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

**Steven A. Knowe, William I. Stein, and L.J. Shainsky**

**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

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**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: $C_2 = \alpha A_2^\theta (C_1/dA_1^\theta)^{A_2/A_1}$.

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:

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

where $C$ is the cover (%), $A$ is the years since disturbance, $\alpha$ is the asymptote, $\theta$ is the shape, $\beta$ is the rate, and $\varepsilon$ 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 ($\alpha$) defines curve shape:

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

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 $\theta$ and $\beta$ in eq. 2 indicate that maximum cover occurs at older ages and at higher levels, and that $\theta$ has a greater effect than $\beta$. The polymorphic cover-projection equation was developed by assuming that the rate ($\beta$) defines curve shape:

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

with terms as previously defined. Large values of $\alpha$ and $\theta$ in eq. 3 indicate that maximum cover occurs at younger ages and at higher levels; $\alpha$ affects the level and $\theta$ 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 ($\beta$) as follows:

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

where $\beta_b$ 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 $\beta_s$ 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 $\beta_z$ 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;

$$\beta_t = \beta_0 + \beta_2T_2 + \beta_3T_3 + \beta_4T_4 + \beta_5T_5 + \beta_6T_6$$

where $\beta_t$ 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 $\beta_{i0}$ terms in $\beta_b$, $\beta_s$, and $\beta_z$ represent an overall rate coefficient, and the $\beta_{i1}$ terms represent adjustments to $\beta_{i0}$ for the respective treatments. In $\beta_t$, the $\beta_0$ term represents the overall rate coefficient, and the $\beta_i$ terms represent adjustments to $\beta_0$ for specific site-preparation treatments. The same approach was used to incorporate the effects of site-preparation treatments into the shape parameter ($\theta$).

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

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**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.

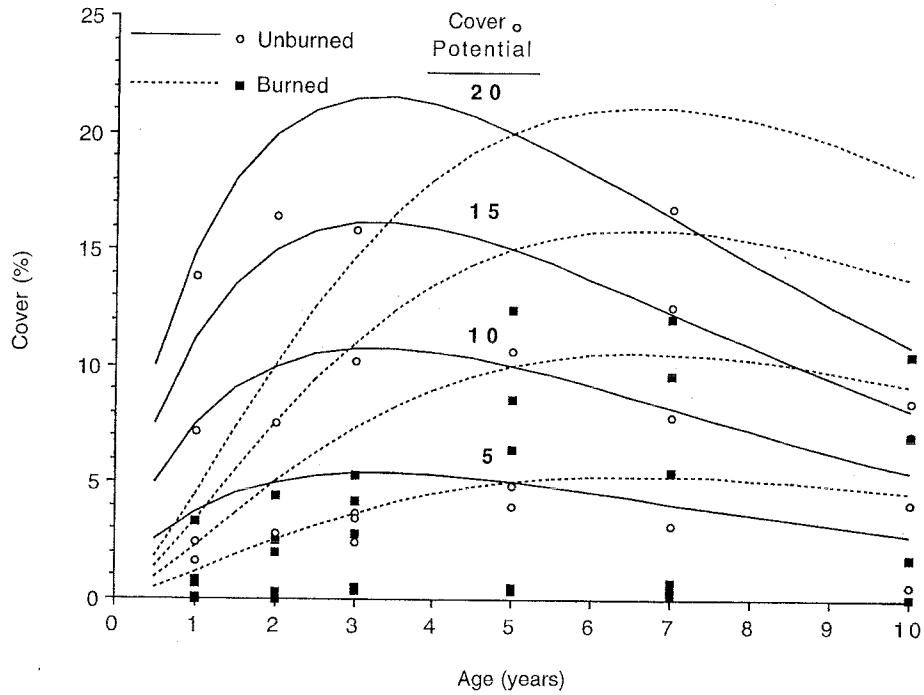


**Table 5.** Explained variation ($R^2$) and partial analysis of variance for testing the effects of site preparation on cover-development curves for thimbleberry in coastal Oregon forests.

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

($p \leq 0.0001$, 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

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**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.

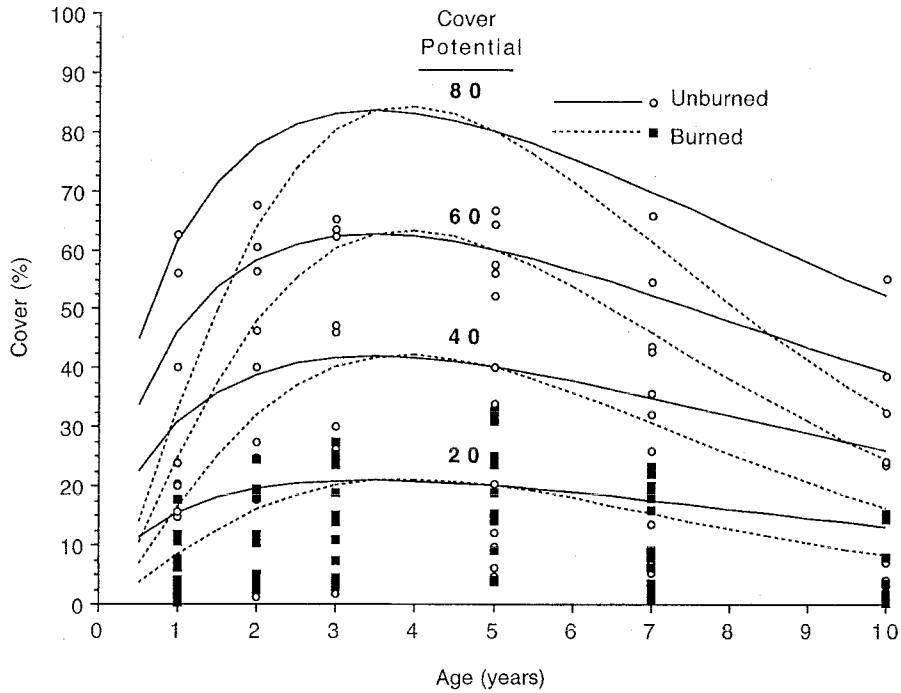


**Table 7.** Explained variation ($R^2$) and partial analysis of variance for testing the effects of site preparation on cover-development curves for all shrubs in coastal Oregon forests.

| 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

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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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