INFLUENCES OF GEOMORPHOLOGY AND GEOLOGY ON ALPINE TREELINE IN THE AMERICAN WEST—MORE IMPORTANT THAN CLIMATIC INFLUENCES?

David R. Butler
Department of Geography
Texas State University–San Marcos
San Marcos, Texas 78666-4616

George P. Malanson
Department of Geography
University of Iowa
Iowa City, Iowa 52242

Stephen J. Walsh
Department of Geography
University of North Carolina
Chapel Hill, North Carolina 27599-3220

Daniel B. Fagre
U.S. Geological Survey
Northern Rocky Mountain Science Center
Glacier National Park
West Glacier, Montana 58836

Abstract: The spatial distribution and pattern of alpine treeline in the American West reflect the overarching influences of geological history, lithology and structure, and geomorphic processes and landforms, and geologic and geomorphic factors—both forms and processes—can control the spatiotemporal response of the ecotone to climate change. These influences occur at spatial scales ranging from the continental scale to fine scale processes and landforms at the slope scale. Past geomorphic influences, particularly Pleistocene glaciation, have also left their impact on treeline, and treelines across the west are still adjusting to post-Pleistocene conditions within Pleistocene-created landforms. Current fine scale processes include solifluction and changes on relict solifluction and digging by animals. These processes should be examined in detail in future studies to facilitate a better understanding of where individual tree seedlings become established as a primary response of the ecotone to climate change. [Key words: alpine treeline, geomorphic facilitation, geologic control, biogeomorphology, ecotone, Rocky Mountains, American West.]

INTRODUCTION

Alpine treeline in the American West is the ecotone between coniferous forest at lower elevations and alpine tundra or bare bedrock above. Conventional wisdom in

Physical Geography, 2007, **28**, 5, pp. 434–450. DOI: 10.2747/0272-3646.28.5.434

studies of alpine treeline in the west and elsewhere states that alpine treeline is primarily a result of some aspect of climatic or edaphic control (e.g., temperature, length of growing season, length of snow cover, soil temperature, or soil moisture, to mention some of the most commonly cited variables; see Holtmeier, 2003, for a magisterial coverage of climatic factors affecting treeline). We assert here, however, that the impact of geology and geomorphology must first be examined as primary determinants of the location and pattern of alpine treeline, rather than climate. This assertion may be expressed most clearly as follows: climate is subservient to the role of geology and geomorphology across both spatial and temporal scales as a determinant of alpine treeline in the American West (although climate is the driver of change).

This perspective on the importance of geomorphology and geology has also been mentioned by Holtmeier (2003) and Holtmeier and Broll (2005), although not to the extent that we assert here. They recognize three fundamental types of treeline: climatic, orographic, and anthropogenic (which we explicitly do not address here). Orographic treeline (Holtmeier, 2003, prefers the term "timberline") is "always located more or less far below the elevation to which the forest would advance at the given climatic conditions" (Holtmeier, 2003, p. 25), and is induced by "steep rocky trough walls, talus cones, slope debris and avalanche chutes" (p. 25). This perspective on the role of geomorphic conditions and disturbances goes partway to our perspective, but does not go sufficiently far, because even climatic treelines illustrate, through the fine-scale patterns of seedling distribution, the role of geomorphic processes and landform patterns. Inherent geological conditions also strongly influence treeline locations and patterns, and also frequently trump climate as the primary causal control on those locations and patterns. Kruckeberg (2002) asserts in effect that all plant distributions are the result of geological control, and although we do not go that far in our perspective on the role of geomorphology and geology as treeline determinants, our position is closer to his than that of Holtmeier. As Wiegand et al. (2006, p. 880) noted, "treeline features are not arbitrary but …. there is a clear signal in the pattern which allows for inference of the underlying processes." We assert that those underlying processes are geomorphic and geologic.

SPATIAL AND TEMPORAL SCALES AT TREELINE

A consideration of scale is critical to our position on geomorphology and geology at treeline. Most studies of treeline have focused on the plants themselves rather than on the broader pattern. Even global scale analyses have been about global patterns of temperature influences on individual plant physiology (e.g., Korner and Paulsen, 2004). Malanson et al. (2007, in this issue) have emphasized multiple scale interactions, but primarily examine how effects at finer scales influence patterns at coarser scales, not vice versa. While we also consider finer scales, we take a somewhat inverted approach and consider the scale question from the perspective of what constraints coarser scale phenomena impose on finer scale process and pattern relations. The importance of coarse scale constraints can affect what happens to individual plants if one follows the constraints down the hierarchy.

Table 1. Specific Locations for Field Observations of Alpine Treeline in the American West

Site	State
Primary sites associated with the Western Mountain Initiative (WMI)	
Glacier National Park	Montana
Rocky Mountain National Park	Colorado
Olympic National Park	Washington
North Cascades National Park	Washington
Sequoia National Park	California
Secondary sites	
Mount Rainier National Park	Washington
Mount Hood	Oregon*
Lemhi Range	Idaho*
Beartooth Mountains	Montana*
Grand Teton National Park (Teton Range)	Wyoming
Wind River Range	Wyoming*
Medicine Bow Mountains (Snowy Range)	Wyoming*
Yosemite National Park	California
White Mountains	Nevada-California*
Spring Mountains	Nevada*
Niwot Ridge	Colorado*
Sangre de Cristo Range	Colorado*

*Western Mountain Initiative (WMI) sites.

In their examination of the Western Cordillera of North America, Malanson and Butler (2002) identified four spatial scales of significance for the study of mountains there—the continental scale, the mountain range scale, a within-range scale, and a within-valley scale. Here, we compress and slightly revise these into three scales of note: the continental-to-range scale, the within-range scale, and the slope scale, the latter term better encompassing the finer processes and landforms associated with local issues of alpine treeline. We examine each of these in sequence below, with specific examples of where treeline conditions are at least moderated, if not outright controlled, by geology and geomorphology. Issues of temporal rates of change at treeline are also addressed where appropriate. Our examples are taken from mountain ranges throughout the American West (Table 1), many of which serve as primary and secondary sites for the U.S. Geological Survey's Western Mountain Initiative program.

Continental-to-Range Scale

At the geographic scale of an individual mountain range or larger, geology trumps climate as a primary control of treeline, because plate tectonics are

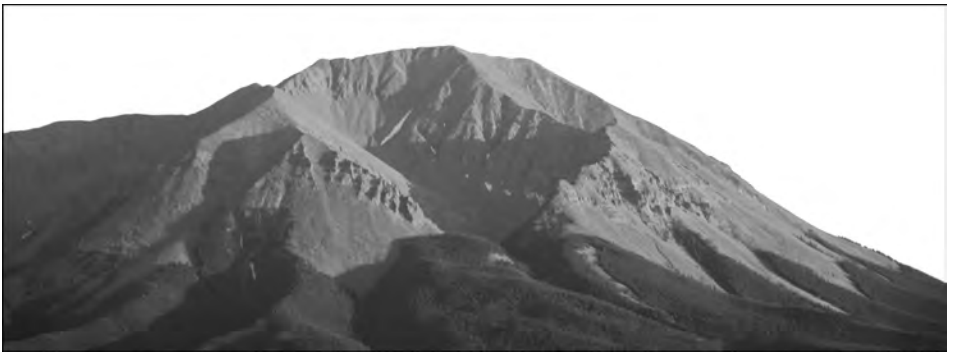

Fig. 1. Treeline as a function of geologic structure—West Spanish Peak, Sangre de Cristo Range, CO.

responsible for the very presence of the mountains (Malanson and Butler, 2002). Kruckeberg (2002, p. 87) conjectures that "(m)ajor weather systems are products of the mountain systems they encounter." From that perspective, all mountain weather and climate is a function of plate tectonics, and thus all treelines are controlled by geological histories associated with each respective mountain range. This perspective does, of course, ignore the post-orogenic reality of varying climates within a mountain range; yet, even with varying climates at the within-range (or finer) scale, geology and geomorphology must be considered as primary treeline determinants, as described below. The north–south trend of the ranges in North America is in line with the global latitudinal energy gradient and perpendicular to the west–east precipitation gradient. This pattern determined the degree of glaciation in the past as a continental gradient in treeline elevation and affected the degree of glaciation in the past and so constrains the degree of variation in landforms and geomorphic processes within ranges. The continental pattern of treeline elevation intersects with these landforms and processes, especially with the degree of past glaciation, and so the effects of glaciation on treeline have a continental scale pattern.

Within-Range Scale

Within an individual range, the geologic structure and glacial history determines the spatial arrangement of major ridges and valleys (Malanson and Butler, 2002), and thus constrains the spatial pattern of treeline. For example, on the West Spanish Peak in the Sangre de Cristo Range of Colorado (Fig. 1), treeline is a function of the structure of the peak (an intrusive stock with radiating dikes) which, upon exhumation, has induced the development of a radial drainage pattern that profoundly affects the upper limits of treeline. The stream channels radiating from the rounded peak create geomorphically active sites where trees are unable to survive at elevations where adjacent ridgecrests are tree covered. The isolated Cascade Range volcanoes are another example where the geologic structure of a stratovolcano is the primary determinant of subsequent erosion patterns, and subsequently of treeline.

Lithology also serves as the primary determinant of treeline within some ranges. In the White Mountains on the Nevada–California border, the location and pattern

Fig. 2. Treeline as a function of lithology—Lower nondolomitic slopes without trees and trees up to climatic limit on dolomite, White Mountains, CA.

of upper treeline is a function of the distribution of sandstone versus dolomitic limestone (Fig. 2; Wright and Mooney, 1965; Sharp and Glazner, 1997; Kruckeberg, 2002). On the sandstones of the White Mountains, treeline is well below the climatic limits where trees may survive, but on the dolomitic sites a zone of bristlecone pine (*Pinus longaeva*) extend up to the climatic limits of tree growth. The dolomitic sites are coarse and nutrient poor, but bristlecone pine is able to survive in such harsh conditions, whereas other trees and sagebrush cannot. On adjacent areas of sandstone, bristlecone pine could survive but is out-competed there, particularly by sagebrush (Wright and Mooney, 1965). Although not exclusive to treeline sites, Parker's work (1991, 1995) also illustrated the significant role of lithology in determining tree species distribution and density in the Sierra Nevada and southern Cascades of California, and Malanson and Butler (1994) argued that soil nutrient status could control treeline elevation by affecting competition between tundra and tree seedlings.

Disturbance treelines (*sensu* the orographic treelines of Holtmeier, 2003) at the within-range scale are also typically a function of underlying geologic control. In Glacier National Park, Montana, for example, the presence of the Lewis Overthrust fault along the eastern edge of the Park powerfully influences the location of the disturbance/orographic treeline produced by large-scale *bergsturz* (Fig. 3; Oelfke and Butler, 1985; Malanson and Butler, 2002). In the same area, Butler and Walsh

Fig. 3. Treeline as a function of mass movement—Yellow Mountain, Glacier National Park, MT.

(1990) and Butler and Malanson (1992) illustrated that lithology and geologic structure exerted primary control over the spatial distribution of snow-avalanche paths, themselves a spatially widespread form of orographic treeline in the Park. Butler and Walsh (1994) showed that debris flows in eastern Glacier National Park severely depress alpine treeline below a hypothetical climatic optimum, and Walsh et al. (1994) did the same for snow-avalanche paths. Both forms of mass movement are widespread throughout the West, and act throughout the region as a geomorphic constraint on the upward advance of treeline.

Within most mountain ranges in the American West, one must also note that current treeline, geomorphic processes, and soils are still adjusting to climatic change covering a variety of time scales, i.e., many ranges are in disequilibrium with current climatic conditions. The effects of the Little Ice Age are probably most prevalent at the slope scale, and are discussed below. However, at the within-range scale, many areas in the West are still adjusting to the geomorphic effects of the Pleistocene. In parts of the Sierra Nevada and Glacier National Park, Montana, the intensity of Pleistocene glaciation produced glacial landforms such as cirque headwalls (Fig. 4) that are simply not going to be invaded by trees within the foreseeable future regardless of whether the current climate would allow it (Fig. 5). Elsewhere, in the Grand Tetons, for example, deep scouring by alpine glaciers descending to the adjacent valley floor removed surface soils and exposed bedrock that has yet to recover with sufficient soils for trees to ascend to elevations where nearby trees exist in areas of deeper soil. In such a situation, conditions are slowly improving and will allow eventual tree establishment and upward movement, but at a rate

Fig. 4. Treeline as a function of glacial topography—Mt. Whitney, Sierra Nevada, CA.

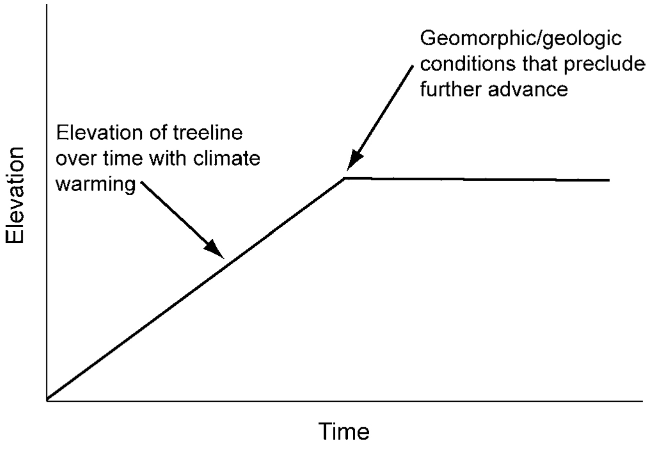

Fig. 5. An upward advance of the treeline ecotone with an ameliorating climate can be halted by unfavorable geomorphic and/or geologic factors.

slower than at sites with better soils/edaphic conditions (Fig. 6). The current-day disturbance treeline (Butler and Walsh, 1994; Walsh et al., 1994; Butler et al., 2003) also acts to preclude upward advance of treeline under currently prevailing climatic conditions.

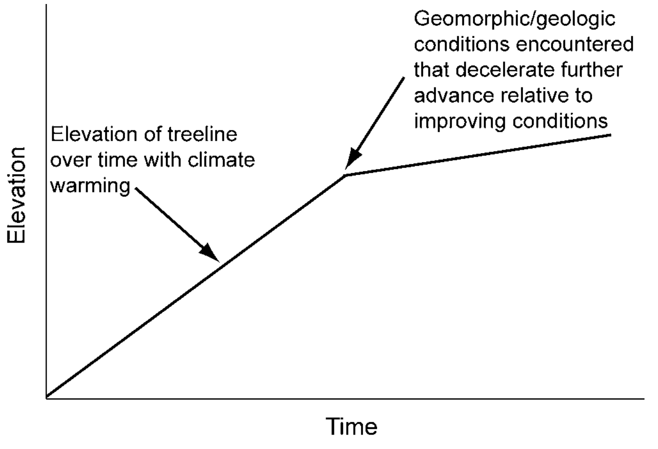

Fig. 6. An upward advance of the treeline ecotone with an ameliorating climate can be slowed by geologic and/or geomorphic factors.

Fig. 7. A relatively straight treeline ecotone may indicate climatic control—Specimen Mountain, Rocky Mountain National Park, CO.

Overall landforms also constrain the patterns that plants can develop within the ecotone because of differences in slopes extents and angles at the right elevation range. Broad gentle slopes exist just above treeline in Rocky Mountain National Park, CO, where treeline is compressed on steeper lower slopes, in contrast to the east slopes of the Snowy Range in Wyoming where treeline is spread across a broad gentle slope below the main peaks. The coincidence of current treeline elevation with landforms determined by past glaciation varies across all of western North America.

Slope Scale

At first glance, the slope scale seems to best represent the influence of climate on treeline. Locations where the upper limit of tree growth approximates a straight line (Fig. 7) suggest an upper altitudinal limit to tree growth imposed by climate

Fig. 8. A relatively straight treeline can be interrupted by avalanches or other geomorphic processes—Mount Dana, Yosemite National Park, CA.

(although even in these cases, geomorphic processes can impose a disturbance treeline upon a climatic treeline; Fig. 8). In such cases, it is posited that seedling establishment above the general horizontal treeline represents a response to changing climatic conditions (e.g., Malanson, 2001; Alftine et al., 2003; Bekker, 2005; Zeng et al., 2007). In some areas in the West, however, the landscape is still adjusting to the end of the Little Ice Age, and upward advance of treeline has *not* occurred; instead, patches of krummholz have become denser and/or taller without upward movement (Butler et al., 1994; Klasner and Fagre, 2002). Such a situation certainly could be a function of a time lag, as suggested by Malanson (1999). However, it is also feasible that the geomorphic setting in the immediate surroundings of the patches is simply inimical for survival as posited in Figures 5 and 6. Conditions immediately adjacent to the established patches were *not* colonized for a reason, whereas the patch was. We suggest that the conditions that were not appropriate for initial establishment were associated with geomorphic and geologic conditions deleterious to seedling establishment and survival.

The issue of tree seedling establishment and survival at the slope scale has been addressed in previous research of the Mountain GeoDynamics Research Group (Allen and Walsh, 1996; Malanson et al., 2002, 2007; Butler et al., 2003, 2004; Walsh et al., 2003; Resler et al., 2005; Resler, 2006; Zeng and Malanson, 2006; Zeng et al., 2007). This body of work has focused particularly on the role of

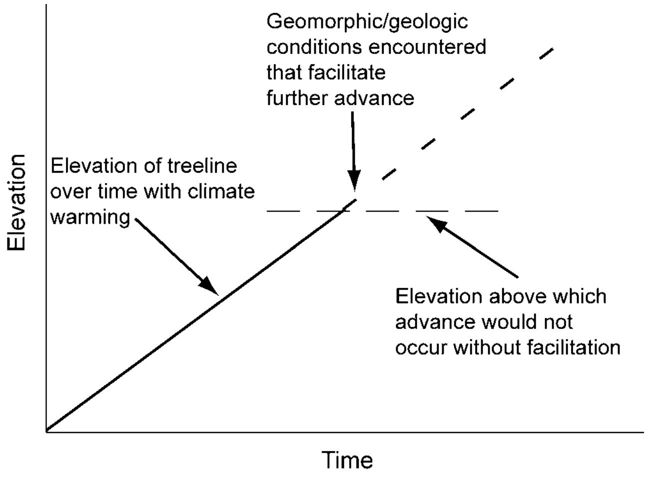

Fig. 9. An upward advance of the treeline ecotone beyond what an ameliorating climate alone would cause can be facilitated by geologic and/or geomorphic factors.

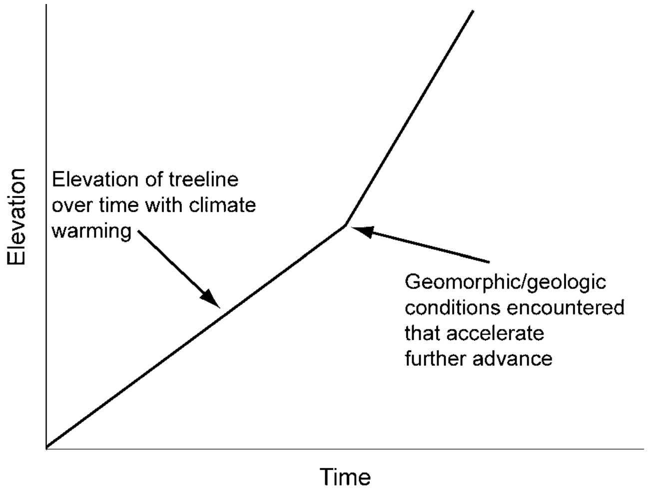

Fig. 10. An upward advance of the treeline ecotone with an ameliorating climate can be accelerated by geologic and/or geomorphic factors.

fine-scale geomorphic processes and landform features as facilitators of tree seedling establishment and survival that may allow any advance (Fig. 9) or accelerate an advance (Fig. 10). This work has illustrated that, even in locations where climate at first glance seems to be the controlling factor at treeline, fine-scale geomorphic processes and landforms ultimately dictate where a tree seedling may become successfully established; or conversely, where a seedling will find geomorphically unfavorable conditions inimical to survival.

Solifluction terraces are a relatively common landform found adjacent to treeline in many ranges in the American West (Fig. 11; e.g., Hansen-Bristow and Price,

Fig. 11. Solifluction forms, bounded by arrows, can develop at the scale of (A) a few meters (Niwot Ridge, CO) or (B) less than 1 m (Lee Ridge, MT).

Fig. 12. Grizzly bears expose surface sediments while digging for food.

1985; Caine, 2001; Walsh et al., 2003). Solifluction treads and risers are very difficult environments on which a tree seedling attempts to become established and survive; risers are comprised of dense tundra vegetation that is difficult if not impossible for seedlings to penetrate, and treads are rocky, barren, and highly susceptible to frost heaving (Butler et al., 2004). On the solifluction surfaces, turf exfoliation (also known by the German term *Rasenabschälung*) facilitates tree seedling establishment by creating fine-textured, penetrable surfaces at the base of risers (Butler et al., 2004). These sites also offer topographic protection from wind and wind-driven ice, as do randomly distributed boulders across the tundra surface, where seedling survival is enhanced (Resler et al., 2005; Resler, 2006). At this fine scale, the geomorphic conditions are what may facilitate upward establishment and migration of the treeline and accelerate the change in pattern. It is also interesting to note that the same geomorphic process (e.g., solifluction) may operate at a different scale in ranges across the West (Fig. 11), but with the same general effect on treeline.

Another slope-scale group of processes that may have profound localized effects on alpine treeline location and pattern is the work of digging by animals. Grizzly bears (*Ursus arctos horribilis*) excavate widespread surfaces on slopes in the treeline ecotone (Fig. 12; Butler, 1992; Hall and Lamont, 2003), and these excavations produce higher concentrations of forms of nitrate than in adjacent, intact meadows (Tardiff and Stanford, 1998) that may benefit tree seedlings. Clark's nutcrackers (*Nucifraga columbiana*) bury whitebark pine (*Pinus albicaulis*) seeds throughout the West from the Sierra Nevada (Tomback, 1982) to northwest Montana (Resler and

Tomback, 2008), and their choice of burial locations determines where whitebark pine seeds sprout. Those choices may, in turn, benefit from localized protection (facilitation) offered by slope-scale geomorphic processes and geologic settings such as at the base of solifluction terraces, rock outcrops, or boulders.

Numerous mammals also create widespread excavations at alpine treeline through the creation of a variety of burrow structures (Butler, 1995; Hall and Lamont, 2003), and their digging activities may have pronounced effects on nitrogen and carbon in soils there (Aho et al., 1998), but virtually no research has been done at present concerning whether or not these excavations aid or hinder tree seedling establishment and survival. Pocket gophers (Geomyidae) in particular have been examined for the role they play in affecting soils characteristics in alpine tundra adjacent to treeline (Seastedt, 2001; Sherrod and Seastedt, 2001; Forbis et al., 2004; Sherrod et al., 2005). No work exists on the roles of gopher digging, gopher mounds, or gopher-induced changes in soil characteristics as facilitators of tree seedling success at alpine treeline. Gopher mounds in Georgia (Simkin and Michener, 2004) illustrated greater longevity of longleaf pine seedlings than in the surrounding matrix, although the difference was not statistically significant. Reichman and Seabloom (2002) noted that mortality of seedlings tends to be very high on gopher mounds, because of exposure to herbivores and dry soil conditions, but they were not specifically addressing tree seedlings. They also pointed out that individual seedlings that survive on mounds are larger and produce more seeds than similar plants embedded in the surrounding plant matrix. Forbis et al. (2004) illustrated that recently created gopher mounds on Niwot Ridge, CO, had lower seedling emergence and survival rates than undisturbed areas in the first five years after mound creation, but also that the mounds had higher seedling emergence density from five years to at least 20 years after disturbance. The study by Forbis et al. (2004) was carried out in alpine tundra, however, and no tree seedlings were found in their seedlings that emerged on gopher mounds. Would mounds in the immediate treeline ecotone show tree seedling emergence and survival? Schütz (2005) examined the question of whether gopher digging damaged young trees on Niwot Ridge, and found no evidence exists that pocket gophers are responsible for visible damage on juvenile conifers there. Given the potential significance of gopher mounds as a geomorphic facilitator or inhibiter at alpine treeline, we suggest that they merit greater examination.

CONCLUSIONS

We are not dismissing the concept of climatic treeline here. Indeed, horizontal, roughly straight-line, treelines such as those illustrated in Figure 7 reflect a primary climatic control. Treelines such as these typically occur in areas of relatively uniform geologic conditions, particularly in areas of homogeneous granitic lithology such as typify parts of the Sierra Nevada and Colorado Rockies where Pleistocene glacial scouring was limited in extent and severity, and where upward advancement of treeline is neither hindered nor facilitated by geomorphic or geologic conditions.

We are, however, emphasizing that treelines throughout the American West are, in many more cases than traditionally recognized, strongly controlled by geological history, geologic structure, lithology, geomorphic processes, and landforms. Furthermore, the distribution of many of the landforms that influence the location and pattern of alpine treeline are themselves directly controlled by geologic structure and lithology. Disequilibrium conditions associated with the profound impacts of Pleistocene glaciation further illustrate the significance of geomorphic processes in controlling present-day treeline. Figure 5 summarizes the situation where geologic and/or geomorphic conditions utterly preclude upward migration of treeline, and Figure 6 does so for situations where upward migration is slow, inhibited by current or past (disequilibrium) conditions, and likely not to be geographically widespread. Even at the slope scale, where a first glance may reveal a relatively uniform, horizontal treeline, we urge a closer inspection. At this scale, the specific location of present-day seedlings is likely the result of fine-scale geomorphic facilitation (*sensu* Butler et al., 2004; Resler et al., 2005) that allows upward migration at an accelerated rate compared to the surrounding landscape. The fine-scale geomorphic effects of digging by animals may serve to facilitate or inhibit seedling establishment on treeline, and "the jury is still out" on which situation is more likely (or if both may occur under varying, site-specific conditions). Future research is needed to expand our knowledge of the significance of animal excavations as facilitators or inhibitors of seedling success in the alpine treeline ecotone.

The relations between geology and geomorphology and the ecological processes and patterns of the treeline ecotone will also change with changing climate in any one place. If a treeline elevation shifts, it may move into an area of different landforms at the within-range scale. Of equal interest will be how changes in climate can affect slope-scale processes such as solifluction and animal activity, which would then change how plants respond to the climate change. In any case, interpretation of the scale dependent influence of geology and geomorphology is necessary to understanding treeline pattern and process because, depending on scale, the influence can be a constraint or a facilitation.

Acknowledgments: This paper is a Contribution of the Mountain GeoDynamics Research Group. Funding for fieldwork came from the USGS Biological Resources Division, Global Change Program's *Western Mountain Initiative*, through the office of Dan Fagre and the Glacier Field Station. The National Park Service provided research permits and access to Glacier, Rocky Mountain, Sequoia/Kings Canyon, Olympic, and North Cascades National Parks. Tim Seastedt organized and hosted an excellent tour of the INSTAAR facilities and landscape of Niwot Ridge, Colorado, and Nel Caine graciously shared his extensive geomorphological experience on Niwot Ridge with us. The field assistance of Dan Weiss, Zehao Shen, Darren Grafius, and Will Butler is gratefully acknowledged.

REFERENCES

Aho, K., Huntly, N., Moen, J., and Oksanen, T. (1998) Pikas (*Ochotona princeps*: Lagomorpha) as allogenic engineers in an alpine ecosystem. *Oecologia*, Vol. 114, 405–409.

Alftine, K. J., Malanson, G. P., and Fagre, D. B. (2003) Feedback-driven response to multi-decadal climatic variability at an alpine forest-tundra ecotone. *Physical Geography*, Vol. 24, 520–535.

Allen, T. R. and Walsh, S. J. (1996) Spatial and compositional pattern of alpine treeline, Glacier National Park, Montana. *Photogrammetric Engineering and Remote Sensing*, Vol. 62, 1261–1268.

Bekker, M. F. (2005) Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, Vol. 37, No. 1, 97–107.

Butler, D. R. (1992) The grizzly bear as an erosional agent in mountainous terrain. *Zeitschrift für Geomorphologie*, Vol. 36, No. 2, 179–189.

Butler, D. R. (1995) *Zoogeomorphology—Animals as Geomorphic Agents*. Cambridge, UK: Cambridge University Press.

Butler, D. R. and Malanson, G. P. (1992) Effects of terrain on excessive travel distance by snow avalanches. *Northwest Science*, Vol. 66, No. 2, 77–85.

Butler, D. R., Malanson, G. P., Bekker, M. P., and Resler, L. M. (2003) Lithologic, structural, and geomorphic controls on ribbon forest patterns. *Geomorphology*, Vol. 55, No. 1–4, 203–217.

Butler, D. R., Malanson, G. P., and Cairns, D. M. (1994) Stability of alpine treeline in Glacier National Park, Montana, USA. *Phytocoenologia*, Vol. 22, 485–500.

Butler, D. R., Malanson, G. P., and Resler, L. M. (2004) Turf-banked terrace treads and risers, turf exfoliation, and possible relationships with advancing treeline. *Catena*, Vol. 58, 259–274.

Butler, D. R., and Walsh, S. J. (1990) Lithologic, structural, and topographic influences on snow-avalanche path location, eastern Glacier National Park, Montana. *Annals of the Association of American Geographers*, Vol. 80, 362–378.

Butler, D. R. and Walsh, S. J. (1994) Site characteristics of debris flows and their relationship to alpine treeline. *Physical Geography*, Vol. 15, 181–199.

Caine, N. (2001) Geomorphic systems of Green Lakes valley. In W. D. Bowman and T. R. Seastedt, eds., *Structure and Function of an Alpine Ecosystem—Niwot Ridge, Colorado*. New York, NY: Oxford University Press, 45–74.

Forbis, T. A., Larmore, J., and Addis, E. (2004) Temporal patterns in seedling establishment on pocket gopher disturbances. *Oecologia*, Vol. 128, 112–121.

Hall, K. and Lamont, N. (2003) Zoogeomorphology in the Alpine: Some observations on abiotic-biotic interactions. *Geomorphology*, Vol. 55, No. 1–4, 219–234.

Hansen-Bristow, K. J. and Price, L. W. (1985) Turf-banked terraces in the Olympic Mountains, Washington, U.S.A. *Arctic and Alpine Research*, Vol. 17, No. 3, 261–270.

Holtmeier, F. K. (2003) *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Dordrecht, The Netherlands: Kluwer.

Holtmeier, F. K. and Broll, G. (2005) Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, Vol. 14, 395–410.

Klasner, F. L. and Fagre, D. B. (2002) A half century of change in alpine treeline patterns at Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, Vol. 34, 49–56.

Korner, C. and Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, Vol. 31, 713–732.

Kruckeberg, A. R. (2002) *Geology and Plant Life*. Seattle, WA: University of Washington Press.

Malanson, G. P. (1999) Considering complexity. *Annals of the Association of American Geographers*, Vol. 89, 746–753.

Malanson, G. P. (2001) Complex responses to global change at alpine treeline. *Physical Geography*, Vol. 22, 333–342.

Malanson, G. P. and Butler, D. R. (1994) Tree-tundra competitive hierarchies, soil fertility gradients, and the elevation of treeline in Glacier National Park, Montana. *Physical Geography*, Vol. 15, 166–180.

Malanson, G. P. and Butler, D. R. (2002) The Western Cordillera. In A. Orme, ed., *The Physical Geography of North America*. Oxford, UK: Oxford University Press, 363–379.

Malanson, G. P., Butler, D. R., Cairns, D. M., Welsh, T. E., and Resler, L. M. (2002) Variability in an edaphic indicator in alpine tundra. *Catena*, Vol. 49, 203–215.

Malanson, G. P., Butler, D. R., and Fagre, D. B. (2007) Alpine ecosystem dynamics and change: A view from the heights. In T. Prato and D. Fagre, eds., *Sustaining Rocky Mountain Landscapes: Science, Policy and Management for the Crown of the Continent Ecosystem*. Washington, DC: RFF Press, 85–101.

Malanson, G. P., Butler, D. R., Fagre, D. B., Walsh, S. J., Tomback, D. F., Daniels, L. D., et al. (2007, in this issue) Alpine treeline of western North America: Linking organism-to-landscape dynamics. *Physical Geography*, Vol. 28, 378–396.

Oelfke, J. G. and Butler, D. R. (1985). Landslides along the Lewis Overthrust Fault, Glacier National Park, Montana. *The Geographical Bulletin*, Vol. 27, 7–15.

Parker, A. J. (1991) Forest/environment relationships in Lassen Volcanic National Park, California, U.S.A. *Journal of Biogeography*, Vol. 18, 543–552.

Parker, A. J. (1995) Comparative gradient structure and forest cover types in Lassen Volcanic and Yosemite National Parks, California. *Bulletin of the Torrey Botanical Club*, Vol. 122, 58–68.

Reichman, O. J. and Seabloom, E. W. (2002) The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology and Evolution*, Vol. 17, 44–49.

Resler, L. M. (2006) Geomorphic controls of spatial pattern and process at alpine treeline. *The Professional Geographer*, Vol. 58, 124–138.

Resler, L. M., Butler, D. R., and Malanson, G. P. (2005) Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography*, Vol. 26, 112–125.

Resler, L. M. and Tomback, D. F. (2008) Blister rust prevalence in krummholz whitebark pine: Implications for treeline dynamics, Northern Rocky Mountains, Montana, USA. *Arctic, Antarctic, and Alpine Research*, Vol. 40, No. 1, 161–170.

Schütz, H-U. (2005) Pocket gopher—Actor under the stage. Studies on Niwot Ridge, Colorado Front Range, U.S.A. In G. Broll and B. Keplin, eds., *Mountain Ecosystems—Studies in Treeline Ecology*. Berlin, Germany: Springer, 153–180.

Seastedt, T. R. (2001) Soils. In W. D. Bowman and T. R. Seastedt, eds., *Structure and Function of an Alpine Ecosystem—Niwot Ridge, Colorado*. New York, NY: Oxford University Press, 157–173.

Sharp, R. P. and Glazner, A. F. (1997) *Geology Underfoot in Death Valley and Owens Valley*. Missoula, MT: Mountain Press Publishing Company.

Sherrod, S. K. and Seastedt, T. R. (2001) Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry*, Vol. 55, 195–218.

Sherrod, S. K., Seastedt, T. R., and Walker, M. D. (2005) Northern pocket gopher (*Thomomys talpoides*) control of alpine plant community structure. *Arctic, Antarctic, and Alpine Research*, Vol. 37, 585–590.

Simkin, S. M. and Michener, W. K. (2004) Mound microclimate, nutrients and seedling survival. *American Midland Naturalist*, Vol. 152, 12–24.

Tardiff, S. E. and Stanford, J. A. (1998) Grizzly bear digging: Effects on subalpine meadow plants in relation to mineral nitrogen availability. *Ecology*, Vol. 79, 2219–2228.

Tomback, D. F. (1982) Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. *Journal of Animal Ecology*, Vol. 51, 451–467.

Walsh, S. J., Butler, D. R., Allen, T. R., and Malanson, G. P. (1994) Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science*, Vol. 5, 657–672.

Walsh, S. J., Butler, D. R., Malanson, G. P., Crews-Meyer, K. A., Messina, J. P., and Xiao, N. (2003) Mapping, modeling, and visualization of the influences of geomorphic processes on the alpine treeline ecotone, Glacier National Park, Montana, USA. *Geomorphology*, Vol. 53, No. 1–2, 129–145.

Wiegand, T., Camarero, J. J., Rüger, N., and Gutiérrez, E. (2006) Abrupt population changes in treeline ecotones along smooth gradients. *Journal of Ecology*, Vol. 94, 880–892.

Wright, R. D. and Mooney, H. A. (1965) Substrate-oriented bristlecone pine in the White Mountains of California. *American Midland Naturalist*, Vol. 73, 257–284.

Zeng, Y. and Malanson, G. P. (2006) Endogenous fractal dynamics at alpine treeline ecotones. *Geographical Analysis*, Vol. 38, 271–287.

Zeng, Y., Malanson, G. P., and Butler, D. R. (2007) Geomorphological limits to self-organization of alpine forest-tundra ecotone vegetation. *Geomorphology*, Vol. 91, No. 3–4, 378–392.