

Post fire regeneration dynamics of white spruce
and aspen in a southern boreal forest in Alberta

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ABSTRACT

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Jianfeng Sun

I used data from 149 repeated aerial photographs taken in (1950s), middle (1970s or 1980s) and recent (1990s) times, together with forest inventory maps prepared by the Alberta Environmental Protection Agency in the year 1999 known as “Phase 3 inventory maps” to analyze changes in spruce crown closure (percentage of canopy cover) and height in mixed forest stands dominated by aspen (*Populus tremuloides* Michx) and white spruce (*Picea glauca* (Moench) Voss) in a boreal forest in Alberta, Canada.

A total of 81 stands located in good (N=11), medium (N=60), and fair (N=10) quality sites were studied for spruce emergence. Site quality and the time since the last fire accounted for about 70% of the variance in spruce canopy cover. A significant correlation between spruce crown closure and age was detected in good ($r^2=0.71$), medium ($r^2=0.81$) and fair ($r^2=0.54$) quality sites. There was no significant correlation between the rate of change in spruce cover (% cover/year) and the time since the last fire. The white spruce reached the main forest canopy height and overtopped the aspen in about 80-100 years since the fire. Results of the present study suggest that a longer time is required for the emergence of spruce through aspen canopy than previous estimates.

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Introduction

Boreal forest ecosystems experience a high frequency of forest fires, and the forest vegetation undergoes successional changes after fire (Johnson, 1992). The concept of forest succession has changed over the years (Drury and Nisbet, 1973; Oliver and Larson, 1990). In general, forest succession is defined as a process where more shade-tolerant species increase their proportion of the biomass, number of individuals or cover with the simultaneous decline of less shade-tolerant species. It is generally agreed, in a very broad sense, that shade-tolerant species are poorly dispersed and grow more slowly than shade-intolerant species under ample light conditions (Greene et al, 2002). The shade-tolerant species often arrive at a disturbed site after the establishment of intolerants or, if they arrive simultaneously, shade tolerants grow slower than shade intolerants. Therefore, in young stands, shade tolerant species are commonly found growing under the canopy of shade-intolerant species (Greene et al, 2002). Since the amount of sunlight reaching the understory is limited, shade-tolerant species need to reach the canopy stratum to receive sufficient light to secure resources for growth and reproduction. The growth rates of shade tolerants in the shade are poor, and opening of canopy gaps are essential for the release of suppressed stems (Bergeron, 2000).

Two forest tree species, the shade intolerant aspen (*Populus tremuloides* Michx.) and shade tolerant white spruce (*Picea glauca* (Moench) Voss), dominate most of the mesic sites in the southern boreal forests of western North America.

Although small plumed seeds of aspen are capable of dispersing throughout a wide geographical range, aspen typically regenerates after a major disturbance through suckering from roots (Peterson and Peterson, 1992). The forest fire, one of the most common disturbances in the boreal forest, recurs at intervals averaging about one hundred years in central Alberta, and perhaps as much as 300 years at the Arctic treeline (Johnson, 1992). Because of their prolific suckering ability, aspen is well adapted for these intense stand-replacing fires. The more shade-tolerant species such as spruce lack suckering ability and regenerates only through seeds from living sources at the burn edge or from residual (surviving) stands within the burnt area. Spruce grows more slowly than aspen stems originated from seeds and far more slowly than vegetatively propagated aspen stems (Bergeron, 2000; Greene and Johnson, 1999). Thus, in young stands of the western North American boreal forest, spruce, if present, is invariably overtopped by aspen (Galipeau et al, 1997; Greene and Johnson, 2000). It has been shown that spruce trees suppressed by overtopping of aspen produce fewer seeds than unsuppressed but similar-sized spruce trees (Greene et al, 2002). Thus, sexual reproduction of spruce is predominantly limited to the individuals that attain canopy status, as suppressed trees receive too little light. Due to the slow growth rate of suppressed spruce and the short fire interval typically found in western North America, the persistence of spruce in the western boreal forests is primarily determined by the rate of ascension of spruce into the canopy.

Immediately after a fire, approximately 35% of the ground comprise exposed mineral soil or thin humus (Lutz, 1956). These optimal seedbeds for white spruce are soon lost (within the first few years) as litter begins to accumulate (Charron and

Greene, 2002; Greene et al, 1999) and seedbeds with exposed mineral soil will become rare for several decades. In about 40 – 80 years after a fire, white spruce seedlings may begin to establish on the decomposing wood derived from original pre-fire trees (Lieffers et al, 1996). However, this second cohort grows even more slowly than the first post-fire cohort due to reduced light availability (Gutsell and Johnson, 2002). Thus, this second cohort may not attain canopy status until about 200 years following the initial fire. Given the short fire rotation times of western boreal forests, the density of the first cohort of spruce is extremely important for the regeneration of spruce. A thorough knowledge of post-fire ascension rate of spruce is critical for understanding the regeneration dynamics of boreal forests.

Estimating spruce ascension rates (rate of increase in height or area covered by spruce) has been hampered by methodological problems. One approach, chronosequence analysis (i.e. a collection of static height or spruce cover from a series of stands differing in their age or time since fire), greatly underestimates the time required for spruce to reach the canopy (e.g. Dix and Swan, 1971). The main source of error stems from the variability in time required for trees to reach the height at which cores are obtained for estimating the age. This error of age estimates is often considerable, leading to underestimation of 10 to 40 years of the true age (Peters et al, 2002). The standard correction factor for the growth period between root collar and the coring height (30 cm) is error prone because of the difficulties in distinguishing the root collar due to adventitious roots (Peters et al, 2002; Desrochers and Gagnon, 1977; Charron and Greene, 2002).

Using the chronosequence approach in a forest stand in Saskatchewan, Kabzems et al (1976) showed that white spruce first enters the lower overstory no earlier than 50—60 years after a fire, and eventually becomes taller than the aspen stand at around 100-120 years. Due to under-estimation of the age due to limitations mentioned earlier, one might assume that the period of emergence is later than the estimates of Kabzems et al (1976). Moreover, the conclusion of Kabzems et al (1976) is intended to be a rough guide, and cannot be used for predicting the mean and variance of ascension rates.

Unlike earlier studies where age underestimation led to the erroneous conclusion that the initial arrival of spruce is delayed (e.g. Dix and Swan, 1971), a recent stand reconstruction study and a permanent plot study have shown that white spruce establishes immediately after the fire along with the vegetatively propagating aspen, and then, at least initially, grows slowly (e.g. Charron and Greene, 2002). The fastest growing spruce stems do not reach the canopy until about 100 years after the fire (Gutsell and Johnson, 2002).

Comparison of aerial photographs taken at various time intervals is useful in assessing the vegetation changes over a relatively long time span. A recent study by Rhemtulla et al (2002) used aerial photographs to assess the change in canopy cover over 80 years in a forested montane landscape in western Alberta. Unfortunately, their analysis was limited to forest cover types (pure hardwood, hardwood-conifer mix) and not focused on individual species level changes. Furthermore, their analysis was based on longitudinal pairs of photographs, and thus they were not able to ascertain temporal

change in the rate of ascension. Moreover, they focused on the regeneration of aspen and lodgepole pine (*Pinus contorta*), and regeneration of white spruce was not studied.

The objective of my study is to examine post-fire changes in cover and growth of white spruce in a southern boreal forest in Alberta using aerial photographs initially taken for a province-wide forest inventory. I have limited my analysis to stands (polygons) where I can confidently determine that only spruce and aspen are present. Further, I constrained the analysis to areas for which I could obtain photographs covering the same region for at least three time periods (1950s, 1970s or 1980s, and 1990s), so that I could obtain data on temporal change in spruce cover, and the time and height of the forest at which spruce emerges through the canopy. To the best of my knowledge, this is the first attempt to use triplicates of aerial photos to estimate the age of spruce emergence through the aspen canopy.

Background on methods for studying stand dynamics

Boreal forest ecosystems experience a high frequency of forest fire and are widely harvested through clear-cutting, especially in the southern portion (the mixedwood dominated by aspen and white spruce). To date, the ecological consequences of the latter activities are not fully understood. However, there is a growing interest in formulating management strategies for boreal forests that emulate natural disturbance regimes with the anticipation of maintaining biodiversity and sustaining essential ecosystem functions (Attiwill, 1994; Bergeron and Harvey, 1997; Bergeron et al, 1999). Fire is one of the major natural disturbances in boreal forests (Johnson, 1992), and is considered to be an integral part of the boreal ecosystem dynamics. The silvicultural practice of clear cutting is believed to emulate the natural disturbance of fire in boreal forests (Bergeron et al, 1999). Although this practice does not totally mimic the effects of fire, the complete removal of vegetation and subsequent seeding or planting leads to a regeneration pattern similar to post-fire regeneration patterns (Bergeron and Dubuc, 1989; Harvey and Bergeron, 1989; Galipeau et al, 1997; Greene et al, 1999).

Several major methodological approaches are used for studying the dynamics of forest ecosystems. The first approach, chronosequence analysis, assumes that stands of different ages are representative of the stages that any single stand goes through. The second approach, permanent plots, directly measures the temporal change in species composition as well as size-specific birth and death rates. A third approach, stand reconstruction, employs plant remains such as dead trees,

the growth rings of living trees, and (occasionally) pollen data to reconstruct the stand history. The fourth approach, modeling, involves simulation of various parameters that affect forest regeneration using computer programs.

Chronosequence analysis. This method involves the use of chronosequences, sets of different-aged stands, assumed to represent stages in a trajectory of species composition change on a single plot (Drury and Nisbet, 1973). This approach assumes that all differences among stands except time are negligible. Chronosequence analysis has been a research tool in ecology since the inception of the field. For example, Cowles (1899) described the vegetation on a series of dunes along the shores of Lake Michigan, U.S.A., and set the foundation for Clements' theories of succession and climax (Clements, 1916). Since that time, vegetation chronosequences have been used repeatedly to describe community and ecosystem changes during primary and secondary succession. Various attributes (e.g., species abundance, net primary production, and soil nutrients) of the communities can be directly measured to obtain precise information about the vegetation.

The utility of chronosequence analysis for studying long-term vegetation dynamics is well illustrated in the study by Walker et al (1981). From the analysis of soils, nutrients, biomass, and forest vegetation across the Cooloola sand dunes in east coastal Australia, these authors were able to show that the composition and structure of forest communities and their recovery following disturbance were dictated primarily by soil changes that took place over several hundreds of thousands of years.

The conventional chronosequence analysis technique has been based on field collection of stand-level data and was therefore limited in its application to a broad geographic area. However, recent advances in remote sensing technology have provided means to overcome some of these limitations. For instance, LIDAR (light detection and ranging) is a relatively new technology that offers an alternative to photogrammetric techniques and radar data for the collection of forest height (St-Onge et al, 2004). The photogrammetric and radar data could only be used to measure the heights of trees at the forest edge, and therefore cannot be used effectively with closed canopy forests. Satellite images, such as American TM & MSS and European SPOT, often are used now to study landscape level forest dynamics (Bergeron, 1991).

Permanent plot data. A more precise assessment of long-term changes of the vegetation can be obtained through repeated measurements of vegetation in permanent plots. Although several long-term ecological research plots have been established within various forest ecosystems, records currently available are relatively short in duration and therefore of limited use in addressing a broad range of questions. For example, secondary succession in some hardwood forests of eastern North America and Europe requires several hundred years to reach a theoretical end point (Hough and Forbes, 1943; Jones, 1945; Raup, 1957; White, 1979). Some west-coast conifer forests may not reach a steady-state for more than 1000 years owing to the dominance of long-lived early successional species (Franklin and Dyrness, 1973; Franklin and Hemstrom, 1981). The longest post-fire

permanent plot in the boreal forest was of only 5 years duration (Charron and Greene, 2002).

Stand reconstruction using plant remains and living trees. Another, very recent, approach is the reconstruction of vegetation changes from plant remains. For relatively short time periods (e.g., 100 years), forest histories can be reconstructed from the growth rings and stem positions of living and dead trees (Stephens, 1956; Henry and Swan, 1974; Oliver and Stephens, 1977; Bergeron 2000). As an example, for understanding species and stand dynamics in the mixed-woods of Quebec's southern boreal forest (Bergeron, 2000), all living and dead stems (> 1 cm DBH) were mapped and cut down in 20m by 20m plots. The cross sections collected at the root collar and at every meter were analyzed using standard dendrochronological techniques. The age of the stand before the last fire was estimated using snags and logs located in, or in the vicinity of, each quadrat. A PCA ordination of all quadrats showed a gradual change with time since fire from stands dominated by hardwoods (aspen and paper birch), to mixedwood stands with an important white spruce component, and finally to coniferous stands (white spruce and balsam fir).

At a longer time scale, palynological data, based on the analysis of pollen grains preserved in lake sediment and on moss layers (Faegri and Iverson, 1975), are valuable for monitoring the vegetation change over very large areas and long time periods. Pollen grains in lake and bog sediments provide continuous records of vegetation change over time. The interpretation of pollen frequencies in terms of vegetation is complicated, however, due to differential pollen production and pollen

dispersal rates of plant species involved and the difficulties in distinguishing many taxa at the species level.

While early pollen studies interpreted vegetation in very general terms, recent work has greatly improved the precision of palynological inferences. One improvement is the use of absolute pollen influx (pollen grains accumulating per square centimeter of sediment per year) rather than relative pollen percentages. Unlike pollen percentages, the pollen influx of any one species is independent of the abundance of pollen from other species. The relationship between pollen influx values and actual plant abundance is still quantitatively different for every species and depends on their pollen production and dispersal characteristics (Davis et al, 1973). This relationship may also vary between sites owing to sedimentation processes unique to each bog or lake (Davis et al, 1973). Several studies attest to the validity of pollen records from small lakes (Brubaker, 1975) and localized organic deposits (Andersen, 1973) for examining the long-term dynamics of individual forest communities. The accuracy of pollen records has increased in recent years by use of the identification of plant macrofossils (leaves, fruits, seeds), which provide conclusive evidence that a species occurred in the immediate vicinity. Finally, in the past few years numerous species-specific identifications have been made possible by the careful measurement of pollen grain dimensions and by the use of scanning electron microscopy.

Computer based forest dynamics simulation models. Computer models have become valuable tools in advancing our understanding of forest dynamics. Three

major types of simulation models, namely historical bioassay, process simulation, and hybrid models are being widely used to simulate the growth and development of forests.

Historical bioassay models take data that define how forests have grown in the past to predict future growth. That is, they extrapolate from recent (often only a few years) relative growth rates of competing stems. For example, a transition probability, Markov-type model was used in an eastern U.S. hardwood forest (Horn, 1975) and in the U.S. Pacific Northwest (Stage, 1973). However, this approach can provide no explanation of the mechanisms of change, and are poor predictors of forest dynamics under different management and environmental conditions.

Process simulation models consider all determinant factors, such as the changing environmental conditions and disturbance regime, but which, in aggregate, are too complex for any simple description. These models are very demanding of computer time. These models include the Douglas-fir growth model in the Netherlands (Mohren 1987) and in coastal British Columbia (Burnett et al, 1996).

To take advantage of the strengths of both historical bioassay and process-based simulation models while overcoming their major drawbacks, many forest ecologists have recently employed a hybrid approach to modeling ecosystems (Kimmins, 1997). These models are driven by historical bioassay growth equations, or empirical growth data, with the predicted growth modified based on the simulation of those processes that are considered to be most important (primarily

the iterative relation between growth and light receipt). This gives the models an empirical foundation, adds sufficient process simulation and provide some flexibility in the face of change, but avoids the complexity of a full process model. There are three groups of hybrid models: the gap models such as JABOWA (Botkin, 1993), which simulate the growth and succession of tree species in a small plot of about 0.01—0.08 ha in size, which represent the canopy gap created by the death of a single large tree; stand level ecosystem management simulation models (e.g. FORCYTE and FORECAST) that deal with individual cells on the order of 1.0 ha in size (Kimmins, 1997); and an emerging group of individual tree growth models such as SORTIE and FORCEE that represent the horizontal as well as the vertical spatial distribution of plants (Kimmins, 1997). With the ever increasing computing power, improved ecological knowledge and the development of GIS techniques, simulation models are becoming a major tool in the conservation and management of forest ecosystems.

Methodology

The study area (Fig. 1) is located within the Central Mixedwood and Wet Mixedwood regions of the boreal forest (Alberta Environmental Protection, 1999) and has a continental climate with long, cold winters, and short, cool summers. The yearly precipitation is low (397mm, with most of this (240mm) falling as rain in July). The mean summer temperature is 13.5°C (May-August), while mean winter temperature is -13.2°C (November-February). The aspen/spruce mixedwood stands are typically on mesic substrates derived from till, which yield the more productive soils in the landscape: Gray Luvisols and Eutric Brunisols (Strong and Leggat, 1992). Westerly and easterly winds alternate in winter under the control of depressions moving east along the trough of low pressure; easterly winds are particularly frequent in late winter and early spring (Kendrew and Currie, 1955).

I have adopted a hybrid approach between stand reconstruction and chronosequence analysis techniques to study post-fire regeneration dynamics of boreal forests in Alberta. I used repeated aerial photographs taken at three time periods (1950s, 1970s or 1980s, and 1990s) of the same area of a given stand or "polygon" to measure the percentage cover of spruce and aspen in each photograph. That is, for each polygon, I have 3 aerial photographs taken at different times. I obtained the stand age data from Phase 3 inventory maps prepared by Alberta Environmental Protection (1999) to examine the relationship of change in spruce and aspen cover as a function of time since fire (age of the forest stand).

The photographs taken by the government of Alberta in the 1950s were incomplete and covered only a part of the province. Therefore these photographs were not used for making forest inventory maps. The Phase 3 forest inventory program began in the early 1970s and was completed in 1984. This inventory evaluated most of the area included in the previous Phase 1 (1949) and Phase 2 (1956) inventories. The main objectives of the phase 3 mapping project were to appraise the province's forest resources to provide a reliable and current data base for the development of management plans; to calculate annual allowable cuts; and to identify and schedule timber stands for harvesting. A series of aerial photographs was taken in the 1990s to update the Phase 3 inventory maps.

The Phase 3 inventory maps are based on aerial photo interpretation supplemented with field-data. In 1976, aerial photographs with the scale of 1:15,000 were adopted in lieu of the previous 1:15,840 scale used in Phase 1 and Phase 2 inventories. The most commonly used film was black and white with modified infrared. A limited number of pictures were taken with panchromatic film. The Phase 3 inventory included the estimation of heights of representative trees in the aerial photographs using stereoscope and parallax bar. These estimated heights were validated with field data (Alberta Environmental Protection, 1988).

In the Phase 3 inventory mapping project, the time since fire or age of the stand was usually determined by felling a sample of trees and sectioning (sawing a one-inch thick disc from the tree bole at stump height (0.3m) or at the diameter at breast height (dbh; 1.3m above the ground). Increment borers were also used at 0.3m

height. If the diameter was exceptionally large, or where decay was present or suspected, the age was determined by sectioning or coring at breast height (typically well above the region of decay). Age correction factors were used for accounting the years of growth prior to a tree reaching stump or breast height.

An index known as "site index" was adopted to describe the quality of a given forest site. The site index is an expression of forest-site quality based on the dominant tree height at a specific age (Alberta Environmental Protection, 1988). For example, a site with a 70 year old stand is classified as good (>20m), medium (15-20m) and fair (<15m) based upon the height of the dominant tree species (Fig. 2).

For the present study, I purchased one hundred and forty-nine aerial photographs and four Phase 3 maps from Alberta Environmental Protection, Land and Forest Service. I selected four townships (TWP 67.10.4, TWP 67.11.4, TWP 91.4.5, and TWP 91.23.4) in Alberta (Figure 1) based on Phase 3 maps. For further analysis, I chose the areas comprising aspen and white spruce with no other conifers present. Initially, I chose a hundred polygons (area range=20-100 ha, mean=60 ha) within the area covered by the air-photos. In this study, I focused on the post-fire spruce only, and excluded the small patches of residual spruce (i.e. those that survived the fire). Since the residual trees were much taller than the surrounding aspen, identification of residual spruce stands in most polygons was accomplished without major difficulties. However, in nineteen stands, it was impossible to confidently distinguish residual spruce trees from post-fire recruited trees. Thus, I excluded those nineteen polygons, and the further analyses were performed with the

remaining eighty-one stands where I could reliably assess the proportion of white spruce crown cover. I used Phase 3 inventory maps for grouping the polygons by site class (good, medium and fair), as well as for determining the stand age.

It was easy to discern the white spruce from aspen in 1:15,000 black and white photographs (Fig. 3). The aspen is much lighter and the form of its crown is “smoother” than white spruce. I chose four stands from township (TWP) 67.11.4 based on photographs taken in 1951, 1977 and 1990; twenty-seven stands from TWP 67.11.4 based on photographs taken in 1951, 1977 and 1993; five stands from TWP 91.4.5 based on photographs taken in 1951, 1978, and 1996; and forty-five stands from TWP 91.4.5 based on photographs taken in 1951, 1983 and 1990 for the present study.

Crown closure, defined as the percentage of ground area covered by the vertical projection of tree crowns, is an important stand density character. Crown density scales from the U.S. Forest Service (Fig. 4), Alberta Environmental Protection (1988) and Chinese Northeast Forestry University (Ma et al., 1988) were used as guidelines to compare with aerial photographs in estimating white spruce crown closure. The precision of this popular method is more than 90% (Ma et al., 1988), and the results were tested twice to make sure the precision.

Among many theoretical growth functions available for modeling forest growth,, the logistic function is considered to be the best for analyzing the relationship between the percentage cover of a single species among competitors .

Likewise, the Richard function is better for investigating the relationship between the vegetation height and age because, if nothing else, it realistically starts at 0 and then asymptotically approaches some site-mediated maximum height. (Richard, 1959; Pienaar et al, 1973; Causton and Venus, 1981; Houllier and Leban, 1991; Meng, X. Y. 1996; Li et al, 1997).

The percent spruce cover data from each site type were analyzed with the logistic function:

$$Y = K / (1 + m \text{Exp} (-rt)),$$

where Y is spruce crown closure (defined as the proportion of canopy comprising spruce); t is time since fire, and K, m and r are independent parameters. Nonlinear regression analysis was performed to estimate the parameters using the SPSS software, version 10.0.

Stand height is defined as the average height of dominant and codominant trees in a forest stand. On a single tree basis, it is the vertical distance from ground level to the upper tip of the tree crown. In order to estimate the height of white spruce and aspen, I selected 108 pure aspen stands representing 29 good, 41 medium, and 38 fair sites, and 82 pure white spruce stands representing 24 good, 40 medium, and 18 fair sites. White spruce and aspen heights estimated by the Alberta Forest Service were obtained from the Phase 3 map. From the Phase 3 map, the height class codes could be found. To apply an accurate height class code to a forest stand,

accurate field data is essential. Care was taken during field work to obtain height of average codominant trees which were representative of the stand being evaluated. Another accurate means of applying stand height codes was by measuring heights of representative trees on aerial photographs using a stereoscope and parallax bar, and its error variation is ± 1.5 -- 2.5 m if the scale of aerial photograph is 1:5000 -- 1:20000 (Ma et al., 1988).

Table 1 Stand height codes

| Height class codes | Actual stand height |
|--------------------|---------------------|
| 0 | 0-6.0 m |
| 1 | 6.1-12.0 m |
| 2 | 12.1-18.0 m |
| 3 | 18.1-24.0 m |
| 4 | 24.1-30.0 m |
| 5 | >30.1 m |

Then the height data was analyzed (sorted by species and site type) with the Richard function (Richard, 1959; Meng, 1996):

$$Y = a (1 - \text{Exp} (-kt))^b,$$

where Y is tree height; t is time since fire; and a, k and b are independent parameters.

Nonlinear regression analysis was performed to estimate parameters using the SPSS version 10.0 software.

Results

White spruce crown closure and ascension rate

Analysis of combined data from all site types showed a weak but significant correlation between spruce cover (closure proportion) and time since fire ($r^2=0.19$; $p=0.03$; $N=81$). However, partitioning the data based upon the site type resulted in much stronger correlations between spruce cover and time since fire (Figure 5a, b, c; $r^2=0.71$, $p<0.001$, $N=33$ for good sites; $r^2=0.81$, $p<0.001$, $N=180$ for medium sites. and $r^2=0.54$, $p<0.001$, $N=30$ for fair sites).

There was no significant correlation between the *rate of change* in spruce cover and the time since fire (Figure 6a, b, c), and this was true even when the data were partitioned based on site type. The visual (qualitative) examination of Figure 6 indicates that the greatest rates of increase (%/yr) occur approximately (71.43%) at 80-120 years after a forest fire. Mean rates of spruce cover change were strongly influenced by the site type (ANOVA; $p<0.05$) with mean values of 0.265, 0.165, and 0.091 %/yr for good, medium, and fair, respectively.

The height of white spruce and aspen

The heights of aspen and spruce as a function of time since fire are shown in Figure 7 ($r^2= 0.72$ and 0.89 , $N= 108$ and 82 for aspen and spruce respectively; both

regressions are significant at $p < 0.001$). The height at which spruce overtopped aspen varied with site type as 22, 20, and 18 m for good, medium, and fair sites, respectively. However, the age at which the average subcanopy spruce overtopped aspen was not correlated with the site type and the corresponding ages were 80, 95 and 85 years for good, medium, and fair site types respectively. Thus, around 80 to 100 years after the fire, white spruce and aspen reached approximately the same height (~20m), and during the subsequent 20 years, spruce overtopped the aspen while maintaining a maximum rate of increase in spruce cover.

Discussion

In this study, I applied a hybrid approach to study forest dynamics. The use of repeated photographs of the same stand is similar to an analysis based on permanent plot data. Conversely, using many such plots simultaneously is similar to the chronosequence approach.

The correlation between percent cover of spruce and time since fire was weak when the data of all three site types (good, medium and fair) were combined, but a strong correlation was detected when data were separated by site type (54 to 81% of the variation explained). This is presumably due to site-mediated differences in growth rates, which affect the rate at which spruce emerge through the aspen and subsequent expansion of their crowns. While many authors (e.g. Fox et al, 1984) have suggested that site differences may affect rates of compositional change (i.e. succession), to the best of my knowledge, this study represents the first quantitative demonstration of the importance of site differences in spruce cover change during the post fire forest regeneration. Similarly, many authors (Clements, 1916) have argued for a general trend in the increase in proportion of shade-tolerant species with time. However, quantitative estimates are lacking, mainly due to methodological limitations. This study clearly shows the quantitative increase in white spruce crown cover as a function of the time since fire.

Nonetheless, about 30% of the variation in spruce percent cover cannot be explained by the combination of time and site type. It could be speculated that the unexplained residual variation can be attributed to recruitment constraints such as variation in nearby seed source densities, occurrence of mast seeding during the first few years following fire when the optimal seedbeds were still common, and the duration of the smoldering combustion of the duff (Dix and Swan, 1971; Greene et al, 1999; Oliver and Larson, 1990; Peters et al, 2002).

In contrast, there was no significant correlation between the rate of spruce cover change and the time since fire, even when I segregated the data by site type. This is due to the fact that the relationship was masked by high variability of the data. Nonetheless, the mean rate of cover change was significantly influenced by the site quality. Qualitatively, it was seen that about three-fourths of the highest rates of change occurred a 75-130 years since fire. The latter result is perhaps not surprising. This maximum rate of spruce cover change coincided with the time when post-fire spruce finally reaches the height of the aspen canopy according to Gutsell and Johnson (2002).

Kabzems et al (1976) argued that spruce emergence in Saskatchewan should occur primarily in the interval 50-80 years but my data for Alberta indicate that the peak emergence tends to occur several decades later than that. Those authors used chronosequence analysis with ages estimated using cores or disks cut at the stump height. This may have lead to under-estimation of ages in white spruce, which grows slowly at young stages. This difference in estimation of emergence rates can have

practical applications. For example, based on Kabzems et al (1976) study, a 60 year old stand can be expected to have many emergent spruce stems which, in turn, can produce many germinants which grow on the rotting wood derived from the previous fire. Such a stand could then be partially harvested assuming that the second cohort and some of the suppressed first cohort stems can stock the new canopy through advance regeneration. However, the results presented here suggest that this augmentation of the advanced regeneration will be greatly delayed, and the spruce will take much longer time to emerge and produce seeds than envisaged by Kabzems et al (1976).

The use of repeat aerial photographs is a promising method for studying forest dynamics and could become a standard approach in studying the boreal forest regeneration dynamics. Aerial photographs taken for inventory purposes during the last 60 years are already available for many boreal forest regions. These photographs will serve as empirical documents to monitor changes in canopy species composition and will provide a practical means to cover much broader area than laborious permanent plot studies. This technique is particularly useful for species- poor communities such as the boreal forest because most tree species are quite difficult to distinguish in air photos.

Nonetheless, there are limitations in application of this methodology. These photographs are of limited utility in identifying taxa in species rich ecosystems. Although newer imaging techniques may permit to record information with higher resolution allowing identification of wider range of species, these newer images may

date back only a few years. A second disadvantage of this method is that this cannot be applied to study sub-canopy dynamics, as one cannot determine the presence or growth rates of a given species in the sub-canopy. A third disadvantage is that this method relies on age estimates supplied with the inventories. These age estimates are dependent on site-specific, height and age relationships developed using labor-intensive field data from a small number of stands. These age estimates and extrapolations are relatively accurate for rapidly growing young stands. However, the variance of age estimates of old trees become large as growth declines, making this method unreliable for studying forest dynamics in old stands. Mainly, in my study, the traditional visual interpretation methods, like parallax bar and crown closure scale, were used to estimate forest height (error variance is ± 1.5 — 2.5 m) and crown closure (the precision is 90%). However, more recently, advances in remote sensing techniques provided a foundation for improved interpretation precision via sophisticated software.

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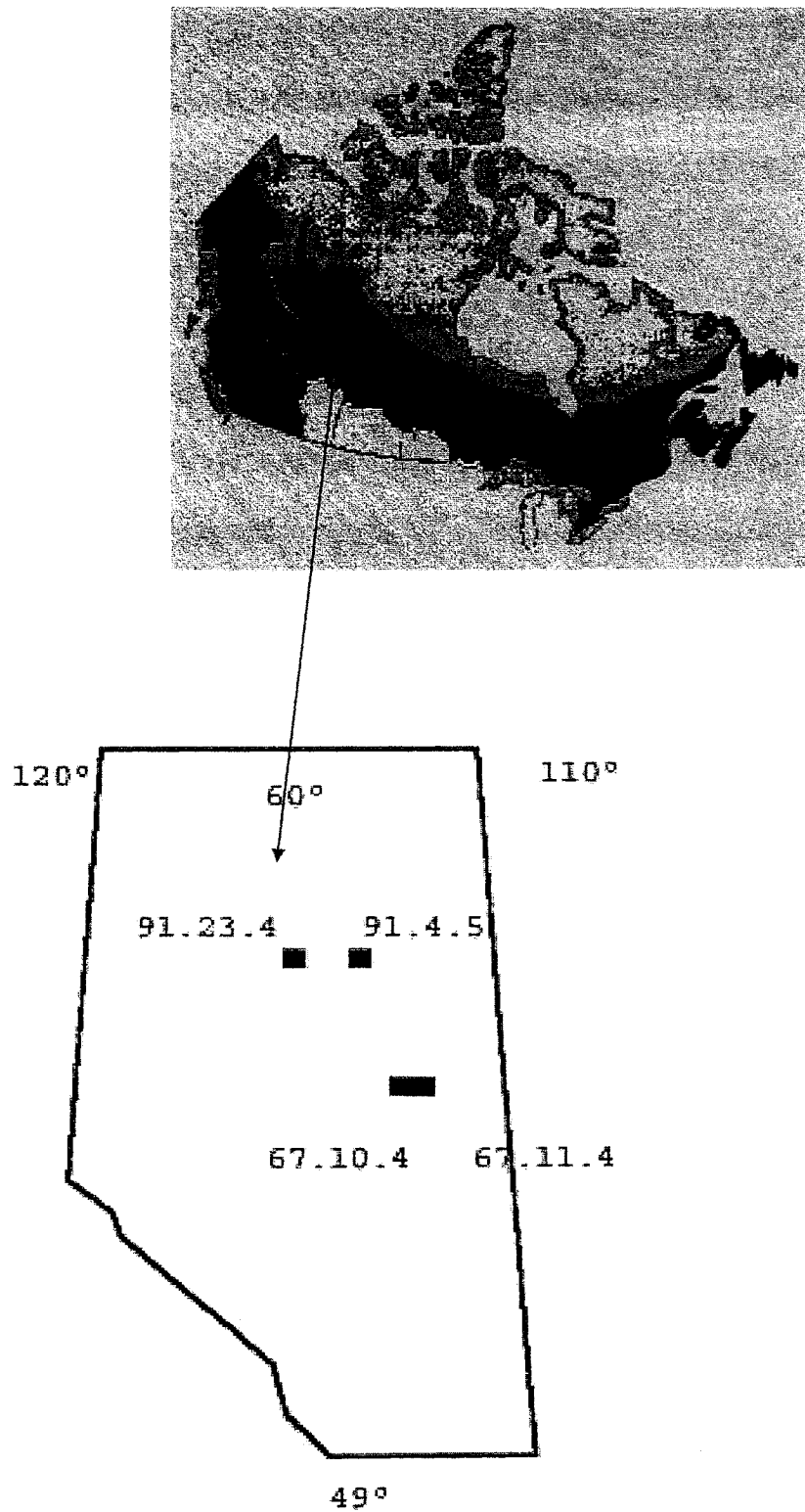
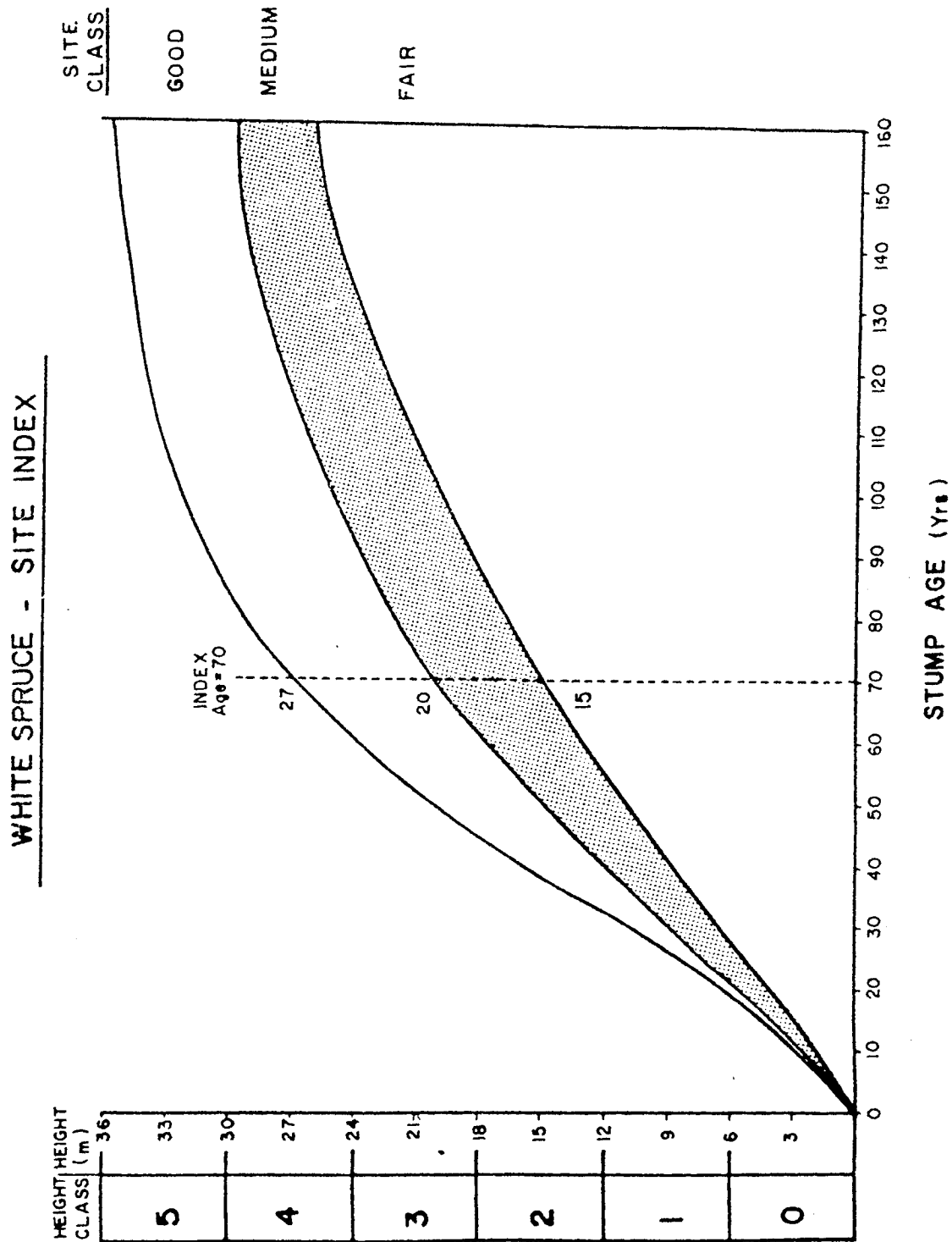


Fig. 1. The map showing the location of study sites in four townships in the southern boreal forest in Alberta.



Redrawn from Kirby and from samples taken in Management Units P6,S5,S8.

Fig. 2. Site index classification system used for the present study.

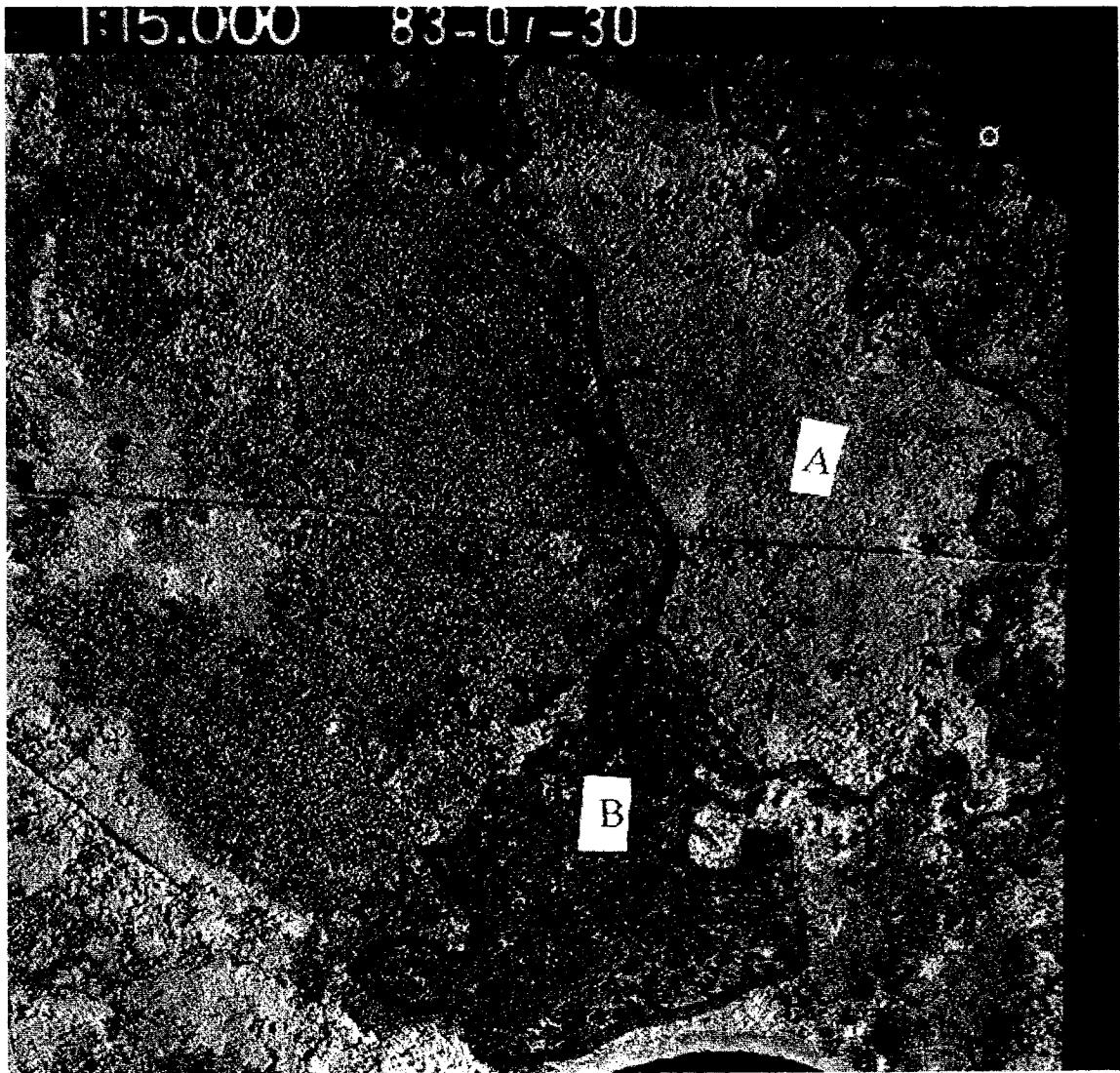


Fig. 3. An aerial photograph to show the interpretation of white spruce and aspen covers. The area "A" depicts aspen, and the area "B" is spruce.

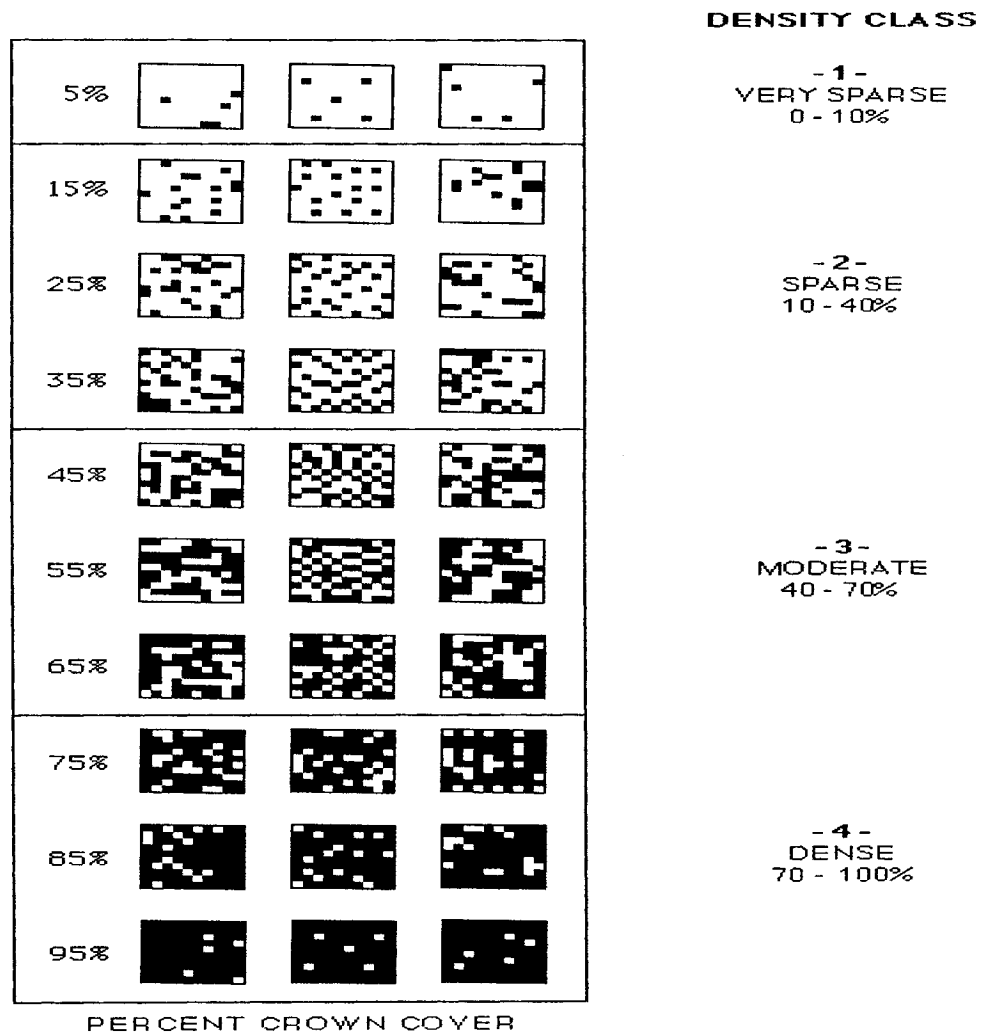


Fig. 4. Crown density scales used as a guideline in estimating crown closure.
 Modified from: U.S. Forest Service, Central states Forest Experiment Station, N.D.
 (Alberta phase 3 forest inventory).

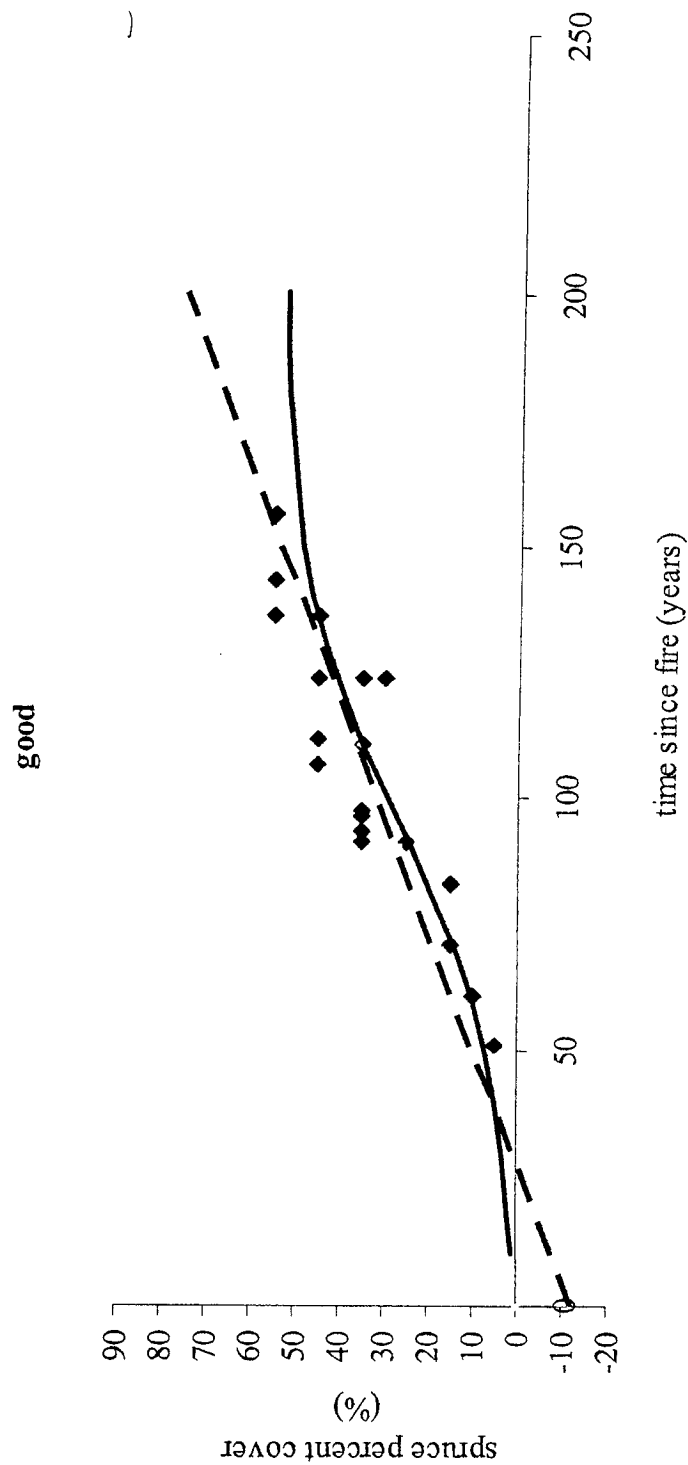


Fig. 5a. The change in percent cover of spruce in relation to time since fire in stands (N=33) in areas with a site index of “good”. The data were fitted to the logistic growth model [$Y = 53.61 / (1 + 43.92 \text{ Exp } (-0.042t))$, $r^2=0.71$] as well as a linear model [$Y = 0.457t - 14.666$, $r^2=0.80$]. Y= spruce crown closure, and t=time since fire in years.

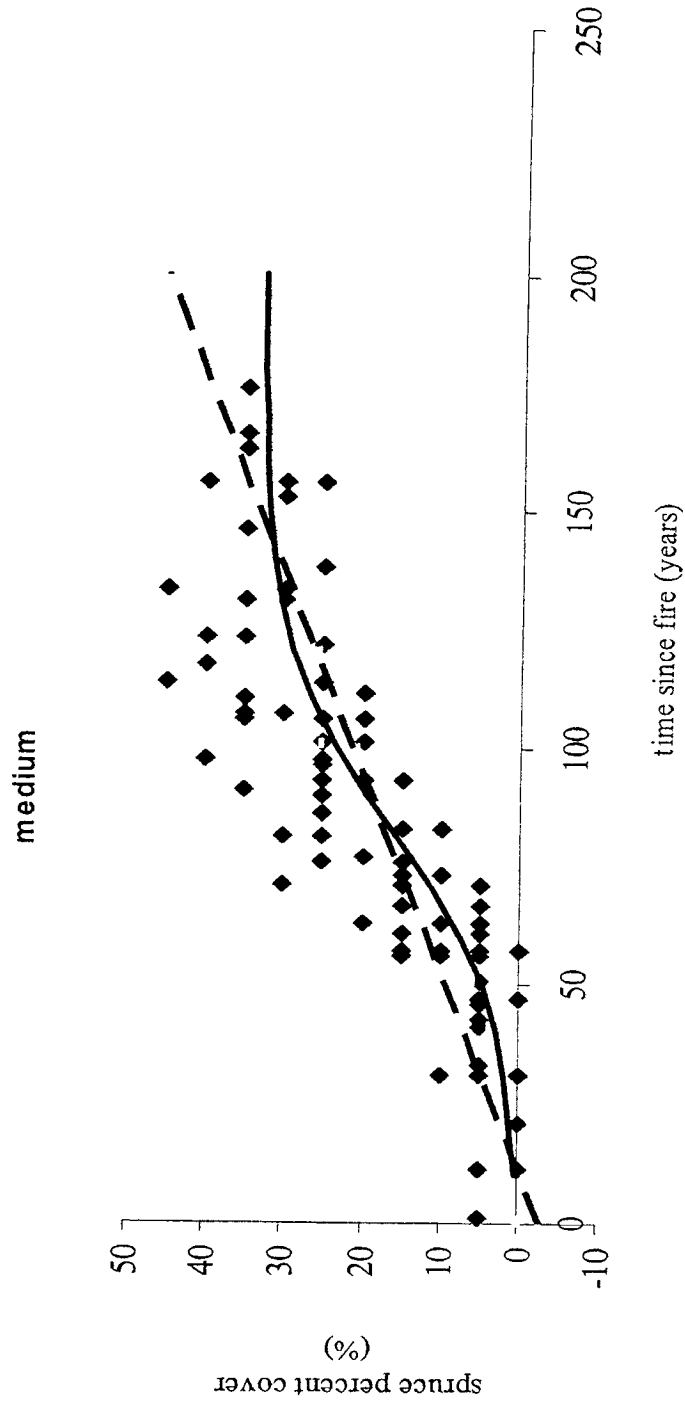


Fig. 5b. The change in percent cover of spruce in relation to time since fire in stands ($N=180$) in areas with a site index of “medium”. The data were fitted to the logistic growth model [$Y = 33 / (1 + 74.19 \text{ Exp } (-0.055t))$, $r^2=0.81$] as well as a linear model [$Y = 0.247t - 3.662$, $r^2=0.74$]. Y = spruce crown closure, and t =time since fire in years.

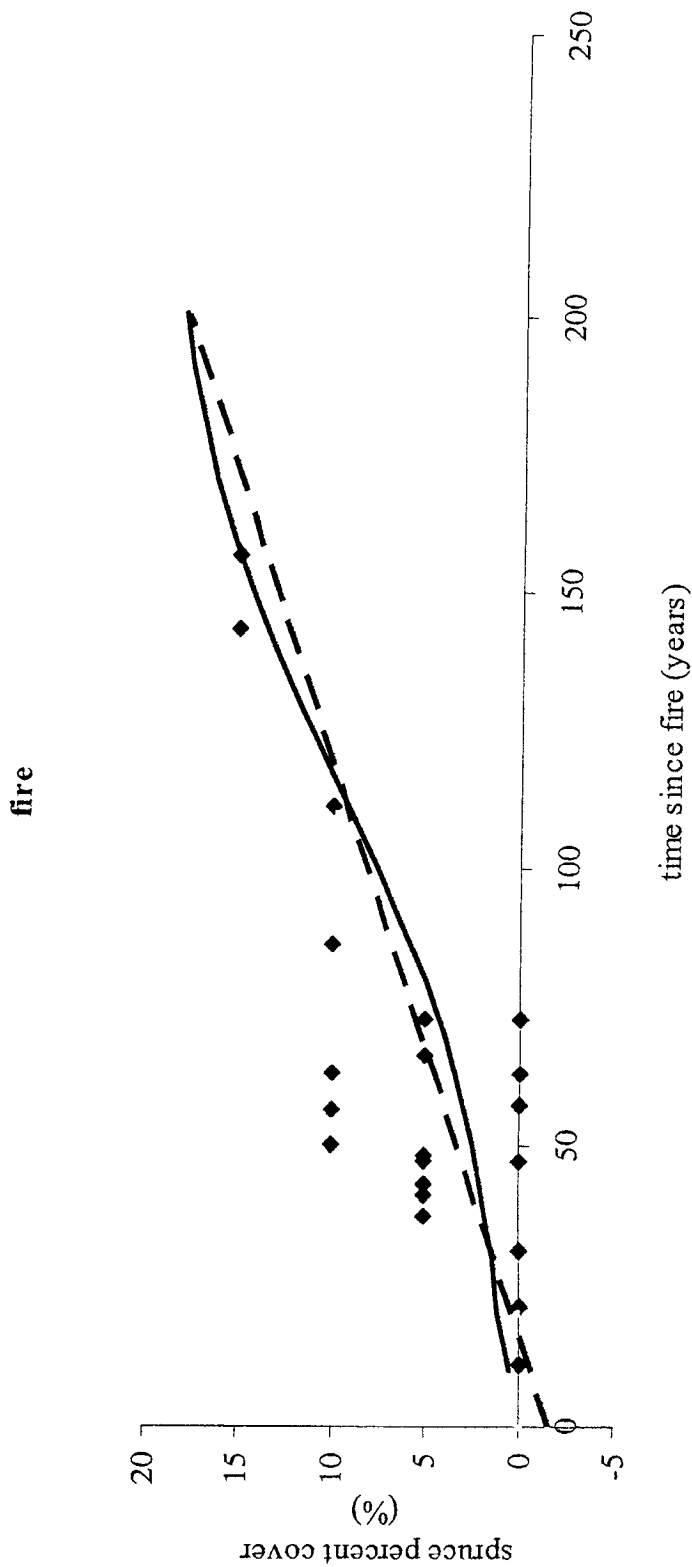


Fig. 5c. The change in percent cover of spruce in relation to time since fire in stands ($N=30$) in areas with a site index of "fair". The data were fitted to the logistic growth model [$Y = 19.49 / (1 + 27 \text{ Exp } (-0.03t))$, $r^2=0.54$] and a linear model [$Y = 0.10 - 1.949t$, $r^2=0.54$]. Y = spruce crown closure, and t =time since fire in years.

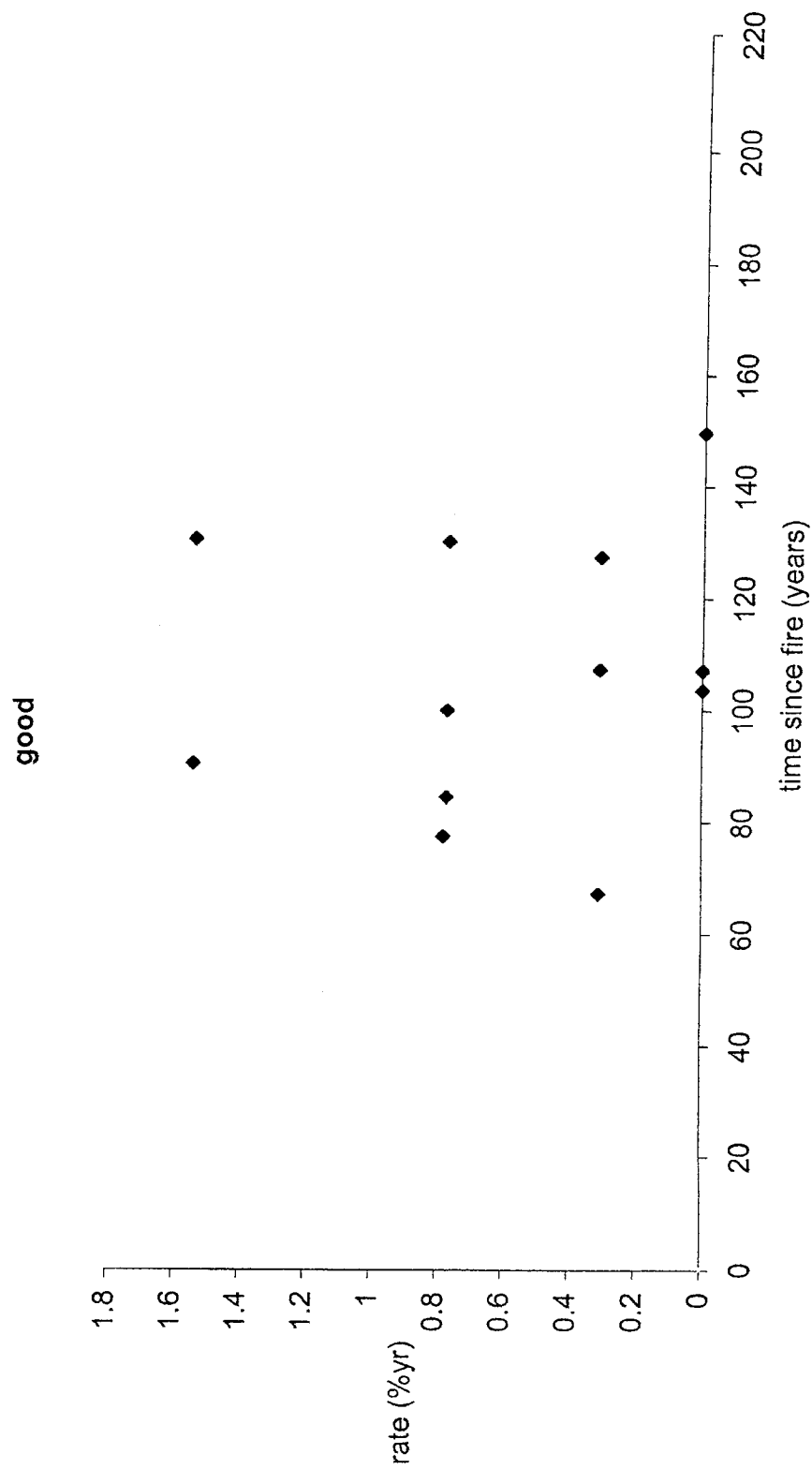


Fig. 6a. The rate of change in percent cover of spruce in relation to time since fire in stands in areas with a site index of “good” (N=22; the correlation is not significant).

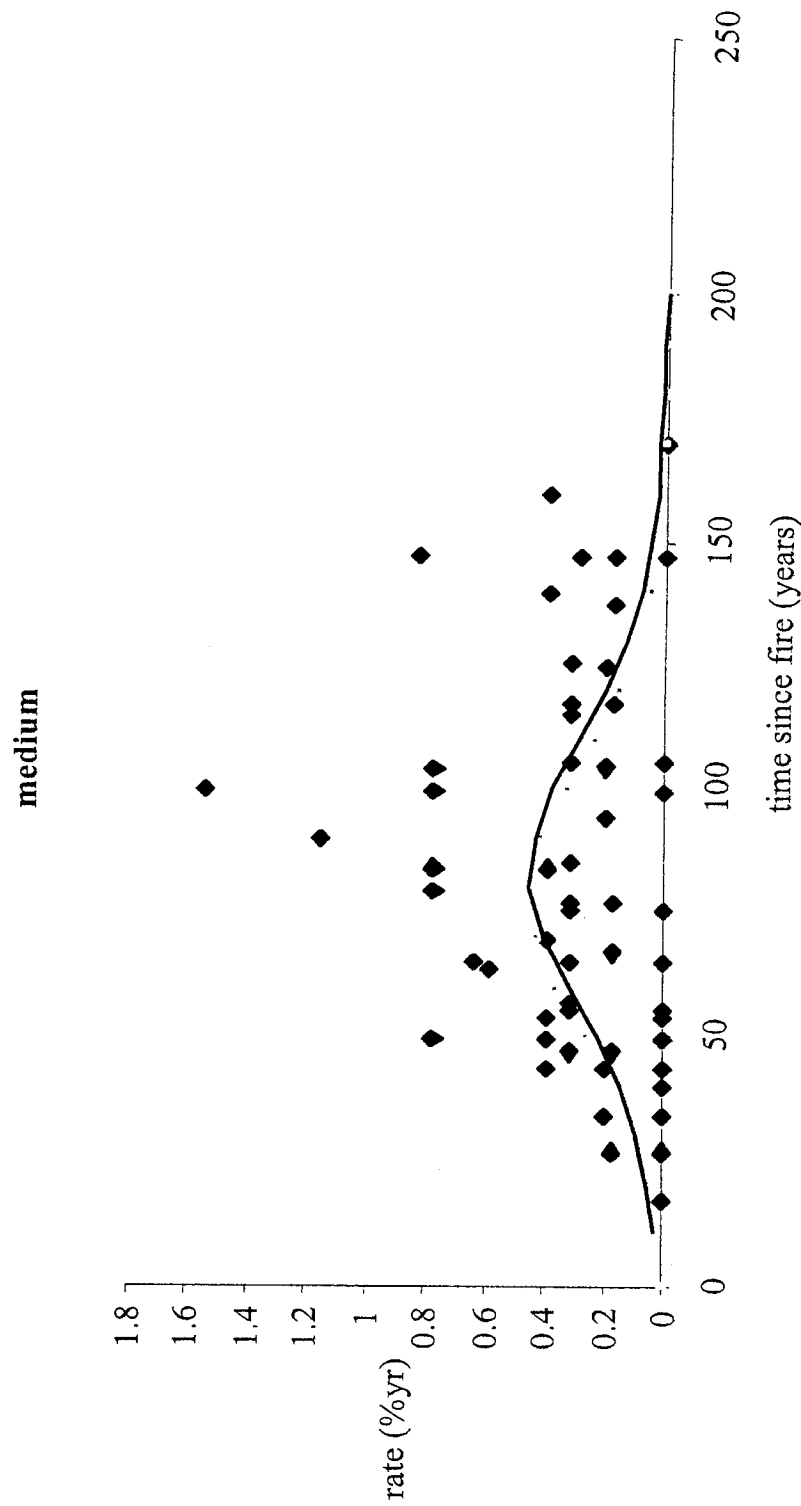


Fig. 6b. The rate of change in percent cover of spruce in relation to time since fire in stands in areas with a site index of “medium” The data were fitted to the model $[Y=33/(1+74.19*EXP(-0.055*t))*0.03*(1-1/(1+74.19*EXP(-0.055*t)))]$, ($N=120$; $r^2=0.20$ and $p=0.26$). Y =growth rate of spruce crown closure, and t =time since fire in years.

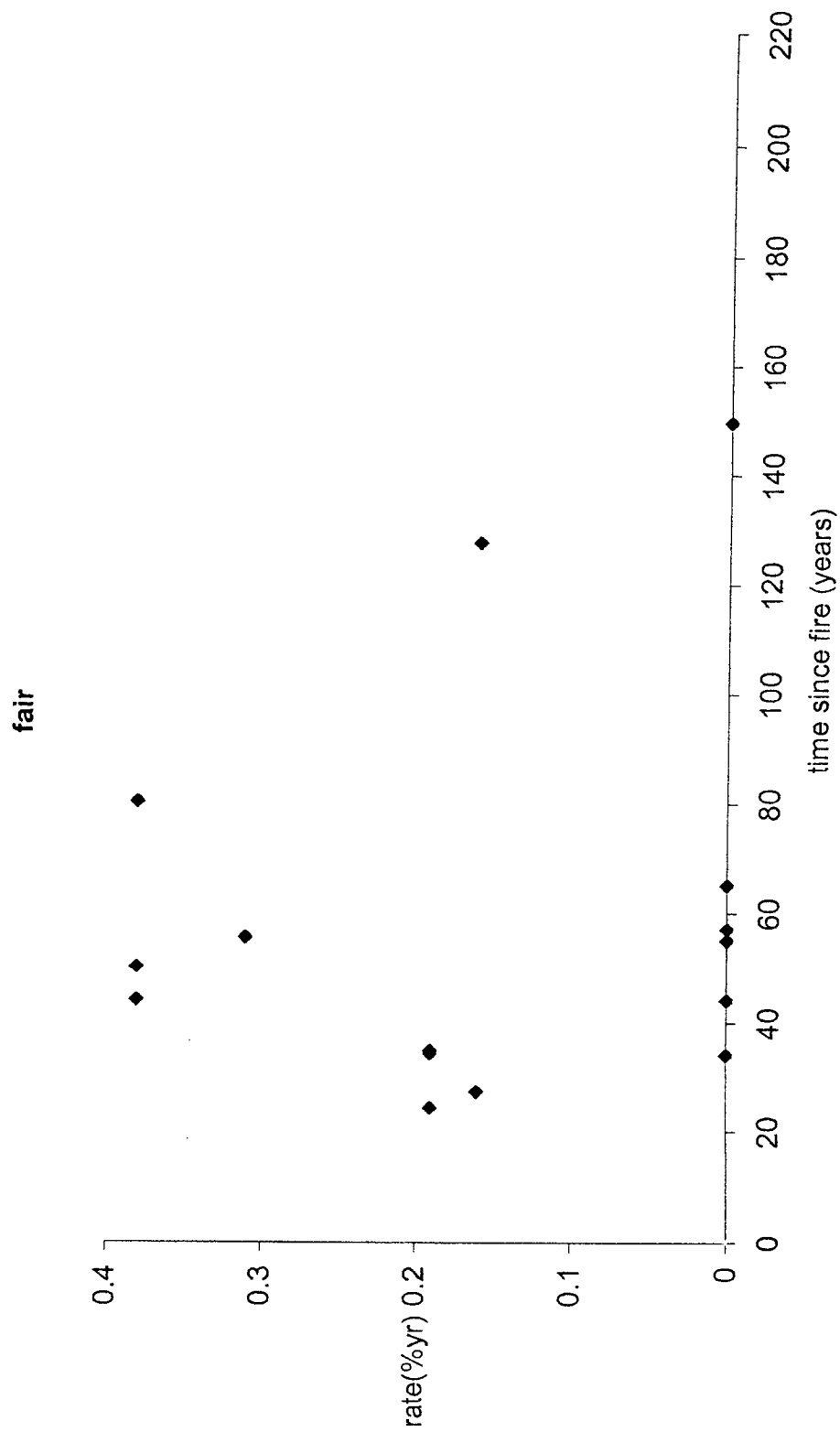


Fig. 6c. The rate of change in percent cover of spruce in relation (not significant) to time since fire in stands in areas with a site index of “fair” (N=20; the correlation is not significant).

good

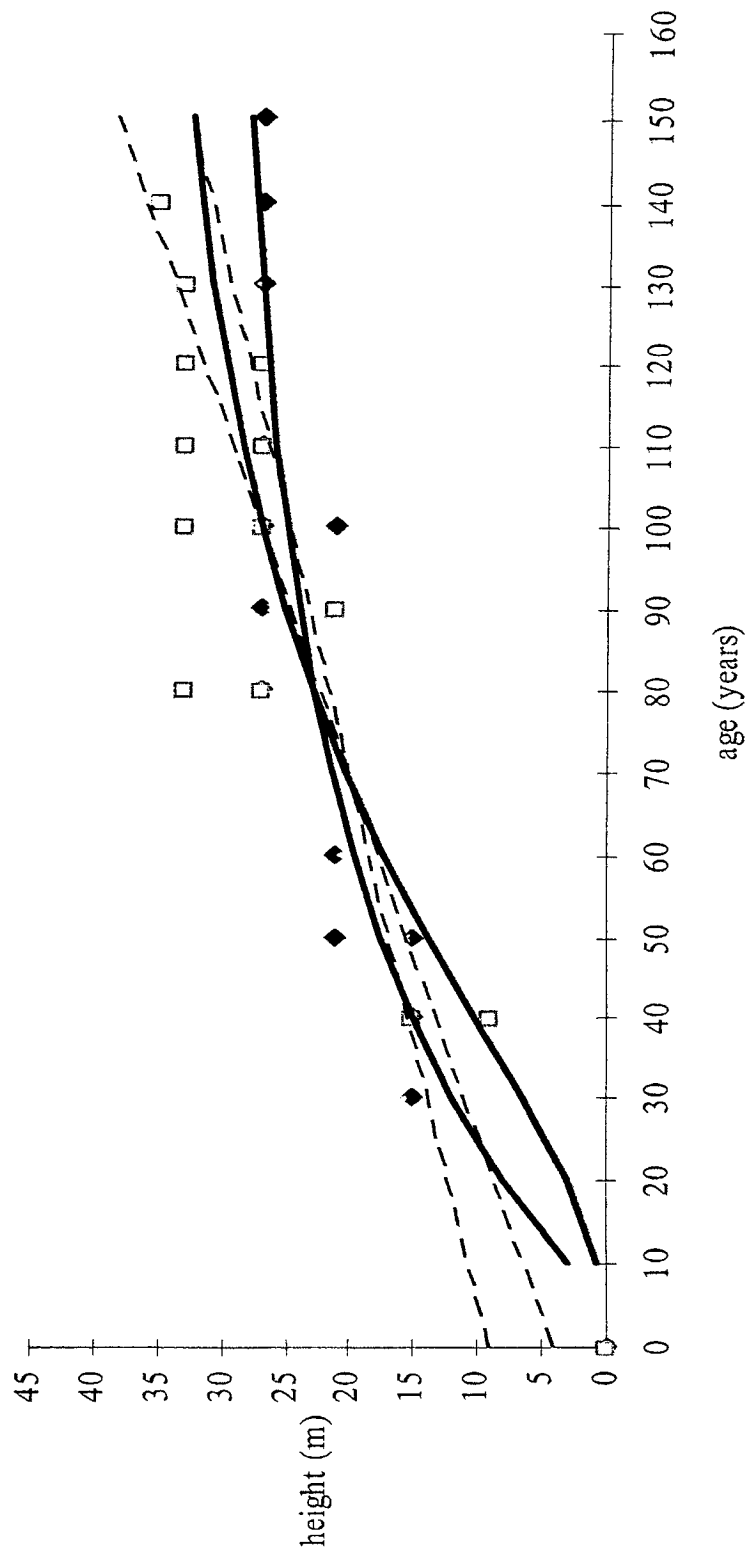


Fig. 7a. The height of white spruce (diamond, N=24) and aspen (square, N=29) in relation to time since fire in stands in areas with a site index of "good". The spruce data were fitted to a Richards function [$Y = 35.61 (1 - \text{Exp} (-0.021t))^{1.899}$, $r^2=0.78$] and a linear model [$Y = 0.2166t + 5.234$, $r^2=0.75$]. Likewise or aspen, the data were fitted to the Richards function [$Y = 29.83 (1 - \text{Exp} (-0.018t))^{0.892}$] and a linear model [$r^2=0.87$; $Y = 0.129t + 11.695$, $r^2=0.82$]. Y= height, and t=time since fire in years.

medium

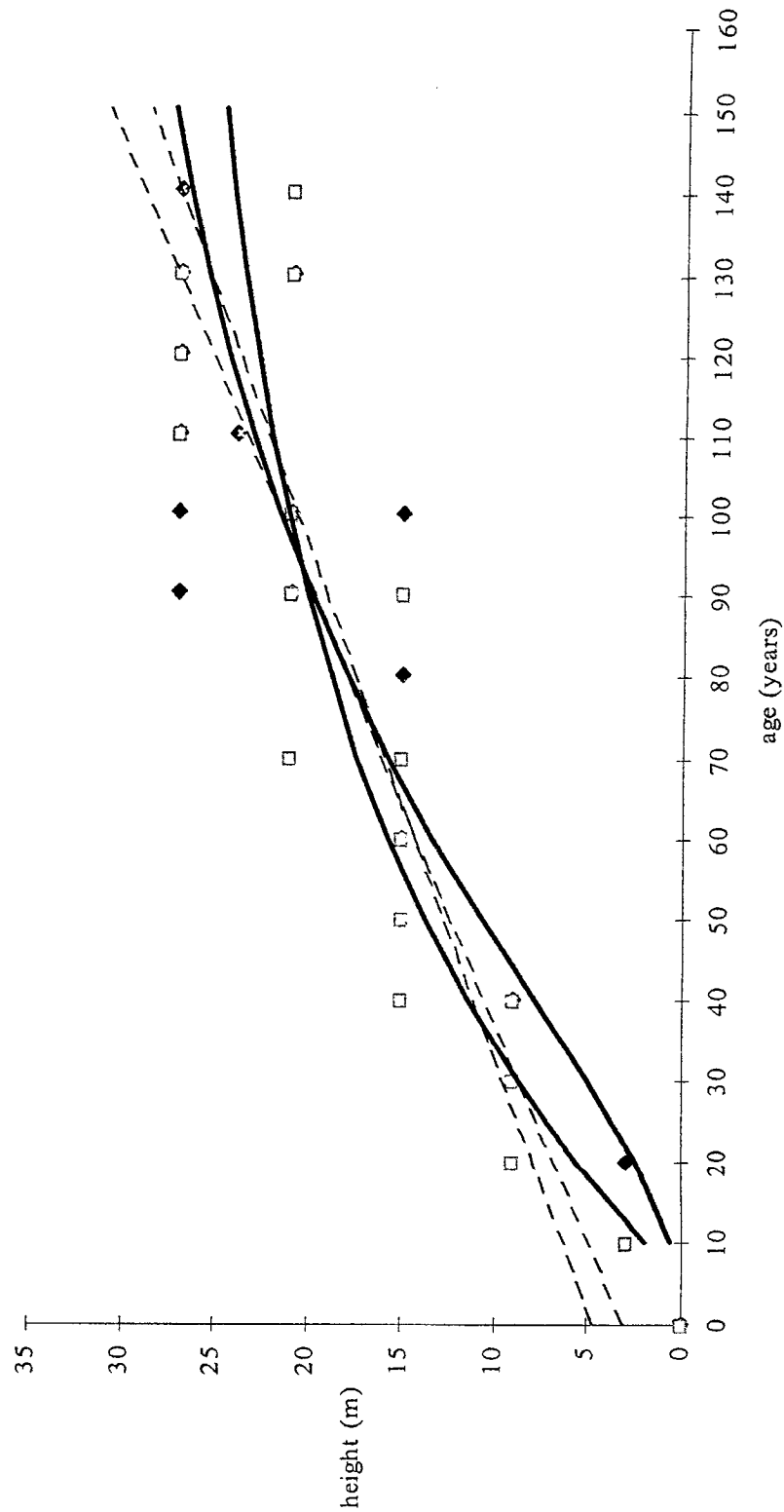


Fig. 7b. The height of white spruce (diamond; N=40) and aspen (square; N=41) in relation to time since fire in stands with a site index of "medium". The data for spruce were fitted to the Richards function $[Y = 31.95 (1 - \text{Exp}(-0.017t))^{1.745}, r^2=0.83]$ and a linear model $[Y = 0.1766t + 3.915, r^2=0.80]$. As for Aspen, the data were also fitted to the same two models $[Y = 27.82 (1 - \text{Exp}(-0.0145t))^{0.989}, r^2=0.85]$ and $[Y = 0.147t + 5.977, r^2=0.80]$. Y= height, and t=time since fire in years.

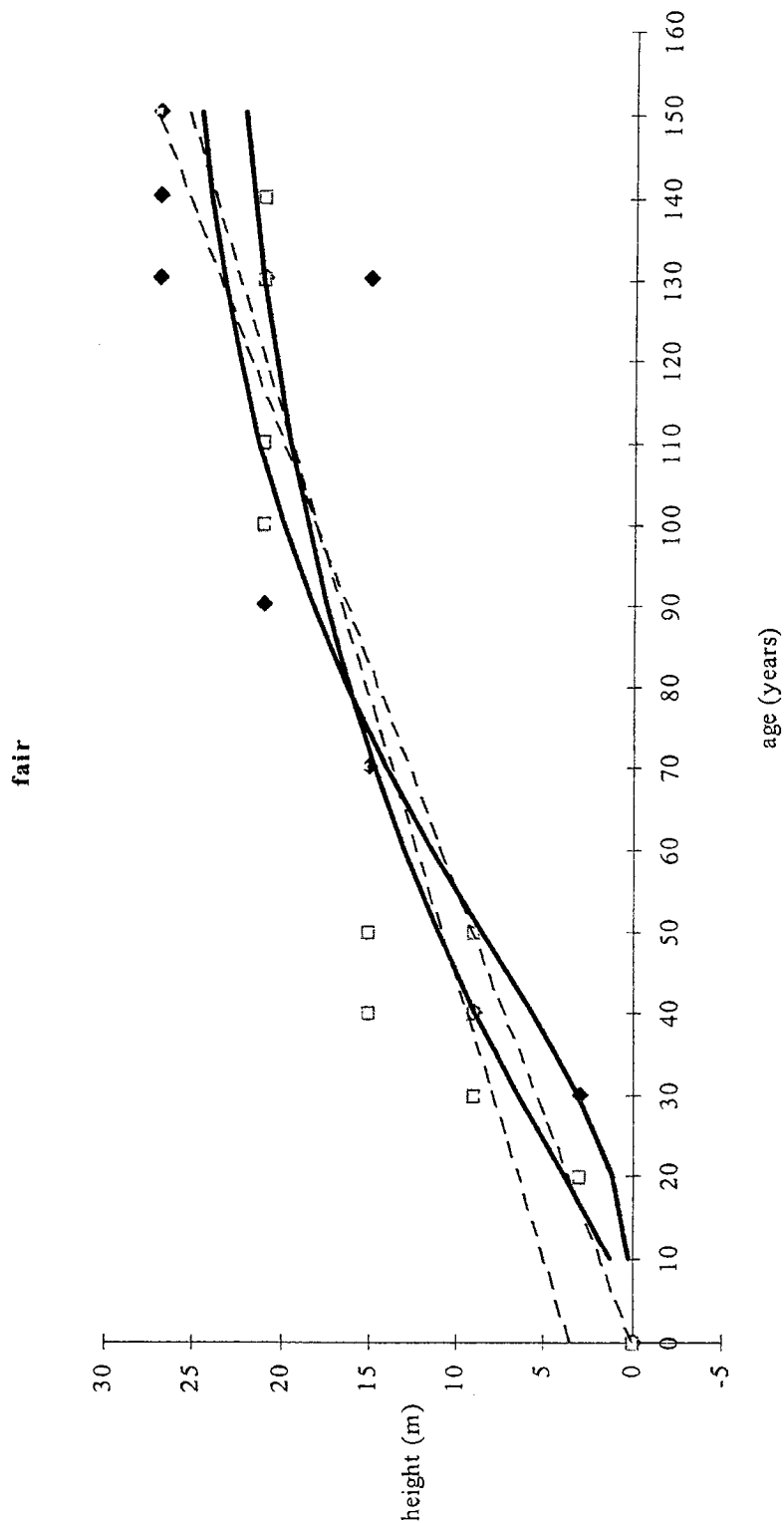


Fig. 7c. The height of white spruce (diamond; $N=18$) and aspen (square; $N=38$) in relation to time since fire in stands in areas with a site index of "fair". The data for spruce were fitted to the Richards function $[Y = 26.94 (1 - \text{Exp} (-0.024t))^{2.760}, r^2=0.83]$ and a linear model $[Y = 0.1819t - 0.116, r^2=0.82]$. Likewise for aspen, the Richard function $[Y = 25.68 (1 - \text{Exp} (-0.015t))^{1.175}, r^2=0.77]$ and linear model $[Y = 0.136t + 4.4745, r^2=0.74]$ were fit to the data. Y = height, and t =time since fire in years.

APPENDIX 1

The raw data collected from aerial photographs and phase 3 maps for the present study.

Township: the standard code of the township.

Stand: stand number based on the phase 3 map.

Site index: an expression of forest site quality (good, medium and fair stand) based on the average height (at a specified age) of dominant and codominant trees.

Density: the percentage of ground area covered by a vertical projection of tree crowns estimated by crown closure “scales” (i.e. categories). A: 6-30%; B: 31-50%; C: 51-70%; D: 71-100%.

Closure: the percentage based on the density.

H: the average height of dominant and codominant trees in a forest stand. On a single tree basis, it is the vertical distance from ground level to the upper tip of the tree crown.

Comp: a listing of tree species in order of decreasing content (based on percentage of crown closure).

A: aspen; Sw: white spruce.

Sc: spruce density based on stand closure and species composition.

Com: reclassified species composition for ANOVA analysis

Com1: the species composition group number for ANOVA analysis

Origin: the year of the stand origin determined by felling trees with a power saw and sectioning the stems at 0.3m above ground or 1.3m.

Age5: stand age for 1950s aerial photographs.

Cov5: spruce crown closure in 1950s.

Age7: stand age for 1970s aerial photographs.

Cov7: spruce crown closure in 1970s.

Cph: stand density from phase 3 map.

Age9: stand age for 1990s aerial photographs.

Cov9: spruce crown closure in 1990s.

R70: spruce density growth rate between 1970s-1990s.

R50: spruce density growth rate between 1950s-1970s.

(Note: m: medium, g: good, f: fair; A: aspen, ASw: aspen with spruce, Sw: spruce)

| Township | Stand | site | density | closure | H | comp | Sc | com | coml | Origin | Age5 | Cov5 | Age7 | Cov7 | Cph | Age9 | Cov9 | R70 | R50 |
|----------|-------|------|---------|---------|---|-------|------|-----|------|--------|------|------|------|------|-----|------|------|-------|-------|
| 67-10-4 | 88 | m | C | 60 | 2 | A | 0 | A | 0 | 1900 | 51 | 5 | 77 | 20 | 0 | 90 | 25 | 0.385 | 0.577 |
| | 65 | g | C | 60 | 4 | ASw | 0.35 | ASw | 2 | 1880 | 71 | 15 | 97 | 35 | 21 | 110 | 35 | 0 | 0.769 |
| | 50 | m | C | 60 | 3 | ASw | 0.35 | ASw | 2 | 1880 | 71 | 15 | 97 | 25 | 21 | 110 | 35 | 0.769 | 0.385 |
| | 58 | f | D | 85 | 1 | A | 0 | A | 0 | 1940 | 11 | 5 | 37 | 5 | 0 | 50 | 15 | 0.769 | 0 |
| 67-11-4 | 86 | m | C | 60 | 3 | Sw(A) | 0.85 | Sw | 3 | 1870 | 81 | 25 | 107 | 30 | 51 | 123 | 35 | 0.313 | 0.192 |
| | 78 | m | C | 60 | 3 | A | 0 | A | 0 | 1910 | 41 | 5 | 67 | 15 | 0 | 83 | 15 | 0 | 0.385 |

| | | | | | | | | | | | | | | | | | | |
|-----|---|---|----|---|--------|------|--------|---|------|-----|----|-----|----|----|-----|----|-------|-------|
| 74 | m | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 10 | 0 | 73 | 10 | 0 | 0.385 |
| 70 | f | C | 60 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 5 | 0 | 63 | 5 | 0 | 0.192 |
| 109 | m | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 10 | 0 | 73 | 10 | 0 | 0.385 |
| 104 | m | C | 60 | 3 | A | 0 | A | 0 | 1900 | 51 | 5 | 77 | 20 | 0 | 93 | 25 | 0.313 | 0.577 |
| 58 | m | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 5 | 0 | 73 | 10 | 0.313 | 0.192 |
| 61 | m | C | 60 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 5 | 0 | 73 | 15 | 0.625 | 0.192 |
| 247 | m | D | 85 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 5 | 0 | 63 | 5 | 0 | 0.192 |
| 227 | m | D | 85 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 5 | 0 | 63 | 5 | 0 | 0.192 |
| 258 | m | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 5 | 57 | 15 | 0 | 73 | 15 | 0 | 0.385 |
| 257 | m | D | 85 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 5 | 0 | 63 | 5 | 0 | 0.192 |
| 260 | m | D | 85 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 5 | 0 | 63 | 5 | 0 | 0.192 |
| 262 | m | D | 85 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 0 | 0 | 63 | 5 | 0.313 | 0 |
| 224 | m | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 0 | 0 | 73 | 10 | 0.625 | 0 |
| 223 | m | D | 85 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 0 | 0 | 63 | 5 | 0.313 | 0 |
| 211 | m | C | 60 | 4 | SwA | 0.65 | Sw | 3 | 1860 | 91 | 35 | 117 | 40 | 39 | 133 | 45 | 0.313 | 0.192 |
| 203 | f | C | 60 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 0 | 0 | 63 | 0 | 0 | 0 |
| 114 | f | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 0 | 0 | 73 | 0 | 0 | 0 |
| 122 | f | D | 85 | 1 | A | 0 | A | 0 | 1930 | 21 | 0 | 47 | 0 | 0 | 63 | 0 | 0 | 0 |
| 52 | f | D | 85 | 1 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 0 | 0 | 73 | 0 | 0 | 0 |
| 55 | m | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 0 | 0 | 73 | 10 | 0.625 | 0 |
| 37 | m | C | 60 | 2 | A | 0 | A | 0 | 1910 | 41 | 5 | 67 | 5 | 0 | 83 | 5 | 0 | 0 |
| 39 | m | C | 60 | 3 | SwA | 0.65 | Sw | 3 | 1870 | 81 | 30 | 107 | 35 | 39 | 123 | 40 | 0.313 | 0.192 |
| 50 | m | D | 85 | 2 | A | 0 | A | 0 | 1920 | 31 | 0 | 57 | 5 | 0 | 73 | 10 | 0.313 | 0.192 |
| 336 | m | C | 60 | 3 | Sw(A) | 0.85 | Sw | 3 | 1880 | 71 | 30 | 97 | 40 | 51 | 113 | 45 | 0.313 | 0.385 |
| 319 | m | C | 60 | 3 | A(Sw) | 0.15 | A(Sw) | 1 | 1880 | 71 | 5 | 97 | 25 | 9 | 113 | 25 | 0 | 0.769 |
| 97 | m | C | 60 | 4 | Aw(Sw) | 0.15 | Aw(Sw) | 1 | 1840 | 111 | 15 | 138 | 15 | 9 | 156 | 30 | 0.833 | 0 |
| 98 | m | B | 40 | 4 | AwSw | 0.35 | AwSw | 2 | 1840 | 111 | 15 | 138 | 25 | 14 | 156 | 40 | 0.833 | 0.37 |
| 101 | m | C | 60 | 3 | Aw | 0 | Aw | 0 | 1840 | 111 | 15 | 138 | 20 | 0 | 156 | 25 | 0.278 | 0.185 |
| 103 | m | C | 60 | 4 | Aw(Sw) | 0.15 | Aw(Sw) | 1 | 1840 | 111 | 15 | 138 | 20 | 9 | 156 | 25 | 0.278 | 0.185 |
| 114 | f | C | 60 | 1 | A(Sw) | 0.15 | A(Sw) | 1 | 1930 | 21 | 5 | 48 | 5 | 9 | 66 | 5 | 0 | 0 |
| 125 | m | C | 60 | 1 | A(Sw) | 0.15 | A(Sw) | 1 | 1940 | 11 | 0 | 43 | 5 | 9 | 56 | 5 | 0 | 0.156 |
| 124 | m | C | 60 | 2 | SwA | 0.65 | Sw | 3 | 1900 | 51 | 5 | 83 | 10 | 39 | 96 | 25 | 1.154 | 0.156 |
| 97 | m | D | 85 | 1 | SwA | 0.65 | Sw | 3 | 1940 | 11 | 5 | 43 | 5 | 55 | 56 | 10 | 0.385 | 0 |

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| | | | | | | | | | | | | | | | | | |
|-----|---|---|----|---|--------|------|--------|------|-----|----|-----|----|----|-----|----|-------|-------|
| 34 | m | C | 60 | 2 | AwSw | 0.35 | AwSw | 1920 | 31 | 5 | 63 | 10 | 21 | 76 | 15 | 0.385 | 0.156 |
| 99 | m | D | 85 | 1 | A(Sw) | 0.15 | A(Sw) | 1940 | 11 | 5 | 43 | 5 | 13 | 56 | 5 | 0 | 0 |
| 37 | m | C | 60 | 1 | SwA | 0.65 | Sw | 1940 | 11 | 5 | 43 | 5 | 39 | 56 | 5 | 0 | 0 |
| 38 | m | C | 60 | 1 | A(Sw) | 0.15 | A(Sw) | 1940 | 11 | 5 | 43 | 5 | 9 | 56 | 5 | 0 | 0 |
| 28 | m | C | 60 | 2 | AwSw | 0.35 | AwSw | 1920 | 31 | 10 | 63 | 20 | 21 | 76 | 25 | 0.385 | 0.313 |
| 33 | m | C | 60 | 1 | Aw(Sw) | 0.15 | Aw(Sw) | 1950 | 1 | 5 | 33 | 5 | 9 | 46 | 5 | 0 | 0 |
| 31 | m | C | 60 | 1 | Aw(Sw) | 0.15 | Aw(Sw) | 1950 | 1 | 5 | 33 | 5 | 9 | 46 | 5 | 0 | 0 |
| 30 | m | C | 60 | 2 | AwSw | 0.35 | AwSw | 1940 | 11 | 5 | 43 | 5 | 21 | 56 | 5 | 0 | 0 |
| 18 | g | C | 60 | 3 | AwSw | 0.35 | AwSw | 1900 | 51 | 5 | 83 | 15 | 21 | 96 | 35 | 1.538 | 0.313 |
| 23 | m | C | 60 | 1 | Aw | 0 | Aw | 1950 | 1 | 5 | 33 | 5 | 0 | 46 | 5 | 0 | 0 |
| 22 | g | C | 60 | 4 | Sw | 1 | Sw | 1860 | 91 | 35 | 123 | 45 | 60 | 136 | 55 | 0.769 | 0.313 |
| 20 | m | D | 85 | 3 | AwSw | 0.35 | AwSw | 1940 | 11 | 5 | 43 | 5 | 30 | 56 | 15 | 0.769 | 0 |
| 102 | m | C | 60 | 3 | SwA | 0.65 | Sw | 1850 | 101 | 25 | 133 | 30 | 39 | 146 | 35 | 0.385 | 0.156 |
| 25 | f | C | 60 | 2 | A(Sw) | 0.15 | A(Sw) | 1910 | 41 | 5 | 73 | 5 | 9 | 86 | 5 | 0 | 0 |
| 26 | m | C | 60 | 3 | SwA | 0.65 | Sw | 1890 | 61 | 15 | 93 | 25 | 39 | 106 | 25 | 0 | 0.313 |
| 50 | m | C | 60 | 1 | Aw(Sw) | 0.15 | Aw(Sw) | 1950 | 1 | 5 | 33 | 5 | 9 | 46 | 5 | 0 | 0 |
| 52 | m | C | 60 | 3 | ASw | 0.35 | ASw | 1890 | 61 | 15 | 93 | 20 | 21 | 106 | 20 | 0 | 0.156 |
| 47 | m | C | 60 | 4 | SwA | 0.65 | Sw | 1820 | 131 | 25 | 163 | 35 | 39 | 176 | 35 | 0 | 0.313 |
| 75 | m | C | 60 | 1 | A(Sw) | 0.15 | A(Sw) | 1940 | 11 | 5 | 43 | 5 | 9 | 56 | 5 | 0 | 0 |
| 83 | m | C | 60 | 3 | ASw | 0.35 | ASw | 1890 | 61 | 5 | 93 | 15 | 21 | 106 | 25 | 0.769 | 0.313 |
| 81 | m | C | 60 | 3 | SwA | 0.65 | Sw | 1890 | 61 | 5 | 93 | 15 | 39 | 106 | 35 | 1.538 | 0.313 |
| 89 | f | C | 60 | 1 | ASw | 0.35 | ASw | 1940 | 11 | 5 | 43 | 5 | 21 | 56 | 15 | 0.769 | 0 |
| 141 | f | C | 60 | 3 | SwAw | 0.65 | Sw | 1840 | 111 | 5 | 143 | 5 | 39 | 156 | 15 | 0.769 | 0 |
| 170 | m | B | 40 | 2 | A(Sw) | 0.15 | A(Sw) | 1910 | 41 | 5 | 73 | 15 | 6 | 86 | 25 | 0.769 | 0.313 |
| 135 | m | C | 60 | 2 | A | 0 | A | 1940 | 11 | 5 | 43 | 5 | 0 | 56 | 5 | 0 | 0 |
| 142 | m | C | 60 | 4 | SwA | 0.65 | Sw | 1830 | 121 | 20 | 153 | 30 | 39 | 166 | 35 | 0.385 | 0.313 |
| 136 | m | C | 60 | 3 | ASw | 0.35 | ASw | 1890 | 61 | 15 | 93 | 20 | 21 | 106 | 20 | 0 | 0.156 |
| 139 | m | C | 60 | 4 | SwA | 0.65 | Sw | 1820 | 131 | 35 | 163 | 35 | 39 | 176 | 35 | 0 | 0 |
| 133 | m | C | 60 | 3 | SwA | 0.65 | Sw | 1890 | 61 | 15 | 93 | 20 | 39 | 106 | 20 | 0 | 0.156 |
| 129 | m | C | 60 | 2 | A(Sw) | 0.15 | A(Sw) | 1940 | 11 | 0 | 43 | 5 | 9 | 56 | 5 | 0 | 0.156 |
| 132 | m | D | 85 | 1 | ASw | 0.35 | ASw | 1940 | 11 | 5 | 43 | 5 | 30 | 56 | 5 | 0 | 0 |
| 48 | g | C | 60 | 4 | SwAw | 0.65 | Sw | 1860 | 91 | 25 | 123 | 35 | 39 | 136 | 45 | 0.769 | 0.313 |
| 41 | m | C | 60 | 1 | Aw(Sw) | 0.15 | Aw(Sw) | 1950 | 1 | 5 | 33 | 5 | 9 | 46 | 5 | 0 | 0 |

| | | | | | | | | | | | | | | | | | | |
|----|---|---|----|---|--------|------|----|---|------|-----|----|-----|----|----|-----|----|-------|-------|
| 43 | g | C | 60 | 4 | SwAw | 0.65 | Sw | 3 | 1860 | 91 | 35 | 123 | 45 | 39 | 136 | 55 | 0.769 | 0.313 |
| 46 | g | C | 60 | 4 | SwAw | 0.65 | Sw | 3 | 1860 | 91 | 25 | 123 | 35 | 39 | 136 | 45 | 0.769 | 0.313 |
| 45 | m | C | 60 | 4 | SwA | 0.65 | Sw | 3 | 1850 | 101 | 15 | 133 | 25 | 39 | 146 | 35 | 0.769 | 0.313 |
| 96 | m | C | 60 | 1 | SwA | 0.65 | Sw | 3 | 1940 | 11 | 5 | 43 | 5 | 39 | 56 | 5 | 0 | 0 |
| 10 | g | C | 60 | 4 | SwAw | 0.65 | Sw | 3 | 1860 | 91 | 25 | 123 | 25 | 39 | 136 | 45 | 1.538 | 0 |
| 14 | g | C | 60 | 4 | SwAw | 0.65 | Sw | 3 | 1860 | 91 | 25 | 123 | 34 | 39 | 136 | 45 | 0.846 | 0.281 |
| 15 | g | C | 60 | 5 | SwAw | 0.65 | Sw | 3 | 1890 | 61 | 10 | 93 | 35 | 39 | 106 | 45 | 0.769 | 0.781 |
| 24 | g | B | 40 | 5 | Sw(Aw) | 0.85 | Sw | 3 | 1840 | 111 | 45 | 143 | 55 | 34 | 156 | 65 | 0.769 | 0.313 |
| 6 | g | C | 60 | 4 | SwAw | 0.65 | Sw | 3 | 1860 | 91 | 25 | 123 | 35 | 39 | 136 | 45 | 0.769 | 0.313 |

APPENDIX 2

The raw data collected from aerial photographs and phase 3 maps. This appendix is an extension of the Appendix 1, and includes additional data on aspen crown closure and residual tree coverage. My interpretation of the results presented in the thesis is based on the data given in the Appendix 1. The purpose of the Appendix 2 is to provide an additional database to facilitate a detailed analysis in future.

Township: the standard code of the township.

Stand: stand number based on the phase 3 map.

Site index: an expression of forest site quality (good, medium and fair stand) based on the average height (at a specified age) of dominant and codominant trees.

Closure: the percentage based on the density.

H: the average height of dominant and codominant trees in a forest stand. On a single tree basis, it is the vertical distance from ground level to the upper tip of the tree crown.

Origin: the year of the stand origin determined by felling trees with a power saw and sectioning the stems at 0.3m above ground or 1.3m.

Age5: stand age for 1950s aerial photographs.

Cov5: spruce crown closure in 1950s.

Cas5: aspen crown closure in 1950s.

Cun5: unclosed area percentage in 1950s.

Age7: stand age for 1970s aerial photographs.

Cov7: spruce crown closure in 1970s.

Cas7: aspen crown closure in 1970s.

Cresidual: residual tree crown closure.

Cun7: unclosed area percentage in 1970s.

Age9: stand age for 1990s aerial photographs.

Cov9: spruce crown closure in 1990s.

Cas9: aspen crown closure in 1990s.

Cun9: unclosed area percentage in 1990s.

R70-90: spruce density growth rate between 1970s-1990s.

R50-70: spruce density growth rate between 1950s-1970s.

| Township | Stand | site | closure | H | Origin | Age5 | Cov5 | Cas5 | Cun5 | Age7 | Cov7 | Cas7 | Cresidual | Cun7 | Age9 | Cov9 | Cas9 | Cun9 | R70-90 | R50-70 |
|----------|-------|------|---------|---|--------|------|------|------|------|------|------|------|-----------|------|------|------|------|------|--------|--------|
| 67-10-4 | 88 | m | 60 | 2 | 1900 | 51 | 5 | 60 | 30 | 77 | 20 | 45 | 5 | 30 | 90 | 25 | 60 | 20 | 0.385 | 0.577 |
| | 65 | g | 60 | 4 | 1880 | 71 | 15 | 50 | 35 | 97 | 35 | 30 | 0 | 35 | 110 | 35 | 45 | 20 | 0 | 0.769 |
| | 50 | m | 60 | 3 | 1880 | 71 | 15 | 50 | 35 | 97 | 25 | 40 | 0 | 35 | 110 | 35 | 50 | 15 | 0.769 | 0.385 |
| | 58 | f | 85 | 1 | 1940 | 11 | 5 | 45 | 45 | 37 | 5 | 85 | 5 | 5 | 50 | 15 | 80 | 5 | 0.769 | 0 |
| 67-11-4 | 86 | m | 60 | 3 | 1870 | 81 | 25 | 40 | 35 | 107 | 30 | 35 | 0 | 35 | 123 | 35 | 55 | 10 | 0.313 | 0.192 |

| | | | | | | | | | | | | | | | | | | | |
|-----|---|----|---|------|-----|----|----|----|-----|----|----|---|----|-----|----|----|----|-------|-------|
| 78 | m | 60 | 3 | 1910 | 41 | 5 | 55 | 35 | 67 | 15 | 50 | 5 | 30 | 83 | 15 | 60 | 25 | 0 | 0.385 |
| 74 | m | 85 | 2 | 1920 | 31 | 0 | 80 | 15 | 57 | 10 | 80 | 5 | 5 | 73 | 10 | 80 | 5 | 0 | 0.385 |
| 70 | f | 60 | 1 | 1930 | 21 | 0 | 40 | 55 | 47 | 5 | 60 | 5 | 30 | 63 | 5 | 65 | 25 | 0 | 0.192 |
| 109 | m | 85 | 2 | 1920 | 31 | 0 | 75 | 20 | 57 | 10 | 80 | 5 | 5 | 73 | 10 | 80 | 5 | 0 | 0.385 |
| 104 | m | 60 | 3 | 1900 | 51 | 5 | 55 | 35 | 77 | 20 | 45 | 5 | 30 | 93 | 25 | 45 | 25 | 0.313 | 0.577 |
| 58 | m | 85 | 2 | 1920 | 31 | 0 | 80 | 15 | 57 | 5 | 85 | 5 | 5 | 73 | 10 | 85 | 0 | 0.313 | 0.192 |
| 61 | m | 60 | 2 | 1920 | 31 | 0 | 55 | 40 | 57 | 5 | 60 | 5 | 30 | 73 | 15 | 55 | 25 | 0.625 | 0.192 |
| 247 | m | 85 | 1 | 1930 | 21 | 0 | 80 | 15 | 47 | 5 | 85 | 5 | 5 | 63 | 5 | 85 | 5 | 0 | 0.192 |
| 227 | m | 85 | 1 | 1930 | 21 | 0 | 75 | 20 | 47 | 5 | 85 | 5 | 5 | 63 | 5 | 85 | 5 | 0 | 0.192 |
| 258 | m | 85 | 2 | 1920 | 31 | 5 | 85 | 5 | 57 | 15 | 75 | 5 | 5 | 73 | 15 | 80 | 0 | 0 | 0.385 |
| 257 | m | 85 | 1 | 1930 | 21 | 0 | 75 | 20 | 47 | 5 | 85 | 5 | 5 | 63 | 5 | 85 | 5 | 0 | 0.192 |
| 260 | m | 85 | 1 | 1930 | 21 | 0 | 80 | 15 | 47 | 5 | 85 | 5 | 5 | 63 | 5 | 90 | 0 | 0 | 0.192 |
| 262 | m | 85 | 1 | 1930 | 21 | 0 | 80 | 15 | 47 | 0 | 90 | 5 | 5 | 63 | 5 | 85 | 5 | 0.313 | 0 |
| 224 | m | 85 | 2 | 1920 | 31 | 0 | 85 | 10 | 57 | 0 | 90 | 5 | 5 | 73 | 10 | 85 | 0 | 0.625 | 0 |
| 223 | m | 85 | 1 | 1930 | 21 | 0 | 85 | 10 | 47 | 0 | 90 | 5 | 5 | 63 | 5 | 85 | 5 | 0.313 | 0 |
| 211 | m | 60 | 4 | 1860 | 91 | 35 | 30 | 35 | 117 | 40 | 25 | 0 | 35 | 133 | 45 | 35 | 20 | 0.313 | 0.192 |
| 203 | f | 60 | 1 | 1930 | 21 | 0 | 60 | 35 | 47 | 0 | 65 | 5 | 30 | 63 | 0 | 70 | 25 | 0 | 0 |
| 114 | f | 85 | 2 | 1920 | 31 | 0 | 70 | 30 | 57 | 0 | 90 | 0 | 10 | 73 | 0 | 95 | 5 | 0 | 0 |
| 122 | f | 85 | 1 | 1930 | 21 | 0 | 65 | 35 | 47 | 0 | 90 | 0 | 10 | 63 | 0 | 95 | 5 | 0 | 0 |
| 52 | f | 85 | 1 | 1920 | 31 | 0 | 65 | 30 | 57 | 0 | 90 | 5 | 5 | 73 | 0 | 90 | 5 | 0 | 0 |
| 55 | m | 85 | 2 | 1920 | 31 | 0 | 85 | 15 | 57 | 0 | 90 | 0 | 10 | 73 | 10 | 80 | 10 | 0.625 | 0 |
| 37 | m | 60 | 2 | 1910 | 41 | 5 | 55 | 40 | 67 | 5 | 60 | 0 | 35 | 83 | 5 | 65 | 30 | 0 | 0 |
| 39 | m | 60 | 3 | 1870 | 81 | 30 | 35 | 35 | 107 | 35 | 30 | 0 | 35 | 123 | 40 | 30 | 30 | 0.313 | 0.192 |
| 50 | m | 85 | 2 | 1920 | 31 | 0 | 75 | 20 | 57 | 5 | 85 | 5 | 5 | 73 | 10 | 80 | 5 | 0.313 | 0.192 |
| 336 | m | 60 | 3 | 1880 | 71 | 30 | 35 | 35 | 97 | 40 | 25 | 0 | 35 | 113 | 45 | 25 | 30 | 0.313 | 0.385 |
| 319 | m | 60 | 3 | 1880 | 71 | 5 | 55 | 35 | 97 | 25 | 40 | 5 | 30 | 113 | 25 | 50 | 20 | 0 | 0.769 |
| 97 | m | 60 | 4 | 1840 | 111 | 15 | 50 | 35 | 138 | 15 | 50 | 0 | 35 | 156 | 30 | 40 | 30 | 0.833 | 0 |
| 98 | m | 40 | 4 | 1840 | 111 | 15 | 40 | 45 | 138 | 25 | 20 | 0 | 45 | 156 | 40 | 30 | 30 | 0.833 | 0.37 |
| 101 | m | 60 | 3 | 1840 | 111 | 15 | 50 | 35 | 138 | 20 | 45 | 0 | 35 | 156 | 25 | 45 | 30 | 0.278 | 0.185 |
| 103 | m | 60 | 4 | 1840 | 111 | 15 | 50 | 35 | 138 | 20 | 45 | 0 | 35 | 156 | 25 | 45 | 30 | 0.278 | 0.185 |
| 114 | f | 60 | 1 | 1930 | 21 | 5 | 35 | 55 | 48 | 5 | 60 | 5 | 30 | 66 | 5 | 65 | 25 | 0 | 0 |
| 125 | m | 60 | 1 | 1940 | 11 | 0 | 60 | 35 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0.156 |
| 124 | m | 60 | 2 | 1900 | 51 | 5 | 60 | 30 | 83 | 10 | 55 | 5 | 30 | 96 | 25 | 45 | 25 | 1.154 | 0.156 |

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| | | | | | | | | | | | | | | | | | | | |
|-----|---|----|---|------|-----|----|----|----|-----|----|----|---|----|-----|----|----|----|-------|-------|
| 97 | m | 85 | 1 | 1940 | 11 | 5 | 60 | 30 | 43 | 5 | 85 | 5 | 5 | 56 | 10 | 80 | 5 | 0.385 | 0 |
| 34 | m | 60 | 2 | 1920 | 31 | 5 | 55 | 35 | 63 | 10 | 55 | 5 | 30 | 76 | 15 | 55 | 25 | 0.385 | 0.156 |
| 99 | m | 85 | 1 | 1940 | 11 | 5 | 75 | 15 | 43 | 5 | 85 | 5 | 5 | 56 | 5 | 85 | 5 | 0 | 0 |
| 37 | m | 60 | 1 | 1940 | 11 | 5 | 55 | 35 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0 |
| 38 | m | 60 | 1 | 1940 | 11 | 5 | 55 | 35 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0 |
| 28 | m | 60 | 2 | 1920 | 31 | 10 | 55 | 30 | 63 | 20 | 45 | 5 | 30 | 76 | 25 | 45 | 25 | 0.385 | 0.313 |
| 33 | m | 60 | 1 | 1950 | 1 | 5 | 40 | 50 | 33 | 5 | 60 | 5 | 30 | 46 | 5 | 65 | 25 | 0 | 0 |
| 31 | m | 60 | 1 | 1950 | 1 | 5 | 35 | 55 | 33 | 5 | 60 | 5 | 30 | 46 | 5 | 65 | 25 | 0 | 0 |
| 30 | m | 60 | 2 | 1940 | 11 | 5 | 50 | 40 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0 |
| 18 | g | 60 | 3 | 1900 | 51 | 5 | 55 | 35 | 83 | 15 | 50 | 5 | 30 | 96 | 35 | 35 | 25 | 1.538 | 0.313 |
| 23 | m | 60 | 1 | 1950 | 1 | 5 | 45 | 45 | 33 | 5 | 60 | 5 | 30 | 46 | 5 | 60 | 30 | 0 | 0 |
| 22 | g | 60 | 4 | 1860 | 91 | 35 | 25 | 35 | 123 | 45 | 20 | 5 | 30 | 136 | 55 | 25 | 15 | 0.769 | 0.313 |
| 20 | m | 85 | 3 | 1940 | 11 | 5 | 55 | 35 | 43 | 5 | 75 | 5 | 15 | 56 | 15 | 65 | 15 | 0.769 | 0 |
| 102 | m | 60 | 3 | 1850 | 101 | 25 | 55 | 15 | 133 | 30 | 35 | 5 | 30 | 146 | 35 | 45 | 15 | 0.385 | 0.156 |
| 25 | f | 60 | 2 | 1910 | 41 | 5 | 55 | 35 | 73 | 5 | 60 | 5 | 30 | 86 | 5 | 65 | 25 | 0 | 0 |
| 26 | m | 60 | 3 | 1890 | 61 | 15 | 45 | 40 | 93 | 25 | 40 | 0 | 35 | 106 | 25 | 55 | 20 | 0 | 0.313 |
| 50 | m | 60 | 1 | 1950 | 1 | 5 | 40 | 50 | 33 | 5 | 60 | 5 | 30 | 46 | 5 | 60 | 30 | 0 | 0 |
| 52 | m | 60 | 3 | 1890 | 61 | 15 | 45 | 35 | 93 | 20 | 45 | 5 | 30 | 106 | 20 | 55 | 20 | 0 | 0.156 |
| 47 | m | 60 | 4 | 1820 | 131 | 25 | 40 | 35 | 163 | 35 | 30 | 0 | 35 | 176 | 35 | 50 | 15 | 0 | 0.313 |
| 75 | m | 60 | 1 | 1940 | 11 | 5 | 55 | 35 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0 |
| 83 | m | 60 | 3 | 1890 | 61 | 5 | 55 | 35 | 93 | 15 | 50 | 5 | 30 | 106 | 25 | 55 | 15 | 0.769 | 0.313 |
| 81 | m | 60 | 3 | 1890 | 61 | 5 | 55 | 40 | 93 | 15 | 50 | 0 | 35 | 106 | 35 | 40 | 25 | 1.538 | 0.313 |
| 89 | f | 60 | 1 | 1940 | 11 | 5 | 35 | 55 | 43 | 5 | 60 | 5 | 30 | 56 | 15 | 55 | 25 | 0.769 | 0 |
| 141 | f | 60 | 3 | 1840 | 111 | 5 | 60 | 30 | 143 | 5 | 60 | 5 | 30 | 156 | 15 | 55 | 25 | 0.769 | 0 |
| 170 | m | 40 | 2 | 1910 | 41 | 5 | 35 | 55 | 73 | 15 | 30 | 5 | 50 | 86 | 25 | 25 | 45 | 0.769 | 0.313 |
| 135 | m | 60 | 2 | 1940 | 11 | 5 | 55 | 35 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0 |
| 142 | m | 60 | 4 | 1830 | 121 | 20 | 40 | 40 | 153 | 30 | 35 | 0 | 35 | 166 | 35 | 45 | 20 | 0.385 | 0.313 |
| 136 | m | 60 | 3 | 1890 | 61 | 15 | 45 | 35 | 93 | 20 | 45 | 5 | 30 | 106 | 20 | 60 | 15 | 0 | 0.156 |
| 139 | m | 60 | 4 | 1820 | 131 | 35 | 25 | 40 | 163 | 35 | 30 | 0 | 35 | 176 | 35 | 50 | 15 | 0 | 0 |
| 133 | m | 60 | 3 | 1890 | 61 | 15 | 45 | 40 | 93 | 20 | 45 | 0 | 35 | 106 | 20 | 55 | 25 | 0 | 0.156 |
| 129 | m | 60 | 2 | 1940 | 11 | 0 | 60 | 35 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0.156 |
| 132 | m | 85 | 1 | 1940 | 11 | 5 | 65 | 25 | 43 | 5 | 70 | 5 | 20 | 56 | 5 | 75 | 15 | 0 | 0 |
| 48 | g | 60 | 4 | 1860 | 91 | 25 | 40 | 35 | 123 | 35 | 30 | 0 | 35 | 136 | 45 | 25 | 30 | 0.769 | 0.313 |

| | | | | | | | | | | | | | | | | | | | |
|----|---|----|---|------|-----|----|----|----|-----|----|----|---|----|-----|----|----|----|-------|-------|
| 41 | m | 60 | 1 | 1950 | 1 | 5 | 45 | 45 | 33 | 5 | 60 | 5 | 30 | 46 | 5 | 65 | 25 | 0 | 0 |
| 43 | g | 60 | 4 | 1860 | 91 | 35 | 25 | 40 | 123 | 45 | 20 | 0 | 0 | 136 | 55 | 15 | 30 | 0.769 | 0.313 |
| 46 | g | 60 | 4 | 1860 | 91 | 25 | 35 | 40 | 123 | 35 | 30 | 0 | 0 | 136 | 45 | 25 | 30 | 0.769 | 0.313 |
| 45 | m | 60 | 4 | 1850 | 101 | 15 | 45 | 40 | 133 | 25 | 40 | 0 | 0 | 146 | 35 | 45 | 20 | 0.769 | 0.313 |
| 96 | m | 60 | 1 | 1940 | 11 | 5 | 55 | 35 | 43 | 5 | 60 | 5 | 30 | 56 | 5 | 65 | 25 | 0 | 0 |
| 10 | g | 60 | 4 | 1860 | 91 | 25 | 35 | 40 | 123 | 25 | 40 | 0 | 0 | 136 | 45 | 35 | 20 | 1.538 | 0 |
| 14 | g | 60 | 4 | 1860 | 91 | 25 | 35 | 40 | 123 | 34 | 31 | 0 | 0 | 136 | 45 | 40 | 15 | 0.846 | 0.281 |
| 15 | g | 60 | 5 | 1890 | 61 | 10 | 50 | 40 | 93 | 35 | 30 | 0 | 0 | 106 | 45 | 35 | 20 | 0.769 | 0.781 |
| 24 | g | 40 | 5 | 1840 | 111 | 45 | 5 | 45 | 143 | 55 | 0 | 5 | 40 | 156 | 65 | 10 | 20 | 0.769 | 0.313 |
| 6 | g | 60 | 4 | 1860 | 91 | 25 | 35 | 40 | 123 | 35 | 30 | 0 | 0 | 136 | 45 | 30 | 25 | 0.769 | 0.313 |