

Germination, survival, and early growth of red alder seedlings in the central Coast Range of Oregon¹

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Abstract: Effects of forest disturbance and soil moisture levels on establishment of red alder (*Alnus rubra* Bong.) seedlings were studied at four sites representing a climatic moisture gradient within the central Coast Range of Oregon. On average, there was no difference in seedling emergence between recent clearcuts and second-growth forests, but emergence was much higher on mineral soil than on organic seedbeds. Emergence, on both types of seedbed, was positively correlated with spring soil moisture conditions ($R^2 = 0.60$). Seedling survival, on the other hand, differed greatly between clearcut and forest. In clearcuts, heat and drought injuries were the primary causes of seedling mortality. In the forest, seedlings had poor vigour and quickly succumbed to pathogens, herbivores, and rain splash. First-year survival rates were strongly correlated with minimum summer soil moisture levels ($R^2 = 0.71$). Height growth of seedlings on clearcuts (2–5 cm after 1 year; 8–23 cm after 2 years) was much slower than rates typically described for red alder. Best establishment occurred on skid trails and landings, suggesting that young seedlings may suffer less from heat or moisture stress on these heavily disturbed microenvironments.

Résumé : Les effets de la perturbation de la forêt et du degré d'humidité du sol sur l'établissement des semis d'aulne de l'Orégon (*Alnus rubra* Bong.) ont été étudiés dans quatre sites distribués le long d'un gradient climatique d'humidité dans la partie centrale de la chaîne côtière en Orégon. En moyenne, il n'y avait pas de différence dans l'émergence entre les coupes à blanc et les forêts de seconde venue, mais l'émergence était beaucoup plus élevée sur le sol minéral que sur les lits de germination organiques. Sur les deux types de lits de germination, l'émergence était positivement corrélée avec les conditions d'humidité du sol au printemps ($R^2 = 0,60$). La survie des semis, par contre, différait beaucoup entre la coupe à blanc et la forêt. Dans les coupes à blanc, les dommages causés par la chaleur et la sécheresse étaient les principales causes de mortalité des semis. En forêt, les semis étaient peu vigoureux et succombaient à l'action des maladies et des herbivores et à l'éclaboussement par la pluie. Le taux de survie après la première année était fortement corrélé au degré minimum d'humidité du sol durant l'été ($R^2 = 0,71$). La croissance en hauteur des semis était beaucoup plus faible dans les coupes à blanc (2–5 cm après 1 an; 8–23 cm après 2 ans) que les taux généralement mentionnés pour l'aulne de l'Orégon. L'établissement était le meilleur sur les sentiers de débardage et les jetées, suggérant que les jeunes semis sont possiblement moins affectés par les stress causés par la chaleur et la sécheresse dans ces micro-environnements fortement perturbés.

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Introduction

Red alder (*Alnus rubra* Bong.), a dominant hardwood species along the Pacific Coast of North America, has traditionally been considered an undesirable competitor with

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and other commercially valuable conifers (Walstad et al. 1987). However, there is growing interest in commercial use of red alder and in its functional role in the ecosystem as a nitrogen fixer and key riparian species (Hibbs et al. 1994).

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Whether red alder is viewed as an undesirable competitor or as an essential component of forest ecosystems, effective management of this species requires knowledge of the ecological factors influencing its establishment.

Red alder is considered a pioneer species, associated with the early stages of forest succession following disturbance (Stettler 1978). It is highly shade intolerant and establishes best on open sites with a mineral soil seedbed (Harrington 1990). Following timber harvest, red alder regeneration commonly occurs in areas where mineral soil is exposed; it tends to be concentrated in those areas where soil disturbance is heaviest, along roadsides, skid trails, and landings (Worthington et al. 1962; Newton et al. 1968). Little if any regeneration is found under mature tree canopies (Carlton 1988). Seedlings can establish in the understory of Douglas-fir stands following disturbances such as thinning, but they rarely survive to reach maturity under a forest canopy (Ruth 1967; Berg and Doerksen 1975).

Availability of moisture appears to be critical for red alder establishment. Throughout its range, red alder occurs most frequently in riparian habitats; however, in areas of humid oceanic climate it can also be found on a wide range of upland sites and soils (Harrington 1990). Within the central Coast Range of Oregon, red alder abundance decreases sharply as one moves inland from the coast (Franklin and Dyrness 1969).

The objective of this study was to determine how disturbance and soil moisture availability affect red alder seedling establishment across a climatic gradient. We hypothesized that forest disturbance, involving removal of the forest overstory and scarification of the seedbed, is required for successful establishment of red alder seedlings, and that severe disturbance increases the likelihood of establishment. We also hypothesized that in moist environments, successful establishment can occur over a broader range of seedbed conditions than in drier environments, thus accounting for the greater abundance and wider distribution of red alder in moist areas. We tested these hypotheses by examining red alder seed losses, germination, emergence, and 1- and 2-year seedling survival and growth on undisturbed and disturbed seedbeds in recent clearcuts and adjacent second-growth forests.

Methods

Study sites

Four sites, two each on south (S) and north (N) aspects, were selected within the central Coast Range of Oregon. The interior sites (IS and IN) were located on the eastern slopes at Woods Creek, near Philomath (44°32'N, 123°28'W; 400 m elevation; 1500–1700 mm annual precipitation); the coastal sites (CS and CN) were on the western slopes near Siletz (44°45'N, 123°7'W; 200 m elevation; 2000–2500 mm annual precipitation). The four sites (IS, IN, CS, and CN) were chosen to represent a climatic gradient of increasingly favourable conditions for red alder. Each study site included a 1- to 2-year-old clearcut and a second-growth forest with similar slope, aspect, and soil type (Haeussler 1987). The cover on clearcut sites was a discontinuous low growth of shrubs and herbs with no natural regeneration of red alder. The cover on forest sites

was pure Douglas-fir at IS (74% overstory cover, 80 year old) and IN (77% overstory cover, 50 years old), a Douglas-fir – red alder mixture at CS (86% overstory cover, 45 year old), and predominantly red alder with some Douglas-fir at CN (62% overstory cover, 45 years old).

Seedbed study installation

During the winter of 1985–1986 we located areas of undisturbed forest floor within the clearcut and forest at each site. The following seedbed treatments were randomly applied to eighteen 1.5 × 1.5 m plots in the clearcut and in the forest: U, undisturbed (forest floor intact); M, moderate disturbance (all aboveground vegetation and surface organic matter removed to expose the mineral soil); and H, heavy disturbance (all aboveground vegetation, surface organic matter, and upper 8 cm of mineral soil removed). Three replicates of each seedbed treatment were randomly selected for seeding in 1986, and another three were left until 1987.

In 1987, because first-year results indicated no significant differences between the M and H treatments for any seedling parameters, we combined these two into a single “disturbed” treatment (D), replicated six times. We redisturbed these unseeded plots to ensure that the mineral soil was freshly exposed. We also increased replication of the U treatment to six by locating three more undisturbed plots in the clearcut and forest at each site.

On each clearcut, we randomly located additional 1.5 × 1.5 m plots on areas of severe logging disturbance adjacent to the U and D plots: S, skid trails (surface soil layers removed during logging, subsurface layers compacted by repeated skidding of logs); L, landings (CS and CN sites only) (surface material pushed aside and replaced with a discontinuous layer of coarse gravel, soil compacted by repeated machine traffic). Three S plots were located on each clearcut in 1986. In 1987, six S plots were located on each clearcut, and six L plots were located on the CS and CN clearcuts.

Before sowing, each plot was divided into quadrants. One randomly selected quadrant was used to sample soil moisture and bulk density. On another (caged subplot), seeds were sown in a circular cage designed to exclude vertebrate seed predators (5-mm mesh hardware cloth, 60-cm diameter with 25-cm sides and a removable mesh lid). In 1986, seeds were also sown within an uncaged 60 cm diameter circle located in the third randomly chosen quadrant (uncaged subplot). No uncaged subplots were sown in 1987. The fourth quadrant (unseeded subplot) was monitored for volunteer red alder seedlings.

Environmental measurements

Soil moisture was determined gravimetrically on 75- to 150-g samples of the <2 mm fraction (Black et al. 1965) taken from 0–5 cm depth within the mineral soil on each plot at monthly intervals from March to September both years. Samples were also taken from 8–12 cm depth on all plots with surviving seedlings in August and September 1986 and monthly on all plots from May to September 1987. The pressure-plate technique (Richards 1949) was used to determine soil water retention values at saturation, –0.33 MPa, and –1.5 MPa for composite samples of mineral soil (0–10 cm depth) from each clearcut and forest.

Soil and air temperature measurements were taken periodically throughout the growing season (Haeussler 1987).

Overstory canopy was estimated in August 1986 by analysing digitized fish-eye photographs (Chan et al. 1986) taken 1 m above five randomly selected plots within each clearcut and forest, with the camera pointing upwards. Percent cover (visual estimate) of understory vegetation was recorded on all seeded 60 cm diameter subplots at monthly intervals during each growing season.

Seed collecting, testing, and sowing

Seeds were collected within a 5-km radius of the study sites in late October and November of 1985 and 1986. Initial viability was determined by germinating four replicates of 100 seeds each in a chamber set for 25°C days and 18°C nights and a 12-h photoperiod (Campbell and Ching 1980; Radwan and DeBell 1981). Caged and uncaged subplots were sown with 200 or 250 seeds (depending on initial viability) in mid-January of 1986 or 1987.

Seed germination and seed losses

In 1987, 10 removable germination containers (80 total) were randomly allocated to the U and D seedbed treatments in both the clearcut and forest at the IN and CN sites. Cylinders (8 cm diameter, 5 cm high) were constructed from polyvinylchloride pipe with fine nylon mesh glued to the base. A core of forest floor or mineral soil was removed from the plot and placed intact into the container. The container was replaced in the core hole with its upper rim protruding 1 cm. Fifty to 70 seeds were sown into each container. A protective cage made of 6-mm plastic mesh (8 cm square, 6 cm high) was staked over each germination container to exclude vertebrates.

The containers were installed and sown on the same date as the caged subplots. Seedlings and empty seed coats were removed and tallied as seedlings emerged. Containers were taken from the field after no further emergence was observed; on clearcuts they were removed after 95 days and in the forest after 137 (CN) and 142 (IN) days.

Containers were refrigerated at 1–4°C until processing. Seeds were retrieved first manually, then by sieving, and finally by flotation in tap water. Each seed was inspected under a dissecting microscope and categorized: (1) seedling emerged, including those removed in the field (split, empty seed coat); (2) germinated but not emerged (dead radicle protruding); (3) partially consumed by invertebrates; (4) no longer viable (embryo visibly deteriorated); (5) apparently viable.

The apparently viable seeds (category 5) were transferred to a germination chamber. Seeds that germinated in the chamber remained in category 5; seeds that failed to germinate were reassigned to category 4 (no longer viable). An adjustment factor was used to account for initial seed viability.

Seedling assessments

At 1- to 2-week intervals from February through mid-September, we counted seedlings on all caged, uncaged, and unseeded subplots. Live seedlings were marked with a 5-cm plastic stake. Apparent causes of seedling mortality were recorded. Lids were removed from the caged subplots in early May after the period of peak seedling emergence. Caged subplots sown in 1986 were monitored during

1987 for new seedling emergence from stored seed. However, second-year emergence could not be monitored on the CS and CN forest sites because of new seeds from alder trees in the overstory.

In late September of 1986 and 1987, we measured seedling height and basal diameter and recorded damage and degree of overtopping by vegetation. In November 1987, we carefully excavated root systems of 106 first-year seedlings (3–16 per plot), measured root and shoot length and the number of root nodules, and noted the presence of mycorrhizal root tips. Second-year seedlings were also examined but could not be excavated intact because of their extensive root systems.

Data analysis

Vertebrate seed predation, seedling emergence (adjusted for volunteers), and survival percentages were normalized with the arcsine transformation prior to ANOVA. Seedling data were analysed separately for each clearcut and forest by treating each group of plots as a completely randomized design with three (1986) or six (1987) replications of each seedbed treatment. To find general trends across all four study sites, we used a randomized block design with individual plot data pooled to produce a single treatment mean for each seedbed. ANOVAs were carried out both with and without data from skid trails and landings. When only U and D plots were considered, the design was a split plot with the paired clearcut and forest units at each site as main plots and seedbed treatments as subplots. When S and L plots were included, the experiment was treated as a single-factor factorial. For unequal sample sizes, a weighted residual sum of squares, based on either the number of subplots or the number of seedlings per plot, was used in the ANOVA. Orthogonal contrasts were used to separate main effect means where more than two treatments were compared (Peterson 1985).

Linear regression was used to examine the relationship between seedling emergence (caged subplots only) and a variety of indices of spring soil moisture (maximum, minimum, mean, by month, etc.). Forest cover (i.e., clearcut vs. forest) and seedbed treatments (U, D, S, and L) were used as indicator variables in the regression (Neter et al. 1983).

We used two-stage sample censoring (Heckman 1976) to model the effect of forest disturbance and soil moisture on seedling survival. First we used the probit technique to predict whether at least one seedling per plot would survive. Then we predicted the rate of survival, given that at least one seedling survived, using weighted least squares regression. Both continuous (soil moisture indices, overstory and understory vegetation cover) and categorical (forest cover, seedbed) independent variables were used.

We used the χ^2 statistic in a contingency table analysis (Snedecor and Cochran 1967) to analyse germination and seed loss data from the germination containers and causes of seedling mortality on the subplots.

Results

Vertebrate seed predation

Vertebrate seed predation (Table 1) was significantly greater than 0 at all four sites in 1986 (p -values between 0.0001 and 0.005). Fewer seedlings emerged on uncaged subplots

Table 1. Mean (with standard error given in parentheses) vertebrate seed predation (%), estimated as the difference in emergence between individually paired caged and uncaged subplots (1986 only).

Treatment	Interior		Coast	
	South	North	South	North
Clearcut				
Undisturbed	46.2 (46.2)	74.7 (20.9)	32.1 (32.1)	20.6 (13.6)
Disturbed	79.5 (8.4)	91.4 (3.8)	70.4 (10.6)	46.1 (7.0)
Forest				
Undisturbed	42.8 (21.5)	56.1 (17.1)	0.0 (0.0)	46.6 (25.2)
Disturbed	70.1 (10.2)	75.3 (4.9)	75.5 (5.9)	88.0 (3.5)

Table 2. Mean (with standard error given in parentheses) seedling emergence, expressed as a percentage of the viable seed sown.

Treatment	Year	Subplot	Interior		Coast	
			South	North	South	North
Clearcut						
Undisturbed	1986	Caged	2.4 (2.4)	4.8 (3.7)	7.2 (5.5)	49.5 (16.8)
		Uncaged	0.9 (0.7)	0.7 (0.4)	2.0 (1.4)	48.0 (7.4)
	1987	Caged	7.0 (2.9)	1.7 (0.7)	7.3 (3.2)	7.0 (1.8)
Disturbed	1986	Caged	23.8 (2.5)	43.0 (10.0)	36.6 (7.3)	65.4 (8.6)
		Uncaged	5.5 (2.4)	4.3 (2.3)	8.9 (2.8)	35.1 (5.5)
	1987	Caged	22.7 (5.7)	6.9 (2.3)	27.3 (5.4)	47.4 (6.4)
Skid trails	1986	Uncaged	6.3 (1.6)	8.3 (1.1)	18.2 (9.1)	40.8 (9.0)
		Caged	10.0 (3.3)	17.4 (6.1)	47.0 (9.8)	40.8 (10.1)
Landings	1987	Caged	—	—	35.3 (9.0)	48.4 (11.1)
Forest						
Undisturbed	1986	Caged	37.6 (5.4)	40.0 (2.4)	1.7 (0.9)	11.6 (4.3)
		Uncaged	21.9 (9.2)	17.5 (7.1)	6.5 (3.5)	4.9 (2.0)
	1987	Caged	2.5 (0.6)	13.7 (5.5)	3.1 (1.4)	1.2 (0.8)
Disturbed	1986	Caged	27.7 (8.0)	42.5 (5.6)	52.1 (4.5)	58.9 (14.1)
		Uncaged	10.0 (4.9)	10.6 (2.6)	13.7 (4.2)	8.2 (2.6)
	1987	Caged	32.1 (4.6)	57.4 (7.9)	54.2 (15.3)	23.4 (4.7)

than on adjacent caged subplots on 15 of 24 U plots and on all D plots (Table 2). Analysis of pooled data from the four sites showed that, on average, there was no difference in predation rate between clearcut and forest ($p = 0.96$) and that the effect of seedbed disturbance on vertebrate seed predation was highly significant ($p = 0.0001$) and was independent of forest cover ($p = 0.78$). The predation rate averaged 38% on U plots and 74% on D plots.

Seedling emergence

On clearcuts, seedling emergence began in late February of 1986 and early March of 1987; it proceeded rapidly and was generally complete by mid-April. In both years, the final seedlings emerged later on the CN (coastal, north-facing) clearcut (early May) than on the other clearcuts (middle to late April). Within the forest, emergence began approximately 1 month later than in corresponding clearcuts

and continued well into June. No seedlings emerged in the fall after the summer drought ended. However, in the spring of 1987, up to 10 seedlings per subplot ($\bar{x} \leq 5$) emerged from the 1986 sowing. This emergence accounted for up to 0.5% of the ungerminated seed in the four clearcuts; in the IS and IN forests the rates were 1.2 and 2.8%, respectively. All but one of the late-emerging seedlings came from a disturbed seedbed.

Fewer seedlings emerged on U than on D seedbeds (Table 2), despite heavier vertebrate seed predation on D plots (Table 1). When only caged subplots were considered, emergence on undisturbed seedbeds averaged 10.6%, whereas on disturbed seedbeds the average was 40.4%. Across all sites, the effect of soil disturbance (seedbed) was highly significant ($p = 0.0017$), but there was no significant difference in mean emergence between clearcuts and forests ($p = 0.51$). Overall emergence was significantly higher in 1986 than in 1987 (38.2 vs. 19.7%; $p = 0.047$). There were no significant factor interactions.

On skid trails and landings, rates of seedling emergence ranged from 6.3 to 48.4% (Table 2) and were not significantly different from those on uncompacted D plots ($p \geq 0.44$).

Regression analysis indicates that mineral soil exposure and soil moisture were the two significant factors affecting seedling emergence on caged subplots. The indicator variable separating plots without mineral soil exposure (U) from those with (D, S, and L) was highly significant ($p = 0.0002$), but indicator variables separating clearcut from forest plots, and uncompacted (U and D) from compacted (S and L) plots, did not contribute significantly to the model. There was also a strong positive correlation between seedling emergence and the mean moisture content of 0–5 cm depth soil samples taken between mid-March and June (Fig. 1). Sixty percent of the variation in seedling emergence is explained by the model equations

$$[1] \quad y = 33.4 + 0.736x$$

for D seedbeds, and

$$[2] \quad y = -16.6 + 0.736x$$

for U seedbeds. This model suggests that emergence increases linearly with increasing soil moisture levels, regardless of substrate; however, at any given level of soil moisture, more seedlings will emerge on D than on U seedbeds. Although the relationship for U seedbeds appears curvilinear (Fig. 1), linearizing transformations on x did not significantly improve the model. On U seedbeds, only plots that averaged above the saturation level (soil moisture of 65–80% or greater) (Table 3) had high rates of seedling emergence (>60%), yet even some of these very wet plots had poor emergence rates (<20%).

Seed germination and seed losses

Seed recovery in the germination containers ranged from 35.0 to 86.6% of all seeds sown. The results presented below and in Fig. 2 represent percentages of recovered seed only.

Total seed germination ranged from 7.0% (CN forest, U seedbeds) to 86.8% (CN clearcut, D seedbeds). As

Fig. 1. Effect of mean March–June soil moisture content (0–5 cm depth) on red alder seedling emergence. $R^2 = 0.6007$, $p = 0.0001$.

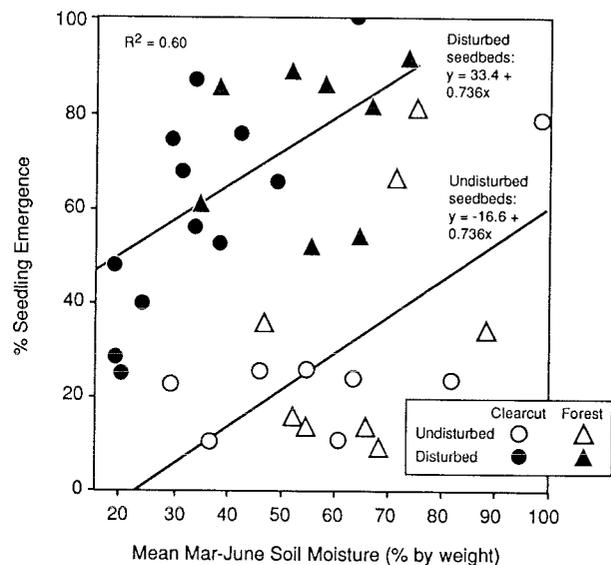


Fig. 2A illustrates, there is a general trend of increasing seed germination with increasing disturbance severity. However, many of the germinants died before reaching the soil surface or expanding their cotyledons, particularly in clearcuts. In clearcuts, between 35 and 48% of germinated seeds failed to emerge; in the forest, only 3 to 18% failed.

In both clearcuts and forests (Fig. 2B), combined losses to invertebrates and decay were significantly higher ($p < 0.001$ in all cases) on U than on D seedbeds. Overall, more than 60% of the seeds on U seedbeds appeared to have been lost to soil organisms, whereas on D seedbeds, only 20% of seeds were lost. Losses due to invertebrate seed predation were the most dramatic. For example, on the IN clearcut, more than 51% of seeds on U plots were partially consumed by invertebrates, compared with only 3% of seeds on D plots. These results underestimate the true magnitude of invertebrate predation because the tally included only those seeds from which fragments of the seed coat could be recovered.

Viable, ungerminated seeds ranged from 5.5 to 24.6% (Fig. 2C). Except in the CN forest, more viable seeds remained on D plots than on corresponding U plots, presumably because of lower predation and decay. There were also more viable seeds left under a forest canopy than in clearcuts, particularly at CN, where the forest (a red alder stand) had 2.5–7 times as many ungerminated viable seeds as the adjacent clearcut (23.3 vs. 3.3% on U plots, $p = 0.001$; 13.9 vs. 5.9% on D plots, $p = 0.003$).

Mortality

Causes of seedling mortality differed significantly among sites, between years and seedbeds and, most significantly, between clearcuts and forests (Table 4). For example, first growing season mortality attributed to heat and drought averaged 58.3% of total mortality in clearcuts, but only 5.2% (drought only) in forests. During the first winter,

Table 3. Mean (with standard error given in parentheses) soil moisture levels (0–5 cm depth) between mid-March and early July on undisturbed, disturbed, and skid trail plots, and moisture retention values for an uncompacted sample of each soil type at saturation, –0.3 MPa, and –1.5 MPa.

	Year	Interior		Coast	
		South	North	South	North
Soil moisture levels (%)					
Clearcut					
Undisturbed	1986	61.7 (3.6)	82.7 (16.7)	63.7 (3.9)	99.2 (24.5)
	1987	29.8 (0.7)	37.0 (0.8)	46.0 (1.9)	55.4 (3.9)
Disturbed	1986	38.3 (2.6)	35.0 (1.0)	50.1 (1.9)	65.0 (3.4)
	1987	19.8 (0.6)	21.1 (0.7)	35.0 (0.8)	43.4 (0.9)
Skid trail	1987 only	20.1 (1.4)	25.1 (1.9)	31.5 (1.0)	32.3 (1.9)
Forest					
Undisturbed	1986	76.8 (3.4)	72.0 (14.2)	66.0 (2.1)	89.2 (4.9)
	1987	47.1 (1.0)	52.0 (1.5)	54.6 (1.8)	69.3 (6.1)
Disturbed	1986	59.3 (5.9)	65.4 (2.6)	67.5 (2.5)	74.5 (3.7)
	1987	39.6 (1.7)	35.4 (1.0)	52.6 (1.3)	56.8 (1.9)
Moisture retention values (%)					
Clearcut					
Saturation		68	83 ^a	68	66
–0.3 MPa		41	45	41	41
–1.5 MPa		24	25	25	25
Forest					
Saturation		68	83	72	68
–0.3 MPa		41	45	48	42
–1.5 MPa		24	25	25	27

^aHydrophobic sample with abundant fungal mycelia.

Table 4. Apparent causes of seedling mortality in clearcuts and forests (% within rows).

	Sample size	Missing	Decay or low light	Heat + drought ^a	Erosion	Frost	Litter or vegetation	Animals	Other	Total (within row)
Clearcut										
First growing season	3201	21.5	12.2	58.3	0.9	1.8	0.3	4.4	0.5	100.0
Overwinter	72	16.7	8.3	0.0	40.3	20.8	9.7	0.0	4.2	100.0
Second growing season	70	18.6	0.0	21.4	2.9	2.9	40.0	5.7	8.6	100.0
Mean	3343	21.3	11.9	56.3	1.8	2.3	1.3	4.3	0.7	100.0
Forest										
First growing season	5288	43.0	38.2	5.2	9.0	0.0	0.0	4.3	0.2	100.0
Overwinter	17	23.5	47.1 ^b	0.0	0.0	0.0	17.6	0.0	11.8	100.0
Second growing season	2	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	100.0
Mean	5307	43.0	38.2	5.2	9.0	0.0	0.1	4.3	0.2	100.0
Overall mean	8650	34.6	28.0	24.9	6.2	0.9	0.6	4.3	0.4	100.0

Note: Results combine data from all four study sites. Overwinter and second growing season data are for the 1986 cohort only.

^aMortality due to heat lesions was observed in clearcuts only.

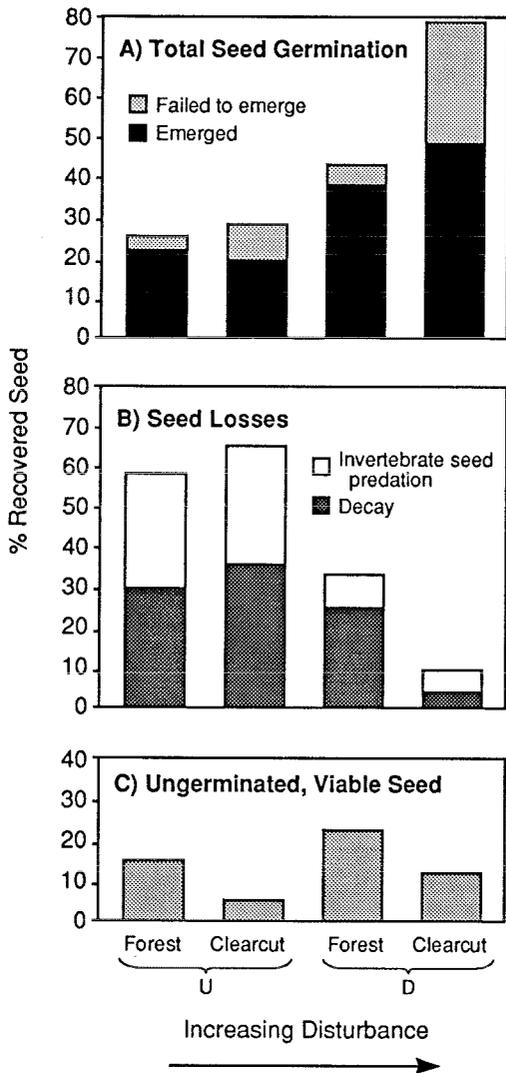
^bThese seedlings “rotted” away. Death may have been caused by freezing of succulent, unsubserved tissues.

soil erosion, frost heaving, and freezing together caused 61.1% of all mortality in clearcuts; crushing under litter or vegetation (40.0%) was the primary mortality factor during the second growing season.

In forests, it was difficult to determine the actual cause of mortality of the frail, succulent seedlings. The largest

category of seedlings (43.0%, on average) simply disappeared, possibly because of herbivory. The second largest category (38.2% average) was labelled “decay and (or) low light.” Most of these seedlings appeared healthy until May; then, while the soil was still moist (40–70% by weight), clusters of seedlings began dying with symptoms

Fig. 2. Seed germination and losses in germination containers on forest and clearcut sites and undisturbed (U) and disturbed (D) seedbeds. (A) Total seed germination, including emerged seedlings and those that failed to emerge (i.e., pre-emergence mortality). (B) Seed losses to invertebrate predation and decay. (C) Ungerminated seeds that remained viable at the end of the experiment.



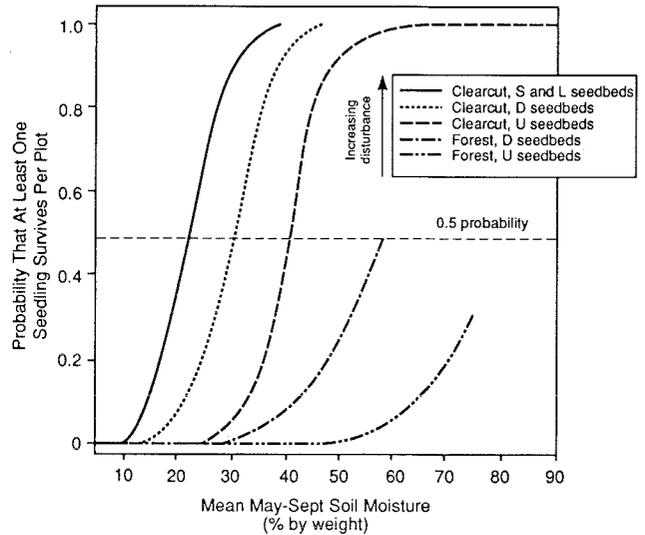
similar to damping-off (limp, slimy, brown root tips). However, no known pathogen could be isolated from a sample of affected seedlings (S. Fischer, personal communication, June 1987). A third important mortality factor was soil erosion and rain splash (range 4–31%; 9.0% average). Of those forest seedlings surviving to the end of the first growing season, all but two died during the first winter, from a combination of litter fall, slow decay, and perhaps freezing of the succulent tissues.

Seedling survival

First- and second-year seedling survival rates, summarized in Table 5, did not lend themselves well to ANOVA because of unequal sample sizes and numerous plots with no survival.

At the interior sites, first-year survival on U and D seedbeds was nil in both years, both in clearcuts and forests.

Fig. 3. Probit model to predict first-year red alder survival as a function of mean May–September soil moisture (0–5 cm depth). S, skid trails; L, landings; D, disturbed; U, undisturbed. Average likelihood = 0.75, correct predictions = 90.5%, *n* = 199.



Survival on coastal clearcut U and D seedbeds averaged 1.7–31.4%. On coastal forest sites there was no survival on U seedbeds; on D seedbeds, survival ranged from 0.2 to 1.6%. Survival on the CN clearcut (8.8–31.4%) was higher than on the CS clearcut (1.7–14.5%), particularly in 1987, when warm, dry early spring weather killed many seedlings on the south aspect. On the CN clearcut there was no significant difference in first-year survival between U and D seedbeds either year. On CS in both years, survival on the U plots was significantly ($p < 0.0065$) higher than on D plots.

The highest rates of first-year seedling survival were observed on skid trails (Table 5); at IN, the only seedlings that survived beyond midsummer in either year were on these trails. At CS, first-year survival on skid trails and landings was higher than on either U or D seedbeds. At CN, survival on skid trails was exceptionally high (49.6%) in 1986, but in 1987 neither skid trails nor landings were significantly different from U and D.

Two models of first-year seedling survival were produced. The first stage probit model (Fig. 3) predicts the probability that at least one seedling per plot will survive to the end of the first growing season. It shows that survival depends on both the degree of forest disturbance and the amount of moisture available in surface soil layers. The model had an average likelihood of 0.75 and correctly predicted seedling survival (yes or no) on 180 of 199 sample plots (90.5%). Indicator variables separating clearcut from forest, undisturbed (U) from disturbed (D, S, and L) seedbeds, and uncompacted (D) from compacted (S and L) disturbed seedbeds were all highly significant ($p < 0.01$). Seedling survival also showed a strong positive correlation with mean May to September soil moisture in the upper 5 cm of soil. As Fig. 3 illustrates, the probability of survival increases logistically with increasing soil moisture. However, for any given level of soil moisture, the

Table 5. First- and second-year survival of red alder seedlings (%).

Treatment	Cohort	First year				Second year			
		IS	IN	CS	CN	IS	IN	CS	CN
Clearcut									
Undisturbed	1986	0	0	14.5	9.2			1.2	3.9
	1987	0	0	7.3	31.4				
Disturbed	1986	0	0	3.7	8.8			1.5	5.7
	1987	0	0	1.7	27.0				
Skid trails	1986	0	5.9	24.8	49.6		0	14.9	36.5
	1987	0	0.4	9.4	26.0				
Landings	1987			12.8	9.8				
Forest									
Undisturbed	1986	0	0	0	0				
	1987	0	0	0	0				
Disturbed	1986	0	0	1.6	0.2			0	0.1
	1987	0	0	0.3	0.4				

Note: Second-year survival rates are for the 1986 seedling cohort only. IS, interior south; IN interior north; CS, coastal south; CN, coastal north.

probability of survival is higher on seedbeds subjected to greater disturbance. Thus, seedlings in clearcuts are more likely to survive than seedlings in the forest, and within these two environments, the probability of survival increases as mineral soil is exposed and compacted.

The second-stage regression model accounts for 71% of the variation in mean first-year survival rates on plots where at least one seedling survived (Fig. 4). Soil moisture levels and forest cover (clearcut or forest) serve as independent variables in the model. Neither the correction term (λ_i) obtained from the first-stage probit model (Heckman 1976) nor environmental variables such as vegetation cover, soil disturbance, and soil compaction contributed significantly to the model. The inclusion of soil moisture levels was highly significant ($p = 0.001$), and highest correlations were obtained when the minimum moisture content of soil samples taken between March and September was used as an index of soil moisture availability. There was a strong interaction between soil moisture and forest cover ($p = 0.0001$); the effect of soil moisture on seedling survival is much stronger in clearcuts ($y = -2.5 + 0.77x$) than in the forest ($y = -2.5 + 0.132x$) (Fig. 4).

After two growing seasons, survival on the coastal clearcuts was below 6% on all U and D plots (Table 5), and none of the differences was statistically significant. However, on S plots, 2-year survival (14.9% at CS; 36.5% at CN) was significantly higher ($p \leq 0.001$) than on corresponding U or D plots. Only one seedling remained alive on the coastal forest plots (0.1% survival; Table 5).

Seedling growth and development

After one growing season, the mean heights of seedlings in clearcuts ranged from 1.8 to 4.7 cm (Table 6); those in the forest were between 0.3 and 2.0 cm tall. Mean basal

diameters on all sites were 0.4–0.7 mm. First-year root length averaged 8–12 cm. Nodulation began just below the root collar when the first true leaves were developing (S. Haeussler, unpublished data). All excavated seedlings had nodules except those rooted in decaying wood. Virtually all roots, on all substrates, were ectomycorrhizal. At 1 year, there were no consistent differences in seedling size among seedbeds, sites, and years, but seedlings on L plots tended to be larger and (or) sturdier than the others, while S plot seedlings were typically short but sturdy. Twelve of the 14 largest 1-year-old seedlings were found either on landings or on skid trails.

Two-year-old seedlings in clearcuts had mean heights ranging from 8.3 to 22.9 cm (Table 6) and mean basal diameters of 1.0–3.2 mm. Roots were 50 to 75 cm long. Most seedlings were still well below the height of associated shrubs and herbs. At both CS and CN, second-year seedlings on U plots were significantly ($p \leq 0.01$) smaller in height and diameter than those on D and S plots, apparently because of greater vegetation interference. The S plot seedlings were significantly ($p < 0.000\ 01$) taller than D plot seedlings at CN, but not at CS. However, the 15 largest 2-year-old seedlings in the study were all found on skid trails.

Discussion

Results of the study confirm that forest disturbance, involving both removal of the forest canopy and exposure of a mineral soil seedbed, is needed for red alder establishment. In general, increasing the severity of disturbance increases the likelihood of successful seedling establishment (Figs. 1–4). However, it is apparent that the role of disturbance is complex; it differentially affects the various

stages of seedling establishment and involves numerous environmental factors: light, moisture, and temperature properties of the seedbed, interference from associated vegetation, predators, and pathogen activity.

We found no difference in seedling emergence between clearcuts and forests, but emergence of both protected and unprotected seed was higher on disturbed mineral soil seedbeds than on undisturbed organic seedbeds (Table 2; Figs. 1 and 2A). For early survival, on the other hand, we found a strong contrast between clearcuts and forests, but comparatively little difference between mineral soil and organic seedbeds, except where soils were compacted (Table 5; Figs. 3 and 4).

How disturbance affects seed losses

Seeds on undisturbed seedbeds are subject to much heavier losses from invertebrates and pathogens than those on disturbed seedbeds (Fig. 2B). Red alder seeds have thin seed coats that offer little protection against predatory and decay organisms. It may be that freshly exposed mineral soil has fewer destructive organisms than an undisturbed forest floor. Seeds on mineral soil seedbeds therefore have a greater likelihood of remaining viable until conditions become favourable for germination. In our germination containers, we found more viable, ungerminated seeds after 5 months in the field on disturbed than on undisturbed seedbeds (Fig. 2C), and on our caged subplots all but one of the seedlings that emerged after more than a year in the soil were on disturbed seedbeds.

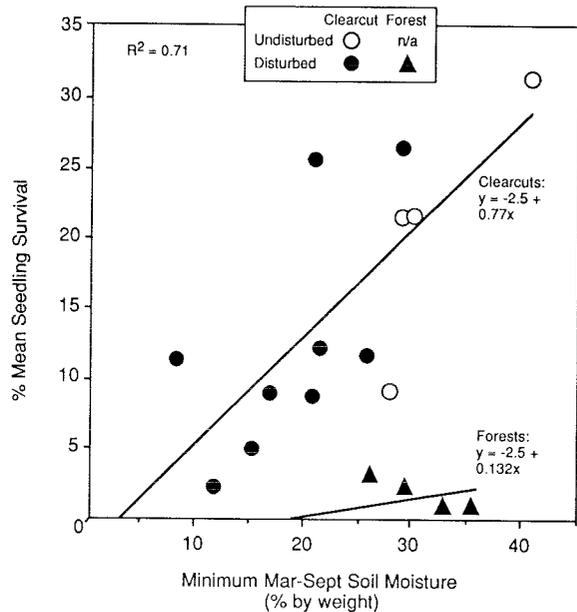
Vertebrate predators such as small mammals and birds also consume large numbers of red alder seeds (Table 1), but in this case, losses were higher on disturbed than on undisturbed seedbeds, presumably because the seeds were easier for seed eaters to locate.

How disturbance affects seed germination

On undisturbed seedbeds, red alder seeds are prone to drying out unless conditions are exceptionally moist (Minore 1972; Fig. 1; also, compare 1986 and 1987 emergence in Table 2). Undisturbed plots have moister mineral soil than disturbed plots (Table 3), but the organic surface material surrounding the seeds is subject to rapid fluctuations in moisture content (Baker 1950); under such conditions, seed germination is likely to be poor. McVean (1955) demonstrated that seeds of European alder (*Alnus glutinosa* (L.) Gaertn.) are sensitive to even minor changes in water availability, and we have observed the same phenomenon in the laboratory with red alder. Continuously moist conditions with relatively minor fluctuations in temperature and evaporative potential are probably necessary for high rates of red alder emergence on organic seedbeds.

The low rate of red alder emergence on undisturbed seedbeds may also be due to the inhibitory effect of light that has filtered through leaf litter, moss, or broad-leaved vegetation (Bormann 1983; Haeussler and Tappeiner 1993). Red alder seed is phytochrome active, and germination is inhibited by light conditions in which far-red wavelengths predominate over red wavelengths, conditions typically found beneath leaf litter, understory vegetation, or a red alder canopy.

Fig. 4. Effect of minimum March–September soil moisture (0–5 cm depth) on mean first-year red alder survival on plots where at least one seedling survived. (No undisturbed forest plots had surviving seedlings.) $R^2 = 0.7055$, $p = 0.0002$.



How disturbance affects early survival

Early survival of red alder seedlings depends on a different set of factors than seedling emergence. There are major differences in mortality factors and survival rates between clearcuts and forests (Tables 4 and 5, Figs. 3 and 4).

In clearcuts, early survival appears to depend on protection from heat, injury, or drought. There is sufficient light to maintain growth, herbivores and pathogens appear to be less important than in forests, and there is little mortality from rain splash because the raindrops are relatively small.

Under a tree canopy, red alder seedlings survive poorly, as also noted by Ruth (1967, 1968) and Harrington (1990). The ability of a species to establish in an undisturbed forest understory is closely correlated with seed size (Salisbury 1942). Unlike large-seeded Pacific Coast hardwoods such as bigleaf maple (*Acer macrophyllum* Pursh) (Fried et al. 1988) or tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) (Tappeiner et al. 1986), red alder lacks sufficient seed reserves to permit root and shoot growth under low light conditions. The tiny germinants are highly susceptible to herbivory, fungi, and rain splash and are too fragile to penetrate litter layers and resist mechanical damage and smothering by debris. Although a mineral soil seedbed may slightly improve a seedling's odds of short-term survival in the forest (Table 5, Fig. 3), such differences are unlikely to be of ecological significance because these seedlings cannot, ultimately, persist beneath a closed forest canopy.

Skid trails and landings

We initially believed that the often-observed success of red alder on skid trails, landings, and roadsides could be explained by lack of competition from other (non-nitrogen-

Table 6. Mean (with standard error given in parentheses) first- and second-year height (cm) and basal diameter (mm) of red alder seedlings.

Treatment	Cohort	IN			CS			CN		
		Sample size	Height (cm)	Diam. (mm)	Sample size	Height (cm)	Diam. (mm)	Sample size	Height (cm)	Diam. (mm)
First-year growth										
Clearcut										
Undisturbed	1986	0			7	2.8 (0.4)	0.4 (0)	92	1.8 (0.1)	0.4 (0.01)
	1987	0						16	3.2 (0.3)	0.4 (0.02)
Disturbed	1986	0			25	4.7 (0.4)	0.5 (0.01)	136	1.8 (0.1)	0.5 (0.01)
	1987	0						110	2.5 (0.1)	0.5 (0.01)
Skid trails	1986	3	3.0 (0.9)	0.7 (0.1)	31	1.9 (0.2)	0.6 (0.02)	94	2.8 (0.2)	0.6 (0.03)
	1987	0						82	3.0 (0.2)	0.5 (0.02)
Landings	1987				26	4.3 (0.4)	0.7 (0.06)	29	4.6 (0.5)	0.6 (0.04)
Forest										
All seedbeds	1986	0			16	1.6 (0.1)	0.4 (0.03)	3	1.6 (0.2)	0.6 (0.1)
	1987	0			3	2.0 (0.2)	0.4 (0)	1	0.3 (0)	0.4 (0)
Second-year growth										
Clearcut										
Undisturbed	1986	0			2	10.9 (0.3)	1.0 (0.4)	57	8.3 (0.6)	1.1 (0.1)
Disturbed	1986	0			11	20.0 (2.9)	2.1 (0.4)	97	12.6 (0.8)	1.8 (0.1)
Skid trails	1986	0			21	16.5 (1.9)	2.9 (0.4)	68	22.9 (2.7)	3.2 (0.3)
Forest										
All seedbeds	1986	0			0			1	2.1 (0)	0.4 (0)

Note: IN, interior north; CS, coastal south; CN, coastal north.

fixing) plant species. However, the rates of early survival we observed on clearcuts appear to be independent of the effects of other vegetation. In our study, higher survival rates on compacted seedbeds were most evident early in the first growing season when both compacted and uncompacted seedbeds were virtually competition free (S. Haeussler, unpublished data). If anything, overtopping vegetation enhanced early survival by providing shade.

The high early survival rates on skid trails and landings within clearcuts (Table 5, Fig. 3) suggest that soil compaction must somehow protect red alder seedlings from heat injury or drought. Soil compaction increases both the thermal conductivity and volumetric heat capacity of soils, thus protecting seedlings from extreme fluctuation in surface soil temperatures (Cochran 1969). Compaction may also increase moisture availability in surface soil layers by reducing macropore volume, thereby improving capillary action and slowing evaporation (Lull 1959).

Differences in soil ecology are another possible explanation for the superior performance of red alder on skid trails and landings compared with less heavily disturbed seedbeds. The survival and fitness of red alder in natural ecosystems is strongly dependent on root symbioses with nitrogen-fixing actinomycetes (*Frankia* spp.) and a limited number of mycorrhizal fungus species (Molina et al.

1994). Perhaps the early development of these symbioses is enhanced on severely disturbed seedbeds by lack of competition from other microbes.

Climatic effects on red alder distribution

Our results support the hypothesis that in moist environments, successful red alder establishment can occur over a broader range of seedbed conditions than in drier environments, especially on clearcuts. In forests, where seedling establishment is poor because of insufficient disturbance, such factors as predators, pathogens, and overtopping vegetation apparently override the effect of moisture.

The four study sites represented a climatic moisture gradient, but temperature extremes may also have been important. There was less temperature variation at the coastal sites than in the interior, particularly from June onwards, when morning fogs were common along the coast (Haeussler 1987). Furthermore, the south-facing coastal clearcut had consistently higher temperature maxima than the north-facing coastal clearcut.

Our seedling emergence and early survival data reflected the natural patterns of red alder abundance within the Coast Range landscape. On our interior plots only a few seedlings on north-facing skid trails survived beyond the middle of the first growing season. In this vicinity, naturally established

red alder is absent from south-facing and level sites but common in sheltered habitats such as gullies, stream channels, and on the steepest portions of north-facing slopes. We believe that low soil moisture and high surface soil temperatures limit seedling establishment in this environment.

In the milder, wetter climate of the coastal sites, there were more microsites available for red alder establishment. On the south-facing slope, seedlings required some shade for survival on uncompacted seedbeds. On the north-facing slope, emergence rates were very high, even on undisturbed seedbeds, and no shade was required for survival. These results support silviculturists' observations that red alder occurs on all slopes and aspects in the coastal environment but is particularly prevalent on north-facing slopes (Knapp et al. 1984).

Year to year variability in weather conditions can dramatically affect red alder establishment. Over just two growing seasons, we observed significant differences in emergence and survival. Both years were warmer and drier than the long-term averages (Redmond 1986, 1987), but in 1987, exceptionally hot, dry weather coincided with the peak period of seedling emergence, a time when seedlings are especially vulnerable. Emergence and survival rates might have been higher, especially at the two interior sites, had the growing seasons been cooler and (or) wetter.

Seedling growth performance

The red alder literature emphasizes the rapid early growth potential of this species, reporting annual height growth of 100–200 cm/year (Harrington 1990). However, the mean heights we recorded (2–5 cm tall after the first growing season; 8–23 cm tall after the second growing season) are far below these rates. The largest 1-year-old seedling measured on our study plots (on a landing) was 10 cm tall, with a 1.8 mm basal diameter. The hot, dry weather of our study years may have influenced growth, but Ruth (1968) reported similar first-year height growth, with mean heights of 2.1 cm on loose mineral soil seedbeds and slightly taller seedlings (2- to 14-cm range) along a skid trail within a thinned Douglas-fir stand. These observations suggest that although red alder is capable of high initial growth rates under favourable conditions, it often takes the plant more than 2 years to develop a sufficient root system and photosynthetic surface to support the rapid juvenile growth for which this pioneer species is known. During those first precarious growing seasons, many of the successful seedlings are sheltered beneath shrubs and herbs, where they are not readily visible to silviculturists.

Conclusions

Our results demonstrate that establishment success in red alder increases with disturbance and soil moisture. Seeds on mineral soil suffer fewer losses from invertebrates and pathogens and remain viable longer than those on undisturbed seedbeds. Because red alder is a highly light-demanding pioneer species with light-sensitive seeds, we anticipated that germination, seedling survival, and seedling growth would all be higher both on clearcuts and on mineral soil seedbeds. Instead, we found that seed germination is equally high in clearcuts and forests, and that early survival is not

affected by mineral soil exposure. It appears that red alder's high moisture requirements for germination, survival, and growth override its need for full sunlight during the earliest stages of seedling establishment. In this study, loose, bare mineral soil with no overhead shade was too harsh an environment for red alder survival except on a very sheltered north slope. The severe soil disturbance and compaction associated with machine traffic seems to create an optimum microenvironment for red alder that provides the necessary protection from drought and heat in an unshaded, competition-free environment.

Kenady (1978) predicted that red alder should be one of the easiest Pacific Northwest tree species to establish by either artificial or natural seeding. At our interior study sites, the range of habitats in which red alder can successfully establish is narrow, especially in dry years. Direct seeding or reliance on natural regeneration does not seem to be a viable option in such an environment. In favourable climates such as at our north-facing coastal site, however, successful establishment from seed seems assured.

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Appendix**Table A1.** ANOVA tables for analysis of pooled arcsine-transformed data from the four study sites.

Source	df	SS	MS	<i>F</i>	<i>p</i> > <i>F</i>
Vertebrate seed predation^a					
Total	71	14.11			
Site(block)	3	1.27	0.42	1.03	0.49
Forest cover	1	0.0012	0.0012	0.00	0.96
Error A (site × cover)	3	1.23	0.41		
Seedbed	2	4.01	2.01	16.00	0.0001**
Cover × seedbed	2	0.064	0.032	0.26	0.78
Error B	60	7.53	0.13		
Contrast					
Undisturbed vs. disturbed (U vs. M and H):	1	3.93	3.93	31.37	0.0001**
Moderate vs. heavy disturbance (M vs. H):	1	0.078	0.078	0.62	0.43
Emergence^b					
Total	167	15.42			
Site(block)	3	0.58	0.19	0.52	0.70
Forest cover	1	0.20	0.20	0.55	0.51
Error A (site × cover)	3	1.11	0.37		
Seedbed	1	3.45	3.45	29.2	0.0017**
Cover × seedbed	1	0.07	0.07	0.61	0.46
Error AB (site × cover × seedbed)	6	0.71	0.12		
Year	1	0.65	0.65	4.89	0.047*
Cover × year	1	0.03	0.03	0.21	0.65
Seedbed × year	1	0.01	0.01	0.10	0.76
Cover × seedbed × year	1	0.14	0.14	1.05	0.33
Error ABC (site × cover × seedbed × year)	12	1.60	0.13		
Sampling error	136	6.07	0.04		

Note: **, $p < 0.01$; *, $p < 0.05$.

^aUses 1986 data from paired caged and uncaged undisturbed (U) and disturbed (M, moderate; H, heavy) plots.

^bUses both 1986 and 1987 data from caged undisturbed and disturbed subplots.