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# Effects of Established Willows on Primary Succession on Lyman Glacier Forefront, North Cascade Range, Washington, U.S.A.: Evidence for Simultaneous Canopy Inhibition and Soil Facilitation

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## Abstract

The effect of established shrub willows (*Salix commutata* and *S. phylicifolia*) was tested in a primary successional ecosystem at Lyman Glacier forefront in the North Cascade Range (Washington, U.S.A.). To examine the hypothesis that early successional plant individuals form centers of establishment for subsequent vascular plant colonizers, two experiments were conducted to assay the effect of shrub willows on the establishment and survival of indigenous plants. First, the occurrence of indigenous plant species under willow canopies was compared with their occurrence beyond the canopies (experiment 1). Second, the separate effects of willow canopies and associated soils on germinant emergence and survival of an indigenous taxon, *Pinus contorta*, were evaluated (experiment 2). Both experiments indicated that the shrub willows do not serve as nuclei that facilitate the establishment of new, emerging plant individuals. In experiment 1, the willow canopy had no effect on the observed frequency of most indigenous taxa. Five species, however, were negatively associated with the willow canopies. In experiment 2, willow canopies inhibited the germinant emergence of *P. contorta*. The greatest emergence occurred in soils transferred from beneath willow canopies to areas beyond the canopies. Results from the two experiments suggest that while the willow canopy is either neutral or inhibitory in its effect on establishment of indigenous plants, the soil developing beneath the willow can actually be a positive factor towards plant establishment.

## Introduction

Primary establishment and survival of new plants may take years of unsuccessful attempts before plant communities develop. Facilitation is one mechanism by which succession occurs in the plant community (see Connell and Slatyer, 1977; Pickett et al., 1987; Matthews, 1992; Callaway, 1995). During facilitation, established individual plants modify their environment (Morris and Wood, 1989; Blundon et al., 1993; Pugnaire and Haase, 1996) and serve as “nurse plants” (Niering et al., 1963; Franco and Nobel, 1988). These established plants enhance both the establishment and survival of new plants and ultimately may place themselves at a competitive disadvantage. Proposed mechanisms for such facilitation include changes in microclimate as well as changes in the physical and chemical properties of soil (Franco and Nobel, 1988; Campbell et al., 1990; Manders and Richardson, 1992; Callaway, 1994; Callaway, 1995; Jacquez and Patten, 1996; Pugnaire and Haase, 1996). A special case of facilitation is a close positive interaction known as nucleation, which refers to early successional plant individuals forming centers (nuclei) of establishment for subsequent colonizers (Yarranton and Morrison, 1974).

Nucleation has been suggested to be a significant mechanism in secondary succession (Campbell et al., 1990). Opportunities to conduct studies addressing questions of successional mechanisms in primary successional ecosystems are rare. Studies of primary successional systems have mainly concentrated on taxa with symbiotic nitrogen fixation ability and their effect on the plant community development (Walker and Chapin, 1986;

Morris and Wood, 1989; Vitousek and Walker, 1989; Blundon et al., 1993; Chapin et al., 1994). Nitrogen-fixing taxa are important during primary succession because nitrogen is limiting during the early stages of community development (Vitousek and Walker, 1989; Walker, 1993; Chapin et al., 1994).

The main objective of this study was to determine the response of indigenous taxa to the physical environment created by a canopy of non-nitrogen-fixing taxa in an ecosystem undergoing primary succession. The forefront of Lyman Glacier in the North Cascade Range, Wenatchee National Forest, Glacier Peak Wilderness Area, Washington, U.S.A., was selected as the study site (Fig. 1). An undisturbed deposit of Mount Mazama ash outside the late 1890s terminal moraine shows that the glacier has not advanced beyond that position in the last ca. 6000 yr (Long, pers. comm., 1989). The glacier has been receding steadily since the 1890s. The site represents natural primary successional communities: no exotic weeds are present. The retreat of the glacier has been frequently recorded over the past century: photos are available for 1900 to 1944 (Lindsley and Harrison photographs at Special Collections Division, University of Washington Libraries, Seattle), for 1940 to 1970 (U.S. Geological Survey), and every year since 1986 (the authors); annual snow survey data of the terminus retreat are available for 1929 to 1943 (Chelan County, Public Utility District No. 1). Consequently, the chronosequence of plant establishment as new substrate emerged from under the melting ice and subsequent community development can be documented with unusual precision (Fig. 2). Nitrogen-fixing *Lupinus latifolius* were present on less than 1% of



FIGURE 1. View of Lyman Glacier forefront, 4 September 1997. The glacier is seen against Chiwawa Mountain with the terminal moraine in the foreground.

over 1000 0.25-m<sup>2</sup> diameter plots on the successional sere (Jumpponen et al., unpublished data), and only one individual of *Alnus sinuata* has been located on the sere. The frequency of these individuals is sufficiently low that any significant effects of biological nitrogen fixation on successional patterns at the glacier forefront would be extremely localized and have little overall impact.

Two separate experiments were conducted to assay the effect of the nuclei formed by shrub willows on the vascular plant establishment at the Lyman Glacier forefront. First, the occurrence of indigenous plant species under willow canopies was compared with their occurrence in the open. Second, the separate effects of willow canopies and associated soils on germinant emergence and survival of an indigenous species, *Pinus contorta*, were evaluated. Because willows affect soil properties, especially organic matter and nitrogen contents, in primary successional substrates, these properties were analyzed from samples along the chronosequence under and away from the willow canopies.

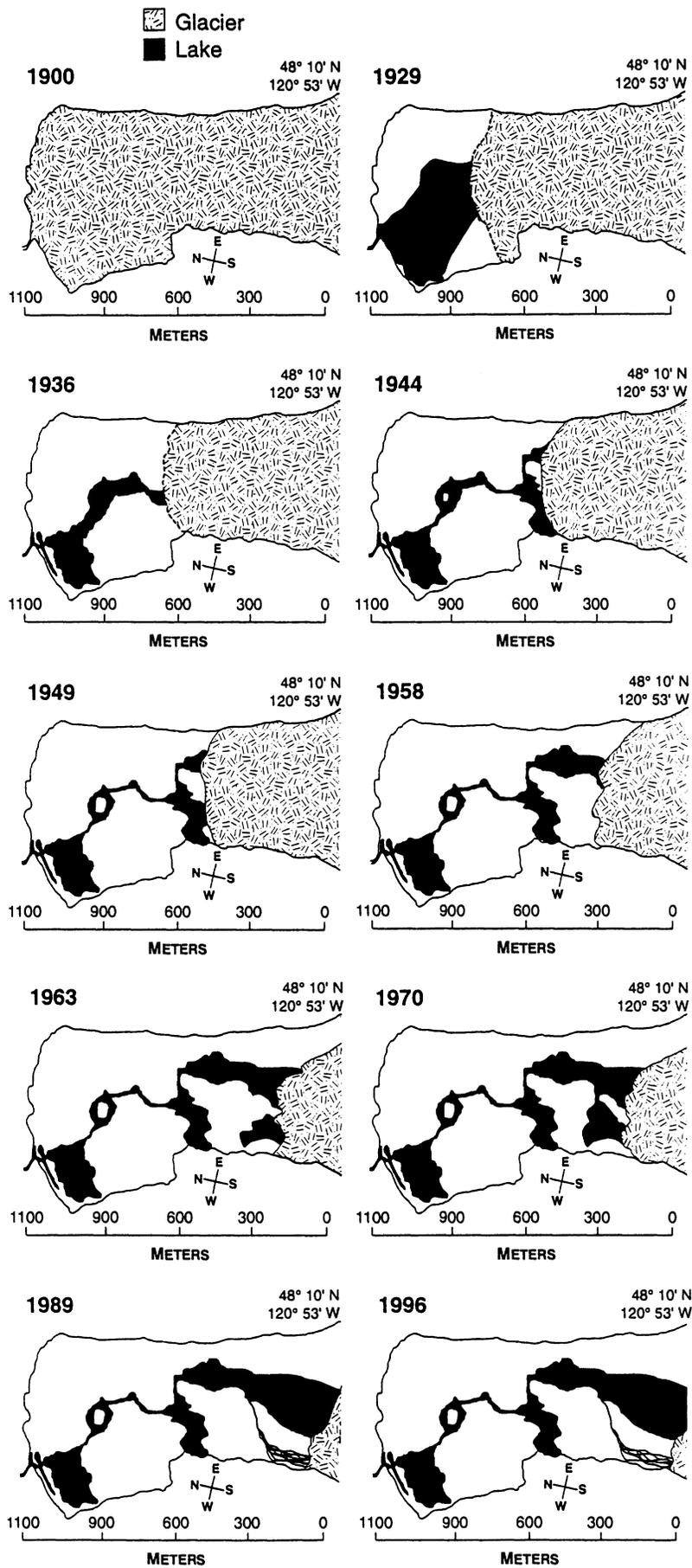
### Study Area

Lyman Glacier is at 48°10'N, 120°53'W; the elevation of the present terminus is about 1800 m. The deglaciated forefront is 1100 m long with an elevational drop of only about 60 m and no distinctive recessional moraines (Fig. 1). The forefront parent material is a heterogeneous glacial till ranging from clay-sized particles to boulders intermingled with deposits of glacial-fluvial sediments (for a description of the chemical characteristics see Cázares, 1992). The glacier and its forefront occupy a cirque and a north-south oriented, U-shaped valley bounded by cliffs that rise up to 600 m above the valley floor and culminate at Chiwawa Mountain (2430 m) at the head of the cirque.

The vegetation on ridges and benches adjacent to the forefront are in the ecotone between the upper parkland subzones of the *Abies lasiocarpa* zone and *Tsuga mertensiana* zone of the North Cascade Range (Franklin and Dyrness, 1973). The primary tree species on and near the forefront are *Abies lasiocarpa*, *Larix lyallii*, and *Tsuga mertensiana*. *Picea engelmannii* and *Pinus*

*contorta* occur on the forefront in small numbers, and *Pinus albicaulis* is common on the higher surrounding ridges but has not been found so far on the forefront itself. Plant communities adjacent to the forefront include heath shrub, lush herb, and dwarf sedge (Franklin and Dyrness, 1973).

The forefront can be divided into the following vegetational phases: (1) A barren phase less than 20 yr old closest to the glacier; (2) a 20- to 30-yr-old phase characterized by scattered individuals or small patches of the early seral species, *Juncus drummondii*, *J. mertensianus*, *Luzula piperi*, *Saxifraga ferruginea*, and *S. tolmiei*, the "rawmark" community of Franklin and Dyrness (1973); (3) a phase roughly 30 to 70 yr old characterized by scattered willow shrubs, principally *Salix phylicifolia* and *S. commutata*, and occasional Pinaceae mixed with the rawmark/low herbaceous communities of Franklin and Dyrness (1973) dominated by species of Cyperaceae, Juncaceae, Onagraceae, Saxifragaceae, and Scrophulariaceae, but including scattered individuals of other families; and (4) a phase roughly 70 to 100 yr old characterized by transition from low herbaceous to early stages of the heath shrub and lush meadow parkland communities containing individuals of *Abies lasiocarpa*, *Larix lyallii*, and *Tsuga mertensiana* among patches dominated by several members of Ericaceae. The boundary between the barren Phase 1 and rawmark community Phase 2 is well defined. The rawmark Phase 2 is also relatively well demarcated from the willow dominated Phase 3. Phase 3, however, merges in a highly variable ecotone with the early stages of heath shrub/lush meadow parklands of Phase 4. Douglas (1971) and Douglas and Bliss (1977) describe plant communities of the North Cascade Range in detail. The vegetation on the forefront has not reached full coverage on any of the phases described above; the communities are still open and have a substantial proportion of exposed mineral soil. Willow shrubs were chosen for the two experiments described here for the following reasons: (1) they are the first larger plants providing enough physical cover to serve as nuclei for subsequent colonizers and (2) their distribution at the site ranges from the 30-yr-old region to the terminal moraine; no willows are present at regions younger than 30 yr old.



**FIGURE 2.** Schematic map of the retreat of Lyman Glacier. Terminus location of 1929 and 1936 (dashed line) estimated based on snow survey data, others on photographs by Lindsley (1900), Harrison (1944), U.S. Geological Survey (1949, 1958, 1963, 1970), and the authors (1989, 1996). Scale bar: distance from the current (1996) glacier terminus.

## Materials and Methods

### EXPERIMENT 1: EFFECT OF WILLOW SHRUBS ON FREQUENCIES OF INDIGENOUS SPECIES

#### Sampling

Presence or absence of indigenous plant taxa were tallied within and beyond willow canopies to study effects of the physical environment created by those canopies on the establishment of new plant individuals. A design modified from Blundon et al. (1993) was employed and the conclusions were based on presence and absence rather than on growth or coverage of a given species.

Six zones representing 10-yr intervals as approximated from the photographic record (Fig. 2) were selected in the area where willows occurred on the forefront: 30–39, 40–49, 50–59, and 60–69 yr old of the Phase 3 willow/rawmark/low herbaceous communities, and 70–79 and 80–89 yr old of the Phase 4 early transitional stage towards heath shrub/lush meadow parkland. Twenty to fifty willow canopies were randomly selected within each of the six zones. The diameter of the vertical projection of each willow canopy was recorded, and it was used as an outer boundary of a plot in which presence or absence of all species were scored. An equal number of plots of similar size were located beyond the willow canopies within the same zone. The diameter of the plots under and beyond canopies ranged from 0.25 to 3.0 m. The plots were never placed closer than 3 m to any willow or conifer canopy to minimize any possible effects of the canopy. This limited the number of possible plots in the oldest zones where canopies were larger and more numerous. As a result, the average size of a plot and the number of plots differed among zones. This sampling scheme resulted in 172 plots within willow canopies and 172 beyond any canopies.

#### Statistical Analysis

The data were analyzed by use of contingency tables and logistic regression. Contingency tables tested for the overall effect of the canopies while logistic regression tested whether the effect of willow canopies varied among zones. Two-by-two contingency tables were used to assess presence and absence data collected for each species (Blundon et al., 1993) and Fisher's exact test was applied to test the effect of canopies. Because of potential problems in tables with low cell counts (SYSTAT, 1992), the tests of species with counts of fewer than five in any of the cells were excluded. The null hypothesis of no canopy effect was tested at alpha of 0.05. Greater frequency of a given species growing under a canopy compared to in the open was interpreted as a positive effect of the canopies, whereas lower frequency was interpreted as a negative effect.

Logistic regression (Hosmer and Lemeshow, 1982) was applied on the presence and absence data of the 12 most prominent species. No logistic regression model was fit with fewer than 40 observations of presence in the 344 plots. A model was used with zone age as a continuous variable, canopy as a categorical variable and interaction of zone age and canopy. No model selection was performed, because the main interest was to see whether the effect of canopy changed over time.

All Fisher's exact tests were performed with SYSTAT (SYSTAT, 1992) and all logistic regression analyses were performed with SAS in CATMOD procedure (SAS, 1989a).

### EXPERIMENT 2: EFFECTS OF WILLOW CANOPIES AND WILLOW SOIL ON EMERGENCE OF *PINUS CONTORTA* GERMINANTS

#### Establishment of Seeding Treatments

Germinant emergence and survival of *Pinus contorta* were assayed for seeds sown in treatments where the presence of willow canopies and soils from beneath willow canopies were controlled. *Pinus contorta* was chosen as a test plant because (1) it occurs naturally at the site but is present at only low frequency, (2) its seeds germinate reliably and are easy to manipulate under laboratory conditions, and (3) *Pinus contorta* seeds were more readily available than seeds of other indigenous conifers (*Abies lasiocarpa*, *Larix lyallii*, *Pinus albicaulis*, and *Tsuga mertensiana*) at the study site.

Seed of *P. contorta* was obtained from high-altitude populations (1540–2430 m) growing in a zone between 4 km west and 172 km east of the crest of the Cascade Range and between 42 and 45°N. The seeds were stratified by soaking in deionized water for 24 h followed by incubation at 4°C for 5 d. They were next treated with 30% H<sub>2</sub>O<sub>2</sub> for 55 min and packed in Ziploc plastic bags with moistened paper towels for transportation to the site. A subsample of the seeds was separated to determine the viability and germination rate in the laboratory. After 3 wk of incubation, 71.5% ( $\pm 1.0\%$ ) of the seeds germinated under these conditions.

Seeds were sown within and beyond willow canopies in four zones representing approximately 30, 45, and 60 yr old of the Phase 3 willow/rawmark/low herbaceous community and 85 yr old of the Phase 4 early transitional stage towards heath shrub/lush meadow parkland. The 30-yr-old zone was at the edge of the boundary between the Phase 2 rawmark community and the Phase 3 community. Within each of these zones, five representative canopies of *Salix* spp. were chosen.

Four soil treatments were applied under each canopy as well as on an open site 3 m from the center of the canopy. Each treatment was applied on a 7 × 13-cm plot, a size defined by the bags used in Soil Trenching and Soil Transfer treatments (see below). The treatments were (1) Control—gentle raking of the top 2 cm of soil to create a seedbed; (2) Soil Mixing—complete mixing of the soil in place to a depth of 10 cm; (3) Soil Trenching—removing the soil to a depth of 10 cm, mixing and placing it into a plastic-lined paper bag (7 × 13 × 10 cm, the bottom perforated for drainage), then replacing the bagged soil back into its pit; (4) Soil Transfer—a Soil Trenching treatment, but instead of replacing the bagged soil into its pit, placing the bag of under-canopy soil in the open-site pit and the bag of open-pit soil in the under-canopy pit.

After the soil treatments were applied, 10 *P. contorta* seeds were sown on each. A "mulch" of either gravel or willow litter was placed on top of the treated soils to represent the conditions at the treatment area. In the case of the transferred soils, the litter was kept with soils taken from under the canopies and placed in the open-sites. Likewise, the surface gravel of the open sites was transferred with those soils to the under-canopy positions.

The soils were thoroughly watered at sowing time and 2 d later; 2 d after watering, heavy rain fell on the study area. The plots received no other treatment prior to recording of surviving germinants 8 wk later. Germinant emergence and survival for the first 8 wk (from here on referred to as emergence) was scored for all plots. Data were treated as proportion of successful events (emergence) in the total number of trials (number of seedlings/number of seed sown in a single plot).

A logistic regression model with zone age (treated as a continuous variable), presence of the canopy (categorical with two levels) and the treatments (three categorical variables with two levels) was fit on the binomial seedling emergence data. Only the main effects were fit because of the large number of empty cells in the experimental design, so interactions could not be tested. To identify the most influential main effects, a model selection based on the Akaike Information Criterion (AIC) (SAS, 1989b) was performed. All analyses were performed in SAS LOGISTIC procedure (SAS, 1989b).

#### CHARACTERIZATION OF SOIL NITROGEN AND ORGANIC MATTER CONTENTS

##### Sampling and Chemical Analysis

The top 10 cm of soil was sampled at the four zones used in experiment 2. All exposed and visible litter and organic debris were removed. One additional sample was collected from the barren zone at <30 yr exposure from under the ice. Two willow canopies were selected in three zones representing ca. 30, 45, and 60 yr old of the Phase 3 willow/rawmark/low herbaceous community, and one was similarly chosen in the 85 yr old of the Phase 4 early transitional stage towards heath shrub/lush meadow parkland. The 30-yr-old zone was at the edge of the boundary between the Phase 2 rawmark community and the Phase 3 community. In each sampled willow, two samples were collected from beneath the willow canopy and two at 3 m from the edge of the canopy.

Soils were sieved through 2-mm mesh and organic matter was determined by loss on ignition (Davies, 1974) with a sub-sample checked against analyses by Leco Carbon-Nitrogen analyzer. Nitrogen was determined by Kjeldahl method (Thomas et al., 1967) and colorimetrically analyzed for total nitrogen concentration (% by dry weight) with an Alpkem Rapid Flow Analysis system Model 300.

##### Statistical Analysis

A multiple linear regression model with zone age (treated as a continuous variable) and presence of the canopy (categorical variable with two levels) was fit on the soil organic matter and nitrogen concentration data. Both main effects and interaction were fit in the full model. Model selection was performed according to suggestions in Ramsey and Shafer (1996). All analyses were performed in SYSTAT using General Linear Models procedure (SYSTAT, 1992).

## Results

#### EXPERIMENT 1: EFFECT OF WILLOW SHRUBS ON FREQUENCIES OF INDIGENOUS SPECIES

Willows did not affect the presence or absence of most indigenous plants tested (Table 1). No species showed a positive association with willow canopies. Negative associations with willows were significant for five species (*Epilobium alpinum*, *E. latifolium*, *Juncus mertensianus*, *Saxifraga ferruginea*, and *S. tolmiei*) of the 18 tested. Logistic regression analysis confirmed the negative effect of willow canopies on *Saxifraga ferruginea* and *S. tolmiei*, but not on *J. mertensianus* or *E. latifolium* (data not shown); observations of *E. alpinum* were too few to complete an analysis. No significant interaction occurred between the zone age and willow canopy, indicating that the effect of willow

TABLE 1

Test of effect of willow canopies on presence/absence of indigenous plant taxa at Lyman Glacier forefront (experiment 1). Canopy effect was tested with Fisher's exact test. Interaction between zone age and canopy was tested with logistic regression

Taxon <sup>a</sup>	Number of plots with taxon present		Canopy effect	Zone age × canopy
	Within canopy	Beyond canopy		
<b>Cyperaceae</b>				
<i>Carex scopulorum</i> Holm	10	8	None	c
<b>Ericaceae</b>				
<i>Cassiope mertensiana</i> (Bong) G. Don	44	34	None	b
<i>Phyllodoce empetriformis</i> (Sw.) D. Don	77	75	None	b
<i>Phyllodoce glanduliflora</i> (Hook.) Cov.	13	14	None	c
<i>Vaccinium deliciosum</i> Piper	38	34	None	<i>P</i> = 0.4867
<b>Juncaceae</b>				
<i>Juncus drummondii</i> E. Meyer	141	145	None	<i>P</i> = 0.3801
<i>Juncus mertensianus</i> Bong.	48	75	Negative**	<i>P</i> = 0.3277
<i>Luzula piperi</i> (Cov.) Jones	96	103	None	<i>P</i> = 0.1696
<b>Pinaceae</b>				
<i>Abies lasiocarpa</i> (Hook.) Nutt.	50	48	None	<i>P</i> = 0.4806
<b>Onagraceae</b>				
<i>Epilobium alpinum</i> L.	10	25	Negative*	c
<i>Epilobium latifolium</i> L.	21	40	Negative*	b
<b>Salicaceae</b>				
<i>Salix commutata</i> Bebb	7	11	None	c
<i>Salix phylicifolia</i> L.	21	25	None	<i>P</i> = 0.1551
<b>Saxifragaceae</b>				
<i>Saxifraga ferruginea</i> Grah.	90	123	Negative***	<i>P</i> = 0.3231
<i>Saxifraga tolmiei</i> T. & G.	21	36	Negative*	<i>P</i> = 0.0994
<b>Scrophulariaceae</b>				
<i>Pedicularis groenlandica</i> Retz.	59	46	None	b
<i>Veronica wormsjoldii</i> Roem. & Schult.	6	12	None	c

<sup>a</sup> Nomenclature follows Hitchcock and Cronquist (1973).

<sup>b</sup> Model with lack of fit; residual  $\chi^2$  of the model significant at 0.05 level.

<sup>c</sup> Too few observations to fit logistic regression model.

\*—*P* < 0.05.

\*\*—*P* < 0.01.

\*\*\*—*P* < 0.001.

canopies did not change over the chronosequence (Table 1). Logistic regression analysis of a few species resulted in a model with a lack of fit, indicating that these patterns of frequency distribution cannot be explained with a logistic regression model (*Cassiope mertensiana*, *Epilobium latifolium*, *Pedicularis groenlandica*, and *Phyllodoce empetriformis* in Table 1).

#### EXPERIMENT 2: EFFECT OF WILLOW SHRUBS ON EMERGENCE OF PINUS CONTORTA GERMINANTS

Only 64 germinants from the total of 1600 *Pinus contorta* seed survived at the study site. This equals an emergence rate

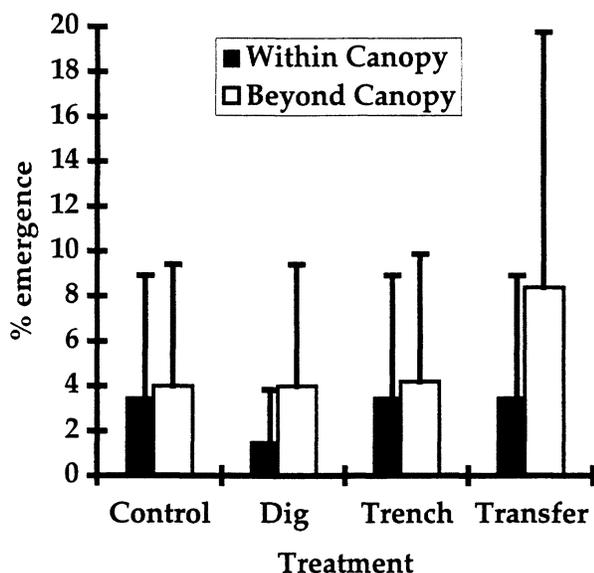


FIGURE 3. Proportion (mean  $\pm$  standard deviation) of *Pinus contorta* seed resulting in germinant emergence in main treatments in experiment 2.

of 4% as opposed to the germination rate of about 70% determined in the laboratory. No mortality among the shoots nor signs of herbivory were detected following the 8-wk period between sowing and data collection.

Neither the soil mixing nor soil trenching treatments significantly affected emergence of *P. contorta*, so these variables were excluded from the final reduced model as inferred from AIC-values. The residual  $\chi^2$  was highly nonsignificant ( $P = 0.6389$ ) indicating that the selected reduced model was well fit.

Zone age negatively affected emergence resulting in a mean decrease of 1.6% per year (95% confidence interval: 1.0–2.3%) over the 30- to 85-yr-old portion of the chronosequence (Table 2). Willow canopies also had a strong negative effect on emergence. Estimated germinant emergence within willow canopies was 57% of that beyond willow canopies (95% confidence interval: 43.7–74.2%). Transfer of soil produced a significant 1.8-fold higher emergence than soil left in place (95% confidence interval: 1.4–2.3; Fig. 3). The highest emergence thus occurred in those treatments where soil from beneath the canopies was transferred to the open.

TABLE 2

Logistic regression model describing *Pinus contorta* germinant emergence in experiment 2. Only the final reduced model is displayed

Variable	df	Odds ratio <sup>c</sup>	95% confidence intervals		Probability
			Lower	Upper	
Intercept	1	0.108	0.074	0.158	0.0001
Zone age (yr) <sup>a</sup>	1	0.984	0.977	0.990	0.0149
Willow canopy (0, 1) <sup>b</sup>	1	0.570	0.437	0.742	0.0332
Soil transfer (0, 1) <sup>b</sup>	1	1.768	1.352	2.313	0.0338

Model likelihood ratio (DF = 2)<sup>d</sup> = 0.6389

<sup>a</sup> Continuous variable.

<sup>b</sup> Indicator (dummy) variable.

<sup>c</sup> Ratio of the proportion of events (emergence) to the proportion of nonevents (see results for interpretation).

<sup>d</sup> Test for goodness of fit.

TABLE 3

Total soil nitrogen and soil organic matter beyond and under the willow canopies at Lyman Glacier forefront. Values are means  $\pm$  standard errors. Sample sizes are 2 for soil nitrogen and 4 for soil organic matter except where otherwise indicated

Age zone	Total soil N % by dry weight		Soil organic matter % by dry weight	
	Under canopy	Beyond canopy	Under canopy	Beyond canopy
<30	— <sup>b</sup>	0.001 $\pm$ — <sup>a</sup>	— <sup>b</sup>	0.001 $\pm$ — <sup>a</sup>
30	0.022 $\pm$ 0.003	0.007 $\pm$ 0.002	1.20 $\pm$ 0.099	0.67 $\pm$ 0.219
45	0.053 $\pm$ 0.038	0.016 $\pm$ 0.002	2.33 $\pm$ 0.739	1.37 $\pm$ 0.114
60	0.097 $\pm$ 0.074	0.006 $\pm$ 0.005	3.03 $\pm$ 1.574	1.04 $\pm$ 0.334
85	0.025 $\pm$ — <sup>a</sup>	0.010 $\pm$ — <sup>a</sup>	1.62 $\pm$ 0.185	0.57 $\pm$ 0.015

<sup>a</sup> Single observation used.

<sup>b</sup> No willows present in this zone.

#### CHARACTERIZATION OF SOIL NITROGEN AND ORGANIC MATTER CONTENTS

Both the nitrogen and organic matter contents of the soil tended to increase with time over the chronosequence through the 60-yr-old zone, although variation was high in samples from some locations (Table 3). The decrease in nitrogen and organic matter at the 85-yr-old sampling site was unexpected, but may be due to its location on the south slope of the rather tall terminal moraine, where leaching and wind or water erosion may be more pronounced than at the other, relatively flat sites. As a result, the zone age did not contribute to the explanatory power of our models, nor did the regression coefficients significantly differ from zero (Table 4). However, zone age was included in the final models for both soil organic matter and nitrogen concentrations as a confounding factor resulting in a reduced, additive model containing no interaction.

Samples under willow canopies consistently produced higher nitrogen and organic matter contents than did those in the nearby open sites (Table 3). Our linear regression model shows that the presence of a willow canopy resulted in an increase of 0.04 percent units (95% confidence interval: 0.01–0.07) in total soil nitrogen and 1.144 percent units (95% confidence interval: 0.13–2.16) in soil organic matter (Table 4). Most of the organic matter in the open sites was probably in the form of fine roots, including mycorrhizae, which passed the sieve mesh. Even sev-

TABLE 4

Reduced, additive, linear regression model describing total soil nitrogen ( $N = 15$ ) and soil organic matter ( $N = 33$ ) beyond and under the willow canopies in the Lyman Glacier forefront

Variable	Total soil N % by dry weight	Soil organic matter % by dry weight
Intercept	−0.003 $\pm$ 0.011 <sup>ns</sup>	0.620 $\pm$ 0.816 <sup>ns</sup>
Zone age (yr) <sup>a</sup>	0.000 $\pm$ 0.000 <sup>ns</sup>	0.007 $\pm$ 0.014 <sup>ns</sup>
Canopy <sup>b</sup>	0.043 $\pm$ 0.015**	1.144 $\pm$ 0.518*
Model (DF = 2)	$R^2 = 0.251$ Model $P = 0.027$	$R^2 = 0.169$ Model $P = 0.098$

<sup>a</sup> Continuous variable.

<sup>b</sup> Indicator (dummy) variable.

\*— $P < 0.05$ .

\*\*— $P < 0.01$ .

\*\*\*— $P < 0.001$ .

<sup>ns</sup>  $P > 0.05$ .

eral meters from the nearest willow and in soil supporting no other plants, an impressive amount of fine roots were evident when samples were extracted.

## Discussion

Both experiments showed that the shrub willows (*Salix commutata* and *S. phylicifolia*) do not serve as “nurse plants” or nuclei that facilitate the establishment of vascular plants from 30 yr onward. In experiment 1, the willow canopy did not affect the observed frequency of most indigenous taxa. The five species negatively associated with the willow canopies suggest that willows inhibit their establishment. In experiment 2, willow canopies inhibited the germinant emergence of *P. contorta*. However, the greatest emergence occurred in soils transferred from beneath willow canopies to areas beyond the canopies (Fig. 3). These findings indicate that although the willow canopy is either neutral or inhibitory in its effect on establishment of indigenous plants, the soil developing beneath the willow can contribute towards successful plant establishment.

Facilitation has been demonstrated in numerous other studies (see Callaway, 1995), although interference may be the major determinant of plant community structure and dynamics (Aarssen and Epp, 1990; Goldberg and Barton, 1992). The existing plants that aid the establishment of new plant individuals have been referred to as “nuclei” (Yarranton and Morrison, 1974; Blundon et al., 1993) or “nurse plants” (Niering et al., 1963; Franco and Nobel, 1988). Given that plants compete directly with one another for resources, one would expect that nucleation is not a typical phenomenon. In fact, where facilitation has been documented, some specific indirect mechanisms existed that resulted in the favored establishment of invading plants within the nucleus. These mechanisms have been described as altered microclimate (Yarranton and Morrison, 1974; Allen and Allen, 1988; Franco and Nobel, 1988; Callaway, 1994; Berkowitz et al., 1995; Pugnaire and Haase, 1996), nutrient accumulation (Yarranton and Morrison, 1974; Campbell et al., 1990; Franco and Nobel, 1988; Pugnaire and Haase, 1996), increased seed input via perching birds (Campbell et al., 1990), alteration of soil conditions by the accumulation of soil organic matter (Morris and Wood, 1989; Blundon et al., 1993; Pugnaire and Haase, 1996), and protection from herbivores (Niering et al., 1963; McAuliffe, 1988; Callaway, 1992). Whether an invading plant successfully establishes and survives within a nucleus is the net outcome of the opposite effects of inhibition and facilitation (Connell et al., 1987; Walker and Chapin, 1987; Franco and Nobel, 1988; Callaway, 1994; Berkowitz et al., 1995; Callaway and King, 1996).

Lower frequency of successful establishment of the five plant taxa and *Pinus contorta* under willow canopies is thought to be due to shading. As indicated by transect data (Jumpponen et al., unpublished), these five species were dominant at the earliest successional stage of glacier forefront, either before or at the point where willows began to occur. In contrast, those taxa not affected by willow canopies had the highest frequencies later in the successional sere. The early seral species are likely adapted to high levels of light and therefore are inhibited by the canopy shade. The same case can be made for *P. contorta*, a shade-intolerant species (Fowells, 1965). Competition for light has been suggested as important in controlling the establishment and performance of neighboring plants under previously established plant individuals (Franco and Nobel, 1988; Callaway, 1992; Berkowitz et al., 1995; Callaway and King, 1996).

Herbivory and seed predation have been hypothesized as

mechanisms of decreased emergence or establishment within nuclei (Morris and Wood, 1989; Callaway, 1992). No signs of herbivory on *P. contorta* were observed within or beyond the canopies in experiment 2 at the 8-wk observation time. Seed and seedling predation, however, cannot be ruled out; small mammals are frequently encountered on the glacier forefront (Cázares and Trappe, 1994) and newly emergent *Abies* seedlings growing in the open are consumed, probably by birds, at the site (Trappe, unpublished data). If the latter were true for the emergent *Pinus contorta* seedlings, it would mean that even more seedlings had emerged in the open than we recorded as emergent/survivors making the suggested canopy inhibition even more obvious.

Morris and Wood (1989) suggested potential effects of allelopathic substances produced by established plants to inhibit plant establishment. This possibility cannot be excluded in experiment 1; however, no such allelopathic mechanism was observed in experiment 2. On the contrary, the logistic regression model suggested that *P. contorta* shoot emergence was almost two-fold higher in transferred soils. If allelopathy that was associated with the soil characteristics were operating, one would expect equally low emergence in the transferred soil.

Enhanced emergence in soils from beneath the willow canopies is hypothesized to result from: (1) higher soil nitrogen or (2) organic matter contents, and (3) higher mycorrhizal inoculum potential in the transferred soil. Primary successional ecosystems are generally low in nitrogen (Vitousek and Walker, 1989; Matthews, 1992). Higher nitrogen concentrations have been observed under willows than in the open at Lyman Glacier forefront (Tables 3 and 4) and under non-nitrogen-fixing poplars at Glacier Bay in Alaska (Crocker and Major, 1955). Furthermore, the addition of nitrogen resulted in significant, almost two-fold, increase in growth of *Pinus contorta* seedlings grown in the greenhouse in soil from the Lyman Glacier forefront (Jumpponen, Mattson and Trappe, unpublished data), showing that plant growth is strongly nitrogen limited and that even small additions may enhance performance. This supports the importance of willow shrubs (vegetation in general [see Chapin et al., 1994]) in storing nutrients in the organic pool. Rapid accumulation of nitrogen during the earlier stages of succession, followed by a plateau, seems to be a general rule in primary successional seres regardless of the type of vegetation (Matthews, 1992; Walker, 1993).

Young soils are naturally low in organic matter; glacial soils begin with extremely low or no organic matter (Jenny, 1980; Matthews, 1992). At Lyman Glacier forefront, the soils are still low in organic matter almost 100 yr after the glacier retreat. However, there is nearly a two-fold increase in soil organic matter beneath the willow canopies compared to beyond them (Table 4). Increased soil organic matter enhances plant performance through a variety of mechanisms, such as increased water-holding capacity, increased nutrient availability, and more favorable rhizosphere environment. Our observations at Lyman Glacier suggest that soil moisture stress can become severe in mid to late summer and strongly limit establishing plants. Soil organic matter may serve as a moisture reservoir during drought.

Cázares (1992) and Trappe and Luoma (1992) hypothesized that the patterns of plant establishment and community development depend on availability of propagules of mycorrhizal fungi. Similarly, the successional change in plant communities is governed by interactions between plant individuals (Bazzaz, 1990; Connell and Slatyer, 1977) as well as the interactions between plants and soil microbiota (Allen and Allen, 1984, 1988, 1990). Root-associated fungi are of special importance because of their ability to access resources not available to plant roots and create below-ground connections between plant individuals

(Harley and Smith, 1983; Read et al., 1985; Newman, 1988; Allen and Allen, 1990). Soil transferred from under the willow canopies may have contained more diverse and viable microflora which could have stimulated seed germination and facilitated survival through the first growing season when the canopy inhibition was excluded.

The logistic regression model indicated that the germinant emergence of *Pinus contorta* decreased with zone age. For example, emergence at the 85-yr-old zone was 54% of that at the 30-yr-old zone. This result should be viewed with caution. The change in emergence over the zones was not linear but rather appeared to display a stepped function where emergence dropped dramatically between the 45-yr-old and 60-yr-old zones. The reduced emergence at the oldest zones may result from factors independent of zone age.

Our data suggest that willow shrubs may be either neutral or inhibitory to other vascular plants and that this interaction is species specific. Callaway (1994) provides a prime example for species-specific interaction: while two winter annuals were clearly positively associated with the perennial shrub, *Arthrocnemum subterminale*, survival of the third was substantially increased by the removal of the *Arthrocnemum* canopies. Our two experiments showed that no net positive effect was created by the physical microenvironment under the canopies. The role of the willow shrubs, however, may be essential in controlling the transition of the plant community from dominance by the early colonizers. The 100 yr of exposure to the environment at the Lyman Glacier forefront may not be enough to unveil possible positive effects of shrub willows on the late seral species. As shown in experiment 2, the willows may modify the substrate favorably for establishment of the later seral species.

In his comprehensive treatise on the ecology of recently deglaciated terrain, Matthews (1992: 271) states: "Many workers have proposed that facilitation is an important process on glacier forelands. In no case, however, has it been demonstrated that the prior occurrence of a particular species is necessary and sufficient for the later occurrence of a different species." Our experiments also show the potential difficulties in pinpointing mechanisms, which may have opposite effects, working simultaneously on any successional sere (Walker and Chapin, 1987). Detailed experimental manipulations are necessary to separate these mechanisms in primary succession. This should be the prerequisite to the introduction of a general theoretical framework and mechanistic models of community development in successional seres.

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