

Forest Colonization of Puget Lowland Grasslands at Fort Lewis, Washington

Abstract

As a result of fire exclusion since the mid-19th century, Douglas-fir has been invading the grasslands of the southern Puget Lowland, Washington, converting them to colonization forests. We studied a chronosequence of these forests, including some that received periodic commercial thinnings, at Fort Lewis Military Reservation to elucidate successional patterns and changes in ecosystem properties associated with tree invasion. In unmanaged colonization forests (ages 27-120 yr), overstory cover and tree density remained constant after 27 yr, while basal area increased. Shrub cover increased with age and, after an initial decrease compared to grasslands, ground cover also increased. Shrub species richness increased over time, while ground-layer richness was much less than in grasslands, and there was a rapid shift from grassland to forest floras. Dead wood (snags and logs) accumulated gradually. The only change in soil properties was lower A-horizon nitrogen. In managed colonization forests (ages 55-91 yr), tree density, overstory cover, and total log length decreased over time, but shrub cover and A-horizon cation-exchange capacity, carbon, and nitrogen increased over time. Although structural and floristic conversion of grassland to forest requires < 30 yr, soil changes are much more gradual, such that the soils underlying colonization forests up to 400 yr old are still classified as grassland soils. Higher tree densities in colonization forests compared to the pre-settlement forests of Fort Lewis mean an increased risk of crown fires during droughts. Even with active management, colonization forests will require many decades to provide northern spotted owl habitat because they lack shade-tolerant conifers and large live trees, snags, and logs.

Introduction

Grassland ecosystems in many regions of the world were once maintained by natural or anthropogenic fire in climates that could support forests or woodlands. However, during the 20th century, human influences have caused drastic reductions in grassland fire frequency. As a result of fire exclusion, trees and shrubs are invading many grasslands (Archer 2003), producing multiple changes in ecosystem properties. Changes in vegetation include dominance by woody as opposed to herbaceous species (Archer 1995, Arabas 2000, Miller and Tausch 2001, Briggs et al. 2002), decreased herbaceous species diversity (Archer 1995, Miller and Tausch 2001), and reduced grass, forb, and sometimes shrub biomass (Bailey and Wroe 1974, Archer 1995, Miller and Tausch 2001, Briggs et al. 2002). Dead wood accumulates also, particularly once woody plant mortality commences. Changes in soils include greater O-horizon and mineral soil depth (Barton and Wallenstein 1997), lower soil pH (Barton and Wallenstein 1997), and

either higher or lower soil carbon, nitrogen, and other nutrients (Archer 1995, Miller and Wigand 1994, Barton and Wallenstein 1997, Gill and Burke 1999). These soil changes suggest the potential for altered site productivity, though no study has specifically examined this possibility. Nor is it clear how long it might take for soil properties to change enough for grassland soils to be reclassified as woodland or forest soils.

Woody plant invasion of grasslands is usually a patchy process (Grimm 1983, Archer et al. 1988, Knight et al. 1994, Barton and Wallenstein 1997), so the resulting changes in vegetation and soil properties can be spatially complex (Miller and Wigand 1994, Archer 1995, Barton and Wallenstein 1997). In addition, alterations in the distribution and amount of live and dead fuels associated with invasion affect wildfire risk (Miller and Tausch 2001, Peterson and Hammer 2001).

Tree invasion of grasslands is ongoing in the southern Puget Lowland and the San Juan Islands of western Washington. An estimated 60,500 ha of grasslands existed in the southern Puget Lowland prior to settlement by European-Americans (Crawford and Hall 1997), and substantial portions of the San Juan Islands were also grassland then (Peterson and Hammer 2001). Fossil pollen records indicate that these grasslands developed during a

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period of warmer, drier climate 7,000 to 10,000 yr ago (Hibbert 1979, Whitlock 1992). As the climate became cooler and wetter, the grasslands persisted because of periodic fires set by Native Americans to perpetuate important food plants, such as camas (*Camassia quamash*) (Perdue 1997). Following settlement in the mid-19th century, grassland fires largely ceased, and Douglas-fir (*Pseudotsuga menziesii*) began invading the grasslands, a process that continues today (Kruckeberg 1991). The early stages of invasion occur in a patchy fashion, with founder trees serving as nuclei for clumps of trees that gradually expand and coalesce to form colonization forests (Giles 1970). The result, as Peterson and Hammer (2001) observed on Orcas Island, Washington, is mosaics of unevenaged colonization forest and remnant prairie patches. Compared to adjacent areas that have been forested for much of the Holocene, colonization forests have few shade-tolerant conifers, possess less-well-developed shrub layers, and lack legacy (large live trees, snags, and logs left over from previous forests occupying the same sites) (Ahrens 1998a, 1998b).

Fort Lewis Military Reservation, a U.S. Army installation located between Tacoma and Olympia, is a good site to study colonization forests, for several reasons. First, forest invasion of prairies is well documented there. Large areas of present-day conifer forest at Fort Lewis are mapped by NRCS soil surveys as growing on grassland soils (Anderson et al. 1955, Pringle 1990). In addition, a comparison of current Fort Lewis vegetation with vegetation recorded by mid-19th century land surveys indicates that 6,600 ha of former prairie are now occupied by conifer forest (Public Forestry Foundation 1996). A second reason is that the installation possesses most of the extant grasslands and colonization forests in the southern Puget Lowland. Elsewhere in the region, grasslands and colonization forests have been heavily fragmented by agriculture and urban development. A third reason is that the majority of Fort Lewis' colonization forests are subject to a consistent regime of silvicultural manipulation, primarily light thinnings (15-20% of basal area removed) at roughly 10-yr intervals, but some have received no timber harvest. Thus, Fort Lewis offers the opportunity to assess the influence of active forest management on the timing and duration of ecosystem changes during tree invasion. For example, does periodic logging differentially affect dead wood accumulation or soil properties in

managed vs. unmanaged colonization forests? A final reason is that Fort Lewis' forests are critical habitat for the northern spotted owl (*Strix occidentalis caurina*) and must be managed in a manner that will hasten the development of late-successional stand structures (e.g., multiple canopy levels and large trees, snags, and logs) that benefit the owl (Public Forestry Foundation 1996). What contribution, if any, can colonization forests make to owl habitat?

The purpose of this study was to describe successional patterns and associated changes in ecosystem properties that have occurred as a result of Douglas-fir invasion of Puget Lowland grasslands following fire exclusion. Specifically, we examined temporal changes in tree size and density, vegetation layering, species diversity, dead wood and litter accumulation, and soil chemical and physical properties. We compared these changes between forests that had received commercial timber harvest and forests that had not been harvested, and we considered the consequences of these changes for forest management, including timber harvest, spotted owl habitat, wildfire risk, and site productivity.

Methods

Chronosequence Approach

Historical records are sketchy, and the oldest aerial photos of Fort Lewis were taken in 1942. Therefore, our primary tool to assess changes over time during tree invasion was to examine vegetation structure and soil characteristics in a chronosequence of sites ranging from open grasslands to 130-yr-old colonization forests. Such space-for-time substitution assumes that the same ecological processes are at work in the past as in the present. Specifically, we assumed that during the past 130 yr, (1) the structure and composition of grassland vegetation at the start of colonization have remained the same, and (2) the direction and magnitude of ecosystem changes during tree invasion have remained the same, regardless of when invasion began.

Available evidence suggests that neither of these assumptions is correct. The starting point of tree invasion has changed in recent years from grasslands dominated by the native perennial bunchgrass, Roemer's fescue (*Festuca roemerii*), to grasslands infested with exotic species, such as the leguminous shrub, Scot's broom (*Cytisus*

scoparius), and sod-forming grasses, especially colonial bentgrass (*Agrostis tenuis*). Scot's broom forms dense, monospecific shrubfields, slowing or preventing forest invasion by shading conifer seedlings. Sod-forming grasses outcompete and eventually exclude Roemer's fescue.

The processes potentially affecting tree invasion have also changed over time. Most of Fort Lewis' grasslands were grazed from the mid-19th century until 1975. In addition, military training has varied in type and intensity since Fort Lewis was established in 1917. For example, tracked-vehicle training on grasslands increased substantially between 1995 and 2001, compared to previous years. The long-term effect of this type of training is a shift in grassland plant species composition toward more dominance by exotics (U.S. Army Corps of Engineers 1994). In addition, in high-use military areas, such as bivouac sites, much of the shrub and ground cover is eliminated and tree establishment is inhibited.

The likely consequence of violations of our two assumptions is an increase in within- and between-site variance of colonization forest structure, making statistical detection of temporal change more difficult.

Study Sites and Sample Plots

We used soil and forest data layers from the Fort Lewis geographic information systems (GIS) lab to compile a map of colonization forests on the installation. The soil layer was derived from detailed soil surveys (Andersen et al. 1955, Pringle 1990), which list the Spanaway, Fitch, and Nisqually series as having formed with grassland vegetation. These soils are gravelly sandy loams with organic matter-rich A horizons, 30-40 cm thick. The forest layer classified stands into age classes (10-yr intervals), which we considered to be rough estimates. Any forests occurring on grassland soils were considered to be colonization forests. Using the forest GIS layer and timber-sale records from the Fort Lewis Forestry Program, we categorized colonization forests according to age class and management status (i.e., managed for timber harvest vs. unmanaged).

There was an insufficient number of stands ($n < 3$) in most of the unmanaged age classes to use stands as statistical replicates. Instead, individual plots, randomly located across the total mapped area of each age class, served as replicates for both unmanaged and managed forests.

This experimental design permitted inferences to be made about individual age classes, but not individual stands, of colonization forest at Fort Lewis.

Managed forests < 50 yr of age do not exist at Fort Lewis because they contain too few commercial-sized trees to justify timber harvest, so that the youngest managed age class in this study was 51-60 yr. Also, for logistical reasons, we chose to sample from only four out of the six available age classes of unmanaged forests.

Sample size was 10 plots in each age class/management status combination ≥ 50 yr of age (except $n = 8$ in 71- to 80-yr-old, managed forests). Since our field observations indicated young colonization forests have greater spatial variability in stand structure than do older colonization forests, we increased sample sizes in age classes < 50 yr old (Table 1). We randomly allocated additional plots, representing year zero of colonization, across the GIS-mapped grasslands at Fort Lewis.

Each sample plot consisted of two nested, circular plots of 1000 m² (17.84-m radius) and 500 m² (12.62-m radius) area. Four 100 m² (5.64-m radius) plots were equally spaced around the edge of the 1000 m² plot, and a fifth 100 m² plot was located at the center of the 1000 m² plot. A 20 m² plot and a 2 m² plot were nested within each

TABLE 1. Available area on Fort Lewis, number of replicate plots, and plot ages (mean \pm 1 SE) for unmanaged and managed forest age classes. Age 0 yr represents grassland plots.

| Age Class (yr) | Area (ha) | No. Plots | Plot Age (yr) |
|-------------------|-----------|-----------------|---------------|
| Unmanaged Forests | | | |
| 0 | ~6,500 | 10 | 0 |
| 11-20 | 85 | 25 ¹ | 27 \pm 2 |
| 21-30 | 199 | 20 ² | 32 \pm 1 |
| 31-40 | 58 | 15 | 47 \pm 5 |
| 51-60 | 56 | 10 | 56 \pm 5 |
| 71-80 | 131 | 10 | 63 \pm 5 |
| 101-110 | 42 | 10 | 92 \pm 4 |
| 121-130 | >40 | 10 | 120 \pm 5 |
| Managed Forests | | | |
| 51-60 | 475 | 10 | 55 \pm 2 |
| 71-80 | 1,688 | 8 | 66 \pm 5 |
| 91-100 | 510 | 10 | 72 \pm 5 |
| 111-120 | 43 | 10 | 91 \pm 7 |

¹n = 24 for age. ²n = 19 for age.

100 m² plot. Values for all variables measured on the 2, 20, and 100 m² plots were averaged to yield a single value for the entire sample plot.

Vegetation Measurements

Overstory age for each plot was determined by coring the nearest dominant or co-dominant tree to the plot center. We cored the tree at dbh (diameter at breast height; 1.37 m above ground) using an increment borer. Age at dbh was estimated by counting tree rings.

For all overstory trees with dbh \geq 15 cm in each 1000 m² plot, we recorded species, dbh, and crown ratio (visual estimate of live crown as percent of total height). Total height was measured directly with a Spiegel Relaskop on 50-75% of the trees per plot. The heights of the rest of the trees were then estimated by visual reference to the trees with known heights. Crown depth was calculated as (live crown ratio \times tree height / 100). Trees forked below dbh were measured as two individual trees.

Percent cover was estimated visually for the overstory and shrub (maximum plant height \geq 0.2 m) layers on the 1000 m² and 500m² plots, and for the ground layer (maximum plant height $<$ 0.2 m) on each 20 m² plot. Plant nomenclature follows Hitchcock and Cronquist (1973).

Presence of all shrub and ground-layer species was recorded in each 20 m² plot, except for grasslands (age zero). We used these data to estimate shrub and ground-layer species richness. For grasslands, we calculated species richness from ground-layer species tallies made in the same year as our study along 100-m-long line transects ($n = 84$) randomly placed in five different Fort Lewis grasslands (Angela Lombardi, Fort Lewis Integrated Training Area Management Program, personal communication). We assumed that the species composition along these transects was similar to that in the 10 plots established in our study.

Dead Wood Measurements

Within each 1000 m² plot, we tallied all snags with dbh \geq 15 cm and height \geq 1 m, and measured the length of all logs with a small-end diameter \geq 10 cm and length \geq 1 m. Branches $<$ 5 cm diameter at the small end, plus twigs, needles, and cones (collectively referred to as litter) on the surface of the forest floor were collected from each 2 m² plot, oven-dried at 30°C for \geq 5 d, and weighed. Litter biomass (g/m²) was calculated by dividing litter dry mass by the area of the plot.

Soil Measurements

We placed a 1 x 1 m frame at each 1000 m² plot center and secured it with metal stakes. The O horizon (forest floor) within the frame was removed and weighed in the field. The sample was mixed and a 20-g subsample weighed, oven-dried at 30° C for \geq 5 d, and reweighed. We calculated biomass (g/m²) of the O horizon as (total sample fresh weight \times [subsample dry weight / subsample fresh weight]).

The A horizon was sampled by excavating a hole with dimensions 30 x 30 x 25 cm depth, centered within the frame. The soil was sieved to remove the coarse fraction (\geq 2 mm), weighed, and a 200-g subsample of the fine fraction ($<$ 2mm) was oven-dried at 30° C for \geq 5 d.

We placed the dried subsamples of the O and A horizons in ziploc bags and sent them to the Analytical Sciences Laboratory at the University of Idaho. There, total nitrogen of the O horizon and total nitrogen and carbon of the A horizon were measured with a Leco high-temperature combustion analyzer; the results are expressed as percent dry mass of the fine fraction. A-horizon pH was measured in a saturated paste and A-horizon cation-exchange capacity (CEC) was determined with the ammonium acetate test (Page et al. 1982).

Statistical Analysis

We analyzed the data with one-way analysis of variance (ANOVA), separately for managed and unmanaged forests, to ascertain differences between age-class means for each variable. The level of significance was 0.05. If an ANOVA was significant, we compared age-class means with the Bonferonni procedure (Day and Quinn 1989). We also compared means of managed and unmanaged forests of similar age using *t*-tests, with a significance level of 0.05. Prior to statistical analysis, we transformed data sets that did not meet the assumptions of normality and homoscedasticity. All analyses utilized SigmaStat 2.0 software (Fox et al. 1995).

Results

Plot Ages

Mean plot ages within each forest age class were highly variable and did not always correspond closely to ages indicated on the GIS age-class map (Table 1). Three pairs of unmanaged/managed age

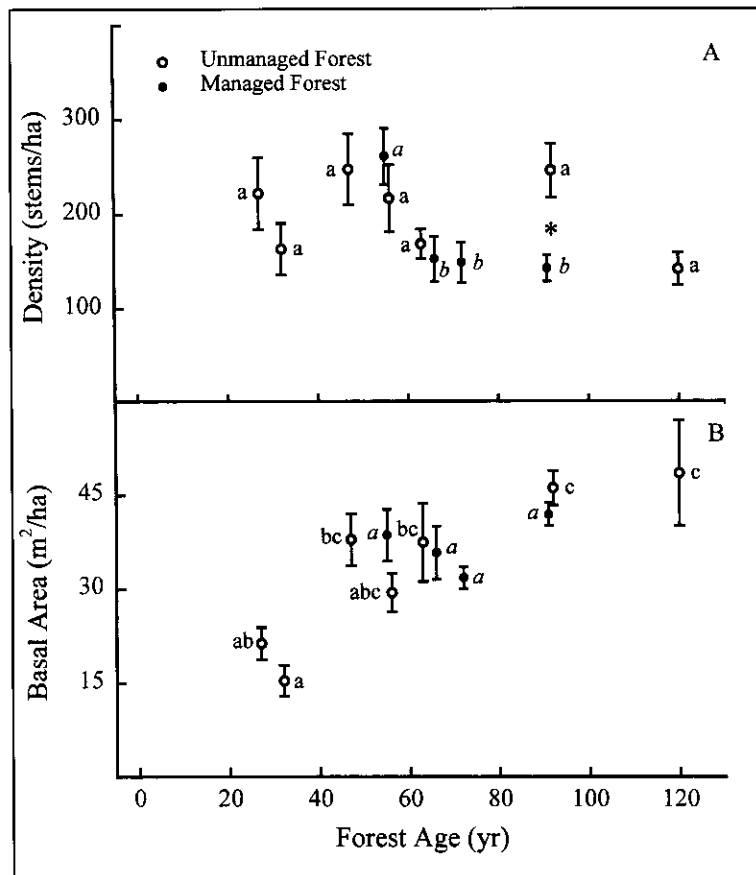


Figure 1. Overstory tree density (A) and basal area (B) in unmanaged and managed forests. Data are means (± 1 SE). Within unmanaged and managed forests, means with the same lowercase letter (normal font for unmanaged forests, italic font for managed forests) are not significantly different. Asterisks indicate when the means of unmanaged and managed forests of similar age are significantly different.

classes (56 vs. 55, 63 vs. 66, and 92 vs. 91 yr) had mean plot ages that did not differ significantly; these were used for comparing unmanaged and managed forests of similar ages.

Vegetation

Virtually all overstory trees were Douglas-fir. Overstory tree density showed no trend over time in unmanaged forests (Figure 1A). In contrast, tree density decreased by 40 stems/ha between 56 and 63 yr in managed forests ($P < 0.01$), and was lower at 92 yr in managed than in unmanaged forests of similar age ($P < 0.01$) (Figure 1A). Overstory basal area increased over time in unmanaged forests ($P < 0.001$), more than doubling between 27-32 yr and 120 yr. There was no

trend in basal area of managed forests, and it did not differ significantly from that of unmanaged forests at any age (Figure 1B). Mean crown depth did not change significantly with age in unmanaged or managed forests, but was 25% lower in 91-yr-old unmanaged forests than in managed forests of similar age ($P < 0.01$) (Table 2).

Overstory cover in unmanaged forests increased gradually between 27-32 yr and 92 yr ($P < 0.001$) (Figure 2A). In managed forests, overstory cover remained constant over time, and was lower than in unmanaged forests at 91 yr ($P < 0.001$) (Figure 2A). Shrub cover in unmanaged forests increased steadily from 3% in grasslands to 45% at 120 yr ($P < 0.001$) (Figure 2B). In contrast, there was no trend in shrub cover in managed forests,

TABLE 2. Mean (± 1 SE) of several vegetation, dead wood, and soil attributes in unmanaged and managed forests. Within columns, means with the same letter superscript are not significantly different. Asterisks indicate significantly different means for unmanaged and managed forests of similar age. Age 0 yr represents grassland plots.

| Forest Age (yr) | Crown Depth (m) | Biomass | | A-Horizon pH (units) | O-Horizon Nitrogen (%) |
|-------------------|-------------------------------|----------------------------|--------------------------------|--------------------------------|--------------------------------|
| | | Litter (g/m ²) | O-Horizon (kg/m ²) | | |
| Unmanaged Forests | | | | | |
| 0 | n/a | 1 \pm 0 ^a | 1.05 \pm 0.12 ^a | 5.44 \pm 0.04 ^a | 1.19 \pm 0.05 ^a |
| 27 | 11.5 \pm 0.8 ^a | 21 \pm 5 ^{abc} | 1.03 \pm 0.27 ^a | 5.40 \pm 0.04 ^a | 1.15 \pm 0.05 ^a |
| 32 | 12.9 \pm 0.8 ^a | 28 \pm 14 ^{bc} | 1.11 \pm 0.13 ^a | 5.22 \pm 0.04 ^{ab} | 1.33 \pm 0.06 ^a |
| 47 | 12.2 \pm 0.7 ^a | 33 \pm 8 ^{bc} | 1.09 \pm 0.14 ^a | 5.33 \pm 0.03 ^{ab} | 1.18 \pm 0.06 ^a |
| 56 | 14.8 \pm 2.8 ^c | 33 \pm 8 ^{bc} | 0.59 \pm 0.07 ^a | 5.26 \pm 0.05 ^{ab} | 1.32 \pm 0.07 ^a |
| 63 | 13.7 \pm 1.2 ^a | 20 \pm 5 ^{ab} | 1.07 \pm 0.20 ^a | 5.18 \pm 0.06 ^{ab*} | 1.39 \pm 0.05 ^{ab*} |
| 92 | 10.5 \pm 0.6 ^{ab*} | 49 \pm 13 ^{bc} | 0.87 \pm 0.29 ^a | 5.34 \pm 0.09 ^{ab} | 1.27 \pm 0.07 ^a |
| 120 | 13.7 \pm 1.5 ^a | 37 \pm 8 ^{bc} | 0.89 \pm 0.21 ^a | 0.29 \pm 0.08 ^{ab} | 1.06 \pm 0.15 ^a |
| Managed Forests | | | | | |
| 55 | 12.7 \pm 1.4 ^a | 31 \pm 5 ^a | 1.02 \pm 0.23 ^a | 5.24 \pm 0.09 ^a | 1.23 \pm 0.16 ^a |
| 66 | 15.2 \pm 1.7 ^a | 36 \pm 8 ^a | 0.99 \pm 0.10 ^a | 5.34 \pm 0.03 ^{ab*} | 1.17 \pm 0.09 ^{ab*} |
| 72 | 14.6 \pm 0.8 ^a | 40 \pm 12 ^a | 0.69 \pm 0.11 ^a | 5.29 \pm 0.06 ^a | 1.54 \pm 0.09 ^a |
| 91 | 14.4 \pm 1.0 ^{ab*} | 25 \pm 5 ^a | 0.69 \pm 0.11 ^a | 5.37 \pm 0.10 ^a | 1.39 \pm 0.04 ^a |

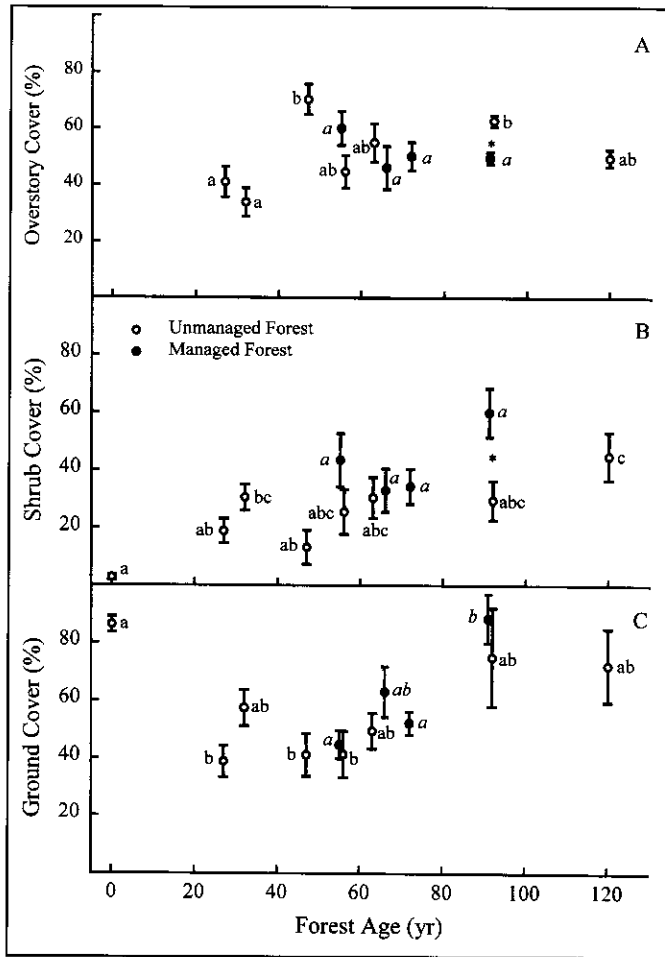


Figure 2. Overstory (A), shrub (B), and ground-layer (C) cover in unmanaged and managed forests. Data are presented in the same manner as Figure 1.

although it was twice as high at 91 yr as in unmanaged forests of similar age ($P < 0.05$) (Figure 2B). Ground cover was generally less in unmanaged forests ≤ 56 -yr-old than in grasslands, but was similar to grasslands in older unmanaged forests ($P < 0.001$) (Figure 2C). In managed forests, ground cover increased between 72 and 91 yr ($P < 0.001$), but did not differ significantly from that of unmanaged forests at any age (Figure 2C).

Species richness in the ground layer was 75% less, but shrub species richness was the same, in 27-yr-old unmanaged forests compared to grasslands ($P < 0.001$) (Figure 3); thereafter, both ground-layer and shrub species richness increased gradually (to 63 yr in unmanaged forests, 72 yr in managed forests) ($P < 0.001$), then remained constant (Figure 3). With increasing age in managed forests, ground-layer species richness increased ($P < 0.01$), but shrub species richness remained constant, and neither differed between

unmanaged and managed forests of similar age (Figure 3). A total of 136 species occurred in grasslands. Eight of these species were present in the oldest (120 yr) unmanaged forests and seven in the oldest (91 yr) managed forests.

Dead Wood

Snag density in 27- to 32-yr-old unmanaged forests was 7-8 stems/ha, then increased 10-fold by 92 yr ($P < 0.001$) (Figure 4A). In contrast, there was no trend in snag density in managed forests, and it did not differ significantly between unmanaged and managed forests of similar age (Figure 4A). Total log length in unmanaged forests increased over time ($P < 0.001$), from near zero at 27-32 yr to 140 m/ha at 120 yr (Figure 4B). Log length did not change over time in managed forests, and by 92 yr it was lower than in unmanaged forests of similar age ($P < 0.05$) (Figure 4B). Litter biomass in unmanaged forests increased

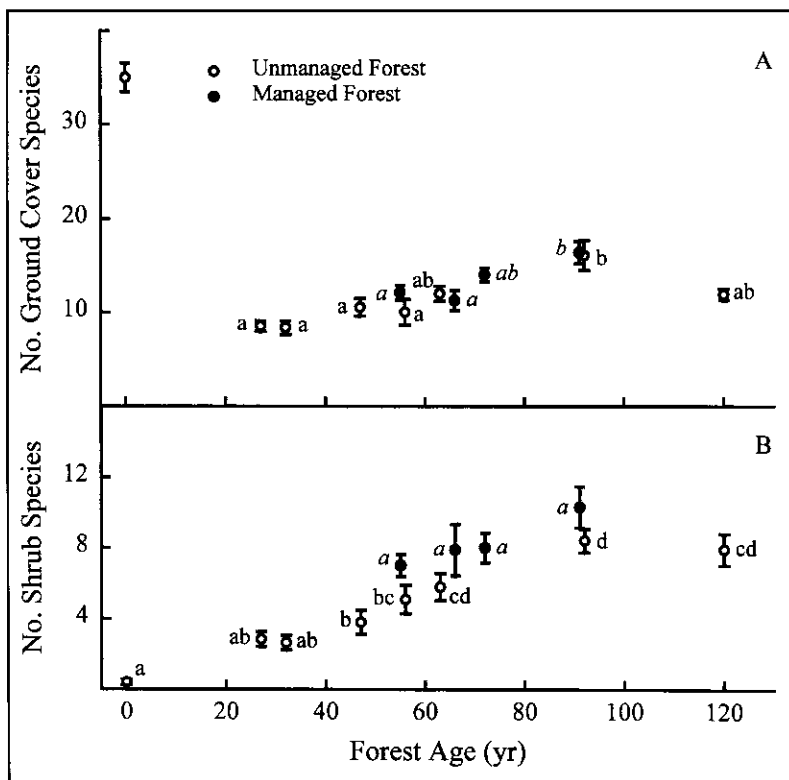


Figure 3. Species richness of ground (A) and shrub (B) layers in unmanaged and managed forests. Data are presented in the same manner as Figure 1. Ground-layer diversity at age 0 yr (grassland) was measured by a different method than the rest of the data, and was excluded from the statistical analysis.

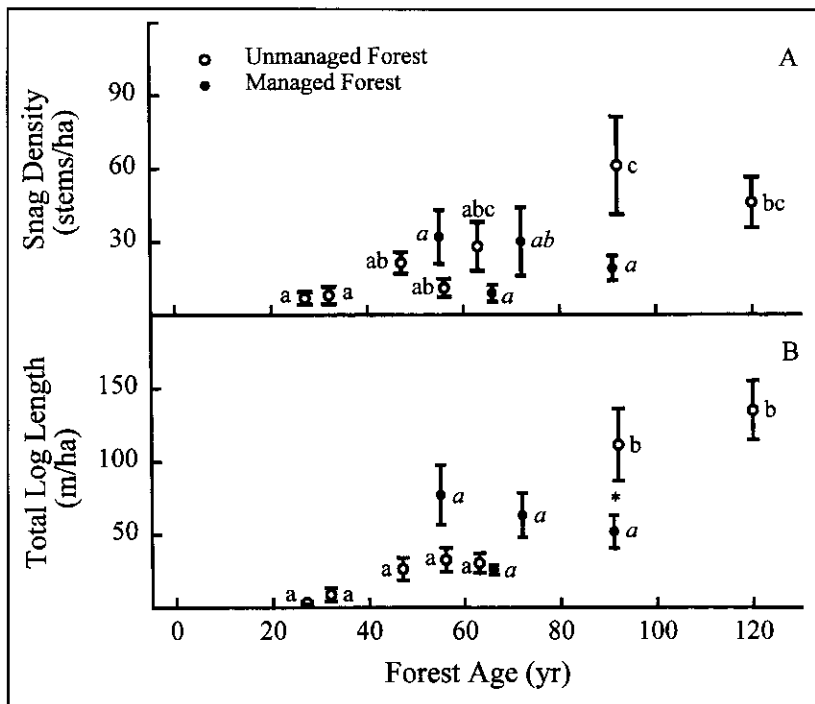


Figure 4. Snag density (A), total log length (B), and forest floor litter (C) in unmanaged and managed forests. Data are presented in the same manner as Figure 1.

from near zero in grasslands to 28 g/m² at 32 yr ($P < 0.001$), and remained constant thereafter; in managed forests, it remained constant over time (Table 2).

Soils

O-horizon biomass showed no temporal trends in either unmanaged or managed forests, and did not differ significantly between unmanaged and managed forests of similar age (Table 2). A-horizon pH did not change over time in either unmanaged or managed forests, and was slightly lower (0.16 units) in 63-yr-old unmanaged forests than in managed forests of similar age ($P < 0.05$) (Table 2). In unmanaged forests, A-horizon CEC varied over time ($P < 0.001$), with a minimum at 27 yr and a maximum at 56-92 yr (Figure 5A). In managed forests, CEC increased nearly two-fold between 55 and 91 yr ($P < 0.001$), from being less than to more than unmanaged forests of similar age ($P < 0.05$) (Figure 5A).

The carbon concentration of the A-horizon in unmanaged forests did not change over time, while that of managed forests increased 50% be-

tween 55 and 91 yr ($P < 0.05$), going from lower than to higher than unmanaged forests of similar age ($P < 0.05$) (Figure 5B). O-horizon nitrogen concentration did not change over time in either unmanaged or managed forests, but was lower in 66-yr-old managed forests than in unmanaged forests of similar age ($P < 0.05$) (Table 2). A-horizon nitrogen in unmanaged forests declined about 40% between 56 and 120 yr ($P < 0.001$), while in managed forests it more than doubled over time ($P < 0.05$), from being less than to more than unmanaged forests of similar age ($P < 0.01$) (Figure 5C).

Discussion

Ecosystem Changes in Unmanaged Forests

The major consequence of fire exclusion in southern Puget Lowland grasslands is rapid (< 30 yr) conversion to forest, with a shift from complete dominance by grasses and forbs to complete dominance by woody species, accompanied by a major floristic turnover from grassland- to forest-associated

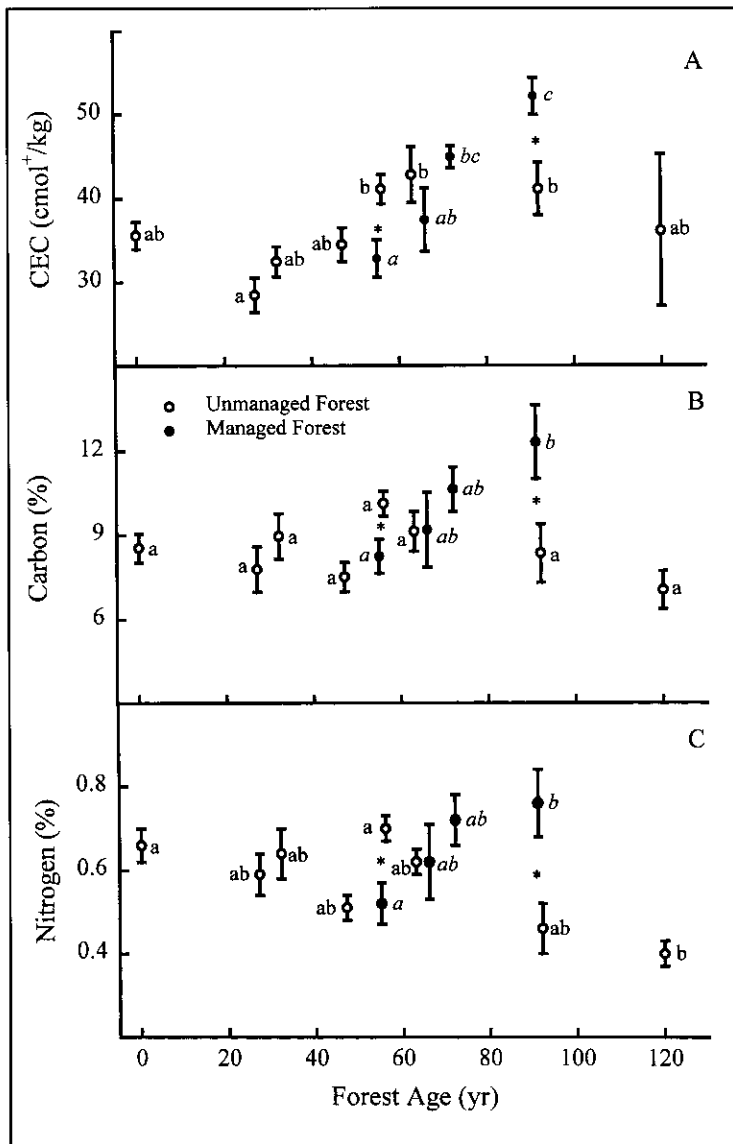


Figure 5. A-horizon cation-exchange capacity (A), and carbon (B) and nitrogen (C) concentrations, in unmanaged and managed forests. Data are presented in the same manner as Figure 1.

species. In the absence of fire, tree or shrub invasion of mesic grasslands in other parts of the world can occur with similar rapidity (Knight et al. 1994, Bruce et al. 1995, Arabas 2000, Briggs et al. 2002). A drastic reduction in herbaceous species richness is also typical of grassland invasions (Archer 1995, Bruce et al. 1995, Briggs et al. 2002, Miller and Tausch 2001).

The wide range of overstory tree ages for the seven age classes of unmanaged forests, 41 ± 5 yr, implies that the trees in Fort Lewis' colonization forests became established over periods of decades, as would be expected if tree invasion was patchy. Peterson and Hammer (2001) also found a wide range (50-95 yr) in overstory Douglas-fir tree ages in a colonization forest on Orcas Island, Washington.

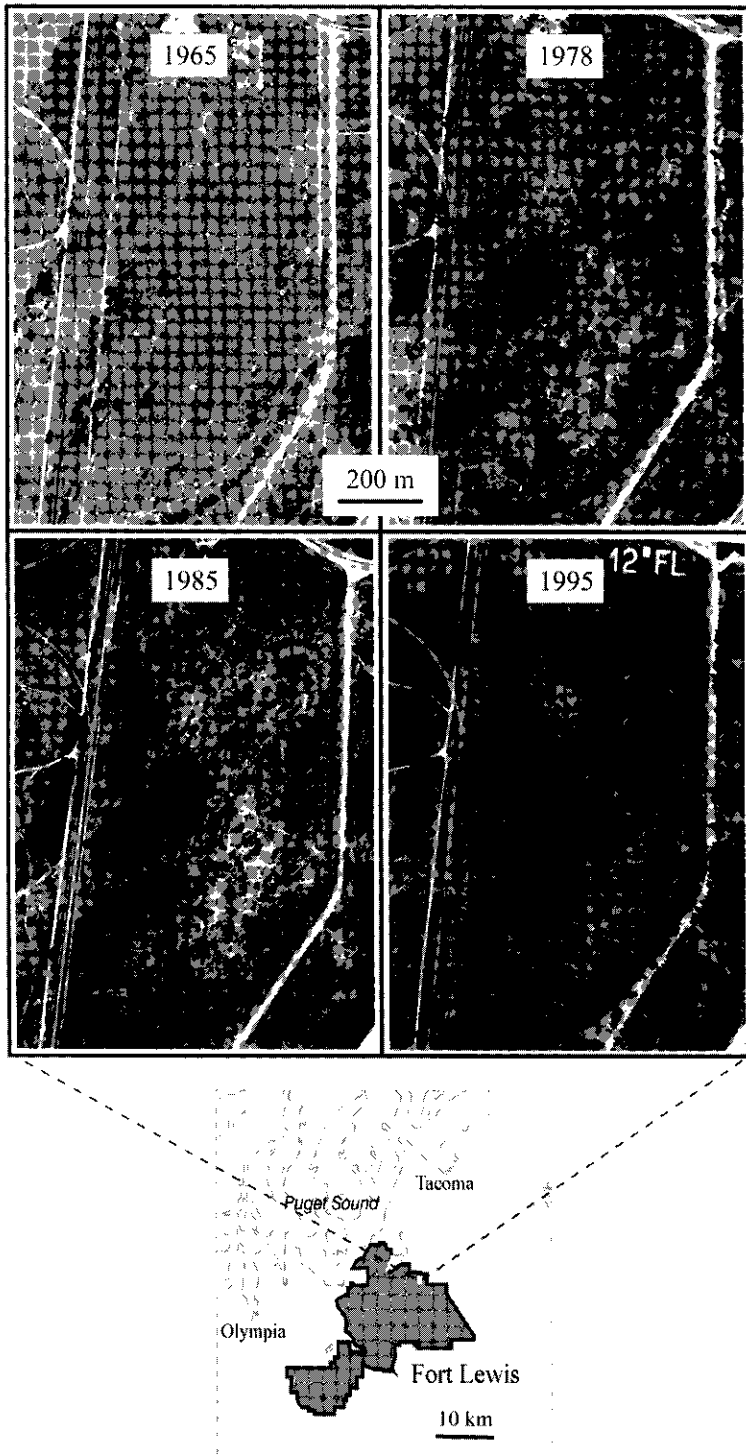


Figure 6. Time series of aerial photographs of a portion of Fort Lewis that has been undergoing Douglas-fir tree invasion.

At Fort Lewis, direct confirmation of the patchy nature of tree invasion is provided by time series of aerial photographs, which reveal that young, unmanaged colonization forests consist of small groves of dense young conifers separated by areas of few or no trees. These groves later merge as newly established trees fill in the remaining openings between the patches (Figure 6). This is the same process observed by Giles (1970) on Mima Prairie, west of Fort Lewis. In southern Texas grasslands, initial invasion by mesquite (*Prosopis glandulosa*) takes the form of scattered shrub clusters. Expansion and coalescence of existing clusters and initiation of new clusters eventually results in conversion to mesquite woodland (Archer et al. 1988). A patchy pattern was also inferred for Virginia pine (*Pinus virginiana*) invasion of serpentine barrens in Pennsylvania (Barton and Wallenstein 1997).

At Fort Lewis, maximum canopy cover of 45-65%, attained by 42 yr, allows sufficient light to reach the forest floor for ground cover to persist and for the gradual development of a shrub layer. In contrast, succession after fire or logging on moister sites in western Washington and Oregon typically passes through a stem-exclusion phase characterized by a dense conifer overstory and almost total absence of ground and shrub cover (Oliver and Larson 1996). Woody plant invasion of grasslands elsewhere in North America results in a decline in herbaceous cover and productivity, initially underneath individual trees or shrubs, and later for the plant community as a whole, while shrub growth is either inhibited or facilitated by the invading species (Archer 1995, Bruce et al. 1995, Briggs et al. 2002, Miller and Tausch 2001).

Another important change in ecosystem structure associated with tree invasion at Fort Lewis is the accumulation of dead wood. However, the absolute amounts, especially of large snags and logs, are much less than in mature conifer forests elsewhere west of the Cascade Mountains. For example, in the oldest (120-yr-old) colonization forests, snag density (≥ 10 cm dbh) was 46 stems/ha and log density (≥ 10 cm diameter) was 222 pieces/ha, compared to 121 stems/ha and 447 pieces/ha for the same size classes of snags and logs in 80- to 199-yr-old Douglas-fir forests in western Oregon (Spies et al. 1988).

The primary effect of tree invasion on Fort Lewis soils is a substantial decrease in A-horizon nitro-

gen. This is likely a consequence of the accumulation and decay of woody litter with a higher C:N ratio than the almost exclusively herbaceous litter of grasslands. Unlike nitrogen, soil carbon does not accumulate, nor are there long-term trends in soil pH or CEC. Everett soils, which occur on dry sites that have been forested for centuries, and which may represent the end-point of forest invasion of Puget Lowland grasslands, have A-horizon nitrogen concentrations that are half those of Spanaway soils, but the two soil types do not differ in pH (Ugolini and Schlichte 1973). Previous studies have found that soil nitrogen increases when junipers (*Juniperus* spp.) invade Great Basin shrub-steppe (Miller and Wigand 1994) and when creosote bush (*Larrea tridentata*) invades New Mexico grasslands (Gill and Burke 1999), and that both soil carbon and soil nitrogen increase when mesquite invades Texas grasslands (Archer 1995). These studies examined soils beneath individual trees or shrub clumps, and thus are not directly comparable to our study. Barton and Wallenstein (1997), however, observed that when Virginia pine invades serpentine barrens, soil organic matter increases beneath individual trees, but there is no difference in soil organic matter between entire stands of pine savanna (earlier stage of succession) and closed pine forest (later stage of succession).

How long might it take for grassland soils to be transformed into forest soils as a result of tree invasion? The answer is certainly centuries, since even the oldest colonization stand on Fort Lewis, 400-yr-old Ellsworth Woods, is partially underlain by grassland soils (Glenn Ahrens, GBA Forestry, Astoria, Oregon, personal communication). In southern Minnesota, fossil pollen reconstruction of Holocene vegetation, when compared to the modern distribution of soils, suggests that it requires several thousand years of oak woodland invasion of grasslands for grassland soils to become woodland soils, and that 300 yr of invasion of woodlands by deciduous forest have not yet converted woodland soils to forest soils (Grimm 1983).

Colonization forests are scattered across Pierce, Thurston, Lewis, Mason, and eastern Grays Harbor counties in the southern Puget Lowland. These are underlain by the same (Spanaway, Fitch, Nisqually) or similar (Carstairs) grassland soil series as Fort Lewis (Crawford and Hall 1997).

Due to the similarities in soils, topography, and climate, we believe the successional trends in unmanaged colonization forests observed at Fort Lewis are typical of trends in unmanaged colonization forests across the region.

Influences of Timber Harvest

The typical stand age at first thinning on Fort Lewis is 50-60 yr and thinnings are relatively light (average removal of stems ≥ 20 cm dbh in 79 thinning sales between 1997 and 2001 was 16%), thus it is not surprising that differences in vegetation structure between unmanaged and managed forests are few (lower canopy cover, higher shrub cover) and do not appear until 91 yr of age. Timber harvest also has no effect on the species richness of the shrub and ground layers, or on the persistence of grassland species in older colonization forests.

The lack of accumulation of snags and logs in managed forests can be attributed to the pre-1991 Fort Lewis policy to remove sound snags and logs during timber harvest. Under current policy, sound snags and logs remain in the woods and most senescent trees, which will eventually become snags, also remain. Therefore, we expect dead wood accumulation in the future in managed forests.

We attribute the positive effect of timber harvest on CEC, nitrogen, and carbon in the A horizon to mixing of the litter layer and the O horizon with the A horizon by heavy logging equipment during timber harvests. The resulting increased organic matter content of the A horizon causes A-horizon CEC, carbon, and nitrogen to increase. Mixing also explains why managed and unmanaged forests have similar amounts of litter, despite the presence of logging-generated slash in managed forests.

Management of southern Puget Lowland colonization forests outside Fort Lewis is usually quite different from that on the installation. Clearcut and shelterwood timber harvests are common, some forests are grazed or managed for firewood, and none has military activity. Therefore, the influences of timber harvest observed in this study may be unique to Fort Lewis.

Management Implications

Most colonization forests on Fort Lewis are < 100 yr old, thus lack large live trees, one component of spotted owl habitat. Colonization forests also

have little large dead wood, e.g., of the snags (≥ 60 cm dbh and 6 m tall) and logs (≥ 50 cm diameter and 6 m long) that are another component of owl habitat (USDA Forest Service & USDI Bureau of Land Management 1994), only one snag and 30 logs occurred across all the plots in this study. In addition, colonization forests have little shade-tolerant western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*), species that contribute to the development of multiple canopy layers, a third component of owl habitat. Therefore, colonization forests are not currently owl habitat, and will not become owl habitat for more than a century. However, continued periodic thinnings, by increasing the growth rates of residual trees, will hasten the appearance of large live trees. Deliberate snag and log creation and underplanting of shade-tolerant species could further accelerate development of owl habitat.

Forest invasion has decreased the likelihood of wildfires at Fort Lewis. The majority of ignitions occur during summer droughts, when fuel moisture is low, and in grasslands, where tracer bullets, pyrotechnics, and artillery shells are used (Joe Reasoner, Fort Lewis Forestry Program, personal communication). Because forest understory fuels take longer to dry out after rain than do grassland fuels, ignitions are less likely in forests than in grasslands. Installation records indicate that between 1986 and 2000, a much greater area of grassland than of forest or woodland burned in wildfires, even though Fort Lewis has more than twice the area of forests and woodlands as it has grasslands. However, during extended droughts, the potential for crown fires is substantial in colonization forests because of large fuel loads, especially midstory fuels (e.g., shrubs) that can carry fire from the ground into the overstory. The difference in wildfire risk during drought between forests and grasslands is probably greater today than prior to settlement because colonization forests have substantially higher tree densities than did the original forests of Fort Lewis, as indicated by land-survey records from the mid-19th century (Public Forestry Foundation 1996). Peterson and Hammer (2001) reached the same conclusion for the colonization forest on Orcas Island, Washington. Miller and Tausch (2001) found that when semiarid grasslands are invaded by junipers, the decrease in understory biomass beneath individual junipers initially reduces wildfire risk, but later, as juniper woodlands with closed canopies develop, the risk of crown fire increases substan-

tially. In southern Minnesota, grassland conversion to oak woodland substantially decreased fire frequency (Grimm 1983).

Will the trend of decreasing soil nitrogen in unmanaged forests eventually reduce tree growth? There is a twofold difference in soil nitrogen between Spanaway and Everett soils (Ugolini and Schlichte 1973), the latter being the putative endpoint of soil development when trees invade Puget Lowland prairies. However, stand inventory data (Lathrop Leonard, Fort Lewis Forestry Program, personal communication) indicate that almost all Fort Lewis forests, on both Spanaway and Everett soils, are Douglas-fir site-index class II (King 1966), suggesting that the reduced soil nitrogen does not influence site productivity. Conversely, if soil nitrogen continues to increase in managed forests, will tree growth eventually increase? This

is difficult to answer because in managed forests, the potential growth effects of higher nitrogen are confounded with those of thinning. Factorial thinning and fertilization trials in unmanaged forests are required to separate these two potential effects.

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