

DISPLACEMENT ECOLOGY OF TREES NEAR UPPER TIMBERLINE

WILLIAM H. MOIR, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO 80521

LAURIE S. HUCKABY, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO 80521

Abstract: Tree invasions into meadows near upper timberline reduce diversity of habitat and diminish high-elevation food sources for black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. How serious is this threat in view of future climate change? Tree invasions observed in the Pacific Northwest to New Mexico suggest that climatic restraints to forest expansion have relaxed since the end of the Little Ice Age. Because climate patterns are large-scale phenomena, geographic synchronicity in tree establishment might be expected if a warming trend began. When tree invasion chronologies from Canada to New Mexico were compared, 2 synchronicities of climate and tree invasions appeared, indicating a possible climatic influence. However, forest retreat and meadow advance are also commonly observed at high elevations. The mechanism of retreat is usually fire followed by slow or unsuccessful regeneration of forest. There is no clear evidence based upon tree seedling chronologies that meadows will continue to be lost on the basis of climate change alone. Climate warming may set the stage for forest advance, but tree invasions are highly sensitive to local conditions. Concentrated grazing by domestic or wild animals in high-elevation meadows may trigger tree invasion by reducing competition to tree seedlings from established meadow vegetation. Prescribed fires or natural fires allowed to burn within prescriptions can be used as a tool for maintaining meadows and bear habitat under some of the projected climate change scenarios for western North America.

Int. Conf. for Bear Res. and Manage. 9(1):35-42

INTRODUCTION

Climate Change

There is abundant evidence that the earth's climate is currently changing, partially as a result of and in concert with extensive deforestation and the outpouring of greenhouse gases into the atmosphere (Schneider 1989). In western North America, the recent warming trend began near the end of the Little Ice Age (a generally cold period lasting several centuries and ending around 1880). Global land surface warming from 1901 to 1987 is shown in Fig. 1. Temperatures mostly increased until around 1940, followed by a cooling trend lasting about 25 years, and subsequent warming to the present (Boden et al. 1990). In western North America regional temperatures followed about the same pattern (Fig. 2 after data from Boden et al. 1990). The warming trends are predicted by some

climatologists to continue into the twenty-first century (Schneider 1989). Trees near upper timberline in mountainous western North America are sensitive to climate temperature trends. What are the consequences if serious global warming continues, and what can wildlife managers do?

Timberlines as Climatically Sensitive Bear Environments

Meadows near upper timberline are important environments for black and grizzly bears primarily because of the diversity of food sources they provide (Jonkel and Cowin 1971, Craighead et al. 1982, Irwin and Hammond 1985). Important bear foods at or near timberline include such plants as *Hedysarum* spp., *Claytonia megarhiza*, *Lomatium cous*, *Pinus albicaulis*, *Vaccinium deliciosum*, and meadow-inhabiting small mammals such as *Spermophilus* spp., and *Thomomys thalpidoides*. In this paper, we review studies of tree invasions into meadows near upper timberlines in western North America. We examine to what degree invasion patterns and densities can be related to variations in climate during the last century. We also look briefly at forest retreat and displacement by meadow or tundra communities.

If the projected global warming has already begun, we expect to see tree invasions adjacent to established forests. The greater the warming, the more extensively we expect a forest microclimate to project beyond the edge of the forest into meadows and the greater the distance of invading trees into adjacent subalpine meadows or tundras. Pronounced warming might cause invading trees to attain high densities throughout meadows and tundras due to improved seedling survival. Similar effects are evident in rates of tree

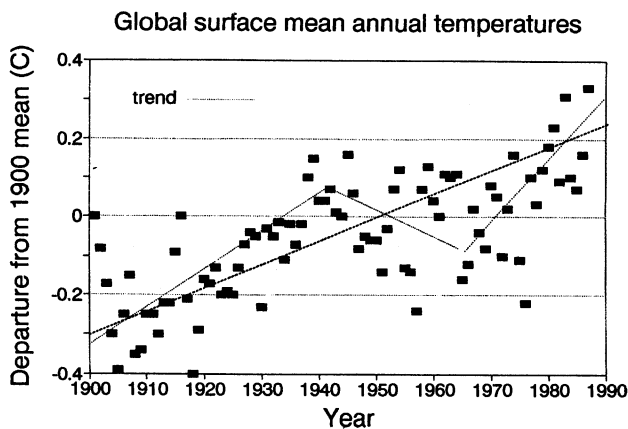


Fig. 1. Global land surface warming, 1901-87 (data from Boden et al. 1990). Lines show overall trend and subtrends.

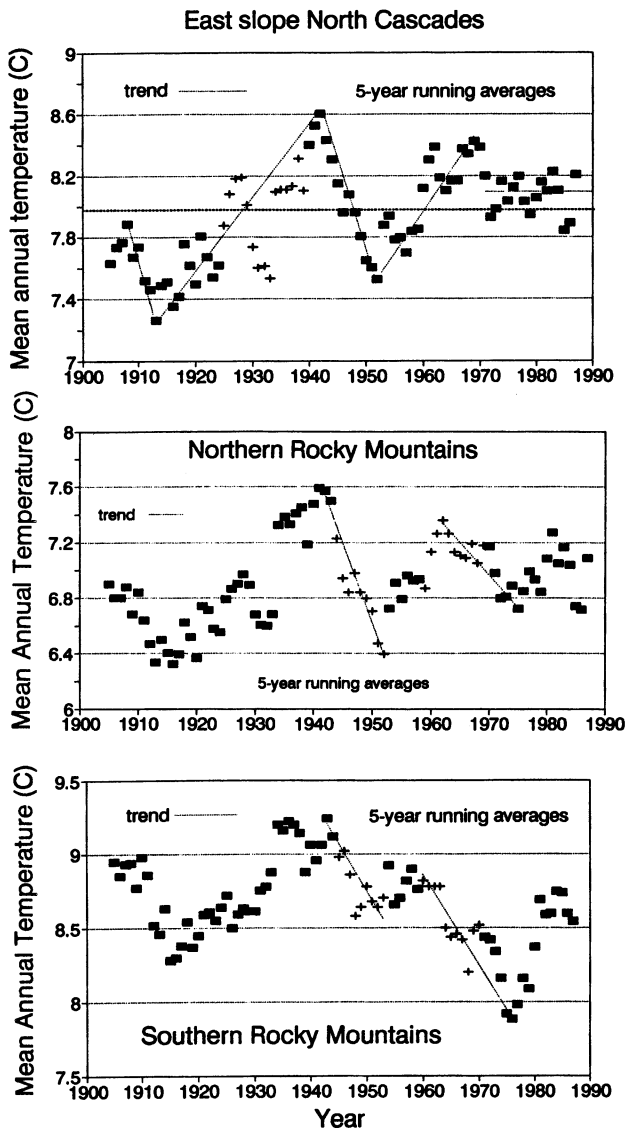


Fig. 2. Regional land surface warming in western North America (data from Boden et al. 1990), as 5-year running averages to better reveal trends. Pluses (+) show synchronistic periods of peak tree invasions at different locations.

regeneration in high-elevation burns. Conversely, cooling or drying trends can lead to displacement of forests by meadows. The play of these opposing phenomena is shown by the fluctuation of the elevation of treeline and the shifting mosaic of meadow and forest in this ecotonal environment.

Forest Advance and Retreat at Timberline

Climate change is the driving force of ecological displacement at all scales (for review, see Stevens and Fox 1991). Timberlines have been correlated to the elevation where a mean 10-12°C isotherm occurs during the warmest month (depending upon geography e.g., Tranquillini 1979, Arno and Hammerly 1984). The cold, wet winters, deep snowpack and short growing seasons of the forest-alpine ecotone favor herbs, dwarf shrubs, and cryptogams over trees (Brink 1959, Franklin et al. 1971). If climates become colder, tundras expand, timberlines decline in elevation, and trees in the forest-tundra ecotone become restricted to elevated microsites where snow accumulation is not so deep (Arno and Hammerly 1984). Mild winters, shallow snowpack, and long growing seasons favor establishment and survival of trees as long as soil moisture is not limiting to seedling establishment (Billings 1969, Noble and Alexander 1977). But on exposed sites, shallow snowpack also removes protection from winter winds, and allows more damage, which kills seedlings. As climates become warmer, timberlines advance and tundras retreat, and fire frequency increases at timberline (Huckaby 1991). On a grand spatiotemporal scale, timberlines respond to the swing of a climatic pendulum whose amplitude is measured in centuries or even millenia (Grant and French 1990).

Climate is modified locally by established vegetation, topography, and soils. Microclimate conditions finally determine whether or not trees will invade meadows, their densities and success rates, and whether they will be deformed krummholz or upright symmetrical trees (Klickoff 1965, Marr 1977, Noble and Alexander 1977, Arno and Hammerly 1984, Hadley and Smith 1987, Scott et al. 1987).

We reviewed tree-invasion data from sites near timberline from Canada to New Mexico to see if overlapping periods of tree invasion from different regions (synchronicities) can be related to warming trends during the last 100 years. Temperature influences snowmelt and the length and warmth of growing season. These factors are critical in determining the nature of plant communities in the forest-alpine ecotone and the success of tree seedlings (Noble and Alexander 1977, Tranquillini 1979, Martinec and Rango 1986, Romme and Turner 1991). We hypothesize that if forest expansion is a response to regional warming, then we might find a correlation

between mean annual temperature and peaks of tree invasion.

METHODS AND STUDY AREAS

Terminology

In this paper "trees" are defined taxonomically, whatever their form. Their forms may range from tall (>15 m), full-canopied, and symmetrical to dwarfed (<15 m) and shrubby, with wind-flagged canopies, to low krummholz canopies developed by snow abrasion and leaf desiccation, but they are the same species found in the forest below. We define "timberline" as the highest elevation at which trees can grow >15 m tall in essentially closed-canopy stands with symmetrical crowns. The "forest-alpine tundra ecotone" is an elevational zone between timberline and "treeline," the highest elevational limit above which tree species cannot survive. The "ecotone" is characterized by mosaics of tundra plant communities and tree-dominated communities (Löve 1970). "Subalpine meadows" refer to herbaceous communities that interrupt forests below timberline. Similarly, "tundras" are plant communities above timberline and do not include trees. "Displacement" implies that a site where the potential vegetation was at one time dominated by one community (trees or meadows or tundra) no longer has that potential; i.e., one kind of vegetation has displaced another. Displacement, as used here, does not include forest succession that might have a temporary herb/shrub stage.

Regional Tree Invasion Data

We selected 7 locations in western North America spanning a broad latitudinal range (Table 1). At each location the number of tree seedlings were tallied into classes based on year of germination. Germination dates were measured in the studies shown in Table 1 by counting tree rings from sections obtained at ground level or from increment cores taken at the lowest possible height along the stems. Tree seedlings occupying severe microsites grow slowly during early years following germination, and exact ring counts are difficult even under high magnification. Missing, frost, and split rings are likely in at least some seedlings.

Our experience suggests that the actual first year (pith) ring can be counted within an accuracy of 1-2 rings for ground level sections. An error arises in estimating the number of growth years from germination level to coring height. This error may be

Table 1. Tree invasion studies at upper timberline, western North America, cited in this paper.

| Location | Symbol | Trees ^a | Reference |
|-------------------------|--------|------------------------|----------------------|
| Jasper Natl Park, Alta. | ALB | Abla, Pien | Kearney 1982 |
| Western Washington | wWA | Tsme, Abla | Franklin et al. 1971 |
| Northwest Wyoming | nWY | Pien | Dunwiddie 1977 |
| Southern Wyoming | sWY | Abla, Pien | this study |
| Central Colorado | cCO | Pien, Pifl | Huckaby 1991 |
| Southern Colorado | sCO | Pien, Piar | Baker 1991 |
| Northern New Mexico | nNM | Pien, Abla, Potr, Abco | Allen 1989 |

^a Abco = *Abies concolor*, Abla = *Abies lasiocarpa*, Piar = *Pinus aristata*, Pien = *Picea engelmannii*, Pifl = *Pinus flexilis*, Potr = *Populus tremuloides*, Tsme = *Tsuga mertensiana*.

as large as 2-4 rings and may bias the resulting distributions left or right along the calendar year axis by as much as 2-3 years. Therefore, we preferred, when available, studies where seedling rings were counted from stem sections obtained at germination level.

Regional Temperature Data

The regional temperature data we used came from weather stations screened on the basis of confidence, missing data, and consistency criteria (Karl et al. 1990). Data from selected stations were adjusted for bias due to time of observation, station and instrument changes, and urban heat island biases (Karl et al. 1988). Four of the timberline sites (nNM, sCO, cCO, and sWY) occurred in the Southern Rockies climatic region, 2 (nWY, ALB) in the region approximated from the Northern Rockies climate region, and the wWA location was situated at the margin of the East Cascades climate region (Fig. 2).

Temperature trends were computed as linear regressions from untransformed data (Fig. 1) or from 5-year running averages (Fig. 2), but were plotted visually. Temperature synchronicities were sought by aligning the seedling age distributions along the calendar year axis and visually examining for common modality between locations. The calendar years within these modes were assigned regional mean annual temperatures. These temperatures were then compared with overall mean annual temperatures since 1900 using simple *t* tests (Norusis 1990).

RESULTS

Pattern and Chronologies of Tree Invasions

In-filling of meadows by tree seedlings occurs from the limits of boreal forest at polar latitudes (Payette and Filion 1985, Scott et al. 1987), southward along mountain cordillera from Canada to New Mexico (see references, Table 1). Invasions are of 2 kinds: establishment of trees near existing forest or tree

borders, and trees establishing 2-3 or more tree height distances beyond borders, sometimes as massive invasions that fill entire meadows (Fig. 3).

The chronologies (Figs. 4ab) all have features in common. All began during the last 100 years. Most invasions began abruptly, and peaks were preceded by a long period of little, if any, tree establishment. Furthermore, many chronologies revealed a subsequent decline of invasions when regional mean annual



Fig. 3. Tree invasions into dry meadows, Snowy Range, southern Wyoming, 1989. The meter-stick banded into 5-dm segments is for scale. The seedlings in foreground are 25-40 years old (in 1989). The meadow behind the meter-stick is too wet to support trees.

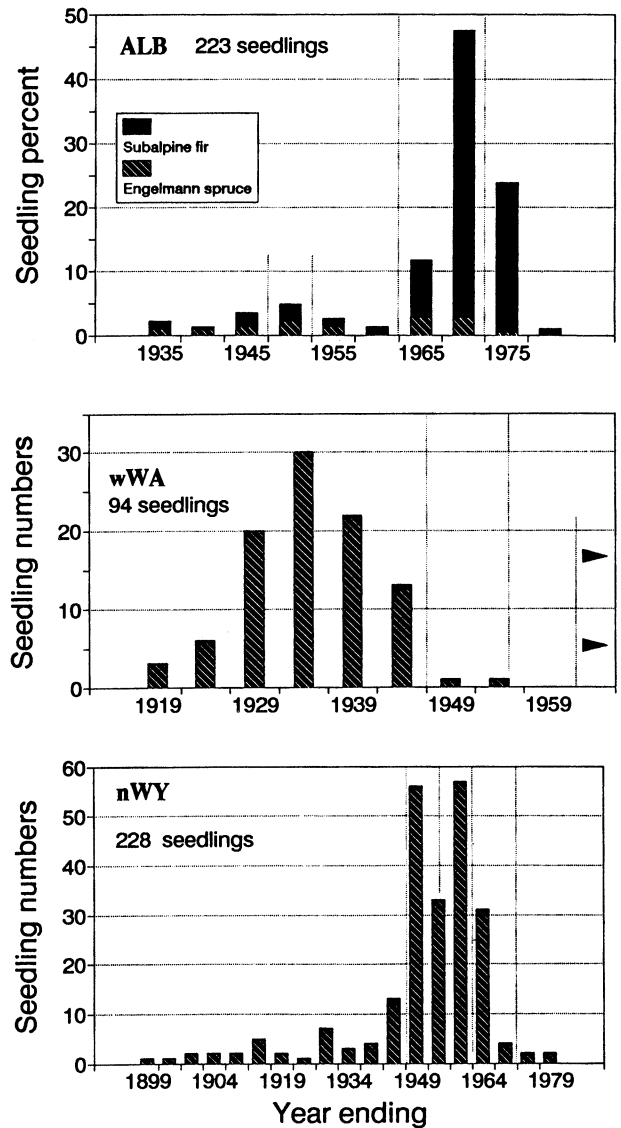


Fig. 4a. Tree invasion chronologies in the Northern Rockies and Washington Cascades. The vertical dotted lines are periods of common peak invasions at the different geographic locations.

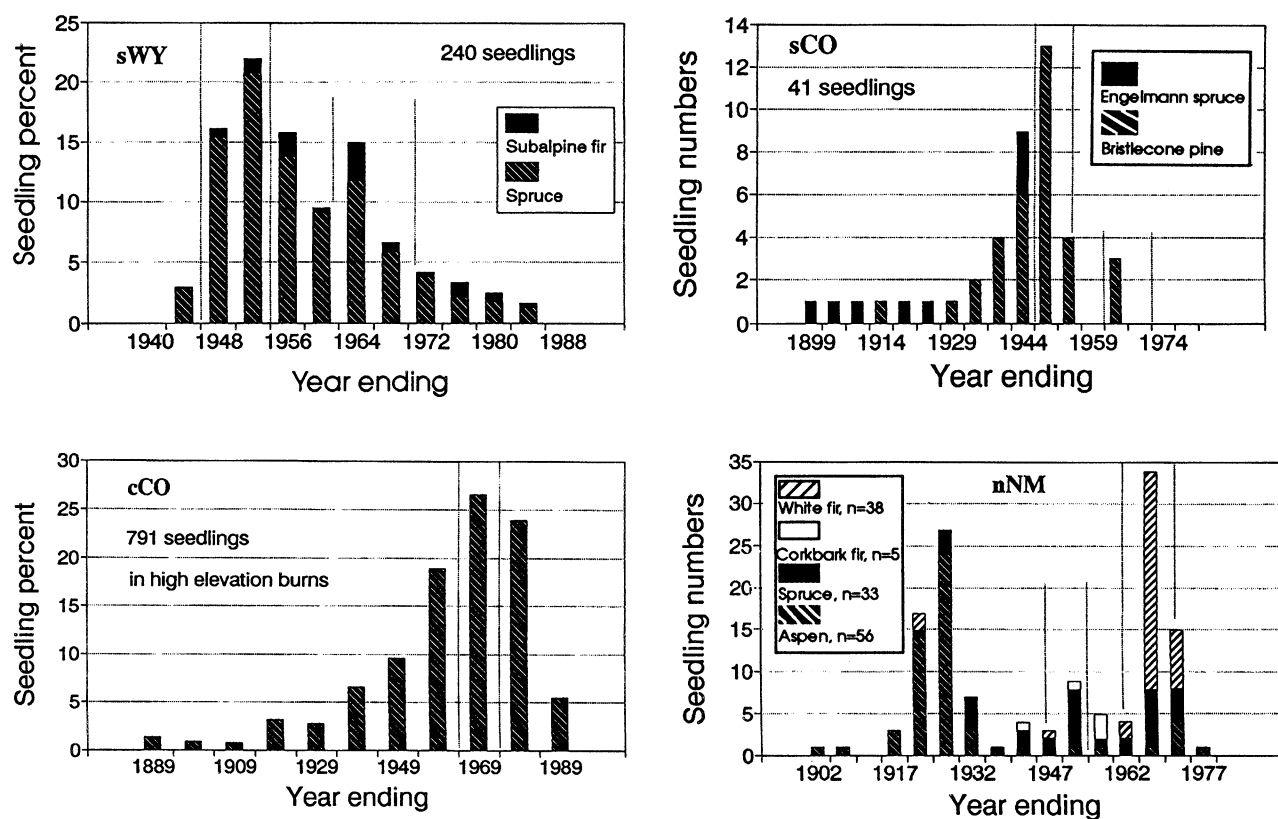


Fig. 4b. Tree invasion chronologies at 4 locations in the Southern Rockies. The vertical dotted lines are periods of common peak invasions at the different geographic locations.

temperatures continued to increase. Clearly, climate warming by itself, as reflected by regional annual mean temperatures, is insufficient to trigger invasions. Several chronologies (ALB, nWY, sWY, nNM) indicated more than 1 period of establishment. In western Washington massive tree invasions in subalpine parklands of Mount Rainier (wWA) peaked during the years 1924-39 and subsequently declined. This chronology differed from most of the others, which generally showed later invasion peaks. In the Jemez Mountains (nNM) a period of aspen invasion peaked between 1918 and 1927, followed by another peak between 1967 and 1971 composed mostly of conifers.

Cross tabulation of the chronologies in the Rocky Mountains revealed most peak periods of tree invasions between 1944-52 and 1959-69. These peak periods accounted for 63% of invading trees at sWY, 57% at ALB, 47% at nWY, and 37-40% at the Colorado and New Mexico locations. At Mount Rainier (wWA), which is located in a very different climatic region, those peak intervals included only 1% of trees in subalpine meadows.

Relationship to Climate Warming

The period from about 1890 to about 1940 was a time of general warming in western North America, followed by a cooling trend from about 1942 to 1974, and then continued warming to the present (Figs. 1-2). The synchronicities of tree invasions (1944-52 and 1959-69 in the Rocky Mountains) occurred during periods of regional cooling, except in wWA. These synchronistic years are indicated by the pluses (+) in Fig. 2. A similar sequence from about 1905 to 1915 did not have tree invasions. This was a period of dramatically increased fire frequency in the Colorado Rockies, which may have prevented invasions. Seedling survival may require a sequence of years of favorable seedbed conditions (Noble and Alexander 1977) that occur perhaps during cooling periods in the Rocky Mountains. Such periods may also produce conditions favorable for heavy tree seed crops, including pine seeds important in bear diets (Mattson and Jonkel 1990).

The average calendar year temperatures for the 2 invasion periods were 8.6 and 8.5°C respectively. We

tested temperatures during these 2 periods for skewness and normality. The tests (Norusis 1990) indicated these data met criteria for normality. We then tested the hypothesis that the invasion periods did not have different temperatures from each other and from the mean background temperature of 8.7°C. Using the 2-tailed Student's *t*, we found no significant differences in regional temperatures during the time the seedlings were at or near their peaks of meadow invasion.

It is possible that other climatic variables are more related to conditions favoring seedling establishment. The synchronistic intervals accounted for only some of the variation in tree invasion patterns, and considerable variation remained (more than half in Colorado and New Mexico sites). While temperature trends in Fig. 1 as well as variation accounted for during the synchronisms both hint at some ultimate, correlative cause for tree invasions, they are not proximate causes. There are many local factor interactions affecting probabilities of successful tree invasions near upper timberlines (Klickoff 1965, Billings 1969, Allen 1989, Stevens and Fox 1991). We suggest that sequences of favorable climatic years only "set the stage" for tree invasions by increasing the odds for tree success at microsites (Moir and Lee 1990). Actual tree establishment depends on events such as grazing or soil disturbance (which reduce vegetation competition), cessation of natural fires, heavy seed crops, and favorable growing conditions at the microsite.

IMPLICATIONS FOR BEAR MANAGEMENT

Loss of Meadow and Tundra Acreage

Should managers be concerned about possible effects of climate change upon bear habitats near timberline? Romme and Turner (1991) discussed potential climate change scenarios with implications for the Greater Yellowstone Ecosystem, prime grizzly and black bear habitat. Depending on the scenario, their model predicted possible contraction of alpine communities, decreases in whitebark pine populations, and fragmentation of forest communities. How likely are any of these possibilities?

Few studies have been done on rates at which meadow and forest-tundra ecotone plant communities are being affected by displacement. Allen (1989) estimated from air photos that grassland areas in the Jemez Mountains, New Mexico decreased 55-85% from 1935 to 1981. In the Snowy Range, Wyoming, Moir and Lee (1990) estimated that about 25% of dry meadow communities have been invaded in the last 50

years. At Mount Rainier, Washington, Franklin et al. (1971) estimated a potential loss over 3 decades of nearly half the forb meadows without management intervention. Despite this rapidity of forest advance, managers often fail to notice because, like a child growing up, it happens gradually over many years.

Role of Fire

High-elevation fires reverse meadow losses and maintain existing meadows. Fires in forest communities near timberline also create herb or shrub dominated seral communities which are slow to regenerate (Shankman and Daly 1988, Huckaby 1991). It is not uncommon to find tundra-like meadows where forests had burned 1-2 centuries before. In areas rapidly invaded by trees, fire can restore important food sources for bears such as huckleberries or currants (Martin 1983, Interagency Grizzly Bear Committee 1987). Fires also help maintain high elevation pine populations, another important food source (Irwin and Hammond 1985, Mattson and Jonkel 1990). Because forests near timberline may be slow to recover after fire, managers must also consider the cover requirements for bears. Extensive or too frequent burns may critically reduce needed forest or krummholz cover.

Role of Grazing

Constriction of meadow habitat has the effect of concentrating both domestic livestock and wild grazing herds on fewer acres. Several studies cited in Table 1 implicated domestic livestock grazing as contributing to tree invasion, particularly where massive invasions occurred. Concentrations of large grazing animals may act as "site preparation" when the balance between trees and subalpine meadow or tundra vegetation is delicate, tipping the scales in favor of trees. Not only is there a reduction in bears' food supply as meadows yield to trees, but unless livestock numbers are reduced (which is seldom), there is more competition from sheep, cows, or elk in the openings that remain (to say nothing about adverse human encounters).

CONCLUSIONS

Tree invasions into high-elevation meadows at 6 sites in the Rocky Mountains have been related to slight-cooling periods in an otherwise warming century. The relationship is weak because tree seedlings also established in years not within this cooling period. This phenomenon demonstrates to wildlife managers the dynamic nature of the forest-alpine tundra ecotone in

western North America. A warming climate as indicated by simple mean annual temperatures, however, was not the direct cause of forest advance, because climate at timberline is strongly modified by local conditions. Nevertheless, future bear management under possible "greenhouse" conditions may require prescribed fires and adjustments in numbers of grazing animals to maintain the best mix of openings and cover for bears at high elevations.

LITERATURE CITED

- ALLEN, C.D. 1989. Tree invasion of ancient grasslands in the Jemez Mountains, N.M. Ph.D. Thesis, Univ. California, Berkeley.
- ARNO, S.F., AND R.P. HAMMERLY. 1984. Timberline, mountain and arctic forest frontiers. *The Mountaineers*, Seattle, Wash. 304pp.
- BAKER, W.L. 1991. Livestock grazing alters succession after fire in a Colorado subalpine forest. Pages 84-90 in S.C. Nodvin and T.A. Waldrop, eds. *Fire and environment: ecological and cultural perspectives*. U.S. Dep. of Agric. For. Serv. Gen. Tech. Rep. SE-69, 429pp.
- BILLINGS, W.D. 1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio* 19: 192-207.
- BODEN, T.A., P. KANCIRUK, AND M.P. FARRELL. 1990. Trends '90, a compendium on global change. Carbon Dioxide Information Analysis Center. ORNL/CDIAC-36, Environ. Sci. Div., Oak Ridge Natl. Lab., Oak Ridge, Tenn., xv, 257pp., append.
- BRINK, V.C. 1959. A directional change in the subalpine forest-heath ecotone in Garibaldi Park, British Columbia. *Ecology* 40:10-16.
- CRAIGHEAD, J.J., J.S. SUMNER, AND G.B. SCAGGS. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. *Wildlife-Wetlands Inst. Monogr.* 1, U of M Found., Univ. Mont., Missoula. 279pp.
- DUNWIDDIE, P.W. 1977. Recent tree invasion of subalpine meadows in the Wind River Mountains, Wyoming. *Arctic & Alpine Res.* 9:393-399.
- FRANKLIN, J.F., W.H. MOIR, G. DOUGLAS, AND C. WIBERG. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic & Alpine Res.* 3:215-224.
- GRANT W.E., AND N.R. FRENCH. 1990. Response of alpine tundra to a changing climate: a hierarchical simulation model. *Ecol. Modelling* 49:205-227.
- HADLEY, J.L., AND W.H. SMITH. 1987. Influence of krummholz mat microclimate on needle physiology and survival. *Oecologia* 67:12-19.
- HUCKABY, L.S. 1991. Forest regeneration following fire in the forest-alpine ecotone in the Colorado Front Range. M.S. Thesis, Colo. State Univ., Ft. Collins. 103pp.
- INTERAGENCY GRIZZLY BEAR COMMITTEE. 1987. Grazing (p 148) and Fire (p 150) in *Grizzly Bear Compendium*. 540pp.
- IRWIN, L.L., AND F.M. HAMMOND. 1985. Managing black bear habitats for food items in Wyoming. *Wildl. Soc. Bull.* 13:477-483.
- JONKEL, C.J., AND I.M. COWAN. 1971. The black bear in spruce-fir forest. *Wildlife Monogr.* No. 27. 57pp.
- KARL, T.R., R.G. BALDWIN, AND M.G. BURGIN. 1988. Time series of regional seasonal averages of maximum, minimum, and average temperature, and diurnal temperature range across the United States. *Nat. Climatic Data Cent., Hist. Climatology Ser.* 4-5. *Nat. Oceanic & Atmos. Adm., Nat. Environ. Satellite, Data, and Inf. Serv.*, Asheville, N.C.
- _____, C.N. WILLIAMS, AND F.T. QUINLAN. 1990. United States Historical Climatology (HCN) serial temperature and precipitation data. NDP-019/R1, Carbon Dioxide Inf. Anal. Cent., Environ. Sci. Div., Oak Ridge Natl. Lab, Oak Ridge, Tenn.
- KEARNEY, M.S. 1982. Recent seedling establishment at timberlines in Jasper National Park, Alberta. *Can. J. Bot.* 60:2283-2287
- KLICKOFF, L.G. 1965. Microenvironmental influence on vegetation pattern near timberline in the central Sierra Nevada. *Ecol. Monogr.* 35:187-221
- LÖVE, D. 1970. Subarctic and subalpine: where and what? *Arctic & Alpine Res.* 2:63-73.
- MARR, J.W. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology* 58:1159-1164.
- MARTIN, P. 1983. Factors influencing globe huckleberry fruit production in northwestern Montana. *Int. Conf. Bear Res. and Manage.* 5:159-165
- MARTINEC, J., AND A. RANGO. 1986. Parameter values for snowmelt runoff modelling. *J. Hydrol.* 84:197-219.
- MATTSON, D.J., AND C. JONKEL. 1990. Stone pines and bears. Pages 223-236 in W.C. Schmidt and K.J. McDonald, compilers. *Proc. symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. U.S. Dep. of Agric. For. Serv. Gen. Tech. Rep. INT-270. 386pp.
- MOIR, W.H., AND KYU-SUNG LEE. 1990. Spatial analysis of tree invasions: a predictive model in a small watershed. *Symposium Internacional, manejo integrado de cuencas para uso multiple*, 26-30 de marzo de 1990, Morelia, Mich. Mexico. U.S. Dep. of Agric. For. Serv. Gen Tech. Rep. RM-198:128-131.

- NOBLE, D.L., AND R.R. ALEXANDER. 1977. Environmental factors affecting natural regeneration of Engelmann spruce in the central Rocky Mountains. *For. Sci.* 23:420-429.
- NORUSIS, M.J. 1990. SPSS/PC+ Statistics 4.0, SPSS Inc, Chicago, Ill.
- PAYETTE, S., AND L. FILION. 1985. White spruce expansion at the treeline and recent climatic change. *Can. J. For. Res.* 15:241-251.
- ROMME, W.H., AND M.G. TURNER. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. *Conserv. Biol.* 5:373-386.
- SCHNEIDER, S.H. 1989. The greenhouse effect: science and policy. *Science* 243:771-781.
- SCOTT, P.A., R.I.C. HANSELL, AND D.C.F. FAYLE. 1987. Establishment of white spruce populations and responses to climatic change at the treeline, Churchill, Manitoba, Canada. *Arctic & Alpine Res.* 19:45-51.
- SHANKMAN, D., AND C. DALY. 1988. Forest regeneration above tree limit depressed by fire in the Colorado Front Range. *Bul. Torrey Bot. Club* 115:272-279.
- STEVENS, G.C., AND J.F. FOX. 1991. The causes of treeline. *Ann. Rev. Ecol. and Systematics* 22:177-191.
- TRANQUILLINI, W. 1979. *Physiological ecology of the alpine treeline.* Springer-Verlag, New York, N.Y. 137pp.