Predicting growth response of shrubs to clear-cutting and site preparation in coastal Oregon forests[1]

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Abstract: Cover-projection models were developed based on algebraic difference formulations of an exponential-power function to describe shrub recovery and development patterns after clear-cutting and site preparation. We tested the effect of six treatments on shrub growth patterns by incorporating indicator variables into the rate and shape parameters of the models for salal (*Gaultheria shallon* Pursh), thimbleberry (*Rubus parviflorus* Nutt.), salmonberry (*Rubus spectabilis* Pursh), and all shrubs. For salal, the shape parameter included an adjustment for burning treatments that delayed maximum cover by several years as compared with unburned treatments. The rate parameter in the thimbleberry model was adjusted for burning treatments; maximum cover occurred about 2 years earlier in burned than in unburned treatments. Both rate and shape parameters in the salmonberry model were adjusted for burning treatments; delayed establishment but increased growth rate and less salmonberry cover are characteristic of burned treatments as compared with the unburned treatments. The rate and shape parameters in the model for the shrub group included adjustments for burning treatments. Overstory removal fostered shrub development, whereas site preparation treatments slowed and curtailed it. The final cover-projection models accounted for 68–92% of the total variation in cover, with the adjustments for burning accounting for 1.5–3.3% of the variation. The predicted growth patterns are consistent with trends in site occupancy and published autecological characteristics.

Résumé : Des modèles de projection du couvert ont été développés à partir de formules de différences algébriques d'une fonction de puissance exponentielle pour décrire la récupération des arbustes et leur patron de développement après la coupe à blanc et la préparation de terrain. Les auteurs ont testé l'effet de six traitements sur les patrons de croissance des arbustes en incorporant des variables indicatrices à l'intérieur des paramètres de taux et de forme des modèles pour le salal (*Gaultheria shallon* Pursh), la ronce parviflore (*Rubus parviflorus* Nutt.), la ronce remarquable (*Rubus spectabilis* Pursh) et l'ensemble des arbustes. Pour le salal, le paramètre de forme incluait un ajustement pour les traitements de brûlage qui décalaient la couverture maximale de plusieurs années par rapport aux traitements n'impliquant pas de brûlage. Le paramètre de taux dans le modèle pour la ronce parviflore a été ajusté pour les traitements de brûlage; la couverture maximale était atteinte 2 années plus tôt dans les traitements avec brûlage que dans ceux sans brûlage. Les paramètres de forme et de taux pour le modèle de la ronce remarquable ont été ajustés pour les traitements de brûlage; un établissement retardé suivi d'une croissance accélérée ainsi qu'un couvert moins dense étaient typiques des traitements de brûlage en comparaison avec les traitements sans brûlage. Les paramètres de forme et de taux pour le modèle de l'ensemble des arbustes incluaient des ajustements pour le brûlage. L'élimination du couvert a favorisé le développement des arbustes, tandis que la préparation de terrain l'a ralenti et réduit. Les modèles finaux de projection du couvert expliquaient 68–92% de la variation du couvert et les ajustements pour le brûlage comptaient pour 1,5–3,3% de la variation. Les patrons de croissance prédits par les modèles étaient cohérents avec les tendances d'occupation des stations et les exigences autécologiques publiées.
[Traduit par la Rédaction]

Introduction

Growth models for young forest stands are being developed to predict the consequences of reforestation practices, including vegetation management. Most growth models have focused on commercial tree species; with few exceptions (e.g., Harrington et al. 1991, 1992; Knowe 1991), associated species have received little attention. The importance of associated vegetation, however, is apparent from its use as an independent variable in some models. For example, growth models for young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Pacific Northwest (Wagner and Radosevich 1991; Knowe et al. 1992; Knowe and Stein 1995) use percent vegetation cover as an independent variable because interspecific competition commonly limits the growth of young trees. To use these models to evaluate tree growth in response to treatments, techniques are needed for predicting the abundance of associated species over time.

Autecological attributes of important Pacific Northwest shrubs have received increasing attention (Haeussler et al. 1990; Tappeiner et al. 1991; Messier 1992; Maxwell et al. 1993; Tappeiner and Zasada 1993; Huffman et al. 1994), including the integration of species ecology and silvicultural practices to prevent vegetation management problems (Wagner and Zasada

Received April 4, 1996. Accepted September 13, 1996.

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Table 1. Description of sites in the Coastal Site Preparation Study (from Stein 1995).

Characteristic	Formader	LBJ	Camp 76	Farmer
Latitude (N)	44°11′	44°29′	44°17′	45°15′
Longitude (W)	123°59′	124°00′	123°45′	123°53′
Distance inland (km)	10	6	27	6
Elevation (m)	290–396	76–198	107–305	183–244
Aspect (degrees)	271	257	3	121
Slope (%)	17	31	59	55
Soil texture	Loam	Loam	Loam	Loam
Vegetation type	Alder–salmonberry	Alder–salmonberry	Alder–salmonberry	Alder–salmonberry – vine maple

Table 2. Description of treatments in the Coastal Site Preparation Study.

Site preparation	Description
None (untreated control)	Only a 30-cm spot was cleared by scalping when each Douglas-fir was planted
Spot clearing	All woody vegetation within a 1.2-m radius of the planted Douglas-fir was cut to a 15-cm height in early 1981
Spraying only	Glyphosate applied aerially as Roundup® in the early fall of 1980 at the rate of 2.52 kg ae/ha at 94 L/ha total mix
Burning only	Slash was broadcast burned after midsummer of 1980
Slashing + burning	All woody vegetation was manually slashed in June 1980 and broadcast burned later in the summer
Spraying + burning	Picloram + 2,,4-D applied aerially as Tordon 101® in May or June 1980 at the rate of 1.49 + 5.97 kg ae/ha in 187 L/ha total mix and then broadcast burned in the summer

Note: ae, acid equivalent.

1991). These studies have provided much life-history information but only limited data useful for predicting cover dynamics as a consequence of silvicultural treatments. Understanding the response of different species to disturbance and competition is critical to assessing harvest and site preparation effects on subsequent plant and tree cover.

Our objective was to develop predictive equations describing the response of shrubs to clear-cutting and site-preparation treatments. Information provided by such equations should be helpful for predicting the growth of young conifer stands, for prescribing vegetation management practices, and for assessing the ecosystem implications in manipulating species composition.

Methods

Data

The Coastal Site Preparation Study was initiated in four areas in 1980 to compare the effects of six site-preparation treatments, and protection from animals, on the survival and growth of Douglas-fir and associated vegetation. Details of the study design, measurements, and results through age 10 years have been presented by Stein (1995) and Knowe and Stein (1995). The four study areas, located on the Siuslaw National Forest, Oregon, are described in Table 1. Dominant woody vegetation present before site preparation included small trees such as vine maple (*Acer circinatum* Pursh); shrubs such as salmonberry (*Rubus spectabilis* Pursh), thimbleberry (*Rubus parviflorus* Nutt.), and salal (*Gaultheria shallon* Pursh); various grasses; bracken-fern (*Pteridium aquilinum* (L.) Kuhn); and sword-fern (*Polystichum munitum* (Kaulf.) Presl.).

The six site-preparation treatments compared at each location included an untreated control, manual spot clearing, aerial spraying, broadcast burning, slashing and burning, and spraying and burning (Table 2). At each location, the six treatments, each on a 2-ha plot, were planted at uniform spacing with 2-0 Douglas-fir seedlings from a seed source appropriate for the site. Spacing for planting varied by location and ranged from 2.4 × 2.4 to 3.0 ×3.0 m. Just before planting, slash, litter, humus, and live vegetation within 15 cm of each planting spot were removed by scalping. After planting, every other seedling was protected from animal damage (browsing or clipping) with an 8 × 75 cm plastic-mesh (Vexar®) tube. Approximately 120 seedlings per plot (104–120) in 4 or 6 rows were marked for repeated measurements. The site-preparation and animal-protection treatments composed a split-plot, randomized block experiment; each location served as a replication, with site-preparation treatments as the main plots and animal-protection treatments as the subplots. We are concerned only with the main plots in the current analyses.

The vegetation associated with each seedling was assessed with a 240-cm line transect centered perpendicular to the marked row at or near each measured Douglas-fir seedling, 1, 2, 3, 5, 7, and 10 years after the seedlings were planted. The uppermost layer of vegetation was recorded by species (or genera for herbs) to the nearest centimetre, with 5 cm being the minimum increment recorded separately for vegetation or bare soil surface. For each location–treatment combination, average cover was calculated based on the 120 line transects for each plot. Because all transects were included in the computations, the average cover is a stand-level estimate of cover for each species.

Table 3. Comparison of explained variation (R^2) and root mean square error (RMSE) for anamorphic and polymorphic cover-projection models.

	Anamorphic model*		Polymorphic model†	
Species	R^2	RMSE	R^2	RMSE
Salal	0.8354	1.98	0.6938	2.70
Thimbleberry	0.6513	2.29	0.4775	2.80
Salmonberry	0.9081	5.66	0.6893	10.42
Shrub group	0.8526	7.82	0.5281	13.99

*Anamorphic model: $C_2 = C_1(A_2/A_1)^{\theta} \exp[\beta(A_2 - A_1)]$.

†Polymorphic model: $C_2 = \alpha A_2^{\theta}(C_1/\mathrm{d}A_1^{\theta})^{A_2/A_1}$.

Inspection of the observed means and frequency data indicated that sufficient data were available to develop models for salal, thimbleberry, salmonberry, and the shrub group (including salal, thimbleberry, salmonberry, Oregon grape (*Berberis* spp.), hazel (*Corylus cornuta* var. *californica* (A. DC.) Sharp), ocean-spray (*Holodiscus discolor* (Pursh) Maxim.), other *Rubus* spp., *Ribes* spp., and *Vaccinium* spp.).

Model development

Because site occupancy curves for herb and shrub groups suggest that maximum cover after a major disturbance is achieved between ages 1 and 10 years and then gradually declines (Newton 1981), a mathematical formula that combines power and exponential functions was selected to represent shrub growth patterns:

$$[1] \qquad C = \alpha A^{\theta} \exp(\beta A) + \varepsilon$$

where C is the cover (%), A is the years since disturbance, α is the asymptote, θ is the shape, β is the rate, and ε is the random error.

An anamorphic cover-projection equation and a polymorphic cover-projection equation were derived through algebraic difference formulations of eq. 1 (Borders et al. 1984). The anamorphic cover-projection equation was developed by assuming that the asymptote (α) defines curve shape:

$$[2] \qquad C_2 = C_1\left(\frac{A_2}{A_1}\right)^{\theta} \exp[\beta(A_2 - A_1)] + \varepsilon$$

where C_2 is the cover (%) at the end of the growth period, C_1 is the cover (%) at the start of the growth period, A_2 is the age (years) at the end of the growth period, A_1 is the age (years) at the start of the growth period, and other terms are as previously defined. The rate and shape parameters interact to produce different curve shapes. Large values of θ and β in eq. 2 indicate that maximum cover occurs at older ages and at higher levels, and that θ has a greater effect than β. The polymorphic cover-projection equation was developed by assuming that the rate (β) defines curve shape:

$$[3] \qquad C_2 = \alpha A_2^{\theta}\left(\frac{C_1}{\alpha A_1^{\theta}}\right)^{A_2/A_1} + \varepsilon$$

with terms as previously defined. Large values of α and θ in eq. 3 indicate that maximum cover occurs at younger ages and at higher levels; α affects the level and θ affects both the level and age of maximum cover.

The anamorphic and polymorphic cover-projection equations are implied growth functions that can be algebraically rearranged to directly predict either C_1 (cover at given values of age and cover-growth potential) or C_2 (future cover or cover-growth potential). Their path-invariant property permits the same future cover to be predicted regardless of whether projections are made for several short intervals or a single, long interval. Desirable features of these equations are that any base age (A_2) may be selected for indexing cover-growth potential and that $C_2 = C_1$ when $A_2 = A_1$.

According to Borders et al. (1988), real-growth series from remeasured plots are less likely to have problems with serial correlation when the data are arranged in nonoverlapping growth intervals rather than all possible intervals. Thus, average cover values for each species and species group were arranged in nonoverlapping intervals (years 1–2, 2–3, 3–5, 5–7, and 7–10), and nonlinear regression was used to fit the cover-projection models.

The anamorphic and polymorphic equations were fit to the data and compared on the basis of explained variation (R^2) and root mean square error (RMSE). The anamorphic formulation consistently had smaller RMSE values and accounted for 14% to 32% more variation than the polymorphic formulation (Table 3). Therefore, the anamorphic equation was selected for use in the final models.

Testing treatment effects

The effects of site preparation on recovery and the pattern of cover development were examined by incorporating indicator variables into the rate and shape parameters of the anamorphic cover-projection equation. The effects of site-preparation treatments were incorporated into the rate parameter (β) as follows:

$$\beta_b = \beta_{10} + \beta_{11}B$$

where β_b is the rate parameter for burning treatments and $B = 1$ for site-preparation treatments involving burning (treatments 4, 5, and 6) or otherwise 0;

$$\beta_s = \beta_{20} + \beta_{21}S$$

where β_s is the rate parameter for spraying treatments and $S = 1$ for site-preparation treatments involving spraying (treatments 3 and 6) or otherwise 0;

$$\beta_z = \beta_{30} + \beta_{31}Z$$

where β_z is the rate parameter for burning or spraying treatments and $Z = 1$ for site-preparation treatments involving burning or spraying (treatments 3, 4, 5, and 6) or otherwise 0;

$$\beta_t = \beta_0 + \beta_2 T_2 + \beta_3 T_3 + \beta_4 T_4 + \beta_5 T_5 + \beta_6 T_6$$

where β_t is the rate parameter for specific treatments, $T_2 = 1$ for the spot-clearing treatment (treatment 2), $T_3 = 1$ for the spraying only treatment (treatment 3), $T_4 = 1$ for the burning only treatment (treatment 4), $T_5 = 1$ for the slashing and burning treatment (treatment 5), and $T_6 = 1$ for the spraying and burning treatment (treatment 6) or otherwise 0. The β_{i0} terms in β_b, β_s, and β_z represent an overall rate coefficient, and the β_{i1} terms represent adjustments to β_{i0} for the respective treatments. In β_t, the β_0 term represents the overall rate coefficient, and the β_i terms represent adjustments to β_0 for specific site-preparation treatments. The same approach was used to incorporate the effects of site-preparation treatments into the shape parameter (θ).

The statistical significance of each treatment effect was determined by performing an F-test on the reduction in the

Table 4. Explained variation (R^2) and partial analysis of variance for testing the effects of site preparation on cover-development curves for salal in coastal Oregon forests.

Parameters modified	Effect	R^2	Partial R^2	df	Error SS	F	$p > F$
None	None (reduced model)	0.8354		88	344.69		
θ (shape)	Burning	0.8551	0.0197	87	303.50	11.802	0.0009
	Spraying	0.8360	0.0006	87	343.51	0.299	0.5859
	Burning–spraying	0.8355	0.0001	87	344.55	0.035	0.8520
	Treatment-specific	0.8613	0.0259	83	290.53	3.095	0.0130
β (rate)	Burning	0.8478	0.0124	87	318.80	7.071	0.0093
	Spraying	0.8369	0.0015	87	341.45	0.826	0.3659
	Burning–spraying	0.8356	0.0002	87	344.29	0.101	0.7514
	Treatment-specific	0.8528	0.0174	83	308.23	1.969	0.0918
θ and β	Burning	0.8552	0.0198	86	303.28	5.865	0.0041
	Spraying	0.8371	0.0017	86	341.04	0.460	0.6328
	Burning–spraying	0.8368	0.0014	86	341.86	0.356	0.7015
	Treatment-specific	0.8750	0.0396	78	261.82	2.466	0.0128

Note: The curve is $C_2 = C_1(A_2/A_1)^{\theta} \exp[\beta(A_2 - A_1)]$.

residual sum of squares between a full model that included treatment coefficients and a reduced model that excluded treatment coefficients (Neter et al. 1985). Cover development curves for salal, thimbleberry, salmonberry, and the shrub group were compared graphically for significant treatment effects.

Results

Salal

The cover-projection equations for salal accounted for 84–88% of the variation in observed cover (Table 4). The burning effect in the shape parameter (θ) alone, in the rate parameter (β) alone, and in both the rate and shape parameters was statistically significant ($p \leq 0.0009$, 0.0093, and 0.0041, respectively) and accounted for 2.0, 1.2, and 2.0% additional variation, respectively, as compared with the reduced model. The indicator variables for specific treatments in the shape parameter alone, and in both the rate and shape parameters, were statistically significant ($p \leq 0.0130$ and 0.0128) and accounted for 2.6 and 4.0% additional variation in salal cover, respectively, as compared with the reduced model.

The final cover-projection equation for salal included the effect of burning in the shape parameter and accounted for 85.5% of the variation:

$$[4] \qquad C_2 = C_1\left(\frac{A_2}{A_1}\right)^{0.740347+0.748220B} \exp[-0.224\,180(A_2 - A_1)]$$

with variables as previously defined. The respective asymptotic standard errors were 0.140 423, 0.196 314, and 0.035 707. Salal cover development reached maximum in years 3–4 in unburned areas, but not until about year 7 in burned areas (Fig. 1). By the end of the decade, salal cover was declining more in unburned areas than in burned areas.

Thimbleberry

The cover-projection equations for thimbleberry accounted for 65–75% of the variation in observed cover (Table 5). The burning effect in the shape parameter alone, in the rate parameter alone, and in both the rate and shape parameters was statistically significant ($p \leq 0.0134$, 0.0006, and 0.0025, respectively) and accounted for 1.8, 3.3, and 3.4% additional variation, respectively, as compared with the reduced model. The indicator variable for burning or spraying (Z) was statistically significant ($p \leq 0.0024$ and 0.0040, respectively) in the rate parameter alone, and in both the rate and shape parameters. Compared with the reduced model, the models with burning or spraying accounted for 2.7 and 3.2% additional variation, respectively. The indicator variables for specific treatments in the rate parameter alone, and in both the rate and shape parameters, were statistically significant ($p \leq 0.0258$ and 0.0001) and accounted for 3.7 and 9.5% additional variation in thimbleberry cover. Because it is impractical to include 12 parameters in a cover-projection model, the final model for thimbleberry includes only the effect of burning on the rate parameter:

$$[5] \qquad C_2 = C_1\left(\frac{A_2}{A_1}\right)^{1.690113} \exp[(-0.278\,243 - 0.160\,387B) \times (A_2 - A_1)]$$

with variables as previously defined. This model accounted for 68.5% of the observed variation, and the respective standard errors were 0.208 218, 0.045 623, and 0.048 453. Thimbleberry cover reached maximum development in burned areas 2–3 years earlier than in unburned areas and declined sooner (Fig. 2).

Salmonberry

The cover-projection equations for salmonberry accounted for 90–94% of the variation in observed cover (Table 6). When the shape and rate parameters were considered alone, only the treatment-specific effect was statistically significant ($p \leq 0.0039$ and 0.0042, respectively) and accounted for 0.3 and 0.2% additional variation, respectively, as compared with the reduced model. When the shape and rate parameters were considered together, however, the burning, spraying, burning or spraying, and treatment-specific effects were all statistically significant

Fig. 1. Projected 10-year cover dynamics for salal on a burned site and an unburned site, based on cover potentials of 5, 10, 15, and 20% at year 5. Each data point represents the average cover on 120 line transects.

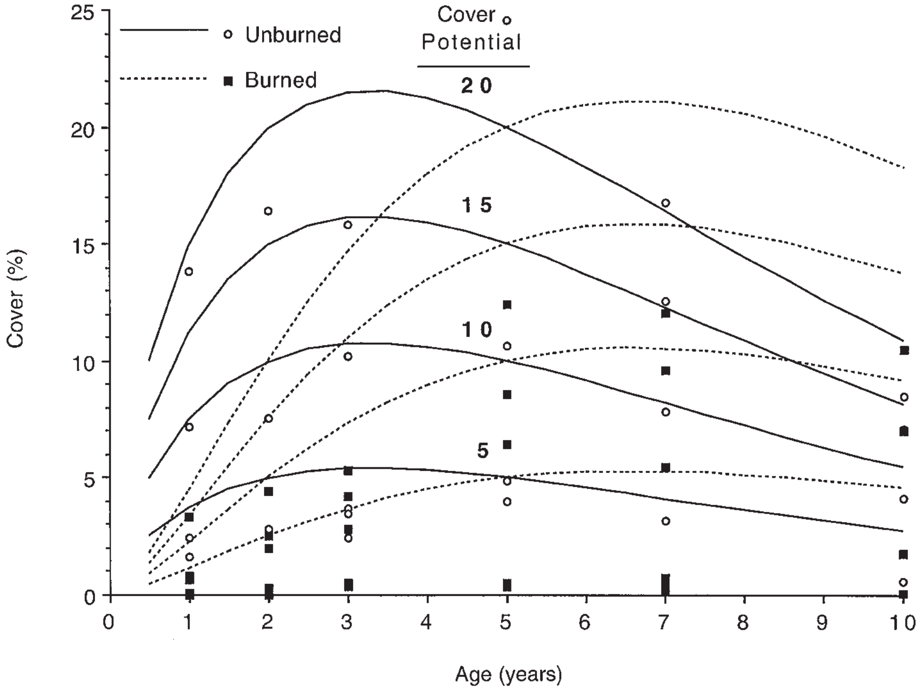


Table 5. Explained variation (R^2) and partial analysis of variance for testing the effects of site preparation on cover-development curves for thimbleberry in coastal Oregon forests.

Parameters modified	Effect	R^2	Partial R^2	df	Error SS	F	$p > F$
None	None (reduced model)	0.6513		118	619.00		
θ (shape)	Burning	0.6692	0.0179	117	587.32	6.311	0.0134
	Spraying	0.6554	0.0041	117	611.70	1.396	0.2398
	Burning–spraying	0.6605	0.0092	117	602.62	3.173	0.0775
	Treatment-specific	0.6742	0.0228	113	578.44	1.584	0.1702
β (rate)	Burning	0.6845	0.0332	117	560.13	12.290	0.0006
	Spraying	0.6546	0.0033	117	613.18	1.111	0.2940
	Burning–spraying	0.6779	0.0266	117	571.85	9.642	0.0024
	Treatment-specific	0.6881	0.0368	113	553.74	2.664	0.0258
θ and β	Burning	0.6856	0.0343	116	558.19	6.321	0.0025
	Spraying	0.6555	0.0042	116	611.61	0.701	0.4982
	Burning–spraying	0.6830	0.0317	116	562.72	5.802	0.0040
	Treatment-specific	0.7467	0.0954	108	449.71	4.069	0.0001

Note: The curve is $C_2 = C_1(A_2/A_1)^{\theta} \exp[\beta(A_2 - A_1)]$.

($p \le 0.0001$, 0.0047, 0.0001, and 0.0001) and accounted for 1.4, 0.8, 1.5, and 2.8% additional variation in salmonberry cover, respectively, as compared with the reduced model.

The salmonberry cover-projection models that included the effects of burning and burning or spraying in the shape and rate parameters had the largest F statistic. Combining the spraying and burning effects into one variable (Z), however, accounted for only slightly more variation than the model with only the burning effect. The final cover-projection model for salmonberry is

$$[6] \quad C_2 = C_1\left(\frac{A_2}{A_1}\right)^{0.574783+0.950649B} \exp[(-0.165\,229 - 0.225\,081B)(A_2 - A_1)]$$

with variables as previously defined. The model accounted for 92.2% of the observed variation in salmonberry cover, and the respective standard errors were 0.071 590, 0.196 714, 0.019 787, and 0.055 636. Salmonberry cover development reached maximum in 3–4 years in unburned areas and about a year

Fig. 2. Projected 10-year cover dynamics for thimbleberry on a burned site and an unburned site, based on cover potentials of 5, 10, 15, and 20% at year 5. Each data point represents the average cover on 120 line transects.

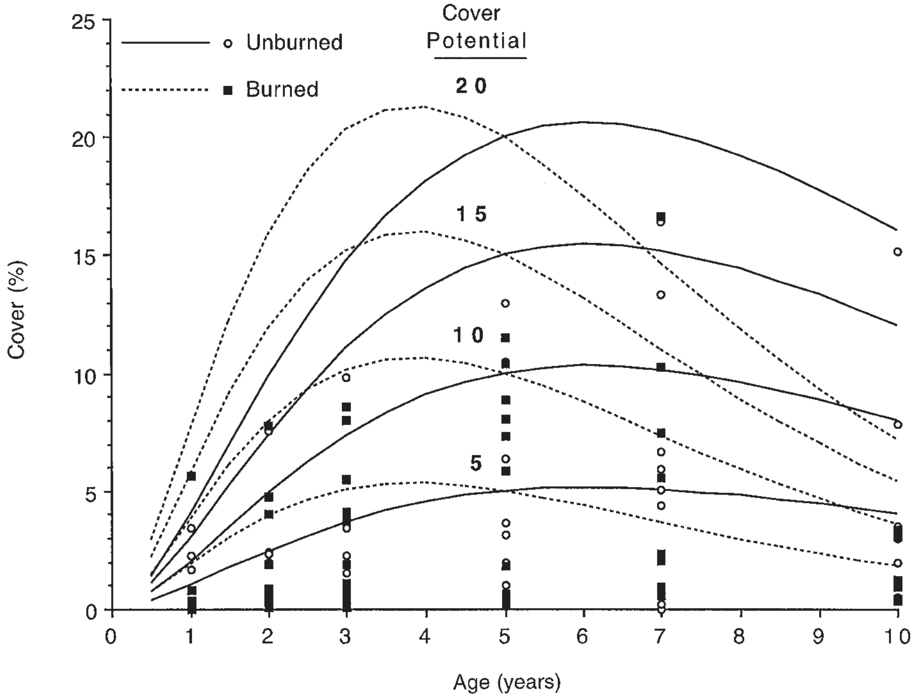


Table 6. Explained variation (R^2) and partial analysis of variance for testing the effects of site preparation on cover-development curves for salmonberry in coastal Oregon forests.

Parameters modified	Effect	R^2	Partial R^2	df	Error SS	F	$p > F$
None	None (reduced model)	0.9081		118	3788.43		
θ (shape)	Burning	0.9100	0.0019	117	3709.78	2.480	0.1180
	Spraying	0.9085	0.0004	117	3770.12	0.568	0.4526
	Burning–spraying	0.9103	0.0022	117	3698.43	2.847	0.0942
	Treatment-specific	0.9111	0.0030	113	3665.02	3.700	0.0039
β (rate)	Burning	0.9084	0.0003	117	3777.66	0.333	0.5650
	Spraying	0.9085	0.0004	117	3770.14	0.568	0.4526
	Burning–spraying	0.9083	0.0002	117	3780.27	2.785	0.0978
	Treatment-specific	0.9101	0.0020	113	3705.56	3.660	0.0042
θ and β	Burning	0.9223	0.0142	116	3202.02	10.623	0.0001
	Spraying	0.9162	0.0081	116	3453.80	5.620	0.0047
	Burning–spraying	0.9227	0.0146	116	3188.39	10.914	0.0001
	Treatment-specific	0.9357	0.0276	108	2651.61	4.631	0.0001

Note: The curve is $C_2 = C_1(A_2/A_1)^{\theta} \exp[\beta(A_2 - A_1)]$.

later in burned areas (Fig. 3). Rate of cover development and decline were faster in burned areas.

Shrub group

The cover-projection equations for the shrub group accounted for 85–89% of the variation in observed cover (Table 7). Only the burning or spraying effect was statistically significant ($p \leq 0.0371$) when incorporated into the shape parameter and accounted for 0.5% additional variation as compared with the reduced model. When the shape and rate parameters were considered together, however, the burning, spraying, burning or spraying, and treatment-specific effects were all statistically significant ($p \leq 0.0001$, 0.0018, 0.0001, and 0.0001) and accounted for 2.3, 1.5, 2.8, and 4.1% additional variation in the cover of all shrubs combined, respectively.

The cover-projection model that included the effect of burning or spraying in the shape and rate parameters had the largest F statistic. As with the cover-projection function for salmonberry, combining the spraying and burning effects into one variable (Z) accounted for only a small amount (<0.5%)

Fig. 3. Projected 10-year cover dynamics for salmonberry on a burned site and an unburned site, based on cover potentials of 20, 40, 60, and 80% at year 5. Each data point represents the average cover on 120 line transects.

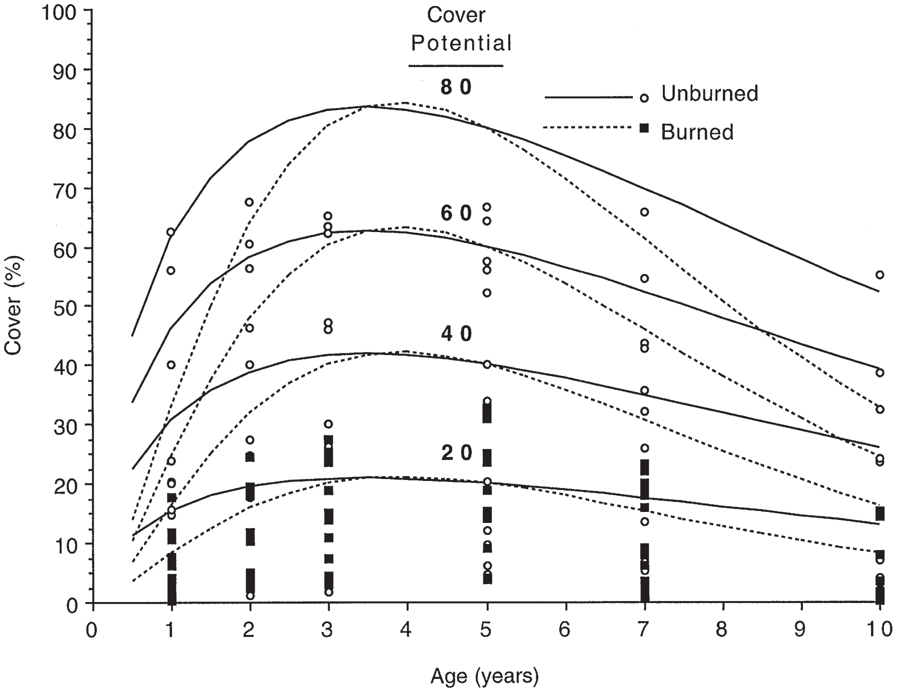


Table 7. Explained variation (R^2) and partial analysis of variance for testing the effects of site preparation on cover-development curves for all shrubs in coastal Oregon forests.

Parameters modified	Effect	R^2	Partial R^2	df	Error SS	F	$p > F$
None	None (reduced model)	0.8526		118	7212.04		
θ (shape)	Burning	0.8564	0.0038	117	7027.02	3.081	0.0818
	Spraying	0.8557	0.0031	117	7057.01	2.570	0.1116
	Burning–spraying	0.8580	0.0054	117	6947.86	4.449	0.0371
	Treatment-specific	0.8594	0.0068	113	6879.67	1.092	0.3688
β (rate)	Burning	0.8528	0.0002	117	7200.17	0.193	0.6612
	Spraying	0.8526	0.0000	117	7209.23	0.046	0.8305
	Burning–spraying	0.8528	0.0009	117	7201.40	0.173	0.6782
	Treatment-specific	0.8535	0.0002	113	7168.89	0.136	0.9837
θ and β	Burning	0.8756	0.0230	116	6083.78	10.756	0.0001
	Spraying	0.8678	0.0152	116	6465.09	6.701	0.0018
	Burning–spraying	0.8804	0.0278	116	5849.86	13.506	0.0001
	Treatment-specific	0.8939	0.0413	108	5189.52	4.209	0.0001

Note: The curve is $C_2 = C_1(A_2/A_1)^{\theta}\exp[\beta(A_2 - A_1)]$.

more variation than the model with only the burning effect. The final model for projecting cover for the shrub group is

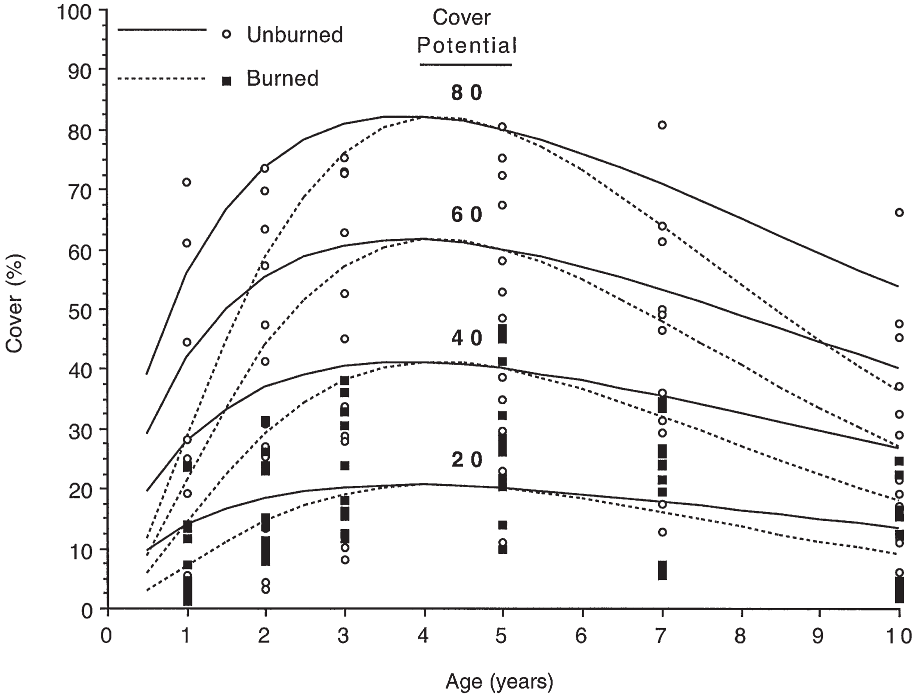
$$[7] \quad C_2 = C_1\left(\frac{A_2}{A_1}\right)^{0.645030+0.935733B}\exp[(-0.169\,356 - 0.208\,268B)(A_2 - A_1)]$$

with variables as previously defined. The final model accounted for 87.6% of the observed variation; the respective standard errors were 0.079 369, 0.193 640, 0.021 075, and 0.051 998. For the shrub group, cover development reached maximum in 4–5 years in both burned and unburned treatments (Fig. 4).

Discussion

The cover-projection models predict shrub recovery after overstory removal and site preparation; initial reduction of residual vegetation was not part of the equations. The effects of site preparation on recovery of shrub cover and patterns of development were intense, as demonstrated by the magnitude and statistical significance of the regression coefficients. Yet, judging by

Fig. 4. Projected 10-year cover dynamics for all shrubs on a burned site and an unburned site, based on cover potentials of 20, 40, 60, and 80% at year 5. Each data point represents the average cover on 120 line transects.



their partial R^2 values (1.5–3.3%), site-preparation treatments were relatively unimportant variables in the final models, even though five of the six treatments composing the reduced model represented site preparation as well as overstory removal effects. The relative importance of overstory removal was determined by fitting the cover-projection equations to cover data from untreated plots only, and computing R^2 for the effect of overstory removal alone. The amount of variation explained in the resulting reduced models was only 0.8–2.4% less than in models containing all treatments; the reduced model for thimbleberry, which accounted for 13.8% less variation, was an exception. These results demonstrate the dominant effect of overstory removal on the development of shrubs. After harvesting, the vigorous residual understory was capable of rapidly reoccupying the site. Site preparation reduced the dominance of the residual vegetation, thus reducing competition for survivors and promoting the establishment of new plants and species.

Cover potential, which is analogous to site index for trees and stem length for shrubs at age 10 years (Minore et al. 1988), is an objective expression for the expected cover of shrubs or other associated species at a given site. This expression allows vegetation development on different sites to be compared directly, which may be useful in forecasting the need for vegetation treatment to release planted conifers. Artificially forcing curves through a common point on a graph is also useful for comparing cover development patterns for different species or vegetation treatments.

After overstory removal, residual shrub cover averaged 27% for the areas receiving no site preparation and 28% for those receiving site preparation. Following site preparation and a decade of recovery with decreasing competition from herbaceous vegetation and increasing competition from hardwoods and planted Douglas-fir, shrub cover averaged 34% in the spot-clearing and no site preparation treatments and 10% in the other treatments. Salmonberry constituted 83% of the shrub cover immediately after site preparation and 72% a decade later. Thus, cover-projection curves for all shrubs (Fig. 4) were predominately influenced by salmonberry and closely resembled those for salmonberry alone (Fig. 3). Shrub cover in all treatments reached maximum in 4–5 years, and the rate of development and decline were faster in the burned than in the unburned areas.

Salmonberry can resprout rapidly after disturbance and also spread laterally by rhizome extension (Wagner 1984; Haeussler et al. 1990; Tappeiner et al. 1991; Stein 1995). These ecological characteristics influenced this shrub's response to site-preparation treatment and were reflected in the projection equations. When manually cut, salmonberry cover regrew to pretreatment levels in about one season; thus, the growth trajectories for spot-clearing and no site preparation treatments were essentially the same over the decade. Salmonberry is moderately affected by picloram + 2,4-D and severely affected by glyphosate (Conard and Emmingham 1984; Stein 1995). It attained only half as much cover after spraying with glyphosate as after any of the burning treatments. Major initial reduction and slow recovery of salmonberry indicated that glyphosate was highly effective, and its subsequent growth rate was more like those in other unburned treatments than in burned treatments. Growth rates were naturally lower in unburned areas, where the residual cover of salmonberry and other vegetation was substantial (44%), than in the relatively competition-free burned areas, where residual cover was very low (4%).

Salal can regenerate from sprouts, rhizomes, and seed and can pre-empt establishment of other species, but its recovery after cutting or burning is often not as rapid as for associated species (Schoonmaker and McKee 1988; Haeussler et al. 1990; Messier and Kimmins 1991; Huffman et al. 1994; Stein 1995). Slow recovery is evident in the projection curves, which show that maximum cover was reached about 4 years later on burned areas than on unburned areas. Recovery after cutting was also slow, but this effect among unburned treatments was countered by the glyphosate treatment, which effectively released salal from salmonberry, a dominant competitor (Stein 1995). The highest level of salal cover (7.1%) was reached in the glyphosate treatment. Glyphosate and picloram + 2,4-D herbicides cause only slight injury to salal itself (Conard and Emmingham 1984).

Thimbleberry can also regrow vigorously from sprouts and rhizomes after cutting or burning (Lafferty 1972; Dyrness 1973; Stickney 1981; Haeussler et al. 1990; Stein 1995). However, its response to site preparation was notably different from that of salmonberry and salal: its cover development in burned areas peaked earlier than in unburned areas (Fig. 2). The most likely explanation for this response is slightly more initial cover and faster regrowth than other shrub species in low competition conditions. After manual cutting, thimbleberry regrew faster than in other treatments; vigorous response to cutting has also been reported by others (Haeussler et al. 1990). Although glyphosate and picloram + 2,4-D cause severe injury to thimbleberry (Conard and Emmingham 1984), neither herbicide treatment impaired its growth relative to that in the other site-preparation treatments. Thimbleberry appears to be less competitive than associated vegetation, as evidenced by slow establishment and growth without site preparation, and rapid decline in burned areas as competition from shrubs and trees increased.

Conclusions

Cover-projection equations are useful for predicting the growth of young conifer stands, for prescribing vegetation-management treatments, and for assessing the ecological consequences of manipulating plant-species composition in forest ecosystems. These models provide us with the ability to forecast the cover development of shrubs, a key variable in growth and yield models for conifers. Based on R^2 values and the distribution of residuals, the maxima function selected for projecting shrub cover adequately described the observed patterns of development.

Although site-preparation treatments were intense, based on the magnitude of their estimated regression coefficients, their effects were relatively unimportant in the final models, based on partial R^2 values (1.5–3.3%). The effects of treatments on the cover-development patterns of the species that we studied were generally consistent with the autecological literature. Shrubs were strongly affected by burning, with maximum cover of salmonberry and salal occurring later on burned areas than on unburned areas but earlier for thimbleberry. The pattern of cover development for salmonberry and all shrubs was very similar because salmonberry constituted such a high proportion of all shrubs.

The cover-projection models represent the recovery and development of shrubs in competition with herbaceous species, hardwoods, natural conifers, and planted Douglas-fir after overstory removal and site preparation by spot clearing, burning, or spraying herbicides. Overstory removal has the overriding effect on shrub development; site-preparation treatments provide a supplemental effect by temporarily reducing cover to allow planted Douglas-fir as well as associated species to establish and develop patterns of rapid growth. In the current model formulation, complex interactions among shrubs and other species and selective browsing by animals are integrated into age and percent cover, which can be easily obtained by foresters and applied ecologists. This model is a simplification compared with existing population dynamics models, which frequently are based on number of stems or ramets (Maxwell et al. 1993). The same general formulation could be expanded to include expressions for the development of competitors, differences in site productivity, or availability of light, moisture, and nutrients.

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