

## FACILITATION BY *PINUS FLEXILIS* DURING SUCCESSION: A HIERARCHY OF MECHANISMS BENEFITS OTHER PLANT SPECIES

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**Abstract.** Studies of facilitation have primarily been limited to single mechanisms, species, or environments. We examined interacting mechanisms governing the facilitative effects of *Pinus flexilis* on two later successional understory species, *Pseudotsuga menziesii* and *Ribes cereum*, in different microhabitats and seasons at the ecotone between the Rocky Mountain forests and Great Plains grasslands in Montana, USA. In field surveys, 69% of *Pseudotsuga* and 91% of *Ribes* were located beneath *P. flexilis* even though *P. flexilis* subcrowns accounted for a small proportion of available habitat. For three years, we monitored the survival of *Pseudotsuga* and *Ribes* seedlings experimentally planted beneath *P. flexilis* and in the open at a windward and a leeward site. Survival of both species was highest beneath *P. flexilis* at a site topographically protected from strong unidirectional winds (38% for *Pseudotsuga* and 63% for *Ribes*), and lowest at a windward site and in the open where tree crowns did not provide shelter from winds (2% and 6%, respectively). These results suggest that wind amelioration contributed to the facilitative effect of *P. flexilis*. However, even at the leeward site, where wind speed was low, survival of *Pseudotsuga* and *Ribes* was higher beneath *P. flexilis*, suggesting the importance of shade. To explore the relative importance of different mechanisms, we designed an experiment with six treatments: “shade,” “shade + wind,” “shade + drift,” “wind,” “drift,” and a “control.” After two years, we found shade to be of overwhelming importance for the survival of *Pseudotsuga* and *Ribes*. Without shade, no other treatments were significant, but once shade was provided, wind amelioration and snow pack accumulation increased survival of *Pseudotsuga*, suggesting that these different facilitative mechanisms functioned in a nested hierarchical manner: some mechanisms were important only when others were already functioning. Many studies have demonstrated multiple interacting mechanisms in the way that plants interact, but to our knowledge hierarchical interactive processes have not been previously documented. If the effects of positive or competitive mechanisms are often hierarchical, then studies of isolated mechanisms may not accurately assess their importance in nature.

**Key words:** community; competition; hierarchical facilitation; interacting mechanisms; *Pinus flexilis*; *Pseudotsuga menziesii*; *Ribes cereum*; shade; snowdrifts; succession; wind.

### INTRODUCTION

Positive interactions among plant species are well documented and a large number of facilitative mechanisms have been demonstrated (Hunter and Aarssen 1988, Bertness 1991, Bertness and Shumway 1993, Callaway 1995, Callaway and Davis 1998, Stachowicz 2001). However, the overall effects of one species on another are often determined by complex interactions between suites of facilitative and competitive mechanisms (Callaway et al. 1991, 1996, Rey and Alcántara 2000). Adding to the complexity, just one mechanism may have positive effects on a neighboring species under some conditions but negative effects on the same species under other conditions (Holmgren et al. 1997). Understanding the relative importance of interacting mecha-

nisms and variation in the importance of single mechanisms can provide important insights into processes that organize plant communities (Bertness 1998), as well as the distributions and abundances of individual species (Callaway 1995).

Facilitative mechanisms may be indirect as neighbors protect other species from herbivores, increase pollinator visits, concentrate animal-dispersed propagules, and enhance the effects of mycorrhizae and soil microbes (Callaway 1995, Stachowicz 2001, Bruno et al. 2003). Facilitative mechanisms may also be direct, in which neighbors ameliorate the physical environment for less hardy species (Vetaas 1992, Callaway 1995, 1997, Hacker and Bertness 1995, Baumeister 1999, Choler et al. 2001). Particular conditions that are ameliorated directly by stress-tolerant benefactors include high temperature and drought (Muller 1953, Muller and Muller 1956, Steenberg and Lowe 1969, Nobel 1984, Everett et al. 1986), low temperature (Carlsson and Callaghan 1991, Blundon et al. 1993, Choler 2001), high salinity (Bertness 1991, Bertness and Shumway 1993,

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Fong et al. 1996), low soil oxygen (Schat and Beckhoven 1991, Bertness and Shumway 1993, Callaway and King 1996), and low nutrients (Connell and Slatyer 1977, Walker and Chapin 1986, Wood and del Moral 1987, Blundon et al. 1993). Despite a wealth of detailed research on the mechanisms governing facilitation, few studies have attempted to identify the relative importance of different mechanisms operating simultaneously in the same ecological system.

We studied the relative importance of different facilitative and competitive mechanisms at the prairie–forest ecotone on the east front of the northern Rocky Mountains in Montana, USA. The forest component of this system is dominated by stress-tolerant limber pine (*Pinus flexilis*), an early successional species after fire, and the only tree species that initially colonizes prairie grassland. Numerous plant species exist under the crowns of *P. flexilis* but not in the open grassland nearby, suggesting the occurrence of facilitative interactions (Baumeister 2002). Several observations suggest that the potential facilitative relationships between *P. flexilis* and some understory species may be unusual. *Pinus flexilis* appears to ameliorate the extraordinarily high winds that occur along the east front (D. Baumeister and J. Dean, *unpublished data*). Wind-related facilitation has rarely been experimentally investigated. Protection from wind may function in addition to the more commonly reported shading of the understory and accumulation of organic material in the subcrown soil. We postulated that amelioration of wind, provision of shade, accumulation of snow pack, alteration of soil characteristics, and protection of seedlings in the understory from herbivores are co-occurring mechanisms through which *P. flexilis* interacts with species that grow beneath its crown. Additionally, we hypothesized that the relative importance of these different mechanisms may depend on abiotic conditions and the beneficiary species considered. For example, the degree to which *P. flexilis* ameliorates wind damage is likely to differ on leeward and windward sides of hills. Secondly, strong spatial associations occur between *P. flexilis* and subcrown species as disparate as the evergreen conifer *Pseudotsuga menziesii* Carr. (Douglas-fir) and the winter-deciduous shrub *Ribes cereum* Dougl. (wax currant). These contrasts provide opportunities to experimentally test theoretical predictions linking abiotic stress with facilitation (Bertness and Callaway 1994) and the mechanistic nature of species specificity in plant interactions (Callaway 1998a). Within this context, we have addressed the following questions: (1) Do patterns of association between *P. flexilis* and seedlings of other species suggest facilitative interactions? (2) What are the mechanisms of facilitation and do these mechanisms interact and/or vary in importance with the severity of environmental conditions? (3) Do the importance of and the mechanisms of facilitation vary among benefactor species? We explored these questions by measuring spatial relationships between *P. flexilis* and two under-



PLATE 1. *Pseudotsuga menziesii* growing beneath canopy of *Pinus flexilis* on leeward side of trunk. Photo credit: D. Baumeister.

story species, *Pseudotsuga menziesii* (see Plate 1) and *Ribes cereum*, by comparing environmental conditions under crowns to the open matrix, and through a series of field experiments over four years.

#### STUDY SITE

All research was conducted at the Theodore Roosevelt Memorial Ranch (TRM Ranch; 48°06'00" N, 112°41'00" W) located at the mountain–forest ecotone 15 km west of Dupuyer, Montana, USA. The Continental Divide to the west and south and the Great Plains to the east delineate the east front of the northern Rocky Mountains. The front is characterized by a very sharp ecotone between Rocky Mountain forests and Great Plains grasslands (Barker and Whitman 1988, Demarchi and Lea 1992). Over 60% of the land cover at the ecotone is prairie that is dominated by *Festuca scabrella* and *F. idahoensis* (Redmond and Prather 1996). The prairie is interspersed with shrub patches, *P. flexilis* stands, aspen (*Populus tremuloides*) groves, and riparian corridors. Annual precipitation in our research area averaged 70 cm over the last 12 years (R. Peebles, *unpublished data*). Snow accounts for 45–75% of annual precipitation (Moeckel 1997). Temperatures can

range from  $-40^{\circ}$  to  $37^{\circ}\text{C}$  annually (Aune and Kasworm 1989). An exceptional feature of the front is the occurrence of very intense catabatic, "Chinook" winds that descend from the mountains onto the prairie (Caprio et al. 1981, BLM 1992). The direction of these winds is predominantly from the west-southwest to the east-northeast. These warming Chinook winds remove and redistribute snow (altering soil moisture and microsite insulation), create some of the most highly diurnally variable temperatures in North America (Western Solar Utilization Network 1980), and severely batter plants, removing needles and branches.

#### METHODS

##### *Spatial relationships between understory species and Pinus flexilis*

To test for positive spatial correlations between *P. flexilis* and *Pseudotsuga* and *P. flexilis* and *Ribes*, we randomly located 50 450-m<sup>2</sup> plots containing at least 15% canopy cover of *P. flexilis* and at least one *Pseudotsuga* individual along a 15-km section of the front near Dupuyer, Montana. The relative proportion of tree cover was calculated by measuring cover of each tree crown using the average crown radius from four readings per tree and then summing the area of all tree canopies in a plot by species (*P. flexilis* or *Pseudotsuga*). The location (beneath a *P. flexilis* crown, beneath a *Pseudotsuga* crown, or in the open) of all individual *Pseudotsuga* and *Ribes* >5 cm in height was recorded. For *Pseudotsuga*, we also recorded whether seedlings occurred on the windward, "neutral," or leeward sides of *P. flexilis* based on observations of the dominant wind direction at each tree (i.e., following the clear pattern of tree "flagging," or the dominant direction of limb growth). Throughout the front, wind direction is highly skewed from the west-southwest. We recorded the approximate age of each *Pseudotsuga* individual >1 m in height beneath a *P. flexilis*, and the overstory *P. flexilis*, by counting rings from 5 mm diameter core samples taken between 0.3 m and 0.5 m above the ground. This allowed us to determine which individual appeared first at each site.

##### *Facilitation experiments*

**Abiotic conditions.**—To measure the general weather conditions at the study area, a Remote Automatic Weather Station (USFS standard issue) was set up at the TRM Ranch on an exposed, open slope (3% slope, 239° aspect). All experimental plots were located within 1 km of this station. Hourly measurements included air temperature, wind speed, wind direction, and maximum wind speed (gust), and direction of that reading. The weather station operated from 16 January 1997 to 27 April 1998, from 1 October 1998 to 23 June 1999, and from 9 September 1999 to 5 October 2000. Non-continuous readings were due to equipment malfunction and sharing the equipment with colleagues.

To incorporate variation in abiotic stress into the sampling design and transplant experiments (see Bertness and Callaway 1994), we selected two stands of low-density *P. flexilis* (<40% canopy cover) that differed in aspect and therefore in wind exposure. One site was fully exposed to the predominant wind (239° aspect), hereafter referred to as the "windward" site, and plants there clearly appeared to experience higher levels of flagging and wind damage, and the site had much lower snow cover during the winter. The other site was on a protected slope (48° aspect), hereafter referred to as the "leeward" site. Both sites were on the opposite sides of the same hill and on the same substrate. *Pinus flexilis* was the dominant conifer species at both sites but the leeward site had *Pseudotsuga* present naturally in the understory. Soils at both sites were predominantly fine, calcareous loams (Montagne et al. 1982, Offerdahl 1989).

To compare abiotic conditions under *P. flexilis* crowns with those of the open grassland matrix, we randomly selected 10 *P. flexilis* trees from each site (windward and leeward) for analyses of soil moisture, light, litter depth, and the thickness of A and O horizons.

We measured soil moisture under *P. flexilis* crowns in PVC monitoring tubes installed to 30 cm in depth beneath each tree; one 1 m from the trunk and one 1–2 m beyond the edge of the crown. A Frequency Domain Reflectometer (Troloxer, Sentry 200-AP; ISM, Malaga, Washington, USA) was used to periodically measure soil moisture at 10 cm and at 25 cm from mid-July 1998 to mid-October 1999. We calibrated reflectometer measurements with gravimetric measurements of soil moisture in 10 soil cores taken beneath trees at the leeward and windward sites. Soil moisture varied dramatically within a single day's measurement, and among the different days of the measurements. Therefore we recorded and analyzed the proportional difference between the outside and subcrown measurements for each individual tree, and used this number as a replicate.

Available nitrogen and phosphorus (mg/cm<sup>3</sup>) were measured using ion exchange resin bags (see Binkley and Vitousek 1991) from 1 May to 1 October 1999, at the leeward site only. One resin bag was buried 15 cm deep within 1 m of the trunk and another 1–2 m beyond the edge of the crown at each of the 10 randomly selected *P. flexilis*. At the end of the 1999 growing season, resin bags were excavated and their extracts colorimetrically analyzed for available nitrate, ammonium, and phosphorus (Binkley and Vitousek 1991).

Light availability was measured using light sensor ceptometers (LI-COR, Lincoln, Nebraska, USA) to take paired, instantaneous photosynthetically active radiation (PAR) measurements directly beneath (within 0.5 m of the trunk) and 1–2 m beyond each of the 10 *P. flexilis* crowns. Under each tree, we sampled light at each of the cardinal directions, halfway between the trunk and the edge of the crown, as the mean of a 45-s reading. The

four measurements were then averaged into a single mean for a tree or for a point in the open. This procedure was repeated on three different days during one growing season on days with <25% cloud cover.

We measured litter depth beneath *P. flexilis* as the average of four measurements taken at the cardinal directions at 1 m from the tree trunk for each of the 10 *P. flexilis* trees used for light measurements. Litter depth in the open was measured at four locations 1–2 m beyond each of the tree crowns. For each tree, the thickness of A and O horizons was measured for one 2 cm in diameter soil core taken at 1 m from the tree trunk and one taken 1–2 m beyond each tree crown.

**Seedling survival.**—At each site (windward and leeward), we chose 25 *P. flexilis* trees >60 years of age for sites for experimental plantings. We monitored the survival of 100, one-year-old *Pseudotsuga* seedlings planted in the open and another 100 under the 25 *P. flexilis*. All seedlings were raised in a greenhouse and kept in cold storage prior to bare root planting (State Conservation Nursery, Missoula, Montana). At planting, seedlings averaged  $3.4 \pm 0.05$  mm (mean  $\pm$  SE) in diameter at base and  $18.0 \pm 2.6$  cm in height. To minimize the effects of local adaptation, seeds for bare root stock were collected at the same elevation as the study site in the Little Belt Mountains of Montana, 200 km southeast of the TRM Ranch. At each of the two sites, in May 1997 four *Pseudotsuga* seedlings were planted next to each of the 25 *P. flexilis* trees; two seedlings within 1 m of the trunk and two seedlings 1–2 m beyond the edge of the *P. flexilis* crown. We planted seedlings in microsites with <50% grass cover and no shrub cover. Survival of seedlings was monitored every six weeks during the growing season beginning in mid-May 1997 and continuing until July 2000. Four seedlings died within the first six weeks of transplanting and were replaced with living seedlings. Survival rates were compared among locations and treatments (leeward/windward site, beneath/beyond crown, and protected/unprotected from herbivory). We considered seedlings to be surviving if at least two green needles were present.

In July 1998, one-year-old *Ribes cereum* seedlings were planted beneath the same *P. flexilis* trees used for the experiment with *Pseudotsuga*. All seedlings were raised in greenhouses and kept in cold storage prior to bare root planting (Bitterroot Restoration, Corvallis, Montana, USA). *Ribes cereum* is common at the study site, but the seeds used in the experiments were collected in Yellowstone County, Montana, ~300 km south from the TRM Ranch. Two *Ribes* seedlings were planted under each *P. flexilis* tree, one <1 m from the trunk and one 1–2 m beyond the edge of the crown. Survival of *Ribes* seedlings among locations and treatments was measured approximately every six weeks during the growing season beginning in mid-July 1998 and continuing until July 2000. Plants were considered alive if at least one green leaf was present. In July 2000, all surviving seedlings of both species were harvested.

Growth rates were measured as the change in total seedling height from the time of planting until the final harvest. Root and shoot masses were measured after drying for 24 h at 65°C.

**Mechanisms.**—Based on spatial associations and observations suggesting facilitation as we followed the experimental plantings, we designed a three-way, fully factorial, blocked experiment to separate the effects of different likely aboveground mechanisms (i.e., snow accumulation (drift), wind amelioration, and shade) by which *P. flexilis* may facilitate the survival and growth of planted *Pseudotsuga* and *Ribes*. The experiment was conducted at TRM Ranch on a level plateau dominated by *Festuca* grasses with scattered *P. flexilis* ranging in age from five to 130 years. A level plateau was selected rather than a windward and/or leeward slope to keep wind exposure constant and to eliminate variation in solar radiation and temperatures experienced by differing aspects. Soil was fine, calcareous loams (Montagne et al. 1982, Offerdahl 1989), and homogeneous within the experimental area. A 2.5 m tall welded wire fence was erected around the  $35 \times 15$  m area to exclude domestic and wild herbivores. Within this treeless experimental enclosure we established different treatments affecting  $1 \times 1$  m plots. Shade treatments (“shade,” “shade + drift,” “shade + no wind,” and “shade + no wind + drift”) were established by fixing green propylene shade cloth ( $1.5 \times 1.5$  m square, 48% shade reduction) over a PVC frame that covered the plots in an umbrella shape. Snow deposition and accumulation treatments (in the form of snow drifts; “drift,” “shade + drift,” “no wind + drift,” and “shade + no wind + drift”) were established by erecting plastic mesh snow fences ( $0.75 \times 1.5$  m, with  $5 \times 10$  cm mesh) directly windward of the plots. These fences allowed wind to scour the plots but substantially increased the accumulation of snow in the plots (D. Baumeister, *personal observation*). Snow fences were installed in October of each year and removed in April. In four wind treatments (“wind,” “shade + no wind,” “no wind + drift,” and “shade + no wind + drift”), wind was blocked with a clear, solid, U-shaped, polycarbonate fence (HYZOD GP, Sheffield Plastics, Sheffield, Massachusetts, USA), 60 cm high  $\times$  150 cm long. This effectively blocked the wind by >80%, but did not increase snow deposition and accumulation (D. Baumeister, *personal observation*). We checked, but did not quantify, the efficacy of the snow fences and the polycarbonate shields every six weeks and observed that the former accumulated a substantial amount of snow whereas the latter did not. The polycarbonate plastic is highly resistant to cold temperatures and transmits 89% of visible light and 86% of solar energy (Sheffield Plastics). An additional treatment with no amendments (“control”) was also established. Although the original design of the experiment was fully factorial, the final results and analysis were not. We excluded treatments “shade + no wind + drift” and “no wind + drift” from final analyses because

TABLE 1. Spatial association between cover types and individual *Pseudotsuga menziesii* and *Ribes cereum* on the east front of the Rocky Mountains, Montana, USA.

Cover type	Proportion of total cover	<i>Pseudotsuga</i> in cover type		<i>Ribes</i> in cover type	
		Observed	Expected	Observed	Expected
		No. (%)	No. (%)	No. (%)	No. (%)
In the open	0.51	131 (19)	360 (51)	43 (8)	264 (51)
<i>Pseudotsuga</i>	0.10	86 (12)	71 (10)	5 (1)	52 (10)
<i>P. flexilis</i>	0.39	489 (69)	275 (39)	470 (91)	202 (39)

Note: We observed 706 *Pseudotsuga* individuals in 50 450-m<sup>2</sup> plots ( $\chi^2 = 315.4$ , df = 1,  $P < 0.0001$ ) and 518 *Ribes* individuals in 33 450-m<sup>2</sup> plots ( $\chi^2 = 583.1$ , df = 1,  $P \ll 0.0001$ ).

they did not reduce wind speeds while simultaneously increasing snow deposition and accumulation.

To investigate the effects of treatments on soil water availability, we installed PVC monitoring tubes 30 cm deep in the center of each plot. Soil moisture as relative water content was measured using Frequency Domain Reflectometry (Troxler, Sentry 200-AP), gravimetrically calibrated using 10 soil cores from the site. Readings were taken at 10 cm and 20 cm depths every month during the growing seasons between 31 May 1998 and 24 August 1999.

Five *Ribes* seedlings and three *Pseudotsuga* seedlings were transplanted into each of 14 replicate quadrats for each of the nine treatment combinations (including the two later excluded). Therefore we planted a total of 530 *Ribes* seedlings and 378 *Pseudotsuga* seedlings at the beginning of the experiment. The replicates were based on the number of seedlings available for the experiment; and our intent was to maximize the number of replicates for a treatment while having an adequate number of seedlings to assess proportional survival within a quadrat. Seedlings were from the same stock as those planted beneath *P. flexilis* trees in the first experiment. We assessed treatment effects on *Pseudotsuga* and *Ribes* survival and growth. Survival (the presence of at least two green needles for *Pseudotsuga* and at least one green leaf for *Ribes*) was determined about every six weeks during the growing seasons of 1998 to 2000. Growth was measured as the change in total seedling height from the time of planting until final harvest in July 2000. Root and shoot masses were measured after drying for 24 hr at 65°C.

Spatial associations and differences in survival among seedlings of the experimental plantings were compared by fitting non-transformed survival numbers to log-normal distribution curves and testing the whole model and paired treatments with  $\chi^2$  analyses. We tested for site  $\times$  canopy interactions using repeated-measures General Factorial Analysis (GLM). Differences in abiotic conditions were assessed using ANOVA with aspect and crown cover as fixed variables. Soil moisture was assessed using repeated-measures GLM in SPSS 8.0 (SPSS 1997). Differences in survival for the field experiment, as well as survival in the multifactorial mechanistic experiment, were assessed using MANOVA

and ANOVA with a post hoc Tukey's test. In this experiment we assessed the effects of treatments as fixed effects, and used the means of all *Ribes* and all *Pseudotsuga* within a single plot for the analysis.

## RESULTS

### *Spatial relationships between understory species and Pinus flexilis*

Most *Pseudotsuga* and *Ribes* were found beneath mature *P. flexilis* (Table 1). Of the 706 *Pseudotsuga* seedlings found, 489 (69.3%) were found beneath *P. flexilis*, even though *P. flexilis* occupied only 39% of the study area. In almost all instances of co-occurrence, *P. flexilis* appeared at the site before *Pseudotsuga*; only 2.6% (or 13) of *Pseudotsuga* trees were older than the associated *P. flexilis*. For *Pseudotsuga* seedlings located beneath *P. flexilis*, the leeward side of the trunk was most preferred (314 of 489 seedlings;  $\chi^2 = 180.1$ , df = 3,  $P < 0.0001$ ). For seedlings located in the open, the leeward side beyond a *P. flexilis* was also preferred over windward and "neutral" (i.e., neither windward nor leeward) (104 of 217 seedlings;  $\chi^2 = 8.5$ , df = 3,  $P = 0.04$ ). The number of *Pseudotsuga* seedlings found beneath other *Pseudotsuga* was not different than would be expected by chance alone (paired *t* test,  $t = -1.9$ , df = 16,  $P = 0.08$ ).

The preference of *Ribes* for *P. flexilis* understories was even greater than that of *Pseudotsuga* (Table 1): 91% of *Ribes* were located beneath *P. flexilis*. We could not accurately age *Ribes*, but 98.3% of *Ribes* individuals occurred beneath trees >60 years old, substantially older than any of the extant stems on *Ribes* shrubs, indicating that *P. flexilis* appeared first at the sample sites.

### *Facilitation experiments*

*Abiotic conditions.*—Data from the weather station confirmed that wind on the front predominantly came from one general direction, the west-southwest (Fig. 1). As such, the leeward experimental site likely experienced a substantial reduction in high-wind events compared to the windward site, although this was not quantified. However, we found evidence of reduced abiotic stress at the leeward site and measured several ecologically important differences between the sites. *Pinus flexilis*

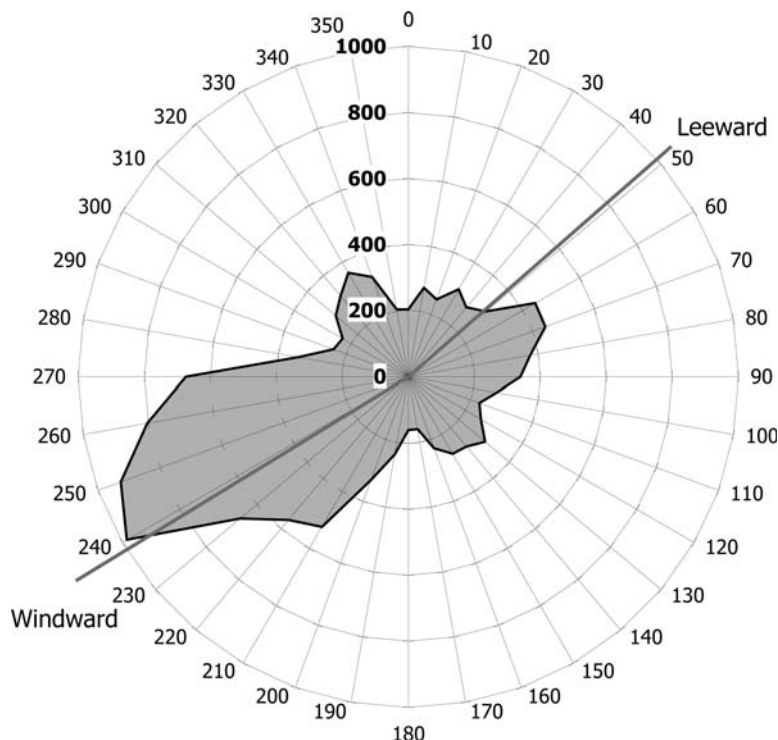


FIG. 1. Number ( $n = 13\,559$ ; scale 0–1000) of hourly readings of wind speeds  $>2.2$  m/s by azimuth (from January 1997 to October 2000). Aspects of experimental sites (windward and leeward) are delineated for reference.

trees were the same age at each site ( $88 \pm 13$  yr [mean  $\pm$  SE] at the windward site and  $97 \pm 9$  yr at the leeward site; one-way ANOVA<sub>age</sub>,  $F = 0.33$ ,  $df = 1, 19$ ,  $P = 0.57$ ), yet *P. flexilis* at the leeward site were much larger than pines at the windward site. At the windward site *P. flexilis* averaged  $3.2 \pm 0.2$  m tall,  $15.1 \pm 1.0$  cm in diameter, and had crown radii of  $1.2 \pm 0.1$  m vs.  $4.5 \pm 0.1$  m,  $22.3 \pm 0.9$  cm, and  $2.3 \pm 0.2$  m, respectively, at the leeward site. Furthermore, we found that A soil horizons were 65% shallower ( $5.0 \pm 1.0$  cm) at the windward site than at the leeward site ( $16.5 \pm 1.9$  cm; one-way ANOVA,  $F = 24.7$ ,  $df = 1, 19$ ,  $P < 0.000$ ). Also, A and O soil horizons were thinnest in the open at the

harsher windward site and thickest in the open at the more moderate leeward site (Table 2).

*Pinus flexilis* reduced PAR by  $40.2\% \pm 4.5\%$ , and this reduction did not significantly differ between the windward and leeward sites. Litter depth was significantly greater beneath trees than in the open at both sites (Table 2). Even though trees commonly improve soil nutrients beneath their canopies (Callaway 1995), we found no significant differences in P, NO<sub>3</sub>-N, or NH<sub>4</sub>-N in soils beneath trees vs. soils in the open grassland at the leeward site. Soil moisture was also unlikely as an important facilitative mechanism because, on average, soil moisture at 10 cm depth over time was  $21.6\% \pm$

TABLE 2. Soil characteristics beneath *Pinus flexilis* vs. in the open on leeward and windward aspects of the study site.

Characteristic	Windward			Leeward		
	<i>P. flexilis</i>	Open	<i>P</i>	<i>P. flexilis</i>	Open	<i>P</i>
	Means $\pm$ SE	Means $\pm$ SE		Means $\pm$ SE	Means $\pm$ SE	
Litter depth (cm)	4.8 $\pm$ 0.6	1.2 $\pm$ 0.3	<0.001	4.2 $\pm$ 0.6	1.2 $\pm$ 0.2	<0.001
A Horizon (cm)	7.1 $\pm$ 1.4	3.5 $\pm$ 1.5	0.097	11.4 $\pm$ 3.4	18.8 $\pm$ 2.7	0.104
O Horizon (cm)	21.4 $\pm$ 2.6	16.2 $\pm$ 1.6	0.104	16.0 $\pm$ 2.9	23.2 $\pm$ 3.0	0.112
P (mg/cm <sup>3</sup> )				0.31 $\pm$ 0.10	0.19 $\pm$ 0.07	0.364
NO <sub>3</sub> -N (mg/cm <sup>3</sup> )				0.13 $\pm$ 0.05	0.04 $\pm$ 0.02	0.079
NH <sub>4</sub> -N (mg/cm <sup>3</sup> )				0.08 $\pm$ 0.02	0.05 $\pm$ 0.01	0.263
Soil moisture, 10-cm depth (relative %)	78.4 $\pm$ 9.0	100.0	0.016	92.2 $\pm$ 8.9	100.0	0.138
Soil moisture, 20-cm depth (relative %)	98.5 $\pm$ 2.5	100.0	0.759	99.3 $\pm$ 2.3	100.0	0.869

Notes: For each location and site aspect,  $n = 10$ . *P* values for soil characteristics are based on one-way ANOVA. Means ( $\pm$ SE) for soil moisture are relative to the open, and *P* values are based on repeated-measures GLM.

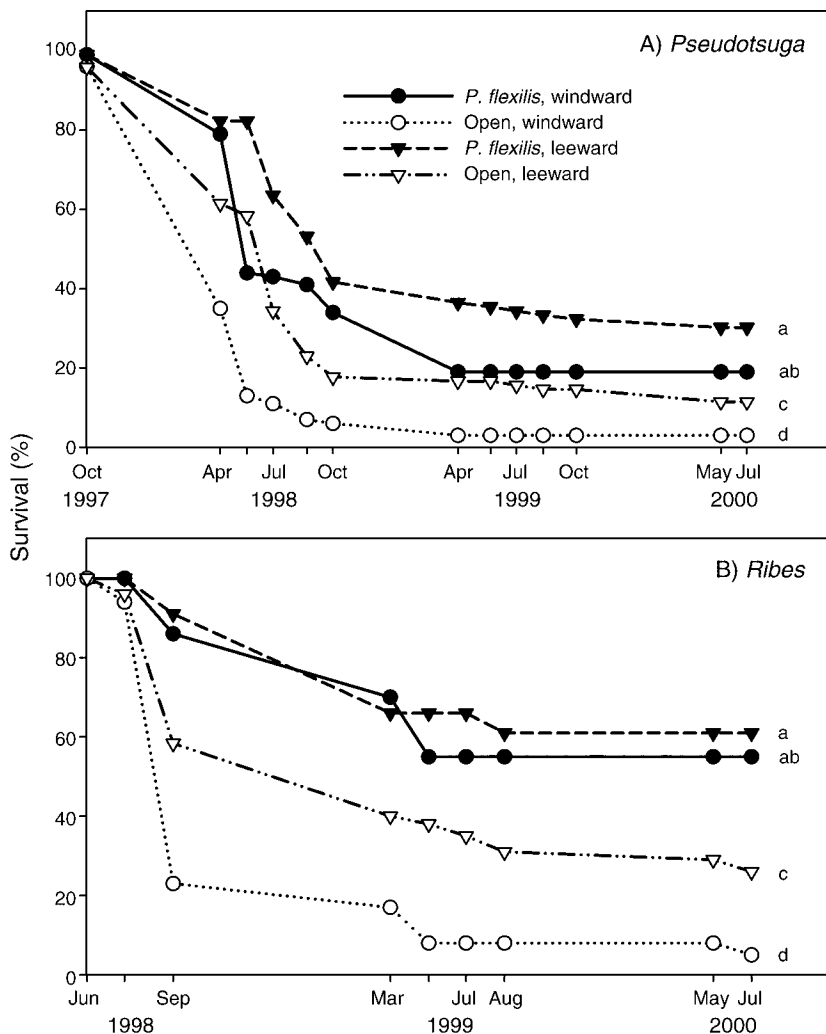


FIG. 2. (A) Survival of planted *Pseudotsuga menziesii* seedlings under *Pinus flexilis* and in the open on windward and leeward sites. On 1 October 1997, the initial number was 100 seedlings for each treatment and site. (B) Survival of planted *Ribes cereum* seedlings under *P. flexilis* and in the open on windward and leeward sites. On 1 June 1998, the initial number was 50 seedlings for each treatment and site. For both species, shared letters on the right designate no significant difference in survival based on  $\chi^2$  analysis of lognormal distribution curves;  $P < 0.05$ .

9.0% lower beneath trees than in the open on the windward side (Table 2; repeated-measures GLM,  $F = 7.13$ ,  $df = 1, 19$ ,  $P = 0.016$ ) and tended toward lower levels under trees on the leeward side (Table 2). The mean soil moisture for trees on the leeward topography averaged  $17.8\% \pm 3.1\%$  vs.  $10.3\% \pm 3.6\%$  on the windward side ( $P = 0.059$ ).

**Seedling survival.**—On 5 July 2000, after three full growing seasons, survival of *Pseudotsuga* was greatest for those seedlings planted beneath *P. flexilis* at the leeward site (37.5%), and lowest for those seedlings planted in the open at the windward site, where only one of 50 seedlings survived (2%; Fig. 2A). At the leeward site, survival beneath live trees and in the open was significantly greater than those respective locations at the windward site ( $\chi^2_{\text{live}} = 6.08$ ,  $df = 1$ ,  $P = 0.011$ ;  $\chi^2_{\text{open}} =$

8.22,  $df = 1$ ,  $P < 0.001$ ). Total survival at the leeward site was 20% compared to 11% at the harsher windward site. Differences in survival under *P. flexilis* vs. in the open were 10 times greater at the windward site (19% vs. 2%,  $\chi^2_{\text{wind}} = 15.33$ ,  $df = 1$ ,  $P < 0.0001$ ), compared to three times greater at the leeward site (30% vs. 11%,  $\chi^2_{\text{lee}} = 9.11$ ,  $df = 1$ ,  $P < 0.001$ ), suggesting that in the abiotically stressful windward site, facilitation is more important than at the leeward site. However, in a test of the relative importance of facilitation by abiotic site condition over time using a repeated-measures GLM, we found no significant interaction effect of site aspect  $\times$  treatment on *Pseudotsuga* survival ( $F = 1.3$ ,  $df = 1, 22$ ,  $P = 0.16$ ). There were, however, significant effects of site aspect and treatment when looked at individually ( $F_{\text{hill}} = 14.2$ ,  $df = 1, 11$ ,  $P < 0.0001$ ;  $F_{\text{trt}} = 3.6$ ,  $df = 1, 22$ ,  $P < 0.001$ ).

These results indicate that wind amelioration is an important facilitative mechanism.

We analyzed the timing of mortality of *Pseudotsuga* among sites to tease apart some of the effects of wind and other potential mechanisms. Differences in the timing of mortality at different sites were statistically significant as early as 25 April 1998 for the windward site ( $\chi^2 = 17.4$ ,  $df = 2$ ,  $P < 0.001$ ) with the greatest mortality occurring during the first winter (42%) and subsequent spring (50%). In contrast, far less mortality occurred at the leeward site in the first winter (26%), but much higher mortality in the second fall (60%). Differences in survival by site were not significant until 15 July 1998 at the leeward site ( $\chi^2 = 8.9$ ,  $df = 2$ ,  $P = 0.012$ ). In sum, shade appeared to have the strongest effects on *Pseudotsuga* in the winter.

The results for *Ribes* were similar to those for *Pseudotsuga*. On 5 July 2000, after three full growing seasons, survival of *Ribes* was highest for those seedlings planted beneath *P. flexilis* at the leeward site (62.5%), and lowest for those seedlings planted in the open at the windward site, where only three of 48 seedlings survived (6.3%; Fig. 2B). This trend follows that of *Pseudotsuga* and supports the importance of wind as a stress at our sites. Furthermore, at the leeward site, the overall survival of *Ribes* was 42.7% compared to 29.2% at the harsher windward site. Also, differences in survival between under *P. flexilis* and in the open were far greater at the windward site than at the leeward site ( $\chi^2_{\text{wind}} = 6.25$ ,  $df = 1$ ,  $P = 0.012$ ;  $\chi^2_{\text{ice}} = 0.33$ ,  $df = 1$ ,  $P = 0.564$ ). Survival in the open at the harsher windward site was significantly less than in the open at the leeward site, whereas there were no significant differences in survival beneath *P. flexilis* between sites ( $\chi^2_{\text{open}} = 20.3$ ,  $df = 1$ ,  $P = 0.020$ ;  $\chi^2_{\text{live}} = 0.14$ ,  $df = 1$ ,  $P = 0.705$ ). Despite these strongly significant differences between leeward and windward, in a repeated-measures GLM we again found no significant effect of site aspect  $\times$  treatment on *Ribes* survival ( $F = 1.2$ ,  $df = 1, 8$ ,  $P = 0.31$ ). There were, however, significant effects of site aspect and treatment individually ( $F_{\text{hill}} = 4.1$ ,  $df = 1, 8$ ,  $P < 0.01$ ;  $F_{\text{trt}} = 10.0$ ,  $df = 1, 8$ ,  $P < 0.01$ ). Survival of *Ribes* was greater beneath *P. flexilis* than in the open at both sites, suggesting as for *Pseudotsuga* that other factors may also play a role in the interactions between *P. flexilis* and *Ribes*.

As for *Pseudotsuga*, differences in the timing of mortality also provided insight into the mechanisms by which *P. flexilis* facilitates *Ribes*. The effect of location (beneath *P. flexilis* vs. in the open) was significant as early as 5 September 1998 (three months after planting) for both sites ( $\chi^2_{\text{wind}} = 12.3$ ,  $df = 2$ ,  $P < 0.01$ ;  $\chi^2_{\text{ice}} = 35.5$ ,  $df = 2$ ,  $P < 0.001$ ). The greatest mortality for *Ribes* at the windward site occurred during the first late summer (45.2%), with additional losses over winter (23.5%) and subsequent spring (25.0%). In contrast, *Ribes* at the leeward site experienced less late summer mortality in 1998 (24.5%), similar mortality during the first winter

(29.6%), and no mortality the following spring (0.0%). In contrast to *Pseudotsuga*, the effect of shade on *Ribes* was strongest in the summer.

Throughout the duration of the experimental planting, facilitation of understory species appeared to be important primarily for survival and not for growth. There were no significant differences among shoot and root mass, root-to-shoot ratio, or change in height for both species when compared among locations and sites. Most surviving seedlings actually lost aboveground tissue over the course of the experiment. For surviving *Pseudotsuga*, 33.4% of seedlings planted beneath *P. flexilis* and 64.3% planted in the open decreased in height due to the mortality of shoot tips. For surviving *Ribes*, 79.6% of seedlings planted beneath *P. flexilis* and 100% planted in the open decreased in height. This concurs with observations during repeated assessments of seedling survival that damaged but living seedlings had living tissue only a few centimeters above ground level.

*Mechanisms.*—In contrast to our interpretations of spatial associations and experimental transplant results, in the second experiment we found that shade and not wind was of primary importance for the survival of both *Pseudotsuga* and *Ribes* (Fig. 3A, B). Without shade no other treatments were significantly different for either species (*Pseudotsuga* one-way ANOVA,  $F = 0.31$ ,  $df = 2, 41$ ,  $P = 0.73$ ; *Ribes* one-way ANOVA,  $F = 0.06$ ,  $df = 2, 41$ ,  $P = 0.94$ ). For *Pseudotsuga*, once shade was provided, other treatments differed significantly (one-way ANOVA<sub>shd</sub>,  $F = 8.68$ ,  $df = 2, 41$ ,  $P = 0.001$ ), suggesting that different mechanisms functioned in a hierarchical manner. In a separate two-way ANOVA assessing only “shade” and “no wind” treatments, both treatments were significant although the interaction of the treatments was not (Table 3). In a two-way ANOVA assessing “shade” and “drift” treatments without “no wind” treatments, both treatments were significant as was the interaction of the two treatments (Table 3), further emphasizing the hierarchical effects of the treatments. Within the shaded plots, *Pseudotsuga* survival was lowest without protection from wind and without enhanced snow deposition and accumulation. Survival was highest with drift fences where snow had accumulated (Fig. 3A). As in the transplant experiments, mortality of *Pseudotsuga* seedlings was greatest during the first winter, averaging 84.1% for plots without shade, 35.9% for shade alone, and 16.7% for shade + wind barrier, yet only 2.4% for shade + drift fence (Fig. 3A). This low winter mortality for *Pseudotsuga* seedlings in plots with snowdrifts was followed by 0% mortality in spring. Snowdrift plots had significantly higher soil moisture at 20 cm depth in spring and early summer than the other shaded plots (repeated-measures ANOVA,  $F = 7.0$ ,  $df = 2, 41$ ,  $P = 0.003$ ).

For *Ribes*, survival was greatest in treatments with shade ( $91 \pm 2\%$  vs.  $29 \pm 4\%$ ; all shade treatments combined vs. all no-shade treatments;  $F = 202.6$ ,  $df = 1$ ,



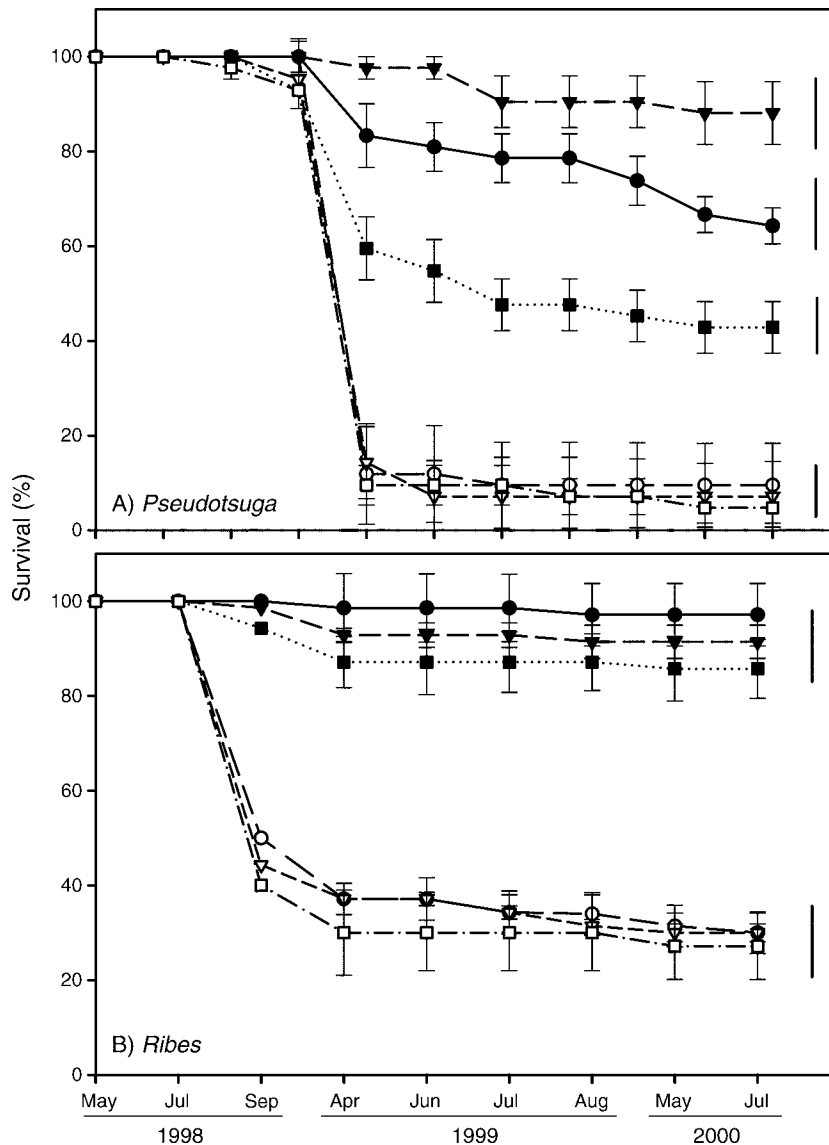


FIG. 3. Survival (mean  $\pm$  SE) of (A) *Pseudotsuga* seedlings and (B) *Ribes* seedlings in experiments designed to test the relative importance of different facilitative mechanisms. Solid symbols represent shade and open symbols represent no shade: circles (●), wind blocked; triangles (▼), treatment to accumulate drifted snow; squares (■), wind not blocked and no accumulated snow. Each treatment had 14 replicates, with three seedlings in each replicate for *Pseudotsuga* and five seedlings per replicate for *Ribes*. For each species, data were analyzed with repeated-measures ANOVA (Table 3) and single ANOVA for mortality on the last day of measurements. Individual bars to the right of the lines indicate significant differences ( $P < 0.01$ ) in final mortality.

83,  $P < 0.001$ ; Fig. 3B). As for *Pseudotsuga*, once shade was provided, wind reduction had a significant positive effect on survival following the first winter (25 April 1999, 1 June 1999, and 16 July 1999;  $P = 0.046$ ; Fig. 3B). However, there were no significant differences in survival among treatments with shade cloth at harvest on 5 July 2000 (one-way ANOVA<sub>shd</sub>,  $F = 2.79$ ,  $df = 2$ , 41,  $P = 0.07$ ). In a two-way ANOVA assessing interactive effects of “shade” vs. “no wind” and “shade” vs. “drift,” only shade was significant ( $F = 117.2$ ,  $df = 1$ , 13,  $P < 0.001$ ;  $F = 100.6$ ,  $df = 1$ , 13,  $P < 0.001$ , respectively).

Shade did not increase soil moisture, corresponding with the lack of crown effects on soil moisture in the field (Table 2). In the experimental plots, soil moisture at 10 cm was  $13.7 \pm 4.1\%$  greater in the treatments without shade (repeated-measures GLM,  $F = 10.1$ ,  $df = 1$ , 83,  $P = 0.002$ ). At 20 cm, there were no significant differences in soil moisture (repeated-measures GLM,  $F = 0.02$ ,  $df = 1$ , 83,  $P = 0.895$ ).

To understand how shade increased survival, as in the first experiment we examined the timing of mortality in plots with and without shade and found that the relative importance of shade differed between species by season.

TABLE 3. Two-way repeated-measures ANOVA analysis of factors affecting survival of *Pseudotsuga menziesii*.

Source of variation	df	MS	F	P
A) Effects of "shade" and "no wind" treatments				
Intercept	1	210.8	751.0	<0.001
Shade	1	17.7	63.0	<0.001
No wind	1	1.6	5.6	0.022
Shade × no wind	1	0.9	3.1	0.086
Error	52	0.3		
B) Effects of "shade" and "drift" treatments				
Intercept	1	227.1	1061.6	<0.001
Shade	1	24.7	115.5	<0.001
Drift	1	3.2	15.1	<0.001
Shade × drift	1	2.9	13.4	0.001
Error	52	0.2		

Note: For "no wind" treatment, wind was blocked with a clear, solid, U-shaped, polycarbonate fence; for "shade" treatment, green propylene shade cloth accomplished a 48% reduction in light; and for "drift" treatment, plastic mesh snow fences were erected on the windward of the plots.

For the evergreen *Pseudotsuga*, shade was crucial in the winter (Fig. 4) with a mortality rate of  $84.1\% \pm 3.4\%$  for seedlings in plots without shade compared to only  $17.5\% \pm 4.7\%$  for those with shade protection (one-way ANOVA<sub>shd</sub>, all shade treatments combined vs. all no-shade treatments,  $F = 130.1$ ,  $df = 1, 83$ ,  $P < 0.0001$ ). In contrast, for the deciduous *Ribes*, shade was crucial in late summer of the first year, with a mortality rate of  $55.2\% \pm 4.3\%$  for seedlings in plots without shade compared to just  $2.4\% \pm 1.2\%$  for those with shade (one-way ANOVA<sub>shd</sub>, all shade treatments combined vs. all no-shade treatments,  $F = 139.8$ ,  $df = 1, 83$ ,  $P < 0.0001$ ). This timing of mortality follows the same trend found for those seedlings planted beneath and beyond *P. flexilis* in the transplant experiments.

Also similar to the experimental plantings, the importance of facilitative mechanisms was manifested primarily in survival and secondarily in growth. Even so, both species were taller in shade treatments than in no shade treatments (Table 4). For both species, there were significantly higher root mass and root-to-shoot ratios for seedlings surviving in the shaded plots as compared to the unshaded plots (Table 4).

#### DISCUSSION

Our results indicate that *P. flexilis* has strong facilitative effects on two co-dominant species on the east front of the northern Rocky Mountains. We found strong positive spatial associations between *P. flexilis* and *Pseudotsuga* and *Ribes*, the beneficiaries were more common on the leeward sides of *P. flexilis*. Experimental plantings demonstrated greater survival for both species beneath *P. flexilis*, and in field experimental plantings more *Pseudotsuga* died on the windward sides of trees, indicating that the most important benefit of *P. flexilis* for *Pseudotsuga* was protection from the wind, and that shade was secondary. For *Ribes*, the effects of wind were important in some parts of our study, but spatial

patterns of mortality and high mortality in late summer in the field transplant experiment suggest that shade was of primary importance, and that wind was secondary. In our experimental manipulation of mechanisms we found that shade was overwhelmingly the primary influence on survival of both species. Wind barriers and treatment to accumulate snowdrifts were also important for *Pseudotsuga*, but only in the presence of shade. As such, the mechanisms governing facilitation appeared to be related to several interacting abiotic factors (wind, snow accumulation, and shade), which appear to function, at least for *Pseudotsuga*, in a nested hierarchical manner. In other words, the effect of particular mechanisms appeared to depend on the presence or absence of other mechanisms. For *Pseudotsuga*, without the effect of the dominant mechanism, shade, other mechanisms were not effective. Many studies have shown that different mechanisms can act synergistically, but to our knowledge this is the first evidence for hierarchical interactions, and in particular hierarchical interactions involving facilitation.

Shade, wind amelioration, and snow accumulation can be produced by other potential facilitators in our system, yet young *Pseudotsuga* and *Ribes* were not preferentially associated with mature *Pseudotsuga*. We do not know why these two conifers differed in their apparent nurse ability, but variation in facilitative effect can be caused by many subtle factors (Callaway 1998b). For example, there appeared to be much less light under *Pseudotsuga* than under *P. flexilis*, raising the possibility that *Pseudotsuga* was providing too much of a good thing. Furthermore, *Pseudotsuga* crowns did not come as close to the ground as those of *P. flexilis* and may have provided less of a wind block. Regardless, this species-specific pattern points to *P. flexilis* as an important ecosystem engineer (Jones et al. 1994, 1997) on the east front of the Rockies, performing functions that other species cannot.

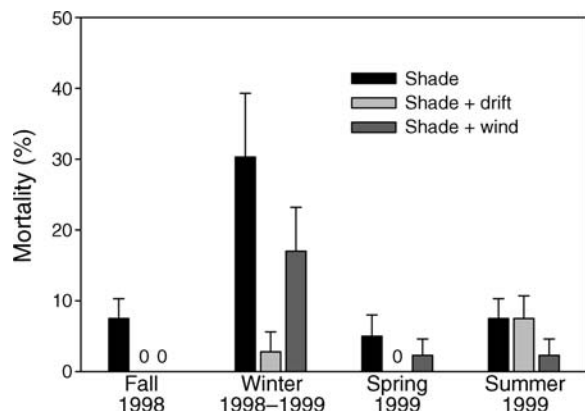


FIG. 4. Mortality (mean + SE) by season for *Pseudotsuga* seedlings in experiments designed to test the relative importance of different facilitative mechanisms. For statistics see Results: Facilitation experiments: Mechanisms.

TABLE 4. Changes in height, shoot mass, dry root mass, and root-to-shoot ratio of surviving *Pseudotsuga menziesii* and *Ribes cereum* from experimental plots at harvest in July 2000.

Source of variation	No shade		Shade		ANOVA		
	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>	<i>F</i>	df	<i>P</i>
<i>Pseudotsuga</i>							
Height (cm)	-7.9 $\pm$ 0.7	9	-1.0 $\pm$ 1.4	38	4.7	1, 47	0.036
Shoot mass (g)	1.4 $\pm$ 0.3	9	1.4 $\pm$ 0.1	38	0.0	1, 47	1.000
Root mass (g)	1.5 $\pm$ 0.5	9	3.2 $\pm$ 0.4	38	4.0	1, 47	0.052
Root:shoot	1.0 $\pm$ 0.2	9	2.2 $\pm$ 0.2	38	6.6	1, 47	0.014
<i>Ribes</i>							
Height (cm)	-11.5 $\pm$ 1.0	30	-6.4 $\pm$ 0.7	47	19.9	1, 76	0.000
Shoot mass (g)	0.9 $\pm$ 0.1	30	0.9 $\pm$ 0.1	47	0.0	1, 76	0.951
Root mass (g)	0.8 $\pm$ 0.1	30	1.2 $\pm$ 0.1	47	20.0	1, 76	0.000
Root:shoot	0.9 $\pm$ 0.1	30	1.4 $\pm$ 0.1	47	19.5	1, 76	0.000

Notes: Shade treatments were pooled because there were no significant effects of other factors. No shade represents the "control," "wind," and "drift" treatments. Shade represents the "shade," "shade + drift," and "shade + wind" treatments. See Table 3 for treatment terminology.

Shade provided by trees has been shown in many studies to facilitate understory species (Walker and Chapin 1986, Jones et al. 1994, Callaway 1995). Shade is important in summer for reducing soil and leaf temperatures and evapotranspiration in understory environments (Smith et al. 1987, Vetaas 1992, Belsky 1994). *Ribes* mortality was highest in summer in those plots without shade. *Ribes* tends to be more drought tolerant than other common shrubs in the area (Lesica 1989), but during our experiments soil moisture decreased to very low levels, particularly in late summer. For *Ribes* planted beneath *P. flexilis*, shade provided by the crown may have offset the effects of lower soil moisture recorded beneath the crown simply by keeping leaf temperatures cooler.

Frequency domain reflectometry measures relative water content of the soil and not water potential. Water potential is correlated with relative water content but varies widely with soil texture. In general, soils in the open had more clay and were denser than soils beneath trees (D. Baumeister, *personal observation*). As such, at equal relative water content values, our measurements of soil water may not have accurately reflected water potential (i.e., water actually available to plants), and it is possible that water availability beneath the crowns was actually higher than in the open. If this is the case, we may have underestimated the importance of crown facilitation of soil water, and we cannot rule out that seedlings, particularly *Ribes*, might also benefit from belowground factors (i.e., water) beneath trees.

Even though shade was primary in a hierarchy of mechanisms, shade appeared to manifest its effects on *Ribes* and *Pseudotsuga* in different seasons, summer and winter, respectively (Fig. 4). In winter, environmental stress for an evergreen species, such as *Pseudotsuga*, includes high irradiation levels because of increased reflectance off of snow and cold temperatures, the ideal conditions for inducing low-temperature photoinhibition in many plants (Öquist 1983, Powles et al. 1983, Germino and Smith 2000). In high light, low temper-

atures can amplify photoinhibition, a light-dependent depression of photosynthetic rate that occurs when leaves absorb more light than can be used (Krause 1994). For young *Pseudotsuga* establishing on the east front without the benefit of shade, chronic, possibly fatal, photoinhibition (Osmond 1994) may be occurring, especially on cold sunny days. In winter, *P. flexilis* crowns may facilitate *Pseudotsuga* by preventing photoinhibition through reduction of PAR and insulation from cold temperatures (DeLucia and Smith 1987, Ball 1994, Germino and Smith 2000).

The far greater abundance of seedlings on the leeward sides of trees, the relative success of transplants at the leeward site, and the significant effects of windbreaks in mechanistic experiments demonstrated the importance of wind amelioration as a facilitative effect. *Pinus flexilis* exhibits a growth form similar to krummoltz with numerous low-lying branches and hence can effectively minimize wind speeds, even at ground level. Wind can adversely affect growth and physiological activities of plants through physical stress as well as physical reduction of the boundary layer (Grace 1977, Nobel 1981, van Gardingen and Grace 1991, Ennos 1997). The latter causes both increased transpiration rates yielding greater water loss and decreased temperatures resulting in slower metabolic rates (Öquist 1983, van Gardingen and Grace 1991). Additionally, in harsh environments similar to the east front, abrasion from windblown soil particles and ice has been found to reduce cuticular wax and increase loss of plant water (Hadley and Smith 1986, van Gardingen and Grace 1991). A few other studies suggest neighbor amelioration of wind may be an important facilitative mechanism. In the Patagonian steppe, average wind velocity is 80% lower on the leeward side of shrubs and evaporation rates are less than half of those for plants on the windward side (Soriano and Sala 1986, Aguiar et al. 1992). In Swedish Lapland, Carlsson and Callaghan (1991) showed that *Carex bigelowii* increased in leaf length and culm height when growing within clumps of *Empetrum hermaphro-*

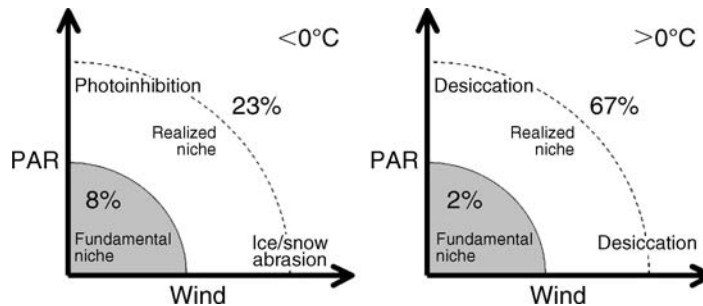


FIG. 5. Conceptual model for the realized niche expansion for *Pseudotsuga* and *Ribes* due to facilitation from *P. flexilis*. *Pinus flexilis* ameliorates PAR, wind, and temperature through crown cover, physical obstruction of wind, and snowdrifts, thereby extending the fundamental niche of these understory species to include the larger realm as their realized niche. Facilitative mechanisms protect *Pseudotsuga* and *Ribes* from desiccation, photoinhibition, and from ice and snow abrasion, depending on the abiotic conditions at a particular time. Approximate percentages of days per annum with each combination of conditions as determined from the weather station are denoted as percentages. Only 10% of days have conditions within the fundamental niches of these species.

*ditum* or *Racomitrium lanuginosum*. They experimentally manipulated the effects of wind by erecting artificial shelters and found that shelters elicited similar responses from *Carex*.

On the east front of the northern Rocky Mountains, wind speeds can be exceptional. During the first winter, from 26 October 1998 to 25 April 1999 (April is still winter in Montana), the mean wind speed was  $4.6 \pm 0.1$  m/s [mean  $\pm$  SE] with gusts up to 47 m/s and sustained winds up to 22.4 m/s, significantly greater than in summer (from 1 May to 30 September;  $n = 1825$ ;  $4.6 \pm 0.1$  m/s vs.  $3.1 \pm 0.05$  m/s). In addition to consistently strong winds, catabatic "Chinook" winds can increase air temperatures as much as  $25^{\circ}\text{C}$  in one hour and have wind speeds exceeding 56 m/s (Brinkman 1971). In Chinook belts, such as the front, snow cover typically lasts only a few days and bare ground is present throughout most of the winter (Western Solar Utilization Network 1980). In general, winter days with above-freezing temperatures were significantly windier ( $4.8 \pm 0.1$  m/s) than those with below-freezing temperatures ( $2.9 \pm 0.1$  m/s). Higher temperatures that come with Chinook winds may create unusually harsh conditions for *Pseudotsuga* by stimulating photosynthesis during a time when the ground remains frozen. The warming of the leaf tissue and subsequent water loss without replenishment from the roots may cause winter desiccation and the mortality we measured at first reading in spring. In contrast to *Pseudotsuga*, Chinook-caused winter mortality for the deciduous shrub *Ribes* was more likely to have been caused by thawing and freezing of stem tissues (see Frey 1983). During the period from 10 October 1998 to 15 April 1999, six freeze-thaw cycles (more than three days of temperature  $< 5^{\circ}\text{C}$  followed by at least one day of temperature  $> 5^{\circ}\text{C}$ ) concurred with Chinooks.

For *Pseudotsuga*, snowdrifts may have prevented photoinhibition, winter desiccation, and abrasion from blowing snow and ice. Snow accumulates in drifts on the leeward side of trees as a result of the fluid dynamics of

wind (Billings and Bliss 1959, West and Caldwell 1983). At our study area, hard-packed snowdrifts formed on the leeward side of trees and most stayed throughout the winter, even during Chinooks (D. Baumeister, *personal observation*). Positive effects of snow cover on plants are many: (1) the maintenance of higher soil temperatures during winter ( $+1$  to  $-3^{\circ}\text{C}$ ), (2) the moderation of temperatures, (3) reduction of cuticular abrasion due to wind during winter, (4) protection against photoinhibition, (5) provision of melt water, (6) protection against winter grazing by animals, (7) accumulation of blown soil, (8) increased availability of nutrients from leaching, and (9) higher annual decomposition rates of soils (Billings and Bliss 1959, Holway and Ward 1963, Bleak 1970, Canaday and Fonda 1974, Weaver 1974, Schwab et al. 1987, Evans and Fonda 1990, Taylor and Jones 1990, Walker et al. 1993, Germino and Smith 2000).

Our evidence for amelioration of wind damage and cold temperature photoinhibition at lower timberline is similar to that described by others for upper timberlines. Egerton et al. (2000) found that protected seedlings of *Eucalyptus pauciflora* at high elevations were less photoinhibited than those in the open. Germino and Smith (1999, 2000) found that *Abies lasiocarpa* and *Picea engelmannii* seedlings were most common in habitats with  $\sim 40$ – $80\%$  of the overhead area open to the sky, and demonstrated that seedlings in these habitats benefited from the way in which overstory canopies ameliorated nighttime temperature and lowered light levels. Based on evidence for wind-based facilitation at upper timberline, Smith et al. (2003) proposed "another perspective on altitudinal limits of alpine timberlines." They argued that mature trees protect recruits from severe mechanical damage from wind and that recruitment away from this protection was severely restricted. In sum, a growing body of evidence indicates that both biotic and abiotic factors play a primary role in development and stability of timberlines.

Our results suggest a relatively minor role for beneficiary species on soil P, N, and water, which contrasts with many other mechanistic studies of facilitation (Tiedemann and Klemmedson 1977, Weltzin and Coughenour 1990, Callaway et al. 1991, Callaway and King 1996, Pugnaire et al. 1996, Kieft et al. 1998). In fact we found either no differences in these variables between tree and open matrix locations or that these resources were more abundant in the open matrix. For nutrients, however, the lack of a crown effect may have been due to inadequate sampling; we only compared understory soils to the open for 10 trees at the leeward site. We do not know why these trees had such weak effects on soil resources, but if *P. flexilis* is shallow rooted its uptake of water and nutrients may exceed inputs via litterfall and shade (see Callaway et al. 1991).

By altering the availability of resources, including nutrients, water, and light, changing the way that energy and materials are cycled, or altering the effects of disturbance plants can potentially reconstruct the realized niches for other species (see Jones et al. 1994, 1997, Laland et al. 1999, Bruno et al. 2003). We found that *Pinus flexilis* appears to expand or even produce realized niches for *Pseudotsuga* and *Ribes* in a number of different ways that are depicted in Fig. 5. Young *Pseudotsuga* and *Ribes* seedlings establishing without the benefits of *P. flexilis* would likely be restricted to those rare niches with moderate temperatures, low wind levels, and low PAR. Through the provision of shade, *P. flexilis* greatly expands the realized niche for *Pseudotsuga* and *Ribes* along the *y*-axes, whereas wind amelioration allows for niche expansion along the *x*-axes of Fig. 5. Snowdrifts, in particular, allow for a larger realized niche along both axes by ameliorating wind, light, and temperature. Indeed, in our mechanistic experiment, we found highest survival for *Pseudotsuga* in the "shade + drift" treatment. Annually, only 10% (8% below zero, 2% above zero) of hourly abiotic readings taken at the weather station were low light and low wind. Over 81% of the days were sunny (data not shown), perhaps helping to explain the importance of shade as a mechanism for both species.

Our results provide strong evidence for the importance of positive interactions during succession at the ecotone of the Rocky Mountain front. Facilitative strength depended not only on the particular beneficiary species involved, but also on environmental conditions and season. In this system, several facilitative mechanisms operated simultaneously, but in a hierarchical manner of relative importance that determined the overall effect of the overstory tree on understory plants. The significance of wind reduction and snow pack was detected only after shade was provided. To our knowledge, the demonstration of hierarchically dependent facilitative mechanisms in interactions is unique in the literature. Understanding the way in which interactive mechanisms function is prerequisite to understanding the shifting roles of competition and facilitation on

abiotic gradients, conditional facilitative effects, and species specificity in facilitation, all of which are important processes determining the structure and function of plant communities. If the effects of positive or competitive mechanisms are often hierarchical, then studies of isolated mechanisms may lead to incorrect conclusions about their importance in nature.

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