



Ecological Assessment of Aspen Communities in the Klamath Network

A Problem Analysis



ON THE COVER

Aspen (*Populus tremuloides*) and Lassen Peak at Lassen Volcanic National Park, 2007.
Photograph by: Daniel Sarr

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Sarah McCullough

Department of Plant Sciences
University of California, Davis
Davis, California

Dr. Kenneth W. Tate

Department of Plant Sciences
University of California, Davis
Davis, California

Daniel A. Sarr

National Park Service
Klamath Inventory and Monitoring Network
1250 Siskiyou Blvd
Ashland, Oregon

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U.S. Department of the Interior
National Park Service
Ashland, Oregon

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This report has been reviewed for accuracy and quality by Klamath Network staff, with input from staff at Lassen Volcanic National Park. No independent peer review was conducted.

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Introduction

As part of the National Park Service (NPS) Inventory and Monitoring Vital Signs process, aspen were identified as keystone ecosystems in forest ecosystems of several of the parks of the Klamath Network. Aspen stands provide an important source of understory plant diversity in the conifer dominated forests of Lassen Volcanic National Park (LAVO) and may be considered a keystone species. However, studies indicate aspen are declining in the region (Di Orio et al. 2005) and throughout the West (Bartos and Campbell 1998). Preliminary results from an aspen inventory and assessment of LAVO indicate a similar trend. Many stands are small in size, heavily browsed by deer, and experiencing competition from lodgepole pine (*Pinus contorta* ssp. *murrayana* Grev. and Balf.) and white fir (*Abies concolor* Gordon and Glend.). This observed pattern has raised the concern that as aspen stands decline in area, the understory plant diversity harbored beneath them and other ecological values will be lost. The Klamath Network and the parks required baseline data to inform the development of long-term monitoring protocols and to provide information about the current condition of the park stands.

The objectives of this project were to:

1. Collect baseline data about the ecological values of aspen communities within the parks to assess whether they function as a keystone species.
2. To assess current condition and environmental trends in park aspen stands, by measuring changes in the total area covered by aspen over the last 50 years, and by measuring browse and conifer encroachment in the stands.

To accomplish these objectives, this study quantified the amount and rate of conifer encroachment in 29 aspen stands at LAVO over the past 50 years. Current aspen stand condition along a gradient of percent conifer canopy cover was measured and the associations between conifer presence and variables representing the ecological values of aspen stands were evaluated. This approach provides managers with information needed to identify management needs and analyze restoration and protection options.

Background

One justification for active aspen management is that aspen has been described as a keystone species by several authors (Bartos 2000, Campbell and Bartos 2001). In California, quaking aspen (*Populus tremuloides* Michaux) occupy a small proportion (~1%) of forests in the Sierra and Southern Cascades (Jones et al. 2005, Shepperd et al. 2006). However, aspen contribute disproportionately to ecosystem goods and services by supporting habitat heterogeneity and biodiversity, increasing available soil moisture and stream baseflows and accelerating nutrient cycling rates (Chong et al. 2000, LaMalfa and Ryle 2008, Legare et al. 2005, Stump and Binkley 1993). The presence of aspen supports and maintains levels of biodiversity that would otherwise not be present (Manley and Schlesinger 2001, Potter 1998). Kuhn (2007) found a mean species richness in 30 northern Sierra Nevada aspen stands of 41 species, compared to a mean of 22 species in conifer stands. In a comparison of aspen and conifer communities, 76% of species were unique to one community. Stohlgren et al. (1997) described aspen as a keystone ecosystem, containing “high plant species richness, distinctive species compositions, or distinctive ecological processes that benefit many other species and ecosystems.” In the context of this usage and current interest and concern about park aspen resources, the keystone designation could be applied to aspen at LAVO.

Aspen is an early successional, clonal species with a relatively short stem lifespan (Shepperd et al. 2001). It is a shade intolerant species; sprouts require sunlight to establish and mature stems deteriorate when they are overtopped and shaded by other tree species (Jones and DeByle 1985a). Mature aspen produce large numbers of seeds, but stringent seedbed requirements (truncated seed viability, bare mineral soil, warm temperatures, and constant moisture in the first growing season) result in infrequent seed establishment (McDonough 1985). Aspen relies on vegetative sprouting from the root system to maintain clones over the long periods between successful seeding events. New sprouts are released when apical meristem hormonal dominance is disrupted by disturbance (Schier et al. 1985).

Fire plays an important role in triggering vegetative reproduction in aspen, but the policy of fire suppression removed fire as an integrated ecological process from the landscape. At LAVO, all fires were suppressed from 1905 until the development of prescribed fire management and fire is still occurring at much smaller spatial scales than in the past (Taylor 1997). Since fire suppression policy began in the early 1900s in California, shifts in forest structure towards increased densities of shade tolerant conifer species have been documented in the Sierra Nevada and the San Bernardino mountains (Ansley and Battles 1998, Beaty and Taylor 2001, 2008, Kilgore and Taylor 1979, Minnich et al. 1995). It has been proposed that this shift is occurring throughout the entire range of mixed conifer forest (Minnich et al. 1995). In the Southern Cascades, similar changes have been observed in the immediate vicinity of Lassen Volcanic National Park (Beaty and Taylor 2001, Bekker and Taylor 2001, Taylor 2000, Taylor and Solem 2001). Taylor concluded that fire suppression was the major driver of twentieth century forest change within Lassen Volcanic National Park (Taylor 2000). Fire suppression affects aspen stand condition through increased competition and shading from conifer species (Shepperd et al. 2006). The frequency of events that stimulate vegetative regeneration is reduced. The ages of current aspen cohorts in California correspond with the end of intensive grazing and the

beginning of fire suppression management early in the twentieth century (Potter 1998, Taylor 2000).

Herbivore pressure further impacts vegetative regeneration. Kay and Bartos (2000) showed that aspen subjected to deer and elk herbivory did not regenerate successfully or regenerated at much lower stem densities than stands protected by exclosures. At LAVO, aspen stands show evidence of impact from both deer and beaver (*Castor canadensis*) herbivory. Deer browsing on aspen suckers is reported to be nearly 100% of current year growth in the majority of aspen stands (Nordensten 2007). Most beaver use is seasonal within LAVO, and there is an established colony in Warner Valley. Aspen is an important food source for beaver (Shepperd et al. 2006), and beaver can have a major impact on individual aspen stands (Beier and Barrett 1987).

An aging or overtopped aspen stand will produce new sprouts annually, but without a release from the double pressure of conifer shading and herbivory on new growth, a clone will die as the carbohydrate stores of the root system become depleted. The death of the clone results in the loss of the ecological services provided by aspen.

Current environmental trends in aspen populations have been studied using stand level studies of age class structure, photo point analysis of historical photos, and GIS-based landscape level change detection studies. Aspen stand surveys from the Rocky Mountains have shown that many stands are currently dominated by mature to decadent trees and lack younger age classes, indicating poor or unsuccessful regeneration (Bartos and Campbell 1998, Mueggler 1989).

The dominance dynamics of aspen persistence and succession to conifer are highly variable between stands (Kashian et al. 2007). The documentation of both persistent and declining aspen stands has prevented consensus on the risk of aspen decline in the western United States. Some studies have found dramatic decreases in aspen stand area and attributed these decreases to successional processes related to fire and herbivory (Bartos and Campbell 1998, Di Orio et al. 2005, Wirth et al. 1996). In southwestern Montana, Wirth et al. (1996) overlaid maps of the current extent of aspen with the historic extent using aerial photos in a GIS and found a 45% decrease of aspen over 45 years. In California, Di Orio et al. (2005) found a 24% decline in aspen stand area over a 48 year period in the Warner Mountains. A similar pattern was observed adjacent to LAVO on the Lassen National Forest, Eagle Lake Ranger District, where 77% of stands were found to be in decline, defined as an almost complete loss of mature aspen with little or no regeneration (Jones et al. 2005). Other studies have found areas of aspen persistence (Binkley 2008, Kulakowski et al. 2004, Kulakowski et al. 2006, Sankey 2008, Zier and Baker 2006). It is important to note that the successional trends described in these papers are a different phenomena than sudden aspen death, which has been implicated in large areas of rapid aspen decline in the Rocky Mountain states but not in California (Worrall et al. 2008). Kashian et al. (2007) reconciled divergent views of aspen stand successional trends by examining the variability in the ecological context of aspen stands and concluding the drivers of aspen dynamics are spatially and temporally heterogeneous. Although drivers of aspen stand decline are present (i.e., fire exclusion, herbivory) in California, few studies have examined aspen stand successional trends (Di Orio et al. 2005). Therefore, management planning at Lassen Volcanic National Park must be preceded by the quantification of aspen stand condition and local successional trends in aspen.

Our overall goal was to determine if successional changes in the levels of conifer have been occurring in these aspen stands over the past half century, and to determine if these changes are associated with the current ecological status or condition of the stands. We associated current percent conifer cover and directional change in conifer cover within aspen stands with a set of aspen forest, understory plant community, and soil litter factors indicative of stand condition. Our first hypothesis was that as percent conifer cover increases, the overall condition of the aspen stand declines, as reflected by the stand condition indicators. The second hypothesis was that percent conifer cover increased in aspen stands over the period 1952-1998. In the context of the concept that local community structure is influenced by regional and historical processes (Ricklefs 1987), our third hypothesis was that factors such as initial percent conifer cover levels from a 1952 reference point and subsequent rate of percent cover change account for an additional portion of the variance in current stand condition. We expected the initial degree of percent conifer cover and rate of conifer cover change to be associated with the stand condition indicators. For example, if conifer cover increases by 25% over the 50 year period, an aspen stand with an initial level of 15% conifer cover has the potential to change more than an aspen stand with an initial level of 75% conifer cover.

The study did not attempt to predict the historical understory diversity of aspen stands in 1952, since it is not possible to know whether understory diversity in 1952 was the product of a lesser degree of encroachment or of other disturbance or climatic factors. However, the study does evaluate the current resource that is at risk of loss, and the rate at which it is changing.

Methods

Study Area

Lassen Volcanic National Park (LAVO) straddles the transition zone between the northern Sierra Nevada and southern Cascade mountain ranges. Elevation ranges from 1650 meters to 3190 meters on Lassen Peak. Lassen Peak is the southernmost large volcano of the Cascade Range. The park is 42,900 ha in area. The area experiences a Mediterranean-type climate; summers are dry with occasional thunderstorm events and winters are cold and wet with deep snowpack formation. Annual precipitation on the east side of LAVO is approximately 100 cm, and mostly occurs as snow. The two most prominent forest types within the range elevations where aspen stands are located (1620 to 1960 meters) are yellow pine (*Pinus ponderosa* and *Pinus jeffreyi*) and red fir (*Abies magnifica*) types.

The three major areas of aspen occurrence are characterized by different geologic disturbance histories within LAVO. Warner Valley is influenced by a major geothermal resource, with activity at the surface in the form of hot springs, pools, and fumaroles. Elevations range from 1650-1950 meters. The mixed hydrologic regime of the valley consists of one perennial stream fed by snowmelt and a series of springs that emerge from beneath the basaltic cap of the valley walls. The springs support a series of wetlands, including a fen. White fir is the most common conifer species occurring in aspen stands.

The Hat Creek drainage was impacted by a catastrophic mudflow during the Lassen Peak eruption in May 1915. All vegetation in the upper drainage was removed and a layer of debris 0.5 to 2.0 meters deep was deposited. The effect of the eruption was limited in the lower drainage to a pulse of debris flow down the creek (Conlin 2007). A 1963 study recorded the occurrence of aspen in several areas 48 years after the disturbance (Bailey 1963). In the Hat Creek drainage, aspen occurs in the alluvial floodplain along the creek, and on higher glacial outwash features underlain by a moisture-holding duripan. The conifer species occurring most frequently in aspen stands is lodgepole pine. Elevations range from 1830-1950 meters.

The Butte/Snag Lakes region is located east of the Lassen massif and is influenced by rain shadow. The area last experienced significant geologic disturbance in the mid 1700s, when lava flowing from a nearby cinder cone dammed the drainage and formed a large, shallow lake. Lodgepole pine and white fir are both found in aspen stands, and elevations range from 1830-1890 meters.

In the selection of aspen stands for enrollment in the study, we first blocked stand selection by geologic disturbance history (Warner Valley, Hat Creek, and Butte/Snag Lakes). Within each block, we identified all known aspen stands. Stands within each block were stratified by percent conifer cover (<20, 20-40, 40-60, >60% conifer cover). A sample of stands was then randomly enrolled from each percent conifer cover level. We limited the study population to aspen stands that had not experienced either significant recreational impact or fire disturbance in the past 20 years, due to the potential impact of fire and human use on understory plant cover. The stands selected for sampling are shown in Figure 1.

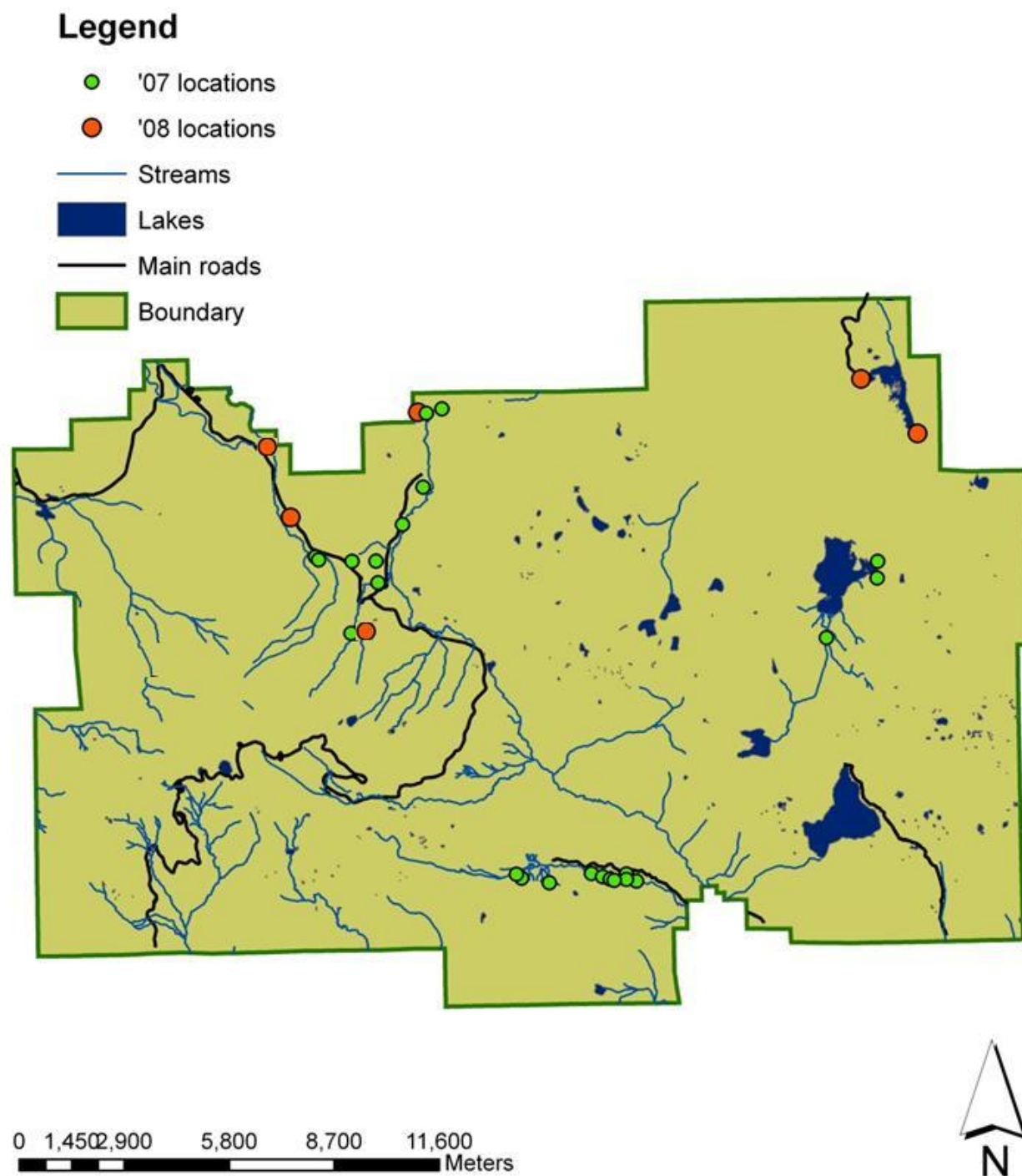


Figure 1. Map of sampled locations in Lassen Volcanic National Park.

Field Data Collection

We selected ten aspen forest, understory plant community, and litter variables as indicators of stand condition. The stand condition indicators used for analysis were recruitment and establishment; understory species richness and diversity; litter depth; total, fine, and woody litter C:N; the ratio of the masses of woody to fine litter; and litter decomposition level (Table 1).

Table 1. Descriptive statistics of stand condition indicators for 29 stands surveyed on Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands.

	<i>Indicator</i>	<i>Rationale</i>	<i>Units</i>	<i>Min</i>	<i>Mean</i>	<i>Max</i>
Stand n=29	Conifer cover	Index of conifer invasion	% cover	2	50	77
	Aspen cover	Forest of interest	% cover	4	24	71
	Recruitment	Measure of stand regeneration	sprouts/100 m ²	3	52	127
	Establishment	Measure of stand recruitment into canopy	m ² /ha	0.0	5.8	35.8
	S-W Diversity	Diversity index	log of the number of species of equal abundance	0.69	1.95	2.74
	Herbaceous species richness	Biodiversity measure	number of species	11	31	54
Soil n=12	Litter depth	Measure of invasion (deeper in conifer forests)	cm	1	5	8
	Litter C:N	Index of litter quality	grams C/grams N	26.0	30.8	36.4
	Fine C:N	Index of fine litter	grams C/grams N	23.3	27.3	35.3
	Woody C:N	Index of woody material quality	grams C/grams N	40.1	50.8	70.2
	Woody:fine mass	Proportion of refractory woody material	grams woody cm ⁻³ /grams fine cm ⁻³	0.11	0.26	0.50
	Decomposition	Evidence of organic soil development	Munsell value	4.6	5.2	5.6

All stand condition indicators used in this study were measured in each of the aspen stands enrolled in the study. All field data collection was based upon a modified Whittaker plot-based design commonly used in studies of coniferous forests (Keeley et al. 2003). We chose a relatively large, multiscale plot design in order to prevent missing locally rare species, an important consideration in aspen stands (Barnett and Stohlgren 2003). The 10 x 10 m sub-plot design allowed flexibility in total plot size, which was necessary to accurately sample stands smaller than the full 1000 m² Whittaker design understory community and soil O horizon. The nested design allowed sampling at the scale of expected variation and permitted the analysis of the plant and litter variables at multiple scales. We placed as many 10 x 10 m plots as would fit within the boundaries of each of the 29 aspen stands, up to a maximum size of ten plots (1000 m²) (Figure 2). The size of many stands was small enough so that most of the stand was included within the Whittaker plot. The plots were aligned with breaks in vegetation, soils, light, and

moisture regime (i.e., wetlands, openings, meadow edges). Each 100 m² plot included five 1 m² subplots, to capture variation in the understory community and soil O horizon.

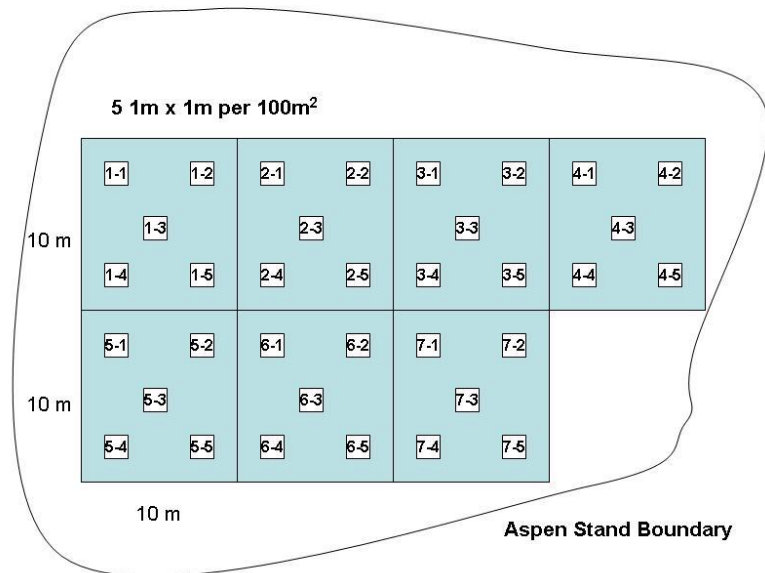


Figure 2. Modified Whittaker Plot Design.

Field data collection occurred July to September 2007 and 2008. For each stand, we recorded elevation and location with a GPS unit from the center of each stand, and also recorded slope and aspect. Forest strata were delineated by stand, and the height of one representative tree from each stratum was measured. The forest stands were divided hierarchically into five strata by height. We labeled any trees taller than the mature aspen stems as strata 4; mature aspen stems, which usually formed a cohesive cohort as strata 3; any trees below the aspen layer but above 3 m as strata 2; and trees between 1.4 m and 3 m tall as strata 1. Sprouts up to 1.4 m were recorded separately. For each tree in the 10 m² plots, we recorded stratum, diameter at breast height, and species. At the center of each 100 m² plot, we read percent overstory cover with a spherical densiometer and measured solar availability with a solar pathfinder. Deer browse on aspen sprouts was recorded as a categorical variable (browsed / hedged / neither) (Keigley and Frasina 1998). We determined understory species composition by percent cover at the 1 m² scale, and recorded species richness data for each 100 m² plot using a standardized search effort.

We measured litter depth (O horizon thickness) to mineral soil from the center of each of the five 1 m² subplots. A subset of four stands per geologic disturbance block was selected for litter sampling, for a total sample size of 12 stands, by choosing stands that encompassed the range of percent conifer canopy cover and soil moisture conditions present in order to account for the effect of different microclimates on decomposition. We collected litter samples of known volume (10 cm x 10 cm x litter depth) from the center of three subplots per 100 m² plot.

Leaf Litter Sample Analysis

We analyzed litter samples for total C and N by a combustion method (AOAC 1997). We composited the three samples per 100 m² plot, sorted out woody litter (defined as twigs and bark greater than 1 mm diameter), and prepared the woody and fine fractions separately. Fine and woody litter were separated in order to distinguish between relatively labile and recalcitrant organic matter pools with different decomposition rates (Maclean and Wein 1978). The samples were dried at 60°C for 36 hours, and loss on ignition was conducted to identify the percentage of organic material from mineral soil collected with the litter sample (Nelson and Sommers 1996). The mass of the litter and woody fractions was determined from the dry sample weight of the fractions and the percentage of organic material from loss on ignition. The ratio of the mass of the woody and fine fractions was expressed as grams woody cm⁻³ / grams fine cm⁻³. We determined the mass of C and N separately for the litter and woody fractions and then summed for total C:N per sample.

The degree of organic matter decomposition of litter was determined through extraction of hemic and fulvic compounds with a pyrophosphate color method (Soil Survey Staff 1999). The pyrophosphate method is a diagnostic tool that estimates the degree of decomposition from the color of a pyrophosphate extract and resolution is best in samples with low to moderate levels of decomposition. The litter samples met this criterion. We treated a sample of 2.5 g fine litter with a solution of 4 mL H₂O and 1 g sodium pyrophosphate decahydrate (Na₄P₂O₇•10H₂O). After 9 hours, we extracted the solution, transferred it to chromatographic paper, and read the degree of darkness as “value” from the Munsell color notation with a colorimeter. The 1-10 scale represents dark (lower numbers representing more decomposed plant material) to light (higher numbers representing less decomposed plant material).

Photo Interpretation

We conducted aerial photo interpretation for all stands with printed black and white panchromatic images, dated 1952 and 1954. Due to a gap in the 1952 photo imagery for the east side of the park, two flightlines from 1954 were substituted. A search of the UC Davis and UC Berkeley aerial photo collections failed to locate additional 1952 east side photos. The photos lack metadata, so information about the flight (plane elevation and tilt) and camera specifications (focal length) was not available. The photos have a nominal scale of 1:20,000 or 1 in = 508 m. Each 9 in x 9 in photo covers an area of almost 2,100 hectares. The photos were scanned at 600 dpi; each pixel width equals 0.85 m on the ground

1952 Photo Quality

The 1952 images were rectified in ERDAS using a “rubbersheeting” method and recent Digital Orthophoto Quarter Quadrangle (DOQQs) imagery as the reference image. The 1952 images have been stretched to match the DOQQ images, but the positional accuracy depends on the number of control points and their quality. High quality rectification requires control points that have clear positional accuracy in the x and y direction and are evenly distributed across the face of the photo. Additional control points are required for areas of topographical relief. The landscape at Lassen is heavily forested with few manmade features and areas of significant relief. The park encompasses an elevation range of over 1,500 m. In this setting, few points have clear x and y positional accuracy. In addition, the long time interval since photo creation reduces the probability of locating the same point in both the historic and current sets of photos.

We rectified the photos in ERDAS software with approximately 30 control points per photo. Points were selected to be repeatable, in an even distribution across the photo, with additional points in areas of high relief. Points were added until the RMS error stabilized, and the photos were then overlaid and examined visually for accuracy. A fairly uniform amount of error across the surface of the photos was obtainable with placement of 30-40 control points. Variable accuracy was achieved but maximum accuracy was estimated to be within 5 meters. An orthorectification methodology was not chosen since this was not a landscape scale application.

1998 Photo Quality

Recent aspen stand status was represented by grayscale Digital Orthophoto Quarter Quadrangle (DOQQs) imagery from panchromatic black and white film, dated August and September 1998. The photos meet national map accuracy standards for 1 m resolution and nominal scale 1:12,000. The appearance of aspen stands varied. The search image for aspen is a blue green color with intermediate texture. Firs have darker green colors with a coarser texture of canopy and shadow, and mature pines show individual bright green canopies. However, color changes depending on time of day, shadow, and location in the photo. Canopy shape is often indistinct for aspen, and easily obscured by the shadow of adjacent conifers. Seam line areas mute the color and resolution further. In addition, overall forest density obscures aspen canopies, resulting in indistinct aspen stand boundaries. Highly encroached stands are not visible. Photo quality is also affected by increasing distortion with distance from the principal point of the photo. Areas at the edge of the original photos show trees at an angle, giving tree canopies an elongated, declining appearance.

We estimated historical and current percent aspen and conifer cover with the USFS- developed Digital Mylar Cover Interpreter for ArcGIS version 9.x (Clark et al. 2004). We read cover as an ocular estimate from a circular buffer (diameter 28 m) around the field-collected GPS point from the center of the full Whittaker plot. This buffer size fit into the plots so that the boundaries of the buffer stayed within the area surveyed in the field. The classification system had an interval width of 10 percentage points per class, and the class midpoint was recorded for each data point. When we estimated a percent cover value at the endpoint of a class, it was recorded as the next higher class (20% conifer cover recorded as 25% rather than 15%) to account for additional cover hidden by shadows. To improve accuracy, we read additive estimates of percent conifer, aspen, and open cover for a total of 100% cover in each plot. Percent total cover was calculated as 100% minus percent open cover. Stands were read in a randomized order and identifying information was blocked out to ensure independence of cover estimates. One person conducted the interpretation for consistency, and the interpreter read the two sets of photos in separate sessions to reduce bias. Validation was conducted against the field-collected densiometer percent cover values for a sample of 12 sites. Percent aspen and conifer cover values from the photointerpretation of the 1998 imagery were regressed on cover values from the field-collected densiometer readings.

Data Organization

Field-collected data is organized with a relational database in Access 2003 SP2. Each stand is identified by a four character field, named Stand ID, that includes the first two letters of the geologic disturbance block and two numeric digits. The 100 m² plots in the stand are linked with a one-to-many relationship based on Stand ID. Each 100 m² plot is identified by a numeric field named KEY. All data collected at the 100 m² plot scale is linked by KEY. The 1 m² plots are

identified by a field named COMBINEKEY that combines KEY and the subplot number (1-5). Understory plant community, litter depth, and litter sample data is linked to the 100 m² plot and Stand ID through COMBINEKEY. Data from the photo interpretation and litter sample laboratory analysis, along with summary data (i.e., species richness and diversity, basal area sums) used in the analysis are also stored in the database, and is linked through the same key fields. Figure 3 illustrates the structure and organization of the database.

Data Analysis

For hypothesis one, we analyzed ten stand condition indicators (Table 1) to examine the relationship between the stand condition indicators and current levels of percent conifer cover. The number of aspen sprouts per 100 m² was considered to be recruitment, and the basal area of aspen in strata 1 and 2 was considered to be evidence of establishment. We calculated species richness and the Shannon-Wiener index of diversity with PC-ORD4 (McCune and Mefford 1999) for each stand. Associations between current percent conifer cover and the stand condition indicators were evaluated using simple linear regression in S-Plus 6.0 (S-Plus 6.0). We analyzed univariate models for each stand condition indicator with current percent conifer cover as the predictor and the stand condition indicator as the response variable. Assumptions of normality and constant homogeneity of variance were confirmed by evaluation of standard residual plots. A probability value of 0.1 ($p < 0.1$) was considered significant due to the number of factors in aspen stands that contribute to variance.

To evaluate hypothesis two, we calculated change in percent conifer, aspen, and total cover over the period 1952 to 1998 as the difference in 1998 and 1952 percent cover values. We assigned stands to two categorical stand dynamics, persistent aspen and increasing conifer. The persistent aspen dynamic was defined as conifer cover change less than or equal to 10%, and the increasing conifer dynamic as conifer cover change greater than 10%. Since change in percent cover was the difference of the midpoints of two cover classes with intervals of 10% cover, each subtracted difference had a potential error $\pm 10\%$. Simple linear regression was employed to test significant differences between stand dynamics, with stand dynamic as the predictor variable and stand condition indicators as the response variables ($p < 0.1$).

For hypothesis three, we employed a backwards stepwise regression approach to develop separate models for each stand condition indicator with generalized least squares regression. The predictor variables for the complete model were geologic disturbance block, stand dynamic, percent total cover, and 1952 percent conifer cover ($p < 0.1$). Data were transformed if necessary to meet the assumption of normality, as determined from standard diagnostic graphs. Variance functions were employed in cases where heteroscedasticity was indicated by residual plots (Pinheiro and Bates 2000).

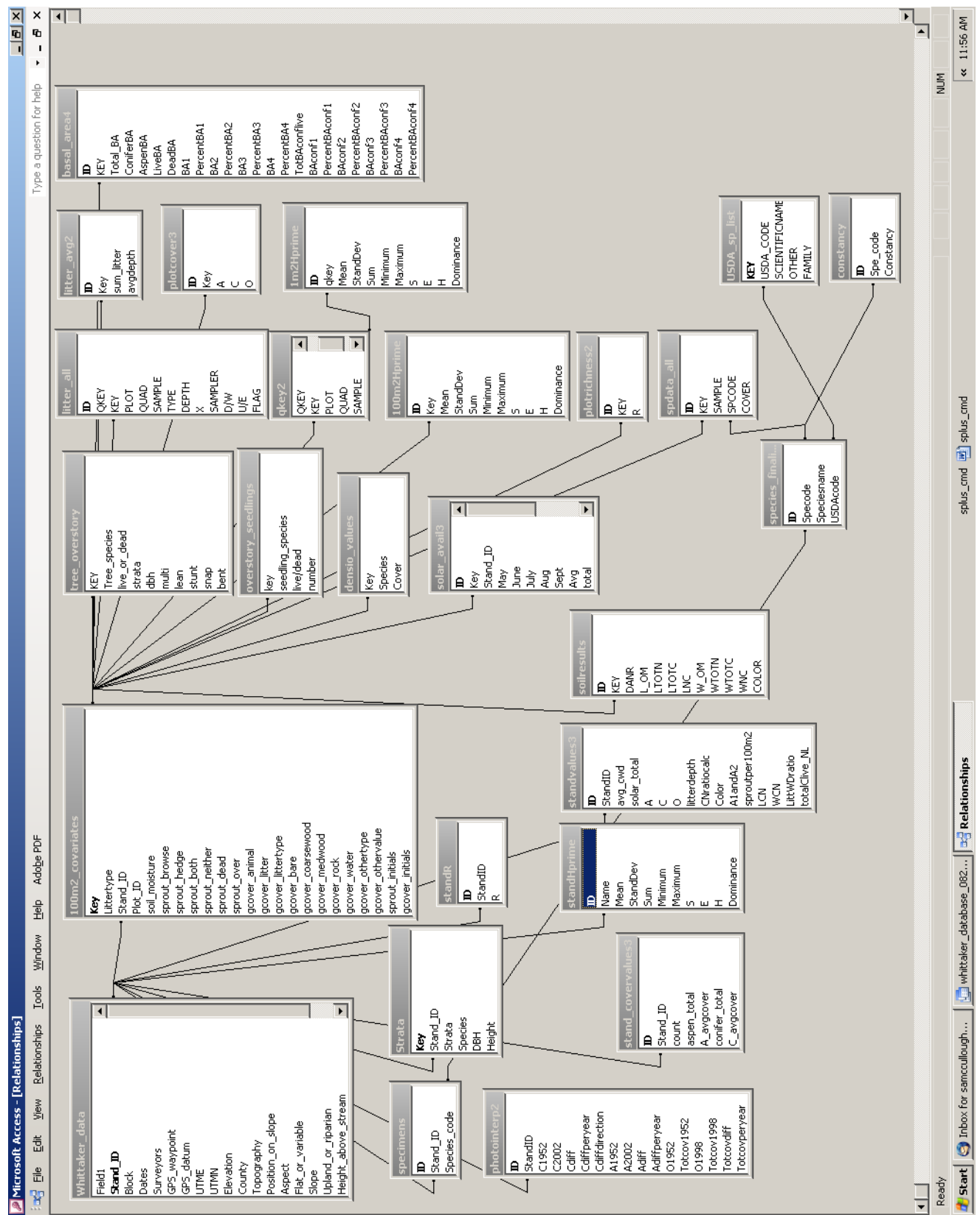


Figure 3. Tables and fields of the relational database.

Results

Correlations between Current Percent Conifer cover and Stand Condition Indicators

Aspen recruitment, herbaceous species richness, and litter depth were significantly associated with current percent conifer cover ($p < 0.1$) (Table 2, Figure 4). We rejected the null hypothesis of no change in aspen stand condition with increasing percent conifer cover. As percent conifer cover increases, the overall condition of the aspen stand declines. For each 10% increase in percent conifer cover, aspen recruitment decreased by six sprouts/100 m², species richness decreased by 1.6 species, and litter depth increased by 0.5 cm. The percentage of sprouts showing evidence of herbivory ranged from 45% to 100% for all stands. The conifer species that accounted for the highest number of records were white fir (35%), lodgepole pine (35%), and red fir (18%).

Table 2. Results for regression analysis with stand condition indicator as the dependent variable and percent conifer cover as the independent variable. All plant variables were measured in the field during summers of 2007 and 2008, for 29 stands surveyed on Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands.

	<i>Indicator</i>	<i>Units</i>	<i>Percent conifer cover coefficient</i>	<i>p value</i>	<i>R²</i>
Plant n=29	Recruitment	sprouts/100m ²	-0.65	0.08*	0.11
	Establishment	m ² /ha	-0.02	0.85	0.001
	S-W Diversity	log of the number of species of equal abundance	-0.002	0.63	0.01
	Herbaceous species richness	number of species	-0.16	0.07*	0.12
	Litter depth	cm	0.05	<0.001*	0.49
Litter n=12	Litter C:N	grams C/grams N	0.01	0.81	0.01
	Fine C:N	grams C/grams N	0.05	0.30	0.1
	Woody C:N	grams C/grams N	-0.06	0.56	0.03
	Woody:fine mass	g woody cm ⁻³ / g fine cm ⁻³	0.001	0.48	0.05
	Decomposition	Munsell value	-0.0004	0.94	0.001

* Results are significant ($p < 0.1$)

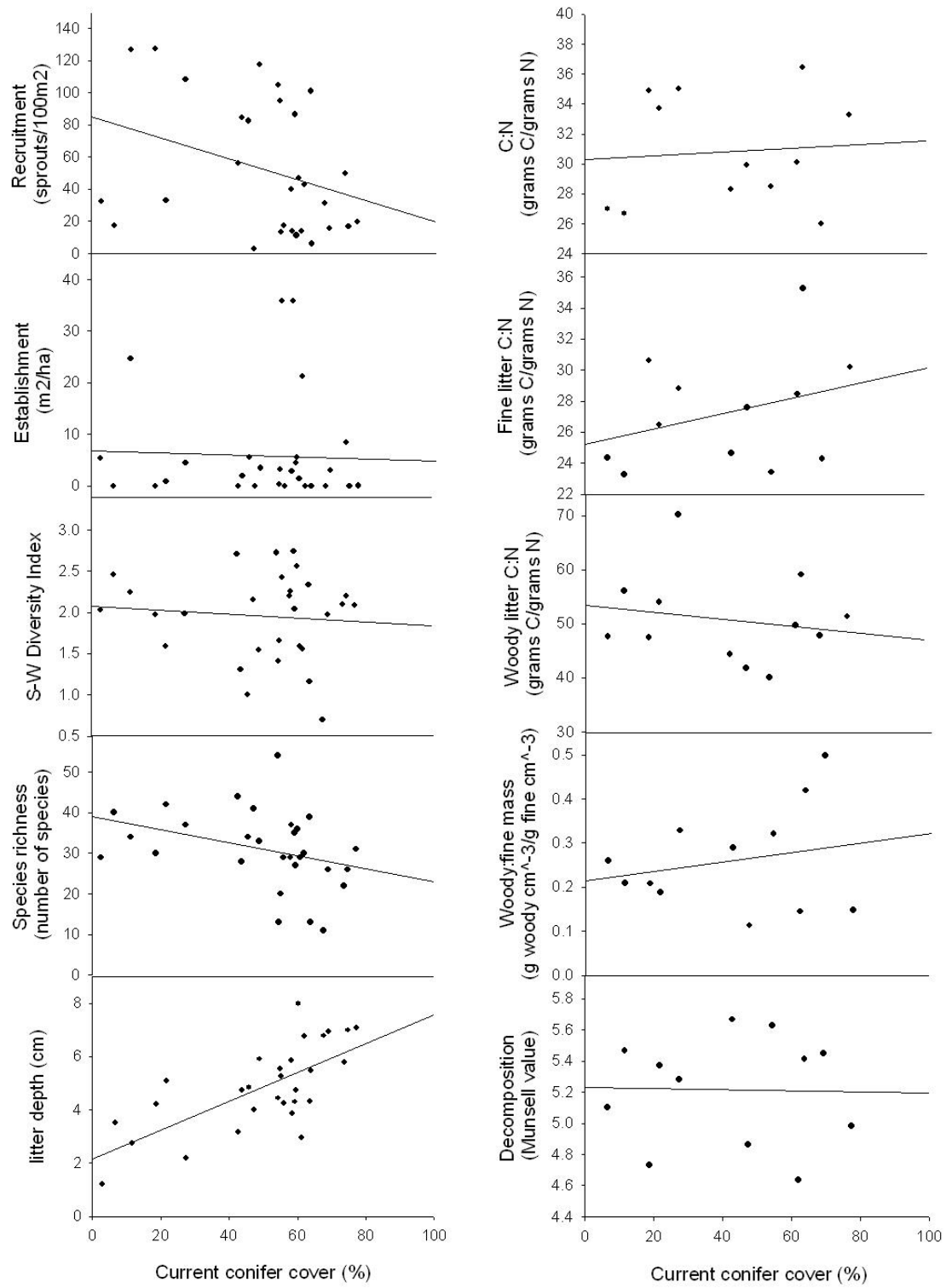


Figure 4. Stand condition indicators from plant samples (n=29) and litter samples (n=12) regressed on percent current conifer cover.

Trends in Conifer Cover within Aspen Stands

Percent conifer cover increased in general; however, we recorded clear evidence of variability in conifer invasion dynamics. About half the sampled stands indicated a persistent aspen dynamic and half indicated a conifer invasion dynamic (Figure 5). The mean rate of change in percent aspen and conifer cover was significantly different for the two dynamics (Table 3). In invaded stands, mean percent conifer cover increased from 22% to 66% over the period, and mean percent total cover increased by 30% to 92%, nearly closing the canopy (Table 3). Percent conifer cover increased by an average of 1% a year, while percent aspen cover declined by 0.3% a year. In persistent aspen stands, mean percent aspen cover increased from 38% to 50%, and mean total cover increased from 62% to 80% (Table 3). Percent total cover increased in these stands as aspen trees filled in the canopy. In the validation of the photo interpretation, percent cover estimates regressed on field densiometer cover values were significant for both aspen and conifer cover (aspen: $p < 0.001$, $R^2 = 0.69$, conifer: $p < 0.001$, $R^2 = 0.73$).

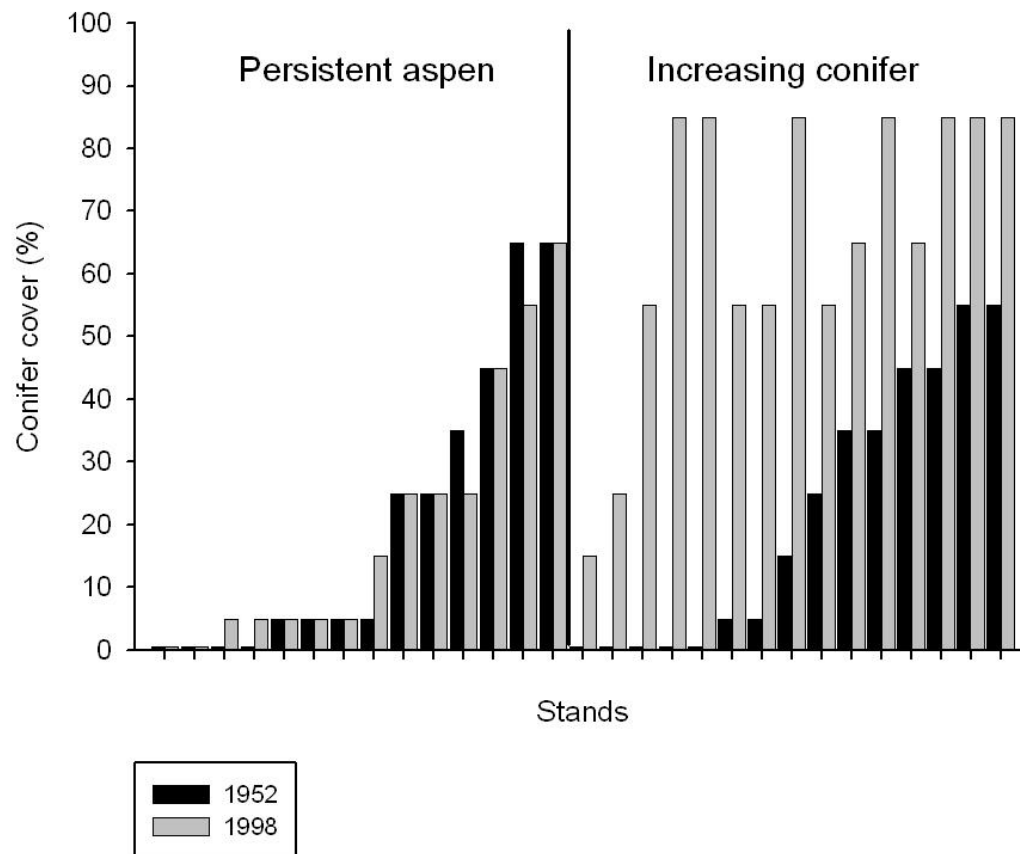


Figure 5. Trends in conifer cover 1952-1998 by stand from photo interpretation. The persistent aspen category is defined as conifer cover change less than or equal to 10% and increasing conifer is defined as conifer cover change greater than 10%.

Table 3. Comparison of conifer, aspen, and open cover values from photo interpretation at the two defined levels of stand dynamic (persistent aspen and increasing conifer).

	<i>Stand dynamic</i>	
	<i>Persistent aspen^a</i>	<i>Increasing conifer^b</i>
Number of stands	14	15
Sample %	48	52
Mean cover values (%)		
Conifer 1952	20	22
Conifer 1998	20	66 *
Conifer Δ /year	0	0.96 *
Aspen 1952	38	35
Aspen 1998	50	21
Aspen Δ /year	0.28	-0.32 *
Total cover 1952	62	61
Total cover 1998	80	92 *
Total cover Δ /year	0.39	0.69

^a Persistent aspen is defined as conifer cover change less than or equal to 10% and increasing conifer is defined as conifer cover change greater than 10%.

^b Results that are significantly different between stand dynamics are marked with an asterisk ($p < 0.1$).

Correlations between Trends in Conifer Cover and Stand Condition Indicators

Aspen recruitment, aspen establishment, Shannon-Wiener diversity, and herbaceous species richness were significantly higher for stands with persistent aspen than for increasing conifer. C:N of the woody litter fraction and the ratio of the mass of woody to fine litter were higher for stands with increasing conifer (Table 4).

Geologic disturbance was not significant for any stand condition indicator and was dropped from the model. We expected that indicator variables would correlate with percent conifer cover at the beginning of the time period studied, but we dropped 1952 percent conifer cover from the model due to lack of significant three way interactions for all variables. We failed to reject the hypothesis that initial percent conifer cover levels from a 1952 reference point and subsequent rate of percent cover change do not influence current stand condition. Instead, significant stand dynamic by percent total cover interactions indicated that the relationship of stand condition indicators to percent total cover depended on stand dynamic (Table 5).

The stand dynamic by percent total cover interaction was significant for aspen recruitment ($p=0.03$). For every 10% increase in percent total cover, the number of aspen sprouts increased by 16 sprouts/100 m² in stands with an increasing conifer dynamic, but decreased by three sprouts/100 m² in stands with persistent aspen (Figures 6a, 6b). Establishment was significantly associated with stand dynamic ($p=0.09$). In stands with an increasing conifer dynamic, the basal area of aspen in understory cohorts was less than in persistent stands. Significant stand dynamic by percent total cover interactions were found for both measures of understory plant community, species richness ($p=0.07$) and the Shannon-Wiener index of diversity ($p=0.08$). For every 10% increase in percent total cover, species richness decreased by less than one species in stands with persistent aspen, but decreased by five species in stands with increasing conifer (Figures 6c, 6d). The Shannon-Wiener diversity index increased by 0.01 for every 10% increase in percent total

cover in stands with persistent aspen, but decreased by 0.05 in stands with increasing conifer (Figures 6e, 6f).

Litter depth was not significantly associated with either stand dynamic or percent total cover, although a positive regression coefficient indicated a trend of increasing litter depth in stands with conifer invasion (Table 5). A significant relationship was not detected in the C:N ratio of the litter as a whole; however, a significant positive relationship between C:N of the woody fraction and percent total cover was observed ($p=0.02$), as well as a significant stand dynamic by percent total cover interaction for the ratio of woody to fine mass ($p<0.01$). For every 10% increase in percent total cover in stands with increasing conifer, the ratio of woody to fine litter increased by $0.2 \text{ g woody cm}^3 / \text{g fine cm}^3$, but the ratio decreased by $0.02 \text{ g woody cm}^3 / \text{g fine cm}^3$ in stands with persistent aspen (Figures 6g, 6h). For decomposition, the measured range of Munsell values was narrow (4.6-5.6) (Table 1). Decomposition was not significantly associated with stand dynamic or percent total cover, but negative coefficients for stand dynamic and percent total cover indicated an apparent decrease in decomposition level in stands with a dynamic of increasing conifer and total cover (Table 5).

Table 4. Descriptive statistics for stand condition indicators by stand dynamic (persistent aspen or increasing conifer). Plant variables were measured in the field during summers of 2007 and 2008, from 29 stands in Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands.

	<i>Indicator</i>	<i>Units</i>	<i>Stand dynamic</i>	
			<i>Persistent aspen^a</i>	<i>Increasing conifer^b</i>
Plant n=29	Aspen cover	% cover	28 (5)	20 (3)
	Recruitment	sprouts/100 m ²	54 (11)	51 (10) *
	Establishment	m ² /ha	7.7 (3.0)	4.0 (2.4) *
	S-W Diversity	log of the number of species of equal abundance	2.1 (0.1)	1.8 (0.1) *
	Species richness	Number of species	34 (2)	28 (3) *
	Litter depth	cm	4.5 (0.5)	5.2 (0.4)
Litter n=12	Litter C:N	grams C/grams N	30.1 (1.7)	31.3 (1.4)
	Fine C:N	grams C/grams N	25.6 (1.4)	28.5 (1.4)
	Woody C:N	grams C/grams N	49.0 (2.8)	52.0 (3.7) *
	Woody:fine mass	g woody cm ⁻³ / g fine cm ⁻³	0.24 (0.02)	0.28 (0.06)*
	Decomposition	Munsell value	5.3 (0.2)	5.2 (0.1)

^a mean (standard error)

^b Results that are significantly different between stand dynamics (from models in Table 5) are marked with an asterisk ($p<0.1$).

Table 5. Regression models for each stand condition indicator, with stand dynamic and total conifer and aspen cover in 1998 as independent variables. Stand dynamic and total cover are from aerial photo interpretation and plant variables were measured in the field during summers of 2007 and 2008, from 29 stands in Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands.

	<i>Indicator</i>	<i>Units</i>		<i>Coefficient^a</i>	<i>p value^b</i>
Plant n=29	Recruitment ^e	sprouts/100 m ²	Intercept	1.79	<0.01
			Stand dynamic ^c : Pers. aspen	0	
			Incr. conifer	-2.63	0.02 *
			Total cover ^d	-0.003	0.55
			Stand dynamic x total cover	0.03	0.03 *
	Establishment ^f	m ² /ha	Intercept	0.29	0.82
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	-1.26	0.09 *
			Total cover	0.02	0.18
	S-W Diversity	log of the number of species of equal abundance	Intercept	1.86	<0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	2.10	0.12
			Total cover	0.003	0.57
			Stand dynamic x total cover	-0.03	0.08 *
	Herbaceous species richness	species	Intercept	40.06	<0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	37.43	0.10 *
			Total cover	-0.07	0.44
			Stand dynamic x total cover	-0.47	0.07 *
	Litter depth	cm	Intercept	5.06	<0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	0.83	0.20
			Total cover	-0.01	0.65
Litter n=12	Litter C:N	grams C/grams N	Intercept	26.96	<0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	0.87	0.72
			Total cover	0.04	0.54
	Fine C:N ^g	grams C/grams N	Intercept	3.1	<0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	0.09	0.25
			Total cover	0.002	0.42
	Woody C:N ^h	grams C/grams N	Intercept	3.43	<0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	0.01	0.88
			Total cover	0.01	0.02 *
	Woody:fine mass	g woody cm ⁻³ / g fine cm ⁻³	Intercept	0.33	0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	-1.05	<0.01*
			Total cover	-0.001	0.29
			Stand dynamic x total cover	0.01	<0.01*
	Decomposition ⁱ	Munsell value	Intercept	1.72	<0.01
			Stand dynamic: Pers. aspen	0	
			Incr. conifer	-0.01	0.83
			Total cover	-0.001	0.54

Table 5. Regression models for each stand condition indicator, with stand dynamic and total conifer and aspen cover in 1998 as independent variables. Stand dynamic and total cover are from aerial photo interpretation and plant variables were measured in the field during summers of 2007 and 2008, from 29 stands in Lassen Volcanic National Park, CA. Litter variables were measured for a subsample of 12 stands (continued).

^a Coefficient for each variable in the linear model. The value of the coefficient indicates the direction (+ or -) and magnitude of the relationship between each predictor variable to the response variable. For continuous predictor variables, the coefficient indicates the change in the response variable associated with each incremental change in the predictor variable.

^b P value associated with each variable. Significant results ($p < 0.1$) are marked with an asterisk.

^c Stand dynamic is a categorical variable with two levels, persistent aspen and increasing conifer cover. The coefficient for the referent condition (persistent aspen) is set to 0.0; the coefficient for increasing conifer represents the estimated difference of the response variable (e.g., stands with increasing conifer dynamic have 10% less aspen cover than stands with a persistent aspen dynamic given that all other variables are held constant).

^d Total cover is the sum of aspen and conifer cover in 1998, from photo interpretation.

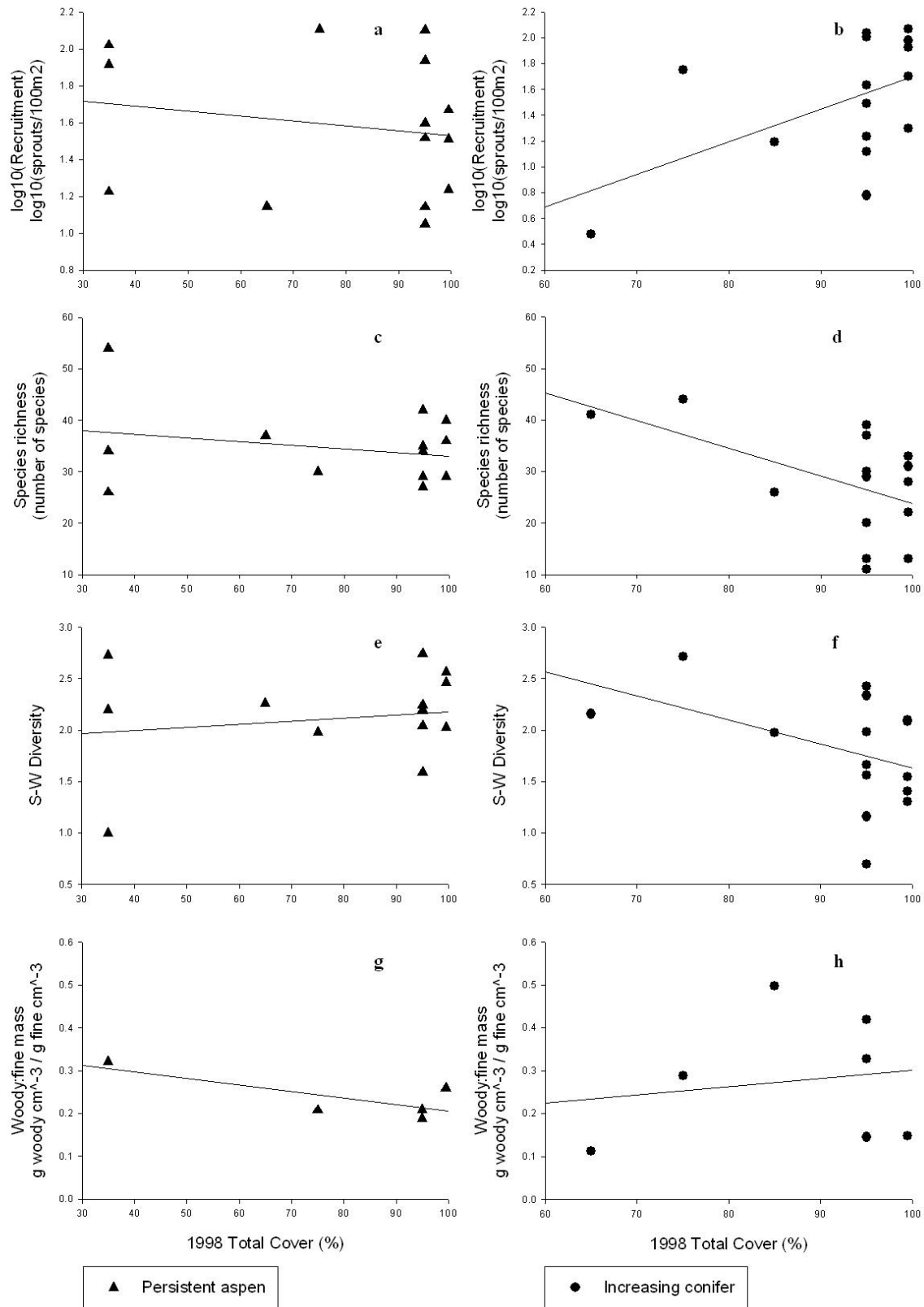
^e Recruitment was log transformed

^f Establishment was square root transformed

^g Fine C:N was ln transformed

^h Woody C:N was ln transformed

ⁱ Decomposition was ln transformed



Figures 6a-h. Regression of stand condition indicators for which the interaction of percent total cover and stand dynamic were significant.

Discussion

Declines in Stand Condition with Increasing Conifer Cover

Along the sampled gradient of current percent conifer cover (3-77%), increasing percent conifer cover was associated with declines in aspen stand condition, as evidenced by decreased herbaceous species richness and increased litter depth (Table 2). Recruitment could be expected to increase as conifer shading disrupts hormonal levels, but the observed decrease may be attributed to lower levels of sprouting as the stand and root system gradually die in response to competition from conifers. The relatively low R^2 values of the regression models indicate that additional factors account for variance in this system, and percent current conifer cover only accounts for a portion of the variability in aspen stands. Aspen are known for their wide ecological amplitude and tolerate a wide range of elevations, climatic conditions, and soil moisture levels (Shepperd et al. 2006). In addition, analyses based on recent field observations are limited to providing a snapshot of current conditions, without taking into account local stand history. Interpretation of aerial photos allowed us to conclude that percent conifer cover has increased in some aspen stands over the period 1952-1998; however, it is clear that variability is present in aspen dynamics within LAVO. All stands are undergoing change, generally afforestation, as gaps in the canopy are filling with either aspen or conifer growth. Determination of the factors behind aspen persistence or conifer increase at each stand was outside the scope of this study; however, the observed variability in stand dynamics is similar to Kashian et al.'s (2007) findings of localized areas of aspen persistence or increasing conifer, and supports the conclusion that the drivers of aspen dynamics are spatially and temporally heterogeneous across the landscape. Differences in stand history, biophysical conditions, and current land uses may affect the invasion process. Prescribed and managed fires and native herbivore populations are also likely drivers of system dynamics at LAVO that warrant further study.

Aspen and Conifer Dynamics

In persistent aspen stands, aspen are present in the canopy with a high percent aspen canopy cover relative to percent conifer canopy cover. Aspen recruitment, establishment, species richness, and diversity are higher. The C:N of the woody fraction and the mass of the woody to fine fractions are lower, and fine litter C:N and litter depth are apparently lower (Table 4). Aspen trees are actually increasing in canopy cover over time. Some stands have a component of conifer; but the mean percent conifer cover level is low, at 20%. In conifer invaded stands, total cover is increasing, but percent aspen cover is decreasing. The mean value of percent conifer cover is higher in these stands, at 66% (Table 3). The divergent stand dynamics suggest differences in the tree dominance hierarchies, such that aspen retain dominance or have lost dominance in persistent aspen and conifer invaded stands, respectively.

Most aspen stands support sprouts in the understory, but in stands with strong apical dominance (dominance by mature stems in the aspen clone), few sprouts may be found. In persistent aspen stands, sprout recruitment decreases with increasing percent total cover; aspen may be directing energy into growth of existing stems, maintaining shoot apical dominance rather than releasing sprouts. Aspen recruitment through sprouting increased sharply in stands with increasing conifer, where conifer species are driving the increase in percent total cover. The steep slope of the recruitment regression line is consistent with a sprout release event. The number of mature aspen trees will decrease as trees die from factors such as age, competition from conifers, and

pathogens. As percent total cover and conifer shading increases, mature aspen stems may be deteriorating and sending the hormonal signal that triggers sprouting.

In terms of aspen establishment, of the sample of 29 stands, only four stands showed more than a minimal amount of establishment in understory strata, and the rest of the stands appeared to have a single age class structure. (Figure 4). The mean basal area of aspen in the establishment cohort is higher in stands with persistent aspen than in stands with increasing conifer, and three of the four sampled stands with the highest levels of establishment are stands with persistent aspen. The low level of successful establishment, even though some stands are releasing large numbers of sprouts in an attempt to regenerate as the canopy closes, may be due to herbivory impacts. The percentage of sprouts showing evidence of herbivory ranged from 81-96% for the four stands with higher establishment, and the level of herbivory appeared similar to the rest of the sample. In addition, only six of 29 stands had more than ten sprouts that had successfully grown above the browse line, indicating that few individuals make the transition from sprout to sapling. More than one mode of stand development occurs in aspen (Kurzel et al. 2007), and either multiple age classes or a single age class may be present. Many aspen stands in California are composed of one cohort that is periodically renewed, often interspersed with a few older conifers (Potter 1998). Stands with a single age class are not necessarily in poor condition, but the apparent impacts of herbivory decrease the probability of a successful sprouting event when stands age and decline.

Aspen stands in good condition support relatively rich and diverse understory plant communities. A higher mean number of species (34 species) was found in stands with persistent aspen than in stands with increasing conifer (28 species) (Table 4). In the Sierra, surveys of intact aspen stands and adjacent meadow and conifer communities also found that aspen and meadows supported significantly higher levels of species richness, diversity, and evenness than conifer communities. In addition, a high degree of dissimilarity between the understory plant species of adjacent aspen, meadow, and conifer communities indicated a high number of unique species in the aspen understory (Kuhn 2007). Among the sampled LAVO stands, herbaceous species richness decreased across all stands as total canopy cover increased, but the decrease occurred more sharply in stands with increasing conifer than in persistent aspen stands. Kuhn (2007) also reported decreases in understory plant richness with increasing percent total cover in aspen stands with little or no percent conifer cover, and attributed it to competition for resources, either above or belowground. However, the measurement of more rapid species loss in stands with increasing percent conifer cover emphasizes the loss of understory species as aspen stands transition to conifer communities. Indeed, conifer dominance is associated with low floristic diversity in temperate forest across North America (Glenn-Lewin 1977).

Understory plant diversity increased slightly with percent total cover in persistent aspen stands, due to either higher numbers of understory species or higher percent cover. The Shannon-Wiener index of diversity accounts for both the number and relative cover of species, and Potter (1998) observed that high levels of diversity in aspen stands are not just due to high numbers of species but also high cover values for a relatively large number of species. Diversity decreased in stands with increasing conifer. Significant decreases in diversity were correlated with increasing canopy cover and litter depth in a Sierra mixed conifer community (Wayman and North 2007). The canopy influences the quantity and quality of light that reaches the forest floor, soil surface

temperatures, and the quantity and quality of litter inputs. Litter directly affects plant community structure by insulating soil from temperature fluctuations, altering moisture retention, and acting as a physical barrier (Facelli and Pickett 1991). Litter impacts seedling germination and establishment, and both litter quantity and type are factors (Xiong and Nilsson 1999).

Experimental work conducted with coniferous litter found germination decreased for all tested herbaceous species as litter depth increased (Horman and Anderson 2003). Seeds fail to come into contact with mineral soil or they may expend their energy stores before the seedlings reach the litter surface. Reduction of conifer cover and litter depth have the opposite effect. Species richness and cover increased in response to a combination of burning (reducing litter and woody debris) and thinning treatments (increasing light and soil moisture) (Wayman and North 2007).

Aspen litter contains higher amounts of N and lower C:N and lignin:N ratios than conifer litter (Stump and Binkley 1993). We expected an association of C:N with percent total cover and increasing conifer dynamic. In fact, the C:N ratio (fine, woody, and total) was apparently higher in stands with increasing conifer than in stands with persistent aspen (Table 4). However, mixing woody and fine litter in the sample masked differences between stands dominated by aspen and stands dominated by conifer. Separating the fractions indicated an increase in woody litter C:N with percent total cover for all stands. All litter has a pool of labile compounds that decompose rapidly, an intermediate pool representing cellulose, and a recalcitrant pool representing lignin (Adair et al. 2008), but in woody litter the pool of labile compounds is small. Woody litter C:N increases as recalcitrant materials build up on the forest floor. Under an increasing aspen canopy, the ratio of woody to fine litter decreases slightly because aspen trees produce a large mass of fine litter annually. In stands with increasing conifer, the ratio of woody to fine litter increases sharply with increasing cover, as relatively large quantities of woody conifer litter accumulate on the forest floor.

In stands with high aspen cover in the canopy, the decomposition of litter initially occurs at higher rates than in stands with high conifer cover (Maclean and Wein 1978, Prescott et al. 2000). Decomposition in forests is driven by litterfall, and rapid decomposition underneath aspen has been attributed to litter quality (Bartos and DeByle 1981, Legare et al. 2005, Stump and Binkley 1993). Aspen litter also contains more labile forms of organic matter resulting in rapid decomposition and nutrient mineralization compared to conifer litter (Taylor and Parkinson 1988). Due to the large proportion of fine litter inputs and rapid decomposition, aspen stands have a thin O horizon (3-4 cm) relative to conifer stands, which consists of accumulated highly decomposed plant materials (Jones and DeByle 1985b).

However, litter depth and decomposition did not show significant associations in this study. The significant differences in forest floor factors found in previous studies came from stands with unmixed canopies of pure aspen or conifer. Prescott et al. (2000) found the presence of deciduous litter mixed with conifer litter did not increase decomposition rates. Differences along the gradient of percent conifer cover may be masked by the persistence and buildup of conifer needles. In other words, the rain of needles and fine woody material from conifers seem to be able to cause substantial changes in litter structure and decomposition rate which are not easily reversed by addition of aspen leaf litter. Conversion of typical thicker conifer litter and duff layers to layers like those under pure aspen may require litter-consuming disturbances, such as fire.

Understory Transitions

We found no evidence that the 1952 reference point for percent conifer cover and subsequent rate of change would account for variance among stands. Percent total cover (in 1998) and stand dynamic were more predictive than the variables originally hypothesized and the significant effects associated with the interaction of percent total cover and stand dynamic suggest that both amount and type of canopy cover influences the forest floor. The canopy determines the quantity and quality of light that reaches the forest floor, soil surface temperatures, and the quantity and quality of litter inputs. Heterogeneity in light availability (along with litter type and litter depth) influences understory plant community structure (Wayman and North 2007).

When succession to conifer is occurring, aspen stand condition may be characterized by increased sprout release and establishment, declining species richness and diversity, and increasing mass ratio of woody to fine litter. In addition, the initial quality of litterfall influences the composition of the microbial communities that become established in the litter, so that aspen and conifer stands support different microbial communities (Giardina et al. 2001). As conifer presence increases in aspen stands, decomposition rates may lag as the existing microbial community is forced to adjust to changes in litter quality. While litter may change rapidly with increasing conifer cover in aspen, associated changes to soil as a result of shifts in vegetation often occur over relatively long time scales. For example, despite differences in litter quality, a comparison of soils under conifer- and aspen-dominated canopies in the Rockies found no difference in soil C:N, even with apparent differences in C mineralization rates (Giardina et al. 2001). In coastal California, differences in soil color, organic carbon, nitrogen, and cation exchange capacity were not yet apparent between invaded and uninvaded meadows an average of 30 years after canopy closure (Popenoe et al. 1992). If we can assume that conifer invasion has the potential to demonstrably change soil characteristics over long-enough time periods, the lack of soil differences in this study provide corroboration with the photoinpretation findings that the conifer invasion process is relatively recent in many of these stands .

Management and Research Recommendations for Aspen Stands in Lassen Volcanic National Park

Maintenance of biological diversity is a primary goal of national parks and wilderness (Cole et al. 2008). A better understanding of the ecosystems and processes supporting diversity will be essential for managers to achieve their goal of preservation in an era of rapid environmental change (Millar 2009). This study demonstrated that aspen are areas of distinct floristic biodiversity on the LAVO landscape, and related research suggests that riparian and isolated upland aspen stands augment landbird diversity (Heath and Ballard 2003, Griffis-Kyle and Beier 2003) and provide habitat for many other wildlife in the region (Shepperd et al. 2006). Whether they fulfill the keystone ecosystem concept (Stohlgren et al. 1997) is open to question, but they are certainly seem worthy of management attention. We also recorded strong evidence that a substantial proportion of the aspen stands in LAVO are undergoing fairly rapid invasion by conifers. Moreover, for conifer invaded stands, the decline in stand condition and diversity appears to be directly proportional to the degree of invasion. Given the rates of invasion in the park and surrounding region, it seems timely to discuss possible management and restoration options for such stands. The finding that nearly half the stands studied support persistent aspen was unexpected and suggests that we have an incomplete knowledge of mechanisms supporting the establishment and long-term viability of this valuable forest type across the park landscape.

We conclude this report by discussing options for management and research in conifer invaded and persistent aspen stands of the park. These are not intended as prescriptions, but to discuss several management and research possibilities from our perspective.

The regeneration of extant aspen stands is a complex process. The disruption of shoot apical dominance can occur by processes as diverse as deterioration of mature stems from pests, pathogens, or age; shading from conifers; fire; stem removal by logging or blowdown; and early spring growth before leaf-out (Schier et al. 1985). Disturbance is widely cited as the main driver of successful stand replacement, although studies suggesting that regeneration also occurs in the absence of catastrophic disturbance have recently been published (Kurzel et al. 2007). As a widely distributed species with relatively broad ecological amplitude, it is likely that aspen stands colonize and regenerate opportunistically wherever conditions intersect with the species' life history traits.

In conifer invaded aspen stands there may be opportunities to mitigate the effects of conifer presence and herbivory through a combination of passive and/or active management. Generally, aspen are considered to be pioneer species that are favored by high severity fire events (Shepperd et al. 2006). Such events certainly occurred in the region in the past, given the mixed severity regime that characterized the mixed conifer and fir forest in much of the park and environs prior to the fire suppression era (Beaty and Taylor 2001). Therefore, there is a possibility that a strategic wildland fire management program could allow natural wildfire-induced rejuvenation of at least some of the stands. Fire return intervals for much of the park landscape range between 15-75 years, but it is uncertain if low severity fire, which is the most frequent and widespread type in the region, would be adequate to return dominance to aspen in conifer invaded stands. Mid to high severity fire in the park landscapes, even if completely unsuppressed, would likely be considerably less frequent (50-300 year return intervals) and perhaps inadequate for timely stand rejuvenation. To improve upon these admittedly speculative projections, research involving simulation modeling could be conducted to provide a more substantive estimate of the likelihood of a rejuvenating fire event on a reasonable management time scale (10-30 years). At current rates of invasion, it seems likely that a number of stands will be lost within 20-30 years at current rates of invasion without fire.

Another set of questions with a passive restoration approach center on whether the pre-European conditions in the environment and the stands themselves can be recreated in the near future. The conditions associated with the initiation of LAVO's aspen stands are poorly understood, but generally appear to have been in a cooler, wetter period than today. The climatic changes and the general pattern of afforestation seen in both conifer invaded and persistent aspen stands suggest that changed stand conditions have limited management options. A common problem in restoration scenarios is the asymmetry (hysteresis) in ecological conditions and dynamics between unimpacted and degraded sites. The implication is that historical dynamics may not be attainable with current conditions and constraints, at least not without one or more intermediate steps (e.g., mechanical thinning of conifers before instituting a "let it burn" wildland fire approach).

Active management may be a preferable alternative given the likely necessity of action to save stands in the near term. The modest size and relative accessibility of most of the park aspen

stands also make active approaches relatively feasible. Prescribed fire has been used as a treatment for encroached canopies in aspen restoration projects elsewhere (Kilpatrick and Abendroth 2000, Perala 1995, Shirley and Erickson 2000), yet no published study refers specifically to LAVO aspen. While fire is considered a fundamental mechanism for stand establishment in most of the range of aspen, and prescribed fire would seem an obvious treatment option, there is a legitimate concern that burning deteriorated stands of aspen such as those common in LAVO may not lead to successful sprouting. If burning “topkills” existing photosynthetic stems and root carbohydrate stores are too depleted by long-term conifer shading and low stem photosynthesis rates, efforts to trigger regeneration through hormonal stimulation may fail (Bartos 2000). It would seem that retaining at least a few mature stems would allow more rapid replenishment of nonstructural carbohydrates in the roots than would new sprouts, which might take several years to reach comparable photosynthetic capacity. Targeted and carefully implemented mechanical removal of dominant conifers could allow stand reinvigoration by lowering conifer dominance, while retaining mature photosynthetically active stems. Moreover, there is evidence that mechanical thinning treatments have proven successful for increasing aspen stem density and promoting aspen growth in treatment trials in Lassen National Forest (Jones et al. 2005).

Once stand initiation processes are begun by passive or active means, recruitment into the canopy is likely to be dependent upon some degree of protection from native herbivory. Most stands had very high levels of browsing, and relatively few sprouts appeared to escape the browse line. Temporary exclusion of ungulates, in particular, may be an important management strategy to ensure that new regeneration results in stand reinitiation.

The discrete and replicated nature of LAVO aspen stands make them excellent targets for experimental restoration research. This study identified focal stands that would be used for such a study. For instance, the sample sites, vegetation sampling protocols, and data from this study provide a background for 29 stands in the park, as well as a database and data sampling protocols. As an example of an experimental approach, a random subsample of the 15 conifer invaded and the 14 persistent aspen stands could be selected for prescribed fire and / or mechanical treatments. One half of such sites could also be selected for ungulate exclusion, with the other half unexcluded, and the remaining untreated stands as controls. Such an approach would foster a better understanding of the various constraints on aspen regeneration and provide insights into the feasibility of management changes to improve stand condition. These are just initial ideas, of course, and we welcome the opportunity to discuss these or any other issues with LAVO managers in the future.

In conclusion, this study provided compelling evidence that aspen stands in LAVO are valuable and many are in decline. It also demonstrated that varied dynamics appear to affect aspen across the park landscape. We submit this report in the hope that these efforts have better defined the resource management concerns stated by the park and provide insights into how to address them through future adaptive management and research.

Reporting

The results of this study were disseminated through peer reviewed presentations and posters, outreach presentations and articles, and annual reporting for the National Park Service. The full list of presentations and reports is provided in Table 6.

Table 6. Peer reviewed abstracts, outreach presentations and reporting.

Peer Reviewed Abstracts:

S.A. McCullough, K.W. Tate, D.A. Sarr, A.T. O'Geen, and M.L. Whiting. 2009. Aspen forest dynamics associated with conifer encroachment at Lassen Volcanic National Park, California. Presentation: North American Forest Ecology Workshop, Logan, UT.

S.A. McCullough, K.W. Tate, D.A. Sarr, A.T. O'Geen, and M.L. Whiting. 2009. Recent trends and current conditions within aspen stands of Lassen Volcanic National Park, California. Poster: George Wright Society, Portland, OR.

S.A. McCullough, K.W. Tate, D.A. Sarr, A.T. O'Geen, and M.L. Whiting. 2009. Plant and soil transitions associated with conifer encroachment in aspen stands of Lassen Volcanic National Park, California. Poster: Society for Range Management, Albuquerque, NM.

Outreach Presentations and Articles:

S.A. McCullough, K.W. Tate, D.A. Sarr, A.T. O'Geen, and M.L. Whiting. 2009. Recent trends and current conditions within aspen stands of Lassen Volcanic National Park, California. Presentation: Lassen Volcanic National Park staff meeting, Mineral, CA.

S.A. McCullough. Aspen stand health and conifer trends at Lassen Volcanic National Park. Klamath Kaleidoscope. Winter/Spring 2009.

K. Tate, B. Jones, T. Kuhn, S. McCullough. 2008. Status of Aspen in the Sierra Nevada and Cascades. Presentation: California Forest Pest Council. Woodland, CA.

Aspen Change Detection at Lassen Volcanic National Park. 2008. Class presentation to ERS 185, Aerial Photo Interpretation, UC Davis.

Reporting:

Investigator's Annual Report 2008

Lassen Volcanic National Park Annual Report 2008

S.A. McCullough, and K.W. Tate. 2008. Ecological Assessment of Aspen Communities in the Klamath Network: A Problem Analysis. Presentation: Klamath Network Board of Directors, Ashland, OR.

Californian Cooperative Ecosystem Studies Unit Annual Report 2008

Investigator's Annual Report 2007

Lassen Volcanic National Park Annual Report 2007

Californian Cooperative Ecosystem Studies Unit Annual Report 2007

K.W. Tate and S.A. McCullough. 2006. Ecological Assessment of Aspen Communities in the Klamath Network: A Problem Analysis. Presentation: Klamath Network Board of Directors, Ashland, OR.

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Appendix A. UTM Coordinates of Sampled Stands

Datum: NAD 83 Zone 10

UTME	UTMN	Elevation	Site Description
629893	4484644	1949	Encroached aspen patch between Paradise Meadows trail and Hat Creek. Sparse understory of <i>Osmorhiza chilensis</i> and <i>Chimaphila menziesii</i> .
631573	4490772	1852	West side of lower Hat Creek, near park boundary. Open canopy of <i>Populus tremuloides</i> and mixed conifer, and understory of <i>Wyethia mollis</i> and <i>Hackelia californica</i> .
630495	4485989	1905	On slope above Hat Creek, within boundaries of Devastated Area. Open overstory of <i>Populus tremuloides</i> and understory dominants of <i>Monardella odoratissima</i> and <i>Lupinus angustiflorus</i> .
630441	4486586	1906	On slope above wetland; located on ridge between old channels of Hat Creek. Open overstory of <i>Populus tremuloides</i> and understory dominants of <i>Elymus glaucus</i> and <i>Hackelia</i> sp.
631176	4487610	1914	Between Emigrant Nobles road and creek at narrows of lower Hat Creek drainage. Mixed overstory of <i>Populus tremuloides</i> and <i>Pinus contorta</i> and sparse understory of <i>Osmorhiza chilensis</i> and <i>Elymus glaucus</i> .
631741	4488646	1868	50 m west of Hat Creek, in vicinity of old creek channel. Overstory of <i>Populus tremuloides</i> and <i>Pinus contorta</i> and thick understory with dominants of <i>Trisetum canescens</i> and <i>Carex angustata</i> .
631834	4490704	1877	Unburned patch between Nobles Emigrant trail and lower Hat Creek south of horse corral. Mixed understory with common forbs of <i>Achillea millefolium</i> and <i>Trifolium</i> sp.
629781	4486583	1975	Dry drainage north of park road at edge of Devastated Area debris flow. Dense overstory of <i>Populus tremuloides</i> , <i>Pinus jeffreyi</i> , and <i>Abies concolor</i> . Sparse understory of <i>Monardella odoratissima</i> and <i>Lupinus angustiflorus</i> .
628764	4486707	1895	Slope above wetland bottom in Devastated Area, between Survivor's Hill and Lost Creek channel. Understory of <i>Monardella odoratissima</i> , <i>Lupinus angustiflorus</i> , and <i>Penstemon gracilentus</i> .
628855	4486624	1899	Stand of <i>Populus tremuloides</i> and mixed conifer adjacent to wetland bottom, between Survivor's Hill and Lost Creek channel in Devastated Area. Understory of <i>Monardella odoratissima</i> and <i>Lupinus angustiflorus</i> .
629857	4484576	1949	Encroached riparian aspen and adjacent wet meadow opening between Paradise Meadows trail and Hat Creek. Sparse understory of <i>Lupinus polyphyllus</i> and <i>Osmorhiza chilensis</i> .
629750	4484579	1962	Encroached riparian aspen between channels of Hat Creek above lake. Understory of <i>Elymus glaucus</i> , <i>Osmorhiza chilensis</i> , and <i>Ribes montigenum</i> .
632262	4490831	1871	Wetland complex south of Badger Flat Trail, with overstory of <i>Populus tremuloides</i> and <i>Pinus contorta</i> , and thick understory dominated by <i>Carex angustata</i> and <i>Lupinus polyphyllus</i> .
628102	4487736	1879	Adjacent to park road between Raker Peak and Hot Rock. Overstory of <i>Populus tremuloides</i> and <i>Abies magnifica</i> , and understory dominants of <i>Monardella odoratissima</i> and <i>Lupinus angustiflorus</i> .
626546	4491131	1694	In vicinity of Lost Creek Campground, east of Lost Creek at park boundary. Small stand of <i>Populus tremuloides</i> . Sparse understory of <i>Carex rossii</i> and <i>Achnatherum occidentale</i> ssp. <i>californicum</i> .

643804	4491622	1860	West shore of Butte Lake north of Fantastic Lava Beds. <i>Populus tremuloides</i> and <i>Pinus contorta</i> overstory with understory dominants of <i>Elymus glaucus</i> , <i>Carex subfusca</i> , and <i>Carex hoodii</i> .
645354	4490192	1821	Wetland on edge of Butte Lake south shore. Mixed overstory of <i>Populus tremuloides</i> and <i>Pinus contorta</i> and understory dominants of <i>Carex angustata</i> and <i>Aster occidentalis</i> .
642887	4484452	1850	West side of Grassy Creek just south of Snag Lake. Mixed understory with <i>Salix lemmonii</i> , <i>Fragaria virginiana</i> and <i>Kelloggia galiodes</i> .
644286	4486113	1872	Wetland slope above east shore of Snag Lake. Open overstory of <i>Populus tremuloides</i> and dense understory with <i>Carex angustata</i> and <i>Carex nervina</i> .
644300	4486583	1821	East side of Snag Lake, between lakeshore and trail. Open overstory of <i>Populus tremuloides</i> and <i>Pinus jeffreyi</i> and understory of <i>Monardella odoratissima</i> and <i>Lupinus arbustus</i> .
637360	4477875	1639	Wetland patch between Hot Springs Creek and Ranger Station in Warner Valley. Understory dominants of <i>Carex amplifolia</i> and <i>Scirpus microcarpus</i> .
637641	4477675	1623	On upper bench, south side of Hot Springs Creek in Warner Valley. Open overstory of <i>Populus tremuloides</i> and <i>Abies concolor</i> , with understory of <i>Trisetum canescens</i> and <i>Hackelia micrantha</i> .
637355	4477722	1629	Meadow and seep complex below talus slope on south side of Warner Valley. Wetland corridor of <i>Salix lemmonii</i> adjacent to meadow opening with <i>Veratrum californicum</i> .
636393	4477889	1716	Small, encroached stand of <i>Populus tremuloides</i> below field of <i>Alnus incana</i> on south side of Warner Valley. Dry understory of <i>Bromus carinatus</i> and <i>Trisetum canescens</i> .
636700	4477802	1684	Small stand of <i>Populus tremuloides</i> below field of <i>Alnus incana</i> on south side of Warner Valley. Dry understory of <i>Elymus glaucus</i> and <i>Achnatherum occidentale</i> ssp. <i>pubescens</i> .
636916	4477730	1672	Small stand of <i>Populus tremuloides</i> on wet slope between talus fields on south side of Warner Valley. Understory of <i>Pteridium aquilinum</i> and <i>Hackelia micrantha</i> .
637019	4477696	1680	South side of Warner Valley. Small stand of <i>Populus tremuloides</i> and mixed conifer on moist, rocky bench between talus slope and <i>Alnus incana</i> field. Understory of <i>Pteridium aquilinum</i> .
635227	4477626	1770	On Drake Lake trail, east of Dream Lake in Warner Valley. Wetland opening in conifer forest with open <i>Populus tremuloides</i> overstory. Dense understory with dominants of <i>Veratrum californicum</i> and <i>Stachys ajugoides</i> .
634466	4477759	1736	Below springs west of Dream Lake in Warner Valley. Stand of <i>Populus tremuloides</i> and conifer surrounded by field of <i>Alnus incana</i> . Sparse understory of <i>Bromus carinatus</i> and <i>Osmorhiza chilensis</i> .
634323	4477865	1734	West end of Drakesbad meadow complex, between Hot Springs Creek and field of <i>Alnus incana</i> . Sparse understory with <i>Osmorhiza chilensis</i> .

Appendix B. Field Supplies – Whittaker Plots

Two 100 m tapes
Two 50 m tapes
Flags
Wooden stakes
1 m² quadrat
1+ site data datasheet
10+ 100 m² species composition datasheets
20+ 1 m² cover datasheets
3+ transect forms for the right layout
Solar pathfinder
White pencil
4 blank pathfinder forms
Spherical densitometer
Clinometer
GPS
Spare GPS batteries
Topo quad sheet
Digital camera
Charged camera battery
Loupe
Gerber for digging specimens
Park Species list
Jepson Manual
Lassen Flora
Plastic collection bags
Plant press
Blotter paper
Newspaper
First aid kit
Radio
Radio call sheet
Spare pencils
Clipboard
15 cm ruler

Appendix C. Field Data Sheets

Whittaker Plot Survey form (adapted from CNPS Rapid Assessment Form dated Sept 20, 2004).

Time _____ Start _____ End _____

I. LOCATIONAL/ENVIRONMENTAL DESCRIPTION				
Stand ID - PreSurvey: _____	Final Coded Stand ID: _____	Date: _____	Name(s) of surveyors: _____	Plot Bearing: _____
GPS waypoint #: _____ Feature taken: Point/Polygon GPS datum: (NAD 83) _____ Is GPS within stand? <u>Yes / No</u> If No, cite from GPS point to stand, the distance _____ (in meters) and bearing _____ (in degrees) GPS Error: $\pm$ _____ ft / m UTM field reading: UTME _____ UTMN _____ UTM zone: <u>Zone 10</u>				
Elevation: _____ ft / m Photo: _____ from GPS spot, bearing: _____ distance: _____ photo bearing: _____ Topography: convex _____ flat _____ concave _____ undulating _____ top _____ upper _____ mid _____ lower _____ bottom _____				
Aspect (circle one and/or enter actual $^{\circ}$): NE _____ NW _____ SE _____ SW _____ Flat _____ Variable _____ Slope (circle one and enter actual $^{\circ}$): 0° _____ $1-5^{\circ}$ _____ $5-25^{\circ}$ _____ $> 25^{\circ}$ _____ Upland or Wetland/Riparian (circle one) Height above stream (m): Top: _____ Bottom: _____ Steps: _____ Surveyor: _____ Distance: _____ Comments: _____ _____ _____				
Stand sketch (stand, plot orientation, major features, major gradients across $10m^2$ quadrants) PLOT LAYOUT: 				

Strata No.	Species	Top	Base	Steps	Initial	DBH	Height

100 m² Plot Species and Cover

Plot ID:[illegible]

Browsed:

Hedged:

Both:

Neither:

Plot ID _____
hedged only _____
browsed only _____
browsed/hedged _____
not browsed/hedged _____
Total _____

Densitometer: (open or species)

	NORTH	EAST	SOUTH	WEST
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				

Species	Live/dead	strata	dbh

Plot ID _____

[illegible]

Appendix D. Protocols

Whittaker Plot Draft Protocol:

The goal is to take a representative measure of the stand. Take two bearings at a 90 degree angle, maximizing the portion of the aspen stand captured in the plot boundaries. Align 10 x 10 plot boundaries with breaks in vegetation, soils, light, and moisture regime (ie wetlands, openings, meadow edges, etc.) Fit as many 10x10 plots in the stand as possible, up to 1000 m². The main analysis will be taken from the stand plots. The 100m² plots will be analyzed separately, as a secondary analysis. Lay out plot to minimize environmental gradients. The data elements should capture some of the unavoidable environmental gradients (such as slope across plot).

Definitions of fields in the protocol

LOCATIONAL/ENVIRONMENTAL DESCRIPTION

Stand ID – Pre Survey. This is the number given to the plot during the preliminary survey.

Final Coded Stand ID: The naming convention for the final plot name is two letters identifying the block, a number identifying the strata, and two numbers representing plot ID.

Date: Date(s) of survey

Name(s) of surveyors: The full names of each person assisting should be provided for the first data sheet. In successive data sheets, initials of each person assisting can be recorded. Please note: The person recording the data on the form should circle their name/initials.

GPS waypoint#: give the number assigned by the GPS unit (will be in the form of a coded date).

GPS datum: Check the unit. It should be set on NAD 83.

Is GPS within stand? Yes / No Circle “Yes” to denote that the GPS waypoint was taken directly within or at the edge of the stand being assessed, or circle “No” to denote the waypoint was taken at a distance from the stand (such as with a binocular view of the stand).

If No cite distance (note ft/m), bearing and view from point to stand: An estimate of the number of feet or meters (please circle appropriate), the compass bearing from the waypoint of GPS to the stand, and the method of view used to verify the plot (e.g. binoculars, aerial photo).

Error: ± The accuracy of the GPS location, when taking the UTM field reading. Please denote feet (ft) or meters (m). Please become familiar with your GPS unit’s method of determining error. Some of the lower cost models do not have this ability. If using one of those, insert N/A in this field.

UTM field reading:

UTM E: This is a 6 digit number starting with 6.

UTM N: This is a 7 digit number starting with 44.

UTM Zone: We are entirely within Zone 10.

Elevation: Recorded from the GPS unit or USGS topographic map. Please denote feet (ft) or meters (m), and note if reading is from GPS unit or map. (Please note: Readings taken from a GPS unit can be hundreds of feet off.)

Photograph #'s: Note the roll number, frame number, direction, and the name of the person whose camera is being used. Take at least two photographs from different directions, and describe the location and view direction from compass bearings for each frame. Additional photographs of the stand may also be helpful. (Also, if using a digital camera or scanning the image into a computer, positions relative to the polygon/stand number can be recorded digitally.)

Topography: Check two of the provided features, characterizing both the local relief and the broad topographic position of the area. First assess the minor topographic features or the lay of the area (e.g. surface is flat, concave, etc.). Then assess the broad topographic feature or general position of

the area (*e.g.* stand is at the bottom, lower (1/3 of slope), middle (1/3 of slope), upper (1/3 of slope), or top).

Sketch stand: Include aspen patch boundaries, plot orientation, major features, and major gradients across 10m² quadrants.

Plot Layout: Circle the letter of the plot layout chosen to match the stand shape.

Aspect (circle one and enter actual °): Read from the center of the stand using a compass with magnetic north correction. Current declination is 15° 8'E.

Make sure to average the reading across entire stand. "Variable" may be selected if the same, homogenous stand of vegetation occurs across a varied range of slope exposures.

Slope: Determine or estimate the height of your eye-level. Looking through the clinometer sight the top of the slope and then fixate on an object or person on the top of that slope that is the same height as your eye-level. Read the degrees. This is the slope.

Height above stream: From stream, sight up to center of Whittaker plot with the clinometer. Use the same method as strata height to obtain height above stream.

Upland or Wetland/Riparian (circle one): Indicate if the stand is in an upland or a wetland; note that a site need not be officially delineated as a wetland to qualify as such in this context (*e.g.* seasonally wet meadow).

Comments: Briefly describe the stand age/seral stage, disturbance history, nature and extent of land use, and other site environmental and vegetation factors. Examples of disturbance history: fire, landslides, avalanching, drought, flood, animal burrowing, or pest outbreak. Also, try to estimate year or frequency of disturbance. Examples of land use: grazing, timber harvest, or mining. Examples of other site factors: exposed rocks, soil with fine-textured sediments, high litter/duff build-up, multi-storied vegetation structure, or other stand dynamics.

VEGETATION DESCRIPTION

Major non-native species: Enter species code.

Defining and recording strata: Identify four strata, as well as a shrub layer if there is one. Record the primary species in the strata. Use the clinometer to record the % number for the top of the canopy (sighted from a representative tree) and the bottom of the canopy. Make sure to stand in a location where the true top of the tree can be seen. Pace the distance to the tree, and multiply by the observer's pace distance (m/pace). The equation for height is:

total height (meters) = (top measurement- bottom measurement) x (distance/100)

Record a representative DBH for each strata using the DBH tape.

We established basic strata levels found in all or most stands, and for each stand applied the framework of these four strata and recorded the local heights of each. In stands occurring on slopes, aspen height was variable- shorter stems at the top of the slope and taller stems at the bottom of the slope. In these cases, average values were estimated using midslope trees.

Strata 4: any trees taller than the mature aspen stems

Strata 3: mature aspen stems- usually a pretty uniform layer

Strata 2: any trees below the aspen layer but above about ten feet tall. This strata had the greatest range of heights.

Strata 1: trees between 4.5 feet and 10 feet tall.

The seedling layer includes seedlings between 1 ft tall and 4.5 feet tall (figuring that seedlings less than 1 ft were captured by the quadrat readings).

Variations from this design are marked with notes on the datasheet. There were a couple of stands that didn't have many Strata 1 trees, or showed a distinct layers of trees just above ten feet tall. In general Strata 2 represents the mid-level trees.

Reading canopy cover by densiometer: Recorded 24 readings in each of the cardinal directions for a total of 96. Readings were taken about a foot above the ground, at the center flag of each 10 x 10 quad. In cases where the center was located under a tree, the densiometer was read from that point. A note was made on the datasheet that the readings were not representative- happened a few times. The densiometer was read by rows from the top, and readings were recorded in that order. A value for each square was read. Partial squares of open space were condensed into whole values. The same was also done as much as possible with tree species. Generally, aspen suckers were excluded from the readings, except in sites with distinct stands of Strata 1 suckers. Dead trees were recorded by species- live/dead status was not necessarily marked. If a dead tree could not be identified it was described in as much detail as possible- as aspen/conifer or just dead. The densiometer readings reflect the species reflected in the mirror, which in dense sites may have been understory rather than overstory species (such as conifer instead of the overstory aspen layer).

Recording overstory species: All trees in each 10 x 10 were measured for dbh and put into categories. Trees above 4.5 feet were recorded with a dbh reading. Some aspen seedlings were too skinny for a dbh reading, but in this case- might have only happened once- they were counted in a separate tally. In general a dbh was recorded for aspen seedlings. Dbh readings below 1 inch may show variation and have some inaccuracy because of the awkwardness of taking such a small reading. Seedlings between 1 ft and 4.5 were recorded in categories and counted with a tally. The seedling tallies are kept separately for live and dead trees of each species- most seedlings were alive- only a few dead were recorded.

The categories used to describe individual trees were:

Multi stem: used in cases where the trunks were fused above ground level- most sets of multistemmed trees are marked sequentially on the datasheet. If the second stem was dead and less than 4.5 feet (including cases where a mature stem had fallen down on the ground) it was not recorded as a multistem- no dbh taken. Recorded as coarse woody debris.

Snap: Used when a treetop was snapped off and the tree did not send up a lateral stem to replace it. It was mostly used for dead standing trees. The strata height was the height of the snap.

Lean: This category was used for trees that were physically leaning, like they were in the process of falling down. It was mostly used for dead trees.

Bent: Used for snow-damaged trees, or trees that had grown around other trees or other obstacles. Alison did not use this category very much.

Stunted: Used for trees with physical damage, like the terminal stem had been broken. This category was used for trees that did not fall into the other classifications.

For all categories, strata height was recorded for the strata that the top of the tree was currently in. We did not try to visualize which strata the tree would be in without the damage or other condition present.

Recording herbivory: All sprouts that were shorter than 4.5 feet were counted.

Hedged: when the terminal branch (as opposed to lateral stems) was browsed more than three times, or it appeared to regrow more than three times.

Browsed: Read from current years growth on the terminal branch. Browse was detected by bare petioles, or green stems that looked like they had been cut short. Insect damage on part of a leaf was not counted. But if there seemed to be cumulative damage to a group of leaves, any sort of appearance of chomping, that was counted. If it was disease-damaged, it was not counted. Live/dead decisions: a sprout with even one leaf was counted as live. Dead was used for sprouts with no sign of life.

Hedged to death: the category was created to group dead sprouts that appeared to be dead because of heavy herbivory- lots of hedged stems. This category was generally used in stands with a large component of that kind of sprout- many of the sprouts actually had one leaf left and were counted in the browsed or hedged categories. On the data sheets this category was sometimes alternatively identified as “Dead” but it means the same thing.

At the end of the season, some heavily hedged sprouts with no obviously browsed leaves or sprouts visible were recorded as hedged only, because the browse damage, while it had probably happened, was not clear.

There were a couple of stands with very large numbers of escaped sprouts just over 4.5 feet. In these cases, a separate tally was kept to capture them. There were also a couple of sites with so many stems that a representative sample of 100 was read, and an overall cover value for those trees was recorded. The sample of 100 was read from trees that were considered accessible to deer- well protected, inner stems were not read. Stems over 4.5 feet that had been damaged so that the live part of the tree (ie, another stem) was shorter than 4.5 feet were not included in this tally, since the tall stem was dead.

100m² plot cover estimates: For each 10 x 10, values were estimated visually for:

Coarse woody debris (also recorded as woody)

Medium woody debris

Animal disturbance- mainly consisted of burrow openings, although in meadow sites it also included places where surface disturbance due to tunneling was visible.

Wildlife trail- we used this at one site in the beginning, but in most sites with animal trails the disturbance was not recorded separately. It probably fell into the litter category.

Rock

Bare mineral ground

Litter (this was split into kinds of litter: combinations of aspen, conifer, and grass/herb)

Solar availability by solar pathfinder: Read 1 foot above ground. When the center point fell under a tree, the pathfinder was generally read from that spot- but the readings were not that affected because of the wide angle of the pathfinder. For afternoon readings affected by direct sunlight, shade was created with the hands (described by the manual) or the solar pathfinder was moved a short distance under a tree for shade. The afternoon readings were the most difficult. Open areas were read; light coming through semi-transparent aspen leaves was excluded. In the rain site, any light that was visible was recorded.

100m² Species Composition

Record plot ID and 100 m² plot number. Start a new page for each of the ten 100m² plots in the Whittaker plot. Start over for each new plot, so that there is a complete species list for each plot. Read the five 1 m² quadrat species and cover first, and then conduct a timed search for additional species by walking a grid pattern through the plot for 10 minutes.

1 m² Plot Species and Cover

Place the quadrat at the correct location on the tape. Place the 1m² quadrats avoiding trampling on the 1m² sample areas. For each species in the 1 m² plot, record species code. No specimens should be collected because they will be identified, or at least given unknown labels, by the 100m² search. Record an ocular estimate of cover, using the marks on the quadrat as guides. The cover estimates will be on the order of 0-100%. We are not using cover classes. Record a numerical value for all species. For species with less than 1% cover (approximately the size of a balled fist), rank using this

numerical convention: 0.99%, 0.98%, 0.97%, etc. Place importance on the relative size and the order of the ranking, rather than the absolute value.

Species Identification

When breaking to identify a species, record where you are in the plot on the data sheet so that you can return to the same place. Record the species code for each specimen seen. If the species can not be identified, take a specimen, keep in a plastic bag, and press when possible. When collecting a specimen, choose specimens with either floral heads or developed seeds. Dig around and under the roots of each specimen, so that a good specimen with complete roots, stem, and flowers is collected. Label each unknown specimen with date, plot and subplot, and a descriptive name. The rule for naming unknowns will be to name them as “Unknown, alphabetical letter, descriptor” The descriptor could be a genera name, if known, or a physical characteristic. Examples: “Unknown A, Tall Poa” or “Unknown B, Short Poa”. These labels will stick with that particular unknown for as many times as it is seen in the entire 1000m² plot. The specimen will be labeled with the first plot that it was seen in, but it may appear on more than one 100m² data sheet. Immature specimens should be identified to species as possible using surrounding individuals. For those that can not be identified reliably, mark as “immature poa” or “immature carex” and move on. The codes for confidence are H- high, M- medium, and L-low.

Leaf Litter

At each 1 m² plot, cut through leaf litter to surface of mineral soil. The cut should be 10cm x 10cm, and should be placed in the middle of the quadrat. For all plots, measure total thickness of leaf litter to soil surface.

Wrapping up

Press specimens in the plant press. Fluff up plot. Place removed leaf litter back in place. Remove all stakes and flags.

Protocol for LAVO Leaf Litter Samples

Materials for sorting:

2 mm sieve
1 large (about 12" x 24") plastic tub
2 medium (12" x 12") plastic tubs
300 5x7 envelopes
300 8 x 11.5 envelopes
100 paper bags (for large samples)
Dissecting needles
Water displacement equipment
Mass balance
Sample drying oven

1. Label all samples with a key number (1-267) for DANR Analytical Lab. Label bags and start data spreadsheet which cross-references the field ID with the DANR ID. DANR ID will be used on all subsequent labels originating from the field sample (e.g, post sorting, recording weights).
2. Dry samples at 60 degrees for 24-48 hours.
3. Weigh all samples within 4 hours after drying.
4. Calculate field bulk density from volume and dried weight.
5. For each sample:
 - a. We first need to sort all woody material out of each sample. We also need to screen all mineral soil and rocks out of the sample. To start, pour the sample into the 2 mm sieve, with the sieve placed in a large tub. Mineral soil will start to pass through the sieve into the large tub. By hand, sort out the identifiable twigs and branches from the sample which are trapped in the sieve. Place all woody material into a small tub. Woody material includes all identifiable twigs, bark, and cones greater than 1 mm in diameter. Within the sieve, hand mix leaf litter gently, breaking up material and picking out trapped woody material, mineral soil and rocks. Grains of mineral soil may be caught on organic material and should be picked off with a dissecting needle as much as possible, without destroying the organic material. Sort fine litter (leaves, petioles, conifer needles, and other material less than 1 mm in diameter) into another small tub. Important: fine litter will include chunks of aggregated organic matter, which may look like a clod of mineral soil but will be very light-weight. Rocks too large to pass through the sieve can be left in the large tub with mineral soil that passed through the sieve and is trapped in the sieve after all woody material and fine litter has been sorted out.
 - b. Mineral soil and some fine litter will remain in sieve. Shake sieve gently to pass remaining mineral soil and fine debris with a 2 mm sieve. Pick any remaining fine litter from sieve and place in fine litter tub. Dump sieve into large tub. Gently "pan" large tub to try and sort fine litter to the edge of the pile. Pick fine litter out and place in fine litter tub.

- c. Transfer all woody material from small tub to a 5 by 7 envelope labeled with the DANR Lab ID.
 - d. Transfer all mineral soil and rocks from small tub to a 5 by 7 envelope labeled with the DANR Lab ID.
 - e. Transfer all fine litter from small tub to an 5 by 7 or 8 by 11.5 envelope labeled with the DANR Lab ID.
6. Sort material in bags that could not be separated with certainty.
7. Dry all material again (same oven and time as first dry-weigh event).
8. Weigh woody material, fine litter, and mineral soil/rock sub-samples, record, account for bag weight (dry 20 bags of each size and weight). Use same scale as first dry-weigh event).
9. Composite fine litter and woody samples (3 subsamples per 100m² plot) separately into 5 by 7" envelopes, with thorough hand-mixing, for submission to DANR Lab for C and N analysis.
10. Determine volume of mineral soil and rocks by loss on ignition.

The Department of the Interior protects and manages the nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

NPS XXXXXX, Month Year

National Park Service
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1250 Siskiyou Boulevard
Ashland, OR 97520-5011

www.nature.nps.gov