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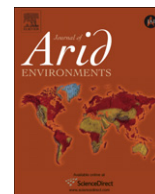Follow this and additional works at: https://digitalcommons.usu.edu/sagestep_articles

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Developing a model framework for predicting effects of woody expansion and fire on ecosystem carbon and nitrogen in a pinyon–juniper woodland

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A B S T R A C T

Sagebrush-steppe ecosystems are one of the most threatened ecosystems in North America due to woodland expansion, wildfire, and exotic annual grass invasion. Some scientists and policy makers have suggested that woodland expansion will lead to increased carbon (C) storage on the landscape. To assess this potential we used data collected from a Joint Fire Sciences Program demonstration area to develop a Microsoft Excel™ based biomass, carbon, and nitrogen (N) spreadsheet model. The model uses input for tree cover, soil chemistry, soil physical properties, and vegetation chemistry to estimate biomass, carbon, and nitrogen accumulation on the landscape with woodland expansion. The model also estimates C and N losses associated with prescribed burning. On our study plots we estimate in treeless sagebrush-steppe ecosystems, biomass accounts for $4.5 \, \mathrm{Mg \, ha^{-1}}$ C and $0.3 \, \mathrm{Mg \, ha^{-1}}$ N this is <10% of total estimated ecosystem C and N to a soil depth of 53 cm, but as tree cover increases to near closed canopy conditions aboveground biomass may account for $62 \, \mathrm{Mg \, ha^{-1}}$ C and $0.6 \, \mathrm{Mg \, ha^{-1}}$ N which is nearly 53% of total estimated ecosystem C and 13% of total estimated ecosystem N to a soil depth of 53 cm. Prescribed burning removes aboveground biomass, C and N, but may increase soil C at areal tree cover below 26%. The model serves as a tool by which we are able to assess our understanding of the system and identify knowledge gaps which exist for this ecosystem. We believe that further work is necessary to quantify herbaceous biomass, root biomass, woody debris decomposition, and soil C and N with woodland expansion and prescribed fire. It will also be necessary to appropriately scale these estimates from the plot to the landscape.

Published by Elsevier Ltd.

1. Introduction

Management of ecosystems for carbon (C) sequestration has become an important issue for private and public land managers (Canadell and Raupach, 2008). The issue is not limited to tropical or mesic environments, but also is a consideration in management of semi-arid and arid ecosystems (Asner et al., 2003). Many sagebrush–steppe (*Artemisia tridentata* Nutt.) ecosystems in the intermountain western U.S. are threatened by expansion and infill of pinyon pine (*Pinus monophylla* Torr. & Frém, *Pinus edulis* Engelm.) and juniper (*Juniperus osteosperma* (Torr.) Little, *Juniperus occidentalis* Hook.) (Miller and Tausch, 2001). Some have suggested that

woodland expansion and infill will provide an offset for greenhouse gas emissions (Norris et al., 2001; Pacala et al., 2001; Asner et al., 2003; Hibbard et al., 2003; Canadell and Raupach, 2008; McKinley and Blair, 2008). However, woodland expansion reduces perennial herbaceous vegetation, which provides forage for native animal species and reduces surface erosion. Woodland infill may also facilitate high severity wildfire and exotic annual grass invasion which may ultimately lead to declines in C storage (Miller and Tausch, 2001; Bradley et al., 2006; Chambers et al., 2007; Rau et al., 2011). Little is currently known about ecosystem C and nitrogen (N) within expansion woodlands, nor about the processes which drive their accumulation.

Fire has an integral role in maintaining sagebrush-steppe ecosystems, and land managers would like to use prescribed fire as a tool for ecosystem maintenance. Because these systems are prone to fire, dense woodlands cannot be maintained on the landscape without dramatically increasing the risk of high severity

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wildfire (Miller and Tausch, 2001). When wildfire burns though dense woodlands large amounts of aboveground C and some soil C are released back to the atmosphere. Prescribed fire also releases C to the atmosphere, but may do so at a more moderate rate.

Scientists and managers currently lack a model that will allow them to account for increasing C in expansion pinyon and juniper woodlands and the effects of land management on C loss and retention. In this paper we initiate development of such a model based on empirical data collected from a Join Fire Science Demonstration area located in central Nevada, USA.

2. Methods

2.1. Experimental area

Underdown Canyon is a Joint Fire Sciences Program demonstration area in the Shoshone Mountain Range on the Humboldt-Toiyabe National Forest (Austin Ranger District) in Nye and Lander Counties, Nevada. The canyon (39°15′11″N, 117°35′83″W) is oriented east to west and contains infrequent springs and an intermittent stream near the top of the drainage. Annual precipitation ranges from 230 to 500 mm and arrives mostly as winter snow and spring rains. Average temperature recorded in Austin, NV ranges from −7.2 °C in January to 29.4 °C in July. Lithology of the Shoshone range consists of welded and non-welded silica ash flow tuff. Soils developed on alluvial fans in this study are classified as coarse loamy skeletal mixed frigid Typic Haploxerolls (Rau et al., 2005).

The vegetation is characterized by mountain big sagebrush (*A. tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beattle) and single leaf pinyon (*P. monophylla* Torr. & Frem) with lesser cover of Utah juniper (*J. osteosperma* (Torr.) Little), and associated understory species. The vegetation occurs in patches of variable tree dominance typical of woodlands in the central Great Basin.

2.2. Study design and data collection

Forty-seven 0.1 ha plots measuring 20 × 50 m were located on northeast facing alluvial fans in order to standardize geomorphic position. Plots ranged in elevation from 2072 to 2346 m. Vegetation and litter assessments were made on all 47 plots prior to burning in June–July 2001, and again post fire in June–July 2002. Tree canopy cover estimated as tree crown area per plot ranged from 5 to 87%, and was independent of elevation. Soil assessments were made at 24 locations due to logistical and budgetary constraints. All 24 soil plots were sampled prior to burning in November of 2001, and again post fire in November 2002. USDA Forest Service fire personnel burned 24 of the vegetation plots including 12 soil plots on May 11–14, 2002 under favorable weather conditions (air temperature < 32 °C, relative humidity > 15%, wind speed < 9 m s^{-1}, and gravimetric fuel moisture ≈40%) 23 vegetation plots including 12 soil plots were left as unburned controls. Fire behavior was characterized by creeping surface fire with single and group tree torching.

2.3. Understory biomass and litter

Understory vegetation in each plot was sampled in fifty 1 × 2 m quadrats located contiguously along belt transects perpendicular to the long axis of the plot. Sampling occurred before burning in 2001 and again after burning in 2002 to determine how much biomass was lost due to prescribed burning. Understory cover and volume were estimated by measuring total vegetation height, crown height, longest crown diameter, crown diameter perpendicular to the longest diameter, and basal diameter for each individual shrub

and herbaceous (grasses and forbs) plant rooted within the 50 quadrats (Reiner et al., 2010). Vegetation was measured and completely removed by species in additional micro-plots outside of the main vegetation plot in order to develop Volume vs. dry mass regression models for each species (Reiner et al., 2010). The volume vs. dry mass regression equations were developed for shrub species by measuring, harvesting, separating by foliage and woody time lag fuel size class, and weighing all shrub parts. Biomass was reported for herbaceous and woody shrub vegetation as live and dead categories of foliage, 1 h (<6.35 mm), 10 h (6.35–25.4 mm), 100 h (25.4–76.2 mm), and 1000 h (>76.2 mm) woody time lag fuels (Anderson, 1990). Time lag is the time required for a fuel particle to reach 63% of the difference between the initial moisture content and the equilibrium moisture content at current atmospheric conditions (Anderson, 1990).

Shrub litter mats were sampled under 18 rabbitbrush (*Chrysothamnus viscidiflorus*) and 36 sagebrush (*A. tridentata vaseyana* and *A. tridentata wyomingensis*) by collecting, drying, and weighing all shrub litter within a 100 cm^2 plot frame (Brown, 1982). Full crown and litter mat dimensions were collected for each sampled shrub. Shrub litter dry weight on the entire plot was estimated for rabbitbrush and sagebrush species using regression equations based on relationships developed between shrub crown area, litter mat area, and litter mat weight (Reiner et al., 2010).

2.4. Tree biomass and litter

Tree biomass was estimated in each plot by measuring total tree height, crown height, longest crown diameter, crown diameter perpendicular to the longest diameter, and trunk diameter just above the root crown for each individual tree rooted within the plot. Crown measurements were of the portion of the crown containing foliage. Sampling occurred before the burning in 2001 and again after burning in 2002 to determine how much biomass was lost due to prescribed burning. Volume vs. dry mass regression equations were used to estimate biomass from tree canopy volume (Tausch, 2009). The volume vs. dry mass regression equations were verified for pinyon and juniper trees by measuring, harvesting, separating by foliage and woody time lag fuel size class, drying, and weighing 18 whole trees from just outside of sub-plots prior to and after burning. Trees ranged in size from 0.5 m to 6.3 m in height. Biomass was reported for trees as live and dead categories of foliage, 1 h (<6.35 mm), 10 h (6.35–25.4 mm), 100 h (25.4–76.2 mm), and 1000 h (>76.2 mm) woody time lag fuels (Anderson, 1990).

Tree litter mats were sampled under 17 pinyon pines with crown diameters ranging from 1.8 to 7.0 m. Complete tree crown and litter mat dimensions were collected in order to derive relationships between tree crown area, litter mat area, and litter mat mass. One to three 33.5 cm diameter rings were evenly spaced on either side of the tree bole depending on its size, and all litter within the ring was collected, dried, and weighed to determine the litter mat mass to area relationships.

2.5. Soil and roots

Due to the large number of vegetation plots sampled and the effort required to determine soil characteristics only a sub-set of representative plots at elevations 2195–2225 m were sampled to determine soil characteristics. Twenty four soil pits were dug at three vegetation microsites (under tree canopy, under shrub canopy, and interspace) to a depth of 53 cm where large grained alluvium was consistently encountered, the soil horizons were identified, texture, and coarse fragment content was quantified, and bulk density was determined using 93 cm^3 soil core. Depth increments for sampling were assigned to the approximate depth

of the soil A_1 horizon and subsequent 15 cm increments due to lack of profile development in the sub-surface (0–8, 8–23, 23–38, and 38–53 cm). Soil samples for chemical analysis were taken from the three microsites using a 10 cm diameter bucket auger. Sampling was conducted for the 53 cm soil profile before the burn in 2001 and again after the fire in 2002 to determine fire effects on soil C and N (Rau et al., 2009a). Estimates for soil mass and C and N concentrations at each microsite were weighted by the microsite's estimated cover percentage on each plot.

Root biomass was estimated at all 24 soil plots, microsites, and soil depths post-hoc in 2005 using a diamond tipped rotary core coupled to a 6.5 hp powerhead (Rau et al., 2009b). Roots were separated from soil and rock by sieve and flotation, dried, and then weighed. Control plots were considered pre-burn and the plots which had prescribed fire implemented in 2002 were considered post-burn. Estimates for root mass and C and N concentrations at each microsite were weighted by the microsite's estimated cover percentage on each plot.

2.6. Carbon and nitrogen

All soil and root samples and six vegetation sub-samples were selected from each biomass component (grass, forb, shrub litter, live and dead shrub foliage, shrub woody 1–100 h fuels, tree litter, live and dead tree foliage and tree woody 1–1000 h fuels) pre and post-burn for chemical analyses. Samples were ground in a Wiley® mill and analyzed for organic C and total N concentration using a LECO Truspec®. The percent organic C and total N for soil and each biomass component was multiplied by the total mass of that component in each sub-plot.

2.7. Model description

The model was created in Microsoft Excel™ and uses 28 regression equations embedded in 10 worksheets for calculating different ecosystem component biomass, C and N. The model uses individual regression equations to calculate soil mass, root biomass, herbaceous biomass (grasses and forbs), shrub litter, shrub foliage, shrub woody fuels, tree litter, tree foliage, tree woody fuels, and C and N pools before and after prescribed fire. The model creates 6 chart graphics based on the input, and returns data on ecosystem biomass, C, and N, before and after prescribed fire based on tree cover (Figs. 1–3).

It was determined that crown area or tree cover could be used in place of crown volume to estimate fuel loads and biomass components with little loss in accuracy. Therefore, the model was designed so that all ecosystem components could be estimated using tree cover rather than canopy volume. A series of regression equations were developed using observed tree cover from 41 of the 47 plots as the independent variable or x-axis, and treating all other pre-burn ecosystem components as dependant variables or y-axis. Individual regressions were developed for pre-burn shrub cover, pre-burn herbaceous cover, and pre-burn herbaceous biomass, shrub litter mass, shrub foliage mass, shrub 1–1000 h woody fuel mass, tree litter mass, tree foliage mass, and tree 1–1000 h woody fuel mass (Table 1). A second set of regressions was developed using 18 of the burned plots to estimate post-burn cover, biomass, and nutrient pools. In most cases the best fitting regression was a second order polynomial (Table 1). Because a second order polynomial has minimum value represented by the apex of a parabola, regression predictions were truncated once the equation crossed the x-axis or the minimum value was obtained. The regressions for shrub cover vs. tree cover were used to determine the weighting for soil and root mass at each microsite, where
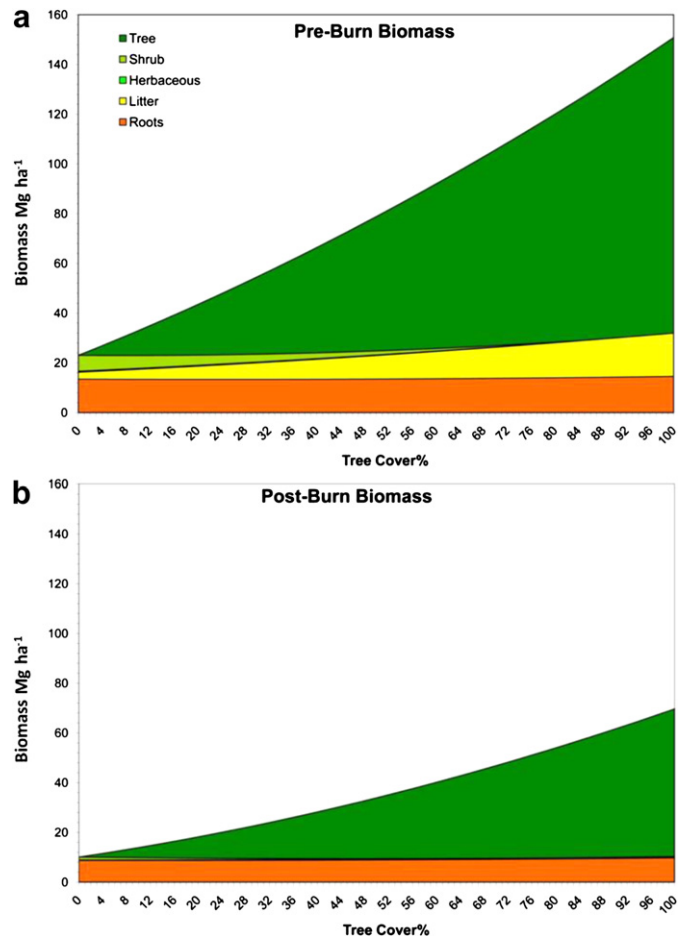

Fig. 1. The output graphics produced for ecosystem biomass pre-burn (panel a) and post-burn (panel b). Post-burn graphics represent the residual biomass found on the site immediately after burning at any given cover percentage. Biomass Mg ha^{-1} is stacked, adding values for each ecosystem component starting at zero, and ending at cumulative ecosystem biomass.

interspace cover was determined to be [100 − (tree cover + shrub cover)].

Six plots were withheld from the development of regressions to verify the predicted values for tree biomass based on tree cover. Observed vs. predicted values were plotted against each other for tree biomass components to determine how well the regression equations predicted field observed data.

3. Results and discussion

3.1. Verification

The plots used to verify the predictions of tree biomass were fit relatively well by the model. The slope of the regression between observed and predicted biomass ranged from 0.84 to 0.99 for pre and post-burn fuels (Table 2). The model is very good at predicting fuels at intermediate tree cover, but additional sample points will be needed to verify high and low tree cover values (Fig. 4). The regression equations developed for tree cover vs. herbaceous biomass and shrub fuels had relatively low r^2 values compared to equations developed for tree fuels (Table 1). We believe this is due to the variability in abiotic conditions across our plots. For example plots at lower elevation have lower mean annual precipitation than plots at higher elevations. Further work is needed to determine how these abiotic factors influence herbaceous and shrub fuels. It
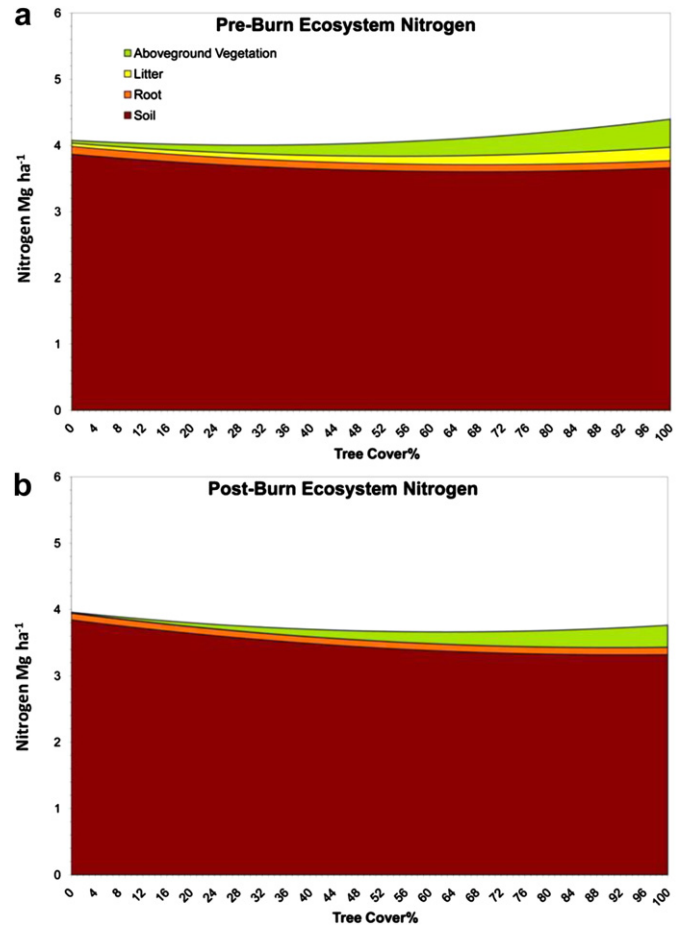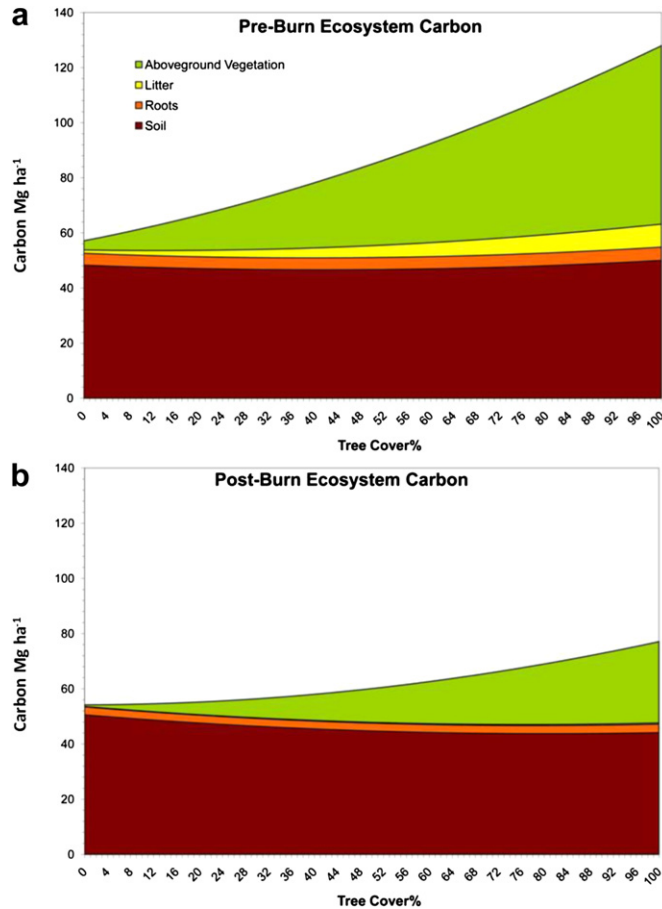
Fig. 2. The output graphics produced for ecosystem C pre-burn (panel a) and post-burn (panel b). Post-burn graphics represent the residual carbon found on the site immediately after burning at any given cover percentage. Mass C Mg ha^{-1} is stacked, adding values for each ecosystem component starting at zero, and ending at cumulative ecosystem C mass.

Fig. 3. The output graphics produced for ecosystem N pre-burn (panel a) and post-burn (panel b). Post-burn graphics represent the residual nitrogen found on the site immediately after burning at any given cover percentage. Mass N Mg ha^{-1} is stacked, adding values for each ecosystem component starting at zero, and ending at cumulative ecosystem N mass.

may be necessary to develop a more complex series of regressions using abiotic factors such as precipitation, temperature, soil depth, and soil texture to more accurately estimate herbaceous biomass. The regression equations developed for tree fuels fit well across all of our plots (Tables 1 and 2; Fig. 4). Trees appear to be less influenced by variation in site characteristics and grow somewhat uniformly over the range of abiotic conditions on our site. Additional work from several other sites indicates that given enough variability in climate and soils, trees may have different height to crown area ratios. Typically trees grow taller for every unit of increased crown area on more productive sites. Therefore, more productive sites typically have taller trees with greater biomass than trees of a similar crown area on less productive sites. Regression equations may need to be calibrated to individual sites with more wide ranging abiotic conditions. We intend to test our regression equations and overall model on plots currently being measured over a broad geographical area with a range of climatic conditions. This may enable us to incorporate climate and soil variables into the model.

3.2. Woodland expansion, aboveground biomass, carbon, and nitrogen

Understory herbaceous and shrub biomass are maximized at the lowest values of tree cover with our site supporting 0.4, 2.8, and 6.4 Mg ha^{-1} of herbaceous, litter, and shrub biomass respectively

(Fig. 1a). This is intermediate to reports for understory biomass from tallgrass prairie at risk of eastern red cedar (*Juniperus virginiana* L.) expansion in Kansas (1—6 Mg ha^{-1}; McKinley and Blair, 2008), and reports from temperate savannas at risk of honey mesquite (*Prosopsis glandulosa* Torr.) expansion in Texas ($\approx$10 Mg ha^{-1}; Hughes et al., 2006). On our sites, shrub and herbaceous biomass accounts for 4.5 Mg ha^{-1} C and 0.3 Mg ha^{-1} N without tree cover, with shrubs and shrub litter accounting for nearly all C and N. Our C values are similar to values for aboveground biomass C reported by Hooker et al. (2008) for treeless sagebrush-steppe ecosystems in Utah (3.8 Mg ha^{-1} C). Our values are higher than aboveground C values reported in tallgrass praire ecosystems (1.63 Mg ha^{-1} C; McKinley and Blair, 2008), but similar to aboveground C values from temperate mesquite savannas ($\approx$5 Mg ha^{-1} C; Hughes et al., 2006).

Adding trees to the landscape rapidly increases total biomass and shifts the balance from herbaceous and shrub fuels to tree fuels. The model estimates that when areal tree cover exceeds 10% tree biomass exceeds total understory biomass, and total aboveground biomass nearly triples to 19.5 Mg ha^{-1} (Fig. 1a). This emphasizes that adding only a few trees to the landscape can dramatically increase the amount of biomass and C stored on a site. This is consistent with Johnson et al. (1992) who reported $\approx$24 Mg ha^{-1} total biomass at 10% tree cover in Arizona pinyon—juniper woodlands. At 25% areal tree cover, our model

Table 1
Best fit regression equations and r^2 values for tree cover (x) vs. shrub and herbaceous cover and biomass components from unburned and burned plots.

	Pre-burn		Post-burn	
	Regression equation	r^2	Regression equation	r^2
Cover				
Herbaceous	$-0.0011x^2 - 0.0039x + 12.096$	0.38		
Shrub	$0.0059x^2 - 1.1437x + 55.37$	0.75		
Biomass				
Herbaceous	$-0.0133x^2 - 2.9919x + 402.67$	0.54	$-0.2796x + 36.245$	0.04
Shrub litter	$0.6108x^2 - 92.772x + 3559.7$	0.71	$0.1106x^2 - 14.88x + 496.9$	0.85
Shrub foliage	$0.0538x^2 - 13.881x + 780.89$	0.71	$0.0121x^2 - 2.2412x + 103.68$	0.78
Shrub 1 h	$0.1801x^2 - 39.392x + 2055.7$	0.80	$0.0343x^2 - 5.9694x + 262.07$	0.87
Shrub 10 h	$0.1593x^2 - 30.55x + 1475.7$	0.76	$0.027x^2 - 4.3368x + 179.23$	0.90
Shrub 100 h	$0.1927x^2 - 40.755x + 2072.5$	0.66	$0.0927x^2 - 14.864x + 606.27$	0.89
Shrub 1000 h	$0.0176x^2 - 1.665x + 42.02$	0.61	$0.0099x^2 - 0.8313x + 17.518$	0.99
Tree litter	$0.0037x^2 + 176.19x$	0.79	$-0.0493x^2 + 13.485x$	0.69
Tree foliage	$0.4714x^2 + 159.14x$	0.99	$0.0718x^2 + 13.51x$	0.99
Tree 1 h	$0.2626x^2 + 125.2x$	0.98	$0.0986x^2 + 30.908x$	0.99
Tree 10 h	$0.4499x^2 + 141.16x$	0.99	$0.2576x^2 + 82.369x$	0.99
Tree 100 h	$0.7038x^2 + 174.27x$	0.97	$0.3588x^2 + 112.95x$	0.99
Tree 1000 h	$0.8396x^2 + 351.88x$	0.96	$1.2953x^2 + 146.75x$	0.97

predicts that aboveground biomass approaches $49\ Mg\ ha^{-1}$ (Fig. 1a). Again these estimates are consistent with estimates made by Johnson et al. (1992) who estimated $54\ Mg\ ha^{-1}$ aboveground biomass at 25% cover in Arizona pinyon–juniper woodlands. Understory biomass continues to decline toward zero as tree cover increases, with shrub biomass decreasing more rapidly than herbaceous biomass (Fig. 1a). By the time tree cover reaches 50%, aboveground biomass is estimated at $65\ Mg\ ha^{-1}$, $34\ Mg\ ha^{-1}$ C, and $0.4\ Mg\ ha^{-1}$ N (Fig. 2a). This level of tree dominance represents a threshold where herbaceous understory has been greatly reduced through competition, and the site is at risk for high severity wildfire and conversion to exotic annual grasses (Miller and Tausch, 2001).

Current estimates suggest that 80% of woodlands have tree cover values <50% (Miller et al., 2008). Landscape scale analysis using remote sensing suggests that woodland cover averages 27% the Colorado plateau (Huang et al., 2009) and 13% on the Owyhee plateau of Idaho (Strand et al., 2008). If woodlands continue to mature and infill at their present rate, than nearly 75% of all woodlands will exceed 50% cover within 30–50 years (Miller et al., 2008). This shift in tree dominance may have dramatic impacts on ecosystem structure and function, increases the risk of high severity fire, and leaves the landscape susceptible to exotic invasive species such as *Bromus tectorum* (Miller and Tausch, 2001). Areal tree cover exceeding 50–60% is rare in most pinyon–juniper woodlands, but could be possible on some very productive sites. The highest observed areal tree cover in our study was 87%. Under these conditions, the model predicts our site in central Nevada would exceed $115\ Mg\ ha^{-1}$ in aboveground biomass, $60\ Mg\ ha^{-1}$ in aboveground C, and $0.6\ Mg\ ha^{-1}$ in aboveground N (Fig. 3a). This is similar to Klopatek et al. (1991) who report $68\ Mg\ ha^{-1}$ C for pinyon–juniper stands located in Arizona. Our values are also similar to the lower value of aboveground biomass reported in eastern red cedar stands ($114–210\ Mg\ ha^{-1}$), and similar to the average values reported for aboveground biomass C in eastern red cedar stands ($\approx 60\ Mg\ ha^{-1}$ C; McKinley and Blair, 2008). This is notable because the mean annual precipitation in eastern red cedar stands in Kansas is greater than 800 mm/year (McKinley and Blair, 2008) compared to our site in central Nevada which ranges from 230 to 500 mm/year.

3.3. Woodland expansion, soil, roots, carbon, and nitrogen

The model produces only small increase in soil C as estimated to 53 cm ($48–50\ Mg\ ha^{-1}$) and a small decrease in soil N ($4–3.6\ Mg\ ha^{-1}$) due to the small absolute differences in C and N content found between microsites (Figs. 2a, 3a). Our results for soil C are similar to observations from red cedar stands where researchers observed small increases in C% near the soil surface, but could not detect a statistically significant change in soil C mass associated with woodland expansion into tallgrass prarie (Spencer et al., 2001; Smith and Johnson, 2003; McKinley and Blair, 2008). The small decrease in soil N has been observed in other grasslands experiencing woody encroachment and could be related to the incorporation of soil N into aboveground plant parts (Jackson et al., 2002). There is at least one documented case where woodland expansion leads to large increases in both soil C and N, where it was observed under the N-fixing mesquite species (Archer et al., 2004). The role that soil N has in soil organic C accumulation cannot be overstated or overlooked. Biomass and litter tend to have C to N ratios of 30:1 or greater. Microbial degradation of biomass results in the respiration of C and the creation of C compounds with average C:N $\approx$ 12. These substances are then subject to aggregation, mineral complexing, and eluviation deeper into the soil profile which can create stable pools over long periods (von Lutzow et al., 2008). Therefore, there are limits to how much C can accumulate in soils under non-N-fixing vegetation, or without N-fertilization.

Root biomass on our plots remains relatively constant with increasing tree cover in our model ($13–15\ Mg\ ha^{-1}$; Fig. 1a). Cold desert shrub-steppe ecosystems have high root densities which are similar to forested ecosystems (Jackson et al., 1996 annual). This is a likely explanation for the slight changes in root mass associated

Table 2
Slope of the correlation and r^2 for observed vs. predicted values on the model verification plots.

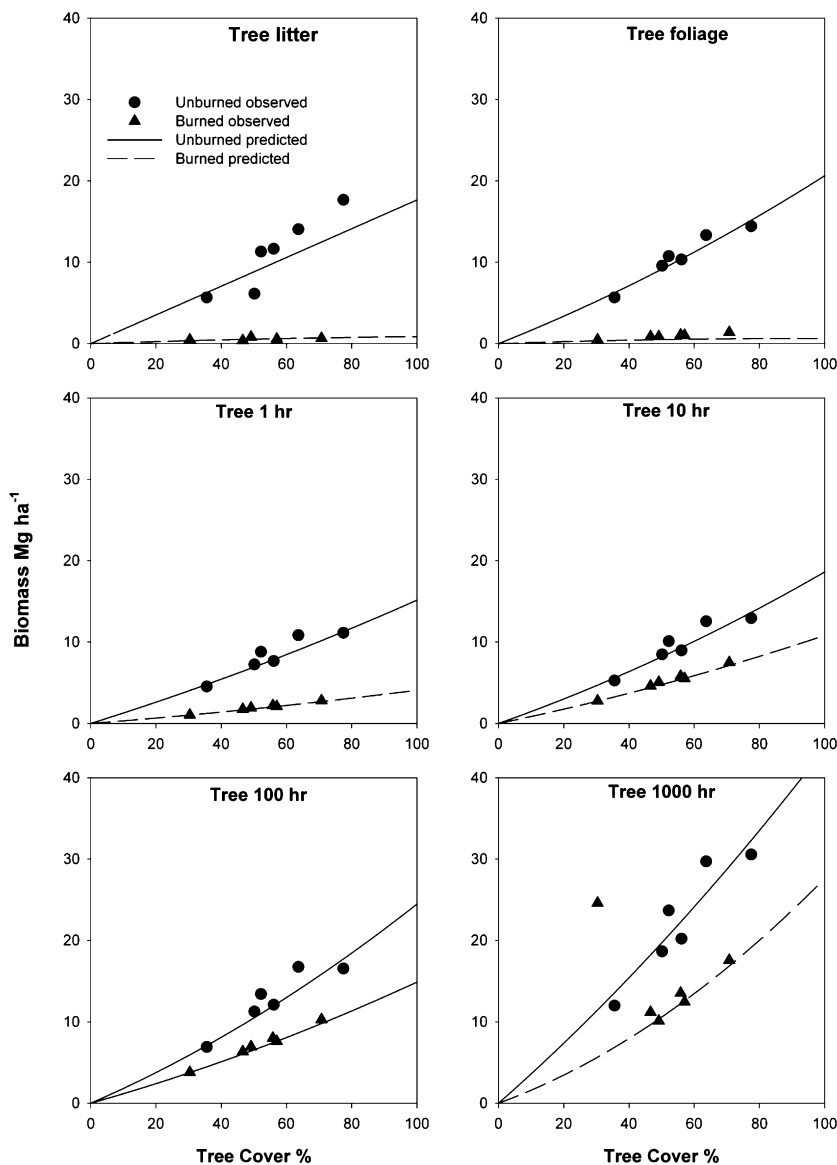|	Slope	r^2
Pre-burn litter	0.84	0.42
Post-burn litter	0.96	0.76
Pre-burn foliage	0.97	0.92
Post-burn foliage	0.95	0.98
Pre-burn 1 h	0.93	0.84
Post-burn 1 h	0.95	0.99
Pre-burn 10 h	0.96	0.86
Post-burn 10 h	0.96	0.99
Pre-burn 100 h	0.94	0.82
Post-burn 100 h	0.95	0.99
Pre-burn 1000 h	0.99	0.82
Post-burn 1000 h	0.95	0.92

Fig. 4. Graphics showing the predicted biomass based on regression equations, and the observed values obtained from individual verification plots.

with woodland expansion. We are working with a more extensive data set from 12 additional sites and a range of tree covers which confirms that root biomass does increase with woodland expansion, but only slightly more on average than estimated by this model. Because modeled root mass remains relatively constant with increasing tree cover, the pools of C and N in roots remain relatively constant as well (Figs. 2a and 3a).

3.4. Prescribed fire, aboveground biomass, carbon, and nitrogen

Prescribed burning at tree cover values near zero removed 83% of aboveground biomass and aboveground C, or 7.9 and 3.7 Mg ha^{-1} respectively (Figs. 1 and 2). Burning released a slightly higher percentage (87%) of aboveground N (0.2 Mg ha^{-1}) due to the high N concentration in herbaceous biomass (Fig. 3). As tree cover increased to 50%, prescribed burning results in a 61% reduction in existing aboveground biomass including 90% of herbaceous vegetation, litter, and shrubs (Fig. 1). Roughly 55% of standing tree biomass was consumed including >90% foliage and 1 h woody fuels; however, the majority of 10, 100, and 1000 h tree woody fuels

remain following the fire. Aboveground biomass consumed by burning at 50% tree cover accounts for 21 Mg ha^{-1} of C and 0.3 Mg ha^{-1} of N released by combustion. These estimates represent 25% and 6% of total estimated ecosystem C and N in our study. It is necessary to mention that the estimates of percent ecosystem C and N lost due to fire are relative to the depth of soil sampled, and other soil physical and chemical factors in our study. Soil depth of 53 cm may be relatively shallow or deep compared to other woodlands in the intermountain western US. Deeper and fine grained soils typically store significantly more C and N than shallow coarse grained soils. These factors will influence the percentage of ecosystem C and N held in soils vs. vegetation.

Although prescribed fire is not likely to be used in woodlands with areal tree cover exceeding 50%, it is worth contemplating this scenario as it may apply to certain wildfire situations. The highest observed areal tree cover in our study was 87%, and although this level of tree cover is rare it may occur on some isolated highly productive sites. Burning at 87% areal tree cover is modeled to remove 56%, 59%, and 49% of existing aboveground biomass, aboveground C, and aboveground N respectively (Figs. 1–3). The

loss of C from aboveground biomass by this type of burn ($37 \, \text{Mg ha}^{-1}$) is nearly than twice the amount lost at 50% tree cover and 10 times the amount lost from burning at tree cover near zero. From a whole ecosystem perspective this represents a 32% decrease in ecosystem C from the estimated pools in our study. Because of the low concentration of N in large woody materials the amount of N lost at high tree cover is not much greater than at intermediate tree cover. Our model estimates that $0.3 \, \text{Mg ha}^{-1}$ of N is lost from aboveground biomass by burning at high tree cover this is less than 6% of estimated ecosystem N in our study.

3.5. Prescribed fire, soil, roots, carbon, and nitrogen

Prescribed burning resulted in an increase in soil C and N concentrations near the soil surface (Rau et al., 2009a). However, losses occurred in several sub-surface horizons following fire (Rau et al., 2009a). The observed increase in near surface soils is likely due to the incorporation of partially burned residues and deposition of organic distillates, while losses could be due to volatilization and decomposition during and following the fire (Johnson and Curtis, 2001). Our model predicts that prescribed burning increases total estimated soil C at tree cover below 26% due to the increased C concentration of near surface soils (Fig. 2). Increases range from 0.4 to $2.3 \, \text{Mg ha}^{-1}$ C, are maximized in treeless sagebrush stands, and decrease with increasing tree cover (Fig. 2). Burning decreased soil N at all tree cover scenarios (Fig. 3). Losses of soil C and N associated with burning became more severe as tree cover increased and ranged from 0.4 to $4.6 \, \text{Mg ha}^{-1}$ of C and $0.02–0.3 \, \text{Mg ha}^{-1}$ of N (Figs. 3 and 4). These relationships indicate that low intensity prescribed fire may have a positive effect on soil C; however, as tree cover and burn severity increase the effects of burning on soil C and N become increasingly negative. In all cases the loss of soil C and N was <10% of the soil pool estimated to 53 cm. These results should be viewed as preliminary and applicable for this site only at this time. Measuring changes in soil C and N is very difficult due to spatial and temporal variation, and more data will be needed from multiple sites and burn conditions to make more definite assertions about the interaction of prescribed burning and soil C and N.

Root biomass, C, and N were all reduced by fire in our model, with root C losses increasing with increasing tree cover, and root N losses decreasing with increasing tree cover (Figs. 1–3). The results for root N pools reflect the C:N ratio of the root material decomposition process which over time reduces the C:N of root material remaining after fire (Entry and Backman, 1995). Herbaceous biomass and shrub roots started with lower C:N values than tree roots. Therefore, these materials will lose more nitrogen over a shorter period of time. Tree roots with a relative high C:N will take longer before they begin to lose N from decomposition processes (Entry and Backman, 1995).

3.6. Ecosystem level budgets

Although burning removed large quantities of estimated ecosystem C and N on our site it must be considered that not all C and N lost from biomass escapes in gaseous form, but a small percentage is incorporated into soils as ash, charcoal, and organic distillates (Johnson and Curtis, 2001). Burning in woodlands below 26% areal tree cover effectively removed aboveground biomass, but may have positive effects on soil C pools due to charcoal and organic distillates being incorporated into soil. Burning woodlands near or above the threshold value of 50% tree cover may be effective at reducing aboveground biomass, but may have negative effects on soil C and N pools. We believe that further losses of remaining roots and large woody fuels will occur via decomposition, but that this is

a relatively slow process due to the arid nature of the system (Conant et al., 1998). Fire induced losses of C and N from the existing condition may not constitute net loss when viewed from the perspective of a woodland developing from a treeless sagebrush–steppe ecosystem. Standing dead biomass, increased root biomass, and materials incorporated into soils may have resulted in a net gain of C and N over the original treeless condition. Ultimately the total net gain or loss of ecosystem C and N caused by woodland expansion and burning will be determined by the severity of the fire, completeness of woody debris decomposition, and the vegetation which returns to this site following the burn. If a healthy sagebrush–steppe or woodland system returns to the site then perhaps C and N is gained following fire, even if all standing dead biomass decomposes. If an annual grass invades the site and the fire return interval decreases, then the ecosystem may become a C source (D'Antonio and Vitousek, 1992). These processes are currently outside of the scope of our model, but are important considerations for land managers and scientists.

4. Model limitations and conclusions

Woodland expansion and the threat of exotic invasions presents land managers with difficult decisions on how best to maintain these ecosystems on the landscape and meet the goals of carbon sequestration.

The empirically derived C and N model we developed is an initial effort to estimate C and N pools in expansion pinyon and juniper woodlands. The model in its current form is likely only applicable for a range of biotic and abiotic conditions similar to our study site, but provides a valuable framework for future work. Further work must be done to incorporate other variables into the model before it would be applicable to a wider range of woodlands. Similarly this model represents stand or plot level estimates, and may not be applicable for landscape scale analysis. Several authors have shown that there are discrepancies between ground based plot level measurements and remotely sensed estimates of woodland cover which must be resolved (Strand et al., 2008; Huang et al., 2009). We believe the model provides insight into our knowledge gaps for belowground processes and decomposition, and provides us with additional hypotheses that need to be addressed. The model shows that >90% of estimated ecosystem C and N on our plots was stored in soils measured to a depth of 53 cm at low areal tree cover, but that as tree cover increases aboveground biomass can account for over 50% of estimated ecosystem C and 13% estimated ecosystem N. Tree cover approaching 50% represents a possible threshold which once passed leaves expansion woodlands prone to high severity wildfire and exotic annual grass invasion. Both intense wildfire and changing fire regimes associated with exotic annual grass invasion could lead this system to become carbon source rather than a sink (D'Antonio and Vitousek, 1992).

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