Low Temperature Extremes: Their Effects on Plants at Timberline[1]

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Abstract. In Rocky Mountain National Park of Colorado cessation of tree growth occurs at 10,947 ± 371 ft. independent of exposure. The cause may be due to a -40°C winter hardiness limit of the dominant timberline trees and other woody flora. Low temperature extremes at timberline are near -40°C and lower at higher elevations.

INTRODUCTION

At timberline a prominent transition occurs in the flora of mountainous regions; cessation of upright tree growth. Above this elevation only low growing woody shrubs and herbaceous alpine plants survive. Timberline, as used here, refers to the 'alpine' timberline of mountainous regions in the temperature zone and not to the northern limit of tree growth, 'boreal' timberline. In Rocky Mountain National Park, this transition is abrupt, occurs at an amazingly uniform elevation, and is at the same elevation on north, south, east, and west facing slopes (Becwar, 1979).

There have been numerous studies attempting to determine the environmental factor responsible for this cessation of tree growth. The findings are summarized in reviews by Arno (1966), Daubenmire (1954), and Tranquillini (1964). The environment at timberline is indeed severe, and increases in severity at higher elevations (Barry, 1973). Severe wind, low temperature, and shortness of growing season are but a few of the environmental stresses at timberline.

There have not been studies conducted to determine the winter hardiness of the timberline flora of this region in relation to the minimum temperatures that occur at the elevation of timberline. In general plant tissue survive winter temperature extremes by either tolerating or avoiding ice formation (Levitt, 1972). Plant cells that survive by tolerance of ice do so by dehydration in winter. The freezing of water occurs outside of the cell, extracellularly, without injury to the living cellular constituents. Such plant tissue in midwinter is extremely hardy and can even survive immersion in liquid nitrogen, -196°C, without injury (Sakai, 1960). Another mechanism of winter survival is for plant cells to remain hydrated and keep the cellular water in a liquid state without ice formation at temperatures well below its normal freezing point. This mechanism of freezing avoidance, deep undercooling (synonymous with deep supercooling), has a low temperature limit of about -40°C (Burke, et al., 1976). This survival mechanism is effective if temperatures remain above -40°C, but lethal if temperatures drop below -40°C. Thus, it is an abrupt 'all or nothing' type of plant response to low temperature extremes.

The sharpness of timberline transition in the Colorado Rocky Mountains suggests that such an abrupt plant stress response may be the cause. In this paper, our recent winter hardiness studies of the timberline flora of this region are summarized. Numerous conifers and hardwoods of this flora have an abrupt -40°C winter hardiness limit. Furthermore, climatological data show that low temperature extremes are near -40°C at timberline elevation and lower at higher elevations.

TIMBERLINE

The discussion here will be restricted to alpine timberline in the temperate region of North America, and in particular to timberline of the Colorado Rocky Mountains. The timberline transition as a function of elevation is shown for the following regions in figure 1.

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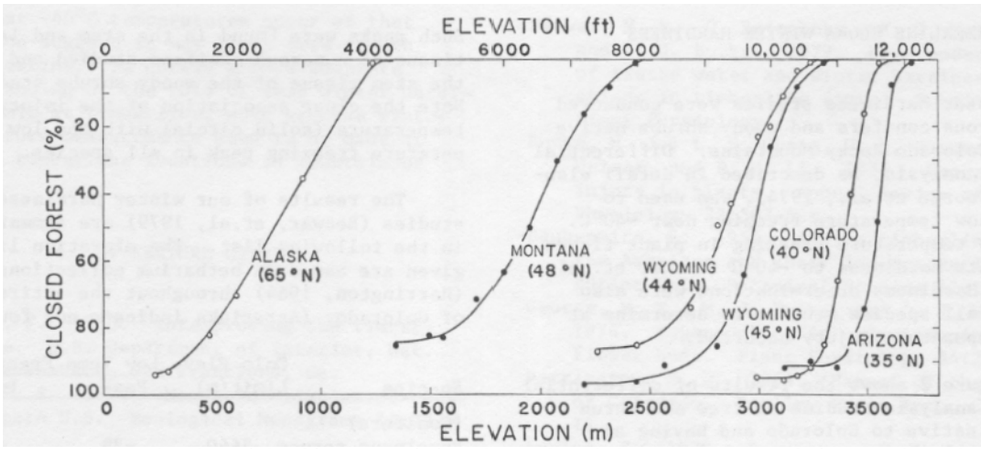

Figure 1. The timberline transition from closed forest to open alpine tundra of six mountainous regions in the western U.S. Percent closed forest values (open and closed circles) were calculated from contour lines on U.S. Geological Survey topographical maps at various elevations.

San Francisco Peaks, AR (35°N)
Rocky Mnt. Nat. Park, CO (40°N)
Teton Nat. Park, WY (44°N)
Yellowstone Nat. Park, WY (45°N)
Glacier Nat. Park, MT (48°N)
McKinley Nat. Park, AK (65°N)

Figure 1 shows two important features of timberline in these regions. First, the transition from closed forest to open alpine tundra is very abrupt in southern regions, Arizona and Colorado, and more gradual in northern regions, Montana and Alaska. In Colorado 80% of the transition occurs over a 500 ft. change in elevation. In contrast, in Alaska 80% of the transition occurs over a 2500 ft. change in elevation (fig. 1). Figure 1 also shows that timberline occurs at higher elevations in southern regions than in northern regions. In general the elevation of timberline decreases about 350 ft. per degree latitude in moving from south to north.

The elevation at which timberline occurs in Colorado is also independent of exposure. To determine this measurements were made on U. S. Geological survey topographical maps of Rocky Mountain National Park. The elevation of timberline was recorded at one mile intervals along the line forming the upper limit of the closed forest. The total distance covered in this manner was 110 miles. These data were averaged to give the following results:

10,947 + 371 ft., all exposures included
10,908 + 307 ft., north "
11,035 + 278 ft., south "
10,911 + 392 ft., east "
10,981 + 441 ft., west "

It is unlikely that one environmental factor would cause timberline to be at 10,911 ft. on east facing slopes and that a different factor would cause it to be at a nearly identical elevation, 10,908 ft. on north facing slopes. The abruptness of the timberline transition in Colorado (fig. 1) and its uniformity of elevation over a large region independent of exposure suggest that one environmental factor is ultimately limiting tree growth.

TIMBERLINE LOW TEMPERATURE *EXTREMES*

There are few weather stations at the elevation of timberline in Colorado. Those near this elevation have recorded low temperature extremes near -40°C (U.S. Dept. of Commerce, climatological data, 1967-1976). An extensive climatological study of the Niwot Ridge area of the Colorado Rocky Mountains by Barry (1973) showed the extreme minimum temperature at 10,000 ft. was -37°C over a eighteen year period. In general there was a 3°C/1000m lapse rate in average yearly extreme temperatures with increasing elevation in this region. This is in close agreement with studies of Baker (1944) on temperature lapse rates in mountainous regions. His results suggest a 5°C decrease in average minimum temperature per 1000m gain in elevation.

Although duration of low temperature, e.g. shortness of growing season, has been implicated as a cause of timberline (Tranquillini, 1964) low temperature extremes have not. This may be due to the fact that there has not been a systematic study of the winter hardinss of the timberline flora of the regions discussed here.

TIMBERLINE FLORA WINTER HARDINESS

Winter hardiness studies were conducted on numerous conifers and woody shrubs native to the Colorado Rocky Mountains. Differential thermal analysis, as described in detail elsewhere (George et al., 1974), was used to detect low temperature freezing near -40°C. Such low temperature freezing in plant tissue limits its hardiness to -40°C (Burke, et. al, 1976). Hardiness determinations were also made on all species studies to determine at what temperature injury occurred.

Figure 2 shows the results of differential thermal analysis studies on tree and shrub species native to Colorado and having an elevational limit at or just below timberline. Peaks in the freezing profiles indicate the freezing of water. All species have a large peak near -10°C which is not injurious to the tissue in midwinter. The presence of freezing peaks near -40°C indicate the freezing of deep undercooled tissue water.

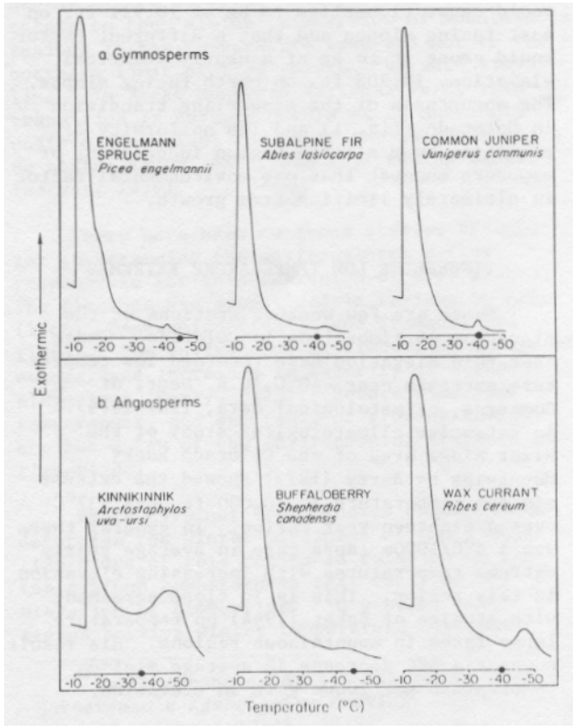

Figure 2.--Freezing profiles for timberline flora native to Colorado Rocky Mountains. Peaks on freezing profiles indicate the freezing of tissue water. Solid circles on the temperature scale indicate the injury temperature (Becwar et al. 1979).

Such peaks were found in the stem and leaf tissue of numerous conifers studied and in the stem tissue of the woody shrubs studied. Note the close association of the injury temperature (solid circle) with the low temperature freezing peak in all species.

The results of our winter hardiness studies (Becwar, et.al, 1979) are summarized in the following list. The elevation limits given are based on herbarium collections (Harrington, 1964) throughout the entire state of Colorado. (Asterisks indicate not found).

Species	Colo Elev. Limit(m)	Low Temp. Freezing (°C) Peak	Injury
(Conifers)			
Engelmann spruce	3660	-39	-45
subalpine fir	3660	-40	-40
limber pine	3660	-46	-45
common juniper	3440	-38	-40
Rocky Mnt. juniper	3350	-41	-45
Douglas fir	3350	-40	-40
lodgepole pine	3350	*	*
blue spruce	2900	*	*
ponderosa pine	2830	*	-45
(Woody Shrubs)			
willow	4270	*	*
kinnikinnik	3570	-37	-35
Rubus sps.	3570	-39	-40
buffaloberry	3510	-40	-45
wax currant	3470	-40	-40
Mnt. maple	3200	-39	-40
snowberry	3200	-39	-35
sagebrush	3080	-34	-35
Mnt. mahogany	3050	-38	-40
ninebark	3050	-40	-40
snakeweed	3050	-38	-35
bitterbrush	2740	-38	-40
skunkbrush	2740	-39	-40
wild grape	2130	-40	-40

SUMMARY

Our results show that in Colorado the timberline transition is abrupt and at an amazingly uniform elevation in Rocky Mountain National Park. This suggests that there is one limiting factor causing the cessation of tree growth in this region. The sharpness of this transition suggests that an abrupt plant stress response to the gradually worsening environment at higher elevations may be the cause. Numerous winter hardiness studies have shown that freezing avoidance to -40°C is a common characteristic in many temperate zone woody plants. This is an abrupt giant stress response; injury occurs below -40 C but not above. The finding of this -40°C winter hardiness limit in the timberline flora, and the

fact that -40°C temperatures occur at that elevation suggest it may limit tree growth at timberline. To obtain a more complete understanding of the role of this winter hardiness limit at timberline, more precise winter temperature measurements need to be made at various timberline locations in mountainous regions.

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