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Biomass and biomass change in lodgepole pine stands in Alberta[†]

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Summary We describe methods and results for broad-scale estimation and mapping of forest biomass for the Canadian province of Alberta. Differences over successive decades provided an estimate of biomass change. Over 1500 permanent sample plots (PSP) were analyzed from across the range of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), the major forest tree species of Alberta. The PSP network is densest in stands aged between 70 and 100 years and is well-represented by stands of all ages to 150 years of age. Stand biomass (Mg ha^{-1}) was estimated for each PSP plot as the sum of the respective biomass components for each tree (live and standing dead). The biomass components for live trees were stem, bark, branches, foliage and roots. The components for standing dead trees excluded foliage. Equations from previous biomass studies were used for biomass component estimation. Biomass estimates of additional non-tree components were attempted, but without much success. Biomass of the soil organic layer was estimated once on 452 PSPs and a mean estimate of total dead fuels on the ground (28.4 Mg ha^{-1}) was available only for the entire distribution of lodgepole pine. However, values of these two components were essentially constant over time and therefore did not alter the analysis or conclusions obtained by analyzing total tree biomass alone. We then used this spatial network of 1549 plots as the basis for mapping biomass across Alberta. Mapping methods were based on Australian National University SPLINe (ANUSPLIN) software, Hutchinson's thin-plate smoothing spline in four dimensions (latitude, longitude, elevation and biomass).

Total tree biomass (mean = 172 Mg ha^{-1}) was dominated by stem biomass (mean = 106 Mg ha^{-1}), which was an order of magnitude greater than the mean estimates for the bark (11 Mg ha^{-1}), branch (12 Mg ha^{-1}) and foliage (12 Mg ha^{-1}) components. A close relationship was found between total tree biomass and stand stem volume ($R^2 = 0.992$ with $n = 3585$; note that volume and biomass were calculated independently). We compared total tree biomass for two decades, the 1980s and the 1990s. After correcting for changes in harvest removals over time, the mean change in total biomass was positive (0.99 Mg ha^{-1} year^{-1}) and differed significantly from zero ($n = 421$; $P < 0.001$). Estimates ranged from −13.9 to 8.0 Mg ha^{-1} year^{-1}. The heart of the lodgepole pine distribution (primarily the Foothills subregions) showed an increase in biomass, whereas isolated pockets of lodgepole pine in the boreal northern subregion indicated a decline in biomass.

Keywords: permanent sample plots, Pinus contorta, productivity, smoothing splines.

Introduction

We are interested in estimating both biomass and change in biomass for lodgepole pine stands across Alberta, Canada, for several reasons. Quantification of forest biomass is useful for estimating available forest resources and understanding changes in forest structure resulting from forest succession and management actions (Cairns et al. 2003). Information on forest biomass is increasingly being used to guide sustainable forest resource management decisions (Parson et al. 1992, UN Division for Sustainable Development 1993, Fournier et al. 2003). Spatially explicit estimates of forest biomass have become critical for improving our capacity to model carbon budgets (Penner et al. 1997, Kurz and Apps 1999) and to predict the effect of global climate change on forest productivity (Monserud et al. 1995, 1996*b*). Biomass estimates are also needed to supply information under the terms of international accords such as criteria and indicators of sustainable forest development (Fournier et al. 2003). With the growing importance of forest-fire hazard management, forest biomass estimation is needed to determine the components of forest fuels (Agee 2000, Edmonds et al. 2000).

As demands on forested lands increase, it is increasingly important to quantify spatial variation in forest productivity (McKenney and Pedlar 2003, Tateno et al. 2004). Such spatial information is essential for managers to make cost-effective decisions about land-use and investment. Because dry biomass density is nearly 50% carbon, tracking biomass change reveals the potential of a forest to be either a carbon source (via burning and deforestation) or a carbon sink (via growth and reforestation) for greenhouse gases (Cairns et al. 2003).

There are two main approaches to creating regional or national biomass inventories (Penner et al. 1997): conversion of

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existing volume inventories to biomass based on broad strata (Birdsey 1992, Alexeyev et al. 1995, Isaev et al. 1995) or direct sampling to measure biomass (e.g., Box et al. 1989, Botkin and Simpson 1990). Converting existing national volume inventories to biomass inventories takes advantage of existing information (Bonnor 1985), but both methods suffer from some of the same weaknesses—the need to estimate all forest biomass components (including non-merchantable parts of the tree stem, understory and roots) from stem wood volume (Penner et al. 1997). In Russia, Isaev et al. (1995) have taken the approach of using plot data to derive volume to biomass conversion factors based on the predominant species, stocking and maturity class of the stand. The stem volume and area in each of these broad classes are then obtained from the national inventory and converted to biomass components. Also in Russia, Monserud et al. (1996*a*) predicted Scots pine (*Pinus sylvestris* L.) needle, crown, stem and root biomass components as functions of stand stem volume and stand age, variables commonly available in inventories. In Canada, Banfield et al. (2002) combined inventory data with relationships between biomass and site factors, such as soil texture or percent clay content.

Forest inventory programs and permanent sample plot (PSP) networks are providing a growing source of information on forest biomass and productivity. Monserud and Huang (2003) assembled over 1000 PSPs from both public and private sources to predict and map lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) site index across Alberta. Fournier et al. (2003) used a large inventory plot network to estimate and map biomass across Newfoundland and Quebec. Kurz et al. (2002) relied on inventory plots to estimate biomass and eventually net primary productivity across Canada. Biomass on a given sample unit is estimated either from existing biomass component equations for each tree (e.g., Singh 1982, Alemdag 1984) or from conversion factors based on volume estimates (Kurz et al. 2002) from stand simulation models such as GYPSY (Huang et al. 2001).

Objectives

Our objectives were to estimate forest biomass by components for lodgepole pine stands across Alberta and then to map the resulting biomass isoclines within and bordering the natural range of lodgepole pine in Alberta. Finally, change in biomass of the same plots was estimated as the difference in biomass between successive decades.

We began by assembling a database of longitude, latitude, elevation and biomass for an extensive network of permanent sample plots. Biomass at each sample location (n =1549) was estimated as the sum of component biomass for each tree (Appendix 1). We then used a thin-plate smoothing spline program (ANUSPLIN; see Hutchinson 2002) to fit this biomass surface as a function of the three topographic variables: longitude, latitude, and elevation. Finally, we combined this fitted surface with a province-wide digital elevation model (DEM) to predict isoclines of biomass for the entire range of lodgepole pine in Alberta. Maps were produced using the ArcView geographic information system (http://www.esri.com/).

Data

We concentrated on naturally regenerated lodgepole pine stands in Alberta. Lodgepole pine, Alberta's provincial tree, is the most common tree species in the Rocky Mountains and Foothills regions (Alberta Environmental Protection 1994), occurring on the eastern slopes of the Canadian Rocky Mountains. It also occurs in a large zone in the boreal regions to the north where it hybridizes with jack pine (*Pinus banksiana* Lamb.). Lodgepole pine comprises about 20% of the mature standing timber in Alberta and accounts for about 40% of the annual provincial harvest (Huang et al. 2001). Lodgepole pine grows well on a wide range of soils and under a wide range of climatic conditions (Wheeler and Critchfield 1985). Lodgepole pine can tolerate sites that have short and irregular growing seasons, poor to very poor nutrient regimes and a distinct soil water deficit (Huang et al. 2001).

We used three PSP networks (Figure 1): (1) the PSP network of Alberta Sustainable Resource Development (2002), which contains 452 lodgepole pine stands; (2) the PSP network of Weyerhaeuser Canada, which contains 261 lodgepole pine stands in Alberta; and (3) the PSP network of Hinton Wood Products Ltd. (formerly Weldwood of Canada Ltd.), which contains 836 lodgepole pine stands in Alberta. These three PSP systems (1549 stands) are established and maintained to similar standards (see Alberta Sustainable Resource Development 2002). A lodgepole pine stand is defined as containing at least 80% lodgepole pine. Many of these plots have been remeasured since 1960. Generally, the remeasurement cycle is every 5 years for stands < 80 years old and every 10 years for older stands. Plot size is mostly 0.08 or 0.1 ha, provided that 50 live trees are available for tagging. Plot size increases to 0.15 or 0.20 ha in low-density stands and decreases to 0.04 ha in young and high-density stands.

An important feature of this PSP network is that the stands are excluded from normal harvesting. Stands are cut and regenerated only if they have undergone severe damage as a result of natural causes such as wildfire, windthrow or bark beetle epidemics. In such an event, a new plot is established in the former stand. Because harvesting is excluded, a harvest adjustment must be made when calculating ecosystem biomass.

One difference among the three PSPs is minimum diameter for measurement. The Alberta Sustainable Resource Development PSPs measure all trees at least 1.3 m tall, equivalent to setting minimum dbh (diameter at breast height) to 0 cm, whereas the Weyerhaeuser minimum dbh is 5 cm, and the Hinton Wood Products minimum dbh is 0 cm on plots measured after 1997, and either 5 cm (if plot size is 400 m^2) or 7.6 cm (if plot size is 800 m^2) in the period 1961–1997 and 11.7 cm on the first PSPs in the 1950s. We reconciled this seeming discrepancy by determining the biomass contribution of trees in each of these dbh classes (0–5 cm, 5–7.6 cm and 7.6–11.7 cm) in the Alberta Sustainable Resource Develop-

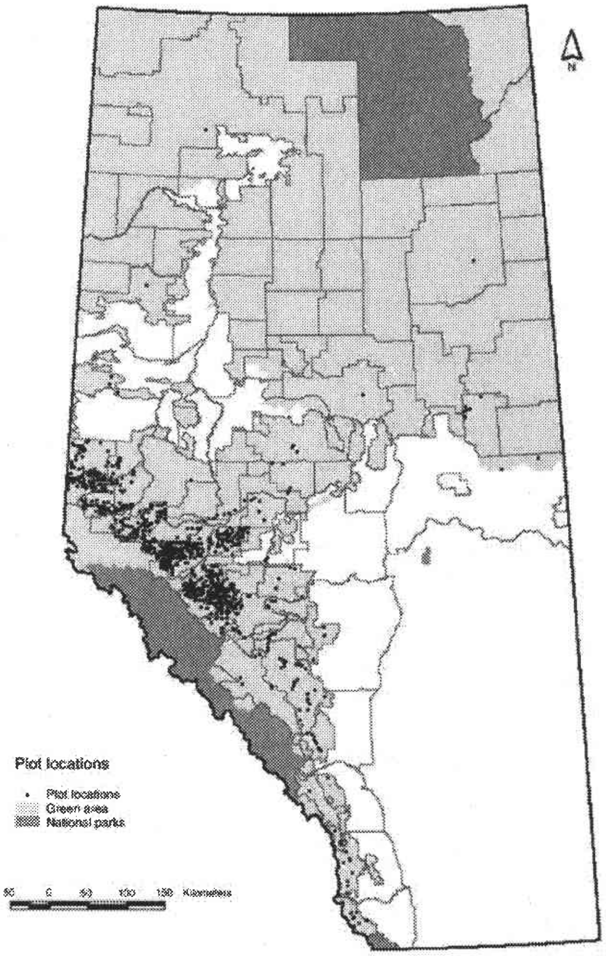

Figure 1. Location of the 1549 permanent sample plots across Alberta. Dark shaded areas are National Parks (Banff and Jasper in the southwest and Wood Buffalo in the north). Agricultural lands, including prairie grasslands in the southeast and the Peace River area in the northwest, are white. Map by the Resource Analysis Section, Forest Management Branch, Alberta Sustainable Resources Development, March 16, 2004.

ment database and then assumed the proportion of total biomass would be the same in the other two PSP networks.

Materials and methods

Biomass estimation

For each sample tree, we estimated the following components of biomass: stem wood, stem bark, branch and foliage. For lodgepole pine, the equations are of the form (Appendix 1; Manning et al. 1984):

$$Y = a + bD^2H \tag{1}$$

where Y is the biomass component of interest, diameter (D) is measured on each tree, height (H) is measured on a subsample of trees on each plot and a and b are parameters to be estimated. The remaining heights are estimated from a local height–diameter curve for each stand and each measurement period.

For stands with admixtures of other species, we used species-specific equations, of similar form to Equation 1, to estimate each of the four biomass components (Appendix 1) from individual tree height and diameter.

Root biomass is rarely measured and modeled in biomass studies (Kurz et al. 1996), although Li et al. (2003) found 49 published studies on root biomass and dynamics. We used regional means. Based on work by Kurz et al. (1996) and Li et al. (2002, 2003), we estimated root biomass as 0.222 of aboveground biomass for Canadian softwood species.

We estimated stand total tree biomass (B; kg ha^{-1}) as the sum of the respective biomass components (B_i) for each tree (live and standing dead):

$$B = \sum_i B_i \tag{2}$$

where the B_i for live trees are stem, bark, branches, foliage and roots. The components for standing dead trees excluded foliage.

Additional non-tree biomass components

Our biomass estimates omitted the understory ground-layer component (shrubs and herbaceous species). Although some of this component has been measured in wildlife habitat surveys, the data have not been coordinated with the PSP remeasurement network. Litton et al. (2003) found no significant differences in stand density associated with the shrub and herbaceous species biomass component and concluded that its effect would not change their results either quantitatively or qualitatively.

Our biomass estimates included standing dead stems. However, there are no inventory data on down and dead woody material (coarse woody debris) on most of the permanent sample plots. The only available information was from a forest fuel survey: the mean of total down and dead fuels = 28.4 Mg ha^{-1} across all lodgepole pine stands in Alberta (C. Tymstra, Forest Protection Division, Alberta Sustainable Resource Development, Edmonton, personal communication).

Soil organic matter Although the Alberta Sustainable Resource Development (2002) data contain mean depth of the litter and duff layers (407 stands), bulk density (mass/volume) was not recorded. Miyanishi and Johnson (2002) obtained a mean duff bulk density of 92 kg m^{-3} in mixed-wood boreal forest stands in central Saskatchewan. The Canadian Forest Fire Weather Index System (van Wagner 1987) assumes a 7-cm layer of duff with a bulk density of 70 kg m^{-3} (our mean depth of the organic layer is 6 cm, with a standard deviation of 4.24 cm). Hirsch and Pengelly (1999) found bulk density estimates averaging 45 kg m^{-3} for litter and 170 kg m^{-3} for duff in lodgepole pine stands in Banff National Park, Alberta. Because the Weyerhaeuser and Hinton Wood Products data do not include measurements of the depth of the organic layer, we assumed that the proportion of total biomass comprising the litter and duff layer on the Weyerhaeuser and Hinton PSPs was the same as on the 407 Alberta Sustainable Resource Development plots.

Based on the mean estimate of 92 kg m^{-3} from Miyanishi and Johnson (2002), we calculated the biomass contribution of the recorded depth of the organic layer for each PSP. This estimate (S) was added to the existing total tree biomass estimate obtained by summing all components on all trees (Equation 2). We also added the mean of total down and dead fuels (DF = 28.4 Mg ha^{-1}). The new estimate is B_2:

$$B_2 = \sum_i B_i + S + \mathrm{DF} \tag{3}$$

We then repeated the analysis with B_2.

ANUSPLIN We used the assembled data set of latitude, longitude, elevation and biomass for each PSP and measurement period for interpolation and mapping. First, we aggregated measurement periods by decade (e.g., 1980–1989). We then built a thin-plate smoothing spline surface for total biomass; we can also build biomass surfaces for important components such as foliage biomass. Monserud and Huang (2003) used this smoothing spline approach with a large network of stem analysis plots to map site index (dominant height at age 50) across Alberta.

The purpose of the Australian National University SPLINe (ANUSPLIN) software is to provide a facility for transparent analysis and interpolation of noisy multivariate data using thin-plate smoothing splines (Hutchinson 2002). The surface fitting procedure was primarily developed for fitting climate surfaces such as temperature and precipitation (e.g., the Alberta Climate Prediction Model; see Anonymous 2004). Thus, there are normally at least two independent spline variables, longitude and latitude (in decimal degrees). A third independent variable, elevation above sea level, is normally included as a third independent spline variable (in km units). Our task is akin to that of fitting a temperature surface based on data from a network of weather stations, except that instead of weather station temperature data, we have PSP location stand biomass data.

The original thin-plate (formerly Laplacian) smoothing spline surface fitting technique was described by Wahba (1979), with modifications for larger data sets detailed by Hutchinson and de Hoog (1985). Thin-plate smoothing splines can be viewed as a generalization of standard multivariate linear regression, in which the parametric model is replaced by a suitably smooth nonparametric function (Hutchinson 2002). The degree of smoothness (or complexity) of the fitted function is determined by minimizing a measure of predictive error of the fitted surface given by the generalized cross validation (GCV; Craven and Wahba 1979).

Wahba (1990) provides a comprehensive introduction to the technique of thin plate smoothing splines. A brief overview of the basic theory and applications to spatial interpolation of monthly mean climate is given in Hutchinson (1991). A comprehensive discussion of the algorithms and associated statistical analyses, and comparisons with kriging, are given in Hutchinson (1993) and Hutchinson and Gessler (1994).

Results

Age

To begin, we plotted total tree biomass versus stand age for all 1549 permanent sample plots (Figure 2). The PSP network is densest between stand ages 70–100 years and is well represented from stand initiation through to 150 years of age. In Figure 2, each of the remeasurements for a given PSP is connected by a line. Note that a few PSPs are newly established (or were abandoned) and appear as solitary values. Mean stand age is 82 years, the standard deviation is 34 years and the maximum is 291 years (Table 1). There were 11 lodgepole pine PSPs older than 200 years, a very advanced age for this species.

Stand variables

Next, we examined total tree biomass versus several common stand variables: site index (Figure 3), elevation (Figure 4) and basal area (Figure 5). The distribution of biomass versus site index (Figure 3) indicated considerable variation throughout the full range of conditions. There was one expected exception: the lack of many plots with both low productivity and high biomass. Although high productivity plots can have both low and high biomass (young versus old stands), the same does not follow for low productivity plots.

The relationship between biomass and elevation (Figure 4) appeared essentially random, indicating that a more complex mapping procedure is needed to capture geographic variation.

A strong sigmoid relationship was apparent between biomass and stand basal area (Figure 5). We used the following model:

$$B = b_0 (e^{b_1/(b_2+\mathrm{BA})})10^5 \tag{4}$$

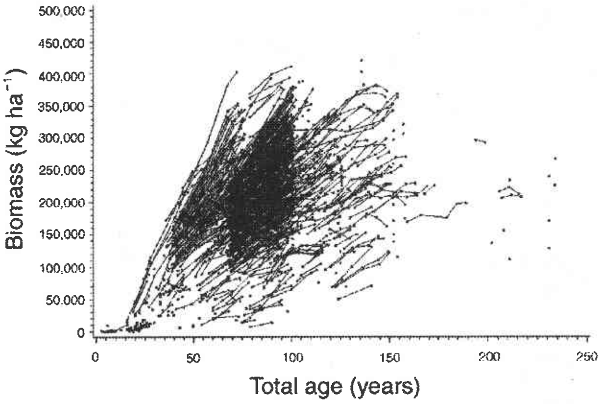

Figure 2. Total tree biomass versus total stand age for all permanent sample plots. Successive measurements are connected by a solid line. The biomass component due to duff and litter is excluded.

Table 1. Summary of lodgepole pine permanent sample plot (PSP) data. "Total" refers to the sum of all trees in the stand, exclusive of duff, litter and woody debris on the ground. Total biomass change is the difference between the periods 1990–2003 and 1980–1989. Abbreviation: SD = standard deviation.

Variable	Units	No.	Mean	Minimum	Maximum	SD
Total volume	(m^3 ha^{-1})	3585	240.57	0.002	603.81	129.41
Total basal area	(m^2 ha^{-1})	3585	31.68	0.004	64.97	13.34
Total density	(trees ha^{-1})	3585	2192.15	12.50	16913.58	1532.80
Total biomass	(Mg ha^{-1})	3585	172.51	0.07	424.76	89.61
Stem biomass	(Mg ha^{-1})	3585	105.51	0.02	265.32	55.26
Standing-dead biomass	(Mg ha^{-1})	3585	2.02	0.00	40.23	4.48
Bark biomass	(Mg ha^{-1})	3585	10.82	0.01	28.20	5.57
Branch biomass	(Mg ha^{-1})	3585	11.70	0.01	31.88	6.06
Foliage biomass	(Mg ha^{-1})	3585	11.53	0.01	36.73	5.38
Root biomass	(Mg ha^{-1})	3585	30.94	0.01	76.41	16.16[1]
Total biomass change	(Mg ha^{-1} year^{-1})	421	2.31	−12.57	9.34	2.06
Stem biomass change	(Mg ha^{-1} year^{-1})	421	1.09	−8.16	5.70	1.45
Standing dead biomass change	(Mg ha^{-1} year^{-1})	421	0.41	−2.48	7.92	1.04
Bark biomass change	(Mg ha^{-1} year^{-1})	421	0.12	−0.74	0.70	0.16
Branch biomass change	(Mg ha^{-1} year^{-1})	421	0.13	−0.80	0.82	0.18
Foliage biomass change	(Mg ha^{-1} year^{-1})	421	0.12	−1.12	1.77	0.22
Root biomass change	(Mg ha^{-1} year^{-1})	421	0.44	−2.14	1.70	0.37
Total biomass change with harvest removals	(Mg ha^{-1} year^{-1})	421	0.99	−13.89	7.98	2.06
Elevation	(m)	3585	1202.57	315.52	2081.89	236.92
Total age	(year)	3517	81.70	1.00	291.00	33.74
Top height	(m)	3208	16.94	1.43	29.88	5.30
Site index	(m)	3208	15.03	2.11	26.66	4.56

[1] The real standard deviation of root biomass is unknown, because we estimated the root biomass component as a constant 22.2% of total biomass (Li et al. 2003).

where BA is basal area in m^2 ha^{-1} ($R^2 = 0.84$). If greater predictive power is desired, then the best model ($R^2 = 0.95$) was a simple power function that used both top height (H) and basal area (BA) to predict total biomass:

$$B = b_0 H^{b_1} BA^{b_2} \tag{5}$$

where $b_0 = 645.9$, $b_1 = 0.7886$, $b_2 = 0.9566$ based on $n = 3508$ observations and H is based on the mean height of the 100 largest diameter trees ha^{-1}. This model is well suited to normal inventory data and does not require site index or age.

Volume

We then examined relationships between total tree biomass and stand stem volume. A close relationship was found ($R^2 = 0.992$ with $n = 3585$; Figure 6). Volume and biomass were calculated independently in Figure 6: volume was estimated based on a slightly modified version of Kozak's (1988) vari-

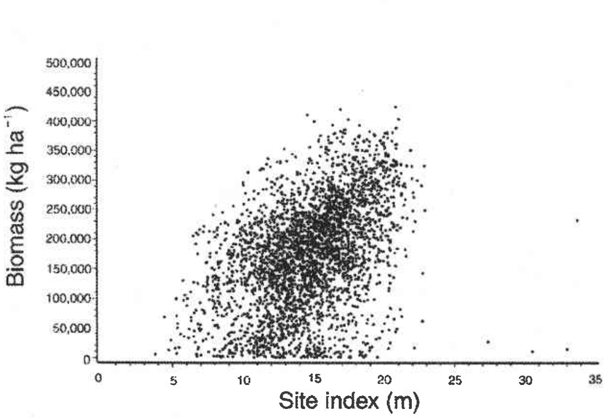

Figure 3. Total tree biomass versus site index (top height in m at breast height age 50).

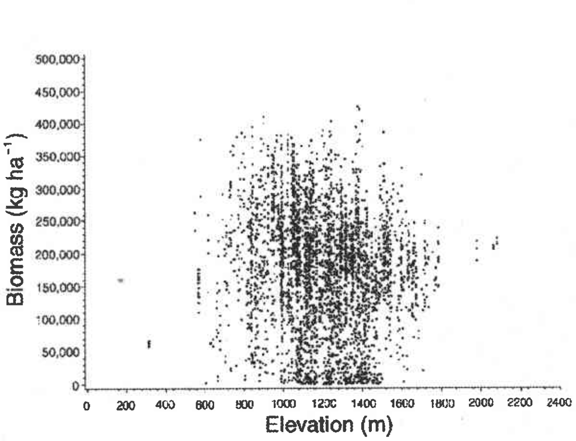

Figure 4. Total tree biomass versus elevation.

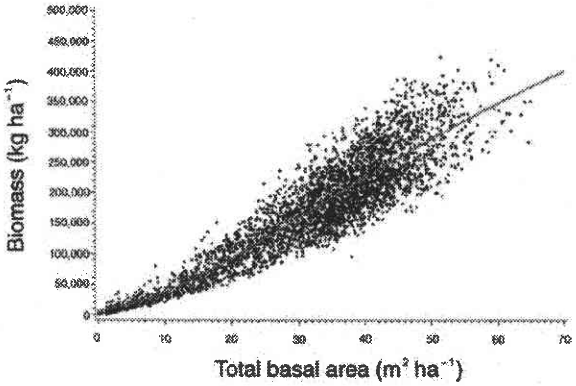

Figure 5. Total tree biomass versus stand basal area.

able-exponent taper equation (see Huang et al. 2001, p 24). The volume equations used for the Hinton Wood Products and Weyerhaeuser PSPs are of a similar form but with coefficients specific to the particular data set. The resulting strong relationship from three different sets of volume predictions provides firm grounds for predicting total tree biomass from stem volumes in stand simulation models, especially in even-aged stands. This relationship has a slight curvature, and is well described by the exponential equation ($R^2 = 0.99$, $n = 3585$):

$$B = b_0(1 - e^{-b_1 V})10^5 \qquad (6)$$

where $b_o = 29.36953$, $b_1 = 0.000253$, B is biomass (kg ha^{-1}) and V is stem volume (m^3 ha^{-1}).

Biomass components

Total stand biomass averaged 172.5 Mg ha^{-1}, with a maximum of 425 Mg ha^{-1} ($n = 3585$; Table 1). We found strong relationships between the individual biomass components and total tree biomass for the stands. As expected, stem biomass dominated the other components of biomass (Table 1). Maximum stem biomass (near 300 Mg ha^{-1}) was a full order of magnitude greater than the maxima of each of the other tree biomass components (near 30 Mg ha^{-1}). The greatest variability was found in the foliage component, although its relationship with total biomass was strong ($R^2 = 0.91$). A simple 2-parameter hyperbolic regression predicting the other three components from total biomass explained 99% of the variation in each case. Because the root biomass component is assumed to be a constant 22.2% of the total biomass (Kurz et al. 1996, Li et al. 2002, 2003), its variation was not observed and cannot be analyzed.

Soil organic matter

When we repeated the analysis with B_2, which contains the additional estimated biomass from the soil organic layer (Equation 3), considerable variation was introduced. No relationship was apparent when the distribution of duff and litter depth was plotted versus stand basal area (Figure 7a). One characteristic of the data, however, is clear. Duff and litter depth was only measured to the nearest cm, and only measured once. When this biomass component was added to aboveground biomass (Figure 7b), additional variation was introduced. An artifact of the 1-cm measurement precision was also introduced—seemingly parallel relationships appear in Figure 7b. This artifact would disappear if the duff and litter depth were measured

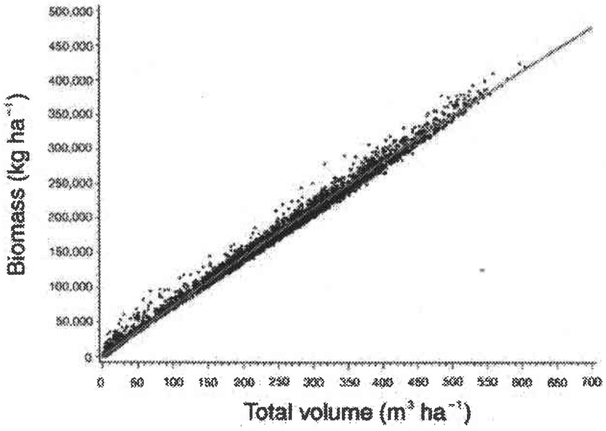

Figure 6. Total tree biomass (excluding duff and litter) versus total volume for all plots combined.

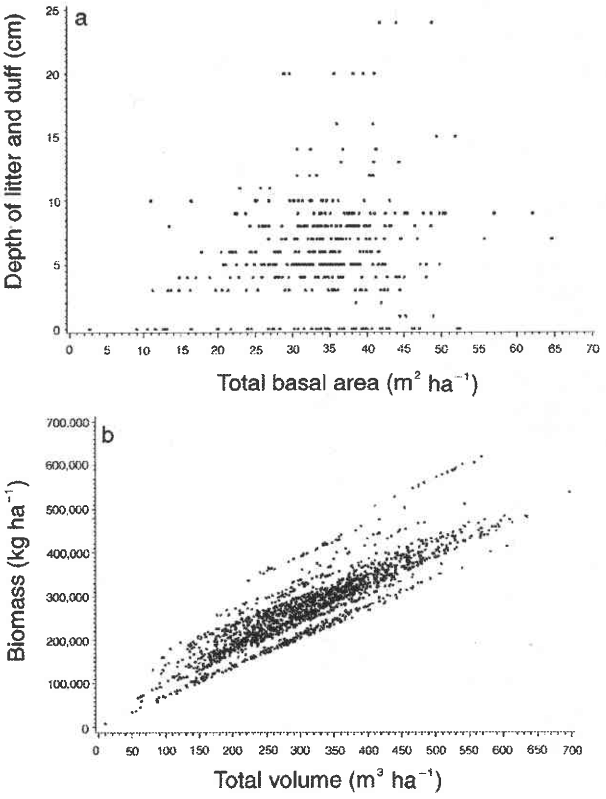

Figure 7. (a) Duff and litter depth versus stand basal area for the Alberta Forest Service data. (b) Total tree biomass plus duff and litter versus total volume for Alberta Forest Service data.

with greater precision and accuracy (i.e., by averaging many more observations per stand) and if it were measured more than once per PSP. We were unable to find any relationship between the different intercepts in Figure 7b and various stand variables (e.g., volume, basal area, stand age, elevation) (e.g., Figure 7a). The addition of a constant 28.4 Mg ha^{-1} for downed and dead fuels (DF) added no variation to the analysis, and was not examined further.

Harvest adjustments

Because harvesting is excluded in the permanent sample plot network, a harvest adjustment is needed to calculate the change in ecosystem biomass. We first looked for bias resulting from changing harvest volumes over time using the harvest and regeneration area data from the Alberta Reforestation Information System (2004). Harvesting of lodgepole pine in Alberta has increased steadily over the past 30 years. For example, lodgepole pine harvest volume in the decade 1980–1989 averaged 3.87×10^6 m^3 year^{-1} and nearly doubled to 7.70×10^6 m^3 year^{-1} in the period 1990–2002. However, the area harvested has also increased steadily over time. The net effect is that harvest removal rate per hectare has increased by 19%, a modest change (Figure 8). The rate of harvest volume in the decade 1980–1989 averaged 242 m^3 ha^{-1} year^{-1} and averaged 289 m^3 ha^{-1} year^{-1} in the period 1990–2002. We then converted the average volume harvest for each decade to mass (Mg ha^{-1} year^{-1}) with Equation 6: 7.40 Mg ha^{-1} year^{-1} (years 1980–1989) and 8.72 Mg ha^{-1} year^{-1} (years 1990–2002). Thus, the rate of harvest removals increased 1.32 Mg ha^{-1} year^{-1}.

An important limitation of this harvest information is that it is a province-wide average, with no spatial stand location data; however, we have some additional but rather diffuse spatial information. Almost all of the harvesting was restricted to three of the 20 subregions of Alberta (Alberta Environmental Protection 1994): the Upper Foothills, the Lower Foothills and the Subalpine. The Central Mixed-wood component of the Boreal Forest subregion contains minor components of lodgepole pine and only 1% of the PSPs are located there.

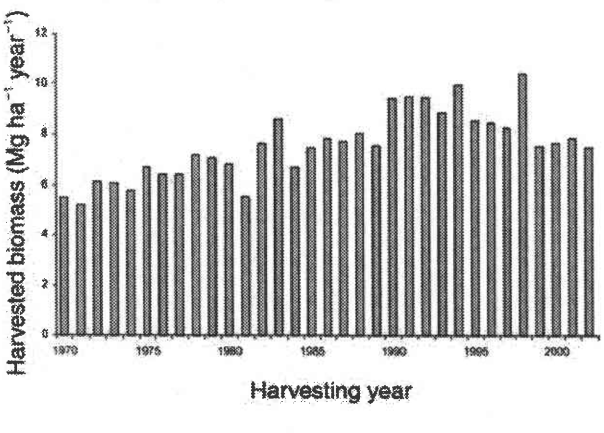

Figure 8. Harvested biomass of lodgepole pine removed in Alberta versus year (1970–2002).

ANUSPLIN mapping

Using our network of 1549 PSPs, we fit thin-plate smoothing spline surfaces (Hutchinson 2002, Monserud and Huang 2003) to decadal total tree biomass across Alberta. Before mapping, we reduced total biomass for decade-specific average harvesting removals on each biomass pixel (picture element) in the three subregions where harvesting is concentrated (Lower and Upper Foothills and Subalpine). We then plotted these decadal biomass surfaces across the distribution map for lodgepole pine (cf. Figure 9 (1980–1989) and Figure 10 (1990–2003)).

Biomass change

The change in total tree biomass between 1990–2003 and 1980–1989 is available for 421 PSPs. This biomass-change surface was then interpolated using ANUSPLIN. Before adjusting for harvest removals, the main range of lodgepole pine showed a significant increase in total tree biomass of 2.31 Mg ha^{-1} year^{-1} (Table 1; $n = 421$, $P < 0.001$). Estimates ranged

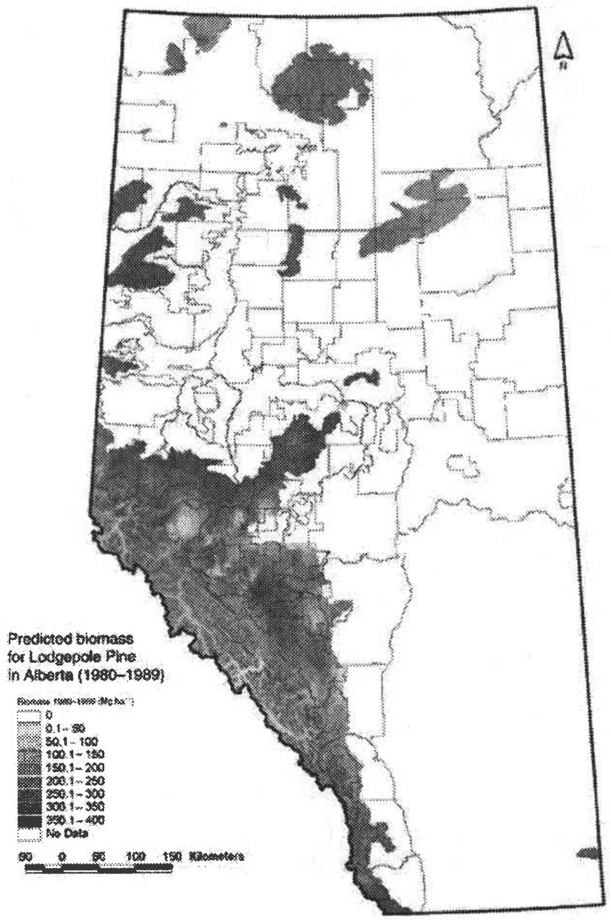

Figure 9. Predicted total tree biomass (Mg ha^{-1}) for the period 1980–1989 across the distribution of lodgepole pine in Alberta. Harvest removals have been subtracted. Map by the Resource Analysis Section, Forest Management Branch, Alberta Sustainable Resources Development, December 10, 2004.

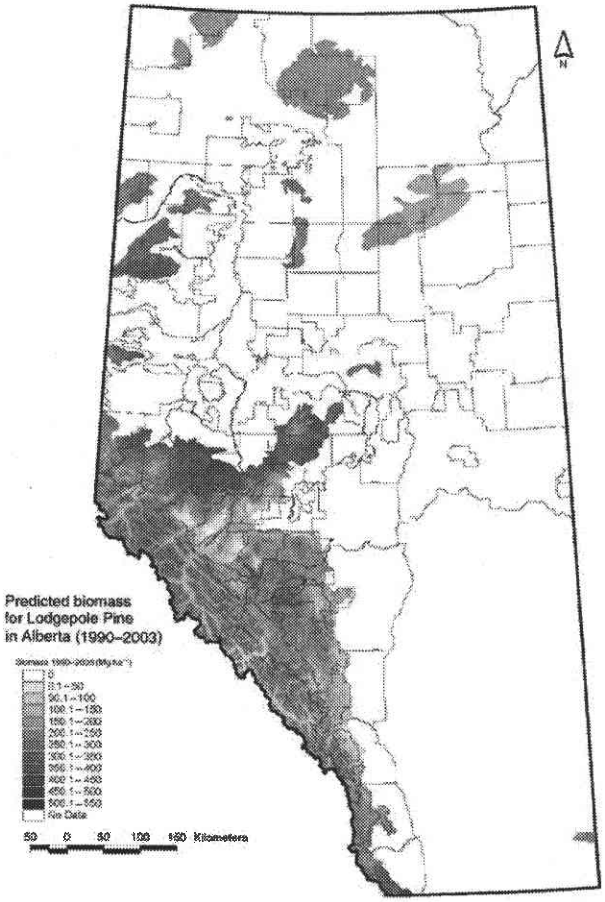

Figure 10. Predicted total tree biomass (Mg ha^{-1}) for the period 1990–2003 across the distribution of lodgepole pine in Alberta. Harvest removals have been subtracted. Map by the Resource Analysis Section, Forest Management Branch, Alberta Sustainable Resources Development, December 10, 2004.

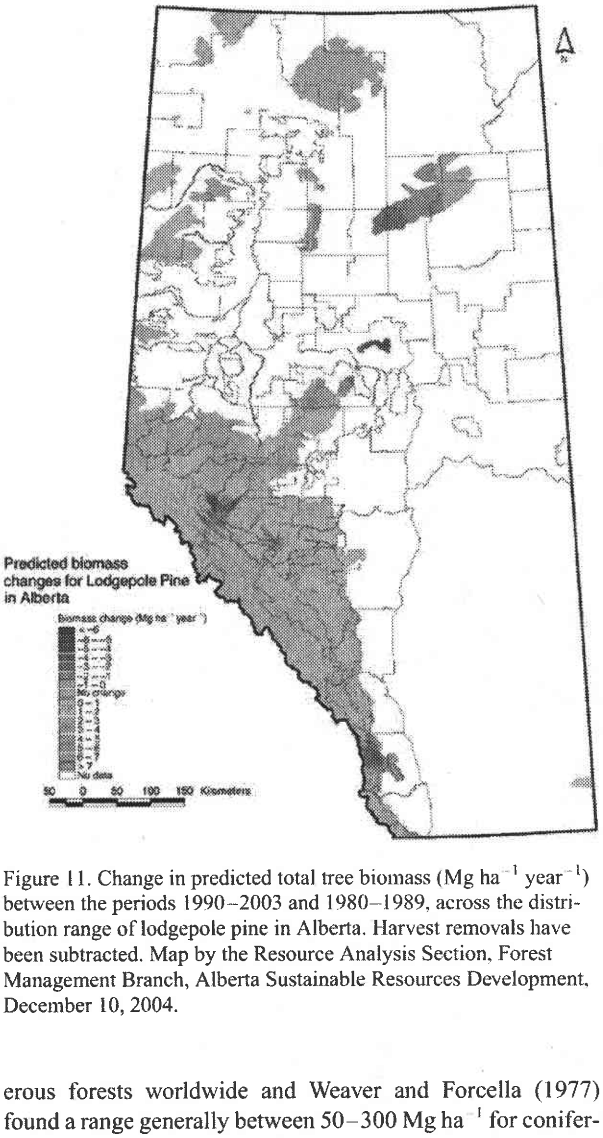

Figure 11. Change in predicted total tree biomass (Mg ha^{-1} year^{-1}) between the periods 1990–2003 and 1980–1989, across the distribution range of lodgepole pine in Alberta. Harvest removals have been subtracted. Map by the Resource Analysis Section, Forest Management Branch, Alberta Sustainable Resources Development, December 10, 2004.

from –12.6 to 9.3 Mg ha^{-1} year^{-1}. After adjusting for harvest removals, the change in total tree biomass between these two most recent decades (1990s minus 1980s) decreased 0.99 Mg ha^{-1} year^{-1}, but was still significant (Figure 11).

Discussion

Stand biomass

Johnstone (1971) found total stand biomass varied from 111 to 192 Mg ha^{-1} in 100-year-old lodgepole stands. Moir (1972) found that stand biomass ranged from 66 to 355 kg ha^{-1} in 70-year-old lodgepole in Colorado. In wetter SE British Columbia, Comeau and Kimmins (1989) found total biomass ranged from 156 to 392 Mg ha^{-1} in 70–78-year-old lodgepole pine stands. Pearson et al. (1984) found total biomass (above- and belowground) was 123–185 Mg ha^{-1} in rather dry Wyoming lodgepole pine stands aged 75–240 years old. Moving to greater generality, Art and Marks (1978) found a range of 60–280 Mg ha^{-1} for pines in a worldwide survey, Rodin and Bazilevich (1967) found a range of 50–350 Mg ha^{-1} for coniferous forests worldwide and Weaver and Forcella (1977) found a range generally between 50–300 Mg ha^{-1} for coniferous forests in the northern Rocky Mountains, although one habitat type had a maximum of 350 Mg ha^{-1}.

The three PSP networks for Alberta cover a full range in ages, site types and densities. As a result, our distribution of predicted total biomass ranges from near zero (newly regenerated stands) to 425 Mg ha^{-1}, although most observations are in the range of 50–350 Mg ha^{-1} (see Figure 2 and Table 1). Mean biomass is 172 Mg ha^{-1} and mean stand age is 82 years. Mean volume is 240 m^3 ha^{-1}, with a maximum of 604 m^3 ha^{-1}. Mean basal area is 32 m^2 ha^{-1}, with a maximum of 65 m^2 ha^{-1}. Tree density averaged 2192 trees ha^{-1}, with a maximum of 16,914 trees ha^{-1} (Table 1). Total tree biomass is dominated by stem biomass (mean = 106 Mg ha^{-1}), which is an order of magnitude greater than the mean estimates for the bark (10.8 Mg ha^{-1}), branch (11.7 Mg ha^{-1}) and foliage (11.5 Mg ha^{-1}) components.

Foliage biomass

Pearson et al. (1984) report foliage biomass of 6.9–12.3 Mg ha^{-1} (ages 70–200 years) and 6.3 Mg ha^{-1} (200 years) for a study by Reid et al. in 1976. Johnstone (1971) reports foliage biomass of 7.4–12.6 Mg ha^{-1} (100 years) and Moir (1972) reports 5.0–17.4 Mg ha^{-1} (70 years). Our foliage biomass estimates average 11.5 Mg ha^{-1} with a standard deviation of 5.4 Mg ha^{-1} (Table 1). The upper bound is essentially 25 Mg ha^{-1}, although one observation reached a maximum of 36.7 Mg ha^{-1}.

Branch biomass

Pearson et al. (1984) report branch biomass of 8–15 Mg ha^{-1} (ages 70–200 years) and 11 Mg ha^{-1} (200 years) for a study by Reid et al. in 1976. Our branch biomass estimates average 11.7 Mg ha^{-1} with a standard deviation of 6.0 Mg ha^{-1} (Table 1). The upper bound is 31.9 Mg ha^{-1}.

Root biomass

Working in young 13-year-old lodgepole pine stands following the Yellowstone National Park fire, Litton et al. (2003) found strong allometric relationships between basal diameter and belowground root biomass. They also observed that total biomass increases regularly with stand age (and stand density) until site occupancy is reached; their young stands had a maximum total biomass of 13.7 Mg ha^{-1}. Pearson et al. (1984) found fine root biomass to be 6% of total stand biomass. Johnstone (1971) found root biomass of 100-year-old lodgepole pine stands in Alberta ranged from 18 to 38 Mg ha^{-1}; fine roots were not measured (Pearson et al. 1984). Using the constant multiplier of 0.222 of aboveground tree biomass reported by Li et al. (2003), we estimated a mean root biomass of 30.9 Mg ha^{-1}. Our estimated maximum is 76.4 Mg ha^{-1}.

Biomass change

We compared total tree biomass for two decades, the 1990s minus the 1980s (Figure 11). After adjusting for harvest removals, the mean change was positive (0.99 Mg ha^{-1} year^{-1}) and significantly different from zero. The heart of the lodgepole pine distribution (primarily the Foothills subregions) showed an increase in biomass (Figure 11). The Lower Foothills subregion showed several areas with concentrations of biomass increasing in the 4–7 Mg ha^{-1} year^{-1} range.

Isolated pockets of lodgepole pine in the boreal northern subregion indicated a decline in biomass (Figure 11). These northern uplands are in the vicinity of Wood Buffalo National Park. One prominent area of decline in the main body of the lodgepole pine distribution in SW Alberta is the Athabasca River Valley draining Jasper National Park. Another is the Porcupine Hills in southern Alberta, near Crowsnest Pass. These are dry montane areas, subject to drying winds and seasonal drought (G. Klappstein, Forest Management Branch, Alberta Sustainable Resource Development, Edmonton, personal communication). Lower precipitation amounts during the past decade would make these areas prone to soil water deficits and bark beetle outbreaks (L. Barnhardt, Forest Management Branch, Alberta Sustainable Resource Development, Edmonton, personal communication). Mountain pine beetle (*Dendroctonus ponderosae*) activity has been observed in these general areas of the Canadian Rockies in recent years (see www3.gov.ab.ca/srd/forests/health/mpb_cond.html). Such areas may have suffered a decline in productivity as a result of increased warming during the past decade, thereby pushing the water balance into a larger deficit relative to the historic average (G. Klappstein, personal communication).

There are a few other areas of negative biomass change that are not Montane (Figure 11), including one region in the Swan Hills and Virginia Hills (central Alberta) where declines reflect, in part, recent fire history and the relatively advanced age of the stands (Figure 2). Other small pockets of negative biomass change were found in the Foothills subregions.

Our biomass change map (Figure 11) was based on interpolating the 421 PSP observations made in both decades. A second way to estimate biomass change is to subtract Figure 9 from Figure 10, pixel by pixel. When we did that, we found that: first, the same general spatial patterns emerged as were apparent on Figure 11; and second, both positive and negative changes in biomass were more extreme than in Figure 11. Direct map subtraction overly accentuates differences that are not close to a PSP observation in one of the two maps being subtracted. The interpolated map of observed differences (Figure 11) is therefore more reliable.

The only stand variable to show a significant relationship with change in biomass was stand age. Total biomass change declined as stand age increased (Figure 12), although this relationship was weak ($R^2 = 0.11$), with a residual mean squared error of 3.85 Mg ha^{-1} year^{-1}. The slope of this simple linear regression is −0.02089 and the intercept is 2.7629. This decline is not unexpected because even-aged lodgepole pine stands become decadent over time.

We also determined the change in biomass by components (stem wood, stem bark, branch and foliage) (Figures 13a–d and Table 1). No patterns were apparent. The greatest variation was in stem biomass, which was by far the largest component.

Plotting change in basal area versus stand age (Figure 14) revealed that no major stand altering events occurred in this set of PSPs. Only one observation indicated a reduction in basal area of more than 1 m^2 ha^{-1} year^{-1}. The prominent feature of

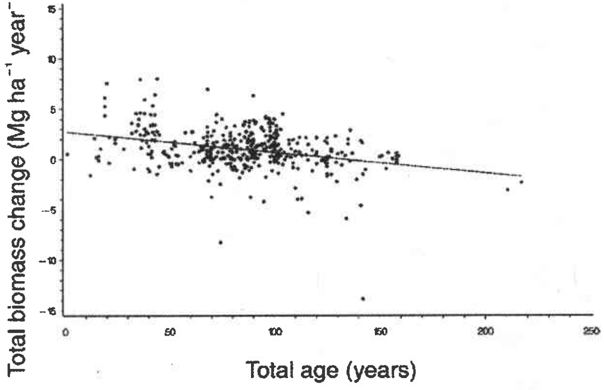

Figure 12. Total biomass change versus stand age between the periods 1990–2003 and 1980–1989.

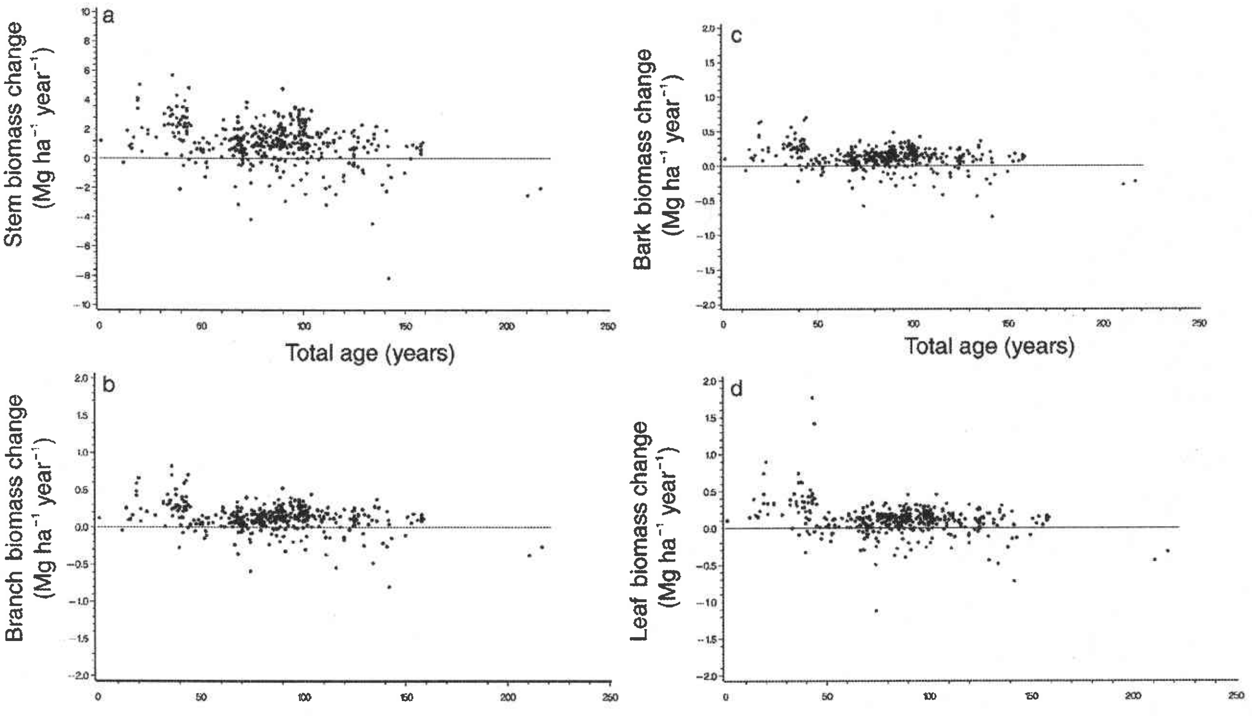

Figure 13. (a–d) Biomass change by component versus stand age between the periods 1990–2003 and 1980–1989. Components are (a) stem, (b) branch, (c) bark and (d) leaf.

Figure 14 is the sharp accumulation of basal area in stands aged 25–40 years. A decline due to advanced age was not apparent. The remaining stand variables (site index, top height and elevation) likewise showed no significant relationship with biomass change.

Our final analysis was to predict total biomass change (ΔB; Mg ha^{-1} year^{-1}) as a function of stem volume change (ΔV; m^3 ha^{-1} year^{-1}), again between the periods 1990–2003 and 1980–1989 (Figure 15):

$$\Delta B = b_0(1 - e^{-b_1 \Delta V}) \quad (7)$$

with $b_0 = 70.2253$ and $b_1 = 0.010061$. This exponential relationship is strong ($R^2 = 0.95$, $n = 421$) and is slightly curvilinear in the range of the data (Figure 15). This result supports the assumption that a model that accurately predicts the change in stand stem volume also predicts change in total biomass, at least for the major tree components.

It is tempting to view our estimate of biomass change (after

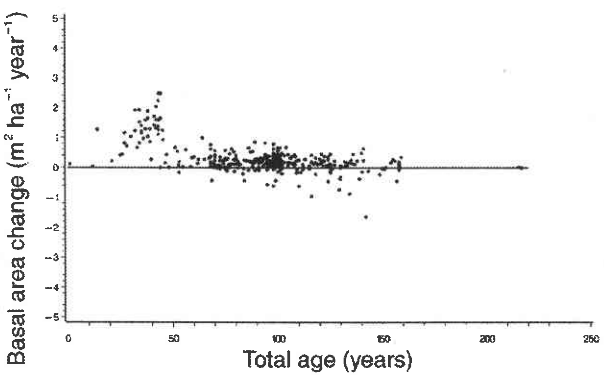

Figure 14. Basal area change versus stand age between the periods 1990–2003 and 1980–1989.

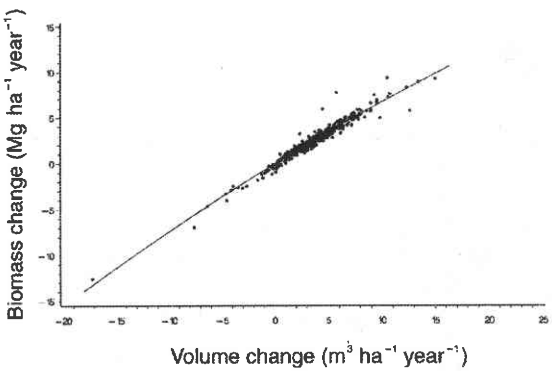

Figure 15. Total biomass change as a function of stem volume change between the periods 1990–2003 and 1980–1989.

converting to carbon) as an initial estimate of net ecosystem production, which is net primary production minus heterotrophic losses in C as a result of respiration (Kirschbaum et al. 2001). However, we lack good estimates of ground layer components (ground vegetation and downed woody debris). We also lack information on decomposition rates and rates of change for litter, dead wood and soil organic matter.

Acknowledgments

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Appendix 1. Species-specific component biomass equations. Abbreviations: B = biomass (kg); D = diameter at breast height (cm); and H = total height (m). The D units are in m for subalpine fir.

Species	Author	Component	Equation form	Coefficients					
				a	*b*	*c*	*d*	*e*	*f*
Lodgepole pine *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.	Manning et al. 1984	Branches	$B = a + bD^2H$	0.2614	0.00171				
		Foliage	$B = a + bD^2H$	1.1011	0.00142				
		Stem bark	$B = a + bD^2H$	0.3064	0.00153				
		Stem wood	$B = a + bD^2H$	0.6301	0.01568				
Balsam fir *Abies balsamea* (L.) Mill.	Ker 1984	Branches	$B = aD^b$	0.0909	1.8405				
		Foliage	$B = aD^b$	0.09982	1.6421				
		Stem bark	$B = aD^bH^c - dD^eH^f$	0.0286	1.9586	0.7794	0.0289	1.9157	0.7625
		Stem wood	$B = aD^bH^c$	0.0289	1.9157	0.7625			
Subalpine fir *Abies lasiocarpa* (Hook.) Nutt.	Standish et al. 1985	Branches	$B = a + bD^2H$	3.6	44.2				
		Foliage	$B = a + bD^2H$	5.7	17.5				
		Stem bark	$B = a + bD^2H$	1	17.2				
		Stem wood	$B = a + bD^2H$	4	107.4				
Paper birch *Betula papyrifera* Marsh.	Alemdag and Horton 1981	Branches	$B = aD^2H$	0.0025581					
		Foliage	$B = aD^2H$	0.0006851					
		Stem bark	$B = aD^2H$	0.0027467					
		Stem wood	$B = aD^2H$	0.016001					
Tamarack *Larix laricina* (Du Roi) K. Koch	Lavigne 1982	Branches	If ($D^2H < 707$), $B = a + bD^2H$, Else $B = c + 707d + e(D^2H - 707)$	0.02902	0.006043	0.02902	0.006043	0.0027842	
		Foliage	If ($D^2H < 707$), $B = a + bD^2H$, Else $B = c + 707d + e(D^2H - 707)$	0.33523	0.004988	0.33523	0.004988	0.0005208	
		Stem bark	If ($D^2H < 707$), $B = a + bD^2H$, Else $B = c + 707d + e(D^2H - 707)$	0.1156	0.001945	0.1156	0.001945	0.002181	
		Stem wood	If ($D^2H < 707$), $B = a + bD^2H$, Else $B = c + 707d + e(D^2H - 707)$	0.10506	0.019636	0.10506	0.019636	0.014877	
White spruce *Picea glauca* (Moench) Voss	Manning et al. 1984	Branches	$B = a + bD^2H$	0.2519	0.001191				
		Foliage	$B = a + bD^2H$	0.9265	0.00241				
		Stem bark	$B = a + bD^2H$	0.1506	0.00193				
		Stem wood	$B = a + bD^2H$	0.277	0.0124				
Black spruce *Picea mariana* (Mill.) BSP	Alemdag 1983	Branches	$B = aD^2H$	0.001288					
		Foliage	$B = aD^2H$	0.003031					
		Stem bark	$B = aD^2H$	0.001726					
		Stem wood	$B = aD^2H$	0.016625					
Jack pine *Pinus banksiana* Lamb.	Alban and Laidly 1982	Branches	$B = aD^bH^c$	0.05842	2.6803	−0.9298			
		Foliage	$B = aD^bH^c$	0.03135	2.4574	−0.7382			
		Stem bark	$B = aD^bH^c$	0.01723	1.8511	0.3206			
		Stem wood	$B = aD^bH^c$	0.01854	1.9774	0.9328			
Balsam poplar *Populus balsamifera* L.	Alemdag 1984	Branches	$B = aD^2H$	0.00315					
		Foliage	$B = aD^2H$	0.000303					
		Stem bark	$B = aD^2H$	0.001888					
		Stem wood	$B = aD^2H$	0.013164					
Aspen *Populus tremuloides* Michx.	Alemdag 1984	Branches	$B = aD^2H$	0.002498					
		Foliage	$B = aD^2H$	0.00051					
		Stem bark	$B = aD^2H$	0.003198					
		Stem wood	$B = aD^2H$	0.014579					