

ALPINE TREELINE OF WESTERN NORTH AMERICA: LINKING ORGANISM-TO-LANDSCAPE DYNAMICS

*George P. Malanson, David R. Butler, Daniel B. Fagre, Stephen J. Walsh,
Diana F. Tomback, Lori D. Daniels, Lynn M. Resler, William K. Smith,
Daniel J. Weiss, David L. Peterson, Andrew C. Bunn, Christopher A. Hiemstra,
Daniel Liptzin, Patrick S. Bourgeron, Zehao Shen, and Constance I. Millar*

**Department of Geography
University of Iowa
Iowa City, Iowa 52242**

Abstract: Although the ecological dynamics of the alpine treeline ecotone are influenced by climate, it is an imperfect indicator of climate change. Mechanistic processes that shape the ecotone—seed rain, seed germination, seedling establishment and subsequent tree growth form, or, conversely tree dieback—depend on microsite patterns. Growth forms affect wind and snow, and so develop positive and negative feedback loops that create these microsites. As a result, complex landscape patterns are generated at multiple spatial scales. Although these mechanistic processes are fundamentally the same for all forest-tundra ecotones across western North America, factors such as prior climate, underlying geology and geomorphology, and genetic constraints of dominant tree species lead to geographic differences in the responses of particular ecotones to climate change. [Key words: climate change, ecotone, establishment, geomorphology, landscape, scale.]

INTRODUCTION

The transition from subalpine forest to alpine tundra is one of the most distinctive features of mountain environments. Though often referred to as alpine *treeline* (which we will do here), this ecotone is a zone rather than a line; it varies in all three spatial dimensions between continuous forest at lower elevations and alpine tundra at upper elevations (Walsh et al., 1992). At a continental scale, the elevation of treeline indicates that it is controlled by temperature, with a decline in elevation at more northerly latitudes and in proximity to coastal locations with maritime climates (e.g., Daubenmire, 1954). Change in the elevation of treeline is an expected outcome of regional climate change (Holtmeier and Broll, 2007), and upslope and downslope movements in response to climate variability during the past 20,000 years have been recorded (e.g., Rochefort et al., 1994; Taylor, 1995; Lloyd and Graumlich, 1997). Such positional change in treeline has important consequences for the adjacent tundra biome. Genetic diversity, habitat for alpine animals, and overall alpine biodiversity are likely to be reduced, and change in tundra areal extent, coupled with changes in treeline community structure, may affect the water and nutrient budgets of mountain watersheds (e.g., Seastedt et al., 2004). However, treeline is controlled by multiple processes (e.g., Kupfer and Cairns, 1996; Holtmeier, 2003), so site-specific responses are likely and a lack of change locally does not necessarily indicate climate stability.

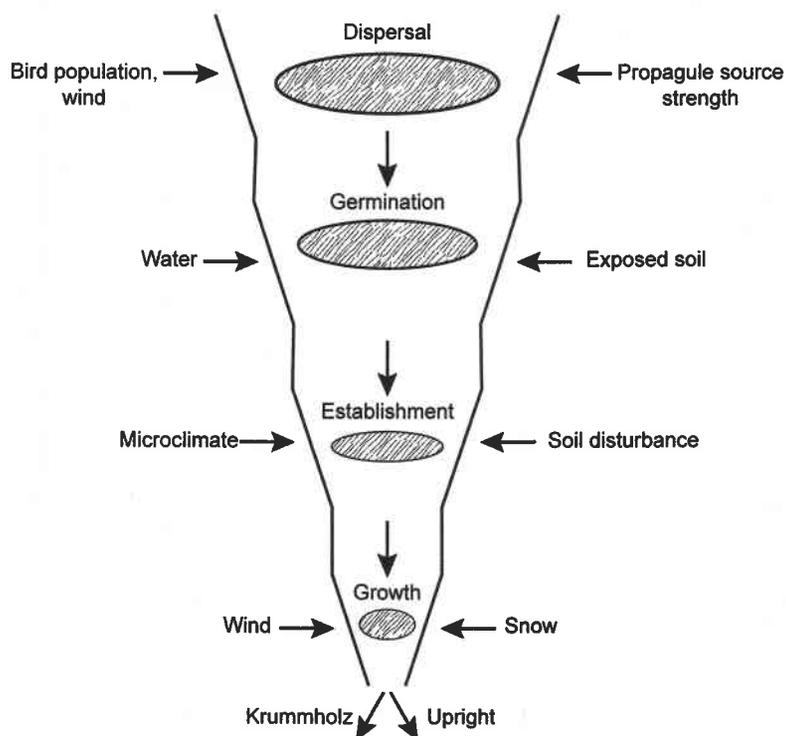


Fig. 1. An environmental sieve indicating the main sequence of processes by which establishment at the alpine forest-tundra ecotone may be limited.

Our purpose here is to examine the processes that link treeline to local and regional controls, and so improve our expectations for their response to climate change. Although the ecological mechanisms that create treeline plant composition, structure and spatial patterns are the same across western North America, the relative importance of processes and responses to the environment varies because the environmental contexts are different. Thus, significant variation in treeline spatial composition and history can occur within and among different mountain ecosystems even with similar climate change, highlighting the notion that there exist many treelines—not one treeline. In this review, we begin with the individual scale and are interested first in the basic biology of tree seedling establishment and, second, in the subsequent development of growth forms (Fig. 1, top to bottom). The establishment of new individual seedlings has such a fundamental potential impact on spatial change at treeline that it should be central to the study of its dynamics (e.g., Smith et al., 2003; Daniels and Veblen, 2004; contrast Korner and Hoch, 2006). We look at patch-scale dynamics where individuals interact, and then we examine the landscape scale and compare it at different locations across the western United States.

INDIVIDUAL OR LOCAL SCALE MECHANISMS

At the scale of individual plants, the mechanisms controlling establishment are largely the same biological processes (Sveinbjörnsson et al., 2002) across western North America. The basic environmental factors of climate, energy and water, directly affect these processes, but the outcomes may differ locally due to abiotic differences and biogeographical history. At what point the combined effects on the carbon balance of seedlings becomes important is unknown (Cairns and Malanson, 1998; Johnson et al., 2004). Climate change may affect successful dispersal, germination and survival by modifying such abiotic conditions as soil availability, quality, and moisture; precipitation fraction arriving as snow; snow redistribution and melt; extent of glacial forefields; extent of permanent snowfields; and disturbance regimes.

Seeds and Germination

Seed production and dispersal vary among conifers (Family Pinaceae), which typically produce moderate to abundant seed crops every 1 to 4 years (e.g., Young and Young, 1992). Because individuals in the ecotone usually produce little seed, dispersal from lower elevations is necessary (Tranquillini, 1979). The winged seeds of most treeline conifers are dispersed by the wind and depend on the proximity and location of seed sources with respect to regional prevailing winds (e.g., Tomback et al., 1990) and surface roughness patterns. In contrast, several large-seeded AFTE pines depend on the seed dispersal services of Clark's nutcracker (*Nucifraga columbiana*, Family Corvidae; e.g., Tomback, 1982, 2001). Nutcrackers harvest seeds from the subalpine forest and transport them to AFTE locations for seed caching (e.g., Tomback, 1986), but may also harvest seeds within AFTEs. Caches are spatial hotspots for regeneration. Nutcracker seed dispersal is a dominant factor for regeneration of interior AFTEs, but more variable regionally in Pacific coastal AFTEs.

The second step in potential spatial change of the treeline is seed germination. Germination follows snowmelt and may be most likely in moist microsites at treelines, such as areas with relatively late-lying snow, (e.g., Mellmann-Brown, 2005; Resler et al., 2005; Maher and Germino, 2006). Butler et al. (2004) associated seedling presence with micro-scale erosion and deposition of fine-grained sediment (likely due to increased penetrability) associated with relict solifluction, a freeze-thaw process that produces patterns such as stripes of coarse and finer substrate (Fig. 2). Differences in substrate texture can thus affect the overall pattern of seedling occurrence. Few data, however, are available describing seed abundance, longevity of seeds and seed banks in the soil, or rates of germination success in treeline environments.

Seedling Survival

Many treelines in North America occur on exposed, high-elevation slopes, with strong and persistent winds. During winter wind damages the leaders, branches,



Fig. 2. Micro-erosion of solifluction risers onto the treads provides an exposed soil seedbed for germination and establishment, Glacier National Park, MT.

buds, and leaves of trees and seedlings. However, many trees and krummholz in treelines obviously survive this damage. Seedling survival is extremely low (<10%) in the first year (Smith et al., 2003), but can increase to >90% within the second or third year (e.g., Germino et al., 2002). Burial beneath snow in winter and reductions in sunlight exposure, low temperatures, water stress, and wind are critical environmental factors influencing new seedling survival in summer, along with adaptive structural attributes for avoiding the severe abiotic environment. Mechanistically, reduction of sky exposure in summer, which lessens night-time cooling and exposure to excessive sunlight, resulted in more favorable microsites and photosynthesis in fir (*Abies lasiocarpa*; Germino and Smith, 1999), which also orient their needles to minimize sky exposure (Smith et al., 2003). Seedling mortality is often attributed directly to a lack of carbon gain, corresponding root growth, and ensuing desiccation in less favorable microsites (e.g., Johnson et al., 2004; Hasselquist et al., 2005; Maher et al., 2005). Favorable conditions must persist for several years (e.g., Taylor, 1995; Hessel and Baker, 1997).

Survival of new seedlings often requires facilitation by microtopographic features, mostly boulders or other plants, that enhance snow burial and reduce abrasion or damage by rime ice, reduce sky exposure, and provide longer-lasting summer soil moisture (Germino et al., 2002; Resler et al., 2005). Even small

changes in microtopography such as solifluction, can provide increased snow coverage and seedling protection during winter, as well as protection from sky exposure during summer.

Biotic interactions also affect seedling survival. Tree seedling competition with alpine tundra species may be important (Malanson and Butler, 1994), but only if the latter are dense; at lower densities tundra plants can facilitate tree seedling survival (Maher et al., 2005). Predation or trampling by vertebrates occurs in treelines, but to a varying degree (e.g., Mellmann-Brown, 2002). Burrowing and digging by mammals of all sizes may create fine-grained sites that are amenable for seedling establishment and survival, but may also expose the excavated sediment to wind erosion (Butler, 1995). Also, the establishment of all conifers in treelines depends on mutualistic root colonization by mycorrhizal fungi (e.g., Cazares et al., 2005).

PATCH SCALE: GROWTH FORMS AND ECOLOGICAL INTERACTIONS

The 3-D pattern at treeline is often patchy, including *krummholz* (prostrate, laterally growing conifers) and dwarf trees (e.g., Weisberg and Baker, 1995; Allen and Walsh, 1996; Cairns and Waldron, 2003). Growth and expansion beyond the initial microsite can be facilitated by other plants (Hättenschwiler and Smith, 1999; Resler, 2006). Here, the individual directly shapes the patch scale and even species-specific tendencies, such as the pioneering nature of whitebark pine into tundra in the Rocky Mountains (e.g., Tomback, 2001), can be critical for patch development. The formation of vegetation structures that add wind protection, snow collection, and soil development at the spatial scales of a tree island allows newly established subalpine forest species to initiate patches and then to have patches expand and become denser in the upper treeline (e.g., Smith et al., 2003). These structures can also affect the infilling of openings in the tree cover lower in the treeline. In addition to patches per se, often, a linear configuration of trees develops with older individuals closest to the initial, facilitating structure (Fig. 3; Holtmeier, 1982; Alftine and Malanson, 2004; Resler, 2006).

The effect of a patch on its surroundings may be a positive feedback (Malanson, 1997, 1999, 2001; Callaway, 1998; Callaway et al., 2002). Once a tree becomes established in a suitable microsite, the growing tree reinforces wind protection and increases snow accumulation and the fine mineral and organic fractions of the soil. This process involves the capability of conifer treeline species to survive as an array of growth forms that include stunted and flagged trees, tree islands, and dense *krummholz* mats (Fig. 4). These growth forms represents a morphological gradient of structural characteristics across the ecotone that enhance snow collection and burial (e.g., *krummholz* mats) or respond to and further avoid blowing snow abrasion (e.g., flagging) in drier, colder treeline sites (e.g., Smith et al., 2003). The effects of micro- and meso-topography can counteract the presumed effects of elevation and create counter gradients of these forms. The *krummholz* shape reduces sky exposure for nearby seedlings as well as providing protection from wind, as indicated by the emergence of vertical stems to form flagged trees on the leeward sides of larger *krummholz* mats (Fig. 4; Smith et al., 2003). Plants also influence soil



Fig. 3. Advance of tree species into tundra is often patchy, including linear forms parallel to the prevailing wind, Lee Ridge, Glacier National Park, MT.



Fig. 4. Patches of krummholz develop into trees islands at their leeward extent, Medicine Bow Mountains, WY.

formation by adding organic material, changing texture, and increasing soil penetrability (Pérez, 1995).

The development of patches also initiates negative feedbacks on seedling establishment. The formation of dense canopies of tree islands adversely affects regeneration within them by shading, decreasing temperature (especially of soil), and accumulating slowly decomposing litter above the mineral soil. Thus dieback is observed at the windward end of migrating tree islands (Benedict, 1984). At the patch scale there is also evidence for reductions in tree species cover; recent diebacks have thinned some patches in the Sierra Nevada during extended droughts (e.g., Millar et al., 2006). More generally, feedbacks and climate conditions must be harsh enough to overwhelm any positive feedbacks for mature individuals. Furthermore, changes in patches influence neighboring patches and create landscape patterns.

LANDSCAPE SCALE

Constraints on Pattern and Process

The constraints that control the dynamics of treelines are the climate at regional scale and landscape scale variation in geomorphology or geology. Studies of the relationship between disturbance and the treeline have emphasized the constraining character of geomorphic processes and structural and lithologic controls (e.g., Butler and Walsh, 1994). The freeze-thaw cycle in the periglacial climate of treeline leads to geomorphologic processes including solifluction, soil creep, landslides, and erosion by wind and water at this scale. Snow avalanches and debris flows can cause tree mortality and limit treeline elevation through disturbance (Butler and Walsh, 1994). Additionally, insects and pathogens are spatially diffuse and spreading and affect AFTE species on a landscape scale. Recent outbreaks in bark beetle (*Dendroctonus* spp.) populations throughout the West are rapidly killing trees in many forests (e.g., Logan and Powell, 2001). Trees in the treeline ecotone may be poor hosts because of reduced stature and slow rates of carbon assimilation, although this status can be affected by climate change. In some areas, the widespread loss of trees will reduce the seeds available for dispersal to AFTEs. White pine blister rust (*Cronartium ribicola*), a fungal pathogen native to Asia, has spread throughout most of the collective ranges of five-needled white pines in the United States and Canada (Tomback and Resler, 2007, in this issue). At a yet coarser scale, the expansion of krummholz or tree-island patches on a landscape may be limited by topographic constraints, such as cliffs, and the ecotone pattern encounters a stable boundary.

Patch Dynamics at Landscape Scale

In alpine systems redistribution of snow by wind is a defining feature of the physical environment. In these landscapes, snow, wind, and topography interact with vegetation to produce a pattern of snow deposition: snow is eroded by wind from



Fig. 5. Late lying snow in the lee of tree islands at Libby Flats, Medicine Bow Mountains, WY.

exposed areas and deposited on the lee sides of hills, trees, and rocks (Fig. 5; Walsh et al., 1994; Hiemstra et al., 2006), creating strong gradients in the distribution of snow. Snow cover at treeline produces both facilitative and inhibitory effects. Snow can protect seedlings and stems in winter from damage by low temperatures and physiological aridity and abrasion due to wind, affect winter soil temperatures, and provide soil moisture through melting in spring and summer. However, snow may also limit the growing season and create avalanches as frequent disturbances.

The effect of established *krummholz* or trees, plus topography, determine how wind and snow alter the pattern and dynamics of habitat across and among slopes, within which trees species can successfully establish in the ecotone. Specifically, facilitation is unimodal, wherein too few or too many neighboring trees reduce the potential for new establishment. Treeline dynamics change when a patch expands to the point where the positive feedback becomes limited by negative feedback. Using a simple, two-state tree-versus-tundra model, Zeng and Malanson (2006) showed that a wide range of patterns exist at simulated treelines, which fluctuate fractally. They explained that establishment of individuals accelerated the advance of treeline, as positive feedback affected a wide number of possible establishment sites. This change led to a coalescence of patches that decreased the number of establishment sites in the vicinity of the trees, which slowed advance. This self organization would seem to override the effect of geomorphic patterns in potential establishment conditions (Zeng et al., 2007).

Coarse-scale constraints limit further landscape development. Geologic control, where forest is terminated by cliffs is primary. Second is lithologic control, where

weathering produces variability in the texture and chemistry of the substrate. Third, snow and debris avalanches greatly lower mapped treelines locally. Next, differences in topography, from the steeply concave U-shaped valleys to the broader convex interfluvies, change the breadth of the ecotone. Finally, the particular species composition creates patchy and fingering krummholz and/or dwarf tree islands. Thus local topography and biogeography modify the mesoscale inputs of energy and water.

REGIONAL SCALE

At regional scales we see commonalities and differences in the constraints on the finer scale processes. Malanson and Butler (2002) arranged the factors that might affect an alpine forest tundra ecotone into a hierarchy and concluded that the continental-scale pattern of AFTE control by temperature is locally modified by moisture. To elucidate the regional variation, we briefly examine differences among regions that bracket the American West: the northern Rockies centered on Glacier National Park (GNP), MT (and adjacent Waterton Lakes NP in Alberta), the southern Rockies centered on Niwot Ridge (NR) and Rocky Mountain National Park (RMNP), CO (but with insights from the Medicine Bow Mountains in WY), the Sierra Nevada centered on the high peaks area of Sequoia and Kings Canyon National Parks (SEKI), and the Pacific Northwest focusing on Olympic National Park (ONP).

Climate

The AFTEs of the entire West are affected by the prevailing west wind and orographic influences. Although the latitudinal gradient produces the most marked continental pattern in the AFTE, maritime environments have lower AFTE elevations than continental AFTEs at the same latitude (Daubenmire, 1954). Maritime climates lack summer warmth, receive much more snow that is denser and less mobile compared with continental climates. Because maritime temperatures are generally lower and snow cover lasts longer, growing seasons are abbreviated compared with continental climates at the same latitude. Among our regional sites, ONP is strongly maritime and NR is strongly continental. SEKI is more continental than maritime, because its highest elevations do not receive much orographic precipitation from the Pacific; the southern Sierra receives more summer precipitation than does the northern Sierra due to monsoon effects. GNP shifts from maritime climate to continental across the divide: the eastern slope is strongly continental in climate. Whereas all regions have experienced extensive glaciation, the more recent effects of the Little Ice Age vary only slightly geographically. Pleistocene glaciation was more extensive and lasted longer on the coastal sites (SEKI and ONP), and as a result their AFTEs are more recent.

Altered productivity of alpine tundra is another consideration. Malanson and Butler (1994) conjectured that competition from denser tundra, due to differences in nutrients, could limit the establishment of tree species and affect upper treeline elevation. Conditions of shorter snow durations in the Pacific Northwest or warmer

and wetter climate elsewhere could favor an increased density of tundra or meadow plants and slow the spatial response of subalpine forest.

Geology

Glacial erosion has left U-shaped valleys in all four locations, but other features and the elevation of AFTE relative to them have more important influences than valley-side slope. In GNP, the AFTE often occurs where the U-shaped valleys become steep, and is not controlled by exposed rock faces and climate. In contrast, climate is limiting east of the Continental Divide, where broad convex ridges with stony shallow soils and small scale (~1 m) relict solifluction exist within and above the AFTE. In RMNP 1 to 10 m scale solifluction and frost boils are more recently active where Precambrian gneiss, schist and granite weather into much coarser fellfields. These slopes are higher in elevation than the northern Rockies, and the glaciation occurred higher also; but, overall there are large extents of broad convex uplands and flatter areas through and above the current AFTE. An important difference in these ranges is that there is considerable input of eolian sediment from the dry basins to their west. This input is not found in the other sites, and while here it is spatially localized, it is potentially extensive across the region.

In SEKI the large Mesozoic granite batholith has AFTE above the deep U-shaped valleys on unglaciated ridges and slopes. The surface material is coarse and often scree, soils are thin, and AFTEs tend to be on steep slopes. The asymmetrical nature of the fault block uplift creates differences in the topography on the east slope vs. the west slope. On both, the AFTE forms both directly and in relation to prevailing winds and attendant orographic precipitation. For example, trees form a scattered, unformed AFTE on the arid and very steep east face of the Sierra, while maintaining a distinct, relatively abrupt transition, on the wetter, gradual west slope.

At ONP the geology is a mix of Cenozoic igneous and sedimentary rocks. Under-sea volcanic activity created the oldest rocks, which then plowed into and under more recent sediments, whereupon the entire area was uplifted as a broad dome that was subsequently eroded by Pleistocene glaciation. Because the rocks are less resistant the glacial forms are less distinct than at the other treeline sites.

Glacial erosion has created glacial topography across western North America, but other geological features have more important influence on the elevation of treeline. Substrate texture varies strongly geographically, with the coarsest developed on the Mesozoic granite batholith in the Sierra Nevada (Fig. 6), which contrasts with the coarse fellfields of Precambrian gneiss, schist and granite mixed with eolian deposition of fine sediments in the Colorado Rockies (Fig. 7). Further contrasts can be seen within the Sierra where fir dominates on finer sediments of other substrates and creates different forms with krummholz patches (e.g., Millar et al., 2004), and in the White Mountains, CA, where bristlecone pine is primarily confined to dolomite at treeline (e.g., Wright and Mooney, 1965; cf. Butler et al., 2007, in this issue).

Perhaps due to the eolian inputs, solifluction forms are large in the southern Rockies but also prevalent further north (Fig. 3). Wetter conditions or more freeze-thaw cycles could increase solifluction activity and forms, which may



Fig. 6. Coarse granitic substrate supports patches of small upright foxtail pine (*Pinus balfouriana*), Inyo National Forest, CA.



Fig. 7. Large solifluction forms develop where the coarse granitic substrate is supplemented by the input of fine eolian sediments in the southern Rocky Mountains, Niwot Ridge LTER, CO.

improve the substrate for seedling establishment (Butler et al., 2004; Resler et al., 2005).

Vegetation

Within all four regions, there is an upslope gradation in community structure from continuous forest to patches of small trees or krummholz. Despite the similarities in structure, some differences are also evident, such as the high elevation open stands of large, upright growth forms of foxtail pine (*Pinus balfouriana*) in SEKI, the fairly straight lines of broad slopes in RMNP without either meadows or tree islands, the importance of high, convex and thus low-snow slopes in ONP (and the North Cascades) and the extreme variability of the AFTE in GNP (Becwar and Burke, 1982).

The variation in alpine AFTE elevation and 3-D community structure are often due to nonclimatic controls, and these are well-illustrated in GNP. Here, geologic/topographic control, where forest is terminated by cliffs that rise above the limits of tree growth (although some lone trees may be seen in crevices high above the forest) is primary. Second is geologic/lithologic control, where weathering produces considerable variability in the texture and chemistry of the substrate. Third, snow and debris avalanches greatly lower mapped AFTEs locally. Next, differences in topography, from the steeply concave U-shaped valleys to the broader convex interfluvies, change the breadth of the ecotone. Finally, the particular species composition creates patchy and fingering krummholz and/or dwarf tree islands. Given these three controls, the effects of climate then manifest themselves as local topography and vegetation patterns modify the mesoscale inputs of energy and water.

Despite general regional similarities in conifer associations, some differences are also evident, such as the high elevation open stands of large, upright growth forms of foxtail pine (*Pinus balfouriana*) in the Sierra Nevada (Fig. 6), densely skirted subalpine fir (*Abies lasiocarpa*) in ONP, or the picturesque shapes of bristlecone pine (*Pinus longaeva*) in the western Great Basin. Elsewhere, *Pinus albicaulis* plays a potentially critical role in the process of patch formation at treeline (Tomback and Resler, 2007, in this issue). These and other high elevation five-needled white pines show idiosyncratic responses to harsh environments, and contribute both to the structural diversity and the biodiversity of western treeline communities.

RESPONSES TO CLIMATE CHANGE

Of the many possible changes in climate, we will elaborate on only two: warmer and wetter climate, and warmer and drier. We will not specifically address CO₂ fertilization; Graumlich (1991) found this scenario unlikely to alter the AFTE. In warmer and wetter conditions we are likely to see significant changes in the three-dimensional structure of the AFTEs at all four of our regional locations. The Pacific Northwest already has ample moisture, and increasing snow is likely to inhibit the establishment and growth of trees. Longer lasting snowpack could limit any expansion of patches of krummholz higher in the ecotone and could expand lower meadows. This effect is dependent on increasing precipitation in the form of snow.

Whereas the period of snow-fall may be shortened, an overall increase in snowpack is quite possible. The other three sites are drier, so increasing moisture will likely improve the conditions for tree species establishment and growth. The effect will possibly be greatest in the southern Rocky Mountains and least in the Sierra Nevada, because of differences in substrate development and water-holding capacity, assuming equivalent climate changes. Millar et al. (2004) and Bunn et al. (2005) reported increased tree-ring widths at SEKI treelines for warmer, wetter periods in the 20th century. Millar et al. (2004) also found increasing invasion of subalpine meadows during drier periods—the elevational switch that we would expect, because deep snow in lower elevation meadows limits establishment even in more continental sites (e.g., Moir et al., 1999).

At all three sites, the effect is likely to be greatest lower in the ecotone where deeper soils and root zones can more readily take advantage of the increased water. In the Rockies throughout the AFTE, warmer and wetter conditions, if just right, could activate relict solifluction, which can create hospitable seed beds, enhancing seedling establishment. The AFTE in the northern Rockies may respond less to increased snow than substrate development would indicate, because much of the upper boundary of tree species is limited both by the total absence of soil and by geomorphic disturbances.

If conditions become warmer and drier, the Pacific Northwest should differ from the other three sites: Less moisture should not reduce tree species establishment and growth in the ecotone. Reduced snow suppression could allow expansion in the upper ecotone and infilling of meadows lower in the zone. Conversely for the other three treeline sites, warmer and drier climate could reduce the number of tree species in the ecotone, as observed recently by Millar et al. (2006) in the Sierra Nevada. While much of the evidence for AFTE response suggests upslope advance during warmer conditions, in many places advanced may be moisture limited. For example, GNP experienced considerable upward expansion of the ecotone in the 19th century (Bekker, 2005). During the 20th century, advanced was limited, but density of existing patches increased (Butler et al., 1994; Klasner and Fagre, 2002). More recent advances in the latter half of the 20th century coincided with the cool, wet, snowy phase of the Pacific Decadal Oscillation (a sea surface temperature phenomenon in the northern Pacific). Advance seemingly stopped coincident with the switch to the warmer, drier phase of the 1980s and 1990s (Alftine et al., 2003). Thus variability in response will be important, but projecting possible scenarios of variability is further out on this limb than we wish to venture.

One of the least understood changes in general could be changes in the density of snow and thus in its mobility. Because of the importance of snow redistribution in determining the relations between landscape and patch scale interaction, this change would have consequences in the overall spatial organization of treeline sites.

In the previous scenarios, we do not explicitly consider the role of increased productivity of alpine tundra. Malanson and Butler (1994) conjectured that competition from denser tundra, due to differences in nutrients, could limit the establishment of tree species and affect upper AFTE elevation. Conditions of shorter snow durations in the Pacific Northwest or warmer and wetter climate elsewhere

could favor an increased density of tundra or meadow plants and slow the spatial response of subalpine forest.

CONCLUSIONS

Alpine treelines have long been considered visual barometers of change in topography where environmental gradients are sharp, and the vegetation patterns are apparent. They have captured the imagination of a broad sector of the public, because many people greatly value high-elevation locations. People see in the wind-flagged, contorted trees the epic struggle of nature against the elements. There is a very real cultural identity associated with the geology, plants, and animals that characterize subalpine and alpine ecosystems—these systems have come to symbolize pristine mountain environments.

As such, treelines simultaneously reflect biological responses and human values, making these ecotones an important focus for management, scientific study, and assessment of ecosystem services. Recent studies of treelines have explored the potential for these locations to record and manifest the effects of climatic variability and change—a possible “canary in the mine” that may portend more extensive ecological changes in mountain ecosystems of western North America. The change clearly will not, however, be a simple upward movement of a line.

While all treelines in western North America share the same sets of mechanisms leading to establishment, landscape responses to climate change are idiosyncratic, based on specific combinations of geology, geomorphology, and climate trends. Yet feedbacks and time-lags in system behavior mean that vegetation and climate are only loosely coupled, and geology and geomorphology may be more important than previously thought. Moreover, given that climate change is not linear, response or lack thereof in any decade or two may not clearly illustrate cause and effect.

Finally, advance of trees into tundra can change high-elevation montane ecosystem services, such as carbon, water, and nutrient cycles, feedbacks to the climate system, and maintenance of biodiversity. Tree establishment at some locations has increased carbon storage through accretion of living vegetation. Transfer of this carbon to dead biomass and soil organic matter results in a long-term carbon sink under cool, wet conditions and/or with less frequent fire in this sparse fuel environment. Advance of trees, or change in pattern in general, also has the potential for altering snow retention and hydrology, with implications for local, soil moisture, and nutrient transport, given how pattern directly affects wind and thus eolian erosion and deposition of snow and sediment, which indirectly affects soil temperatures and runoff (Seastedt et al., 2004). Changes in albedo and surface roughness are other feedbacks to the climate system, although of lesser impact. Potentially of most importance, habitat for alpine animals and biodiversity in the tundra are likely to be affected by changes in treeline landscapes.

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