

Soil nutrient differences between two krummholz-form tree species and adjacent alpine tundra

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Abstract

Above treeline at Goliath Peak, Colorado, *Pinus aristata* (bristlecone pine) and *Picea engelmannii* (Engelmann spruce) grow as krummholz tree forms. Due to the harsh alpine climate, these trees are dwarfed in size (approximately 0.5 to 3.0 m tall) and root along a horizontal stem. Soil nutrients, including carbon, nitrogen, and phosphorus fractions were examined to 10-cm depth beneath *P. aristata* krummholz and *P. engelmannii* krummholz, as well as from adjacent, undisturbed alpine soils. Plant available phosphorus was higher under *P. engelmannii* than *P. aristata*, suggesting that although these two species exist in the same environment, they have a different effect on the availability of labile soil phosphorus. Mineral soils under *P. aristata* were not significantly different than under *P. engelmannii* for total carbon, total nitrogen, and total phosphorus. Soil phosphorus differences are important in this ecosystem because of the proposed P limitation in some alpine ecosystems. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Just above treeline on Goliath Peak, Colorado, Engelmann spruce (*Picea engelmannii* (Parry) Engel.) and bristlecone pine (*Pinus aristata* Engel.) have growth forms that allow them to persist in the harsh alpine climate, which is dominated by strong and frequent winds, as well as heterogeneous snow cover for much of the year. Krummholz are dwarfed trees (approximately 0.5 to 3.0 m tall) that root along a horizontal stem. Although it is not known whether *P. aristata* krummholz are capable of moving across the alpine tundra, *P. engelmannii* and *Abies lasiocarpa* (Hook) Nutt. krummholz have been reported to migrate across the alpine tundra from windward to leeward at rates of approximately 2–4 cm year⁻¹ (Marr, 1977; Benedict, 1984). Migration of krummholz across the tundra is a result of die back on their windward side from climatic injuries, and elongating to the leeward side via layering (Marr, 1977; Benedict, 1984; Holtmeier, 1987; Holtmeier and Broll, 1992).

Plant species composition, productivity, and litter quality have long been recognized as factors affecting soil characteristics (Shaw, 1930; Jenny, 1941; Birkeland, 1984; Schlesinger, 1991). Phosphorus (P) availability, from both labile and nonlabile soil fractions, directly affects plant production because plants cannot grow without a reliable supply of this nutrient (Schachtman et al., 1998). For most soils, more than 80% of the soil P becomes immobile and unavailable for plant uptake because of adsorption, precipitation, or conversion to the organic form (Holford, 1997). Labile, or plant available P, is generally thought to be available to microbes and vegetation in the short term because it rapidly desorbs from the surface of soil particles (Cross and Schlesinger, 1995). Hence, labile P, or that portion of P that is most readily available for plant uptake in the short term, is crucial for plant survival in any ecosystem. Furthermore, while nitrogen (N) is the primary limiting nutrient in most ecosystems, P availability may limit plant production in the alpine (Körner, 1989). Alternatively, both N and P may be co-limiting (Bowman et al., 1993). However, in a more recent study, Parker and Sanford (1999) found high soil P concentrations in krummholz and tundra communities, suggesting P may not be limiting in these environments in the Colorado Front Range.

Several previous studies have measured soil characteristics in the presence and absence of krummholz in the alpine. Burns (1980) compared soil chemical and physical characteristics between krummholz soils and uninvaded tundra soils. Holtmeier and Broll (1992) conducted more extensive studies on soil properties between windward, interior, and leeward areas of the tree islands in the Colorado Front Range. Although they reported significant differences in concentrations of carbon (C), total N, and plant available P for some microenvironments, the leeward areas of tree islands did not represent undisturbed tundra soils. Pauker and Seastedt (1996) conducted a krummholz study on Niwot Ridge, Colorado, that included soil samples from adjacent leeward, interior, and

windward sites, as well as undisturbed tundra soils directly upslope and downslope from krummholz trees. The results of their study indicated that the krummholz tree forms and/or the associated soil biota consumed soil C as they moved from windward to leeward. Also on Niwot Ridge, Parker and Sanford (1999) conducted detailed analysis of soil P in samples pooled from beneath two krummholz tree species (*P. engelmannii* and *A. lasiocarpa*), as well as from the adjacent tundra. Their findings indicated that there were no significant differences in labile, occluded, or non-occluded soil P concentrations between windward, leeward, and tundra soils. There have been no previous studies that compare soils between krummholz forming tree species. All of these studies compared open tundra soils with krummholz soils, but treated krummholz as a physiognomic form, and did not account for species (Burns, 1980; Holtmeier and Broll, 1992; Pauker and Seastedt, 1996; Parker and Sanford, 1999). In contrast, Barrick and Schoettle (1996) compared foliar nutrient status among varying krummholz species and symmetrically formed tall trees growing at timberline in the Colorado Front Range. Their findings indicated that *P. engelmannii* krummholz, but not *P. aristata* krummholz, had significantly lower mean foliar P concentrations compared with tall trees.

This study was designed to test for krummholz species effects on alpine soils. Specifically, we compared the following characteristics between *P. aristata* krummholz, *P. engelmannii* krummholz, and the adjacent undisturbed tundra: depth of litter layer (O horizon), soil moisture, soil pH, and soil nutrients, with an emphasis on soil P fractions. P fractions included labile P (Resin Pi, Bicarb Po, Bicarb Pi) and refractory P (NaOH Pi, NaOH Po, Sonic Pi, Sonic Po, HCl Pi, Residual Pi).

We present two sets of predictions: the first set is for krummholz vs. tundra and the second set is for krummholz species effects. We propose that O horizon depth, soil moisture, and total C, N, and P will be higher under *P. engelmannii* krummholz and *P. aristata* krummholz when compared to the adjacent tundra soils. Likewise, for P fractions, we expect that under *P. engelmannii* krummholz and *P. aristata* krummholz, labile and refractory P will be higher than from undisturbed tundra soils. For species comparisons, we hypothesize that C, N, and all P fractions will be higher under *P. engelmannii* than under *P. aristata* because of the denser foliage and a more prominent litter layer of the former.

2. Study area

Tree islands, composed of *P. engelmannii* and *P. aristata*, were studied on a 15% slope with a SE aspect on Goliath Peak (39°38'N, 105°35' W), just east of the Continental Divide in the Colorado Rocky Mountains. Some tree islands grow at elevations up to approximately 3650 m on Goliath Peak, but the

krummholz patches used in this study were in a saddle-shaped drainage located between 3300- and 3500-m elevation. The study site was uniform with respect to slope, elevation, and aspect. Additionally, the study area straddled a border between alpine grassland upslope to the south and a mixed species stand of bristlecone pine (*P. aristata*) and Engelmann spruce (*P. engelmannii*) to the north. Thus, the study site was just beyond the forest edge, as well as within the area containing the highest density of tree islands on Goliath Peak.

The climate on Goliath Peak has a short growing season that lasts from May to August. Wind direction is primarily from the southwest, and air temperature averaged -4.8°C from October 1996 through June 1997 (Rick Boyce, personal communication). The soils at treeline are Cryic Inceptisols that have been preliminarily classified as Dystocryepts (Mike Petersen, personal communication).

3. Materials and methods

Twenty tree islands, 10 with *P. engelmannii* and 10 with *P. aristata*, were selected for sampling within the study area. Two criteria were used in the selection of tree islands for this study. First, to exclude small patches, areas of $> 13 \text{ m}^2$ of continuous tree vegetation were selected. Second, the islands were not immediately leeward (20 m or closer) to other islands (Pauker and Seastedt, 1996) and were separated by an upslope distance of more than 15 m from adjacent tree islands. Out of the islands that met these criteria, those selected for the study were chosen randomly. The horizontal (windward–leeward) lengths and maximum widths (perpendicular to the horizontal axis at the widest point) were measured for each tree island. Following removal of any O horizon (litter layer), mineral soils were sampled from within the middle of each tree island to a depth of 10 cm using a 1.905 cm diameter corer. For comparison, in adjacent undisturbed tundra meadow, 0–10 cm-deep mineral soils were sampled 5 m upslope from the upslope edge of each tree island. Three samples from each site were composited separately (20 tree, 20 tundra) for a total of 40 samples. Finally, the depth of the O horizon was measured in the center of each krummholz sample area. Field samples of soil were obtained in October 1997, before the first significant snow fall.

Freshly collected soil samples were weighed, dried for 24 h at 105°C , and reweighed to determine gravimetric soil moisture for each sample (Topp, 1993). The dried soil samples were passed through a 2-mm mesh sieve. Soil pH was measured by mixing 2 g of soil with 2 ml of distilled water to form a paste.

Soil samples were analyzed for P by following a modified, Hedley sequential fractionation procedure (Hedley et al., 1982a). This method has been widely used in recent years for determination of soil P fractions (Lajtha et al., 1997), and it allows the same soil sample to be sequentially treated with reagents that

mimic many of the plant–soil interactions. These fractions provide a measure of the proportions of plant available and refractory P. Plant available P includes resin inorganic P (Pi), bicarbonate inorganic P (Pi), and bicarbonate organic P (Po). The resin fractionation simulates ion uptake action of plant roots, and like active roots, provides a strong sink for P released into solution (Lajtha et al., 1997). The alkaline bicarbonate extract mimics respiration activity of plant roots and is able to mineralize some additional soil P (Lajtha et al., 1997; Cross and Schlesinger, 1995). The plant available pool, also called labile P, is the most biologically available form of P. Conversely, refractory, or unavailable P, includes all other fractions (NaOH Pi, NaOH Po, Sonic Pi, Sonic Po, HCl Pi, Residual Pi). An alternative interpretation of the Hedley fractionation proposed by Cross and Schlesinger (1995) recognizes organically bound or biological P (Bicarb Po, NaOH Po, Sonic Po), and geochemical P (Resin Pi, Bicarb Pi, NaOH Pi, Sonic Pi, HCl Pi, Residual Pi).

The modified soil P sequential fractionation procedure followed Tiesson and Moir (1993) through the diluted HCl fractionation with the exception that 1 g of soil was used instead of 0.5 g. Following the HCl fractionation, ultrasonication was performed to derive the second NaOH (NaOH (2)) soil Pi and Po extraction. Finally, the residual P was determined using the Smith and Bain (1982) sodium hydroxide fusion method for determination of total P. Fractionation sequence aliquots were prepared according to Tiesson and Moir (1993) and analyzed colorimetrically for P content using Method B of the Orthophosphate procedure for Lachat Instruments QuikChem AE automated flow injection ion analyzer (Prokopy, 1996).

Total C and total N analysis were done with LECO Carbon–Hydrogen–Nitrogen IR Gas Analyzer (LECO, 1993). Soil samples were finely ground with a mortar and pestle. Approximately 0.1 g of the sample was weighed and placed in the analyzer chamber where sample combustion allowed for the measurement of the concentrations of gaseous C and N emitted from the soil sample.

A PROC *t*-test was performed on the total C, total N, sequential P, pH, and soil moisture tundra data to determine if there were differences between *P. aristata* tundra soils and *P. engelmannii* tundra soils (SAS Institute, 1996). This was a conservative way to assure there were no differences between tundra soils upslope from the two krummholz species tree islands. Once no difference was found ($P > 0.10$), a PROC GLM one-way ANOVA was performed on each of the measurements using SAS (SAS Institute, 1996). Levels of significance ($P < 0.05$) were examined for each measured soil nutrient with respect to *P. aristata* krummholz, *P. engelmannii* krummholz, and tundra. Tukey's test (Milliken and Johnson, 1992; Steel and Torrie, 1980) was also performed when a significant *F* value was found. Additionally, a Student's one-tailed *t*-test (Brower et al., 1997) was performed on the O horizon depths to determine if *P. engelmannii* had a significantly deeper ($P < 0.05$) O horizon than *P. aristata*.

4. Results

The O horizon depth beneath *P. engelmannii* krummholz was significantly deeper ($P < 0.05$) than that of *P. aristata* ($df = 18$) (Fig. 1). There was no significant difference for soil pH ($df = 37$; $P > 0.05$). Average pH values were 6.1 ± 0.1 , 6.2 ± 0.1 , and 6.3 ± 0.1 , for *P. engelmannii*, *P. aristata*, and tundra, respectively. Although average soil moisture (% fresh weight) was not significantly different ($P > 0.05$) between sites, both *P. aristata* (9.4%) and *P. engelmannii* (11.9%) krummholz sites had slightly higher soil moisture than the tundra sites (8.6%).

Soil P fractionation pools are summarized for each site (Fig. 2) showing the general trend that for most proportions of soil P, *P. aristata* had lower concentrations than *P. engelmannii*. Despite this, total soil P did not significantly differ between sites ($P > 0.05$).

Resin Pi and Bicarb Po were significantly greater ($P < 0.05$) under *P. engelmannii* than *P. aristata* and the tundra (Table 1). When the three forms of plant available P were summed (Resin Pi + Bicarb Pi + Bicarb Po), analysis revealed *P. engelmannii* had significantly greater ($P < 0.05$) mean concentrations of labile P (Table 1). There were no significant relationships for refractory forms of soil P (NaOH Pi + NaOH Po + Sonic Pi + Sonic Po + HCl Pi +

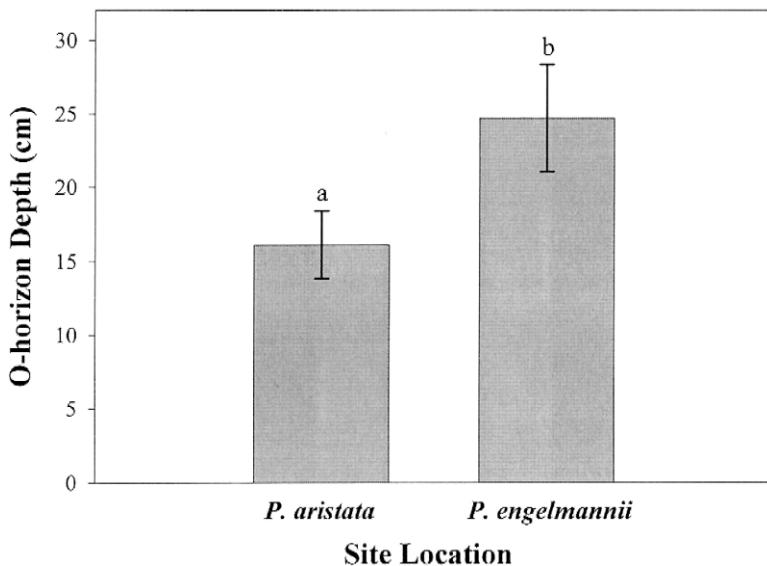


Fig. 1. Depth of the O horizon (cm) beneath krummholz patches of *P. aristata* and *P. engelmannii* on Goliath Peak, Colorado. Different letters indicate significant differences from *t*-test analysis ($P < 0.05$). Error bars represent standard error values ($n = 10$ for each site location).

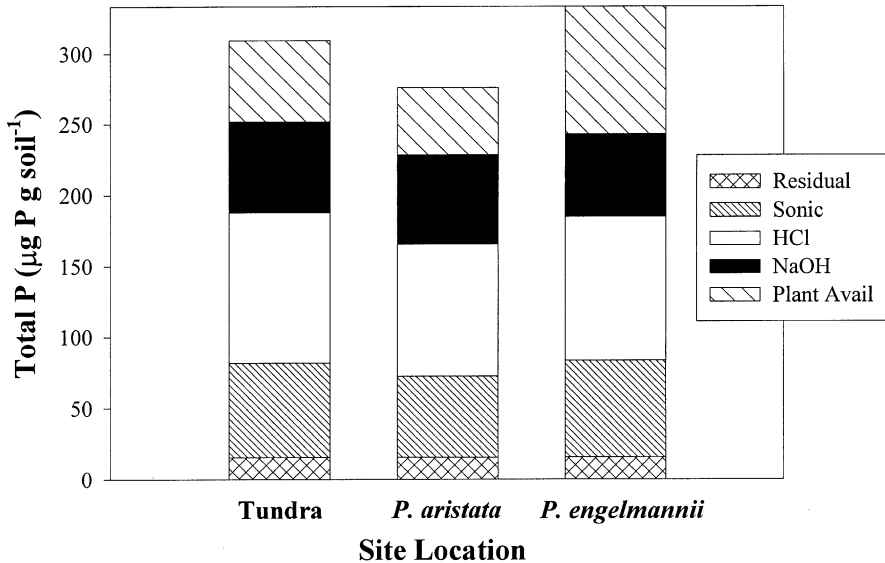


Fig. 2. Soil phosphorus fractions for *P. aristata* and *P. engelmannii* krummholz, and for adjacent undisturbed tundra.

Residual P), nor were there significant relationships for the individual pools of refractory P ($P > 0.05$) (Table 2).

When the distribution of soil P was divided into biological and geochemical pools for each site, mean concentrations of biological P (Bicarb Po + NaOH Po + Sonic Po) represented approximately one-third of total P. Although the proportion of biological P was slightly higher for *P. engelmannii* (36%) compared to tundra (32%) and *P. aristata* (31%), there was no significant difference ($P > 0.05$) between sites. Likewise, there was not a significant difference between geochemical P ($P > 0.05$).

Total soil N and total soil C concentrations did not differ significantly between sites ($P > 0.05$). The average values of total soil N were 1.6 ± 0.2 , 1.9 ± 0.3 , and 2.3 ± 0.3 mg N g⁻¹ soil for *P. aristata*, tundra, and *P.*

Table 1

Mean (and standard error) plant available soil phosphorus fractions and total plant available soil phosphorus ($\mu\text{g P g}^{-1}$ soil) for each site on Goliath Peak, Colorado

Site	Resin Pi	Bicarb Pi	Bicarb Po	Total plant available
Tundra	15.35 ± 1.49^a	5.03 ± 0.46^a	37.24 ± 3.21^a	57.62 ± 4.37^a
<i>Pin. aristata</i>	15.66 ± 1.76^a	5.02 ± 1.17^a	26.78 ± 5.34^a	47.46 ± 7.05^a
<i>Pic. engelmannii</i>	23.71 ± 2.63^b	7.20 ± 1.20^a	59.25 ± 9.74^b	90.16 ± 12.28^b

Different letters within each column indicate significant differences in mean concentrations from Tukey's test ($P < 0.05$).

Table 2
 Mean (and standard error) refractory soil phosphorus fractions ($\mu\text{g P g}^{-1}$ soil) for each site on Goliath Peak, Colorado

Site	NaOH Pi	NaOH Po	HCl Pi	Sonic Pi	Sonic Po	Residual Pi
Tundra	28.85 \pm 3.45	34.98 \pm 4.32	106.21 \pm 12.87	40.36 \pm 3.92	25.81 \pm 2.60	15.60 \pm 0.60
<i>Pin. aristata</i>	26.12 \pm 4.22	36.56 \pm 7.44	93.00 \pm 11.51	34.73 \pm 6.01	22.48 \pm 3.69	15.54 \pm 0.31
<i>Pic. engelmannii</i>	25.44 \pm 2.90	32.40 \pm 5.39	101.62 \pm 21.20	40.27 \pm 5.81	27.64 \pm 3.30	15.67 \pm 1.08

Table 3

Soil C:N:P ratios for each site on Goliath Peak, Colorado, where P is used for basis of comparison

Site	C	N	P
Tundra	104	6	1
<i>Pin. aristata</i>	107	6	1
<i>Pic. engelmannii</i>	123	7	1

engelmannii, respectively. Average values of total soil C in the mineral soil were 29.4 ± 3.4 , 32.3 ± 6.5 , and 41.0 ± 4.9 mg C g⁻¹ soil for *P. aristata*, tundra, and *P. engelmannii*, respectively.

Although there were no significant differences for soil C and N, their ratios varied consistently with respect to P, with highest C:P ratios in the vicinity of *P. engelmannii*, intermediate under *P. aristata*, and lowest in the tundra (Table 3). Additionally, C:N ratios were the same for *P. aristata* and *P. engelmannii* krummholz (18:1), and similar for the tundra (17:1).

5. Discussion and conclusions

The significantly higher plant available P concentrations below *P. engelmannii* krummholz compared to both *P. aristata* krummholz and the adjacent tundra is evidence that a krummholz species effect is present in the alpine tundra on Goliath Peak, Colorado. Although differences in soil nutrients could be a result of heterogeneous soil conditions prior to krummholz establishment, we suggest that a more plausible explanation is that *P. engelmannii* tree islands are altering the soil chemistry of the alpine predominantly by their existence and growth in this alpine environment.

We propose that the differences in plant available forms of soil P in this study were due, in part, to the presence of deep O horizons (organic litter layer) that are generated by krummholz tree forms. Although geochemical and biological processes control P availability and distribution, the plant available pool is influenced predominately by biological processes and it is mostly derived from soil organic matter (SOM) (Ballard, 1980; Cross and Schlesinger, 1995). The soils sampled in the undisturbed tundra had a 0–1 cm deep O horizon, while the conifer needles and additional organic matter trapped beneath *P. aristata* krummholz (5–26 cm deep) and *P. engelmannii* krummholz (12–52 cm deep) provide a significant organic reservoir containing nutrients, such as P, that accumulate above the mineral soil. Holtmeier and Broll (1992) concluded that leaching seems to be confined to tree islands and not the wind-exposed tundra. We found a significantly deeper O horizon beneath *P. engelmannii* krummholz

than under both *P. aristata* krummholz (Fig. 1) and the surrounding tundra, presenting a correlation between litter layer and plant available P concentration beneath *P. engelmannii* krummholz.

Because of the increased O horizon depth beneath *P. engelmannii* compared to *P. aristata* and the tundra, it is curious that there was not a significant difference in soil C concentrations among these habitats. However, Pauker and Seastedt (1996) provide evidence that the tree islands and/or their respective soil biota consume soil C. This may account for the lack of difference in soil C between habitats in spite of increased C inputs from the krummholz litter layer.

We were surprised that *P. aristata* krummholz soils did not have higher concentrations of plant available P when compared to tundra soils (Table 1). While *P. aristata* had a significantly deeper O horizon than the tundra, levels of plant available soil P were not significantly different from those of the tundra. This similarity in plant available P, as well as the differences in plant available P between *P. aristata* and *P. engelmannii* krummholz, may be explained by varying foliar nutrient concentrations between the two krummholz species.

Barrick and Schoettle (1996) compared foliar nutrients of conifer species of krummholz and lower elevation trees in the Colorado Front Range and found that *P. engelmannii* krummholz had lower foliar P (0.11% dry weight) than that of *P. aristata* krummholz (0.16% dry weight). Therefore, the lower concentration of plant available soil P under *P. aristata* krummholz (vs. *P. engelmannii* and the adjacent tundra) may be due to *P. aristata* absorbing and retaining more soil P for foliar tissue than *P. engelmannii*. Under this scenario, *P. aristata*, which lives up to 2100 years in the Colorado Front Range (Brunstein and Yamaguchi, 1992), may be a very long-term sink for P.

Although a deeper O horizon was present over the mineral soils with the highest plant available P concentrations beneath *P. engelmannii*, soil moisture and pH did not significantly differ between krummholz species and tundra. This result was surprising given the deeper, acidic conifer O horizon below both tree island species when compared to the tundra.

While plant available forms of soil P significantly differed in this study, total soil P did not differ significantly. Soil P concentrations in this study (275–333 $\mu\text{g P g}^{-1}$) were lower than those 50 km north at Niwot Ridge (Pauker and Seastedt, 1996; Parker and Sanford, 1999), where total soil P concentrations ranged from 988 to 1127 $\mu\text{g P g}^{-1}$ soil (Parker and Sanford, 1999). Although Niwot Ridge and Goliath Peak both lie within the Colorado Front Range, variations in parent material between these two mountains, as well as the degree of weathering of parent material, could account for the substantial difference in soil status and nutrients between these two sites. Both Niwot Ridge and Goliath Peak have similar bedrock and age, but Goliath Peak has more exposed bedrock (Nel Caine, personal communication). Hence, the lower soil P values on Goliath Peak compared to Niwot Ridge is likely the result of more exposed, and therefore more weathered, parent material.

There were no significant differences for total soil C and N in this study. It is surprising that total C and total N values were not more closely related to soil P because P is arguably the dominant element controlling C and N immobilization (Paul and Clark, 1989). In fact, soil C and N appear to be acting somewhat independently of soil P. Where P is at least co-limiting the system, as Bowman et al. (1993) experimentally demonstrated, a converging C:P ratio should be observed where the P concentration should increase proportionally with C gains (McGill and Cole, 1981). However, this is not the case with this study (Table 3).

Future studies should focus on decomposition rates and the chemical content of krummholz litter, N availability, soil microbial activity, and species production rates to determine further the causes of the soil nutrient differences between krummholz species that have been found in this study. Furthermore, in order to understand the effects of krummholz tree forms in the alpine tundra, future krummholz comparisons should specifically compare species, as well as understand that general conclusions regarding krummholz biogeochemistry in the alpine may not hold for cross site comparisons.

The findings of this study suggest that these two krummholz tree species have quite different effects on soils in this alpine tundra ecosystem. While *P. engelmannii* krummholz is significantly changing soil chemistry as it passes over soils in this ecotone, *P. aristata* krummholz appear to be successfully inhabiting the ecotone without significantly changing the soil chemistry. The significantly larger organic litter layer below *P. engelmannii* krummholz is a major nutrient source that may be providing more plant available P than the less deep litter below both *P. aristata* krummholz and the adjacent tundra. Additionally, the lower plant available P in mineral soils under *P. aristata*, compared to *P. engelmannii*, may be accounted for by the requirement for higher foliar P in *P. aristata* compared to *P. engelmannii*. The plant available soil P concentrations beneath these two krummholz species are significantly different, raising the spectra that woody plants above treeline on Goliath Peak both modify the soil and utilize soil nutrient fractions in very different ways.

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References

- Ballard, R., 1980. Phosphorus nutrition and fertilization of forest trees. In: Khasawneh, F.E., Sample, E.C., Kamprath, E.J. (Eds.), *The Role of Phosphorus in Agriculture*. Am. Soc. of Agronomy, Madison, WI, USA, pp. 763–804.
- Barrick, K.A., Schoettle, A.W., 1996. A comparison of the foliar nutrient status of elfinwood and symmetrically formed tall trees, Colorado Front Range, USA. *Can. J. Bot.* 74, 1461–1475.
- Benedict, J.B., 1984. Rates of tree-island migration, Colorado Rocky Mountains. *Ecology* 65, 820–823.
- Birkeland, P.W., 1984. *Soils and Geomorphology*. Oxford Univ. Press, New York, NY, USA.
- Bowman, W.D., Theodose, T.A., Schardt, J.C., Conant, R.T., 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* 74, 2085–2097.
- Brower, J.E., Zar, J.H., von Ende, C.N., 1997. *Field and Laboratory Methods for General Ecology*. 4th edn. McGraw-Hill, New York, NY, USA.
- Brunstein, F.C., Yamaguchi, D.K., 1992. The oldest known Rocky Mountain bristlecone pines (*Pinus aristata* Engelm.). *Arct. Alp. Res.* 24, 253–256.
- Burns, S., 1980. *Alpine soils of the Indian Peaks, Colorado*. Dissertation, Dept. of Geological Sciences, University of Colorado, Boulder, CO, USA.
- Cross, A.F., Schlesinger, W.H., 1995. A literature review and evaluation of the Hedley fractionation: applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. *Geoderma* 64, 197–214.
- Hedley, M.J., Steward, W.B., Chauhan, B.S., 1982a. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Sci. Soc. Am. J.* 46, 970–976.
- Holford, I.C.R., 1997. Soil phosphorus: its measurement, and its uptake by plants. *Aust. J. Soil Res.* 35, 227–239.
- Holtmeier, F.-K., 1987. Der Baumwuchs als klimaökologischer Faktor an der boeren Waldgrenze. *Munstersche Geogr. Arb.* 27, 145–151.
- Holtmeier, F.-K., Broll, G., 1992. The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arct. Alp. Res.* 24, 216–228.
- Jenny, H., 1941. *Factors of Soil Formation*. McGraw-Hill, New York, NY, USA.
- Körner, C., 1989. The nutritional status of plants from high altitudes. *Oecologia* 81, 379–391.
- Lajtha, K., Driscoll, C., Jarrell, W., Elliott, T., 1997. Soil phosphorus characterization and total element analysis. In: Robertson, P., Coleman, D., Bledsoe, C., Sollins, P. (Eds.), *Standard Soil Methods for Long-term Ecological Research*, Oxford Univ. Press, New York, NY, USA.
- LECO, 1993. *Simultaneous carbon, hydrogen, and nitrogen analysis*. LECO, St. Joseph, MI, USA.
- Marr, J.W., 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology* 58, 1159–1164.
- McGill, W.B., Cole, C.V., 1981. Comparative aspects of cycling organic C, N, S, and P through soil organic matter. *Geoderma* 26, 267–286.
- Milliken, Johnson, 1992. *Analysis of Messy Data, Vol. I: Designed Experiments*. Chapman and Hall, New York.
- Parker, E.R., Sanford Jr., R.L., 1999. The effects of mobile tree islands on soil phosphorus concentrations and distribution in an alpine tundra ecosystem on Niwot Ridge, Colorado Front Range, USA. *Arct. Antarct. Alp. Res.* 31 (1), 16–20.
- Pauker, S.R., Seastedt Jr., T.L., 1996. Effects of mobile tree islands on soil carbon storage in tundra ecosystems. *Ecology* 77, 2563–2567.
- Paul, E.A., Clark, F.E., 1989. *Soil Microbiology and Biochemistry*. Academic Press, San Diego, CA, USA.

- Prokopy, W.R., 1996. QuikChem Method 10-115-01-1-B: determination of orthophosphate by flow injection analysis colorimetry. Lachat Instruments, Milwaukee, WI, USA, pp. 1–19.
- SAS Institute, 1996. SAS Procedures Guide, Version 6.19. SAS Institute, Cary, NC, USA.
- Schachtman, D.P., Reid, R.J., Ayling, S.M., 1998. Phosphorus uptake by plants: from soil to cell. *Plant Physiol.* 116, 447–453.
- Schlesinger, W.H., 1991. *Biogeochemistry: An Analysis of Global Change*. Academic Press, New York, NY, USA.
- Shaw, C.F., 1930. Potent factors in soil formation. *Ecology* 11, 239–245.
- Smith, B.F.L., Bain, D.C., 1982. A sodium hydroxide fusion method for the determination of total phosphate in soils. *Commun. Soil Sci. Plant Anal.* 13, 185–190.
- Steel, R.G.D., Torrie, J.H., 1980. *Principles and Procedures of Statistics*. 2nd edn. McGraw-Hill, New York, NY, USA.
- Tiesson, H., Moir, J.O., 1993. Characterization of available P by sequential extraction. In: Carter, M.R. (Ed.), *Soil Sampling and Methods of Analysis*. Lewis Publishers, Ann Arbor, pp. 75–86.
- Topp, G.C., 1993. Soil Water Content. In: Carter, M.R. (Ed.), *Soil Sampling and Methods of Analysis*. Lewis Publishers, Ann Arbor, pp. 541–543.