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Representative regional models of post-disturbance forest carbon accumulation: Integrating inventory data and a growth and yield model

Crystal L. Raymond *, Sean Healey, Alicia Peduzzi, Paul Patterson

USDA Forest Service, Rocky Mountain Research Station, 507 25th St, Ogden, UT 84401, United States

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ABSTRACT

Disturbance is a key driver of carbon (C) dynamics in forests. Insect epidemics, wildfires, and timber harvest have greatly affected North American C budgets in the last century. Research is needed to understand how forest C dynamics (source duration and recovery time) following disturbance vary as a function of disturbance type, severity, forest type, and initial C stocks. We used the Forest Vegetation Simulator (FVS) to simulate total C stocks (excluding soil) for 100 years following three types of disturbance (fire, harvest, and insects) with four levels of severity. We initiated the model using empirical data from a large representative sample of forest conditions on the national forest ownership in the Rocky Mountain region (Forest Inventory and Analysis data). Unlike analyses based on stand age, an ambiguous quantity with respect to disturbance history, our approach enables explicit consideration of disturbance type and severity, as well as pre-disturbance forest C. On average, stands became a C sink after fire in 5, 6, 14, and 23 years for low to high-severity fire. Pre-fire C stocks were reached 25–55 years later. Following bark beetle epidemics, on average stands continued to be a C source for 10 years longer than fire and up to 40 years longer in some cases, but pre-disturbance C stocks were reached in a similar amount of time. C stocks following harvest showed the largest initial decline, but on average stands became a sink sooner at 1, 5, 15, and 12 years post-harvest for low to high-severity harvests. Differences in C dynamics based on disturbance type and severity, initial conditions, and forest type demonstrate the importance of considering this variability when modeling forest C dynamics. The regionally averaged models of C response quantified in this study can be combined with remotely sensed data on disturbance type and severity and used with C accounting approaches that rely on growth and yield or state and transition models.

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1. Introduction

Disturbance is well recognized as an important driver of carbon (C) dynamics in forests. In the last century, national and continental C budgets have been greatly affected by insect epidemics (Kurz et al., 2008; Kurz and Apps, 1999), wildfires (Amiro et al., 2001; Houghton et al., 2000), and timber harvest (Houghton and Hackler, 2000; Masek et al., 2011). Forest regrowth following disturbance is a major contributor to the current C sink in forests of North America (Birdsey et al., 2006; Goodale et al., 2002; Houghton et al., 1999). More research is needed to understand how forest C dynamics after disturbance vary by forest type and disturbance type and severity. This information can improve estimates of C stocks and fluxes for reporting under national and international policies. It can also inform the development of management practices to maintain or enhance forest C sinks, thereby reducing greenhouse gas (GHG) emissions that contribute to climate change.

The effects of disturbance on forest C dynamics are often quantified at individual sites or national and continental scales, but similar information is needed at regional and sub-regional scales to inform management decisions that are implemented at these intermediate scales. For example, the United States Forest Service (USFS) Climate Change Response Strategy (USFS, 2008) and Performance Scorecard (USFS, 2010), require national forest administrative units to report baseline C stocks, as well as changes in these stocks caused by disturbance and forest management. A 2012 revision to the USFS planning rule, which guides development of all unit-level land and resource management plans, requires national forests to assess ecological conditions and trends relevant to forming baseline assessments of C stocks and fluxes (USFS, 2012). These assessments are useful to managers considering actions to

* Corresponding author at: City of Seattle, 700 5th Avenue, Suite 3200, Seattle, WA 98124-4023, United States.
E-mail address: Crystal.Raymond@Seattle.gov (C.L. Raymond).

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maintain or enhance ecosystem services, such as C sequestration. The USFS owns one fifth of all forestland in the US (Smith et al., 2009), so management of these lands can affect national C budgets.

Baseline C stocks at any time can be quantified with forest inventory data collected as part of the USFS Forest Inventory and Analysis (FIA) program (Smith et al., 2006; Van Deusen and Heath, 2010). As of 2005, estimates from FIA indicate that forestland owned by the USFS contains a mean of 192 Mg C ha^{-1} on 60 million ha for a total of 11604 TgC (Heath et al., 2011). Estimates based on changes in C stocks between two times indicate that these lands are currently sequestering 150 $TgCO_2$ $year^{-1}$ on average (Heath et al., 2011). These estimates of stocks and stock changes are useful baselines under current conditions, but they cannot be attributed to particular management actions or disturbance trends. Ground-based inventory approaches, such as FIA, are limited in their ability to describe the effects of infrequent disturbances, characterize effects for specific forest conditions, or attribute C fluxes to specific disturbance types and severities (Masek and Healey, 2012). Further obscuring the relationship in the FIA data between disturbance and C dynamics is that only 10% of plots are measured per year, making it difficult to capture short-term C response following disturbance.

A more dynamic method is needed to assess the effects of disturbance on past and potential future changes in C stocks. The critical information needed for a dynamic method is the amount of C remaining after disturbances of different types and severities and subsequent changes in total C stocks with time since the disturbance. The rate at which C accumulates on a site can show the long-term effect of the disturbance on forest C stocks by showing the amount of time that the site functions as a source of C to the atmosphere and the time required to sequester the C emitted to the atmosphere from the disturbance and subsequent decomposition. This information can be summarized by models of total forest C as a function of time since disturbance. These models of C accumulation with time since disturbance can be combined with several approaches commonly used to estimate the effects of disturbance on C storage, such as growth and yield tables or state and transition models. Models based on growth and yield tables use pre-defined functions to track forest characteristics (e.g. C stocks) over time as forests change through succession and transition to new conditions via disturbance or management. Two such models commonly used for decision support are the Vegetation Dynamics Development Tool (VDDT; Kurz et al., 1999) and the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3; Kurz et al., 2009). The latter is the primary tool used for national reporting of GHG emissions in Canada. A third model of this type, the Forest Carbon Management Framework (ForCaMF; Healey et al., 2014), is being applied across the US National Forest System to respond to C reporting requirements for the USFS. ForCaMF uses a Monte Carlo-based uncertainty framework to assign average C accumulation functions across the landscape based upon remotely sensed data of vegetation and disturbance patterns. The predefined functions of C accumulation with time since disturbance vary based on initial forest conditions and disturbance type and severity.

Biogeochemical process models can also provide a dynamic method for accessing past and future trends in C stocks (e.g. Zhang et al., 2012), but disturbance is represented in only a limited way (Liu et al., 2011). In the last decade, significant progress has been made to represent timber harvests (e.g. Masek et al., 2011), bark beetle epidemics (e.g. Edburg et al., 2011), and fire (e.g. Lenihan et al., 2008). However, most process models simulate only stand-replacing disturbances (e.g. Zhang et al., 2012) because C dynamics following disturbances are calibrated with empirical models based on forest age (He et al., 2012; Williams et al., 2012) making it difficult to represent partial disturbances (i.e. disturbances that emit and transfer C but do not reset stand age). If partial disturbances are represented, it is often with simplifications that can affect the rate at which C accumulates after a disturbance. Process models do not simulate individual trees, thus they are unable to capture variation in the species and size of dead trees, residual trees, and woody debris caused by disturbances of different types and severities. This variation can greatly affect C release and accumulation after disturbance (Amiro et al., 2010; Pfeifer et al., 2011) because these factors influence rates of decomposition, regeneration, and tree growth.

The objective of our study was to quantify average C accumulation rates following disturbance using a method that takes advantage of US national inventory data and is sensitive to the effects of disturbance type and severity on C without relying on stand age. We quantified average rates of total forest C (excluding soil) accumulation over 100 years following three types of disturbance (fire, harvest, and insects) with four levels of severity and for six forest types. We investigated multiple levels of severity because partial disturbances are common. Approximately 60% of forest harvests in the US are only partial harvests (Smith et al., 2009), and 68% of the area burned in the U.S. between 1984 and 2010 was categorized as moderate or low severity (Finco et al., 2012).

Our method for quantifying average rates of C accumulation following disturbance, which we demonstrate on the national forest ownership in the USFS Northern Region, combines publically available, nationally consistent FIA data and a commonly used growth and yield model, the Forest Vegetation Simulator (FVS) (Dixon, 2002). Unlike most biogeochemical process models, FVS simulates mixed-species and uneven-aged stands, enabling detailed simulation of disturbance effects specific to tree species and size. We modeled average functions for C accumulation following disturbance by grouping forest stands based on pre-disturbance levels of aboveground live tree C, forest type, and disturbance type and severity – all factors that that can be included in the growth and yield-based accounting systems mentioned above. We initiated FVS with a large dataset drawn from FIA's spatially balanced simple random sample (Bechtold and Patterson, 2005). Thus, the average functions for C accumulation are representative of a wide range of pre-disturbance conditions. By simulating the effects of three disturbance types with four levels of severity, we capture a wide range of responses in total forest C in terms of disturbance type, severity, and pre-disturbance forest conditions. This approach differs from studies that have observed or modeled C response following disturbance for one or a few sites which represent only a small sample of possible initial conditions and disturbance types and severities that could exist in a region.

2. Methods

2.1. Study area

We quantified the average rate and amount of C accumulation with time since disturbance for the forested area of the national forest ownership in the Northern Region (northeastern Washington, northern Idaho, Montana, and northwestern South Dakota, Fig. 1). The Northern Region includes 12 national forests covering 9 million hectares spanning from west to east of the Rocky Mountain Range and into the northern Great Plains. Forests are primarily coniferous, but the large elevation and associated climatic gradient gives rise to diverse forest types. Lower elevation forests west of the Rocky Mountains are a mix of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), *Abies* spp., western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don) and are some of the most productive forests in the region. Higher elevation forests are dominated by subalpine fir (*Abies lasiocarpa*

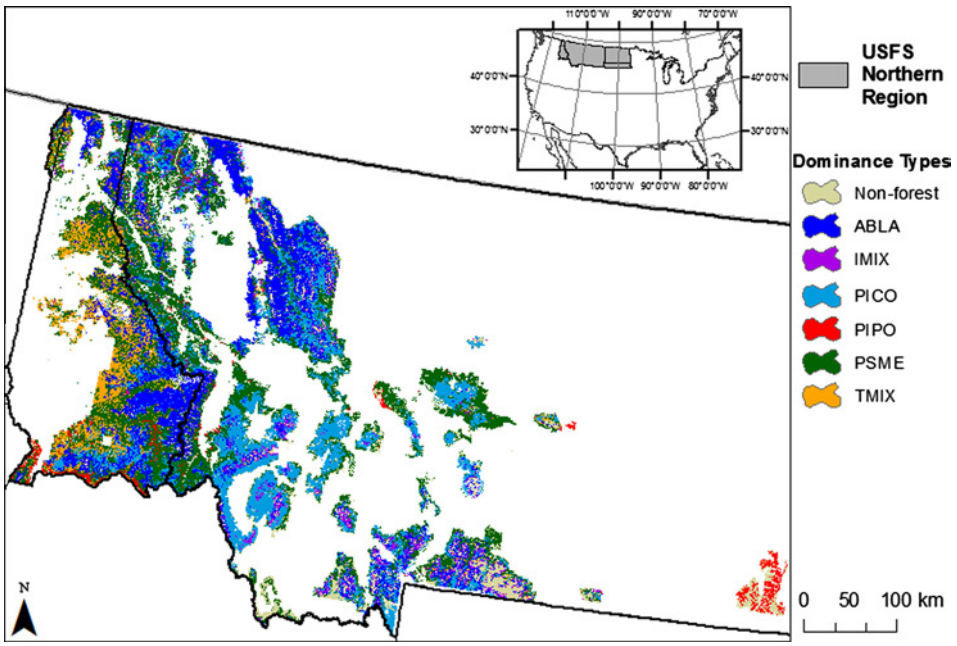

Fig. 1. The distribution of dominance type groups for the National Forest lands in the USFS Northern Region. Dominance type groups were assigned to stands using a series of algorithms based on the species with at least 60% abundance as measured by canopy cover, basal area, or stem density. Dominance type names are the first two letters of the scientific name of the dominant species: *Abies lasiocarpa* (ABLA), *Pinus contorta* (PICO), *Pinus ponderosa* (PIPO), *Pseudotsuga menziesii* (PSME), and two mixed species groups (shade-intolerant [IMIX] and shade-tolerant [TMIX]).

(Hook.) Nutt.), lodgepole pine (*Pinus contorta* Doug. ex Loud.), and Engelmann spruce *(Picea engelmannii* Parry ex Engelm). Species at treeline include whitebark pine (*Pinus albicaulis* Engelm.) and limber pine (*Pinus flexilis* James). Forests in eastern Montana and South Dakota are dominated by Douglas-fir and ponderosa pine and transition from forests to woodlands and grasslands.

2.2. Inventory data

We used inventory data from 5432 FIA plots on the USFS ownership in the Northern Region. Plots are located at a rate of one for each 2400-hectare cell in a hexagonal sampling grid that extends across the country (Reams et al., 2005). Plots were measured as part of either the older periodic inventory or the more recent annualized inventory. One objective for using FIA data was to maximize the amount of randomly distributed inventory data to define initial conditions and inform simulations, so we used inventory data from both inventory designs. For the older periodic inventory design, all plots on national forest lands in a state were measured at one time. For the current annual inventory design, the sample is distributed randomly among 5–10 "panels," which are measured at a rate of one panel per year. Of the 5432 plots used in this analysis, 3239 plots were measured in the periodic inventory between 1993 and 2010 and 2193 plots were measured in the annual inventory between 2001 and 2010.

All FIA inventory plots were classified into groups based on dominance type, a forest type classification used by national forests in the Northern Region (Fig. 1). The dominance type for each plot was determined using a series of algorithms implemented as a post-processor to FVS (Barber et al., 2011). The dominance type is assigned based on the lifeform and species with at least 60% abundance as measured by canopy cover, basal area, or stem density. We aggregated plots into six groups of dominance types: *Abies amabalis* (ABLA), *Pinus contorta* Douglas var. *latifolia* (Engelm.) (PICO), *Pinus ponderosa* (PIPO), *Psuedotsuga menseizii* (PSME), TMIX, IMIX. The TMIX group is comprised of plots dominated by other shade-tolerant species including grand fir (*Abies grandis* (Dougl.) Lindl. (Pinaceae)), Engelmann spruce, western hemlock, western redcedar, and mountain hemlock (Tsuga mertensiana (Bong.) Carriere. The IMIX group is comprised of plots dominated by other shade-intolerant species including western larch (*Larix occidentalis* Nutt. [Pinaceae]), whitebark pine, and Douglas-fir. We excluded from the analysis FIA plots that had multiple forested conditions because these plots are inherently ambiguous with respect to a forest type classification such as dominance type. An FIA plot is designated as having multiple conditions if portions of the plot have different forest types, ages, land uses, or structures. However, we did include plots with multiple conditions if only one condition was forested, in which case forest attributes were weighted by the forested area of the plot. The number of excluded plots was 283, less than 5% of the total plots (from both periodic and annual inventories) on national forest lands.

2.3. Modeling carbon accumulation with the Forest Vegetation Simulator

We used FVS to model 100-years of total C stocks (excluding soil) for all 5432 FIA plots without disturbance and following three types of disturbance: fire, bark beetle, and harvest. FVS is a semi-distance-independent growth and yield model (Dixon, 2002) that uses a stand (i.e. FIA plot) as the population and simulates growth and density-dependent mortality of individual trees over time. Growth and mortality are a function of site conditions (aspect, slope, elevation, plant association and habitat type), stand characteristics (basal area and crown competition factor), and tree characteristics (species, height, live crown ratio, and site index) (Dixon, 2002). Model variants of FVS have regional parameters for growth and mortality functions by species. We used the Inland Empire variant (Keyser, 2008) because it is the most commonly used and well-validated variant for the Northern Region. We calibrated the growth increment models for small-tree height and large-tree diameter for each of the six dominance type groups using the self-calibration feature in FVS. Calibration uses an independent dataset of diameter and height growth increment measurements

to predict multipliers, which we applied to the base growth increment models for each species (Vandendriesche, 2010).

FVS requires as input tree-level variables of live and dead trees (species, height, diameter, crown ratio, and number of trees represented by the record) and site-level variables (e.g. slope, aspect, and habitat type). We used FVS to estimate total C in all above and belowground live and dead biomass pools for each FIA plot (referred to hereafter as a "stand") (Hoover and Rebain, 2011; Rebain, 2010). We used the option in FVS to calculate biomass in aboveground components of live trees with equations from Jenkins et al. (2003), which predict biomass based on tree diameter, height, and species. The FIA inventory includes measurements of standing dead trees, which FVS converts to volume and then biomass using wood density (Rebain, 2010). Of the 5423 FIA plots, 197 included field observations of downed woody debris and forest floor (litter and duff), which we used as initial estimates of biomass in non-tree C pools for these plots. For all other FIA plots, we used the Fire and Fuels Extension (FFE) to FVS to estimate biomass in downed woody debris, understory vegetation, and forest floor. Downed woody debris and forest floor biomass are estimated as a function of the dominant cover type and percent canopy cover (Rebain, 2010). Understory biomass is estimated as a function of dominant tree species and percent cover (Rebain, 2010). Cover type, dominant species (by basal area), and percent cover are calculated from the input tree data. Biomass is converted to C using a conversion factor of 0.5, except forest floor biomass which uses a factor of 0.37 (Rebain, 2010). FFE-FVS simulates snag fall, litter fall, and decomposition of these dead C components over time after initialization.

We simulated 100-years of total stand C with and without disturbance for all 5432 stands individually. We used FVS as a deterministic model because, although it can be run stochastically, current model structure makes it computationally prohibitive to simulate and process multiple iterations for a large number of stands. Furthermore, stochasticity in FVS is implemented as small variations in diameter increment, which introduce only a small amount of variability in growth relative to the high variability in initial conditions represented by many stands (e.g. Hummel et al., 2013). FVS uses model extensions to simulate disturbance effects on multiple tree-level processes including consumption, mortality, growth release, regeneration, and transfer between C pools. Growth and mortality are simulated in 10-year time steps in the Inland Empire variant, so live C pools change only at the boundaries of the 10-year time steps (Rebain, 2010). Decomposition and transfer among dead C pools are simulated in annual time steps, but dead pools receive input from live pools only every 10 years.

We quantified the effects of five silvicultural treatments, clear-cutting and four levels of thinning, on total C for each stand. We selected treatments to represent the range of treatments commonly used in the region to attain forest management objectives of timber production, wildfire habitat, or fuel reduction. The clear-cutting treatment removed all trees with a diameter >12.7 cm. For the four thinning treatments, stands were thinned starting with the smallest dbh until a prescribed level of residual basal area (m^2 ha^{-1}) was met: 5, 14, 23, and 32. We simulated harvest only for stands that met minimum basal area requirements. All C from harvested trees was assumed to be transferred off site except roots, which were transferred to dead C pools (Hoover and Rebain, 2011).

We quantified the effects of fire on total stand C by simulating a fire, followed by 100 years of growth, mortality, and regeneration. In FVS, fire-caused tree mortality is a function of species and fire behavior, which is driven by fuel availability, fuel moisture, and fire weather. Fires consume 100% of foliage and 50% of small branches (<0.6 cm) for the portion of the tree crown that is within the fire and the remaining mortality is transferred to dead C pools (Scott and Reinhardt, 2001). Similarly, consumption of dead biomass is a function of fire behavior, fuel moisture, and fuel size (Rebain, 2010). We simulated two fire scenarios for each stand, one with mild fire weather and wet fuel moisture and one with moderate fire weather and drier fuel moisture (Appendix A, Table A.1).

We quantified the effects of bark beetle epidemics on total stand C by simulating additional tree mortality added to background mortality as a function of tree species and size, and stand density. Bark beetle species preferentially select trees of a specific species, with larger diameters, and in stands with higher densities of host species (Bentz, 2000; Cole and McGregor, 1983), so mortality rates were set higher for larger trees and susceptible species. We simulated tree mortality from bark beetles for four years, followed by 96 years of density-dependent growth, regeneration, and mortality. Stands were included in bark beetle simulations if they had a sufficient density of host species that are large enough to be susceptible to beetles (Randall et al., 2010). Epidemics of mountain pine beetle (*Dendroctonus ponderosae* Hopk.) in forests with Pinus spp. are more common in higher density stands (Bentz, 2000), so beetle-caused mortality was triggered in FVS when stands had a minimum basal area of 11.5 m^2 ha^{-1} of lodgepole pine or ponderosa pine or a minimum basal area of 6.9 m^2 ha^{-1} of whitebark pine or limber pine. Beetle-caused mortality in Douglas fir and *Abies* spp. is dependent on having large trees in a stand (Bentz, 2000), so for these tree species beetle-caused mortality was triggered in stands that had trees greater than 25.4 cm in diameter. As with fire, we simulated two scenarios of bark beetle epidemics, a mild and extreme event for each stand (n = 4559) (Appendix A, Table A.2).

We classified the severity of fires and bark beetle epidemics as the percent change in percent canopy cover (the difference between pre-disturbance canopy cover and post-disturbance canopy cover divided by pre-disturbance canopy cover). We grouped all simulation results (10,864 for fire and 9118 for bark beetle epidemics) into quartiles of percent change in percent canopy. We used change in percent canopy cover as a metric of disturbance severity because of its applicability for detecting disturbances of different severity with Landsat-based remote sensing (Healey et al., 2006). For harvest simulations (15,446), we quantified severity as percent change in aboveground live tree C (ABGLTC) and grouped all simulation results into quartiles of percent change in ABGLTC. We used live tree C as a metric of harvest severity because historical data on harvest volume (USFS, 2013) can be converted to live tree C (Smith et al., 2006) and used to constrain estimates of harvests for national forest units.

Regeneration is simulated automatically in the Inland Empire variant but regeneration parameters vary by disturbance type. The variant simulates a pulse of seedling regeneration for up to 20 years following fires and harvests that significantly reduce tree density (Dixon, 2002). The density of regeneration and the time over which it is added depend on how much the simulated fires and harvests reduce tree density. The variant also periodically simulates ingrowth, the addition of seedlings and small trees, in the absence of disturbance and when stocking is below maximum potential. Simulated ingrowth is a function of overstory tree density and species composition. A short-term pulse of regeneration is not simulated following bark beetle epidemics, but lower stocking because of insect-caused tree mortality will increase ingrowth rates.

2.4. Statistical analysis

We fit regression models of total stand C as a function of time since disturbance (or time since initial measurement in undis-

Table 1
Summary statistics of pre-disturbance stands by dominance type and initial level of aboveground live tree carbon (ABGLTC).

	N	Aboveground live tree carbon (Mg ha^{-1})		Total stand carbon (Mg ha^{-1})		Basal area (Mg ha^{-1})		Percent canopy cover	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Abies lasiocarpa (ABLA)									
1	177	11.9	8.0	51.9	19.8	5.6	4.0	20	15
2	184	40.3	7.5	103.4	19.5	18.1	4.2	41	14
3	191	64.9	6.9	141.2	18.8	27.7	5.0	48	12
4	169	104.0	28.5	189.2	37.0	39.7	9.1	54	12
Shade-intolerant mix (IMIX)									
1	167	13.4	8.9	43.6	23.9	6.7	4.6	22	17
2	173	39.9	8.2	85.8	21.7	19.0	4.9	42	15
3	159	66.7	7.5	126.1	21.8	29.4	6.0	53	13
4	164	108.9	24.7	185.7	43.8	44.5	11.0	63	12
Pinus contorta (PICO)									
1	314	17.5	13.0	58.2	24.0	9.4	7.0	30	20
2	309	46.8	5.0	95.8	15.2	24.6	4.5	50	12
3	317	63.9	5.0	118.4	13.3	32.6	5.6	57	11
4	306	92.6	16.3	155.8	23.9	44.8	8.9	63	9
Pinus ponderosa (PIPO)									
1	63	9.3	5.7	20.0	12.8	4.5	2.8	14	11
2	57	27.0	4.9	42.7	7.9	11.8	3.2	28	12
3	54	46.1	6.0	70.0	11.0	19.1	4.8	38	13
4	67	91.4	30.3	128.0	40.4	31.6	9.8	45	12
Psuedotsuga menseizii (PSME)									
1	354	25.0	13.0	52.4	23.0	9.0	4.9	30	17
2	353	61.0	8.9	100.6	16.7	20.8	4.7	48	13
3	338	91.6	8.3	141.7	16.6	30.8	5.3	57	12
4	344	140.2	33.6	202.9	46.4	43.4	10.8	64	11
Shade-tolerant mix (TMIX)									
1	271	22.6	14.3	72.8	37.4	9.6	6.0	31	20
2	316	66.2	10.6	147.2	33.8	26.4	5.9	55	17
3	303	100.2	9.5	194.0	30.2	38.2	5.9	61	15
4	282	158.0	40.8	274.2	61.3	54.2	12.8	69	14

turbed stands) to the 100-year simulations because FVS effectively only simulates C in 10-year time steps creating discontinuous functions of C stocks with time. For statistical analysis, we grouped stands by disturbance type (undisturbed, fire, harvest, and bark beetle), disturbance severity (four levels of percent change in percent canopy cover), dominance type (six types), and pre-disturbance ABGLTC (four levels) (Table 1). The four levels of ABGLTC were calculated by dominance type as quartiles (25, 50, 75, and 100) of the frequency distribution of the initial values of ABGLTC for all stands. Groups were combined when they included less than five stands. We assumed dominance types remained constant for the 100-year simulation. To maintain independence for statistical analysis, we did not include the same stands in a group if the stands were classified as the same severity level, despite different scenarios. For example, if the high and low fire scenarios caused less than 25% loss of canopy cover for the same stand, we randomly selected one scenario to include in a group.

We used generalized estimating equations (GEE) (Hardin and Hilbe, 2003) to fit models of total C as a function of time since disturbance (year) for each group separately. GEE account for correlation among repeated measures of the same subject over time. We treated total C in each 10-year time step as a repeated measurement of the same stand. We fit GEE models using the geeglm function in the R statistical software package (R Core Development Team, 2013). We used an AR(1) correlation structure to account for the temporal autocorrelation of individual stands. This correlation structure was determined using *quasilikelihood under the independence model information criterion* (QIC). QIC is an adaptation of *Akaike's information criterion* (AIC) for GEE, which are quasilikelihood-, rather likelihood-based models (Hardin and Hilbe, 2003; Pan, 2001). For most groups the relationship between the log of total C and year appeared non-linear and variance increased with time, so we used nonparametric B-spline methodology (Racine, 2012) to fit polynomial functions. A B-spline is defined by its degree (as with a polynomial equation) and the number of internal knots, which increase flexibility in the shape of the curve. We used the default value (the median) for the location of internal knots. For each group, we fit linear, cubic, and quadratic B-splines with and without internal knots. We selected the best fitting model based on QICu (Burnham and Anderson, 2010; Hardin and Hilbe, 2003). If a model with additional terms reduced QICu by 2 or more, we selected the model with more terms. For most groups, the best fitting model was a three-degree B-spline without an internal knot, but an internal knot improved model fit for some groups.

The regression models are the mean response for multiple initial conditions (i.e. FIA plots within groups), and thus are representative regional trends in C stocks following disturbance for each combination of dominance type, ABGLTC level, disturbance type, and disturbance severity. For example, we fit one model for all TMIX stands with 50–75 percentile ABGLTC, and a fire that caused 50–75% canopy cover loss (Fig. 2). Thus each fitted model represents at least 5 and up to hundreds of simulated stands all with the same grouping factors but high variability among individual stand responses (Fig. 2). We compared these fitted models of post-disturbance C accumulation in terms of three aspects of C dynamics: (1) number of years before the mean stand response shows a C sink (i.e. positive net ecosystem productivity); (2) mean number of years necessary to accumulate to pre-disturbance stocks (i.e. positive net ecosystem C balance); and (3) mean number of years for C accumulation of disturbed stands to meet or exceed that of undisturbed stands (fire only). We compare the latter for C accumulation after fire only because, unlike fire simulations, bark beetle epidemics and harvest were not simulated for all stands and are thus not directly comparable. Bark beetle epidemics and harvests were simulated on a subset of stands meeting minimum requirements for susceptibility to disturbance.

Table 2
Mean (S.D.) and percent (S.D.) of carbon (Mg ha^{-1}) released from fire for each of the four severity classes. Severity classes are defined as percent change in percent canopy cover form before and after the fire: 0–25%, 25–50%, 50–75%, and 75–100%. Groups with less than five stands (indicated by NA) were combined.

Dominance type	Severity 1				Severity 2				Severity 3				Severity 4			
Initial ABGLTC	Mean (S.D)		Percent (S.D)		Mean (S.D)		Percent (S.D)		Mean (S.D)		Percent (S.D)		Mean (S.D)		Percent (S.D)	
Abies lasiocarpa (ABLA)																
1	NA		NA		12.24	(4.56)	29.1	(13.5)	17.10	(6.67)	32.6	(13.5)	16.6	(10.31)	42.2	(16.1)
2	NA		NA		17.96	(7.00)	17.6	(7.0)	21.79	(8.09)	21.5	(8.1)	45.2	(2.84)	41.3	(6.9)
3	NA		NA		19.30	(7.72)	13.9	(5.8)	24.44	(8.70)	17.2	(6.1)	39.3	(10.97)	29.6	(7.6)
4	NA		NA		25.44	(8.97)	13.5	(5.0)	25.22	(9.19)	14.5	(5.5)	48.7	(3.67)	27.4	(3.7)
Shade-intolerant mix (IMIX)																
1	7.99	(3.62)	28.1	(19.2)	7.77	(4.13)	19.7	(10.9)	10.89	(7.65)	25.3	(13.9)	13.6	(16.72)	38.2	(18.8)
2	9.69	(4.35)	14.5	(6.2)	12.80	(7.06)	14.6	(6.5)	17.37	(8.97)	18.9	(7.8)	26.7	(11.75)	30.8	(6.9)
3	10.45	(4.54)	8.8	(3.6)	14.39	(7.88)	11.4	(5.2)	21.52	(11.15)	15.7	(6.6)	31.1	(12.91)	22.1	(7.6)
4	17.01	(12.63)	8.2	(3.7)	17.74	(10.48)	9.7	(5.3)	22.28	(9.03)	12.7	(5.0)	41.1	(11.54)	20.8	(5.1)
Pinus contorta (PICO)																
1	NA		NA		10.32	(3.45)	25.7	(16.7)	12.02	(3.97)	20.7	(8.2)	18.7	(6.78)	41.7	(15.9)
2	NA		NA		13.35	(4.06)	14.1	(4.8)	14.15	(5.22)	15.1	(6.0)	27.3	(4.05)	28.5	(5.0)
3	NA		NA		14.22	(4.60)	12.0	(4.2)	15.04	(5.45)	12.9	(4.9)	29.8	(3.66)	25.1	(3.4)
4	NA		NA		14.37	(4.55)	9.2	(3.4)	14.83	(4.78)	10.1	(3.6)	32.9	(3.01)	21.0	(2.7)
Pinus ponderosa (PIPO)																
1	2.35	(1.24)	20.2	(21.1)	2.27	(0.82)	11.6	(3.5)	2.77	(1.26)	26.8	(19.3)	5.33	(2.62)	31.1	(16.7)
2	2.65	(0.59)	6.8	(1.8)	4.30	(1.09)	9.7	(2.3)	NA		NA		8.43	(2.99)	19.2	(5.4)
3	3.86	(0.90)	5.9	(1.4)	5.38	(1.35)	7.4	(1.6)	NA		NA		10.79	(4.38)	15.0	(4.8)
4	5.53	(1.58)	4.7	(2.0)	6.55	(2.58)	5.6	(1.9)	NA		NA		13.31	(3.31)	10.8	(2.9)
Psuedotsuga menseizii (PSME)																
1	7.62	(2.94)	19.3	(15.6)	7.66	(2.00)	15.5	(8.2)	7.88	(3.03)	29.2	(16.1)	15.8	(4.52)	33.5	(12.9)
2	7.95	(2.23)	8.2	(2.7)	8.02	(1.75)	8.1	(2.1)	NA		NA		20.0	(3.10)	20.0	(3.7)
3	8.09	(1.69)	5.8	(1.3)	8.07	(1.17)	5.8	(1.0)	NA		NA		22.6	(3.89)	16.0	(2.8)
4	8.18	(1.63)	4.2	(1.2)	8.58	(2.40)	4.7	(1.2)	NA		NA		25.1	(4.22)	12.9	(2.6)
Shade-tolerant mix (TMIX)																
1	10.83	(6.43)	31.8	(15.8)	14.51	(6.71)	20.6	(11.7)	16.19	(7.52)	25.6	(13.7)	23.2	(15.13)	34.8	(15.2)
2	17.56	(7.29)	12.1	(5.2)	21.60	(10.92)	14.3	(6.1)	23.59	(10.83)	16.38	(6.1)	46.7	(13.59)	28.6	(6.9)
3	22.97	(7.45)	12.4	(4.1)	23.18	(11.49)	11.6	(5.1)	22.83	(9.83)	11.86	(4.3)	49.5	(13.82)	24.3	(5.0)
4	23.95	(12.20)	8.2	(3.6)	25.92	(11.17)	10.0	(4.0)	24.72	(13.85)	9.71	(4.5)	53.8	(12.54)	19.5	(3.8)

3. Results

3.1. Forest carbon accumulation following fire

Following fire, the time required for the mean response to show a C sink and return to pre-fire C stocks increased with increasing severity and levels of ABGLTC. Fires of all severities caused an initial decline in C through consumption, and this decline increased with increasing severity. The absolute value of C released by fire generally increased with increasing severity and initial levels of ABGLTC (Table 2). The percentage of C released by fire was as low as 4% of total C for low-severity fires in stands with high initial ABGLTC. For the highest severity fires, the percentage C released was as high as 30–40% in stands with low initial ABGLTC (Table 2). For stands with high initial ABGLTC, the highest severity fires released 11–27% of initial C and this varied among dominance types with PIPO having the lowest consumption and ABLA having the highest (Table 2).

After initial consumption, total C stocks continued to decline for most groups. Averaged for all dominance types and levels of ABGLTC, the mean response showed stands becoming a C sink in 5, 6, 14, and 23 years for low- to high-severity fires (Table 3). The time before stands became a C sink was more similar among levels of ABGLTC. Averaged for all dominance types and severities, stands became a C sink in 9, 14, 20, and 16 years for low to high levels of ABGLTC (Table 3). On average, pre-fire C stocks were recovered in an additional 25–55 years after stands became a sink. Averaged for all dominance types and levels of ABGLTC, the mean recovery time was 35, 41, 56, and 78 years for low to high severities (Table 4). Similarly, the C recovery time averaged for all dominance types and severities was 30, 44, 56, and 72 years for low to high levels of ABGLTC (Table 4). For most groups, C stocks did not reach or exceed undisturbed stands in 100 years, except for stands with the lowest severity fires and lowest two levels of ABGLTC (Figs. 3 and 4).

Variability, as indicated by the standard error of the model (the uncertainty associated with predicting a new value) was greatest for the highest severity fires and increased with time for these models, indicating divergence in C accumulation in individual stands. Models for the lowest level of initial ABGLTC had the least differences among severity classes and this was consistent across all dominance types, suggesting that disturbance severity exerts less influence on C dynamics when initial C stocks are low at the time of disturbance. For two dominance types, PIPO and PSME, models for moderate-severity fires also showed little distinction except for the highest levels initial ABGLTC.

Post-fire C recovery patterns varied among dominance types. The ABLA and PICO dominance types showed similar mean response for C accumulation for three levels of severity (0–50%, 50–75%, and 75–100% canopy cover loss, Fig. 3). Carbon released by fire increased with increasing severity, but was much higher for the highest severity class than the lower classes. After initial consumption, the decline in C stocks lasted longer in ABLA and PIPO than other dominance types (10–45 years), and increased with increasing severity and levels of ABGLTC. In 100 years, C stocks recovered to pre-fire levels or above for all but the two highest severity classes and the highest level of initial ABGLTC. Of the groups that did recover to pre-fire C stocks, recovery times for ABLA and PICO were generally longer than for other dominance

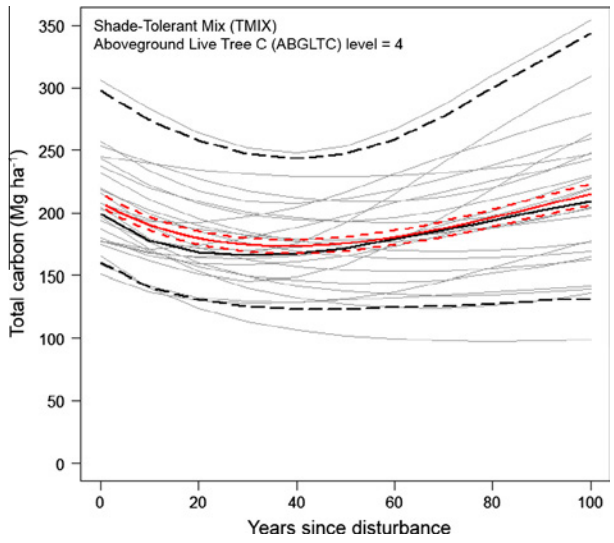

Fig. 2. An example of a GEE model of total stand carbon (C) as a function of time since disturbance for one group of stands: dominance type is shade-tolerant mix (TMIX), ABGLTC level is 4, disturbance type is fire, and disturbance severity is level 3 (50–75% canopy cover loss). Grey lines show C accumulation for individual stands. Black lines are the mean, and 2.5 and 97.5 percentiles for all stands in the group. The solid red line is the fitted model and the dashed red lines are +/− one standard error of the model. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Mean time (years) until stands become a carbon sink after disturbance as a function of disturbance type, disturbance severity, and initial carbon level.

Disturbance severity class	Disturbance type		
	Fire	Bark beetle	Harvest
0–25	5	4	1
25–50	6	17	5
50–75	14	25	15
75–100	23	34	12
Live aboveground tree carbon level			
1	9	11	3
2	14	16	7
3	20	22	10
4	16	31	13

Table 4
Mean time (years) before stands recover pre-disturbance carbon stocks as a function of disturbance type, disturbance severity, and initial carbon level.

Disturbance severity class	Disturbance type		
	Fire	Bark beetle	Harvest
0–25	35	7	25
25–50	41	41	54
50–75	56	60	66
75–100	78	76	61
Live aboveground tree carbon level			
1	30	23	12
2	44	35	43
3	56	52	62
4	72	74	88

types, with a low of 35 years and a high of 99 years. In 100 years, C stocks following fire in almost all groups remained below that of undisturbed stands, except for the lowest severity and lowest ABGLTC in the PICO dominance type.

Carbon accumulation post-fire in the four other dominance types (IMIX, PIPO, PSME, and TMIX) showed greater variability among severities and levels of ABGLTC than did PICO and ABLA. For PSME, post-fire C accumulation was similar for the two lowest severity classes (0–25% and 25–50% canopy cover loss) (Fig. 4). On average, stands with low-severity fires, s became a sink in the first year and recovered to pre-fire C stocks within 20 years, but total C remained below that of the undisturbed stands for the full 100 years. In contrast, stands with the highest severity fires (50–100% canopy cover loss) became C sinks in 15–30 years, recovery of pre-fire C stocks required 40–95 years, and all groups remained well below undisturbed groups regardless of ABGLTC level. Post-fire C accumulation in PIPO, IMIX, and TMIX forests was more rapid and more C accumulated in 100 years than in ABLA, PICO, and PSME forests. For low-severity fires (0–25% and 25–50% canopy cover loss), stands became a C sink in the first year. Total C stocks exceeded pre-fire stocks for all groups except moderate-severity fires (50–75% canopy cover loss) and high levels of ABGLTC in TMIX and IMIX forests. C accumulation in stands with low levels of ABGLTC, including some for the highest severity fires, exceeded C accumulation in undisturbed stands within 100 years. For these three dominance types, C accumulation following the highest severity fires was more rapid than following moderate-severity fires (50–75% canopy cover loss) and more C accumulated in 100 years. Moderate-severity fires had the least accumulation of C in 100 years and on average stands remained a C source for the longest time (up to 40 years).

3.2. Forest carbon accumulation following bark beetle epidemics

Relative to fire, C accumulation following bark beetle epidemics generally showed less recovery to pre-disturbance C stocks in 100 years and on average stands remained a source of C for longer, especially for high-severity epidemics and high levels of initial ABGLTC. C accumulation following the highest severity epidemics did not show rapid rates of accumulation, as did those after high-severity fires (Figs. 5 and 6). For a given severity and ABGLTC level, stands were a C source for an average of 10 years longer than after fire (Table 3) and up to 40 years longer for some groups. Only IMIX stands became a C sink sooner after bark beetle epidemics than after fire. In contrast, the time required to recover pre-disturbance C stocks was similar for bark beetle epidemics and fire, except for the lowest severity epidemics, which generally recovered pre-disturbance stocks sooner than fire (Table 4). For low-severity epidemics, pre-disturbance C stocks were recovered in 7 years on average, but most groups recovered to pre-disturbance C stocks in the first year. The time required to reach pre-disturbance C stocks was longer for the three higher severity classes at 41, 60, and 76 years. As with fire, the time required to reach pre-disturbance C stocks increased with increasing levels of initial ABGLTC.

Model error was generally smaller and differences among models by severity class were greater for the mean response following bark beetle epidemics compared to fire. Differences among severity classes increased with increasing levels of initial ABGLTC for all disturbance severities and only a few models had similar rates of C accumulation, indicating the strong dependence of post-disturbance C accumulation on disturbance severity, regardless of forest type and initial levels of ABGLTC.

Carbon accumulation following bark beetle epidemics was generally more similar among dominance types than it was following fire. Forest types dominated by pine species (PIPO, IMIX, and PICO, Fig. 5) showed similar patterns to forest types dominated by Douglas-fir and *Abies* spp. (PSME, ABLA, TMIX, Fig. 6). Carbon accumulation in PIPO showed the most rapid recovery to pre-disturbance C stocks, the shortest amount of time as a

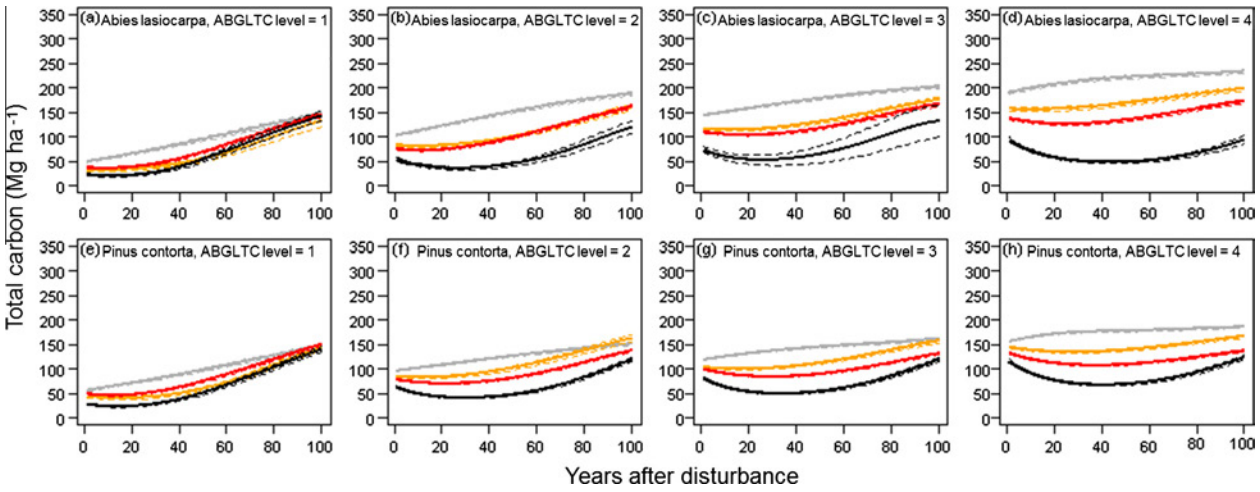

Fig. 3. Total stand carbon (C), excluding soil, as a function of time since fire for two dominance types: *Abies lasiocarpa* (ABLA), *Pinus contorta* (PICO). Within each dominance type, stands were grouped by quartiles of aboveground live tree C (ABGLTC). Solid lines are the mean stand response for three levels of fire severity, defined as percent change in percent canopy cover: orange (0–50%), red (50–75%), and black (75–100%). Dashed lines are +/− one standard error of the model. Grey lines are the mean response of stands without disturbance. The transition to a C sink occurs at the minimum point on all curves.

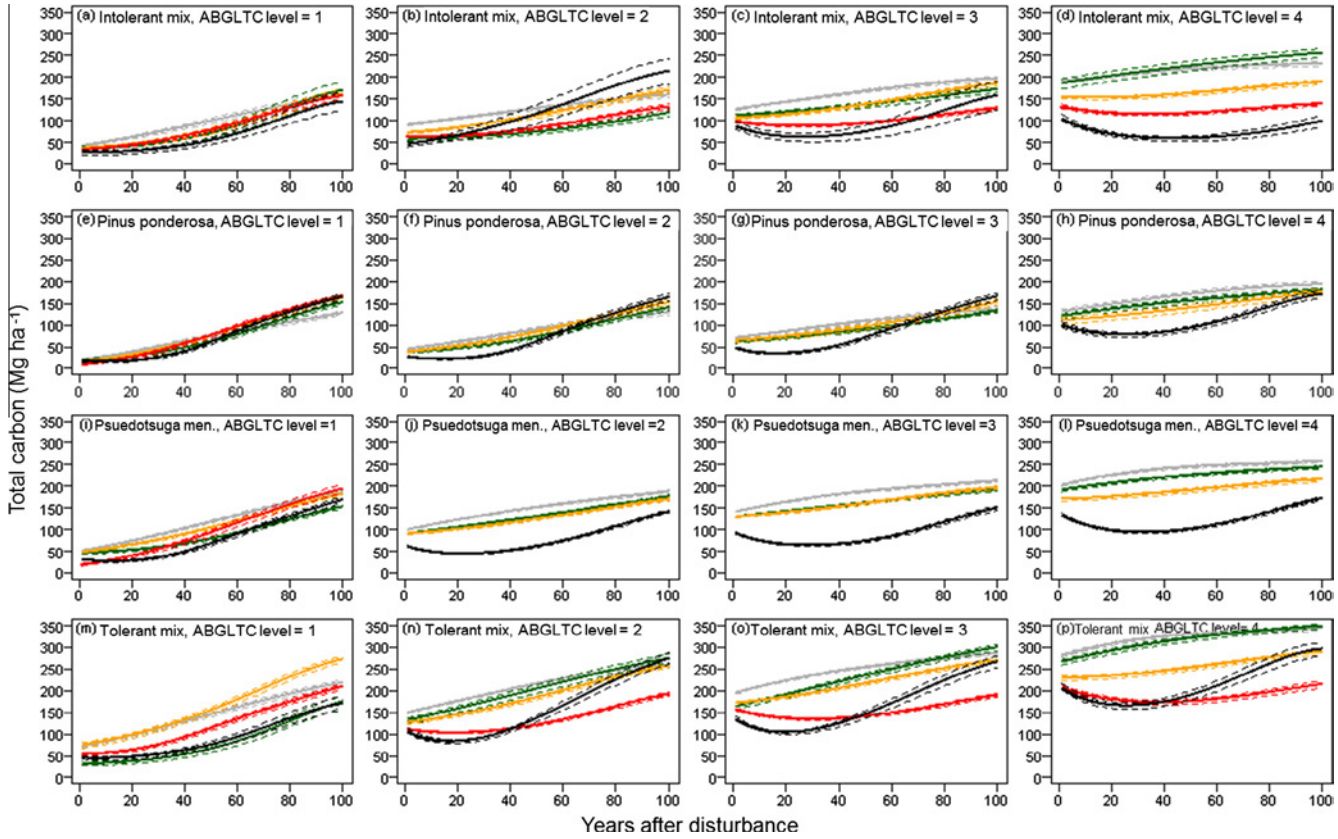

Fig. 4. Total stand carbon (C), excluding soil, as a function of time since fire for four dominance groups: *Pinus ponderosa* (PIPO), *Pseudotsuga menziesii* (PSME), and two mixed species groups (shade-intolerant [IMIX] and shade-tolerant [TMIX]). Within each dominance type, stands were grouped by quartiles of aboveground live tree C (ABGLTC) based on quartiles of pre-disturbance conditions. Solid lines are the mean response for four levels of fire severity, defined as percent change in percent canopy cover: green (0–25%), orange (25–50%), red (50–75%), and black (75–100%). Dashed lines are +/− one standard error of the model. Grey lines are the mean response of stands without disturbance. The transition to a C sink occurs at the minimum point on all curves.

C source, and all groups recovered to pre-disturbance C stocks in 100 years (Fig. 5). Among dominance types, the time required to reach pre-disturbance C stocks was longest for ABLA, IMIX, and PICO, and several groups with high-severity disturbance and high levels of ABGLTC did not reach pre-disturbance C stocks in 100 years.

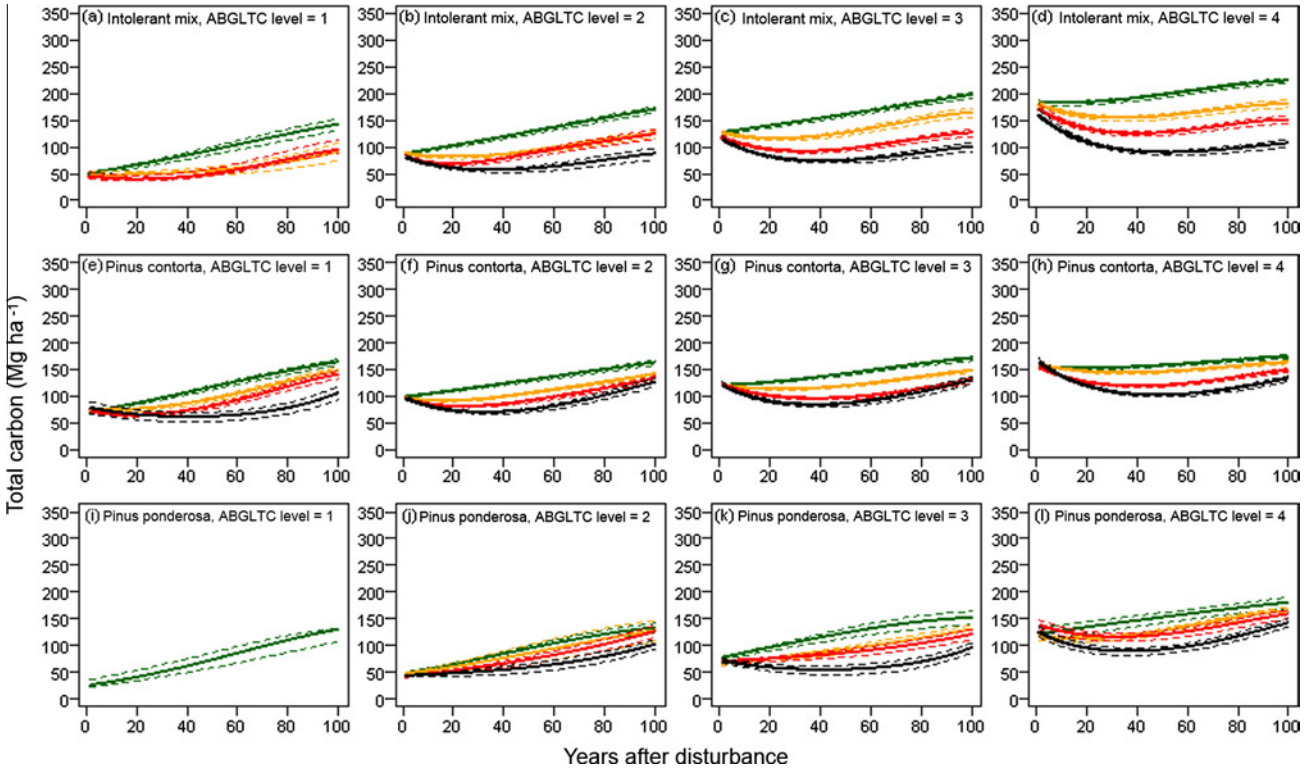

Fig. 5. Total stand carbon (C) as a function of time since, excluding soil, after bark beetle epidemics for three dominance type groups with susceptible pine host species: *Pinus contorta* (PICO), *Pinus ponderosa* (PIPO) a mixed-species group (shade-intolerant [IMIX]). Within each dominance type, stands were grouped by quartiles of aboveground live tree C (ABGLTC). Solid lines are the mean stand response for four levels of severity of insect-caused tree mortality, defined as percent change in percent canopy cover: green (0–25%), orange (25–50%), red (50–75%), and black (75–100%). Dashed lines are +/− one standard error of the model. PIPO and IMIX with an ABGLTC level equal to 1 had only one and three disturbance severity classes respectively. The transition to a C sink occurs at the minimum point on all curves.

3.3. Forest carbon accumulation following harvest

Relative to fire and bark beetle epidemics, trends in C stocks following harvest generally showed a larger initial decline but stands became a C sink sooner (Figs. 7 and 8). Averaged for all dominance types and levels of ABGLTC, stands showed a C sink in 1, 5, 15, and 12 years for low to high severity (Table 3). For harvest, the variability among severity levels was lower, with levels of ABGLTC showing little variation. Averaged for all dominance types and severity classes, stands became a C sink in 3, 7, 10, and 13 years for low to high levels of ABGLTC (Table 3). As with fire, the highest severity harvests showed the most rapid rate of C accumulation and stands became a C sink sooner than moderate-severity harvests in several groups, despite larger initial declines in C. The time required to reach pre-disturbance C stocks increased with increasing ABGLTC and severity, with the exception of the highest-severity harvests, which generally reached pre-disturbance C levels sooner than the next highest severity level. The time required to accumulate to pre-disturbance C stocks varied from 1 year for the lowest severity level and ABGLTC to more than 100 years for moderate-severity harvests and the highest ABGLTC. Higher levels of ABGLTC had a greater effect on increasing recovery time than did higher disturbance severity levels. Relative to bark beetle epidemics and fire, C accumulation after harvest was more similar among dominance types. PSME and TMIX (Fig. 8) showed greater differences among levels of severity and ABGLTC than did the other four dominance types.

Model error decreased and the differences among harvest severities increased with increasing levels of ABGLTC. This pattern was consistent for all dominance types. For the lowest levels of ABGLTC, several dominance types had little difference between models, with the exception of the highest severity class.

4. Discussion

Differences in the response of C stocks following disturbance quantified in our study demonstrate the importance of representing variability in disturbance effects as a function of initial C stocks, forest type, and disturbance type and severity when modeling the effects of disturbance on forest C. The rate and amount of C accumulation varied as a function of all four factors. For example, the high-severity fires simulated in this study are similar to the fires represented in most biogeochemical process models. Differences in post-fire C accumulation between high-severity fires and other levels of severity show the information that is lost when fire effects on C stocks are simplified to only high-severity (stand-replacing) disturbances. Furthermore, differences among forest types in C accumulation after high-severity fire demonstrate that species-specific tolerances and responses to fire can affect the timing and magnitude of C accumulation. In contrast to fire, C accumulation following bark beetle epidemics were more similar among forest types indicating less of an interaction effect between forest type and the severity of the bark beetle epidemic or initial levels of ABGLTC in stands with sufficient density to be susceptible to bark beetle epidemics.

4.1. Processes driving observed carbon dynamics

As documented in previous studies, forest stands often act as a C source following disturbance (Amiro et al., 2010) and the magni-

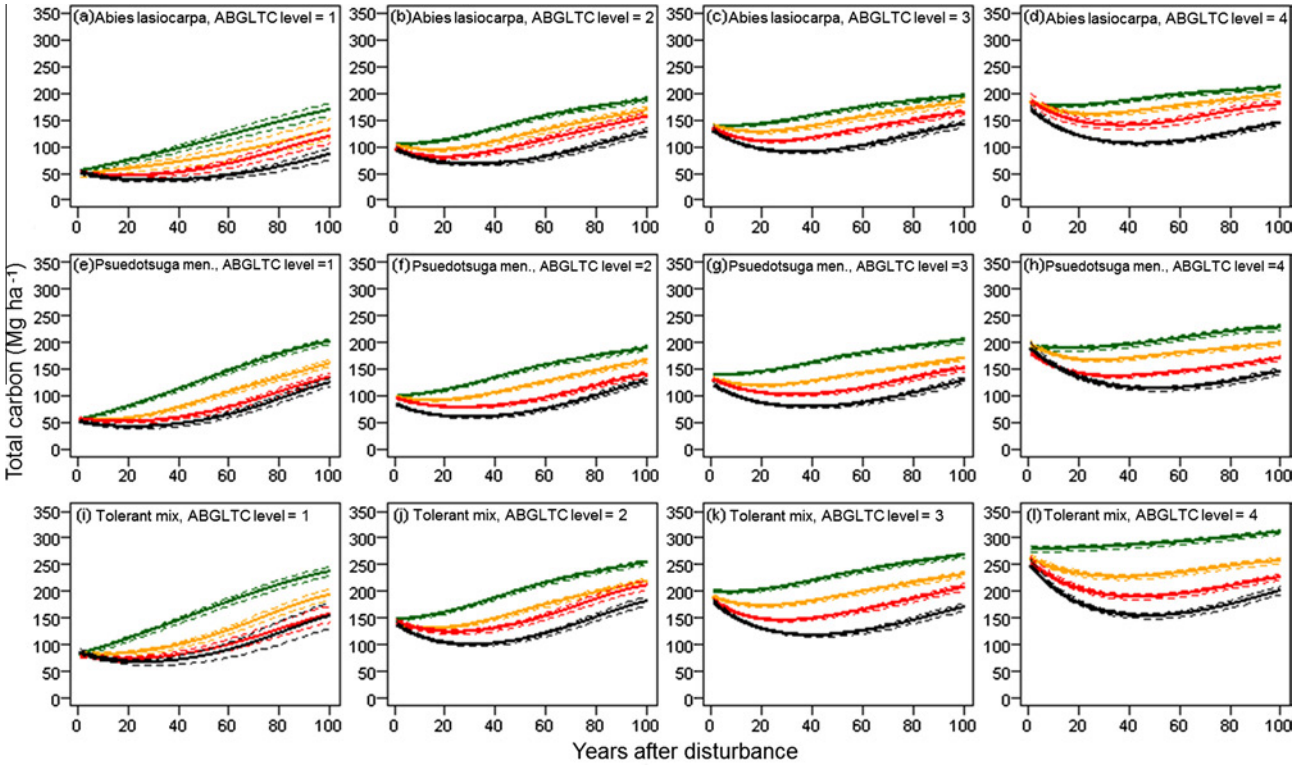

Fig. 6. Total stand carbon (C) as a function of time since, excluding soil, after bark beetle epidemics for three dominance type groups with less susceptible Douglas-fir and *Abies* spp.: *Abies lasiocarpa* (ABLA) and *Pseudotsuga menziesii* (PSME) and a mixed species group (shade-tolerant [TMIX]). Within each dominance type, stands were grouped by quartiles of aboveground live tree C (ABGLTC). Solid lines are the mean stand response for four levels of severity of insect-caused tree mortality, defined as percent change in percent canopy cover: green (0–25%), orange (25–50%), red (50–75%), and black (75–100%). Dashed lines are +/− one standard error of the model. The transition to a C sink occurs at the minimum point on all curves.

tude and duration of the source depends partially on disturbance severity for fire (Irvine et al., 2007; Meigs et al., 2009,) and bark beetle epidemics (Hicke et al., 2012; Pfeifer et al., 2011). During this time, net primary productivity is typically reduced and C dynamics are dominated by heterotrophic respiration (Hicke et al., 2012; Irvine et al., 2007), although lags have been observed in the decomposition of dead biomass from disturbance-caused tree mortality in ponderosa pine forests (Meigs et al., 2009). In our study, C emissions from heterotrophic respiration exceeded productivity for as little as 1 year following low-severity disturbances and up to 50 years following high-severity disturbances in stands with high levels of initial C. Following low-severity disturbances, less biomass is transferred to dead pools (Meigs et al., 2009) and more of the transferred biomass is in small trees that decompose rapidly (Harmon et al., 1986), which results in stands with low-severity disturbances becoming a C sink within 10 years in our study. Although high-severity fires emit more C initially through combustion, they also transfer more biomass to dead pools because of higher fire-caused tree mortality (Meigs et al., 2009) that includes more large trees which decompose slower.

In our study, differences in dominance types caused differences in the pattern and timing of C recovery following high-severity fire and harvest. After an initial 10–30 years as a C source, stands in four dominance types for fire and all six dominance types for harvest showed rapid rates of C accumulation, and within 100 years, C stocks exceeded that of stands with moderate-severity disturbances and even low-severity or no disturbances for some dominance types. These rapid rates of C accumulation likely can be attributed to three factors: (1) high growth rates of young regenerating trees, (2) high growth rates (due to growth release) of residual trees that survive fire, and (3) and lower rates of density-dependent mortality compared to stands with more trees surviving low-severity disturbances. The highest severity fires and harvests cause the greatest reduction in stem density, and tree regeneration and growth respond favorably to this reduction. In contrast, this pattern was not observed following high-severity fires in ABLA and PICO. Species in these dominance types are the most fire-intolerant, so few trees survive to experience density-dependent growth release. This fire-intolerance also causes high tree mortality, regardless of tree size, so large and small trees are transferred to dead biomass pools causing stands to act as a C source for longer.

The time necessary to reach pre-disturbance C stocks was similar following bark beetle epidemics and fire, despite differences in the fate of C affected by the disturbance. Relative to bark beetle epidemics, fire caused a larger initial loss of C, but C accumulated more rapidly. In contrast, the time before stands showed a C sink was generally higher for bark beetle epidemics than fire and lowest for harvest. Unlike fire, which releases C to the atmosphere immediately through combustion, bark beetle epidemics transfer all C in killed trees to dead pools. Furthermore, bark beetles preferentially kill large trees, thus a greater proportion of the biomass that is transferred to dead pools is in large trees which decompose slower (Kurz et al., 2008; Pfeifer et al., 2011). Both factors contribute to a longer period as a C source following bark beetle epidemics.

Differences in regeneration following fire, bark beetle epidemics, and harvest contribute to differences in carbon recovery. These differences are both ecological and a function of regeneration assumptions in FVS. In the northern Rocky Mountains, regeneration of several conifer species responds favorably to fire. Regeneration of ponderosa pine increases with mineral soil exposure. Cone serotiny in lodgepole pine causes high post-fire regeneration. However, these ecological differences in regeneration may be exaggerated by regeneration assumptions in FVS. For the Inland Empire

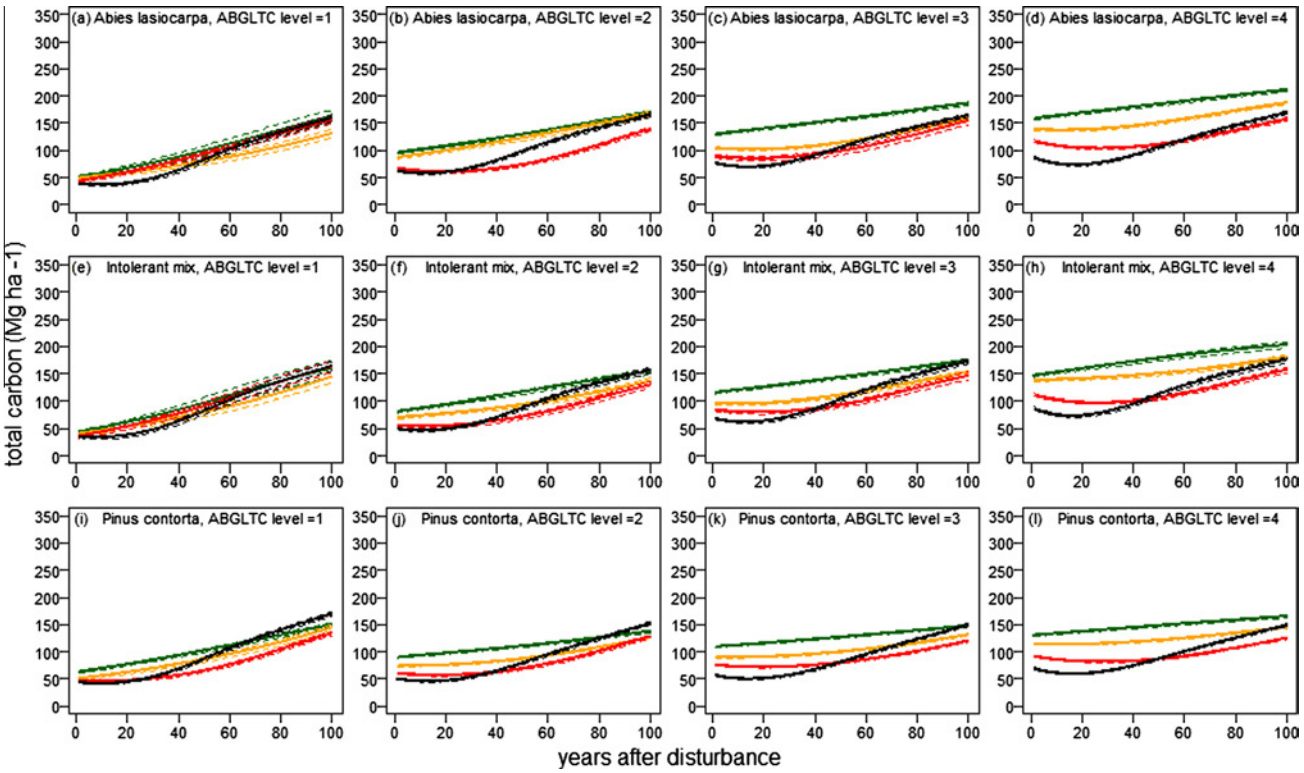

Fig. 7. Total stand carbon (C), excluding soil, as a function of time since harvest for three dominance types: *Abies lasiocarpa* (ABLA), *Pinus contorta* (PICO) and a mixed species group (shade-intolerant [IMIX]). Within each dominance type, stands were grouped by quartiles of aboveground live tree C (ABGLTC). Solid lines are the mean stand response for four levels of harvest severity, defined as percent change in percent aboveground biomass: green (0–25%), orange (25–50%), red (50–75%), and black (75–100%). Dashed lines are +/− one standard error of the model. The transition to a C sink occurs at the minimum point on all curves.

variant, regeneration after fire and harvest is simulated automatically, but regeneration after beetle epidemics must be initialized by the user. Thus C accumulation patterns following bark beetle epidemics do not reflect a pulse of regenerating trees. Additional trees are automatically simulated in the form of ingrowth at 20-year intervals and lower stand densities following bark beetle epidemics will trigger greater ingrowth. Therefore, the lack of immediate post-disturbance regeneration likely causes only a short delay in C recovery relative to fire and harvest, and the effect would be minimal after 20-years when ingrowth is simulated. Initializing regeneration immediately after bark beetle epidemics might increase productivity slightly, but it could also lead to earlier density-dependent mortality (Pfeifer et al., 2011). The consequences of regeneration for post-disturbance C recovery for all disturbance types remains an important area for further research (Kashian et al., 2006).

The post-disturbance patterns of C accumulation quantified in our study are the mean response of simulations of many individual stands. They encompass the range of post-disturbance C response for individual stands that have been measured with eddy covariance (Amiro et al., 2010; Hicke et al., 2012) or modeled with FVS (Pfeifer et al., 2011). Previous studies show that C release and accumulation following disturbance is a function of disturbance severity because of its influence on the amount of tree mortality; the amount, size, and species of residual trees; and the amount and size of biomass transferred to dead pools (Hicke et al., 2012; Pfeifer et al., 2011). It is difficult to compare our mean functions of C stocks with time since disturbance to observations of C accumulation following disturbance because most studies include only limited information on disturbance severity and emphasize stand-replacing disturbances and chronosequences based on stand age. However, in a review of disturbance effects on forest C, Amiro et al. (2010) found that eddy covariance measurements of disturbed forests show recovery to positive NEP in 20 years on average. In our study, stands with high-severity fire, bark beetle epidemics, and harvests generally required more than 20 years to show positive NEP, whereas stands with low-severity harvests and bark beetle epidemics showed positive NEP in less than 20 years and stands with low-severity fires showed positive NEP in less than 10 years. Unlike studies of individual stands, our study shows the mean response for a group of stands by forest type, initial C stocks, and disturbance type and severity.

FIA is likely the most comprehensive source of data on the variability in initial conditions of forest type and stand C. The goal of using FIA data in our study was not to estimate forest conditions across the region, which is a common use of FIA data, but to quantify average C accumulation following disturbance for a full range of initial forest conditions. We make use of FIA's designed sample (Reams et al., 2005) in populating simulations for each group of initial conditions, but our modeling dataset is not a true designed sample. Nevertheless, we describe the derived models of C stocks with time as "representative" because the simulations were initiated from as many randomly distributed FIA plots as possible from across National Forest lands in the region.

4.2. Variability and model assumptions

Prediction errors were small because the regression models were the mean response of many stands, but some models had higher prediction errors and more variability. Models for the lowest level of ABGLTC had the highest variability because these stands had large differences in dead biomass remaining from previous disturbances. This variability demonstrates that the legacy of past disturbances can continue to affect C dynamics even after

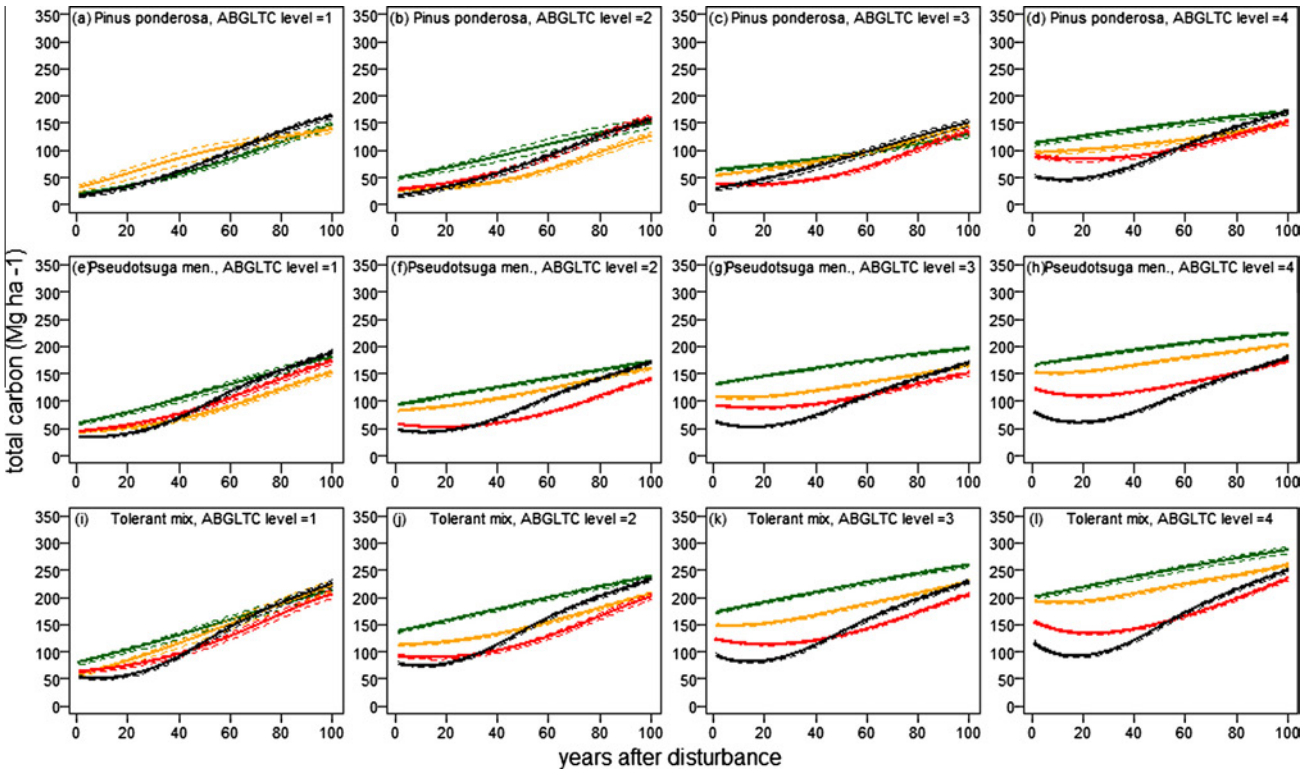

Fig. 8. Total stand carbon (C), excluding soil, as a function of time since harvest for three dominance types: *Pinus ponderosa* (PIPO), *Pseudotsuga menziesii* (PSME), and a mix of shade-tolerant species (TMIX). Within each dominance type, stands were grouped by quartiles of aboveground live tree C (ABGLTC). Solid lines are the mean stand response for four levels of harvest severity, defined as percent change in percent aboveground biomass: green (0–25%), orange (25–50%), red (50–75%), and black (75–100%). Dashed lines are +/− one standard error of the model. The transition to a C sink occurs at the minimum point on all curves.

subsequent disturbances. Prediction errors for models for high-severity disturbance increased with time, reflecting the greater variability introduced by differences in regeneration, ingrowth, and growth release of residual trees that is typical of high-severity disturbances.

Several assumptions in FVS are important to consider when evaluating the C stocks simulated in this study. FVS does not simulate the effects on tree growth of nutrient availability or fine root dynamics, so it cannot capture how changes in these factors following disturbance might increase or decrease growth of residual trees and thus C recovery (Rebain, 2010). FVS simulates only first order disturbance mortality. It does not simulate tree mortality caused by secondary factors such as root mortality or subsequent insect or pathogen outbreaks. We simulated all three disturbance types separately, so the models of C stocks as a function of time do not reflect the combined effects of interacting disturbances such as changes in fire severity in stands that previously experienced insect outbreaks (Hicke et al., 2012; Parker et al., 2006). FVS does not simulate C dynamics in soil layers below the organic layer (i.e. litter and duff). Carbon in mineral soil layers can increase or decrease following high-severity fires and harvests (Boerner et al., 2008; Johnson and Curtis, 2001), but disturbances primarily affect soil organic layers. Growth, decomposition, mortality, and regeneration are not driven by climate in FVS, so the model cannot simulate direct effects of climatic variability and change on these processes, although a climate-sensitive version of the model is in development (Crookston et al., 2010). The direct effects of climate will be an important driver of C stocks locally and in the long term, but in the short term, changes in disturbance extent and severity will likely have greater consequences for regional C budgets (Caspersen et al., 2000).

4.3. Applications for carbon accounting and modeling

The approach used in our study relies on publically available empirical data to refine the current understanding of post-disturbance C dynamics. These models quantify the mean C response as a function of forest type, initial stand C, and disturbance type and severity. The models can be used as a parsimonious alternative to biogeochemical process models or in combination with C accounting models that rely on a growth and yield tables. Knowledge gained through this approach has at least two applications: (1) assessing past C dynamics on landscapes when combined with remotely sensed data on vegetation and disturbance (e.g. Healey et al., 2014) and (2) quantifying the effects on C dynamics of potential shifts in disturbance regimes. Although, we present 100 years of C response for comparison, these models are not intended to be used to project 100 years in the future and will be better applied retrospectively or for shorter time periods in the future.

For retrospective assessments, regionally averaged models of C stocks following disturbance can be used to account for C storage associated with historical vegetation conditions and disturbance patterns monitored using remote sensing. The four forest attributes used to group the stands (forest type, disturbance type, disturbance severity, and ABGLTC) can be mapped using optical sensors such as Landsat and MODIS, calibrated and validated with inventory data. Disturbances from the last few decades have been mapped by type and severity (Eidenshink et al., 2007; Healey et al., 2008; Nelson et al., 2009; Schroeder et al., 2011), as have forest structural attributes such as biomass (Healey et al., 2006; Powell et al., 2010). Likewise, forest types similar to those used in our study can be mapped with inventory data and satellite imagery (Ruefenacht et al., 2008). Linking these regionally averaged models

of C response with spatial data on the four forest attributes provides a dynamic method for assessing the effects of disturbance on forest C in the last few decades (Healey et al., 2014).

Furthermore, by not relying on forest age, our method overcomes challenges associated with defining and mapping forest age. Spatial data on forest age is limited and maps of forest age do not distinguish between disturbance types, represent partial disturbances, or account for repeated disturbances in the same location (e.g., Pan et al., 2011). Thus models that rely on forest age cannot take advantage of remotely sensed data on disturbance severity, which is increasingly available through efforts such as the Monitoring Trends in Burn Severity program (Eidenshink et al., 2007) and the Interagency Aerial Detection Surveys for insects and diseases. Methods to detect disturbances from Landsat data are improving (e.g., Kennedy et al., 2010) and can now detect timber harvests (Healey et al., 2006) and fires (Meigs et al., 2011) of different severity.

Quantifying differences in C response as a function of forest type and disturbance severity is also important for quantifying consequences for forest C of climate-driven changes in disturbance regimes. Climate change is projected to increase the area affected by fire (Littell et al., 2009; Westerling et al., 2011) and bark beetles (Raffa et al., 2008), and it may also increase the severity of these disturbances (Bentz et al., 2010; Dillon et al., 2011), making it increasingly important to assess the effects of disturbance severity on C budgets. For example, our results suggest that a shift towards more high-severity fire would lead to longer delays in C recovery in some forest types. In other forest types, it could lead to more rapid recovery and greater C accumulation in 100 years because of regeneration and growth release of surviving trees.

Differences in C response among disturbance types is important for understanding potential positive feedbacks between increasing disturbance rates and GHG emissions from disturbances. Although C stocks recover faster after fire than after bark beetle epidemics, post-fire emissions of GHG may have greater consequences for climate change. The higher initial releases of GHG via combustion will reside in the atmosphere longer, thus contributing to warming more than would the same amount of GHG released slowly over time via decomposition of insect-caused tree mortality. Even if fire and insect epidemics reach the same level of C recovery in 100 years, the upfront release of C via fire will likely have greater consequences for climate change in the short term.

The response of C stocks to disturbance quantified in our study are based on a representative sample of forest conditions used to initiate a growth and yield model that simulates tree- and stand-level processes. Our approach captures a wider range of disturbance effects on forest C than is currently implemented in most biogeochemcal process models. By not relying on forest age, our method can take advantage of high-resolution Landsat-based data that can now detect disturbances of all severities, not just stand-replacing disturbances. When linked to spatial data as described above, these C accumulation models can be used to assess the effects of disturbance type and severity on forest C stocks over time and at regional and subregional scales in support of forest management policies at similar scales.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.09.038.

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