IMPACTS OF FIRE EXCLUSION ON FOREST DYNAMICS AND PROCESSES IN CENTRAL IDAHO

Peter F. Kolb[1] and David L. Adams
College of Forestry, Wildlife and Range Resources, University of Idaho, Moscow, ID 83844-1133

Geral I. McDonald
U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Moscow, ID 83843

ABSTRACT

Fire exclusion in forests of central Idaho during the past century may have resulted in overstocked stands of shade-tolerant species that are predisposed to drought, pest and pathogen attack, increased mortality, and subsequent catastrophic fires. Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and subalpine fir (*Abies lasiocarpa*), ranked according to increasing shade tolerance, are the four tree species that dominate the climax plant associations along xeric to mesic moisture gradients and warm to cool temperature gradients, respectively. Prevailing climatic patterns coupled with the mountainous topography of central Idaho create a mosaic of distinct plant communities and successional pathways across a relatively small geographic area. Where tree species overlap, shade-tolerant species eventually dominate the climax community although they also exhibit less drought tolerance. Fire tolerance is positively correlated with drought tolerance for these species. This has led to the hypothesis that, historically, naturally occurring fires with a frequency of 5–10 years on the warm dry sites and 15—30 years on the mesic sites maintained old-growth stands of ponderosa pine and Douglas-fir, the most drought-tolerant species.

Plots established during 1994 in naturally occurring stands of each of the major forest habitat types in central Idaho were measured for stand mortality and symptoms of disease and insect infestation, tree species composition, age, growth, crown size, soil water availability, and soil carbon and nitrogen content. Our data indicate that stand structure and composition on the majority of habitat types is comprised of >150-year-old seral species and a majority of shade- tolerant climax species that are under 90 years old. Stands with large components of shade-tolerant species have significantly higher basal areas and incidence of disease than stands of older shade-intolerant species. Correlations among stand structure, soil water availability, and soil carbon indicate that stands with basal areas greater than 40 square meters per hectare may deplete available soil water by early August. Soil carbon and nitrogen content, on the other hand, increase in stands of shade-tolerant species with higher basal areas. The implications of a shift from historically frequent ground fires to less frequent catastrophic crown fires on ecological processes and ecosystem management are discussed.

Citation: Kolb, Peter F., David Adams, and Geral I. McDonald. 1998. Impacts of fire exclusion on forest dynamics and processes in central Idaho. Pages 210–218 *in* Teresa L. Pruden and Leonard A. Brennan (eds.). Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20. Tall Timbers Research Station, Tallahassee, FL.

INTRODUCTION

Disturbances, such as frequent fire, represent a variable in the site-species relationship that should be considered a natural environmental gradient. A fire-resistant species such as ponderosa pine, with frequent ground fires, can be the *defacto* climax species where less fire resistant and more shade-tolerant species such as Douglas-fir or grand fir could otherwise dominate. Left free of human management activities, including fire exclusion, the structure of a ponderosa pine forest increases the likelihood of ground fires prevailing as opposed to fir-dominated sites where the likelihood of stand-replacing fires is increased (Wright and Bailey 1982, Agee 1990, Arno et al. 1995). The importance of tree species adaptations and their interspecific relationships with respect to light availability, soil water, nutrient cycling, and disturbances such as fire have been largely overlooked for predicting long-term forest productivity and resilience.

In forested areas of the northwestern United States, sites have been classified by their potential climax plant communities (where climax refers to the development of a stable plant community in the absence of disturbance) and defined as forest habitat types. The differentiation among habitat types is linked to the combined effects of topography, climate, parent material, time, and biotic processes (Daubenmire 1952, Pfister and Arno 1980, Hironaka et al. 1991, Steele and Pfister 1991). As a result, habitat type is used as an ecological index for potential site productivity and mechanisms of disturbance. Similarly, it is a useful tool for targeting species and successional preferences in managed forests.

In the inland Northwest, natural disturbances such as fire have historically prevented significant proportions of the landscape from developing into old-growth climax communities (Losensky 1995). Evidence suggests that stands of seral species, such as ponderosa pine, were maintained with old-growth characteristics by frequent ground fires (Habeck 1988, 1994, Arno et al. 1995, 1997) However, since the early 1900's the attempt has been made to exclude fire from these eco-

[1] Present address: School of Forestry, University of Montana, Missoula, MT 59812.

systems. In the absence of fire or other large disturbances a gradual progression from seral plant communities towards climax communities will occur (Odum 1969, Halpern 1988, McLendon and Redente 1990, Botkin 1993). In most forested environments, the ability to regenerate in the light-limited conditions of an understory environment is the overriding factor that determines climax tree species (Kramer and Kozlowski 1979, Smith and Huston 1989). In the inland Northwest, a xeric condition can exclude shade-tolerant species and, therefore, is also considered an important factor determining climax tree species (Daubenmire 1968, Pfister et al. 1977, Steele et al. 1981). From xeric to mesic sites in central Idaho, ponderosa pine, Douglas-fir, grand fir, and subalpine fir are the climax tree species, respectively (Daubenmire 1968, Steele et al. 1981). Shade-intolerant species such as ponderosa pine and Douglas-fir are seral to grand fir or subalpine fir where adequate soil moisture allows these later shade-tolerant species to survive. The ecotones where one species becomes climax over another due to water availability or shade tolerance can be highly variable, in part because the shade-tolerant species have been historically excluded from many sites by fire.

A noticed increase in stand dominance by shade-tolerant tree species in the last decades and associated increases in stand level mortality and occurrence of catastrophic fires have been attributed to fire exclusion practices (Habeck 1988, Agee 1990, Harvey 1994, Sampson et al.1994, Arno et al. 1995, 1997). The effects of shifts in species dominance and density due to fire exclusion on potential site productivity, insect and disease occurrence, and tree species longevity are poorly understood. It is, therefore, difficult to predict the consequences of management practices that maintain shade-tolerant species or attempt to restore historic seral stands. The primary objective of this study was to measure stands of the dominant climax tree species in central Idaho, ponderosa pine, Douglas-fir, grand fir, and subalpine fir, for their growth attributes, insect and disease occurrence, and susceptibility to drought stress following 90 years of fire exclusion practices. Furthermore, we examined these attributes with respect to slope, aspect, elevation, soil water availability, soil carbon, soil nitrogen, stand habitat type, composition, successional stage, and competition.

Physical Environment

The general climate in central Idaho is characterized by cold winters and warm and dry summers, with the majority (55–60%) of the annual precipitation occurring as snow (Steele et al. 1981). Steep topography with elevations varying from 900 meters to 2800 meters creates an environmental mosaic where slopes with southerly aspects are particularly warm and dry. On average, high potential summer evapotranspiration (evaporative demands that exceed 16 grams per cubic meter at 28 °C) and less than 27 centimeters precipitation for the months of July, August, and September create drought conditions (Steele et al. 1981). Therefore, the vegetation must rely on stored soil water during the major part of the growing season.

Most of the soils are Entisols that are granitic in origin and lie on the southern portion of the Idaho Batholith. They have been characterized as sandy loams ranging in depth between 2 meters on moderate slopes to less than 0.1 meter on steeper slopes (Rasmussen 1981, Noe 1991). In addition, they tend to be well drained with rapid water permeability, and low water holding capacities. Often mean fine litter depth is in excess of 7.5 centimeters, apparently due to dry summers and cold winters which hinder decomposition. It has been hypothesized that, historically, frequent fires played a major role in nutrient cycling and in maintaining forest stand species and structural attributes (Harvey 1994, Sampson et al. 1994).

METHODS

To measure stand characteristics and monitor soil water and nutrient availablility, sixty-three permanent plots were established on the Boise National Forest, Idaho between May and October, 1994. All plots were located on the southern portion of the Idaho Batholith, consequently the soils were relatively homogenous in texture and origin. Plots were randomly located among the major forest habitat types, which included ponderosa pine, Douglas-fir, grand fir, and subalpine fir series. Approximately ten different habitat types within each of the latter three were sampled, although data was pooled by series for most analyses. A vegetation cover type map of the Boise National Forest, developed from LANDSAT imagery by the Idaho Department of Water Resources (Boise) was used to stratify sampling to ensure a representative sample from each of the major habitat type series. With the exception of four plots located on Boise Cascade Corporation lands, where some logging had previously occurred, all stands sampled consisted of naturally occurring forest with no apparent history of human manipulations other than fire exclusion.

Each plot consisted of a 0.04 hectare intensively measured microplot and a 1.0 hectare macroplot. Microplot measurements included soil depth of A and C horizons in two places, elevation, slope, aspect, and air temperature and relative humidity 1.4 meters above the soil surface at plot center, measured at either 10:00 or 14:00. Two samples of the A and C horizons each were collected per plot using a 50 cubic centimeter cylindrical probe. These samples were stored in sealed 120 cubic centimeter containers, placed in coolers and later analyzed for bulk density, water content, water potential and total carbon, nitrogen, and hydrogen. Water potential was measured with a ten chamber thermocouple psychrometer (Decagon DC-10) and soil C, N, and H (% mass) with an atomic absorption/thermal conductivity elemental analyzer (LECO CHN-1000). For relative site comparisons, total soil carbon was estimated by multiplying the percent carbon by A-horizon depth (centimeters). This approach was used as opposed to calculating absolute carbon mass based on soil bulk density since variations in soil texture and mineral content can bias estimates of total carbon.

Measurements of vegetation included habitat type, stand successional stage (based upon stand species and structural components according to Johnsen et al. 1993 and Oliver et al. 1994), tree basal area, tree species, a tree crown vigor classification (healthy, thinning, dead), height, diameter at 1.4 meters, crown length, total tree height, cross sectional crown width, and physical damage. Crown measurements were used to calculate relative crown volume (cubic meters crown space = $\{\text{mean crown diameter}/2\}^2 \{\pi\}\{\text{crown length}\}$) as an index of crown position in the canopy (dominant, codominant, suppressed, etc.) and as an estimate of photosynthetic area. In addition, the first two trees of each species (clockwise from north) per plot were increment cored twice at 90 ° angles to determine sapwood thickness, growth rate, and age. Finally, a macroplot stand health survey was conducted for pests, pathogens, and stand level mortality. This included intensively examining every tree on the microplot for insect pests, excavating around the tree bases to search for evidence of root diseases, and conducting a 100-meter radius survey from plot center for indications of root disease, such as windblown stems, exposed root systems, fungal fruiting bodies, crown thinning, crown defoliation, bark beetle attack, and percent stand mortality.

To estimate the water relations of trees, predawn water potentials of major species were measured weekly. This was done by shooting off tree branches with a 22 caliber rifle from the mid-crown area of trees during the first morning light in a plot measured the previous day. Water potentials were determined with a pressure-bomb (PMS instruments, Corvallis, OR). In addition, three permanent plots were established near Cascade, Idaho, each with a ponderosa pine, Douglas-fir, and grand fir present to compare seasonal variations among these species on a common site. These plots were measured in late spring, mid-summer, and early fall for soil water content and tree predawn water potentials.

Statistical analysis was performed using SigmaStat and SigmaPlot software (Jandel Scientific). One way analysis of variance, student's t-test, the Bonferroni-t procedure and regression analysis were used to test for significant differences ($\beta = 0.05$) between means and for correlations.

RESULTS

Stand Characteristics

Based upon the LANDSAT cover type map and our sampling across the Boise National Forest, Douglas-fir habitat types cover approximately 45% of the forest and are prevalent below 1800-meter elevations with subalpine fir sites comprising approximately 40% of the forest predominantly occurring at elevations greater than 1800 meters. True ponderosa pine habitat types were restricted to minor areas of the southern portion of the Boise National Forest and grand fir habitat types to the broad mid-elevation valleys on the western edge of the forest.

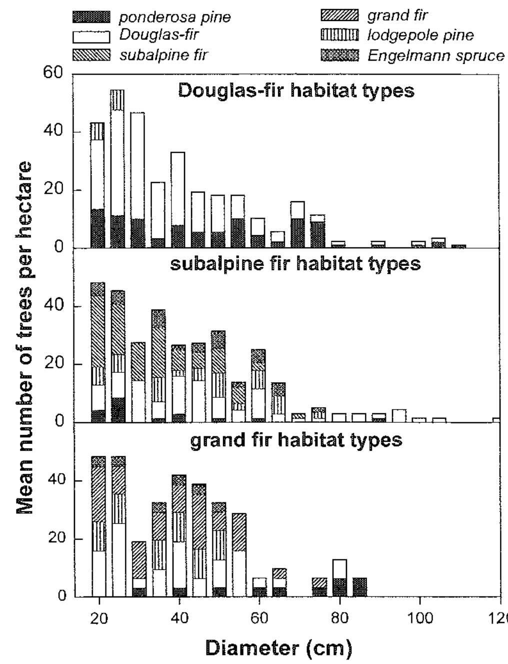

Fig. 1. Diameter distributions of tree species in the three major habitat type series in central Idaho.

Two predominant tree species, ponderosa pine and Douglas-fir, were found on all of the habitat type series sampled either as climax species on xeric sites or seral components on more mesic sites. Species diameter distributions in the three major habitat type series (Douglas-fir, subalpine fir, and grand fir) showed that ponderosa pine was a dominant old-growth seral component on Douglas-fir and grand fir sites (Figure 1). Douglas-fir was the old-growth seral component on subalpine fir sites and appears to be replacing ponderosa pine as the dominant seral species on grand fir sites. In all three series, the shade-tolerant climax species are more dominant in the small diameter classes and drought-tolerant seral species are dominant in the large diameter classes. The mean age threshold under which climax species became more abundant than seral species was 75 years. Ponderosa pine trees, on average, attained the highest mean age of all species measured. Trees reached ages in excess of 300 years on xeric habitat types and 200 years or less on more mesic sites. Douglas-fir trees also attained ages greater than 300 years on xeric habitat types but closer to 150 years on more mesic sites. Almost all of the larger diameter trees of these two species had basal fire scars. Although species longevity varied among habitat types, tree size (mean diameter and height) did not (Table 1).

Three of the four basic successional stand structures as outlined by Johnsen et al. (1993) and Oliver et al. (1994) for "stand development after partial disturbance" were commonly found. The "stand initiation stage" consisting of a parklike structure of mature seral trees with little understory regeneration was more commonly found on southern aspects. Open seral

Table 1. Mean values of characteristics of the four dominant tree species, ponderosa pine (pp), Douglas-fir (Df), subalpine fir (saf), and grand fir (gf). Data are presented for trees that are healthy or visually declining from pest and pathogen attack for each forest habitat type. Douglas-fir habitat types are separated into dry and mesic sites due to the broad ecological range of this species in central Idaho.

Species	Diameter at 4.5 m (cm)	Height (m)	Crown height (%)	Crown width (m)	n	Sapwood (% DBH)	Sapwood (rings/cm)	Age	n
				Douglas-fir habitat types					
pp—dry									
healthy	47.2	20.8	38	3.4	16	46	7.5	235	6
declining	73.4	30.1	46	3.7	1	no	data		
pp—mesic									
healthy	57.0	28.2	45	3.1	41	41	8.4	180	17
declining	39.0	22.5	52	1.8	22	40	10.7	130	7
Df—dry									
healthy	62.2	27.5	36	4.2	8	23	5.7	316	2
declining	no	data							
Df—mesic									
healthy	34.5	22.8	65	3.0	116	20	6.7	109	27
declining	32.0	19.6	49	1.8	48	9	24	133	3
				Subalpine fir habitat types					
pp									
healthy	38.1	21.3	44	2.0	12	41	10.2	223	5
declining	26.2	23.7	53	1.1	19				
Df									
healthy	43.4	20.3	30	3.3	41	17	7.1	130	12
declining	49.5	22.5	40	2.4	33	12	8.9	133	6
saf									
healthy	29.5	17.3	29	1.6	49	17	11.1	111	12
declining	34.3	21.1	36	1.3	24	8	12.4	159	4
				Grand fir habitat types					
pp									
healthy	62.5	32.3	53	2.4	10	44	2.7	174	3
declining	no	data							
Df									
healthy	44.2	25.0	44	2.9	20	20	7.4	149	7
declining	29.0	19.3	62	1.5	16	14	8.5	174	2
gf									
healthy	37.1	24.0	44	2.3	13	39	4.6	109	5
declining	35.8	21.1	52	2.2	20	18	8.3	123	3

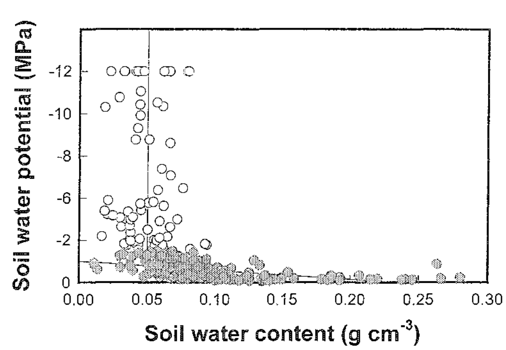

Fig. 2. Soil water release curve generated from 240 soil samples collected from June until October, 1994. Filled symbols indicate soils with water available for plant uptake. Two regression lines represent mean plant-available water content of the soil.

stands with a well-established pole-sized understory component of shade-tolerant species, (i.e., understory reinitiation), and stands that had a mixed overstory of seral and climax species, (i.e., old growth), were more commonly found on northern aspects. Plots with northern aspects also had higher basal areas with a mean (± standard error) of 42 ± 5 square meters per hectare than southern aspects that had a mean of 35 ± 4 square meters per hectare.

Analysis of soil water measurements showed significant variation in soil water availability among habitat types and stand basal areas. Soil water release curves indicate that the soils sampled have a mean plant-available water holding capacity of 0.15 grams per cubic centimeter (Figure 2) which is depleted at a water potential of approximately −1.5 megapascals. Using these values, measurements of A and C soil horizon water potentials on Douglas-fir habitat types indicated that mean soil water was depleted by the second week in August, subalpine fir habitat types by the

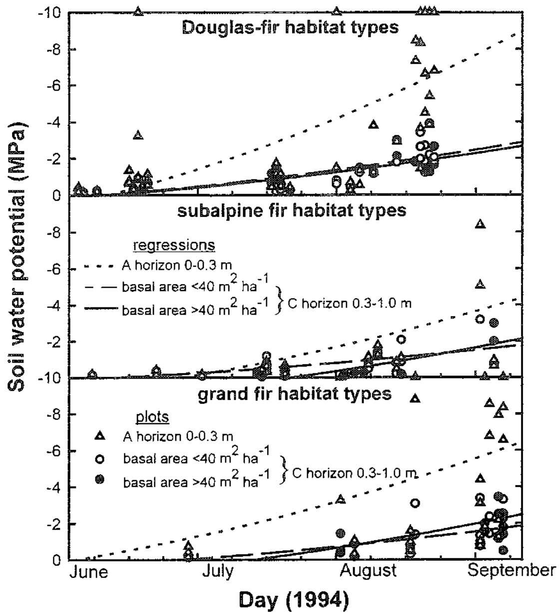

Fig. 3. Soil water potentials at two depths measured across three major habitat type series on the Boise National Forest, 1994. Significant regressions (r^2 = 0.75 for Douglas-fir sites, 0.91 for subalpine fir, and 0.72 for grand fir) were developed for deeper soils supporting basal areas greater than 40 square meters per hectare. Weaker regressions (r^2 = 0.57, 0.40, and 0.56 respectively) were developed for sites with basal areas less than 40 square meters per hectare.

last week in August, and grand fir habitat types by the first week in September (Figure 3). Mean depths of the A-horizon and C-horizon were 0.07 meters and 0.87 meters, respectively. Decreases in soil water potentials of A-horizons generally preceded C-horizon decreases by 1 to 2 weeks. Soils on subalpine fir and grand fir sites with basal areas greater than 40 square meters per hectare reached water potentials lower than −1.5 megapascals 1 to 4 weeks earlier in the summer than plots with lower basal areas. The variability of water potentials on Douglas-fir sites was too high for significant correlations with basal area.

Predawn water potentials measured from selected plot trees indicated a significant correlation between soil water potentials and tree water potentials (Figure 4). Douglas-fir trees reached the lowest water potentials during the summer. Ponderosa pine maintained significantly higher water potentials than Douglas-fir on similar sites. Grand fir and subalpine fir, which grow on the more mesic sites, showed a later seasonal depression in predawn water potential but a more rapid decrease to levels similar with Douglas-fir. A three dimensional model of soil water availability developed from all plots showed that soils in stands with basal areas near 80 square meters per hectare reached drought levels as much as 4 weeks earlier in the season than stands with basal areas near 40 square meters per hectare (Figure 5). Stands with basal areas less than 40 square meters per hectare had highly variable soil water potentials.

Soil carbon and nitrogen analysis also showed significant differences among habitat types and stand suc-

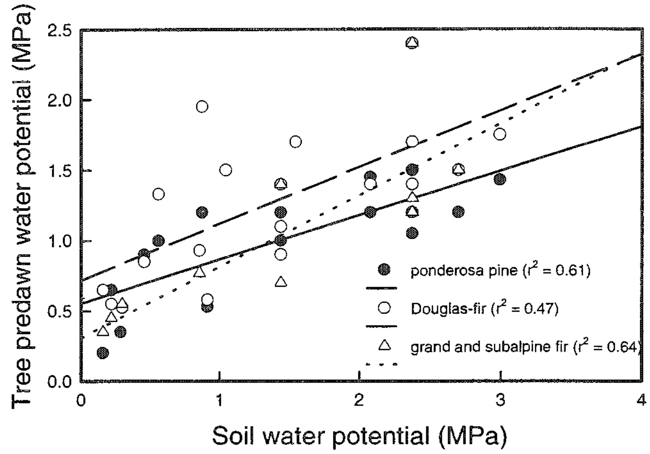

Fig. 4. Predawn water potentials measured for dominant tree species in central Idaho, 1994, plotted against the corresponding C-horizon water potentials.

cessional stages. The percent of total soil nitrogen and carbon was found to be higher in the A-horizon than the C-horizon by a factor of 10. Most C-horizon samples indicated carbon percentages (by weight) below 0.01 %. Total soil nitrogen content was significantly correlated with total soil carbon (Figure 6). This correlation allowed soil carbon content to be considered equivalent with total soil nitrogen content for this study. Comparisons between percent carbon and A-horizon depth showed no significant relationships. The correlations between soil carbon content and habitat type, stand mortality, species composition, elevation, aspect and slope were not significant. However, when plots were stratified by habitat type and stand structure, mean A-horizon carbon and nitrogen levels were significantly higher (β = 0.05) for mature climax (old-growth) stands than seral (stand initiation) stands in Douglas-fir habitat types and somewhat higher (β = 0.15) for mature climax stands than seral in subalpine fir and grand fir habitat types (Figure 7).

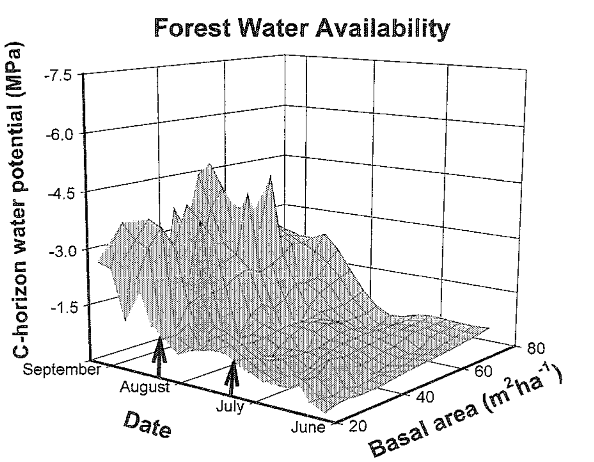

Fig. 5. Soil water potentials of the C-horizon plotted as a function of basal area and date for central Idaho, 1994. Vertical arrows (↑) indicate dates when soil water potentials became too low for plant use.

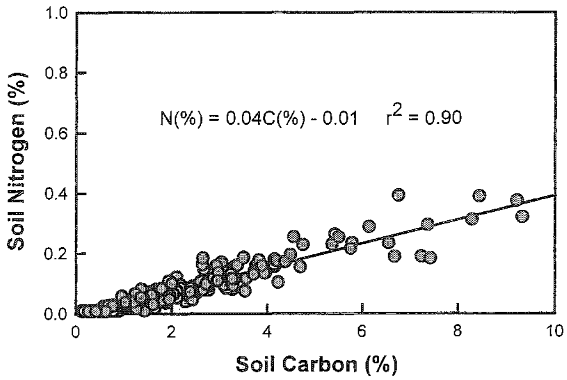

Fig. 6. Linear regression of total soil nitrogen as a function of total soil carbon for soils of central Idaho (n = 240).

Tree Growth

A mean of 34% of all trees sampled on the Boise National Forest exhibited symptoms of decline such as poor needle retention, root disease, stem decays and recent (less than 5 years) mortality (Table 2). This percentage varied among the habitat type series. Ponderosa pine/Douglas-fir sites had a mean of 28.5% trees affected, subalpine fir sites 35.4%, and grand fir sites 44.2%. In general, seral species experienced the highest mortality on south and west facing slopes on sites with higher than average (38 square meters per hectare) basal areas. Climax species mortality was greatest in mature stands of shade-tolerant species on north and east facing slopes. Individual trees with symptoms of decline or recent mortality had small crowns and less sapwood area than trees deemed healthy, regardless of diameter size (Table 1). Ponderosa pine trees experienced scattered mortality in either dense pole-sized, or very old senescent trees, and had the lowest total mortality compared to other tree species. Douglas-fir mortality was highest as a seral component on subalpine fir sites, particularly on south aspects where stand structures consisted of open grown >150-year-old trees with a subalpine fir understory. Often more than 60% of the trees in these stands were affected. On Douglas-fir and grand fir habitat types, however, Douglas-fir mortality was highest among suppressed and codominant trees in densely stocked stands. Grand fir and subalpine fir mortality consisted of dominant and codominant trees in mature climax stands. Regression analysis for grand fir sites showed a significant correlation between mortality and stand density (coefficient of determination = 0.83). Few disease-free grand fir and subalpine fir trees older than 150 years were found in climax "old-growth" stands. Mean maximum ages were 114 and 120 years, respectively.

Recent (less than 50 years) tree growth was measured from annual sapwood ring measurements, from which mean cross-sectional growth increments (square centimeters per year) were calculated. A significant relationship between crown volume and sapwood mean annual increment was found for each species (coefficient of determination = 0.76: ponderosa pine, 0.53: Douglas-fir, and 0.67: grand fir and subalpine fir, combined). To determine the effect of stand density on tree growth, mean annual increment, stratified by crown volume, was plotted against basal area (Figure 8). Measured ponderosa pine trees showed little correlation with increasing basal area, whereas Douglas-fir, grand fir, and subalpine fir trees showed decreased growth at basal areas above 60 square meters per hectare. Trees on sites with basal areas less than 30 square meters per hectare also showed decreased growth rates for all species. Mean annual increment stratified by crown volume was also plotted against total A-horizon carbon (Figure 9). As with basal area, increasing soil carbon (and nitrogen) showed no correlation with ponderosa pine growth. Douglas-fir growth also showed no significant correlation with soil carbon. Grand fir and subalpine fir showed an increasing growth rate with an increase in total soil carbon (and nitrogen) from 0 to 0.3 centimeters.

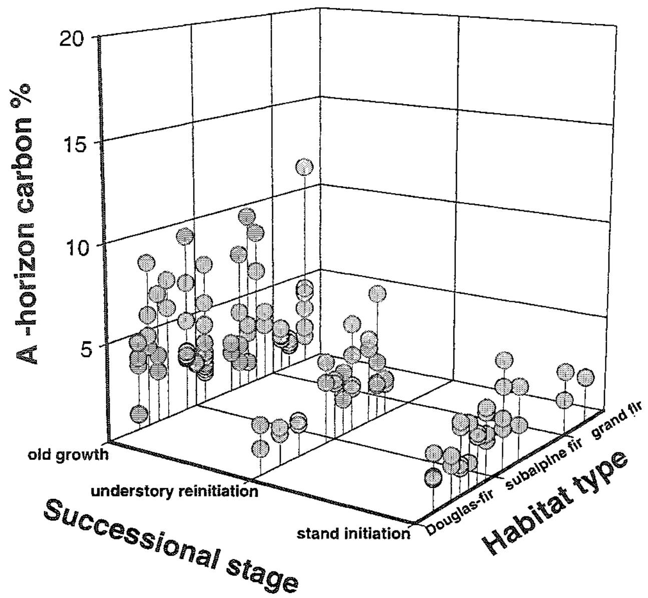

Fig. 7. Total carbon of the A-horizon plotted as a function of habitat types and stand successional stage. Habitat types within each series are ordered from dry to wet (left to right).

DISCUSSION

Our data support claims that forested stands which were composed of open grown shade- intolerant species

Table 2. The percentage of trees found to be either symptomatic of decline (%S) of dead (%D) within the last 5 years. Totals refer to the number of trees per habitat type (right column) or trees by species within each habitat series (bottom).

	Tree species							
	Ponderosa pine		Douglas-fir		Subalpine fir		Grand fir	
Habitat type	%D	%S	%D	%S	%D	%S	%D	%S
Douglas-fir	6	23	5	22	0	50		
Subalpine fir	0	33	15	29	8	25		
Grand fir	0	0	11	36	0	33	18	42
Total %	4	17	11	22	8	26	18	42
Sample size	121		283		77		33	

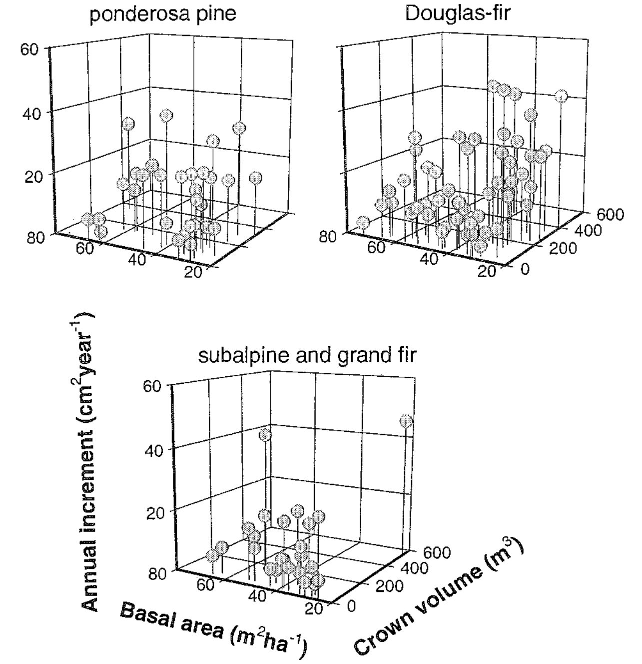

Fig. 8. Mean diameter growth of the sapwood for dominant tree species in central Idaho plotted as a function of crown volume and basal area. Basal area is used as an indicator of increasing competition for soil water. Crown volume can indicate tree canopy position (dominant, suppressed). Annual increment and crown volume are significantly correlated for each species (r2 = 0.76 for ponderosa pine. 0.53 for Douglas-fir, and 0.67 for pooled grand and subalpine firs).

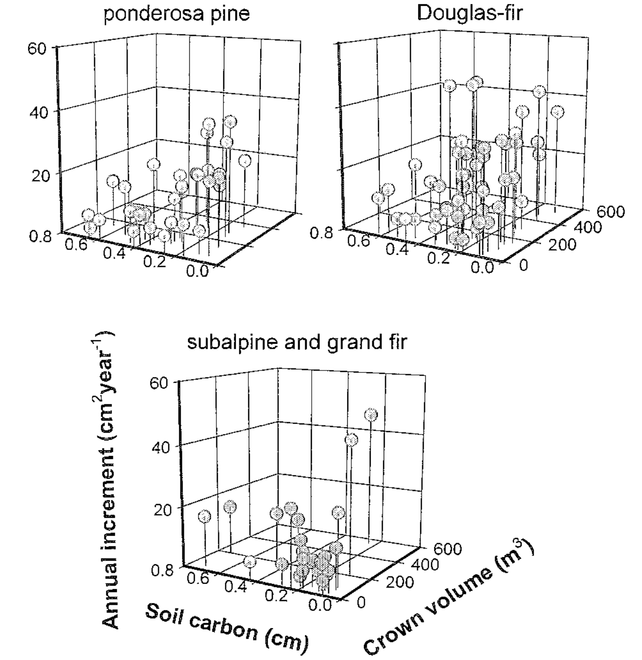

Fig. 9. Mean diameter growth of the sapwood for dominant tree species in central Idaho plotted as a function of crown volume and total soil carbon (which is equivalent to total soil nitrogen). Crown volume can indicate tree canopy position (dominant, suppressed). Annual increment and crown volume are significantly correlated for each species.

and maintained by frequent fire, are shifting in structure and composition to more dense stands of shade-tolerant species. However, differences in stand structure, composition, and successional status that were correlated with aspect and habitat type suggest that patterns and frequency of disturbance, such as fire, varied considerably across the landscape. Significant proportions of southern aspects may have experienced frequent ground fires which maintained large open-grown ponderosa pine and Douglas-fir stands. Northern aspects appear to convert much more rapidly to dense stands of climax species, which do not support frequent understory fires but rather stand-replacing fires.

Climax stands with high basal areas had higher occurrences of insect- and disease-related mortality than seral stands on similar habitat types. Pests and pathogens can act as thinning agents and may be a natural nutrient cycling process as important as fire (Harvey 1994, Castello et al. 1995), increasing nutrient and water availability to remaining trees (Matson and Boone 1984, Gale and Grigal 1987, Knight 1991, Knight et al. 1991, Riegel et al. 1992). Ponderosa pine, which showed the lowest drop in predawn water potentials during the summer, also showed the least incidence of pest and pathogen infection, which lends support to the theory from Mattson and Haack (1987) that drought predisposes trees to attack from insects and diseases. In addition, the apparent independence of ponderosa pine growth from soil nitrogen levels may indicate lower soil nutrient requirements, another characteristic attributed to increased resistance to pests and pathogens (Chapin et al. 1993).

Stands of shade-tolerant species with basal areas greater than 40 square meters per hectare were experiencing drought conditions, presumably from competition for water. A preliminary comparison between the effects of soil nitrogen and soil water on tree growth indicated that soil water depletion had a greater negative effect on tree growth than the positive effect realized from soil nitrogen. Schulze (1991) indicated that numerous studies have shown that any limitation in the availability of water affects almost all plant functions, including the roots ability to take in nutrients. Tree species appeared to have different sensitivities to competition for and location of soil water and soil nitrogen, however. The historically dominant tree species, ponderosa pine, showed the lowest growth correlation to either soil water depletion or increasing soil nitrogen. Grand fir, subalpine fir, and to a lesser extent Douglas-fir, on the other hand, showed correlations with both competition for soil water and increasing soil nitrogen.

It has been shown that soil water and soil nutrient fluxes may differentially affect growth and survival of plant species with dissimilar patterns of root development and resource acquisition (Parrish and Bazzaz 1976, Caldwell and Richards 1986, Gale and Grigal 1987, Franco and Nobel 1990, McLendon and Redente 1990). Ponderosa pine has been shown to extract significant amounts of water from parent rock strata (Zwieniecki and Newton 1994), indicating a deep root system that may allow trees to function with relative independence of soil resources. Douglas-fir and particularly grand fir and subalpine fir have been shown to develop shallower root systems that may increase the dependence of these species on surface soil resources (Jackson and Spomer 1979). During extended periods without precipitation, such as typically occurs in central Idaho during the summer, plants can rely exclusively on water stored in the soil (Little et al. 1995, Nepstad et al.1994, Zwieniecki and Newton 1994, Phillips and Ehleringer 1995). Our measurements from central Idaho indicate that shallow soils with poor water holding capacity provide a limited sink, however.

Significant carbon accumulation (and total nitrogen) with advanced successional stage on Douglas-fir sites, and to a lesser extent on subalpine fir and grand fir sites, may reflect the influence of stand structure and composition on carbon and nitrogen cycling. Decomposition rates have been correlated with nutrient balances of litter (Black and Harden 1995, Johansson 1994, Ladd et al. 1994) and stand structural attributes which affect light, temperature, and moisture regimes of the forest floor (Carlyle 1995, Morrison et al. 1994, Knight et al. 1991, Toda and Haibara 1994, Tyrell and Crow 1994). The development of climax stands may, therefore, enhance the long-term soil nutrient status, as indicated by increased soil carbon (Entry and Emmingham 1995).

Fire, which historically has had a significant role in shaping central Idaho forest ecosystems, may be important for perpetuating seral species and reducing stand densities, climax species establishment, and litter accumulations. It has been suggested that fire exclusion in forests of central Idaho has allowed stands to reach densities that are above the water and nutrient carrying capacities of most sites (Sampson et al. 1994). The inclusion of fire as a natural process may require a redefinition of climax plant communities for areas of central Idaho. Alternatively, the absence of fire in historically fire-shaped ecosystems may enhance equally important biotic communities that rely on insects and fungal organisms as a mechanism of disturbance.

ACKNOWLEDGMENTS

We thank Alan E. Harvey, USDA Forest Service Intermountain Research Station, Moscow, Idaho and Robert D. Pfister, School of Forestry, University of Montana, Missoula, Montana for reviewing this paper. We also would like to thank Karin Dial for laboratory help and soil analysis, Duane Andrews for technical assistance, and the staff at the USDA Forest Service Intermountain Research Station, Moscow for their support. Funding was provided by the Boise National Forest and Boise Cascade Corporation.

LITERATURE CITED

Agee, J.K. 1990. The historical role of fire in Pacific Northwest forests. Pages 25–38 *in* J.D. Walstad, S.R. Radosevich, and D.V. Sandberg (eds.). Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis.

Arno, S.F, J.H. Scott, and M.G. Hartwell. 1995. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. Research Paper INT-RP-481, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Arno, S.F, H.Y. Smith, and M.A. Krebs. 1997. Old growth ponderosa pine and western larch stand structures: influences of pre-1900 fires and fire exclusion. Research Paper INT-RP-495, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Black, T.A., and J.W. Harden. 1995. The effect of timber harvest on soil carbon storage at Blodgett Experimental Forest, California. Canadian Journal of Forest Research 25:1385–1395.

Botkin, D.B. 1993. Forest dynamics, an ecological model. Oxford University Press, New York.

Caldwell, M.M., and J.H. Richards. 1986. Competing root systems: morphology and models of absorption. Pages 251–273 *in* T.J. Givnish (ed.). On the economy of plant form and function. Cambridge University Press, New York.

Carlyle, J.C. 1995. Nutrient management in a *Pinus radiata* plantation after thinning: the effect of thinning and residues on nutrient distribution, mineral nitrogen fluxes, and extractable phosporus. Canadian Journal of Forest Research 25:1278–1291.

Castello, J.D., D.J. Leopold, and P.J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45:16–24.

Chapin, F.S., III, K. Autumn, and F. Pugmaire. 1993. Evolution of suites of traits in response to environmental stress. American Naturalist 142:S78-S92.

Daubenmire, R.F. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecological Monographs 22:301–330.

Daubenmire, R.F. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology 49: 431–438.

Entry, J.A., and W.H. Emmingham. 1995. Influence of forest age on nutrient availability and storage in coniferous soils of the Oregon Coast Range. Canadian Journal of Forest Research 25:114–120.

Franco, A.C., and P.S. Nobel. 1990. Influences of root distribution and growth on predicted water uptake and interspecific competition. Oecologia 82:151–157.

Gale, M.R., and D.F. Grigal. 1987. Vertical root distributions of northern tree species in relation to successional status. Canadian Journal of Forest Research 17:829–834.

Habeck, J.R. 1988. Old-growth forests in the Northern Rocky Mountains. Natural Areas Journal 8:202–211.

Habeck, J.R. 1994. Using general land office records to assess forest succession in ponderosa pine/Douglas-fir forests in western Montana. Northwest Science 68:69–78.

Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69: 1703–1715.

Harvey, A.E. 1994. Integrated roles for insects, diseases and decomposers in fire dominated forests of the Inland Western United States: past, present and future forest health. Journal of Sustainable Forestry 2:211–220.

Hironaka M., M.A. Fosberg, and K.E. Neimann, Jr. 1991. The relationship between soils and vegetation. Pages 29–31 *in* A.E. Harvey and L.F. Neuenschwander (eds.). Proceedings-management and productivity of western-montane forest soils. General Technical Report INT-280, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Jackson, P.A., and G.C. Spomer. 1979. Biophysical adaptations of four western conifers to habitat water conditions. Botanical Gazette 140:428–432.

Johansson, M.B. 1994. Decomposition rates of scots pine needle litter related to site properties, litter quality, and climate. Canadian Journal of Forest Research 24:1771–1781.

Johnsen, C.G., R.R. Clausnitzer, P.J. Mehringer, and C.D. Oliver.

1993. Biotic and abiotic processes of eastside ecosystems: the effects of management on plant and community ecology, and on stand and landscape vegetation dynamics. Pages 36–100 *in* P.F. Hessburg (ed.). Eastside forest ecosystem health assessment. Volume III. Assessment. U.S. Department of Agriculture, Forest Service, National Forest System, Forest Service Research, Wenatchee, WA.

Knight, D.H., J.B. Yavitt, and G.D. Joyce. 1991. Water and nitrogen outflow from a lodgepole pine forest after two levels of tree mortality. Forest Ecology and Management 46:215–225.

Knight, D.H. 1991. Pine forests: a comparative overview of ecosystem structure and function. Pages 121–135 *in* N. Nakagoshi and F.B. Golley (eds.). Coniferous forest ecology from an international perspective. SPB Academic Publishing, The Hague, Netherlands.

Kramer, P.J., and T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Ladd, J.N., M. Amato, Z. Li-Kai, and J.E. Schultz. 1994. Differential effects of rotation, plant residue and nitrogen fertilizer on microbial biomass and organic matter in an Australian Alfisol. Soil Biology and Biochemistry 26:821–831.

Little, R.L., D.L. Peterson, D.G. Silsbee, L.J. Shainsky, and L.F. Bednar. 1995. Radial growth patterns and the effects of climate on second-growth Douglas-fir (*Pseudotsuga menziesii*) in the Siskiyou Mountains, Oregon. Canadian Journal of Forest Research 25:724–735.

Losensky, B.J. 1995. Historical vegetation types of the Interior Columbia River Basin. Contract Report RJVA-94951. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Matson, P.A., and R.D. Boone. 1984. Natural disturbance and nitrogen mineralization: wave-form dieback of mountain hemlock in the Oregon Cascades. Ecology 65:1511–1521.

Mattson, W.J., and R.A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. BioScience 37:110–118.

McLendon, T., and E.F. Redente. 1990. Succession patterns following soil disturbance in a sagebrush steppe community. Oecologia 85:293–300.

Morrison, I. K., N.W. Foster, and P.W. Hazlett. 1994. Carbon reserves, carbon cycling, and harvesting effects on three mature forest types in Canada. New Zealand Forestry Science 23:403–412.

Nepstad, D.C., C.R. De Carvalho, E.A. Davidson, P.H. Jipp, and P.A. Lefebvre. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372:666–669.

Noe, H.R. 1991. Soil survey of Elmore county area, Idaho, parts of Elmore, Owyhee, and Ada counties. U.S. Department of Agriculture, Soil Conservation Service, Moscow, ID.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164:262–270.

Oliver, C.D., D.E. Ferguson, A.E. Harvey, H.S. Malany, J.H. Mandzak, and R.W. Mutch. 1994. Managing ecosystems for forest health: an approach and the effects on uses and values. Journal of Sustainable Forestry 2:113–133.

Parrish, J.A.D., and F.A. Bazzaz. 1976. Underground niche separation in successional plants. Ecology 57:1281–1288.

Pfister, R.D., B.L. Kovalchik, S.F. Arno, and R.C. Presby 1977. Forest habitat types of Montana. General Technical Report INT-34, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Pfister, R.D., and S.F. Arno. 1980. Classifying forest habitat types based on potential climax vegetation. Forest Science 26:52–70.

Phillips, S. L., and J. R. Ehleringer. 1995. Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt.). Trees:Structure and Function 9:214–219.

Rasmussen, L.M. 1981. Soil survey of valley area, Idaho, parts of Adams and Valley counties. U.S. Department of Agriculture, Soil Conservation Service, Moscow, ID.

Riegel, G.M., R.F. Miller, and W.C. Krueger. 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. Ecological Applications 2:71:85.

Sampson, R.N., D.L. Adams, S. Hamilton, S.P. Mealey, R. Steele, and D. Van DeGreeff. 1994. Assessing forest ecosystem health in the inland West. American Forests 100: 13–16.

Schulze, E.D. 1991. Water and nutrient interactions with plant water stress. Pages 90–101 *in* H.A. Mooney, W.E. Winner, and E.J. Pell (eds.). Response of plants to multiple stress. Academic Press, Inc. New York.

Smith, T., and M. Huston. 1989. A theory of spatial and temporal dynamics of plant communities. Vegetatio 83:49–69.

Steele, R., and R.D. Pfister. 1991. Western-montane plant communities and forest ecosystem perspectives. Pages 20–28 *in* A.E. Harvey and L.F. Neuenschwander (eds.). Proceedings-management and productivity of western-montane forest soils. General Technical Report INT-280, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Steele, R., R.D. Pfister, R.A. Ryker, and J.A. Kittams. 1981. Forest habitat types of central Idaho. General Technical Report INT-114, U.S. Department of Agriculture, Forest Service, Intermountain Forest Research Station, Ogden, UT.

Toda, H., and K. Haibara. 1994. Kinetics of mineralization of nitrogen in forest soil (I.) Characteristics of soil nitrogen mineralization of different aged stands, slope positions, and soil depths. Journal of the Japanese Forestry Society 76: 144–151.

Tyrell, L.E., and T. R. Crow. 1994. Dynamics of dead wood in old-growth hemlock-hardwood forests of northern Wisconsin and northern Michigan. Canadian Journal of Forest Research 24:1672–1683.

Wright, H.A., and A.W. Bailey. 1982. Fire ecology, United States and Canada. John Wiley and Sons, New York.

Zwieniecki, M.A., and M. Newton. 1994. Root distribution of 12-year-old forests at rocky sites in southwestern Oregon: effects of rock physical properties. Canadian Journal of Forest Research 24:1791–1796.