

Biomass distributions in dwarf tree, krummholz, and tundra vegetation in the alpine treeline ecotone

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Abstract: Alpine treeline ecotones are expected to respond to climate change with shifts in biomass patterns and carbon dynamics; however the nature of these shifts and the current structure of carbon storage at treeline remain poorly understood. Biomass at treeline sites in Glacier National Park, Montana was measured in different aboveground carbon pools. Notably large proportions of biomass were recorded in compartments of dead material (~64% in upright tree cover, ~82% in krummholz). The storage of proportionally so much carbon in dead material complicates predictions of alpine treeline response to climate change, given the expectation of increased respiration losses through decomposition in a warmer climate. Although conventional belief holds that treeline advance will result in sequestration of carbon as tundra is replaced by trees, carbon release by decomposition may deviate from this expectation. This work represents a descriptive study that highlights the importance of conducting similar work at broader spatial scales and in more varied locations to further determine the magnitude and extent of its implications.

Key words: alpine tundra, carbon, climate change, decomposition, timberline

Introduction

Carbon sequestration is a globally important ecosystem service that varies among different ecosystems (Nelson *et al.*, 2009; Buckingham 2014). Climate change is expected to alter the spatial distribution of ecosystems, which in turn will affect carbon storage and sequestration (Wu *et al.*, 2013a; Wu *et al.*, 2013b). This is likely to be particularly true of complex landscapes with shifts between starkly different vegetation types over short distances. One such landscape can be found at alpine treelines, where subalpine forest transitions to alpine tundra (Holtmeier 2009). Climate imposes a broad upper limit for tree reproduction and growth in these environments, leading to an overall gradient effect from upright trees to tundra with increasing altitude; however these factors are also constrained by pre-existing geomorphology and modified by dynamic processes including wind, snow accumulation and redistribution, animal activity, and feedbacks with existing patterns of vegetation (e.g. Hiemstra *et al.*, 2006; Butler *et al.*, 2007; Malanson *et al.*, 2007; Holtmeier 2009; Holtmeier and Broll 2010; Elliott 2011; Malanson *et al.*, 2011). The result of these diverse and interrelated factors is a highly complex landscape, the changing structure of which remains relatively poorly understood.

In many locations, clear evidence is already present of treeline response to recent anthropogenic climate warming through shifts in their location, density, and biodiversity (Juntunen *et al.*, 2002; Kullman 2002; Alftine *et al.*, 2003; Klanderud and Birks 2003; Holtmeier and Broll 2005; Walther *et al.*, 2005; Kullman 2007; Shiyatov *et al.*, 2007; Hallinger *et al.*, 2010; Rundqvist *et al.*, 2011; Elliott 2012). It has been hypothesized that the greater aboveground carbon storage of alpine forest over tundra will lead to a net increase in carbon storage as treelines change and advance to higher altitude in a warming climate (Kupfer and Cairns 1996; Zhang and Welker 1996; Steltzer 2004); however research on advancing polar treelines in

Alaska has suggested that these gains may be offset by losses to carbon storage below ground (Wilmking *et al.*, 2006). Although alpine and polar treelines exhibit many similarities with regard to their driving forces and potential results, they also differ in key aspects such as soil depth. It is therefore important to determine in greater detail how much biomass and carbon are present and in what component pools of the ecotone they are distributed so accurate assessments can be made, both of current states and future potential (e.g. Wilson 1994; Kammer *et al.*, 2009).

To this end, this study sought to explore and inventory the manner in which carbon is stored in different structural components and vegetative cover types at the alpine treeline ecotone in Glacier National Park, Montana, USA. The main objective of the study was to determine biomass per unit area (g m^{-2}) for each main aboveground component pool of the three vegetation types characteristic of alpine treelines: upright dwarf trees, krummholz, and open tundra. In order to gain an understanding of carbon distribution relevant to treeline dynamics, we focused on variation within these cover types and their component carbon pools. The work detailed here is a descriptive study that highlights a critical gap in our understanding of alpine treeline dynamics in the context of global climate change, and calls for additional research on biomass distribution at treelines worldwide. In addition to exploring the overall structure of biomass distribution at treeline, the specific expectation that tree and krummholz cover types store carbon in greater quantity than tundra was tested.

Background

Given current interest in feedbacks of carbon dynamics and climate change, recent research has addressed carbon flux in several environments (e.g. Wieser *et al.*, 2005; Wieser and Stohr 2005; Blanken *et al.*, 2009; Hagedorn *et al.*, 2010), including carbon storage in ecosystem

compartments (e.g. Michaelson *et al.*, 1996; Dai *et al.*, 2002; Lal 2005; Li *et al.*, 2010; Hertel and Schöling 2011). Remote mountain environments have received relatively little attention and remain poorly understood regarding their capacity to store and exchange carbon, but alpine ecosystems differ from lower elevations (Prichard *et al.*, 2000; Zimmermann *et al.*, 2010; Moser *et al.*, 2011). In addition to their remoteness, spatial patterns of carbon storage in alpine forests and meadows exhibit a high degree of spatial heterogeneity relative to many ecosystems, complicating their study. In particular, carbon content in the O-horizon of soils at alpine treeline differs considerably between land cover types, and remains too variable to allow the isolation of any spatial trends in mineral horizons (Sanscrainte *et al.*, 2003). Treeline soils also have the potential to release carbon through increased decomposition rates more quickly than new plant growth is able to capture and store carbon (Hagedorn *et al.*, 2010).

Treeline carbon dynamics are particularly important to overall ecotone dynamics according to the carbon sink limitation hypothesis, which proposes that the primary limit on tree growth at treeline is the prevention by low temperatures of trees from applying stored non-structural carbohydrates to biomass growth (Hoch and Körner 2003; Körner 2003; Piper *et al.*, 2006; Bansal and Germino 2008; Hoch and Körner 2009; Holtmeier 2009). Given the complex and distinctive environments found at treeline, however, gaps remain in current knowledge of how carbon is distributed there. In comparison to tundra, tree cover stores considerably more biomass above ground, exhibits a higher carbon flux, and a lower albedo. Within tree cover at treeline, however, the ecotone includes stunted upright trees, fragmented patches, and a twisted, prostrate growth form called krummholz. Krummholz in particular exhibits a considerably different canopy structure from upright trees, storing a greater proportion of biomass toward the top of its canopy as opposed to the 'cone-shaped' nature of biomass distribution in upright

coniferous trees. This architecture forms a dense mat that shelters the ground underneath, potentially altering temperature and soil profiles under them (Cairns 2005). These differences scale up to impact regional and global atmospheric carbon in diverging ways (Thompson *et al.*, 2004).

Below ground, rates of decomposition in alpine soils are limited largely by temperature, and climate warming scenarios include the potential for some of the greatest changes in carbon flux to occur at high elevations and latitudes (Osono and Takeda 2006; Tewksbury and Van Miegroet 2007). At treeline, soil carbon storage may be determined not only by vegetation productivity and characteristics but also by underlying patterns of soil depth and parent material (Sanscrainte *et al.*, 2003). For these reasons there remains a need for more detailed research on soil carbon dynamics at treeline.

Methods and materials

Study area

We chose Glacier National Park, Montana (GNP) for this study as it provides a favorable laboratory for conducting treeline research for a combination of reasons (Fagre 2009). Complex glacial topography has a large influence on local climate from regional to micro scales, resulting in a very diverse treeline environment so numerous landscape types can be easily studied and compared (Cairns 1995; Walsh *et al.*, 2009). Additionally, treelines have remained relatively pristine since the Park's creation in 1910, limiting human modifications relative to many other possible study locations (Butler *et al.*, 1994; Resler 2006). Despite this, road and foot access to a variety of sites is uncommonly feasible for treeline elevations in the American Rocky Mountains.

Spanning the continental divide, the west side of the Park is predominantly influenced by maritime air masses, whereas the east side is more continental (Finklin 1986). Vegetation at treeline in GNP is dominated by two tree species; subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) (Walsh *et al.*, 2009). Together these two species, especially the former, are the most prominent tree species at treelines across North America, ranging through most of the American and Canadian Rockies as well as the Cascade and Coastal ranges (Holtmeier 2009). These advantages make GNP a favorable place to conduct treeline research, and the diversity of the Park's landscapes mean that a wide range of differences and factors can be studied with relative ease. This diversity imparts a greater potential relevance to treelines in other locations; however the intense variability of treeline environments creates a need for more detailed research to be conducted at various sites to determine the degree of spatial variability in research results.

Site selection

We selected treeline sites believed most likely to be caused directly by the altitudinal climate gradient rather than local orographic or terrain-based effects (e.g, local rain shadows and slope angle, sensu Butler *et al.*, 2007; Holtmeier 2009) and where all three cover types were present. We sampled in seven locations distributed across the east side of the Park and two just outside the Park's boundaries in the Blackfeet Indian Reservation: Logan Pass, Preston Park/Siyeh Pass, Baring Creek, Scenic Point, Lunch Creek, Lee Ridge, Apikuni Falls, and Divide and White Calf Mountains (in the Reservation) (Fig. 1, Table 1). Sites at Logan Pass and Lunch Creek were near enough the continental divide to potentially exhibit wetter conditions than other sites, with the former perched on the divide. Twenty site pairs were selected in each of

three cover types: dwarf trees (Fig. 2), krummholz (Fig. 3), and open tundra (Fig. 4) for a total of 60 pairs with two subsample points each. At each location, site pairs were chosen visually to be representative of cover types present and involve relatively homogenous patches of a single cover type to ensure sampling consistency. Between study locations, sites and cover types were distributed as evenly as possible but were dependent on land cover present, as the primary goal was to obtain data representative of the studied cover types. The number and location of the sites throughout GNP were chosen as a compromise between qualitatively representing the landscapes and climate regimes present in the park, and feasibility of access. The spatial patterns and rugged locations of treeline environments in GNP precluded the use of conventional ecological approaches such as random or gridded sampling design. Site-level methods (detailed below) introduced a local random element to where measurements were taken at each location. Average elevation across treeline sample sites was approximately 2100 meters, which is consistent with previous research (e.g. Cairns and Malanson 1997; Cairns and Malanson 1998).

Field and lab methods

To inventory aboveground biomass distribution at treeline we adapted the sampling and estimation methods proposed by Brown et al. (1982) since destructive sampling was both physically unfeasible and counter to National Park policy. These methods, detailing biomass estimation for the American West, present a comparatively efficient and practical way to gather biomass data without a need for intense destructive sampling. The methods described by Brown et al. (1982) were originally intended for estimation of fire fuel load in the forests of the western United States, but the resulting data in the form of biomass per unit area are equally applicable to the goal of understanding biomass distribution (e.g. Malanson and Butler 1984; 1991). The

method established equations to relate basal area to biomass for small trees (which we recreated for krummholz), a planar intercept method for dead stems, and destructive methods for subsamples of litter and herbaceous biomass that are extended to multiple areas by visual assessment of cover.

At all sites we recorded elevation, aspect, and slope. At dwarf tree and krummholz sites (which were generally patchy in occurrence amidst a matrix of alpine tundra), two interior points were chosen by random number generation along a transect running along the long axis of the patch and approximately crossing its center (edges might differ; Cairns 2005; Mori and Hasegawa 2007). At each sample point we described a circle of 57-cm radius (from Brown *et al.*, 1982, as 1/4000 of an acre) (Fig. 5). We recorded the basal area and height of trees in the circle, and downed woody material intersecting a vertical sampling plane along a random direction radius of the circle was grouped into size classes. The relatively short length of the transect for measuring downed woody material was a necessary modification from Brown *et al.*'s methods owing to the extremely high density of dead material along the ground in many cases as well as the small size of debris (most ranging from zero to 3 cm in diameter); the use of a longer transect was deemed unnecessary and unfeasible. The proportional area of the sampling circle covered by litter, herbaceous cover, and bare rock was visually estimated. For biomass measures, litter and herbaceous plants were collected in all three cover types (where present) from separate 10 x 10 cm quadrats (12 of 40 for herbs and 34 of 40 for litter) and scaled the resulting weight relative to the visually estimated area. We calculated tree biomass per unit area based on size class-weight relationships given in Brown *et al.* (1982). For all cases where material was present but too small to measure (e.g., a single twig), we estimated the biomass at 10% of the lowest biomass recorded for that category.

At krummholz sites, we recorded stems originating within the area. In most sites we chose one plant for destructive sampling to substitute for the relations for trees created by Brown et al. (1982). The stem was cut, measured and weighed, and a small woody sample kept. The woody sample's density was measured after oven drying. We took a separate sample of the plant's crown needle mass and later dried and weighed it. This destructive sampling was done for krummholz and not dwarf trees due to the comparatively poor understanding of krummholz size/biomass relationships. Methods exist to accurately estimate tree biomass based on size characteristics; however the high variability of krummholz as a growth form meant that destructive sampling was necessary to calculate these relationships ourselves.

At tundra sites we used Brown et al.'s (1982) methods for sampling grasses and herbaceous cover in four 30- x 60-cm sampling frames evenly spaced on the circumference of a circle of 57 cm radius. We estimated relative cover within each frame for herbaceous growth and litter, and sampled both in 10- x 10-cm subareas in whichever of the four frames had the highest cover.

We deviated from the original methods in Brown et al. (1982) in order to more appropriately address the unique environments of the alpine treeline ecotone. Given the short stature and high density of treeline plants (Girardin *et al.*, 2013), the unique canopy structure of krummholz (Cairns 2005), and the desired data, we modified the sampling techniques in the field (e.g., shorter transects and smaller sampling areas, detailed above) and the calculations in the lab. The spatially smaller samples are justified given the high density of stems, especially in krummholz, but the results are still minimum estimates and the smaller samples contribute to high variance; therefore we deleted one large piece of woody debris as an outlier given the plot size (we did not see anything similar outside the sample areas in any plot). Brown et al.'s

methods were originally devised for forest ecosystems, including small diameter (2.5cm) trees and shrubs (i.e., not only dead and downed wood), and the methods used in this study for upright dwarf trees remained closest in practice to and within the size ranges of the original procedures.

To obtain mass measures, we oven dried and weighed herbaceous, litter, and krummholz wood and crown samples at 93.3° C (200° F) for a period of ~12 hours given the nature and small size of the samples. We recorded dry weights, and for krummholz wood samples we measured volume by displacement in a graduated beaker of water.

Although we attempted to measure belowground carbon, the difficulties presented by stony and impenetrable soils complicated sampling of soil and root biomass. Additionally, understanding of aboveground/belowground biomass relationships at treeline remains sparse in the literature, so that estimation of soil and root carbon would require multiple assumptions. After consideration, we decided that the uncertainty caused by these difficulties and assumptions was too great to justify further reporting and analysis of belowground carbon pools in this study.

Analysis Methods

We compartmentalized constituent biomass pools for dwarf upright tree sites into aboveground tree biomass, downed woody material, herbaceous biomass, and litter. For krummholz sites, component pools were aboveground plant biomass and litter; no herbaceous biomass was present. For open tundra sites, components were herbaceous biomass and litter.

These methods led to a complete summary in g m^{-2} of biomass in each main aboveground component pool of dwarf trees, krummholz, and open tundra. In order to explore what structural

relationships were present, we compared distributions of biomass among the different cover types and across different components using ANOVA (Excel 2010 v. 14.0).

Results

Relative biomass amounts in constituent compartments of each cover type are shown in Figure 6. Total aboveground biomass differed significantly between the dwarf tree and krummholz types versus tundra (ANOVA, $p < .001$, $F=13.619$). Although the mean biomass in stands of upright dwarf trees was nearly twice that of the dense prostrate growth form of krummholz (Table 2), the variance was high in both cover types. Tundra, by comparison, had lower and less variable biomass which matched expectation.

The division of biomass among constituent compartments measured in this study proved informative and also showed significant differences (ANOVA, $p < .001$, $F=17.04$). Standard error for all constituent carbon pools in each cover type is shown in Table 3. Within dwarf tree cover, litter biomass made up the largest component, exceeding aboveground tree biomass (1918.1 vs. 1078.1 g m⁻²). Downed woody biomass was observed to play a significant role in many dwarf tree sites, but it was irregular (the outlier mentioned above and removed from analysis measured ~120 kg m⁻²). Many dwarf tree sites contained no downed woody material, while one contained as many as nine occurrences. Dwarf tree stem occurrence ranged from zero to ten. Herbaceous cover generally occupied between zero and 20% of the sampling area, with some sites as high as 90%. In most sites, the majority of the ground cover was litter.

In krummholz cover, litter also made up a majority of the biomass due to low living material and a thick accumulation of needles, often melded into a dense mat. In contrast to the

relationship between aboveground plants, krummholz stored the most biomass as litter, with dwarf trees marginally less and tundra the lowest (ANOVA $p < 0.001$, $F=32.869$). Stem occurrence in krummholz ranged from zero to 13. Litter exceeded the biomass of living woody material by a high degree in both dwarf tree and krummholz cover. In concert with the dead woody material measurements, this suggests that a considerable majority of the carbon in both dwarf tree and krummholz areas is stored in dead material.

In tundra, herbaceous biomass made up the overwhelming majority of biomass. Only one tundra site contained measurable litter. Each cover type included at least one sample of 0 g m^{-2} , due to the patchy occurrence of bare or stony ground locations and the randomized nature of sampling.

Discussion and Conclusions

Overall, our research found a biomass distribution within the treeline ecotone that matched expectation in some ways, particularly with respect to the relative proportions of total biomass between the three cover types. At the same time, the findings highlighted more surprising patterns in the biomass structure within component pools of each cover type. A much greater proportion of carbon was stored in dead material than expected, which may have implications for treeline dynamics under climate warming scenarios.

Dwarf tree cover possessing the highest biomass density was unsurprising given the environmental gradients within the alpine treeline ecotone that relate plant growth to altitude and climate. Previous studies reported similarly high biomass of tree islands relative to alpine meadows (Prichard *et al.*, 2000; Sanscrainte *et al.*, 2003; Liptzin and Seastedt 2010), and

krummholz slightly below dwarf trees but still considerably higher than tundra (Cairns 1999). The sampling methods used in this study resulted in dwarf tree biomass possessing a particularly high degree of variability; however it is important to note that these methods deviated the least from Brown et al.'s (1982) original methods upon which all sampling methods used in this study were based. The recorded variability likely reflects the actual variability in the ecotone.

A possible explanation for the finding of krummholz possessing greater dead biomass than dwarf tree cover is that the relatively more sheltered environment beneath the krummholz canopy facilitates accumulation of litter more effectively than the more exposed ground under upright trees. This sheltering effect could reduce potential wind erosion of organic matter. Additionally, the unique canopy structure of krummholz creates lower levels of insolation and temperature within both canopy and soils, which could reduce decomposition relative to dwarf trees.

In dwarf tree cover, the high measures of litter and dead material relative to living biomass were unexpected. Prichard et al. (2000) in a similar study found much less woody debris in Washington, but their sites contrasted forests and meadows and did not include dwarf tree and krummholz sites. Krummholz showed a similar relationship, with litter accounting for considerably more biomass than krummholz above ground. These relatively high proportions of biomass in downed woody material (note outlier removal) and litter in both dwarf tree and krummholz patches have implications for response to climate change. At present, low temperatures and short growing seasons at the alpine treeline ecotone limit decomposition and cause carbon to be stored in dead plant material longer than in lower-elevation forests (cf. Prichard *et al.*, 2000; Dai *et al.*, 2002; Garcia-Pausas *et al.*, 2007). Future changes in both temperature and moisture availability could therefore alter these dynamics.

Shifts toward a warmer and drier climate, predicted to be likely in many locations, could lead to an increased risk of wildfires (Power *et al.*, 2011), and a large store of dead organic material at treeline would then represent a source of fuel, causing fire to become a more important disturbance at many treeline sites and a fast transfer of carbon to the atmosphere. Fire disturbances are infrequent at most high-latitude treeline sites and are believed to be insignificant as drivers of treeline change (Lloyd 2005), and are particularly unlikely in a monitored landscape such as Glacier N.P. However, the potential of this dead material as a fuel source may remain a noteworthy consideration as conditions change.

Increases in temperature would cause higher rates of decomposition at treeline (all else remaining equal), which again could lead to the quicker breakdown of this carbon store (Osono and Takeda 2006; Hagedorn *et al.*, 2010). An increase in moisture availability would also positively impact decomposition rates (e.g. Lu and Cheng 2009); however decreased sheltering by snow packs in the event of drier conditions would extend the effective growing season and potentially allow decomposition to take place for longer each year (O'Lear and Seastedt 1994; Brooks *et al.*, 1996). Results would therefore tend to be region- or site-specific, given the complex and variable relationships between temperature, moisture, and snowpack (Hiemstra *et al.*, 2006; Pederson *et al.*, 2011). Alpine environments in all parts of the world are expected to experience changes to their carbon storage potential, being sensitive to the impacts of climate change on biomass allocation (Wu *et al.*, 2013a; Wu *et al.*, 2013b).

The scope of this study was restricted to Glacier National Park, which limits the ability to draw regional or global conclusions about treeline dynamics from its findings. The intense variability of the alpine treeline ecotone exacerbates this issue. Nonetheless, the implications of the results are significant enough to warrant further study. Future research should be carried out

to explore similar biomass dynamics in other treeline locations around the world with a goal of determining how common these patterns are. Additionally, soil and root biomass at treeline remain poorly understood and would benefit from further study in light of these findings.

Whereas the carbon distribution at treeline sites in Montana alone may have a negligible influence on global climate dynamics, if the same trends are present at treeline ecotones elsewhere in North America and around the world they could represent an important modifier in our assumptions about how global change will affect tree and forest dynamics at the climate frontier. The proportionally large amount of dead material this study found present in the alpine treeline ecotone suggests that decomposition rates, known to be limited by the low temperatures present in these environments, may act as a significant limiting factor in the ecotone's carbon cycle. If true, the distribution of carbon within the ecotone structure may be one of the first features of treeline to be affected by climate change. This possibility is supported by observations at Arctic treelines (Grace *et al.*, 2002; Aerts 2006) and could result in faster cycling of carbon through the ecotone. If carbon release outpaces carbon uptake and growth by plants, it may result in a significant change to treeline carbon flux and even a net loss to the atmosphere, at least in the short term (cf. Kammer *et al.*, 2009). Such a trend would be at odds with the conventional understanding that treeline advance will result in a net carbon sink due to increased productivity in the long term, so greater study will be important to determine not only the magnitude but the very direction of change in the decomposition and biomass dynamics of treelines around the world.

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Table 1. Sample site locations in and near Glacier National Park, MT. Location coordinates represent geographic centroids of sample sites at that location.

Study Sites	Latitude N	Longitude W
Apikuni Falls	48.8150	113.6416
Baring Creek	48.6955	113.6088
Divide Mountain	48.6666	113.3875
Lee Ridge	48.9218	113.6505
Logan Pass	48.6840	113.7366
Lunch Creek	48.7043	113.7043
Preston Park/Siyeh Pass	48.7168	113.6409
Scenic Point	48.4815	113.3411
White Calf Mountain	48.6562	113.3939

Table 2. Total aboveground biomass for dwarf trees, krummholz, and tundra in g m^{-2} .

	Dwarf Tree	Krummholz	Tundra
Mean	2896.4	1996.9	702.9
Median	1970.4	1709.3	468.1
Maximum	9369.7	8698.9	5215.0
Minimum	0	0	0
Standard Deviation	2523.1	1864.6	932.8
Sample Size	40	40	40
Skew	1.1	1.8	3.1
Kurtosis	0.6	4.1	13.4

Note: all means significantly different according to ANOVA.

Table 3. Standard error in g m^{-2} for constituent carbon pools in each cover type.

	Dwarf Trees	Krummholz	Tundra
Aboveground Woody	299.90	61.58	n/a
Downed Woody	80.24	n/a	n/a
Herbaceous	43.65	n/a	102.14
Litter	301.06	343.35	90.00

Figure 1. Sample site locations in and near Glacier National Park, MT.

Figure 2. Dwarf tree habitat in Glacier National Park, MT.

Figure 3. Krummholz habitat in Glacier National Park, MT.

Figure 4. Alpine tundra habitat in Glacier National Park, MT.

Figure 5. Example diagram of sampling site layout for a) dwarf trees/krummholz, and b) tundra.

Features include: 1. a transect along the long axis of the patch; 2. a point along the transect chosen by random number generation for sample site location; 3. a sample site within the patch consisting of a circle with a radius of 57 cm, within which tree stems were counted and measured and percentage of herbaceous ground cover was measured; 4. a transect along a randomly selected radius of the circle along which downed woody material intersecting a vertical plane was measured; 5. a 10 x 10 cm plot in which herbaceous cover was collected and measured, with a second for litter; and 6. in tundra sites, four 30 x 60 cm plots in which percentage of herbaceous cover was measured.

Figure 6. Total and component aboveground carbon biomass pools by cover type.

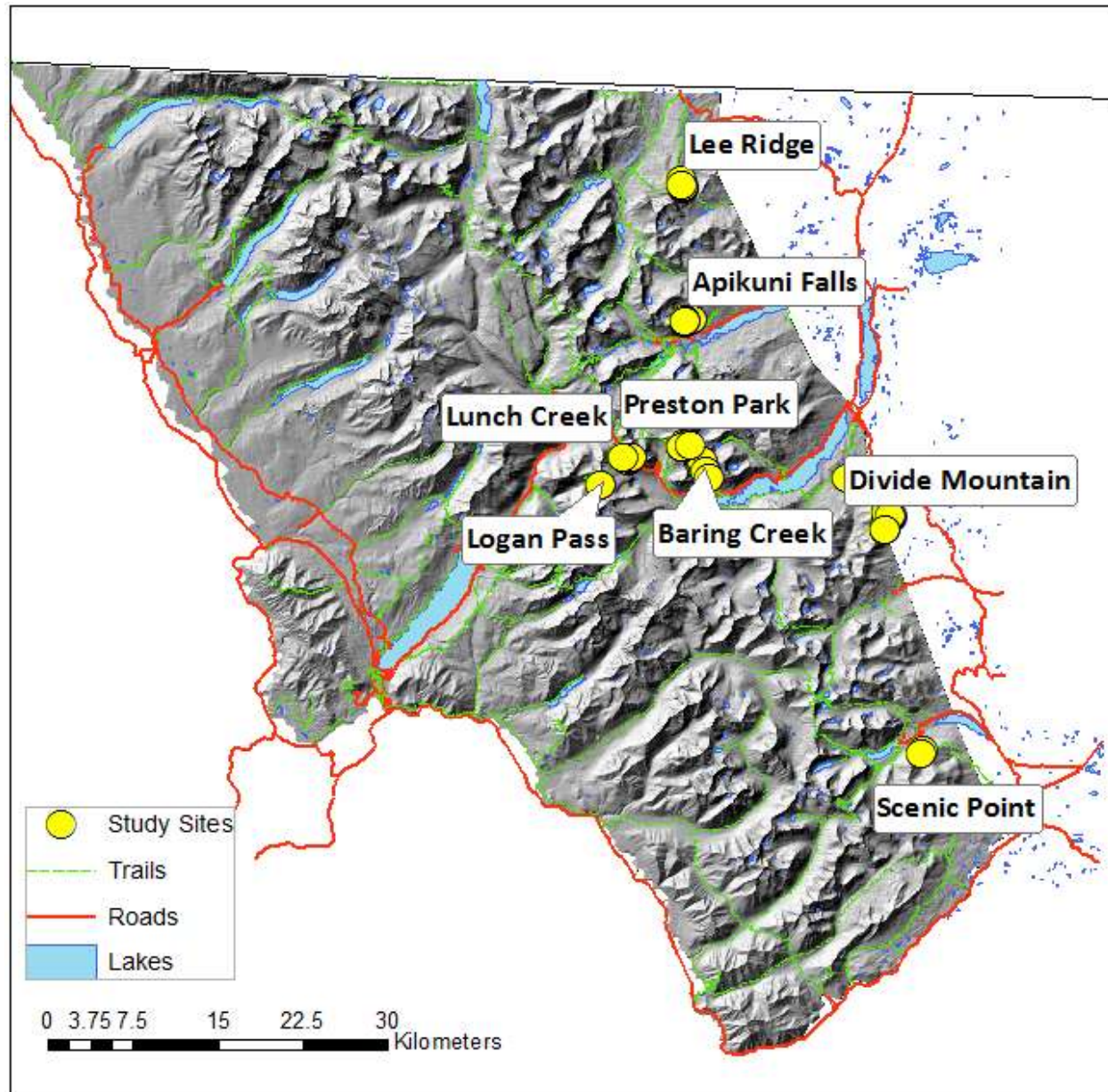


Figure 1



Figure 2



Figure 3



Figure 4

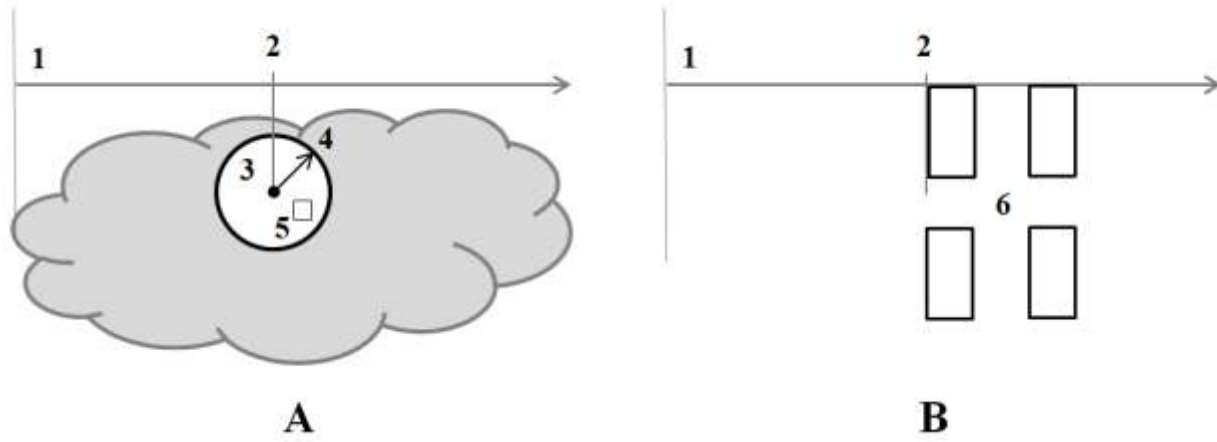


Figure 5

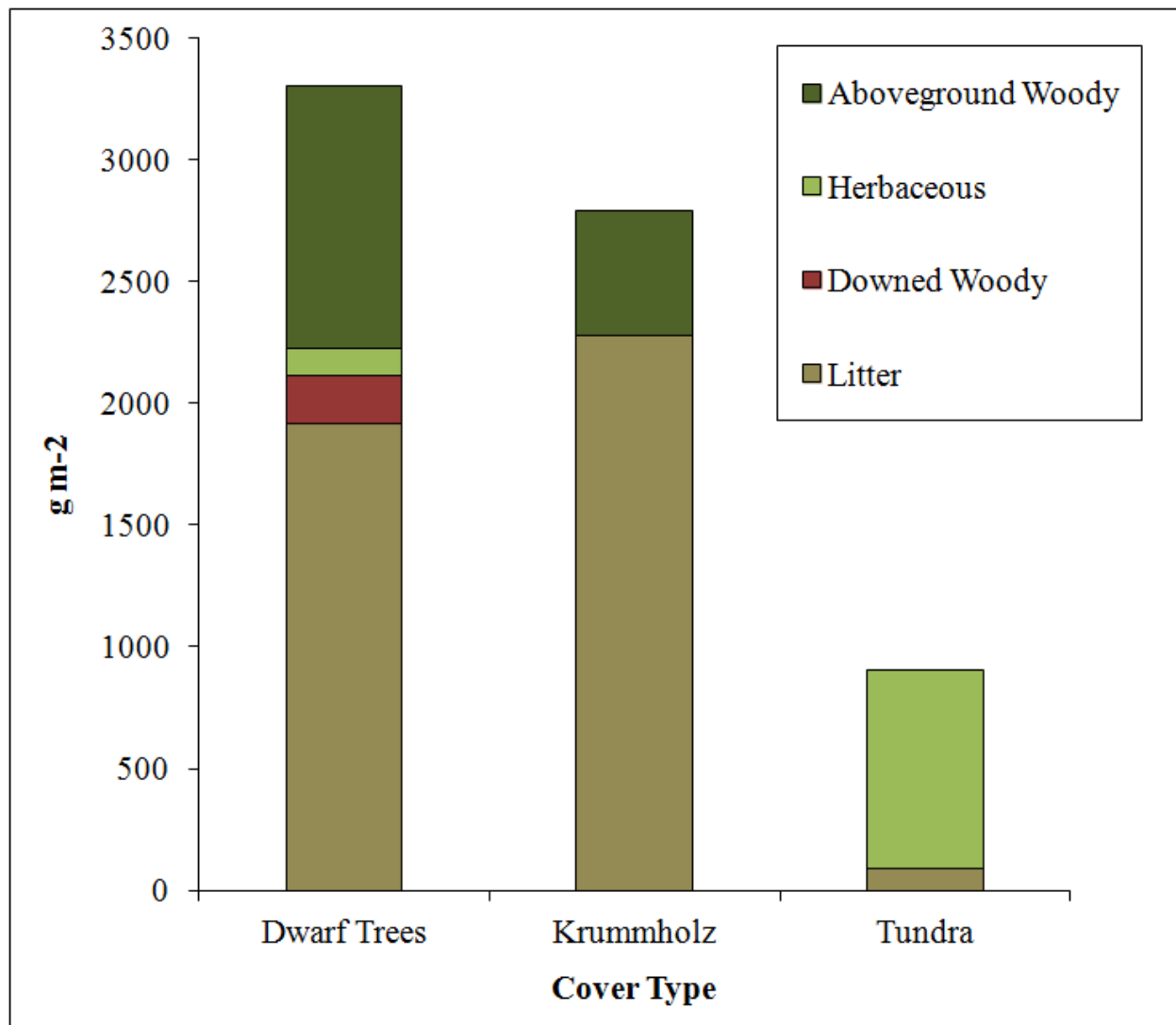


Figure 6

Biomass distributions in dwarf tree, krummholz, and tundra vegetation in the alpine treeline ecotone

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