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Estimation of snag carbon transfer rates by ecozone and lead species for forests in Canada

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Abstract. Standing dead trees (snags) and downed woody debris contribute substantially to the carbon (C) budget of Canada's forest. Accurate parameterization of the C transfer rates (CTRs) from snags to downed woody debris is important for forest C dynamics models such as the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3), but CTRs are rarely measured or reported in the literature. Therefore, forest C models generally use snag fall rates (FRs) available in the literature, as a proxy for CTRs. However, FRs are based on stem counts while CTRs refer to mass transfers. Stem mass and stem number are not linearly related, with small diameter trees representing disproportionately lower C mass transfers. Therefore this proxy, while convenient, may bias C transfer from standing dead to downed woody material. Here, we combined tree data from 10 802 sample plots and previously published species-specific individual-tree relationships between tree diameter (diameter at breast height, dbh) and fall rate to derive stand-level estimates of CTRs for the CBM-CFS3. We estimated CTRs and FRs and used the FR values to validate this approach by comparing them with standardized FR values compiled from the literature. FRs generally differed from CTRs. The overall CTR (4.78% ± 0.02% per year, mean ± SE) was significantly smaller than the overall FR (5.40% ± 0.02% per year; mean ± SE). Both the difference between FR and CTR (FR – CTR) and the CTR itself varied by ecozone, with ecozone means for CTR ranging from 3.94% per year to 10.02% per year. This variation was explained, in part, by heterogeneity in species composition, size (dbh distribution), structure, and age of the stands. The overall mean CTR estimated for the Snag_Stemwood (4.78% per year) and the Snag_Branches (11.95% per year) pools of the CBM-CFS3 were approximately 50% and 20% higher than the current default rates used in the CBM-CFS3 of 3.2% and 10.0%, respectively. Our results demonstrate that using CTRs to estimate the annual C transfer from standing dead trees to downed woody biomass will yield more accurate estimates of C fluxes than using a FR proxy, and this accuracy could be further improved by accounting for differences in ecozone, stand component (hardwood or softwood), or lead species.

Key words: Canadian forests; carbon modeling; carbon transfer rate; ecozones; forest carbon; snag; snag fall rate; standing dead wood; woody debris.

Introduction

Historically, studies of the dynamics of dead wood have focused on the role of woody debris in ecological functions such as provision of wildlife habitat and biodiversity, nutrient cycling, and regeneration. In their original synthesis of data on the ecology of coarse woody debris in temperate ecosystems, Harmon et al. (1986) presented principles that remain relevant today (Harmon et al. 2004). Increasing interest in the role of forests in the global carbon (C) cycle has made understanding the role of dead wood in forest C dynamics a more recent research focus (Sharik et al. 2010). However, data needs and types of analyses differ for these various topics of dead wood research. Understanding the role of woody debris in habitat management and conservation of biodiversity is often a research priority when developing site-specific management goals for maintaining target levels of woody debris, usually in the form of large standing dead trees (snags) and coarse woody debris. In contrast, understanding the contribution of dead wood to forest C dynamics requires accurate estimates of the size of the C pools in standing and downed dead wood, including all size fractions of stemwood and branches, and the fluxes from these pools to the atmosphere and soil at regional or national scales.

Snags can form a large component of forest C stocks (Smith et al. 2003, Woodall et al. 2008), typically contributing from 5% to 35% of aboveground forest mass in Canada and the contiguous United States (Aakala et al. 2008, Vanderwel et al. 2008). In Canada, large-scale fire and insect disturbances can result in large numbers of snags (Stocks et al. 2002, Kurz et al. 2008,

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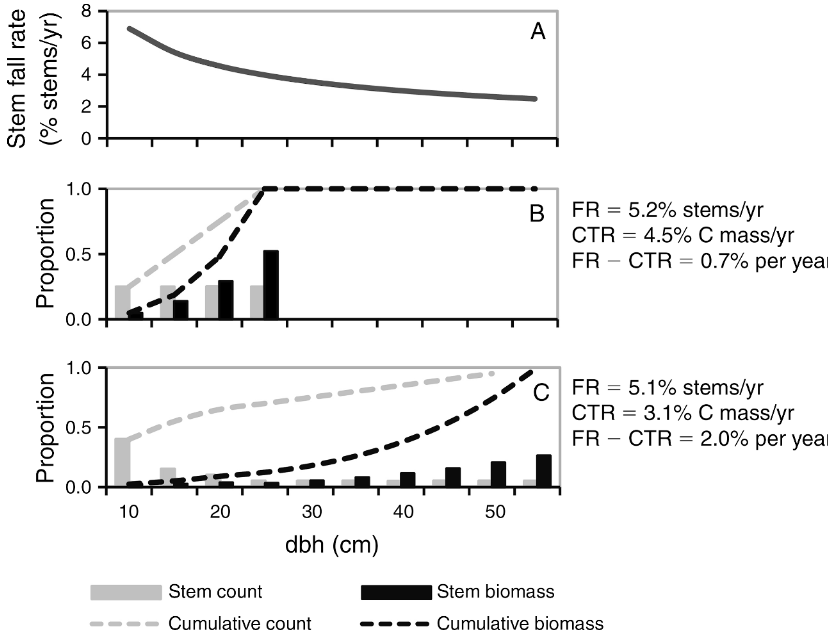

FIG. 1. (A) The effect of diameter (dbh) on snag stem fall rates and the calculated stand-level fall rates (FR) and C transfer rate (CTR) for two hypothetical stands with (B) narrow or (C) wide dbh distributions. The *y*-axis shows the proportion of the total number of stems or of the total biomass, in each diameter class.

Axelson et al. 2009, Dymond et al. 2010*a*, Metsaranta et al. 2010), with important implications for C dynamics (Kurz et al. 2008). After disturbance, aboveground C stocks may consist largely of snags (Hagemann et al. 2010, Lavoie et al. 2010, Moroni et al. 2010), which will remain on site if management is of low intensity, with little salvage harvest, as is common in Canadian forests (Dymond et al. 2010*b*). In addition, the decay and combustion dynamics of snags differ from those of standing live trees or downed dead wood. Relative to downed woody debris, snags have slower decay rates (Harmon et al. 1986, Boulanger and Sirois 2006) and the proportion combusted during fire is lower (de Groot et al. 2002, Hessburg et al. 2010).

Explicitly accounting for dead wood dynamics can enhance the predictive accuracy of forest C models (Kurz et al. 2009). However, the dynamics of these pools must also be adequately parameterized. Of particular importance is the rate of C transfer from snag to downed woody debris, which affects the balance of C in standing and downed dead wood and thus can influence estimates of present and future forest C stocks and fluxes. In C accounting models that include snag pools (Nalder and Wein 2006, Kurz et al. 2009), parameterization of C transfer rates from snag to downed woody debris is often based on literature rates for snag fall, even though most studies report rates based on number of stems and not on a biomass or C basis. Fall rates based on stem counts may not be accurate proxies for stand-level C transfer rates because large (high C) trees fall at a slower rate than small trees (Harmon et al. 1986) and therefore stand size distributions can affect the discrepancy between fall rate (percentage stems per year) and C transfer rate (percentage C mass per year). Stands with a narrow diameter at breast height (dbh) distribution would be expected to show a closer relationship between fall and C transfer rates than those with broader dbh range (Fig. 1). Snag fall rate is influenced by many site-scale factors (Keen 1929) including: tree species and size (Harmon et al. 1986); the cause of tree death (Raphael and Morrison 1987); soil type and soil moisture conditions (Lewis 2009); microclimate, elevation, and topography of the site (Everett et al. 1999); and stand density and management regime (Harmon et al. 1986, Garber et al. 2005, Russell et al. 2006). It is impossible to account for all of these factors at a national scale, because the understanding of their interactions is incomplete and national data sets for all of the explanatory variables are lacking. However, data on tree species and size, factors that have consistent effects across studies (Harmon et al. 1986), are collected nationally at forest inventory and research sample plots. These data are potentially useful for developing parameters that reflect some of the large-scale variability in snag fall and C transfer rates.

The consistently observed inverse relationship between snag stem size and snag fall rates (Harmon et al. 1986) has been incorporated into regional models of snag dynamics (Storaunet 2004, Garber et al. 2005, Huggard and Kremsater 2007, Parish et al. 2010). Here, we combine one such inverse relationship (Huggard and Kremsater 2007) with a large data set of inventory sample plots (n = 10 802) as a novel approach to estimating ecozone and species-specific snag stemwood

TABLE 1. Distribution of sample plots of forest stands representative of species composition and diameter distribution across Canadian ecotones.

Ecozone	Default age (yr)	Stand age group (% of plots)				Stand type (% of plots)		
		Young	Default	Old	NA	SW	HW	MW
Pacific Maritime	300	97	1	1	0	96	2	2
Boreal Cordillera	175	100	0	0	0	96	4	0
Montane Cordillera	150	79	16	4	0	91	3	6
Taiga Plains	125	70	23	6	1	48	39	13
Boreal Plains	125	62	25	6	7	65	23	13
Prairies	75	0	50	50	0	50	25	25
Taiga Shield West	100	17	50	33	0	100	0	0
Boreal Shield West	75	16	39	29	16	66	15	19
Boreal Shield East	125	79	14	2	5	43	36	20
Hudson Plains	75	0	20	0	80	100	0	0
Mixedwood Plains	125	60	5	0	36	19	67	14
Atlantic Maritime	125	96	4	0	0	38	35	27
All ecozones	% of plots	73	16	6	4	76	14	10
	No. of plots	7902	1750	697	453	8198	1491	1113

Notes: Ecozones are as in Kull et al. (2011). Default age represents the default return interval for stand-replacing disturbance in the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3). For categorization of plots by age: default, plots within 20% of default age; young, plots younger than default; old, plots older than default; NA, not available (i.e., age unknown). For categorization of plots by stand type: SW, softwood; HW, hardwood; MW, mixedwood. For provinces and territories: BC, British Columbia; AB, Alberta; SK, Saskatchewan; MB, Manitoba; ON, Ontario; QC, Quebec; NB, New Brunswick; NS, Nova Scotia; PE, Prince Edward Island; NT, Northwest Territories.

fall and C transfer rates using individual tree data from the sample plots. The calculation method was validated by comparing calculated snag stemwood fall rates to fall rates compiled from literature data. We developed recommendations for specific snag C transfer rates by ecozone (ESWG 1996), lead species, and stand component (hardwood, softwood, all) for use in the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3; Kurz et al. 2009).

METHODS

Model framework for analysis

The CBM-CFS3 is the core model of Canada's National Forest Carbon Monitoring, Accounting and Reporting System (NFCMARS; Kurz and Apps 2006, Kurz et al. 2009). The model calculates stand-level C pools and fluxes at annual time steps and integrates the estimates of C stocks and fluxes over the defined region of analysis. The model represents 10 biomass and 11 dead organic matter and soil C pools, including four snag pools; Snag_Stemwood and Snag_Branches for both the HW (hardwood or angiosperm) and SW (softwood or gymnosperm) components of a stand. The Snag_Stemwood pools consist of dead stemwood of merchantable-sized trees including bark, but not tops or stumps. The Snag_Branches pools include not only attached dead branches, but also the top and stump (non-merchantable parts) of dead merchantable trees, as well as all wood and bark of dead small (non-merchantable) trees and saplings. Woody material in the snag pools varies in size from one jurisdiction to another because merchantability limits vary across Canada (Boudewyn et al. 2007). Biomass is transferred to snag pools through annual turnover, stand mortality (indicated by a declining yield curve), and through disturbances that kill trees. Decomposition of the Snag_Stemwood, Snag_Branches, and downed woody pools is simulated by decay functions with pool-specific decay rates, which are further affected by mean annual temperature (Kurz et al. 2009).

Snag C is transferred to downed woody debris pools in two ways: as a pulse when disturbance events cause snag fall and at a fixed annual rate (expressed as percentage of snag C; Kurz et al. 2009). The fixed annual C transfer rate (CTR, the subject of this paper) presumes an exponential fall pattern for snags, consistent with other models of snag dynamics (Everett et al. 1999, Verkerk et al. 2011). For both HW and SW components, the default annual rates of C transfer are 3.2% per year for the Snag_Stemwood pool and 10.0% per year for the Snag_Branches pool, values that were determined through qualitative assessment of snag fall rates reported in the literature (although these rates were biased toward productive west coast forests). However, recent studies (Hagemann et al. 2010, Moroni et al. 2010) have indicated that these default rates may be too low for less productive boreal forests, which typically consist of smaller diameter trees. The analysis presented here is designed to provide improved estimates of annual C transfer rates for the Snag_Stemwood pools and, where possible, to provide insight into transfer rates for the Snag_Branches pools, for which fewer data are available.

Comparison of fall and C transfer rates for snag stemwood

Data for individual trees from 10 802 sample plots were used to calculate plot-level fall rates for snag stems

TABLE 1. Extended.

Province or territory (no. plots)	Total no. plots
BC (2526)	2 526
BC (28)	28
BC (2967), AB (354)	3 321
BC (76), AB (60), NT (2)	138
BC (79), AB (1130), SK (102)	1 311
AB (4)	4
AB (6)	6
AB (6), SK (27), MB (66), ON (1270)	1 369
ON (1951), QC (10)	1 961
MB (5)	5
ON (105), QC (2)	107
QC (9), NB (6), NS (10), PE (1)	26
	10 802

(FR) and C transfer rates for snag stems (CTR). These data were obtained from four sources: British Columbia permanent sample plots (BC-PSPs; *available online*),[4] the Ontario Ecological Data Repository (EDR) (ELCG 2005), Forest Ecosystem Carbon Database (FECD) plots from across Canada (Shaw et al. 2005), and Alberta Ecological Site Inventory System (ESIS) data (Resource Data Branch 2002). These data were representative of species composition and diameter distributions for stands across Canadian ecozones (ESWG 1996) and jurisdictions (Table 1). Plots with location information (latitude and longitude) and data for predefined variables (specifically, species, dbh [at 1.3 m], height, and status [live or dead]) and having at least four live, merchantable trees were included in the analysis. Data for stand age were also included when available. For plots with repeated measurements, only the most recent data were used, to avoid pseudoreplication.

The plot data provided a sample of diameter distributions, species mix, and ages representative of forest stands in Canada. We limited our analysis to data for live trees for three reasons: the size distribution of snags produced in a stand generally corresponds to that of live trees (Ferguson and Archibald 2002), there were more live than dead trees per plot from which to infer the diameter distribution, and species identification was complete for live trees, whereas the species of dead trees was often not recorded.

Snag fall rates at the level of individual trees were calculated according to the following equation:

$$r_i = F_{40}(40/D)^{0.6} \quad (1)$$

where r_i is the snag fall rate for individual trees (percentage of stems per year), F_{40} is a species-specific parameter (base fall rate, percentage of stems per year for trees with dbh of 40 cm), and D is dbh (cm). This equation is based on equations and parameterization developed by Huggard and Kremsater (2007; see sections 2.1 and 2.2, and equation in 2.4.1 of that paper). Briefly, Huggard and Kremsater derived the generalized relationship between snag fall rates and dbh and determined the influence of species from meta-analysis of snag fall data reported in 13 studies having two or more diameter classes (Huggard and Kremsater 2007; see section 2.1 of that paper). Using this relationship, they then derived the effects of species groups on the half-life values (T_{50}) for trees of standardized dbh (40 cm; Huggard and Kremsater 2007; see Table 2.2 of that paper). The species-group specific values for F_{40} are based on those half-life values and are described in Appendix A.

Plot-level FR, representing the average percentage of stems falling per year, was calculated as follows:

$$\mathrm{FR} = \sum_{i=1}^{n} r_i \left(\frac{1}{n}\right) \quad (2)$$

where r_i is the fall rate (percentage of stems per year) of the ith tree calculated from Eq. 1 and n is the number of merchantable trees in a plot. For each plot, FR was calculated for all trees and for the HW and SW components separately, where n was the number of merchantable trees in each component.

Plot-level CTR, representing the average percentage of C transferred from snags to downed wood per year, was calculated as a rate, weighted by the proportion of plot stemwood biomass contributed by each merchantable tree:

$$\mathrm{CTR} = \sum_{i=1}^{n} r_i \left(\frac{C_i}{\sum_{i=1}^{n} C_i}\right) \quad (3)$$

where C_i is the stemwood C mass of the ith tree for n merchantable trees per plot (equal to the product of stemwood biomass and the constant C fraction of 0.5) and r_i is the individual-tree fall rate from Eq. 1. As for FR, plot-level CTR was calculated for all trees and for the HW and SW components separately. Tree biomass was calculated for EDR and BC-PSPs using dbh-based allometric equations (Lambert et al. 2005, Ung et al. 2008). Tree biomass for FECD plots provided by Shaw et al. (2005) was calculated using published allometric equations (Appendix B) where selection of the appropriate equation was based on tree species and plot location (combination of province or territory and ecozone).

Each plot was classified by ecozone, stand type, lead species, stand component, and age group to determine if FR and CTR were affected by these characteristics. Ecozone was determined from geographic coordinates. Stand type was based on the proportion of total biomass

[4] http://www.for.gov.bc.ca/hts/vri/psps/psp.html

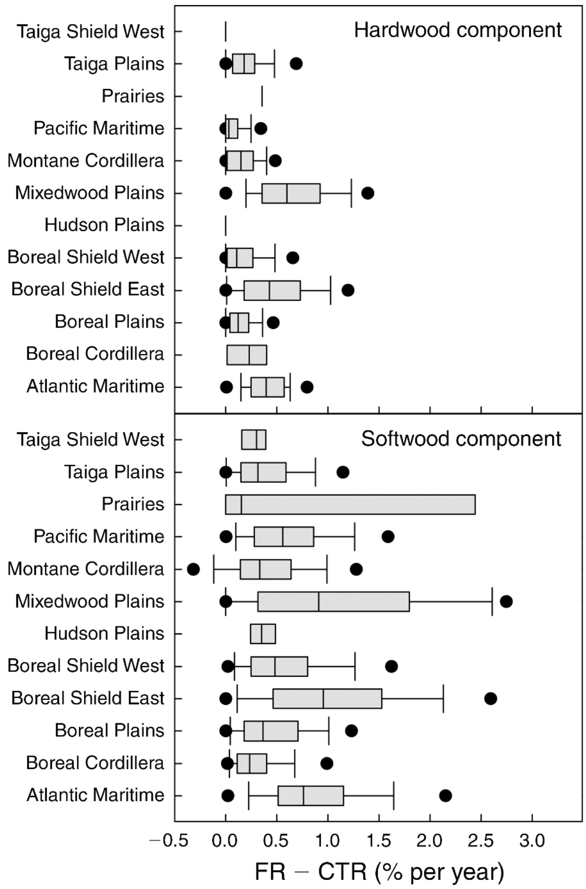

FIG. 2. Distribution of the difference between calculated fall rates and carbon transfer rates for Snag_Stemwood (FR − CTR) for the hardwood and softwood components of plots, grouped by ecozone. Box plots show the following features: median (line), 25th to 75th percentile or interquartile range (IQR; box), 10th and 90th percentiles (whiskers), and 2.5th–97.5th percentile (solid dots).

accounted for by SW and HW species, as follows: plots where >75% of the stemwood biomass was SW or HW were designated as SW ($n = 8337$) or HW ($n = 1685$), respectively; all others were designated as mixedwood (MW; $n = 1119$). The lead species for each plot was the species with the largest proportion of biomass in the dominant stand component (i.e., the stand component [HW, SW] accounting for >50% of the total stemwood biomass for the plot). Plots for which age data were available ($n = 10\,349$) were binned into three age groups: default, young, or old. The default age category for each ecozone was defined as tree age within 20% of the "average stand age" used for that ecozone in the CBM-CFS3, which represents the average return interval for stand-replacing disturbances for the ecozone (Kurz et al. 2009). The young and old age categories referred to tree ages younger and older than the default age category, respectively.

To determine if stand structure influences the magnitude of the difference between FR and CTR, we also calculated the Gini coefficient for the dbh distribution at each plot and regressed these coefficients against the absolute difference in rates. The Gini coefficient is an expression of size inequality (Lexerod and Eid 2006) that approaches a value of zero when all trees are essentially equal in diameter. We used two-tailed paired *t* tests to test for differences between mean FR and CTR values for groups of plots. We used analysis of variance to test for effects of plot classifiers on FR, CTR, and the difference between them, with a post hoc test of differences using least squares means with separate error terms for variances. Here, we report the standard deviation (SD) of the mean to express the variation or scatter of data points and the standard error (SE) of the mean to express differences between means or comparisons of means (Altman and Bland 2005). All statistical analyses were conducted with SYSTAT12 (2007).

Database of snag fall rates

Snag fall and breakage data were collected from literature sources pertinent to Canadian boreal and temperate forests (Supplement). We used these data to indirectly validate the method used to calculate CTR by comparing our calculated FR with measured FR values reported in the literature. We also used these data to estimate CTRs for the Snag_Branches pool as defined for the CBM-CFS3.

RESULTS

Comparison of calculated FR and CTR

The values of FR and CTR were strongly correlated both overall and within ecozones (Appendix C: Fig. C1), with FR being higher in 93% of plots. Across all plots, FR was significantly higher than CTR (grand means 5.40% ± 0.02% per year, vs. 4.78% ± 0.02% per year, mean ± SE; paired *t* test, $P < 0.05$). Within each ecozone, FR was significantly greater than CTR (paired *t* test, $P < 0.05$) except for the Prairies ecozone, where few plots were available. The magnitude of the difference between rates (i.e., FR − CTR) varied by stand component type and ecozone (Fig. 2). The overall mean difference between rates (with 95% confidence interval [CI]) was 0.62% per year (95% CI 0.61% per year to 0.63% per year) for all plots, so on average, CTR was 11.5% lower than FR. There was a greater difference for SW components (0.61% per year, 95% CI 0.60% per year to 0.62% per year) than for HW components (0.28% per year, 95% CI 0.27% per year to 0.29% per year). The differences also varied by ecozone, with the largest mean difference (for all trees), 1.11% per year (95% CI 1.08% per year to 1.14% per year), in the Boreal Shield East and the smallest mean difference, 0.24% per year (95% CI 0.10% per year to 0.37% per year), in the Taiga Shield West. The difference in rates also varied by stand type, with mean differences of 0.88% ± 0.02% per year for MW, 0.78% ± 0.02% per year for HW, and 0.56% ± 0.01% per year for SW.

The difference between FR and CTR was also affected by inequality of the dbh distribution, species composition, and stand age, all of which influence the distribution of biomass among stems. The variability among ecozones (Appendix B: Fig. B1) can be attributed, in part, to differences in these factors. Across sample plots, the Gini coefficient for dbh distribution ranged from 0.02 to 0.46, with a significant positive correlation between the magnitude of the difference between rates and the Gini coefficient ($y = 5.66x - 0.32$, where y is the difference between rates and x is the Gini coefficient; $R^2 = 0.43$, $P < 0.001$, $n = 10\,802$). In three of the ecozones, the difference between FR and CTR was statistically significant but relatively small (mean difference <4% of the value of FR); 0.24 in the Taiga Shield West, 0.20 in the Boreal Cordillera, and 0.36 in the Hudson Plains. In these ecozones, the values of the Gini coefficient were also small (means <0.10), and the plots were predominantly SW, with no more than four species. Thus differences between CTR and FR were greatest in stands with a wide range of stem diameters, and were small in stands with a narrow diameter distribution.

Stand age can affect both the dbh distribution and species composition of stands. Most of the plots (73%) were classified as young, with only 22% in the default or old age groups (Table 1). For ecozones where all three age groups were represented, the difference between FR and CTR was larger for older than for younger stands (Fig. 3A), a pattern that was evident across most ecozones and significant ($P < 0.05$) for some. Gini coefficients were also higher for older stands (Fig. 3B). Stand age had the greatest effect on the difference between FR and CTR in the Pacific Maritime ecozone, where the difference between the two rates was three times larger for old than for young stands (1.86 vs. 0.60; the latter difference was similar to the national average of 0.62).

Comparison of calculated and published values for FR

The literature yielded 184 estimates of annual FR from 55 studies. The compiled data set includes sources, estimated values, and associated metadata (Supplement). Most values are from North American sites (Canada, $n = 77$; United States, $n = 97$), the remainder being from other regions climatically similar to Canada (Russia, $n = 8$; Norway, $n = 2$). Reported FR values were highly variable, with similar ranges of values for studies from Canada and the United States (means 7.04% per year, SD 6.91% per year, and 8.75% per year, SD 8.38% per year, respectively). We compared FR values obtained from the literature with the range and central tendency of calculated FR by ecozone (Fig. 4) and by leading species (Fig. 5). Rates obtained from the literature were within the range of calculated rates for all but the Mixedwood Plains ecozone (Fig. 4), for which all literature values were from a single study (Vanderwel et al. 2006) and were higher than the

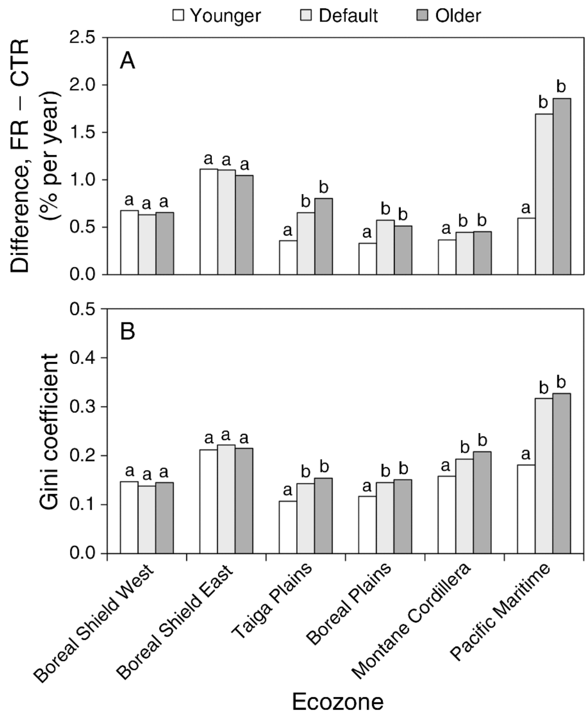

FIG. 3. Effect of stand age group on (A) mean difference between fall rate for Snag_Stemwood (FR) and carbon transfer rate for Snag_Stemwood (CTR) and (B) mean Gini coefficients for plots, grouped by ecozone. The Gini coefficient approaches a value of zero when all trees are essentially equal in diameter. Age ranges for plots in the default age group are 60–90 years for the Boreal Shield West; 100–150 years for the Boreal Plains, Boreal Shield East, and Taiga Plains; 120–180 years for the Montane Cordillera; and 240–360 years for the Pacific Maritime. Within each ecozone, differing lowercase letters indicate significantly different means for age groups ($P < 0.01$).

calculated rates. For leading species (Fig. 5), literature-derived and calculated values were reasonably similar for most species, except the category "other HW" for which the literature-derived rates tended to be higher than the calculated rates, and jack pine (*Pinus banksiana* Lamb.) for which they tended to be lower.

Values of CTR for use in the CBM-CFS3

The overall CTR was estimated at 4.78% ± 0.02% per year (mean ± SE; Table 2), which is ~50% higher than the current default rate of 3.2% per year used in the CBM-CFS3 for the Snag_Stemwood pool. The absolute ranges in mean CTR values across ecozones (6.59% per year) and across lead species (5.92% per year) were large relative to the overall mean of 4.78% per year, which indicates that the accuracy of modeling CTR could be improved if rates were assigned by ecozone or by lead species. These large ranges were due primarily to the influence of the SW component, which had a greater range than the HW component (6.21% per year vs. 1.32% per year; Table 2).

Fall rates for the Snag_Branches pool could not be calculated for our plots but could be estimated from the

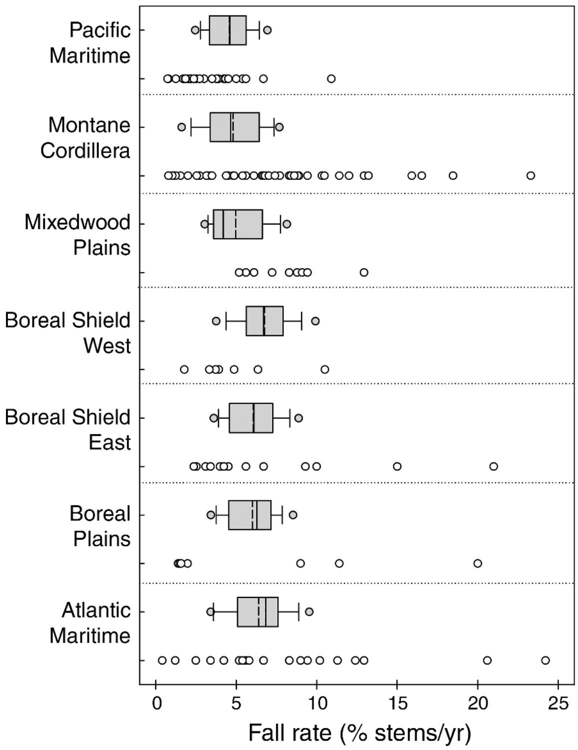

FIG. 4. Fall rates for Snag_Stemwood (FR) calculated from sample plot data (solid box plots) compared with fall rates for Snag_Stemwood compiled from the literature (open dot plots), grouped by ecozone. Box plots show the following features: median (solid line), mean (dashed line), 25th–75th percentile or interquartile range (IQR; box), 10th and 90th percentiles (whiskers), and 2.5th–97.5th percentile (solid dots).

literature; ranging from 5% per year to 36% per year (Appendix D). Regression of the fall rate for the Snag_Branches pool (y) against the fall rate for the Snag_Stemwood pool (x) yielded the relationship: $y = 2.5x$ ($R^2 = 0.88$, $P < 0.0001$; Appendix D: Fig. D1). Thus, we estimated an overall mean CTR for the Snag_Branches pool of 11.95% per year, calculated as the product of the overall mean CTR (4.78% per year) and the slope of the regression (2.5). This rate is about 20% higher than the current CBM-CFS3 default value of 10.0% per year.

DISCUSSION

Standing and downed dead wood, and the fluxes from them, are important components of the C budget of Canada's forest (Stinson et al. 2011). Snag fall rates based on stem counts (FR) reported in the literature are often used as a proxy for snag C transfer rates (CTR) in models that track C transfer from snags to downed woody debris (e.g., Nalder and Wein 2006, Kurz et al. 2009). However, FRs reported in the literature may not be equivalent to CTRs, and do not provide sufficient representation of typical stand composition and structure for all ecozones and lead species in the forests of Canada. For this reason we developed and validated a method to provide estimates for FRs and CTRs representative of the ecozones and lead species (Tables 2 and 3) in the forests of Canada that can be used to improve estimation by the CBM-CFS3.

We show that FR should not generally be substituted for CTR because these rates were significantly different, with the magnitude of the difference varying by ecozone and stand characteristics. Although the overall mean difference between FR (5.40% per year) and CTR (4.78% per year) is small (0.62% per year), it represents an 11.5% reduction in the annual C flux. Our result is supported by data from Wilson and McComb (2005) for HW stands where decadal snag fall was about 20% higher on a stem-count basis than on a volume basis. Also, using the data of Dahms (1949) for ponderosa pine (*Pinus ponderosa* P. Laws. ex C. Laws.) stands we estimated that fall rates based on stem counts (6.7% per

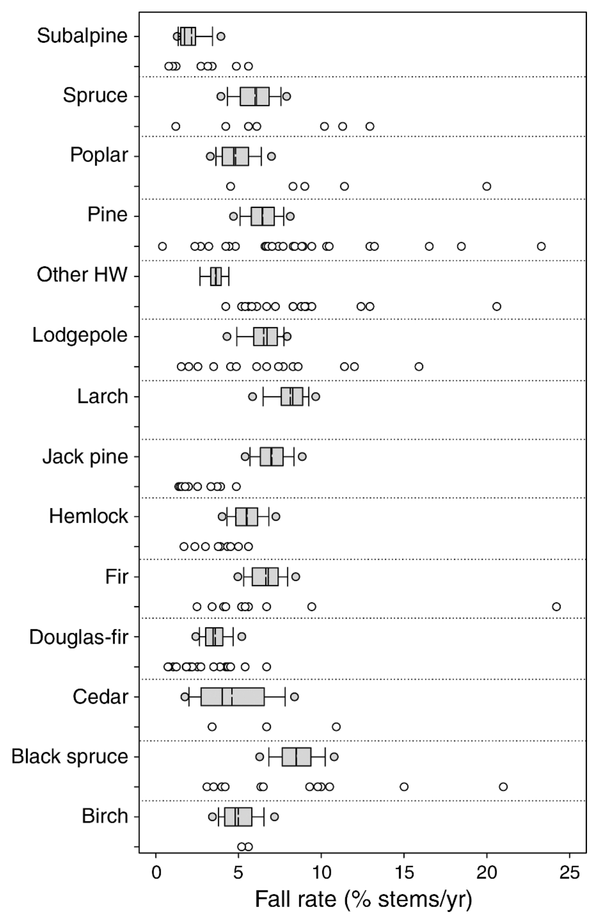

FIG. 5. Fall rates for Snag_Stemwood (FR) calculated from sample plot data (solid box plots) compared with fall rates for Snag_Stemwood compiled from the literature (open dot plots), grouped by lead species. For some species groups, no values could be found in the literature. "Lodgepole" represents lodgepole pine; hardwoods is indicated by HW. Box plots show the following features: median (solid line), mean (dashed line), 25th–75th percentile or interquartile range (IQR; box), 10th–90th percentiles (whiskers), and 2.5th–97.5th percentile (solid dots).

TABLE 2. Stand-level Snag_Stemwood C transfer rates (CTR) by ecozone, for all, softwood, and hardwood components, calculated for *n* plots.

	CTR (% per year)								
	All components			Softwood component			Hardwood component		
Ecozone	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*N*
Prairies	3.43	0.38	4	3.81	0.94	3	3.74	0.19	2
Mixedwood Plains	3.92	0.15	107	7.03	0.24	56	3.16	0.07	101
Pacific Maritime	3.94	0.03	2 526	3.99	0.03	2 506	3.10	0.03	508
Montane Cordillera	4.42	0.03	3 321	4.50	0.03	3 274	3.76	0.02	1 278
Boreal Shield East	4.95	0.04	1 961	6.72	0.04	1 686	3.43	0.02	1 580
Taiga Plains	5.56	0.14	138	7.38	0.13	110	3.74	0.07	107
Boreal Plains	5.60	0.04	1 311	6.48	0.04	1 088	3.55	0.03	659
Atlantic Maritime	5.65	0.35	26	7.62	0.22	21	3.81	0.13	20
Boreal Shield West	6.09	0.05	1 369	7.04	0.04	1 279	3.54	0.03	668
Taiga Shield West	6.87	0.32	6	6.96	0.32	6	4.42	0.24	3
Boreal Cordillera	7.42	0.17	28	7.55	0.14	28	3.82	0.35	3
Hudson Plains	10.02	0.24	5	10.02	0.24	5			
Range	6.59			6.21			1.32		
Total, all ecozones	4.78	0.02	10 802	5.35	0.02	10 062	3.51	0.01	4 929

Notes: Ecozones are as in Kull et al. (2011). For "all components," *n* includes all plots; however, not all plots have both softwood and hardwood components.

year) were almost 40% higher than rates calculated on the basis of basal area (4.8% per year). The FR-CTR difference (and proportional change) in transfer rates varied widely by ecozone (Fig. 2) because of differences in stand component or species composition, dbh distribution and age structure; higher structural and compositional diversity resulted in greater differences between the two rates.

The HW stand component had a smaller mean difference (0.28% per year) than the SW stand component (0.61% per year), but this is partly methodological because only one base fall rate (2.5% per year) was available for all HW species, whereas many base fall rates (ranging from 1.00% per year to 6.30% per year) were available for SW species (Appendix A). These differences by stand component and type explain some of the variation by ecozone, given that the fraction of SW sample plots ranged from 100% in the Hudson Plains and Taiga Shield West to 19% in the Mixedwood Plains (Table 1). The Boreal Shield East had a greater proportion of MW or HW than did the Boreal Shield West (57% vs. 34%) and also had greater FR-CTR differences (Fig. 2).

Stands with more unequal dbh distribution (high Gini coefficient) had greater discrepancy between FR and CTR. In such stands, FRs are influenced to a greater extent by the more numerous small (faster-falling) stems, whereas CTRs are influenced to a greater extent by the few, large (slower-falling) stems. Consider the example of two plots analyzed (Fig. 6). FR is almost the same as CTR where stems are small, dbh distribution is narrow, and the species composition simple (Fig. 6A). CTR is

TABLE 3. Stand-level Snag_Stemwood C transfer rates (CTR) for all components, by lead species group for the plot, calculated for *n* plots.

Lead species group for plots	Group description	CTR (% per year) Mean	SE	*n*
Black spruce	*Picea mariana* (Mill.) BSP	7.92	0.053	668
Jack pine	*Pinus banksiana* Lamb.	6.38	0.038	730
Lodgepole pine	*Pinus contorta* Dougl. ex Loud.	6.23	0.026	1 604
Fir	all *Abies* spp. except those in subalpine group	6.00	0.079	203
Larch	all *Larix* spp. except those in subalpine group	5.94	0.091	240
Other pine	all *Pinus* spp. except jack pine and lodgepole pine	5.39	0.042	467
Other spruce	all *Picea* spp. except those in subalpine group and black spruce	5.25	0.037	1 026
Hemlock	all *Tsuga* spp.	4.78	0.029	1 261
Poplar	all *Populus* spp.	3.91	0.021	1 140
Birch	all *Betula* spp.	3.90	0.045	312
Cedar	all *Thuja* spp.	3.78	0.109	305
Other softwood	all coniferous (gymnosperm) species not found in other groups	3.39	0.512	3
Other hardwood	all deciduous (angiosperm) species not found in other groups	3.26	0.029	481
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*	3.06	0.018	1 903
Subalpine	subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.); subalpine larch (*Larix lyallii* Parl.)	2.00	0.053	459
Range		5.92		
Total	all species groups	4.78	0.018	10 802

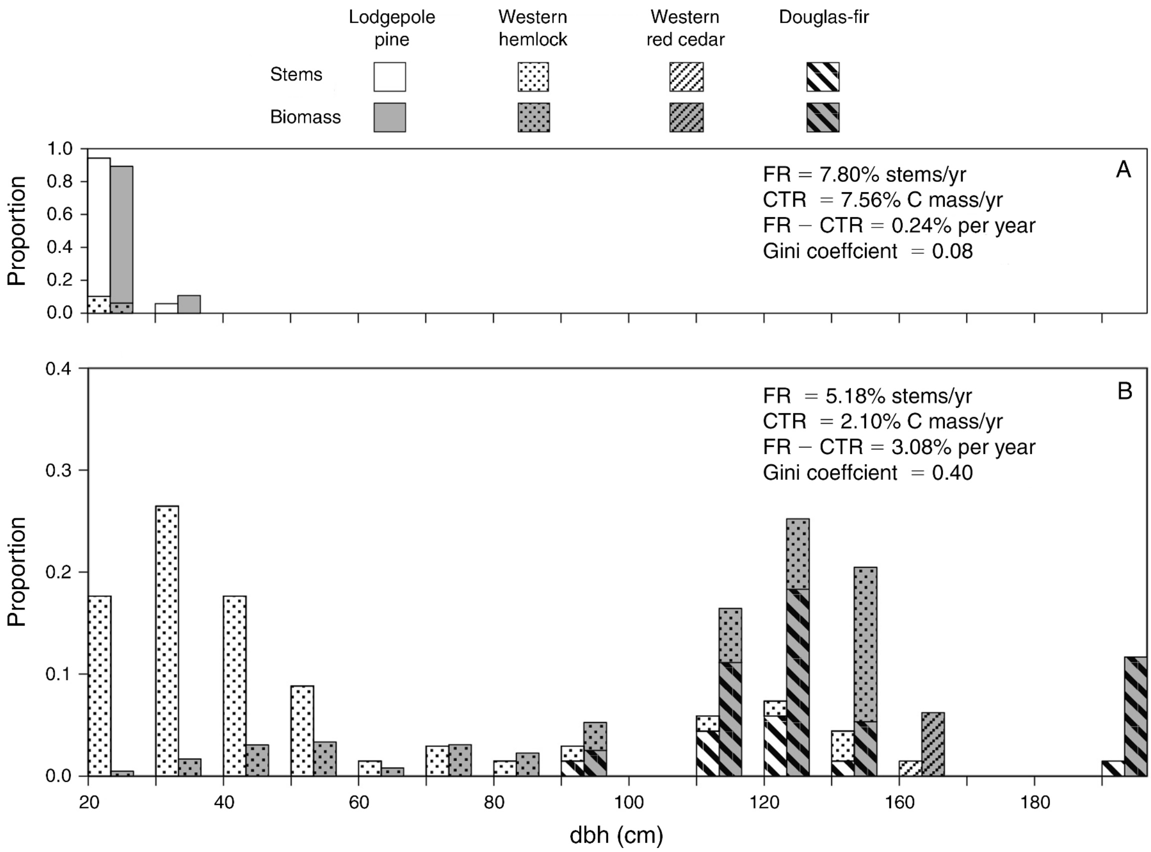

FIG. 6. Species distribution by size class (dbh), based on both proportion of stems and proportion of biomass, and its impact on fall rates (FR), carbon transfer rates (CTR), and the Gini coefficient for Snag_Stemwood. The contrast is between two sample plots with (A) narrow or (B) wide dbh distributions. Species were lodgepole pine (*Pinus contorta* Dougl. ex Loud. var *latifolia* Engelm.); western red cedar (*Thuja plicata* Donn ex D. Don); Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*); and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.).

almost half FR when the range of dbh is wide, species are diverse, and larger stems are species with lower base rates than the species with smaller stems (Fig. 6B). If we remove the effect of species for the example in Fig. 6B by using a single base rate (that of the lead species, Douglas-fir), the stem size (dbh) effect remains. FR and CTR are both lowered (2.5% per year and 1.3% per year, respectively), but CTR is still almost half FR.

Stand age influenced the FR-CTR difference (Fig. 3), probably because both the species compositional diversity (Bradford and Kastendick 2010) and dbh distribution change with age; both FR-CTR difference and Gini coefficient for dbh increased with stand age. The age effect was strongest for the Pacific Maritime ecozone, where trees grow to old ages because of long return intervals between stand-replacing natural disturbances, and they can become very large (e.g., Fig. 6B) because of the high productivity of this ecozone.

These results suggest that FRs should not be used as a proxy for CTRs, especially in high productivity ecosystems where trees grow to old ages and achieve very large sizes. The small difference (<4% of FR) between FR and CTR in the Taiga Shield West, Boreal Cordillera, and Hudson Plains ecozones indicates that FR could potentially be substituted for CTR in these ecozones; however we found no FRs for these ecozones in the literature. Thus, our analysis demonstrates that the CTRs calculated in this study are the best available estimates for Canada's forest at this time.

The overall mean CTR (4.78% per year) from this analysis was almost 50% higher than the current default CBM-CFS3 rate of 3.20% per year (Kurz et al. 2009), largely because of higher CTR values for SW components in ecozones other than the Pacific Maritime (Table 2). Estimated CTR rates for the Pacific Maritime ecozone (3.94% per year) and for the lead species that were most common in this ecozone (Douglas-fir 3.06% per year and cedar 3.78% per year) were close to the default rate, probably because these are most characteristic of the available literature on which the default rates were based. The absolute ranges of CTR across ecozones (6.59% per year) and across lead species (5.92% per year) were large relative to the overall mean (4.78% per year), which indicates that using ecozone or species-specific CTR values would improve the accuracy of dead wood dynamics in forest C models. The large ranges of CTR (across ecozones and lead species) were due primarily to the influence of the SW component (range 6.21% per year) rather than the HW component (range 1.32% per year).

Ecozone, lead species, and tree size are related classifiers in Canada because some species are largely restricted to certain ecozones and some ecozones are more productive than others. For example, >80% of plots with lead species groups of birch (*Betula* spp.), black spruce (*Picea mariana* (Mill.) BSP), jack pine, pine (*Pinus* spp.), or poplar (*Populus* spp.) were in the Boreal Shield East ecozone, whereas plots with lead species Douglas-fir, cedar (*Thuja* spp.), hemlock (*Tsuga* spp.), and other SW or subalpine species were largely restricted to the Pacific Maritime and Montane Cordillera ecozones. Within ecozones, analysis of variance showed significant ($P < 0.05$) effects of lead species group on CTR for all ecozones except the Prairies, Taiga Shield West, and Hudson Plains. For the Atlantic Maritime and Mixedwood Plains ecozones, CTRs were lower for plots with any HW lead species than for plots with any SW lead species, but did not differ otherwise. Tree size is implicit in the calculation of CTR, and ecozones and species also differ in this respect. Plots in the Pacific Maritime ecozone had the largest trees and those in the Hudson Plains, Boreal Cordillera, and Taiga Shield West ecozones had the smallest trees, with mean quadratic dbh values for merchantable trees of 37.7 (SE 0.3), 12.3 (SE 0.5), 16.1 (SE 0.4), and 18.8 (SE 2.1) cm, respectively. Lower CTR values were associated with productive west coast species (cedar, Douglas-fir), subalpine species, and HW species (Table 3), and the ecozones where these species commonly occur, for example, cedar and Douglas-fir in the Pacific Maritime ecozone (see Plate 1), subalpine species in the Montane Cordillera ecozone, and HW species in the Mixedwood Plains and Atlantic Maritime ecozones. Higher CTR values were associated with low-productivity, small-diameter species occurring in stands dominated by a single species and commonly generated by stand-replacing disturbances such as fire (e.g., black spruce, jack pine, and lodgepole pine) or the ecozones where these stand types dominate (Hudson Plains, Taiga Shield West, Boreal Cordillera, Boreal Shield West; see Plate 1).

The most reliable CTR estimates (i.e., those with large sample sizes and good agreement on validation) were for the Pacific Maritime (3.94% per year), Montane Cordillera (4.42% per year), Boreal Shield East (4.95% per year), Boreal Shield West (6.09% per year), and Boreal Plains (5.60% per year). Accuracy in estimation for these ecozones could be further increased by accounting for the effect of species or by assigning different CTRs to the HW and SW stand components. Within the Pacific Maritime and Montane Cordillera ecozones, use of species-specific values could improve accuracy because of the high diversity of SW species and their CTR values

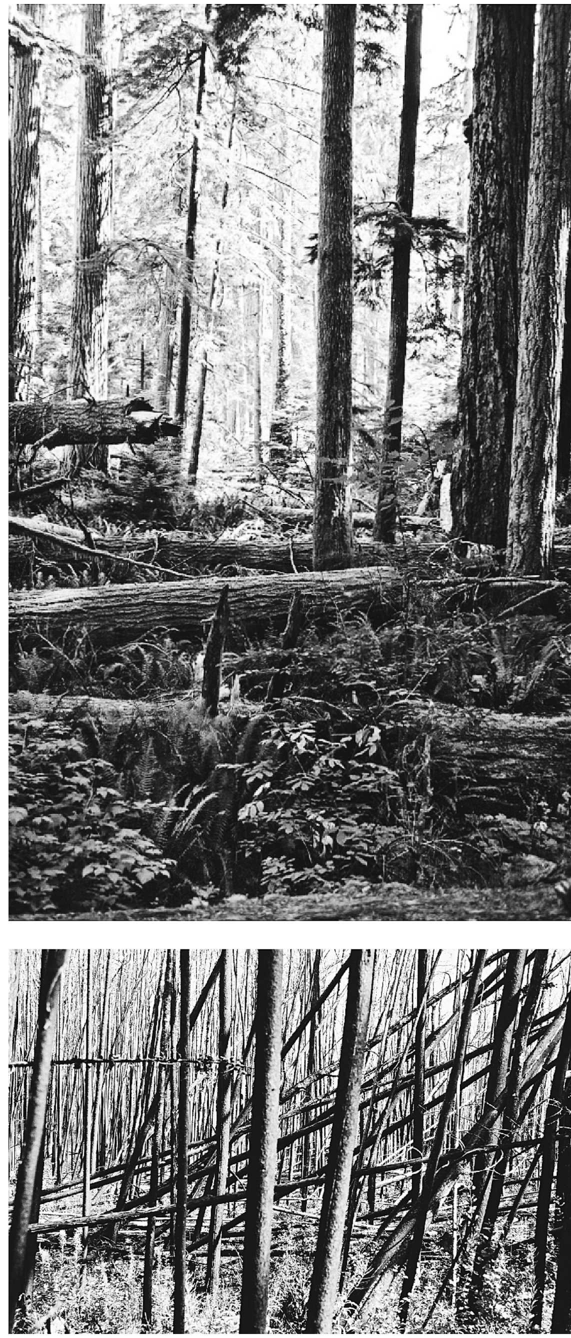

PLATE 1. Standing and downed dead wood contrasting (upper) a Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*] stand in the Pacific Maritimes ecozone characterized by snags of large diameter, wide diameter distribution, and a low C transfer rate with (lower) a post-fire black spruce [*Picea mariana* (Mill.) BSP] stand in the Boreal Shield West ecozone characterized by snags of small diameter, narrow diameter distribution, and a high C transfer rate. Photo credits: W. A. Kurz.

(Table 3). For the Boreal Shield East, Boreal Shield West, and Boreal Plains ecozones, accuracy could be increased by using different CTR values for the HW and

SW components, because the difference between rates for these components was large (Table 2).

Greater uncertainty of CTRs is associated with ecozones where plot sample sizes were relatively small (4–138). Small sample size may not be of great concern for the Mixedwood Plains and Atlantic Maritime ecozones, which occupy small areas of Canada, because sufficient numbers of snag fall rates were found in the literature to validate the methodology for these ecozones. Literature-derived fall rates were somewhat higher than calculated FR values for plots in the Mixedwood Plains ecozone (Fig. 4), so CTR calculated for plots in this ecozone (mean 3.92% per year) may also be somewhat low. In the Mixedwood Plains 62% of plots had "other HW" species as the leading species (e.g., maple (*Acer* spp.), oak (*Quercus* spp.), and other eastern shade-tolerant hardwood species). The single base rate for hardwoods used in this analysis was developed mainly from studies of boreal hardwoods (Huggard and Kremsater 2007). Thus, estimation of CTR by our method could be improved if more specific base rates were developed for eastern HW species.

Estimates of CTR were most uncertain for the remaining ecozones with small sample sizes (Prairies, Taiga Plains, Taiga Shield West, Boreal Cordillera, and Hudson Plains). However, the CTR estimates provided here are the best available for these ecozones, because no FR or CTR values were found for them in the literature. Overall average CTR estimates for these ecozones were 3.43% per year for the Prairies, 5.56% per year for the Taiga Plains, 6.87% per year for the Taiga Shield West, 7.42% per year for the Boreal Cordillera, and 10.02% per year for the Hudson Plains. For most of these ecozones, accuracy would be improved by assigning CTRs on the basis of lead species, because sample size and validation were reasonable for the species most common in these five ecozones (e.g., other spruce [25%], lodgepole pine [21%], aspen poplar [25%], and black spruce [9%]; Table 3). Estimation of rates for these ecozones could be improved if more field study data become available.

The overall mean CTR estimated for the Snag_Branches pool, 11.95% per year, was ~20% higher than the current default value of 10.0% per year used in the CBM-CFS3. In the absence of better data, the derived multiplier of 2.5 (Appendix D) can be used with CTR values (Tables 2 and 3) to estimate CTRs for the Snag_Branches pool for each ecozone and lead species. Snag stem breakage has been reported as a significant process in some boreal forests (Ganey and Vojta 2005, Angers et al. 2010). However, because the Snag_Stemwood pool in the CBM-CFS3 includes only the merchantable portion of the bole, C transfer associated with reported rates of snag breakage (Appendix D) is accounted for by C transfer rates for the Snag_Branches pool of CBM-CFS3, which includes entire non-merchantable trees as well as branches and tops of merchantable trees (see Appendix D).

Accurate characterization of density reduction due to snag decay is important for carbon accounting methods that rely on allometrics of tree cohorts, and as such is the subject of recent research (Domke et al. 2011, Harmon et al. 2011). However, the CBM-CFS3 does not track tree cohorts, and implements C losses due to decay of snag pools, with annual decay rates as a function of mean annual temperature, separately from snag fall. In addition, the CBM-CFS3 uses yield curves as input and for BC, where trees are large and decay in live trees important, the yield curves have been netted down to account for rot. Decay rates for snag pools in the CBM-CFS3 were not the subject of this analysis.

The implications for C accounting of increasing the snag C transfer rates beyond the default rates in the CBM-CFS3 is to move more C to the more rapidly decomposed and combusted downed woody debris pools. Evidence that doing so may improve the fit of modeled to measured field plot data comes from Moroni et al. (2010), for black spruce stands in Newfoundland. They found the best-fit parameterization of Snag_Stemwood carbon transfer rates of 9.0 % per year.

The snag C transfer rates estimated here can be applied in forest ecosystem models other than the CBM-CFS3, provided that snag pool structure and dynamics are modeled similarly to the CBM-CFS3. For models with alternative constructs of snag dynamics, the calculation and validation approach described here can easily be adapted to reestimate snag C transfer rates. Further improvements to the underlying species and dbh-specific fall rate relationships would be useful, and in particular the development of these relationships for eastern hardwood species, which are currently lacking.

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Supplemental Material

Appendix A

Determination of F_{40} values (*Ecological Archives* A022-113-A1).

Appendix B

References used for biomass equations (*Ecological Archives* A022-113-A2).

Appendix C

Plots of FR on CTR for all sample plots and by ecozone (*Ecological Archives* A022-113-A3).

Appendix D

Methods to determine Snag_Stemwood and Snag_Branches annual fall rates from literature sources (data in Supplement) (*Ecological Archives* A022-113-A4).

Supplement

Data compiled for Snag_Stemwood and Snag_Branch annual fall rates from literature sources, with site and tree information, and methods used to compile values (*Ecological Archives* A022-113-S1).