The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta* – *Picea engelmannii* forest

E. A. JOHNSON, K. MIYANISHI* and H. KLEB†

Division of Ecology, Department of Biological Sciences and Kananaskis Field Stations, University of Calgary, Calgary, Alberta, Canada T2N 1N4 and *Department of Geography, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Summary

1 Stand reconstruction methods which involved the dating of live and dead trees were used to demonstrate the major flaws inherent in the common approach of using static stand structure to infer stand dynamics. To illustrate the problems with this approach we tested two hypotheses on conifer forest succession: (i) that the empty middle age classes in static stand age-class distributions are the result of a period in stand development in which recruitment was prevented, and (ii) that understorey trees have replaced canopy trees.

2 Reconstructions of age-class distributions at 20-year intervals into the past for five stands ranging in age from 58 to 222 years revealed a short postfire period of high recruitment of both *Pinus contorta* and *Picea engelmannii* followed by low and sporadic recruitment for the rest of the life of the stands. The initial postfire cohort also had a lower mortality rate than the subsequent cohorts. This pattern of low recruitment and high mortality for the understorey cohort resulting in the disappearance of these cohorts over time explains the false impression of a period of prevented recruitment in the middle age class of the static stand age distribution.

3 Height–date curves for individual standing live and dead trees, obtained by sectioning trees at 1-m intervals and ageing the disks, showed little, if any, canopy replacement by trees which were once in the understorey. Again, the combination of low recruitment and high mortality precludes any trees in the subsequent (understorey) cohorts from surviving and growing into the canopy.

4 This study of the dynamics of *Pinus contorta* – *Picea engelmannii* forest points out that forests must be viewed as a collection of species populations of stacked cohorts and that succession (dynamics) can be understood by studying the recruitment and mortality rates of these cohorts.

Keywords: age distributions, conifer forest dynamics, fire frequency, forest reconstruction, tree population dynamics


Introduction

The essence of traditional forest succession is that understorey saplings replace canopy trees. The temporal pattern of this canopy replacement process depends on the patterns of understorey tree recruitment, survival and growth in height. A major problem in our understanding of succession has been our inability to observe the actual dynamics involved in the process of canopy replacement. Thus, forest ecologists have generally relied on a static stand structure (age distribution at one point in time) or a chronosequence (age distributions of stands of different ages) to make inferences about the dynamics that produced the stand (e.g. for conifer stands: Miller 1970; Day 1972; Leak 1975; Whipple & Dix 1979; Balogh & Grigal 1988; Butson et al. 1987; Hytteborn et al. 1987; Knowles & Grant 1983; Kohyama 1984; Léger & Payette 1981; Shea, 1985; Stewart 1986; Veblen

†Present address: Department of Biology, McGill University, Montreal, Quebec H3A 2T5, Canada.
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1986a,b; Veblen et al. 1991). In terms of population dynamics, the assumptions underlying these two approaches are the same, i.e. that recruitment and mortality schedules are identical for all cohorts. However, such assumptions are rarely supported by empirical evidence. In fact, the evidence indicates that the initial cohort establishing soon after a disturbance and the subsequent cohorts usually have significantly different recruitment and mortality rates (e.g. Johnson & Fryer 1989; Lertzman & Krebs 1991; Lertzman 1992). Although most studies acknowledge that these assumptions limit their ability to make inferences about stand dynamics from static age distributions, they often then proceed to make such inferences (e.g. Day 1972; Whipple & Dix 1979; Knowles & Grant 1983).

In order to actually study stand dynamics, it is necessary to track the changes in a given stand over time. This can be accomplished by observing permanent plots at regular intervals over decades (Peet & Christensen 1980; Harcombe 1986) and determining recruitment and mortality by the appearance and disappearance of trees between inventories. An alternative method which does not require this long-term commitment is to produce a reconstruction of the age distributions at different times in the stand's history (Johnson & Fryer 1989). The stand reconstruction method requires the ability to detect and date trees that have died in the past. The purpose of this study was to use the stand reconstruction method to show clearly why static stand structures should not be used to infer stand dynamics. We tested two current hypotheses about canopy replacement in conifer forests by examining the dynamics of lower subalpine Pinus contorta – Picea engelmannii forests in the southern Canadian Rockies using stand reconstruction techniques.

A good example of how static stand structure has been used to infer stand dynamics is provided by a hypothesis concerning the temporal pattern of recruitment during stand development. Oliver (1981) postulated an initial wave of recruitment following a disturbance which kills the canopy. The recruits may arise from seeds, sprouts or advance regeneration. After these initial recruits form a canopy, further recruitment is prevented until a later stage when recruitment begins again. The explanation offered for this hiatus in recruitment is the monopolization of available resources by the canopy of the initial cohort, preventing successful establishment of any new individuals. Thus, no further recruitment occurs as long as the canopy trees retain control of the resources. This postulated temporal pattern of recruitment during stand development was based on an interpretation of static stand structures of older forest stands. These stands showed empty age classes following the initial postdisturbance recruits. We used stand reconstruction techniques which dendrochronologically date dead trees (Fritts 1976) to reconstruct a more complete age distribution of a specific stand at different times in its past. With these reconstructions we tested Oliver's hypothesis that a recruitment pause occurs following initial canopy development. If Oliver's interpretation is correct, the pause in recruitment should be obvious in these reconstructions as illustrated in Fig. 1. The empty age classes shown in this hypothetical 120-year-old stand must be shown to be empty throughout the development of the stand. We defined recruitment as any individuals that survive to the end of their first year of growth.

The second hypothesis we tested concerns the growth of understory trees into the canopy. The current modification of traditional successional theory (Pickett & White 1985; Platt & Strong 1989) holds that understory trees can replace canopy trees through the formation of gaps in the canopy caused by the death of one or more trees. These gaps allow recruitment of new individuals or release in growth of understory trees which then enter the canopy. In order to document or detect such dynamics, it is necessary to trace the growth in height of understory trees into the canopy. This can be accomplished using the fact that forest trees preserve in their rings at different heights above the ground a history of their growth in height over time. Consequently it is possible to produce height-date curves which show the height of each tree at any particular date (Fig. 2). The steepness of the curve indicates the rate of growth in height.

There is a continuum of ways that height–date curves can show progress of trees into the canopy. At one extreme (Fig. 2a), all trees recruit in one discrete period of time (in a large gap) and grow into the

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Fig. 1 Hypothetical age distributions at different periods in a stand's history. Example shows recruitment hiatus. Notice that after disturbance, there is a period of high recruitment. This is followed by a period in which recruitment is prevented and a later period in which recruitment begins again.
canopy. There is no subsequent growth into the canopy. At the other extreme (Fig. 2d), trees recruit continuously and grow into the canopy through the life of the stand. This situation would occur through continuous formation of gaps by random mortality of canopy trees. Trees may grow into the canopy and then die; such trees are still included as canopy replacement. Two intermediate situations could be imagined: sporadic growth into the canopy (Fig. 2b) or a discrete period of growth into the canopy in older aged stands (Fig. 2c). The situation in Fig. 2(b) could occur through infrequent formation of moderate-sized gaps while that illustrated by Fig. 2(c) could result from age-related canopy tree mortality. Understory trees can grow into the canopy either by constant increase in height over time or by one or more periods of slow growth followed by relatively rapid growth (suppression–release periods). These various pathways for reaching the canopy would be apparent in the height–date curves.

Thus the second hypothesis to be tested is that understory trees replace canopy trees through the formation of gaps. Height–date curves resembling any of Fig. 2(b–d) would support the hypothesis of canopy replacement by understory trees while the pattern depicted in Fig. 2(a) would indicate no canopy replacement.

**Study area and methods**

The five stands used in this study, ranging from 58 to 222 years in age, were located within a 5-km radius of each other in the lower subalpine zone (following La Roi & Hnatiuk 1980) in the Kananaskis River watershed (51°15′N, 116°03′W). The stands were dominated by lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and all originated from forest fires which completely killed the previous stand. Stand descriptions are given in Table 1. A more detailed description of the study area can be found in Johnson & Fryer (1987).

The disturbance history of this forest indicates the primary role of stand-replacing fires. Lightning-caused fires have burned an area equal in size to the 1300 km² Kananaskis watershed on average every 90 years (the fire cycle) since the mid-1700s. Before this, the fire cycle was 60 years (Johnson & Larsen 1991). Large areas of wind-thrown trees have not occurred in the study area despite the high winds during Chinooks (Foehns). Epidemics of mountain pine beetle or other insects and pathogens have not been recorded. Although logging occurred between 1883 and 1945 in the region, the area in which the stands occur was never logged. Furthermore, logging does not appear to have affected either the fire frequency or the species composition of the Kananaskis watershed (Johnson & Fryer 1987).

In order to test the first hypothesis concerning the temporal pattern of recruitment, it was necessary to determine changes in the age distributions of each stand over time. Within each of five 100-m² stands, all live, standing dead and fallen dead trees (including seedlings and saplings) were aged using disks obtained at the tree base. Dead trees were identified to species by microscopic examination of the wood and were dated by standard dendrochronological techniques (see Johnson & Fryer 1989). Because dead trees decompose, there is a limit to how far back in time the complete age distributions can be reconstructed. As a rule of thumb, decomposition prevents reconstruction beyond half the stand age (Johnson & Greene 1991). Detailed discussions of the methods of stand reconstruction can be found in Johnson & Fryer (1989) and Johnson & Greene (1991). The reconstruction limits imposed by decomposition are given in Table 1.

For each stand a Lexis diagram (Keyfitz 1968) was
Table 1  Stand descriptions

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>1798</th>
<th>1790</th>
<th>1524</th>
<th>1736</th>
<th>1676</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age oldest live tree (year)</td>
<td>58</td>
<td>99</td>
<td>118</td>
<td>215</td>
<td>222</td>
</tr>
<tr>
<td>Reconstruction limit (years back from present)</td>
<td>-</td>
<td>60</td>
<td>62</td>
<td>80</td>
<td>95</td>
</tr>
<tr>
<td><em>Picea engelmannii</em></td>
<td>25</td>
<td>54</td>
<td>60</td>
<td>70</td>
<td>85</td>
</tr>
<tr>
<td><em>Pinus contorta</em></td>
<td>162</td>
<td>35</td>
<td>37</td>
<td>25</td>
<td>14</td>
</tr>
<tr>
<td>Density of live trees &gt; 3 cm DBH (stems 100 m⁻²)</td>
<td>100</td>
<td>39</td>
<td>77</td>
<td>7</td>
<td>72</td>
</tr>
<tr>
<td>Relative density of live trees in 1981 (%)</td>
<td>0</td>
<td>60</td>
<td>14</td>
<td>89</td>
<td>16</td>
</tr>
<tr>
<td><em>Pinus contorta</em></td>
<td>0</td>
<td>1</td>
<td>9</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td><em>Picea engelmannii</em></td>
<td>0</td>
<td>1</td>
<td>9</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td>Abies lasiocarpa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The reconstructed age distributions consist of two groups of trees – those alive at the time of sampling and those trees which were dead at the time of sampling but could still be dendrochronologically dated. Beyond the decomposition limit indicated in Fig. 3, the reconstructed age distributions would be incomplete since they would be missing a third group of trees, those that died and decomposed and therefore of which there is no record. However, in the Results it will become evident why this limitation poses no major problem in the conclusions drawn.

In order to test the second hypothesis concerning height growth of understory trees into the canopy, all standing trees > 1 m in height (live and dead) within each stand were sectioned at 1-m intervals up the boles. Standing dead trees were largely intact as the tops do not tend to break off in these forests. The sections were dated to produce a height–date curve for each tree. The tops of fallen dead trees are often broken off and height measurements are not available for these trees. Therefore, the height–date curves represent a subset of the tree population which does not include either trees that died, fell to the ground and decomposed or trees that died and fell to the ground but could still be dated. Johnson & Greene (1991) give the rate at which trees fell over in these stands.

To determine from the height–date curves whether any canopy trees had originated from the understory trees, criteria for the canopy and understory had to be established. The bottom and top of the crown of each live tree (including saplings and seedlings) were plotted for each stand to determine the structure of the canopy. To simplify the diagrams, the trees were ranked by height from the shortest to the tallest. These diagrams provided a visual representation of the canopy structure in each stand and allowed selection of a height criterion for the canopy.

Results

To test the first hypothesis on the temporal pattern of recruitment (i.e. that a recruitment pause occurs following initial canopy development), the age dis-
tributions at 20 year intervals for each stand were reconstructed (Fig. 4). The decomposition limit for each stand (given in Table 1) is also indicated. The static age distributions (i.e. age distribution at the time of sampling in 1980) show the pattern described by Oliver (1981) with empty age classes evident, particularly in the oldest stands (E and A). Such empty age classes had been interpreted as evidence for a lack of recruitment during this period in the development of the stand. However, examination of the reconstructed age distributions indicates that the empty age classes were often filled at earlier periods in the stand’s history. The empty age classes are therefore due to mortality of trees in these age classes and not due to lack of recruitment. For example, the empty 160 year age classes in stands E and A (Fig. 4) which are evident in 1980 can be seen to have had trees in them for 140 years from the date of recruitment in 1820 right up until 1960.

Although the youngest stand (stand I) might appear to support Oliver’s hypothesis with its empty 0–20-year age classes, it should be noted that the much older stands (stands H, O and A) also show a lack of recruitment in this same time period (i.e. the 20 years preceding the date of this study). Since these stands range in age from 58 to 222 years, this lack of recruitment is more likely indicative of unfavourable conditions for seedling establishment during this particular time period rather than to any conditions due to stand development.

It is clear in these reconstructions that, following the fire that killed the canopy, initially recruitment was large and then was followed by a period to the present of reduced recruitment. Because the lower numbers of recruits in the later cohorts are also subject to higher mortality (see Johnson & Fryer 1989 and Fig. 4), these later cohorts will have fewer or no surviving members. The result could be age classes with no trees in them in the static age distributions of old stands (e.g. stands E and A). One important limitation of this stand reconstruction method is the inability to detect small seedlings which decompose rapidly. Although there is no information available on the dynamics of these young (5–10-year) age classes in the past, this problem results in an underestimate of the actual recruitment and mortality occurring.

Fig. 4 Reconstructed age distributions for five stands at 20-year intervals.
Therefore, the conclusion of rejecting the hypothesized pause in recruitment is robust even under this limitation of the data.

Before testing the second hypothesis concerning canopy replacement, the structure of the live canopy for each stand at the time of the study was graphed (Fig. 5). Looking only at the group of the tallest trees in each stand that are obvious members of the canopy, it would appear that, although the top of the canopy shows an increase in height with age of the stand (from stands I to A), the base of the canopy establishes at 4–7 m above the ground within 60 years of stand establishment and remains remarkably stable beyond 200 years. While the 222-year-old stand (A) does show a canopy bottom at approximately 10 m, the bottom of the canopy for the 215-year-old stand (E) is still at 4–8 m above the ground. Therefore, 6 m was selected as the criterion for the base of the canopy.

Using the height-date curves for all live and dead standing trees, the growth of individual live and dead standing trees in each stand which are or were ever in the canopy (i.e. at some period their height reached 6 m) can be traced and the date when they recruited can be determined (Figs 6–10a). Figs 6–10(b) also show the growth curves for all the remaining trees that did not make it into the canopy. Stands I, E and A (Figs, 6, 9 and 10) all show a discrete period of recruitment and growth into the canopy with no subsequent growth into the canopy as depicted in Fig. 2(a). All of the canopy trees in the youngest stand (I) recruited prior to 1940. Although recruitment has continued, none of the subsequent recruits have reached the canopy (Fig. 6). The two oldest stands (A and E) also show a discrete period of growth into the canopy although extended over a longer period of time (Figs 9 and 10). None of the trees that recruited after c. 1840 made it into the canopy. Stands H and O (Figs 7 and 8) show slightly more continuous growth into the canopy although the number of later recruits is very small and a good number of them are dead at

Fig. 5 Top and base of crown of individual live trees at the time of sampling by stand. Trees are ranked from shortest to tallest and stands are presented in order of increasing age.

Fig. 6 Height-date curves for 93 live and standing dead trees in stand I: (a) canopy (> 6 m) trees and (b) understorey (< 6 m) trees.

Fig. 7 Height-date curves for 63 live and standing dead trees in stand H: (a) canopy (> 6 m) trees and (b) understorey (< 6 m) trees.
present. However, again no trees recruited after c. 1925 grew up into the canopy. A more stringent criterion for a canopy tree (e.g. setting the centre of the canopy rather than the base as the limit) would provide even stronger support for our conclusion that no canopy replacement by understorey trees has occurred. Note that in most stands there has been continuous recruitment in the understorey over the life of the stand.

Discussion

From this study of the dynamics of five lower subalpine Pinus contorta – Picea engelmannii stands, it appears that after thinning starts there is a reduction in the number of trees recruited in the understorey; however, there is no evidence of any real stop in recruitment (hypothesis 1). Neither is there much evidence of canopy replacement by understorey trees in mature stands (hypothesis 2).

The results presented here have some limitations bearing on testing of the hypotheses. One problem may be that these stands are not old enough for canopy replacement to be occurring to any extent. The oldest stands were approximately 200 years old. In the Kananaskis watershed, however, stands greater than 200 years old in the lower subalpine zone are very rare, occupying less than 5% of the area, because of recurrent fires (Johnson & Larsen 1991). A second problem may be the size of the sample, i.e. it is possible that with a greater number of stand reconstructions, more evidence of canopy replacement might have been found.

However, this study clearly points out the limitations of using static age distributions to infer stand dynamics. The static approach to studying stand dynamics assumes (1) that the lack of trees in any age class at the present is evidence that there never were any individuals in that age class or (2) that the understorey trees will eventually replace the canopy. These assumptions ignore the fact that the canopy and understorey cohorts differ, not only in their initial numbers (recruitment) but also in their mortality.

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Fig. 8 Height-date curves for 53 live and standing dead trees in stand O: (a) canopy (> 6 m) trees and (b) understorey (< 6 m) trees.

Fig. 9 Height-date curves for 59 live and standing dead trees in stand E: (a) canopy (> 6 m) trees and (b) understorey (< 6 m) trees.

Fig. 10 Height-date curves for 25 live and standing dead trees in stand A: (a) canopy (> 6 m) trees and (b) understorey (< 6 m) trees.
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rates. As shown in this study, the presence of understory trees of any species does not ensure that any of them will enter the canopy. Even with continued recruitment, the mortality rates operating on these low numbers of individuals in the understory cohorts almost ensures that the cohorts will have virtually no survivors in the time required for them to grow into the canopy. Unlike the static age distribution approach with its often untenable assumptions, the reconstruction approach allows us to examine the stand dynamic processes of recruitment and mortality to which rates can be assigned.

Forests are made up of tree populations of cohorts that are diagonally stacked in the Lexis diagram (Fig. 3). The amount of recruitment and subsequent patterns of mortality of these stacked cohorts determine the sequence of forest tree population succession. *Pinus contorta* and *Picea engelmannii* provide an example of such a succession.

Recruitment patterns of both *Pinus contorta* and *Picea engelmannii* are similar (Johnson & Fryer 1989). Both recruit in large numbers immediately following fires which have removed the canopy and exposed large areas of mineral soil. After this initial high recruitment, recruitment is low and similar for both species despite differences in their shade-tolerance. These lower subalpine populations of *Pinus contorta* and *Picea engelmannii* can thus be thought of as consisting of two cohorts: a fire cohort that is recruited in the first few years after a forest fire and an understory or nonfire cohort that is recruited after the development of a canopy by the fire cohort.

These two cohorts are distinguished not only by their different recruitment rates but also by their different mortality schedules (Johnson & Fryer 1989). Trees of the fire cohort would have established under low competition, open canopy conditions on a mineral substrate while trees of the understory cohort would have established on a shaded organic substrate. The fire cohort of shade-intolerant *Pinus contorta* has a U-shaped mortality curve indicating a period of decreasing mortality associated with seedling establishment, then a period of low mortality, followed by an increase due to thinning once the trees are large enough. The understory cohort of *P. contorta* has a high and constant mortality rate. For the relatively shade-tolerant *Picea engelmannii*, the fire and understory cohorts have mortality curves that are similar in both magnitude and shape. These cohorts have, in fact, at least two mortality functions, one discussed above which operates in the interval between fires, and the other due to fire. These mortalities operate at different temporal and spatial scales, the former more or less continuously on the local population and the latter on the regional population.

Consequently both *Pinus contorta* and *Picea engelmannii* have very similar dynamics which affect the ability of the understory cohorts to replace the canopy. In both species, the understory cohorts show low recruitment and high establishment and thinning mortality rates (Johnson & Fryer 1989 and Figs 4 and 6–10). Therefore, the understory cohorts have a very low chance of replacing the canopy. In order for succession (i.e. canopy replacement) to occur, the population dynamics would have to change so as to increase the survivorship of the understory cohorts into older age classes. This can be accomplished through increased recruitment, decreased thinning and establishment mortality, and/or less frequent fires.

Forest succession cannot be viewed as simply a sequence of species replacements based on shade tolerance. We have shown that canopy replacement can only occur if the dynamics (recruitment and mortality rates) of the understory cohorts are such that they have a significant probability of replacing the canopy. Shade tolerance of species in the understory is not sufficient to ensure canopy replacement as shown by this study in which replacement of *Pinus contorta* by the more shade-tolerant *Picea engelmannii* does not occur. Only a population dynamics approach can provide the information necessary to reach conclusions about species replacements in succession. Furthermore, such studies must include all forces of mortality (e.g. establishment, thinning, disturbance, chance).

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