COMPOSITION, FORM, AND DISTRIBUTION OF THE FOREST-ALPINE TUNDRA ECOTONE, INDIAN PEAKS, COLORADO, USA

With 2 figures and 8 photos

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Zusammenfassung: Zusammensetzung, Form und Verbreitung des Übergangssaumes zwischen der Waldstufe und der alpinen Tundrastufe im Indian Peaks Gebiet, Front Range, Colorado, USA

Die außergewöhnlich starke touristische Beanspruchung des Indian Peaks Gebietes (Colorado) hat zur Degradation aller Ökosysteme geführt, wobei insbesondere die Pflanzengesellschaften des Übergangssaumes (Ökotons) zwischen der oberen Waldstufe und der alpinen Tundrastufe schwere Schädigungen erfuhren. Als Grundlagenstudie für eine Überwachung zukünftiger Schäden werden die gegenwärtige Form, Zusammensetzung und Verbreitung der Baumarten innerhalb des Ökotons untersucht. Im Höhenbereich von unterhalb der Waldgrenze bis zur Obergrenze der Baumarten können fünf vorherrschende Wuchsformen der Bäume unterschieden werden. Drei Baumarten dominieren innerhalb des Ökotons, daneben sind drei weitere Arten von nachgeordneter Bedeutung vertreten. Die räumliche Verbreitung des Ökotons zeigt mancherlei Abwandlungen aufgrund mikroklimatischer und topographischer Unterschiede, geomorphologischer Einflüsse sowie im Gefolge anthropogener Einwirkungen.

Introduction

The Indian Peaks area of the Colorado Front Range trends roughly north-south and forms the Continental Divide. Transected by latitude 40° N., the highest summits exceed 4,000 m within 30 km of the western edge of the High Plains. They have been moderately glaciated during the Late Cenozoic ice ages which has produced two distinctive landform assemblages – cirques, aretes, horns, and U-shaped valleys, comprising the "glacial assemblage", often separated by broad east-west trending interfluves with gentle slopes characterized by periglacial landforms – the "periglacial assemblage".

The Indian Peaks lie within four distinct management areas: the Indian Peaks Wilderness; the Niwot Ridge Biosphere Reserve; the City of Boulder Watershed; and contiguous sections of Roosevelt-Arapahoe National Forest. These few management areas collectively form the Indian Peaks Study Area (Fig. 1). The Indian Peaks Wilderness was designated in 1978 following a prolonged political campaign by Congressman Timothy Wirth and local conservationist groups. The area, encompassing 294 km², is one of the smallest wilderness areas in the United States, yet one of the most popular, with more than 150,000 overnight stays per season and many more day visits. This popularity can certainly be attributed to the spectacular vistas, pristine appearances, and extensive areas of alpine meadow (hereafter referred to as "alpine tundra"); however, its close proximity to the so-called Denver-Boulder-Fort Collins urban corridor is an equally important factor.

The Niwot Ridge Biosphere Reserve was established by Unesco and the United States Federal Government in 1979. The ridge is the longest of the east-west interfluves on the eastern side of the Continental Divide, extending approximately 9 km from Navajo Peak (4087 m) on the divide, to Bald Mountain (3490 m). Its gently-rolling upper slopes support extensive areas of alpine meadow and fell fields which give way to a broad ecotonal belt of wind-deformed trees (cripple trees or elfin wood: HOLTMEIER 1981) and finally to the upper montane forest (Photos 1–3). Niwot Ridge and the adjacent City of Boulder Watershed constitute the site of an intensive research effort by the University of Colorado. The research, supported by the National Science Foundation, is part of a "Long-Term Ecological Research" programme.

The Indian Peaks Study Area is the focus of an environmental atlas mapping programme funded by the National Aeronautics and Space Administration. The atlas, still in progress, includes maps on a scale of 1:50,000 illustrating relief, vegetation, soils, natural hazards, landforms, the visual landscape, and human impacts (IVES a. DOW 1982; DOW et al. 1981; BAUMGARTNER 1983, 1984).

Each year several hundred thousand visitors enter the Indian Peaks area in search of a wilderness experience, a

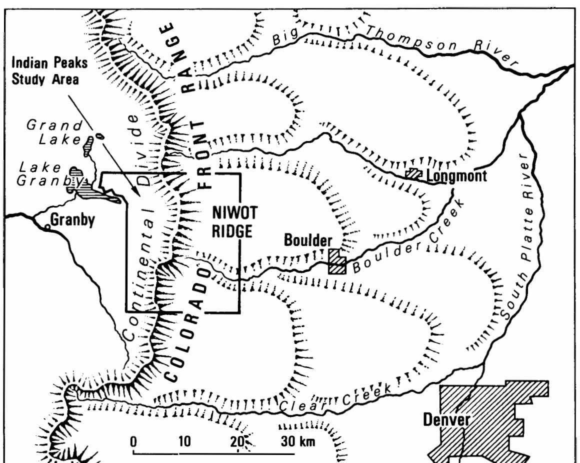

Fig. 1: The Indian Peaks lie within three management areas: the Indian Peaks Wilderness area, the Niwot Ridge Biosphere Reserve, and the City of Boulder Watershed

Photo 1: Low-level oblique air photo looking southwestward onto the east slope of the Continental Divide across the Indian Peaks Wilderness. Niwot Ridge is the long, broad interfluve in the upper left. Note the forest-alpine tundra ecotonal forms, especially in the foreground, and the glacial and periglacial landforms

weekend of camping and fishing, and simply a relief from their urban lifestyles. The resultant impact has been large. Most has occurred on the eastern side of the Continental Divide which provides easiest access from the neighbouring urban centers. Trampling of vegetation, removal of wood for campfires, stream water pollution (Hansen-Bristow et al., 1982), soil erosion along trails, and littering have contributed to a progressive degradation of the region. To check these processes of environmental deterioration the United States Forest Service has prohibited campfires and camping in several of the east slope drainages, and has introduced a camping permit system in other areas. Efforts are being made to stabilize trails and revegetate heavily damaged campsites. The campfire prohibition was introduced partly to prevent widespread destruction of the timberline and forest-alpine tundra ecotone belts. Trees within the ecotone, displaying extensive dwarfing by strong westerly winds, snow fungus, and short growing seasons, were being stripped of their wood for campfires (Hansen-Bristow 1981). It was postulated that these trees, growing only a few millimeters each year and depending upon vegetative reproduction, may be unable to regenerate under present-day climatic conditions (Ives a. Hansen-Bristow 1983).

Serving as a basis for monitoring changes induced naturally or by human impact in the forest-alpine tundra community, the study presented herein discusses the present-day form, composition, and distribution of tree species within the ecotone. It should provide a framework upon which future studies and evaluations of vegetational changes can be structured. Additionally, it is conceived as an aid to understanding the environmental controls on the upper altitudinal limit of tree growth on continental North American mountains (cf. Tranquillini 1979).

Definitions and species composition

The forest-alpine tundra ecotone of the Indian Peaks area is defined as the mosaic of forest and alpine meadow species extending between the upper timberline (upper limit of tall,

Photo 2: The southern flank of Niwot Ridge shows the forest-alpine tundra ecotone with the strong east-west wind alignment of the cripple-wood forms of *Picea engelmanii* and *Abies lasiocarpa.* Oblique air photo. Note the 1906 forest fire site in bottom left.

Photo 3: View looking due west along the length of Niwot Ridge onto the Continental Divide. Scattered patches of cripple-wood in foreground. The small Isabell Glacier with its Neoglacial moraine can be seen in the upper centre

symmetrical, closely-spaced trees of the montane forest: average elevation 3168 m) and the treeline (upper limit of tree-species: average elevation 3365 m). This is the equivalent of the "subalpine belt" as defined by Löve (1970). Its vertical width varies with exposure, slope, and substrate but exceeds 250 m in places with the species limit extending as high as 3760 m. It is characterized by a gradual upslope progression in reduction in the number of individuals, increase in deformation, and reduction in tree height until, at the uppermost levels, prostrate shrub forms prevail. This ecotone has been studied with increasing vigor over the past two decades (Hansen-Bristow 1981; Hansen-Bristow a. Ives 1985; Holtmeier 1978, 1981, 1982; Ives 1973; Ives a. Hansen-Bristow 1983; Marr 1977; Shankman 1984; Wardle 1965, 1968, 1974). The late professor Carl Troll visited Niwot Ridge in the 1950's. Holtmeier, in particular, has introduced several of his graduate students to the region and has made important comparisons between the treeline problems of the Alps, Northern Europe, and the Colorado Rocky Mountains. For a research topic that is often confused by the use of conflicting and misleading terminology and definitions, Holtmeier's distinction between the genetically-controlled krummholz of the upper Alpine Forests in Europe and the predominantly crippled forms or elfin wood of the Indian Peaks area is especially valuable (Holtmeier 1981).

The dominant conifer species of the Indian Peaks forest-alpine tundra ecotone are *Picea engelmanni* (Parry) Engelm., *Abies lasiocarpa* (Hook) Nutt., and *Pinus flexillis* James. The common names are Engelmann spruce, subalpine fir, and limber pine respectively. *Pinus contorta* Dougl. var. *latifolia* Engelm. (lodgepole pine) is found only rarely in the ecotone, despite its widespread occurrence in the lower parts of the upper montane forest belt. *Pinus aristata* Engelm. (bristlecone pine or fox-tail pine) reaches its most northerly position in the southern section of the Indian Peaks area. The most northerly occuring stand of bristlecone pine, displaying an extreme wind deformed treeline form, occurs on Caribou Mountain immediately south of Niwot Ridge.

Populus tremuloides Michx. (quaking aspen) is the only deciduous tree found within the ecotone, although deciduous shrub species occur. The aspen is not a common ecotonal tree but is found in several localities on the south an southeast slopes of Niwot Ridge occuring in both flagged and mat forms (see below for terminology).

The conifer species within the ecotone are distributed along environmental gradients. Limber pine which favors xeric sites, is found at the highest elevations along dry, wind-swept secondary ridges. It does not appear in snow accumulation sites nor in extremely moist sites. It does not appear to compete well with Engelmann spruce and subalpine fir in the more sheltered sites.

Moisture stress measurements (Hansen-Bristow 1981) indicate that limber pine are more tolerant of dry conditions than the other two co-dominants of the ecotone, thus explaining its location on wind-swept sites. Where spruce and fir are extensively distorted by wind, the pine will often display erect or flagged forms, appearing to withstand winter desiccation (Wardle 1968) more easily. Along a north-south spur on Niwot Ridge, limber pine extends higher on the leeward than on the windward side of the slope. This is expected because the winds striking the windward slope are exceptionally harsh. Limber pine, however, does extend higher upslope on the windward side than does any other tree species. Seedlings and saplings appear to survive on these windy slopes only if located to the lee of a boulder, a willow (*Salix* spp.) shrub, or another limber pine. By providing shelter from the harsh winds, as well as a small site for snow deposition (providing moisture later during the growing season), these micro-sites allow limber pine establishment today. In exceptional areas newly established seedlings actually constitute the tree-species limit as defined here.

The elevational limit of limber pine is controlled by the existence or absence of wind-exposed ridges and knolls where competition and snow accumulation is minimal. One of the lower sites for limber pine on Niwot Ridge is a major north-south ridge extending from the southeast side of the main ridge. Here, many large diameter, old, limber pine exist, which appear to have established during a different climate than that of today. The limber pines at this site are more symmetrical than those which appear to have been established more recently.

Spruce and fir are co-dominants throughout most of the ecotone. Although spruce may be more abundant than fir in some locations the two occupy the same habitat having what appears to be very similar ecologic requirements. *P. engelmannii* below timberline, in general, has a greater diameter, height and longevity than *A. lasiocarpa* (FRANKLIN a. DRYNESS 1973). Also, the two species have slightly differing habitat requirements for establishment and survival as seedlings. Spruce and fir form treeline where pine does not. In treeline areas where snow accumulates and winds are not extremely harsh, the spruce and fir are dominant.

At the uppermost ranges the trees are found only where some type of shelter exists providing protection from the winds. The shelter provides protection from the dry winter winds which carry many rock, snow, and ice particles. Additionally, the shelter, acting as a snow fence, creates an eddy which causes snow to be deposited on its lee side. The snow cover provides insulation to the soil and foliage during the winter and a moisture supply in spring and early summer. A good example is found on the south-facing slope of Niwot Ridge. The individuals in mat form are found downwind of turf-banked terrace risers which provide a protective micro-environment. A *P. contorta* has been found in this area where shelter exists (ELLIOTT-FISK, pers. comm.). Other such shelters are provided by willow shrub, boulders, other tree species, knolls, and ridges.

In cases where spruce and fir presently appear not to have adequate shelter, the windward side of the individual is damaged and often killed. These individuals, established perhaps long ago when climatic conditions were milder (IVES a. HANSEN-BRISTOW 1983), most likely began behind a shelter and have migrated through layering to more exposed sites.

In the flag mat and flag sub-belts (see below), great depths of winter snow accumulate and spruce and fir are the only tree species found here. They are much more tolerant of moisture and less tolerant of desiccation than is the pine. However, seedlings are excluded from areas where snow depths are so great as to drastically decrease the length of the growing season.

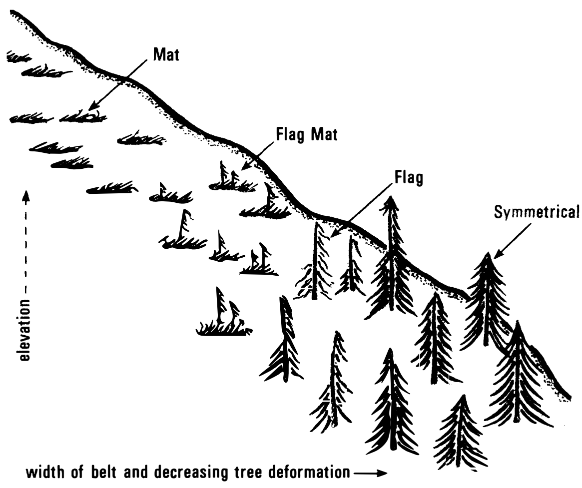

Fig. 2: A transect from timberline to above treeline indicates the changes in tree form with increasing severity of climate and altitudinal increase

Ages of individual trees have been estimated at 700 to 1,000 years (IVES 1973, 1978). The oldest tree so far identified in the Colorado Front Range is a bristlecone pine dated at 1,700 (KREBS 1973).

Tree forms

Throughout the ecotone, as environmental conditions become more harsh, the trees take on an appearance or form less like "normal" trees (Fig. 2). These changes in form reflect growth differences induced by an increase in severity of climate with altitudinal increase and topographic exposure.

Within the closed forest, below timberline, the coniferous and deciduous trees are of the characteristic shape with a vertical trunk and symmetrical branching (Photo 4). The conifers may attain heights of 40 m, with average heights of 20 m to 35 m. Shading of the understory is great, and hence, little understory vegetation exists in the dark, and often damp, closed forest of the upper montane forest belt. The trees are relatively closely spaced; canopy cover nears 100 percent. A great increase in species diversity usually occurs in sun-lit areas.

At timberline the trees continue to support branches on both sides of a main, vertical trunk. Occasionally branches found on the 'ecotone' side of the tree may be slightly less developed than the others. The conifers become less dense, often growing more in a grove or island fashion. The trees are usually shorter at timberline than within the closed forest, normal height being approximately 15 m. The upper symmetrical trees at timberline have narrower and more pointed crowns than the trees found lower in the forest. This may be a population response to heavy snowfalls, as

Photo 4: Within the closed forest the trees are of a characteristic conifer form with normal, symmetrical branching

Photo 5: At timberline the trees have narrower and more pointed crowns than the trees found lower in the forest. The conifers become less dense, often growing more in a grove or island fashion. The trees are usually shorter at timberline than within the closed forest, normally about 15 m height

narrow crowns hold less snow and reduce the danger of branch and leader breakage (Photo 5).

Many of the timberline trees have a characteristic wide trunk at the base and a much narrower trunk at the top. This form is characteristic of many old conifers up to 700–1000 years(IVES 1973, 1978). Additionally, the form may be due to exposure to winds from many different directions and to swaying in the wind. The tree develops an increased growth in the lower stem, exhibiting a pronounced trunk taper. The adaptive significance of these changes seems to be that conifering additional strength to the tree (JACOBS 1954).

As shading is much less at timberline due to the wide-spacing of trees, the understory species are more numerous. Additionally, with the abundance of light, the trees have living branching along the entire trunk. At timberline, in many cases, wide, open meadows exist which are sites of heavy snow accumulation. The species here are predominantly of forest affiliation. Occasional mixing with alpine tundra species is seen in these meadows depending on local micro-environments and proximity to the alpine tundra communities.

Upslope from timberline the trees gradually become deformed due to a variety of factors, predominantly wind, winter desiccation, freezing injury and mechanical abrasion (WARDLE 1968; HANSEN-BRISTOW 1981; BECWAR et al., 1981, HOLTMEIER 1981). The first arboreal vegetation forms seen above timberline are groves of flagged trees similar to YOSHINO's Type 2 (1975) (Photo 6). These trees, often found in elongated groves aligned parallel to the prevailing westerly wind direction, create a special microclimate within the grove. Herbaceous understory vegetation is diverse, composed of both forest and alpine tundra species. Because snow cover often exists late into the growing season, diversity and lushness of growth may be slightly diminished. Also, the late-lying snow allows the growth of a snow fungus (*Herpotrichia nigra* Hartig.) which parasitizes the needles on the lower branches. Many of the flag trees, therefore, have no needle growth within the lower 1.0 to 1.5 m of the trunk. The flag trees support a main, vertical trunk with branching mainly on the leeward side of the trunk. Slight windward branching is found on the lower trunk and occasionally along its mid-sections. The precise height of windward branching on these flag trees appears to be controlled by winter snow depth. In all cases, the upper section of the trunk supports no branching on the windside. The upper flag is normally exposed above the winter snow cover (Photo 7).

On the flag trees found in the lowest section of the ecotone it appears that at some time in the past branching was supported along almost the entire windward side of the trunk. Branch scars are found on the windward side and occasionally a very short branch with a terminal bud and perhaps some lateral buds is found protruding from the lower half of the trunk. Some of the buds will produce needles during a favourable year; however, it was consistently found that these needles were destroyed during their first winter (HANSEN-BRISTOW 1981). This sparse windward growth along with branch scars is a clue to a changing climate within the ecotone. The conditions that allowed

Photo 6: Upslope from timberline, the increasingly harsh conditions produce a distorted tree form, similar to YOSHINO's Type 2 (1975). Living foliage is found only on the leeward side of the main vertical trunk

Photo 7: Within the ecotone, snow cover often exists late into the growing season, allowing the growth of a snow fungus (*Herpotrichia nigra* Hartig.) which parasitizes the needles on the lower branches of the already-stressed conifers

more symmetrical branching in the past appear to no longer prevail and harsher conditions now exist.

With an increase in altitude and increasingly harsh conditions, the trees take environmentally stunted (WARDLE 1974) forms. The first cripple form upslope from the flag trees is termed a flag mat. The trees support only short, often scrawny vertical trunks. Often the main trunk is misshapen and bent. Branching from the trunk, close to the ground, is a mat, cushion or shrub growth. Although branching is found on all sides of the mat, most branches extend from the trunk towards the lee direction. This mat varies in height from 1.5 to 2 m and the length may exceed 6 m. WARDLE (1965) suggests the name "infranival cushion" for this mat because it is protected by the winter snowpack. Often the flag mat trees grow in elongated clumps, forming a ribbon extending in an west-east or wind-lee direction. The clump or island may actually be composed of several individuals. From the lower mat, frequently an upright branching leader is found. This upright leader, exposed to windy winter conditions may be called "supranival flag" (WARDLE 1965). This leader is flagged supporting branching only on the lee side. Although able to withstand the environmental conditions to which it is subjected, it appears stressed. If the climatic conditions were to deteriorate even slightly these leaders would most likely die back.

The second cripple form, found at the highest altitudes within the forest-alpine tundra ecotone, is the mat or cushion similar to YOSHINO's Type 3 (1975). In this form the tree is dwarfed to a mat, usually no higher than 1.5 m, but up to 5 m long. Rarely are vertical branching or upright leaders found. The horizontal trunk usually lies close to the ground and extends leeward (Photo 8).

The mat forms frequently grow in islands. Each island appears to have a size and shape that is adapted or adjusted to its specific topo-environment. Reproducing only through vegetative layering, the islands grow downwind. In many cases the mother tree has died back leaving a daughter tree surviving to the lee. As more wind branches die and more lee branches layer the tree gradually migrates downwind. Remnants of mother trees in the form of macrofossils are found upwind of the mat forms. Occasionally the mats now found in sites downwind from where the original seedling

Photo 8: At the highest altitudes within the ecotone, an elfin or crippled wood conifer is found. Dwarfed to a mat rarely higher than 1.5 m, yet up to 5 m in length, the horizontal trunk usually lies close to the ground and extends leeward

was established appear "out of place", being in a particularly harsh site. These may have migrated to these spots, from protected microsites by vegetative layering (Marr 1977).

The plant tissues on the wind side of the mats are mostly a contorted mass of broken and brown needles and distorted branches. These deformations are mainly the result of mechanical abrasion by wind-carried particles. Little snow cover exists on the windward sides of these mats. The survival of the mat forms is largely dependent on winter snow cover as shoots that project above the snow are severely damaged or destroyed. The mat form, when viewed from the side, is assymmetrical and triangular. The windward side has a gentle slope, while the lee side is more nearly vertical. This is a result of wind-shaping. The mats are widely spaced and occur in an matrix of herbaceous and dwarf shrub alpine tundra vegetation. Rarely are sexually reproduced seedlings found in this sub-belt. The characteristics of this zone suggest that climatic conditions were less harsh than today when the individuals became established. Another characteristic of this uppermost sub-belt of the ecotone is the increasing frequency of bare soil patches, caused by wind deflation, frost-sorting and needle-ice action. Occasional small sporadic patches of permafrost begin to occur (Ives a. Fahey 1971; Ives 1973).

On stressed sites the growth period may be less hospitable than on more optimal sites, and thus the trees may not be as tall and the crown may become more spherical and flattened. Wardle (1968) found a very strong correlation between the distribution of growth forms and exposure to winds on Niwot Ridge, and Brandegee (1880), Griggs (1938, 1946), Yoshino (1973, 1975), Marr (1977) and Holtmeier (1981) considered wind to be most important in affecting the changes in growth forms throughout the forest-alpine tundra ecotone. Klikoff (1965) found the degree of contortion and dwarfing to be directly related to the protection afforded by microtopographic features. Grant and Mitton (1977) demonstrated substantial differentiation of peroxidase enzymes along an elevational gradient of trees on Niwot Ridge marked by the different growth forms. Löve et al. (1970) advanced the view that various growth forms are the result of an interaction between coumarin, and its derivatives, and high elevational environmental parameters such as ultraviolet radiation. Wardle (1968) considered snow mould to be a significant feature of tree deformation. Finally Holtmeier presented a strong case for discounting the hypothesis of genetic control (Holtmeier 1981) and in this manner underlined one of the major differences with the Alpine upper timberlines.

Distribution

The forest-alpine tundra ecotone within the Indian Peaks region exhibits many variations resulting from microclimatic and topographic differences, geomorphic influences and human-impact consequences. The ecotone ranges from a wide belt of wind-shaped forms, as on Niwot Ridge, to a narrow, almost non-existent belt, such as above Arapahoe Creek on the western slope. Within the Indian Peaks Study Area, coniferous symmetrical trees cover 45 percent of the total ground surface. The forest-alpine tundra ecotone covers a total of 12 percent of the study area, with flag mat and mat forms covering 10 percent, and flag trees covering 2 percent.

The ecotone, treeline, and timberline at most sites are natural, with limits formed by climatic or geomorphic (e.g. avalanches, rockfall, or debris cones) controls. In a few sites these limits have been influenced by human activities, such as burning, logging or mining. The ecotone and timberline near the town of Nederland particularly have been influenced by logging and mining. Mean elevations of timberline and treeline within the Indian Peaks Study Area are 3168 and 3365 m, respectively with extremes of 2957 m and 3760 m (Hansen-Bristow 1981). These values were determined through sampling 100 points, along treeline and timberline, as mapped on 1:24,000 topographic quadrangles during the production of the Indian Peaks Environmental Atlas.

Topography influences treeline by providing differing topoclimates and potential habitats for tree growth, as well as an altitudinal change. Increasing elevation, normally accompanied by increasing environmental stress, reduces the capability of an individual to produce new biomass. This is evident not only in the change of tree form from the forest to the tree species limit, but also in the reduction of needle-length and seasonal growth increment as elevation increases (Steward 1977; Hansen-Bristow 1981). Topography also influences tree growth by affecting the severity of the wind, the distribution and depth of snow, temperature inversions, incoming solar radiation, and geomorphic events. Wardle (1968) found trees more abundant and to ascend higher on convex surfaces than on concave surfaces. Holtmeier (1973) develops a similar hypothesis stating that the natural regeneration above timberline follows the ridges first. The topographic influence on treeline is important on Niwot Ridge especially through its effect on the distribution of the more critical environmental needs of the treeline species, such as moisture, temperature, photoperiod, and wind.

The effect of active geomorphic processes in Colorado can be seen by depressed treelines bordering avalanche chutes, rock glaciers, talus slopes, and debris flows (Ives et al. 1976). Coniferous trees on many of the steep slopes are eliminated by the effect of the pressure of avalanches, and often are replaced by flexible deciduous species or an herbaceous meadow cover, leaving the ridges with trees where, undisturbed, they may attain great ages. In alpine valleys with glaciers in the headwalls, one observes the ecotone dropping down in the direction of the valley; a result of cold winds. Moraines of Triple Lakes age, 5000 to 3000 BP (Benedict 1973) or greater than 4750 BP (Davis et al. 1979), are often revegetated by cripple forms. This interesting correlation between geomorphic history and vegetative growth needs further study.

On Niwot Ridge periglacial processes are an important influence on the limit of the ecotone. Solifluction terraces may be too active for seedling establishment and maintenance and may cause root damage, especially in spring. Often, however, cripple forms are found established in the lee of the terrace risers where snow accumulation and protection from winds allow survival. In fact, treeline extends very high on Niwot Ridge on the solifluction terraces. Active solifluction, talus, rockfall, avalanches, soil creep, rock rubble, and stone stripes all provide very harsh environments for woody plant survival. Where vegetation cover does not exist, soil fines are subject to frost churning in frost boils. Needle-ice activity is a common process in barren areas within the Indian Peaks. Often seedlings may be uplifted by needle ice and their roots may be broken or damaged.

On Niwot Ridge treeline and timberline vary considerably according to micro- and meso-habitats. On the north slope of the ridge timberline is depressed by avalanche activity to as low as 3212 m elevation. Further east and upslope from, or south of, Lefthand Reservoir, timberline reaches 3375 m where winds are deflected and the conifers are not deformed. At the eastern edge of Lefthand Reservoir the wind-shaped trees exist at elevations below 3300 m as a result of cold, icy, westerly winds funnelling down valley and moving across the open reservoir at high speeds. The ecotone extends for as much as 200 m in elevational range on the north slope.

On the south slope timberline is depressed to 3300 m where an early 1900's burn eliminated the forest. Timberline here has been subjected to fire on numerous occasions (Grulke 1978). Timberline reaches a high altitude of 3375 m in a sheltered, south-facing site where *A. lasiocarpa* trees aging 700 to 800 years (Löve, pers. comm., cited in Ives 1978) exist. These symmetrical trees were not burned during the fires which have destroyed large areas of timberline on the south side of Niwot Ridge. Treeline extends as low as 3400 m above some of the burned areas and reaches as high as 3600 m on protected knolls. The ecotone belt on the south side of the ridge has an elevational rise of up to 300 m.

East versus west slopes of the Continental Divide

The geographical distribution and extent of the forest-alpine tundra ecotone exhibits a large contrast between the east and west sides of the Continental Divide.

On the west slope of the Continental Divide the ecotone is relatively narrow and often non-existent. In most cases, it is composed of flagged trees with the occasional flag mat tree. There are a few exceptions where mat forms exist where channelled winds occur at relatively high speeds. In some cases symmetrical and flag trees together form treeline and timberline with no actual ecotone.

On the east side of the Divide, in contrast, the ecotone is very broad in many areas, particularly as seen on Niwot Ridge, Mt. Audubon, and St. Vrain Mountain. The lower ecotone and timberline are depressed to much lower elevations into the forest on this side of the Divide. The differences in the extent and distribution between the two sides can be explained through differing wind patterns. The prevailing winds are westerly to north-westerly. As the winds pass through and over the forest of the west slope, a mutual sheltering effect occurs. This effect allows trees to ascend to the maximum altitude in the lee of their neighbours (Wardle 1965) and no extremely harsh climatic effects on the uppermost trees are found.

The winds continue upslope over the alpine tundra and the Continental Divide. Once crossing over the Divide, the winds move downslope. With little interference from the small alpine plants, the wind moves at ground level with high velocity as compared to the west slope situation. In many cases this downslope wind carries particles of snow, ice crystals, and sediments which are abrasive to plant materials causing a sand-blasting effect. In the ecotone and timberline areas, these westerly downslope winds may be lethal to plant tissues. Mechanical abrasion of exposed plant tissues, deflation of snow, and desiccation are the major impacts (Hansen-Bristow 1981). The destructive winds affect a wide belt of trees and move timberline low into the 'forest'. The winds begin to drop their snow load once they have entered the ecotone. This is the result of a gradual or slight decrease in the wind speed with additional friction resulting as the wind strikes the uppermost mat forms and produces multiple small eddy effects from interaction with the tree islands.

Within the lower flag mat and the flag sub-belts, snow depths were found to reach 5.2 m during late winter–early spring (Hansen-Bristow 1981). This deep snow accumulation is a hindrance to seedling establishment and tree growth due to an extreme shortening of the growing season with late melt-out. The deep snow deposition continues into the forest below timberline.

An additional explanation for the difference in the extent of the ecotone on opposite sides of the Divide may relate to moisture conditions. Although precipitation data for the west slope are very scarce, the lushness and diversity of vegetational species is greater, suggesting more mesic conditions. The apparent increase in moisture and snowfall may be adequate to alleviate the increased evapotranspiration rates and desiccation which are apparently greater on the east slope.

Avalanches are most prevalent on the west slope of the Divide than on the east slope (Dow et al. 1981). The increased activity is the result of a higher amount of precipitation and snow deposition on the west slope. Within many avalanche tracks, revegetation by coniferous species is prohibited by frequent avalanche activity and only aspen, willow, and alder are able to withstand the avalanche pressure. Treeline and timberline are depressed into the valleys by some of the avalanches, and in a few cases, trees on the opposite valley side have been removed by the avalanching.

Slope aspect

Additional obvious differences in environmental factors and tree distribution are found between west-facing and east-facing slopes. Westerly winds remove snow from the upper section of a west-facing slope. The lack of an insulating snow cover results in extremely low soil temperatures and, hence, increased periglacial activity. The soil instability and lack of soil water both limit tree growth. An east-facing slope, in contrast, receives a large accumulation of wind-deposited snow. This snow provides insulation, moisture, and wind-protection to the plants it covers, promoting tree growth and viability. Too much snow, however, causes a delay in the onset of the growing season (Hansen-Bristow 1981) and promotes attack of needles by the snow fungus.

The differences between north-facing and south-facing slopes in the distribution of the ecotone are apparent, but because of a different spatial scale the differences are not quite as obvious as are the east-west differences. The major difference between the north-facing and the south-facing slopes is the amount of incoming solar radiation. The fact that radiation levels are higher on the south-facing than the north-facing slopes has a variety of implications. First, on the south-facing slope the snowmelt is earlier and more rapid. The earlier snowmelt, providing moisture to the trees early in the growing season, as well as permitting warming of the soils, allows the initiation of growth earlier than on north slopes. This results in a longer growing season, which appears to be a key factor for the survival of plant tissues (Hansen-Bristow 1981).

Solar radiation levels during winter, being higher on the south-facing than the north-facing slopes, can also be a detrimental factor. High rates of incoming solar radiation during winter may warm the exposed tree tissues to a point at which evapotranspiration takes place. With frozen soils and evapotranspiration (especially in late winter), an increase in water stress often leads to desiccation of tissues. Additionally, solar radiation during winter months is subjected to considerable reflection due to the high albedo of the snow cover. This reflection has been observed to sunscald the tissues of the exposed tree parts. In many cases, the chorophyll appears to be deactivated by the snow re-radiation, the tissues turning yellow. Often the underside of a clump of needles appears "burned" whereas the upper side remains green.

Conclusion

With an increase in mountain ecosystem use, possible artificial alteration of the forest-alpine tundra ecotone will jeopardize its geographical position. Trampling of young trees, compaction of soils, firewood gathering, drainage changes through trail establishment, and campfire-related forest fires could result in drastic changes to the ecotonal community. Additionally, assuming that the ecotone is stressed under the present day climatic condition, it may not regenerate within its present geographical range if severely disturbed. The analysis of the form, composition, and distribution of the forest-alpine tundra ecotone discussed herein will serve as a historical statement upon which to monitor future change.

The forest-alpine tundra ecotone is a dynamic vegetational belt, but it is also in precarious balance. Management regulations must be strictly enforced and public education about the geography of the ecotone is a necessity.

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