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Contribution of actinorhizal shrubs to site fertility in a Northern California mixed pine forest

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Abstract

Bitterbrush (*Purshia tridentata*) and mahala mat (*Ceanothus prostratus*) are common N-fixing shrubs in interior forests of the western United States, yet their contribution to ecosystem N pools is poorly characterized. We compared N fixation and soil N accretion by these shrubs in old-growth ponderosa pine (*Pinus ponderosa*)–Jeffrey pine (*Pinus jeffreyi*) stands versus stands that had been harvested 50 years earlier. No differences ($\alpha = 0.10$) in cover, biomass, or percent N derived from fixation by bitterbrush or mahala mat were found between harvested and uncut stands. Approximately 46% of bitterbrush N was derived from symbiotic N fixation as measured by the ^{15}N natural abundance method. No accurate measure of percent N derived from fixation was attained for mahala mat using this technique due to the absence of a well-matched reference plant. Estimates of total N fixation rates in both stand types were 0.2 kg ha^{-1} year^{-1} for bitterbrush and 0.3 kg ha^{-1} year^{-1} or less for mahala mat. No appreciable soil N accretion resulted due to the presence of bitterbrush or mahala mat in either stand type. Nitrogen addition by these shrubs, although small, accounts for 10–60% of annual N input in these dry forest ecosystems.

Keywords: Symbiotic nitrogen fixation; Bitterbrush; Mahala mat; *Purshia tridentata*; *Ceanothus prostratus*; Natural ^{15}N abundance; Old-growth; Timber harvesting

1. Introduction

Maintaining site nutrient capital is a tenet of sustainable forestry. This holds particular relevance in many ponderosa pine forests on the east side of the Cascade Range and the Sierra Nevada Mountains in California (hereafter, eastside pine forests), where vegetation growth is limited by low annual precipitation. Nutrient pools in these forests are considerably lower than in more mesic forests of the western United States (e.g. Little and Shainsky, 1995; Page-Dumroese and Jurgensen, 2006). Thus, nutrient losses during logging or fire result in proportionally larger reductions to the total pool size of these infertile ecosystems. As an example, volatilization loss of N during wildfire can exceed 800 kg ha^{-1} in eastside forests (Grier, 1975), or approximately 25% of the total ecosystem N in some stands (Little and Shainsky, 1995). Even the popular management practice of prescribed burning to reduce unwanted fuel buildup and overstocking can release 50–400 kg N ha^{-1} in eastside pine forests (Shea, 1993; Caldwell et al., 2002). Nitrogen loss associated with logging varies considerably depending on harvest intensity. For example, clear-cut harvesting and removal of whole trees may remove between 100 and 200 kg N ha^{-1} from these forests (Little and Shainsky, 1995).

Symbiotic N fixation by actinorhizal shrubs is an important mechanism to offset N losses from logging and fire disturbances (Jurgensen et al., 1997; Johnson and Curtis, 2001). For example, snowbrush (*Ceanothus velutinus*) fixes between 4 and 75 kg N ha^{-1} annually in eastside pine and mixed-conifer forests (Youngberg and Wollum, 1976; Busse, 2000). Site factors, such as overstory density, shrub cover, shrub age, length of growing season, and annual precipitation, contribute to the large range of reported N fixation rates. However, even at its lowest N fixation rate of 4 kg ha^{-1} year^{-1}, snowbrush can replace most disturbance-caused N losses within a 100-year rotation.

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Other actinorhizal shrubs in addition to snowbrush are common in eastside forests. Bitterbrush (*Purshia tridentata*) is a highly-valued species for wildlife browse (Guenther et al., 1993), and is distributed across more than 100 million hectares of forest and range lands in the interior west of North America (Hormay, 1943). Limited information shows that bitterbrush responds well to logging disturbance, preferring open stands with minimal forest floor cover for seedling establishment (Edgerton, 1983; Busse and Riegel, 2005). Mahala mat (*Ceanothus prostratus*) is also common in eastside forests, and its mat-like growth form is considered valuable for reducing soil erosion (Conard et al., 1985). How mahala mat responds to logging disturbance is unknown, although resilience is suggested given its growth form, large root system with multiple taproots, and ability to tolerate other disturbances such as prescribed fire (G.M. Riegel, unpublished data).

Knowledge of bitterbrush and mahala mat and their contribution to N budgets in eastside forests is surprisingly incomplete given their importance to these systems. Both Dalton and Zobel (1977) and Busse (2000) measured N fixation rates by bitterbrush in ponderosa pine forests of central Oregon as less than 1 kg N ha^{-1} year^{-1}. They attributed the low rates to either poor nodulation resulting from restrictive soil temperature and moisture (Dalton and Zobel, 1977), or slow growth rate and thus low N demands by the host plant (Busse, 2000). Whether this low rate is common throughout bitterbrush's wide geographic and climatic range is unknown. Presently, no estimates of N fixation rates have been reported for mahala mat.

A long-term study of eastside pine forests was established at Blacks Mountain Experimental Forest (BMEF) in northeastern California between 1938 and 1947. The study compared the effects of harvest intensity (0, 16, 54, 74, and 95% volume removal of trees larger than 29 cm in diameter) on resulting stand structure and growth. No additional management or major disturbance has occurred since the initial entry. Findings indicated that post-harvest tree growth was greatest for the 74% removal treatment and that in-growth of small diameter trees was high in all treatments (Dolph et al., 1995). Regardless of overstory condition, both bitterbrush and mahala mat are found throughout BMEF (Oliver, 2000).

The objectives of our study were to: (1) quantify N fixation and soil N accretion by bitterbrush and mahala mat at the BMEF study site, (2) determine the long-term effects of old-growth harvesting on the distribution and biomass of these two N-fixing shrubs, and (3) test the hypothesis that the rapid growth of pine regeneration following harvesting would limit N fixation and soil N accretion due to competition for site resources. At question was whether N fixation by bitterbrush and mahala mat offsets or surpasses N losses from the harvesting of old-growth pine.

2. Materials and methods

2.1. Study area and treatment design

The study was located at BMEF (lat. 40°40′N, long. 121°10′W), about 60 km northwest of Susanville, CA on the eastern slope of the southern Cascade Range. The forest is an eastside pine type (Society of American Foresters Forest Cover Type 237; Barrett et al., 1980) and has an overstory dominated by mixed-age ponderosa pine and Jeffrey pine (Youngblood et al., 2004). The climate is continental with cold, wet winters and warm summers with occasional thundershowers. Mean annual precipitation is about 50 cm, primarily in the form of winter snow (Oliver, 2000). The soil is a loamy-skeletal, mixed, mesic Typic Argixeroll, about 1 m deep above basalt bedrock. Mineral soil properties in the surface 0–15 cm include: 46 g kg^{-1} organic matter content, 0.9 g kg^{-1} total N, pH 6.9, and <10% clay content. Understory vegetation is 5–10% cover of perennial grasses and forbs and 10–15% shrub cover (Oliver, 2000).

We selected two treatments in the long-term harvesting study (74% removal and 0% removal) to test the cumulative effect of harvesting on bitterbrush and mahala mat distribution, coverage, and N-fixation. Three replicate plots (8.2 ha) of each treatment were arranged in a randomized complete block design. The 74% volume-removal treatment was typical of "heavy selection" harvesting on national forests that favored cutting of large-diameter trees. Basal area was reduced by harvesting from 24.7 to 10.5 m^2 ha^{-1}, and stand density declined from 281 to 205 trees ha^{-1} (Dolph et al., 1995).

2.2. Plant cover, biomass, and age

Canopy cover of bitterbrush and mahala mat was determined within three randomly-selected subplots (0.05 ha) per plot. Length and width of each plant (to the nearest 1 cm) were measured, and coverage was estimated assuming a rectangular-shaped canopy. Total cover was calculated as the sum of the canopy sizes of all individual plants within the subplots. Predictive equations of shrub biomass and age were developed to avoid unwanted destructive sampling within the subplots. Twenty-eight bitterbrush and 54 mahala mat plants, spanning all size classes, were measured for canopy length and width, and then excavated for above- and below-ground (roots >0.4 cm diameter) dry weight determination. Plant age was determined on all excavated samples by counting annual rings at ground level. Annual rings were counted on all tap roots of individual mahala mat, and the oldest tap root was used as the estimate of plant age. Linear regression analysis (SAS, 2000) was used to produce the predictive equations of biomass and age as a function of canopy size. Total biomass within each subplot was calculated as the sum of individual plant estimates as derived from the regression equations.

2.3. Quantification of N fixation

Few actinorhizal shrubs obtain their N solely from N fixation (Boddey et al., 2000). Nitrogen from the atmosphere and from soil solution are complementary sources whose proportional use by N-fixing plants depends on host-plant physiology, microsymbiont efficiency and environmental constraints, such as site fertility. Therefore, the percentage of N derived from the atmosphere (%Ndfa) must be quantified when assessing N fixation. We used the natural abundance method (Shearer and Kohl, 1993) to determine %Ndfa by bitterbrush and mahala mat. This method capitalizes on inherent differences between atmospheric $\delta^{15}N$ (0‰ by definition) and plant $\delta^{15}N$ to determine %Ndfa. Plants that meet all of their N demands from fixation have a $\delta^{15}N$ signature of 0‰, whereas those plants that fail to obtain any of their N from the atmosphere have $\delta^{15}N$ signatures equal to a non-fixing reference plant. Plants that obtain 50% Ndfa have $\delta^{15}N$ signatures at the mid-point between 0‰ and the $\delta^{15}N$ of a reference plant.

Foliage from five bitterbrush, mahala mat, and manzanita (*Arctostaphylos patula*) plants was collected from each subplot, for a total of 90 samples of each species (5 samples × 3 subplots × 3 reps × 2 treatments). Manzanita was selected as the non-N-fixing reference plant based on its similar root distribution and N uptake pattern as bitterbrush (Busse, 2000). No other plants were sampled since manzanita was the only non-N-fixing shrub found throughout the study area. Five clusters of adjacent bitterbrush, mahala mat, and manzanita were sampled within the subplots to account for anticipated spatial variation in ^{15}N natural abundance across treatment plots (Sutherland et al., 1991). Foliage was clipped from current-year growth in November 1995 and analyzed for $\delta^{15}N$ ($^{15}N/^{14}N$ relative to atmospheric $^{15}N/^{14}N$) and N concentration by mass spectrometry on duplicate samples at the Stable Isotope Research Unit, Oregon State University.

The need for a well-matched reference plant to estimate N fixation is minimized in soils with low ^{15}N variability in the rooting profile (Boddey et al., 2000). In such ‘‘homogeneous’’ soils, plants have access to similar ^{15}N abundance regardless of any differences in rooting depth or architecture between N-fixing and non-N-fixing plants. To test the variation in ^{15}N abundance with rooting depth, composite soil samples were collected from each harvested and unharvested plot at 0–18; 18–36; 36–54; 54–72 cm depths and analyzed for $\delta^{15}N$ by Isotope Services, Inc., Los Alamos, New Mexico.

Nitrogen derived from fixation (%Ndfa) was calculated by the equation:

$$\%\mathrm{Ndfa} = \left(\frac{[\delta^{15}\mathrm{N_r} - \delta^{15}\mathrm{N_a}]}{\delta^{15}\mathrm{N_r}}\right) \times 100 \qquad (1)$$

where $\delta^{15}N_r$ is the per mil ^{15}N natural abundance of the reference plant and $\delta^{15}N_a$ is the per mil ^{15}N natural abundance of the N-fixing plant. Total N fixed was then calculated by the equation:

$$\text{Total N fixed}(\mathrm{kg\,ha^{-1}}) = (\%\mathrm{Ndfa}) \times (\text{plant biomass}) \times (\text{plant N concentration}) \qquad (2)$$

Plant N concentration was determined by mass spectrometry using five randomly-selected, whole-plant samples of each species. Total N fixed was converted to an annual rate by dividing by the estimated mean age of all plants within the subplots for bitterbrush or the actual mean age of the 54 mahala mat plants selected for destructive sampling.

2.4. Soil N accretion

Fifteen randomly-selected organic and mineral soil (30 cm depth) samples were collected in each subplot with a 10 cm-diam. core sampler (Jurgensen et al., 1977) from: (1) beneath the canopy of bitterbrush, (2) beneath the canopy of mahala mat, and (3) in openings free of understory vegetation (a minimum of 1 canopy-width from the nearest shrub). All cores were separated in the field by forest floor (O_i, O_e, and O_a horizons combined), soil wood, and mineral soil at two depths (0–15 and 15–30 cm). Roots were hand-separated from the forest floor, soil wood, and mineral soil samples in the laboratory. Soil and root samples were dried at 80 °C, weighed, and the mineral soil was passed through a 2 mm sieve to remove coarse fragments. All samples were ground to pass a 0.04 mm mesh, and analyzed for total N content with a LECO-600 analyzer (LECO Corp., St. Joseph, MI). Mineral soil N content was extrapolated to an area basis using the fine-fraction bulk density (Cromack et al., 1999).

2.5. Statistical analyses

Foliar and soil $\delta^{15}N$ data were normally distributed based on the Kolmogorov-Smirnov test (SAS, 2000). Paired *t*-tests were used to test for differences in foliar $\delta^{15}N$ between the N-fixing shrubs and manzanita. A significant difference in foliar $\delta^{15}N$ between reference plants and putative N-fixing plants is a prerequisite to show active N fixation (Shearer and Kohl, 1993). Paired *t*-tests were also used to determine the effect of harvesting on shrub cover, biomass, and N fixation, and to identify differences in soil N accretion due to the presence or absence of N-fixing shrubs. Estimates of shrub biomass were determined by linear regression using average canopy diameter ((length +width)/2) as the independent variable and total dry weight from destructively sampled shrubs as the dependent variable.

3. Results and discussion

3.1. Plant cover, biomass, and age

No significant difference in bitterbrush cover ($P = 0.70$) or mahala mat cover ($P = 0.71$) was found between the 74% harvest treatment and the uncut control (Table 1). Thus, our hypothesis that bitterbrush and mahala mat would be less prevalent following old-growth harvesting due to greater in-growth and shading from young trees was not substantiated,

Table 1
Cover and biomass of bitterbrush and mahala mat 50 years after harvesting old-growth ponderosa pine at Blacks Mountain Experimental Forest

Shrub	Treatment	Cover (%)	Biomass (kg ha^{-1})
Bitterbrush	Harvested	6.4 (3.4)	724 (403)
	Unharvested	8.3 (3.3)	856 (384)
Mahala mat	Harvested	14.4 (3.8)	1968 (550)
	Unharvested	13.3 (5.3)	1588 (671)

Values in parentheses are S.E. ($n = 3$).

Table 2
Predictive equations of bitterbrush and mahala mat biomass (g plant^{-1}) and age (year) as a function of their canopy diameter (cm)

Species	Component	*n*	Predictive equation	R^2
Bitterbrush	Biomass	28	$\ln(Y) = -5.6 + 2.66 \ln(\text{canopy diameter})$	0.80
	Age	10	$Y = 1.70 + 0.235$ (canopy diameter)	0.91
Mahala mat	Biomass	54	$\ln(Y) = -5.3 + 2.54 \ln(\text{canopy diameter})$	0.89
	Age	52	$Y = 14.5 + 0.078$ (canopy diameter)	0.15

Canopy diameter was determined as the average of a plant's canopy length and perpendicular width. Biomass predictions include both aboveground and belowground weights.

even though stand densities were higher on harvested plots (1124 trees ha^{-1}) compared to unharvested plots (914 trees ha^{-1}) (Dolph et al., 1995). This agrees with findings from central Oregon that indicate bitterbrush and manzanita growth is restricted when tree density exceeds 309 trees ha^{-1} and basal area exceeds 19 m^2 ha^{-1} (Busse et al., 1996).

Plant canopy size was a good predictor of individual plant biomass for both bitterbrush and mahala mat (Table 2). As a result, large-scale destructive sampling was avoided in predicting total biomass per hectare. No difference in total biomass between harvest treatments was found for bitterbrush ($P = 0.82$) or mahala mat ($P = 0.68$) (Table 1).

The relationship between bitterbrush age and canopy size was also excellent (Table 2). Consequently, a bitterbrush age-class distribution was developed in order to examine potential differences in community structure between harvested and unharvested plots. The distribution pattern of the two treatments was similarly skewed in favor of young plants; the majority of bitterbrush plants were 20 years old or younger (Fig. 1), with a median age of 13.8 years for harvested plots and 13.3 years for unharvested plots. In contrast, a poor relationship between canopy size and age was found for mahala mat (Table 2). Consequently, a comparison of age distribution between harvest treatments was not made for mahala mat.

3.2. Suitability of the ^{15}N natural abundance method at BMEF

Average soil-available δ^{15}N at the study site, as estimated by the ^{15}N signature of manzanita, was -3.2 ± 0.2‰ (Fig. 2). This was significantly different than atmospheric δ^{15}N at $P < 0.001$, satisfying a key condition of the natural abundance method that the δ^{15}N signatures of the soil and atmosphere are unique. Mean foliar δ^{15}N of bitterbrush (-1.7 ± 0.2‰) was significantly different than manzanita ($P < 0.001$), indicating active N fixation. No differences in δ^{15}N of bitterbrush were found between the control and harvested treatments ($P = 0.34$). Additional evidence of active N fixation by bitterbrush included higher total foliage N than manzanita (1.86% versus 1.32%, respectively; $P < 0.001$), plus nodule formation on most plants examined in spring when soil moisture was near optimal. These factors, particularly the combined differences in δ^{15}N and total N between putative N-fixing and reference plants, are strong indicators of *in situ* N fixation (Delwiche et al., 1979; Virginia and Delwiche, 1982; Roggy et al., 1999) and substantiate the validity of the natural abundance method to estimate N fixation by bitterbrush at BMEF.

In contrast, the difference in δ^{15}N between mahala mat and manzanita (-2.7‰ versus -3.2‰, respectively) was not significant ($P = 0.192$), nor was the difference in total N content between the species (1.29% versus 1.32%, respectively; $P = 0.274$). Nodules were found on nearly all mahala mat plants and served as the lone indication of potential N fixation. Currently, no information exists to confirm or refute *in situ* N

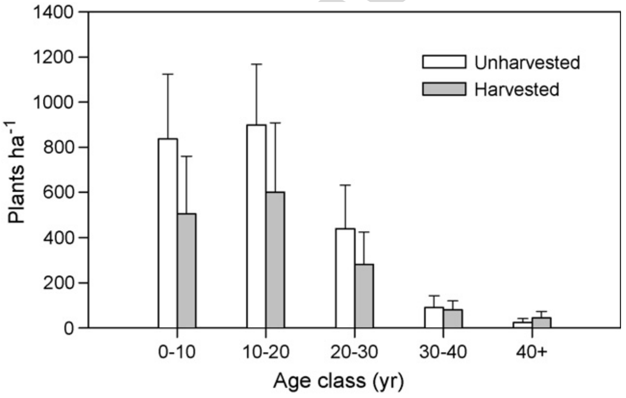

Fig. 1. Age-class distribution of bitterbrush 50 years after old-growth harvesting at Blacks Mountain Experimental Forest. Bars represent mean and S.E. ($n = 3$).

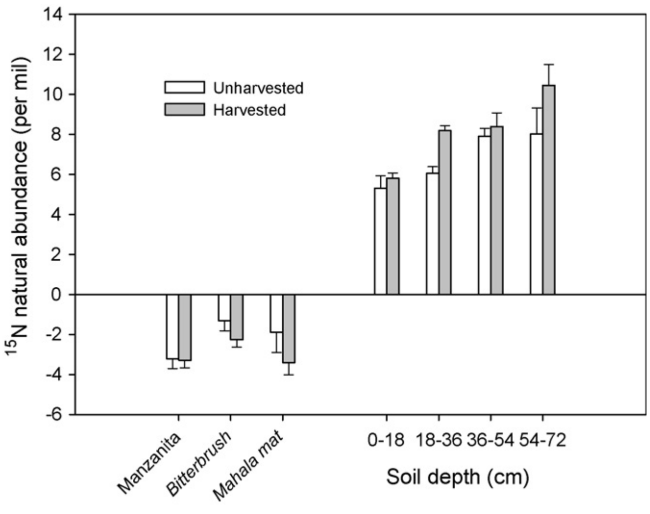

Fig. 2. ^{15}N natural abundance (δ^{15}N) of vegetation and mineral soil 50 years after old-growth harvesting at Blacks Mountain Experimental Forest in northeast California. Manzanita is a non-N-fixing shrub with similar rooting profile and seasonal N uptake pattern as bitterbrush. Bars represent mean and S.E. ($n = 45$ for each shrub-treatment combination except mahala mat-control, $n = 30$; $n = 3$ for each soil depth × harvest treatment combination).

fixation by mahala mat, although high rates of $^{15}N_2$ fixation have been shown using excised nodules (Delwiche et al., 1965). Either mahala mat did not fix N at our study site, or N fixation was not detected due to a poor reference-plant match with manzanita. The natural abundance method assumes that rooting profiles and temporal N demands are similar between N-fixing and reference plants. However, mahala mat has multiple taproots and a high proportion of fine roots in the upper soil surface, which is considerably different from the upright, single-taproot system of manzanita. The alternative method of sampling several reference plants to provide a range of rooting patterns and estimates of %Ndfa (Högberg, 1997; Boddey et al., 2000) was not an option in our study since manzanita was the only non-N-fixing shrub on all plots.

Our attempt to circumvent high spatial variability across treatment plots by sampling adjacent N-fixing and non-N-fixing plants met limited success. Spatial variability of $\delta^{15}N$ among plants was high, ranging from −8.5 to 1.4‰ for manzanita, −6.0 to 2.7‰ for bitterbrush, and −7.6 to 4.4‰ for mahala mat. Although $\delta^{15}N$ was normally distributed, the respective coefficients of variation for the three species were 66, 83, and 128%. Average subplot CV was 53% for manzanita, 61% for bitterbrush, and 55% for mahala mat. The high variability of $\delta^{15}N$ contributed to unrealistic values of %Ndfa by mahala mat – greater than 100% or less than 0% – in 8 out of 18 subplots.

Other studies have reported impossible %Ndfa values (Sanginga et al., 1990; Hansen and Vinther, 2001), and support the concern of Broadbent et al. (1980) that excessive variation in $\delta^{15}N$ can limit the use of the natural abundance method to obtain quantitative estimates of N fixation. Guinto et al. (2000) also was unable to estimate N fixation by *Acacia* sp. in the understory of native eucalyptus forests using the natural abundance method. Similar to our results for mahala mat, they found substantial variation in foliar $\delta^{15}N$ and no significant differences in $\delta^{15}N$ between N-fixing and reference plants. In contrast, favorable results using the natural abundance method have been reported for a variety of crops (Bremer and van Kessel, 1990; George et al., 1993; Androsoff et al., 1995; Doughton et al., 1995; Ramos et al., 2001) and tree species (Shearer et al., 1983; Domenach et al., 1989; Ladha et al., 1993; Salas et al., 2001; Galiana et al., 2002). Common experimental conditions in these studies included: (1) a well-matched reference plant, or, when available, selection of several reference species to provide a range of %Ndfa; (2) growing N-fixing and reference plants in proximity to overcome inherent spatial variability in $\delta^{15}N$; (3) plant-available $\delta^{15}N$ with an absolute value at least 4‰ greater than atmospheric $\delta^{15}N$. These conditions were generally met for bitterbrush but not mahala mat at our study site. Because the combination of site factors (soil, plant, climate) required to meet condition 3 is poorly understood, we agree with Shearer and Kohl (1993) that preliminary testing of non-N-fixing plants for their $\delta^{15}N$ signature is needed prior to selecting an experimental site.

3.3. N fixation estimates

Average %Ndfa for bitterbrush was 46%, with no statistically significant differences between harvest treatments ($P = 0.59$; Table 3). Only a rough approximation of %Ndfa was possible for mahala mat given the unrealistic %Ndfa values found for many of the subplots. Accepting this weakness, one-third of mahala mat's N was derived from fixation based on whole-plot averages. No statistical difference in %Ndfa was detected between harvest treatments for mahala mat ($P = 0.54$). Annual N fixation averaged 0.2 kg ha^{-1} for bitterbrush and 0.3 kg ha^{-1} for mahala mat, reflecting both the low %Ndfa values and the low biomass production by these shrubs. Again, the rate of N fixation from mahala mat should be interpreted with caution, and considered as an upper limit for these stands.

Even if these shrubs received all their N from the atmosphere (100% Ndfa), their N fixation rate would only reach 0.4 kg ha^{-1} year^{-1} for bitterbrush and 0.9 kg ha^{-1} year^{-1} for mahala mat. Such low N input by bitterbrush is similar to results found in central Oregon pine stands (Dalton and Zobel, 1977; Busse, 2000). Nevertheless, the combined estimate of 0.2–0.5 kg N fixed ha^{-1} year^{-1} by bitterbrush and mahala mat accounts for 10–60% of the annual N added to eastside forests in California, with the remaining 0.3–2.0 kg ha^{-1} year^{-1} provided by precipitation (Johnson et al., 1997).

3.4. Soil N accretion

We could find no appreciable differences in soil N accretion between the harvested and uncut stands due to the presence of bitterbrush or mahala mat. Total N content in the forest floor, mineral soil, and fine roots was similar beneath N-fixing plants and the open stand. About 90% of the total N was found in mineral soil where there was no clear trend between shrub and non-shrub soil (Table 4). Differences in N content beneath N-fixing plants and the open stand in the harvested treatment were not significant for roots ($P = 0.224$) or the O horizon ($P = 0.547$).

Table 3
Nitrogen-fixing characteristics of bitterbrush and mahala mat 50 years after harvesting of old-growth pine at Blacks Mountain Experimental Forest

Shrub	Treatment	Plant N (kg ha^{-1})	Ndfa (%)	Total N fixed (kg ha^{-1})	Annual N fixed (kg ha^{-1} year^{-1})
Bitterbrush	Harvested	5.3 (2.6)	37 (12)	2.0 (1.0)	0.1 (0.1)
	Unharvested	6.2 (2.9)	55 (23)	3.6 (1.6)	0.2 (0.2)
Mahala mat	Harvested	21.5 (6.0)	20 (20)	4.1 (1.2)	0.2 (0.1)
	Unharvested	16.0 (6.8)	44 (15)	7.0 (3.0)	0.3 (0.2)

Values in parentheses are S.E. ($n = 3$).

Table 4
Total N content (g m^{-2}) in roots, O horizon, and mineral soil sampled between understory shrubs (Open) or directly beneath bitterbrush and mahala mat plants

Treatment	Sample location	Roots	O horizon	Mineral soil		Total
				0–15 cm	15–30 cm	
Harvested	Open	1.9 (0.2)	9.4 (1.7)	87.7 (15.4)	66.7 (9.1)	165.7 (26.3)
	Bitterbrush	2.6 (0.4)	15.9 (5.7)	84.0 (12.1)	59.7 (9.4)	162.1 (25.4)
	Mahala mat	2.3 (0.2)	19.0 (8.5)	94.7 (10.3)	49.3 (9.1)	165.3 (27.0)
Unharvested	Open	2.6 (0.2)	17.5 (6.9)	77.3 (9.4)	63.0 (0.0)	160.1 (16.0)
	Bitterbrush	2.7 (0.1)	14.5 (0.6)	98.3 (15.1)	56.3 (9.4)	171.8 (20.0)
	Mahala mat	3.0 (0.4)	13.9 (9.8)	80.7 (9.4)	45.7 (9.1)	143.3 (19.7)

Values in parentheses are S.E. ($n = 3$).

Nitrogen accretion beneath other actinorhizal species is well documented (Youngberg and Wollum, 1976; Binkley et al., 1982; Johnson, 1995). Recently, Johnson et al. (2005) reported rapid replenishment of O horizon and mineral soil N by snowbrush after wildfire in the eastern Sierra Nevada range, with N accretion estimated at 36–48 kg ha^{-1} $year^{-1}$. Erickson et al. (2005) found soil beneath *Ceanothus cordulatus* (whitethorn) thickets had considerably higher N content and N mineralization rates than open canopy soils in the central California Sierras. Unlike snowbrush and whitethorn, which serve an ecological function by improving soil productivity or providing ‘‘islands of fertility’’, we found no evidence of soil N accretion by bitterbrush or mahala mat. This divergence between mahala mat and the other ceanothus species can be attributed to inherent differences in biomass production. Snowbrush biomass, for example, can approach 25 Mg ha^{-1} in similar climatic and soil conditions (Busse, 2000), or more than 10-fold greater biomass than mahala mat produced at BMEF.

4. Management implications

The ecological benefits of N fixation by bitterbrush and mahala mat are subtle. Clearly, no gross improvements in soil N content or soil productivity should be expected. Instead, these shrubs serve as a long-term source for replenishing site N following disturbance. Approximately 150 kg N ha^{-1} were removed by the 74% harvest treatment at BMEF, based on values for total volume removal (Dolph et al., 1995) and N concentration in bolewood and crowns typical of eastside pine (Little and Shainsky, 1995). This N loss would be replaced in 100 years or less given the combined input of 0.2–0.5 kg ha^{-1} $year^{-1}$ from the two shrubs, 1.0 kg ha^{-1} $year^{-1}$ from rainfall, and <0.5 kg ha^{-1} $year^{-1}$ from nonsymbiotic N fixation (Jurgensen, unpublished results). Full restoration of site N by bitterbrush and mahala mat following prescribed fire is unlikely; however, Johnson et al. (1998) estimated that a moderate-severity prescribed fire would volatilize about 200 kg N ha^{-1} from a forest ecosystem similar to ours. Thus, nearly 7 kg N ha^{-1} $year^{-1}$ are needed to replace the anticipated N loss for a 30-year fire return interval, or 14-times more N than is supplied by the two shrubs. Shorter fire-return intervals would result in even greater N replacement needs, as would fires of higher severity. Management implications for eastside forests like BMEF are clear: restoration of soil N by bitterbrush and mahala mat after forest disturbance (e.g. harvesting, fire) will be incomplete without: (1) uncharacteristically long return intervals between disturbance events, (2) logging methods and light prescribed burns that limit N losses, (3) alternative methods of fuel reduction that do not use fire, or (4) additional N input from native or introduced legumes. Reducing excessive fuel loads and catastrophic fire risk is currently the top priority in these forests from an ecological and a social perspective. Whether soil N losses due to preferred management practices such as repeated prescribed fire are inevitable or ecologically acceptable requires further scrutiny.

5. Conclusion

The natural abundance method was used successfully to quantify %Ndfa by bitterbrush. Estimates for mahala mat were compromised, however, by the lack of a well-matched reference plant and high spatial variability of plant ^{15}N. Combined N fixation by bitterbrush and mahala mat was meager regardless of harvest treatment (0.2–0.5 kg ha^{-1} $year^{-1}$). As a result of this low rate, soil N pools in the O horizon and mineral soil 50 years after harvesting were not enriched beneath N-fixing shrubs, nor were changes in site fertility indicated. Harvesting old-growth pine at BMEF had no effect on cover, biomass, or N-fixing capacity of bitterbrush or mahala mat. We suspect this was a consequence of the lack of post-harvest treatment aimed at reducing pine seedling density, and not a direct effect of harvesting per se, as both harvested and unharvested treatments had high stand densities that likely limited understory production after 50 years. Although N fixation rates were low, the addition of N by these shrubs accounts for 10–60% of annual N input in these forests, approaching the amount added by atmospheric N deposition.

References

Androsoff, G.L., van Kessel, C., Pennock, D.J., 1995. Landscape-scale estimates of dinitrogen fixation by *Pisum stivum* by nitrogen-15 natural abundance and enriched isotope dilution. Biol. Fertil. Soils 20, 33–40.

Barrett, J.W., McDonald, P.M., Ronco Jr., F., Ryker, R.A., 1980. Interior ponderosa pine. In: Eyre, F. (Ed.), Forest Cover Types of the United States and Canada. Society of American Foresters, Bethesda, Maryland.

Binkley, D., Cromack Jr., K., Fredriksen, R.L., 1982. Nitrogen accretion and availability in some snowbrush ecosystems. For. Sci. 28, 720–724.

Boddey, R.M., Peoples, M.B., Palmer, B., Dart, P.J., 2000. Use of the ^{15}N natural abundance technique to quantify biological nitrogen fixation by woody perennials. Nutr. Cycling Agroecosyst. 57, 235–270.

Bremer, E., van Kessel, C., 1990. Appraisal of the nitrogen-15 natural-abundance method for quantifying dinitrogen fixation. Soil Sci. Soc. Am. J. 54, 404–411.

Broadbent, F.E., Rauschkolb, R.S., Lewis, K.A., Chang, G.Y., 1980. Spatial variability of nitrogen-15 and total nitrogen in some virgin and cultivated soils. Soil Sci. Soc. Am. J. 44, 524–527.

Busse, M.D., 2000. Suitability and use of 15N-isotope dilution method to estimate nitrogen fixation by actinorhizal shrubs. For. Ecol. Manage. 136, 85–95.

Busse, M.D., Riegel, G.M., 2005. Managing ponderosa pine forests in central Oregon: who will speak for the soil? In: Ritchie, M.W., D.A. Maguire, A. Youngblood (Tech. coordinators), Proc. Symposium on Ponderosa Pine: Issues, Trends, and Management. USDA For. Serv. PSW-GTR-198, pp. 109–122.

Busse, M.D., Cochran, P.H., Barrett, J.W., 1996. Changes in ponderosa pine productivity following removal of understory vegetation. Soil Sci. Soc. Am. J. 60, 1614–1621.

Caldwell, T.G., Johnson, D.W., Miller, W.W., Quallis, R.G., 2002. Forest floor carbon and nitrogen losses due to prescription fire. Soil Sci. Soc. Am. J. 66, 262–267.

Conard, S.G., Jaramillo, A.E., Cromack Jr., K., Rose, S., 1985. The Role of the Genus Ceanothus in Western Forest Ecosystems. USDA Forest Service GTR PNW-182.

Cromack Jr., K., Miller, R.E., Helgerson, O.T., Smith, R.B., Anderson, H.W., 1999. Soil carbon and nutrients in a coastal Oregon Douglas-fir plantation with red alder. Soil Sci. Soc. Am. J. 63, 232–239.

Dalton, D.A., Zobel, D.B., 1977. Ecological aspects of nitrogen fixation by *Purshia tridentata*. Plant Soil 48, 57–80.

Delwiche, C.C., Zinke, P.J., Johnson, C.M., 1965. Nitrogen fixation by *Ceanothus*. Plant Physiol. 40, 1045–1047.

Delwiche, C.C., Zinke, P.J., Johnson, C.M., Virginia, R.A., 1979. Nitrogen isotope distribution as a presumptive indicator of nitrogen fixation. Bot. Gazette 140 (Suppl.), S65–S69.

Dolph, K.L., Mori, S.R., Oliver, W.W., 1995. Long-term response of old-growth stands to varying levels of partial cutting in the eastside pine type. West. J. Appl. For. 10, 101–108.

Domenach, A.M., Kurdali, F., Bardin, R., 1989. Estimation of symbiotic dinitrogen fixation in an alder forest by the method based on natural ^{15}N abundance. Plant Soil 118, 51–59.

Doughton, J.A., Saffigna, P.G., Vallis, I., Mayer, R.J., 1995. Nitrogen fixation in chickpea. II. Comparison of ^{15}N enrichment and ^{15}N natural abundance methods for estimating nitrogen fixation. Aust. J. Agric. Res. 46, 225–236.

Edgerton, P.J., 1983. Response of the bitterbrush understory of a central Oregon lodgepole pine forest to logging disturbance. In: Tiedemann, A.R., K.L. Johnson (Compilers), Proc. Research and Management of Bitterbrush and Cliffrose in Western North America. USDA For. Serv. Gen. Tech. Rep. INT-152, pp. 99–106.

Erickson, H.E., Soto, R., Johnson, D.W., Roath, B., Hunsaker, C., 2005. Effects of vegetation patches on soil nutrient pools and fluxes within a mixed-conifer forest. For. Sci. 51, 211–220.

Galiana, A., Balle, P., N'Guessan Kanga, A., Domenach, A.M., 2002. Nitrogen fixation estimated by the ^{15}N natural abundance method in *Acacia mangium* Willd. inoculated with *Bradyrhizobium* sp. and grown in silvicultural conditions. Soil Biol. Biochem. 34, 251–262.

George, T., Singleton, P.W., van Kessel, C., 1993. The use of nitrogen-15 natural abundance and nitrogen yield of non-nodulating isolines to estimate nitrogen fixation by soybeans (*Glycine max* L.) across three elevations. Biol. Fertil. Soils 15, 81–86.

Grier, C.C., 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Can. J. For. Res. 5, 599–607.

Guenther, G.E., Wambolt, C.L., Frisina, M.R., 1993. Characteristics of bitterbrush habitats that influence canopy cover and mule deer browsing. J. Environ. Manage. 36, 175–181.

Guinto, D.F., Xu, Z., House, A.P.N., Saffigna, P.G., 2000. Assessment of N2 fixation by understorey acacias in recurrently burnt eucalypt forests of subtropical Australia using ^{15}N isotope dilution techniques. Can. J. For. Res. 30, 112–121.

Hansen, J.P., Vinther, F.P., 2001. Spatial variability of symbiotic N2 fixation in grass-white clover pastures estimated by the ^{15}N isotope dilution method and the natural ^{15}N abundance method. Plant Soil 230, 257–266.

Högberg, P., 1997. ^{15}N natural abundance in soil-plant systems. New Phytol. 137, 179–203.

Hormay, A.L., 1943. Bitterbrush in California. USDA Forest Service. California Forest and Range Experiment Station Research Note 34.

Johnson, D.W., 1995. Soil properties beneath ceanothus and pine stands in the eastern Sierra Nevada. Soil Sci. Soc. Am. J. 59, 918–924.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. For. Ecol. Manage. 140, 227–238.

Johnson, D.W., Susfalk, R.B., Dahlgren, R.A., 1997. Nutrient Fluxes in forests of the eastern Sierra Nevada mountains. United States of America. Global Biogeochem. Cycles 11, 673–681.

Johnson, D.W., Susfalk, R.B., Dahlgren, R.A., Klopatek, J.M., 1998. Fire is more important than water for nitrogen fluxes in semi-arid forests. Environ. Sci. Pol. 1, 79–86.

Johnson, D.W., Murphy, J.F., Susfalk, R.B., Caldwell, T.G., Miller, W.W., Walker, R.F., Powers, R.F., 2005. The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. For. Ecol. Manage. 220, 155–165.

Jurgensen, M.F., Larsen, M.J., Harvey, A.E., 1977. A soil sampler for steep, rocky sites. USDA For. Serv. Res. Note INT 217.

Jurgensen, M.F., Harvey, A.E., Graham, R.T., Page-Dumroese, D.S., Tonn, J.R., Larsen, M.J., Jain, T.B., 1997. Impacts of timber harvesting, productivity, and health of inland northwest forests. For. Sci. 43, 234–251.

Ladha, J.K., Peoples, M.B., Garrity, D.P., Capuno, V.T., Dart, P.J., 1993. Estimating dinitrogen fixation of hedgerow vegetation using the nitrogen-15 natural abundance method. Soil Sci. Soc. Am. J. 57, 732–737.

Little, S.N., Shainsky, L.J., 1995. Biomass and Nutrient Distributions in Central Oregon Second-Growth Ponderosa Pine Ecosystems. U.S. Department of Agriculture, Forest Service Res. Pap. PNW-RP-481, 17 pp.

Oliver, W.W., 2000. Ecological Research at the Blacks Mountain Experimental Forest in northeastern California. USDA Forest Service General Technical Report PSW-GTR-179.

Page-Dumroese, D.S., Jurgensen, M.F., 2006. Soil carbon and nitrogen pools in mid- to late successional forest stands in the northwestern United States: potential impact of fire. Can. J. For. Res. 36, 2270–2284.

Ramos, M.G., Villatora, M.A.A., Urquiaga, S., Alves, B.J.R., Boddey, R.M., 2001. Quantification of the contribution of biological nitrogen fixation to tropical green manure crops and the residual benefit to a subsequent maize crop using ^{15}N-isotope techniques. J. Biotechnol. 91, 105–115.

Roggy, J.C., Prévost, M.F., Gourbiere, F., Casabianca, H., Garbaye, J., Domenach, A.M., 1999. Leaf natural ^{15}N abundance and total N concentration as potential indicators of plant N nutrition in legumes and pioneer species in a rain forest of French Guiana. Oecolog. 171–182.

Salas, E., Nygren, P., Domenach, A.M., Berninger, F., Ramírez, C., 2001. Estimating biological N2 fixation by a tropical legume tree using the non-nodulating phenophase as the reference in the ^{15}N natural abundance method. Soil Biol. Biochem. 33, 1859–1868.

Sanginga, N., Danso, S.K.A., Zapata, F., Bowen, G.D., 1990. Influence of reference trees on N2-fixation estimates in *Leucaena leucocephala* and *Acacia albida* using ^{15}N-labelling techniques. Biol. Fertil. Soils 9, 341–346.

SAS, 2000. SAS User's Guide, Version 6.0. SAS Institute, Cary, NC.

Shea, R.W., 1993. Effects of prescribed fire and silvicultural activities on fuel mass and nitrogen redistribution in *Pinus ponderosa* ecosystems of central Oregon. M.S. Thesis. Oregon State Univ., Corvallis, Oregon.

Shearer, G., Kohl, D.H., 1993. Natural abundance of 15N: fractional contribution of two sources to a common sink and use of isotope discrimination. In: Knowles, R., Blackburn, T. (Eds.), Nitrogen Isotope Techniques. Academic Press, New York, pp. 89–96.

Shearer, G., Kohl, D.H., Virginia, R.A., Bryan, B.A., Skeeters, J.L., Nilsen, E.T., Sharifi, M.R., Rundel, P.W., 1983. Estimates of N2-fixation from variation in the natural abundance of ^{15}N in Sonoran desert ecosystems. Oecolog. 56, 365–373.

Sutherland, R.A., van Kessel, C., Pennock, D.J., 1991. Spatial variability of nitrogen-15 natural abundance. Soil Sci. Soc. Am. J. 55, 1339–1347.

Virginia, R.A., Delwiche, C.C., 1982. Natural ^{15}N abundance of presumed N2-fixing and non-N2-fixing plants from selected ecosystems. Oecolog. 54, 317–325.

Youngberg, C.T., Wollum, A.G., 1976. Nitrogen accretion in developing *Ceanothus velutinus* stands. Soil Sci. Soc. Am. J. 40, 109–112.

Youngblood, A., Max, T., Coe, K., 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. For. Ecol. Manage. 199, 191–217.