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SOIL IMPACTS OF BRISTLECONE PINE (*PINUS LONGAEVA*) TREE ISLANDS ON ALPINE TUNDRA, CHARLESTON PEAK, NEVADA

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Soils are modified by the presence and growth of vegetation throughout biomes and across latitudes (Jenny 1941, Callaway and King 1996). In addition to the presence of vegetation, species type can modify soil nutrients and affect colonizing biota (Walker and Chapin 1987, Callaway et al. 1991, Hobbie 1992). Patches of vegetation in open or relatively stressful environments, such as low-elevation deserts or high-elevation alpine-tundra, can facilitate biotic activity (Bertness and Callaway 1994, Schlesinger et al. 1996) by acting as fertile islands that elevate resources such as soil nutrients and organic matter (Garner and Steinberger 1989, Jackson and Caldwell 1993, Bolling and Walker 2002).

Fertile tree islands in high-elevation alpine ecosystems provide habitat for a variety of life-forms (Seastedt and Adams 2001) and can potentially modify and enrich their vegetation-poor surroundings (Burns 1980, Holtmeier and Broll 1992, Malanson and Butler 1994). However, soil physical and chemical properties are not always altered by the existence of tree islands (Parker and Sanford 1999, Shiels and Sanford 2001). For example, Shiels and Sanford (2001) found that soil alterations might be species specific, as *Picea engelmannii* Parry ex Engelm. (nomenclature follows Hickman 1993) but not *Pinus aristata* Engelm. (Rocky Mountain bristlecone pine) altered soil nutrients. Modifications to belowground environments by vegetation may therefore provide more favorable refuge and heightened resources below some tree species and not others, thereby producing habitat heterogeneity that may ultimately affect ecosystem function.

Pinus longaeva D.K. Bailey (Great Basin bristlecone pine), well known for its pronounced longevity (Schulman 1958, LaMarche 1969), occurs above Great Basin treelines as islands in a krummholz (dwarfed and gnarled) growth form. Stands of *P. longaeva* are common on the upper elevations of Charleston Peak, Nevada, particularly on south-southwestern–facing slopes, and krummholz-shaped tree islands formed by *P. longaeva* exist above the treeline (the area where trees are ≥4 m tall; Arno and Hammerly 1984). While some krummholz life-forms move across mountainsides (Marr 1977, Benedict 1984), the lack of adventitious roots makes migration of *P. longaeva* krummholz unlikely (A. Shiels personal observation, R. Lanner personal communication). This study examines the influence of *P. longaeva* krummholz tree islands on soil chemical and physical properties just above treeline on Charleston Peak. Because of the presence of a substantial litter layer and the greater potential for snow and particle capture associated with the krummholz growth form (Tranquillini 1979, Hadley and Smith 1987, Barrick and Schoettle 1996), we expected that soil moisture and soil nutrients such as nitrogen (N) and phosphorus (P) would be higher, that pH values would be lower, and that soil particle size would be smaller beneath tree islands on Charleston Peak than in open tundra.

The study was conducted above treeline on Charleston Peak (elevation 3632 m asl), located in the Spring Mountains in southern Nevada (36°25′N, 115°63′W), approximately 56 km northwest of Las Vegas. The study site, at 3495 m, was a 150 × 120-m area (1.8 ha) on a

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southwest-facing ridge where *P. longaeva* tree islands are present. We chose this area because of its close proximity to a trail ascending Charleston Peak and because the density of krummholz tree islands was large enough to select a sufficient number of individuals to sample. Treeline was approximately 50 m in surface distance and 15 m in elevation below the lower edge of the sampling area. Soils have not been previously classified at this site, but the parent material is dominated by carbonates (D. Merkler personal communication), and there is minimal soil formation. Estimated slope was 15%. Based on the physiognomy of the tree islands, prevailing winds appeared to be from the southwest. Mean annual precipitation at the nearest weather station (Kyle Canyon, 2135 m) is 780 mm with 10–35 m of snow each winter (S. Brittingham personal communication). Mean annual temperatures at Kyle Canyon range from –20° to +32°C (mean = 8°C). Our study site receives more snow and has cooler temperatures than Kyle Canyon (Brittingham personal communication).

On 26 October 2001, densities of *P. longaeva* trees and seedlings (individuals <50 cm tall) were determined by delineating 3 randomly chosen 10×10-m plots within the study area and counting all live individuals. The only other noticeable vegetation at the site during the sampling period consisted of a few *P. flexilis* James seedlings.

We collected soil and leaf litter samples, when present, from 10 tree islands and 10 tundra sites that were randomly selected within the study area. Only tree islands >13 m^2 were used. Tundra sites were 3 m uphill from the upslope edge of each of the 10 tree islands and at least 1.5 m from any adjacent trees. Tundra sites were free of vegetation and dominated by flat rocky surfaces with little exposed soil.

We measured litter layer (O-horizon) depth beneath each tree island in a 20×20-cm area and sampled litter layer (representing recently senesced leaves) for nutrient analyses. Tundra sites were free of litter and frequently consisted of exposed limestone rock. Live needles, both young (distal tip) and old (5th cohort from distal tip), were sampled from 4 randomly chosen tree islands ($n = 8$ samples). We sampled mineral soil with a trowel to 10-cm depth in the same 20×20-cm area used for litter collection at each tree island and in a similar set of plots in the tundra site ($n = 20$ samples).

Rocks and roots were removed by passing the soil through a 2-mm mesh sieve.

We determined available N (NH_4^+ and NO_3^-) under tree islands and in tundra by 2 M potassium chloride (KCl) extraction techniques followed by colorimetric analysis (Binkley and Vitousek 1989, Alpkem Corporation 1992). Potential nitrogen mineralization and potential nitrification rates were determined by first extracting subsamples of fresh soil (pre-incubation) with 2 M KCl 15 hours after field collection (refrigerated until extraction; Binkley and Vitousek 1989). A 2nd set of soil subsamples was incubated (post-incubation) in loosely capped containers for 14 days at $20 \pm 1.5°C$ (Kandeler 1996) prior to 2 M KCl extraction, with water added dropwise as needed to maintain the initial mass of each sample. Rates of potential N mineralization and nitrification were determined by subtracting pre-incubation from post-incubation values. Total Kjeldahl N and total Kjeldahl P were determined by digesting soil samples in acid prior to colorimetric analysis (Alpkem Corporation 1992).

We determined available P using the first 3 sequential extractions of the Hedley fractionation (Hedley et al. 1982). These 3 extractions, constituting the forms of P most available to plants, included resin P (extracted with anion-cation exchange resin strips) and bicarb P_i (inorganic P) and bicarb P_o (organic P; both extracted with sodium bicarbonate solutions). The sequential extractions were used to determine available P because they closely mimic plant-soil interactions (Cross and Schlesinger 1995) and because they allow comparison with past tree island studies that implemented the same technique (Parker and Sanford 1999, Shiels and Sanford 2001). Resin fractionation simulates the ion uptake action of plant roots, providing a strong sink for P released into solution (Lajtha et al. 1997), while the bicarbonate extraction is able to mineralize additional soil P through mimicking the respiration activity of plant roots (Cross and Schlesinger 1995, Lajtha et al. 1997).

In addition to analyzing soil nutrients, we analyzed soil samples for gravimetric soil moisture (% dry mass; Topp 1993), soil organic matter (SOM; % loss on ignition; Nelson and Sommers 1996), pH (1:1 paste of soil and deionized water; Hendershot and Lalande 1993), and particle size (Scheldrick and Wang 1993). We ground litter and foliar samples and passed

TABLE 1. Soil properties (mean ± standard error) in tree islands and tundra on Charleston Peak, Nevada. *P*-values of each *t* test are noted with * when significantly different (*P* < 0.05). Results of MANOVA showed a significant treatment effect (Wilks' Lambda = 0.047; *F* = 7.29; Num. d.f. = 14, Den. d.f. = 5; *P* = 0.0192).

Variable	Tree islands (*n* = 10)	Tundra (*n* = 10)	*P*-value
Total N ($\mu g \cdot g^{-1}$)	3231.66 ± 538.03	1574.14 ± 200.34	0.0200*
Available N ($\mu g \cdot g^{-1}$)	2.55 ± 1.14	1.18 ± 0.42	0.0735
NH_4^+ ($\mu g \cdot g^{-1}$)	1.65 ± 0.55	0.65 ± 0.17	0.0998
NO_3^- ($\mu g \cdot g^{-1}$)	0.90 ± 0.59	0.53 ± 0.25	0.5740
N Mineralization ($\mu g \cdot g^{-1}$ soil d^{-1})	0.29 ± 0.10	0.33 ± 0.08	0.7700
Nitrification ($\mu g \cdot g^{-1}$ soil d^{-1})	0.347 ± 0.10	0.345 ± 0.10	0.9877
Total P ($\mu g \cdot g^{-1}$)	661.14 ± 50.84	607.50 ± 36.74	0.4037
Available P ($\mu g \cdot g^{-1}$)	39.42 ± 10.82	14.76 ± 1.88	0.0367*
Resin P ($\mu g \cdot g^{-1}$)	5.19 ± 0.99	2.71 ± 0.32	0.0287*
Bicarb P_o ($\mu g \cdot g^{-1}$)	13.86 ± 2.83	5.33 ± 1.02	0.0109*
Bicarb P_i ($\mu g \cdot g^{-1}$)	20.36 ± 7.29	6.73 ± 1.17	0.0814
Organic matter (%)	12.97 ± 2.03	5.79 ± 0.53	0.0030*
pH	7.46 ± 0.03	7.65 ± 0.02	<0.0001*
Moisture (%)	12.00 ± 1.00	7.00 ± 1.00	0.0017*
Sand (%)	52.63 ± 1.75	55.75 ± 1.50	0.1928
Silt (%)	43.13 ± 1.73	41.50 ± 1.35	0.4691
Clay (%)	4.25 ± 0.68	2.75 ± 0.55	0.1033

them through a 1-mm mesh before analyzing for total N, total P, and pH (litter only) using the methods described above.

A multivariate analysis of variance (MANOVA) was used to compare tree island and tundra environments for all 17 soil variables (Table 1). A significant treatment effect led to univariate (Student's *t* tests) analysis for each individual soil variable. We log-transformed total soil N, available N, and NH_4^+ to meet assumptions of equal variance and normal distribution. All analyses used SAS (SAS Institute 1996). Significance was determined at *P* < 0.05 and means are presented ± $s_{\overline{x}}$.

Tree islands create heterogeneity in the otherwise vegetation-poor tundra, and their presence has physical and chemical effects on the soils below them. Tree island density averaged 6.3 *P. longaeva* trees and 1.7 *P. longaeva* seedlings per 100 m^2. The litter layer, which averaged 10.1 ± 2.7 cm (mean ± $s_{\overline{x}}$; *n* = 10) below tree islands, provides a year-round source of organic matter and nutrients that appears to be impacting chemical and physical conditions of the soil. The litter layer also may insulate soil beneath it and contribute to the significantly higher soil moisture below tree islands compared with tundra (*P* = 0.0017; Table 1), a condition common when organic matter is elevated (Seastedt and Adams 2001). The acidic litter layer (litter pH: 5.98 ± 0.23; *n* = 5) beneath tree islands is likely causing the signifi-

cantly lower soil pH values compared with tundra soils (*P* < 0.0001), which is typical of soils beneath conifer litter (Zinke 1962).

Tree island foliar material provides an important nutrient source for biotic uptake once it is incorporated into the soil through decomposition processes. Total N of the litter averaged 1.31% ± 0.03%, and total P averaged 0.12% ± 0.02%. Unexpectedly, live needles from the youngest cohort tended to have lower N concentrations than litter, averaging 0.98% ± 0.05%, whereas total P averaged 0.15% ± 0.01% (*n* = 4). Old living needles also showed lower average N (0.88% ± 0.06%), as well as lower P (0.07% ± 0.01%; *n* = 4), than the litter samples below the tree islands. The slightly higher N (and P in the case of older needles) in the litter compared with living needles could be attributable to association with microbial organisms in the litter, such as fungi, which concentrate nutrients through the process of immobilization (Cairney 1992, Dighton 1997). Fungal mycelia were noted in the litter layer beneath tree islands during sampling, but not in tundra sites (Shiels personal observation), supporting the proposed importance of tree islands as potential habitats for other organisms (Seastedt and Adams 2001).

While differences in parent material and microbial communities may account for variable findings with regard to nutrient limitations in the alpine tundra (e.g., compare findings of

Körner 1989 to Parker and Sanford 1999), N and P have been proposed as the 2 major limiting nutrients to plant production in this type of ecosystem (Bowman et al. 1993). Thus, patches of higher N and P concentrations may distinguish particularly important areas across the mountainside for plant and animal development. Although available soil N was not significantly different beneath tree islands and in tundra ($P > 0.05$), total soil N was higher beneath the tree islands ($P = 0.020$). While NH_4^+ and NO_3^- are thought to be the most available forms of N for plants and microbes, organic N in the total soil N pool may also be a substantial N source for alpine plant uptake in this environment (Paul and Clark 1989). Total soil N is mainly derived from soil organic matter, which was significantly higher ($P = 0.0030$) beneath tree islands than in tundra sites.

The concentration of N available to plants at a given time is largely affected by soil temperature and moisture (Körner 2003). Under the controlled conditions of our 14-day incubation, there was no significant difference in N mineralization ($P > 0.05$) or nitrification ($P > 0.05$) between open tundra and tree island soils, and the available N pool was nearly entirely composed of soil NO_3^- after 14 days (98% for tree islands and 94% for tundra). These results indicate that soil microbes are able to mineralize organic N at comparable rates at both sites under the same environmental conditions.

While the majority of P in soil is derived from parent material, the plant-available portion is often derived from SOM and is the most critical for biological use (Paul and Clark 1989). Total soil P was not significantly different between tree islands and tundra ($P > 0.05$). This finding, coupled with the lack of significant difference in soil particle sizes between sites ($P > 0.05$), suggests that soil weathering and soil particle capture are similar between the tree island and tundra environments on Charleston Peak. However, the mean concentration of available soil P was approximately twice as high beneath tree islands as in tundra soils and this difference was significant ($P = 0.0376$). Of the soil fractions comprising available P, resin P ($P = 0.0287$) and bicarb P_o ($P = 0.0109$) were significantly higher in tree island soils, but bicarb P_i was not significantly different between environments despite the relatively higher mean soil values beneath tree islands

and tundra ($P > 0.05$). Microsite conditions will influence the availability of P, as higher root respiration is likely beneath the tree islands, increasing bicarb P, and the higher soil moisture and soil organic matter beneath tree islands likely increased both resin P and bicarb P (Cross and Schlesinger 1995, Lajtha et al. 1997). Shiels and Sanford (2001) also found a similar correlation between litter layer and plant-available P concentration (resin P and bicarb P_o) below tree islands and in tundra in the Colorado Rocky Mountains, supporting our hypothesis that some tree island species (and associated litter layers) can alter available P in the alpine tundra environment.

Pinus longaeva tree islands are significantly altering soils in the alpine tundra on Charleston Peak, Nevada. The presence of trees in a relatively vegetation-free alpine environment increases foliar inputs to the soil surface. Once the foliar material decomposes and is incorporated into the soil, it increases SOM and soil nutrients that are critical for plant growth and survival in this severe, high-elevation environment.

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