Using dendrochronology to obtain annual data for modelling stand development: a supplement to permanent sample plots

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Summary

Permanent sample plots (PSPs), measured at 5- to 10-year intervals, are presently used to monitor stand development in boreal forests in Canada. These data cannot easily be used to study inter-annual variability in stand development processes nor can they monitor the effects of transient factors affecting stands annually because of their coarse temporal resolution. It also takes a considerable period of time to obtain time series of data for regions without PSPs. Long re-measurement intervals are necessary because instruments like diameter tapes, calipers and clinometers cannot discern annual growth in these slow-growing forests. Dendrochronological stand reconstruction techniques are a method that can be used to obtain annual data on forest growth and stand development. We show that these techniques can provide annual information on stand development patterns while periodic measurements of PSPs cannot, and that these data can be obtained in a short period of time, relative to waiting to obtain data from PSPs established today. Detailed, annual data will become more important in the future, as climate change will affect both forest growth and stand dynamics. Annual resolution data on these processes will be required to describe and account for these effects.

Introduction

Presently, there are three primary methods that can be used to monitor the growth and dynamics of forests: permanent sample plots (PSPs), eddy covariance flux towers and dendrochronology. The vast majority of data presently used to monitor forest growth and stand dynamics of boreal forests in Canada are obtained by periodic remeasurement of the breast height diameter, height and condition of trees at PSPs. Plot designs vary

by jurisdiction, but re-measurements are typically made at only 5- to 10-year intervals. In the past, it has been often been argued that these long intervals are adequate (e.g. Ranneby and Rovianen, 1995; West, 1995), but this may not be true in the future if we wish to monitor or model the effects of processes that operate at an annual timescale. Eddy covariance studies (e.g. Kljun *et al.*, 2006; Barr *et al.*, 2007; Dunn *et al.*, 2007) have clearly demonstrated the magnitude of inter-annual variability of ecosystem processes in Canadian

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forests, but because of the high cost, the density of such installations will never be very high. As climate change begins to have significant impacts (e.g. Ogden and Innes, 2007), monitoring their magnitude and direction will be required to adapt forest management practices to these effects. In this paper, we suggest that dendrochronological methods may be a powerful, complementary method to PSPs, and demonstrate some of their advantages particularly for obtaining more detailed, annual resolution data on forest growth and stand dynamics.

Studies of the relationship between environmental variability and forest growth and stand dynamics address two separate types of questions: the direction and causes of long-term trends and the magnitude and causes of inter-annual variability. PSPs provide accurate estimates of the size and condition of trees at these fixed intervals that can be used to investigate the magnitude of long-term trends (e.g. Zeide, 2001), but they are not well suited for study of inter-annual variability of forest growth or stand dynamics due to their coarse temporal resolution. Statistical methods exist for annualizing data from periodic measurements (e.g. McDill and Amateis, 1993; Cao, 2000; Nord-Larsen, 2006), however, to determine the true magnitude and causes of interannual variability in tree growth and mortality requires measurements at an annual resolution. An additional consideration for most boreal tree species is slow growth rates. Even if undertaken, vearly re-measurement of PSPs usually cannot obtain annual data because instruments like tapes, calipers and clinometers used to make field measurements of tree diameters and heights have difficulty resolving the small annual growth increments typical of boreal forests. Further, in regions where PSPs are absent, data from plots established elsewhere must be used to parameterize models used to make local management decisions. Investments made in local PSPs will not return useful monitoring data for a considerable period of time.

Dendrochronology techniques can overcome the weaknesses of PSPs related to their coarse temporal resolution. Ring widths measured on increment cores can be resolved annually and can provide detailed time series of diameter growth decades into the past without waiting for PSP re-measurements. For example, Biondi (1999) showed how tree-ring data can be used to obtain insight into stand growth patterns over longer historical periods than is possible using PSPs. In this paper, we show that dendrochronology techniques can be used to retrospectively obtain much of the data that are presently normally acquired by periodically re-measuring PSPs. We demonstrate three particular types of data: stand-level volume growth, stand-level mortality and standlevel biomass dynamics, owing to the importance of these values in forest management. These represent only a portion of the growth and stand development trajectories that could be examined using these data. We show that the data obtained by these techniques can provide more information than the data obtained from periodic remeasurement of PSPs, and that they can quickly obtain long time series of data in areas currently lacking a PSP infrastructure, relative to waiting to observe changes at a PSP established today. We also compare and contrast the possible sources of error between the stand reconstruction and PSP methods, and discuss some possible methods of minimizing that error.

Materials and methods

Data collection and processing

We use data from a 900-m² stem-mapped plot located in an unmanaged, fire-origin jack pine (Pinus banksiana Lamb.) stand located near Candle Lake, Saskatchewan, Canada (latitude 53.9° N and longitude 104.7° W). We sampled this stand in June 2005 as part of our studies on the growth and dynamics of jack pine forests in the region. The plot was a c1.2 site type (jack pine/ black spruce/green alder/feather moss) on SM1 (moist/sandy) soil (Beckingham et al., 1996) and was located in the boreal plains ecozone (Ecological Stratification Working Group, 1996). We recorded breast height diameter and height for all living trees, breast height diameter for all dead trees, extracted two randomly oriented cores at breast height for living trees and cut a crosssectional disc at breast height from both standing and fallen dead trees. This was a full census of all living trees, standing snags and downed logs present in the stand at the time of sampling. The stand originated in 1916, so was 90 years old,

with a mean height of 15.9 m, quadratic mean diameter of 17.7 cm, a total density of 1767 trees per hectare and a live density of 1267 trees per hectare. We air-dried the core and disc samples, mounted the cores on grooved boards and cut cross-sectional discs into 1- to 2-cm thick slices. These were polished with up to 600 grit sandpaper, scanned as 1600 dpi grev scale images and imported into WinDendro (Regent Instruments, Quebec, Canada) for ring-width measurement. When suppressed, jack pine can form light rings (Volney and Mallett, 1992) that were not always visible on the scanned images. We simultaneously examined suppressed samples with a microscope and added rings not visible on the scanned images to the WinDendro file. We considered trees functionally dead when radial growth ceased at breast height (Mast and Veblen, 1994), which may have underestimated year of death in some cases of extreme suppression (<5 per cent of samples).

Reconstructing stand volume growth

The vast majority of studies that investigate the volume growth of trees or stands do not actually measure volume. Instead, they measure either diameter and/or height, and use equations to predict volume from these measurements. In this paper, we calculated the diameter (inside bark D_{ib}) of each tree from the arithmetic average of the cumulative radii measured on the two increment cores extracted from each tree. In the cases where samples did not hit the pith, we used the outside bark diameter (D_{ob}) measured in the field to estimate the amount of missing radius. We used the difference between the total of the mean cumulative radial measurements and the diameter measured in the field (corrected for bark thickness) as an estimate of the missing distance between the final ring measured on an off-centre core and the true centre of the tree. In practice, other methods of estimating the distance to pith could also be used (Applequist, 1958; Liu, 1986).

We then used $D_{\rm ob}$ to predict cumulative volume for each individual tree. This required (1) a bark thickness equation, (2) a height-diameter equation and (3) a taper equation, as shown in Figure 1. Volume increment was obtained by subtracting volume in year y - 1 from volume

in year y and was expressed in cubic meter per year. Stand-level volume and increment were obtained by summing the individual tree values for each year and annual mortality was obtained by summing the volume of trees that died in a given year. These methods are further detailed in Metsaranta and Lieffers (2008b). We chose the equations used here because we could (1) parameterize them from data readily available to us or (2) easily obtain parameters for them from the existing literature for our study region. We admit that the particular equations that we chose are rather simple, but argue that they are adequate for demonstrating the advantages of the dendrochronological method for obtaining annual data on forest stand development.

Reconstructing mortality

To reconstruct past mortality, we cross-dated dead samples against the living trees in order to determine their year of death. We did this against a master chronology developed from 25 of the largest trees at the site by visual reference to narrow marker years (Yamaguchi, 1991), induced primarily by jack pine budworm defoliation (Volney, 1988). Gross dating errors were quantitatively detected by calculating the correlation between sample raw ring widths and the master chronology, as well as shifting sample dates ±1 to 5 years, repeated iteratively until most samples (94.1 per cent) had the highest correlation at the final assigned date (97.7 per cent for ±1 year). The average correlation with the master chronology at the assigned date was $r^2 = 0.89$ (SD = 0.09, range = 0.76-0.98, n = 171). Ring widths could be measured on 93 per cent of n=171 sample trees at the study site. The rest were too decomposed. For decomposed trees, we used the mean year of death of the three larger and three smaller trees nearest in diameter and of the same class (snag or downed log) as the decomposed sample as an estimate of its year of death, and the mean ring widths of these same trees as an estimate of its growth (Metsaranta et al., 2008). We have tested the accuracy of this method, and found that it provided unbiased estimates of year of death, with a mean absolute difference between the measured and estimated year of death of 3.3 (SD 2.4) years.

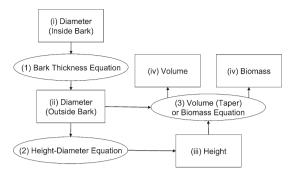


Figure 1. The steps required to estimate annual volume or biomass using dendrochronlogy data and equations predicting inside bark diameter, height, whole tree volume and biomass. Equations required in steps (1), (2) and (3) used in this study are given in Metsaranta and Lieffers (2008b) but in other studies they should be the best available for a given region, species and management question being considered.

Reconstructing stand biomass growth

We also reconstructed trajectories for stemwood biomass of living trees, snags and downed logs. We estimated total stemwood biomass using the equations of Lambert *et al.* (2005), where biomass is predicted from diameter and height of individual trees, the values of which are summed to obtain stand biomass. The equations provide reasonably accurate estimates of tree biomass relative to localized equations in this region of Canada (Case and Hall, 2008).

Reconstructing coarse woody debris

Trees that die become standing snags and then fall down to become downed logs. We estimated a time of falling for each snag based upon Gore *et al.* (1985), which uses data on the time since death of standing snags and downed logs to estimate snag fall rates, based on an assumption of exponential fall-down rate. In practice, other methods of estimating the fall-down rate of snags could also be used if they were more appropriate to local stand conditions (e.g. Johnson and Greene, 1991; Storaunet and Rolstad, 2004). These results are further detailed in Metsaranta *et al.* (2008). This allowed us to estimate when a snag fell to

the ground, determine the number of years *t* that it had been on the ground and so estimate how much it decomposed since it fell. We did this using a natural log-transformed simple exponential decay model of the per cent mass remaining

$$In(MR\%) = a - kt. \tag{1}$$

We obtained parameters (a = 4.617 and k = 0.009) from the nearest study plot (Prince Albert) in Trofymow *et al.* (2002). Using these methods, and assuming that snag decomposition was minimal, we could reconstruct annual trajectories of stemwood biomass in living trees, snags and downed logs for the study plot.

Results and discussion

Annual volume, mortality and biomass trajectories

From the resulting series of volume growth data for individual trees, we calculated (1) annual volume growth (gross and net), (2) cumulative volume growth (gross and net), (3) annual volume mortality and volume of fallen snags and (4) cumulative stemwood biomass in living trees, snags and downed logs. Net growth refers only to gross growth minus mortality, and does not account for decay. In Figure 2, we plotted the incremental and cumulative volume growth series alongside what the data for these series would like if this plot had been established as a PSP in 1950, and re-measured on a 10-year interval up to the present time. We chose the year 1950 because our previous assessments suggested that stand reconstruction likely underestimates growth prior to that time in jack pine forests in this region due to loss of trees that have died and subsequently decomposed beyond recognition (Metsaranta et al., 2008). The data obtained from tree-ring reconstructions demonstrated significant annual variation in volume growth (Figure 2a). These variations were not evident if the data were summarized at 10-year intervals, as they would be if this plot was a PSP that was remeasured every 10 years (Figure 2b). Similarly, in Figure 3, we plotted the annual volume mortality and volume of falling snags. Like the volume increment data, tree-ring reconstruction demonstrates significant annual variation in mortality and snag

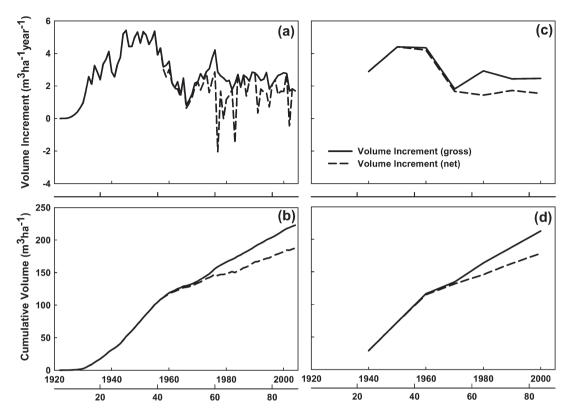


Figure 2. On the left are the patterns of gross and net incremental (a) and cumulative (b) volume growth for a 900-m² plot in a jack pine stand in Saskatchewan, Canada, calculated from a complete ring-width reconstruction of all living and dead trees. On the right (c and d) is what we would know about these patterns of growth if a PSP had been established at the site in 1950 and re-measured every 10 years. Net growth refers only to gross growth minus mortality and does not account for decay. The data are plotted since stand origin, but are likely underestimates prior to 1950 due to loss of trees that have died and subsequently decomposed beyond recognition.

fall (Figure 3a). These variations were again not evident if the data were summarized at 10-year intervals (Figure 3b). In Figure 4, we integrated the growth data, mortality data, snag falling data and log decomposition data to plot trajectories of cumulative stemwood biomass (tonnes per hectare) in living trees, standing snags and downed logs at the study site.

Possible sources of error

Undoubtedly, the data plotted in Figures 2, 3 and 4 contain error and are probably biased to some extent. This error could be one of four types: (1)

measurement error; (2) error due to the incorrect choice of allometric equations (model error); (3) errors related to selection of inappropriate plot size for the question being addressed and (4) the error resulting from sample plots that are not representative of the population of interest (Chave et al., 2004). Because we are dealing here only with the reconstruction of the growth of a single plot, only measurement error and model error are of immediate relevance to the methods that we describe. In the following, we discuss some potential impacts of measurement and model error on the dendrochronology method, and compare them with analogous errors that would occur in PSP re-measurements. A detailed analysis of error

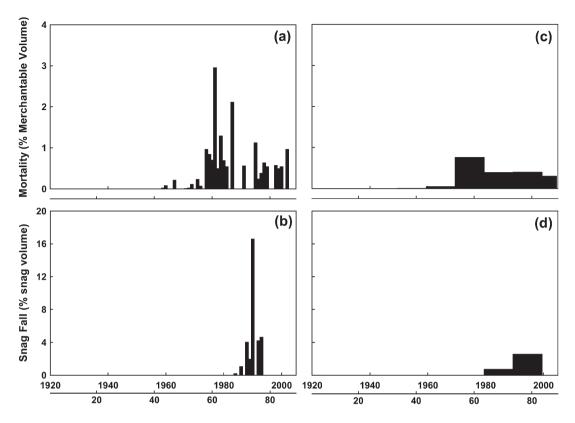


Figure 3. On the left are annual estimates of volume mortality (a) and volume of snag fall (b), expressed as a proportion of the standing stemwood volume or standing snag volume at that time for a 900-m² plot in a jack pine stand in Saskatchewan, Canada, calculated from a complete ring-width reconstruction of all living and dead trees. On the right (c and d) is what we would know about these patterns if a PSP had been established at the site in 1950 and re-measured every 10 years. The data are plotted since stand origin, but are likely underestimates prior to 1950 due to loss of trees that have died and subsequently decomposed beyond recognition.

propagation would be valuable for both the dendrochronology and PSP methods if it accounts for all possible errors, but we consider a quantitative assessment to be outside of the scope of our paper.

The methods that we describe are dependent upon being able to reconstruct past diameters. In the absence of measurement error, the nominal precision of laboratory ring-width instruments are typically \pm <0.01 mm, which is much better than the precision of diameter tapes or calipers (typically \pm 1 mm). This immediately means that the tree-ring measurements can resolve diameter growth rates of less than 1 mm per year, while PSPs cannot. However, both the dendrochronol-

ogy method and the PSP method may have several possible errors that reduce the accuracy of either method. When extracting core samples, the increment borer may not have been inserted exactly perpendicular to the tree nor exactly at breast height. A similar error in PSP remeasurements is induced by changing from tapes to calipers between successive measurements (e.g. Gregoire et al., 1990) or not placing the instruments at breast height or the same location at each successive measurement. Another possible error occurs when air-drying cores prior to measurement, which induces shrinkage that may vary as a function of wood density, and so differ for each ring. A similar error in PSP re-measurements

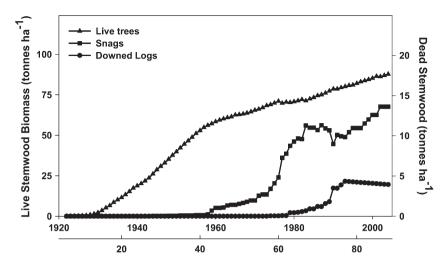


Figure 4. Trajectories of cumulative stemwood biomass (tonnes per hectare) in living trees, standing snags and downed logs at a 900-m² plot in a jack pine stand in Saskatchewan, Canada, calculated from a complete ring-width reconstruction of all living and dead trees using biomass equations, estimates of the fall-down rate of snags and estimates of the decomposition rate of downed logs. The data are plotted since stand origin, but are likely underestimates prior to 1950 due to loss of trees that have died and subsequently decomposed beyond recognition.

may relate to differential amounts of swelling of the wood and bark, depending upon the season in which the measurements are made or the amount of soil moisture. Both the stand reconstruction and the PSP method will have difficulty resolving the issue of measuring diameter on an object that is not round (Biging and Wensel, 1988).

A weakness of the stand reconstruction approach is that it does not provide data on past height growth, which is needed to estimate volume. Traditionally in many growth and yield studies, missing heights have been predicted using height-diameter regression equations (e.g. Huang et al., 1992; Peng et al., 2001), which in the simple form that we used here assume that all trees of a given diameter are the same height and likely result in biased predictions of height growth (Hasenauer and Monserud, 1997). Height prediction equations that are sensitive to the effects of stand conditions on height growth (e.g. Sharma and Zhang, 2004a; Newton and Amponsah, 2007) help alleviate some of this error. Since we are describing here methods for obtaining annual data, however, a more relevant question is how much measurement error would occur in annual height measurements made at a PSP? When collecting

data for this study, we measured the height of 79 trees twice, on separate days, with a laser clinometer. The mean absolute difference between the two measurements was 0.79 m (SD=0.68). From full stem analysis data in Varem-Sanders and Campbell (1998), we estimate that the annual height increment of jack pine trees in this region averages 0.16 m (SD=0.09). In other words, unless our height measurements were exceptionally sloppy, repeated annual height measurements, though probably unbiased, would have difficulty resolving the small annual height increment in these forests. Hasenauer and Monserud (1997) came to a similar conclusion about error in height measurement.

There may also be error related to estimating true year of death for snags or true year of fall for downed logs. For a PSP, it is only possible to know that a tree died or fell to the ground some time during the re-measurement interval. This means that the error associated with dendrochronological dating of dead trees would have to be greater than the re-measurement interval in order for PSP methods to be a better estimate of both of these quantities. This is unlikely to be the case for year of death, except in the case of

extreme suppression. In this study, we considered trees without detectable radial growth to be functionally dead (e.g. Mast and Veblen, 1994), which may underestimate the true year of death by some unknown amount in this situation. Our method of estimating when snags fell to the ground (Gore et al., 1985) is the most uncertain of the all the methods that we describe because it makes several assumptions that may not hold under all conditions (e.g. Johnson and Greene, 1991). We do not know if the error associated with this method is less than the typical PSP re-measurement interval. Another consideration is that the dendrochronological method likely underestimates growth with increasing time from the present due to the loss of trees that have died and decomposed. In this forest type, our evidence suggests that dead trees remain standing long enough and downed logs decompose slowly enough that stand reconstructions can be reliable for ~50 years into the past (Metsaranta et al., 2008). Other studies suggest that this period is one-half of the life a stand in subalpine forests. regardless of stand age (Johnson and Fryer, 1989). Operationally, the reliable reconstruction period in other forest types would need to be assessed and would likely be less in warmer and wetter regions and for species with wood that is more susceptible to decay.

In measurement studies comparing different ways of estimating annual volume or biomass increment, LeBlanc (1990) noted that volume estimates based on breast-height measurements were highly correlated with whole-tree volume measurements regardless of the equation used to estimate volume, while Bouriaud et al. (2005) suggested that breast-height samples may underestimate growth during drought. For biomass prediction, (Case and Hall, 2008) have demonstrated that the national scale equations of Lambert et al. (2005) provide reasonable estimates of biomass relative to more localized equations in this region. The relationship between diameter and height and tree volume or biomass may also change as a stand develops (e.g. Morris and Forslund, 1992; Muirhawe et al., 1994; Bond-Lamberty et al., 2002; Sharma and Zhang, 2004b). Improvements in these equations would help to reduce error and bias of volume and biomass estimates made by both dendrochronological stand reconstruction and PSP methods.

Conclusions

This paper shows that dendrochronological reconstruction of stands offers a way to quickly collect annual scale information on the growth and mortality of trees for several decades into the past. Annual resolution data obtained by dendrochronological measurement facilitate the analysis of many ecological processes that could not be investigated with periodically obtained data (Metsaranta and Lieffers, 2008a, b). We detailed the reconstruction of stand volume and biomass growth because of the primary importance of these characteristics of the forest in management planning. Such data provide opportunities to link growth and stand dynamics models to climate and other factors that are best modelled with data on an annual timescale. Models derived from PSPs may have unknown biases because they must assume average weather conditions owing to a lack of data on inter-annual variability in growth (e.g. Kangas, 1998). The development of growth models that account for environmental factors that operate at annual timescales (e.g. Wensel and Turnblom, 1998; Snowdon, 2001; Matala et al., 2005) could be accelerated if annual data on stand-level productivity were available across larger regions.

The immediate cost of establishing a stand reconstruction plot is clearly higher than the cost of establishing a PSP. The data that we used in this study were obtained in 2005, from samples collected over the course of 2 days by three people in the field, and processed in the laboratory over the course of about 2 months by a single person. While this procedure may have taken more effort than establishing and re-measuring a PSP five times, the data could be obtained in less than 3 months instead of 50 years. The benefits of the more detailed data that can be obtained by stand reconstruction would arise primarily from the reduced costs of incorrect decisions taken as a result of not knowing the magnitude or causes of inter-annual variability in forest processes. The importance of this error will increase in the future as average weather conditions are affected by climate change. Across a landscape, sampling design considerations are likely similar for both PSP and stand reconstruction methods, with additional complications like the degree to which inter-annual variability is spatially correlated across a landscape for different species. An

advantage of PSPs is that methods have already been developed for using the data as part of annual forest inventory and rolling sample designs (e.g. Van Deusen, 1997; Johnson *et al.*, 2003; Arner *et al.*, 2004). Additional research would be required to use dendrochronology data in these designs.

In this study, we obtained a complete census from all living and dead trees present at the time of sampling, but it is also possible to conduct such reconstructions with sampling (Garcia, 1992; Osawa et al., 2000; Osawa and Abaimov, 2001; Osawa et al., 2001), which would reduce the costs and time effort significantly, but would also add a degree of sampling error within plots. In any case, the analytical infrastructure required to do these analyses is not extensive. Software and hardware for obtaining ring-width measurements are readily available. As mentioned by Biondi (1999), the cost of obtaining the infrastructure for tree-ring analysis capabilities is likely no more than that required for Geographic Information Systems analysis capabilities, which are ubiquitous decision support tools for forest and natural resource management agencies. Because a given data collection budget would likely allow for a larger number of PSPs to be established at a finer resolution than tree-ring reconstruction plots, it would be useful if the relative costs, benefits and error structures of the two techniques were further quantified. Though more labour intensive in the short term than PSPs, dendrochronological samples need only be collected once so have no costs associated with plot maintenance and re-measurement. Also, the plots are not subject to risks from vandalism, industrial damage or fire after they have been established because the data on past growth have already been collected. While periodic remeasurement of PSPs provides accurate estimates of tree condition and size at fixed intervals, the dendrochronology approach that we report can provide annual resolution data that also follows the fates of individuals over time. Stand reconstruction techniques can also retrospectively provide long time series of data for areas without a PSP infrastructure—compared with long delays if normal PSPs were established today. These techniques should therefore also be of interest in regions that either do not have a PSP infrastructure or where the present PSP infrastructure has coverage gaps in certain stand types.

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