

INFLUENCES OF ANIMAL ACTIVITY ON TREELINE POSITION  
AND PATTERN: IMPLICATIONS FOR TREELINE RESPONSES  
TO CLIMATE CHANGE

*David M. Cairns and Charles Lafon*  
**Department of Geography**  
**Texas A&M University**  
**College Station, Texas 77843-3147**

*Jon Moen*  
**Department of Ecology and Environmental Science**  
**Umeå University**  
**SE-901 87 Umeå**  
**Sweden**

*Amanda Young*  
**Department of Geography**  
**Texas A&M University**  
**College Station, Texas 77843-3147**

*Abstract:* The alpine treeline is a potentially sensitive indicator of vegetation response to climate change. However, there is not a generally accepted single hypothesis that explains treeline position and pattern at multiple scales. Recently a set of five hypotheses has been proposed for treeline explanations (Körner, 2003b). The impacts of animals are not explicitly included in any of these hypotheses, however, they can and should be included. In this review we discuss Körner's five hypotheses and explain how animal activity can be included within them to make them more applicable to treeline environments experiencing a changing climate. We utilize the conceptual model proposed by Cairns and Moen (2004) as an organizing framework for the inclusion of animal activity with existing hypotheses. Finally we suggest that the equivocal nature of treeline response to climate change may be in part related to animal activity. [Key words: alpine treeline, herbivory, climate change.]

## INTRODUCTION

The Earth's climate is expected to change considerably in the near future. Global temperatures are predicted to rise between 1.4°C and 4.4°C over the next century, and precipitation patterns are also expected to be altered (Allen et al., 2000; Boer et al., 2000; Dai et al., 2001). Changes are expected to be greatest near the poles and more moderate in the tropics. Vegetation communities are thought to be in quasi-equilibrium with climate; as climate changes, so should vegetation communities (Walther et al., 2002). Many vegetation communities may exhibit predictable changes in location, species composition, biomass, and pattern on the landscape. Such changes are expected to be most visible at ecotones between adjacent

vegetation types, because at these locations small changes in environmental conditions are likely to push vegetation communities from one stable state to another (Hansen et al., 1988).

One ecotone of particular interest in this regard is the forest-tundra transition, because it has the potential to be a sensitive bioindicator of climate change (Kupfer and Cairns, 1996; Kullman, 1998; Burga and Perret, 2001) and it can be viewed as an analog to other zonal biome transitions (Stevens and Fox, 1991). Transitions between forest and tundra occur in both Arctic and alpine locations. In both cases, as the thermal environment becomes more severe there is a switch from the arboreal growth forms of a low-latitude or low-elevation forest to short-stature tundra. This transition may be gradual or sharp and may include an intermediate shrub-like growth form of trees in a matrix of tundra. In this paper, we use the term "treeline" to describe the ecotone between the timberline and the tree limit. The timberline is the altitudinal or latitudinal limit of continuous forest, while tree limit is the altitudinal or latitudinal limit of tree-forming individuals, which may be scattered among tundra vegetation.

Predictions of how treelines will respond to changing climates routinely concentrate on the effects of climate (e.g., Cairns and Malanson, 1997; Bekker et al., 2001; Moen et al., 2004) but rarely consider the influence of animals. Animal activity in a wide range of environments has been hypothesized to have effects at least as important as climate in the shifting of major ecotones (e.g., Zimov et al., 1995). Niemela et al. (2001) argue that understanding the response of northern forests to climate change can not be achieved without considering the effects of herbivores. Payette et al. (2002) similarly urge that future research should concentrate on finding nonclimatic factors that influence treeline migrations. Yet very little is known about how animal activity may limit or augment contemporary treeline response to climate change. Therefore, in this paper we discuss the importance of animal activity for each of the major treeline hypotheses currently being debated (Körner, 2003a). Our discussion is based on the conceptual model proposed by Cairns and Moen (2004) for treelines.

#### DETERMINANTS OF TREELINE POSITION AND PATTERN

There is no single accepted explanation for the formation of treelines. Treelines occur worldwide under climatic conditions that are both seasonal and aseasonal, thereby complicating the search for an explanation of their formation. Körner (2003a) proposed separating the drivers of treeline formation into two categories: modulative (regional) and fundamental (global). The global drivers are those that can be applied to worldwide treelines. Currently there are five general hypotheses related to these global drivers that are being debated. The stress hypothesis holds that repeated damage to trees such as from freezing, desiccation or phototoxic effects limits the expression of the arboreal growth form above a certain elevation. A related hypothesis focuses on disturbance and relies on mechanical damage, pathogens, and herbivory to explain treelines. The key process in this hypothesis is the removal of biomass from trees in amounts that are detrimental to tree survival. The reproduction hypothesis focuses on the regeneration of trees. For this

hypothesis, any or all stages between pollen production and seedling establishment (including germination, dispersal, and seed development) are limited, thereby preventing the recruitment of seedlings at high elevations. Carbon balance is also hypothesized to control treeline elevation. The carbon balance hypothesis states that treeline occurs where either the uptake of carbon or carbon uptake less losses of carbon due to senescence and damage is not enough to support the maintenance and growth demands of a tree (cf. Cairns and Malanson, 1998). Finally, treelines may be due to growth limitations. Under this hypothesis, the amounts of photosynthetic input to the tree are sufficient to keep the tree alive, but growth processes are limited and do not meet the minimum growth requirements necessary to keep the tree alive. Animal activity may act as a modulative driver under any of these hypotheses.

### CONCEPTUAL MODEL OF ANIMAL/TREELINE INTERACTIONS

Cairns and Moen (2004) proposed a conceptual model that summarizes the modes of interaction of animals and arboreal vegetation at the forest tundra ecotone. Three types of interaction were proposed. Type 1 responses are those where the field layer vegetation is more palatable to animals than the arboreal vegetation. In these cases, when animal activity is low, growth of the field layer vegetation is relatively unimpaired and competition between herbaceous plants and trees (especially seedlings) is high resulting in a low upslope migration potential of the treeline. Type 2 responses occur when the relative palatability of the vegetation at treeline is shifted toward the trees. In these cases, animal populations preferentially consume the foliage, buds and stems of trees rather than the field layer vegetation. Growth may be limited in these cases due to a reduction of photosynthetically active tissue thereby inhibiting the growth and reproduction of trees at all stages from seedling to sapling to adult. Cairns and Moen (2004) also present an intermediate case (designated Type 3) in which the migration potential of treelines is highest at intermediate levels of animal activity. This last case represents tradeoffs between the positive and negative impacts of animals with regard to migration potential. At low levels of animal activity, migration is relatively low due to the lack of site preparation either due to mechanical disturbance of the soil or because under low animal activity the field layer plants outcompete the trees. Also, for species that are dispersed by animals, low levels of animal activity would inhibit their ability to migrate. At high levels of animal activity the consumption of foliage or seeds by animals restricts their ability to grow, produce seeds, and disperse to new sites thereby reducing their migration potential. Type 3 responses are likely influenced by multiple animal species.

Cairns and Moen (2004) presented examples of Type 1 and Type 2 responses. Deciduous treelines such as those found in northern Fennoscandia are expected to exhibit Type 2 responses to animal activity due to reindeer herbivory. *Pinus sylvestris* treelines were presented as an example of a treeline likely to show a Type 1 response.

## THE HYPOTHESES

The hypotheses discussed below utilize terminology as put forth by Körner (2003a). The definitions of stress and disturbance are therefore somewhat different from the standard definitions proposed by Grime (2001) where disturbance is defined as any mechanism that limits plant biomass by causing its partial or total destruction in contrast to stress which is defined as external constraints that limit the rate of dry matter production. Because in this review we are concerned with the hypotheses proposed by Körner (2003a) we chose to utilize his terminology.

### *Stress Hypothesis*

Trees at their upper elevational limit are living in a stressful environment where small increases in the amount of stress that they endure may result in their demise. The treeline could therefore be controlled primarily by these stresses. The stresses most commonly cited as potential controlling factors at treeline are freezing and desiccation. Freezing can kill large portions of the overwintering canopy due to either extremely low temperatures (Wardle, 1981) or due to precocious dehardening (Hadley et al., 1991; Perkins et al., 1991; Strimbeck et al., 1995). Desiccation stress develops during the winter due to insufficient maturation of the cuticle (DeLucia and Berlyn, 1984; Herrick and Friedland, 1991), cuticular abrasion by wind-blown snow (Hadley and Smith, 1986), or stomatal damage (Grace, 1990; van Gardingen et al., 1991). In all cases, the amount of damage sustained by the trees is variable both within the canopies and within the broader forest—tundra transition (Cairns, 2001).

The activity of animals within the treeline ecotone can influence the ability of trees to survive these stresses. These effects can be either direct or indirect. Direct effects of animals would be those in which the activity of the animal reduces the vigor of the tree thereby predisposing it to damage and subsequent death. There are cases where the feeding of an herbivore on a tree at treeline during one season reduces the foliage quality in the subsequent growing season (e.g., Asshoff and Hattenschwiler, 2006) but there are no reported cases where this reduction in foliage quality significantly affects the ability of foliage to survive harsh treeline winter conditions.

A more likely pathway for animals to influence treeline position or pattern under the stress hypothesis would be through some indirect route. For example, animal activity may lead to an opening up of the ecotone due to consumption of foliage either of the trees or the shrubs and field layer plants. More open vegetation would have greater exposure to wind, hence would be more stressful. This would be most evident when woody shrubs are major components of the ecotone. Shrubs have the potential to trap blowing snow (Sturm et al., 2001; Mcguire et al., 2003; Sturm et al., 2005) thereby providing protection from exposure to extremely cold temperatures and desiccation stress. Cairns (2001) documented patterns of winter desiccation damage in subalpine fir *krummholz* patches at treeline in Glacier National Park, Montana and noted that desiccation was nearly always greatest on the windward side of *krummholz* patches. While shrubs are not a particularly important

component of the treeline in the Rocky Mountains, they are in other treeline environments (e.g., Scandinavia) where their presence could significantly alter the pattern of snow accumulation within the ecotone.

### *Disturbance Hypothesis*

The disturbance hypothesis relies on the mechanical damage of trees to explain the treeline. Under this hypothesis, the structure of the trees and their life history traits are detrimental to survival above the treeline when disturbed. Disturbances likely to have an effect on the trees are damage due to high winds and snow/ice blasting (Marchand, 1991; Kullman, 2005), animal activities, fire (Noble, 1993; Proctor et al., 2007), human activities (Baker and Moseley, 2007), disease outbreaks (Arno and Hammerly, 1984; Shen et al., 2001; Holtmeier, 2003), and mass wasting events such as avalanches and debris flows (Butler et al., 1992; Butler and Walsh, 1994; Walsh et al., 2003). The expression of such disturbances within the treeline ecotone can be either ubiquitous or localized. For example, the presence of high winds at the treeline may be a relatively ubiquitous disturbance within a region whereas avalanches and debris flows would have a more limited expression.

We interpret animal activity to fit into this hypothesis when the damage to trees is fatal, for example, when trampling breaks the primary stem of a tree, or when the entire tree is consumed. Cases of animal damage or herbivory that do not kill the tree directly are considered under the reproduction hypothesis and the carbon balance hypothesis below. Mortality-causing events are uncommon at treeline and in the case of consumption of the entire tree are confined to the juvenile stages of the trees' development. In *Polylepis* forests in the Andes, trampling of seedlings by cattle was proposed as a possible explanation for treeline (Cierjacks et al., 2008). However, no evidence existed for such an influence at the relatively low cattle densities. Higher densities of cattle could, however, inhibit the growth of *Polylepis* at treeline. Similarly, Pérez (1992) suggested that consumption of seedlings of an Andean paramo rosette (*Coespeletia timotensis*) by cattle may inhibit the reproduction and survival of the species. Moreover, damage to larger *C. timotensis* plants by cattle browsing and rubbing may contribute to mortality or reduced plant vigor. Animals may contribute indirectly to tree mortality by slope failures, for example, because of slope loading by large mammals or slope undermining by digging animals (Hall and Lamont, 2003).

Insect herbivory that causes the death of the trees is the most widely reported mode of animal activity that fits within the disturbance hypothesis. The autumnal moth (*Epirrita autumnata*) in Scandinavia attacks mountain birch (*Betula pubescens* ssp. *czerepanovii*) at treeline, leaving behind stands of dead trees and a depressed treeline (Nuorteva, 1963; Kallio and Lehtonen, 1973; Fig. 1). Over a more limited spatial extent at a tropical coniferous treeline, Biondi et al. (2005) found that an outbreak of roundheaded pine beetle (*Dendroctonus adjunctonus* Blandford) killed most of the trees at one of their study sites.

These treelines would be typical Type 2 treelines where higher densities of herbivores slow the migration rate of the treeline. Conversely, disturbance by animals could favor trees by causing field layer mortality (i.e., Type 1 response). Animal



**Fig. 1.** A mountain birch (*Betula pubescens* ssp. *czerepanovii*) treeline forest that has recently been severely defoliated by the autumnal moth (*Epirrita autumnata*) near the border of Sweden and Norway west of Abisko.

digging, trampling, and browsing have been demonstrated to kill tundra plants and provide open sites (e.g., Butler, 1995; Tardiff and Stanford, 1998), which could be colonized by trees.

### *Reproduction Hypothesis*

In order for the treeline to advance upslope, tree seeds must be able to reach upslope locations, germinate, and grow beyond the seedling and sapling stages into mature trees. Smith et al. (2003) have stressed the importance of seedlings and processes that affect them rather than adult trees as determinants of the treeline position. All three treeline types proposed by Cairns and Moen (2004) are relevant for reproduction limited treelines.

One mode of interaction between animals and the regeneration of trees occurs when the animals act as dispersal agents for the tree seeds. This mode of interaction would have the most impact on ecto- and endo-zoochorous species. Birds are the primary agents of dispersal at treeline (Tranquillini, 1979).

When animals consume large numbers of seeds, the migration potential of a treeline species would be limited due to the reduction of new immigrants to an area. Seed predation has been hypothesized as a major control on the regeneration of Scots pine (*Pinus sylvestris*) at Spanish treelines (Castro et al., 1999), but has been shown to be negligible at *Polylepis* treelines in South America (Cierjacks et al., 2008).

The establishment of trees within the current treeline ecotone and above it may be limited by competition between existing vegetation and invading seedlings (Malanson and Butler, 1994; Hobbie and Chapin, 1998; Moir et al., 1999; Dullinger et al., 2003). Camarero and Gutierrez (2007) attributed the lack of substantial expansion of *Pinus uncinata* treelines in Spain to competition between existing herbaceous vegetation and tree seedlings. Competition by field layer vegetation can be reduced by grazing (Castro et al., 2002). If the relative palatability of the field layer vegetation is greater than that of the trees, animals may increase the migration rate of trees into the upslope tundra under a warmed climate, following the Type 1 response proposed by Cairns and Moen (2004).

Large herbivores may inhibit the ability of seedlings to establish by compacting the soil. Soil compaction by herbivores has been shown to influence establishment in other vegetation systems (den Herder et al., 2003; Cuevas and Le Quesne, 2006), but has yet to be demonstrated at alpine treeline. In some cases, the effect of large animals in a system may be to reduce existing vegetation cover, thereby increasing soil temperatures and facilitating vascular plant growth (van der Wal and Brooker, 2004). Digging and burrowing by both large animals (e.g., grizzly bears, *Ursus arctos horribilis*) and small animals (e.g., northern pocket gophers, *Thomomys talpoides*) also expose soils to higher insolation, which enhances soil temperatures (Tardiff and Stanford, 1998; Sherrod and Seastedt, 2001). Körner (2003a) has proposed that soil temperatures are important determinants of the treeline elevation worldwide; higher soil temperatures due to animal activity above the present treeline might foster increased tree establishment and accelerated upslope/poleward migration of treeline. Further, these animal impacts on soils alter nutrient availability, expose the soil to erosion, and contribute to redistribution of soil mass and nutrients (e.g., Butler, 1995; Sherrod and Seastedt, 2001). For example, Tardiff and Stanford (1998) found that nitrogen availability was higher in grizzly bear digs than in undisturbed meadows. Such influences on soil condition could create sites favorable for tree seedling establishment.

Finally, for many treelines, the primary mode of plant/animal interaction at the seedling stage is through herbivory (Type 2 treelines). Coppiced forms of mountain birch are common within the treeline ecotone in Fennoscandia where populations of reindeer or sheep are high (Oksanen et al., 1995; Hofgaard, 1997). The form of the mountain birch treeline (i.e., whether abrupt or gradual) has been linked to herbivory (Oksanen et al., 1995). In South America, guanaco (*Lama guanicoe*) herbivory can be high on seedlings of *Nothofagus* spp. and has been suggested to prevent treeline advance under a warming climate (Cuevas, 2002). For Finnish treelines, reindeer browsing has been associated with low seedling survival of mountain birch in the 50–100 cm height range (Helle, 2001). At *Pinus leucodermis* treelines in southern Italy, the reduction in grazing pressure over the past 30 years has contributed to an increase in the number of saplings (Todaro et al., 2007).

### *Carbon Balance Hypothesis*

Carbon balance is defined as the difference between photosynthetic inputs to the vegetation system and the balancing outflows of carbon due to respiration and



**Fig. 2.** Reindeer (*Rangifer tarandus*) browsing mountain birch (*Betula pubescens* ssp. *czerepanovii*) at the treeline in northern Sweden.

tissue loss. The carbon balance hypothesis has been evaluated for treelines in Montana using a simulation modeling approach (Cairns and Malanson, 1997, 1998). Under the carbon balance hypothesis, animals may influence carbon balance directly through the removal of tissue from the system (Fig. 2), or indirectly due to a reduction of photosynthesis subsequent to the consumption of foliage. Treelines controlled by carbon balance are Type 2 treelines (sensu Cairns and Moen, 2004).

Because carbon balance is important in determining annual growth of trees, any factors that reduce the ability of trees to sequester carbon through photosynthesis should be evident as reduced growth. Annual tree-ring increment in treeline environments is sensitive to a suite of climatic conditions (Innes, 1991; Lloyd and Graumlich, 1997; Linderholm, 2002; Lloyd and Fastie, 2002). However, the influence of herbivory on tree growth can be strong (Trotter et al., 2002; Zhang and Alfaro, 2002), and must also be considered when interpreting the dynamics of tree growth at treeline.

Outbreaks of the autumnal moth occur on a cycle of approximately 10 years in Scandinavian treeline environments (Sonesson and Hoogesteger, 1983; Hoogesteger and Karlsson, 1992). These outbreaks usually occur at the beginning of the growing season and can result in severe defoliation of mountain birch. Experimental research has shown that simulated moth defoliation has a significant impact on radial growth of mountain birch (Hoogesteger and Karlsson, 1992; Karlsson et al., 2004). Annual ring-width in the year of defoliation is severely reduced, and the



reduction continues to be evident for 2–3 years following the defoliation (Hoogesteger and Karlsson, 1992). Growth release subsequent to outbreaks is also evident in tree-ring records because of the increased amount of light available to new foliage (Eckstein et al., 1991).

### *Growth Hypothesis*

The growth hypothesis is the least affected by herbivory of all the major hypotheses discussed here. Under the growth hypothesis, carbon balances at treeline are positive, but growth limitations prevent the upslope advance of trees (Körner, 1998). These growth limitations usually are attributed to low temperatures preventing the transformation of nonstructural carbon to structural carbon. These kinds of limitation have been observed for treelines in the European Alps (Hoch et al., 2002; Körner, 2003b), the Tibetan Plateau (Shi et al., 2006), and for the Andes (Hoch and Körner, 2005; Piper et al., 2006). Because the hypothesized mechanism of treeline control is primarily related to the biochemistry of the growth process, there is little opportunity for animals to play a role in treeline determination under this hypothesis.

## CONCLUSION

Körner (2003a) argues that the current position of the treeline reflects an integration of processes occurring over centuries and therefore is not in equilibrium with contemporary climate. The consequence of this is that treeline position should be used with caution as an indicator of climate change. Although Körner does not consider animal activities explicitly in his explanation of treelines, it is clear that animals may have modulatory effects on treelines in a variety of environments. This has been particularly clear for managed ecosystems where the removal of animals has led to an increase in seedling establishment above the current treeline (Stutzer, 2000) which will presumably lead to its upslope advance (Camarero and Gutierrez, 2007; Gehrig-Fasel et al., 2007; Todaro et al., 2007). When choosing monitoring locations for the impacts of climate change, care should be taken to ensure that the treeline is not controlled by factors, such as herbivory or other animal influences, that are unrelated or only indirectly related to climate. This has previously been noted for the Swedish and Norwegian Scandes (Hofgaard, 1997; Dalen and Hofgaard, 2005), but our synthesis of the literature suggests that the issue of animal activity at treeline is more widespread and may have both positive and negative effects on the migration potential of treeline trees.

## REFERENCES

- Allen, M. R., Stott, P. A., Mitchell, J. F. B., Schnur, R., and Delworth, T. L. (2000) Quantifying the uncertainty in forecasts of anthropogenic climate change. *Nature*, Vol. 407, 617–620.
- Arno, S. F. and Hammerly, R. P. (1984) *Timberline: Mountain and Arctic Forest Frontiers*. Seattle, WA: The Mountaineers.

- Asshoff, R. and Hattenschwiler, S. (2006) Changes in needle quality and larch bud moth performance in response to CO<sub>2</sub> enrichment and defoliation of treeline larches. *Ecological Entomology*, Vol. 31, 84–90.
- Baker, B. B. and Moseley, R. K. (2007) Advancing treeline and retreating glaciers: Implications for conservation in Yunnan, P.R. China. *Arctic, Antarctic, and Alpine Research*, Vol. 39, 200–209.
- Bekker, M. F., Malanson, G. P., Alftine, K. J., and Cairns, D. M. (2001) Feedback and pattern in computer simulations of the alpine treeline ecotone. In A. C. Millington, S. J. Walsh, and P. E. Osborne, eds., *GIS and Remote Sensing Applications in Biogeography and Ecology*. Boston, MA: Kluwer Academic Publishers, 123–138.
- Biondi, F., Hartsough, P. C., and Estrada, I. G. (2005) Daily weather and tree growth at the tropical treeline of North America. *Arctic, Antarctic, and Alpine Research*, Vol. 37, 16–24.
- Boer, G. J., Flato, G., and Ramsden, D. (2000) A transient climate change simulation with greenhouse gas and aerosol forcing: Projected climate to the twenty-first century. *Climate Dynamics*, Vol. 16, 427–450.
- Burga, C. A. and Perret, R. (2001) Monitoring of eastern and southern Swiss alpine timberline ecotones. In C. A. Burga and A. Kratochwil, eds., *Biomonitoring: General and Applied Aspects on Regional and Global Scales*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 179–194.
- Butler, D. R. (1995) *Zoogeomorphology: Animals as Geomorphic Agents*. Cambridge, UK: Cambridge University Press.
- Butler, D. R., Malanson, G. P., and Walsh, S. J. (1992) Snow avalanche paths: Conduits from the periglacial alpine to the subalpine-depositional zone. In J. C. Dixon and A. D. Abrahams, eds., *Periglacial Geomorphology*. New York, NY: John Wiley and Sons, 185–202.
- 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.
- Cairns, D. M. (2001) Patterns of winter desiccation in krummholz forms of *Abies lasiocarpa* at treeline sites in Glacier National Park, Montana, USA. *Geografiska Annaler*, Vol. 83A, 157–168.
- Cairns, D. M. and Malanson, G. P. (1997) Examination of the carbon balance hypothesis of alpine treeline location in Glacier National Park, Montana. *Physical Geography*, Vol. 18, 125–145.
- Cairns, D. M. and Malanson, G. P. (1998) Environmental variables influencing carbon balance at the alpine treeline ecotone: A modeling approach. *Journal of Vegetation Science*, Vol. 8, 679–692.
- Cairns, D. M. and Moen, J. (2004) Herbivory influences tree lines. *Journal of Ecology*, Vol. 92, 1019–1024.
- Camarero, J. J. and Gutierrez, E. (2007) Response of *Pinus uncinata* recruitment to climate warming and changes in grazing pressure in an isolated population of the Iberian system (NE Spain). *Arctic, Antarctic, and Alpine Research*, Vol. 39, 210–217.

- Castro, J., Gomez, J. M., Garcia, D., Zamora, R., and Hodar, J. A. (1999) Seed predation and dispersal in relict Scots pine forests in southern Spain. *Plant Ecology*, Vol. 145, 115–123.
- Castro, J., Zamora, R., and Hodar, J. A. (2002) Mechanisms blocking *Pinus sylvestris* colonization of Mediterranean mountain meadows. *Journal of Vegetation Science*, Vol. 13, 725–731.
- Cierjacks, A., Ruhr, N. K., Wesche, K., and Hensen, I. (2008) Effects of altitude and livestock on the regeneration of two tree line forming *Polylepis* species in Ecuador. *Plant Ecology*, Vol. 194, 207–221.
- Cuevas, J. G. (2002) Episodic regeneration at the *Nothofagus pumilio* alpine treeline in Tierra del Fuego, Chile. *Journal of Ecology*, Vol. 90, 52–60.
- Cuevas, J. G. and Le Quesne, C. (2006) Low vegetation recovery after short-term cattle exclusion on Robinson Crusoe Island. *Plant Ecology*, Vol. 183, 105–124.
- Dai, A., Wigley, T. M. L., Boville, B. A., Kiehl, J. T., and Buja, L. E. (2001) Climates of the twentieth and twenty-first centuries simulated by the NCAR climate system model. *Journal of Climate*, Vol. 14, 485–519.
- Dalen, L. and Hofgaard, A. (2005) Differential regional treeline dynamics in the Scandes Mountains. *Arctic, Antarctic, and Alpine Research*, Vol. 37, 284–296.
- DeLucia, E. H. and Berlyn, G. P. (1984) The effect of increasing elevation on leaf cuticle thickness and cuticular transpiration in balsam fir. *Canadian Journal of Forest Research*, Vol. 14, 2423–2431.
- den Herder, M., Kytoviita, M. M., and Niemala, P. (2003) Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. *Ecography*, Vol. 26, 3–12.
- Dullinger, S., Dirnbock, T., and Grabherr, G. (2003) Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps, Austria. *Arctic, Antarctic, and Alpine Research*, Vol. 35, 434–441.
- Eckstein, D., Hoogesteger, J., and Holmes, R. L. (1991) Insect-related differences in growth of birch and pine at northern treeine in Swedish Lapland. *Holarctic Ecology*, Vol. 14, 18–23.
- Gehrig-Fasel, J., Guisan, A., and Zimmerman, N. E. (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, Vol. 18, 571–582.
- Grace, J. (1990) Cuticular water loss unlikely to explain tree-line in Scotland. *Oecologia*, Vol. 84, 64–68.
- Grime, J. P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Chichester, UK: John Wiley & Sons
- Hadley, J. L., Friedland, A. J., Herrick, G. T., and Amundson, R. G. (1991) Winter desiccation and solar radiation in relation to red spruce decline in the northern Appalachians. *Canadian Journal of Forest Research*, Vol. 21, 269–272.
- Hadley, J. L. and Smith, W. K. (1986) Wind effects on needles of timberline conifers: Seasonal influence on mortality. *Ecology*, Vol. 67, 12–19.
- Hall, K. and Lamont, M. (2003). Zoogeomorphology in the Alpine: Some observations on abiotic-biotic interactions. *Geomorphology*, Vol. 55, 219–234.

- Hansen, A. J., di Castri, F., and Risser, P. G. (1988) A new SCOPE project. Ecotones in a changing environment: The theory and management of landscape boundaries. *Biology International Special Issue*, Vol. 17, 137–163.
- Helle, T. (2001) Mountain birch forests and reindeer husbandry. In F. E. Wielgolaski, ed., *Nordic Mountain Birch Ecosystems*. New York, NY: Parthenon, 279–291.
- Herrick, G. T. and Friedland, A. J. (1991) Winter desiccation and injury of subalpine red spruce. *Tree Physiology*, Vol. 8, 23–36.
- Hobbie, S. E. and Chapin, F. S., III. (1998) An experimental test of limits to tree establishment in Arctic tundra. *Journal of Ecology*, Vol. 86, 449–461.
- Hoch, G. and Körner, C. (2005) Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. *Functional Ecology*, Vol. 19, 941–951.
- Hoch, G., Popp, M., and Körner, C. (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggest sink limitation of growth at the Swiss treeline. *Oikos*, Vol. 98, 361–374.
- Hofgaard, A. (1997) Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. *Global Ecology and Biogeography Letters*, Vol. 6, 419–429.
- Holtmeier, F.-K. (2003) *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Dordrecht, The Netherlands: Kluwer Academic Publishers
- Hoogesteger, J. and Karlsson, P. S. (1992) Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* ssp. *tortuosa*). *Functional Ecology*, Vol. 6, 317–323.
- Innes, J. L. (1991) High-altitude and high-latitude tree growth in relation to past, present and future global climate change. *The Holocene*, Vol. 1, 168–173.
- Kallio, P. and Lehtonen, J. (1973) Birch forest damage caused by *Oporinia autumnata* (Bkh.) in 1965–66 in Utsjoki, N Finland. *Reports of the Kevo Subarctic Research Station*, Vol. 10, 55–69.
- Karlsson, P. S., Tenow, O., Bylund, H., Hoogesteger, J., and Weih, M. (2004) Determinants of mountain birch growth in situ: Effects of temperature and herbivory. *Ecography*, Vol. 27, 659–667.
- Körner, C. (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, Vol. 115, 445–459.
- Körner, C. (2003a) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. 2nd ed. Berlin, Germany: Springer
- Körner, C. (2003b) Carbon limitation in trees. *Journal of Ecology*, Vol. 91, 4–17.
- Kullman, L. (1998) Tree-limits and montane forests in the Swedish Scandes: Sensitive biomonitors of climate change and variability. *Ambio*, Vol. 27, 312–321.
- Kullman, L. (2005) Wind-conditioned 20th century decline of birch treeline vegetation in the Swedish Scandes. *Arctic*, Vol. 58, 286–294.
- Kupfer, J. A. and Cairns, D. M. (1996) The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography*, Vol. 20, 253–272.
- Linderholm, H. W. (2002) Twentieth-century Scots pine growth variations in the central Scandinavian Mountains related to climate change. *Arctic, Antarctic, and Alpine Research*, Vol. 34, 440–449.

- Lloyd, A. H. and Fastie, C. L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, Vol. 52, 481–509.
- Lloyd, A. H. and Graumlich, L. J. (1997) Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*, Vol. 78, 1199–1210.
- Malanson, G. P. and Butler, D. R. (1994) Tree-tundra competitive hierarchies, soil fertility gradients, and treeline elevation in Glacier National Park, Montana. *Physical Geography*, Vol. 15, 166–180.
- Marchand, P. J. (1991) *Life in the Cold: An Introduction to Winter Ecology* (2nd edition). Hanover, NH: University Press of New England
- Mcguire, A. D., Sturm, M., and Chapin, F. S. (2003) Arctic transitions in the land-atmosphere system (ATLAS): Background, objectives, results, and future directions. *Journal of Geophysical Research—Atmospheres*, Vol. 108 (D2), Art. No. 8166.
- Moen, J., Aune, K., Edenius, L., and Angerbjorn, A. (2004) Potential effects of climate change on treeline position in the Swedish mountains. *Ecology and Society*, Vol. 9, 16.
- Moir, W. H., Rochelle, S. G., and Schoettle, A. W. (1999) Microscale patterns of tree establishment near upper treeline, Snowy Range, Wyoming, USA. *Arctic, Antarctic, and Alpine Research*, Vol. 31, 379–388.
- Niemela, P., Chapin, I., Stuart, F., Danell, K., and Bryant, J. P. (2001) Herbivory-mediated responses of selected boreal forests to climatic change. *Climatic Change*, Vol. 48, 427–440.
- Noble, I. R. (1993) A model of the responses of ecotones to climate change. *Ecological Applications*, Vol. 3, 396–403.
- Nuorteva, P. (1963) The influence of *Oporinia autumnata* (Bkh.) (Lep., Geometridae) on the timber-line in subarctic conditions. *Annales Entomologici Fennici*, Vol. 29, 270–277.
- Oksanen, L., Moen, J., and Helle, T. (1995) Timberline patterns in northernmost Fennoscandia. *Acta Botanica Fennica*, Vol. 153, 93–105.
- Payette, S., Eronen, M., and Jasinski, J. J. P. (2002) The circumboreal tundra-taiga interface: Late Pleistocene and Holocene changes. *Ambio*, Vol. 12 (Special Report), 15–22.
- Pérez, F. L. (1992) The ecological impact of cattle on caulescent Andean rosettes in a high Venezuelan paramo. *Mountain Research and Development*, Vol. 12, 29–46.
- Perkins, T. D., Adams, G. T., and Klein, R. M. (1991) Desiccation or freezing? Mechanisms of winter injury to red spruce foliage. *American Journal of Botany*, Vol. 78, 1207–1217.
- Piper, F. I., Cavieres, L. A., Reyes-Diaz, M., and Corcuera, L. J. (2006) Carbon sink limitation and frost tolerance control performance of the tree *Kageneckia angustifolia* D. Don (Rosaceae) at the treeline in central Chile. *Plant Ecology*, Vol. 185, 29–39.
- Proctor, J., Edwards, I. D., Payton, R. W., and Nagy, L. (2007) Zonation of forest vegetation and soils on Mount Cameroon, West Africa. *Plant Ecology*, Vol. 192, 251–269.

- Shen, Z.-H., Fang, J.-Y., Liu, Z.-L., and Wu, J. (2001) Structure and dynamics of *Abies fabri* population near the alpine timberline in Hailuo clough of Gongga Mountain. *Acta Botanica Sinica*, Vol. 43, 1288–1293.
- 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.
- Shi, P. L., Körner, C., and Hoch, G. (2006) End of season carbon supply status of woody species near the treeline in western China. *Basic and Applied Ecology*, Vol. 7, 370–377.
- Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M. (2003) Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, Vol. 23, 1101–1112.
- Sonesson, M. and Hoogesteger, J. (1983) Recent tree-line dynamics (*Betula pubescens* Ehrh. ssp. *tortuosa* [Ledeb.] Nyman) in northern Sweden. *Nordicana*, Vol. 47, 47–54.
- Stevens, G. C. and Fox, J. F. (1991) The causes of treeline. *Annual Review of Ecology and Systematics*, Vol. 22, 177–191.
- Strimbeck, G. R., Schaberg, P. G., DeHayes, D. H., Shane, J. B., and Hawley, G. J. (1995) Midwinter dehardening of montane red spruce during a natural thaw. *Canadian Journal of Forest Research*, Vol. 25, 2040–2044.
- Sturm, M., McFadden, J. P., Liston, G. E., Chapin, F. S., Racine, C. H., and Holmgren, J. (2001) Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. *Journal of Climate*, Vol. 14, 336–344.
- Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J., and Romanovsky, V. E. (2005) Winter biological processes could help convert arctic tundra to shrubland. *BioScience*, Vol. 55, 17–26.
- Stutzer, A. (2000) Forestline and treeline on Saualpe: A comparison of old and new pictures. *Fortwissenschaftliches Centralblatt*, Vol. 119, 20–31.
- 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.
- Todaro, L., Andreu, L., D'Alessandro, M., Gutierrez, E., Cherubini, P., and Saracino, A. (2007) Response of *Pinus leucodermis* to climate and anthropogenic activity in the National Park of Pollino (Basilicata, Southern Italy). *Biological Conservation*, Vol. 137, 507–519.
- Tranquillini, W. (1979) *Physiological Ecology of the Alpine Timberline, Tree Existence at High Altitudes with Special Reference to the European Alps*. New York, NY: Springer-Verlag
- Trotter, R. T., III, Cobb, N. S., and Whitham, T. G. (2002) Herbivory, plant resistance, and climate in the tree ring record: Interactions distort climatic reconstructions. *Proceedings of the National Academy of Science, USA*, Vol. 99, 10197–10202.
- van der Wal, R. and Brooker, R. W. (2004) Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, Vol. 18, 77–86.
- van Gardingen, P. R., Grace, J., and Jeffree, C. E. (1991) Abrasive damage by wind to the needle surfaces of *Picea sitchensis* (Bong.) Carr. and *Pinus sylvestris* L. *Plant, Cell and Environment*, Vol. 14, 185–193.

- Walsh, S. J., Butler, D. R., Malanson, G. P., Crews-Meyer, K. A., Messina, J. P., and Xiao, N. C. (2003) Mapping, modeling, and visualization of the influences of geomorphic processes on the alpine treeline ecotone, Glacier National Park, MT, USA. *Geomorphology*, Vol. 53, 129–145.
- Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. D., Fromentin, J-M., Hoegh-Guldberg, O., and Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, Vol. 416, 389–395.
- Wardle, P. (1981) Winter desiccation of conifer needles simulated by artificial freezing. *Arctic and Alpine Research*, Vol. 13, 419–423.
- Zhang, Q. B. and Alfaro, R. I. (2002) Periodicity of two-year cycle spruce budworm outbreaks in central British Columbia: A dendro-ecological analysis. *Forest Science*, Vol. 48, 722–731.
- Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., III, Reynolds, J. F., and Chapin, M. C. (1995) Steppe-tundra transition: A herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist*, Vol. 146, 765–794.