

Restoration planting options for limber pine (*Pinus flexilis* James) in the Southern Rocky Mountains¹

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Abstract. Limber pine *Pinus flexilis* James populations in the southern Rocky Mountains are threatened by the combined impacts of mountain pine beetles and white pine blister rust. To develop restoration planting methods, six *P. flexilis* seedling planting trial sites were installed along a geographic gradient from southern Wyoming to southern Colorado. Experimental treatments included: high or low overstory canopy density from existing trees, presence/absence of a nurse object, and presence/absence of hydrogel. Of the *P. flexilis* seedlings planted, 72% were alive after four growing seasons. There were interactions between nurse object, seedling height at planting, and percent canopy cover that affected the number of healthy seedlings. Denser canopy cover was positively correlated with healthier planted seedlings and hydrogels had no effect. Nurse objects promoted healthier seedlings, particularly when canopy cover was low (0–50% cover), and the specific orientation to the nurse object affected seedling health under all levels of canopy cover. In conclusion, for best growth and survival in the first four years after planting, *P. flexilis* seedlings should be planted under an overstory canopy and on the north or west side of a nurse object, particularly if the canopy cover is low or absent.

Key words: *Cronartium ribicola*, *Dendroctonus ponderosae*, exotic disease, five-needle pine, mountain pine beetle, tree planting white pine blister rust

Pinus flexilis James, commonly known as limber pine, is a North American five-needle pine that grows at a wide range of elevations on xeric sites (Schoettle and Rochelle 2000). Its range extends from northern New Mexico north to Alberta, and west to California, Oregon, and British Columbia (Steele 1990). *Pinus flexilis* grows in similar habitats and overlaps in range with *Pinus albicaulis* Engelm. (whitebark pine) in the northern part of its

range and *Pinus aristata* Engelm. (Rocky Mountain bristlecone pine) in the southern part of its range (Steele 1990). *Pinus flexilis* and *P. albicaulis* seeds are dispersed by birds, primarily by *Nucifraga columbiana* Wilson, Clark's Nutcracker (Tomback and Linhart 1990).

On harsh sites, *P. flexilis* grows in monocultures and performs many important ecosystem functions, including decreasing erosion,

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facilitating other plant growth, and stabilizing snowpack (Schoettle 2004). Its large seeds are an essential food for *Ursus americanus* Pallas (American black bear; McCutchen 1996), corvids, and small mammals (Lanner and Vander Wall 1980; Tomback 1982).

In the Rocky Mountains, all *Pinus* species are susceptible to mortality by *Dendroctonus ponderosae* Hopkins, hereafter referred to as mountain pine beetle (MPB), and several species, including *P. flexilis*, have experienced extensive mortality with 75% of stands affected with up to 35% mortality on some mountain ranges in the recent outbreak (Schwandt *et al.* 2010; Cleaver 2015). Additionally, *P. flexilis* is susceptible to the introduced fungal pathogen *Cronartium ribicola* J.A. Fisch., which causes white pine blister rust (WPBR; Hoff, Bingham, and McDonald 1980). Although *P. flexilis* has rebounded from MPB outbreaks in the past, the additional threat of WPBR threatens the survival of *P. flexilis* in some areas of the southern Rocky Mountains (Schoettle, Goodrich *et al.* 2011; Cleaver 2014).

While genetic resistance to WPBR naturally occurs in some *P. flexilis* families, these resistant trees are threatened by MPB outbreaks (Schoettle, Sniezko *et al.* 2011; Schoettle *et al.* 2014). As climate change shifts the lifecycle of these beetles, this impact may intensify (Schwandt *et al.* 2010). Since MPB kills mature seed-bearing *P. flexilis* trees (Gibson *et al.* 2008), which may be resistant to WPBR, and WPBR can girdle and kill young trees rapidly, natural regeneration may be seriously restricted. However, since MPB primarily attacks large diameter trees (Raffa *et al.* 2008), and *P. flexilis* trees grow slowly (Schoettle and Rochelle 2000) and the current MPB outbreak has subsided, seedlings outplanted now are unlikely to be attacked by MPB during the current outbreak (Cleaver 2014).

Currently, researchers are identifying trees that are genetically resistant to WPBR (Schoettle *et al.* 2014), which can eventually provide a means of restoring *P. flexilis* in some sites or establishing *P. flexilis* in newly suitable habitat (Schwandt *et al.* 2010; Schoettle, Goodrich *et al.* 2011; Schoettle, Sniezko *et al.* 2011). Outplanting WPBR-resistant planting stock will be an important management strategy to sustain the species (Schoettle and Sniezko 2007; Burns *et al.* 2008). To plant WPBR resistant trees, *P. flexilis* seedlings will

need to be propagated in a nursery and outplanted into areas of particular concern (Burns *et al.* 2008). Prescribed planting methods and techniques that optimize survival exist for *P. albicaulis*, which is similarly threatened by both MPB and WPBR (Scott and McCaughey 2006), but have not been developed for *P. flexilis* (Schwandt *et al.* 2010). Thus, the objective of this study was to develop planting protocols for *P. flexilis* seedlings for use by land managers in the southern Rocky Mountains.

Planting techniques that ameliorate water stress may be important because desiccation is a major challenge to seedling survival on xeric sites (Coop and Schoettle 2009). Compounding the challenge of achieving planting success on xeric sites, planted seedlings experience higher water stress for 2 to 4 yr after planting, due to poor root/soil contact following transplant (Baldwin and Barney 1976; Burdett 1990). Hydrogels, or polyacrylimide gels, may improve seedling survival and growth in some arid environments and in horticulture (Rowe *et al.* 2005; Agaba *et al.* 2010). However, the literature does not indicate a universal positive effect. Soil type and nutrient availability can be important factors influencing the effect of hydrogels (Rowe *et al.* 2005; Agaba *et al.* 2010). Nurse objects improve successful natural establishment of *P. flexilis* and *P. aristata* and may also improve survival of planted seedlings (Coop and Schoettle 2009). In planting studies of *Picea engelmannii* Parry ex Engelm. (Engelmann spruce), nurse objects have been beneficial for seedling survival (Ronco 1970a; Jacobs and Steinbeck 2001). These objects provide protection from the sun; increase snowpack, which protects seedlings from cold temperatures; increase soil moisture; and may enhance mycorrhizal infection (Callaway and Walker 1997; Germino, Smith, and Resor 2002). Nurse objects may also protect seedlings from low-temperature photoinhibition early in the day (Germino and Smith 1999).

Since *P. flexilis* is a poor competitor but establishes well postdisturbance (Rebertus, Burns, and Veblen 1991, Coop and Schoettle 2009, Smith *et al.* 2011), *P. flexilis* studies often focus on establishment in disturbed areas. However, stand dynamics and establishment patterns of *P. flexilis* postdisturbance are not inherently the same as those for

continued establishment in an existing stand (Johnson, Miyanishi, and Kleb 1994).

Pinus flexilis seedlings do not only establish in disturbed areas, as there is evidence of prolonged, continuous establishment of *P. flexilis* in the Southern Rocky Mountains (Brown and Schoettle 2008; Coop and Schoettle 2009). Because nurse objects and tree cover are important in seedling establishment and survival on harsh sites (Germino *et al.* 2002, Coop and Schoettle 2009), canopy cover provided by existing overstory trees may provide protection for *P. flexilis* seedlings during initial establishment, as has been found with the shade-intolerant *Pinus pinaster* Aiton (maritime pine; Rodriguez-Garcia, Bravo, and Spies 2011). Additionally, planted *P. flexilis* seedlings may have different establishment requirements than natural regeneration, as suggested by a *P. flexilis* planting study in Waterton Lakes National Park, Canada, that indicated vegetation cover may increase planted *P. flexilis* survival (Smith *et al.* 2011).

Even though the planting guidelines for *P. albicaulis* recommend removal of overstory canopy (McCaughey, Scott, and Izlar 2009), studies specific to *P. flexilis* are necessary to understand the impact of canopy on survival, growth, and maturation of planted *P. flexilis* seedlings. Planting WPBR resistant *P. flexilis* has been identified as an important management strategy (Schoettle and Sniezko 2007), so information about the success of seedling survival in areas with partial canopy versus more exposed areas will help guide management in areas where the overstory is still present, but is significantly impacted by MPB and WPBR.

To help determine planting protocols for *P. flexilis*, we established a study to address the following questions: (a) do seedlings planted next to a nurse object have higher survival rates than seedlings planted in the open; (b) will hydrogels improve seedling survival; and (c) does existing tree canopy density impact seedling survival.

Methods. In the spring and early summer of 2009, we planted 2,160 *P. flexilis* seedlings at five study sites in Colorado and one site in Wyoming: (a) Trout Creek, Salida Ranger District, San Isabel National Forest (NF); (b) Buffalo Peak, South Park Ranger District, Pike NF; (c) Columbine, Boulder Ranger District, Arapaho NF; (d) Killpecker, Canyon

Lakes Ranger District, Roosevelt NF; (e) Pilot Hill, Laramie Ranger District, Medicine Bow NF; and (f) Mosca Pass, Great Sand Dunes National Park and Preserve (Fig. 1, Table 1). The planting sites were selected based on the following criteria: *P. flexilis* is currently a component of the forest, different amounts of canopy cover either naturally or from forest management operations were available, and future planting of *P. flexilis* might be expected to occur at or near that site.

The seedlings were grown at the Colorado State Forest Service Nursery, Fort Collins, CO, from seeds collected from natural stands of *P. flexilis* growing at 2,895 m near Rollinsville, CO (39.9164°N, 105.5008°W; Fig. 1). Seeds were sown June 2006 in 2.5 × 17.8 cm cone-tainers and filled with a 50/50 peat and vermiculite soilless mix in a greenhouse. Seedlings were watered and fertilized with 150, 100, 150 ppm NPK mix twice a week except in January through March, when they were hardened off. During hardening off, seedlings were fertilized with a solution of 50, 100, 150 ppm NPK and watered as needed (approximately once a week). In March 2007, seedlings were moved into a shade house, where they lived until they were planted in the field in April–June 2009. The average height of the seedlings at planting was 22 cm (SE 0.12).

PLANTING TREATMENTS. The study used a randomized block design, using sites as blocks, with nested plots. Each planting site was systematically divided into sections of high and low density canopy cover from existing trees. Crown density varied from open canopy (clear-felled areas or old wildfire areas) to thinned and unthinned forests with higher density canopy cover. Canopy cover was measured by taking convex densitometer readings at the four cardinal directions at 1 m above each group of two or four planted seedlings for analysis and comparison across sites, since high and low canopy densities were relative within study sites. This resulted in a total of 48 readings at sites without hydrogel and 96 readings at hydrogel sites. These measurements allowed us to analyze canopy as a continuous, rather than categorical, variable.

At each planting site, three plots (repetitions) were established in each of the high and low canopy cover areas, for a total of six plots per site. Within each plot, nurse object and

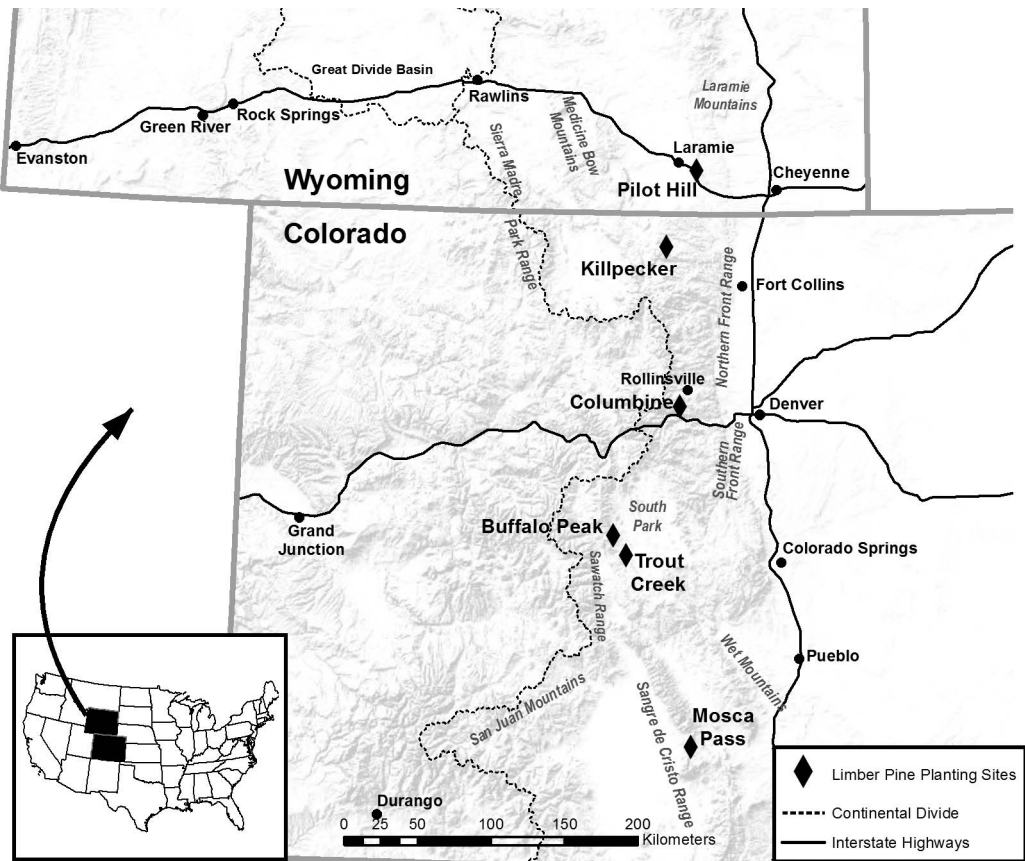


FIG. 1. Location of six *Pinus flexilis* planting sites.

hydrogel treatments were randomly assigned to seedlings. Trout Creek and Mosca Pass did not have hydrogel treatments due to a limitation in the number of available seedlings and challenges in obtaining permission to use hydrogels in Great Sand Dunes National Park and Preserve. In areas without hydrogel treatment, nurse object and control treatments were randomly located in a 2×6 m grid at 2 m apart, for a total of six control plantings (two seedlings each) and six nurse object plantings (four seedlings each) per plot, and 216 seedlings across all six plots at a site. In areas with hydrogel treatment, a 4×6 m grid was used, for a total of six plantings for each nurse object/control and hydrogel/no hydrogel combination per plot, and 432 seedlings across all six plots at a site (Buffalo Peak, Columbine, Killpecker, and Pilot Hill). When necessary, we modified the grid shape to fit the planting location, maintaining randomization and at least a 2 m spacing.

Nurse objects were created by cutting stem sections (approximately 20 cm wide by 50 cm tall) from dead and downed conifer trees in the vicinity. Each nurse object was buried in the ground 5–15 cm to provide stability. Four seedlings were planted as close as possible to the nurse object at the cardinal directions. A wood stake marked the location for sites with no nurse object and two seedlings were planted 40 cm apart on the east and west sides of the stake. With this planting method we purposefully doubled the number of seedlings planted without a nurse object because we were concerned that high mortality would hinder analyses.

Hydrogel treatment used the following procedure: seedling roots were dipped in a slurry of Terra-sorb hydrogel (Plant Health Care Inc., Pittsburg, PA), mixed to the manufacturer's specifications (142 g per 19 L), prior to planting. All seedlings that were not treated with hydrogel (in both the mixed sites and in

Table 1. *Pinus flexilis* planting sites¹ in Colorado and southern Wyoming, 2009.

Variable	Pilot Hill	Killpecker	Columbine	Buffalo Peak	Trout Creek	Mosca Pass
UTM Northing	13 T 0462953	13 T 0442451	13 S 0452012	13 S 0406271	13 S 0415082	13 S 0459417
UTM Easting	4568390	4516571	4407606	4320156	4306549	4176079
Elevation ² (m)	2680 (54)	2998 (17)	2843 (17)	3196 (9)	2952 (39)	2948 (30)
Slope ³ (%)	2 (1)	8 (4)	1 (1)	4 (2)	4 (2)	3 (1)
Aspect ⁴ (degrees)	138 (9)	234 (161)	30 (14)	175 (186)	15 (7)	260 (23)
July-2009 Temp. ⁵ (°C)	13.6 (12.3)	12.6 (12.5)	12.7 (11.4)	— ⁹	15.1 (9.8)	14.2 (10.7)
Jan-2010 Temp. ⁵ (°C)	−7.5 (12.6)	−9.4 (14.8)	−6.1 (12.6)	−8.4 (13.6)	−7.8 (15.8)	−6.7 (13.5)
July-2010 Temp. ⁵ (°C)	14.8 (2.2)	13.8 (12.4)	13.8 (11.5)	12.6 (11.8)	15.9 (10.2)	15.0 (11.2)
Total Summer Precip. 2009 ⁶ (cm)	2.9	2.3	9.7	3.4	3.8	7.8
Total Summer Precip. 2010 ⁶ (cm)	— ⁹	2.7	— ⁹	4.1	9.6	15.3
Total Summer Precip. 30 yr ave. ⁷ (cm)	16.0	14.0	17.4	16.5	13.4	19.1
Soil Moisture ⁸ ls mean (%)	11.9 (0.6)	10.4 (0.6)	10.4 (0.6)	15.6 (0.6)	11.9 (0.6)	8.1 (0.6)

¹ Each site consists of six plots. Pilot Hill is in the Laramie Ranger District, Medicine Bow National Forest (NF); Killpecker is in the Canyon Lakes Ranger District, Roosevelt NF; Columbine is in the Boulder Ranger District, Arapaho NF; Buffalo Peak is in the South Park Ranger District, Pike NF; Trout Creek is in the Salida Ranger District, San Isabel NF; and Mosca Pass is in the Great Sand Dunes National Park and Preserve.

² Arithmetic mean elevation (SD) of six plots at each site, elevation was recorded from a Garmin eTrek GPS.

³ Arithmetic mean percent slope (SD) of six plots, slope was measured using an inclinometer.

⁴ Arithmetic mean aspect (SD) of six plots, aspect was recorded using a compass.

⁵ Arithmetic mean (SD) for each month’s temperature data taken every half hour, *n* = 1488.

⁶ Total summer precipitation July–September in 2009 and 2010.

⁷ Total summer precipitation – Sum of 30 year average of PRISM data from July–September 1981–2010 (PRISM, 2014).

⁸ Gravimetric soil moisture was collected in each plot (6 per site) four times in 2009 and twice in 2010, numbers are least square means of these six data points across time adjusted for site and canopy level (dense or open, relative within site).

⁹ Data logger malfunction caused the loss of July 2009 temperature data at Buffalo Peak and 2010 precipitation data at Columbine.

the entirely hydrogel-free sites) had their roots dipped in water prior to planting. All seedlings were watered only once at the time they were planted when they received either 0.5 or 1 liter of water, as determined by site soil moisture at the time.

METEOROLOGICAL DATA. We installed an automated HOBO weather station (Onset Computer Corporation, Pocasset, MA) to measure temperature, relative humidity, and precipitation near one of the plots with low canopy density at each site. Temperature and relative humidity measurements were recorded every 30 min from planting in spring 2009 until late fall 2010, while precipitation was recorded by HOBO tipping rain gauges (Onset Computer Corporation, Pocasset, MA) from May/June to October/November of 2009 and 2010. Thirty year monthly average precipitation totals were obtained for the six planting sites from an 800 m resolution GIS layer (PRISM Climate Group 2014).

SOIL DATA. Soil samples were taken to determine nutrient content at planting, and samples were collected for soil moisture analysis each time seedlings were assessed in the summers of 2009 and 2010. For all samples, we collected three 18-cm deep soil samples in each plot by removing the duff layer and sieving the soil through 0.64 cm wire mesh. The three soil samples were located equal distances across the middle of each plot. Soil moisture samples were collected in metal soil sample cans and nutrient samples were collected in sample bags.

In the lab, soil moisture samples were weighed and then placed in a drying oven at 40 °C for a minimum of 72 hr, and then reweighed to obtain the dry weight. Nutrient analysis samples were dried and sieved through a 1 mm wire mesh. The three soil nutrient samples from each plot were then combined and sent to AgSource Laboratories (Harris, Lincoln, NE) for analysis of soil pH, buffer pH,

sodium, soluble salt, nitrate, phosphorus, potassium, magnesium, calcium, estimated CEC, percent base saturation, organic matter, and particle size.

SEEDLING ASSESSMENT. Seedlings were assessed the fall following planting in 2009, in early summer 2010, and in late summer 2010, 2011, and 2012. Overall health status was determined by rating them on a standard 1 to 4 scale, using the following classifications: (a) tree was healthy with less than 5% dead needles or branches; (b) tree had 5–50% dead needles and/or branches; (c) tree had 50% to 99% dead needles and/or branches; and (d) tree was recently dead (died within the last five years), and still had needles and fine branches intact. In 2010, current year terminal growth and needle length were measured, as well as basal diameter. In 2012, current year terminal growth and overall seedling height were measured.

To assess the existing stand structure at planting sites, we installed one transect (4 m × 50 m) directly on each of the seedling planting plots. The middle of the transect was placed at the middle of the seedling planting plot and the long axis (50 m) of the plot followed the contour lines. In each transect we measured diameter at breast height (1.35 m, dbh) to the nearest 1.0 cm for each tree, and heights to the nearest 0.1 cm for seedlings less than 1.35 m tall.

At the end of each transect, we recorded percent slope; elevation (m); presence of any major damage agent on the trees within the subplot, including presence of MPB, WPBR, or *Arceuthobium cyanocarpum* A. Nelson ex Rydberg (dwarf mistletoe); and signs of historical fire.

DATA ANALYSIS. All data analysis was done using SAS software, Version 9.3 for Windows XP. Copyright © 2002–2008 SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA. Prior to data analysis we carried out some data manipulations. Temperature data from our remote stations were averaged by week and month for July and January temperatures (Table 1), while precipitation data was summed by growing season (June to October 2009, July to October 2010; Table 1). Soil nutrient values were averaged across high and low canopy cover plots within

a site. Gravimetric soil moisture was averaged over all samplings. Due to a malfunction of the data loggers at Columbine and Pilot Hill, the 2010 precipitation data was not included in modeling efforts. Thirty-year average precipitation data for each site was obtained from the PRISM Climate Dataset (Table 1; PRISM 2014). Canopy cover was used as a continuous variable in models since the open and dense canopy blockings were relative within a site and highly variable across sites, with open canopy ranging from 8–42% and dense canopy ranging from 56–93% (Table 2). Densiometer readings for each object location (*i.e.*, stump or stake) were averaged to get a canopy cover value for the object, then averaged across the plot for a plot average. Since the effect of hydrogel was not significant in any model, all other analyses were performed averaging over this treatment. For seedling health analysis, averages for each plot were created (*e.g.*, average health for trees on the west side of a stump in plot one at Pilot Hill) since variables being tested were all measured at the plot level.

Site and stand variable means, as well as planted seedling health data (Table 1, 2; Fig. 2) are arithmetic means or percentages (PROC MEANS). To protect for multiple comparison errors we used Fisher's protected *t* test/least significant difference.

Backward stepwise regressions were used for modeling (PROC GLIMMIX, with the Laplace method). The basic model design was a randomized block (sites) with plots as subsamples. Although the random site effect was significantly larger than the plot within site variance, the orientation to nurse object by site interaction was not larger than the orientation to nurse object by plot within site interaction, so those two variances were pooled.

Models predicting the percent of healthy seedlings in each year (data only presented for 2012) and 2012 terminal growth length (Fig. 3–6; Table 3, 4) all used PROC GLIMMIX models starting with the following variables as covariates: seedling height at planting, mean soil moisture, mean canopy cover, elevation, percent slope, aspect, percent clay, mean dbh of surrounding trees, mean basal area of surrounding trees, total summer 2009 precipitation, mean July 2009 and 2010 temperature, and mean January 2010 temperature. Orientation to object was included as

Table 2. Stand characteristics of *Pinus flexilis* planting sites.

Site	Canopy	Basal area (m ² /ha) ¹	Stems per ha ²	dbh ³			Percent canopy cover ⁴		
		dbh > 10 cm	dbh > 10 cm	n (trees)	Mean	SD	n (plots)	Mean	SD
Pilot Hill	Dense	24	583	35	20.9	9.9	72	93.1	6.0
	Open	17	233	14	28.0	11.8	71	29.4	13.5
Killpecker	Dense	58	983	59	25.8	9.0	72	72.3	7.8
	Open	4	317	19	12.0	2.4	72	11.5	8.7
Columbine	Dense	24	550	33	21.9	9.0	72	77.5	6.1
	Open	17	267	16	27.7	6.8	72	34.0	8.6
Buffalo Peak	Dense	13	250	15	23.5	9.8	72	55.8	12.6
	Open	2	50	3	20.5	15.1	70	8.1	5.4
Trout Creek	Dense	31	600	36	24	9.4	36	81.1	6.5
	Open	18	400	24	23.0	7.4	36	41.5	6.2
Mosca Pass	Dense	32	1,083	65	18.3	6.6	36	81.1	8.7
	Open	16	500	30	18.8	7.5	36	27.3	9.3

¹ Basal area is from the 4×50 m transects in the center of the planting plots and includes all live trees 10 cm dbh or larger, of any species.

² Stems/ha includes all live trees 10 cm dbh or larger, of any species, at from the 4×50 m plot in the center of the planting plot.

³ Dbh (diameter at breast height, 135 cm) is from all trees of all species in the 4×50 m plots in the center of the planting plot and was measured in cm. Trees less than 135 cm in height were not included in this measurement.

⁴ A canopy measurement using a convex densitometer at the four cardinal direction was taken over each stump or stake, then averaged over all replication within a low or high canopy treatment.

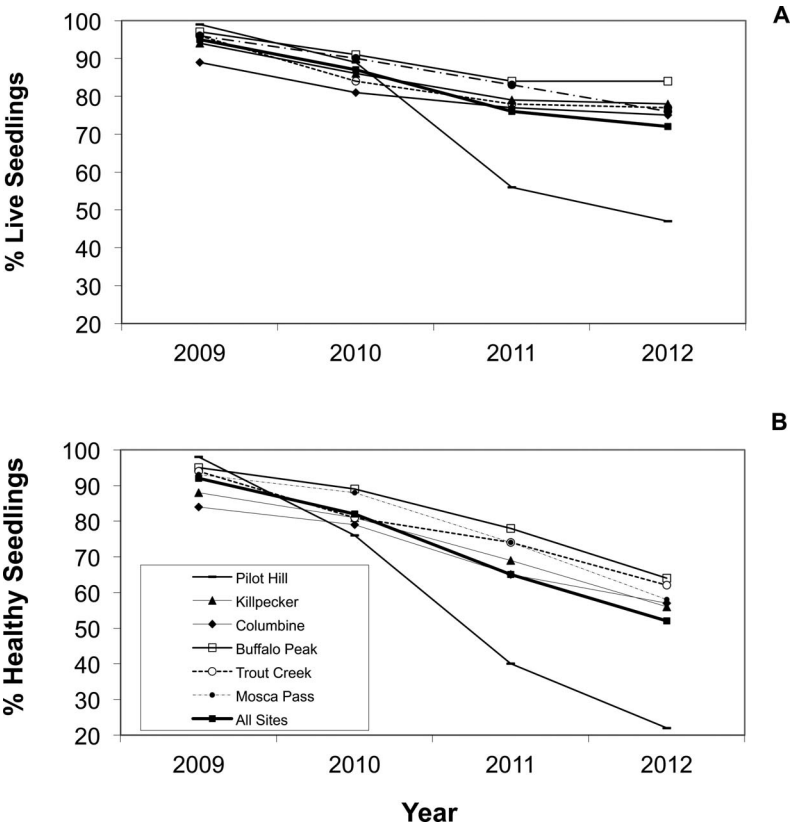


FIG. 2. (A) Percentage of live seedlings; (B) percentage of healthy (health status = 1) seedlings in August by site for six *Pinus flexilis* planting sites planted at the beginning of the 2009 growing season.

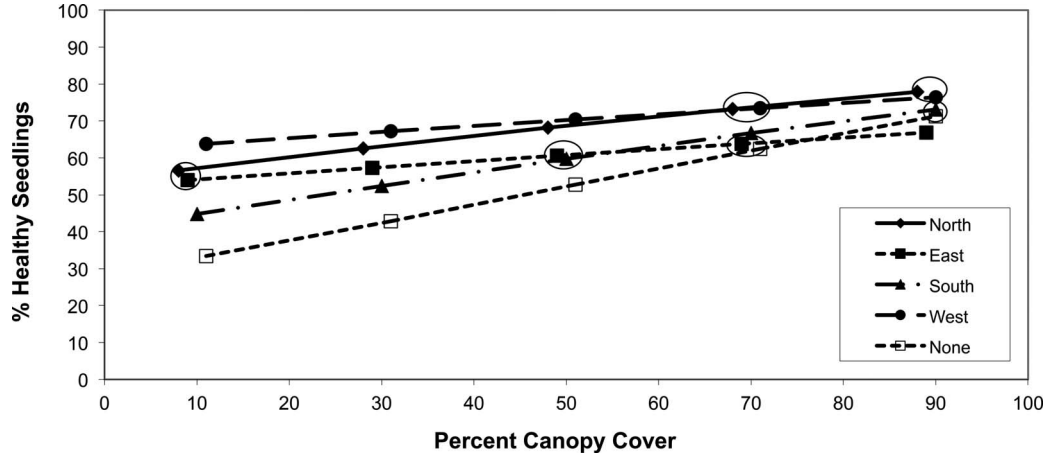


FIG. 3. Percentage of healthy seedlings by percent canopy cover and orientation to nurse object, for six *Pinus flexilis* planting sites, planted at the beginning of the 2009 growing season, based on linear regression model that includes canopy cover, seedling height at planting, orientation to nurse object, and the two-way interactions between these variables, holding seedling planting height constant at the mean (22.3 cm; Table 3).

¹ Seedlings were rated as healthy (health status = 1) if they had less than 5% dead needles or branches. In this analysis, healthy seedlings (health status = 1) were compared with all other health status categories (declining, dying, and dead).

a fixed effect of north, south, east, west, or no object. Hydrogel treatment was also initially included as a fixed effect, but was removed when it was found to be not significant. Additionally, seedling health in 2012 was included as a covariate for the model predict-

ing 2012 terminal leader growth. We did not use basal area by species in the stands we planted under because several of the species were specific to one or two sites, and the tree species that were common across sites were correlated with overall basal area (live and

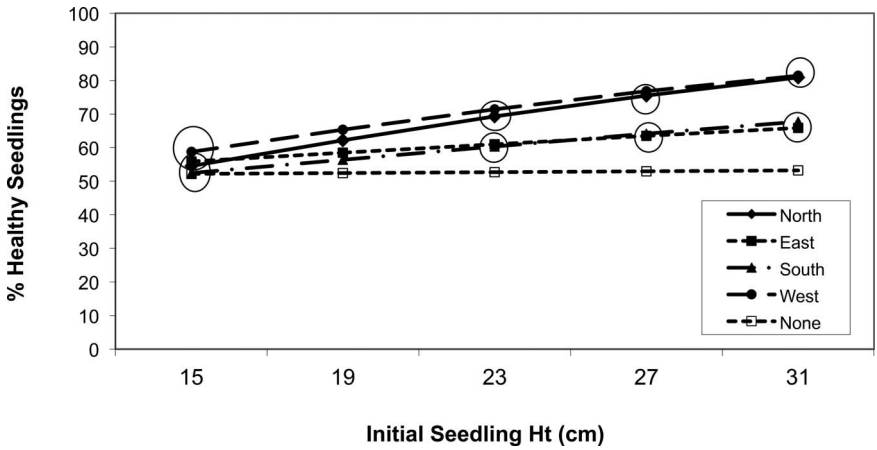


FIG. 4. Percentage of healthy seedlings by initial seedling height at planting and orientation to nurse object, for six *Pinus flexilis* planting sites, planted at the beginning of the 2009 growing season, based on linear regression model that includes canopy cover, seedling height at planting, orientation to nurse object, and the two-way interactions between these variables, holding percent canopy cover constant at the mean (50%; Table 3). Circles indicate data points that are not statistically significant from each other, at a given seedling height.

¹ Seedlings were rated as healthy (health status = 1) if they had less than 5% dead needles or branches. In this analysis, healthy seedlings (health status = 1) were compared with all other health status categories (declining, dying, and dead).

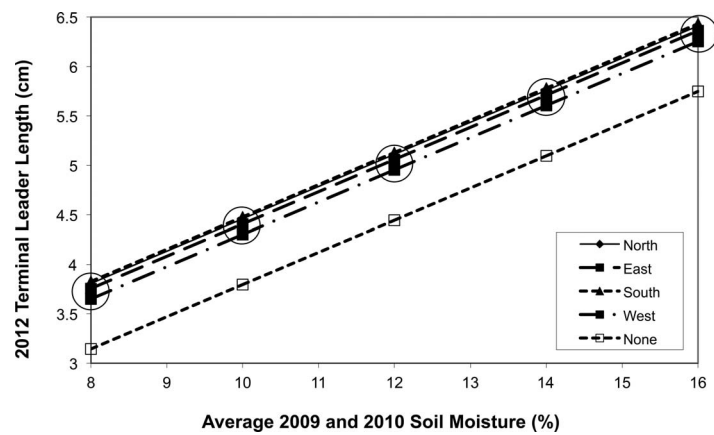


FIG. 5. Mean 2012 terminal leader growth (cm) by average 2009 and 2010 percent soil moisture and orientation to nurse object for six *Pinus flexilis* planting sites planted at the beginning of the 2009 growing season and based on linear regression model that includes canopy cover, average 2009/2010 percent soil moisture, 2012 health, and orientation to nurse object (Table 3). Circles indicate groups of data points that are not statistically significant from each other, at a given percent soil moisture.

standing dead), which prevented the model from converging. Live basal area was also not included in the initial model because it caused similar problems, due to its correlation with total basal area. Site and plot nested within site were in the random statement of the model. Variables were left in the model when they had a significance of $P < 0.05$.

Because the PROC GLIMMIX procedure does not provide a goodness of fit, we used PROC GLM to determine pseudo R^2 values for the models. We ran PROC GLM with the full model (r^2_{full}) and with only the random factors (r^2_{random}) factors and used the formula $(r^2_{full}-r^2_{random})/(1-r^2_{random})$ to de-

termine the pseudo R^2 for the PROC GLIMMIX models.

Results. SEEDLING PLANTING SITE CHARACTERISTICS. Site characteristics varied among the planting study sites yet were generally similar (Table 1). Elevations ranged from 2,680 m at Pilot Hill to 3,196 m at Buffalo Peak, and slopes were gradual (0–12%) at all sites.

Forest structure varied between sites and between open and closed canopy at each study site (Table 2). The total live basal area of stems 10 cm dbh or greater, including species, ranged from 2 to 18 m²/ha the open canopy plots while in the dense canopy plots basal area ranged

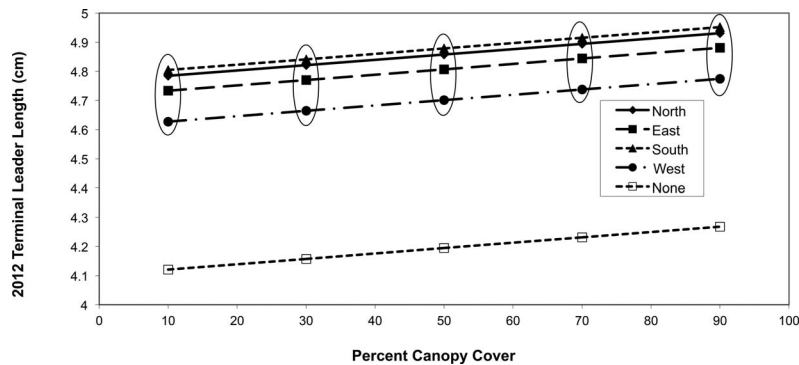


FIG. 6. Mean 2012 terminal leader growth (cm) by percent canopy cover and orientation to nurse object for six *Pinus flexilis* planting sites planted at the beginning of the 2009 growing season and based on linear regression model that includes canopy cover, average 2009/2010 percent soil moisture, 2012 health status, and orientation to nurse object (Table 4). Circles indicate groups of data points that are not statistically different from each other, at a given percent canopy.

Table 3. Linear multiple regression model parameters for predicting proportion of healthy¹ *Pinus flexilis* seedlings in 2012, which were planted in 2009, from a backward stepwise regression modeling based on site characteristics. Positive estimates indicate a positive relationship with healthy trees.

Parameter	Estimate	s.e.	d.f.	P value	
Intercept	−1.08	0.73	5	0.198	
Mean Canopy Cover (%)	0.01	0.01	131	0.304	
Planting Height (cm)	0.07	0.02	131	<0.001	
Parameter ^{2,3}	Orientation to object	ls means	s.e.	d.f.	P value
Side of Object	East	0.5813	0.4516	131	0.2003
Side of Object	None ⁴	0.1324	0.3553	131	0.7100
Side of Object	North	−0.5434	0.4220	131	0.2002
Side of Object	South	−0.1818	0.4447	131	0.6833
Side of Object	West	0	.	.	.
Canopy*Side Interaction	East	−0.00081	0.001777	131	0.6507
Canopy*Side Interaction	None	0.012390	0.001440	131	<0.0001
Canopy*Side Interaction	North	0.004772	0.001802	131	0.0091
Canopy*Side Interaction	South	0.007515	0.001771	131	<0.0001
Canopy*Side Interaction	West	0	.	.	.
Planting Ht.*Side Interaction	East	−0.04390	0.01835	131	0.0181
Planting Ht.*Side Interaction	None	−0.06766	0.01467	131	<0.0001
Planting Ht.*Side Interaction	North	0.008817	0.01709	131	0.6068
Planting Ht.*Side Interaction	South	−0.02986	0.01816	131	0.1025
Planting Ht.*Side Interaction	West	0	.	.	.

¹ Seedlings were rated as healthy (health status = 1) if they had less than 5% dead needles or branches. In this analysis, trees rated 1 were compared with all other health status categories (declining, dying, and dead).

² Least square means are reported for categorical values instead of estimates from model.

³ Least square means are the proportion of seedlings classified as a health status = 1, compared to all other health status categories. *P* < 0.0001 for comparing mean of seedlings around an object (north, east, south, west) to those without an object.

⁴ Indicates seedlings with no nurse object.

from 13 to 58 m²/ha. The mean dbh of all species ranged from 2.0 to 32.6 cm across all plots. In the open canopy sites the density of stems greater than 10 cm dbh for all species ranged from 50 to 500 stems/ha. In the dense canopy sites the density of stems greater than 10 cm dbh of all species ranged from 250 to 1,083 stems/ha. The average percent canopy

cover in open areas ranged from 8.1–41.5% and from 55.8–93.1% in dense areas. The canopy in planting sites was composed of primarily conifer species with *Populus tremuloides* Michx., (aspen) being the only hardwood present. The northern sites had more homogenous forests, whereas the sites farther south had more heterogeneous forests, incorporating up to six

Table 4. Linear multiple regression model parameters for predicting 2012 terminal leader length (cm) of live planted *Pinus flexilis* seedlings planted in 2009 from a backwards stepwise regression modeling based on site characteristics.

Parameter	Estimate	s.e.	d.f.	P value	
Intercept	1.08	2.06	5	0.6209	
Mean Canopy Cover (%)	0.001	0.006	138	0.7666	
2012 Health Status ¹	−0.3	0.24	138	0.2195	
Planting Height (cm)	0.02	0.05	138	0.6498	
Mean Soil Moisture (2009/10)	0.32	0.12	138	0.0072	
Parameter ²	Orientation to object	ls means	s.e.	d.f.	P value
Orientation to Object	East	0.11	0.28	138	0.7043
	None	−0.51	0.25	138	0.0446
	North	0.16	0.27	138	0.5658
	South	0.18	0.28	138	0.5219
	West	0	.	.	.

¹ Seedlings were rated as healthy (health status = 1) if they had less than 5% dead needles or branches. In this analysis trees rated 1 were compared with all other health status categories (declining, dying, and dead).

² Least square means are reported for categorical values instead of estimates from model.

species at a site. Mature tree species located within the planting sites included *P. flexilis* and *Populus tremuloides* at Pilot Hill; *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir), *P. flexilis*, and *Picea engelmannii* at Killpecker; *Pinus contorta* Douglas ex Loudon (lodgepole pine) and *Populus tremuloides* at Columbine; *Pinus contorta*, *Picea engelmannii*, and *Populus tremuloides* at Buffalo Peak; *Abies lasiocarpa*, *Pinus contorta*, *Pinus ponderosa* Lawson & C. Lawson, (ponderosa pine), *Picea engelmannii*, *Populus tremuloides*, and *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) at Trout Creek; and *Abies lasiocarpa*, *Juniperus scopulorum* Sarg. (Rocky Mountain juniper), *P. flexilis*, *Pinus ponderosa*, *Populus tremuloides*, *Pinus aristata*, and *Pinus edulis* Engelm (pinyon pine), at Mosca Pass. Soil characteristics were not strikingly different between sites, with little variation within sites. Between sites, pH ranged from 6.3 to 7.5, texture ranged from sandy loam to clay loam, percent organic matter ranged from 1.6–5.6%, nitrate ranged from 1.0 to 6.5 ppm, P ranged from 11.6 to 57.0 ppm, and K ranged from 78 to 228 ppm.

Overall, mean January 2010, July 2009, and 2010 temperatures followed similar fluctuation patterns across sites, and only varied by a few degrees between sites (Table 1). Excluding Buffalo Peak's missing data, July 2009 average temperatures were similar across all sites and ranged from 13 °C at Columbine and Killpecker to 15 °C at Trout Creek. The small difference of 2 °C falls well within the standard deviations, which ranged from 9 °C at Trout Creek to 12 °C at Pilot Hill and Killpecker. July 2010 mean temperatures were similar, ranging from 13 °C at Buffalo Peak to 16 °C at Trout Creek, with standard deviations that ranged from 10 °C at Trout Creek to 12 °C at Pilot Hill and Killpecker. January 2010 temperatures were also similar, and ranged from –9 °C at Killpecker to –6 °C at Columbine, with standard deviations that ranged from 12 °C at Pilot Hill and Columbine, to 16 °C at Trout Creek.

Total monthly precipitation in 2009 and 2010 was similar or lower than 30-yr averages for the planting sites (Table 1). In 2009, the year the seedlings were planted, precipitation ranged from 3.1 cm at Killpecker to 31.7 cm at Columbine, in the 17 weeks from June 7th to October 3rd. Least-square-mean soil moisture from six readings, four in 2009 and two in 2010, ranged from 8.1–15.6% across all sites

and variations did not reflect the precipitation amounts (Table 1).

SEEDLING SURVIVAL AND GROWTH. Overall, 72% of seedlings were alive after four growing seasons (in 2012), and 52% were classified as healthy (health status = 1; Fig. 2). The percentage of live seedlings by site ranged from 47–84%, and the percentage of healthy seedlings ranged from 22–78% (Fig. 2). Pilot Hill had much lower percentages of live (47%) and healthy (22%) seedlings than the other sites. Due to these overall high levels of health and survival, and since classification as live but not healthy (2 or 3) was a good predictor for seedling death (86% of planted seedlings classified as a 2 or 3 in fall 2009 to August 2010 were dead by August 2011), all treatment effect analyses were performed comparing seedlings classified as healthy to all others (status rating 1 vs. 2–4).

Overall, seedling health and survival gradually declined each growing season (Fig. 2). Each site had approximately 5–10% mortality per growing season, except Pilot Hill, which had a 33% decline in live seedlings between the end of the second (2010) and third (2011) growing seasons. The percentage of healthy seedlings declined in a similar pattern, with declines of approximately 5–15% of healthy seedlings per growing season. Between growing seasons two (2010) and three (2011), a 36% decline was observed in the seedling at Pilot Hill.

TREATMENTS. Hydrogel, canopy cover, and nurse object treatments differed in their impact on seedling health. Hydrogel treatment did not have a significant effect in any model; therefore, variables were averaged over this treatment. Canopy cover was a significant variable in models predicting tree health but not 2012 terminal leader length (Table 3, 4; Fig. 3, 6). Orientation to nurse object was a significant variable in models predicting both tree health and 2012 terminal leader length (Table 3, 4; Fig. 3, 6).

MODELING PLANTED SEEDLING HEALTH. The regression model predicting the percentage of healthy seedlings remaining after four growing seasons included mean canopy cover (%), seedling height at planting (cm), orientation to object, the interaction between orientation to object and canopy cover, and the interaction between seedling height at planting and orientation to an object (Table 3; pseudo

$R^2 = 0.27$). All variables were positively correlated with planted seedling health. Due to the significance of the interaction terms the fixed effects cannot be simply interpreted from the model. However, Fig. 2, 3 graphically represent the interactions.

Orientation to object had a stronger effect on the health of seedlings under lower canopy densities, while holding planting height constant at the mean height (Fig. 3). At low- to midcanopy density (10–50%), there were more healthy seedlings when located next to an object, regardless of their orientation. The percentage of healthy seedlings overall increased as canopy cover increased. At 10% canopy cover, the percentage of healthy seedlings ranged from 33% (no object) to 64% (west side of object), whereas at 90% canopy cover, the percentage of healthy seedlings ranged from 67% (east side of object) to 78% (north side of object). Overall, the highest percentage of healthy seedlings were on the west side of an object (64–70%) for lower percent canopy cover (10–50% cover), and on both the north (73–78% healthy) and west sides (73–76% healthy) for higher percent canopy cover (70–90% cover). Seedlings on the north side of an object had similar percent of healthy seedlings (56–78%), across all canopy levels. The percentage of healthy seedlings on the east side of an object changed the least with increasing canopy, ranging from 54–67%. Seedlings on the south side of an object with low canopy cover did the poorest of all seedlings planted next to an object with only 45% of the seedlings healthy at 10% canopy (full range: 45–73%). The percentage of healthy seedlings without an object ranged from 33–71%.

Seedlings that were taller at planting were more sensitive to their orientation to the object than seedlings that were initially shorter (Fig. 4). For the seedlings that were small at time of planting (15 cm), the percentage of healthy seedlings ranged from 52% without an object to 59% on the west side of an object. For seedlings taller at time of planting (31 cm), the percentage of healthy seedlings ranged from 53% without an object to 81% on the west and north sides of an object. For midheight and tall seedlings (23–31 cm), the percentage of healthy seedlings fell into three clusters: no object, east and south, and north and west. Each of these three clusters are

significantly different from each other $P < 0.05$).

Seedling height at initial planting did not influence the percentage of healthy seedlings after four years when seedlings were not protected by a nurse object, holding canopy cover constant (Fig. 4). However, the percentage of healthy seedlings next to a nurse object increased for each additional 2.5 cm in planting height by 7% on the north side, 2% on the east side, 4% on the south side, and 6% on the west side ($R^2 > 0.99$ for all regression lines).

MODELING PLANTED SEEDLING GROWTH. Seedling terminal height growth in the 2012 growing season varied greatly; at the end of the growing season, terminal growth ranged from 0 to 43.5 cm, suggesting it may be a good indicator of establishment. The significant variables in predicting 2012 terminal growth in our regression equation were 2009–10 mean soil moisture (more recent data was not available) and orientation to the object (Table 4; pseudo $R^2 = 0.11$). In addition, percent canopy cover, 2012 health rating, and seedling height at planting were retained in the model, despite not being statistically significant, due to theoretical importance.

Higher mean soil moisture in 2009–10 is correlated with longer terminal growth in 2012 (Fig. 5). Seedlings planted without a nurse object had shorter terminal leader growth than seedlings planted next to a nurse object, regardless of orientation to object (Fig. 5, 6; $P < 0.05$). While 2012 seedling health was not statistically significant in the model, no data for this variable were entered for dead seedlings, since they had no terminal leaders to measure.

SEEDLING DAMAGES. For the four growing seasons of this study, seedling mortality appeared to be caused by poor establishment. We did not observe any WPBR infection on the seedlings and evidence of damage due to other diseases, insects, herbivory, or snow pack was rare. White pine blister rust was present in the surrounding stands at Mosca Pass and Pilot Hill but has not been detected within and around the other study sites. There were no seedlings with insects, disease, or herbivory as a direct cause of death. Less than 1% of seedlings had damage that may have been caused by herbivory. Most insects noted were sucking insects, and there were only two seedlings that appeared to be damaged directly

by sucking insects. In August 2012, several blown-down overstory trees were found at Columbine but only one seedling was killed.

The Pilot Hill site had high levels of disturbance by *Thomomys talpoides* Richardson, hereafter referred to as pocket gopher, with gopher mounds present in 100% of the plots. However, except for three seedlings that were covered by a gopher mound and missing in August 2012, we did not observe any clear evidence of seedlings being killed by pocket gopher activity. Dead seedlings did not pull out of the ground easily, as would be expected with pocket gopher root damage. Pocket gopher activity was also observed at Columbine, but only near one planting plot, not directly next to the planted seedlings. While neither pocket gopher activity nor other indications of rodent disturbance were observed at Killpecker, in 2012 one seedling was found that had been chewed off below root line. Only the two most northern sites, Pilot Hill and Killpecker, had a few seedlings (< 0.5%) damaged and killed by heavy and prolonged snow pack.

Discussion. We had high levels of planted seedling survival, with 72% of seedlings still alive and 52% classified as healthy after four growing seasons in the field (Fig. 2). Seedling health was affected by the presence of a nurse object, canopy density, and soil moisture (Table 3; Fig. 3, 4). While further long-term studies across larger elevation and seasonal moisture gradients are necessary for generalized conclusions, the results after four growing seasons indicate that planting *P. flexilis* seedlings near objects, under canopy cover, and in areas with higher soil moisture is a viable way to establish regeneration cohorts.

Our plots occurred across a relatively small elevation gradient, 2,680 to 3,196 m, but with a comparatively wide latitudinal gradient (Fig. 1; Table 1). The planting sites were also in different forest types (Table 2). Therefore, while our highest proportion of healthy planted seedlings was at the highest elevation site at midlatitude, and the lowest was at the lowest elevation site furthest north, it is likely that elevation and latitude are confounded, preventing us from making clear recommendations about those factors for planting guidelines. Our planting protocols should be applied to different elevations with caution since the elevation gradient of our plots was only a small

portion of *P. flexilis*'s elevation range in the Central Rocky Mountains (1,600–3,300 m; Schoettle and Rochelle 2000).

We used seedling health and fourth-season terminal shoot growth lengths to determine which site characteristics are important for seedling survival to develop planting protocols useful for land managers. Due to the high number of healthy and surviving seedlings, and a high death rate of seedlings classified with a health status of 2 and 3 during early assessments, health data analysis only compared seedlings classified as healthy (status rating 1) to all others (2 to 4).

PLANTING TREATMENTS. Overall, *P. flexilis* seedlings benefit from denser canopy cover during their first four growing seasons following outplanting (Fig. 3). Seedling health varied more by canopy density when a seedling was not protected by a nurse object. The healthiest seedlings at low canopy cover were on the west side of a nurse object, followed by seedlings on the north and east sides, the south side, and lastly those unprotected by a nurse object. Seedling terminal leader growth in 2012 (year 4) was longer under denser canopy, regardless of orientation to object. Based on our seedling results, the *P. flexilis* planting study by Smith *et al.* (2011), research on the shade-intolerant *P. pinaster* by Rodriguez-Garcia *et al.* (2011), and Germino and Smith's (1999) research on photoinhibition in seedlings without canopy cover, we recommend planting seedlings under canopy cover and on the north or west side of an existing nurse object, particularly under lower levels of canopy cover. We found a positive linear relationship between seedling health and canopy cover, and did not find a negative impact of high levels of canopy cover on seedling health (Fig. 3). However, over a longer period it is possible that canopy cover may slow *P. flexilis* maturation or impact tree reproduction. Therefore, further studies are needed to understand the long-term impact of canopy cover on planted *P. flexilis* seedling survival, maturation, and reproduction.

The positive correlation between the proportion of healthy seedlings and canopy density may indicate that planted *P. flexilis* seedlings benefit from canopy cover despite being a shade-intolerant species, since the conditions needed for natural establishment of seedlings may be different than those required for planted seedlings. Seedlings expe-

rience higher water stress for two to four years posttransplant due to poor root/soil contact, known as planting check, or growth check (Burdett 1990, Grosnickle 2005). In Burdett's (1990) model of planted seedling establishment for conifer seedlings, high initial water potential allows for photosynthesis to occur immediately, which, in turn, allows the seedlings to enter a positive cycle of root growth, higher water potentials, and more photosynthesis. These high levels of root growth and photosynthesis are important for seedlings to extend their roots into the surrounding soil, increasing root/soil contact, and allowing them to move beyond growth check (Burdett 1990).

The protection provided by canopy cover and nurse objects in our study may have allowed seedlings in these treatments to have higher water potentials that, in turn, led to better establishment. Additionally, seedlings height ranged from 9 to 28 cm tall at the time of planting. Once established, taller seedlings would be better competitors with surrounding vegetation than newly emergent seedlings. Therefore, the benefit of canopy cover for planted seedlings may, at least initially, outweigh the negative effect of competition from other trees that provide the canopy cover.

Nurse Object. The high percentage of healthy seedlings with a nurse object (73%) versus without a nurse object (63%) suggests that nurse objects help improve seedling survival and health (Fig. 3; $P < 0.0001$; Colak 2003; Barbeito *et al.* 2009; Coop and Schoettle 2009). The higher percentage of healthy seedlings on the north side of the nurse object concurs with the findings of previous studies that nurse objects protect seedlings from intense solar radiation, which is believed to cause photoinhibition and reduce soil moisture, leading to desiccation (Germino and Smith 1999, Castro *et al.* 2004). The higher number of healthy seedlings on the west side of an object may be a result of protection from high intensity sunlight early in the day when needles are cold. High intensity sunlight during cold temperatures causes photoinhibition in Engelmann spruce and subalpine fir (Ronco 1970b, Germino and Smith 1999).

Due to our use of artificial nurse objects, we cannot make any recommendations about the type of naturally occurring object to plant next to. In a study of natural *P. flexilis* regeneration, Coop and Schoettle (2009) found that

seedlings were associated with small objects, such as cobbles, boulders, fallen logs, and tree trunks, but they did not find that type of object mattered. Digging holes next to objects can be difficult. For example, it may not be possible to plant directly against stumps or living trees due to root flares. Instead, seedlings may need to be placed a few to several centimeters away from the object. Large rocks on the landscape may indicate rocky areas with shallow rocky soil that prevents digging and may negatively impact seedling survival.

Jacobs and Steinbeck's (2001) success with artificial shelters and Ronco's (1970a) success with shingles to protect *Picea engelmannii* seedlings in the central and southern Rocky Mountains indicates that plastic shelters or wooden shingles may be a viable option for use in protecting planted *P. flexilis* seedlings as well. While these shelters have the possible drawback of introducing artificial materials into the landscape, they solve the problems caused by planting near naturally occurring objects. Wooden shingles do not introduce artificial materials into the environment, but require removal overwinter so they do not damage the seedlings by flattening under snowpack (Ronco 1970a).

Hydrogels. While further research on hydrogels under different soil and moisture conditions may provide alternative results, we currently do not recommend the use of hydrogels in *P. flexilis* plantings because it had no effect in any of the parameters we measured. The placement of compounds that have an unknown half-life and long-term effects in natural ecosystems is another concern for the use of hydrogels in planting projects. Even though the precipitation at the planting sites was not higher than average (Table 1), it is possible that the type of seedlings we used for planting influenced the effectiveness of our hydrogel treatment. The lack of any positive effect of the hydrogels in our study may have been because the seedlings were well prepared for outplanting. Additionally, the seedlings were cone-tainer grown, and not bare root; therefore, the hydrogels might not have been in direct contact with the inside of the root plug.

Other research on hydrogels indicates that they are most effective in sandy soils; therefore, it is possible that hydrogels could have a beneficial effect in areas with sandier soils than our study sites, which ranged from sandy

loams to clay loams (Agaba *et al.* 2010). Hydrogel effect is also linked to tree species and brand of hydrogel (Agaba *et al.* 2010). Since there have been no *P. flexilis*-specific hydrogel studies and hydrogel ingredients are proprietary, we cannot make direct comparisons between our results and other studies for either of these two factors.

GROWTH PARAMETERS. Seedling height and health ratings are good measures of establishment and survival in a research test such as ours (Pinto *et al.* 2011, Smith *et al.* 2011, Walsh and Redente 2011). Seedlings that are experiencing water stress will photosynthesize less, and put the energy they do have into developing their root system (Burdett 1990). Mean percent canopy cover was not statistically significant in the terminal growth model (Table 4; $P = 0.7666$), but a nonsignificant positive trend in terminal leader growth with increasing canopy is apparent when the data points are graphed (Fig. 6). Similarly, seedling height at planting was also not statistically significant ($P = 0.5498$), indicating that the initial height at planting does not have a significant influence on terminal leader growth by the fourth growing season.

It is not surprising that soil moisture was correlated with seedling growth, as water stress is a frequent cause of seedling death (Fig. 5; Bernier 1993; Grosnickle 2005). The positive correlation between seedling health and height at planting suggests that the taller seedlings had more stored resources to enhance survival during the initial growth check and root establishment that occurs following outplanting (Fig. 4; Grosnickle 2005). However, it is unlikely that taller seedlings will always be better for planting. Because taller seedlings also require more resources for survival, height can become limiting. The interaction between planting height and nurse object indicates that taller seedlings only had a survival advantage when they had protection, which likely decreased water stress and planting shock (Fig. 4; Burdett 1990).

HERBIVORY, INSECTS, DISEASE, AND ABIOTIC DAMAGES. We observed little evidence of seedling damages from animals, insects, or snow creep. When insects were observed, they were not directly damaging the trees. In a few cases, herbivory by large ungulates was suspected because a few trees had several centimeters of terminal growth removed between

site visits. The low impact of herbivory in our study is similar to Ronco's (1970a) low levels of herbivory in his *Picea engelmannii* planting experiments. The combination of Ronco's (1970a) and our results indicate that in the Colorado and Southern Wyoming Rocky Mountains herbivore exclusion from planting sites may be unnecessary. However, our planting sites represented a small portion of the forests they were in. Thus, if the plantings were larger they may have attracted more herbivores.

We did not have a problem with snow creep uprooting trees or knocking over artificial stumps. Only one stump in the entire study was leaning following the first winter, and it has remained stable at its angle since. Because all of our sites had mild slopes, ranging from 0% to 12%, we do not know how snow creep would influence seedlings or artificial nurse objects on steeper slopes. However, in steep mountain terrain, the protection objects provide may include protection from snow creep (Scott and McCaughey 2006).

Future studies would help understand the important factors for successful natural and artificial regeneration of *P. flexilis*. We did not carry out an operational planting trial, so future planting trials are needed where seedlings are planted operationally. In the future, studies are necessary that consider larger sample sizes and longer durations of monitoring, greater elevation ranges, greater diversity in canopy densities including clearcuts, alternative nurse objects such as tree shelters (Ronco 1970a, Jacobs and Steinbeck 2001), and various other factors. These future studies will further our understanding of microsite characteristics, the long-term influence of canopy cover on seedling maturation and survival, and nurse object factors that are important for natural *P. flexilis* regeneration, continuing to expand on the work of Coop and Schoettle (2009).

Conclusions. In conclusion, for optimum survival and growth in the first four years, we recommend planting *P. flexilis* seedlings in areas with higher soil moisture, under canopy cover, and next to a nurse object; preferably on the north or west side of the object. While nurse objects had a diminishing effect as canopy cover increased, at 90% canopy cover there were still significantly higher numbers of healthy seedlings on the north or west side of a nurse object, compared to seedlings on the

east or south side, or seedlings without an object.

While the survival of well-planted seedlings without a nurse object was acceptable (53%) four growing seasons after planting, continued monitoring of seedling health is needed to determine the long-term outcome. Overall we observed 5–11% annual mortality rate of seedlings during each growing season, approximately a 10% decrease in healthy seedlings in each of the first two growing seasons, a 17% decrease in healthy seedlings between the second and third growing seasons, and a 12% decrease in healthy seedlings between the third and fourth growing seasons (Fig. 2). Therefore, seedling survival and health results may differ five or ten years after planting. Future monitoring of the planted seedlings will provide answers to some of these questions.

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