

NOTE

Effect of the light environment on seed germination of red alder (*Alnus rubra*)¹SYBILLE HAEUSSLER² AND JOHN C. TAPPEINER II³

Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR 97331, U.S.A.

Received June 17, 1992

Accepted January 12, 1993

HAEUSSLER, S., and TAPPEINER, J.C., II. 1993. Effect of the light environment on seed germination of red alder (*Alnus rubra*). Can. J. For. Res. 23: 1487-1491.

Red alder (*Alnus rubra* Bong.) seed showing strong phytochrome activity in the laboratory was tested to determine whether the phytochrome effect could influence germination under light conditions experienced in the field. Seeds in sealed Petri dishes were placed beneath three types of overstory cover (clearcut (no overstory); Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (coniferous evergreen overstory); and red alder (broad-leaved deciduous overstory)) and seven types of understory cover (control (complete darkness); uncovered; 1-cm mineral soil; leaf litter; moss; swordfern; and non-evergreen herbs). Germination was highest in clearcuts (68.6%), intermediate in Douglas-fir stands (47.4%), and lowest in red alder stands (11.7%). Covers of understory vegetation, leaf litter, and mineral soil significantly reduced germination, with the greatest reduction occurring where understory vegetation was dense enough to significantly reduce the ratio of red:far-red light. These findings concur with field studies of red alder seedling establishment and suggest that the phytochrome sensitivity of red alder seed plays an important role in this species' success on disturbed habitats.

HAEUSSLER, S., et TAPPEINER, J.C., II. 1993. Effect of the light environment on seed germination of red alder (*Alnus rubra*). Can. J. For. Res. 23: 1487-1491.

Des graines d'aulne de l'Orégon (*Alnus rubra* Bong.) exhibant une forte activité du phytochrome en laboratoire ont été testées pour vérifier si l'effet du phytochrome pouvait influencer la germination dans les conditions lumineuses rencontrées sur le terrain. Des graines placées dans des plats de Pétri scellés furent exposées sous trois types de couvert typiques de l'étage dominant (coupe rase (pas d'étage dominant), sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) (couvert de résineux à feuilles persistantes) et aulne de l'Orégon (couvert de feuillus à feuilles caduques)) ainsi que sous sept types de couvert typiques du sous-étage (témoin (complète noirceur), absence de couvert, 1 cm de sol minéral, litière de feuilles, mousse, fougère et herbacées à feuilles non persistantes). La germination était la meilleure (68,6%) dans la coupe rase, moyenne (47,4%) sous le peuplement de sapin de Douglas et la moins bonne (11,7%) dans les peuplements d'aulne de l'Orégon. Les couverts de végétation de sous-étage, la litière de feuilles et le sol minéral ont significativement réduit la germination, la plus forte réduction se produisant où la végétation de sous-étage était assez dense pour réduire le ratio de lumière rouge par rapport au rouge éloigné. Ces résultats concordent avec les expériences d'établissement de semis d'aulne de l'Orégon sur le terrain et suggèrent que la sensibilité du phytochrome chez les graines d'aulne de l'Orégon joue un rôle important dans le succès de cette espèce dans les habitats perturbés.

[Traduit par la rédaction]

Introduction

Among the forest trees of the North American Pacific Coast, red alder (*Alnus rubra* Bong.) is considered a pioneer species, associated with the early stages of forest succession following disturbance (Stettler 1978). Unlike many other hardwoods, red alder has a short life-span and a limited ability to regenerate vegetatively (Harrington 1984, 1990). However, it is a prolific seeder, and its establishment and persistence in the ecosystem depend almost entirely on regeneration from seed. A knowledge of red alder's seed ecology and the factors involved in successful seed germination are therefore particularly important for effective management of this species.

Laboratory experiments by Bormann (1983) indicate that red alder seed is highly sensitive to light. Seeds kept in complete darkness have very low rates of germination, and the germination rate increases steadily as the amount of light

increases. However, light saturation is reached after as little as 5 min of bright white or red light. Bormann (1983) also demonstrated that red alder seed germination is phytochrome mediated: red light stimulates seed germination, far-red light inhibits it, and the effect of each light treatment can be reversed by the alternative treatment. Bormann was able to simulate the far-red effect by using a red alder leaf as a light filter. A one-leaf filter caused a slight reduction in seed germination. A two-leaf filter substantially inhibited germination. In contrast, a filter made of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) needles significantly increased seed germination.

In nature, a host of factors in addition to light (for example, moisture, temperature, predators, pathogens, and plant competition) interact to regulate germination and seedling establishment. However, the sensitivity of red alder seed to the red:far-red (R:FR) light ratio may help explain why the establishment of red alder seedlings is tied to disturbances that remove vegetative cover and expose mineral soil.

We tested the light sensitivity of red alder seed in a field experiment designed to exclude predators and decay organisms, maintain constant high humidity, and provide favourable temperatures for germination. This experiment was part of a larger study examining red alder seedling establishment and growth in forest environments exposed to varying levels

¹Paper 2825, Forest Research Laboratory, Oregon State University, Corvallis.

²Author to whom all correspondence should be addressed. Present address: Skeena Forestry Consultants, RR 2 Moncton Road, Site 81 C-2, Smithers, BC V0J 2N0, Canada.

³Present address: College of Forestry, Bureau of Land Management Cooperative Research Unit, Oregon State University, Corvallis, OR 97331, U.S.A.

TABLE 1. Results of two laboratory experiments testing for light sensitivity and phytochrome activity in red alder seed lots

Treatment	Mean percent germination	
	This study	Bormann (1983)
No light	1.0 (1.3)	1.0
5 min white light	87.1 (3.2)	22.8
5 min red light	84.6 (7.0)	29.3
10 min far-red light	0.0 (0.0)	1.4
5 min red light followed by 10 min far-red light	0.0 (0.0)	3.2
10 min far-red light followed by 5 min red light	84.9 (7.6)	16.1

NOTE: In this study, standard error for comparing means (untransformed data) = 1.4. $N = 10$ for each observation; numbers in parentheses are standard deviations.

of disturbance (S. Haeussler and J.C. Tappeiner, in preparation). We hypothesized that light filtering through the forest overstory, understory vegetation, and forest floor layers significantly influences seed germination.

Methods

Seed collection and processing

Red alder seed was collected along Woods Creek, near Philomath, Oregon (44°32'N, 123°28'W), in late October 1985. The seed lot was processed with an air blower to remove most of the unfilled seeds; seeds were then stored at 4°C until needed. Viability was determined by germinating four replicates of 100 seeds each in a chamber set for 25:18°C (day:night) under a 12-h photoperiod. This regime produces near-complete germination of viable red alder seed within 5–14 days (Campbell and Ching 1980; Radwan and DeBell 1981). Viability of the seed lot at the start of the experiment was 95%.

Laboratory experiment

We repeated the first experiment of Bormann (1983) in the laboratory to determine whether the red alder seed was phytochrome active. The experiment was a completely randomized design with 10 replications of six treatments. Sixty Petri dishes, each containing 50 seeds on two sheets of Whatman filter paper moistened with 10–15 mL distilled water, were sealed with tape to prevent moisture loss, then placed in complete darkness for 24 h to allow the seeds to imbibe the water. Ten Petri dishes were then randomly allocated to each of the six light treatments listed in Table 1. The light treatments were produced by using Corning plexiglass filters (red light: 650 nm; far-red light: 750 nm), with two 15-W cool white fluorescent tubes for the white and red light treatments and one 75-W incandescent bulb for the far-red treatment. Following treatment, the seeds were transferred in darkness to a germination chamber (25:18°C, day:night) and left to germinate in complete darkness for 14 days.

Field experiment

The field experiment was a two-factor split plot arranged in a randomized complete block design with six replications. In each of 126 Petri dishes, 50 red alder seeds were sown on a thick germination pad moistened with 30 mL distilled water. The dishes were then sealed with tape and surrounded with clear polyethylene wrap to prevent moisture loss, and were placed in sealed steel cans to exclude light. The seeds were allowed to imbibe water for 24 h and were then transferred to the field.

Of the six field sites selected, three were along Woods Creek and three were near Logsdan, Oregon (44°45'N, 123°46'W). Each site consisted of (i) a recent (1- to 3-year-old) clearcut, (ii) an adjacent stand of pure Douglas-fir, and (iii) an adjacent stand of pure red alder. Within each of these three overstory treatments, we created the following understory treatments:

- (1) Control: dish placed in complete darkness within sealed steel can
- (2) Uncovered: dish placed on mineral soil surface with no overtopping understory vegetation.
- (3) Mineral soil: dish buried beneath 1 cm mineral soil with no overtopping understory vegetation.
- (4) Leaf litter: dish buried beneath approximately 3 cm loose alder swordfern, and (or) herbaceous litter.
- (5) Moss: dish placed beneath healthy *Kindbergia oregana* (Sull) Ochyra moss carpet.
- (6) Swordfern: dish placed beneath the foliage of *Polystichum munitum* (Kaulf.) Presl., an evergreen fern.
- (7) Non-evergreen herbs: dish placed beneath vigorous non-evergreen understory herbs of variable species composition and leaf area.

The Petri dishes were placed in the field on May 1–2, 1987, when the red alder canopy was almost fully developed. On June 6, 1987, they were retrieved from the field in darkness and placed in sealed steel cans. Because field temperatures during this period were well below the 25:18°C (day:night) optimum (Haeussler 1987) and may have inhibited germination, and because there was considerable temperature variation among sites and treatments, the dishes were then transferred to a germination chamber (25:18°C, day:night) and kept in complete darkness for 12 days before the germinants were counted. Substantial germination occurred after the seeds were placed in the germination chamber. Chamber-germinated seeds were readily distinguished from the field-germinated seeds by germinant age and coloration.

Data analysis

Analyses of variance (ANOVA) were carried out on arcsine-transformed germination percentages, and orthogonal contrasts of the means were used to test for differences among treatments (Peterson 1985). For the field experiment, separate ANOVA were carried out for field-germinated seeds and for the combined total of field- plus chamber-germinated seeds.

Results

Laboratory experiment

Results of the laboratory experiment indicated a strong phytochrome effect (Table 1). Germination was extremely low in the absence of light (1.0% on average) and was completely inhibited (0.0% in all cases) when far-red light was the final treatment. Exposure to a short period of white or red light resulted in high rates of germination (84.6–87.1%) and reversed the effect of far-red light. The results are similar to those obtained by Bormann (1983) (see Table 1) but more dramatic, reflecting both higher seed quality and a higher degree of phytochrome sensitivity in our seed lot.

Field experiment

We have presented only the total (field + chamber) germination results in Tables 2–4 in order to best isolate the effect of light conditions and minimize the confounding effects of temperature differences among sites and treatments. Most of the germination that took place after the Petri dishes were placed in the germination chamber occurred in dishes exposed to the most heavily shaded (presumably coolest) treatments, but there was considerable variability among treatments and sites. The trends in the field-germination data set were virtually identical with those in the field + chamber germination data set but were weaker and had higher coefficients of variation and less definitive p -values.

Germination of seeds kept in complete darkness (control treatment) was poor for all three overstory treatments (0.0–11.3%), and differences among treatments were not statistically significant ($p = 0.7115$).

TABLE 2. ANOVA of total (field + chamber) red alder seed germination in the field experiment

Source	df	SS	MS	F	<i>p</i> > <i>F</i>
Total	125	31.927			
Block	5	0.1695	0.0339	0.65	0.6703
Overstory	2	12.5375	6.2688	119.70	0.0001
Block × overstory	10	0.5237	0.0524	0.85	0.5789
Understory	6	9.8632	1.6439	26.80	0.0001
Overstory × understory	12	3.3129	0.2761	4.50	0.0001
Error	90	5.5205	0.0613		

TABLE 3. Mean percent germination of red alder seeds exposed to different light environments

Understory treatment	Overstory			Understory mean
	Clearcuts	Fir stands	Alder stands	
Control (complete darkness)	11.3 (9.3)	3.0 (6.4)	0.0 (0.0)	4.8
Uncovered	95.3 (4.1)	92.7 (7.1)	47.0 (22.0)	78.3
1 cm mineral soil	87.0 (15.2)	59.0 (25.0)	20.0 (18.9)	55.3
Leaf litter	94.0 (1.8)	47.3 (15.9)	7.3 (6.9)	49.6
Moss	80.6 (31.5)	43.3 (18.5)	2.7 (3.5)	42.2
Swordfern	71.0 (37.0)	40.3 (11.0)	3.3 (5.3)	38.2
Non-evergreen herbs	41.0 (29.0)	46.3 (26.0)	1.7 (4.1)	29.7
Overstory mean	68.6	47.4	11.7	42.6

NOTE: Means are calculated from total germination counts (seeds that germinated in the field plus seeds that germinated subsequently in the germination chamber). *N* = 6 for each observation; numbers in parentheses are standard deviations.

There was a highly significant overstory × understory interaction ($p = 0.0001$) (Table 2). Although the response to understory cover varied from one type of overstory to another, it is apparent that overall germination was highest in clearcuts (68.6% on average), intermediate in Douglas-fir stands (47.4%), and lowest in red alder stands (11.7%) (Table 3). Furthermore, among the understory treatments, germination was always highest when seeds were uncovered (78.3% on average). An understory cover of vegetation, leaf litter, or mineral soil significantly reduced germination (29.7–55.3% on average; $p < 0.002$ for all three overstory types) (Table 4). The soil layer inhibited germination somewhat less than vegetation or leaf litter, but differences among these cover types were not significant ($p = 0.052$ – 0.14).

In the clearcuts, most understory treatments did not substantially reduce germination. Germination averaged between 71.0 and 94.0% beneath swordfern, leaf litter, moss, and soil, compared with 95.3% for uncovered seeds. Under dense non-evergreen herbs, however, mean germination was only 41.0%.

In the Douglas-fir stands, where the cover of non-evergreen herbs was relatively sparse, leaf litter, moss, swordfern, and non-evergreen herbs all produced similar rates of germination (40.3–47.3%). These rates were all substantially lower than the rate for uncovered seeds (92.7%, $p = 0.0006$).

In the red alder stands, seed germination was relatively poor even for uncovered seeds (47.0%), but the combination of a broad-leaved overstory and additional vegetative or organic understory layers produced exceptionally low rates of seed germination (1.7–7.3%).

Discussion

A forest canopy not only reduces the intensity of light that reaches the forest floor, but also affects light quality by dif-

ferentially absorbing and reflecting light of various wavelengths. Under open conditions, red light (650–700 nm) predominates over far-red wavelengths (700–750 nm), with the ratio of R:FR light energy averaging between 1.1 and 1.5 on a clear day (Vezina and Boulter 1966; Atzet and Waring 1970; Smith 1982; Messier and Bellefleur 1988; Messier et al. 1989). When light passes through a canopy, however, the R:FR ratio drops. The amount of the reduction depends on the structure and composition of the canopy (Smith 1982). Under a deciduous forest canopy, the R:FR ratio drops substantially because the broad-leaved foliage selectively absorbs red light and substantially increases the proportion of far-red light. Morgan and Smith (1981) reported that R:FR ratios measured beneath a variety of broad-leaved deciduous canopies ranged from 0.08 to 0.28 on clear days. Other researchers have reported a much smaller effect from coniferous evergreen canopies on the quality of incoming radiation, with R:FR ratios typically ranging from 0.6 to 1.0 (Vezina and Boulter 1966; Atzet and Waring 1970; Ross et al. 1986). Apparently, in coniferous canopies, the relatively thick needles transmit little light, and most of the light that enters the forest passes through spaces between needles and through other canopy gaps.

Less information exists on the effect of understory cover on light quality. Stoutjesdijk (1972) measured radiation spectra beneath a variety of deciduous tree and shrub communities; his results show that the denser the vegetation is and the more layers it contains, the lower the R:FR ratio will be. Bliss and Smith (1985) measured light spectra beneath different types of leaf litter and varying depths of mineral soil. They found that oak leaf litter dramatically reduced the R:FR ratio, while pine needles were a relatively neutral density filter; and that in soil, shorter wavelengths were rapidly attenuated, while

TABLE 4. Planned orthogonal contrasts of the effect of light environments on red alder seed germination

Contrast		Conclusion	<i>p</i>
Overstory means			
Is germination higher in clearcuts than in Douglas-fir or red alder stands?		Yes	0.0001
Is germination higher in Douglas-fir stands than in red alder stands?		Yes	0.0001
Overstory × understory means			
Is germination lower in the controls than in seeds exposed to natural light?	Clearcuts	Yes	0.0001
	Fir stands	Yes	0.0001
	Alder stands	No	0.1949
Is germination higher in uncovered seeds than in seeds under soil, leaf litter, or vegetation?	Clearcuts	Yes	0.0017
	Fir stands	Yes	0.0001
	Alder stands	Yes	0.0002
Is germination higher under 1 cm of soil than under leaf litter or vegetation?	Clearcuts	Probably not	0.0521
	Fir stands	Probably not	0.0989
	Alder stands	Probably not	0.1407
Is germination higher under moss than under leaf litter?	Clearcuts	No	0.3240
	Fir stands	No	0.7811
	Alder stands	No	0.7439
Is germination higher under moss and litter than under swordfern or non-evergreen herbs?	Clearcuts	Yes	0.0001
	Fir stands	No	0.8246
	Alder stands	No	0.8047
Is germination higher under swordfern than under non-evergreen herbs?	Clearcuts	Yes	0.0010
	Fir stands	No	0.5754
	Alder stands	No	0.9073

NOTE: *P*-values of tests are for arcsine-transformed germination percentages.

longer wavelengths, particularly in the far-red range, penetrated more deeply. Variation in soil particle size, structure, and moisture content, however, had a major effect on the R:FR ratios.

We made no measurements of light quality or quantity or of R:FR ratios in our field experiment. Our assumption was that the phytochrome pigment, through perception of R:FR light quality, is the mechanism by which red alder seeds detect and respond to vegetation shade (Smith 1982). Thus, we tried to re-create the range of overstory and understory environments encountered by red alder seeds to determine whether light sensitivity could explain some of the germination patterns we were observing in our other field studies. In selecting the understory test environments, we assumed that thick dark materials such as evergreen fern foliage, moss, and soil, which, like conifer needles, appear opaque to the visible spectrum, would have a relatively neutral effect on the light quality compared with broad-leaved deciduous or herbaceous vegetation and leaf litter.

Our experimental results support the laboratory findings of Bormann (1983), which showed that red alder seed germination decreases with decreased light intensity and that an alder-leaf light filter significantly inhibits seed germination. Our results also support Bormann's finding that germination drops off rapidly when there is more than one layer of leaves filtering out sunlight. Apparently, a threshold level in the R:FR ratio exists, below which germination rates are substantially reduced. This threshold is unlikely to be approached in large forest openings such as clearcuts unless the shrub and herbaceous vegetation on those sites is very dense. Nor would an overstory of evergreen needles alone create light conditions below this threshold, which explains the high rate of seed

germination on bare ground beneath Douglas-fir stands observed in our study.

The timing of our field experiment may have affected the red alder overstory results somewhat. In coastal Oregon, most red alder germination takes place in early April, when the leaves of deciduous tree and shrub species are just beginning to expand (Haeussler 1987). Thus, under natural conditions, inhibition of seed germination by a broad-leaved overstory is unlikely to be as pronounced as it was in this experiment, which was carried out in May. However, many understory herbs do emerge before red alder seed germination occurs, and the presence of leaf litter, mosses, and evergreen plants such as swordfern under broad-leaved overstories also will tend to reduce seed germination.

The field experiment was designed to minimize the effects of factors other than light on seed germination by excluding predators and decay organisms, maintaining constant high humidity, and providing favourable temperatures for germination. Nevertheless, temperature differences among the field treatments may have influenced the results, as indicated by the control (complete darkness) data. In this treatment, although the differences in germination among the three overstory types were not significant, germination was highest in clearcuts (11.3%) and lowest in alder stands (0.0%) (Table 3). Perhaps more of the clearcut seeds were able to germinate in darkness because they were subjected to higher temperatures and larger diurnal temperature fluctuations than seeds in the Douglas-fir or red alder stands. Similar temperature-related phenomena have been observed in other plant species with light-sensitive seed germination, including *Alnus crispa* (Ait.) Pursh and *Alnus tenuifolia* Nutt. (Densmore 1979). Work by Tanaka et al. (1991) suggests that stratification of the red alder

seeds might have reduced this temperature-related variability by improving germination rates at the suboptimal temperatures we experienced in the field.

The sensitivity of red alder seeds to the R:FR ratio (i.e., to the degree of vegetation shade) serves two ecologically important functions: it cues seeds to when a disturbance exposes seedbeds to open, full-light conditions, and it synchronizes germination to the favourable early spring period when moisture is normally abundant. Most likely, the light cue works in conjunction with temperature stimuli that also indicate open, full-light conditions (i.e., major diurnal temperature fluctuations) or the onset of spring (warming after a lengthy period of chilling).

Stoutjesdijk (1972) has questioned the extent to which far-red light inhibition affects the regulation of seed germination under natural conditions, where factors such as substrate moisture level may be so much more important. Our field studies of red alder seedling establishment (Haeussler 1987; S. Haeussler and J.C. Tappeiner, in preparation) indicate that moisture level probably is the primary regulator of germination, but that when ample moisture is available, light inhibition does play an important regulatory role. To illustrate, during a wet spring, we observed good alder germination in clearcuts, in Douglas-fir stands with sparse, mossy understories, and on bare ground beneath red alder that had not yet leafed out, and in contrast, very poor germination below undisturbed herb and leaf litter understories in the same leafless red alder stands, results that correspond closely to those of the current study. On the other hand, during the following spring, which was dry, germination was poor on all organic substrates regardless of light conditions.

It appears that the light sensitivity of red alder seed encourages maximum seed germination in the most favourable circumstances; that is, immediately following disturbances. Disturbance-cued seed germination is a phenomenon found in many pioneer tree species (Brokaw 1985), but it has survival value for a species only if dormant seeds are present in the forest floor when disturbance occurs. Red alder lacks a hard seed coat, and on an undisturbed forest floor, the seed probably does not retain viability for long (Haeussler 1987; S. Haeussler and J.C. Tappeiner, in preparation). This species is therefore unlikely to persist in a stand's seedbank through the latter stages of forest succession, when red alder trees no longer are present in the stand. However, short-term seed storage (1–2 years) may permit a flush of light-stimulated germination following logging or a natural disturbance of a mature red alder stand.

Acknowledgements

Partial funding for this study was provided by a Boise-Cascade Fellowship to the senior author. We thank D. Minore, T. Robinson, and an anonymous reviewer for their helpful comments.

- Atzet, T., and Waring, R.H. 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. *Can. J. Bot.* **48**: 2163–2167.
- Bliss, D., and Smith, H. 1985. Penetration of light into soil and its role in the control of seed germination. *Plant Cell Environ.* **8**: 475–483.
- Bormann, B.T. 1983. Ecological implications of phytochrome-mediated seed germination in red alder. *For. Sci.* **29**: 734–738.
- Brokaw, N.V.L. 1985. Community structure in tropical forests. In *The ecology of natural disturbance and patch dynamics*. Edited by S.T.A. Pickett and P.S. White. Academic Press, Orlando, Fla. pp. 53–69.
- Campbell, A., and Ching, K.K. 1980. Genetic differences in red alder populations along an elevational transect. *Oreg. State Univ. For. Res. Lab. Res. Note* 64.
- Densmore, R.A. 1979. Aspects of the seed ecology of woody plants of the Alaskan taiga and tundra. Ph.D. thesis, Duke University, Raleigh, N.C.
- Haeussler, S. 1987. Germination and first-year survival of red alder seedlings in the central Coast Range of Oregon. M.S. thesis, Oregon State University, Corvallis.
- Harrington, C.A. 1984. Factors influencing initial sprouting of red alder. *Can. J. For. Res.* **14**: 357–361.
- Harrington, C.A. 1990. *Alnus rubra* Bong. Red alder. In *Silvics of North America*. Vol. 2. Hardwoods. Edited by R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654. pp. 116–123.
- Messier, C., and Bellefleur, P. 1988. Light quantity and quality on the forest floor of pioneer and climax stages in a birch – beech – sugar maple stand. *Can. J. For. Res.* **18**: 615–622.
- Messier, C., Honer, T.W., and Kimmins, J.P. 1989. Photosynthetic photon flux density, red:far-red ratio, and minimum light requirement for survival of *Gaultheria shallon* in western red cedar – western hemlock stands in coastal British Columbia. *Can. J. For. Res.* **19**: 1470–1477.
- Morgan, D.C., and Smith, H. 1981. Nonphotosynthetic responses to light quality. *Encycl. Plant Physiol.* **12A**: 109–134.
- Peterson, R.G. 1985. Design and analysis of experiments. *Statistics: textbooks and monographs*. Vol. 66. Marcel Dekker, Inc., New York.
- Radwan, M.A., and DeBell, D.S. 1981. Germination of red alder seed. *USDA For. Serv. Res. Note* PNW-370.
- Ross, M.S., Flanagan, L.B., and La Roi, G.H. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. *Can. J. Bot.* **64**: 2792–2799.
- Smith, H. 1982. Light quality, photoperception and plant strategy. *Annu. Rev. Plant Physiol.* **33**: 481–518.
- Stettler, R.F. 1978. Biological aspects of red alder pertinent to potential breeding programs. In *Utilization and management of red alder*. Compiled by D.G. Briggs, D.S. DeBell, and W.A. Atkinson. *USDA For. Serv. Gen. Tech. Rep.* PNW-70. pp. 209–222.
- Stoutjesdijk, P. 1972. Spectral transmission curves of some types of leaf canopies with a note on seed germination. *Acta Bot. Neerl.* **21**: 346–350.
- Tanaka, Y., Brotherton, P.J., Dobkowski, A., and Cameron, P.C. 1991. Germination of stratified and non-stratified seeds of red alder at two germination temperatures. *New For.* **5**(2): 67–76.
- Vezina, P.E., and Boulter, D.W.K. 1966. The spectral composition of near ultraviolet and visible radiation beneath forest canopies. *Can. J. Bot.* **44**: 1267–1284.