, SI 22.5 m @ 70 years[c]	130[f]	494[f]	32.7[f]	29[f]	20.4[f]	130.6

Note: na, not available; SI, site index.
[a]Data from Ball & Walker 1997.
[b]Data from Kirby 1962.
[c]Data from Johnstone 1977.
[d]Arithmetic mean diameter.
[e]Stand average that includes spruce component, 34.4% by volume.
[f]Stand average that includes spruce component, 72.9% by volume.

that some white spruce were in far less competitive situations and were able to maintain greater rates of height and diameter growth.

The Fort Nelson results for codominant stands are in contrast with the classic boreal mixedwood succession descriptions, where both species regenerate at the same time, and the trembling aspen and white spruce are described as codominant in the canopy at roughly 70–100 years post-disturbance (Kabzems 1971; Day and Harvey 1981; Strong and La Roi 1983; Cogbill 1985; Chen and Popadiouk 2002). The spruce-dominated stages have been documented to start as early as 75 years in Ontario (Day and Harvey 1981) and at 100–150 years in Alaska (Van Cleve and Viereck 1981; Foote 1983), Alberta (Lacate et al. 1965; Strong and La Roi 1983; Corns and Annas 1986), and Saskatchewan (Kabzems 1971; Kabzems et al. 1986).

The vigor and longevity of trembling aspen in Fort Nelson appear to be the key in explaining the observed differences in succession for these mixed species stands. Average heights of trembling aspen in the Fort Nelson stands were 27–31 m compared with less than 27 m in other studies from western Canada (Table 4). Similarly, stand characteristics such as basal area and total volumes are lower in other western boreal locations compared with Fort Nelson (Table 4).

With such a prolonged period of trembling aspen domination, when could domination by spruce conceivably occur? There was an 18- to 21-m average height difference between the spruce layer and the dominant trembling aspen in the stratified stands (Table 1). Assuming maintenance of current average white spruce height increments, it would require approximately 80 years for white spruce to achieve the current trembling aspen heights. Depending on the particular stand, this could be 166–200 years after trembling aspen initiation. Both codominant and stratified mixedwood types in Fort Nelson would appear to require successional development well beyond 150 years to achieve white spruce domination.

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