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Influence of stocking, site quality, stand age, low-severity canopy disturbance, and forest composition on sub-boreal aspen mixedwood carbon stocks

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Abstract: Low-severity canopy disturbance presumably influences forest carbon dynamics during the course of stand development, yet the topic has received relatively little attention. This is surprising because of the frequent occurrence of such events and the potential for both the severity and frequency of disturbances to increase as a result of climate change. We investigated the impacts of low-severity canopy disturbance and average insect defoliation on forest carbon stocks and rates of carbon sequestration in mature aspen mixedwood forests of varying stand age (ranging from 61 to 85 years), overstory composition, stocking level, and site quality. Stocking level and site quality positively affected the average annual aboveground tree carbon increment (C_{AAI}), while stocking level, site quality, and stand age positively affected tree carbon stocks (C_{TREE}) and total ecosystem carbon stocks (C_{TOTAL}). Cumulative canopy disturbance (DIST) was reconstructed using dendroecological methods over a 29-year period. DIST was negatively and significantly related to soil carbon (C_{SOIL}), and it was negatively, albeit marginally, related to C_{TOTAL}. Minima in the annual aboveground carbon increment of trees (C_{AI}) occurred at sites during defoliation of aspen (*Populus tremuloides* Michx.) by forest tent caterpillar (*Malacosoma disstria* Hubner), and minima were more extreme at sites dominated by trembling aspen than sites mixed with conifers. At sites defoliated by forest tent caterpillar in the early 2000s, increased sequestration by the softwood component (*Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss) compensated for overall decreases in C_{AI} by 17% on average. These results underscore the importance of accounting for low-severity canopy disturbance events when developing regional forest carbon models and argue for the restoration and maintenance of historically important conifer species within aspen mixedwoods to enhance stand-level resilience to disturbance agents and maintain site-level carbon stocks.

Key words: forest carbon, forest disturbance, defoliating insects, resilience, dendroecology, aspen mixedwoods.

Résumé : Les perturbations peu sévères du couvert forestier influencent probablement la dynamique du carbone forestier au cours du développement d'un peuplement bien que ce sujet ait été relativement peu étudié. C'est surprenant parce que de tels événements se produisent souvent et que la fréquence et la gravité de ces perturbations pourraient augmenter à cause des changements climatiques. Nous avons étudié les impacts d'une perturbation peu sévère du couvert forestier et d'une défoliation périodique par les insectes sur les stocks de carbone forestier et le taux de piégeage du carbone dans des peuplements mixtes de peuplier mature qui variaient en termes d'âge (de 61 à 85 ans), de composition du couvert forestier, de densité et de qualité de station. La densité du peuplement et la qualité de station ont influencé positivement l'accroissement annuel moyen du carbone aérien des arbres (C_{AAM}) alors que la densité et l'âge du peuplement ainsi que la qualité de station ont influencé positivement le stock de carbone des arbres (C_{ARBRE}) et le stock de carbone total de l'écosystème (C_{TOTAL}). Les perturbations cumulatives du couvert forestier ont été reconstituées sur une période de 29 ans en utilisant des méthodes dendroécologiques. Les perturbations cumulatives du couvert forestier ont été négativement et significativement reliées au carbone du sol (C_{SOL}) et ont été négativement reliées, quoique marginalement, au C_{TOTAL}. Les valeurs minimales de l'accroissement annuel du carbone aérien des arbres (C_{AA}) ont été observées sur les stations dont les peupliers faux-trembles (*Populus tremuloides* Michx.) ont été défoliés par la livrée des forêts (*Malacosoma disstria* Hubner) et ces valeurs minimales étaient plus extrêmes sur les stations dominées par le peuplier faux-tremble que sur celles où le peuplier était mélangé à des conifères. Sur les stations défoliées par la livrée des forêts au début des années 2000, une augmentation du piégeage par les résineux (*Abies balsamea* (L.) Mill. et *Picea glauca* (Moench) Voss) a compensé la diminution globale moyenne de 17 % du C_{AA}. Ces résultats soulignent l'importance de tenir compte des épisodes de perturbation peu sévère du couvert forestier lors de la mise au point de modèles régionaux de carbone forestier. Ils plaident aussi en faveur de la restauration et du maintien d'espèces résineuses historiquement importantes dans les peuplements mixtes dominés par le peuplier pour améliorer la résilience de ces peuplements face aux agents de perturbation et maintenir les stocks de carbone des stations. [Traduit par la Rédaction]

Mots-clés : carbone forestier, perturbation forestière, insectes défoliateurs, résilience, dendroécologie, peuplements mixtes de peuplier.

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Introduction

Forest management practices that enhance forest carbon stocks have been proposed as a mechanism to mitigate the effects of climate change (Millar et al. 2007; Bosworth et al. 2008). Specific strategies are aimed at increasing both carbon sequestration (i.e., change in forest carbon mass over time) and total forest carbon stocks (i.e., total ecosystem carbon mass at a given point in time). Strategies to achieve the former include manipulating landscape level age structures in favor of younger, faster growing stands with greater sequestration rates (Alban and Perala 1992); strategies to achieve the latter include extending rotation ages (Alban and Perala 1992; Bradford and Kastendick 2010), improving stocking levels (Woodall et al. 2005; Birdsey et al. 2006), and promoting complementary species mixtures to enhance on-site carbon stocks (Cavard et al. 2010). Regional implementation of these strategies requires a sound understanding of complex relationships between carbon storage and forest attributes commonly influenced through management, including stand age, stocking level, disturbance frequency and severity, and species composition. Moreover, accounting for the constituent effects of these factors, particularly the influence of lower severity disturbances, on carbon stocks is a critical step for improving regional carbon models and management approaches intended to maximize forest carbon stocks.

The importance of low- to moderate-severity disturbances in structuring the development and composition of temperate and boreal forests is well documented (McCarthy 2001; D'Amato et al. 2008). Although the effects of lower severity disturbances on forest-stored carbon have received relatively little attention, Campbell et al. (2009) documented the ability of understory woody stems and fine roots to maintain carbon sequestration following lower severity disturbance (i.e., fuel-load thinning) in mature ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands, and Coomes et al. (2012) demonstrated that low- to moderate-severity canopy disturbances (i.e., earthquakes, insect outbreaks, snow storms, and wind) can cause prolonged regional oscillations in total ecosystem carbon stocks. These examples aside, most studies have focused on age-related patterns of carbon storage following high-severity, stand-replacing disturbances (e.g., catastrophic fire or clearcut harvest), with far less emphasis placed on the effects of the lower severity events that predominate over the course of stand development for many forest types (Pregitzer and Euskirchen 2004). For example, Bradford and Kastendick (2010) examined a 133-year aspen mixedwood chronosequence originating from clearcut harvests and found that total ecosystem carbon stocks increased while carbon sequestration rates decreased with stand age. In a similar chronosequence study spanning 80 years in clearcut aspen mixedwoods, carbon sequestration rates increased up to stand age 40 years, and total ecosystem carbon stocks increased to stand age 66 years, both declining thereafter (Alban and Perala 1992). The wide range of forest structural outcomes that can arise from variability in disturbance severity (Zenner 2005; D'Amato et al. 2008) implies that a correspondingly wide range of carbon stocks or sequestration likely exists during stand development. As a result, there is a need to better understand the relationships between lower severity disturbances and carbon dynamics to refine predictions regarding forest ecosystem carbon stocks and sequestration. This is especially important given that the frequency and severity of low- to moderate-severity disturbances are expected to increase in response to global climate change (Dale et al. 2001).

The southern boreal mesic aspen (*Populus tremuloides* Michx.) mixedwood forests (hereafter referred to as "aspen mixedwood") of northern Minnesota, USA, are an ideal system for examining the role of low- to moderate-severity disturbances on forest carbon dynamics for two reasons. First, these forests hold significant potential for both rapid sequestration and long-term storage of atmospheric carbon (Alban and Perala 1992; Bradford and Kastendick 2010). Second, the development of aspen mixedwood forests are largely governed by low- to moderate-severity canopy disturbance fueled by insect, fungi, and wind events (Bergeron 2000; McCarthy 2001), but the impacts of these disturbances on forest carbon stocks and sequestration have received relatively little attention — leaving key knowledge gaps regarding the influence of high-frequency, low-severity disturbances on carbon stocks.

Here, we utilize detailed carbon measurements and stand-level dendroecological reconstructions of canopy disturbance, including discrete canopy mortality events and the influence of defoliating insects, for 48 compositionally varied, similarly aged plots within mature aspen mixedwoods. These data provide an excellent opportunity to link disturbance processes with carbon dynamics to address the following specific objectives: (*i*) quantify the effects of cumulative low-severity disturbance over the last three decades on total ecosystem carbon stocks and sequestration, (*ii*) assess the relative importance of potential predictors (i.e., disturbance, stocking, site quality, stand age, and tree species composition) on carbon stocks and sequestration, and (*iii*) characterize how compositional susceptibilities to insect-induced disturbance influence recovery of the annual aboveground carbon increment of trees following defoliation events.

Methods

Study region

Forty-eight study plots were selected from nine study sites located in the Laurentian Mixed Forest Province of northern Minnesota, USA. Sites were located using forest inventory data provided by the Minnesota Department of Natural Resources (MNDNR) based on three criteria: age (mature stands >50 years), composition (classified as MHn44, aspen mixedwoods, based on the state community classification system) (MNDNR 2003), and stand size (≥3 ha). The study region is governed by a continental climate of short, warm, and moderately wet summers followed by long, cold, and snowy winters (Albert 1995). Average precipitation ranges from 530 to 810 mm and mean annual temperature ranges from 1 °C in the north to 4 °C in the south of the forest province (MNDNR 2003). Soils were moderately well to poorly drained aqualf soils originating from clayey glaciolacustrine deposits or fine textured glacial till.

Owing to intensive land-use over the last century, younger aspen mixedwoods composed chiefly of *P. tremuloides* dominate much of the contemporary landscape (Schulte et al. 2007). *Populus tremuloides* is a wide-ranging, shade-intolerant, pioneer species that vigorously regenerates from underground root systems and has a pathological rotation between 50 and 100 years (Burns and Honkala 1990). *Populus tremuloides* comprised 34%–84% of the basal area of the overstory composition in the sites examined, with *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss making up lesser components. Other overstory species included *Acer rubrum* L., *Betula papyrifera* Marsh., *Fraxinus nigra* Marsh., *Populus balsamifera* L., *Ulmus americana* L., and *Pinus strobus* L.

Field measurements

Carbon estimates

Three to six 0.04 ha circular plots (11.3 m radius) were established at each of the nine sites (site codes A–I). Plots were installed systematically every 30 to 50 m starting from a random point on one to two transects depending on stand shape and size. Plot perimeters were never closer than 30 m to stand edge to minimize edge effects (Fraver 1994). Species and diameter at breast height (DBH; measured at a height of 1.37 m) were recorded for all living and standing dead trees >10.0 cm DBH, and three to five representative upper canopy trees were measured for height using a clinometer. Increment cores were taken from all trees >10.0 cm DBH for reconstructing growth dynamics and disturbance history. Understory trees (1.0 cm < DBH ≤ 10.0 cm) were tallied by species

within eight 5.0 m² subplots within the main plot. Allometric equations for understory trees were calibrated to trees >2.5 cm DBH and applied to understory trees >1.0 cm DBH. Biomass estimates for understory trees only included the aboveground portion of the plant, potentially leading to slight underestimates of total carbon stocks. Overstory and understory live tree aboveground biomass was estimated using DBH measurements and species-specific allometric equations provided by Jenkins et al. (2003). As is often the case when using allometric equations, there are assumptions, limitations, and error associated with modeling live tree biomass and carbon based on DBH measurements (see Domke et al. 2012). As such, we have included a summary of the species-specific models used to estimate biomass in this study from Jenkins et al. (2003) in the supporting materials (Appendix A, Table A1). All standing dead trees were assigned one of four fragmentation classes (I = recently dead, full crown; II = some crown missing; III = bole only; and IV = snapped bole) following Tyrrell and Crow (1994). Standing dead biomass includes coarse roots and was estimated using species, fragmentation class, and component biomass estimates that corresponded to fragmentation class definitions (i.e., branches, wood) (Jenkins et al. 2003).

Downed woody debris (DWD; diameter >10.0 cm) and fine woody debris (FWD; diameter ≤10.0 cm) were sampled on each plot using the line-intercept method described by Brown (1974). DWD was sampled on each plot using three 20 m transects radiating from the plot center at 60°, 180°, and 300° where species, diameter, and decay class of each encountered piece >10.0 cm were noted. Decay classes (from I = sound to IV = heavily decayed, collapsed) were assigned following Fraver et al. (2002), and DWD volume was calculated following methods described by Brown (1971), with decay class IV volumes reduced to account for the elliptical cross-section resulting from collapse (Fraver et al. 2002). FWD volume was also calculated following methods outlined by Brown (1974). Total DWD biomass was calculated as DWD volume multiplied by decay-class specific wood density reduction factors to account for the effects of decomposition (Harmon et al. 2008). Carbon in live and dead woody pools was calculated by multiplying pool biomass by 0.5.

Carbon content was estimated for the herbaceous understory, forest floor, and upper 20 cm of soil horizons. Three 0.25 m² subplots located 5 m from the plot center on three transects radiating from the center at 90°, 210°, and 330° were destructively sampled for herbaceous and forest floor biomass in each plot. Herbaceous samples and forest floor were oven-dried at 70 °C, weighed, and ground. Within the same nested subplot, three 6.4 cm diameter soil cores were collected to a depth of 20 cm. Soil samples were oven-dried at 100 °C and sieved to remove rocks and roots (2.0 mm screen). Roots ≤2.0 mm (fine roots) were included in soil carbon samples, and roots >3.0 cm (coarse roots) were modeled using biomass component ratios from Jenkins et al. (2003) and were included in estimates of tree carbon (C_{TREE}; see below). All herbaceous, forest floor, and soil samples were analyzed for carbon content using a Leco TruSpec (model 630-100-400).

Four response variables related to ecosystem carbon dynamics (C_{AAI}, C_{TREE}, C_{SOIL}, and C_{TOTAL}, as follows) were calculated for use in linear regression analyses testing a priori hypotheses regarding the influence of live-tree stocking, site quality, stand age, disturbance history, and overstory composition. The average annual increment of carbon (C_{AAI}) was calculated for the previous 29 years (1980–2008) and included aboveground tree biomass only. C_{AAI} was calculated as the mean change in carbon from one year to the next based on reconstruction of diameters from tree ring measurements. Allometric equations were used to convert reconstructed tree diameters to tree carbon content (Jenkins et al. 2003). Tree carbon (C_{TREE}), or the carbon stored within live trees >10.0 cm DBH, included coarse roots and was calculated from DBH measurements and allometric equations. Soil carbon (C_{SOIL}) was measured to a depth of 20.0 cm and included fine root

material <2.0 mm in diameter. Finally, total ecosystem carbon (C_{TOTAL}) was calculated as the sum of all measured carbon pools, including C_{TREE}, standing dead, DWD, understory trees, forest floor, and C_{SOIL}.

Stand characteristics

A measure of site occupancy, namely relative density (RD), and a measure of site quality, namely aspen site index (SI), were examined as potential predictors of carbon stocks. RD was calculated as a measure of live tree occupancy within each plot and was composition specific. That is, the stand density index (SDI) was calculated using the summation method outlined by Shaw (2000) and tailored to better estimate species-specific RD as per Woodall et al. (2005). This method was adapted from Reineke's (1933) SDI based on even-aged, single-species stands. To better quantify the RD of multispecies stands, the summation method was calculated as

$$ SDI = \sum tph_i \left(\frac{DBH_i}{25} \right)^{1.6} $$

where tph_i is trees per hectare for an individual observation, i, and DBH_i is the DBH for an individual observation, i. At the plot level, the summation of SDI for each observation, i, yields total SDI for the plot. RD was then calculated as

$$ RD = \frac{SDI}{SDI_{99}} $$

where SDI was calculated from stand measurements in this study (above), and SDI_{99} is the observed 99th percentile SDI from forests with similar species composition based on plot mean wood specific gravity (WSG) published by Woodall et al. (2005). Plot WSG for the sampling unit was calculated as the arithmetic mean where each sampled tree >10.0 cm DBH was assigned an unweighted WSG value (Harmon et al. 2008). SI represents the average height in metres of a *P. tremuloides* stem at age 50 years, and was calculated using a regional *P. tremuloides* site index equation:

$$ SI = C_1 H^{C_2} (1 - e^{C_3 A})^{C_4 H^{C_5}} $$

where $C_1 = 0.0612$, $C_2 = 1.4390$, $C_3 = -0.0050$, $C_4 = -3.9080$, and $C_5 = -0.4350$, A is the median age of the oldest aspen cohort at the plot, and H is mean height of canopy aspen within the plot (Carmean et al. 1989).

Expecting that RD and SI would explain a significant portion of the variation in carbon stocks, we were interested if additional measures of composition and disturbance would strengthen predictions. Compositional predictors were thus calculated to account for the proportion of overstory functional groups present. Functional groups were defined as intolerant hardwoods of the genus *Populus* (PW), including *P. tremuloides* and occasionally *P. balsamifera*; tolerant hardwoods (HW), including *A. rubrum*, *B. papyrifera*, *F. nigra*, *Tilia americana* L., and *U. americana*; and tolerant softwoods (SW), including *A. balsamea*, *P. glauca*, and rarely *P. strobus*. Additionally, interaction terms were included between RD and the proportion of RD occupied by each functional group, as past investigations of compositional effects on productivity justify the inclusion of these terms (Edgar and Burk 2001). Plot composition was calculated as the proportion of plot RD occupied by each functional group (RD_{PW}, RD_{HW}, and RD_{SW}).

Disturbance chronology, defoliation history, and stand age

We rely on a previously published plot-level record of percent canopy area disturbed that was constructed using tree-ring analysis and measurements of recently formed and dated canopy gaps (see Reinikainen et al. 2012). The disturbance-based predictor,

DIST, was calculated as the sum of percent canopy area disturbed from 1980 to 2008 (the last complete ring of tree core samples), as reconstructed following the approach outlined by Lorimer and Frelich (1989). Release events were tallied by decade and weighted by exposed crown area as predicted by tree DBH. Since stand age also affects patterns of carbon stocks and sequestration, we included age (AGE, calculated as median age of the oldest *P. tremuloides* cohort) in several models. Cohort definition in this study was based purely on similarities in age. Recognizing that recruitment of the first cohort can take place over an extended period of time, we confined the initial cohort to the first two decades of stand development. In addition to these metrics, periods of defoliation by forest tent caterpillar (FTC; *Malacosoma disstria*) and eastern spruce budworm (SBW; *Choristoneura fumiferana*) were detected using a host–nonhost analysis between *P. tremuloides*, for FTC, and *A. balsamea*, for SBW, in the dendroecological program OUTBREAK (Holmes and Swetnam 1996). Defoliation events were further verified using a disturbance etiology created by identifying documented defoliation events for the region in the peer-reviewed literature, historical documents, and aerial surveys (see Reinikainen et al. 2012). Reconstruction of defoliating disturbances dates aided in assessing the effects of insect-induced disturbance on rates of carbon sequestration.

Statistical analysis

Given the patchy nature of aspen mixedwood forests (Chavez and Macdonald 2010), and the ample replication of measurements, we used the 0.04 ha main plot as the sampling unit ($n = 48$). As such, models were fit separately for each response variable (C_{AAI}, C_{TREE}, C_{SOIL}, and C_{TOTAL}) using mixed linear regression within PROC MIXED in SAS v. 9.2 (SAS Institute Inc. 2008) where site and plots nested within site were treated as random error terms. A set of 24 mixed-effects models, including a null model with only an intercept term and error terms, were constructed based on a priori hypotheses regarding the effects of composition, stocking, and disturbance on carbon stocks. Hypotheses ranged from simple, few-termed models using single measures of stocking or site quality (i.e., RD and SI) to more complex, multiterm models including compositional and disturbance-based predictors (i.e., RD_{PW}, RD_{HW}, RD_{SW}, and DIST) and several compositional interactions (i.e., RD × RD_{PW}, RD × RD_{HW}, and RD × RD_{SW}).

To assess the impact of disturbance history, in addition to the other variables of interest (i.e., stand stocking, site quality, stand age, and composition), on carbon stocks and sequestration (objectives 1 and 2), models were fit to the data for all four response variables (C_{AAI}, C_{TREE}, C_{SOIL}, and C_{TOTAL}) and ranked using the corrected Akaike's information criterion (AIC_c). AIC_c favors the best-fitting, parsimonious models in a given set by penalizing overly parameterized models and quantifying fit based on model negative log-likelihood (Johnson and Omland 2004). Thus, the best models were those that had the lowest AIC_c scores. In addition to AIC_c scores, model goodness-of-fit was assessed based on the Pearson's correlation coefficient (r) between predicted and actual values for each model (cf. Canham et al. 1994) and root mean squared error (RMSE). The relative competitiveness of models within a given set was determined by calculating the difference (Δ_i) between the AIC_c of any model in the set and the best-fit model (lowest AIC_c, $\Delta_i = 0$). We considered competitive models to be those with $\Delta_i < 2.0$. Additional evidence of model strength is reflected by the Akaike weight, w_i, which expresses the probability that a given model is the best candidate in the model set (Johnson and Omland 2004). During model construction, the need to transform predictors to meet regression assumptions was assessed using histograms of predictor values and scatter plots of model residuals on predictor values.

To further explore tree compositional effects on carbon dynamics (objective 2), we examined relationships between C_{AAI}, C_{TREE}, C_{SOIL}, C_{TOTAL} and composition, particularly of the most prevalent

functional groups RD_{PW} and RD_{SW}. Models included interaction terms to account for differences in prediction slopes resulting from compositional effects (Edgar and Burk 2001). To characterize how tree species composition influences the susceptibility of carbon sequestration to insect defoliation (objective 3), we examined the reconstructed carbon accumulation, or annual aboveground carbon increment (C_{AI}), of trees >10.0 cm DBH from 1980 to 2008 and highlighted the varied disturbance history of sites and the impact of known defoliation events on carbon stocks. C_{AI} was calculated as the annual change in tree carbon stocks estimated using tree-ring reconstructed diameter increments and allometric equations relating diameter to biomass (Jenkins et al. 2003). We assumed that the reconstructed diameter was of a circular tree cross-section and not an ellipse. We further assumed that the core sample represented the "average" radius of the tree, and we went to great efforts when coring trees to sample what we determined to be a representative radius. Onset of the most recent FTC and SBW defoliation events were pinpointed, and a measure of resilience (RES), or the ability of a post-disturbance forest to attain pre-disturbance productivity, was calculated as

$$RES = \frac{C_{AI\text{-}POST}}{C_{AI\text{-}PRE}}$$

where $C_{AI\text{-}POST}$ is the mean C_{AI} for the 5 years after the initial year of defoliation and $C_{AI\text{-}PRE}$ is the mean C_{AI} for the 5 years prior to the onset of defoliation (calculation of RES does not include the initial year of defoliation) (Kohler et al. 2010). RES was calculated to better assess the performance of aspen mixedwoods of various composition during periods of disturbance that selectively affect a given functional group.

Results

Stand and plot characteristics

Stand ages, defined as the median age of the oldest cohort, ranged from 61 to 85 years, whereas plot ages (AGE) ranged from 58 to 88 years since stand-initiating disturbance (Tables 1 and 2). Overstory composition, by relative basal area, was dominated by *P. tremuloides* (34%–84%) and *A. balsamea* (8%–43%), with lesser amounts of *A. rubrum* (0%–20%), *P. glauca* (0%–18%), *F. nigra* (0%–14%), and *B. papyrifera* (0%–13%) (Table 1). Composition, based on the proportion of RD, varied considerably, with mean values for *Populus* species (RD_{PW}), softwoods (RD_{SW}), and hardwoods (RD_{HW}) of 58%, 25%, and 16%, respectively (Table 2). Tree density varied greatly from 175 to 1025 stems·ha⁻¹, while SDI_{99} and RD ranged from 1062 to 1288 stems·ha⁻¹ and 0.23 to 0.71, respectively (Table 2). The median SI for *P. tremuloides* was 20.1 m (height) at 50 years (Table 2).

Carbon pools were similar across sites with the exception of site G, which had considerably lower carbon stored in overstory tree, standing dead, and DWD pools (Appendix A, Table A2). This finding was presumably due to the lower tree densities at this site relative to the other stands examined. Study-wide total ecosystem carbon (C_{TOTAL}) averaged 193.2 ± 4.5 Mg C·ha⁻¹ (sites pooled; Appendix A, Table A2), and the carbon increment (C_{AAI}) ranged from 0.49 to 2.65 Mg C·ha⁻¹·year⁻¹ with a median of 1.33 Mg C·ha⁻¹·year⁻¹ (Table 2). Plot tree carbon (C_{TREE}) and C_{TOTAL} ranged considerably, from 36.9 to 138.4 Mg C·ha⁻¹ and 135.6 to 264.0 Mg C·ha⁻¹, respectively (Table 2). Study-wide mean carbon-pool values were 82.3 ± 3.5 (C_{TREE}), 28.4 ± 1.8 (understory tree), 11.7 ± 1.1 (standing dead), 14.4 ± 1.0 (DWD), 18.0 ± 1.1 (forest floor), and 38.3 ± 1.9 (C_{SOIL}) Mg C·ha⁻¹ (Appendix A, Table A2).

Controls over carbon sequestration and stocks

Examination of scatterplots for average annual increment of carbon (C_{AAI}), tree carbon (C_{TREE}), and total ecosystem carbon

Table 1. Compositional and physiographic characteristics for aspen mixedwood study sites in northern Minnesota, USA.

Characteristic	Site								
	A	B	C	D	E	F	G	H	I
Plots (no.)	6	5	6	3	6	6	6	4	6
Stand area (ha)	7	12	30	3	10	13	13	10	3
Stand age (years)	80	61	73	82	81	84	85	78	69
Site index (m)	19.6 (0.2)	24.3 (0.7)	23.6 (1.2)	18.8 (0.9)	22.0 (1.4)	18.8 (0.4)	18.0 (0.5)	19.4 (1.2)	22.3 (0.6)
Composition (%)									
PW									
Populus tremuloides	83.7	53.8	50.4	39.2	34.1	67.9	65.7	71.0	48.6
Populus balsamifera	—	—	1.0	—	4.5	—	—	3.6	—
HW									
Acer rubrum	—	12.6	10.9	—	18.2	9.7	20.2	0.4	1.0
Betula papyrifera	—	13.3	12.0	—	3.4	4.6	2.6	—	6.7
Fraxinus nigra	—	—	9.0	—	1.6	0.1	0.0	9.6	13.5
Ulmus spp.	—	—	1.0	—	—	0.2	—	2.1	0.5
SW									
Abies balsamea	14.6	14.2	11.4	43.1	38.1	15.7	7.9	12.9	25.0
Picea glauca	1.7	6.1	3.8	17.7	—	1.8	3.6	—	3.0
Pinus strobus	—	—	—	—	—	—	—	—	1.8

Note: Stand age refers to the median age of the oldest *P. tremuloides* cohort. For site index, values in parentheses are SEs of the mean. Composition is based on percent of total basal area and is grouped by functional group. PW, *Populus* species; HW, hardwood species; and SW, softwood species.

Table 2. Carbon pool, composition, stocking, and disturbance characteristics for all 48 aspen mixedwood plots in northern Minnesota, USA.

Characteristics	Range	Mean	Median
C_{AAI} (Mg C·ha^{-1}·year^{-1})	0.49–2.65	1.38	1.33
C_{TREE} (Mg C·ha^{-1})	36.9–138.4	82.3	82.8
C_{SOIL} (Mg C·ha^{-1})	14.0–70.4	38.3	34.0
C_{TOTAL} (Mg C·ha^{-1})	135.6–264.0	193.2	190.1
RD	0.23–0.71	0.43	0.41
SI (m)	16.5–27.8	20.9	20.1
AGE (years)	58–88	77	79
DIST	0.00–0.40	0.12	0.08
RD_{PW}	0.00–1.00	0.58	0.64
RD_{HW}	0.00–0.69	0.16	0.11
RD_{SW}	0.00–0.84	0.25	0.21
Density (trees·ha^{-1})	175–1025	604	575
SDI_{99} (trees·ha^{-1})	1062–1288	1222	1242
WSG (g·cm^{-3})	0.34–0.44	0.39	0.38

Note: C_{AAI}, the average annual increment of carbon in trees; C_{TREE}, carbon stocks in trees >10.0 cm diameter at breast height (1.37 m); C_{SOIL}, soil carbon stocks to 20.0 cm depth including fine roots <2.0 mm in diameter; C_{TOTAL}, total ecosystem carbon; RD, relative density calculated following Woodall et al. (2005); SI, site index or the average tree height (m) at age 50 years for *Populus tremuloides*; AGE, stand age or the median age of the oldest *P. tremuloides* cohort; DIST, cumulative canopy disturbance from 1980 to 2008; RD_{PW}, the proportion of relative density composed of *Populus* species; RD_{SW}, the proportion of relative density composed of softwood species; RD_{HW}, the proportion of relative density composed of hardwood species; SDI_{99}, 99th percentile of maximum observed stand density index from Woodall et al. (2005); and WSG, mean wood specific gravity.

(C_{TOTAL}) responses clearly indicate the importance of the predictors stocking level (RD), age (AGE), site index (SI), and cumulative past disturbance severity (DIST) (Fig. 1*a*–1*d*, 1*g*, 1*j*, 1*m*, and 1*p*). Ranked model fits demonstrated that the strongest effects on C_{AAI} were all positive and attributed to RD, SI, and to a lesser degree, AGE and DIST (Table 3; Appendix A, Table A3). The top model included only RD and SI, and both predictors were significantly and positively related to C_{AAI} ($R^2 = 0.73$; RMSE = 0.21). Similarly, the top models for predicting tree carbon (C_{TREE}) revealed the positive effects of RD, SI, and AGE, but also the proportion of plot RD attributed to *Populus* species (RD_{PW}) and its interaction with RD (Tables 3 and A3). C_{SOIL}, the second largest carbon pool following C_{TREE}, was best predicted by a model that included AGE, DIST, and an interaction term including AGE and DIST ($R^2 = 0.17$; RMSE =

1.01) (Tables 3 and A3, Fig. 2). The best model for predicting C_{TOTAL} indicated a positive effect of RD, SI, and AGE and a negative effect of DIST and its interaction with AGE ($R^2 = 0.55$; RMSE = 0.01) (Tables 3 and A3).

Aspen mixedwood resilience to defoliation

Notable minima in the annual aboveground carbon increment of trees (C_{AI}) over the 29-year period can be attributed to FTC and SBW defoliation of *Populus* spp. (PW) and softwoods (SW), respectively (Fig. 3). Total C_{AI} lows coincided with FTC defoliations. The most noticeable FTC defoliations occurred from 1989 to 1995 at all sites except F and I, as well as in the early 2000s at all sites except D, E, and H (Fig. 3). RES calculated for the most recent FTC defoliation event indicated nearly complete recovery with a mean RES of 0.97 for all sites (Table 4). During that same FTC event in the early 2000s, sites A, B, C, F, G, and I (pooled) displayed average decreases in total $C_{AI-POST}$ of 0.38 Mg C·ha^{-1}·year^{-1} (24% decrease), decreases in PW C_{AI} of 0.48 Mg C·ha^{-1}·year^{-1} (41% decrease), and increases in SW C_{AI} of 0.08 Mg C·ha^{-1}·year^{-1} (68% increase) (Fig. 4). Reductions in C_{AI} were most severe at sites A, B, and F, which showed reductions in C_{AI} of 50%, 31%, and 44%, respectively (Table 4). These reductions in carbon sequestration occurred during a documented FTC event, but other unconsidered abiotic factors such as growing season drought or freeze–thaw events may also have contributed to these trends (Hogg et al. 2002). All other sites had RES values ranging from 0.88 (site G) to 2.16 (site D) indicating a 12% reduction and a 116% increase in $C_{AI-POST}$, respectively (Table 4). Following defoliation of softwoods by SBW, RES values greater than 1.0 were documented at all sites (Table 4). RES values ranged from 1.12 (site G) to 1.90 (site A) indicating an average C_{AI} increases of 12% and 90%, respectively, in the 5 years following the initial year of defoliation. In both periods of FTC and SBW defoliation, estimates of RES and defoliation severity were negatively correlated (FTC: $r = -0.58$; SBW: $r = -0.38$) and estimates of RES and time since the onset of defoliation were negatively correlated (FTC: $r = -0.47$; SBW: $r = -0.48$). Furthermore, stand composition by percent basal area of host species was positively correlated to defoliation severity of PW by FTC ($r = 0.60$) and negatively correlated to SW by SBW ($r = -0.56$).

Discussion

Disturbance effects on carbon stocks

Our findings demonstrate that in addition to the positive effects of stocking level, site quality, and stand age, recent canopy distur-

Fig. 1. Relationships between the response variables average annual increment of carbon (C_{AAI}; *a–f*), tree carbon stocks (C_{TREE}; *g–l*), and total ecosystem carbon stocks (C_{TOTAL}; *m–r*) and the predictors relative density (RD), site index (SI), stand age (Age), disturbance severity (DIST), *Populus* spp. contribution to relative density (RD_{PW}), and softwood species contribution to relative density (RD_{SW}). Mean function and R^2 values are displayed for statistically significant relationships ($p < 0.05$).
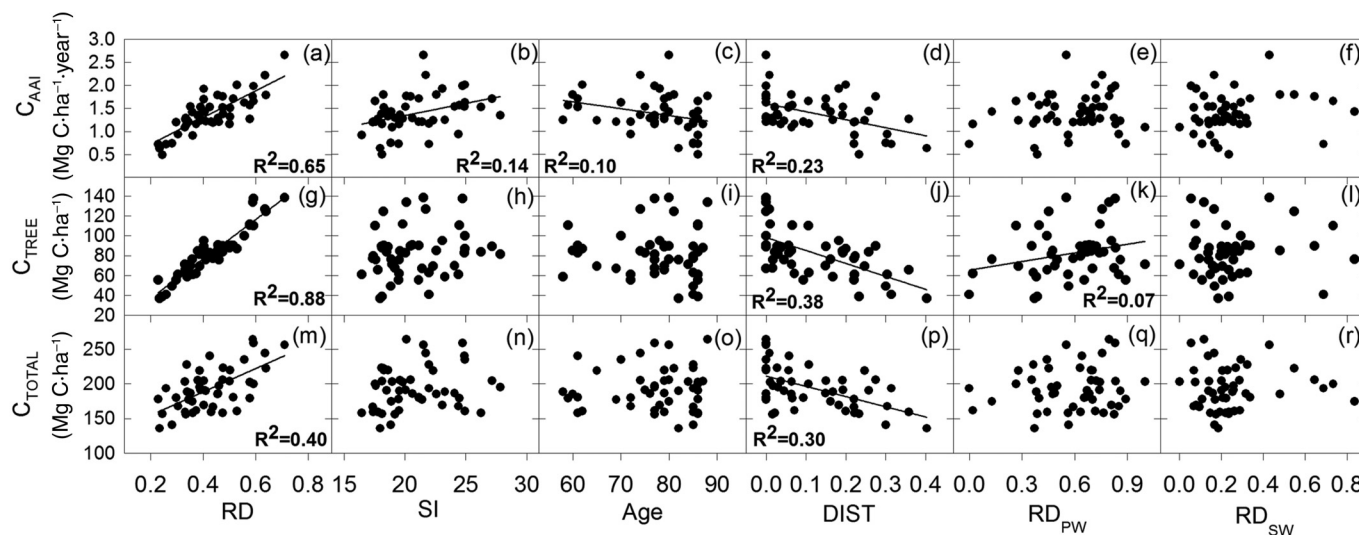
Table 3. Results from AIC_c selection of mixed-effects models for predicting carbon increment (C_{AAI}), tree carbon stocks (C_{TREE}), soil carbon stocks (C_{SOIL}), and total ecosystem carbon (C_{TOTAL}) as a function of factors related to stocking level, species composition, and disturbance history.

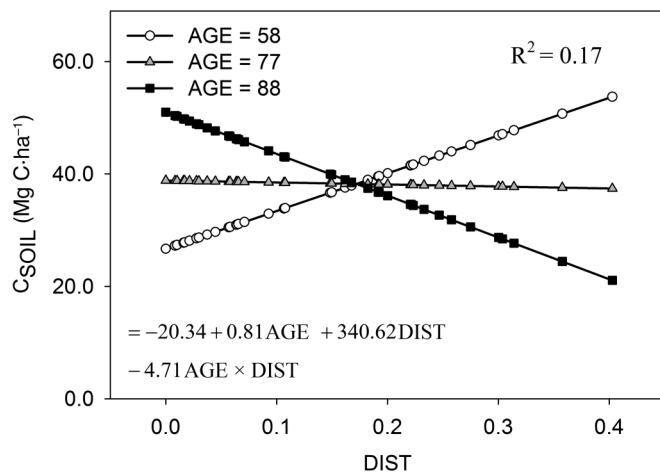| Model	Model rank	K	AIC_c	Δ	w	R^2	RMSE
$C_{AAI} = -0.61^b + 2.80RD^a + 0.04SI^a$	1	5	−1.5	0.00	0.33	0.73	0.21
$= -0.82^b + 3.12RD^a + 0.04SI^a + 0.50DIST$	2	6	−0.7	0.76	0.23	0.74	0.20
$= -0.19 + 2.80RD^a + 0.03SI^b + 0.00AGE$	3	6	0.5	1.98	0.12	0.74	0.20
$= -0.73^c + 3.02RD^a + 0.04SI^a + 0.27RD_{PW} − 0.42RD × RD_{PW}$	7	7	3.2	4.72	0.03	0.73	0.20
$= -0.43 + 3.12RD^a + 0.03SI^b + 0.00AGE + 1.16DIST − 0.01AGE × DIST$	10	8	4.1	5.55	0.02	0.74	0.20
$= 1.40^a$	24	4	56.8	58.33	<0.01	0.00	0.38
$C_{TREE} = -71.00^a + 200.46 RD^a + 1.54SI^a + 0.46AGE^a$	1	7	343.4	0.00	0.28	0.91	1.00
$= -30.82^a + 201.85RD^a + 0.84SI^c + 17.64RD_{PW} − 4.83RD × RD_{PW}$	2	8	343.4	0.04	0.27	0.90	1.05
$= -13.00 + 198.16RD^a + 17.14RD_{PW} + 1.05RD × RD_{PW}$	3	7	344.1	0.74	0.19	0.90	1.00
$= -69.68 + 198.00RD^a + 1.53SI^a + 0.46AGE^a − 3.70DIST$	4	8	346.2	2.81	0.07	0.91	1.00
$= 82.29^a$	22	3	448.1	104.76	<0.01	0.00	0.01
$C_{SOIL} = -20.34 + 0.81AGE^b + 340.62DIST^b − 4.71AGE × DIST^b$	1	7	385.2	0.00	0.27	0.17	1.01
$= 42.22^a − 30.88DIST^b$	2	5	386.4	1.18	0.15	0.06	1.02
$= 38.49^a$	4	4	387.9	2.72	0.07	0.00	1.02
$C_{TOTAL} = -61.71 + 115.66RD^a + 3.05SI^b + 1.96AGE^b + 527.70DIST − 7.66AGE × DIST^c$	1	8	445.8	0.00	0.45	0.55	0.01
$= -11.73 + 128.22RD^a + 3.26SI^b + 1.17AGE^b − 67.79DIST^c$	2	7	446.7	0.92	0.29	0.51	1.00
$= 144.52^a + 132.12RD^a − 66.44DIST^c$	4	6	450.8	4.97	0.04	0.43	1.01
$= 118.15^a + 174.56RD^a$	5	5	451.1	5.32	0.03	0.40	1.01
$= 193.16^a$	22	3	470.9	25.09	<0.01	0.00	0.00

Note: Displayed models include the most competitive (Δ < 2.0), the null, and examples of the least parameterized and most parameterized models. *K* refers to the number of terms included in the model, AIC_c is the corrected Akaike's information criterion, Δ is the difference between a given model's AIC_c and the minimum observed AIC_c, *w* is the Akaike weight, RMSE is the root mean squared error, and R^2 is the square of Pearson's correlation coefficient. [a], Parameter is significant at $p < 0.01$; [b], parameter is significant at $p < 0.05$; and [c], parameter is significant at $p < 0.10$.

bances had a negative effect on soil carbon (C_{SOIL}) and total ecosystem carbon (C_{TOTAL}) stocks in mature aspen mixedwood forests. We observed a gradient of cumulative canopy disturbance across the study stands, ranging from 0.0% to 40.0%; FTC and SBW defoliation severity and duration varied among sites. In the boreal mixedwoods of Canada, prolonged and severe FTC defoliation tripled the stand area in gaps (12.3%–43.7%) and increased mean gap size to 12 times that of undefoliated stands (Moulinier et al. 2011). Similarly, Kneeshaw and Bergeron (1998) observed a range of 7.1%–40.4% of stand area in gaps in mixed *Betula alleghaniensis* Briton – *A. balsamea* forests impacted by SBW. Furthermore, the duration and severity of FTC defoliation events vary, imparting variation in gap formation and the resulting change in structure and composition of the forest (Moulinier et al. 2013). We observed similar gap formation following species-specific defoliation events and found

that increases in canopy gap area resulted in decreases in C_{SOIL} and C_{TOTAL}.

Bradford and Kastendick (2010) proposed an age-based model for predicting carbon storage in regional aspen mixedwood stands that produced a similar C_{TOTAL} value (183 Mg C·ha⁻¹ at 77 years old) for the mean aged aspen mixedwoods in this study (193 Mg C·ha⁻¹ at 77 years old). Examinations of study plots based on the levels of disturbance experienced over the past 29 years suggest that undisturbed plots conform to Bradford and Kastendick's (2010) age-related carbon model; however, disturbed plots deviated from their predictions and stored less carbon (results not shown). Decreased C_{TOTAL} could be attributed to disturbance and its effects on the allocation of carbon among large live tree, deadwood, and forest floor pools. Gap formation and the resulting in-growth can shift annual accumulation of carbon from

Fig. 2. Effects of stand age in years since stand initiating disturbance (AGE; $p = 0.0201$), cumulative proportion of the canopy disturbed from 1980 to 2008 (DIST; $p = 0.0308$), and the interaction of AGE and DIST ($p = 0.0187$) on soil carbon stocks (C_{SOIL}). Levels of AGE correspond to the observed minimum (open circle), midpoint (shaded triangle), and maximum (solid square) values from the data set.

within detrital pools could have occurred as a result of increased canopy gap area and the short- and long-term effects of gap formation on detrital inputs and understory light and temperature conditions (Bhatti et al. 2002).

Compositional effects on resilience

We examined mature stands with varying composition ranging from nearly "pure" *P. tremuloides* to nearly "pure" conifer (*A. balsamea* and *P. glauca*) and many "mixed" stands where *P. tremuloides* and conifers were more equally represented. Several studies have demonstrated that production is greatest in "pure" *P. tremuloides* stands when compared with varying mixtures of *P. tremuloides* and conifers such as *A. balsamea*, *P. glauca*, and *Picea mariana* (Mill.) BSP (Edgar and Burk 2001; Cavard et al. 2010). Other findings have identified enhanced biomass production within aspen mixedwoods containing a fully stocked overstory of *P. tremuloides* with an understory of *P. glauca* (MacPherson et al. 2001). It is thought that conflicting findings, such as these, may result from interactions among variables describing stand composition and commonly utilized measures of stand stocking (e.g., basal area and stand density) (Pretzsch 2005; Long and Shaw 2010). Thus, controlling for stand stocking is imperative when assessing the effects of composition on carbon stores.

We used RD to control for stocking differences, a measure of site occupancy advanced by Woodall et al. (2005) as a more robust estimate of stand stocking in uneven-aged and mixed species stands. RD adequately accounts for the natural limits placed on maximum stand density by architectural differences among tree species. By employing RD, we were better equipped to detect differences that may exist as an artefact of stand composition. It is worth noting that RD can be readily calculated using typical stand inventory data (see Woodall et al. 2005).

We found that C_{TREE} was often higher in stands with fewer tree species and higher proportions of *P. tremuloides.* These findings were similar to those found in Canadian boreal mixedwoods, where mixtures of *P. tremuloides* and softwoods, while storing more tree carbon than "pure" softwood stands, stored less tree carbon than "pure" *P. tremuloides* stands (Cavard et al. 2010). Similarly, other work in Minnesota found a positive influence of *P. tremuloides* on stand productivity that outweighed the effects of softwood or hardwood groups (Edgar and Burk 2001). These findings are attributed to rapid juvenile growth rates of *P. tremuloides* and subsequent canopy dominant and codominant positions, which lead to high levels of tree biomass and thus carbon. Nonetheless, examination of the annual aboveground carbon increment of trees (C_{AI}) and resilience in these systems over the past three decades suggested that mixed stands were as productive during that time period and more resilient to defoliation relative to purer stands. These results demonstrate possible benefits of mixed stands in sustaining productivity rates in systems affected by host-specific disturbance agents, as well as changing climatic regimes (cf. Drobyshev et al. 2013).

Another important area of interest beyond productivity effects in mixtures is the susceptibility (sensu Su et al. 1996) to disturbance of mixed versus pure plant communities and the ability of additional species in a mixture to compensate for production losses incurred by a single species (Man and Lieffers 1999; Pretzsch 2005). The patterns of C_{AI} and resilience documented in this study highlighted the importance of overstory tree diversity in compensating for host-specific defoliating agents (i.e., FTC and SBW) (Fig. 4). We observed that RES during the most recent FTC event was negatively correlated to both defoliation severity ($r = -0.58$) and percent basal area occupied by *P. tremuloides* ($r = -0.63$) such that stands with a greater proportion of *P. tremuloides* were defoliated more severely and had not completely recovered production in the 5 years after the onset of FTC defoliation. During the FTC outbreak in the early 2000s, we observed that *A. balsamea* and *P. glauca* were able to compensate for losses in C_{AI} by 17% on average (Fig. 4). Ultimately, less pure stands experienced less

fewer large stems to many small stems that reoccupy gaps (Ryan et al. 1997). The ability of carbon stocks to recover under these circumstances requires adequate stocking of tree regeneration in gaps; however, this condition can be delayed in mature aspen mixedwoods because of limited shade tolerant seed source, limited seeding substrate, and unfavorable light conditions related to recalcitrant *Corylus cornuta* Marsh. and *Acer spicatum* Lamb. shrub layers (Lieffers et al. 1999). As observed in other forest systems, the slow rates at which canopy gaps are reoccupied can generate prolonged periods of lower C_{AAI} and C_{TOTAL} (Coomes et al. 2012), underscoring the importance of accounting for disturbance effects when predicting the range of carbon stocks to be expected for a given stand developmental stage (Gough et al. 2008).

Although low- to moderate-severity natural disturbances intuitively should reduce live tree stocking, thus reducing carbon stocks in forest systems, these effects have generally been overlooked in studies of stand development and forest-carbon accrual (but see Campbell et al. 2009; Coomes et al. 2012). Disturbances redistributed carbon stored in live trees to deadwood pools, but our data did not indicate elevated deadwood pools in stands with elevated disturbance rates (results not shown). However, these data indicate relationships between soil carbon and the interaction of stand age and cumulative canopy disturbance ($p < 0.05$; $R^2 = 0.17$; RMSE = 1.01). Our results suggest that the relationship between C_{SOIL} and canopy disturbance depends on stand age. Specifically, the best model for C_{SOIL} is positively related to disturbance when stand age is less than ~77 years and negatively related to disturbance when stand age is greater than ~77 years. Consistent with our result suggesting an interaction between age and disturbance history, previous work has found that age-related trends in C_{SOIL} can be mixed (Bradford and Kastendick 2010) and that both patterns of continuous C_{SOIL} accrual and fluctuation have been observed depending on the disturbance history (Bhatti et al. 2002).

Our results suggest that increased tree mortality led to increases in below- (i.e., fine root mass) and above-ground (i.e., FWD, leaves) detritus. Following a pulse of detrital inputs related to insect-induced overstory mortality, annual detrital inputs likely decreased and the understory light environment changed as canopy gap area increased. Detrital inputs and C_{SOIL} are closely and positively related, such that decreased detrital inputs following disturbance events could be responsible for reductions in C_{SOIL} (Bhatti et al. 2002). Significant loss of C_{SOIL} to the atmosphere due to elevated heterotrophic respiration

Fig. 3. Aboveground annual carbon increment (C_{AI}) of trees (>10.0 cm diameter at breast height) for aspen mixedwood study sites A–I. Total C_{AI} (shaded square) is displayed, as well as that of the functional groups including *Populus* species (PW; *Populus tremuloides* and *Populus balsamifera*; open circle), softwood species (SW; *Abies balsamea* and *Picea glauca*; solid triangle), and hardwood species (HW; *Acer rubrum*, *Betula papyrifera*, *Fraxinus nigra*, *Tilia americana*, and *Ulmus americana*; shaded circle). Resilience values (RES) are displayed to demonstrate the ability of sites to recover rates of C_{AI} following the most recent forest tent caterpillar (FTC; *Malacosoma disstria*) outbreak. The aboveground average carbon increment (C_{AAI}) is displayed as a horizontal dotted black line. Notable lows in C_{AI} were associated with FTC defoliation of PW (onset denoted by black arrows) as well as eastern spruce budworm (SBW; *Choristoneura fumiferana*) defoliation of SW (onset denoted by shaded arrows). The placement of arrows indicating the onset of defoliation events were determined using a host–nonhost dendroecological reconstruction of defoliation events in the OUTBREAK program (see Reinikainen et al. 2012).
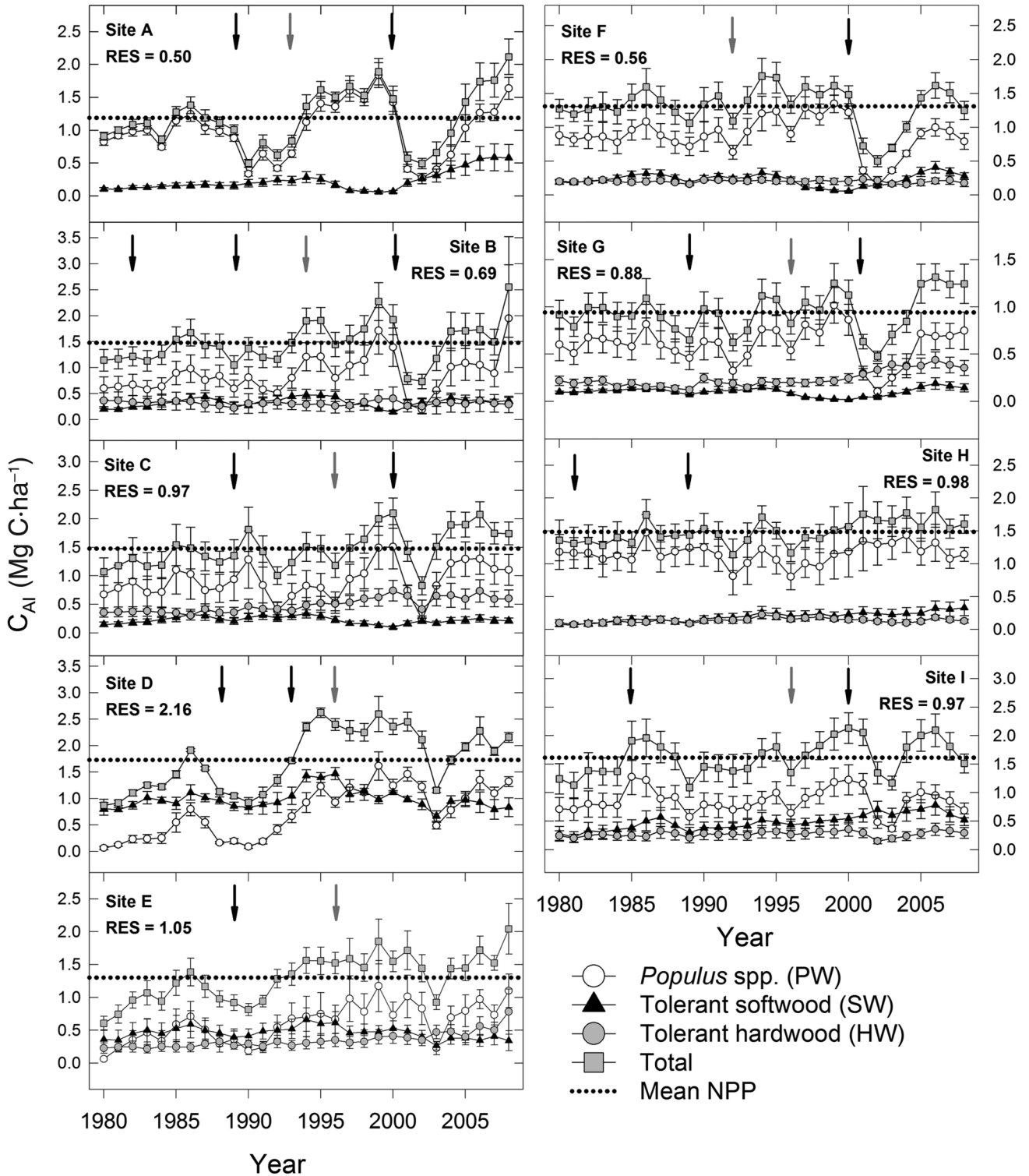
Table 4. Defoliation history and measures of resilience (RES) for aspen mixedwood study sites over the last three decades based on analyses in the dendroecological OUTBREAK program (see Reinikainen et al. 2012).

Site	n, POTR (FTC)	Initial year of recent FTC event	Percent defoliated (FTC)	RES to FTC	n, ABBA (SBW)	Initial year of recent SBW event	Percent defoliated (SBW)	RES to SBW
A	51	2000	76.5	0.50	12	1993	16.7	1.90
B	53	2000	63.0	0.69	44	1994	11.6	1.42
C	21	2000	19.1	0.97	19	1996	84.2	1.30
D	20	1993	15.0	2.16	45	1996	11.1	1.31
E	21	1989	23.8	1.05	34	1996	14.7	1.22
F	35	2000	31.4	0.56	28	1992	32.1	1.22
G	38	2001	18.4	0.88	11	1996	90.9	1.12
H	36	1989	36.1	0.98	36	—	—	—
I	38	2000	21.1	0.97	57	1996	19.3	1.25
Mean/mode	35	2000	33.8	0.97	32	1996	35.1	1.34

Note: Sample size as well as host tree and defoliating insect species denoted as "n, tree species (insect species)", and "percent defoliated" refers to mean percent of trees defoliated during documented defoliation years. FTC, forest tent caterpillar (*Malacosoma disstria*); SBW, spruce budworm (*Choristoneura fumiferana*); POTR, *Populus tremuloides*; and ABBA, *Abies balsamea*.

Fig. 4. Aboveground tree carbon increment (C_{AI}) for *Populus* species (open bars), softwood species (solid bars), and all species combined ("total"; shaded bars) during the 5 years pre- and post-defoliation by forest tent caterpillar (FTC), as well as the initial years of defoliation (2000 or 2001). Values are pooled for sites A, B, C, F, G, and I that shared a common defoliation event by FTC in the early 2000s. Pre-defoliation (C_{AI-PRE}) and post-defoliation C_{AI} ($C_{AI-POST}$) are averages for the 5 years preceding and following the initial year of defoliation ($C_{AI-INITIAL YEAR}$), respectively. Also shown are differences in the aboveground tree carbon increment ($C_{AI-POST} - C_{AI-PRE}$) (fourth group from left) and percent change (($C_{AI-POST} - C_{AI-PRE}$)/C_{AI-PRE}) of C_{AI} (right group of bars corresponding to right-hand y axis). Tolerant hardwood (HW) C_{AI} values are not shown.
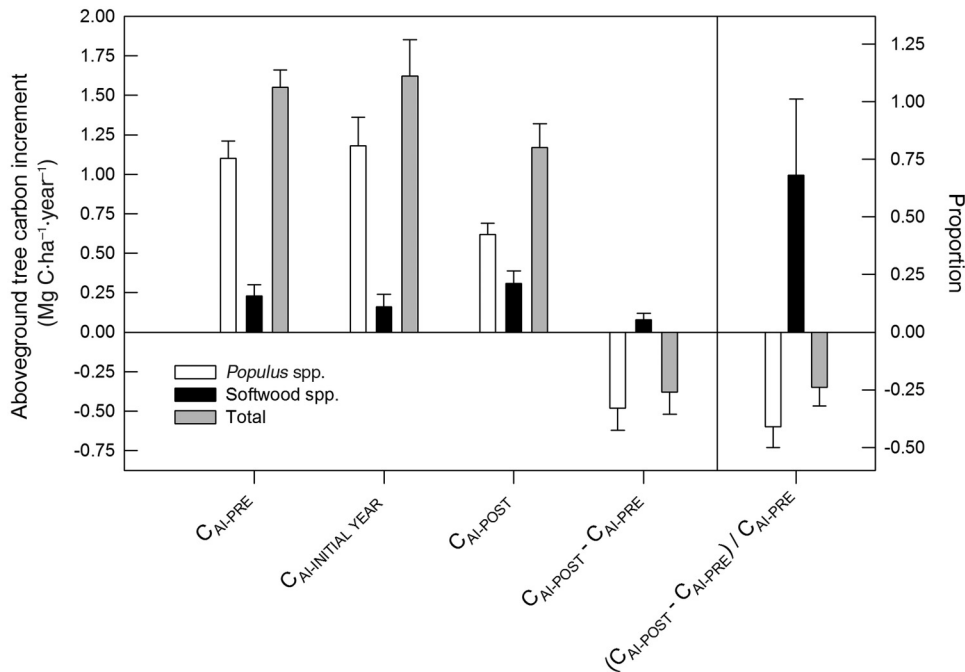
severe outbreaks and recovered more completely in the 5 years following defoliation. This complementarity between tolerant softwood and intolerant hardwood species, most notably during the recent FTC defoliation, highlights the ability of those species less susceptible to a defoliating agent to mitigate carbon losses during defoliation. A similar trend was observed in aspen-dominated mixed species forests of Michigan, USA, where diverse, multistoried stands mitigated losses in production during breakup of the aging aspen overstory (Gough et al. 2010). Pretzsch (2005) referred to this benefit of mixed species forests as "risk reduction", which is particularly important for aspen mixedwoods given the chronic levels of defoliation these systems experience by species-specific defoliators (see Reinikainen et al. 2012). Our findings confirm the ability of diverse

mature aspen mixedwoods to minimize production loss resulting from defoliation.

Conclusions

Regional management goals aimed at curbing climate change and bolstering the resilience of forested ecosystems to changing conditions are becoming increasingly common; however, important tradeoffs may exist in the ability to simultaneously achieve these goals (Bradford and D'Amato 2012). Where carbon sequestration or protecting carbon stocks is a management objective, the findings from this study offer support for the notion of favoring *P. tremuloides* on shorter rotations to increase carbon sequestration, yet document the limited resilience of broadleaf-dominated plots to defoliating

insects, namely FTC. While we confirmed past studies (Edgar and Burk 2001; Cavard et al. 2010) that highlight the ability for stands dominated by mature aspen to store more tree carbon relative to mixed stands, the greatest resilience to defoliation and average annual aboveground carbon increment of trees (C_{AI}) was observed at site D, an *A. balsamea* – *P. tremuloides* mixture with the largest proportion of *P. glauca* (17% by basal area) on the whole. Extending the rotation age of aspen mixedwoods is another alternative to enhance carbon stocks, but because of a number of factors related to land-use history, the abundance of mid- to late-successional species capable of long-term carbon storage, such as *P. glauca*, *P. strobus*, and *Thuja occidentalis* L., are limited (Schulte et al. 2007). Thus, older stands contain a similar suite of species as younger stands (Reinikainen et al. 2012), and canopy gaps are often slow to fill following disturbance leading to declining carbon stocks on disturbed sites. Deliberate efforts to restore historically important long-lived conifer species in aging aspen mixedwood stands could confer multiple benefits, including bolstering resilience to SBW (Batzer 1969). However, given a suite of factors including recalcitrant shrub layers and a low abundance of on-site seed sources, efforts to restore these conifer species may require significant investment in site preparation, planting, and competition control to ensure establishment and growth to increase long-term carbon storage potential and resilience (Lieffers et al. 1996).

Acknowledgements

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Appendix A

Table A1. Parameters and equation used to estimate total aboveground biomass for stems >2.5 cm DBH (1.37 m) for *Populus* (PW), hardwood (HW), and softwood (SW) species sampled in this study.

Functional groups	Species sampled in this study	Parameters		Data points (n)	Max. DBH (cm)	RMSE (log units)	R^2
		β_0	β_1				
PW	*Populus balsamifera* and *Populus tremuloides*	−2.2094	2.3867	230	70	0.507441	0.953
HW	*Acer rubrum* and *Betula papyrifera*	−1.9123	2.3651	316	66	0.491685	0.958
	Fraxinus nigra, *Tilia americana*, and *Ulmus americana*	−2.4800	2.4835	289	56	0.360458	0.980
	Quercus macrocarpa	−2.0127	2.4342	485	73	0.236483	0.988
SW	*Abies balsamea*	−2.5384	2.4814	395	230	0.182329	0.992
	Pinus strobus	−2.5356	2.4349	331	180	0.253781	0.987
	Picea glauca	−2.0773	2.3323	212	250	0.250424	0.988

Note: DBH, diameter at breast height (cm); and RMSE, root mean square error. The equation used to calculate biomass was as follows: biomass (kg, dry mass) = $\exp(\beta_0 + \beta_1 \ln\text{DBH})$, where exp is an exponential function and ln is the natural log base "e" (2.718282). Table adapted from Jenkins et al. (2003).

Table A2. Total ecosystem and carbon pool values (Mg C·ha^{-1}) for aspen mixedwood study sites in northern Minnesota, USA.

Site	Total ecosystem carbon	Overstory trees*	Understory trees	Standing dead	Downed woody debris	Forest floor†	Soil‡
A	183.9 (6.5)	73.9 (5.0)	26.8 (3.3)	10.4 (1.6)	18.8 (3.2)	16.7 (1.9)	37.3 (3.4)
B	183.6 (14.8)	91.0 (5.1)	21.5 (9.8)	10.6 (2.1)	14.6 (3.1)	18.2 (2.5)	27.9 (3.9)
C	202.5 (16.3)	87.9 (14.4)	28.2 (3.9)	7.6 (1.8)	14.8 (2.3)	30.6 (2.6)	33.5 (4.2)
D	209.2 (6.6)	108.1 (10.1)	15.8 (4.0)	12.9 (0.7)	17.2 (3.8)	19.7 (1.1)	35.5 (1.1)
E	191.0 (9.7)	67.3 (6.6)	30.2 (5.9)	18.5 (4.1)	17.2 (5.2)	11.7 (1.1)	46.0 (4.6)
F	196.9 (18.2)	86.6 (11.1)	36.4 (3.9)	20.0 (4.0)	13.2 (1.5)	13.0 (1.8)	27.8 (4.5)
G	170.5 (11.1)	68.8 (11.9)	22.4 (4.4)	12.8 (2.7)	15.9 (1.9)	12.1 (0.5)	38.5 (3.5)
H	201.3 (12.0)	87.4 (4.1)	29.1 (5.3)	6.0 (2.2)	8.7 (3.0)	14.1 (4.0)	56.0 (10.6)
I	208.6 (13.5)	85.8 (12.3)	38.1 (3.8)	5.3 (1.9)	8.7 (2.0)	25.6 (2.4)	45.0 (5.4)
Mean (SE)	193.2 (4.5)	82.3 (3.5)	28.4 (1.8)	11.7 (1.1)	14.4 (1.0)	18.0 (1.1)	38.3 (1.9)

Note: Values in parentheses are the SE.

*Overstory trees include coarse roots >3.0 cm diameter.

†Forest floor includes herbaceous plants, fine woody debris, and leaf litter.

‡Soil measured to a depth of 20 cm and includes fine roots ≤2.0 mm diameter.

Table A3. Parameter estimates and AIC$_c$ ranking of mixed-effects models for predicting carbon increment (C$_{AAI}$), tree carbon stocks (C$_{TREE}$), soil carbon stocks (C$_{SOIL}$), and total ecosystem carbon (C$_{TOTAL}$) as a function of factors related to stocking level (relative density (RD)), age (AGE), site quality (site index (SI)), disturbance history (DIST), and species composition (RD$_{PW}$, *Populus* spp.; RD$_{SW}$, softwood species including *Abies balsamea* and *Picea glauca*).

Response	Model rank	Intercept	RD	SI	AGE	DIST	RD$_{PW}$	RD$_{SW}$	RD× DIST	RD× RD$_{PW}$	RD× RD$_{SW}$	AGE× DIST	K	AIC$_C$	Δ	w	RMSE	R^2
					Predictors													
C$_{AAI}$	1	−0.61[b]	2.80[a]	0.04[a]	—	—	—	—	—	—	—	—	5	−1.50	0.00	0.33	0.21	0.73
	2	−0.82[b]	3.12[a]	0.04[a]	—	0.50	—	—	—	—	—	—	6	−0.70	0.76	0.23	0.20	0.74
	3	−0.19	2.80[a]	0.03[b]	0.00	—	—	—	—	—	—	—	6	0.50	1.98	0.12	0.20	0.74

Table A3 (*continued*).

Response	Model rank	Intercept	RD	SI	AGE	DIST	RD$_{PW}$	RD$_{SW}$	RD×DIST	RD×RD$_{PW}$	RD×RD$_{SW}$	AGE×DIST	K	AIC$_C$	Δ	w	RMSE	R²
	4	−0.37	3.14[a]	0.03[b]	0.00	0.51	—	—	—	—	—	—	7	1.20	2.70	0.09	0.20	0.74
	5	0.88[b]	2.87[a]	—	−0.01[b]	—	—	—	—	—	—	—	5	2.90	4.34	0.04	0.21	0.69
	6	0.11	2.82[a]	—	—	−1.44	—	—	5.29[b]	—	—	—	6	3.20	4.72	0.03	0.20	0.67
	7	−0.73[c]	3.02[a]	0.04[b]	—	—	0.27	—	—	−0.42	—	—	7	3.20	4.72	0.03	0.20	0.73
	8	−0.72[c]	2.64[a]	0.04[b]	—	0.40	—	−0.45	—	—	1.39	—	8	3.40	4.85	0.03	0.20	0.75
	9	0.69[c]	3.19[a]	—	−0.01[b]	0.48	—	—	—	—	—	—	6	3.80	5.34	0.02	0.20	0.70
	10	−0.43	3.12[a]	0.03[b]	0.00	1.16	—	—	—	—	—	−0.01	8	4.10	5.55	0.02	0.20	0.74
	11	0.15	2.87[a]	—	—	—	—	—	—	—	—	—	4	4.20	5.72	0.02	0.21	0.65
	12	−0.57[b]	2.33[a]	0.04[a]	—	—	—	−0.42	—	—	1.44	—	8	4.40	5.92	0.02	0.21	0.74
	13	−0.05	3.20[a]	—	—	0.51	—	—	—	—	—	—	5	5.00	6.54	0.01	0.21	0.64
	14	−0.15	2.93[a]	—	—	0.67[c]	0.17	—	—	0.40	—	—	7	6.50	7.95	0.01	0.19	0.64
	15	0.10	2.62[a]	—	—	—	0.17	—	—	0.24	—	—	6	7.00	8.45	<0.01	0.20	0.64
	16	0.28	2.58[a]	—	—	—	—	−0.48	—	—	1.13	—	6	8.80	10.31	<0.01	0.21	0.65
	17	0.06	2.95[a]	—	—	0.51	—	−0.48	—	—	1.01	—	7	9.90	11.41	<0.01	0.20	0.64
	18	1.59[a]	—	—	—	−1.63[a]	—	—	—	—	—	—	4	45.60	47.07	<0.01	0.34	0.23
	19	1.16	—	0.03	0.00	−1.52[a]	—	—	—	—	—	—	6	46.10	47.64	<0.01	0.32	0.32
	20	2.38[a]	—	—	−0.01[c]	−1.58[a]	—	—	—	—	—	—	6	48.60	50.08	<0.01	0.33	0.28
	21	1.64[b]	—	—	0.00	5.29	—	—	—	—	—	−0.09	7	49.40	50.91	<0.01	0.32	0.31
	22	2.53[a]	—	—	−0.01[b]	—	—	—	—	—	—	—	4	52.00	53.50	<0.01	0.37	0.10
	23	0.35	—	0.05[b]	—	—	—	—	—	—	—	—	5	54.60	56.11	<0.01	0.36	0.14
	24	1.40[a]	—	—	—	—	—	—	—	—	—	—	4	56.80	58.33	<0.01	0.38	0.00
C$_{TREE}$	1	−71.00[a]	200.46[a]	1.54[a]	0.46[a]	—	—	—	—	—	—	—	7	343.40	0.00	0.28	1.00	0.91
	2	−30.82[a]	201.85[a]	0.84[c]	—	—	17.64	—	—	−4.83	—	—	8	343.40	0.04	0.27	1.05	0.90
	3	−13.00	198.16[a]	—	—	—	17.14	—	—	1.05	—	—	7	344.10	0.74	0.19	1.00	0.90
	4	−69.68	198.00[a]	1.53[a]	0.46[a]	−3.70	—	—	—	—	—	—	8	346.20	2.81	0.07	1.00	0.91
	5	−29.20[a]	204.89[a]	1.13[a]	—	—	—	—	—	—	—	—	6	346.60	3.19	0.06	2.06	0.88
	6	−14.61	200.36[a]	—	—	3.89	17.30	—	—	1.43	—	—	8	346.90	3.53	0.05	1.00	0.90
	7	−76.75[a]	195.20[a]	1.50[a]	0.58[a]	73.11	—	—	—	—	—	−1.00	9	348.70	5.34	0.02	1.00	0.91
	8	−5.11	203.62[a]	—	—	—	—	—	—	—	—	—	5	348.90	5.54	0.02	1.00	0.88
	9	−29.00[a]	204.61[a]	1.13[a]	—	−0.45	—	—	—	—	—	—	7	349.30	5.94	0.01	1.32	0.88
	10	−25.07[b]	210.18[a]	0.97[b]	—	—	—	−5.88	—	—	−12.85	—	8	349.60	6.27	0.01	1.15	0.89
	11	−18.76	203.05[a]	—	0.18	—	—	—	—	—	—	—	6	350.30	6.90	0.01	1.00	0.89
	12	−5.88	213.80[a]	—	—	—	—	−2.99	—	—	−24.99	—	7	350.60	7.25	0.01	1.01	0.89
	13	−3.15	200.41[a]	—	—	−4.71	—	—	—	—	—	—	6	351.40	8.04	<0.01	1.00	0.88
	14	−26.06[b]	211.79[a]	0.97[b]	—	2.05	—	−5.63	—	—	−13.75	—	9	352.70	9.29	<0.01	1.17	0.89
	15	−16.55	198.33[a]	—	0.19	−6.87	—	—	—	—	—	—	7	352.80	9.41	<0.01	1.00	0.89
	16	−6.05	214.13[a]	—	—	0.41	—	−2.94	—	—	−25.19	—	8	353.50	10.14	<0.01	1.02	0.89
	17	−4.62	203.74[a]	—	—	11.15	—	—	−42.85	—	—	—	7	354.00	10.59	<0.01	1.00	0.88
	18	98.32[a]	—	—	—	−130.64[a]	—	—	—	—	—	—	5	430.40	87.02	<0.01	1.01	0.38
	19	82.26[a]	—	—	0.21	−133.55[a]	—	—	—	—	—	—	6	432.60	89.24	<0.01	1.00	0.38
	20	33.41	—	—	0.84[c]	312.04	—	—	—	—	—	−5.66[c]	7	432.60	89.25	<0.01	1.00	0.41
	21	29.22	—	1.46	0.50	−130.71[a]	—	—	—	—	—	—	7	433.90	90.55	<0.01	1.00	0.40
	22	82.29[a]	—	—	—	—	—	—	—	—	—	—	3	448.10	104.76	<0.01	0.01	0.00
	23	51.18[b]	—	1.49	—	—	—	—	—	—	—	—	4	449.00	105.61	<0.01	1.00	0.03
	24	93.67[a]	—	—	−0.14	—	—	—	—	—	—	—	4	450.40	107.01	<0.01	0.01	0.00
C$_{SOIL}$	1	−20.34	—	—	0.81[b]	340.62[b]	—	—	—	—	—	−4.71[b]	7	385.20	0.00	0.27	1.01	0.17
	2	42.22[a]	—	—	—	−30.88[b]	—	—	—	—	—	—	5	386.40	1.18	0.15	1.02	0.06
	3	25.35	46.83[c]	—	—	—	—	5.58	—	—	−72.61	—	7	387.90	2.69	0.07	1.20	0.05
	4	38.49[a]	—	—	—	—	—	—	—	—	—	—	4	387.90	2.72	0.07	1.02	0.00
	5	22.23	—	—	0.26	−30.66[b]	—	—	—	—	—	—	6	388.00	2.83	0.07	1.01	0.09
	6	27.83[a]	24.55	—	—	—	—	—	—	—	—	—	5	388.10	2.88	0.06	1.06	0.01
	7	38.80[a]	6.70	—	—	−26.64	—	—	—	—	—	—	6	388.90	3.70	0.04	1.04	0.05
	8	18.38	—	—	0.26	—	—	—	—	—	—	—	5	389.50	4.27	0.03	1.02	0.02
	9	34.19[b]	31.18	—	—	−19.91	—	2.92	—	—	−63.68	—	8	389.60	4.44	0.03	1.75	0.07
	10	9.91	23.28	—	0.24	—	—	—	—	—	—	—	6	389.90	4.72	0.03	1.03	0.04
	11	35.41[b]	—	0.15	—	—	—	—	—	—	—	—	5	390.40	5.18	0.02	1.03	0.00
	12	32.08[c]	48.68[c]	−0.34	—	—	—	6.36	—	—	−77.69	—	8	390.50	5.36	0.02	1.19	0.05
	13	11.31	—	0.33	0.31	−29.83[c]	—	—	—	—	—	—	7	390.60	5.40	0.02	1.01	0.09
	14	25.47	24.47	0.12	—	—	—	—	—	—	—	—	6	390.70	5.47	0.02	1.07	0.01
	15	20.23	4.67	—	0.25	−27.65	—	—	—	—	—	—	7	390.70	5.53	0.02	1.02	0.09
	16	−25.69	−6.66	0.22	0.86[b]	347.30[b]	—	—	—	—	—	−4.85[b]	9	390.90	5.73	0.02	1.01	0.17
	17	48.51[b]	−38.53	—	—	—	−32.40	—	—	100.42	—	—	7	391.20	6.02	0.01	1.06	0.04
	18	36.18[a]	12.73	—	—	4.46	—	—	−84.37	—	—	—	7	391.30	6.06	0.01	1.04	0.60
	19	38.31[b]	6.73	0.02	—	−26.58	—	—	—	—	—	—	7	391.60	6.45	0.01	1.05	0.05
	20	−3.13	22.46	0.41	0.30	—	—	—	—	—	—	—	7	392.40	7.18	0.01	1.04	0.04

Table A3 (*concluded*).

Response	Model rank	Intercept	RD	SI	AGE	DIST	RD_{PW}	RD_{SW}	RD×DIST	RD×RD_{PW}	RD×RD_{SW}	AGE×DIST	K	AIC_C	Δ	w	RMSE	R^2
	21	41.58[b]	32.87	−0.37	—	−20.23	—	3.71	—	—	−68.88	—	9	392.40	7.22	0.01	1.46	0.07
	22	58.42[a]	−52.15	—	—	−24.06	−33.05	—	—	97.59	—	—	8	392.60	7.40	0.01	1.09	0.07
	23	9.51	4.51	0.33	0.30	−26.94	—	—	—	—	—	—	8	393.40	8.24	<0.01	1.03	0.09
	24	49.61[b]	−38.72	−0.05	—	−32.38	—	—	—	100.74	—	—	8	394.10	8.90	<0.01	1.06	0.04
C_{TOTAL}	1	−61.71	115.66[a]	3.05[b]	1.96[a]	527.70	—	—	—	—	—	−7.66[c]	8	445.80	0.00	0.45	0.01	0.55
	2	−11.73	128.22[a]	3.26[b]	1.17[b]	−67.79[c]	—	—	—	—	—	—	7	446.70	0.92	0.29	1.00	0.51
	3	−35.23	170.21[a]	3.40[b]	1.10[b]	—	—	—	—	—	—	—	7	450.20	4.39	0.05	1.01	0.47
	4	144.52[a]	132.12[a]	—	—	−66.44[c]	—	—	—	—	—	—	6	450.80	4.97	0.04	1.01	0.43
	5	118.15[a]	174.56[a]	—	—	—	—	—	—	—	—	—	5	451.10	5.32	0.03	1.01	0.40
	6	103.27[a]	130.45[a]	—	0.55	−72.33[c]	—	—	—	—	—	—	7	451.80	5.96	0.02	1.01	0.45
	7	132.33[a]	159.88[a]	—	—	63.62	—	—	−352.00	—	—	—	7	451.90	6.04	0.02	1.01	0.45
	8	87.14[a]	171.54[a]	1.55	—	—	—	—	—	—	—	—	6	452.30	6.46	0.02	1.01	0.41
	9	116.37[a]	133.31[a]	1.30	—	−61.33	—	—	—	—	—	—	7	452.50	6.65	0.02	1.01	0.44
	10	80.60[b]	176.79[a]	—	0.48	—	—	—	—	—	—	—	6	452.60	6.77	0.02	1.01	0.41
	11	93.60[a]	242.46[a]	—	—	—	—	83.91	—	—	−230.73	—	7	453.70	7.91	0.01	1.00	0.42
	12	159.96	48.92	—	—	—	−71.55	—	—	212.47	—	—	7	454.10	8.24	0.01	1.01	0.42
	13	186.85[a]	13.80	—	—	−63.68	−75.30	—	—	205.30	—	—	8	454.30	8.45	0.01	1.00	0.45
	14	118.68[a]	196.50[a]	—	—	−58.19	—	79.88	—	—	−205.76	—	8	454.40	8.54	0.01	1.00	0.45
	15	71.41[b]	233.58[a]	1.20	—	—	—	78.10	—	—	−209.26	—	8	455.80	9.95	<0.01	1.00	0.43
	16	130.53[a]	53.72	1.40	—	—	−69.48	—	—	200.94	—	—	8	455.80	9.95	<0.01	1.00	0.43
	17	56.74	—	3.16[b]	1.15[b]	−149.4[a]	—	—	—	—	—	—	6	456.00	10.15	<0.01	1.42	0.37
	18	98.33[a]	191.32[a]	1.04	—	−55.42	—	74.60	—	—	−188.66	—	9	456.70	10.91	<0.01	1.00	0.45
	19	81.08	—	—	1.70[a]	682.15[b]	—	—	—	—	—	−10.63[b]	7	457.10	11.24	<0.01	1.01	0.39
	20	211.30[a]	—	—	—	−148.13[a]	—	—	—	—	—	—	5	458.80	13.00	<0.01	1.01	0.30
	21	169.59[a]	—	—	0.55	−155.36[a]	—	—	—	—	—	—	6	459.90	14.11	<0.01	1.01	0.32
	22	193.16[a]	—	—	—	—	—	—	—	—	—	—	3	470.90	25.09	<0.01	0.00	0.00
	23	148.11[a]	—	2.16	—	—	—	—	—	—	—	—	4	471.30	25.47	<0.01	0.99	0.04
	24	183.54[a]	—	—	0.12	—	—	—	—	—	—	—	4	473.20	27.42	<0.01	1.00	0.00

Note: K refers to the number of terms included in the model, AIC_c is the corrected Akaike's information criterion, Δ is the difference between a given model's AIC_c and the minimum observed AIC_c, w is the Akaike weight, RMSE is the root mean squared error, and R^2 is the square of Pearson's correlation coefficient. Models are ranked in descending order. [a], Parameter is significant at $p < 0.01$; [b], parameter is significant at $p < 0.05$; and [c], parameter is significant at $p < 0.10$.