Effects of Pinus flexilis on the dynamics and structure of plant communities on the northern Rocky Mountain front and Training biologists for emerging niches in non-traditional jobs

Dayna Baumeister

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EFFECTS OF PINUS FLEXILISON THE DYNAMICS AND STRUCTURE OF PLANT COMMUNITIES ON THE NORTHERN ROCKY MOUNTAIN FRONT

and

TRAINING BIOLOGISTS FOR EMERGING NICHES IN NON-TRADITIONAL JOBS

by

Dayna Baumeister
M.S. The University of Montana, Montana 1996
B.A. New College, Florida 1992
Presented in partial fulfillment of the requirements For the degree of Doctor of Philosophy
The University of Montana May 2002

Approved by:
Chair
Dean, Graduate School

Date
S-31-02
Effects of *Pinus flexilis* on the dynamics and structure of plant communities on the Northern Rocky Mountain Front

and

Training biologists for emerging niches in non-traditional jobs

Director: Ragan C. Callaway

My research examines the relative importance of interacting mechanisms (amelioration of wind, provision of shade, accumulation of snow pack, and alteration of soil characteristics) governing facilitation between *Pinus flexilis* and two understory species, *Pseudotsuga menziesii* and *Ribes cereum* in Montana. Survival of understory species was greatest beneath *P. flexilis* at a leeward site (*Pseudotsuga*, 38% and *Ribes*, 63%), and lowest in the open at a windward site (2% and 6%, respectively). The effects of wind amelioration, shade provision, and snowdrift accumulation were separated experimentally and after two years, shade was of overwhelming importance for the survival of both species. Once shade was provided, effects of wind amelioration and increased snow pack increased survival, suggesting a hierarchical functioning of mechanisms. High winter mortality of *Pseudotsuga* suggests *P. flexilis* canopies may prevent photo-inhibition and winter desiccation through reduction of light and insulation from variable temperatures. High summer mortality of *Ribes* suggests *P. flexilis* canopies may reduce transpiration through lowering leaf temperatures, thereby decreasing vapor pressure deficits. In this system, several mechanisms governing facilitation operated simultaneously, but in a hierarchical manner of relative importance thereby determining the overall effect of *P. flexilis* on understory plants.

I also studied facilitation and secondary succession by examining understory species composition beneath individual *P. flexilis* and in *P. flexilis* stands. As *P. flexilis* trees and stands aged, understory species richness increased, as did cover of forbs and shrubs, but cover of grasses decreased. Stands currently dominated by *P. flexilis* are shifting towards dominance by *Pseudotsuga* primarily in mesic sites, with corresponding increases in litter and shrub cover and decreases in grasses and *P. flexilis* recruitment. Since the 1860's succession from grasslands to forest on the Front has been characterized by invasion of *P. flexilis* and subsequent shifts in understory species composition apparently facilitated by *P. flexilis*.

Lastly, I examined the role of the emerging science of biomimicry in providing employment for biologists. Biomimicry as a discipline seeks design solutions inspired by nature. Industries employing this tool require biologists with an understanding of biology from a functional perspective, good communication skills, and a background in applied natural history.
Acknowledgements

Although the conferring of a doctor of philosophy is upon the individual, the process and product of the degree is the work of numerous individuals. My own dissertation is no exception. I have been extremely fortunate to have interacted with a suite of individuals and organizations whose contributions over the last six years were essential and invaluable. Of foremost, I am forever indebted to my husband, Thomas Baumeister, whose unwavering interest in my well-being provided the support I needed throughout this entire endeavor. From our first walk on the Rocky Mountain Front in January of 1995 and the seeding of questions about limber pine to the final stages of dotting my “i’s” and crossing my “t’s” during the spring of 2002, this dissertation is as much his as it is mine.

Several individuals contributed a substantial amount of time collecting field data in both beautiful and nasty weather. I am particularly grateful to Sandra Bierne, Justin Dean, Regan Choi and Damian Cremins for their help. Dean Snyder was incredibly patient with me and the GIS work he did that was ultimately not included. In addition, many fabulous summer days were spent in the company of a suite of “help as you can” field assistants including Meagan Barnett, Dulcie Belanger, Lisa Flowers, Jochen Baumeister, Lisa Classen, Levia Jones, Gus Motte, Justin Dean, Lori Harger, Mark Robertson, Bruin Herr, Kristi Tranter, Ray Callaway, and the students of the BIOL524 Vegetation Sampling class.
Funding for this research came primarily from my National Science Foundation Training Within Environmental Biology fellowship and the Boone and Crockett Wildlife Conservation Program. Additional seed funding was provided by the Bureau of Land Management, The Nature Conservancy, Montana Fish, Wildlife & Parks, and the Rocky Mountain Elk Foundation.

Logistical support from the Boone and Crockett Club was critical to the success of this project. I am extremely grateful to have had the opportunity to conduct research on the Club’s Theodore Roosevelt Memorial Ranch in Dupuyer, Montana. Access to the amazing landscape of the ranch, as well as consultations with the “local expert” and ranch manager, Bob Peebles, was the best support the Club could have provided.

My committee was extremely supportive of my work, as well as trusting my mid-process expansion in interest to Biomimicry, the subject of my third chapter. In particular, it was a very positive experience working with my advisor, Dr. Ray Callaway, whose sharp intellect and carefree energy complemented the process nicely. Dr. Anna Sala provided critical insight into the processes at work in this ecosystem, but equally important, became a great friend. Lastly, I have a tremendous amount of appreciation for Janine Benyus, who wrote the inspiring book on Biomimicry, serendipitously lived just 30 minutes away, and has become my respected mentor and, hopefully, a lifelong friend.

This dissertation is dedicated to my great grandfather, Dr. Watson, the only other biologist in the family, and my son, Alexander Orion, whose smile and endless love at such a tender young age helped see this dissertation to fruition.

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Chapter 1

Hierarchical effects of shade, wind protection, and snowpack benefit species beneath *Pinus flexilis*
Abstract:

Mechanistic studies of facilitation have primarily been limited to single mechanisms, species, or environments. This research examines the relative importance of interacting mechanisms governing facilitation between *Pinus flexilis* and two 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, an environment known for strong uni-directional winds, highly variable temperatures, and frequent winter Chinooks. I studied the relative importance of the amelioration of wind, provision of shade, accumulation of snow pack, and alteration of soil characteristics by *P. flexilis* for both species growing in its understory. In field surveys, 69% of *Pseudotsuga* and 91% of *Ribes* were located beneath *P. flexilis*. Under *P. flexilis* canopies, I found reduced PAR and increased litter depth under *P. flexilis*, but no significant differences in soil nutrients or moisture. For three years, I monitored the survival of *Pseudotsuga* and *Ribes* seedlings planted beneath *P. flexilis* and in the open at a windward and leeward site. Survival of both species was greatest beneath *P. flexilis* at the leeward site (*Pseudotsuga*, 38% and *Ribes*, 63%), and lowest in the open at the windward site (2% and 6%, respectively). These results suggest that wind amelioration was a dominant mechanism. However, survival of both species was greatest beneath *P. flexilis* at both sites suggesting the existence of other important mechanisms. To separate
the effects of wind amelioration, shade provision, and snowdrift accumulation, I
designed an experiment creating six combinations of treatments: shade,
shade+wind, shade+drift, wind, drift, and a control. After two years, I found
shade to be of overwhelming importance for the survival of both *Pseudotsuga*
and *Ribes*. Without shade, no other treatments were significant, yet once shade
was provided, effects of wind amelioration and increased snow pack increased
survival, suggesting that these different mechanisms functioned in a hierarchical
manner. For the evergreen *Pseudotsuga*, shade was crucial in winter, with 84% 
mortality for seedlings growing without shade compared to only 18% for those
with shade protection. High winter mortality of *Pseudotsuga* suggests *P. flexilis*
canopies may prevent photoinhibition and winter desiccation through reduction
of PAR and insulation from variable temperatures. In contrast, for the deciduous
*Ribes*, shade was crucial in late summer, with 55% mortality for seedlings
growing without shade compared to just 2% for those with shade. High summer
mortality of *Ribes* suggests *P. flexilis* canopies may reduce transpiration through
lowering leaf temperatures, thereby decreasing vapor pressure deficits. In this
system, several mechanisms governing facilitation operated simultaneously, but
in a hierarchical manner of relative importance thereby determining the overall
effect of *P. flexilis* on understory plants.
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INTRODUCTION

Positive interactions among species are well documented in plant communities 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 determined by complex interactions between facilitative and competitive mechanisms (Callaway et al. 1991, Callaway et al. 1996, Rey and Alcántara 2000). Adding to the complexity, just one mechanism may have positive effects on a neighboring species in some conditions but negative effects on the same species in other conditions (Holmgren et al. 1997). Understanding the relative importance of interacting mechanisms and the variation in the importance of single mechanisms can provide insight into processes that regulate plant communities (Bertness 1998), as well as the distribution 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 et al. 1991, Stachowicz 2001). Facilitative mechanisms may also be direct, in which neighbors ameliorate the physical environment for less hardy species (Vetaas 1992, Callaway 1995, Hacker and Bertness 1995, Callaway 1997,

I studied the relative importance of different facilitative and competitive mechanisms in a low elevation forest at the prairie-forest ecotone on the eastern front of the northern Rocky Mountains in Montana. The forest is dominated by stress-tolerant limber pine (*Pinus flexilis*), the only tree species that initially colonizes prairie grassland in the absence of fire. Numerous plant species exist in the understory of *P. flexilis* but not the open grassland nearby, suggesting the occurrence of facilitative interactions. Several observations suggest that the potential facilitative relationships between *P. flexilis* and understory species may be unique. Unlike previously reported facilitative mechanisms for other species, *P. flexilis* accumulates snow pack and ameliorates the extraordinarily high winds
averaging 25 m sec\(^{-1}\) that occur along the east Front. These mechanisms may function in addition to the more commonly reported shading of the understory and accumulation of organic material in the sub-canopy soil. I 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 mechanisms through which \(P. \textit{flexilis}\) interacts with species that grow beneath its canopy. Additionally, I hypothesize that the relative importance of these different mechanisms depends on abiotic conditions and the beneficiary species considered. For example, the strength of positive interactions between \(P. \textit{flexilis}\) and understory species appears to differ on leeward and windward sides of hills. Secondly, strong spatial associations occur between \(P. \textit{flexilis}\) and understory species as disparate as the evergreen conifer, \(Pseudo\textit{tus} \textit{g}a \textit{menziesii}\) Carr. (Douglas-fir), and the winter-deciduous shrub, \(Ribes \textit{cereum}\) 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).

Here I have addressed the following questions: 1) do different facilitative and competitive mechanisms interact and does the relative importance of these mechanisms vary with the severity of environmental conditions? 2) Is facilitation of understory species by \(P. \textit{flexilis}\) more important in abiotically stressful habitats
than moderate habitats? 3) Are different beneficiary species of *P. flexilis*
facilitated by different mechanisms? I explored these questions by measuring
spatial relationships between *P. flexilis* and two understory species, *Pseudotsuga*
*menziesii* and *Ribes cereum*, and through a series of field experiments over four
years.

*Study Site*

All research was conducted at the Theodore Roosevelt Memorial Ranch
(TRM Ranch) (N48°06′00″, W112°41′00″) located at the mountain-forest ecotone
15 km west of Dupuyer, Montana (Figure 1). The Continental Divide to the west
and south and the Great Plains to the east delineate the eastern “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 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. Abiotic
conditions on the Front resemble those of timberline environments, with long
cold winters and short warm summers. Annual precipitation in my research
area averaged 70 cm over the last 12 years (R. Peebles, unpubl. data). Snow
accounts for 45-75% of annual precipitation (Moeckel 1997). Temperatures can range from -40° to 37° 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. Chinook winds remove and redistribute snow (altering soil moisture and microsite insulation), create some of the most highly diurnally variable temperatures in North America (Anonymous 1980), and severely batter plants.

METHODS

Spatial relationships between understory species and *P. flexilis*

To test for positive spatial correlations between *P. flexilis* and *Pseudotsuga* and *P. flexilis* and *Ribes*, I randomly located 50, 450 m² 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 (Figure 1). All individual *Pseudotsuga* and *Ribes* were recorded by location (beneath a *P. flexilis* canopy, beneath a *Pseudotsuga* canopy, or in the open). For *Pseudotsuga*, I also recorded whether seedlings occurred on the windward 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). The relative proportion of tree cover was calculated by measuring cover of each tree canopy using the average canopy radius from four readings and summing across all trees in a plot by species (*P. flexilis* or *Pseudotsuga*). For each *Pseudotsuga*, I recorded the age of each *Pseudotsuga* individual beneath a *P. flexilis* and the overstory *P. flexilis* by counting rings from 5-mm core taken 0.5 m above the ground. This allowed me 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 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 air temperature, wind speed, and wind direction were determined from 600 readings taken over 10 minutes every hour. The maximum wind speed (gust) and direction of that reading were also recorded each hour. 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 until 5 October 2000. Non-continuous readings are due to sharing the station with another project and equipment malfunction.
To incorporate experimental variation in abiotic stress (see Bertness and Callaway 1994), I selected two stands of low-density *P. flexilis* (<40% canopy cover) that varied strongly in aspect and therefore in wind exposure. One site was fully exposed to the predominant wind (aspect of 239°± 2°), hereafter referred to as the “windward” site, and experienced high levels of desiccation, snow cover loss, and physical battering. The complementary site was on a protected slope (aspect of 48°± 1°), hereafter referred to as the “leeward” site. Both sites occurred on the same hill and had similar habitats, *P. flexilis* dominated; the leeward site had *Pseudotsuga* present in the understory. The windward site had less ground cover of biomass and more bare ground than the leeward site. Soils at both sites were predominantly fine, calcareous loams (Montagne et al. 1982, Offerdahl 1989).

To directly measure abiotic conditions under and beyond *P. flexilis* canopies, I randomly selected 10 live *P. flexilis* trees from each site (windward and leeward) for analyses of soil moisture, nutrients, light reduction, litter depth, and depth of A and O horizons. To determine soil moisture under *P. flexilis* canopies, I installed PVC monitoring tubes to 30-cm depths at each tree, one within 1-m of the trunk and one 1-2 m beyond the canopy. Gravimetric soil moisture was measured periodically at 10-cm and 25-cm depths from mid-July 1998 to mid-October 1999 using Frequency Domain Reflectometry (Troxler, Sentry 200-AP). The reflectometer was calibrated from 10 soil cores taken.
beneath trees at the leeward and windward sites. Available nitrogen and phosphorous were measured with ion exchange resin bags (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 canopy 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 phosphorous (Binkley and Vitousek 1991).

Light availability was determined using light sensor ceptometers (LI-COR, Inc., Lincoln, Nebraska, USA) to take paired, instantaneous PAR measurements directly beneath and 1-2 m beyond each of the 10 *P. flexilis* canopies. To calculate proportional light intensity differences between under each tree and the open, I took four paired samples of 100 readings over a 45-s period, and averaged the differences in PAR. This procedure was repeated three times during one growing season on days with less than 25% cloud cover.

Litter depth beneath *P. flexilis* was averaged from four measurements of a meter stick plunged into litter within 1-m of the tree trunk. Litter depth in the open was measured in four locations 1-2 m beyond the tree canopies. For each tree, the depths of A and O horizons were measured using 2-cm diameter soil cores taken within 1-m of the tree trunk and 1-2 m beyond the tree canopy.
Facilitation experiments: Seedling survival

At each site (windward and leeward), I chose 25 living *P. flexilis* trees > 60 years of age for transplant experiments. I planted and monitored the survival of 200, one-year old *Pseudotsuga* seedlings planted in the open and under these *P. flexilis* trees. All seedlings were bareroot, raised in greenhouses, and kept in cold storage prior to planting (State Conservation Nursery, Missoula, Montana). Seeds were collected at the same elevation as the study site in the Little Belt Mountains of northcentral Montana, 200 kilometers to the southeast of the TRM Ranch. In May 1997, four *Pseudotsuga* seedlings were planted next to each of the 25 *P. flexilis* trees per site; two seedlings within 1-m of the trunk and two seedlings 1-2 m beyond the edge of the *P. flexilis* canopy. I planted seedlings only in microsites with <50% grass cover and no shrub cover. To test for affects of herbivory, one seedling beneath each tree and one beyond each tree canopy was protected from herbivory with a 60-cm tall plastic mesh tube. Survival of seedlings was monitored every six weeks during the growing season beginning in mid-May 1997 and continuing until July 2000. I found four seedlings that died within the first six weeks of transplanting and assumed they underwent transplant shock and were subsequently replaced with live seedlings. I considered seedlings to be alive if at least two green needles were present. I compared survival rates among locations (leeward/windward site, beneath/beyond canopy, and protected/unprotected from herbivory).
In July 1998, one-year-old Ribes seedlings were planted beneath the same P. flexilis trees used for the experiment with Pseudotsuga. All seedlings were bareroot, raised in greenhouses, and kept in cold storage prior to planting (Bitterroot Restoration, Inc., Corvallis, Montana). Seeds were collected in Yellowstone County, Montana, ∼300 kilometers 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 canopy. Because Ribes appears to be rarely browsed on the Front (D. Baumeister, pers. obser.) protection from herbivory was not incorporated. Survival of Ribes seedlings among locations and treatments were 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-hr at 65°C.

Facilitation experiments: mechanisms

Based on observations during the ongoing transplant experiment, I designed a 3-way, full factorial, blocked experiment to separate different
potential mechanisms (i.e. snow accumulation, wind amelioration, and shade) by which *P. flexilis* may facilitate *Pseudotsuga* and *Ribes*. The experiment was conducted at TRM Ranch on a level plateau dominated by *Festuca* species with scattered *P. flexilis* aging from five to 130 years of age. 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 entire area to exclude domestic and wild herbivores. Within this experimental exclosure, shade treatments (‘shade’, ‘shade+drift’, ‘shade+no wind’ and ‘shade+no wind+drift’) were established by fixing green propylene shade cloth (1.5 x 1.5 m square, 48% shade reduction) over a PVC frame that covered the 1 x 1 m 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 m x 1.5 m, with 5 cm x 10 cm mesh) directly leeward of the plots. These fences allowed wind to scour the plots but substantially increased the accumulation of snow in the plots (pers. obs., D. Baumeister, every 6 weeks). 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, Inc.), 60 cm high x 150 cm long. This effectively blocked the wind by >80%, but did not increase snow deposition and accumulation (pers.
obs., D. Baumeister, every 6 weeks). The polycarbonate plastic is highly resistant to cold temperatures and transmits 89% of visible light and 86% of solar energy (Sheffield Plastics, Inc., Sheffield, MA). An additional control treatment with no amendments ('control') was also established. Although the design of the experiment was fully factorial, the analysis was not. I excluded treatments shade+no wind+drift and no wind+drift from final analyses because I found that they did not reduce wind speeds while simultaneously increasing snow deposition and accumulation.

To investigate the effects of treatments on soil water availability, I 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 98 and 24 August 99.

Five *Ribes* seedlings and three *Pseudotsuga* seedlings were transplanted into 14 replicate quadrats for each of the nine treatment combinations (including the three later excluded). Based on the number of available seedlings for the experiment, this maximized replicates while still providing an adequate number of seedlings to assess survival. Seedlings were from the same stock as those planted beneath *P. flexilis* trees in the facilitation experiments. I 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 approximately every six weeks during the growing seasons of 1998-2000. 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 of the transplant experiment were compared using Chi-squared. Differences in abiotic conditions were assessed using ANOVA, except for those monitored over time (e.g. soil moisture), which were assessed using a GLM repeated measures procedure. Differences in survival for the mechanistic experiment were assessed using MANOVA, ANOVA and GLM with a post-hoc Tukey's test. Results of means are reported ± one standard error. All statistical values were computed using standard statistical software (SPSS version 8.0 for Windows, SPSS, 1997).

**RESULTS**

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

Most *Pseudotsuga* and *Ribes* were found near mature *P. flexilis* (Table 1). Of the 706 *Pseudotsuga* seedlings found, 489 (69.3%) were found beneath *P.
*fle xilis* 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% (13 trees) of *Pseudotsuga* were older than the associated *P. flexilis*. For *Pseudotsuga* seedlings located beneath *P. flexilis*, the leeward side of the trunk was most preferred (χ²=180.1, df=3, p<0.000). For seedlings located in the open, the leeward side of a *P. flexilis* was also preferred (χ²=8.5, df=3, p=0.04). The number of *Pseudotsuga* seedlings found beneath other *Pseudotsuga* was not significantly different than expected by chance alone (paired t-test obs vs. exp, 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). Ninety-one percent of *Ribes* were located beneath *P. flexilis*. I could not accurately age *Ribes*, but 98.3% of *Ribes* individuals occurred beneath trees >60 years old, substantially older than at least the extant stems on *Ribes* shrubs, strongly indicating *P. flexilis* appeared first at the sample sites.

*Facilitation experiments: abiotic conditions*

Data from the weather station shows that wind on the Front predominantly comes from one general direction, the west-southwest (Figure 2). Because of this dominant wind direction, the leeward experimental site likely
experienced a substantial reduction in high wind events compared to the windward site, although this was not quantified. However, I found evidence for reduced abiotic stress at the leeward site and measured several ecologically important differences between the sites. *Pinus flexilis* trees were the same age at each site (88 ± 13 years at the windward site and 97 ± 9 years old at the leeward site) (one-way ANOVA_{age}, F=0.33, 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 ± 0.2 m tall, 15.1 ± 1.0 cm in diameter, and had canopy radii of 1.2 ± 0.1 m versus 4.5 ± 0.1 m, 22.3 ± 0.9 cm, and 2.3 ± 0.2 m, respectively, at the leeward site. In further support of the harsh conditions at the windward site, I found that A horizons were 65% shallower (5.0 ± 1.0 cm) than at the leeward site (16.5 ± 1.9 cm) (one-way ANOVA_{A horizon}, F=24.7, p<0.000). Also, A and O horizons were shallowest in the open at the harsher windward site and greatest in the open at the more moderate leeward site (Table 2).

*Pinus flexilis* effectively reduced PAR by 40.2 ± 4.5% and this reduction did not significantly differ between the windward and leeward sites. Litter depth was significantly greater beneath canopies than in the open at both sites (Table 2). Surprisingly, considering the majority of relevant literature, there were no significant differences in P, NO\textsubscript{-}N, or NH\textsubscript{4}•-N beneath live trees compared to the open. Soil moisture was generally similar beneath the canopy and in the open, as well as between sites (Table 2). The only significant difference in soil
moisture suggests that *P. flexilis* reduced soil moisture. At 10-cm depth soil moisture over time was 21.6 ± 9.0% lower beneath trees than in the open on the windward site alone (repeated measures GLM, F=7.13, df=1, p=0.016).

*Facilitation Experiments: 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 1 of 50 seedlings survived (2%) (Figure 3). At the more moderate leeward site, survival beneath live trees and in the open was significantly greater than those respective locations at the windward site ($\chi^2_{\text{live}}=4.67$, df=1, p=0.031; $\chi^2_{\text{open}}=5.28$, df=1, p=0.022). Overall survival at the leeward site was 20% compared to 11% at the harsher windward site. These combined results suggest that wind amelioration is a dominant facilitative mechanism. However, at both sites, survival of *Pseudotsuga* was greater beneath *P. flexilis* than in the open, suggesting that, in addition to wind, other factors likely play a role in the dynamics between *P. flexilis* and *Pseudotsuga*. Even so, differences in survival under *P. flexilis* and in the open were greater for the windward site than the leeward site ($\chi^2_{\text{windward}}=13.1$, df=1, p<0.000; $\chi^2_{\text{leeward}}=10.2$, df=1, p=0.001), suggesting that in the abiotically stressful windward site, facilitation is more important for *Pseudotsuga* survival 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, I found no significant effect of site aspect*treatment on overall *Pseudotsuga* survival (*F*=1.3, df=22, *p*=0.16). There were, however, significant effects of site aspect and treatment individually (*F*_{hillside}=14.2, df=11, *p*=0.00; *F*_{treatment}=3.6, df=22, *p*=0.00).

After one winter, differences in survival due to herbivory were not significant with only 4 of 100 seedlings showing evidence of non-fatal browsing. Protective cages were therefore removed in May 1998 from all locations and this treatment was subsequently excluded from final analyses.

I analyzed the timing of mortality among sites to tease apart some of the effects of wind and other potential mechanisms. Differences in survival by location were significant as early as 25 April 1998 for the windward site (*X^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%) as compared to the second fall (60%). Differences in survival by location were not significant until 15 July 1998 at the leeward site (*X^2*=8.9, df=2, *p*=0.012). High winter and spring mortality at the windward site suggests winter desiccation, photoinhibition, or snow/ice abrasion of the cuticle as possible causes. Indeed, average wind speeds in winter (1 Oct to 30 April) were significantly greater than in summer (1 May to 30 Sep).
(n=1825) (4.6± 0.1 m sec\(^{-1}\) vs. 3.1± 0.05 m sec\(^{-1}\)) (one-way ANOVA\(_{\text{wind}}\), F=105.2, p<0.001). In contrast to the windward site, the late summer and fall mortality at the leeward site is more likely due to summer water stress.

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 3 of 48 seedlings survived (6.3%) (Figure 4). This trend is identical to that of *Pseudotsuga* and supports the importance of wind amelioration as a mechanism. Indeed, at the more moderate leeward site, the overall survival of *Ribes* was 42.7% compared to 29.2% at the harsher windward site. Additionally, differences in survival between under *P. flexilis* and in the open were far greater at the windward site than the leeward site ($\chi^2_{\text{windward}}=6.25$, df=1, $p=0.012$; $\chi^2_{\text{leeward}}=0.33$, df=1, $p=0.564$). Survival in the open at the harsher windward site was significantly less than the open at the leeward site, whereas there were no significant differences in survival beneath *P. flexilis* among 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 strong significant differences leeward and windward, in a repeated measures GLM, I found no significant effect of site aspect*treatment on *Ribes* survival (F=1.2, df=8, $p=0.31$). There were, however, significant effects of site aspect and treatment individually ($F_{\text{hillside}}=4.1$, df=8, $p<0.01$; $F_{\text{treatment}}=10.0$, df=8, p<0.01). Nonetheless, survival of *Ribes* was greater beneath *P. flexilis* than in the open at both sites, suggesting

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that, in addition to wind, other factors may also play a role in the interactions between *P. flexilis* and *Ribes*.

As for *Pseudotsuga*, differences in the timing of mortality provided insight into the mechanisms by which *P. flexilis* facilitates *Ribes*. The treatment affect of location (beneath *P. flexilis* vs. open) was significant as early as 5 September 1998 (3 months after planting) for both sites ($X^2_{\text{windward}}=12.3$, df=2, $p<0.01$; $X^2_{\text{leeward}}=35.5$, 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%). At both sites, late summer mortality was likely due to water stress, whereas winter mortality for a deciduous shrub is likely due to thawing and freezing of stem tissues (Frey 1983). During the period 10 October 98 to 15 April 99, six freeze-thaw cycles (>3 days of $T<-5\, ^\circ\text{C}$ followed by at least one day of $T>5\, ^\circ\text{C}$) concurred with Chinooks. In general, the occurrence of the Chinooks likely contributed to the overall loss of seedlings independent of where they were transplanted. Significantly greater winter mortality at the windward site can also be explained by the winds associated with Chinooks. The spring mortality that occurred only at the windward site was likely due to severe wind events (as opposed to freeze/thaw cycles, which would cause mortality at both sites).
Between 15 April 99 and 5 Jun 99 (spring), 20 days had sustained winds greater than 5 m/s and the average wind speed was 3.8 ± 0.1 m/s. Wind gusts exceeded 10 m/s in at least 290 different hours.

For the duration of this experiment, facilitation of understory species appeared to be important primarily for survival but not for growth. There were no significant differences among shoot and root mass, root to shoot ratio, change in height for both species when compared among locations and sites. Most surviving seedlings actually lost biomass 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 visual observations during repeated assessments of seedling survival that damaged, but living seedlings had living tissue only a few centimeters above ground level.

*Facilitation experiments: mechanisms*

In contrast to the analyses of spatial associations and previous experimental results, in the second experiment I found that shade and not wind was of overwhelming importance for the survival of both *Pseudotsuga* and *Ribes* (Figures 5 and 6). Without shade no other treatments were significantly different
for either species (one-way ANOVA \textit{Pseudotsuga}, F=0.31, df=2, p=0.73; one-way ANOVA \textit{Ribs}, F=0.06, df=2, p=0.94). For \textit{Pseudotsuga}, once shade was provided, other treatments were highly significant (one-way ANOVA \textit{shade}, F=8.68, df=2, 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, \textit{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 (Figure 5). Like in the transplant experiments, mortality of \textit{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 plus wind barrier, yet only 2.4% for shade plus drift fence (Figure 7). This low winter mortality for \textit{Pseudotsuga} seedlings in plots with snowdrifts was followed by 0% mortality in spring. These plots had significantly higher soil moisture at 20-cm deep in spring and early summer than the other shaded plots (repeated measures GLM, F=7.0, df=2, p=0.003).
For *Ribes*, survival was greatest in treatments with shade (91 ± 2% versus 29 ± 4%; F=202.6, df=1, p<0.001) (Figure 6). As for *Pseudotsuga*, once shade was provided, then wind reduction also had a significant positive effect on survival following the first winter, including 25 April 99, 1 June 99, and 16 July 99 (p=0.046) (Figure 6). However, there were no significant differences in survival among treatments with shade cloth at harvest on 5 July 2000 (one-way ANOVA shade, F=2.79, df=2, p=0.07). In a two-way ANOVA assessing interactive effects of ‘shade’ and ‘no wind’ and ‘shade’ and ‘drift’, only shade was significant (F=117.2, df=1, p<0.001, F=100.6, df=1, p<0.001, respectively).

The importance of shade for both species was not related to increased soil moisture, corresponding with the lack of canopy effects on soil moisture in the field (Table 2). In the experimental plots, at 10-cm, soil moisture was 13.7 ± 4.1% greater in the treatments without shade (repeated measures GLM, F=10.1, df=1, p=0.002). At 20-cm, there were no significant differences in soil moisture (repeated measures GLM, F=0.02, df=1, p=0.895).

To better understand the importance of shade, I examined the timing of mortality in plots with and without shade and found that the relative importance of shade differed between species by season. For the evergreen *Pseudotsuga* shade was crucial in the winter, with a mortality rate of 84.1 ± 3.4% for seedlings in plots without shade compared to only 17.5 ± 4.7% for those with shade.
protection (one-way ANOVAshade, $F=130.1$, df=1, $p<0.000$). 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 ANOVAshade, $F=139.8$, df=1, $p<0.000$). This timing of mortality is the same trend found for those seedlings planted beneath and beyond *P. flexilis* in the transplant experiments.

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

**DISCUSSION**

My results indicate that *P. flexilis* has strong facilitative effects on two co-dominant species on the eastern front of the northern Rocky Mountains. I found strong positive spatial associations between *P. flexilis* and *Pseudotsuga* and *Ribes* and transplant experiments demonstrated greater survival for both species beneath *P. flexilis*. The mechanisms governing facilitation appeared to be related...
to several interacting abiotic factors (wind, snow accumulation, and shade), which appear to function in a strongly hierarchical manner. In other words, without the effect of the dominant mechanism, the others do not function. In field transplant experiments, the timing of *Pseudotsuga* mortality indicated that the most important benefit of *P. flexilis* for *Pseudotsuga* was protection from the wind, and shade was secondary. For *Ribes*, although wind had highly significant effects, high mortality in late summer in the field transplant experiment suggests shade was of primary importance, and wind secondary. However, in my experimental mechanism plots, I found that shade was overwhelmingly the primary influence on survival of both species. Wind barriers and snowdrifts were significant, particularly for *Pseudotsuga*, but these were only important in the presence of shade.

In mechanistic experiments, shade was crucial for both species, and without it, no other factors are important. Once shade is present, the effects of wind amelioration and increased snow pack increase substantially in importance. Interestingly, shade appears to affect *Pseudotsuga* and *Ribes* in different seasons, winter and summer, respectively. Shade provided by trees has been shown in many studies to have important facilitative effects for understory species (Walker et al. 1993, Jones et al. 1994). Shade is important in summer for reducing soil and leaf temperatures and evapotranspiration in below-crown environments (Smith et al. 1987, Vetaas 1992, Belsky 1994). *Ribes* mortality was
highest in summer in those plots without shade and water loss due to higher transpiration rates in higher temperatures may have been the limiting factor. Although, *Ribes* tends to be more drought-tolerant than other common shrubs in the area (Lesica 1989), during my experiments soil moisture decreased to very low levels, particularly in late summer. *Ribes* seedlings survived the first ten weeks following planting ruling out transplant shock, but not eliminating the possibility of short acclimatization time. During the first summer, when *Ribes* mortality was highest, soil moisture in the root zone at 10-cm depth on 11 July was just 7.0±0.4% and by 3 September was undetectable (0.0±0.0%). For the *Ribes* seedlings growing in high light and strong winds, increased water pressure deficits and the resulting higher water demands likely proved fatal under these low soil moisture conditions. For those seedlings located beneath *P. flexilis*, the competitive effects of lower soil moisture beneath the canopy compared to the open on the windward site may have been offset by the benefits of shade, which likely reduced transpiration rates by lowering leaf and soil temperature and thereby leaf-air vapor pressure deficits. Furthermore, shade may be crucial at low water potentials when stomatal cooling is not possible.

I measured lower soil moisture beneath canopies than in the open, however, 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 were
more clayey and dense than soils beneath canopies (D. Baumeister, pers. obs.).

As such, at equal relative water content values, it is possible that the water potential (i.e. water available to plants) beneath the canopies was actually higher than in the open. If this is the case, I cannot rule out that seedlings, particularly *Ribes*, might also be benefiting from below-ground factors (i.e. water) beneath canopies.

In contrast to *Ribes*, shade was only important for *Pseudotsuga* in the field transplant experiment in the winter. In winter, environmental stress for an evergreen species includes high irradiation levels because of increased reflectance off snow and cold temperatures—ideal conditions for inducing low-temperature photoinhibition in many plants (Öquist 1983, Powles et al. 1983, Germino and Smith 2000). In high light, low temperatures 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 Front without the benefit of shade, chronic, possibly fatal, photoinhibition (Osmond 1994) may be occurring, especially on cold, sunny days. In winter, *P. flexilis* canopies may benefit *Pseudotsuga* by preventing photoinhibition through reduction of PAR and insulation from cold temperatures (DeLucia and Smith 1987, Ball 1994, Germino and Smith 2000). Forest and solitary tree canopies can increase temperature minima by trapping solar radiation during the night and re-radiating long-wave irradiation. Man and
Lieffers (1996) transplanted *P. glauca* seedlings in *Populus tremuloides* understories and in the open and found photosynthetic parameters were depressed in open-grown seedlings in the spring and autumn when frosts were common at night. Leaf temperatures at night are strongly influenced by the exposure to the sky, and leaves exposed to the night sky will experience low levels of long-wave irradiation and leaf temperatures may drop to levels well below (up to 7°C) ambient air temperatures (Jordan and Smith 1994). For young seedlings not yet adapted to these conditions, mortality might result.

As a mechanism, shade can be facilitative and competitive. For *Ribes* and *Pseudotsuga*, shade likely protected understory species from high and low temperatures and reduced solar irradiance. However, in summer, reduced PAR may have also limited growth of these understory species, resulting in shade functioning as a competitive mechanism. The length of my experiment, coupled with the young age of the seedlings used, did not allow me to fully assess this possibility. Nonetheless, the results indicate that shade was more facilitative than competitive, particularly with regards to survival.

The far greater abundance of seedlings on lee 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. 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 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 studies have documented significant reductions in wind and the benefit of this for neighboring plants. In the high steppe of Patagonia, where strong, dry winds blow predominantly from one direction all year, the average wind velocity is 80% lower on the lee 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). Osmond et al. (1987), in a review of stress physiology for plants, state that in environments where wind is the limiting factor to growth and survival, plant species that do not adapt to the wind through mechanisms such as leaf area reduction, thickened cuticle, or stronger root base must avoid wind by sheltering beneath or behind other plants or topographic structures.

On the Front, wind speeds can be exceptional. During the first winter 26 Oct 98 to 25 April 99 (April is still winter in Montana), the mean wind speed was
3.4 ± 0.05 m/s with gusts up to 47 m/s and sustained winds up to 22.4 m/s. In addition to consistently strong winds, the Front is frequently subjected to Chinook winds. A Chinook can increase air temperatures as much as 25°C in one hour and have wind speeds exceeding 56 m/s (Brinkman 1971). In general, winter days with above-freezing temperatures were significantly windier (4.8 ± 0.1 m/s) than those with below-freezing temperatures (2.9 ± 0.1 m/s) (ANOVA, F=186, df=1, p>0.001). In Chinook belts, such as the Front, snow cover typically lasts only a few days and bare ground is present throughout most of winter because of the tremendous desiccating power of the winds (Anonymous 1980). Consequently, Chinook winds are often associated with drought conditions (Nkemdirim 1991). The presence of Chinook winds on the Front significantly increased the air temperature during the first winter on numerous occasions. Defining a Chinook as wind speeds > 7 m/s and T > 10° C, there were seven Chinooks during winter 98-99; on 14 separate days between Nov 1 and March 1 the temperature exceeded 10° C. In all but two of those days, the high T the day before and day after were less than 0° C.

Higher temperatures with high winds that come with Chinooks may create unusual conditions for evergreen species such as *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 might have directly caused winter desiccation and the mortality I
measured at first reading in spring. The loss of seedlings might have been due to a single Chinook event, or cumulative effects of several Chinooks.

It is possible that desiccation caused the greatest mortality for seedlings and that the strong effects seen in the shade treatments may not actually be related to reduced PAR. Instead, cooler temperatures beneath the shade cloth might have reduced the likelihood of photosynthesis while the ground is still frozen. In addition, due to the high winds in my experimental plots, shade cloths were established at ground level. This effectively resulted in complete shade throughout the entire day, ineffectively mimicking *P. flexilis* canopies which have some PAR in the understory at various times of the day. In addition to moderating temperature fluctuations, the shade cloths likely provided wind protection and I did find evidence of snow drifts in those treatments with shade cloths. These drifts were not as large nor did they last as long as those in the shade+drift treatments.

For *Ribes*, a winter-deciduous species, wind was not as important as shade, although higher survival at the leeward site and in the experimental treatment of shade and protection from wind combined suggests that wind affects survival at least secondarily, perhaps in concert with snowdrifts. Snowdrifts reduce wind and PAR (preventing photosynthesis) simultaneously, which might explain the greater survival of both species in those treatments in the mechanistic experiment.
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). I found in my study area that hard-packed snowdrifts formed on the lee side of trees and most stayed throughout the winter, even during Chinooks (D. Baumeister, *pers. obs.*).

Positive effects of snow cover on plants are many: (1) the maintenance of higher soil temperatures during winter (+1 to -3°C), (2) the moderation of air-leaf temperatures, (3) reducing 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, Taylor and Jones 1990, Walker et al. 1993, Germino and Smith 2000).

On the Front, for *Pseudotsuga* and *Ribes*, the effects of snowdrifts on temperature, shade provision, and wind protection were likely more important than other effects of snowdrifts. In a similar study, Callaway (1998b) found that young *Abies lasiocarpa* were facilitated by *P. albicaulis* at high elevation, wind swept sites, but did not need facilitation by *Pinus albicaulis* at a sub-alpine site when seedlings appeared to be protected by deeper snowpack. Evans (1990) and
Billings (1959) found that the accumulation of snow both within stands and on the leeward side of individual trees altered the micro-environment to the extent that snow cover, rather than just temperature or wind acting alone, was a major influence on the plant community.

In this study, the relatively minor role of P and N and soil structure is in contrast to many other mechanistic studies of facilitation, which have found soil to play a much greater role (e.g. Tiedemann and Klemmedson 1977, Weltzin and Coughenour 1990, Callaway et al. 1991, Callaway and King 1996, Pugnaire et al. 1996, Kieft et al. 1998). Soils beneath tree crowns often have significantly higher concentrations of organic matter, N, Ca, K, and P, higher microbial biomass, reduced bulk density, and increased water infiltration than open-grassland soils, all related to greater heterogeneity in litter and faster decomposition rates (reviewed in Vetaas 1992). Holtmeier and Broll (1992) found that in sub-alpine zones on the windward sides of tree islands, bare mineral soil is exposed by wind erosion and very little litter accumulates. In contrast, within islands and on the leeward side, thick humus layers and lush herbaceous vegetation enriched soil high organic matter and nutrient content. Similarly, I found that total A horizon depth increases as *P. flexilis* age (see Chapter 2) and is significantly greater beneath trees than in the open. Monitoring understory plants over time might reveal greater importance of nutrients, but for *Pseudotsuga* and *Ribes*, the
protection from wind and insolation for survival clearly took precedence over mechanisms related to growth.

Plants can favorably alter the availability of all fundamental resources, including nutrients, water, and light. Plants can also change the way that energy and materials are cycled, and profoundly alter the course of natural disturbance. By doing this they can potentially reconstruct the realized niches for other species (see Jones et al. 1994, Jones et al. 1997, Laland et al. 1999). From this research, I have found that *Pinus flexilis* appears to reconstruct the realized niches for *Pseudotsuga* and *Ribes* in a number of ways that are depicted in Figure 8. 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 x-axis. Additional temperature moderation extends the niches along the y-axis, and wind amelioration allows for niche expansion along the z-axis. Snowdrifts, in particular, allow for a larger realized niche along all three axes, by providing all three ameliorative effects. Indeed, in our mechanistic experiment, we found highest survival for *Pseudotsuga* in the shade+drift treatment. The relative amount of each abiotic condition (denoted at corners of the box) was determined from data from the weather station. The large proportion of sunny days (81%).
helps explain the relatively high importance of shade as a mechanism for both species.

My results demonstrate 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 which determines the overall effect of the overstory tree on understory plants. The significance of wind reduction and snowpack was detected only once shade was provided. To my 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.
ACKNOWLEDGEMENTS:

This project received primary funding through a graduate fellowship from NSF Training Within Environmental Biology grant # NSF- GRT#9553611, awarded to P. Kukuk, C. Brewer and F. Allendorf. I also thank the Boone and Crockett Club Wildlife Conservation Program for access to Theodore Roosevelt Memorial Ranch and additional research funding. Bob Keane, from the USFS, arranged for use of the weather station for this study. For field assistance over this five-year project, I thank Regan Choi, Sandra Bierne, Justin Dean, Damian Cremins, Ragan Callaway and Thomas Baumeister. Invaluable comments on this chapter were provided by Ragan Callaway, Thomas Baumeister, Anna Sala, and Bob Keane.
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TABLES
Table 1. Spatial association between cover types and individual *Pseudotsuga menziesii* (n=706) observed in 50,450 m² plots on the Rocky Mountain Front, Montana ($\chi^2=315.4$, df=1, $p<0.0001$) and individual *Ribes cereum* (n=518) observed in 33,450 m² plots on the Rocky Mountain Front, Montana ($\chi^2=583.1$, df=1, $p<0.0001$).

| Cover type | Proportion | Associated *Pseudotsuga* | | Associated *Ribes* | |
|------------|------------|--------------------------|-----------------|-------------------|
|            |            | Number (%) | Expected       | Number (%) | Expected |
| Open       | 0.51       | 131 (19%)  | 360 (51%)      | 43 (8%)    | 264 (51%) |
| *Pseudotsuga* | 0.10     | 86 (12%)   | 71 (10%)       | 5 (1%)     | 52 (10%)  |
| *P. flexilis* | 0.39     | 489 (69%)  | 275 (39%)      | 470 (91%)  | 202 (39%) |
Table 2. Below-ground characteristics by location and site aspect. Sample size for each location*site aspect is 10. P-values for soil characteristics are from a one-way ANOVA. Means for soil moisture are relative to the OPEN and p-values are based on a repeated measures GLM.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>WINDWARD</th>
<th></th>
<th>LEEWARD</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P. flexilis OPEN p</td>
<td></td>
<td>P. flexilis OPEN p</td>
<td></td>
</tr>
<tr>
<td>Litter Depth (cm)</td>
<td>4.8 ± 0.6 1.2 ± 0.3 &lt;0.001</td>
<td></td>
<td>4.2 ± 0.6 1.2 ± 0.2 &lt;0.001</td>
<td></td>
</tr>
<tr>
<td>A Horizon (cm)</td>
<td>7.1 ± 1.4 3.5 ± 1.5 0.097</td>
<td></td>
<td>11.4 ± 3.4 18.8 ± 2.7 0.104</td>
<td></td>
</tr>
<tr>
<td>O Horizon (cm)</td>
<td>21.4 ± 2.6 16.2 ± 1.6 0.104</td>
<td></td>
<td>16.0 ± 2.9 23.2 ± 3.0 0.112</td>
<td></td>
</tr>
<tr>
<td>P (mg/cm³)</td>
<td>0.31 ± 0.10 0.19 ± 0.07 0.364</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NO₃-N (mg/cm³)</td>
<td>0.13 ± 0.05 0.04 ± 0.02 0.079</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NH₄-N (mg/cm³)</td>
<td>0.08 ± 0.02 0.05 ± 0.01 0.263</td>
<td></td>
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<tr>
<td>Soil Moisture (%)</td>
<td>78.4 ± 9.0 100.0 0.016</td>
<td></td>
<td>92.2 ± 8.9 100.0 0.138</td>
<td></td>
</tr>
<tr>
<td>(% relative @ 5 cm)</td>
<td>98.5 ± 2.5 100.0 0.759</td>
<td></td>
<td>99.3 ± 2.3 100.0 0.869</td>
<td></td>
</tr>
<tr>
<td>(% relative @ 20 cm)</td>
<td></td>
<td></td>
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<td></td>
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</table>

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Table 3. Two-way ANOVA analysis of factors affecting survival of *Pseudotsuga menziesii* using a repeated measures GLM. A) The relationship of shade and no wind treatments on survival. B) The relationship of shade and drift treatments on survival.

<table>
<thead>
<tr>
<th>A)</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>210.8</td>
<td>1</td>
<td>210.8</td>
<td>751.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SHADE</td>
<td>17.7</td>
<td>1</td>
<td>17.7</td>
<td>63.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NO WIND</td>
<td>1.6</td>
<td>1</td>
<td>1.6</td>
<td>5.6</td>
<td>0.022</td>
</tr>
<tr>
<td>SHADE * NO WIND</td>
<td>0.9</td>
<td>1</td>
<td>0.9</td>
<td>3.1</td>
<td>0.086</td>
</tr>
<tr>
<td>Error</td>
<td>14.6</td>
<td>52</td>
<td>0.3</td>
<td></td>
<td></td>
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<table>
<thead>
<tr>
<th>B)</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>227.1</td>
<td>1</td>
<td>227.1</td>
<td>1061.6</td>
<td>&lt;0.001</td>
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<tr>
<td>SHADE</td>
<td>24.7</td>
<td>1</td>
<td>24.7</td>
<td>115.5</td>
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<tr>
<td>DRIFT</td>
<td>3.2</td>
<td>1</td>
<td>3.2</td>
<td>15.1</td>
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</tr>
<tr>
<td>SHADE * DRIFT</td>
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<td>1</td>
<td>2.9</td>
<td>13.4</td>
<td>0.001</td>
</tr>
<tr>
<td>Error</td>
<td>11.1</td>
<td>52</td>
<td>0.2</td>
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<td></td>
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</tbody>
</table>
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<table>
<thead>
<tr>
<th></th>
<th>No shade</th>
<th>Shade</th>
<th>2-way ANOVA</th>
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<td></td>
<td>Mean</td>
<td>N</td>
<td>Mean</td>
</tr>
<tr>
<td><strong>Pseudotsuga</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δ height (cm)</td>
<td>-7.9 ± 0.7</td>
<td>9</td>
<td>-1.0 ± 1.4</td>
</tr>
<tr>
<td>Shoot mass (g)</td>
<td>1.4 ± 0.3</td>
<td>9</td>
<td>1.4 ± 0.1</td>
</tr>
<tr>
<td>Root mass (g)</td>
<td>1.5 ± 0.5</td>
<td>9</td>
<td>3.2 ± 0.4</td>
</tr>
<tr>
<td>Root: Shoot</td>
<td>1.0 ± 0.2</td>
<td>9</td>
<td>2.2 ± 0.2</td>
</tr>
<tr>
<td><strong>Ribes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δ height (cm)</td>
<td>-11.5 ± 1.0</td>
<td>30</td>
<td>-6.4 ± 0.7</td>
</tr>
<tr>
<td>Shoot mass (g)</td>
<td>0.9 ± 0.1</td>
<td>30</td>
<td>0.9 ± 0.1</td>
</tr>
<tr>
<td>Root mass (g)</td>
<td>0.8 ± 0.1</td>
<td>30</td>
<td>1.2 ± 0.1</td>
</tr>
<tr>
<td>Root: Shoot</td>
<td>0.9 ± 0.1</td>
<td>30</td>
<td>1.4 ± 0.1</td>
</tr>
</tbody>
</table>

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*Pinus flexilis* ameliorates PAR, wind, and temperature through canopy cover, physical obstruction of wind, and snowdrifts, thereby extending the fundamental niche of these understory species to include the entire box as their realized niche. Facilitative mechanisms prevent the conditions of desiccation, photoinhibition, and ice & snow abrasion, depending on the abiotic conditions at that time. Approximate proportion of days annually with each combination of conditions as determined from the weather station are denoted at each corner. For example, 7% of days experience below-freezing temperatures, winds less than 5 m/s, and high irradiance levels—conditions likely to cause photoinhibition.
CHAPTER 2

Facilitation and Succession: the effect of *Pinus flexilis* on the eastern front of the Rocky Mountains
CHAPTER 2

Facilitation and Succession: the effect of Pinus flexilis on the eastern front of the Rocky Mountains
ABSTRACT

Most examples of facilitation as a mechanism in succession are for primary succession in harsh environments. On the Rocky Mountain Front in Montana, I studied secondary succession of grassland to forest during a prolonged era of fire exclusion by examining understory species composition beneath individual Pinus flexilis and in P. flexilis stands. At both the individual plant and stand scales, species composition was more highly correlated with the age of P. flexilis than any other environmental variable. As P. flexilis trees and stands aged, understory species richness increased, as did cover of forbs and shrubs, but cover of grasses decreased. Fifteen important species varied significantly in abundance under different aged P. flexilis trees and stands. Stands currently dominated by P. flexilis are shifting towards dominance by Pseudotsuga primarily in mesic sites, with corresponding increases in litter/duff ground cover and shrub cover and decreases in grasses and P. flexilis recruitment. Since Euro-American settlement and fire suppression in the late 1860’s succession from grasslands to forest at the forest prairie ecotone on the northern Rocky Mountain Front has been characterized by invasion of P. flexilis and subsequent shifts in understory species composition apparently facilitated by P. flexilis.
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INTRODUCTION

Frederick Clements claimed, “the climax is thus a product of reaction [effects of early species on the environment] operating within the limits of the climatic factors of the region concerned” (Clements 1928, pp. 105, 107, Walker and del Moral in press). The role of facilitation in succession has been a hotly debated topic since the earliest experiments contradicted Clements’ assertion by demonstrating that prior site amelioration was not necessary for subsequent community development (Keever 1950, McCormick and Buell 1968, Keever 1979, Sousa 1979). In Connell and Slatyer’s seminal paper (1977) facilitation remained a major conceptual model for succession, but their statement that experimental demonstrations of facilitated succession were lacking seemed to “sour ecologists on invoking positive processes in explaining successional patterns” (Bertness and Callaway 1994). As Walker and del Moral (in press) pointed out, subsequent theoretical shifts and experimental advances further de-emphasized the importance of facilitation in succession (Drury and Nisbet 1973, Sousa 1979).

Recently, however, facilitation has experienced an upsurge in experimental studies and community theory (Bertness and Callaway 1994, Callaway 1995, Callaway and Walker 1997, Brooker and Callaghan 1998, Callaway and Davis 1998, Callaway and Pugnaire 1999, Mulder et al. 2001), and some studies have demonstrated that facilitation can, in fact, be an important
mechanism in succession (Morris and Wood 1989, Kellman and Kading 1992, Callaway and Davis 1993, Chapin III et al. 1994, Shumway and Bertness 1994, Jumpponen et al. 1998, Meiners and Gorchov 1998, Bellingham et al. 2001). Yet, none of these investigations found facilitation as the sole explanatory ‘model’ (e.g. Connell and Slatyer 1977), but rather it occurred as one among many mechanisms driving succession (see Walker and del Moral in press), supporting Pickett et al.’s (1987) contention that single mechanisms might only explain succession when considered at the scale of an individual sere or between individual species.

The effects of positive interactions on whole communities and succession are not well understood (Stachowicz 2001), although facilitative interactions at the species level are well documented (Rousset and Lepart 1999). For example, at the species level facilitation generally increases in importance as environmental conditions become more extreme (Callaway and Bertness 1994, Callaway 1998, Bertness et al. 1999). At the scale of whole communities, this relationship has not been clearly demonstrated, although severe abiotic conditions might be important for facilitation to drive community succession (Turner 1983, Walker et al. 1993, Chapin III et al. 1994) as supported by examples of facilitation cited in primary succession (see Walker and del Moral in press).

Generally, facilitation appears to be more important in stressful environments (Choler et al. 2001, Callaway et al. in press). However, more recent work has
found examples of facilitation in secondary succession in more moderate environments (Berkowitz et al. 1995, Sans et al. 1998, Rousset and Lepart 1999).

The Rocky Mountain Front in Montana (N48° ± 1°; W112°48' ± 24') is an ideal ecosystem in which to examine the role facilitation might play in secondary succession in harsh environments. The Front represents the ecotone between the Rocky Mountain forests and the Great Plains grasslands (Barker and Whitman 1988, Demarchi and Lea 1992). Abiotic conditions on the Front resemble those of timberline environments with long, cold winters and short, warm summers. Changes in fire frequency and intensity, climate, exotic pathogens, and human land use patterns have dramatically altered the historic composition and structure of the flora at this ecotone (Ayers 1996). Since Euro-American settlement in the mid-1800s, ecological processes have shifted from frequent fires (Arno 1980) and annual grazing by wintering bison to anthropogenic fire exclusion and moderate livestock grazing (Baumeister, T. et al. 1996). These landscape changes appear to have initiated succession in the fescue-dominated prairie by allowing expansion of fire-intolerant limber pine (*Pinus flexilis* James) and creating a savanna-like landscape. *Pinus flexilis*, once restricted to dry, windswept ridges and riparian zones (sites protected from fire), is now much more common and as the dominant conifer it currently comprises 15-20% of the land cover (Redmond and Prather 1996).
Previous work demonstrated that *P. flexilis* facilitates Douglas-fir (*Pseudotsuga menziesii* Carr.), an evergreen conifer, and wax currant (*Ribes cereum* Dougl.), a deciduous shrub (see Chapter 1). *Pinus flexilis* facilitates these understory species through amelioration of a hierarchy of abiotic conditions, including light, wind, and temperature—mechanisms that likely also benefit other understory species. Here, I hypothesize that for facilitation to play a predominant role in successional dynamics of communities the benefactor species must either facilitate many other species (sensu Connell and Slatyer 1977) or facilitate a dominant species of a later seral stage (sensu Rebertus et al. 1991), and either of these effects must scale up to the level of the stand (Pickett et al. 1987). To test if facilitation drives secondary succession in *P. flexilis* communities at the Rocky Mountain Front, I addressed the following questions: (1) does understory species composition and richness change with the age of individual overstory *P. flexilis* trees? (2) Does species composition and richness change as the canopy cover of late-seral *Pseudotsuga* increases in a stand of *P. flexilis*? (3) Are shifts in species composition and richness that occur at the scale of individual *P. flexilis* also occurring at the scale of stands?
Study Site and Species

Montana's Rocky Mountain Front is geographically delineated by the Continental Divide to the west and south, US Highways 200, 89, and 287 to the east, and the Canadian border to the north (Figure 1). Over 60% of the land cover is Festuca grassland and small patches of shrub, conifer, aspen and riparian corridors comprise the remaining cover (Redmond and Prather 1996). Annual precipitation in the study area averaged 70 cm over the last 12 years (R. Peebles, unpubl. data) with snow accounting for 45-75% of annual precipitation (Moeckel 1997). Temperatures can range from -40° to 37°C annually (Aune and Kasworm 1989). A unique feature of the Front is the occurrence of very intense catabatic, "Chinook" winds that blow off the mountains onto the prairie (Caprio et al. 1981, BLM 1992) and remove and redistribute snow, reduce water availability, create highly diurnally variable temperatures (Anonymous 1980), and severely damage plants.

Pinus flexilis' northern range includes most of the Northern Rocky Mountains into Alberta and British Columbia (Steele 1990). In its range north of the 40th parallel, P. flexilis is typically found at the lower tree line and on dry, windswept sites. At lower elevations such as those of the Front, it grows in semi-forested areas characterized by a continental climate with low precipitation, low humidity, and wide annual and diurnal temperature ranges (Steele 1990). In
these harsh growing conditions *P. flexilis*, with its high drought and wind
tolerance (Tomback and Linhart 1990) can be a ‘climax’ species (Fischer and
Clayton 1983), although *P. flexilis* can be succeeded by less drought tolerant
species in some xeric sites (Patten 1963). In these dry areas, the presence of *P.
flexilis* may create moister conditions (through shade, greater snow
accumulation, and/or reduction of wind) conducive for less drought resistant
mesic species, such as spruce (*Picea spp.*), sub-alpine fir (*Abies spp.*) (Shankman
and Daly 1988, Donnegan and Rebertus 1999), and Douglas fir (Butler 1986). At
mesic sites, *P. flexilis* is usually a seral species that is successionaly replaced by
*Pseudotsuga*, Engelmann spruce (*Picea engelmannii*), and less frequently by
lodgepole pine (*Pinus contorta*) (Butler 1986, Donnegan and Rebertus 1999).

At the Front, the density of *P. flexilis* stands ranges from 15% in the
savanna-like habitats of the foothills to 70% with a *Pseudotsuga* understory on
mountain toe-slopes (Lesica 1989, Offerdahl 1989, Ayers 1996). The majority of
trees are pole size (4-10 cm DBH), 50-100 years old (D. Baumeister, *unpubl. data*),
probably because of relatively recent expansion of *P. flexilis* into sites where fire
is now excluded (Ayers 1996). Clark’s Nutcracker (*Nucifraga columbiana*) is the
only known dispersal agent of *P. flexilis* (Lanner and van der Wall 1980). These
birds cache the large *P. flexilis* seeds in areas commonly free of snow in winter
(Benkman et al. 1984, Lanner 1996). Unrecovered caches germinate and grow in
clumps of trees as a result of multiple seeds within a cache (Linhart and Tomback 1985, Carsey and Tomback 1994).

METHODS

I examined the role of *P. flexilis* on successional change at the individual scale (beneath *P. flexilis* canopies) and at the stand scale. Data for the individual scale were collected at the Boone and Crockett Club’s Theodore Roosevelt Memorial Ranch (TRM Ranch) (N48°05’, W112°43’) (Figure 1). Stand scale data were collected at four study sites along the Front: the Nature Conservancy’s Pine Butte Ranch (N47°52’, W112°33’), Montana Fish, Wildlife and Park’s Blackleaf Wildlife Management Area (N48°00’, W112°39’), TRM Ranch, and Montana Department of Natural Resources and Conservation lands near Swift Reservoir (N48°09’, W112°51’). All study sites were representative of the savanna-like ecotone characteristic for the eastern front of the Rocky Mountains.

**Individual Scale**

On a wind-exposed site at TRM Ranch, aspect 237° with 15-30% canopy cover of *P. flexilis*, the percent plant cover for all understory species was determined within 1-m² quadrats located on the leeward side of 68 *P. flexilis* trees. Cover was estimated in 5% increments by sub-dividing the quadrat into 82

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100, 100-cm$^3$ units. Plots were located in the lee of trees to standardize the effects of wind (Aguiar et al. 1992). *Pinus flexilis* trees >2-cm basal diameter were aged using a 5-mm corer, 20 cm above ground. No age correction was made to account for height of corer. Smaller trees were aged by cutting them at the base and counting growth rings. An additional 18 quadrats were placed in open sites within the stand beyond any tree canopy. For all trees, I recorded diameter at base (cm), live crown (%) (estimated visually in increments of 10%), and height (m). As an estimate of a tree’s ability to ameliorate light and wind under its canopy, a variable of “volume” was calculated as diameter x height x % live crown. To estimate changes in soil condition with tree age, the depth of A and O soil horizons in each quadrat were measured using a 2-cm soil corer. In addition to slope and aspect, I recorded microtopographical characteristics (concave, convex, flat).

*Stand Scale*

I sampled species composition in 80 *P. flexilis* stands with at least 5% tree canopy cover and in ten grassland plots located within 100-m of a *P. flexilis* stand. Plots were located in diverse topographies along the Front. Each circular, 0.05 hectare plot was assessed for canopy cover of woody species by size class, total grass and forb cover, topographic characteristics, ground cover (litter/duff, bare ground, wood, gravel, rock, lichen/moss), and the average age of the
overstory. Cover (%) was assessed in the following classes: 0, 1, 3, 5, 10, 20...90, 100. Size classes of trees were seedlings (<1 cm DBH), saplings (1-4 cm DBH), pole trees (5-10 cm DBH) and large trees (>10 cm DBH). The mean age of each plot was determined by counting the growth rings from 5-mm cores of four *P. flexilis* trees that represented the largest and oldest size class. As an estimate of a stand’s ability to ameliorate wind and light, I computed a structural diversity index (SDI) as the total number of tree cover size classes (seedling, sapling, pole trees, medium trees) with at least 5% canopy cover * total tree canopy cover (%); values were then scaled from 0 to 1. I determined species richness in each plot by counting the total number of shrub species with at least 1% canopy cover. I computed northness and windiness values for each plot based on aspect and slope. Northness was calculated as cos(azimuth)x sin(2*slope (%)) modified after Borchert (1989). Sites with aspects that have northerly aspects and with steeper slopes approach a northness value of one, whereas those plots with little or no slope are close to zero. Southern slopes have negative northness values. Windiness was computed in the same way as northness, but adjusted for the dominant wind direction of 250° (see Chapter 1). An additional harshness index was computed as -1(northness) + windiness + % bare ground following Rebertus et al. (1991).

In plots with *Pseudotsuga*, I recorded all *Pseudotsuga* individuals by location: beneath *P. flexilis*, beneath another *Pseudotsuga*, or in open.
computed the degree of facilitation as: $\# $ of *Pseudotsuga* beneath *P. flexilis*/ total $\# $ of *Pseudotsuga* in plot (see Chapter 1).

**Ordination**

I conducted two different indirect ordination analyses using detrended correspondence analysis (DCA) (PC-ORD; McCune and Mefford 1997). The first was for samples collected under individual trees and the second was for samples collected in stands. In both analyses, the corresponding environmental matrix was used to overlay bi-plot scores on the axes. Default settings were used for all DCA’s; rare species were not down-weighted. All environmental variables were tested for normality and correlated with DCA axes 1 and 2. The results are presented when $r^2>0.25$ (Gauch 1995). In addition, cluster analysis (PC-ORD, McCune and Mefford 1997) was used to split the plots into four groups based on species associations. Indicator species analysis (Dufrene and Legendre 1997) was used to identify up to three dominant species for each group using indicator values (IV), a computation based on relative frequency and abundance of each species in each plot. Significant values based on a post-hoc Monte Carlo test were used to rank indicator species for each group. To assess the relationship between *Pseudotsuga* abundance and understory community characteristics, I removed *Pseudotsuga* from the species matrix, performed another DCA, and
subsequently correlated relative canopy cover of *Pseudotsuga* with the
ordination axes, with species richness and with cover of understory species.

**RESULTS**

*Succession at the scale of individual* *P. flexilis*:

DCA ordination of all 1-m² plots produced eigenvalues of 0.464 and 0.317
for axis 1 and 2, respectively. DCA Axis 1 was more highly correlated with the
age of *P. flexilis* trees than with other environmental variables (Table 1; second-
order regression, \( r^2_{\text{age}}=0.56, F=50.6, \text{df}=81, P<0.001; \) Fig. 2a). The age of trees
ranged from 5 to 450 years. Mean DCA Axis 1 scores were significantly different
among those quadrats without trees, those aged 5-50 years (seedlings and
saplings), those aged 51-90 years (pole size trees) and those greater than 91 years
old (medium and large trees) (one-way ANOVA, \( F=27.0, \text{df}=3, P<0.001; \) Fig. 3a).
The volume of the canopy tree (Fig. 2b), depth of A horizon (Fig. 2c), and O
horizon depth were significantly correlated with both DCA axis 1 and with age
(Table 1). Species richness did not correlate with DCA axis 1, but was positively
correlated with tree age (Table 1; Fig. 2d). The slope of plots was weakly
correlated with axis 2 (Spearman rho, \(-0.270, P=0.012\)).

I used cluster analysis to the fourth level to group plots and one to three
indicator species were identified for each group (Table 2). The mean age of the
plots in the four different groups was significantly different among groups (one-
86
plots in the four different groups was significantly different among groups (one-way ANOVA, $F_{age\ class}=9.1$, df=3, $P<0.001$). Ten species, primarily forbs and shrubs significantly increased in cover while three species, a forb and two grasses significantly decreased (Table 3). As trees aged, total forb cover did not change significantly (one-way ANOVA, $F_{age\ class}=0.85$, df=3, $P=0.473$), but total grass cover decreased significantly and total shrub cover increased significantly (Fig. 4a).

**Succession at the scale of *P. flexilis* stands**

DCA ordination of the stand scale plots produced eigenvalues of 0.391 and 0.320 for axis 1 and 2, respectively. The age of stands ranged from 12 to 164 years and like the results at the individual scale, DCA Axis 1 was more highly correlated with the average age of the oldest cohort of *P. flexilis* in a stand than other variables (Table 4). In a second-order regression, $r^2_{age}$ was 0.46 ($F=36.1$, df=86, $P<0.001$; Fig. 5a). DCA Axis 1 scores were not significantly different between plots in grassland (without trees) and stands 5-50 years old, but stands 51-90 years old and stands $\geq$ 91 years old were significantly different from all others (Fig. 3b). SDI, the estimate of wind and light amelioration, was positively correlated with DCA axis 1 and with age (Table 4; Fig. 5b), as were two correlated measures of ground cover: bare ground and litter/duff (Table 4; Fig. 5c). In contrast to results at the scale of individual trees, species richness was
significantly correlated with both DCA axis 1 and with age (Table 4; Fig. 5d). Cover of *Pseudotsuga* was correlated with DCA axis 2 (Spearman rho, 0.459, \( P<0.001 \)). Topographical variables (northness, windiness, and slope) were not strongly correlated with either axis; however, DCA axis 1 was significantly correlated with the harshness index (Table 4).

In the cluster analysis, one to three indicator species for each group were identified (Table 2). Mean ages of these plots were significantly different between at least two groups (one-way ANOVA, \( F=13.9, \text{df}=3, P<0.001 \)). Significant increases and decreases in cover of common and important understory species are listed by stand age in Table 5. Six species—five shrubs and one tree, significantly increased with the age of the stand while no species significantly decreased in cover. Total forb and shrub cover increased significantly, whereas total grass cover decreased significantly (Fig. 4b).

*Facilitation of Pseudotsuga*

Of the 80 forested stands sampled, 54 plots (60%) contained *Pseudotsuga* with 78.3 ± 3.6% of the trees (\( n=717 \)) found directly beneath the canopies of *P. flexilis* indicating possible facilitation by the latter (see Chapter 1). In 22 of these plots, 100% of *Pseudotsuga* were under *P. flexilis*. The degree of facilitation (# of *Pseudotsuga* beneath *P. flexilis*/ # of *Pseudotsuga* in plot) was not related to the total canopy cover of *P. flexilis* in plots (\( r^2=0.000, F=0.01, \text{df}=1, P=0.941 \)), the age
of the stand ($r^2=0.000$, $F=0.01$, $df=1$, $P=0.931$), or the harshness index ($r^2=0.053$, $F=2.72$, $df=1$, $P=0.106$). However, facilitation was more prevalent in plots with lower structural diversity ($r^2=0.260$, $F=15.1$, $df=43$, $P<0.001$). Canopy cover of *Pseudotsuga* and the number of individual trees increased as canopy cover of larger *P. flexilis* increased (i.e., created more potential sites for *Pseudotsuga* to establish) (regression through origin, $r^2_{\text{cover}}=0.366$, $F=30.4$, $df=1$, $P<0.001$; $r^2_{\text{trees}}=0.268$, $F=19.6$, $df=1$, $P<0.001$).

Succession from *P. flexilis* stands to *Pseudotsuga* did not occur at all sample sites. In plots where *Pseudotsuga* was present, I only found large (i.e. older) *Pseudotsuga* in *P. flexilis* stands older than 50 years (Figure 6). Similarly, as *P. flexilis* stands aged the relative proportion of pole size *Pseudotsuga* ($25.5 \pm 2.5$ years) increased and was significantly greater in stands older than 90 years than those less than 90 years (one-way ANOVA, $F_{\text{age class}}=7.82$, $df=2$, $P=0.001$; Fig. 6). In stands with *Pseudotsuga* present, the replacement of *P. flexilis* by *Pseudotsuga* appears to be occurring as evidenced by a strong positive correlation between cover of large dead *P. flexilis* and relative cover of large living *Pseudotsuga* (Spearman rho = 0.476, $p<0.001$).

Several measured stand characteristics were significantly different among plots with 40-80% relative canopy cover of *Pseudotsuga*, those with <40% relative canopy cover and those without any *Pseudotsuga* (Table 6). Relative cover of *Pseudotsuga* increased with the total cover of *P. flexilis* and the age of
the stand. In addition, as the relative cover of *Pseudotsuga* increased, bare ground decreased and litter/duff increased. With the establishment of more trees, structural diversity in stands increased, species richness increased, the cover of dead *P. flexilis* increased, and recruitment of *P. flexilis* declined (Table 6). Cover of forbs and grasses tended to decrease as relative cover of *Pseudotsuga* increased while shrub cover increased (Figure 7). Plots without *Pseudotsuga* had significantly higher harshness index values compared to those with 40-80% relative cover of *Pseudotsuga* (Table 6).

When *Pseudotsuga* was excluded from DCA to prevent autocorrelation, the eigenvalue for DCA axis 1 was 0.407 and 0.222 for axis 2. The proportional cover of *Pseudotsuga* (cover of *Pseudotsuga* / total tree cover) was only weakly correlated with DCA axis 1 (Spearman rho, 0.253, p=0.028). Furthermore, mean DCA axis 1 values were greatest for plots with relatively greater *Pseudotsuga* cover and lowest for plots with no *Pseudotsuga* cover (two-way ANOVA, $F=24.8$, df=2, $p<0.001$; Fig. 7). To more directly assess the relationship between *Pseudotsuga* and understory species, I created three groups of plots from the complete species matrix (i.e. with *Pseudotsuga* included) using cluster analysis followed by an indicator species analysis. Cluster analysis resulted in group A (n=57) with grasses as the significant indicator species group (IV=$67.6$, $p<0.001$), group B (n=26) with *Arcostaphylos uva-ursi* and *Juniperus horizontalis* as significant indicator species (IV$_{arcuva}$= 67.4, $p<0.001$, IV$_{junhor}$=60.8, $p<0.001$), and
group C (n=7) with *Symphoricarpus albus*, *Rosa sayii*, and *Potentilla fructosa* as significant indicator species ($IV_{symaib}=88.7$, $p<0.001$; $IV_{rossay}=75.2$, $p<0.001$; $IV_{potfru}=55.1$, $p=0.006$). Although not as strong as indicator, *Pseudotsuga* was significant in group C ($IV_{psemen}=50.2$, $p=0.017$), and mean relative cover of *Pseudotsuga* was significantly greater in group C (38 ± 10%) than groups A (9 ± 2%) and B (15 ± 3%) (Tukey’s post-hoc in GLM, $F=10.9$, df=2, $p=0.002$).

**DISCUSSION**

Facilitation by *Pinus flexilis* appears to be a predominant mechanism driving secondary succession from grasslands to forests on the eastern front of the Rocky Mountains. In the absence of fire and bison grazing, the expansion and maturing of *P. flexilis* in grasslands is highly correlated with substantial changes in species composition. Overall, the species richness of these developing forested communities appears to be increasing with increasing age of individual *P. flexilis* trees, with increasing age of *P. flexilis* stands, and with increasing canopy cover of the secondary successional species, *Pseudotsuga menziesii*. At both the individual and the stand scale, the cover of grasses decreased while the cover of forbs and shrubs increased. Of nine understory species recorded at both scales, all but *Rosa sayii* exhibited similar trends in relative abundance over time.

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Of 24 dominant and/or important species, 11 showed significant increases in cover with the age of *P. flexilis* and four showed significant declines.


The mechanisms governing facilitation of understory species may be related to above- or below-ground ameliorative effects by *P. flexilis*. The age of individual trees correlated strongly with organic material in the soil, which suggests that changes in soil characteristics may affect the establishment and growth of understory plants. Similarly, at the stand scale, I found that ground
cover of litter and duff was positively correlated with age of *P. flexilis*, which might indicate changes in the organic content of soil over time. Improved fertility and structure of soils below tree canopies is common. Understory soils often have significantly higher concentrations of organic matter, N, Ca, K, and P, greater microbial biomass, reduced bulk density, and increased water infiltration than soils of open-grassland (reviewed in Vetaas 1992, Callaway 1995, Scholes and Archer 1997). Hoitmeier and Broll (1992) found that in windy sub-alpine zones, thick humus layers and lush herbaceous vegetation enriched soil organic matter as well as nutrients on the lee side and within islands of trees. Pugnaire et al. (1996) and Moro et al. (1997) found that *Retama sphaerocarpa* facilitated succession of understory species by ameliorating soil texture, nutrient content and capacitance of water. However, in contrast, Anderson et al. (2001) found greater nutrient availability beneath *Quercus fusiformis*, but did not find a corresponding response of understory productivity. Instead, shade appeared to be of greater importance than soil characteristics underneath a tree canopy. Similarly, Baumeister (see Chapter 1) found that *Pseudotsuga* and *Ribes* growing under the canopy of *P. flexilis* were strongly influenced by shade and wind and found no clear relationship between soil characteristics and facilitative effects.

The importance of shade and wind amelioration by *P. flexilis* for *Pseudotsuga* and *Ribes* (see Chapter 1) appears to extend to other understory species as well. My estimates of the ameliorative ability of *P. flexilis* — volume 93
and stand structural diversity, were both strongly correlated with their corresponding DCA axis 1, suggesting that aboveground influences of *P. flexilis* on the overstory were important. In other studies, stands of trees have been shown to modify environmental conditions of a site by increasing soil moisture, ameliorating wind, decreasing evapotranspiration, reducing light, and increasing snow accumulation and duration (Tupas and Sajise 1977, Caprio et al. 1981, Belsky and Canham 1994). For example, in savannas, trees can reduce the mean sub-canopy solar radiation by as much as 45-60% (Tiedemann and Klemmedson 1977, Belsky et al. 1989), thereby reducing both soil and plant temperatures and evapotranspiration in below-crown environments (Smith et al. 1987, Vetaas 1992, Belsky 1994). In addition, it is well established that individual plants and stands of vegetation can ameliorate wind (Hadley and Smith 1986, van Gardingen and Grace 1991, Aguiar et al. 1992). Baumeister and Dean (1997) found that high-density *P. flexilis* stands (>40% cover) had lower wind speeds, less light and less variable temperatures than low-density stands (<15% canopy cover).

Given my observations and the findings of others it is likely that *P. flexilis* plays an important role in facilitating the growth of a suite of woody understory species by ameliorating the harsh abiotic conditions that are characteristic of the Front. Two additional indirect measures support this contention. First, the DCA axis 1 at the community scale was highly correlated with the harshness index independent of *P. flexilis* stand age. Second, the degree of facilitation, with
respect to just one species—*Pseudotsuga*, was highest in those stands with lower structural diversity, suggesting that ameliorative effects by individual *P. flexilis* compensated for the lack of stand level amelioration in low density *P. flexilis* stands.

*Pseudostuga* seedlings experience high mortality in the absence of *P. flexilis* (see Chapter 1) and facilitation of *Pseudotsuga* by *P. flexilis* appears to create a pathway for eventual shifts to *Pseudotsuga*-dominated stands, especially in more mesic sites. As *P. flexilis* stands aged and the amount of *Pseudostuga* increased, total tree cover increased, which reduces available light to the understory and, in turn, tends to create cooler temperatures (Baumeister and Dean 1997). Understory species composition was different in stands with *Pseudotsuga* than in those without *Pseudotsuga*, and I found that a decline in forb and grass cover and an increase in shrub cover correlated with the relative cover of *Pseudotsuga*. However, it is likely still too early to determine if these changes are due to *Pseudotsuga* specifically or are simply a function of the presence of larger and older *P. flexilis* and their effects over longer time periods. Nonetheless, there was a correlation between DCA axis 2 at the stand scale and the cover of *Pseudotsuga*. Current vegetation trends in stands with low relative cover of *Pseudotsuga* suggest that an increase in cover will likely result in further shifts in species composition and richness.
*Pinus flexilis* appears to facilitate *Pseudotsuga* by ameliorating limiting physical conditions, but only below a certain threshold of abiotic severity, a phenomena also noted in old-field succession (Sans et al. 1998). In extremely harsh sites, the positive effects of *P. flexilis* did not appear to drive successional change toward *Pseudotsuga* since *P. flexilis* remained the only dominant conifer in stands and there was little or no recruitment of *Pseudotsuga*. It appears that *P. flexilis* is a climax species in xeric sites and a seral species in more mesic sites, as indicated by studies of *P. flexilis* elsewhere (Fischer and Clayton 1983, Butler 1986, Shankman and Daly 1988, Rebertus et al. 1991). For example, Rebertus et al. (1991) on the Colorado Front Range found that *Picea engelmannii* and *Abies lasiocarpa* succeeded *P. flexilis* in mesic sites but in xeric, harsh sites, *P. flexilis* maintained its presence and dominance.

In sites where *Pseudotsuga* appears to be succeeding *P. flexilis*, I found that as the cover of large *Pseudotsuga* increased, so did the cover of dead *P. flexilis* (Figure 5). Likewise, Donnegan and Rebertus (1999) found that *Picea* and *Abies* establishing near the canopy of *P. flexilis*, in turn, appeared to promote the early demise of *P. flexilis*. Increased mortality of benefactors due to competition by beneficiaries has also been documented for *P. albicaulis* and *Abies* in upper timberlines in Montana (Callaway 1998) and for *Opuntia* and *Larrea* in deserts (Yeaton 1978). For *P. flexilis* and *Pseudotsuga*, the rate of this change is difficult to quantify due to the relatively recent changes in disturbance regimes. The
timeframe for assessing successional change on the Front is relatively short; *Pinus flexilis* expanded its distribution only after extermination of bison and severe reduction in fire frequency following settlement by Euro-Americans in the 1860s (Ayers 1996). As such, the landscape still resembles an early stage of secondary succession. Since most stands are less than 150 years old, it is too early to determine where, when and how quickly *Pseudotsuga* will succeed *P. flexilis*. When Donnegan and Rebertus (1999) assessed rates of succession of *P. flexilis*, they found them to be relatively slow, partially due to the nature of the species’ longevity relative to that of its successors. Rebertus et al. (1991) observed a time lag of 10-100 years before *Picea* and *Abies* established following *P. flexilis* in mesic sites and predicted, given the longevity of *P. flexilis*, that replacement on xeric sites might take up 500 years. As the time frame for observing secondary succession on the Front is limited to a little more than a century, observations of increased mortality in the relatively long-lived *P. flexilis* due to increased presence of *Pseudotsuga* — an indicator of a shift in seral stage — is difficult to quantify. In addition, the widespread mortality of *P. flexilis* currently seen on the Front has been more directly linked to several beetle infestations, and more recently, widespread infection of trees by pine blister rust (Kendall et al. 1996, Baumeister, *unpubl. data*), rather than from competition with *Pseudotsuga* per se.
Connell and Slatyer (1977) proposed that in facilitated succession, only certain species are able to colonize a disturbed area and over time, create more favorable conditions for the establishment of later seral species. In my study, it appears that facilitation is driving succession in the *P. flexilis* dominated ecotone of the Front through the amelioration of abiotic conditions specifically by a certain species, *P. flexilis*. However, as predominant as facilitation appears to be in this particular system, it is not possible to ascribe one process to a series of events that occur over long-periods of time, with a multitude of different species, in a heterogeneous environment. As such, it is critical when attributing mechanisms of succession to a community that researchers carefully identify the species involved, the spatial and temporal scale of reference, dynamics of individual life-stages, and the frame of reference for the interactions described (e.g. for an interacting pair of species, one might be inhibited while the other is facilitated). Nonetheless, for *P. flexilis* on the eastern front of the Rocky Mountains, secondary succession from grasslands to mixed *P. flexilis*/*Pseudotsuga* forests appears to be dominated by facilitation.
ACKNOWLEDGEMENTS:

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LITERATURE CITED:


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TABLES
Table 1. Significant correlations and regressions for environmental variables with DCA axis 1 and age of the individual *P. flexilis* trees.

<table>
<thead>
<tr>
<th>Variable</th>
<th>DCA Axis 1</th>
<th>Age</th>
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<tbody>
<tr>
<td></td>
<td>Spearman rho coefficient</td>
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<tr>
<td>Age</td>
<td>0.706</td>
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<tr>
<td>Tree volume</td>
<td>0.703</td>
<td>&lt;0.001</td>
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<tr>
<td>A Horizon depth</td>
<td>0.555</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>O Horizon depth</td>
<td>0.565</td>
<td>&lt;0.001</td>
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<tr>
<td>Species richness</td>
<td>0.081</td>
<td>0.461</td>
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*second order regression*
Table 2. Indicator species for groups identified in cluster analysis at the individual and stand scales. Indicator values (IV) and significances based on a Monte Carlo procedure are given. Ages are means ± 1 S.E.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Group</th>
<th>Age of <em>P. flexilis</em></th>
<th>n</th>
<th>Species</th>
<th>IV</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual</td>
<td>A</td>
<td>20.7 ± 6.3</td>
<td>20</td>
<td><em>Festuca idahoensis</em></td>
<td>30</td>
<td>0.045</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Phlox muscoïdes</em></td>
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<td>0.002</td>
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<tr>
<td></td>
<td>B</td>
<td>49.1 ± 10.2</td>
<td>27</td>
<td><em>Poa spp.</em></td>
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<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Juniperus horizontalis</em></td>
<td>49</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>86.8 ± 23.2</td>
<td>19</td>
<td><em>Festuca scabrella</em></td>
<td>56</td>
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<tr>
<td></td>
<td>D</td>
<td>151.1 ± 28.8</td>
<td>20</td>
<td><em>Shepherdia canadensis</em></td>
<td>69</td>
<td>0.001</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Arcostaphylos uva-ursi</em></td>
<td>46</td>
<td>0.001</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Ribes cereum</em></td>
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<td>0.002</td>
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<tr>
<td>Stand</td>
<td>A</td>
<td>58.3 ± 8.8</td>
<td>20</td>
<td><em>Arcostaphylos uva-ursi</em></td>
<td>60</td>
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<td></td>
<td><em>Juniperus horizontalis</em></td>
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<td></td>
<td>B</td>
<td>72.0 ± 5.4</td>
<td>36</td>
<td>No significant indicator species</td>
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<td></td>
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<tr>
<td></td>
<td>C</td>
<td>84.9 ± 5.8</td>
<td>26</td>
<td>Grass spp.</td>
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<tr>
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<td>D</td>
<td>122.9 ± 7.8</td>
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<td><em>Symphoricarpus albus</em></td>
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<td><em>Rosa sayii</em></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Shepherdia canadensis</em></td>
<td>47</td>
<td>0.006</td>
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</table>
Table 3. Mean cover ± 1 S.E. of a selection of the important and common species identified in 1-m² quadrats in the open and under individual *P. flexilis*, stratified by age class. Different letters denote significant differences among age classes for each species at *P*<0.05 based on a post-ANOVA Tukey's test. Species that significantly increase with *P. flexilis* age are underlined; those that significantly decrease with *P. flexilis* age are italicized (Pearson's correlation, *P*<0.05).

<table>
<thead>
<tr>
<th>Sample size</th>
<th>18</th>
<th>26</th>
<th>24</th>
<th>18</th>
<th>86</th>
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</thead>
<tbody>
<tr>
<td><strong>Age of associated <em>P. flexilis</em></strong></td>
<td>no tree</td>
<td>&lt;50 yrs.</td>
<td>50-100 yrs.</td>
<td>&gt;100 yrs.</td>
<td>Pearson Coeff.</td>
</tr>
<tr>
<td><strong>Achillea millefolia</strong></td>
<td>0.0 ± 0.0*</td>
<td>0.0 ± 0.0*</td>
<td>0.9 ± 0.5*</td>
<td>2.5 ± 0.9*</td>
<td>0.48</td>
</tr>
<tr>
<td><strong>Anemone nuttalliana</strong></td>
<td>0.1 ± 0.1*</td>
<td>0.2 ± 0.1*</td>
<td>0.5 ± 0.3*</td>
<td>2.4 ± 0.8*</td>
<td>0.35</td>
</tr>
<tr>
<td><strong>Arcostaphylos uva-ursi</strong></td>
<td>1.6 ± 1.0</td>
<td>1.2 ± 0.7</td>
<td>5.1 ± 1.6</td>
<td>3.0 ± 1.1</td>
<td>0.11</td>
</tr>
<tr>
<td><strong>Artemisia frigida</strong></td>
<td>4.1 ± 1.1*</td>
<td>2.0 ± 0.6*</td>
<td>1.9 ± 0.6*</td>
<td>1.0 ± 0.5*</td>
<td>-0.20</td>
</tr>
<tr>
<td><strong>Balsamorhiza sagittata</strong></td>
<td>0.1 ± 0.1</td>
<td>0.3 ± 0.2</td>
<td>0.8 ± 0.3</td>
<td>1.0 ± 0.5</td>
<td>0.32</td>
</tr>
<tr>
<td><strong>Carex filifolia</strong></td>
<td>2.7 ± 1.0*</td>
<td>0.8 ± 0.4*</td>
<td>0.0 ± 0.0*</td>
<td>0.1 ± 0.1*</td>
<td>-0.22</td>
</tr>
<tr>
<td><strong>Clematis columbiana</strong></td>
<td>0.0 ± 0.0*</td>
<td>0.0 ± 0.0*</td>
<td>1.6 ± 0.6*</td>
<td>2.3 ± 0.8*</td>
<td>0.33</td>
</tr>
<tr>
<td><strong>Festuca idahoensis</strong></td>
<td>7.5 ± 1.9*</td>
<td>2.4 ± 0.6*</td>
<td>4.0 ± 1.2*</td>
<td>1.7 ± 0.9*</td>
<td>-0.22</td>
</tr>
<tr>
<td><strong>Festuca scabrella</strong></td>
<td>6.4 ± 1.9</td>
<td>5.2 ± 1.5</td>
<td>6.5 ± 1.3</td>
<td>6.0 ± 1.3</td>
<td>0.05</td>
</tr>
<tr>
<td><strong>Juniperus communis</strong></td>
<td>0.0 ± 0.0*</td>
<td>0.0 ± 0.0*</td>
<td>0.0 ± 0.0*</td>
<td>0.9 ± 0.5*</td>
<td>0.37</td>
</tr>
<tr>
<td><strong>Juniperus horizontalis</strong></td>
<td>1.9 ± 0.9*</td>
<td>9.4 ± 1.8*</td>
<td>9.2 ± 1.8*</td>
<td>7.5 ± 1.8*</td>
<td>0.00</td>
</tr>
</tbody>
</table>

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<table>
<thead>
<tr>
<th>Species</th>
<th>Mean ± SE</th>
<th>Mean ± SE</th>
<th>Mean ± SE</th>
<th>Mean ± SE</th>
<th>p-value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lithospermum ruderale</em></td>
<td>0.2 ± 0.2</td>
<td>0.3 ± 0.2</td>
<td>0.2 ± 0.1</td>
<td>1.5 ± 0.6</td>
<td>0.53</td>
<td>0.000</td>
</tr>
<tr>
<td><em>Phlox muscoides</em></td>
<td>1.8 ± 0.8</td>
<td>0.7 ± 0.3</td>
<td>0.3 ± 0.2</td>
<td>0.0 ± 0.0</td>
<td>-0.27</td>
<td>0.049</td>
</tr>
<tr>
<td><em>Potentilla fructosa</em></td>
<td>0.2 ± 0.1</td>
<td>0.6 ± 0.5</td>
<td>0.9 ± 0.4</td>
<td>0.0 ± 0.0</td>
<td>-0.08</td>
<td>0.445</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em></td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.2 ± 0.2</td>
<td>1.0 ± 0.8</td>
<td>0.11</td>
<td>0.320</td>
</tr>
<tr>
<td><em>Ribes cereum</em></td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.8 ± 0.8</td>
<td>2.9 ± 1.2</td>
<td>0.44</td>
<td>0.000</td>
</tr>
<tr>
<td><em>Rosa sayii</em></td>
<td>0.9 ± 0.5</td>
<td>1.0 ± 0.4</td>
<td>2.4 ± 1.0</td>
<td>1.3 ± 1.0</td>
<td>-0.02</td>
<td>0.861</td>
</tr>
<tr>
<td><em>Shepherdia canadensis</em></td>
<td>0.2 ± 0.2</td>
<td>0.7 ± 0.7</td>
<td>5.4 ± 1.6</td>
<td>6.5 ± 1.7</td>
<td>0.26</td>
<td>0.017</td>
</tr>
<tr>
<td><em>Solidago missouriensis</em></td>
<td>0.2 ± 0.1</td>
<td>1.0 ± 0.5</td>
<td>1.5 ± 0.6</td>
<td>2.7 ± 0.8</td>
<td>0.33</td>
<td>0.002</td>
</tr>
<tr>
<td><em>Symphoricarpus albus</em></td>
<td>0.1 ± 0.1</td>
<td>1.0 ± 0.7</td>
<td>3.4 ± 1.3</td>
<td>4.8 ± 1.3</td>
<td>0.32</td>
<td>0.002</td>
</tr>
</tbody>
</table>
Table 4. Significant correlations of environmental variables at the scale of stands with DCA axis 1 and age of the *P. flexilis* stand.

<table>
<thead>
<tr>
<th>Variable</th>
<th>DCA Axis 1</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spearman rho coefficient</td>
<td>$p$</td>
</tr>
<tr>
<td>Age</td>
<td>0.700</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Structural Diversity Index (SDI)</td>
<td>0.500</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bare ground (%)</td>
<td>-0.505</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Litter/duff (%)</td>
<td>0.452</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species richness</td>
<td>0.656</td>
<td>0.461</td>
</tr>
<tr>
<td>Harshness Index</td>
<td>-0.482</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

* regression through origin
** second-order regression

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Table 5. Mean cover ± 1 S.E. of important and common species identified in stand scale quadrats in open grasslands and *P. flexilis* stands, stratified by % cover of pole size *P. flexilis*. Different letters denote differences among cover classes for each species at *P*<0.05 based on a post-ANOVA Tukey's test. Species that significantly increase with *P. flexilis* age are underlined; those that significantly decrease with *P. flexilis* age are italicized (Spearman bivariate correlation, *P*<0.05).

<table>
<thead>
<tr>
<th>Sample size</th>
<th>Age of <em>P. flexilis</em> stands</th>
<th>Spearman</th>
<th>Coeff.</th>
<th><em>p</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No trees</td>
<td>10-50 yrs.</td>
<td>51-90 yrs.</td>
<td>91-170 yrs.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>25</td>
<td>33</td>
</tr>
<tr>
<td><em>Acer rubrum</em></td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.3 ± 0.3</td>
<td>0.2 ± 0.2</td>
</tr>
<tr>
<td><em>Amelanchier alnifolia</em></td>
<td>1.0 ± 0.5</td>
<td>0.1 ± 0.1</td>
<td>1.9 ± 1.1</td>
<td>0.5 ± 0.3</td>
</tr>
<tr>
<td><em>Arcostaphylos uva-ursi</em></td>
<td>5.3 ± 2.9</td>
<td>10.8 ± 4.0</td>
<td>14.1 ± 3.5</td>
<td>3.4 ± 1.5</td>
</tr>
<tr>
<td><em>Artemesia frigida</em></td>
<td>0.2 ± 0.1</td>
<td>0.0 ± 0.0</td>
<td>0.2 ± 0.1</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td><em>Juniperus communis</em></td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>3.2 ± 1.2</td>
<td>4.3 ± 2.1</td>
</tr>
<tr>
<td><em>Juniperus horizontalis</em></td>
<td>9.3 ± 4.0</td>
<td>22.4 ± 3.1</td>
<td>11.7 ± 2.5</td>
<td>12.1 ± 4.1</td>
</tr>
<tr>
<td><em>Potentilla fructosa</em></td>
<td>6.7 ± 2.2</td>
<td>7.8 ± 1.5</td>
<td>6.5 ± 1.0</td>
<td>8.6 ± 2.6</td>
</tr>
<tr>
<td><em>Prunus virginiana</em></td>
<td>0.7 ± 0.4</td>
<td>0.1 ± 0.1</td>
<td>1.0 ± 0.6</td>
<td>0.6 ± 0.3</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em></td>
<td>0.0 ± 0.0</td>
<td>1.0 ± 0.3</td>
<td>8.0 ± 2.0</td>
<td>9.5 ± 2.6</td>
</tr>
<tr>
<td><em>Ribes spp.</em></td>
<td>0.0 ± 0.0</td>
<td>0.3 ± 0.2</td>
<td>2.5 ± 1.3b</td>
<td>2.3 ± 0.9b</td>
</tr>
<tr>
<td><em>Rosa sayii</em></td>
<td>1.1 ± 0.3a</td>
<td>0.1 ± 0.1a</td>
<td>1.4 ± 0.4a</td>
<td>11.3 ± 3.4b</td>
</tr>
<tr>
<td><em>Shepherdia canadensis</em></td>
<td>0.1 ± 0.1a</td>
<td>3.0 ± 0.6a</td>
<td>11.2 ± 1.8b</td>
<td>13.9 ± 2.6b</td>
</tr>
<tr>
<td><em>Spirea betulifolia</em></td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.5 ± 0.3</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td><em>Symphoricarpus albus</em></td>
<td>0.0 ± 0.0a</td>
<td>0.1 ± 0.1a</td>
<td>2.3 ± 0.7a</td>
<td>20.7 ± 4.6b</td>
</tr>
</tbody>
</table>

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Table 6. Significantly different stand characteristics (means ± 1 S.E.) among *P. flexilis* stands without *Pseudotsuga*, those with <40% relative cover of *Pseudotsuga* and those with 40-80% relative cover of *Pseudotsuga*.

Different letters denote significant differences among *Pseudotsuga* cover classes using a post-ANOVA Tukey's test at *p*<0.05.

<table>
<thead>
<tr>
<th>Variable</th>
<th>No <em>Pseudotsuga</em></th>
<th>of <em>Pseudotsuga</em> &lt;40% rel. cover</th>
<th>of <em>Pseudotsuga</em> 40-80% rel. cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare ground (%)</td>
<td>26.8 ± 4.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.8 ± 1.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.8 ± 2.7&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Litter/Duff (%)</td>
<td>52.5 ± 4.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>65.4 ± 2.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>80.0 ± 3.7&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Structural Diversity Index</td>
<td>0.21 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.40 ± 0.04&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.60 ± 0.12&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead <em>P. flexilis</em> (%)</td>
<td>5.9 ± 1.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>12.6 ± 1.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>14.2 ± 2.7&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>P. flexilis</em> (%)</td>
<td>23.9 ± 5.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>37.0 ± 2.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>31.3 ± 2.7&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>P. flexilis</em> seedlings (%)</td>
<td>3.0 ± 0.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.8 ± 0.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.0 ± 1.0&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>P. flexilis</em> pole trees (%)</td>
<td>10.5 ± 2.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>23.6 ± 2.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>26.7 ± 3.8&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Harshness Index</td>
<td>0.63 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.33 ± 0.10&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>-0.16 ± 0.26&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Species Richness</td>
<td>3.8 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.0 ± 0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.0 ± 0.4&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Age of stand (yrs.)</td>
<td>56.8 ± 5.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>87.3 ± 4.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>101.3 ± 11.4&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
FIGURES
Figure 1. Map of study area on the Rocky Mountain Front, Montana. All individual scale data were collected at Theodore Roosevelt Memorial Ranch. Community scale data were collected within the dashed line.
Figure 2. The relationship between the age of individual *P. flexilis* with a) DCA axis 1 scores, b) volume (cm$^3$), c) depth of A horizon (cm), and d) species richness. Regression values are reported in Table 1.
Figure 3. Mean DCA axis 1 scores ± 1 S.E. for age classes of *P. flexilis* at the a) individual and b) stand scales. Significant differences among classes at $P<0.05$ using a post-ANOVA Tukey’s test are denoted by different letters.
Figure 4. Mean cover ± 1 S.E. for forbs, grasses and shrubs stratified by age classes of *P. flexilis* at the a) individual and b) stand scales. Significant differences among classes at *P*<0.05 using a post-hoc Tukey’s test are denoted by different letters.

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Figure 5. The relationship between the age of *P. flexilis* stands and a) DCA axis 1 scores, b) structural diversity index, c) depth of litter (cm), and d) species richness. Regression values are reported in Table 4.
Figure 6. Relative cover of seedlings, saplings, pole trees and large trees of *Pseudotsuga* by age class of *P. flexilis* stands (n=54). Seedlings and pole trees significantly differed among age classes (two-way ANOVA, df=2; $F_{\text{seedling}}=8.9, P<0.001, F_{\text{pole}}=7.8, P=0.001$).

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Figure 7. Mean cover ± 1 S.E. for each taxonomic group stratified by classes of relative cover of *Pseudotsuga*. Significant differences among classes at $P<0.05$ using a post-ANOVA Tukey’s test are denoted by different letters.
Figure 8. Mean DCA axis 1 scores ± 1 S.E. for classes of relative cover of *Pseudotsuga*. Significant differences among classes at $P<0.05$ using a post-ANOVA Tukey's test are denoted by different letters.
CHAPTER 3

Training biologists for emerging niches in non-traditional jobs
Each year, America's more than 4,200 institutions of higher learning churn out almost 74,000 bachelors, masters, and PhDs with non-medical biology degrees\(^1\). And every year, a startling 45% of these budding biologists don't find work in the biological sector\(^2\). That's 33,000 graduates with degrees in biology who have spent four or more years of their lives studying cell biology, genetics, organismic biology, and ecology and all their sub-disciplines appear to not have the opportunity to make use of their hard-earned knowledge filling specialized niches in the job market, primarily in research, health care, "the great outdoors", and education\(^3\). With a quality education and 4+ years of time and energy, why aren't 33,000 enthusiastic, well-trained graduates finding work in the biological sector?

The simple answer is there just aren't enough niches for our well-trained specialists. According to the office of National Occupational Employment, in 2000 there were just 157,380 individuals employed in non-medical, biological sectors. Given this limited number of biological positions, it would take a phenomenal 50% annual growth in the biological sector to employ all biology graduates. In reality, the Bureau of Labor Statistics forecasts only 16% growth in jobs in biological sectors over the next decade, primarily for biological technicians. That's just 0.6% annual growth, equating to approximately 3,600 new positions each year, based on anticipated growth and net replacement needs—3,600 jobs for 33,000 "extra" graduates. Each June, natural selection (i.e.
market forces) chooses only those individuals best adapted for available niches; the rest don't find a niche to occupy and are forced to migrate to other sectors or face extinction. Given the investment of both students and professors (a K-adapted strategy), losing 45% of graduates (offspring) might not be a very-adaptive strategy in the long haul.

In ecology classes, students learn that K-adapted species in limited habitats follow one of several different strategies. 1) Individuals may migrate to unoccupied niches—as we're currently seeing with the many biology graduates who find work in other fields. 2) Individuals may specialize and either out-compete current or potential niche occupants or fill yet unexplored local niches. The competition strategy appears to predominate in most biological science departments today, and in some sub-disciplines, particularly molecular biology, the niche expansion through specialization strategy is also employed. 3) Individuals may adopt a generalist strategy rather than one of a specialist, thereby partially occupying several different niches in the local habitat. This adaptive strategy of niche expansion employed by some species is more common in highly variable environments. In our current dynamic labor market, these last two strategies of niche expansion might provide many of the job opportunities needed for the extra 30,000 graduates annually.

In other academic disciplines, we have seen niche expansion through private sector employment; the growing number of chemists employed by
industry is a recent example. Indeed, industry is fertile ground for new niches.

In biology, we have seen niche expansion in industry via the biotechnology sector, as evidenced by the proliferation of "life science" companies and the race to decode the human genome. More than one economic analyst has called the next 100 years the "century of biology". That's great news for graduating molecular biologists, bioinformaticists, and geneticists, who, in fact, have the greatest prospects for employment following graduation. However, I argue that there are great prospects for other disciplines as well. Emerging niches in biology outside of the biotech sector are not nearly as widely known, but are growing rapidly and will likely fully blossom in the next decade and flourish for many years to come. Biologists trained with a broad overview of biology (generalists) and those trained in applying biological knowledge (specialists) are filling emerging niches in industry by helping design biologically-inspired, more sustainable solutions for human needs, a field termed "biomimicry" by Benyus (1997). Here, I define the niche and discuss training biologists for this new career path.

The demand for "biologists at the design table" (the generalists) and for biologists researching industry-specific questions (the specialists) will only expand over the next decade and beyond. This growth is related to evolving trends in industry. As we enter the 21st century, industry is becoming increasingly aware that the earth's resources are finite, the public is demanding
more responsible corporate behavior, and governments are imposing ever-
 stricter laws and regulations. While many industries fight these tightening boundaries, others are embracing the power of limits, just as nature does, and seeking new innovative solutions outside their traditional scope. Evidence of this shift can be found in the emerging fields of industrial ecology and ecological economics, in popular books such as “Natural Capitalism”, “A Living Company”, and “What We Learned in the Rainforest”, and in new non-profit organizations like The Natural Step and Global Futures Foundation. The tie that binds these together is the application of biological principles to the design of systems created by humans. Organizations turning towards nature for inspiration are employing a tool of inquiry called “biomimicry”. Biomimicry is a emerging field of science that seeks solutions from nature and uses these lessons in design within the fields of engineering, materials science, organizational development, chemistry, and industrial design, among others. Currently, students in these disciplines tend to have very little biology training, and design challenges are addressed solely with tools commonly available within the specific discipline. Biomimicry breaks this barrier by integrating biological solutions into the design process by asking: “What would nature do here? What wouldn’t nature do here? Why and Why not?” (Benyus 1997). With this set of questions, biologists are introducing designers and engineers to life’s designs.
and strategies, while helping them understand biological principles that can lead to sustainable practice.

Biomimetic examples are now found in a number of different disciplines including agriculture, computing, energy generation, architecture, materials science, organizational development, and medicine. Innovators in these fields have teamed up with biologists from all specialties. To give the reader an idea of the wide spectrum of possibilities that biologists have for symbioses with specialists in other fields, I provide just a handful of examples. These are excerpted from Benyus (1997), as well as from an Internet search with keywords “inspired by nature,” “biomimicry,” and “biomimetic”.

**Botanists and Paint Manufacturers**

Prof. Dr. Wilhelm Barthlott, a German botanist studying the leaf structure of the lotus leaf spent years researching its amazing ability to keep clean. Microscopic bumps on the leaf surface reduce electro-static forces of dirt particles and keep water droplets rolling to carry away dirt, a phenomena now known as the Lotus Effect (Barthlott and Neinhuis 1997). Dr. Barthlott teamed up with a façade manufacturer, IPSO, which now produces and markets an exterior paint façade that mimics the microscopic structural features of the lotus leaf. Taking lessons from the lotus, German buildings wearing Lotusan™ are kept clean by rain alone.
Evolutionary biologists and whiskey makers

One of the marvels of evolution is the ability for natural selection to filter multiple genotypes in a population resulting in an adaptive genome. The rules of mating and natural selection are being applied to non-biological models in the form of genetic algorithms (Holland 1992). For example, a whiskey manufacturer in Scotland, United Distillers, trying to determine the right combination of brewing secrets (e.g. the species of wood for the barrel, the length of time in each fermentation process, ratios for blending, and optimizing the movement of whiskey casks) used a computer model and self-defined selection criteria to randomly mate different combinations of genotypes. Those offspring meeting selection criteria were then mated and genes were randomly combined. This $F_1, F_2, \ldots, F_n$ process was repeated until several well-adapted whiskey making strategies were born. The result is a streamlined production process that has saved the company money, reduced waste, and resulted in a better whiskey. Evolution at its finest.

Molecular biologists and car manufacturers

Nacre, the inner lining of an abalone shell is a natural ceramic that is 2-3x stronger than our best attempt using traditional "heat, beat, and treat" methods ($3000^\circ F$ for up to 120 hours, often involving toxic or rare elements)$^5$. In contrast, at ambient temperatures ($34^\circ F$), the abalone builds its nacre, a microlaminate
composite of calcium carbonate (chalk) and proteins, using minerals readily available in seawater and proteins built from metabolized plankton. Jeff Brinker and Alan Sellinger, researchers at Sandia Labs, mimicked the self-assembly process of the abalone based on work of molecular biologist Dr. Daniel Morse at UCSB (Belcher et al. 1998) and created a transparent ceramic stronger than any of its human-made predecessors using minimal energy and materials. They expect windshields and protective paint coatings to be marketable within just a few years.

Other unusual pairs include a marine naturalist and a manufacturer of piston pumps, a lepidopterist and a silicon chip manufacturer, a crustacean biologist and the Department of Defense, plant physiologists and a solar cell company, a neurobiologist/entomologist and a hearing-aid manufacturer and even an ecologist and the CEO of a multi-million dollar carpet company. The opportunities for interdisciplinary work and applications (i.e. niches for biologists) are phenomenal. Biomimicry just might be one of the niche expansions that graduating biologists need. In fact, biomimicry allows biologists to earn a living while simultaneously fulfilling their passions: studying nature, learning her strategies, sharing her mysteries with others, and possibly even making a difference in this world.

While the interest in biomimicry is keen, industry’s ability to practice biomimicry has been hampered by one limited resource: biologists trained as
biomimics. Currently, only 7% of biologists employed in research and development in the private sector are involved in design\(^1\). But, the niches are there. Janine Benyus speaks of a presentation she did for over 100 energy executives at the annual E-Source Conference in Aspen, Colorado in 1999. At the end of her talk on biomimicry, she asked the audience how many had a biologist on staff. Not a single hand was raised. She then asked how many were planning to hire a biologist in the near future, and almost every hand went up. Linking 30,000 "biologists-in-waiting" with these jobs will require broadening the educational training of these graduates. Biology departments need to cultivate students so that all adaptive strategies for limited and dynamic habitats are options: migration, competition, and niche expansion through specialization or generalization.

While formal education has become quite adept at the competition strategy, there is great potential for growth with respect to niche expansion. Within the realm of biomimicry, there are three important skills and knowledge bases with which we must send our next generation of biologists into the emerging biomimetic niche. These apply equally to biologists choosing the specialist or the generalist strategy. Biomimetic biologists or biomimics must be able to: (1) access their biological knowledge base functionally. (2) They must be able to communicate this information to a non-biological interdisciplinary team. (3) They need to rediscover and learn the field of applied natural history.
Biology Organized Functionally

If you look at the suite of classes offered in any biology department, you’ll find that they are primarily organized taxonomically by sub-discipline and secondarily by geography: Zoology 101, Vertebrate Anatomy and Physiology, Plants of the Tropics, etc. Because classes, textbooks, and journals are organized in this way, from the outset, students specialize according to the same hierarchy, and access the knowledge in their memory in the same way—by taxa and geography. Yet, the designers that I work with in my workshops do not think in terms of taxa and geography: they are trying to solve functional problems—how to clean surfaces without toxins, how to resist combustion, how to cushion a surface. If a designer were to ask a traditional biology student “how does nature adhere to smooth surfaces?” where would he or she go to look for the answer?

The lack of a functional organization scheme makes the application of biological knowledge cumbersome, expensive, and time-consuming. As a supplement to traditional biological education, imagine classes, texts, or journals organized by function: Aerodynamics 101, Adhesives, Filtering, Color, Interspecific Interactions, etc. By studying nature’s solutions from this perspective, students would learn biology in a way that relates directly to human design challenges. Not surprisingly, organizing, teaching, and accessing biological knowledge functionally will be a monumental task. To assist biology
departments, biomimics, and designers in this endeavor, Janine Benyus and
myself, the Rocky Mountain Institute, and the San Diego Super Computing
Center have submitted a five-year, $5 million proposal to the Information
Technology Research division of the National Science Foundation to develop an
internet-based digital library that maps the web of connections between biology
concepts and engineering concepts. The initial building of this database will be
biologist-driven, but eventually will be designed to grow electronically with
carefully programmed searchbots and database builders. The result will be a
library of biological knowledge accessible by engineering and design search
terms. The database will assist a biomimic the way that a product catalogue,
showing existing human-made solutions, assists engineers when they are
designing. An engineer designing your next dishwasher or an architect building
a shelter in Finland or an earthquake-safe bridge will be able to access
information on the suite of organisms that clean, or filter, or keep warm, or
cushion, etc. As part of this project, we will design and implement
interdisciplinary pilot courses at twelve universities that bring together
biologists, designers, engineers, and business majors teaching them to access and
utilize biological knowledge.
Communication

Although the relative quality of information is questionable, it has been estimated that our knowledge of the natural world doubles every five years. A biomimic translates the vast volumes of biological knowledge as needed for a particular design problem. Once the information has been obtained, conveying this knowledge to a non-biological audience is an essential skill for biomimics. Currently, very few programs require biology students to take classes in communication skills, and even fewer teach how to share scientific information with non-technical audiences. Yet sharing information across disciplines is at the very core of biomimicry. In a design team that includes engineers, materials scientists, architects, business marketers, industrial designers, and more, a biologist must be able to communicate biological knowledge not only accurately, but in a way that others can understand. This can be a challenge, given that most people's last exposure to biology was dissecting a frog with Mrs. Jones in 10th grade biology class.13

A good analogy for the role of biomimics in information transfer can be found in the nucleus of a cell. Assume for a moment that the biological information generated through research is akin to information coded in DNA. Research biologists perform the transcription process of the living cell, publishing biological information, and like strands of messenger RNA, their research papers float out of the nucleus of the lab. A biomimic essentially acts as
a ribosome, translating messenger RNA so that it can be used to build amino acids. Designers of human systems (i.e. industry, banks, governments, non-profits, etc.) can then use these amino acids to build the proteins of the goods and services that humans demand. Inherent in this translation process is an understanding of the needs of the designers. Biomimics that are versed in the jargon of architecture, industrial design, materials science, engineering, or business can further facilitate the application and mimicry of nature’s best design strategies to human systems by having some background in these disciplines.

This means that students exposed to classes outside of biology (e.g. in rudimentary engineering or business) will be more effective biomimics, just as an environmental lawyer might excel with some understanding of biology or a construction engineer might improve her designs by studying hydrology.

**Applied Natural History**

Natural history is the study of the patterns and processes of the natural world from a holistic viewpoint. Natural history involves an interest in and study of natural sciences (botany, zoology, geology), historical geography (history, geography), anthropology (human development and history within an ecological framework), and conservation. In writing this article, when I searched for university programs in natural history, the few that existed were limited to educating the general public about nature, primarily through associations with
natural history museums. Natural history is generally regarded as an out-of-date branch of knowledge that formed the foundation for modern biology and is therefore, no longer required. According to Juan Armesto (1998), “the purposes, context, and field methods of Natural History are all-too-often dismissed as non-scientific and insufficient for understanding of biological phenomena.” For this reason, the study of natural history has been de-emphasized in biology departments and relegated to a specialty of museum science. Yet natural history emphasizes “meticulous description, direct observation, experience, and comparison, [while] embracing emotions such as admiration and respect, [providing] sound grounds for understanding and valuing ecosystems and becoming aware of our strong connections with the biosphere and the history of life on Earth.”

Armesto goes on to say:

Because of the technological emphasis of modern reductionist science, progress in understanding has generally been associated with human domination and appropriation of "wild" ecosystems for human profit. The occidental belief that science and technology are tools that empower us to control and transform "nature" to better serve our needs has, to a great extent, promoted our current environmental crisis. Natural History lacks this connotation of superiority over nature, as its aim is to understand ecosystems as our place of living. In this context, knowledge of Natural History may play a fundamental role in increasing human appreciation of ecosystems and in generating a positive link between natural scientists, managers and environmentalists that can foster a new environmental ethics for the 21st century. (Armesto 1998).
Encouraging an exploration of natural history for students will not be difficult. The 74,000 aspiring biologists each year were motivated to study biology because of their fascination with the natural world. They are curious about the creatures of land and sea, about the way plants capture sunlight, how whales circumnavigate the globe, or where memories are stored in their brains. In fact, budding biologists tend to be those that as children asked a lot of why’s about the natural world around them. Why do birds sing more in the morning? Why is my bruise black and blue? Why does my sister look like my dad? A biologist’s enchantment with the natural world is inevitable. It is written in our (Homo sapiens) genes.

The earliest humans survived and prospered because of their ability to observe the natural world and their keen interest in how things worked. The gazelle comes to the watering hole in the evenings. Fresh new leaves come with the rains. Birds and small mammals don’t eat the poison dart frog. Polar bears stay warm by burying in the snow. That chimpanzee is sick and is eating Ficus. The knowledge gained from these observations likely increased the survival of these observant humans. Is it surprising that genes coded for an interest in nature were passed on? Or, that our biology departments are filled with enthusiastic students with curious analytical minds and a passion for life? Adding natural history to the curriculum should come quite naturally.
Taking natural history one step deeper and applying this knowledge to human systems design can further strengthen symbioses between biologists, educational organizations, industry, and the public. Renewing an interest in natural history is an essential component of training biomimics. In many of my research endeavors for companies interested in a specific “how does nature?” inquiry, such as an interest in how nature deals with cold temperatures, I find that I must turn to pre-1980’s scientific literature, when natural history type inquiries were more dominant in research. Coupling basic knowledge with new technologies and methods of research allows industry to more successfully learn from and incorporate some of nature’s strategies. For example, natural history observations by desert ecologists of the tenebrinoid beetle inhabiting the Namibian desert revealed in the early 1960s that the beetle appeared to acquire water by condensing fog on its back. Recently, technological advances in methodology found that this was achieved due to a pattern of hydrophilic and hydrophobic bumps on the beetle’s back. Using modern methods of material science and nanotechnology, researchers are working to mimic this water-collection strategy in the form of fog-collecting tents for human-inhabitants of deserts (Parker and Lawrence 2001).

By learning applied natural history, biologists can delve into biomimicry at several levels. Benyus (1997) defines these as “nature as model, measure, and mentor”. The examples of the lotus, genetics algorithms, the abalone, and beetle
are studying “nature’s models and then [imitating or taking] inspiration from these designs and processes to solve human problems”. Nature as measure provides “an ecological standard to judge the “rightness” of our innovations. After 3.8 billion years of evolution, nature has learned: What works. What is appropriate. What lasts.” In other words, what is adaptive, and what is not? At the deepest level, as individuals learn to apply nature’s lessons to design, an even greater appreciation of the natural world’s wonders develops. Nature as mentor is a “new way of viewing and valuing nature. It introduces an era based not on what we can extract from the natural world, but on what we can learn from it.” With this in mind, biomimicry differs from biotechnology by focusing on lessons, ideas, and strategies of nature, rather than actually using her creatures or her genes. Although it is feasible to employ biotechnology, there are advantages to emulating an organism, whether it be its processes, functions, or by-products, as opposed to using the actual organism. For example, green algae can be induced to produce hydrogen, which in turn is a valuable fuel product. Emulating the functional site of the hydrogenase enzyme within green algae using a catalyst allows us to produce the hydrogen in a simple biochemical reaction, without the costs of maintaining living creatures (Gloaguen et al. 2001).

Sustainability and biomimicry have great potential to complement each other. The possibility that biomimetic designs might be also sustainable designs lies in the assumption that the strategies we find in nature today are examples
honied to the environment in which we live. Adaptations by non-human organisms, both behavioral and physiological, help sustain individuals in the short term, and ultimately lead to genetic adaptations that sustain a species in the long term. The same can be said for humans, yet many of our adaptations are proving themselves biologically maladaptive, and there is considerable evidence that we are pushing the limits of our existence. If industry and biologists can consult nature for hints on how to adapt and survive given the constraints of earth’s habitats, the resulting processes and products might contribute to our long-term survival.

Biomimicry encourages biologists to study life, not just for the sake of study, but to mimic life’s strategies so that we might live more sustainably. Industry adopting biomimicry values biological knowledge relative to how well it assists them in meeting their own sustainability challenges. In contrast, biologists often value knowledge for its ability to advance our understanding of the natural world—from “little is known” to “well-documented”. The more a research effort can bridge this gap, the more we value it. Imagine the additional value this knowledge could have if it could help bring about a more-adaptive strategy for Homo sapiens sapiens on this Earth. Chances are good that new sources of funding could open up, and even more biological research (more niches) could be created. For example, researchers may be funded to study the microstructure of a feather, not only to understand how the peacock creates a
colorful display, but to learn how we might emulate structural color, and thereby reduce the use of toxic dyes in the print and paint industry.

I believe, as a biologist and a recent graduate, that biologists can fill an incredible niche in our global society. Colleges and universities have the responsibility to train enthusiastic, passionate budding biologists in such a way that they can add to the diversity and adaptability of the field of biology. The current system works and 41,000 biologists find work each year, but resources, talents, and passions are wasted by losing the remaining 45% of biologists upon graduation each year. By providing education in functional biology, communication skills, and applied natural history, colleges and universities can help these graduates fill expanding niches in an otherwise limited habitat, while earning a livable income, pursuing their interests, and in many cases, helping to “create conditions conducive for life” (Benyus 1997).

Biomimicry isn’t revolutionary or an entirely new paradigm. It’s surprisingly quite logical. Biologists don’t need to abandon what they know or change the work that we do. Not every strategy in nature will be helpful or useful, but many can be. Biomimicry doesn’t prevent us in the least from doing pure science, and therein lies the beauty of it. However, to expand into these developing niches requires a different perspective and an openness to the possibility that research labs, students, and pure knowledge might have a wider application than increasing the knowledge base. The neurobiologist/
entomologist Dr. Ron Hoy, whose work with the Ormia fly is being incorporated into new hearing-aid designs, stated “when I realized this [research application] could turn out to be something out there in the real world...this has been one of the highlights of my life” (National Public Radio 1999). Benyus (1997) believes biomimicry is the “conscious emulation of nature’s genius”. My genes tell me it’s why we all became biologists in the first place.
LITERATURE CITED:


ENDNOTES:

1 National Science Foundation Office for Science Statistics.

2 This figure is based on a survey of graduates 18 months following graduation and already accounts for those students returning to school for advanced degrees. Within the fields of science and engineering (excluding social science) only the field of mathematics has a higher rate: 53%. The average of 45% for biology breaks down as: 46% of students with bachelor degrees, 31% with Master’s, and 3.4% with PhD’s. In 1999, there were almost 3,800 PhD’s in biology who wanted full-time work in their field of study and could not find it1.

3 www.aibs.org/careers

4 Humans have always looked towards nature for inspiration. In cultures closely tied to and dependent on nature, this phenomena continues. In cultures more removed from nature, interest in learning from nature has been periodic. Its recent reemergence as a science appears to be a new approach.

5 www.superiortechceramics.com/methods/

6 www:animatedsoftware.com/pumpglos/glrecess.htm

7 www.wired.com/news/technology/0,1282,10163,00.html
Some functional biology classes do exist, e.g. biomechanics, but these are the exception rather than the rule.

In rare instances, however, a team member might be a "hidden" biologist, removed from the gene pool upon college graduation and now working in an unrelated field. In my work conducting workshops on biomimicry and biology for industry, I find about 1 out of every 10 people have a formal training in biology that they were never able to use.

This description might be more accurate of a more recent evolution of natural history, given that the earliest natural historians made many observations through systematic and widespread "collection" of specimens—hence the current connection with museums.