Landschaftsökologie

The regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, Montana and Wyoming

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Contents

1 Introduction

The timberline in the Rocky Mountains of Montana, Wyoming and Idaho is dominated by three tree species: Subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) (Arno and Hammerly 1984; Arno and Hoff 1989; Holtmeier 1989; McCaughey and Schmidt 1990, 2001). While the seeds of subalpine fir and Engelmann spruce are wind distributed, the heavy, wingless seeds of whitebark pine are primarily dispersed by the Clark's nutcracker (*Nucifraga columbiana*) (Hutchins and Lanner 1982; Tomback 1982).

Whitebark pine is the only North American member of the stone pines, all classified as genus *Pinus*, subgenus *Strobus*, section *Strobus*, and subsection *Cembrae* (Critchfield and Little 1966; Price et al. 1998; McCaughey and Schmidt 2001). The Cembrae subsection includes the five pines worldwide: whitebark pine, Swiss stone pine (*Pinus cembra*), Korean stone pine (*Pinus koraiensis*), Japanese stone pine (*Pinus pumila*), and Siberian stone pine (*Pinus sibirica*). All stone pine are characterized by five needles per fascicle, essentially indehiscent cones, and wingless seeds that are dispersed by two nutcrackers, *Nucifraga columbiana* and *Nucifraga caryocatactes* (Hutchins and Lanner 1982; Lanner 1982, 1990; Holtmeier 1999a). Stone pines also have in common the severe environment in which they are able to grow (Lanner 1990). Korean stone pine can be found in subarctic forest zones. The other four members of this group occur, though not exclusively, in subalpine zones up to timberline, where they are commonly associated with spruce species.

The relationship between the Clark's nutcracker and whitebark pine is mutually beneficial (Tomback 1978, 1982, 2001; Lanner 1982, 1996, Tomback and Linhart 1990). Whitebark pine seeds are harvested by Clark's nutcrackers in late summer and early fall. They are transported to a variety of storage areas throughout the subalpine zone, as well as to areas below and above the current elevational distribution of whitebark pine. Seeds are stored in caches of 1-15 seeds, 2-3 cm under the surface. Germination occurs in unretrieved caches (Tomback 1982, Tomback and Linhart 1990).

The influence of the European nutcracker *(Nucifraga cariocatactes*) on the spatial distribution of Swiss stone pines has been documented by several studies (Holtmeier

1965, 1966, 1974, 1993; Kuoch and Amiet 1970; Mattes 1978, 1982, 1985). Mattes (1982) and Holtmeier (1993, 1999a, 2000) proposed that the selective site preferences of the nutcracker's caching activity coincide with favorable growing conditions for Swiss stone pine regeneration, causing higher regeneration densities on convex land forms compared to concave slopes and depressions.

Regeneration of Japanese stone pine, *Pinus pumila*, is restricted to open, wind exposed patches near mature pine scrub, despite a more widespread seed distribution by the Japanese nutcracker (*Nucifraga cariocatactes* var. *japonica)* into closed coniferous forest (Hayashida 1994, Kajimoto et al. 1998). Tomback (1982) also reported discrepancies between the most frequent caching environments and sites with the highest seedling recruitment potential for the closely related North American species, the Clark's nutcracker and whitebark pine, on the eastern slope of the Sierra Nevada.

The patterns of whitebark pine regeneration after fire were investigated by Tomback et al. (1993, 2001a; Tomback 1994). McCaughey and Weaver (1990; McCaughey 1993) studied the influence of shade, seedbed type, and predator densities on germination and survival of whitebark pine in a subalpine clearcut. The general implications of avian seed dispersal on tree distribution patterns in the timberline ecotone are discussed by Holtmeier (1993, 1999a, 2000). However, detailed, regional studies documenting the regeneration of whitebark pine at its upper elevational limit are not available.

2 Objectives

This study investigated the relationship between distribution, seed dispersal, and site characteristics of whitebark pine in the timberline ecotone of the northern Rocky Mountains. Field work was conducted primarily from 1991 to 1994, with survival and growth data collected annually until 2001. In particular, the study focused on regeneration patterns and prevailing microsite conditions which may limit or promote germination and survival of whitebark pine at its upper elevational limit.

Central questions to this study were:

- What are the patterns of natural whitebark pine regeneration?
- What are characteristic site conditions for areas with high regeneration densities? Which factors may be limiting a successful recruitment of whitebark pine?
- What is the responsible agent for the spatial distribution of whitebark pine in the timberline ecotone? If a particular site has no regeneration, does the nutcracker not cache seeds in these sites, or do the site characteristics not permit germination and survival?

The spatial variability of whitebark pine regeneration was described by mapping stand structure and regeneration pattern in several transects through the timberline ecotone of the Beartooth Plateau. Successful reproduction from seed depends on several factor complexes: a sufficient seed bank, suitable conditions for germination, and suitable conditions for survival and establishment.

To supplement the mapping results, germination and survival rates of whitebark pine were determined in a controlled field experiment. The observed patterns of whitebark pine distribution were compared with the results of the germination and survival study. Convergent results would indicate that viable seeds are available wherever microsite conditions allow the recruitment of whitebark pine in the studied timberline ecotone. Divergent results would suggest that whitebark pine regeneration is not found on sites with the highest potential for tree establishment, but in locations determined by the nutcracker's selective caching activity.

Furthermore, the amount of regeneration, natural and experimental, may provide information about the reproductive potential of whitebark pine under present climatic conditions. Successful regeneration in the upper timberline ecotone is essential for an altitudinal advance of timberline due to global warming. Possible implications of changing climatic conditions on the regional development of timberline stands will be discussed.

In summary, the comparison of observational and experimental regeneration data should allow further insight into 1) the relative importance of the nutcracker’s caching activity versus other environmental limitations, 2) the status of the timberline ecotone in relation to the climatic situation, and 3) the sensitivity of the ecotone to future climatic changes.

3 The study area

3.1 Geographic setting

The study was conducted in the Beartooth Mountains of Montana and Wyoming, approximately 40 km east of Yellowstone National Park (Fig. 3.1; Fig. 4.1, page 17). U.S. Highway 212, also called the “Beartooth Highway”, crosses the Beartooth Plateau and allows easy access to subalpine and alpine areas. This region is part of the

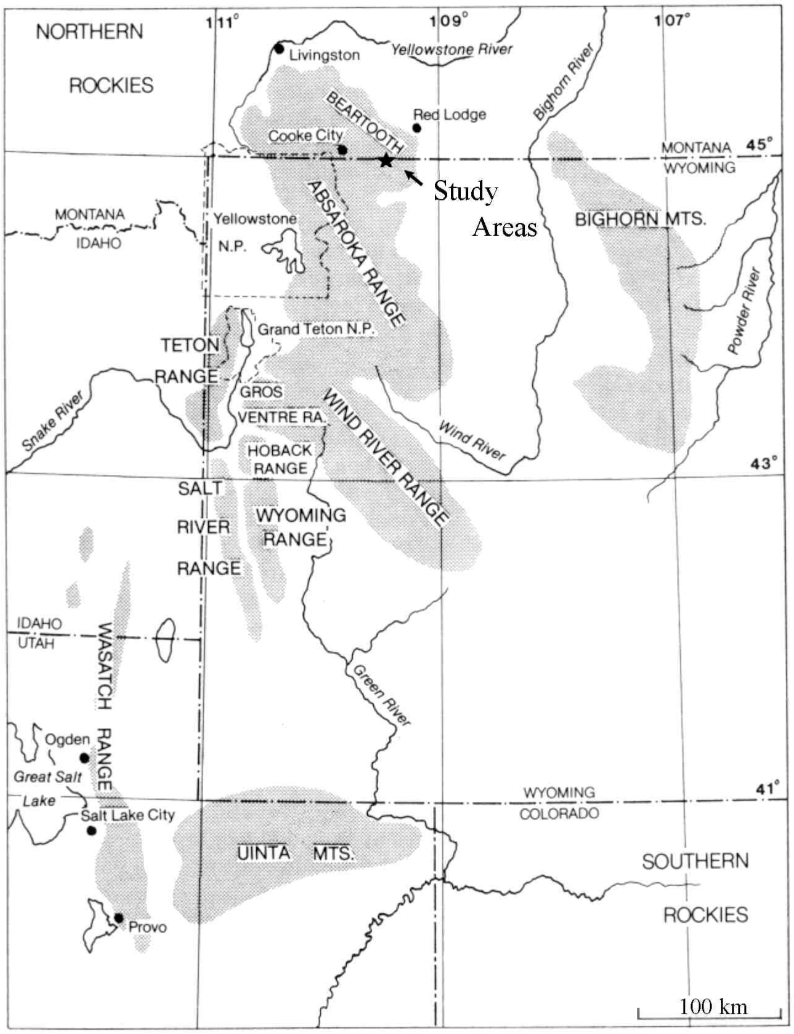


Figure 3.1: Location of study areas in the middle Rocky Mountains (modified from Arno and Hammerly 1984). See Fig. 4.1 for detailed map of study areas.

eastern range of whitebark pine, which forms extensive stands in the high elevation forests of the Greater Yellowstone Ecosystem in Montana, Wyoming, and Idaho (McCaughey and Schmidt 2001).

Four study areas were established in the upper timberline ecotone of the Beartooth Plateau. Study areas were selected according to the following guidelines: 1) the upper timberline was judged to be caused by climate rather than by orographic or edaphic factors, 2) no recent disturbances from fire, grazing or recreation were apparent, and 3) sites were reasonably accessible (≤ 1 hr walking distance from road).

The Tibbs Butte study area is located in Wyoming, on the gentle, north to northwest exposed slope of Tibbs Butte, approximately 3 km south of the Gardner Lake trailhead on U.S. Highway 212 (Photo 3.1 and 3.2). The study area is part of an extensive timberline ecotone characterized by Engelmann spruce tree islands and groups of whitebark pine. From an open subalpine forest at an elevation of 3050 m, the ecotone stretches more than 100 altitudinal meters to the upper-most trees at approximately 3170 m. Study sites are located at altitudes from 3095 to 3105 m.

The Littlerock Creek drainage separates Tibbs Butte from the southwest exposed Littlerock Creek study area, 2 km to the east. From the distance, the timberline in this area appears like an abrupt edge between pine–spruce forest and the alpine (Photo 3.3). Compared to Tibbs Butte, the ecotone is narrow. Slopes are slightly steeper than in other study areas. The elevation of the Littlerock Creek study areas varies from 3070 to 3105 m.

The Wyoming Creek and Rock Creek study areas are located in Montana, approximately 10 km north of Tibbs Butte and Littlerock Creek (Photo 3.4). The lower section of the Rock Creek study area is characterized by dense prostrate growth of Engelmann spruce and subalpine fir mixed with whitebark pine. This section is located on an almost level area at the edge of the Beartooth plateau, bound to the north by the steep walls of the Rock Creek valley, and to the east by the headwaters of Quad Creek, a tributary to Rock Creek (Photo 3.5). The upper section of this study area is situated on the northeast exposed slopes of Twin Mountain. Most of this section is dominated by alpine vegetation, with occasional pockets of prostrate trees. Study sites were established at elevations of 2990 to 3020 m.

In the Wyoming Creek study area, east of the highway, a strip of open whitebark pine woodland developed on a short, gradual, northeast exposed slope (Photo 3.6). This area is located leeward of a small ridge, on a bench above the steep slopes of

Wyoming Creek. Study sites are at 2970 to 2995 m elevation.

Photo 3.1: *Gentle, north exposed slope of Tibbs Butte, on May 15, 1993. Study area is marked with arrow. View to SE.*

Photo 3.2: *Tibbs Butte study area, marked with arrow, on June 1, 1992. View to SW.*

Photo 3.3: *Littlerock Creek study area, on June 1, 1992. View to N.*

Photo 3.4: *Wyoming Creek (left) and Rock Creek (right) study areas on the northeastern part of the Beartooth Plateau, on June 1, 1992. Study areas are marked with arrows. View to SW.*

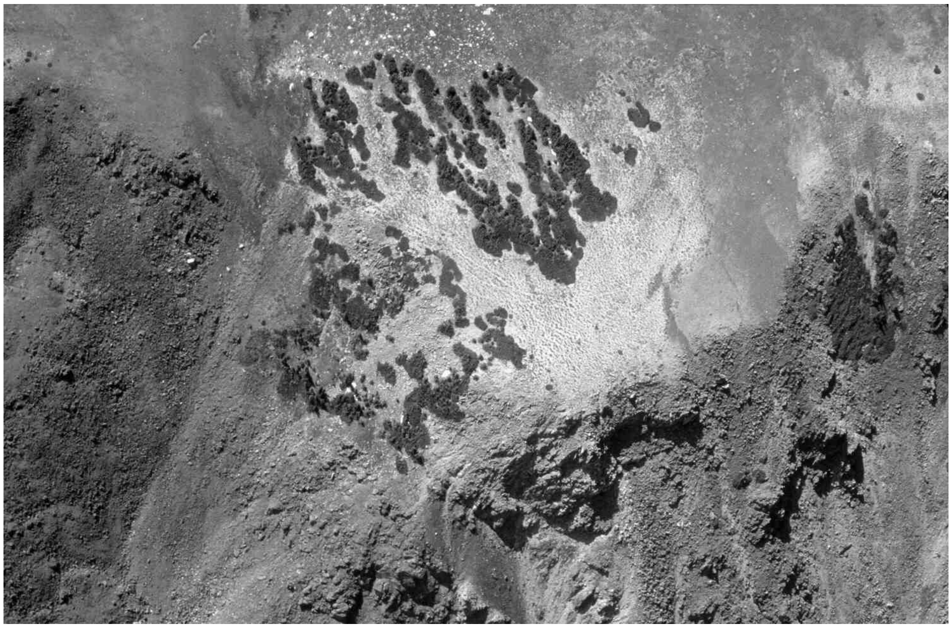


Photo 3.5: *Rock Creek study area on June 28, 1993. View to SE.*

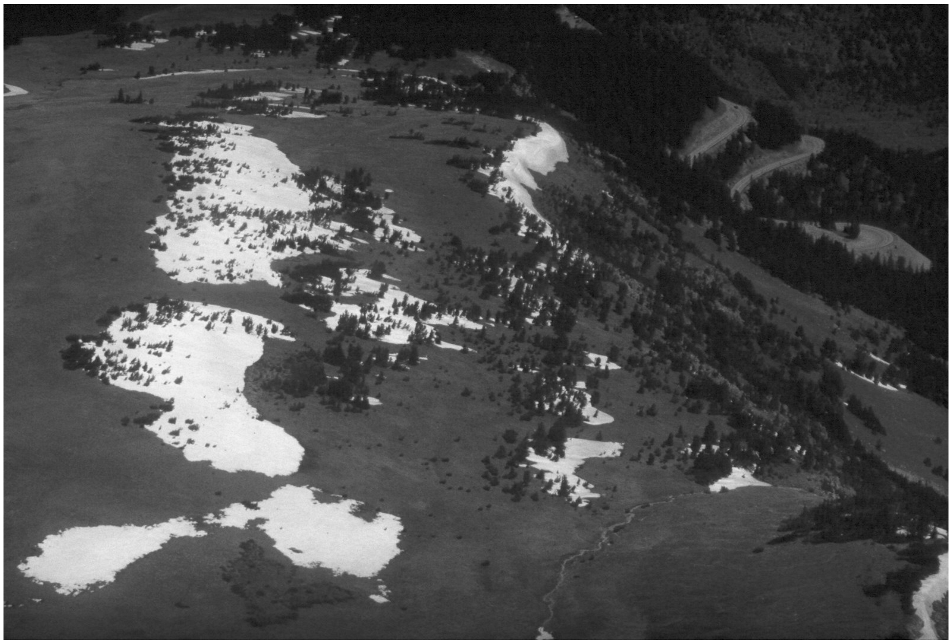


Photo 3.6: *Wyoming Creek study area, on June 1, 1992. View to NW.*

3.2 Geology and soils

The Beartooth Mountains are a large, uplifted fault block of early Precambrian crystalline rocks (Poldervaart and Bentley 1958; Foose et al. 1961; James 1995). The uplift is divided into three parts, the North and the South Snowy blocks, and the Beartooth block, the largest and southeastern-most block. It was uplifted higher than its neighboring sections, and during that process tilted southwestward and thrust northeastward. The southern and eastern part of this block are characterized by five distinct erosional surfaces, one of which is the Beartooth Plateau at the Montana–Wyoming border.

The mountain building events that resulted in the major uplift of the Beartooth Mountains occurred during the Late Cretaceous and early Tertiary. The Paleozoic and Mesozoic sediments that were deposited on the crystalline basement complex were also uplifted, or slid southward of the plateau. Major volcanic activity during the Eocene resulted in the deposition of volcanic rocks on a large part of the South Snowy block. The uplift of the Beartooth Mountains continued through the middle and late Tertiary, and may have been completed as late as early Quaternary time. By the end of the Tertiary period, nearly all sediments had eroded from the Beartooth and North

Photo 3.7: *View of the Beartooth Mountains, northeastern section. May 15, 1992.*

Snowy blocks, exposing large areas of Precambrian rocks. The present landscape was formed by three major periods of glaciation during the Pleistocene. The majority of the uplift was covered by icefields. Today, U-shaped valleys and other glacial features dissect the uplifted fault block, creating distinctive plateau-type benches characteristic for this mountain range (Photo 3.7).

The Beartooth block which includes the Beartooth Plateau is predominantly composed of gneisses, migmatites, and granitoids, intruded by mafic dikes (Lafrenz et al. 1986). The parent material in all selected study areas is composed of granitic rocks (Pierce 1965).

Soil development in upper subalpine and alpine areas of the Rocky Mountains has been studied intensively in the Colorado Front Range (Osburn and Cline 1967; Komárková 1979; Burns 1980; Holtmeier and Broll 1992). Little published information is available for the Beartooth Mountains. A soil survey in the Wyoming Beartooth Mountains has been conducted by the Shoshone National Forest, and is scheduled for completion in 2003 (Houston 2002). Soil descriptions from alpine areas on the Beartooth Plateau are included in Bamberg (1961) and Nimlos and McConnell (1962). In their monograph about the alpine vegetation of the Beartooth Plateau, Johnson and Billings (1962) assigned the alpine soils found under different vegetation types to four categories which are based on a classification system by Retzer (1956): alpine turf soils, alpine meadow soils, alpine bog soils, and lithosols.

The lack of a uniform soil classification system at the time of these early surveys and recent changes in soil taxonomy (Soil Survey Staff 1999) make comparisons between studies challenging. Under the current soil taxonomy definitions (Soil Survey Staff 1999), Johnson and Billings (1962) alpine turf soils as well as their alpine meadow soils may be classified generally as Inceptisols, and more specifically as Eutrocryepts or Dystrocryepts, depending upon the amount of base saturation in the mineral soil between 25-75 cm. Eutrocryepts have base saturations greater than 60% (NH_4OAc method, Soil Survey Staff 1999), Dystrocryepts have base saturations less than 60%. These soils show little development and are also typical of well- to medium-drained alpine areas of the Colorado Front Range (former Cryumbrepts or Cryochrepts, Burns 1980; now probably classified as Dystrocryepts).

Subalpine and alpine soils of wetlands, fens, and riparian areas are less uniform in their classification than the soils of relatively dry alpine meadows. Walford et al. (2001) used the 1994 version of soil taxonomy (Soil Survey Staff 1994). They reported the occurrence of Cryaquents (Entisol order), Cryaquepts (Inceptisol order), and Cryaquolls (Mollisol order) in alpine and upper subalpine wetlands and riparian corridors of the Beartooth Plateau. In alpine fens with high peat accumulation, Cryofibrists (Histosol order) were developed (Walford et al. 2001).

Johnson and Billings (1962) documented the occurrence of permafrost in alpine fens at a depth of less than 1 meter. Collins et al. (1984) found permafrost along the southeast portion of the Beartooth Plateau in the Sawtooth peatbeds, the only known fen-palsa in the contiguous United States. Where permafrost is present, soils would classify to the new Gelisol order (Soil Survey Staff 1999). Gelisols are defined by the presence of permafrost in less than 1 m depth, or by the presence of 'gelic material' (materials exhibiting characteristics of cryoturbation processes) and permafrost in less than 2 m depth. Possible classifications include Historthels, Aquorthels, or subgroups within the Fibristels great group.

Soils on outcrops or under late-melting snowbanks are usually shallow with a high content of skeletal material. These poorly developed soils are Cryorthents, in the soil order of Entisols (Shoshone National Forest 1996).

Alpine soils on the Beartooth Plateau do not show chemical evidence of a 'spodic horizon', which is defined by the translocation of organic materials, aluminum, and iron (Johnson and Billings 1962; Nimlos and McConnell 1962; Shoshone National Forest 1996). This is consistent with observations from the Southern Rocky Mountains by Komárková (1979) and Burns (1980) and is generally attributed to the continental climate character of these regions. Subalpine forest soils in the Beartooth Mountains exhibit weak morphological characteristics of a 'spodic horizon', but laboratory data do not substantiate these observations (Houston 2002, pers. comm.). Forest soils are in the Inceptisols order and classify as either Dystrocryepts or Eutrocryepts (Shoshone National Forest 1992, Soil Survey Staff 1999).

3.3 Climate

Few climatic data are available characterizing the subalpine or alpine environment of the Beartooth Mountains. The general climate character is continental. Prevailing winds are from the southwest, west, and northwest throughout the year. SNOw TELemetry (SNOTEL) sites are automated climate stations operated by the USDA

Natural Recources Conservation Service for water supply and drought forecasting. The SNOTEL site located near the Beartooth Lake Campground (WY9E10S) at 2727 m elevation is the only permanent, high elevation weather station in the vicinity of the study areas.

The average annual precipitation at Beartooth Lake (1980-1997) was 860 mm (Fig. 3.2). At Fischer Creek, a subalpine SNOTEL site northeast of Cooke City, MT and approximately 25 km west of Beartooth Lake at 2774 m elevation (MT09D06S), the average annual precipitation during the same time period amounted to 1338 mm, indicating increasingly dryer conditions towards the eastern part of the Beartooth Mountains. Seventy-eight percent of the precipitation at Beartooth Lake occurred as

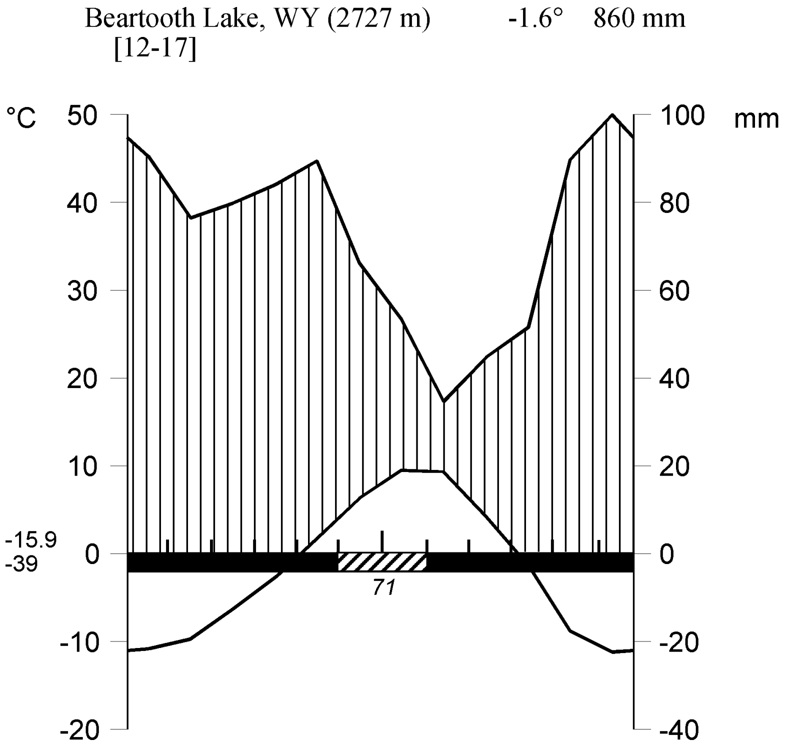


Figure 3.2: *Climate diagram after Walter and Lieth (1960) for the Beartooth SNOTEL station in subalpine spruce-fir forest, 1980-1997. Data following the station name are: elevation, mean annual temperature in °C, annual precipitation, and years of record for temperature and precipitation data. The upper line shows monthly precipitation, the lower line shows mean monthly temperature. Black bars indicate months with mean minimum temperature < 0°C, diagonally hatched bar indicates months with absolute minimum temperature < 0°C. Number of frost free days is 71; average daily minimum of coldest month is -15.9°C; coldest temperature on record is -39°C.*

snow in the winter and spring. Wind exposed areas on the Beartooth Plateau are commonly swept clear of snow, while snow banks on leeward slopes and depressions may persist until August. The relocation of snow on the Beartooth Plateau creates a small-scaled mosaic of different site conditions and vegetation characteristics in the upper subalpine and alpine areas.

The mean annual temperature from 1985 to 1997 was -1.6°C. July and August are the warmest months during the year, with average temperatures of 9.5°C and 9.3°C, respectively. The number of frost-free days between 1986 and 1998 ranged from 41 to 89 days. Frost and snow may occur any month of the year (Fig.3.2).

Short term temperature data during 1958 and 1959 from alpine environments on the Beartooth Plateau were published by Johnson and Billings (1962). From mid-June until the beginning of September 1959, 82% of days were frost-free at their instrument shelter 1.2 m above ground. Temperatures near ground level (2.5 cm above surface) were more severe, with 29 - 58% frost-free days, depending on the site.

During the main years of this study, the precipitation at Beartooth Lake was above average in 1992, and below average in 1993 and 1994, with 978 mm, 760 mm, and 676 mm, respectively. Precipitation patterns during the growing season were more differentiated: July precipitation was above average in all three years; August precipitation was close to normal for 1993 and 10 - 20 mm below average in 1992 and 1994; September precipitation was 20 - 40 mm below average in September 1993 and 1994. Temperature conditions in July 1992 and in June, July, and August 1993 were 2-3°C below average. In 1994, the average air temperatures were close to normal during June, July, and August, but 2°C above average during September.

3.4 Vegetation

The Beartooth Mountains of Montana and Wyoming are part of the Southern Rocky Mountain floristic region (Peet 1988). Arno and Hammerly (1984) and Scott (1995) use different subdivisions and consider the Beartooth Mountains as part of the Middle Rockies (see Fig. 3.1, page 5). While the southern border of the region varies depending on the classification used, the border to the north is consistently defined as the limit of Pacific air masses that result in the inland-maritime climate and Cascadian vegetation character of the northern Rocky Mountains (Arno and Hammerly

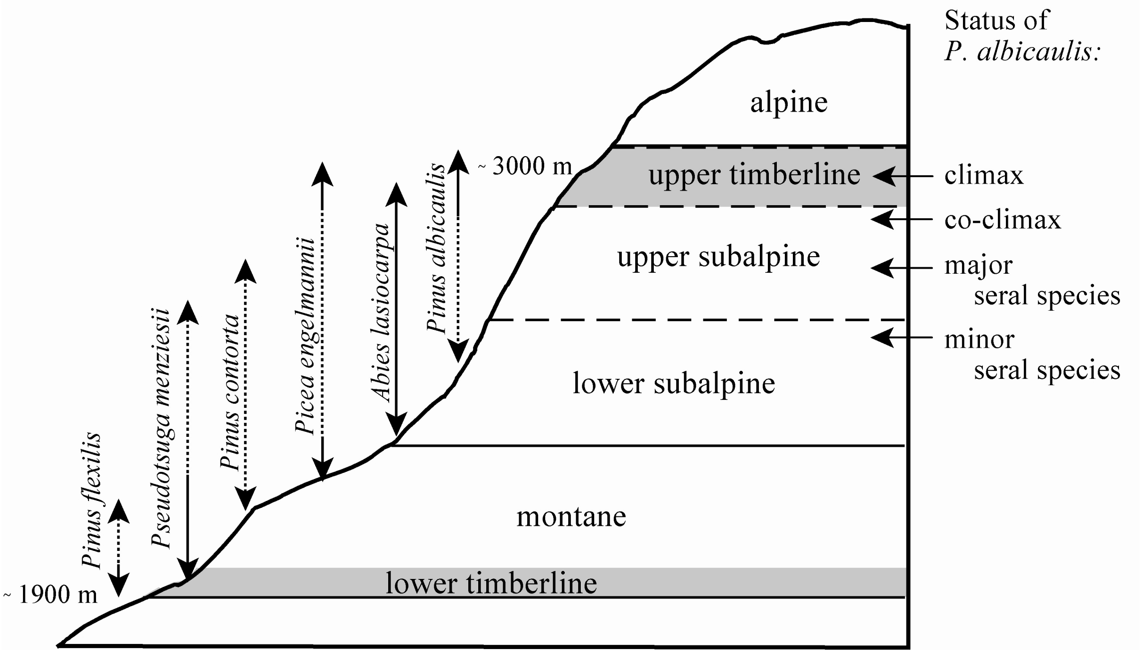


Figure 3.3: *Generalized elevational distribution of forest trees and successional status on noncalcareous geological substrates in the Beartooth Mountains, Montana and adjacent Wyoming. Solid portion of arrow indicates where a species is the potential climax, and dotted portion shows where it is seral. (Modified from Pfister et al. 1977 and Arno 2001).*

1984; Peet 1988; Barbour and Christensen 1993). The Rocky Mountains south of Livingston, Montana, are characterized by a dryer and generally more continental climate; forests are composed of few conifers either tolerant to summer heat and drought or to the severe conditions of high elevations.

The narrow forested zone of the Beartooth Mountains is mostly dominated by four conifer species: lodgepole pine (*Pinus contorta*), Engelmann spruce, subalpine fir, and whitebark pine (Fig. 3.3). Toward the lower timberline, pockets of Douglas-fir (*Pseudotsuga menziesii*) and limber pine (*Pinus flexilis*) can be found in warm microsites and are more widespread on calcareous substrates (Arno and Hammerly 1984). Groves of quaking aspen (*Populus tremuloides*) occur in moist areas throughout the lower forest zone.

Whitebark pine is mainly restricted to the upper subalpine and timberline zones. In the lower part of its range, whitebark pine forms successional communities with lodgepole pine, subalpine fir, and Engelmann spruce (Fig. 3.3). As a slow growing, moderately shade-tolerant species (Arno and Hoff 1989), whitebark pine will gradually be replaced by the more shade-tolerant subalpine fir and Engelmann spruce in the absence of disturbance. On cold or dry sites, however, whitebark pine is a climax species. It occurs in pure stands, but also coexists indefinitely with subalpine fir and Engelmann spruce throughout the timberline ecotone (Arno and Hoff 1990, Arno 2001).

The upper timberline in the Beartooth Mountains is situated at 2900 m to 3200 m. The top of the Beartooth Plateau is mostly occupied by alpine communities. In some areas, conifers are restricted to steep canyon slopes, and timberline appears to coincide with the edge of the upper plateau surface. In other places, the subalpine forest continues onto the ‘plateau top’, and broad timberline ecotones can be found.

The alpine communities on the Beartooth Plateau have been documented by Johnson and Billings (1962). They describe a broadly defined *Geum rossii* turf on summits, ridges, and upper slopes. *Deschampsia cespitosa* meadows occur on moist to mesic slopes and depressions. Wetlands are commonly occupied by *Carex scopulorum* communities or *Salix* thickets.

3.5 Disturbances

Many Rocky Mountain forests are in some stage of recovery from prior disturbances. Fire, wind, insects, disease, browsing, avalanches, landslides, weather extremes, volcanism, and humans all impact vegetation pattern in a landscape, resulting in a mosaic of communities within local elevational zones (Peet 1988).

Historically, fire has been the most important natural disturbance in Rocky Mountain coniferous forests. Subalpine lodgepole pine and spruce-fir forests in Yellowstone National Park burned every 300-400 years; fires in these forests were commonly widespread and stand-replacing (Romme 1982). In the northeastern part of Yellowstone National Park, stand replacing fire intervals of more than 350 years in high elevation whitebark pine forests have been documented (Barrett 1994). Fires starting in the subalpine forests may eventually reach timberline. Because of the relatively cold and moist conditions and a general lack of continuous fuels, destructive and large fires are uncommon in the timberline ecotone (Arno and Hammerly 1984). Many fires are started by lightning strikes, but may not spread beyond the tree group from which they originated.

No signs of recent fire were observed in or adjacent to the selected study areas on the Beartooth Plateau. However, many soil samples from study sites included small pieces of charcoal, indicating past fire incidents in all study areas.

Presently, whitebark pine populations are declining. This loss can be attributed to fire suppression policies during the 1900's and the subsequent successional replacement of whitebark pine by Engelmann spruce and subalpine fir (Murray et al. 2000). Declining populations are aggravated by mountain pine beatle epidemics and particularly by white pine blister rust infections (Arno 1986, 2001; Tomback et al. 2001b). White pine blister rust (*Cronartium ribicola*) is an introduced fungal disease that has infected and killed many whitebark pine stands in the mesic parts of its range (Kendall and Keane 2001). Dry and cool continental climates appear to limit the destructive character of white pine blister rust. Recent surveys in Yellowstone National Park and adjacent National Forests found infection rates of 2-12% and low mortalities of whitebark pine (Kendall et al. 1996a, 1996b; Harris 1999). However, if regional climatic conditions change toward milder temperature regimes and higher moisture during summer and fall, blister rust infections could intensify rapidly. Such weather fluctuations and the evolution of new blister rust races may eventually cause increased mortality rates in presently little-affected geographic regions (Kendall and Keane 2001).

Many subalpine and alpine areas in the Beartooth Mountains have been grazed at some time in the past. Sheep grazing was most common at higher altitude. Grazing of alpine areas in the Montana portion of the Beartooth Plateau ceased more than 30 years ago (Custer National Forest, pers. comm.). Some sheep grazing is still permitted in the Wyoming portion of the Beartooth Plateau, but is restricted to a short period during late July and August (Shoshone National Forest, pers. comm.). Domestic sheep have been observed in the Littlerock Creek and Tibbs Butte study areas. Cattle frequently travel the creek bottoms to the timberline area near Littlerock Creek. The study sites themselves, however, were not disturbed by domestic animals during the years of this study.

4 Methods

4.1 Terminology

The definitions of the boundary between the contiguous forest and alpine vegetation are as diverse as the physiognomy of this vegetational limit (see Wardle 1974; Körner 1999; and Holtmeier 2000 for discussion). This study follows the terminology used by Holtmeier (2000).

Timberline and timberline ecotone are treated as synonyms and describe the transition zone between closed subalpine forest and the most advanced trees of the same species that form the forest below, regardless of their growth form or height. The term 'subalpine' is defined as the altitudinal belt below the timberline ecotone, contrary to suggestions by Löve (1970) who favored the use of 'subalpine' for the timberline ecotone itself.

Tree clusters, multi-stemmed trees, and tree islands are phrases referring to different growth morphologies. A cluster is a group of individual trees (seedlings or older) with different genotypes. Whitebark pine seedlings usually start out as clusters since they originate from nutcracker caches. The growth form of mature whitebark pine is frequently described as multi-stemmed. Multiple stems originating from the base may be caused by an early loss of apical dominance in a single tree, or may have developed from a tree cluster, where single individuals can no longer be distinguished (Linhart and Tomback 1985). Regeneration by layering causes clonal growth (Cooper 1911; Kuoch and Amiet 1970). The resulting, well-defined vegetational units that occur at timberline are called tree islands. Theoretically, tree islands have one genetic origin, even though this can only be proven by genetic analysis or extensive site excavation. Finally, a tree clump is a nonspecific term for any tree group, clonal or not, which may even consist of different tree species.

All of the above described growth forms may occur as erect trees or tree groups, or, as a response to adverse growing conditions at high altitude, may be growing more or less decumbent, with no or few apical shoots extending above the average winter snow cover. At timberline, exposed tree branches are usually wind flagged or wind shorn, and are likely to exhibit severe needle damages.

4.2 Composition and structure of the timberline ecotone

At two locations in the upper timberline ecotone, 10 m wide transects were established along altitudinal isoclines. The Tibbs Butte transect, at 3100 m elevation, is 300 m long. It begins at the eastern edge of an open stand of tree islands and continues toward the western end of the NW exposed slope (Fig. 4.1, area a).

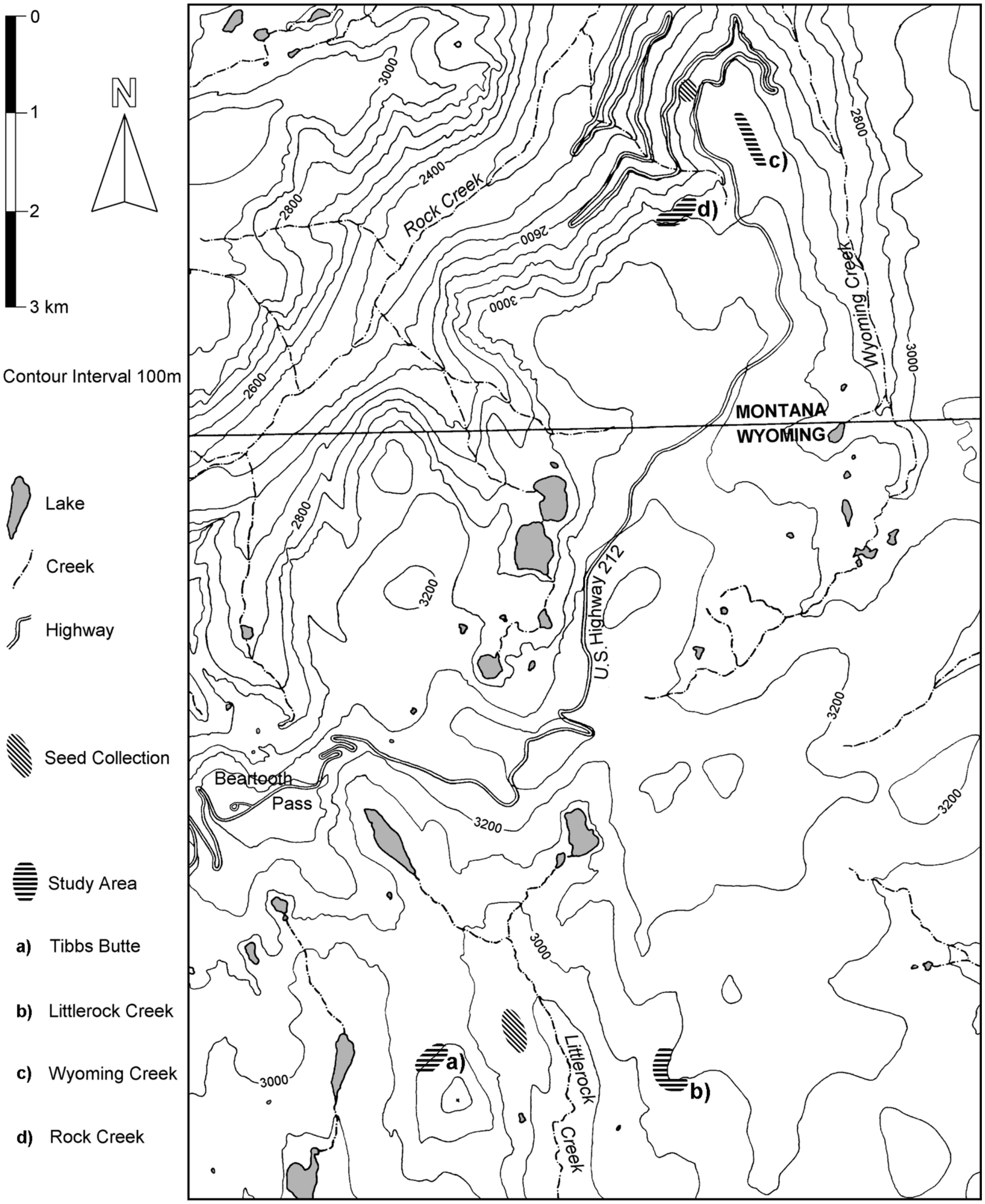
At Wyoming Creek (Fig. 4.1, area c), three transects were established at an elevation of 2985 to 2995 m, parallel to each other, with a distance of 25 m between them: the upper transect is 100 m long and runs windward of the woodland, the 85 m long center transect cuts through the woodland, and the lowest 100 m long transect is located on the leeward side of the woodland, where the woodland opens to a treeless meadow.

Combined, the transects cover 5850 m^2 of timberline ecotone. While the starting points of the transects were subjectively selected, all transects were established perpendicular to the main slope direction and transverse through a random selection of treeless meadows, tree islands and woodland sites.

The locations of all tree individuals, including snags, found within the transect borders were mapped. Additionally, the canopies of trees ≥ 1.5 m tall were recorded in graphs. The percent canopy cover values of the overstory were derived from calculating the areas on the field graphs. During the field seasons of 1992 to 1994, the following data were collected for all tree individuals: species, growth form (clonal, multi or single stemmed, erect or decumbent), diameter of the thickest stem at ground level, height (estimated for trees taller than 2 m), and vitality (good, fair, poor, or dead). A tree island was treated as a singular entity and its length and width were recorded.

For all whitebark pine shorter than 1.5 m, the location relative to rocks, logs, trees or other characteristic site features was described. The number of individuals per cache, needle length of the tallest leader, and needle losses and their probable causes were analyzed. Young seedlings were aged by counting the nodes on the main stem. Measurements on whitebark pine clusters refer to the largest and healthiest seedling.

Often the transect covered only part of a tree island. It was included in the analysis as long as some of its stems originated from the transect area. On Tibbs Butte an exemplary tree island was mapped entirely in an 17 by 27 m area. These data were



Base: USGS 7.5 Minute Series (Topographic): Black Pyramid Mountain, Montana - Wyoming 1986 and Deep Lake, Wyoming 1987.

Figure 4.1: *Location of study areas on the Beartooth Plateau, Montana and Wyoming. Transects were established in areas a) and c). The sites for the germination experiment are in area a) T1-T8, b) L1-L8, c) W1-W10, and d) R1-R5.*

used in a separate graphic display. Saplings and trees outside the standard 10 m transect were excluded from statistical analysis.

New germinants and seedlings lower than the surrounding herbaceous vegetation can easily be missed while mapping larger areas. Circular subplots of 10 m^2 area were established every 10 m along the transect centerline, amounting to 10% of the total transect area. In August and September 1993, and again in August 1994, 28 circular plots in the Wyoming Creek transects were carefully searched for new germinants and one- to three-year-old seedlings. The 30 circular plots in the Tibbs Butte transect were surveyed in September 1994. The number of caches, seedlings per cache, vitality, litter depth, and the location relative to rocks, logs, trees, or other microsite characteristics were recorded. Distance and direction from the center pole of the subplot helped relocating germinants and seedlings in September 1995, 1996, and 1997 for determination of survival rates. Each time, the vitality of seedlings was re-evaluated and the diameter and height measured with calipers.

The snow distribution and the patterns of snow melt on the transects were studied in 1993. The snow depths of the Tibbs Butte transect were measured on May 15, May 30, June 13, June 26, and July 13. The snow depths of the Wyoming Creek transects were mapped on May 18, June 11, June 26, and July 12. Snow depth measurements were taken with a 2.20 m long fiberglass pole in 5 m intervals at the upper boundary,

Photo 4.1: *Weather station on Tibbs Butte, WY, at 3100 m elevation.*

the center, and the lower boundary of the 10 m wide transects.

An automated weather station was established just below the Tibbs Butte transect at 3100 m, in an open meadow (Photo 4.1). A LI-COR quantum sensor, mounted horizontally at 1.5 m above ground on a Meteorological Instrumentation Tripod, measured the photosynthetically active radiation (PAR) between 400 to 700 nm wavelength (MIT EA-136, OMNIDATA and LI-190SZ Quantum Sensor, LI-COR). Sensors for air temperature and relative humidity (ES-110, OMNIDATA) were housed in a white solar radiation shield at 1.5 m above ground. Two soil temperature sensors (TP10 Thermistor Temperature Probe, OMNIDATA) were installed at the weather station at the depths of 3 cm and 10 cm. A data recording system (OMNIDATA EasyLogger EL-824) scanned and saved measurements from all sensors in 10 minute intervals and reported hourly averages, daily minima, and daily maxima of air and soil temperatures, relative humidity, and radiation.

4.3 Germination and survival of whitebark pine

The germination and survival rates of whitebark pine were analyzed in a field and laboratory experiment. On September 11, 1991, whitebark pine cones were collected from two stands approximately 100 m below timberline, in the Littlerock Creek and Rock Creek drainages (see Fig.4.1, p. 16). The cones were air-dried and the seeds were extracted and X-rayed to discard poorly developed seeds (Simak 1980).

For the laboratory experiment, 150 X-rayed whitebark pine seeds from each location (300 seeds total) were surface sterilized by soaking in 40 % household bleach for 10 minutes. The seeds were rinsed thoroughly, placed in cheesecloth bags, and soaked in running tap water for 48 hours. For moist stratification, seeds were placed between moistened blotter paper and stored in a plastic bag in the refrigerator at 1.5°C (Jacobs and Weaver 1990). After one month, the stratified seeds were transferred into 6 plastic germination boxes lined with moistened blotter paper. Each germination box contained 50 seeds from either Littlerock Creek, Rock Creek, or mixed to equal parts from both locations.

The boxes were placed into a germination chamber on June 16, 1993, with a 25°C day, 15°C night, and a 10 hour photoperiod (Jacobs and Weaver 1990). The seeds were remoistened periodically, and the number of germinants were recorded biweekly until October 1994.

At the end of September 1991, a total of 2325 whitebark pine seeds, mixed from both locations in equal parts, were planted in 31 experimental field sites on Tibbs Butte (T1-T8), and in the Littlerock Creek (L1-L8), Rock Creek (R1-R5) and Wyoming Creek (W1-W10) study areas (Fig. 4.1, p.17). While the general area of each experiment site was chosen subjectively to represent a diversity of aspects, topographic positions, wind exposures, and existing vegetation patterns, the specific location was determined randomly. Experiment sites were established in areas with homogeneous vegetation cover. A uniform vegetation cover was hypothesized to be an indicator for similar environmental conditions throughout the experiment site. All experiment sites were located away from permanent creeks or other open water.

In each experiment site, 15 artificial caches of 5 whitebark pine seeds were buried to a depth of 3 - 4 cm, resulting in a total of 75 seeds/site. Depending on the thickness of the organic layers, whitebark pine seeds were located in different soil horizons. Seeds were placed in the O_e and O_a horizons on sites T4, T5, T6, W4, and W9, in the transition between O and A horizons on sites W2, W3, and R5, and in the A horizon on all remaining sites. The specific depth instead of a specific horizon for the seed location results in different moisture, nutrients, and temperature regimes at the microsite scale. The planting followed a strict systematic pattern displayed in Fig. 4.2. If a planting location fell on a rock or log, the closest possible planting spot was chosen instead, and its location was recorded. To minimize the impact on microclimatic conditions, all sites were left unprotected from possible rodent or bird predation. The only markers consisted of one 50 cm long PVC pipe at both ends of each experiment site (Fig. 4.2). During the summers of 1992 and 1993, the

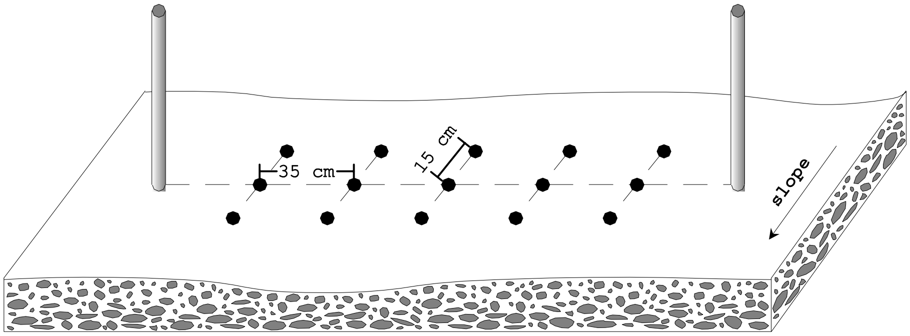


Figure 4.2: *Planting pattern of the 31 germination sites. Black circles indicate individual planting locations. The centerline between stakes runs perpendicular to the general slope.*

germination sites were monitored for seedling emergence and survival on an approximate biweekly schedule. In 1994 the sites were visited monthly. From September 1994 to 1999 and in 2001, the heights and stem diameters of surviving seedling clusters (represented by the largest healthy seedling) were measured annually with calipers, and their growth characteristics and vitality were recorded.

Germination and seedling emergence are different processes. Germination starts with the development of the primary root, underground, followed by the elongation of the hypocotyl, which eventually emerges above the soil surface. The time between germination and emergence may range between a few days to possibly a few weeks (McCaughey and Tomback 2001). Initially, germinated seeds are not visible above ground. Successful germination is identified by seedling emergence, and, for practical purposes, is termed germination throughout this report.

The planting in artificial seed caches was intended to imitate seed dispersal by the nutcracker. Germination and survival rates are reported for individual seedlings and for seedling clusters, to facilitate comparison with other studies. As seedlings get established, a seedling cluster is a more meaningful unit for survival and growth measurements, since there is little to no morphological difference between a single multi-stemmed whitebark pine and a whitebark pine cluster.

The snow melt on all experiment sites was monitored each spring from 1992 - 1995. When the Beartooth Highway opened in May or June, the sites were visited and the snow cover was recorded twice a month until all sites were melted out.

The cover of vascular plants was recorded using the Braun-Blanquet method (Braun-Blanquet 1964; Mueller-Dombois and Ellenberg 1974). General plot size for the vegetation analysis was 5 x 5 m, with the germination experiment site in the center. For some experiment sites, the vegetation was too heterogeneous to sample a 5 x 5 m area. In these cases either the shape or size of the sample was altered to maintain homogeneity, but still included the entire regeneration site. Vascular plant nomenclature follows Dorn (1992) and for some genera Hitchcock and Cronquist (1973). Species magnitudes of all vascular plants were recorded separately for the herbaceous layer (< 0.3 m), shrub layer (0.3 - <1.5 m), and tree layer (≥1.5 m). The following scale values were used: r = solitary, with small cover; + = few, with small cover; 1 = ≤ 5% cover, scattered to numerous; 2 = >5 - 25% cover; 3 = >25- 50% cover; 4 = >50 - 75% cover; and 5 = >75% cover. A site description including altitude; slope; aspect; topographic position and relief; cover of rocks, woody debris, litter, moss, lichen, and mineral soil; and signs of disturbances complemented the vegetation analysis.

Slope and aspect were used to determine the potential annual solar radiation of a site (Frank and Lee 1966). To reflect relative moisture conditions, a topographic moisture index was created similar to the index suggested by Parker (1982). Topographic positions were assigned to the following values: valley bottom = 10, lower slope = 8, middle slope = 5, upper slope = 2, ridge top = 0. Relief features were rated as: depression = 10, concave = 9, concave/straight = 8, straight = 5, convex/straight = 2, convex = 1, mound = 0. Values assigned to slope steepness ranged from 0 (≥30°) to 10 (<3°), according to Parker (1982). These three variables were summed to form an index ranging from 0 (relatively dry) to 30 (relatively wet), and can be considered a "moisture supply index" (see Donnegan and Rebertus 1999). The aspect was not included because it adds a temperature related variable (solar radiation) to the moisture index, and because of the interaction between aspect and slope.

Partial to complete shading of germinated whitebark pine clusters by trees, shrubs, rocks, or logs was recorded at each planting location. To measure the surface temperature at the soil/air interface, wax pellets with defined melting points (TEMPIL Pellets) were placed on characteristic surface materials (litter, mineral soil, or scree) in all experiment sites. In summer 1992, eight pellets with melting temperatures ranging from 45°C and 93°C were used. Pellets with high melting points proved unnecessary for the actual temperature ranges, and in summer 1993, six pellets with melting points at 38°C, 41°C, 45°C, 52°C, and 59°C were distributed. Melted or lost wax pellets were replaced at least twice a month. This method provides a crude measurement of the maximum temperatures reached in the past time interval. However, it is an inexpensive and simple approach to collect temperature data on all experiment sites. To calculate an average maximum temperature index for each site, maximum surface temperatures were first scaled from 1 (<38°C) to 6 (≥59°C) and then averaged for July and August.

On experiment sites T4, T5, and T6 on Tibbs Butte and W7, W8, and W10 in the Wyoming Creek study area, soil temperatures were measured digitally with OMNIDATA sensors at a depths of 3 and 10 cm. For the Tibbs Butte sites, the weather station data logger recorded the hourly averages and daily extremes of soil temperatures for the same periods as all other weather data collected (see chapter 4.2).

The six sensors in the Wyoming Creek study area were connected to a second data recording system (OMNIDATA EasyLogger EL-824) installed inside a tree island. The data logger requested measurements in 10 minute intervals and recorded hourly averages as well as daily minima and maxima during summer and fall of 1992, 1993, and 1994.

At all germination experiment sites, the depth and kind of organic litter was mapped, and soils of the A horizon were sampled at 0 - 5 cm in a systematic pattern (6 samples at each germination site). The soil profiles of 15 selected experiment sites were mapped and classified following the USDA Soil Taxonomy (Soil Survey Staff, 1999). If feasible, soil pits were dug to the C horizon or the depth of 100 cm, and soils from each horizon were sampled.

All soil samples were air-dried and passed through a 2 mm sieve. Dry and moist soil colors refer to crushed and smoothed soil samples, using Munsell Soil Color Charts. Root contents and percentage of skeletal material (≥ 2 mm) were estimated. The texture of the fine earth fractions (< 2 mm) of mixed topsoil samples were determined by hand using the U.S. system of soil textural classes. The particle size distributions of the profile samples were analyzed in the laboratory with the pipette method (Page 1982). Particle size classes refer to the International system (Birkeland 1984).

Chemical soil analysis included the determination of soil pH with a glass electrode in a 1:2.5 dilution of destilled water and in a 0.01 M $CaCl_2$ solution; for litter samples a 1:10 dilution was used. Total nitrogen and organic carbon of ground soil samples were determined by an elemental analyzer (Carlo Erba NA 1500).

4.5 Statistical analysis

The statistical analysis of stand structure and whitebark pine germination and survival was performed with SAS (SAS Institute 1999).

Snow depth and snow melt graphs were created using the Geographic Information System IDRISI (Eastman 1995). The IDRISI routine INTERPOL was used to calculate a digital elevation model with 16 cells/m², from the original 5 m measurements of snow depth. This image was smoothed three times using a mean filter (low pass). The resulting data were classified for the graphic display of snow depth and snow free areas during spring 1993.

The vegetation data of the germination sites were summarized with the aid of a detrended correspondence analysis (DCA, CANOCO program, Ter Braak 1988). Plants with magnitude value “r” were excluded from the analysis. The magnitude value “+” was converted to 0.5, all other magnitudes were directly used in the ordination. This approach ensured that species with high cover did not dominate the ordination. The sample scores of the first two axes were used in visual and statistical analysis to explore the relationship between vegetation cover and germination and survival of whitebark pine.

Temperature data were not recorded continuously due to repeated instrument failures. Linear multiple regression analysis of acquired data (PROC REG, SAS Institute 1999) was used to model missing daily average, minimum, and maximum temperature data during July and August 1992-1994. Stepwise variable selection with $\alpha = 0.01$ chose a maximum of five predictor variables from other soil or air temperature measurements during the same time period at Tibbs Butte, Wyoming Creek, or Beartooth Lake. Resulting temperature models had adjusted r^2s that were usually above 0.80 (min = 0.71, max = 0.91), with $n \geq 60$. Modeled data are identified as such whenever they are used in graphs, tables, or text.

The relationship between germination, survival, and a set of environmental variables was investigated with logistic and linear regression analysis (PROC LOGISTIC and PROC REG, SAS Institute 1999). The general model was designed prior to analysis and based on literature (Holtmeier 2000; Jacobs and Weaver 1990; McCaughey and Weaver 1990; McCaughey and Tomback 2001; Tomback et al. 2001a; and others) as well as field observations. Final variable selection was aided by univariate statistical analysis and Pearson or Spearman correlation coefficients between variables that reflect moisture and temperature conditions of the experiment sites.

All variables used in logistic regressions were checked for linearity in their logit (Hosmer and Lemeshow 1989, Agresti 1990). Variables with few values, e.g. maximum surface temperature and time of snow melt, still have underlying interval scales and were treated as continuous variables, as long as they did not violate the assumption of linearity.

For the survival analysis, the variable snow melt had only four values with nonlinear trends. Values 5 and 6 with late to very late snow melt were combined.

Snow melt was entered into linear regression analysis with two design variables. Shading was a binary variable indicating the presence or absence of shade on any whitebark pine clusters of a site.

Model selection followed suggestions from Burnham and Anderson (1998) and Anderson et al. (2000). Akaike's information criterion modified for small sample size AIC_c and Akaike weights w_i were used for model evaluation. The AIC_c is an estimate of the relative Kullback-Leibler information, i.e., the information that is lost when a model is used to approximate the full reality. The model with the lowest AIC_c is considered the best approximating model in the group of proposed models. The Aikaike weights range from 0 to1 and express the probability that a specific model is the best one in the group of models considered (Burnham and Anderson 1998).

Generalized multiple correlation coefficients $\bar{r}^2$ and adjusted multiple correlation coefficients r^2_{adj} are given for logistic and linear regression analysis, respectively. The r^2_{adj} is the classical r^2 adjusted for the degrees of freedom for the specific model and expresses the proportion of explained variance (SAS Institute 1999). For logistic models, residual variance cannot be calculated. Here the r^2 is defined as $1-\{L(0)/L(\beta)\}^{2/n}$, where $L(0)$ and $L(\beta)$ are the likelihoods of the intercept-only model and the fitted model, respectively (Cox and Snell 1989). Since this value has a maximum less than 1, $\bar{r}^2$ is defined as $r^2/\max(r^2)$ (Nagelkerke 1991). The $\bar{r}^2$ does not include any adjustment for the number of parameters in the model, leading to higher $\bar{r}^2$ as more parameters are included in the equation. However, this commonly does not improve the quality of the model, as explained in detail by Burnham and Anderson (1998, chapter 1.4). The generalized multiple correlation coefficients were not used for model selection but are provided as a classical, familiar measure of success of predicting germination and survival from a number of environmental factors measured in this study.

5 Results

5.1 Composition and structure of the timberline ecotone

5.1.1 Tree composition and distribution of juvenile whitebark pines

The composition and structure of ecotonal forest and woodland stands were different in the two sites studied. The Tibbs Butte transect was dominated by Engelmann spruce, contributing 89% of the total canopy cover in the overstory (Fig. 5.1). Whitebark pine was the dominant overstory species in the Wyoming Creek transects. Subalpine fir did not occur in the overstory in the Tibbs Butte transect and was only a minor component in the Wyoming Creek area.

The change in composition was paralleled by differences in growth forms. On Tibbs Butte, Engelmann spruce commonly grew in decumbent, asymmetrically shaped tree islands, with a narrow, low-growing windward side and a progressively taller and

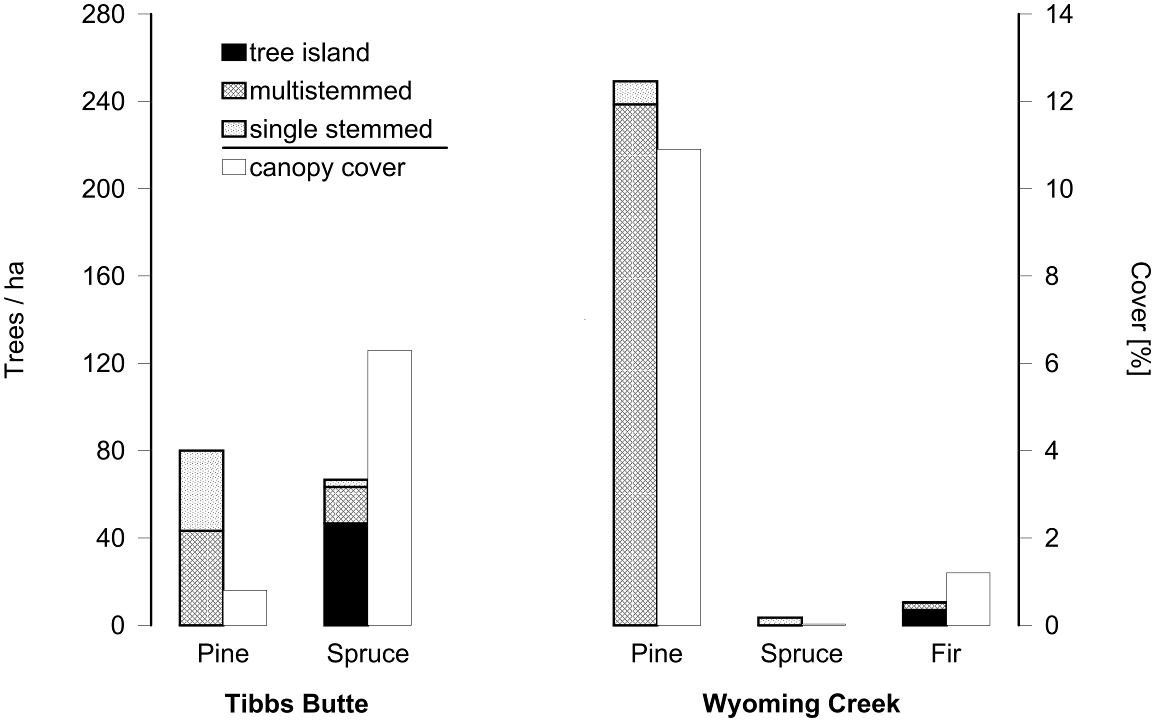


Figure 5.1: *Species composition, growth forms, and canopy cover of the overstory (≥ 1.5 m) on the Tibbs Butte and Wyoming Creek transects. Growth forms are displayed in trees/ha on the left axis, canopy covers refer to the right axis of the diagram.*

broader growth habit toward the leeward side. This growth form is the result of directional clonal growth (by layering) on the wind-protected side of the tree island (Marr 1977; Benedict 1984; Holtmeier 1999b). Mature whitebark pine were scattered inside or at the leeward side of the island. In these protected microsites whitebark pine was frequently found with an upright, single stemmed growth form. A tree island was treated as a single entity, despite the possibility of several genetic origins. Therefore the Tibbs Butte tree count resulted in a relative small number of Engelmann spruces covering 6% of the transect area, compared to less than 1% canopy cover of whitebark pine (see Fig. 5.1).

The timberline ecotone at the Wyoming Creek location can be described as a whitebark pine woodland. Due to the gentle, northeast-facing slope, trees were less exposed to wind than on Tibbs Butte. Only two tree islands — formed by subalpine fir — were mapped on the transect windward of the woodland. Most whitebark pines in the overstory were multi-stemmed and may possibly be tree clusters, that is, stems may have different genotypes. Only 19% of these multi-stemmed whitebark pines exhibited a decumbent growth form with possible layering. The rooting of decumbent whitebark pine branches was only observed once on Tibbs Butte, while excavating parts of the stem system. Rooting had occurred in a single location at the lowest part of a buried branch. Compared to Engelmann spruce or subalpine fir, layering of whitebark pine occurs very infrequently.

Stand structure and wind exposure resulted in variable snow regimes in both study locations. On the windswept slope of Tibbs Butte, tree islands acted as effective snow fences and created a mosaic pattern of snow patches during winter and spring (Photo 3.2, page 7; Fig. 5.2). The northeast-facing slope at Wyoming Creek is moderately wind protected by a minor ridge just west of the transect and collected windblown snow. Differences in snow cover were on a different scale at Wyoming Creek than on the Tibbs Butte transect. The snow cover on the transect windward of the woodland was low, compared to a high and long cover on the inside and leeward transects (Fig. 5.3).

For the winter of 1992-1993, the SNOTEL site at Beartooth Lake, WY (2727 m), approximately 11 km west of the Tibbs Butte study area, measured a maximum snow water equivalent of 580 mm, 14% below the 17 year average on this site. The highest snow water equivalent during the winter 1992-1993 was registered on May 6, eight days before snow depth was measured for the first time on the Tibbs Butte transect. During this time the maximum air temperature at the Tibbs Butte weather station

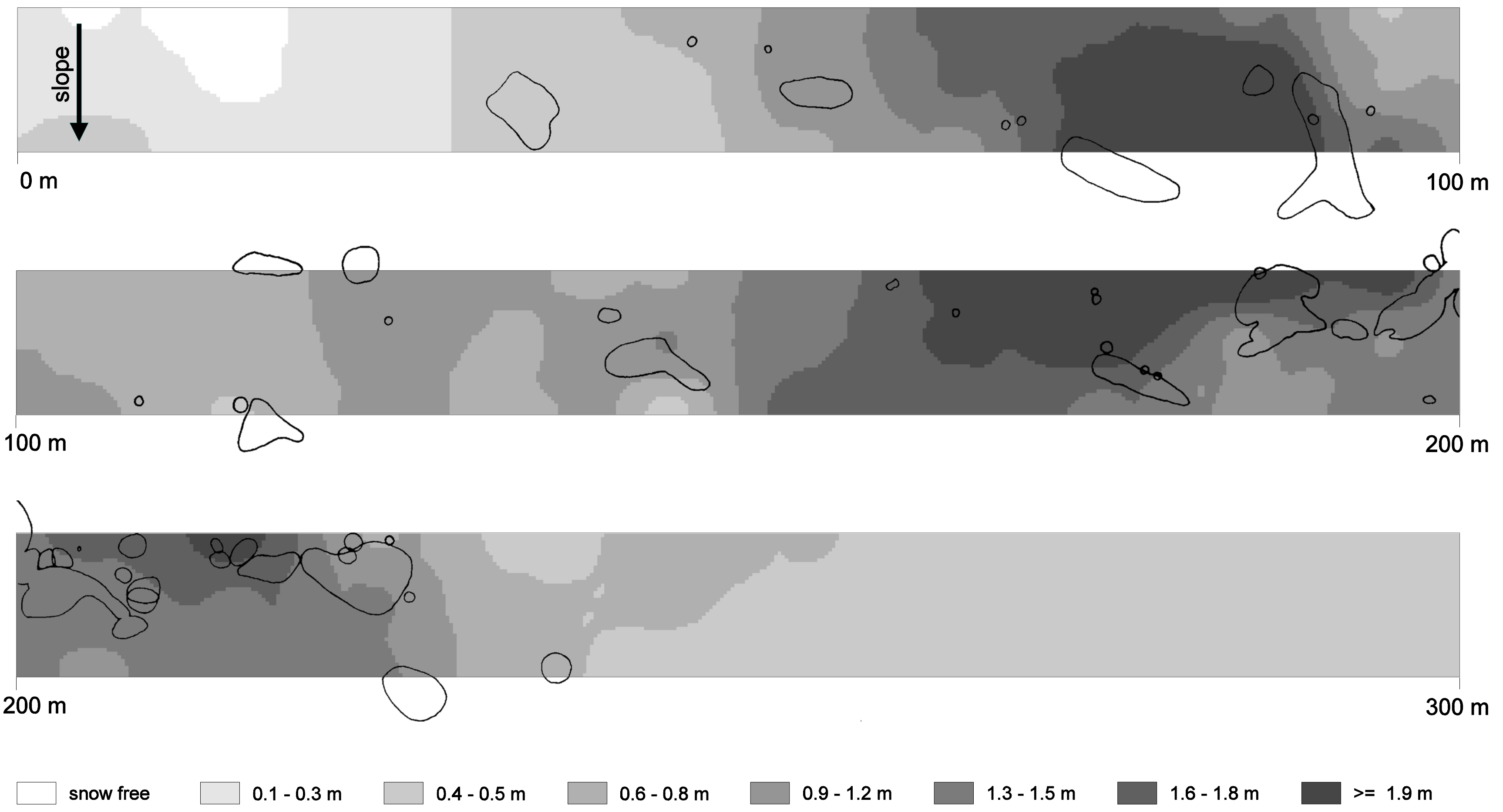


Figure 5.2: *Snow depth on May 15, 1993, on the Tibbs Butte transect at 3100 m. The image of snow depths is derived from linear interpolation of snow depth measurements and displayed in shades of grey. Black lines show the canopy cover of the overstory. The three sections of the diagram represent one continuous transect, perpendicular to the main slope. The aspect varies from 300°-350°.*

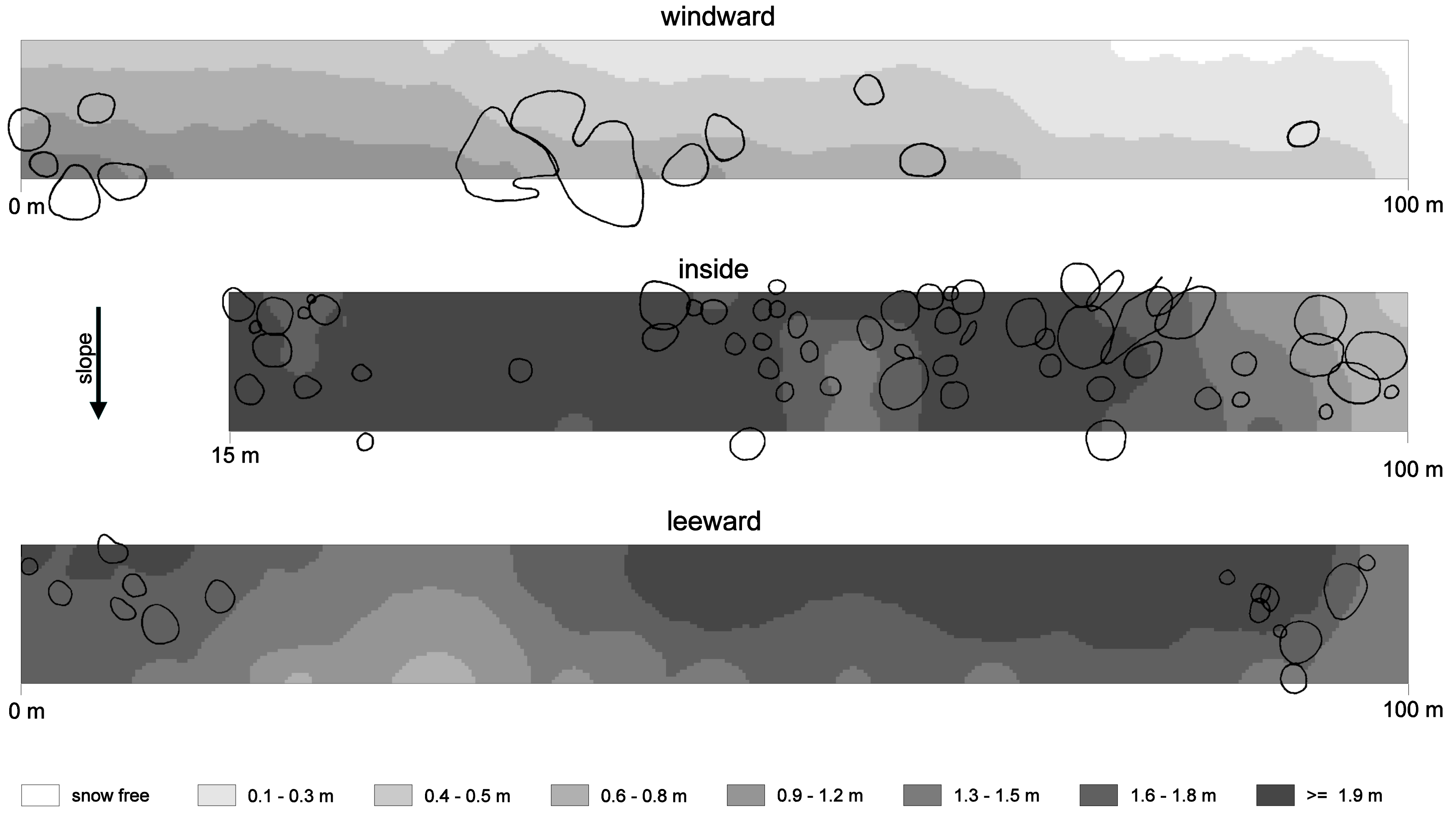


Figure 5.3: *Snow depth on May 18, 1993, on the three Wyoming Creek transects at approx. 2990 m. The image of snow depths is derived from linear interpolation of snow depth measurements and displayed in shades of grey. Black lines show the canopy cover of the overstory. All transects run perpendicular to the slope. The aspect varies from 30°-60°.*

climbed above freezing on six days and the snow pack compacted and started melting. Nevertheless, it can be assumed that the snow depths displayed in Fig. 5.2 and 5.3 are close to the maximum snow depths on the transects during the winter of 1992-1993.

Very few juvenile Engelmann spruce were located in both study locations, despite the abundance of this species in the overstory on Tibbs Butte. Fig. 5.4 shows the diameter distribution of all tree species on the Tibbs Butte and Wyoming Creek

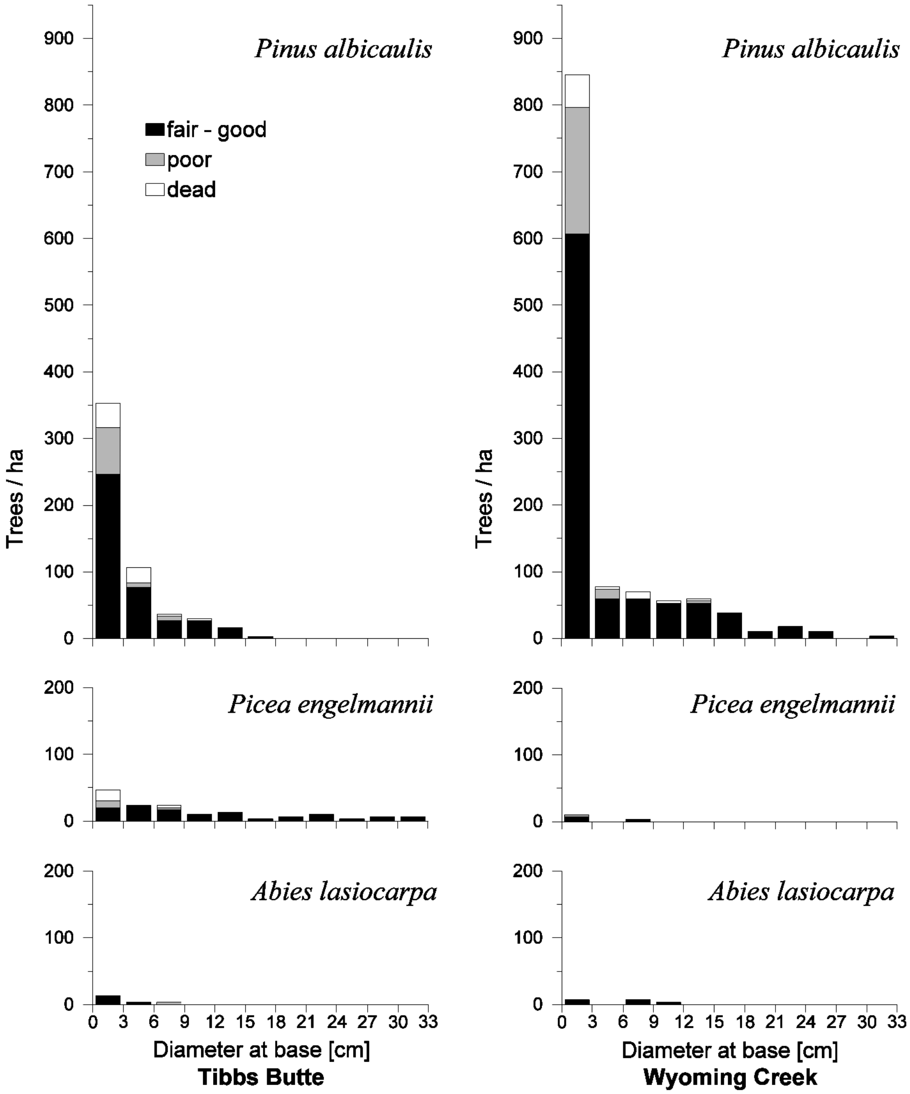


Figure 5.4: *Size class distribution and condition of all tree species older than three years for the Tibbs Butte and Wyoming Creek transects. For multi-stemmed individuals and tree islands the largest stem diameter was taken. Clusters of whitebark pines that appeared to originated from the same seed cash were treated as singular units.*

transects. Subalpine fir was neither common in the overstory nor in the understory. The only tree species with abundant regeneration in the studied transects was whitebark pine. The distribution curve for this species roughly resembles a reversed-J shape (negative exponential distribution).

The 0-3cm class in the graph does not include new germinants and one- to three-year-old seedlings found on the transects. In 1992, three whitebark pine clusters with new germinants and two clusters with seedlings germinated in 1991 were located on the Tibbs Butte transect while mapping the tree cover. In 1994 on the Wyoming Creek transects, there were two clusters of new germinants, two clusters of 1-year-old seedlings, four clusters of 2-year-old seedlings, and ten clusters of 3-year-old seedlings (germinated in 1991). All seedlings were whitebark pines. The natural tree regeneration on the transects is discussed in further detail in chapter 5.1.3.

Younger whitebark pines were often growing in groups of several seedlings, originating from the same seed cache. For whitebark pines <1 cm in diameter, 38% of regeneration sites contained clusters of two or more individuals. This percentage decreased with increasing diameter. In the diameter class 1-<2 cm it was only 20%; at 2-<3 cm basal diameter the percentage decreased to 7%. For older saplings it was difficult to distinguish between multiple individuals with intertwined rootstocks or multiple stems from the base. Most whitebark pines ≥1 cm in basal diameter were multi-stemmed. With increasing diameter, the percentage of whitebark pines with multiple stems from the base also increased, from 2% (diameter class < 1 cm) to 48% and more (diameter classes ≥3cm). These whitebark pines may have originated from one or several seedlings.

Height growth of all tree species in the timberline ecotone appeared limited. None of the trees were taller than 5 m in the study areas. Few trees were between 1.2 m and 1.5 m tall; therefore 1.5 m was a practical height to separate the over- and understory. Of all live whitebark pines shorter than 1.5 m, 99% had a basal diameter of less than 6 cm. Only 1% of all live whitebark pines taller than 1.5 m were smaller than 6 cm in basal diameter. The relationship between diameter and height of whitebark pines in the lower diameter classes is displayed in Fig. 5.5. While there is no significant difference in average tree height of the lowest diameter class (Wilcoxon Two-sample test, $z = 1.49$, $n = 46,76$, two-sided $p = 0.1350$), whitebark pines between 1 - 6 cm were significantly taller on the Wyoming Creek transects than on Tibbs Butte ($z = -2.11$, $n = 87,79$, two-sided $p = 0.0352$).

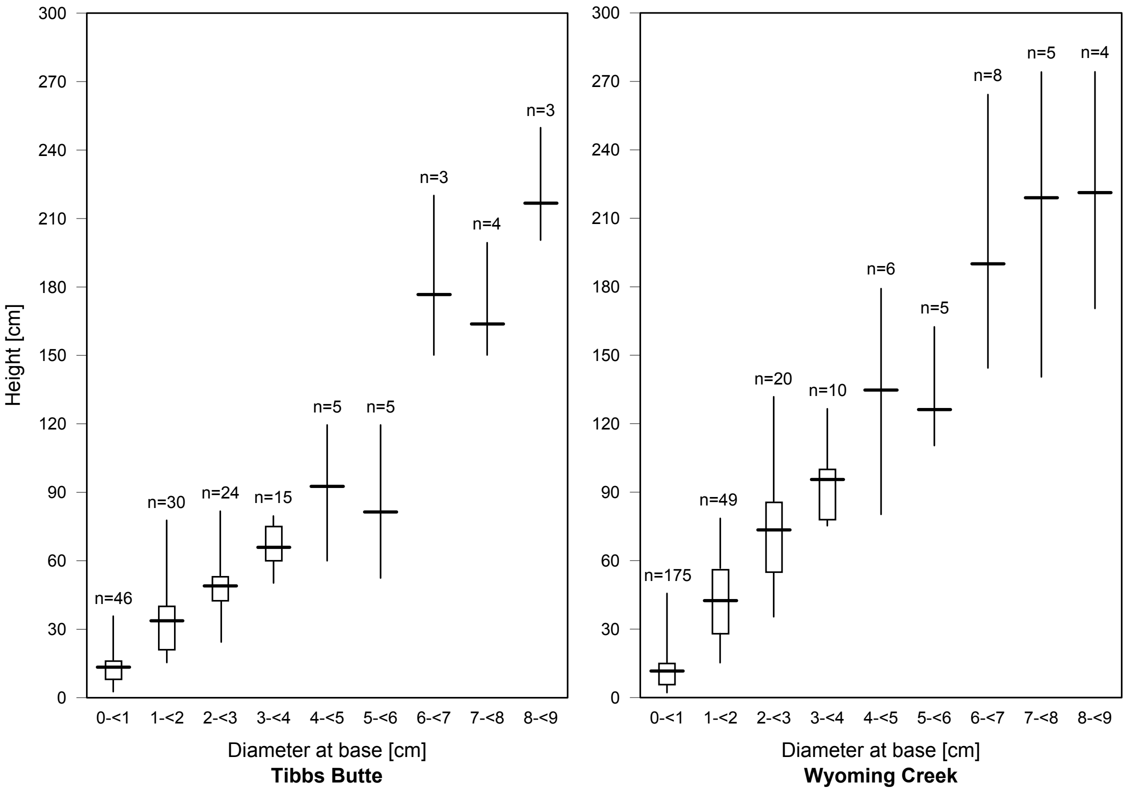


Figure 5.5: *Relationship between height and stem diameter for live whitebark pine (stem diameter < 9 cm) in the studied transects. The vertical bars show the range of all values in each diameter class, and the horizontal bars represent the arithmetric average. For diameter classes with n ≥ 10, the 25% and 75% quantiles are displayed with boxes.*

Needle length of whitebark pines shorter than 1.5 m varied from 0.5 to 5.0 cm and increased with increasing stem diameter (Spearman rank correlation $r_s = 0.7427$, $n = 374$). For stem diameters smaller than 1 cm, average needle length was 2.4 cm, with no significant difference between the Wyoming Creek and Tibbs Butte transects (Wilcoxon Two-sample test, $z = 1.61$, $n = 41{,}172$, two-sided $p = 0.1079$). Needles from whitebark pines with stem diameters between 1-6 cm were significantly longer at Wyoming Creek (mean = 3.8 cm, $n = 84$) than Tibbs Butte (mean = 3.2 cm, $n = 76$) (Wilcoxon Two-sample test, $z = -5.79$, $n = 84{,}76$, two-sided $p < 0.0001$).

Young seedlings on the Wyoming Creek and Tibbs Butte transects were aged by counting nodes on the main stem. All encountered seedling clusters younger than 5 years were aged ($n = 33$), and the range of basal diameter and stem length was small (Fig. 5.6). For seedlings younger than 5 years the annual growth rate was approximately 0.1 mm/yr in basal diameter and 0.2 cm/yr in stem length. Juvenile trees 5 years and older did not always show distinguishable nodes. Only 42 specimens

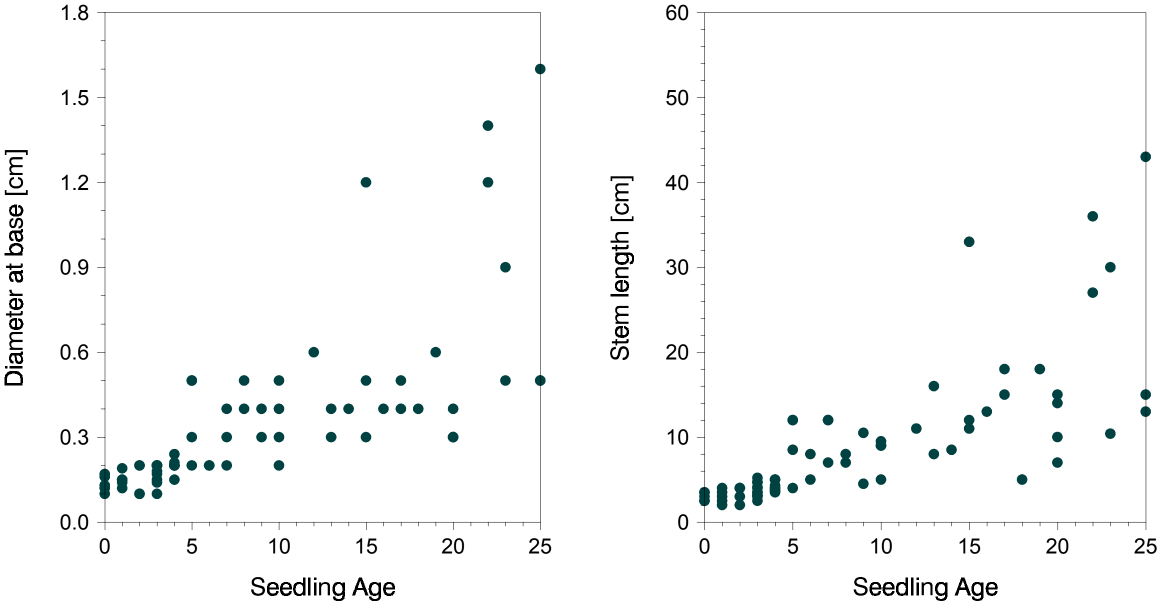


Figure 5.6: *Seedling age, diameter (left), and stem length (right) for selected whitebark pine ≤ 25 yrs on the Tibbs Butte and Wyoming Creek transects.*

between 5-25 years were aged using this method. The variation in basal diameter and stem length increased with age. This could be due to the increasing probability of missing nodes resulting in inaccurate age counts. It also may reflect accumulative effects of variable site conditions. Annual growth rates for trees 5 - <15 years old were 0.3 mm/yr in basal diameter and 0.7 cm/yr in stem length.

The distribution of whitebark pines smaller than 1.5 m was strongly clustered on all mapped transects (see Fig. 5.10 and Fig. 5.11, pages 40-41). Whitebark pine regeneration occurred commonly close to the base of adult trees, adjacent to rocks, and in the vicinity of tree islands (Fig. 5.7). Differences in locations between the Tibbs Butte and the Wyoming Creek transects mirrored the characteristics of these sites.

The Tibbs Butte transect was rocky, and tree islands created variable site conditions in a relative small area. Whitebark pine regeneration was located close to the main features of this area, rocks and tree islands. A total of 145 whitebark pine regeneration sites with seedlings and saplings <1.5 m were mapped on the transect, a density of approximately five singles or clusters /100 m^2. Three whitebark pine clusters and sixteen solitary whitebark pines were dead. Of the remaining 126 regeneration sites, 44% were found near rocks, and 47% were associated with tree islands.

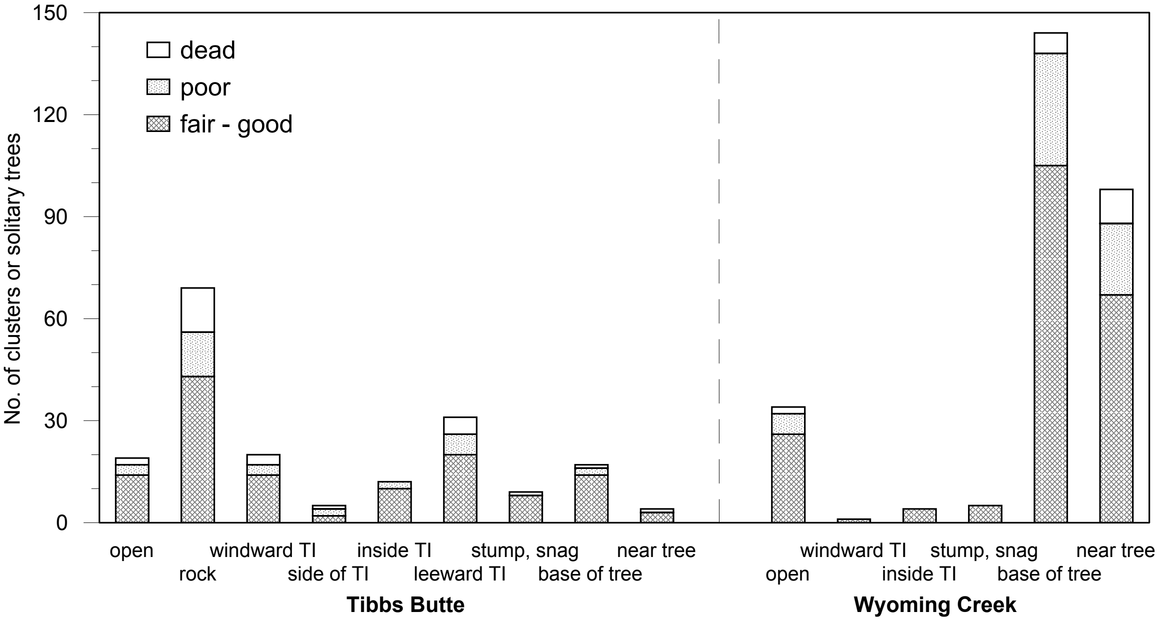


Figure 5.7: *Location and vitality of whitebark pines < 1.5 m on the Tibbs Butte and Wyoming Creek transects. (TI = tree island; base of tree = less than 1 m from base; near base = 1 - < 5 m from base.) For each whitebark pine regeneration site, all suitable descriptions are listed.*

While whitebark pines occurred windward, to the side, and inside of tree islands, they were commonly located on the leeward side. Inside of tree islands, none of the mapped whitebark pines was > 1 cm basal diameter. Sixty-three percent of regeneration sites inside and leeward of tree islands consisted of whitebark pines < 1 cm basal diameter. The diameter distribution of whitebark pine regeneration growing windward of or to the side of tree islands was relatively flat, and only 33% of sites were represented by trees < 1 cm basal diameter. Few juvenile whitebark pines were found ‘in the open’, in a distance > 5 m from the next tree and > 1 m from extruding rocks or other objects (Fig. 5.7). This group included seedlings and saplings of all diameter classes < 6 cm. The detailed drawing in Fig. 5.8 illustrates the distribution of whitebark pine regeneration commonly encountered in the Tibbs Butte study area.

At Wyoming Creek, the terrain contained little microrelief and few rocks. Tree islands were uncommon, and the transects did not cover a leeward part of a tree island. The major feature of this site is the location relative to the open whitebark pine woodland. Due to the small ridge to the west, the upper transect on Wyoming Creek is less exposed than the Tibbs Butte sites. However, of the three Wyoming Creek transects the upper exhibits the most severe site conditions with low snow cover and

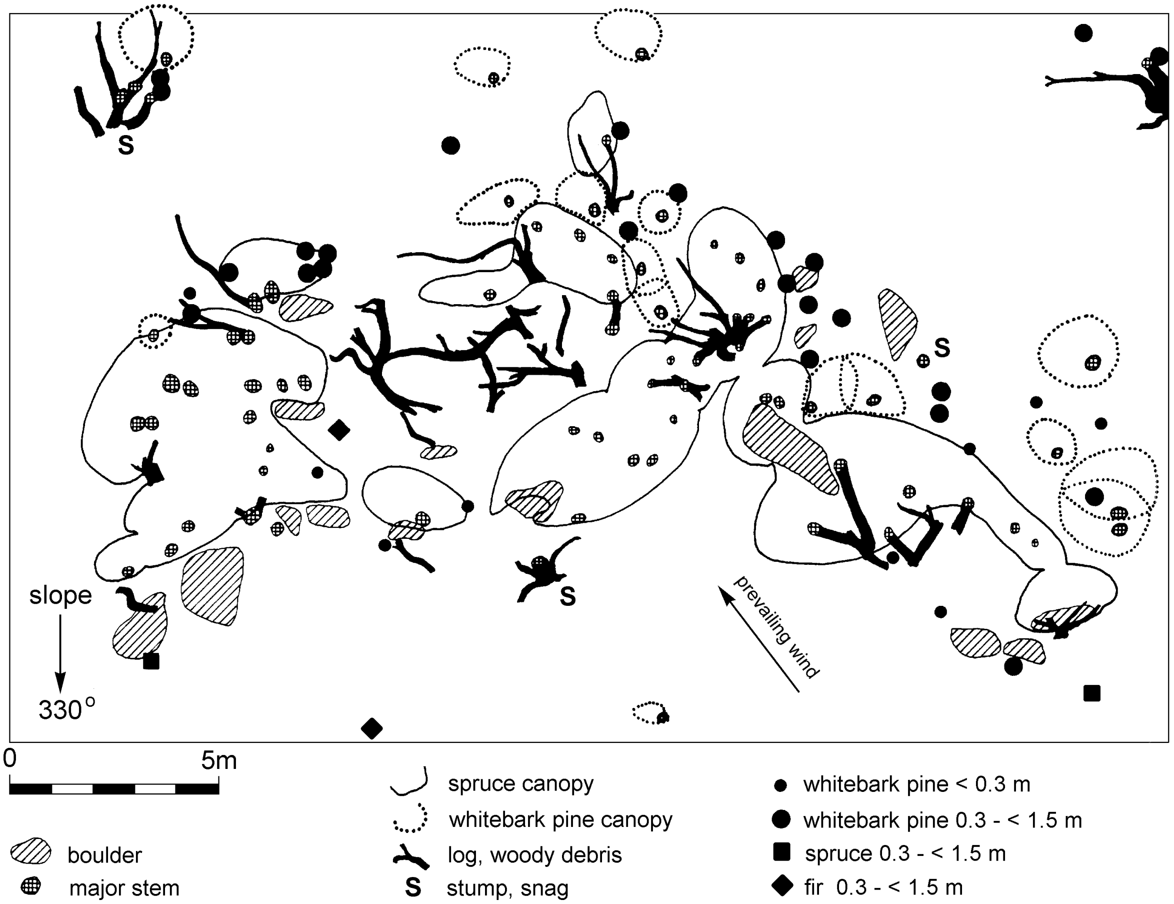


Figure 5.8: *Tree regeneration at a complex tree island with an unknown number of origins in the Tibbs Butte study area. The transect runs through the lower part of the tree island, at approximately 3100 m. Canopies are shown for trees ≥ 1.5 m, only. Clusters of whitebark pines are represented by their largest and healthiest individual.*

high wind exposure (see Fig. 5.10, page 40). On this windward transect, 47 regeneration sites with whitebark pine < 1.5 m tall were mapped (5 trees or clusters /100 m^2). Inside the woodland, 122 regeneration sites (14 trees or clusters /100 m^2), and on the leeward transect 115 regeneration sites (12 trees or clusters /100 m^2) were found. Four clusters and 14 solitary whitebark pines were dead, leaving a total of 266 regeneration sites of poor, fair, and good vitality on all three Wyoming Creek transects. Of these regeneration sites, 52% were located less than 1 m from the base of a tree (usually a whitebark pine), while another 33% were found 1 - < 5 m from the base of a tree. The diameter distribution for juvenile whitebark pines at the base of trees resembled a negative exponential curve (reversed-J) with 83% of sites consisting of seedlings and saplings < 1 cm in basal diameter. Only 23 regeneration sites (17%)

included live whitebark pines with basal diameters ≥1 cm.

For whitebark pine regeneration located 1 - < 5 m from a tree, the diameter distribution was less steep and only remotely resembled a reversed-J shape. In 45 of these regeneration sites (51%), live whitebark pines with diameters ≥ 1 cm were recorded.

A few whitebark pines were mapped as growing ‘in the open’. The majority of these sites were located leeward of the woodland and were less exposed than whitebark pines growing in ‘open’ locations on Tibbs Butte.

Areas inside and leeward of tree islands, close to the base of trees, and in woodland have a higher snow accumulation and melt out later than open and wind exposed sites in the timberline ecotone (Fig. 5.10 and 5.11). Even small rocks can influence snow accumulation and therefore may protect small seedlings from wind and dessication. Derived from a 5 x 5 m grid of measurements, the maps in Fig. 5.10 and 5.11 show the approximate time of snow melt in relation to tree cover and tree regeneration.

Despite the coarse sample grid, the tabulation of snow melt dates and whitebark pine regeneration revealed a non linear relationship (Fig. 5.9). In general, regeneration densities increased with increasing length of snow cover, with the exception of areas with very late snow melt, where low regeneration densities were found.

Few sites on the Tibbs Butte and Wyoming Creek transects were snow free before May 15, 1993 and May 18, 1993, respectively. No whitebark pine regeneration was

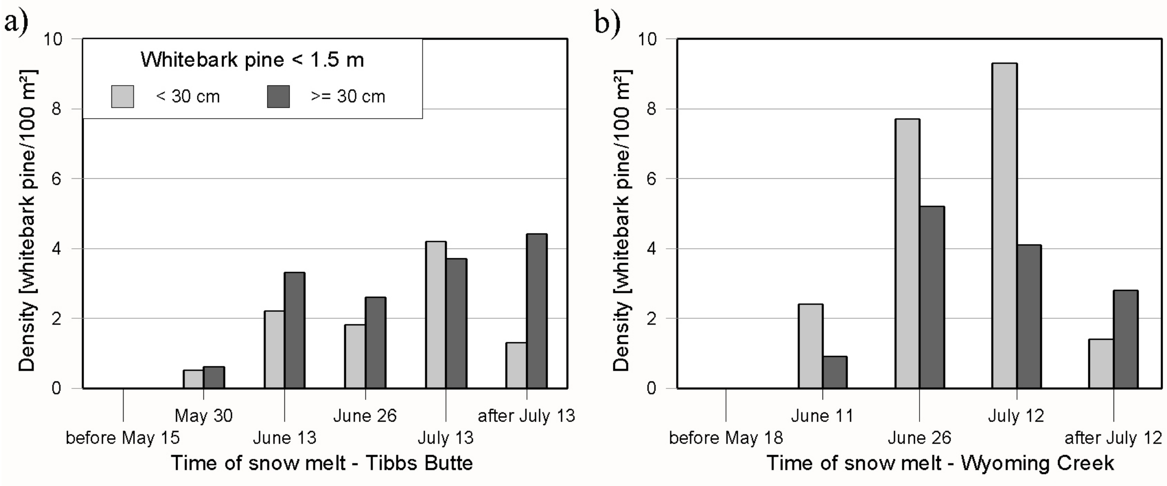


Figure 5.9: *Density of live whitebark pine regeneration in relation to the date of snow melt in 1993 on a) the Tibbs Butte transect and b) the Wyoming Creek transects. Snow melt data are derived from interpolation of snow depth measurements on the transects.*

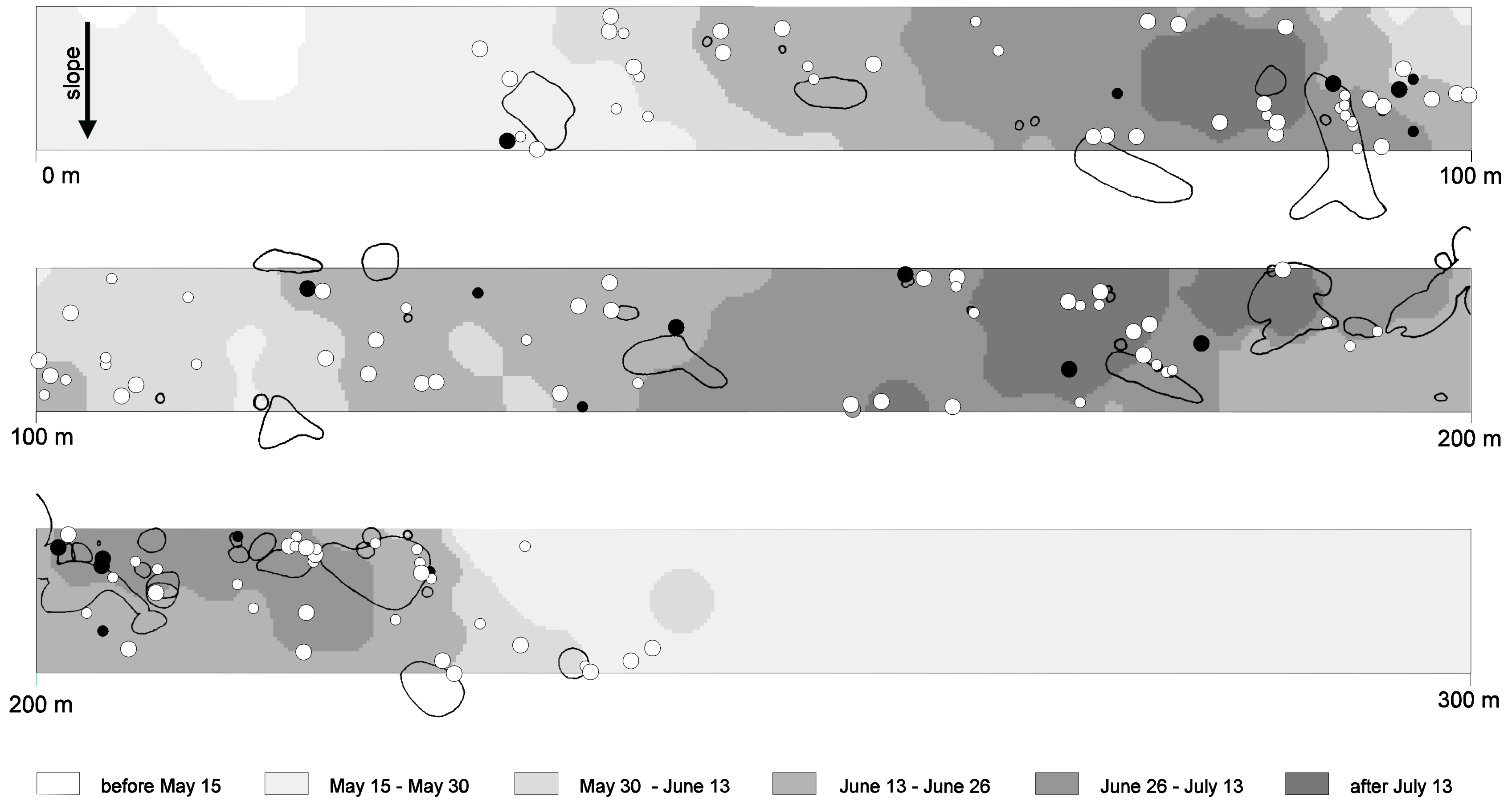


Figure 5.10: *Snow melt, canopy cover, and whitebark pine regeneration on the Tibbs Butte transect in 1993. Dates of snow melt are displayed in shades of grey. Black lines show the canopy cover of trees ≥ 1.5 m. Large dots display whitebark pines 0.3 m - < 1.5 m in height, small dots stand for whitebark pines < 0.3 m in height. Dot color indicates the vitality of whitebark pine regeneration, with life whitebark pine = white, and dead whitebark pine = black.*

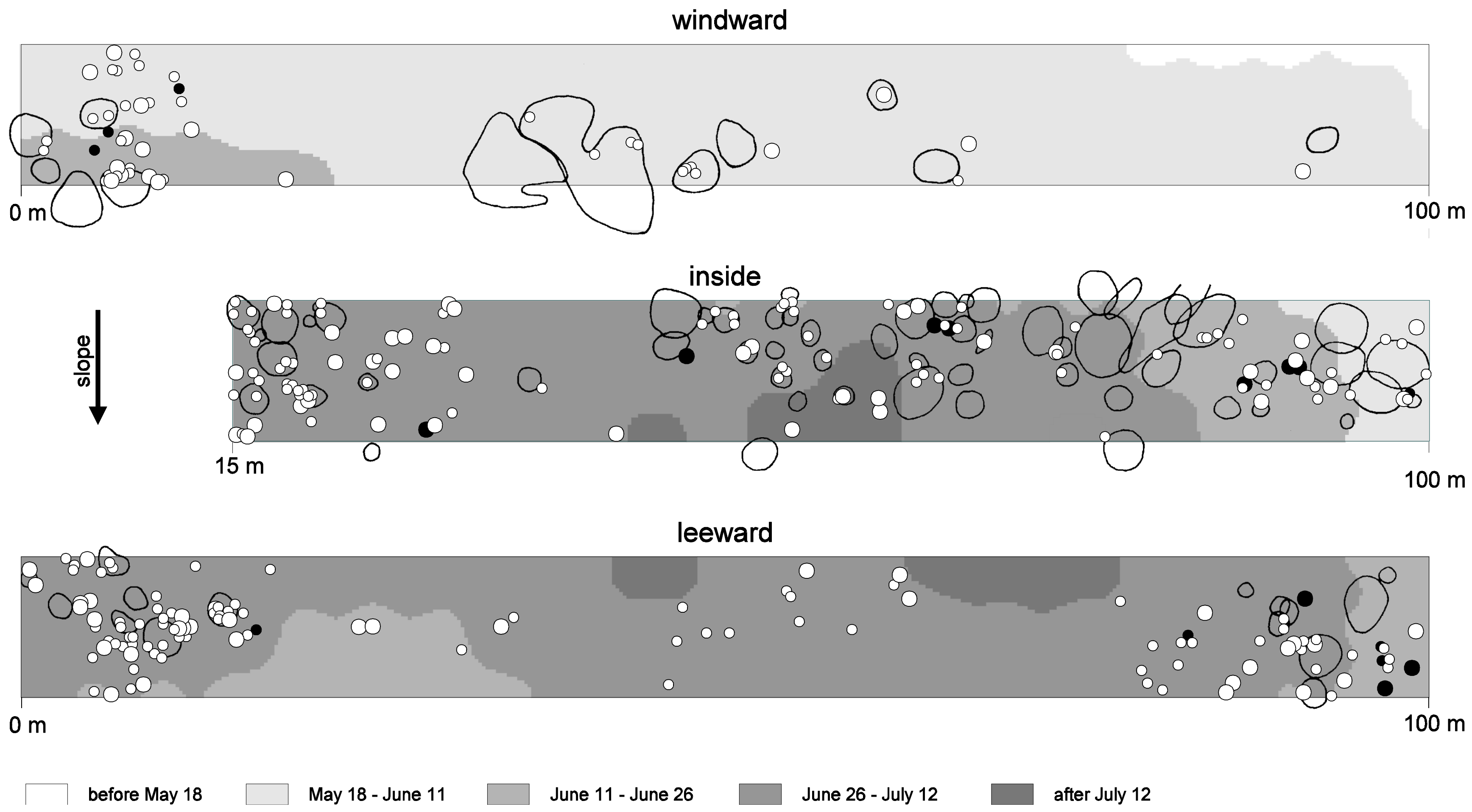


Figure 5.11: *Snow melt, canopy cover, and whitebark pine regeneration on the Wyoming Creek transects in 1993. Dates of snow melt are displayed in shades of grey. Black lines show the canopy cover of trees ≥ 1.5 m. Large dots display whitebark pines 0.3 - < 1.5 m in height, small dots display whitebark pines < 0.3 m in height. Dot color indicates the vitality of whitebark pine regeneration, with live whitebark pine = white, and dead whitebark pine = black.*

located in the early snow free sites. Thirty-four percent of the transect area melted out between June 26 and July 13, 1993. However, 59% of all regeneration sites with live whitebark pine were found in these areas, eight sites/100 m^2 on Tibbs Butte, and thirteen sites/100 m^2 on Wyoming Creek. Late snow beds were found leeward of tree groups or in topographic depressions, and here regeneration densities were lower than in areas with intermediate dates of snow melt. On July 12/13, 1993, 7% of the entire transect area was still snow covered. These late snow beds include only 5% of all live whitebark pine regeneration sites, a density of six sites/100 m^2 on Tibbs Butte and on Wyoming Creek (Fig. 5.9).

5.1.2 Whitebark pine growth and survival in relation to climatic conditions

Many trees in the transects showed signs of damage to needles and new growth. On Tibbs Butte, 65% of live whitebark pines shorter than 1.5 m had lost one or more apical shoots. On the Wyoming Creek transects, this kind of damage was seen on 43% of live whitebark pines shorter than 1.5 m. Needle losses were observed on windward branches, at the base of trees, and throughout a tree without distinguishable pattern. The amount of needle loss appeared similar on Wyoming Creek and Tibbs Butte: 45% of live whitebark pines smaller 1.5 m were estimated to have lost 30 - 70% of their needle mass. On 11% of juvenile trees the damage was severe, with needle losses > 70%.

The majority of damage to whitebark pine needles and shoots was attributed to frost during the growing season or winter dessication. A comparison of temperature data between the Beartooth Lake SNOTEL site (2727 m) and the Tibbs Butte weather station (3100 m) showed only minor differences in average air temperatures during the summer months June through September of 1992 to 1994 (Fig. 5.12). Growing season means (June - September) for the Tibbs Butte weather station were 6.1°C in 1992, 4.3°C in 1993, and 8.1°C in 1994. At Beartooth Lake, means of average air temperatures over the same time periods were 0.2 - 0.9°C higher, depending on year. The daily minima were on average 2°C higher on Tibbs Butte than at Beartooth Lake. The largest differences in air temperatures were observed in average daily maxima. Tibbs Butte daily maximum temperatures were 3°C to 4°C below the measured daily maxima at Beartooth Lake, indicating a large difference in the cumulative amount of heat these two sites receive during the summer.

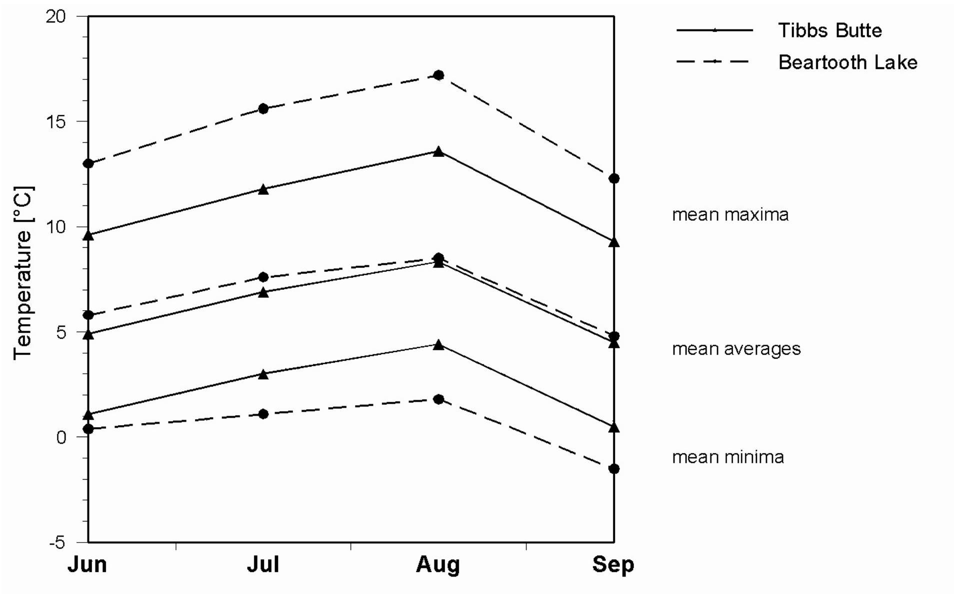


Figure 5.12: *Mean daily maximum, average, and minimum air temperatures from 1992 to 1994 at the Tibbs Butte weather station and the Beartooth Lake SNOTEL site.*

Freezing events during the growing season were no more common on Tibbs Butte than at Beartooth Lake. All freezing events below 2°C between June 15 - September 15, 1992 -1994 are listed in Table 5.1. The absolute minima were often lower at the Beartooth Lake site, which is located in a cold air pocket in subalpine spruce/pine forest. The first severe frost of the season in 1992 and 1993 was recorded at the end of August, with temperatures at or below -5°C. In 1994, minimum air temperatures at Tibbs Butte did not drop below -2°C before September 21. Compared to the subalpine site at Beartooth Lake, the length of the growing season at Tibbs Butte was not shortened by early frost, but by a later start in spring due to high snow accumulation in part of the transect.

The 1992/1993 winter temperatures at Tibbs Butte were on average 1°C below the air temperatures at Beartooth Lake, with mean minimum temperatures 1°C higher, and mean maximum temperatures 3°C lower than Beartooth Lake (Fig. 5.13). The largest differences in mean maximum temperatures were observed during March, April, and May (mean daily maxima 4-6°C lower at Tibbs Butte). The lowest air temperature recorded at the Tibbs Butte weather station was -30.2°C, in February 1993. Average soil temperatures at 10 cm depth dropped to -10.8°C at the weather station, a site that was swept clear of snow for long periods during winter (Fig. 5.13). At 3 cm depth, the lowest temperature recorded was -18.0°C, in December 1992. On sites with longer and

Table 5.1: *Freezing events with air temperatures below -2°C during the growing seasons 1992 to 1994 (June 15 - September 15*)

Date	**Tibbs Butte min. air temperature**	**Beartooth Lake min. air temperature**
August 24-26, 1992	-6°C	-7°C
September 6-8, 1992	-11°C	-12°C
September 12-14, 1992	-5°C	-4°C
June 16-18, 1993	-5°C	-4°C
June 23-25, 1993	-6°C	-4°C
June 30, 1993	-1°C	-3°C
July 17-18, 1993	-2°C	-3°C
August 27, 1993	-1°C	-3°C
August 29-30, 1993	-5°C	-6°C
September 12-14, 1993	-10°C	-8°C
June 15-17, 1994	-6°C	-8°C
July 11, 1994	3°C	-3°C
September 4-5, 1994	0°C	-4°C

deeper snow cover, the soil temperatures at 3 cm and 10 cm depth commonly remained between 0° and -5°C (Appendix 9.3).

In 1993, the average soil temperature at 10 cm depth of the "light snow site" at the weather station did not rise above 0°C before the end of May. Spring soil temperatures at sites with deep snow cover remained at -1° to 1°C until the snow melted in late June. From October 1992 until September 1993, soil temperatures at 10 cm depth at the weather station were above 0°C for 138 days. The mean maximum air temperature in May 1993 was 6.8°C, only slightly lower than in June or September 1993 (7.1°C and 8.2°C, respectively). The air temperature stayed above freezing on 16 days in May 1993. The mean maximum incoming photosynthetically active radiation (PAR) amounted to1971 $\mu E \cdot m^{-2} \cdot s^{-1}$ in May 1993, and 1912 $\mu E \cdot m^{-2} \cdot s^{-1}$ in June 1993. This does not differ considerably from the maximum PAR of a sunny day at sea level (2000 $\mu E \cdot m^{-2} \cdot s^{-1}$), and is approximately 85% of the mean maximum PAR received at Tibbs Butte during July 1993.

Damages due to winter dessication were most clearly seen on dense Engelmann spruce or subalpine fir islands, where all shoots extending beyond the spring snow cover had turned reddish brown by late spring. However, shoot and needle damage of whitebark pine was not restricted to tree parts protruding above the spring snow. Shoot and needle damages may be caused by dessication or may be attributed to frost during the growing season.

High elevation forests with long snow cover are often impacted by snow-mold fungi (*Herpotrichia* spp.). *Herpotrichia coulteri* causes brown felt blight on snow-covered branches of whitebark pine. Small trees and seedlings that are entirely covered by snow during late winter may be killed. Despite the late snow melt inside and leeward of tree groups, brown felt blight was not common in the study area. On the Wyoming Creek transects, only two juvenile whitebark pines were affected by *Herpotrichia coulteri*. Eight whitebark pines shorter than 1.5 m were affected on the Tibbs Butte Transect. Several of the ten whitebark pines affected by brown felt blight had high needle losses and poor vitality, but none of them were dead.

A number of other diseases can affect the vitality of whitebark pine. Of biggest concern is white pine blister rust (*Cronartium ribicola*), a widespread disease that causes high mortality in many whitebark pine stands. No case of blister rust infection was recorded in the study area. The absence of active, fruiting cankers indicates that blister rust was not a serious problem in the investigated timberline areas during the years of field study.

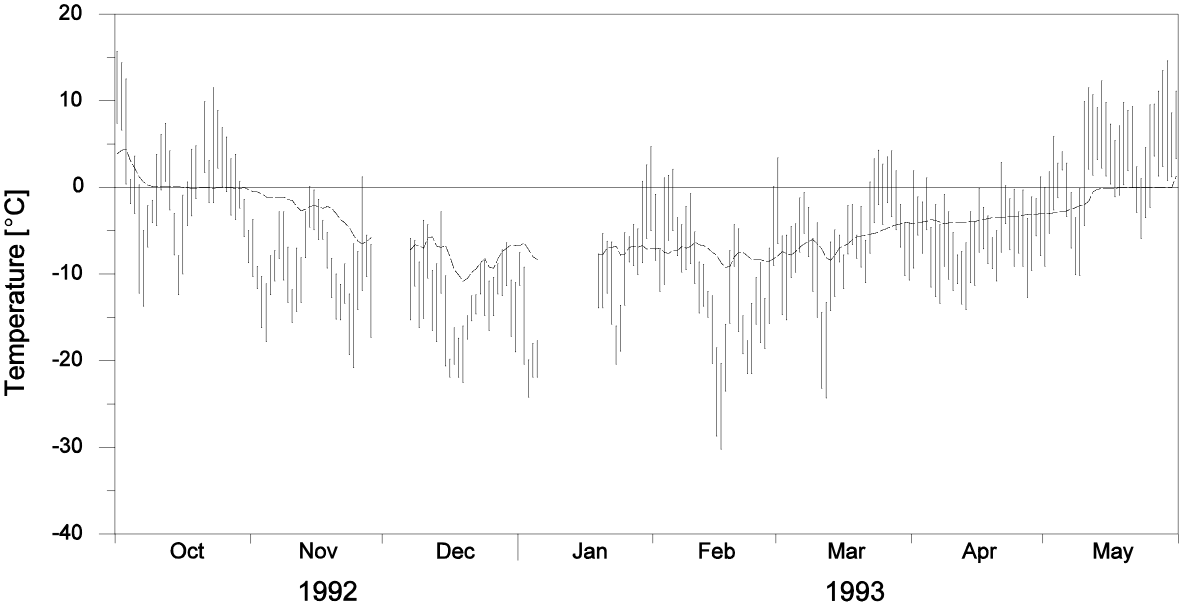


Figure 5.13: *Daily maximum and minimum air temperatures (vertical lines) and average soil temperatures (dashed line) at the Tibbs Butte weather station at 3100 m during the winter 1992/1993. Air temperatures were measured 1.5 m above ground level, soil temperatures 10 cm below the soil surface.*

5.1.3 Natural regeneration in the timberline ecotone

The seed production of whitebark pine is known to vary significantly between years (Weaver and Forcella 1986, Arno and Hoff 1989). Data on cone production are available from subalpine whitebark pine stands in the Republic Creek drainage south of Cooke City, approximately 40 km east of the study areas. Cone production of whitebark pine in the Republic Creek drainage was good in 1989 and 1991, there were some cones in 1992, and little to no production in 1990 and 1993 (Tomback et al. 2001a). This is consistent with observations about whitebark pine seed crops on the Beartooth Plateau between 1991 and 1994. During August and early September 1991, Clark's nutcrackers were seen with filled sublingual pouches near the Tibbs Butte and Wyoming Creek transects. On occasion, nutcrackers were observed caching whitebark pine seeds in the study areas.

Subalpine spruce/fir forests in drainages west and east of Tibbs Butte provide seed sources for Engelmann spruce and subalpine fir. For the Wyoming Creek transects, the closest spruce and fir seed sources are the subalpine forests in the Wyoming Creek drainage, east of the study area.

All new regeneration located in 1993 and 1994 on the Wyoming Creek and Tibbs Butte transects consisted of whitebark pine seedlings. During this study, not one Engelmann spruce or subalpine fir seedling was located on the transects, neither a new germinant nor a one- to three-year old seedling.

In 1993, 24 seedling clusters with 86 newly germinated whitebark pine seedlings were found in 29 10-m² circular plots at Wyoming Creek (covering 10% of the transect area). The plots also included two clusters with three one-year-old seedlings and five clusters with 13 two-year-old seedlings. The density of new germinants amounted to 29.7 seedlings and 8.3 seedling clusters/100 m². For one- to three-year-old whitebark pine regeneration, the density was 5.5 seedlings and 2.4 clusters/100 m².

In 1994, a new survey of the 10 m² plots on the Wyoming Creek transects resulted in five seedling clusters with 16 new germinants. Delayed germination was observed at three clusters from 1993, where seedlings germinating in 1993 were supplemented with three additional seedlings germinating in 1994. The whitebark pine regeneration densities were 6.5 seedlings and 1.7 seedling clusters/100m² germinated in 1994, and 8.6 seedlings and 4.8 clusters/100m² for one- to three-year-old regeneration surviving to 1994. On the Tibbs Butte transect, only one new seedling from 1994 and one cluster

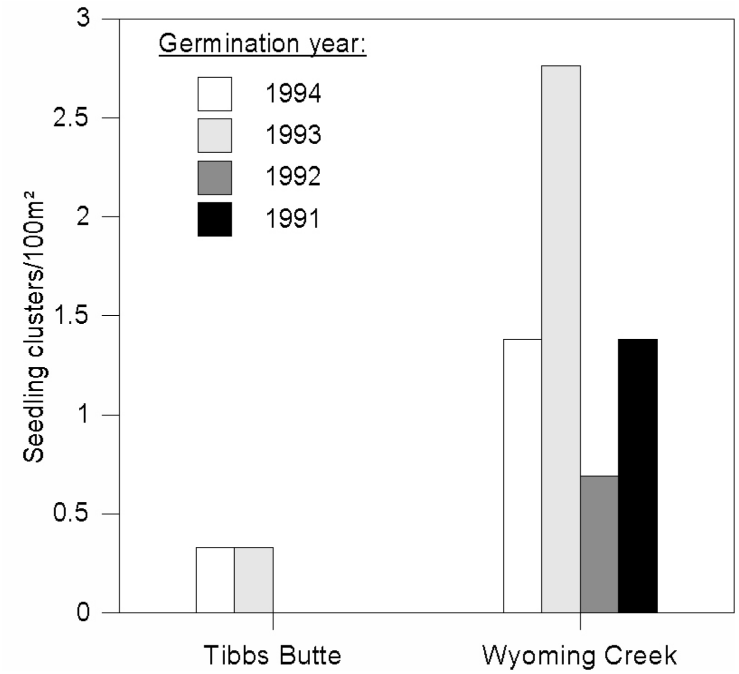


Figure 5.14: *Natural whitebark pine regeneration in 1994 on the Tibbs Butte and Wyoming Creek transects. Results are from 59 plots, 10 m² each. Only live seedling clusters are included.*

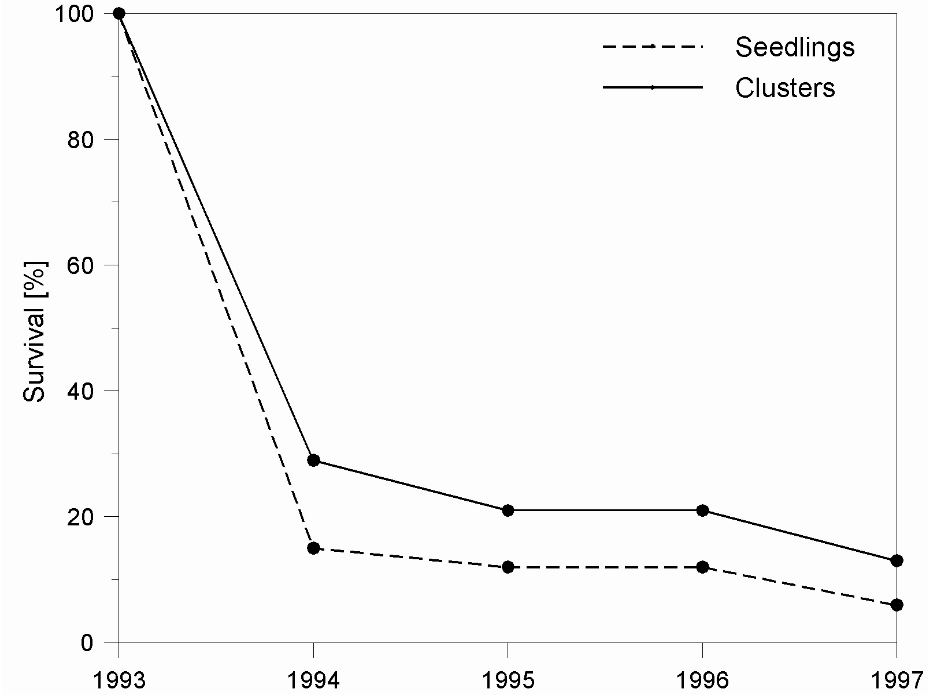


Figure 5.15: *Survival of natural whitebark pine regeneration that germinated in 1993 on the Wyoming Creek transects.*

of three seedlings surviving from 1993 were located in the 30 10m²-plots; surveys were not completed for 1993. Figure 5.14 shows the densities of live whitebark pine regeneration on the Tibbs Butte and Wyoming Creek transects. For comparison purposes, the density of whitebark pine older than three years was 11.2 trees or clusters/100 m² on Wyoming Creek , and 4.8 trees or clusters/100 m² on Tibbs Butte.

On Wyoming Creek, 43% of 1993 germinants were dead by the end of the summer season. Another 42% died during the winter of 1993/1994. After the first year, the seedling mortality dropped to 3%, 0%, and 6% from 1995 to 1997, respectively (Fig. 5.15). This resulted in the survival of three clusters (13%) with five seedlings (6%) from 1993 to 1997. Seedling mortality appeared to be distributed evenly among most clusters, resulting in less seedlings per cluster and higher survival rates for clusters than for individual seedlings.

The mortality for 1994 regeneration was similar, but the numbers are small due to lower initial germination. In 1997, a total of seven regeneration clusters (19%) with 13 seedlings (11%) located on Wyoming Creek in 1993 and 1994 were still alive (Fig. 5.16).

The distribution of whitebark pine germination followed a pattern similar to the distribution of juvenile whitebark pines. Of seedling clusters ≤ three years in age,

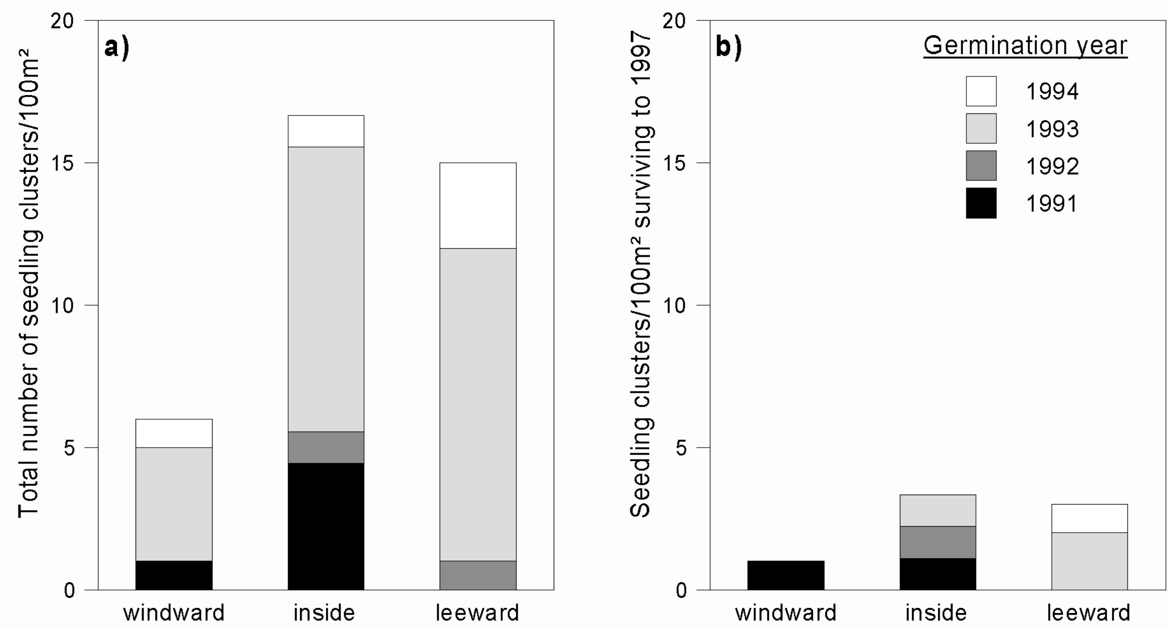


Figure 5.16: Whitebark pine regeneration densities on the Wyoming Creek transects, windward, inside, and leeward of the woodland. a) displays the total densities of seedling clusters ≤ 3 years found in the circular subplots, b) shows the density of seedling clusters surviving to 1997.

42% were located less than one meter from the base of another whitebark pine; 45% were found in one to three meter distance to a tree base.

The regeneration density on Wyoming Creek varied between the windward, inside, and leeward transects (Fig. 5.16a). Inside and leeward of the woodland, the density of whitebark pine clusters germinated between 1991 and 1994 were two to three times as high as on the windward transect. Mortality rates appeared similar on the three transects. Only one whitebark pine cluster/100 m² survived to 1997 on the windward transect, compared to 3.3 clusters/100 m² on the inside and 3 clusters/100 m² on the leeward transect (Fig. 5.16b).

5.2 Germination and survival of whitebark pine

5.2.1 Germination of whitebark pine in the laboratory

The results of the germination experiment in the germination chamber showed variable success depending on the seed source. The highest germination rate was achieved with seeds that originated from the Rock Creek drainage, with 56% and 42% germination for both seed boxes. Seeds from the Little Rock Creek source had germination rates of 26% and 18%, less than half as high as those from Rock Creek. The two boxes with seeds mixed from both locations also had intermediate germination rates (36% and 28%) (Fig. 5.17).

A total of 103 seeds (34%) germinated over a period of 16 months. The highest amount of germination occurred in August 1993, four to six weeks after placement in the germination chamber. Germination continued on a decreasing trend until March 1994. Afterward, few seedlings germinated in any of the seed boxes.

5.2.2 Regeneration of whitebark pine — a field experiment

5.2.2.1 Description of the experiment sites

All 31 experiment sites are situated in the upper timberline ecotone, at altitudes from 2970 m to 3105 m. Slopes varied from 4 - 19°. The Tibbs Butte sites are the highest in elevation, at 3095 m to 3105 m, with N to NW exposures. The S to W exposed sites on Littlerock Creek are at a similar altitude, ranging from 3070 m to 3105 m

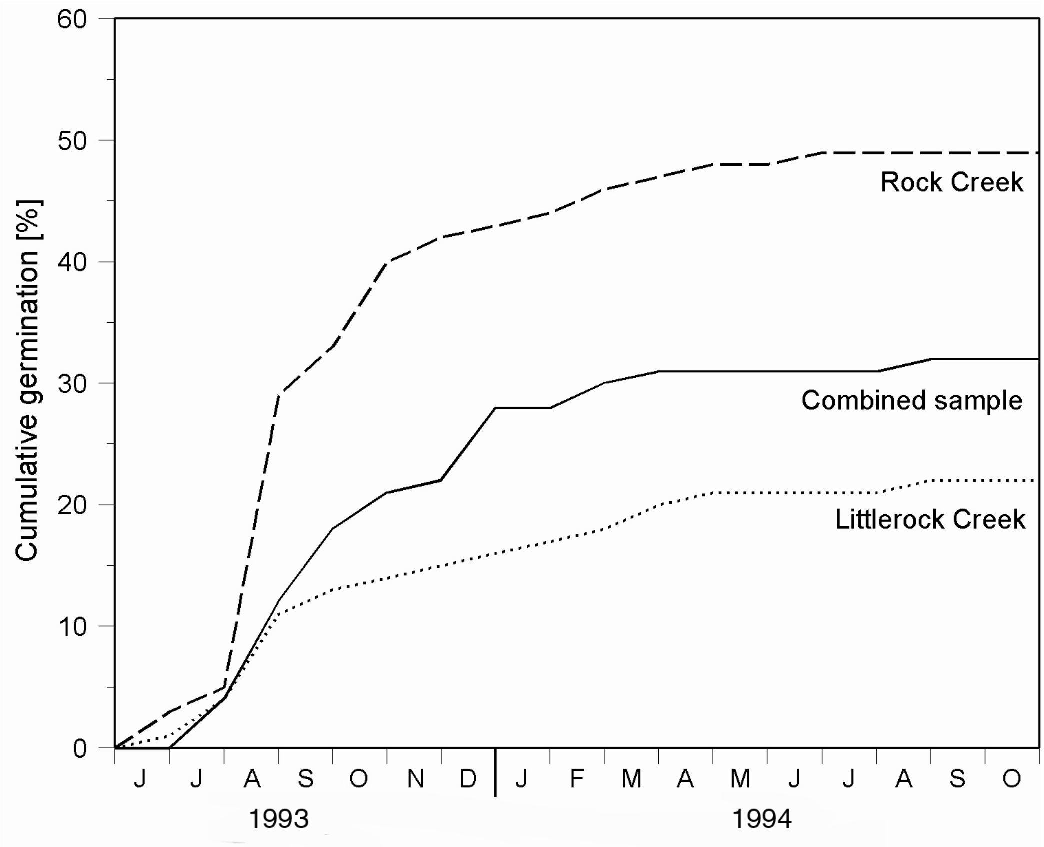


Figure 5.17: *Cumulative germination of whitebark pine seeds in the germination chamber. Displayed are the averages from two separate sets of 50 seeds each, from Rock Creek, Littlerock Creek, and a combined sample.*

elevation. At Rock Creek, the five experiment sites are N to NE exposed and at 2990 m to 3020 m altitude. The Wyoming Creek sites are the lowest in elevation (Photos 5.1-5.6). They are at 2970 m to 2995 m altitude and have NE to E exposed slopes. Table 5.2 includes further descriptions of the experiment sites.

The time of snow melt varied by four weeks between different years of the study. In 1994, snow melted early, compared to the two previous years. Of all 31 sites, 25 were free of snow by the end of May. By June 20, 1994, all sites were snow free. In 1995, a late snow melt was observed. Only one site was snow free by the end of May, and the last site did not emerge from snow until the middle of July (see Table 5.2). More persistent snowbanks can be found on leeward slopes in the higher alpine areas, and in comparison, even the experiment sites with the latest snow release have to be considered early snow-beds (compare Johnson and Billings 1962).

Photo 5.1: *Wyoming Creek study area, view to NW. The shrub communities in the lower right and the center of the photo are dominated by Salix glauca, and include experiment sites W1 and W3. October 1991.*

Photo 5.2: *Experiment site W2 in the Wyoming Creek study area, marked by 2 PVC pipes. This site is located up slope of a Salix glauca community which includes site W3. View to NE. July 1993.*

Photo 5.3: *Experiment site W6 in an open Salix glauca community in the Wyoming Creek study area. View to W. October 1991.*

Photo 5.4: *Experiment site W7 windward of a tree island intermingled with whitebark pines in the Wyoming Creek study area. View to NE. July 1996.*

Photo 5.5: *Experiment site W8 leeward of a tree island in the Wyoming Creek study area. View to W. August 1995.*

Photo 5.6: *Experiment site W9 in whitebark pine woodland in the Wyoming Creek study area. View to W. October 2, 1991.*

Table 5.2: *Site descriptions for regeneration experiment sites on Tibbs Butte (T1 - T8), Littlerock Creek (L1 - L8), Rock Creek (R1 -R5), and Wyoming Creek (W1 - W10).*

Site	altitude (m)	aspect	slope (°)	snow melt*	site description
T1	3105	N	10	June 1-10	open
T2	3095	N	8	July 1-10	depression between tree islands
T3	3095	N	8	June 21-30	between tree islands
T4	3095	N	8	June 21-30	open meadow below group of tree islands
T5	3100	N	12	June 21-30	windward spruce/pine tree island
T6	3105	N	11	July 1-10	leeward spruce tree island, next to whitebark pine
T7	3105	NW	11	July 1-10	between spruce tree islands
T8	3100	N	8	July 1-10	depression between spruce tree islands
L1	3070	S	11	June 21-30	uphill from low group of whitebark pines
L2	3070	S	11	May 21-30	open
L3	3080	SW	15	June 11-20	edge of whitebark pine/spruce woodland
L4	3095	SW	5	June 1-10	uphill from whitebark pine/spruce woodland
L5	3105	SW	17	June 11-20	open, rocky slope below top of ridge
L6	3085	W	19	June 11-20	edge of whitebark pine/spruce woodland, rocky
L7	3075	SW	9	July 1-10	small depression, at edge of pine/spruce woodland
L8	3070	W	13	June 21-30	edge of whitebark pine/spruce woodland
R1	2990	NE	6	June 11-20	wind eroded area windward tree islands
R2	2990	NE	5	July 1-10	leeward tree islands
R3	3020	NE	13	July 1-10	in group of low whitebark pines
R4	3020	N	14	June 11-20	open, on rocky edge of plateau
R5	3020	N	9	June 11-20	open, on gentle slope with solifluction
W1	2995	NE	6	June 21-30	small depression leeward of small rise
W2	2990	NE	8	June 21-30	leeward of small ridge, above depression
W3	2980	NE	9	June 21-30	small depression leeward of small ridge
W4	2970	NE	7	June 21-30	uphill from small drainage, below depression
W5	2995	E	12	June 21-30	leeward small ridge, windward pine woodland
W6	2990	E	8	July 1-10	opening in whitebark pine woodland
W7	2985	NE	7	June 11-20	windward subalpine fir tree island
W8	2985	N	6	July 1-10	leeward subalpine fir tree island
W9	2990	NE	13	July 11-20	inside whitebark pine woodland
W10	2985	NE	4	June 21-30	leeward whitebark pine woodland

*The dates of snow melt show the snow conditions in 1995

5.2.2.2 Vegetation

The topographic position and the resulting length of the snow cover have long been considered crucial factors in controlling vegetation composition of alpine sites (Cox 1933; Billings and Bliss 1959; Braun-Blanquet 1964; and others). At timberline, tree clumps act as snow fences and as black bodies, altering site conditions significantly (Billings 1969; Holtmeier 1982, 1987). The position of a site relative to trees may be as important as general topographic features.

The vegetation cover of the experiment sites consists of xeric windblown cushion plant communities, turf vegetation, mesic to moist meadows, tree groups, and open whitebark pine woodlands. Tabular analysis and ordination (Detrended Correspondence Analysis, DECORANA) of the vegetation composition resulted in the classification of nine vegetation types. Some of these groups may be described as distinct plant communities, while others are diverse and would likely be split into several, related communities, if adequately sampled. The first two DECORANA axes had eigenvalues larger than 0.2. They were used for classification and further analysis. The first ordination axis appears to arrange the sites along a moisture gradient, from dry to moist (Fig. 5.18). The length of snow cover increases with the first and second ordination axis. Cushion plant communities and xeric turf vegetation are displayed on the lower left side of the diagram, while moist willow communities and sites in snowbeds are arranged toward the upper center or on the right side of the diagram. The topographic moisture index exhibits a weak positive correlation with the first ordination axis (r = 0.426, n = 31), while annual potential solar radiation shows a decreasing trend (r = -0.532, n = 31). The pH of the topsoil (0-5 cm) decreases with the first ordination axis (r = -0.912, n = 31).

A total of 121 vascular species were recorded on the experiment sites. Five of these species, *Geum rossii, Potentilla diversifolia, Festuca brachyphylla, Luzula spicata,* and *Trisetum spicatum* had a high constancy occurring in 90% or more of all sites. Another 26 species were found in only one site. Most of these infrequent species had low magnitudes and therefore were not considered for classification purposes. The vegetation composition of all sites is tabulated in Appendix 9.1.

Site R1 is a cushion plant community dominated by *Dryas octopetala* (Appendix 9.1, Table 9.1). The site occurs in a wind eroded area at the edge of the Beartooth Plateau, windward of a large subalpine fir tree island. *Dryas octopetala* grows in large patches providing 60% of ground cover, surrounded by scree. Other species are typically found inside the *Dryas* mats and have a low cover. The occurrence of *Arenaria obtusiloba, Silene acaulis, Eritrichium nanum, Trifolium nanum,* and *Phlox pulvinata* is typical for cushion plant communities in this area. *Dryas octopetala* mats are uncommon on the Beartooth Plateau (Johnson and Billings 1962). Similar *Dryas*

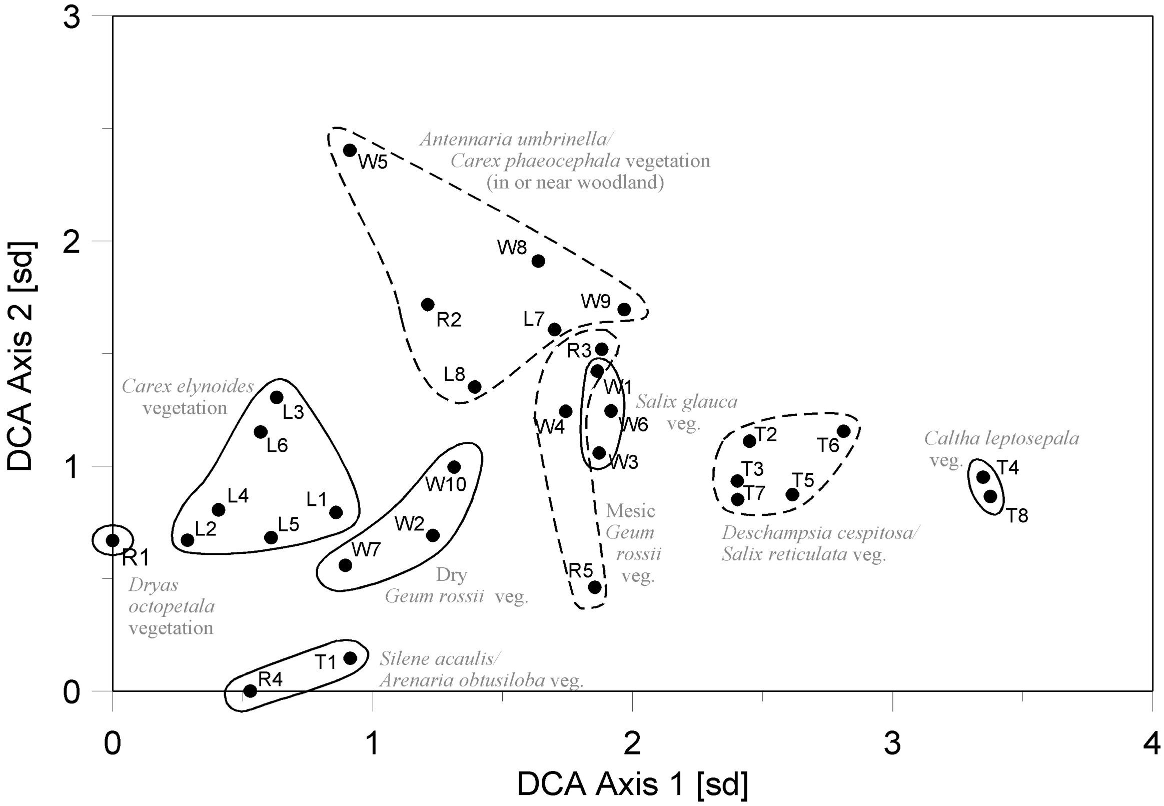


Figure 5.18: *DECORANA ordination diagram of the vegetation composition of 31 experiment sites. Lines indicate the classification into nine vegetation types further described in the text. (Dashed lines are used for diverse groups of sites.)*

dominated communities have been described for Montana by Bamberg (1961, *Dryas* island stand type) and Cooper and Lesica (1992, *Dryas octopetala/Carex rupestris* c.t.). The community appears to be closely related to the *Eritricho aretioidis-Dryas octopetala* association of the Front Range, Colorado (Komárková 1979).

The sparsely vegetated dry sites R4 and T1 are physiognomically similar to the *Dryas octopetala* community (Appendix 9.1, Table 9.1). The vegetation cover is 50-75% and is dominated by cushion or mat-forming plants interspersed with rock and scree. *Dryas octopetala* is missing on these sites, but *Arenaria obtusiloba, Selaginella densa, Silene acaulis, Eritrichium nanum, Erigeron rydbergii,* and *Phlox pulvinata* are common and dominate the appearance of this community. While *Geum rossii* is quite abundant on these sites, its plant size is small and it does not form dense mats as seen on more mesic slopes.

Johnson and Billings (1962) include the cushion plant communities of the Beartooth Plateau in their *Geum* turf continuum, but mention its status as a distinct community. Similar cushion plant communities that occupy the driest, most windswept sites with little or no snow accumulation have been reported from other alpine areas in Montana and Wyoming (fellfield stand type, Bamberg 1961; *Geum rossii/Arenaria obtusiloba* c.t., Cooper and Lesica 1992), as well as Colorado (*Sileno acaulis-Paronychietum pulvinatae,* Komárková 1979; Willard 1979).

The mostly south to southwest exposed sites L1 to L6 have low winter snow cover, comparable to the cushion plant communities. The vegetation consists of cushion plants and a number of taller vascular species, with high covers of exposed rock and scree (Appendix 9.1, Table 9.2). *Carex elynoides* is co-dominant with *Arenaria obtusiloba, Selaginella densa, Phlox pulvinata,* and *Geum rossii*. Other characteristic species are *Elymus scribneri, Polemonium viscosum,* and *Carex albonigra* which were rarely encountered in other vegetation types. *Carex elynoides*-dominated communities are considered climax alpine vegetation for the Beartooth Plateau (*Carex elynoides* turf, Billings and Johnson 1962) and parts of the Colorado Rocky Mountains (*Caricetum elynoidis*, Willard 1979). They have been described for many alpine areas in Montana and Wyoming (Bamberg 1961; Potkin and Munn 1987; Cooper and Lesica 1992; Lesica 1993).

Sites W2 and W10 can be considered dry *Geum rossii* turf (Photo 5.2, page 51; Appendix 9.1, Table 9.2). These species rich sites are dominated by *Arenaria obtusiloba, Selaginella densa, Lupinus argenteus, Geum rossii,* and *Potentilla diversifolia*. They are superficially similar to *Carex elynoides* turf, however, *Carex elynoides* and other characteristic species for that vegetation type are absent. The vegetation on site W7 is an intermediate between *Carex elynoides* turf and dry *Geum rossii* turf (Photo 5.4, page 52). It was included in the latter on floristic similarities.

Geum rossii appears to be one of the most ubiquitous alpine species in the central Rocky Mountains. The described vegetation fits into Johnson and Billings (1962) broadly defined *Geum* turf for the Beartooth Plateau. Similar communities were reported from southwest Montana (*Carex-Geum* stand type, Bamberg 1961; *Carex scirpoidea/Geum rossii* c.t., Cooper and Lesica 1992; Lesica 1993), Wyoming (*Geum rossii/Selaginella densa* c.t., Potkin and Munn 1987), and Colorado (*Acomastylidetum,* Komárková 1979; Willard 1979). Willard (1979) considers the *Geum rossii* dominated communities on Trail Ridge, Colorado, as zootic-controlled by small mammals. This relationship was not observed on the Beartooth Plateau sites.

Sites R5, W4 and R3 support a mesic *Geum rossii* turf characterized by the occurrence of *Deschampsia cespitosa* (Appendix 9.1, Table 9.3). They have a dense ground cover of 70-90%. *Geum rossii, Deschampsia cespitosa,* and *Lupinus argenteus* are dominating species with moderate abundance of *Solidago multiradiata*, *Polygonum bistortoides*, *Potentilla diversifolia*, *Festuca brachyphylla,* and *Carex scirpoidea*. Cushion plants are uncommon. The vegetation of these sites appears to be an intermediate between *Geum rossii* and *Deschampsia cespitosa* dominated communities. The *Deschampsia* meadow vegetation described by Bamberg (1961) and Johnson and Billings (1962) refers to moister sites with longer snow cover. Lesica (1993) mentioned *Deschampsia cespitosa* and *Geum rossii* dominated sites for the Line Creek Plateau, just east of the study area (included in *Carex scirpodea/Geum rossii* c.t.). Potkin and Munn (1987) described a similar community for the Wind River Range in Wyoming.

The next vegetation type includes sites with high and long snow cover. Sites L8, L7, W8 and R2 are leeward of tree islands or subalpine woodland (Photo 5.5, page 53). W5 is located between woodland and a small ridge and W9 is inside of open whitebark pine woodland (Photo 5.6, page 53). The vegetation of these sites is diverse (Appendix 9.1, Table 9.3). Besides the abundant species *Geum rossii, Potentilla diversifolia*, and *Carex scirpoidea* the vegetation is characterized by the occurrence of *Antennaria umbrinella, Arenaria congesta, Carex phaeocephala,* and *Poa secunda.* Several sites have high covers of *Festuca idahoensis* and *Danthonia intermedia*. Lesica (1993) described a similar community on warm slopes near the timberline of the adjacent Line Creek Plateau (*Festuca idahoensis/Geum rossii* c.t.). Some resemblance also exist with lower alpine and subalpine communities reported from the Wind River and Front Ranges (*Festuca ovina* c.t., Potkin and Munn 1987; *Solidagini spathulatae-Danthonietum intermediae*, Komárková 1979).

Small depressions leeward a ridge or whitebark pine woodland support open shrub communities. Sites W1, W3, and W6 are dominated by *Salix glauca* forming a shrub cover not much taller than surrounding forbs and graminoids (Photos 5.1-5.3, pp. 51-52; Appendix 9.1, Table 9.4). Common associated species are *Festuca brachyphylla, Lupinus argenteus, Selaginella densa*, and *Arenaria obtusiloba*. Other characteristic species include *Arenaria congesta, Solidago multiradiata, Aster alpigenus, Sibbaldia procumbens,* and *Lewisia pygmaea.* All three sites are situated in or below snow catchment areas with medium to late snow release. *Salix glauca* communities with variable understories have been described for southwest Montana (Cooper and Lesica

1992; Lesica 1993), Wyoming (Potkin and Munn 1987), and Colorado (*Bistorto viviparae-Salicetum villosae,* Komárková 1979). They usually occupy medium to late snow melt areas that are dryer than sites dominated by *Salix planifolia*.

With the exception of the cushion plant community on T1, the vegetation composition of all Tibbs Butte sites differs considerably from other studied locations. Besides the ubiquitous *Festuca brachyphylla* and *Potentilla diversifolia,* the Tibbs Butte sites have moderate to high covers of *Deschampsia cespitosa, Poa alpina, Carex scirpoidea, Polygonum viviparum, Artemisia scopulorum, and Salix reticulata* (Appendix 9.1, Table 9.5). These are the coldest of all experiment sites, due to high elevation, north facing exposure, and moderate to late snow melt.

Sites T2, T3, and T5-T7 represent a heterogenous vegetation type. The cover of the herb layer amounts to 40-65%. In addition to the above mentioned species, the sites can be characterized by *Arenaria obtusiloba, Antennaria media*, and *Lewisia pygmaea*. *Vaccinium scoparium* is a significant component on sites T2 and T6. Most sites in this group appear to be intermediate between *Deschampsia cespitosa* communities (discussed under mesic *Geum rossii* turf) and *Salix reticulata/Salix arctica* communities reported from north exposed, mesic, and cool alpine slopes of other Rocky Mountains ranges (*Bistorto viviparae-Salicetum reticulatae,* Komárková 1979; *Salix arctica/Polygonum bistortoides* c.t., Potkin and Munn 1987; Cooper and Lesica 1992).

Sites T4 and T8 are the wettest sites included in this study. They are water saturated in spring and remain moist through most of the growing season. *Caltha leptosepala, Salix reticulata,* and *Deschampsia cespitosa* are important species. Site T8 also contains appreciable amounts of *Phyllodoce sp.* The vegetation composition appears similar to the *Deschampsia cespitosa/Caltha leptosepala* meadow (Cooper and Lesica 1992; Lesica 1993) and the *Salix reticulata/Caltha leptosepala* c.t. (Potkin and Munn 1987; Cooper and Lesica 1992) described for southwest Montana and Wyoming. According to Johnson and Billings (1962), the occurrence of *Caltha leptosepala* indicates the transition from *Deschampsia* meadow vegetation to *Carex scopulorum* bog.

Disturbance by pocket gophers (*Thomomys talpoides*) was noted in ten of the experiment sites. Four sites showed evidence of vole activity (*Microtus sp.).* Some domestic sheep grazing occurs in the Littlerock Creek and Tibbs Butte area. Wapiti (*Cervus elaphus*) and mule deer (*Odocoileus hemoinus)* have been observed near the

Littlerock Creek and Wyoming Creek sites. However, the experiment sites did not appear to be impacted by larger mammals. Disturbance by pocket gophers seems to have the largest impact on vegetation and the resulting sparsely vegetated gopher mounds or “gopher gardens” on gravel mulch are obvious features for many years (see Osburn 1958, Willard 1979). Gopher activity was recorded in all vegetation types with the exception of cushion plant communities and the moist cold sites on Tibbs Butte.

5.2.2.3 Soils

The 15 soil profiles studied revealed only minor differences in soil development between germination experiment sites. Detailed data on soil profiles are given in Appendix 9.2. All examined profiles are Inceptisols and classify either as Eutrocryepts or Dystrocryepts, depending upon the amount of base saturation ($\geq 60\%$ or $< 60\%$, respectively) (Soil Survey Staff 1999).

Base saturation of subsurface soil horizons was not a critical parameter for classification purposes at the time of the soil survey, and therefore not measured in this study. Alpine soils in the Colorado Front Range are reported to have base saturations < 50% in horizons more than 25 cm below the surface (Burns 1980; Litaor 1987). Unpublished data from an alpine pedon developed from glacial till in the Beartooth Mountains show high base saturations (>70%) down to 94 cm depth. This soil would be classified as a Eutrocryept (Shoshone National Forest 1992). Soils in the study area, however, are shallow and developed from granitic materials. Field measured pH’s (in H_2O) less than 5.6 are generally accepted to indicate base saturations below 60% (Houston 2002), but this is inconsistent with pH and base saturation values of the alpine Eutrocryept mentioned above.

In this study, pH values of B and C horizons varied between 5.3 and 6.1 (Appendix 9.2). Following the pH rule, classifications of some soils would depend on pH differences as little as 0.1. Such a difference between classified Eutrocryepts or Dystrocryepts does not appear useful for soil interpretations. Lacking further data for the Beartooth Plateau, all soils were classified as Dystrocryepts, consistent with reported soils from the Colorado Front Range. The presence of an umbric epipedon (dark surface horizons with low base saturation) is an important diagnostic feature separating humic (umbric epipedon present) and typic (ochric epipedon) Dystrocryepts. Most soils classified in this project fall into these two subgroups (Soil

Survey Staff 1999).

Soils in the study area contain high amounts of rock fragments (> 2 mm in diameter). Gravel, cobbles, stones, and boulders increase with depth and comprise 90% of the soil materials in the C/B horizon of site W9. The soils of sites with tree cover tend to contain higher amounts of rock fragments than treeless sites.

On windy, rocky slopes usually covered with cushion plant communities or dry turf (sites L5, T1, W2, W10, and R1), soils are shallow with an ochric epipedon and a weakly developed cambic horizon. These soils are classified as typic Dystrocryepts. Topsoils (0-5 cm) of the most wind-exposed sites L1, T1, R1, and R4 contain high amounts of sand. The textures of the fine earth fractions are loamy sands in contrast to the sandy loam or loam of other experiment sites (Table 5.3). PH values (in $CaCl_2$) of the dry rocky sites are the highest found in the study area, varying between 4.7 and 5.5 for the upper 5 cm topsoil and decreasing with increasing depth (Table 5.3). The amount of organic matter in the A horizon is low (3.4% - 5.3%).

In the whitebark pine woodland on site W9, and leeward a fir tree island on site R2, the soil profiles were only slightly more developed than the soils of wind-exposed, rocky slopes. Their upper horizons did not meet the color and depth requirements of an umbric epipedon. Therefore these are still typic Dystrocryepts, tending toward humic Dystrocryepts.

Sites W2, W3, and W4 are located along a transect running downhill from the upper part of a ridge (W2) through a willow patch (W3) to a small seasonal drainage (W4). The A horizons increase in depth toward site W4. While the soil profile of W2 is classified as a typic Dystrocryept, humic Dystrocryepts can be found on the lower part of the transect. The organic matter of the A horizon also increases toward site W4, but the pH values of the topsoil (0-5 cm) are the lowest on the willow site W3, (4.4 in $CaCl_2$, Table 5.3).

Sites W4 and R5, with a dense cover of grasses and herbaceous plants, developed A horizons thicker than 20 cm. At site R5, the profile revealed a buried A and B_w horizon that is attributed to solifluction activity.

The experiment sites on Tibbs Butte show the highest variation in soil development and texture. Leeward and inside a tree island, the A horizon is generally better developed than in wind exposed locations. At sites T5 and T6, the epipedon is dark enough to classify as umbric. Site T5 is located windward of a tree island. The soil profile exposed old root and stem parts that occurred to be part of the tree island, suggesting that this site was, at one time, covered by trees and protected from wind erosion. While the soil texture at the wind exposed site T1 is loamy sand to sandy loam with 62.1% coarse sand in the A horizon, the topsoils of sites T4, T5, and T6 show a high accumulation of clay and silt particles as high as 59.6% at site T5 (silt loam). Clay and silt components decrease with depth while the amount of coarse sand and rock fragments increase. The clay and silt accumulation of the A horizon is most pronounced on site T5.

Table 5.3: *Characteristics of mixed soil samples from experiment sites (A horizon, 0-5 cm)*

Site	roots [%]	color dry	color moist	pH ($CaCl_2$)	texture	Soil classification*
T1	< 5	10YR 4/3	10YR 3/2	5.1	loamy sand	Typic Dystrocryept, sandy-skeletal
T2	< 5	10YR 3/3	10YR 2/2	4.2	sandy loam	
T3	< 5	10YR 3/2	10YR 2/1	4.4	loam	
T4	0	10YR 3/3	10YR 2/2	4.2	loam	Oxyaquic Dystrocryept, loamy-skeletal
T5	0	10YR 3/2	10YR 2/1	4.4	silt loam	Humic Dystrocryept, sandy-skeletal
T6	< 5	10YR 3/2	10YR 2/1	4.3	loam	Humic Dystrocryept, sandy skeletal
T7	< 5	10YR 3/3	10YR 2/2	4.3	sandy loam	
T8	< 5	10YR 3/3	10YR 2/2	4.2	sandy loam	
L1	< 5	10YR 4/3	10YR 3/2	5.2	loamy sand	
L2	< 5	10YR 3/3	10YR 2/2	5.5	sandy loam	
L3	< 5	10YR 3/2	10YR 2/1	5.1	sandy loam	Humic Dystrocryept, loamy-skeletal
L4	< 5	10YR 3/3	10YR 2/1	5.5	sandy loam	Humic Dystrocryept, sandy-skeletal
L5	0	10YR 3/3	10YR 2/2	5.4	sandy loam	Typic Dystrocryept, sandy-skeletal
L6	< 5	10YR 3/3	10YR 2/2	5.4	sandy loam	
L7	10	10YR 3/3	10YR 2/2	4.6	sandy loam	
L8	< 5	10YR 3/3	10YR 2/2	5.0	sandy loam	
R1	< 5	10YR 3/2	10YR 2/1	5.5	loamy sand	Typic Dystrocryept, loamy-skeletal
R2	< 5	10YR 3/3	10YR 3/2	5.1	loamy sand	Typic Dystrocryept, loamy-skeletal
R3	< 5	10YR 4/3	10YR 3/2	4.6	sandy loam	
R4	0	10YR 4/3	10YR 3/2	4.8	loamy sand	
R5	< 5	10YR 3/3	10YR 2/2	4.5	loam	Humic Dystrocryept, loamy-skeletal
W1	< 5	10YR 3/3	10YR 2/2	4.7	sandy loam	
W2	< 5	10YR 3/3	10YR 2/2	4.7	sandy loam	Typic Dystrocryept, loamy-skeletal
W3	< 5	10YR 3/3	10YR 2/2	4.4	sandy loam	Humic Dystrocryept, loamy-skeletal
W4	< 5	10YR 3/3	10YR 2/2	4.7	sandy loam	Humic Dystrocryept, loamy-skeletal
W5	< 5	10YR 3/3	10YR 3/2	5.0	sandy loam	
W6	< 5	10YR 3/3	10YR 3/2	4.5	sandy loam	
W7	0	10YR 3/3	10YR 3/2	5.5	sandy loam	
W8	0	10YR 3/3	10YR 3/2	4.6	sandy loam	
W9	0	10YR 3/3	10YR 3/2	4.4	sandy loam	Typic Dystrocryept, sandy-skeletal
W10	< 5	10YR 4/3	10YR 3/2	4.9	sandy loam	Typic Dystrocryept, loamy-skeletal

*soil classification for sites with analyzed soil profile

An oxyaquic Dystrocryept developed under site T4 which is located in a slight depression influenced by snow melt water each spring. The vegetation is dominated by *Caltha leptosepala* and *Deschampsia cespitosa*, indicating water saturation during the early part of the growing season. In spring 1994, water collected in the soil pit to a depth of 50 cm below the surface. Silt and fine sand particles accumulated in elongated lenses in the B_{w2}, B/C, and C horizons, possibly as the result of subsurface water runoff. The variable watertable caused reddish mottling in the B_{w2} and B/C horizons, especially above the silt lenses.

PH values of the moist Tibbs Butte sites are among the lowest measured. They varied from 4.2 to 4.4 in the topsoil (in $CaCl_2$, 0-5 cm depth, Table 5.3). There is generally a slight increase of the pH values with depth. The organic matter contents of the A horizons are high, reaching a maximum of 31% on site T5 (see soil profiles, Appendix 9.2)

Little to no organic material can be found under cushion plant communities like on sites T1, R1, and R4. In wind protected sites, organic litter may accumulate. Leeward of tree islands or inside of whitebark pine woodland the organic horizons are well developed, and separate O_i and $O_{e/a}$ horizons can be recognized (see sites T6 and W9, Appendix 9.2) Despite a thick layer of decomposed organic matter at site T5, the O_i horizon is missing. This suggests the beginning erosion of the soil profile due to changed microsite conditions. Most experiment sites with a dense cover of herbs, grasses, or willows developed a recognizable $O_{e/a}$ horizon, with little accumulated O_i material. The boundaries to the A horizons are usually gradual.

Soils in the timberline ecotone are influenced by pocket gopher activities. Organic soil horizons are often covered with mineral soil material from pocket gopher excavations, making it difficult to recognize soil horizon boundaries. Root content and skeletal material in the organic layers can be as high as in the mineral topsoil horizons.

5.2.2.4 Surface and soil temperatures

In 1993, maximum measured surface temperatures of the experiment sites ranged from < 38°C on site T1 (none of the wax pellets melted) to ≥ 59°C on L3 and W9 (all wax pellets melted). Figure 5.19 shows the frequency of surface temperatures reached during July and August 1993 in the four study areas. Maximum surface temperatures

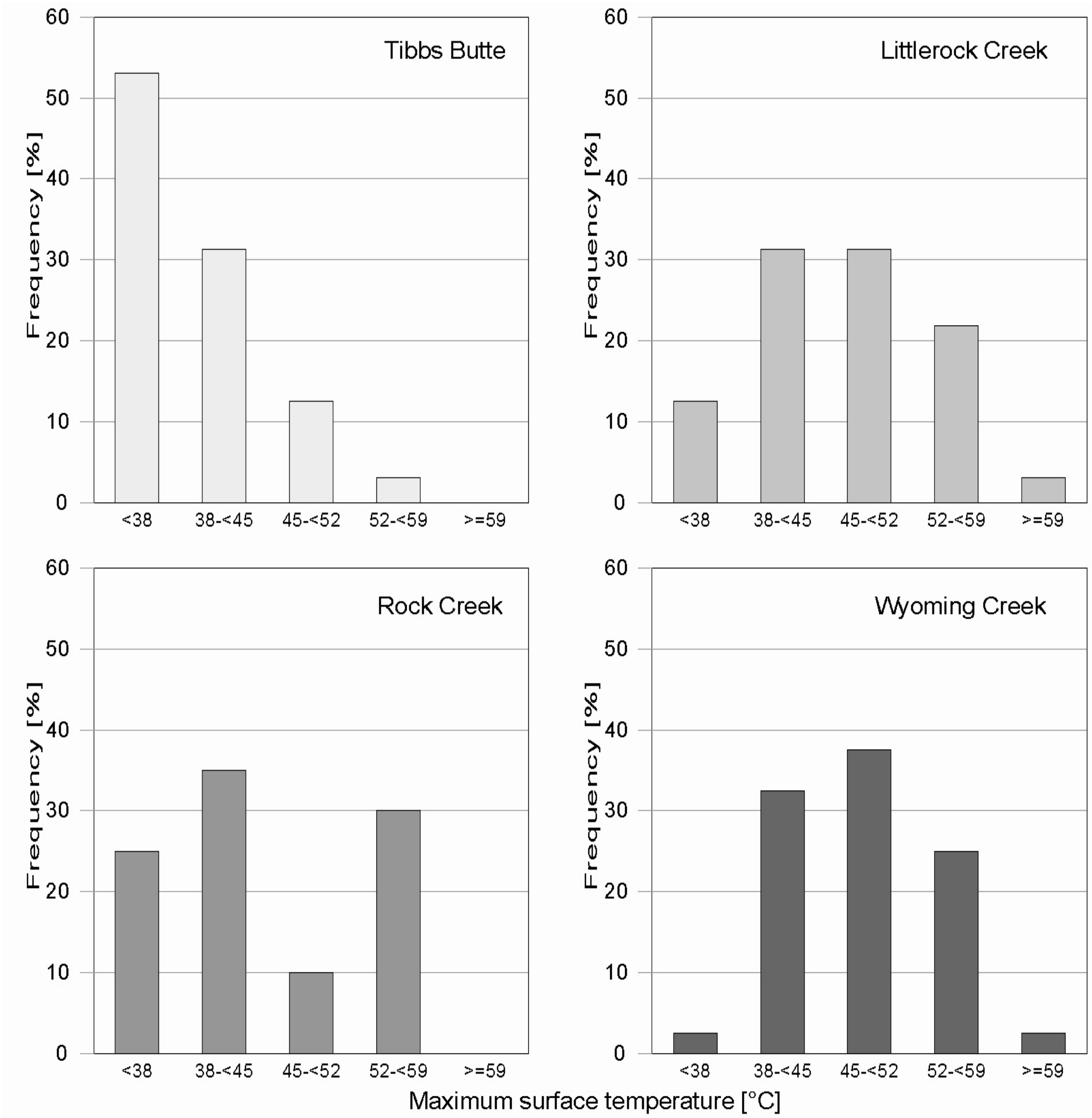


Figure 5.19: *Frequency of maximum surface temperatures during July and August 1993. Included are four semi-monthly readings for each experiment site, with 8 sites in the Tibbs Butte and in the Littlerock Creek area, 5 sites in the Rock Creek area, and 10 sites in the Wyoming Creek area.*

were noticeably lower on Tibbs Butte than in any other study area. More than 50% of all maximum surface temperature measurements were below 38°C. On the Wyoming Creek experiment sites, 65% of maximum surface temperature readings were ≥ 45°C, indicating that Wyoming Creek was the warmest of all study areas.

Differences among Littlerock Creek, Rock Creek and Wyoming Creek were minor compared to the Tibbs Butte sites. The Rock Creek frequency diagram of maximum surface temperatures (Fig. 5.19, bottom right) shows a bimodal distribution, indicating the high diversity of sites. The surface temperatures on sites R2 and R4 warm up to more than 52°C in the latter part of July and during August, whereas surface temperatures of site R1 never climbed above 41°C. This low temperature may be due to wind exposure and the high coverage of light-colored scree on this site.

The average daily soil temperatures at 3 cm and 10 cm depth were strongly correlated on Tibbs Butte and Wyoming Creek. The soil temperatures on the three measured Wyoming Creek experiment sites (WYCR) were generally higher than on the three examined Tibbs Butte sites (TIBU). Linear regression analysis results in the following model for temperatures at 3 cm depth [°C]: WYCR = 1.828 + 1.244 * TIBU ($r^2_{adj} = 0.888$, $n = 172$). The relationship of temperatures in °C at 10 cm depth is best described with a cubic model: WYCR = 2.713 - 0.002 * TIBU + 0.301 * TIBU² - 0.019 * TIBU³ ($r^2_{adj} = 0.950$, $n = 114$). Temperature graphs of all measured experiment sites can be found in Appendix 9.3.

In 1992 and 1993, soil temperatures were highest in August. In 1994, July soil temperatures were as high or higher than August temperatures. Figure 5.20 shows a comparison of August soil temperatures for T5, T6, and T4 on Tibbs Butte and W8, W7, and W10 on Wyoming Creek. The average soil temperatures at 3 cm depth varied between 5.3 and 9.9°C on Tibbs Butte, and between 10.0 and 12.9°C on Wyoming Creek (data were modeled to fill gaps, see method section). The coolest year measured was 1993.

The differences in soil temperatures between Tibbs Butte and Wyoming Creek are also apparent examining heat sums and frequency distributions (Table 5.4). In August 1994, the soil temperature at 3 cm depth was above 10°C for 319 hours on the warmest Tibbs Butte site T4, and 423 hours on the coolest Wyoming Creek site W8. The sum of temperatures 10°C and above was 6474°C on W8 and only 4479°C on T4.

Table 5.4: *Frequencies of average hourly soil temperatures at 3 cm depth (n = 744), and heat sums for temperatures ≥ 10°C for August 1994 in six selected sites at Tibbs Butte (T4, T5, T6) and Wyoming Creek (W7, W8, W10).*

Temperatures	T5	T6	T4	W8	W10	W7
-5 to < 0°C	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
0 to < 5°C	38.6%	8.9%	9.5%	4.8%	3.0%	2.0%
5 to < 10°C	33.9%	55.2%	47.6%	38.3%	38.3%	37.6%
10 to <15°C	20.3%	27.2%	26.9%	27.4%	25.8%	30.1%
15 to < 20°C	6.9%	8.6%	15.7%	24.1%	16.8%	20.3%
20 to < 25°C	0.4%	0.1%	0.3%	5.4%	12.0%	9.9%
25 to < 30°C	0.0%	0.0%	0.0%	0.0%	4.2%	0.0%
Heat sum (≥ 10°C)	2753	3577	4479	6474	7348	6991

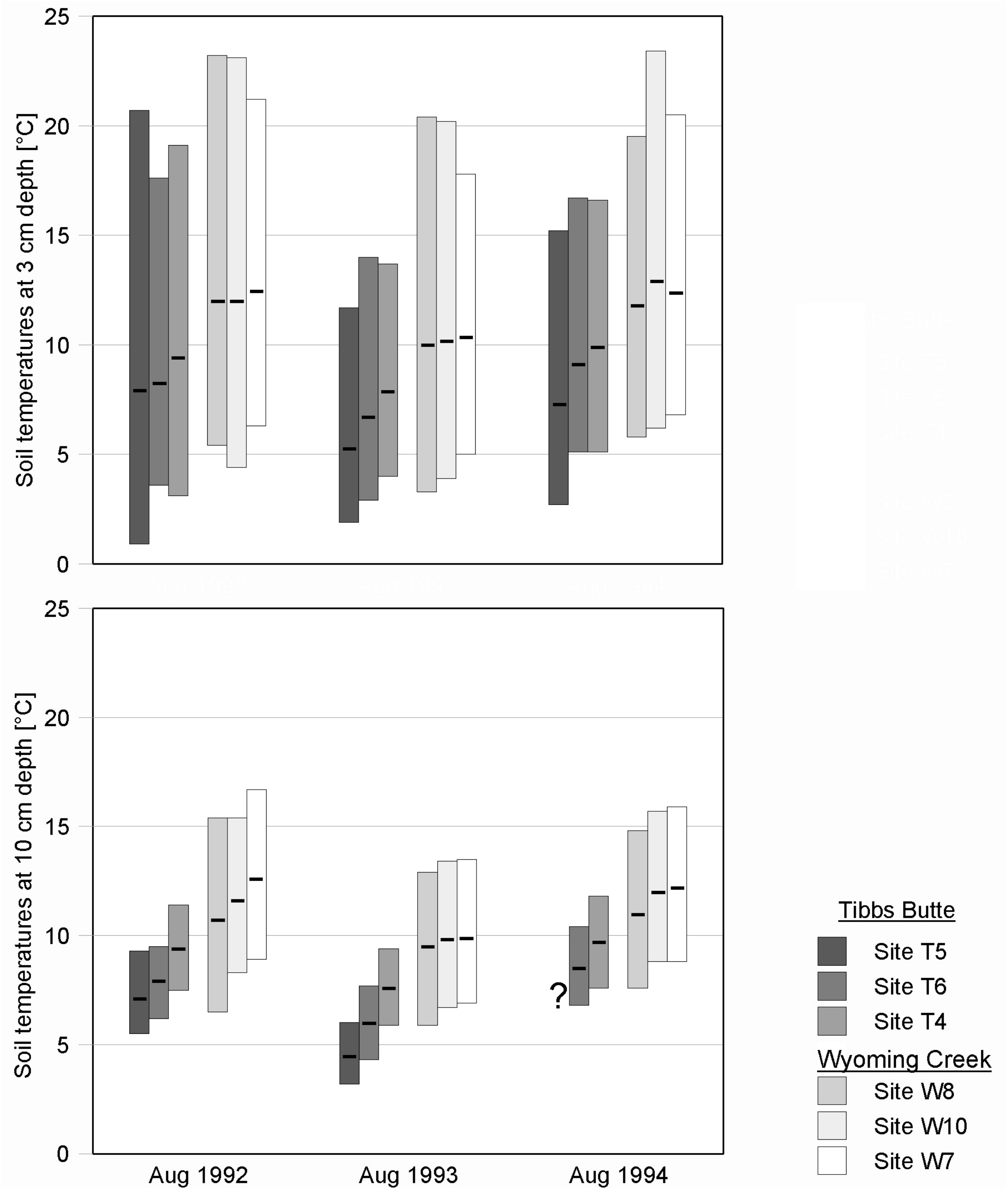


Figure 5.20: *Average daily minima, maxima, and mean soil temperatures at 3 cm and 10 cm depth for selected germination sites in the Tibbs Butte and Wyoming Creek study areas. Temperatures include modeled data for 3 cm depth measurements at sites W8 and W10 in 1992, and for 3 cm and 10 cm depth measurements at sites T5, W7, W8, and W10 in 1993. See method section for further detail.*

5.2.2.5 Germination of whitebark pine

The germination of planted whitebark pine seeds was delayed by one year in nearly all experiment sites. In 1992, only four seedlings in two planting locations (caches) germinated on site W9 in the Wyoming Creek study area (Photo 5.7). Site W9 is also the only site with germination occurring in 1994 (nine additional seedlings).

Photo 5.7: *New whitebark pine germinants on experiment site W9. July 1992.*

In 1993, the second year after planting, 543 seeds (23.4%) germinated in the experiment sites (Fig. 5.21). Seedling emergence in 1993 started in the second half of June (Table 5.5). By the end of September, germination had not entirely ceased. On October 4, 1993, during the last survey of the season, ten new seedlings were found on sites W3 and W9. Most of these had not emerged completely from the ground and did not survive the winter. Of the 1993 germination, 79% occurred in July. In summary, from 1992 to 1994 23.9% of all planted seeds germinated; germination occurred in 38.3% of all caches.

The results of the germination experiment varied between study areas (Table 5.5). None of the 600 seeds planted on the eight Tibbs Butte sites germinated. In the Littlerock Creek area, four of the eight experiment sites had at least four whitebark pine seedlings, and sites L7 and L8 had 22 and 28 seedlings, respectively. A total of 9.7% of the 600 planted seeds germinated in the Littlerock Creek area.

Germination success was also variable on the five Rock Creek sites. Sites R4 and

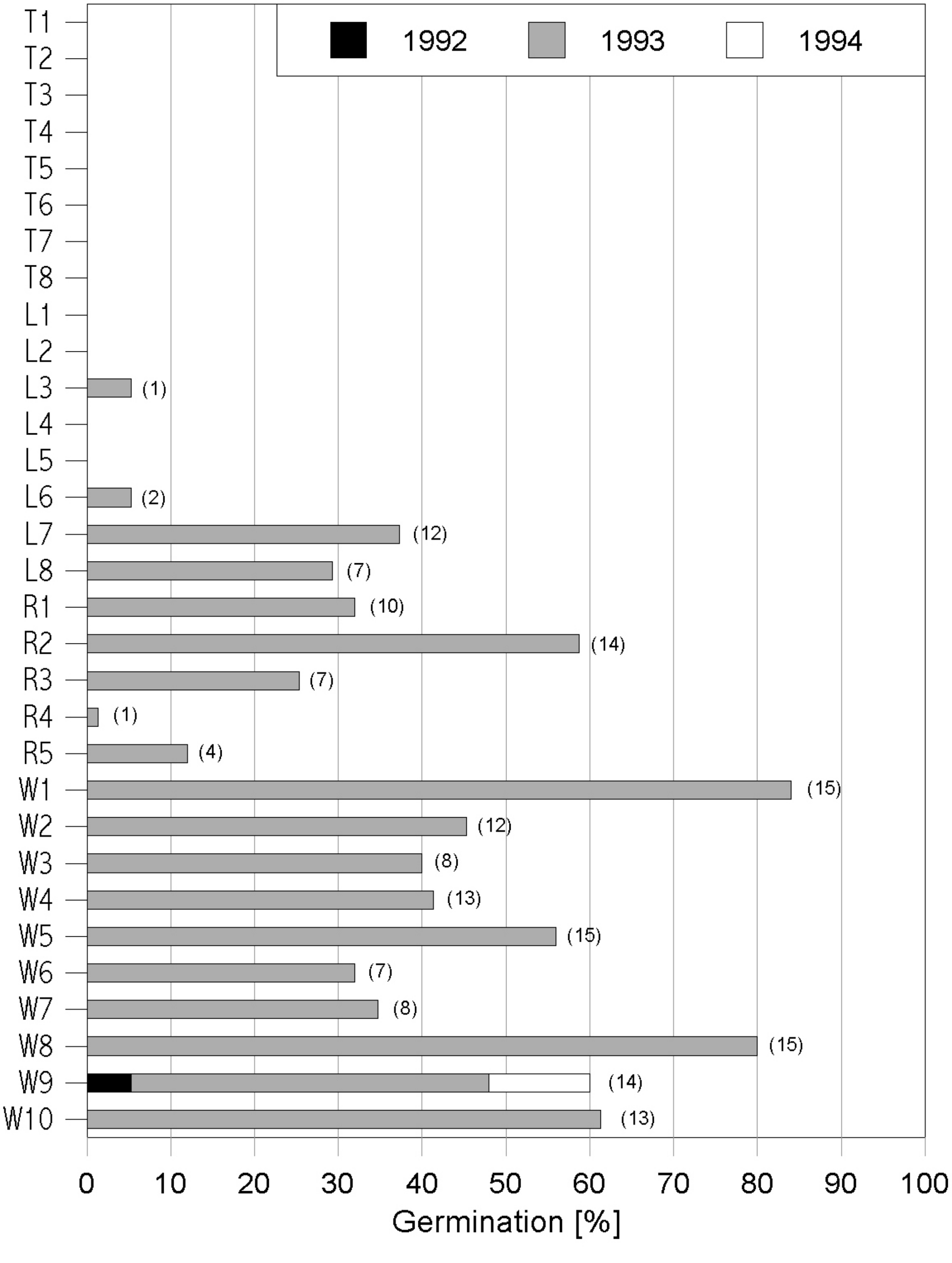


Figure 5.21: *Germination of planted whitebark pine seeds in all experiment sites. Numbers in parenthesis indicate the number of planting locations (caches), out of 15, with germination success in each site.*

Table 5.5: *1993 germination (%) of planted whitebark pine seeds in four study areas*

Study Area	– mid June	– end June	– mid July	– end July	– mid Aug.	– end Aug.	– mid Sept.	– end Sept.	Total for 1993
Tibbs Butte (N=600)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Little Rock Creek (N=600)	0.0	0.2	2.0	3.7	3.7	0.2	0.0	0.0	9.7
Rock Creek (N=375)	0.0	0.0	17.9	5.6	0.8	1.6	0.0	0.0	25.9
Wyoming Creek (N=750)	0.0	2.3	22.0	19.1	2.8	3.3	0.8	1.5	51.7
All Areas (N=2325)	0.0	0.8	10.5	8.0	2.0	1.4	0.3	0.5	23.4

R5 (highest in elevation in this area) had germination rates of 1% and 12%, respectively. Germination on the other three sites varied between 25% and 59%. Of the 375 seeds planted in the Rock Creek area, 97 seeds (26%) germinated in 36 seedling clusters.

The germination of whitebark pine seeds was most successful in the Wyoming Creek study area. On all ten Wyoming Creek sites, germination rates were higher than 30%. The wind protected site W8 (leeward a tree island) and the moist willow site W1 had the highest germination with 80% and 84%, respectively, and germination occurred in all 15 caches of each site. For the entire area, 52% of planted seeds germinated.

Germination was not uniformly distributed over an experiment site (Fig. 5.22). Apparently, site conditions of caches were either favorable or unfavorable for germination, and these conditions varied significantly across an experiment site, from one planting location to the next.

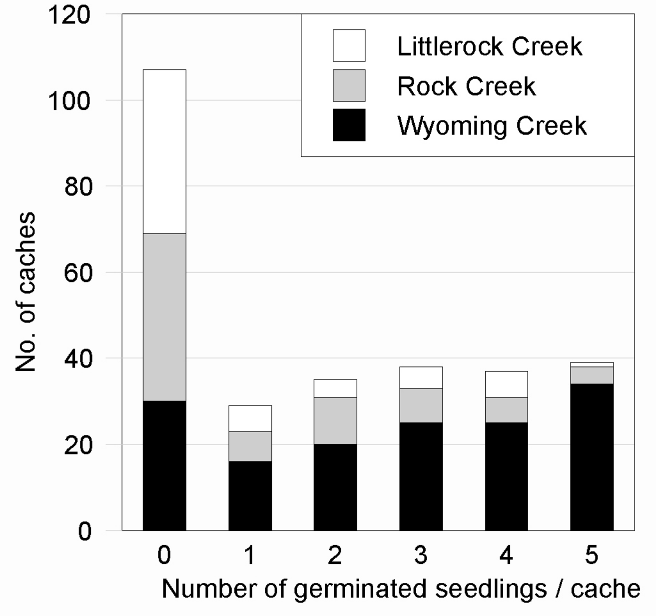


Figure 5.22: *Number of seedlings per planting location (cache) on experiment sites with germination success. (Included are 19 sites with 285 caches).*

Generally, germination was

highest on the moderately moist, wind protected sites adjacent to or inside tree islands and woodland, in dry to mesic *Geum rossii* turf, and in open *Salix glauca* communities (Fig. 5.23). With exception of the *Dryas octopetala* community, dry wind exposed sites with *Carex elynoides* or cushion plant vegetation had little to no germination success. While the *Dryas octopetala* community on site R1 is floristically similar to cushion plant vegetation, it may primarily be a pioneer community on wind eroded soils and may be less dry than *Carex elynoides* or cushion plant vegetation. No germination occurred on the moist to wet, cold, north exposed sites on Tibbs Butte.

Logistic regression analysis was used to investigate the effect of topographic location, temperature conditions, and moisture availability on the success or failure of whitebark pine regeneration. Variables entered into the analysis were altitude, topographic relative moisture index, maximum surface temperatures in July, average maximum surface temperature index, and time of snow melt. For further explanation of these variables see chapters 4.4 and 4.5.

Potential annual solar radiation was not used in the logistic regression analysis,

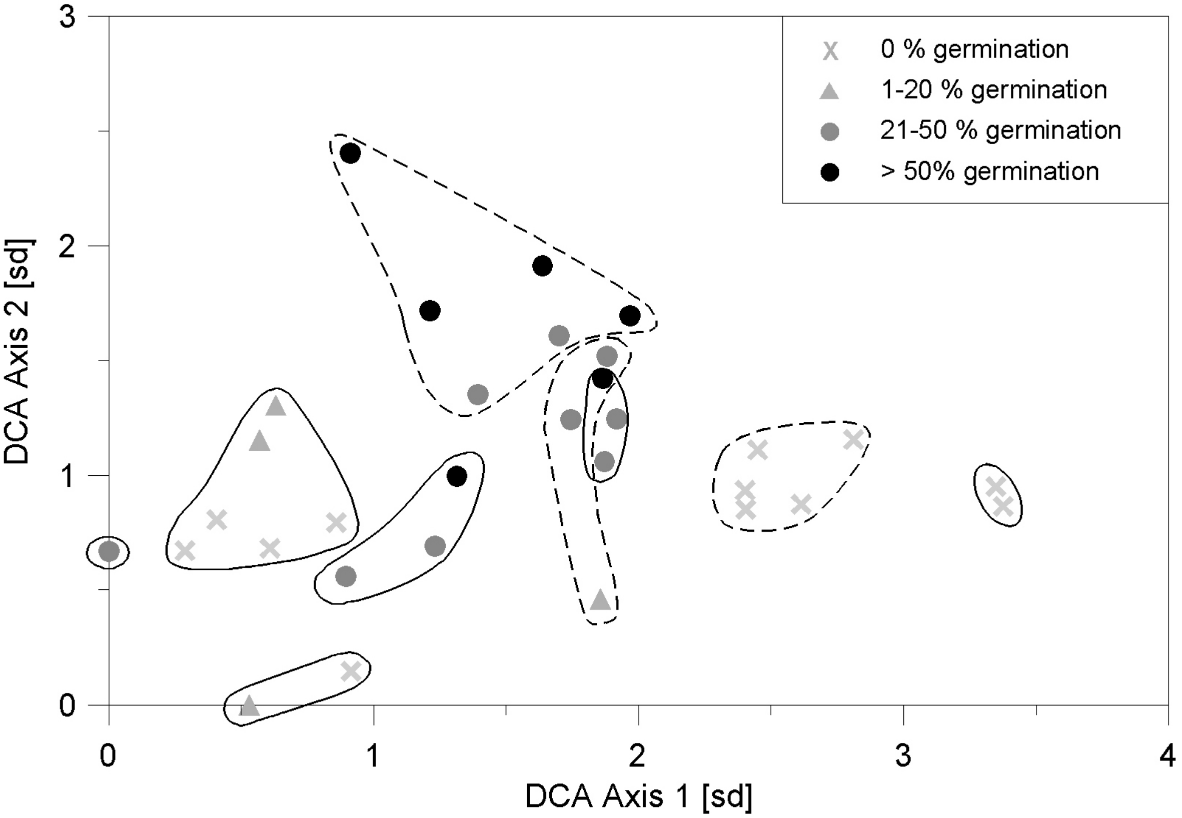


Figure 5.23: *Germination of planted whitebark pine seeds displayed in the DECORANA ordination diagram of the vegetation composition of 31 experiment sites.*

since this variable is not linear in the logit. Sites with both, low and high solar radiation values were more likely to have no germination compared to sites with intermediate solar radiation. The Pearson correlation coefficient between solar radiation and germination of ‘caches’ is low with r = - 0.048 (n = 31).

Detailed soil temperatures were only available for six germination sites (T4, T5, T6, W7, W8, and W10). However, for July 1993, maximum surface temperatures, as measured with wax pellets, correlated strongly with average mean and average maximum soil temperatures at 3 cm depth on those sites (r_s = 0.928 and r_s = 0.754, respectively, n = 6).

The AIC_c values and their weights for all considered models are given in Table 5.6. The first three models investigate the effect of topographic position on germination probabilities. Models 4 to 15 consider the effects of temperature and moisture conditions. The number of variables in each model was kept small, due to

Table 5.6: *Summary of logistic regression results for 15 models for the analysis of germination success. Variables included in the models are defined as following: A = altitude; M = topographic relative moisture index;* T_{Jul} *= maximum surface temperature in July;* T_i *= average maximum surface temperature index; and S = time of snow melt. K denotes the number of estimable parameters;* AIC_c *is Aikaike’s information criterion adjusted for small samples;* Δ_i *is the difference between* AIC_c *and the smallest* AIC_c *value in the set;* w_i *is the Aikaike weight; and* $\bar{r}^2$ *is the generalized coefficient of determination adjusted to range from 0 to 1.*

No.	Model	K	AIC_c	Δ_i	w_i	$\bar{r}^2$
1	A	2	16.848	0.000	0.629	0.824
2	M	2	44.160	27.312	0.000	0.070
3	A, M	3	18.784	1.936	0.239	0.833
4	T_{Jul}	2	24.868	8.020	0.011	0.666
5	T_{Jul}, S	3	25.443	8.595	0.009	0.707
6	T_{Jul}, M	3	23.953	7.105	0.018	0.738
7	T_{Jul}, S, M	4	25.985	9.138	0.007	0.750
8	T_{Jul}, S, T_{Jul}*S	4	21.838	4.991	0.052	0.826
9	T_{Jul}, M, T_{Jul}*M	4	26.308	9.461	0.006	0.744
10	T_i	2	28.261	11.413	0.002	0.587
11	T_i, S	3	29.236	12.388	0.001	0.623
12	T_i, M	3	30.257	13.409	0.001	0.598
13	T_i S, M	4	31.791	14.944	0.000	0.625
14	T_i, S, T_i*S	4	23.238	6.391	0.026	0.802
15	T_i, M, T_i*M	4	32.735	15.888	0.000	0.602

a very small sample size, and a global model that includes all variables considered for analysis was not calculated.

The AIC$_c$ selected model is the first model of Table 5.6, with the single variable altitude as predictor. Elevation ranges 135 meters between all experiment sites. The parameter estimate of -0.1192 (se = 0.059; intercept = 366.9, se = 180.6) indicates decreasing germination probabilities with increasing altitude, as is expected in the upper timberline ecotone (Figure 5.24). The predictive ability of the model is high with $\overline{r}^2 = 0.824$ and a concordance of 96.5% (percentage of all possible pairs in which a site with observed germination has a higher predicted germination probability compared to a site with germination failure, see SAS Institute 1999). An inspection of Pearson and deviance residuals does not indicate a lack of fit of the logistic model. All residuals are < 2 in absolute value. The Littlerock Creek sites L1, L2, and L6 have the highest residuals and are not well explained by the model. At an altitude of 3070 m, the calculated germination probability of L1 and L2 is 0.72, however, these sites had no germination success. Sites L8 and L6 are at the same or higher altitude, and germination was good or at least occurred in a few subsites (L6). On these Littlerock Creek sites, other factors besides altitude must influence germination.

The Akaike weight for the altitude as best model is only 0.649, leaving some model selection uncertainty. The second best model has a weight of 0.246 and

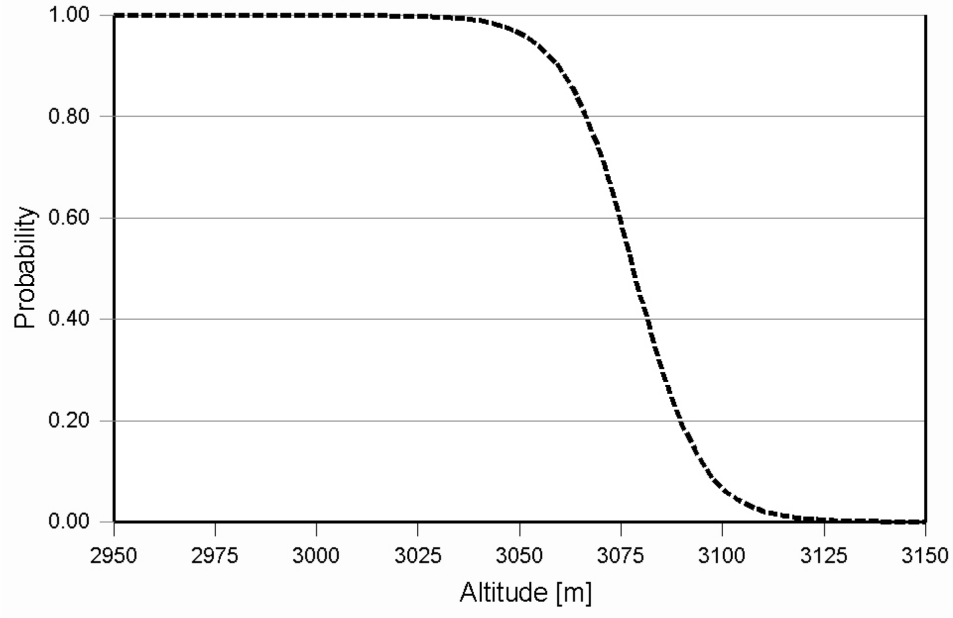


Figure 5.24: *Calculated germination probabilities with altitude as sole predictor (see model 1, Table 5.6).*

includes the topographic relative moisture index (M) with altitude in the equation (Model 3, Table 5.6). However, the difference in AIC_c to the best model is nearly two, and model 2 with M as the sole predictor is very weak. There is little support for including M as an additional variable into the model.

Models 4 to 9 are very similar to models 10 to 15 (Table 5.6). The only difference is the use of the T_{Jul} (maximum surface temperature in July) for the first set, and T_i (maximum surface temperature index, July and August) for the second. Both variables are strongly correlated ($r = 0.867$). A comparison of the AIC_c values reveals that the inclusion of T_{Jul} consistently results in better models than the inclusion of T_i. The Akaike weights for all models with T_i amount to 0.031 compared to 0.102 for models with T_{Jul}. This provides evidence that the maximum temperatures during the first part of the summer are more important for germination success than high temperatures during most of the growing season. The best temperature/moisture model is number 8, with T_{Jul}, S (time of snow melt), and the interaction between T_{Jul} and S. The AIC_c difference to the selected altitude model is 4.991. Considering the small sample size and a 95% confidence set of models (sum of Akaike weights from largest to smallest until the sum ≥ 0.95; Burnham and Anderson 1998), model 8 is a likely best approximating model.

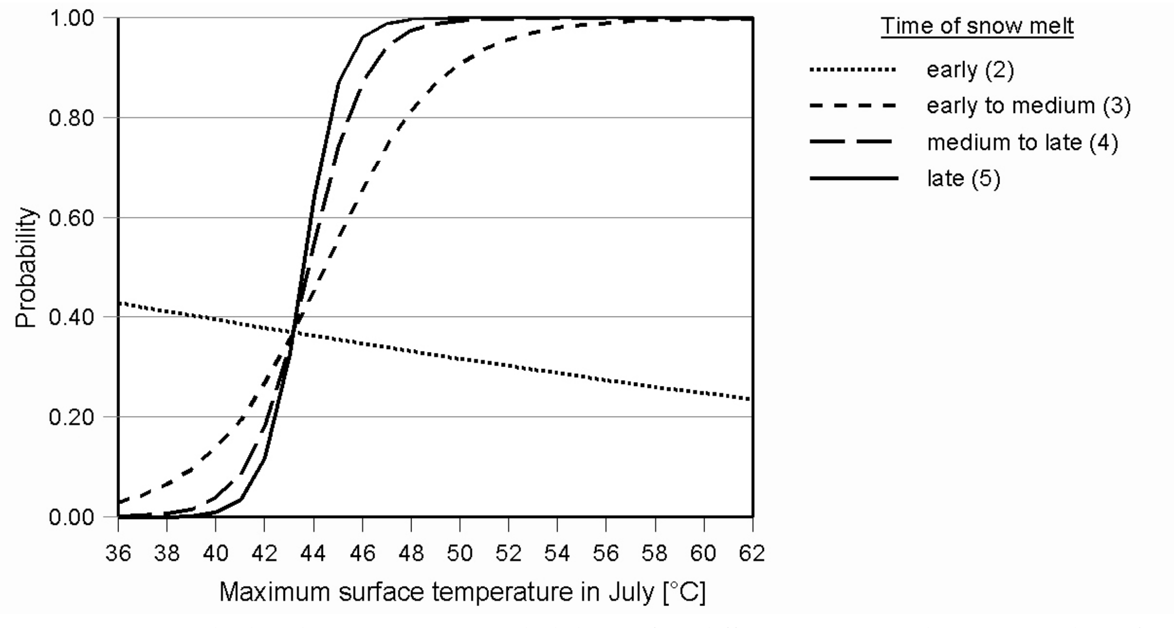


Figure 5.25: *Calculated germination probabilities for different snow melt times and surface temperatures, according to the logistic model 8, Table 5.6.*

Model 5 with only T_{Jul} and S as predictors (no interaction) does not fit the data particularly well compared other models in the set. The inclusion of the interaction factor in model 8 decreases the AIC_c value by 3.6, and indicates the importance of the interaction. The model suggests that germination success can be explained or predicted by July surface temperatures and the time of snow melt, and that the effect of temperature is dependent on snow melt and vice versa. Calculated probabilities for different snow melt and temperature conditions are displayed in Fig. 5.25, the parameter estimates for the regression equation are listed in Table 5.7. In general, the higher the maximum July surface temperature, the higher the probability for successful germination on this site. An exception is sites with very early to early snow melt. Here, the modeled relationship between surface temperatures and germination probabilities is reversed. However, there are only three sites in these snow melt categories. The model has a predictive ability comparable to the AIC_c selected model 1, with a concordance of 96.5% and $\bar{r}^2 = 0.826$. With the exception of site R1, all Pearson and deviance residuals are smaller than 2 in absolute value. The probability for germination success on site R1 is low, due to early to medium snow melt and low maximum surface temperatures. However, the observed germination results were good. On this site, surface temperatures may not reflect actual soil temperatures because of the physical properties of the surface material (light-colored scree) and the high wind exposure of the site (see chapter 5.5.4). A second, poorly fitted observation is site T1, with low maximum surface temperatures and early snow melt. The germination probability is 0.43, whereas no germination was observed on this site. The results of this site are highly influential on the estimates of the logistic regression coefficients. Nevertheless, the results of the germination experiment on site T1 were plausible and retained in the analysis.

Table 5.7: *Estimated logistic regression coefficients for germination model 8. See Table 5.6 for variable definitions.*

Variable	Estimate	Standard Error (se)
Intercept	39.55	26.46
T_{Jul}	-0.93	0.61
S	-19.30	10.09
T_{Jul} * S	0.45	0.23

The relationship between soil temperatures at 3 cm depth and germination for sites T4, T5, T6, W7, W8, and W10 is shown in Fig. 5.26. The average mean soil temperatures in July were 8-9°C on the Wyoming Creek sites. In August 1993, they were 10°C. Tibbs Butte average mean soil temperatures during the same periods were at least 2°C colder than the Wyoming Creek temperatures. Average maximum soil temperatures for the Wyoming Creek sites were 16-18°C in July and 18-20°C in August, at least 4°C warmer than on Tibbs Butte. Average mean soil temperatures seem to be a predictor for the success or failure of germination, but not the percentage of germinated seeds (Fig. 5.26 bottom). Germination increased with increasing average daily temperature maxima (Fig. 5.26 top). For both variables the relationship with germination is not linear.

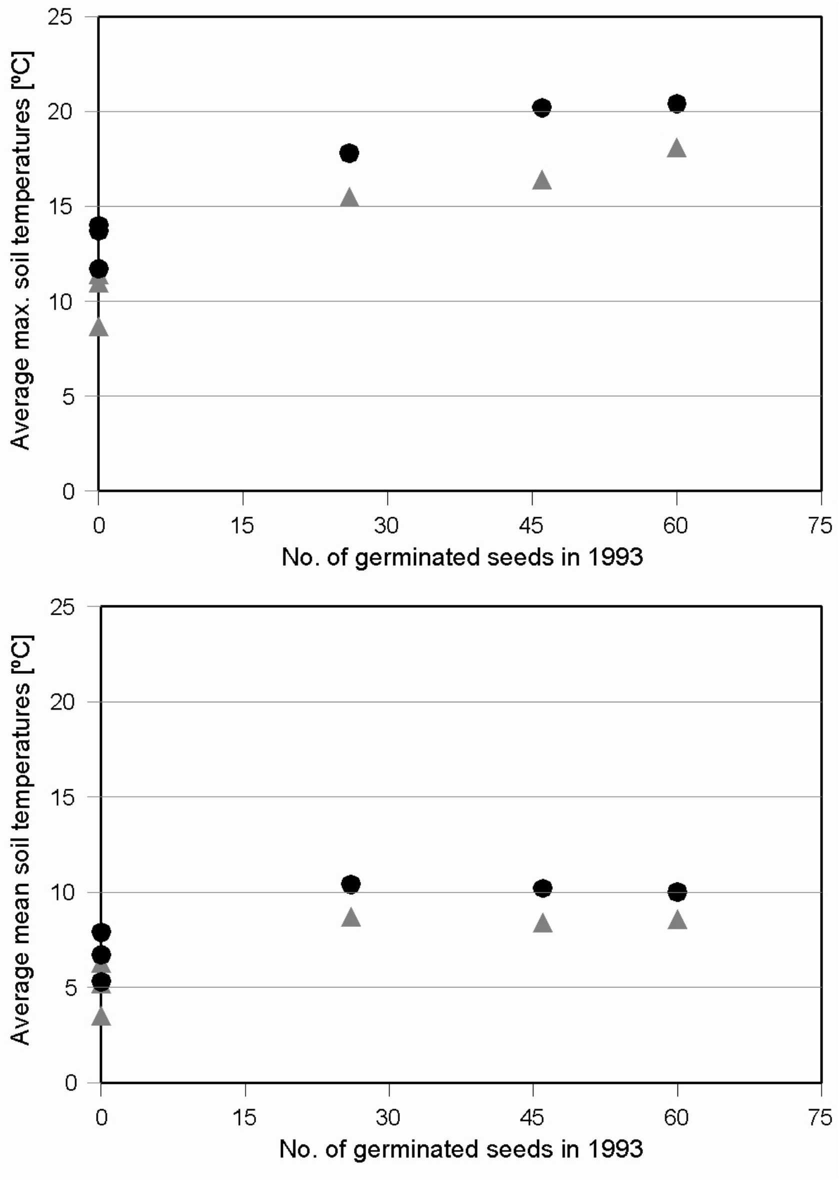


Figure 5.26: *Average soil temperatures at 3 cm depth and seedling germination on six experiment sites. (Soil temperatures include modeled data to fill gaps.) Triangles and circles display temperatures in July 1993 and August 1993, respectively.*

Pearson correlation coefficients were used to investigate the effect of site conditions on the amount of germination on each site (Table 5.8). After eliminating the high and cool sites of Tibbs Butte and Littlerock Creek with no germination, only 19 sites were left in the analysis. While the altitude of a site is a good predictor for germination success and failure, its correlation with the number of germinated seedling clusters is less strong (r = -0.593). For the 19 experiment sites with germination success, altitude is considerably correlated with slope (r = 0.707) and solar radiation (r = 0.516), i.e., experiment sites at higher altitude tend to be steeper and have higher annual radiation values than sites at lower altitude. These interactions may interfere with the "true" relationship between altitude and germination. In fact, the partial correlation coefficient between altitude and germinated seedling clusters, eliminating the influence of slope and solar radiation, is only -0.414. The intercorrelation between altitude and solar radiation also interferes with the strength of the correlation coefficient between solar radiation and cluster germination. Excluding the influence of altitude, solar radiation and cluster germination are weakly correlated (r = 0.465).

Slope steepness may affect the water relations of a site and is therefore one of the three topographic factors that form the topographic moisture index. The topographic moisture index (M) and the time of snow melt (S) are both positively correlated with

Table 5.8: *Pearson correlation coefficients between the number of germinated seedling clusters and selected variables (n=19).*

	Germination (clusters)	Altitude	Solar radiation	Moisture index	Time of snow melt	Max. surface temp. (July)	Max. surface temp. index
Germination (clusters)	1.000						
Altitude	-0.593	1.000					
Solar radiation	0.014	0.516	1.000				
Moisture index	0.553	-0.601	0.072	1.000			
Time of snow melt	0.599	-0.245	0.003	0.239	1.000		
Max. surface temp. (July)	-0.441	0.176	-0.009	-0.240	0.068	1.000	
Max. surface temp. index	-0.119	0.288	0.283	-0.052	0.204	0.696	1.000

cluster germination. The number of germinated clusters did not increase with increasing surface temperatures. The correlation with the maximum surface temperature index is very low, the correlation with maximum surface temperatures in July is weak and negative. This indicates a reverse relationship compared to the analysis of germination success.

In summary, steep sites on mounds or convex landforms (low topographic moisture index) with comparably early snow melt tended to have low numbers of germinated whitebark pine clusters. The relationship can be described with multiple regression analysis, resulting in the following equation: No. of clusters = -10.23 + 2.64*S + 0.52*M ($r^2_{\text{adj}} = 0.479$).

5.2.2.6 Development of whitebark pine clusters

Whitebark pine seedling development was slow during the years of this study. Cotyledons persisted for one to two years after germination. In fall 1994, 80% of all seedlings had some cotyledons, by fall 1995, 96% of surviving seedlings had lost them entirely. Adult fascicles developed slowly. Seventeen percent of one-year-old seedlings had no adult fascicles in fall 1994; 47% of whitebark pine seedlings only

Photo 5.8: *Five-year-old whitebark pine cluster on experiment site W3. The tallest seedling of this cluster is 6.2 cm in height. Oct. 1, 1998.*

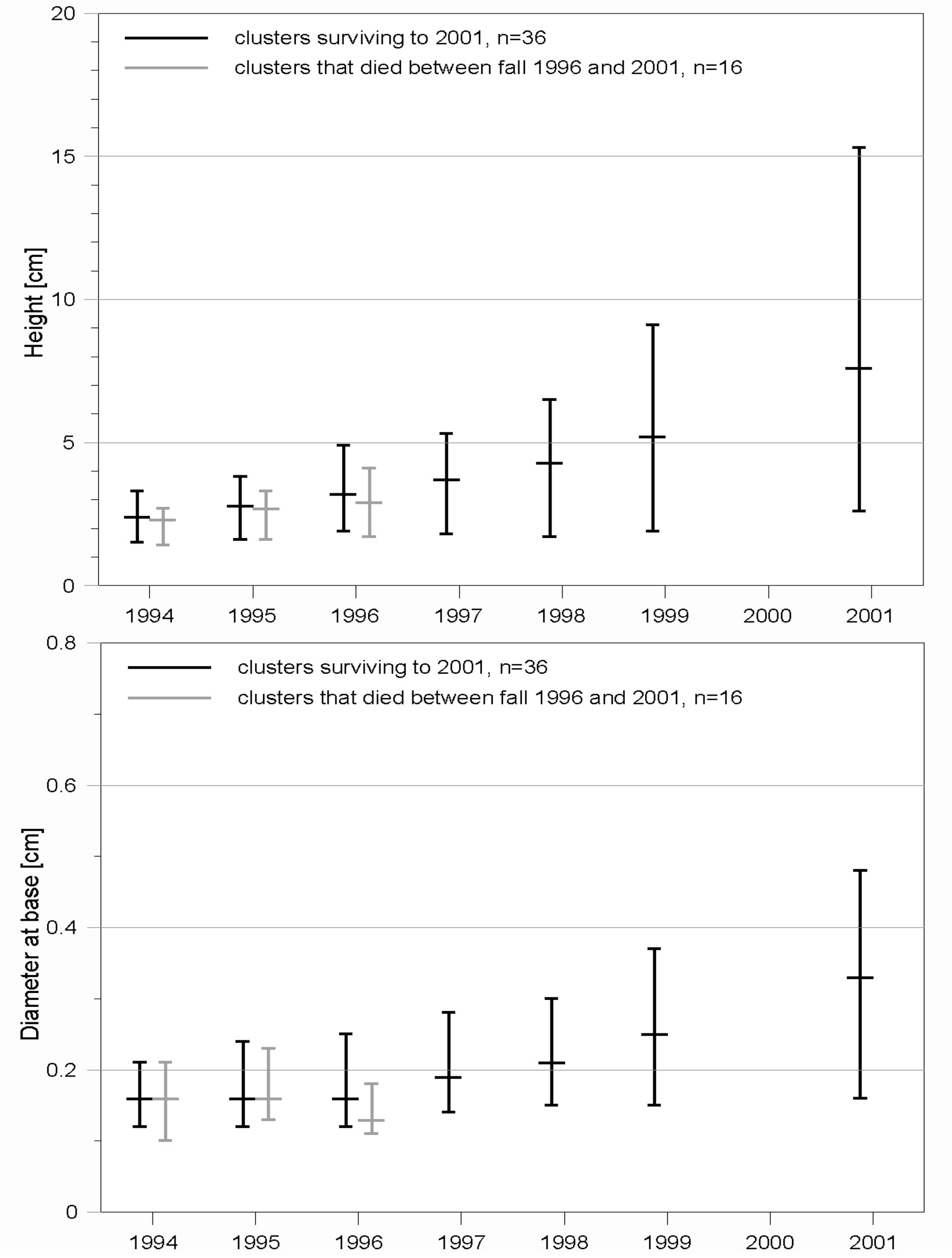


Figure 5.27: *Growth of whitebark pine clusters germinated in 1993 on the experiment sites. The diagram displays maxima, minima, and arithmetic averages of clusters represented by their largest, healthy seedling.*

had one to three fascicles. By fall 1995, 16% of the two-year-old seedlings still had not developed more than three adult fascicles.

The average stem diameter of new whitebark pine clusters was 1.6 mm and did not change during the first three years (Fig. 5.27, bottom). From 1996 to 2001, diameter growth averaged 0.3mm/year. Height growth followed similar patterns. One- to three-year-old seedling clusters (represented by their tallest healthy seedling) grew on average 0.4 cm/year (Fig. 5.27, top). From 1996 to 2001, the average yearly growth of surviving seedling clusters has been steadily increasing to 1.2 cm/year.

However, some seedlings do not appear to develop much at all. The smallest eight-year-old seedling is only 2.6 cm tall, from 1.7 cm as a one-year-old. In contrast, several seedling clusters on sites W1 and W6 were between 10 and 15cm in height in 2001, with annual growth rates of more than 2 cm (Appendix 9.4).

The differences in height and diameter growth of surviving and not surviving whitebark pine clusters were minor. Figure 5.27 displays the growth of clusters that died between fall 1996 and fall 2001 in comparison to the growth of surviving whitebark pine clusters. The tallest seedlings were usually “survivors”, but the average height differed only by 0.3 cm in 1996. The diameter graph (Fig.5.27, bottom) shows that seedlings that did not survive had a smaller diameter in 1996, compared to prior years and to their “survivors”. This may indicate low vigor and a beginning desiccation. However, the diameter difference amounts to 0.3 mm and may also be an artifact of measuring inaccuracies and small sample sizes.

Branching and a loss of apical dominance is common in all experiment sites. On a few seedlings, branching was already apparent in the fall of 1994. By fall of 1996, 17% of all seedlings were recorded to be multi-stemmed. This percentage increased steadily until 2001, with 66% of surviving seedlings developing a bushy growth form.

5.2.2.7 Survival of whitebark pine germinants

Only 13 seedlings emerged during 1992 and 1994, and they were on just one experiment site, W9. Most of those 13 seedlings survived their first summer, but subsequent mortality rates were high. None of the 13 seedlings survived past 1996.

Of the 543 seedlings that germinated in 1993, 374 (69%) survived their first summer (Figure 5.28). The survival rate after the following winter was 45% of 1993 germinants; in fall 1994, 36% of 1993 germinants were still alive. More seedlings died during the first growing season than during the following year. Seedling mortality

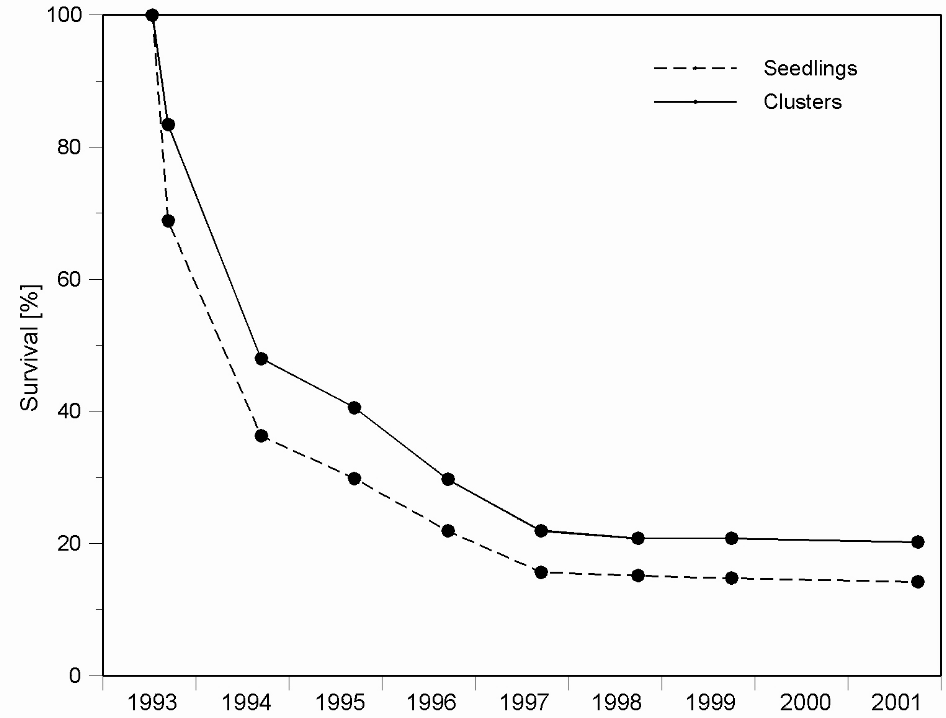


Figure 5.28: *Survival of whitebark pine regeneration germinated in 1993 in 19 experiment sites of the timberline ecotone (n=543 seedlings and 175 clusters).*

decreased significantly after 1994. The annual mortality varied from 6% to 7% from fall 1994 to 1997 and dropped to less than 1% from fall 1997 to 2001 (Figure 5.28). Detailed data are listed in Appendix 9.4.

Seedling mortality was often distributed evenly over all seedling clusters of a site. This resulted in fewer seedlings per seedling cluster and higher survival rates for seedling clusters compared to single seedlings. Ten years after planting and eight years after the major germination event, 14% of all seedlings (79) and 20% of all seedling clusters (36) were still alive (Table 5.9).

Immediately after emerging from the ground, seedlings appeared to be most vulnerable to injury and death

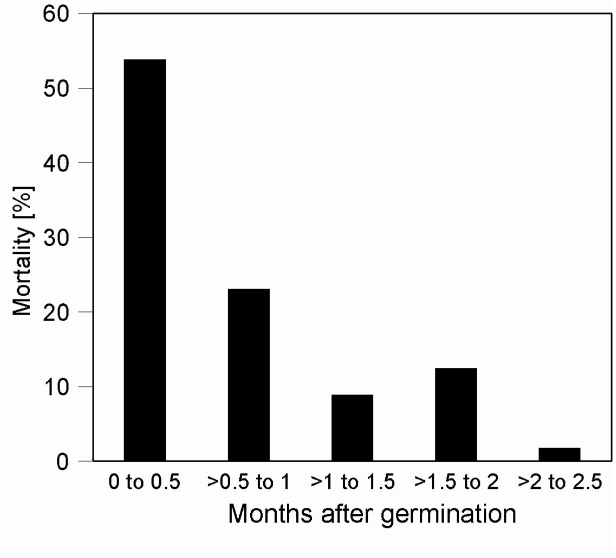


Figure 5.29: *Mortality of 1993 whitebark pine seedlings during the first months after germination.*

Table 5.9: *Survival of whitebark pine seedlings and clusters in % of total germination, in 2001, 10 years after planting.*

	Germination			**Survival**				
Site	seedlings	clusters	seedl./cluster	seedlings	clusters	seedl./cluster	avg. vitality	**Vegetation type**
W6	24	7	3.4	88%	100%	3.0	3.0	*Salix glauca*
W1	63	15	4.2	33%	47%	3.0	2.7	*Salix glauca*
W7	26	8	3.3	38%	50%	2.5	2.3	dry *Geum rossii*
W10	46	13	3.5	22%	46%	1.7	2.5	dry *Geum rossii*
W3	30	8	3.8	20%	38%	2.0	2.4	*Salix glauca*
W2	34	12	2.8	18%	42%	1.2	1.8	dry *Geum rossii*
L8	22	7	3.1	9%	14%	2.0	2.0	*Antennaria umbrinella / Carex phaeocephala*
R1	24	10	2.4	8%	20%	1.0	1.5	*Dryas octopetala*
R2	44	14	3.1	2%	7%	1.0	1.0	*Antennaria umbrinella / Carex phaeocephala*
W8	60	15	4.0	0%	0%	0	0	*Antennaria umbrinella / Carex phaeocephala*
W9	45	14	3.2	0%	0%	0	0	*Antennaria umbrinella / Carex phaeocephala*
W5	42	15	2.8	0%	0%	0	0	*Antennaria umbrinella / Carex phaeocephala*
W4	31	13	2.4	0%	0%	0	0	mesic *Geum rossii*
R3	19	7	2.7	0%	0%	0	0	mesic *Geum rossii*
L7	28	12	2.3	0%	0%	0	0	*Antennaria umbrinella / Carex phaeocephala*
R5	9	4	2.3	0%	0%	0	0	mesic *Geum rossii*
L6	4	2	2.0	0%	0%	0	0	*Carex elynoides*
L3	4	1	4.0	0%	0%	0	0	*Carex elynoides*
R4	1	1	1.0	0%	0%	0	0	*Silene acaulis / Arenaria obtusiloba*
sum/avg.	556	178	3.0	14%	20%	1.9*	2.1*	

*averaged for sites with live clusters, only

(Fig. 5.29). Of all seedlings that died during their first summer, 77% died during the first month after germination and emergence. A major cause for this early mortality may have been insolation damage to the succulent stem (Fig.5.30; see Tranquillini 1979; McCaughey 1990; McCaughey and Tomback 2001 for comparison). Discoloring of the stem was observed at the bend neck of the hypocotyl before the cotyledons emerged, and as a ring immediately above ground surface. The maximum survival temperature with long exposure for plants is generally believed to be about 55°C (Kimmins 1987). A high portion of the mortality during the later part of the summer was attributed to insufficient moisture availabily. Seedlings decreased in vitality and appeared wilted. Heat scorching and insufficient moisture availability may have accounted for 77% of the entire mortality during the first growing season.

Photo 5.9: *New whitebark pine germinants with fatal injuries to the hypocotyl. Two seedlings lost the entire apical bud with all cotyledons. One 'seedling top' is visible below the remaining seedling stem. July 1993.*

Trampling by deer or elk were noted on several sites, but had only minor impact on the total survival rates (Fig.5.30). The apical bud (including all coyledons) of 11 seedlings on site W8 and three seedlings on site W9 may have been browsed by blue grouse (*Dendragapus obscurus*). Several other seedlings on these two sites had severely clipped cotyledons, possibly caused by browsing. Clipped cotyledons may also be the result of insufficient emergence from the seed coat. While the impact of

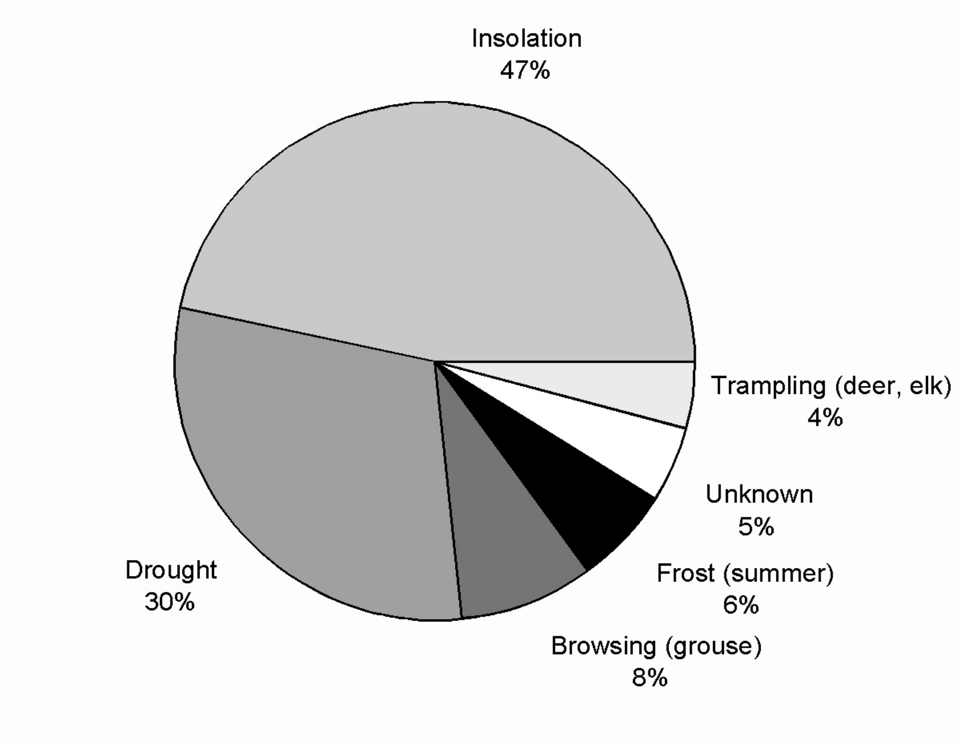


Figure 5.30: *Probable causes for 1993 seedling mortality (169 dead seedlings) during the first growing season.*

browsing was low considering all sites, it was a significant factor on site W8. Up to 28% of all seedlings on this site may have died during the first year due to browsing effects. Browsing other than by grouse was not observed at any time during this study. Burying by pocket gophers, and uprooting due to burrowing activities and soil erosion was occasionally observed in later years of this study.

Early frost was an important mortality cause on site L7. This site is located in a light depression and may be a cold air drainage. In September 1993, a few days after a severe freezing event with air temperatures on Tibbs Butte dropping to -5°C, several seedlings on the Littlerock Creek site L7 were brown colored and "wilted". At least 10 seedlings (36%) may have died due to early frost exposure on this site.

Survival rates varied between study sites (Fig.5.31 and Table 5.9). The best survival rates were recorded on sites W1 and W6, with 21 seedlings and seven clusters surviving to 2001 on both sites (47% and 100% of germinated clusters, respectively). Fig. 5.32 displays the seedling survival rates of the experiments sites in the DECORANA diagram of floristic similarities. Sites W1 and W6 are both dominated by *Salix glauca*, which forms a low and open shrub layer. A third site with similar

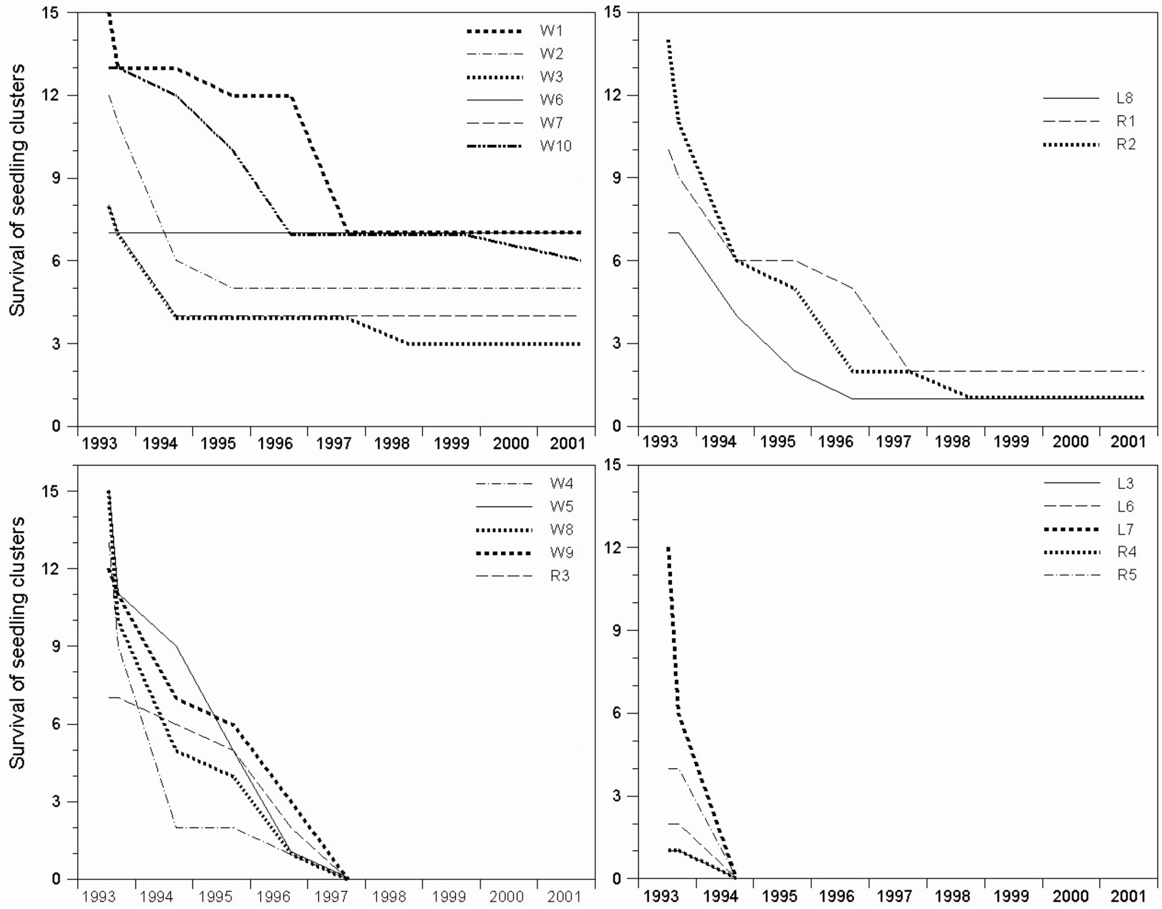


Figure 5.31: *Survival of whitebark pine seedling clusters from 1993 to 2001 in 19 experiment sites.*

willow vegetation is W3. This site had medium seedling densities (30) and medium survival rates with six seedlings in three clusters still alive in 2001 (38% of germinated clusters).

A second group of sites with medium to good seedling survival was classified as dry *Geum rossii* vegetation. In all, 18-38% of seedlings and 42-50% of clusters survived to 2001. The vitality of seedlings was fair to good, with exception of site W2. Here seedlings numbers have continued to decline during the past years, and most clusters consist of only one seedling with poor to fair vitality. Further mortality of seedlings is expected on this site.

Low survival rates were recorded on sites L8, R1, and R2. On these sites, only 1-2 seedlings in 1-2 clusters survived to 2001. The vitality of the few remaining seedlings was poor to fair. Seedlings on site R1 were in particular poor conditions — and have been this way since 1997.

Despite germination rates of more than 50% on W5, W8, and W9, all seedlings had died by 1997. These sites were classified as moderately moist and were associated with woodlands or tree islands. Sites W4 and R3, characterized by a dense herbaceous cover (mesic *Geum rossii* turf), showed a similar mortality with no survival after 1997 (Fig. 5.31 and 5.32).

On the Littlerock Creek sites L3, L6, and L7 as well as on the Rock Creek sites R4 and R5, low germination and high mortality resulted in a short term failure of whitebark pine regeneration. All seedlings on these sites were dead by fall 1994 (Fig. 5.31).

In summary, of the 19 site with germination success only six sites had cluster survival rates > 30%, and another three sites had poor survival rates with 1 - 2 clusters remaining. Short term survival data were insufficient in differentiating between sites with good or poor seedling establishment. Survival rates of 2001 were correlated with rates of 1994 (one year after the major germination event) and with rates of 1997. The short term correlation was low (1994 and 2001 data, $r^2 = 0.483$), whereas the

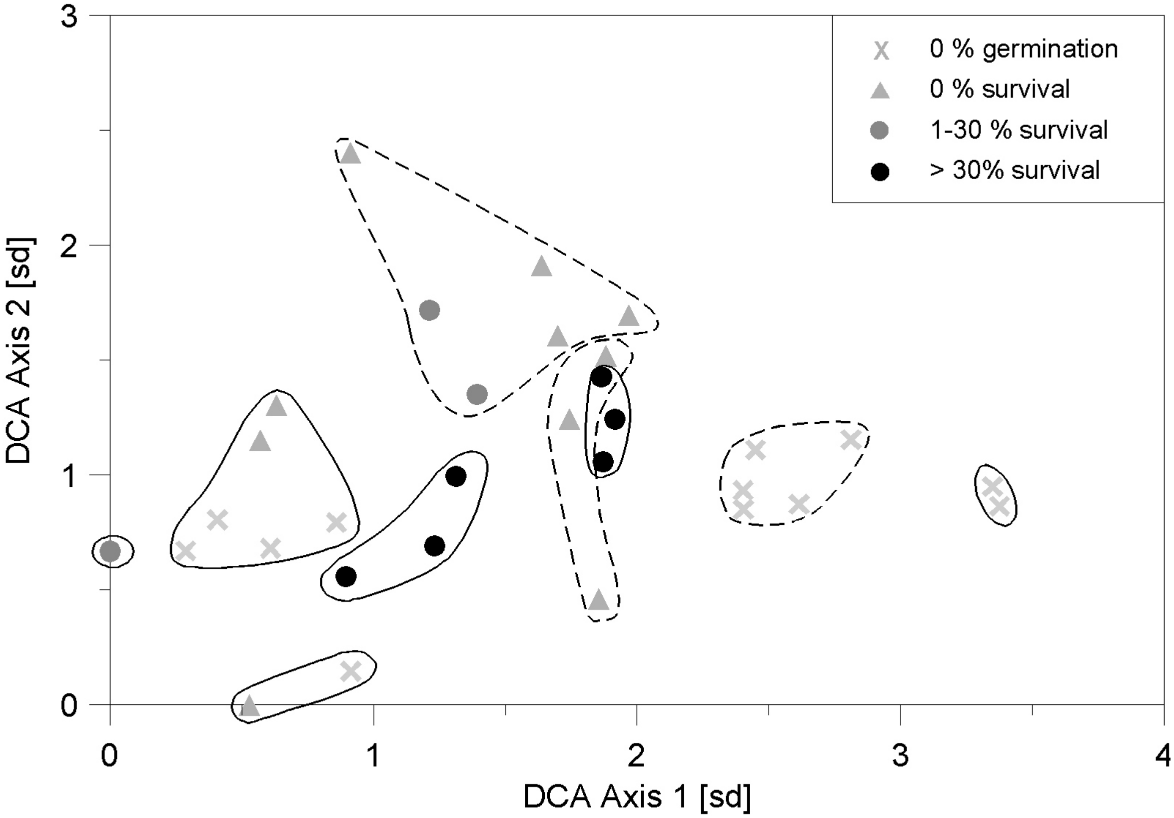


Figure 5.32: *Survival of whitebark pine seedling clusters displayed in the DECORANA ordination diagram of the vegetation composition of 31 experiment sites.*

longer term correlation was high (1997 and 2001 data, $r^2 = 0.985$). This indicates that long term studies of four or more years are needed to study whitebark pine recruitment in the severe environments of the timberline ecotone.

The relationship between selected site conditions and survival was analyzed with multiple linear regression. After removing all sites with no germination, only 19 observations were left for the analysis. Survival was expressed as percent of live seedling clusters in 2001 compared to seedling clusters germinated. Since insolation damage and drought are believed to be the major mortality factors for young seedlings, the analysis included variables that may reflect temperature and moisture conditions of a site. Altitude (A), potential solar radiation (P), and topographic moisture index (M) characterize the topographic position. While a higher topographic moisture index suggests better moisture conditions, it may also indicate a higher probability for cold air pockets and frequent freezing events. Moisture conditions are influenced by the time of snow melt (S) - a categorical variable for this analysis. The time of snow melt also indicates the presence and quality of winter protection and the length of the growing season on a site. High maximum surface temperatures (T_{max}) were surmised to increase seedling mortality, particularly during the first summer. However, simple correlations between variables derived from maximum temperature measurements (TEMPIL pellets) and survival data were very low (The Pearson correlation coefficient between T_{max} and 2001 cache survival was -0.072). Litter cover (L, coniferous needles) and partial to complete shading of planting sites (C, binary variable) also influence temperature conditions, which in turn affect the moisture regime of a site. The Pearson correlation coefficients of these two factors with 2001 survival rates were 0.289 and 0.466, respectively. These variables were used instead of the wax pellet measurements to model the influence of extreme versus moderate temperature conditions on the experiment sites. Considering the multiple causes of seedling mortality, it became evident that more than one environmental factor had to be included into the survival model. No single variable examined in this study explained more than 22% of the total variance observed. Interactions between variables were not considered due to the small sample size.

All analyzed survival models and their AIC_c values are listed in Table 5.10. The model with the lowest AIC_c value (model 9) contains the variables litter, shading, and the topographic moisture index as predictors. Survival of whitebark pine clusters increased with increasing values of the topographic moisture index, decreasing litter

Table 5.10: *Summary of linear regression results for 10 models for the analysis of survival. Variables included in the models are defined as following: A = altitude; P = potential annual solar radiation; M = topographic relative moisture index; S = time of snow melt (early to medium, medium to late, late); L = litter cover (coniferous needles) in % of area; and C = presence of partial to complete shading by trees, shrubs, logs, or rocks. The adj. r^2 is the multiple correlation coefficient adjusted for the degrees of freedom. See Table 5.6 for further explanation.*

No.	Model	K	AIC_c	Δ_i	w_i	adj. r^2
1	A, P	4	128.779	7.181	0.019	0.224
2	A, M	4	130.885	9.287	0.007	0.133
3	A, P, M	5	132.404	10.806	0.003	0.178
4	M, S	5	134.703	13.104	0.001	0.072
5	M, C	4	123.885	2.286	0.222	0.400
6	M, S, C	6	130.285	8.686	0.009	0.374
7	L, C	4	127.495	5.896	0.036	0.274
8	L, C, S	6	135.285	13.687	0.001	0.186
9	L, C, M	5	121.598	0.000	0.695	0.534
10	L, C, S, M	7	130.678	9.080	0.007	0.476

Table 5.11: *Estimated linear regression coefficients for survival model 9. Variables are defined as following: L = litter cover in %; C = presence of partial to complete shading; and M = topographic moisture index.*

Variable	Estimate	Standard Error
Intercept	-47.71	19.92
L	-0.54	0.23
C	33.25	9.20
M	3.46	1.10

covers, and the presence of shade (Table 5.11). The adjusted r^2 is 0.534, and the model fits well, with normal distributed residuals, and studentized residuals < 2.5 in absolute value. The Akaike weight of 0.695 leaves some model selection uncertainty. Considering a 95% confidence set of models, model 5 and model 7 would be competitive. The predictors of model 5 and 7, topographic moisture content, litter and shade, are all included in the selected model. The difference to model 9 is one less predictor and therefore a lower K value, which decreases the AIC_c value by more than 2. Model 5, with the predictors M and C, an Akaike weight of 0.222 and an adjusted r^2 of 0.4 appears superior to model 7. In model 7, the topographic moisture index (M) is excluded, in favor of the variables litter and shade. The environmental factor shade is included in every model of the 95% confidence set.

The topographic position of the experiment site by itself, characterized by altitude, potential solar radiation, and the topographic moisture index, did not explain much of the observed variance in whitebark pine cluster survival. Models 1 through 3 performed poorly in predicting survival rates. The length of snow cover also did not appear to limit the survival of whitebark pine clusters. The best survival was observed on W6 with late snow melt, while other sites with comparable snow melt had no survival (W8, W9).

The analysis of survival data was less successful than the analysis of whitebark pine germination. Many variables affect the survival of whitebark pine, and considering the small sample size, factors like animal behavior cannot be modeled for this study. However, it was possible to select one model that explains more than 50% of the variance observed in the 8-year survival data.

6 Discussion

6.1 Status of the timberline ecotone

Differences found in the composition, structure and regeneration of the timberline stands on Tibbs Butte and Wyoming Creek can be mostly explained by a number of site factors. Of particular importance are site history, altitude, wind exposure, moisture conditions, and seed availability. General soil conditions, however, do not differ considerably between both study areas (see Table 5.3, page 62).

Tibbs Butte study area

Engelmann spruce is the dominant tree species on Tibbs Butte, where it commonly forms decumbent tree islands. Based on diameter distributions (see Fig. 5.4, page 33), and tree island dimensions (see Fig. 5.8, page 38), it is likely that Engelmann spruce established before whitebark pine on the Tibbs Butte transect. In the absence of detailed dendrochronological data, it is not possible to estimate the age of these tree islands. Whitebark pine can live more than 1200 years, as documented by Perkins and Swetnam (1996), but subalpine fir and Engelmann spruce may persist indefinitely, due to their ability to reproduce by stem layering.

Ives (1978) estimated the age of spruce and fir tree islands on Niwot Ridge, Colorado, as 800 - 1,000 years. Benedict (1984) aged three spruce and fir tree islands at timberline of Niwot Ridge, where he found that the minimum age varied between 388 and 528 years, with an unknown number of inner growth rings missing, and the uncertainty whether sampling occurred on the initial stem of the tree island. Most of the current live stems of any one tree island on Tibbs Butte are clonal growth that developed on the wind protected side of the original tree. Fragments of the oldest original stems may have rotted away, burned, or moved down slope. The largest stem diameters of Engelmann spruce tree islands only indicate the minimum ages of the clones, but these stems are nonetheless larger than the stem diameters of whitebark pines.

Regeneration of Engelmann spruce from seed is poor on this study area in spite of the dominance of this species in the overstory. Most juvenile trees (< 1.5 m tall) mapped on the transect were whitebark pines, growing in relatively protected and moist microsites next to and inside of spruce tree islands. The density of juvenile whitebark pines is only half as high as on Wyoming Creek. Regeneration of whitebark pine on Tibbs Butte has therefore occurred in the recent past, but is not occurring on a year to year basis, as indicated by the low number of natural whitebark pine seedlings and the failure of the germination experiment (see Fig. 5.14 and 5.21, pages 47 and 68).

Wyoming Creek study area

The Wyoming Creek transects are dominated by whitebark pine. Spruce and fir are rare in the over- and understory, possibly due to a lack of viable seeds for these species. Seeds produced at timberline are commonly of poor quality (Dahms 1984, in Holtmeier 2000). The closest lower elevation seed source for Engelmann spruce and subalpine fir are the subalpine slopes of Wyoming Creek, directly east and downwind of the study area. The amount of wind distributed seeds decreases exponentially with increasing distance from the seed source, and most spruce and fir seeds will fall to the ground near the parent tree (McCaughey et al. 1986). Thermal slope winds facilitate seed dispersal uphill (Shearer 1980), but dispersal against strong, prevailing western winds greatly reduces the chances of viable seeds reaching suitable germination beds. The Clark's nutcracker, however, has been observed to transport whitebark pine seeds up to a distance of 12.5 km and 800 m in elevation (Tomback 1978). Seed dispersal by nutcrackers may give whitebark pine an advantage over its competitors early in succession (Tomback 1994, 2001). Whitebark pine may play a pioneering role for the colonization of alpine areas removed from viable seed sources, if changes in climatic conditions allow such an advance (Holtmeier 1993, 1995).

In comparison to the Tibbs Butte study area, the timberline stand at Wyoming Creek is more closed, and the border with alpine meadow appears sharp. This might be explained by the topographic position of the Wyoming Creek ecotone immediately leeward of a minor ridge. Wind exposure and unfavorable moisture conditions may impair the ability of trees to advance into alpine meadows further uphill and windward of this ridge. Regeneration densities are low on the upper, windward side of the woodland, and whitebark pine seedlings and juvenile trees that do occur on this transect are generally located adjacent to larger established trees (see Fig. 5.11 and 5.16, pages 41 and 48). However, whitebark pine regeneration is frequent on the inside and the leeward transects, and the meadow below the woodland is being invaded by trees. Whitebark pine seeds germinated on all experiment sites.

Relict status of timberline on Tibbs Butte

The lack of new germinants and comparably low numbers of juvenile trees suggest that the timberline stand on Tibbs Butte may be a relict of past climatic conditions. Ives and Hansen-Bristow (1983) and Benedict (1984) proposed that tree establishment of relict tree islands in the Colorado Front Range may have happened during a post-glacial warm period. Both, above average temperatures and higher summer precipitation, would constitute favorable climatic conditions for seedling establishment in continental mountains like the Colorado Front Range and the Beartooth Plateau (see chapter 6.2).

A further argument for the relict status of timberline stands on Tibbs Butte is the relatively high altitude of the ecotone (3050 - 3170 m). Compared to Wyoming Creek, the timberline ecotone on Tibbs Butte is more than 100 m higher in elevation. This disparity appears too large to be explained by a minor variation in slope exposure (N to NW exposed on Tibbs Butte versus NE exposed on Wyoming Creek). It is possible that the timberline on Wyoming Creek is below its climatic potential, due to fire or grazing history, but there is no evidence supporting either of these factors. While pieces of charcoal were found in soil samples from Wyoming Creek, they were present in almost all soil samples from other study areas as well. Grazing did occur in the past, but is presently not permitted in the Wyoming Creek study area, contrary to the Tibbs Butte and Littlerock Creek study areas. If past grazing caused a marked decline in timberline elevation, it is not apparent in current regeneration patterns. Alpine areas above the current timberline are not being reclaimed by trees, and regeneration densities decline toward the upper edge of the ecotone.

Natural regeneration in the timberline ecotone

Although the position and structure of the timberline ecotones of Tibbs Butte and Wyoming Creek appear to be controlled by different factors, several general conclusions regarding tree regeneration are possible: 1) Whitebark pine regeneration does occur in the timberline ecotone of the Beartooth Plateau, but is infrequent at the upper edge of the ecotone and equally uncommon in relict stands reflecting past climate conditions. 2) Readily available, viable seeds appear to give whitebark pine an advantage over Engelmann spruce and subalpine fir. 3) Regeneration of Engelmann spruce and subalpine fir in the timberline ecotone is poor. During the main years of this study (1991-1994), no new or recent recruitment of spruce or fir by seeds was recorded throughout the study areas.

Comparison to other studies

A number of recent studies have investigated the structure, growth, and regeneration of timberline stands in order to analyze the sensitivity of this vegetational boundary to climatic variability. However, comparisons between studies are complicated by the diverse timberline definitions used by different authors. Daly and Shankman (1985) reported widespread tree regeneration above the ‘tree limit’ on Niwot Ridge, Colorado, which was defined as the boundary above which trees are decumbent and do not usually extend above the average winter snow pack. What Daly and Shankman (1985) considered above tree limit, would be below the upper limit of the timberline ecotone as defined in this study (see chapter 4.1). Similar to the regeneration patterns documented for the Beartooth Plateau, regeneration densities on Niwot Ridge decreased strongly with increasing elevation. Few young seedlings (< 10 yrs) and no new germinants were recorded, suggesting that regeneration did not occur to any extent in at least a decade prior to their study. These results are consistent with the prior assessment of Niwot Ridge by Ives and Hansen-Bristow (1983), who hypothesized that the upper timberline ecotone must have been established during a more favorable climate period.

In the Medicine Bow Mountains, Wyoming, Resor (1996) found no current year germinants or young seedlings ≤ 5 cm tall in the upper parts of the timberline ecotone. Seedling establishment in the Rocky Mountain National Park, Colorado, was uncommon in openings toward the upper limit of matted tree growth and even more infrequent in the alpine zone above (Weisberg and Baker 1995a). Increased height growth of prostrate trees and the presence of tree regeneration in the lower parts of the timberline ecotone suggest a possible change in ecotone structure, from open parkland with decumbent growth forms to denser forest with erect trees (Weisberg and Baker 1995a, 1995b). Lavoie and Payette (1992, 1996) came to similar conclusions for the boreal timberline in Canada, where the forest limit has been unresponsive to climate change over the last 2000-3000 years, but recent changes in growth forms have been observed. The authors proposed that "only major temperature changes of the order of several degrees Celsius can induce back-and-forth movements of the boreal forest" (Lavoie and Payette 1996).

A common characteristic of the above mentioned studies is the assessment that the timberline ecotones are stable and the current positions of their upper boundaries are not rising significantly in altitude. These findings are consistent with the results of this study.

Response of timberline to climatic changes

The advance of timberline to a higher altitude or latitude will not solely depend on temperature, but on the entire climate character (Holtmeier 1994, 1995, 2000). While most models predict an increase of average temperatures as a response to elevated atmospheric CO_2 concentrations, there is considerable uncertainty about regional patterns of precipitation (Romme and Turner 1991; Bartlein et al. 1997). Regional projections of climate change in the Greater Yellowstone Ecosystem suggest an increase of January precipitation and a decrease of July precipitation at higher elevation (Bartlein et al. 1997). According to this model, the Beartooth Plateau climate will become milder and moister in winter, but increasingly dry during the summer months.

High densities of whitebark pine regeneration were associated with moderately late to late snow melt areas on the Tibbs Butte and Wyoming Creek transects (see Fig. 5.9, page 39). Moisture availability also appeared to be a crucial factor for whitebark pine establishment in the germination and survival experiment (see chapter 6.2). Increased snow packs during winter may therefore be beneficial for regeneration, but persisting snow covers late into summer are likely to be detrimental, due to shortened growing seasons, delayed warming of soils, and increased risks of conifers for infections with parasitic fungi. Possible positive effects of winter precipitation may be more than offset by an extensive summer drought. Additionally, it is difficult to predict how climatic changes will influence the intensity of blister rust infections of whitebark pine in this currently little-affected mountain range. For the Greater Yellowstone Ecosystem, moist and warm fall weather conditions which are conducive to blister rust spread are predicted to increase in frequency (Koteen 1999). At high elevation, however, a decrease in summer precipitation as predicted by Bartlein et al. (1997) may limit the occurrence of optimal conditions for blister rust spore germination

(McDonald and Hoff 2001; Kendall and Keane 2001). Considering these conflicting scenarios regarding regional precipitation patterns, as well as their inherent uncertainty, it is not possible to predict the blister rust infection risk for whitebark pines at high altitude.

In summary, how the timberline ecotone in general, and whitebark pine in specific, will react to predicted climatic changes is based more on subjective interpretations than on science. We currently do not know the details of regional climatic changes, nor their time frame. True timberline advances — where tree regeneration invades previously non-forested alpine meadows — are dependent on successful sexual reproduction of trees (Holtmeier 1994, 1995). Sufficient moisture during the growing season may be a decisive factor for tree regeneration in continental mountain ranges, but altered precipitation and snow regimes may have positive as well as negative effects on regeneration and growth. These effects are likely to vary between species and specific conditions of a site.

The variable environmental conditions at timberline are mirrored in a mosaic of plant communities, some of which have been shown to be favorable or unfavorable for tree regeneration (see discussion in chapter 6.2). It is quite unlikely that the timberline ecotone will react uniformly to climatic change and advance upward in a continuous front. It is equally unlikely that timberline will advance rapidly (Slatyer and Noble 1992). Seedling growth rates during the past decade were very slow (see Fig. 5.27, page 78). If these growth rates are any indication of future conditions, it may take several decades before pioneering seedlings will extend above the average height of their surrounding vegetation. Only then will they begin to have an ameliorating effect on microclimate, which in turn creates conditions favorable for further tree establishment. On Tibbs Butte, current climatic conditions do not allow sexual reproduction of spruce and limit reproduction of whitebark pine to a few sheltered microsites inside the ecotone. Any effect of global warming must first compensate for the relict nature of this timberline.

6.2 Germination and survival experiment

Seed storage, stratification, and germination

The germination rates of whitebark pine reached higher percentages in the field than under laboratory conditions and differed between seed sources. Germination rates of whitebark pine are greatly dependent on the maturity of the seed lot, measured by the size of the embryo relative to the embryo cavity (McCaughey 1994b; Burr et al. 2001). Storage of whitebark pine seeds may lower germination rates significantly, especially if seeds are immature. New studies have resulted in improved stratification procedures compared to those reported by Jacobs and Weaver (1990) and Eggleston and Meyer (1990) and used in this study. Seeds that are placed into a 28-day warm and moist stratification to facilitate after-ripening, and into a 60-day cold and moist stratification to break dormancy, had high germination rates after nicking the seed coat (Burr et al. 2001). The use of surface sterilants, as done in this study, may actually reduce germination rates (Burr et al. 2001).

The whitebark pine seeds used in the laboratory experiment were stored for two winters at temperatures around 2°C. Harmful storage conditions, insufficient stratification procedures, and variable seed maturity may all have decreased the germination success in the laboratory compared to favorable sites in the field. The seed lot originating from the Littlerock Creek drainage may have had a higher percentage of immature seeds than the Rock Creek seed lot, and may therefore have been more affected by storage and stratification procedures. Both seed lots were used as a mixture in the field experiment, but whether the seed source influenced field germination rates cannot be assessed with the available data.

Delayed germination

The majority of germination in the experiment sites occurred in 1993, two years after planting. Delayed germination of one to several years has been observed in other whitebark pine studies (McCaughey 1993, 1994a; Tomback et al. 1993, 2001a; Tomback 1994), and is also known for Swiss stone pine, Korean stone pine, and Japanese stone pine (Kuoch and Amiet1970; Krugman and Jenkinson 1974; Kajimoto et al. 1998). Two nonexclusive reasons have been given for delayed germination: 1) the need for after-ripening due to underdeveloped embryos and endosperm, and 2) a strong seed dormancy requiring long or multiple stratification periods (Leadem 1986; Pitel and Wang 1990; Burr et al. 2001). Both explanations are plausible reasons for the observed delayed germination in almost all experiment sites. First year germination occurred only on W9, the site that experiences the longest snow cover but very warm surface temperatures during late summer.

The formation of a soil seed bank is rare in conifers, but may have advantages for seedling recruitment of whitebark pine by delaying germination until conditions are favorable for germination and survival (Tomback et al. 2001a). Furthermore, good whitebark pine seed crops are infrequent (Arno and Hoff 1989; Weaver and Forcella 1986), and seed banks allow seedling recruitment in years with low seed production (Tomback et al. 2001a).

Germination in relation to altitude

The statistical results of the germination and survival analysis are based on small sample sizes and should be regarded as exploratory. Reviewing the germination results, two models stand out in explaining a high amount of observed variation while having low AIC_c values: Model 1, with altitude as the only predictor, and Model 8, with maximum July surface temperatures, time of snow melt, and the interaction between these two variables (see Table 5.6, page 71). While model 1 was the AIC_c selected model, model 8 is biologically more meaningful.

That germination decreases with increasing altitude in the upper timberline ecotone is not “new”, but was expected. The altitudinal gradient may be the most commonly used variable to explain any directional vegetation change (i.e., Whittaker and Niering 1963; Peet 1981; Vankat 1982 and others). Noteworthy is the strength of the correlation (see Table 5.6, page 71), despite the small elevational range of 135 meters between all study sites. Other topographic factors like slope, aspect (combined in the variable solar radiation), and relief (included in the topographic moisture index) did not alter or improve the germination-altitude relationship when all study sites were considered. The selection of study sites may, however, explain some of the findings above. The four study locations vary in altitude: Tibbs Butte sites are the highest, followed by Littlerock Creek, Rock Creek, and Wyoming Creek at the lowest elevation. The altitudinal variation between the sites in each study area is small. The high correlation between altitude and germination may be an artifact of the study design. The four different study areas surely differ in more than just altitude from each other, but these differences were best expressed in the variation of this one variable.

Altitude itself is a complex gradient. It is not the altitude of a site that “causes” tree regeneration to cease. Altitude is an indicator for a number of climatic variables that influence the temperature and moisture regimes of a site, which in turn affect germination and survival of seedlings. These variables are better encompassed in model 8, which may provide a more detailed definition of decisive environmental factors for successful germination of whitebark pine.

Germination in relation to temperature and moisture regimes

In this study, higher maximum July surface temperatures and a late snow melt, as indicators for soil temperature conditions and soil moisture in the early part of the growing season, correspond with a higher germination probability of whitebark pine. Cool or dry sites, that is, sites with July maximum surface temperatures ≤ 43°C, average July soil temperatures at 3 cm depth < 8°C, and average maximum July soil temperatures < 16°C, or sites with the earliest snow melt, tended to have no germination success.

The temperature requirements for the germination of whitebark pine have been studied by Jacobs and Weaver (1990). Germination of stratified seeds occurred from 10° - 40°C, and root growth occurred at a similar temperature range. The temperature threshold for both germination and root growth was lowered by long stratification periods (5 months at 1.5°C). In high elevation field studies near Yellowstone National Park, McCaughey and Tomback (2001) observed whitebark pine germination immediately after snow melt, before the soil could warm up to 10°C. The germination of Japanese stone pine begins at 2°C, after a long stratification under moist and cold conditions (Asakawa 1957, in Kajimoto et al. 1998). High germination rates at such low temperatures, however, would not be advantages for whitebark pine regeneration. The germination of whitebark pine is not dependent on light, and could occur in fall or spring under deep snow cover with no chance of survival. Optimum germination conditions for the closely related Swiss stone pine have been reported as approximately 20°C with more than 50% of moisture saturation (Tranquillini 1979).

Several studies have emphasized the importance of moisture for the regeneration of stone pines. Kajimoto et al. (1998) found that the episodic recruitment of Japanese stone pine seedlings in Northern Japan was related to high early summer precipitation, but not to temperature regimes. The regeneration of whitebark pine corresponded to higher May through August precipitation in post-fire forests of western Montana, an area that can experience severe summer drought (Tomback et al. 1993). Tomback et al. (2001a), in a study about whitebark pine regeneration following the Yellowstone fires, concludes that the moisture availability might modify patterns of germination in the more arid parts of whitebark pine's range.

In his experimental study in a subalpine clearcut north of Yellowstone National Park, McCaughey (1994a) found lower first year germination of whitebark pine in a year with below-average precipitation compared to a year with close to average precipitation. Germination rates tended to increase with increased shade levels of the site and were higher on mineral soil sites compared to litter or burned seedbeds (McCaughey and Weaver 1990; McCaughey 1993).

Temporal variations of moisture and germination rates over several years were not analyzed in this study. However, spatial pattern of germination and site factors indicating moisture availability support the results of the studies cited above. The germination probability of whitebark pine is higher in areas with late snow release, if temperature conditions are sufficient for germination. Holtmeier (2000) points out that the influence of snow melt water on the moisture regime is dependent on the water capacity of the soil. Melt water in sandy and poorly developed soils will quickly move to deeper soil horizons and downhill in subsurface runoff. Nevertheless, in continental climates like the central Rocky Mountains, any additional moisture during the generally dry summer months is beneficial for germination and seedling development, despite shallow soils and coarse substrates.

Most of the above mentioned studies were carried out in subalpine forests well below timberline. At lower altitude, minimum temperature thresholds necessary for seed development are assumed to be reached on a regular basis and would not constitute a limitation to successful regeneration. Soil temperatures appear to be an important, facilitating factor for whitebark pine germination at its upper limit of distribution. An exact definition of required temperature conditions is difficult, since plants do not respond to statistical averages. However, soil temperatures on Tibbs Butte generally stayed below 15°C. The largest differences between the temperature regimes of sites with germination success and sites with failure were found in the total amount of heat received during the growing season. Temperature heat sums (≥ 10°C) on Tibbs Butte ranged from 40 - 70% of the heat sums measured on Wyoming Creek (see Table 5.4, page65). A long exposure to warm soil temperatures would also ensure after-ripening of immature embryos in years prior to germination.

Increased surface temperatures above the required threshold did not necessarily improve germination rates (Fig. 5.26 and Table 5.8, pages 75 and 76). In fact, maximum July surface temperatures showed a weak negative correlation with germination rates. High temperatures by itself have been shown to inhibit germination (Tranquillini 1979, Jacobs and Weaver 1990), but recorded soil temperatures rarely reached 30°C. The observed negative trend is more likely the result of the interaction between soil temperatures and soil moisture regimes. Soils with high amounts of organic matter or small particle sizes that are saturated by snow melt water (sites below late snow banks or in depressions) will warm up slower than gravelly to sandy soils in relatively dry microsites (convex, wind exposed slopes with low snow cover). The three experiment sites with the earliest snow melt had no germination success. For sites with successful germination, high germination rates correlated with late snow melt dates and high topographic moisture indices.

The germination model 8 includes an interaction term between temperatures and snow melt dates. Optimal moisture conditions or optimal temperature ranges alone are not sufficient for the successful regeneration of whitebark pine, and the effect of soil moisture on germination success or failure is dependent on temperature and vice versa. Within the parameters of this study, the germination model fits reasonably well. However, early snow melt conditions were only represented by three study sites with medium to high surface temperature conditions. Extrapolation of the model to sites with early snow melt and low surface temperatures (cold and dry conditions) — which may be found on wind exposed north slopes above timberline — would falsely predict a high germination probability of whitebark pine. Successful germination under cold and dry conditions is not likely.

The depth and duration of the snow cover also modified the winter soil temperatures of the experiment sites. Soil temperatures under high snow accumulation leeward of tree groups were approximately 5 - 10°C warmer than soils on wind exposed sites with little or no snow. Dormant seeds are considered very resistant to frost, particularly if they have a low water content (Sakai and Larcher 1987). Low soil temperatures may not affect seed viability for many alpine and subalpine species. Swiss stone pine seeds are commonly stored at -5 to -10°C, after their water content has been lowered to < 15% (Frehner and Schönenberger 1994). Fresh whitebark pine seeds often have a moisture content of 12 - 15%, and cannot be frozen until they are dried to a moisture content of less than 9% (Burr et al. 2001).

Exposed sites that experience the most severe soil temperatures are usually also dry during late summer and fall, and seeds should be able to dry sufficiently.

Exceptions may be found on slopes with little relief and high wind exposures, where wetlands can occupy relatively smooth areas below large snow fields. The Tibbs Butte experiment site T4 is characterized by moist *Caltha leptosepala* vegetation, periodically high water tables, and little or no snow accumulation during winter. Winter soil temperatures on this site were the coldest measured (absolute min = -17.8°C); summer soil temperatures were the highest of all Tibbs Butte sites. If soil moisture conditions did not allow whitebark pine seeds to dry sufficiently before winter, the germination failure on this site could be related to frost damage of seeds.

Survival in relation to temperature and moisture regimes

Ten years after seeding, and eight years after the major germination event, mortality rates of whitebark pine seedlings are approximating zero. Most surviving caches appear established. The 465 seed caches planted in 1991 resulted in 36 live whitebark pine clusters in 2001 (8% of planted seed caches, and 20% of germinated caches). Survival rates are lower for natural whitebark pine clusters than for experimental clusters, which may be due to a higher portion of underdeveloped seeds in natural versus experimentally planted caches (Fig.5.15 and 5.28, pages 47 and 80).

Environmental conditions favorable for whitebark pine germination were not necessarily favorable for seedling survival and establishment. Seedling germination rates for sites with *Antennaria umbrinella/Carex phaeocephala* vegetation varied from 29-80%, and were on average 54% (86% of planted caches). There was no survival in four of six sites, and only one cluster survived in the remaining two sites (Fig. 5.23 and 5.32, pages 70 and 85; Table 5.9, page 81). Sites in this vegetation group are associated with tree islands or woodland, and they are characterized by long snow covers and thick litter accumulations. Nevertheless, the long duration of snow does not explain the lack of survival. On W6, a site with *Salix glauca* vegetation surrounded by whitebark pine woodland and the best survival rates of all sites (87% of seedlings and 100% of clusters), the snow cover was comparable to sites with poor survival (W8, W9, and R2). High survival rates were, however, associated with high topographic moisture indices, presence of shade, and low cover percentages of conifer litter, all variables that indicate relatively moist site conditions and moderate surface temperatures.

Tomback et al. (2001a) reported higher survival rates (40 - 89%) of 1 - 5 year old whitebark pine clusters in recent subalpine burns, actual survival depending on moisture conditions and fire severity. Several studies have suggested that seedling survival of high elevation conifers is related to exposure to the sun and ground cover (Ronco 1970; Noble and Alexander 1977; Knapp and Smith 1982; Cui and Smith 1991; Resor 1996). Generally, those sites most exposed to the sun and with greater litter cover had reduced seedling survival. Thus, the ability of the seedling to grow a root that reaches moist mineral soil aids survival.

Under optimal laboratory conditions (25 - 35°C), whitebark pine root extension of new germinants varied between 5 - 15 mm per day (Jacobs and Weaver 1990). Even though root growth in nature occurs at suboptimal temperature conditions, McCaughey (1988) found that natural whitebark pine germinants have 5 - 18 cm tap roots with several lateral and fine root hairs. Dead whitebark pine germinants in this study had developed taproots longer than 10 cm and had penetrated mineral soil layers. While the observed mortality of whitebark pine on coniferous litter may still be caused by water stress, it is not likely that it is due to rooting in dry litter layers.

McCaughey and Weaver (1990) found higher surface temperatures on litter seedbeds than on mineral soil, and attributed this to increased light reflectance off light-colored needles and reduction of downward heat transmittance due to the insulating properties of litter. Shading significantly decreased mortality presumably caused by insolation.

In this study, high litter coverage correlated weakly with high maximum surface temperatures during July and August, but there was no correlation between maximum surface temperatures and survival. This may be due to insufficient measurements of surface temperatures. Temperature conditions are likely to be highly variable between microsites, and measurements were derived from only one to two locations per experiment site. In addition, the variable used in this study does not include any information about the frequency and duration of high temperatures. A higher frequency or duration of the same maximum temperature would increase the evapotranspiration and potentially increase the water stress seedlings experience. High covers of litter may therefore be associated with relatively high temperatures as well as with insufficient moisture availability.

According to McCaughey and Weaver (1990), shade appears to be an important factor for the survival of whitebark pine clusters. This is consistent with the results of this study, where the variable shade is included in all three models considered competitive in the survival analysis. Both factors, the presence of shade and the absence of litter, moderate maximum temperatures and drought conditions.

The third variable included in the survival model is the topographic moisture index. Sites with little slope, a concave hillside, or a depression are generally moister than wind exposed sites with a convex topography; a higher number of seedling clusters survived in these relatively moist sites.

As mentioned above, the temperature regime of a site inadvertently influences soil moisture and moisture requirements of plants. It therefore appears difficult to separate temperature and moisture variables and determine their individual importance. Mortality during the first growing season may often be directly related to high surface temperatures. Older seedlings with woody hypocotyl may be less susceptible to heat scorching; thus water availability, also indicated by the same set of variables, may become the most important factor for survival.

Survival in relation to animal activity and frost

The selected survival model focuses on two major hypothesized mortality causes: insolation or heat damage, and drought. It disregards mortalities caused by animal activity and by frost during the growing season.

During the first growing season, 12% of whitebark pine seedling mortality was attributed to browsing and trampling. Small mammals, particularly deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*), are known to forage on whitebark pine seeds (McCaughey 1994a; McCaughey and Tomback 2001), but there was no indication of seed predation in this study.

The highest amount of animal caused damage was attributed to blue grouse, who are known to feed on whitebark pine buds and needles (Arno 1970). Blue grouse often roost at timberline and are most likely seen near or in tree patches, which provide thermal and hiding cover (see Kendall and Arno 1990). Both sites that experienced seedling damage caused by browsing are indeed located in, or directly adjacent to, mature groups of trees.

Seedling survival was impacted only to a small extend by the burrowing activities of pocket gophers (*Thomomys talpoides)* and voles (*Microtus* or *Phenacomys* spp., Pattie and Verbeek 1967). In ribbon forests of the Colorado Front Range, Holtmeier (1987) reported 14-16% of meadows covered by pocket gopher eskers and mounds. Pocket gopher densities were higher in mesic meadows between tree ribbons than inside tree ribbons or adjacent shrub communities. These species-rich meadows are also attractive grazing areas for mule deer and elk (Holtmeier 1999a).

Within the parameters of this study, however, it was not feasible to model animal behavior in relation to seedling survival rates. Considering the low frequency of animal related damages, it appeared to be more a matter of chance than a predictable risk whether the infrequent elk stepped on or next to a tree seedling, and a pocket gopher mound landed on or beside a whitebark pine planting location.

Seedling mortality presumably caused by frost was only observed on one experiment site on Littlerock Creek, and amounted to 6% of the observed first year mortality. Nevertheless, frost damage should be considered a common risk factor in the timberline ecotone.

Data regarding the frost resistance of whitebark pine are not available. The frost resistance of current season needles of Swiss stone pine during the growing season is given as -2°C (Tranquillini 1979). One-year-old needles of Japanese stone pine can survive a two-hour exposure down to -7°C (Sakai and Otsuka 1970). When air temperatures at the Tibbs Butte weather station dropped to -5°C at the end of August 1993, temperatures at the ground were likely lower than measured at 1.5 m height, and may have significantly varied between study areas. Since no climate data were collected in the Littlerock Creek study area, the exact temperatures conditions which may have caused the observed frost damage are not known. It is likely, however, that prolonged exposure to temperatures below -5°C are lethal to immature needles and seedlings.

Thermal radiant loss and freezing risk at the soil surface is reduced by a forest canopy, shrub layer, or dense herbaceous cover, while insulating layers of peat and litter increase the probability of frost events by preventing heat transfer from the ground (Larcher 1984; Sakai and Larcher 1987). The presence of shade has a moderating effect on day and nighttime temperatures as well as a positive influence on soil moisture relations, whereas thick layers of coniferous litter covers may magnify the effects of minimum and maximum temperatures. The risk of frost damage is increased in cold air drainages, e.g., concave hillsides and depressions, possibly mitigating the positive effect of higher soil moisture in these topographic positions.

In this study, however, the topographic relative moisture index correlated positively with cluster survival rates, indicating either that cold air drainage is less important than soil moisture, or that freezing risks cannot be modeled with this variable (Table 5.10 and 5.11, page 87).

Plant communities as indicators for the regeneration success of whitebark pine

While whitebark pine germination in the experiment sites is mostly explained by a small number of environmental variables (altitude or July maximum surface temperatures and snow cover), attempts to model cluster survival were less successful. Too many variables determine the fate of seedlings, and observations were too few to develop complicated models. Nevertheless, in this study, regeneration success of whitebark pine was restricted to two plant communities: *Salix glauca* vegetation and dry *Geum rossii* turf (Fig. 5.23 and 5.32, pages 70 and 85; Table 5.9, page 81). Furthermore, all sites in these two vegetation types had good germination and survival, evidence that plant composition is a suitable indicator for site conditions favorable for whitebark pine regeneration (Table 6.1).

Salix glauca forms one of few alpine shrub communities (extending above the herbaceous layer) on the Beartooth Plateau, outside of wetlands and riparian zones. It is possible, that the community structure by itself is advantageous to tree regeneration: scattered open shrubs provide shade on soil surfaces free of thick layers of coniferous litter. However, moisture conditions also appear favorable. *Salix glauca* is typically found in the transition between wetland and "upland" habitat, often growing on the edge of wetlands and riparian areas characterized by *Salix planifolia*, or in snowdrift areas as documented in the Wyoming Creek study area (Lesica 1993; Walford et al. 2001; Photo 5.1, page 51). *Salix glauca* also occurs in moist environments on Tibbs Butte, but plants are scattered and have a prostrate growth form. The described *Salix glauca* vegetation type is a conspicuous plant community that supports natural regeneration (juvenile trees) of Engelmann spruce, some subalpine fir, and whitebark pine, surrounded by herbaceous meadows without obvious tree recruitment.

The beneficial conditions of dry *Geum rossii* turf for whitebark pine regeneration are less apparent. Snow release was earlier than on *Salix glauca* sites, but not as early as on wind exposed cushion plant communities. Dry *Geum rossii* sites are intermediately warm, intermediately moist, protected during winter by snow, are not shaded by conifers, and therefore do not have coniferous litter layers. While conditions may not appear optimal for tree regeneration, they are better than in most other vegetation types.

If sufficient soil moisture is a decisive factor for whitebark pine regeneration, the seeding experiment on mesic *Geum rossii* sites should have resulted in live whitebark

Table 6.1: *Regeneration success of whitebark pine in different vegetation types of the timberline ecotone. Germination, survival, and growth data are arithmetic averages for each vegetation type and refer to % germination of planted caches, % survival of germinated caches to 2001, and annual apical shoot extensions of seedling clusters between 1998 and 2001 (5-8 year old clusters).*

Vegetation type (no. of sites)		Site characteristics	Gemination	Survival	Growth
Silene acaulis/ Arenaria obtusiloba	(2)	wind exposed, dry, low snow cover	poor 3%	none 0%	—
Dryas octopetala	(1)	wind eroded soil, low to moderate snow cover	good 67%	poor 20%*	very poor 2mm/yr
Carex elynoides	(6)	dry, low to moderate snow cover	poor 3%	none 0%	—
Dry *Geum rossii*	(3)	dry to mesic, moderate snow cover	good 73%	good 46%	fair 7mm/yr
Antennaria umbrinella/ Carex phaeocephala	(6)	in or near woodland, leeward tree island, high and long snow cover	very good 86%	poor 4%	poor 4mm/yr
Mesic *Geum rossii*	(3)	mesic, moderate snow cover, dense herb and grass layer	fair 53%	none 0%	—
Salix glauca	(3)	mesic, in slight depressions, moderate to high snow cover	good 67%	very good 62%	good 17mm/yr

*represents only 1 cache with 1 seedling

pine clusters. The lack of survival on these sites is not easily explained by the available data. A possible cause may be competition with herbs and grasses for moisture and nutrients, as has been suggested for the regeneration of other tree species (Auer 1948, in Holtmeier 2000; Dunwiddie 1977; Schönenberger 1975; Moir et al. 1999). Two of the three mesic *Geum rossii* sites have herb layers of 90% cover, with *Deschampsia cespitosa* abundant in all sites (Appendix 9.1, Table 9.3).

A number of studies describe spatial relationships between tree regeneration and plant communities in the subalpine parkland and the lower part of the timberline ecotone. Brink (1959) noticed that the establishment of small trees was limited to moderately moist *Phyllodoce-Cassiope* heath, in the timberline ecotone of Garibaldi Park, British Columbia. Intense tree invasion of cool and wet *Phyllodoce-Vaccinium* communities of forest openings near timberline of Mt. Rainier was reported by Franklin et al. (1971) and Henderson (1973, in Franklin and Dyrness 1988). A positive relationship between new tree establishment and communities dominated by ericaceous species was also documented in the Olympic Mountains, Washington (Fonda and Bliss 1969; Agee and Smith 1984; Woodward et al. 1995). Some researchers limit this tree invasion in the generally moist Pacific Northwest to a regional drying trend in the early- to mid-1900's (Franklin et al. 1971; Lowery 1972; Agee and Smith 1984), while others indicate an ongoing phenomenon depending on temporal and spacial pattern of mesic (moderately moist) conditions (Fonda and Bliss 1969; Henderson 1973; Woodward et al. 1995).

In the comparably dry and continental timberline ecotone of the Rocky Mountain National Park, Colorado, high densities of tree regeneration were found in wet areas dominated by *Salix* spp. (Weisberg and Baker 1995a). Hessl and Baker (1997) suggested that both, high temperatures and high snow depth, must occur simultaneously for several years to allow successful tree establishment in the lower part of the ecotone. This is consistent with findings from Jakubos and Romme (1993) in subalpine meadows of Yellowstone National Park. In continental mountain ranges, tree establishment therefore benefitted from above average warmth and moisture, a result supported by the germination and survival analysis of this study.

The common denominator of the above mentioned studies appears to be moderate moisture conditions within certain plant communities, which facilitate recruitment of timberline forming tree species (compare with Woodward et al. 1995). In maritime climates, tree invasion was observed under relatively dry climatic conditions or in comparably dry microsites, whereas in continental climates tree recruitment occurred under moist climatic conditions or in comparably moist microsites. However, it seems more than coincidental that all these mesic communities indicating suitable conditions for regeneration are dominated by shrubs. In addition to mesic moisture conditions, seedlings also receive necessary protection from climatic extremes (both, low and high temperatures, radiation, wind).

The results of this study substantiate the importance of moderate temperature and moisture regimes for whitebark pine germination and survival in the timberline ecotone. Whitebark pine is successfully regenerating in specific timberline sites of the Wyoming Creek study area, particularly in open, mesic willow communities near already established trees. Recruitment in exposed sites or areas at higher elevation was unsuccessful, providing no evidence that whitebark pine is invading alpine meadows above the current timberline ecotone.

6.3 Spacial distribution of whitebark pine

The regeneration studies on the transects show that moderate snow cover and intermediate snow releases concur with high densities of whitebark pine regeneration in the < 30 cm and 30- ≤ 150 cm height classes. Germination and survival of whitebark pine seedlings in the experimental sites followed similar trends, with best recruitment in mesic areas with at least moderate snow cover during winter. Suitable site conditions for successful whitebark pine regeneration are indicated by *Salix glauca* and dry *Geum rossii* communities. However, regeneration results of this study are not consistent with reported caching preferences of the Clark's nutcracker (Table 6.2).

According to Tomback (1978, 2001) and Holtmeier (1993), nutcracker caches are frequently established in areas with low snow cover and early snow release. Holtmeier (1993) described higher densities of young limber pines (mostly dispersed by nutcrackers) on wind exposed, convex landforms than on concave surfaces in the timberline ecotone of the Colorado Front Range (also see Wardle 1968). He suggested that these patterns resulted from selective caching preferences of the Clark's nutcracker. However, this is contrary to observed patterns of recent whitebark pine recruitment on the Beartooth Plateau.

Whether the nutcracker preferably caches seeds on convex slopes, or whether caches are established in almost any exposure, topography, and microsite (Hutchins and Lanner 1982), the spatial distribution of whitebark pine regeneration on the Beartooth Plateau does not appear to be primarily caused by cache distribution pattern. There is no obvious explanation why the nutcracker should prefer areas leeward of tree groups or depressions, where snow tends to linger until midsummer. To the contrary, these sites seem unfavorable for caching, because heavy snow cover restricts access to seeds. There are, however, a number of environmental factors that explain patterns of tree regeneration (see chapter 6.2), and favorable site conditions are well reflected in the vegetational composition of the understory (Table 6.1).

These results indicate that a sufficient number of whitebark pine seeds are available wherever microsite conditions allow the successful regeneration of whitebark pine, even if these microsites do not coincide with spacial caching preferences of the Clark's nutcracker. Only nutcracker caches that were not retrieved

Table 6.2: *Site characteristics for seed caching by the Clark's nutcracker, germination, and survival of whitebark pine (literature and study results).*

	Site characteristics
Preferred caching sites of Clark's nutcracker	Communal seed storage areas are frequently on steep, often windswept, often south facing slopes that accumulate little snow and experience rapid snow melt. (Tomback 1978, 2001) In a wide variety of microsites (at base of trees, under tree canopies, in open terrain, next to roots or fallen trees, at edge of meadows, among plants, etc.). (Tomback 1982, 2001) "... on all exposures, near a spring, on a streambank, and even in a puddle of water." (Hutchins and Lanner 1982) Common characteristics are the relative low snow cover and short duration of snow. (Holtmeier 1993)
High densities of whitebark pine germinants	Areas with high to moderate snow cover, inside and leeward of woodland and tree islands, often at base of tree, mostly in Wyoming Creek study area. (study results, transects) Areas with high to moderate snow cover and warm microclimate, in slight depressions with mesic *Salix glauca* vegetation, inside and leeward of woodland, leeward of tree islands, particularly at lower altitudes of the ecotone. (study results, experiment sites)
High densities of successful whitebark pine recruitment	Areas with moderate snow cover, inside and leeward of woodland, leeward to tree islands, near tree (but less common directly at base). (study results, transects) Mesic areas, usually with moderate snow cover, somewhat wind protected, no coniferous litter, some shade, in *Salix glauca* or dry *Geum rossii* vegetation. (study results, experiment sites)

and were established in relatively moist and protected microsites, contribute to the recruitment of whitebark pine in the timberline ecotone. These microsites are more commonly found on concave hillsides, in slight depressions, and adjacent to tree groups than on exposed ridges. In general, concave landforms have ecological disadvantages for tree establishment, i.e., lack of drainage, higher likelihood of avalanches and persisting snow cover late into summer, higher risk of infections with parasitic fungi, and higher probability of nocturnal temperature inversions (Wardle 1968; Senn et al. 1994). On the other hand, ecological conditions on convex landforms are not entirely favorable, either. These sites have little to no protection during winter, experience extreme maximum and minimum soil temperatures throughout the year, and may be excessively dry during the latter part of the growing season.

Tree growth on the Beartooth Plateau is generally absent, or at least very stunted, on extreme topographic positions such as pronounced drainages with wetlands and highly exposed ridges. However, many timberline areas on the Beartooth Plateau have little relief, and the danger of creeping snow or avalanches is considerably lower than in rugged mountain ranges. Differences between convex and concave sites are often subtle. The tree regeneration of timberline ecotones with continental climate character may require the additional moisture found in snowdrifts of small depressions or tree groups. This is supported by studies from the Rocky Mountain National Park, where high densities of regeneration coincided with mesic sites parameters or periods of higher precipitation (Weisberg and Baker 1995a; Hessl and Baker 1997).

The presented relationship between concave landforms and tree recruitment are the result of current environmental conditions. Trends may be reversed in years of high snow accumulation. It is feasible that in years with high and prolonged snow cover slightly convex landforms are more favorable to seedling establishment. However, the distribution pattern of juvenile trees showed similar trends as the distribution pattern of younger whitebark pine seedlings, indicating that critical parameters have not changed significantly during the past 30 - 40 years.

Cox concluded for the timberline ecotone on James Peak, Colorado, that “the presence or absence of the tree species appears frequently to be a matter of enough but not too much snow” (Cox 1933, p.322). This assessment seems well suited for regeneration pattern of whitebark pine on the Beartooth Plateau. In wind exposed gentle terrain (e.g., Tibbs Butte study area), however, trees themselves act as major snow fences, and the question remains how the first trees ever populated these slopes (see Holtmeier 1996, 2000). A common denominator of ‘pioneering’ tree groups may be the coarse substrate they tend to grow on (Arno and Hoff 1989; Körner 1998). The protection found between rocks and in small depressions may have been sufficient to allow establishment of isolated tree individuals, which in turn altered the environment around them (Holtmeier 1996). A second, but not exclusive explanation could be the initial establishment of trees under more favorable (in continental areas warmer and moister) climatic conditions, as proposed for the Tibbs Butte study area. Once established, these ‘remnant’ trees persist despite moderate climatic variation (Holtmeier 1995; Slatyer and Noble 1992), and may even allow further tree recruitment in sheltered microsites within already established tree clumps.

Considering the lack of tree regeneration above the ecotone, the slow growth rate of tree seedlings at this altitude, and the ability of spruce and fir to regenerate vegetatively, the current position of timberline on the Beartooth Plateau appears stable, no matter whether vegetation patterns are a relict of past climate periods or a reflection of the current reproductive potential.

7 Summary

Whitebark pine (*Pinus albicaulis*) is a high elevation stone pine characterized by heavy, wingless seeds that are primarily dispersed by the Clark's nutcracker (*Nucifraga columbiana*). The relationship between seed dispersal, site characteristics, and tree distribution of whitebark pine was studied in the timberline ecotone of the Beartooth Plateau, Montana and Wyoming. The study focused on regeneration patterns and prevailing microsite conditions which may limit or promote germination and survival of whitebark pine at its upper elevational limit.

The composition and structure of ecotonal forest and woodland stands were different in the two areas studied. Engelmann spruce (*Picea engelmannii*) was the dominant tree species on Tibbs Butte, where it formed decumbent tree islands. Whitebark pines were usually growing inside or leeward of tree islands and were younger than Engelmann spruce. In the Wyoming Creek study area, whitebark pine was the dominant tree species, forming an open woodland leeward of a minor ridge.

Regeneration of Engelmann spruce and subalpine fir (*Abies lasiocarpa*) was poor in both study areas. No young fir or spruce seedlings (≤ 3 years) were located during the study. Juvenile whitebark pines were more abundant in areas with moderate to late snow release. Only few young whitebark pine seedlings and germinants were located on Tibbs Butte, whereas in the Wyoming Creek study area, young whitebark pine seedlings clusters (≤ 3 years) were present in all transects. Regeneration densities inside and leeward of the woodland were higher than on the windward side.

Germination of whitebark pine seeds generally occurred two years after planting. Between 1992 and 1994, 24% of all planted seeds germinated in 38% of all seed caches. Germination rates in experiment sites varied between 0 and 84% of planted seeds, with no germination on Tibbs Butte or on sites with the earliest snow melt. Higher maximum July surface temperatures and late snow melt corresponded with a higher germination probability of whitebark pine.

Environmental conditions favorable for whitebark pine germination were not necessarily favorable for seedling establishment. Seedlings were most vulnerable to injury or death immediately after germination. Insolation damage and drought were judged to be major causes of mortality during the first growing season. Eight years after the major germination event, 14% of all seedlings and 20% of germinated

seedling clusters (8% of planted seed caches) were still alive. High survival rates were correlated with high topographic moisture indices, presence of shade, and low covers of coniferous litter. Plant composition was a suitable indicator for site conditions favorable for whitebark pine regeneration. All experiment sites with *Salix glauca* vegetation and dry *Geum rossii* turf had good germination and survival success.

Regeneration results were not consistent with reported caching preferences of the Clark's nutcracker. Sites with moderate to long snow cover, leeward of tree groups or in depressions, appear unfavorable for caching, because of restricted access to stored seeds, but were favorable for germination and survival of whitebark pine. Only nutcracker caches that are not retrieved and that are established in relatively moist and protected microsites contribute to recruitment.

Descriptive and experimental data show that regeneration of whitebark pine does occur in parts of the timberline ecotone. Recruitment in exposed sites or areas at higher elevation was unsuccessful. The lack of sexual reproduction of tree species on Tibbs Butte suggest that the timberline stand in this area may be a relict reflecting past climatic conditions. The results of this study do not provide any evidence that whitebark pine is invading alpine meadows above the current timberline ecotone.

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9 Appendix

9.1 Vegetation tables of experiment sites

Table 9.1: Cushion plant comm.: *Dryas octopetala and Silene acaulis/Arenaria obtusiloba* veg.

Site number	**R1**	**R4**	**T1**
Tree layer (%)	0	0	0
Shrub layer (%)	0	0	0
Herb layer (%)	60	75	50
Mosses and lichen (%)	1	10	10
Number of species (vascular plants)	36	29	26
Arenaria obtusiloba	1	2	2
Selaginella densa	1	2	1
Silene acaulis	+	2	2
Eritrichium nanum var. *elongatum*	1	1	1
Trifolium nanum	1	2	.
Oxytropis lagopus var. *atropurpurea*	1	1	.
Poa pattersonii	+	1	1
Erigeron rydbergii	+	1	1
Phlox pulvinata	+	1	+
Arenaria rubella	+	+	+
Castilleja pulchella	r	+	+
Lupinus argenteus var. *depressus*	2	.	1
Douglasia montana	+	1	.
Carex elynoides	+	r	.
Senecio canus	+	.	+
Smelowskia calycina var. *americana*	r	.	+
Dryas octopetala var. *hookeriana*	3	.	.
Carex rupestris	1	.	.
Calamagrostis purpurascens	.	2	.
Mertensia alpina	.	+	1
Carex albonigra	.	+	+
Geum rossii var. *turbinatum*	+	2	2
Festuca brachyphylla	+	1	1
Potentilla diversifolia	r	1	1
Luzula spicata	.	1	1
Carex scirpoidea var. *pseudoscirpoidea*	.	1	1
Polygonum bistortoides	+	1	+
Trisetum spicatum	+	+	2
Sedum lanceolatum	+	.	.
Poa secunda var. incurva	1	.	+
Bupleurum americanum	r	+	.
Draba cana	+	.	.
Draba crassifolia	+	.	.
Saxifraga bronchialis var. *austromontana*	+	.	.
Lesquerella alpina	+	.	.
Campanula uniflora	+	.	.
Poa alpina	+	.	.
Trifolium parryi var. *montanense*	r	.	.
Festuca baffinenesis	r	.	.
Pinus albicaulis	r	.	.
Elymus scribneri	.	+	.
Artemisia scopulorum	.	+	.
Helictotrichon hookeri	.	+	.
Agoseris glauca	.	+	.
Senecio fuscatus	.	+	+
Carex capitata	.	.	+
Gentiana algida	.	.	+
Cerastium beeringianum var. *capillare*	.	.	+

Table 9.2: Well drained turf communities: *Carex elynoides* and dry *Geum rossii* vegetation

Site number	**L2**	**L4**	**L3**	**L6**	**L5**	**L1**	**W7**	**W2**	**W10**
Tree layer (%)	0	0	3	0	0	0	0	0	0
Shrub layer (%)	0	0	0	3	5	3	15	0	5
Herb layer (%)	60	75	70	70	45	50	45	80	75
Mosses and lichen (%)	5	5	2	2	10	3	5	10	3
Number of species (vascular plants)	28	32	37	34	33	36	38	41	37
Tree layer									
Pinus albicaulis	.	.	1	.	.	.	.	.	.
Shrub layer									
Pinus albicaulis	.	.	.	1	2	1	2	.	1
Herb layer									
Arenaria obtusiloba	2	2	2	2	2	2	2	2	2
Silene acaulis	2	1	1	1	2	2	1	2	+
Selaginella densa	+	2	2	2	1	2	2	2	+
Phlox pulvinata	1	2	2	2	2	1	1	1	1
Poa pattersonii	2	2	1	1	1	1	+	2	+
Erigeron rydbergii	1	1	+	1	1	1	1	1	+
Arenaria rubella	+	1	+	+	+	+	1	+	1
Lupinus argenteus var. *depressus*	.	2	2	+	+	+	1	2	2
Antennaria umbrinella	1	2	1	+	+	+	+	+	2
Myosotis alpestris	+	1	1	1	+	1	+	+	+
Bupleurum americanum	+	+	+	+	+	+	+	+	.
Castilleja pulchella	+	+	.	+	+	1	.	+	1
Carex elynoides	2	2	1	2	2	1	+	.	.
Elymus scribneri	1	1	2	2	1	+	.	.	.
Polemonium viscosum	+	1	+	1	.	+	.	.	.
Carex albonigra	+	1	1	1	1	.	.	.	.
Senecio canus	1	1	+	+	1	.	.	.	.
Mertensia alpina	+	.	+	+	+	+	.	.	.
Oxytropis lagopus var. *atropurpurea*	2	1	.	1	1	1	+	.	.
Smelowskia calycina var. *americana*	+	+	.	.	1	+	+	.	.
Eritrichium nanum var. *elongatum*	1	1	.	.	1	+	+	.	.
Douglasia montana	1	+	.	.	+	+	+	.	.
Solidago multiradiata var. *scopulorum*	.	.	.	+	.	.	1	1	1
Erigeron simplex	.	.	+	.	.	.	+	1	1
Pedicularis cystopteridifolia	.	+	+	.	.	.	+	1	+
Saxifraga rhomboidea	.	.	r	.	+	+	+	+	+
Calamagrostis purpurascens	.	1	.	.	.	.	1	+	.
Artemisia scopulorum	.	.	.	.	.	.	+	1	.
Draba paysonii var. *treleasii*	.	.	.	.	.	.	+	.	+
Androsace septentrionalis var.*subulifera*	.	.	.	.	.	.	+	.	+
Draba crassifolia	.	.	.	.	.	+	.	+	+
Carex paysonis	.	.	.	.	.	.	.	+	1
Agoseris glauca	.	.	.	.	.	.	.	1	1
Geum rossii var. *turbinatum*	2	2	2	2	2	2	2	2	2
Festuca brachyphylla	1	1	1	1	1	1	2	1	+
Luzula spicata	1	1	1	1	1	1	+	1	1
Sedum lanceolatum	1	+	2	1	1	1	1	+	+
Potentilla diversifolia	+	1	.	1	1	1	1	2	2
Polygonum bistortoides	.	+	1	.	+	1	1	1	1
Trisetum spicatum	.	+	+	+	+	1	+	+	+
Carex scirpoidea var. *pseudoscirpoidea*	.	.	1	1	1	2	1	1	2
Poa secunda var. *elongata*	1	.	1	1	.	.	.	1	.
Pinus albicaulis	+	.	.	+	.	+	+	.	.
Draba cana	.	+	+	.	.	.	.	+	.
Cerastium arvense	.	+	.	+	+	.	.	.	1

Table 9.2 (continued)

Site number	**L2**	**L4**	**L3**	**L6**	**L5**	**L1**	**W7**	**W2**	**W10**
Agrostis mertensii	.	.	.	+	.	+	.	1	+
Arabis lyallii	.	.	+	.	.	+	.	.	+
Arabis nuttallii	.	.	+	.	.	.	+	.	+
Potentilla concinna	.	.	2	.	.	.	.	.	.
Festuca idahoensis	.	.	1	.	.	.	+	.	.
Elymus trachycaulus var. *tachycaulus*	.	.	+	+	.	.	.	.	.
Carex phaeocephala	.	.	+	.	.	1	.	.	.
Cerastium beeringianum var. *capillare*	.	.	+	.	.	.	.	.	.
Oxytropis campestris var.*cusickii*	.	.	.	+	.	.	.	r	.
Saxifraga bronchialis var. *austromontana*	.	.	.	+	.	.	.	.	.
Poa secunda var. incurva	.	.	.	.	1	.	.	.	.
Aster alpigenus	.	.	.	.	.	+	.	1	r
Penstemon procerus	.	.	.	.	.	+	.	+	.
Trifolium nanum	.	.	.	.	.	.	1	.	.
Anemone patens var. *multifida*	.	.	.	.	.	.	1	.	.
Carex rupestris	.	.	.	.	.	.	+	.	.
Sibbaldia procumbens	.	.	.	.	.	.	.	1	.
Deschampsia cespitosa	.	.	.	.	.	.	.	+	.
Koeleria macrantha	.	.	.	.	.	.	.	+	.
Draba incerta	.	.	.	.	.	.	.	+	.
Danthonia intermedia	.	.	.	.	.	.	.	+	.
Helictotrichon hookeri	.	.	.	.	.	.	.	+	.
Achillea millefolium var. *lanulosa*	.	.	.	.	.	.	.	.	+
Claytonia lanceolata	.	.	.	.	.	.	.	.	+
Lewisia pygmaea	.	.	.	.	.	.	.	.	+

Table 9.3: Mesic turf and woodland communities: Mesic *Geum rossii* turf and *Antennaria umbrinella/Carex phaeocephala vegetation*

Site number	**R5**	**W4**	**R3**	**W5**	**L8**	**L7**	**W9**	**W8**	**R2**
Tree layer (%)	0	0	10	0	0	0	30	0	0
Shrub layer (%)	0	0	5	0	0	0	1	1	0
Herb layer (%)	90	90	70	60	60	85	80	50	70
Mosses and lichen (%)	20	1	1	10	35	2	1	15	5
Number of species (vascular plants)	31	36	25	32	30	33	28	30	26
Tree layer									
Pinus albicaulis	.	.	2	.	.	.	3	.	.
Shrub layer									
Pinus albicaulis	.	.	1	.	.	.	1	.	.
Abies lasiocarpa	.	.	.	.	.	.	.	+	.
Herb layer									
Antennaria umbrinella	.	1	2	2	3	1	2	2	1
Arenaria congesta	.	1	2	2	.	+	2	2	+
Androsace septentrionalis var.*subulifera*	.	+	+	1	+	+	+	+	1
Penstemon procerus	.	+	2	1	+	+	.	+	2
Lewisia pygmaea	.	+	1	+	.	+	+	+	1
Lupinus argenteus var. *depressus*	2	2	1	2	1	.	.	2	.
Cerastium arvense	1	1	.	1	1	2	.	+	1
Solidago multiradiata var. *scopulorum*	2	2	.	.	.	1	2	1	.
Erigeron simplex	+	+	+	.	1	+	2	.	+
Draba crassifolia	+	+	+	.	.	+	.	+	+
Carex paysonis	+	.	+	.	1	2	+	.	.
Myosotis alpestris	+	+	.	+	1	+	.	+	.
Artemisia scopulorum	1	1	.	.	+	1	+	.	.
Festuca idahoensis	.	2	.	2	.	.	1	2	.
Danthonia intermedia	.	1	.	+	.	2	2	+	.
Agoseris glauca	.	.	+	1	.	1	.	+	.
Agrostis mertensii	.	1	.	.	1	1	.	+	.
Aster alpigenus	.	+	1	+	.	.	2	1	.
Sibbaldia procumbens	.	.	1	.	+	.	+	.	.
Deschampsia cespitosa	2	2	2	.	.	.	1	+	.
Pedicularis cystopteridifolia	1	+	.	.	.	.	+	.	.
Saxifraga rhomboidea	+	+	.	.	.	.	.	.	.
Bupleurum americanum	+	+	.	.	+	.	.	.	.
Carex phaeocephala	.	.	.	2	2	3	2	.	.
Poa secunda var. incurva	.	.	.	.	2	1	.	.	+
Poa secunda var. *elongata*	.	.	.	1	1	1	.	1	2
Achillea millefolium var. *lanulosa*	.	.	.	.	.	2	1	1	2
Geum rossii var. *turbinatum*	3	1	2	1	2	2	1	.	1
Polygonum bistortoides	2	1	1	1	+	1	1	+	1
Potentilla diversifolia	1	1	1	1	2	2	+	2	2
Carex scirpoidea var. *pseudoscirpoidea*	1	1	1	1	2	1	1	1	1
Festuca brachyphylla	1	1	2	.	2	2	.	+	.
Luzula spicata	1	1	.	1	1	1	+	+	.
Trisetum spicatum	+	1	1	+	1	1	+	+	+
Sedum lanceolatum	+	+	+	1	+	.	.	+	1
Arenaria obtusiloba	1	+	1	.	1	+	1	.	.
Selaginella densa	.	1	.	2	.	1	+	1	.
Phlox pulvinata	+	.	1	1	+	.	.	.	.
Arenaria rubella	+	.	.	.	+	.	.	.	1
Carex elynoides	.	.	.	2	.	1	.	.	.
Poa pattersonii	1	.	.	.	.	.	.	.	1
Poa alpina	+	.	.	.	.	.	.	.	+
Stellaria longipes	+	.	.	.	.	1	.	.	.

Table 9.3 (continued)

Site number	**R5**	**W4**	**R3**	**W5**	**L8**	**L7**	**W9**	**W8**	**R2**
Gentiana algida	1	.	.	.	.	.	.	.	.
Senecio fuscatus	1	.	.	.	.	.	.	.	.
Carex capitata	+	.	.	.	.	.	.	.	.
Caltha leptosepala	+	.	.	.	.	.	.	.	.
Lloydia serotina	+	.	.	.	.	.	.	.	.
Castilleja pulchella	.	+	.	.	.	.	+	.	.
Claytonia lanceolata	.	+	.	.	.	.	.	.	.
Campanula rotundifolia	.	+	.	.	.	.	.	.	.
Ranunculus glaberrimus var. *ellipticus*	.	+	.	.	.	.	.	.	.
Dodecatheon pulchellum	.	r	.	.	.	.	.	.	.
Rumex paucifolius	.	r	.	.	.	.	.	.	.
Trifolium parryi var. *montanense*	.	.	1	.	.	.	.	.	.
Pinus albicaulis	.	.	+	.	.	.	+	+	.
Geum triflorum	.	.	.	2	.	.	.	.	.
Anemone patens var. *multifida*	.	.	.	+	.	.	.	.	.
Carex rossii	.	.	.	1	.	.	.	.	.
Besseya wyomingensis	.	.	.	1	.	.	.	.	.
Erigeron umbellatum var. *majus*	.	.	.	1	.	.	.	.	.
Poa rupicola	.	.	.	+	.	.	.	.	.
Arabis lyallii	.	.	.	+	+	.	.	.	+
Erigeron rydbergii	.	.	.	+	+	.	.	.	.
Polemonium viscosum	.	.	.	.	+	.	.	.	.
Silene acaulis	.	.	.	.	+	.	.	.	+
Senecio integerrimus var. *exaltatus*	.	.	.	.	.	+	.	+	.
Antennaria lanata	.	.	.	.	.	+	+	.	.
Poa nervosa var. *wheeleri*	.	.	.	.	.	.	1	+	.
Epilobium angustifolium	.	.	.	.	.	.	.	.	1
Trifolium dasyphyllum	.	.	.	.	.	.	.	.	+
Eritrichium nanum var. *elongatum*	.	.	.	.	.	.	.	.	+
Oxytropis lagopus var. *atropurpurea*	.	.	.	.	.	.	.	.	+

Table 9.4: Upland willow community: *Salix glauca vegetation*

Site number	**W1**	**W3**	**W6**
Tree layer (%)	5	0	0
Shrub layer (%)	5	20	20
Herb layer (%)	60	80	50
Mosses and lichen (%)	15	15	30
Number of species (vascular plants)	31	38	29
Tree layer			
Abies lasiocarpa	1	.	.
Shrub layer			
Pinus albicaulis	.	1	2
Abies lasiocarpa	+	.	.
Picea engelmannii	.	1	.
Salix glauca var. villosa	.	2	.
Herb layer			
Salix glauca var. *villosa*	3	2	2
Arenaria obtusiloba	1	2	1
Selaginella densa	1	2	2
Arenaria congesta	1	1	1
Solidago multiradiata var. *scopulorum*	1	1	1
Aster alpigenus	1	1	1
Erigeron simplex	1	1	+
Lewisia pygmaea	1	+	1
Pedicularis cystopteridifolia	1	1	r
Danthonia intermedia	+	2	+
Penstemon procerus	1	+	+
Androsace septentrionalis var.*subulifera*	+	+	+
Bupleurum americanum	+	1	r
Antennaria umbrinella	2	1	.
Antennaria media	.	.	1
Sibbaldia procumbens	.	2	1
Agrostis mertensii	+	1	.
Artemisia scopulorum	+	1	.
Draba crassifolia	+	+	.
Carex phaeocephala	+	.	+
Deschampsia cespitosa	.	1	.
Festuca brachyphylla	2	2	2
Trisetum spicatum	+	+	+
Lupinus argenteus	1	2	2
Polygonum bistortoides	1	1	+
Sedum lanceolatum	+	+	+
Luzula spicata	+	1	+
Potentilla diversifolia	.	1	1
Geum rossii var. *turbinatum*	.	+	1
Carex scirpoidea var. *pseudoscirpoidea*	+	.	1
Pinus albicaulis	+	.	+
Poa secunda var. *elongata*	1	.	.
Festuca idahoensis	+	.	.
Koeleria macrantha	+	.	.
Poa alpina	+	.	.
Vaccinium scoparium	.	1	.
Arenaria rubella	.	1	.
Cerastium arvense	.	+	.
Saxifraga rhomboidea	.	+	.
Castilleja pulchella	.	+	.
Phlox pulvinata	.	+	.
Myosotis alpestris	.	+	.
Carex paysonis	.	r	.
Picea engelmannii	.	.	+
Agoseris glauca	.	.	+
Poa secunda var. incurva	.	.	+

Table 9.5: Moist snowbeds and meadows: *Deschampsia cespitoa/Salix reticulata* and *Caltha leptosepala* vegetation

Site number	**T6**	**T5**	**T2**	**T3**	**T7**	**T4**	**T8**
Tree layer (%)	40	20	0	0	0	0	0
Shrub layer (%)	0	0	0	15	15	0	5
Herb layer (%)	40	60	40	55	65	85	70
Mosses and lichen (%)	1	10	55	3	3	40	5
Number of species (vascular plants)	24	22	25	31	28	21	25
Tree layer							
Pinus albicaulis	.	2	.	.	.	.	.
Picea engelmannii	3	2	.	.	.	.	.
Shrub layer							
Pinus albicaulis	.	.	.	1	2	.	1
Abies lasiocarpa	.	.	.	1	.	.	.
Picea engelmannii	.	.	.	1	1	.	2
Herb layer							
Deschampsia cespitosa	1	2	2	2	2	2	3
Poa alpina	2	2	1	1	1	1	1
Cares scirpoidea var. *pseudoscirpoidea*	1	1	2	2	2	2	2
Polygonum viviparum	1	1	+	1	1	2	1
Artemisia scopulorum	1	1	1	1	1	+	1
Salix reticulata var. *nana*	+	+	1	2	3	2	3
Salix glauca var. *villosa*	.	.	.	2	1	+	1
Gentiana algida	.	1	.	+	+	1	+
Carex paysonis	.	.	.	.	1	+	1
Caltha leptosepala	.	.	.	.	.	3	2
Vaccinium scoparium	2	.	2	.	.	.	.
Arenaria obtusiloba	+	2	1	1	2	.	.
Antennaria media	1	.	+	1	1	.	.
Aster alpigenus	+	.	2	.	+	.	.
Lewisia pygmaea	.	+	+	+	+	.	.
Stellaria longipes	.	1	+	1	.	.	+
Festuca brachyphylla	1	3	2	1	1	1	2
Potentilla diversifolia	2	2	1	2	1	1	1
Luzula spicata	+	2	1	+	+	+	1
Geum rossii var. *turbinatum*	1	+	1	2	2	.	+
Trisetum spicatum	+	.	+	+	1	+	.
Polygonum bistortoides	+	+	1	1	.	.	.
Sedum lanceolatum	+	1	1	1	+	.	.
Saxifraga rhomboidea	+	+	+	.	.	.	.
Lupinus argenteus var. *depressus*	+	.	.	1	+	.	+
Agrostis mertensii	.	.	+	1	1	1	.
Erigeron simplex	.	.	.	+	1	+	.
Poa nervosa var. *wheeleri*	1	.	.	.	.	.	.
Poa secunda var. incurva	+	.	.	+	.	.	.
Senecio fuscatus	r	+	.	.	.	.	.
Mertensia alpina	.	+	.	.	.	.	.
Poa arctica var. *grayana*	.	+	.	.	.	.	.
Selaginella densa	.	.	2	1	.	.	.
Sibbaldia procumbens	.	.	1	.	.	.	.
Antennaria lanata	.	.	1	.	.	.	+
Draba crassifolia	.	.	+	+	.	.	.
Arenaria rubella	.	.	.	1	+	.	.
Silene acaulis	.	.	.	+	1	.	.
Phlox pulvinata	.	.	.	.	+	.	.
Carex elynoides	.	.	.	.	+	.	.

Table 9.5 (continued)

Site number	**T6**	**T5**	**T2**	**T3**	**T7**	**T4**	**T8**
Carex albonigra	.	.	.	.	.	1	.
Pedicularis oederi	.	.	.	.	.	1	.
Gentiana prostrata	.	.	.	.	.	+	.
Gentianella tenella	.	.	.	.	.	+	.
Dodecatheon pulchellum	.	.	.	.	.	r	.
Phyllodoce glanduliflora	.	.	.	.	.	.	2
Phyllodoce empetriformis	.	.	.	.	.	.	1
Senecio cymbalarioides	.	.	.	.	.	.	+
Salix arctica var. *petraea*	.	.	.	.	.	.	+
Carex capitata	.	.	.	.	.	.	+

9.2 Soil profiles of selected experiment sites

Table 9.6: *Soil profile on site L3 — Humic Dystrocryept, loamy-skeletal, mixed*

Horizon	**$O_{e/a}$**	**A**	**A/B**	**B_{w1}**	**B_{w2}**	**C**
Depth [cm]	2.5 - 0	0 - 7	7 - 11	11 - 50	50 - 72	72+
Color moist		10YR 2/2	10YR 3/2	10YR 3/3	10YR 3/3	10YR 3/3
Color dry		10 YR 3/3	10 YR 4/3	10YR 5/3	10YR 5/4	10YR 5/4
Skeletal [%]		25	25	40	40	40
Texture		sandy loam	sandy loam	sandy loam	loamy sand	sandy loam
pH in H_2O	6.2	5.5	5.6	5.5	5.5	5.5
pH in $CaCl_2$	5.5	4.8	4.7	4.6	4.5	4.5

Table 9.7: *Soil profile on site L4 — Humic Dystrocryept, sandy-skeletal, mixed*

Horizon	**$O_{e/a}$**	**A**	**B_w**	**B/C**	**C**
Depth [cm]	1.5 - 0	0 - 10	10 - 29	29 - 50	50 - 80+
Color moist		10YR 2/2	10YR 3/2	10YR 3/3	10YR 3/3
Color dry		10 YR 3/3	10 YR 4/3	10YR 5/4	10YR 5/4
Skeletal [%]		45	45	45	45
Texture		sandy loam	sandy loam	loamy sand	loamy sand
pH in H_2O	6.4	5.9	5.4	5.5	5.4
pH in $CaCl_2$	6.0	5.2	4.5	4.6	4.7

Table 9.8: *Soil profile on site L5 — Typic Dystrocryept, sandy-skeletal, mixed*

Horizon	**$O_{e/a}$***	**A**	**B_w**	**B/C**	**C**
Depth [cm]	2 - 0	0 - 12	12 - 15	15 - 35	35 - 50+
Color moist		10YR 2/2	10YR 3/3	10YR 3/3	10YR 3/4
Color dry		10 YR 4/3	10YR 4/4	10YR 5/4	10YR 5/4
Skeletal [%]		65	65	65	65
Texture		sandy loam	sandy loam	loamy sand	loamy sand
pH in H_2O	6.2	5.7	5.7	5.6	5.7
pH in $CaCl_2$	5.6	4.9	4.8	4.7	4.8

* Organic horizon patchy

Table 9.9: *Soil profile on site T1 — Typic Dystrocryept, sandy-skeletal, mixed*

Horizon	**A**	**B/A**	**B_w**	**C**
Depth [cm]	0 - 8	8 - 13	13 - 50	50 - 100+
Color moist	10YR 3/2	10YR 4/3	10YR 4/4	10YR 4/4
Color dry	10YR 4/3	10YR 5/4	10YR 6/4	10YR 6/4
Skeletal [%]	40	45	45	60
Texture	sandy loam	sandy loam	sandy loam	loamy sand
Clay [%]	8.1	5.5	4.5	3.1
Silt [%]	11.5	10.4	15.7	7.3
Fine Sand [%]	18.3	27.3	28.5	17.6
Coarse Sand [%]	62.1	56.9	51.4	72.0
pH in H_2O	6.0	5.8	5.6	5.8
pH in $CaCl_2$	5.0	4.5	4.4	4.5
C_{org} [%]	2.5	0.6	0.5	0.1
N [%]	0.20	0.04	0.03	0.01
C/N	12.9	15.8	15.0	13.0
Org. Matter [%]	4.3	1.1	0.8	0.2

Table 9.10: *Soil profile on site T4 — Oxyaquic Dystrocryept, loamy-skeletal, mixed*

Horizon	**O_a[†]**	**A_1**	**A_2**	**B_{w1}**	**B_{w2}**	**B/C**	**C**
Depth [cm]	4 - 0	0 - 10	10 - 25	25 - 37	37 - 65	65 - 87	87 - 110+
Color moist		10YR 2/2	10YR 2/2	10YR 4/4	10YR 4/4	10YR 4/4	10YR 5/4
Color dry		10YR 3/3	10YR 3/3	10YR 5/6	10YR 6/4	10YR 6/4	10YR 7/4
Skeletal [%]		10	10	30	50	50	55
Texture		loam	loam	sandy loam	sandy loam	sandy loam	sandy loam
Clay [%]		17.6	15.6	2.9	7.8 / 1.4*	5.7 / 3.2*	4.1 / 3.2*
Silt [%]		21.8	21.0	14.3	15.7 / 26.5*	15.3 / 31.2*	12.8 / 22.8*
Fine Sand [%]		25.5	25.2	36.8	30.9 / 41.8*	30.8 / 48.4*	29.3 / 48.6*
Coarse Sand [%]		35.1	38.2	46.0	45.6 / 30.3*	48.2 / 17.2*	53.8 / 25.4*
pH in H_2O	5.4	5.2	5.3	5.4	5.5	5.5	5.5
pH in $CaCl_2$	4.4	4.1	4.2	4.3	4.4	4.4	4.3
C_{org} [%]		–	4.8	0.9	0.9	0.4	0.1
N [%]		–	0.37	0.05	0.06	0.03	0.00
C/N		–	13.3	17.3	15.3	13.3	–
Org. Matter [%]		–	8.3	1.5	1.6	0.7	0.2

[†] $O_{i/e}$ horizon above O_a, 0.5 cm thick, not sampled

*Silt lenses (texture = silt loam) in B_{w2}, B/C, and C horizons. Color of silt lenses 10YR 4/4 to 5/4 moist, 10YR 6/4 dry; with mottling of higher chroma, 10YR 4/6 to 7.5 YR 5/6 moist and 10YR 6/6 to 7.5 YR 6/6 dry. Reddish mottling of soil in B_{w1} and B_{w2}, strongest above silt lenses.

Table 9.11: *Soil profile on site T5 — Humic Dystrocryept, sandy-skeletal, mixed*

Horizon	O_e	O_a	A_1	A_2	B/A	B_w*	C
Depth [cm]	6 - 4	4 - 0	0 - 8	8 - 23	23 - 36	36 - 72	72 - 100+
Color moist			10YR 2/1	10YR 2/2	10YR 3/3	10YR 4/4	10YR 4/4
Color dry			10YR 3/2	10 YR 4/2	10 YR 4/3	10YR 5/4	10YR 6/4
Skeletal [%]			30	30	40	70	70
Texture			silt loam	loam	sandy loam	loamy sand	loamy sand
Clay [%]			26.9	14.4	11.0	5.9	2.8
Silt [%]			32.7	19.4	11.4	5.1	3.9
Fine Sand [%]			26.1	26.5	21.7	9.1	23.2
Coarse Sand [%]			14.3	39.7	55.9	79.9	70.2
pH in H_2O	5.7	5.6	5.4	5.5	5.6	5.6	5.7
pH in $CaCl_2$	5.1	4.9	4.7	4.4	4.3	4.3	4.5
C_{org} [%]			17.7	4.4	1.4	0.3	0.2
N [%]			1.04	0.30	0.11	0.02	0.01
C/N			17.1	14.8	12.7	14.5	40.0
Org. Matter [%]			30.6	7.6	2.4	0.5	0.3

*Structure was "massive", with no pores and few roots, similar to the C horizon.

Table 9.12: *Soil profile on site T6 — Humic Dystrocryept, sandy-skeletal, mixed**

Horizon	O_i	O_e	O_a	A	B/A	B_w
Depth [cm]	7 - 5	5 - 2	2 - 0	0 - 15	15 - 25	25 - 33+
Color moist				10YR 2/1	10YR 3/3	10YR 3/4
Color dry				10YR 3/2	10YR4/3	10YR 5/4
Skeletal [%]				30	30	40
Texture				loam	loam	sandy loam
Clay [%]				19.4	14.3	12.5
Silt [%]				27.8	26.0	20.0
Fine Sand [%]				27.7	26.5	25.8
Coarse Sand [%]				25.1	33.2	41.7
pH in H_2O	5.5	5.4	5.0	5.1	5.2	5.3
pH in $CaCl_2$	5.0	4.9	4.4	4.1	4.1	4.1
C_{org} [%]				9.2	2.1	1.2
N [%]				0.60	0.15	0.09
C/N				15.3	13.7	14.1
Org. Matter [%]				15.8	3.5	2.1

* Soil profile only analyzed to 33cm, adjacent soil profiles show high percentages of sand in lower horizons.

Table 9.13: *Soil profile on site W2 — Typic Dystrocryept, loamy-skeletal, mixed*

Horizon	**O**	**A**	**B_{w1}**	**B_{w2}**	**B/C**	**C**
Depth [cm]	3 - 0	0 - 7	7 - 17	17 - 50	50 - 80	80 - 92+
Color moist		10YR 3/2	10YR 3/4	10YR 4/4	10YR 4/4	7.5YR 4/6
Color dry		10YR 4/3	10 YR 5/4	10YR 5/6	10YR 6/4	7.5YR 6/6
Skeletal [%]		20	25	35	45	75
Texture		sandy loam	sandy loam	sandy loam	sandy loam	sandy loam
Clay [%]		9.2	6.4	4.5	7.3	6.0
Silt [%]		11.3	16.3	19.2	19.5	9.6
Fine Sand [%]		29.7	36.3	43.0	42.2	36.0
Coarse Sand [%]		49.7	41.0	33.3	31.0	48.5
pH in H_2O	6.2	5.5	5.5	5.5	5.5	5.6
pH in $CaCl_2$	5.0	4.5	4.3	4.1	4.1	4.1
C_{org} [%]		3.1	1.1	0.5	0.2	0.1
N [%]		0.26	0.10	0.08	0.05	0.02
C/N		11.8	11.5	6.8	4.5	5.5
Org. Matter [%]		5.3	2.0	0.9	0.4	0.2

Table 9.14: *Soil profile on site W3 — Humic Dystrocryept, loamy-skeletal, mixed*

Horizon	**O**	**A**	**B/A**	**B_{w1}**	**B_{w2}**	**B/C**	**C**
Depth [cm]	3 - 0	0 - 14	14 - 24	24 - 38	38 - 72	72 - 92	92 - 105+
Color moist		10YR 2/2	10YR 3/3	10YR 3/4	10YR 4/4	10YR 4/4	10YR 5/6
Color dry		10YR 3/3	10YR 5/3	10YR 5/4	10YR 5/4	10YR 6/4	10YR 7/4
Skeletal [%]		10	20	20	40	50	60
Texture		sandy loam	sandy loam	sandy loam	sandy loam	sandy loam	sandy loam
Clay [%]		11.2	9.2	2.0	4.3	7.0	7.0
Silt [%]		9.8	16.3	24.5	16.3	18.0	18.9
Fine Sand [%]		30.5	32.8	32.7	36.2	38.4	39.2
Coarse Sand [%]		48.6	41.7	40.9	43.3	36.7	34.9
pH in H_2O	6.2	5.2	5.4	5.5	5.6	5.5	5.5
pH in $CaCl_2$	5.0	4.2	4.2	4.3	4.3	4.2	4.2
C_{org} [%]		3.1	1.2	0.8	0.6	0.2	0.1
N [%]		0.24	0.09	0.06	0.05	0.04	0.02
C/N		13.1	14.2	12.8	10.8	4.8	5.3
Org. Matter [%]		5.3	2.1	1.3	1.0	0.3	0.2

Table 9.15: *Soil profile on site W4 — Humic Dystrocryept, loamy-skeletal, mixed*

Horizon	**$O_{i/e}$**	**O_a**	**A**	**B/A**	**B_{w1}**	**B_{w2}**	**B/C**
Depth [cm]	4.5-4	4 - 0	0 - 22	22 - 28	28 - 50	50 - 78	78 - 89+
Color moist			10YR 2/2	10YR 3/3	10YR 4/4	10YR 4/4	10YR 4/4
Color dry			10YR 3/3	10YR 4/3	10YR 5/4	10YR 5/4	10YR 6/4
Skeletal [%]			10	15	30	45	60
Texture			sandy loam	sandy loam	sandy loam	sandy loam	sandy loam
Clay [%]			14.5	2.6	6.0	6.3	8.3
Silt [%]			14.2	25.4	14.8	16.3	17.9
Fine Sand [%]			31.1	30.7	39.7	37.8	35.2
Coarse Sand [%]			40.3	41.3	39.5	39.7	38.6
pH in H_2O	not	5.9	5.4	5.6	5.6	5.6	5.9
pH in $CaCl_2$	sampled	5.0	4.5	4.4	4.4	4.4	4.6
C_{org} [%]			4.3	1.0	0.5	0.3	0.2
N [%]			0.38	0.10	0.05	0.06	0.03
C/N			11.2	10.0	10.6	4.5	7.1
Org. Matter [%]			7.3	1.7	0.8	0.5	0.4

Table 9.16 : *Soil profile on site W9 — Typic Dystrocryept*, sandy-skeletal, mixed*

Horizon	**$O_{i/e}$**	**O_a**	**A**	**B/A**	**B_{w1}**	**B_{w2}**	**C/B**
Depth [cm]	4.5 - 3	3 - 0	0 - 12	12 - 21	21 - 36	36 - 53	53 - 80+
Color moist			10YR 3/2	10YR 3/3	10YR 3/4	10YR 3/4	10YR 4/4
Color dry			10YR 3/3	10YR 5/4	10YR 5/4	10YR 5/4	10YR 6/4
Skeletal [%]			15	30	45	70	90
Texture			sandy loam	sandy loam	sandy loam	sandy loam	loamy sand
Clay [%]			10.0	5.6	3.1	4.3	4.4
Silt [%]			15.0	13.4	12.0	10.4	7.3
Fine Sand [%]			34.0	34.3	36.8	37.3	33.2
Coarse Sand [%]			40.9	46.7	48.2	48.0	55.2
pH in H_2O	5.2	5.9	5.4	5.4	5.5	5.5	5.6
pH in $CaCl_2$	4.4	4.6	4.3	4.2	4.3	4.3	4.3
C_{org} [%]			2.5	1.1	0.5	0.2	0.1
N [%]			0.17	0.08	0.04	0.05	0.02
C/N			14.8	13.5	12.3	5.2	5.2
Org. Matter [%]			4.2	1.9	0.8	0.4	0.2

*Epipedon is ochric, tending towards umbric (soil tending towards a Humic Dystrocryept)

Table 9.17: *Soil profile at site W10 — Typic Dystrocryept, loamy-skeletal, mixed*

Horizon	**O**	**A**	**B/A**	**B_{w1}**	**B_{w2}**	**B/C**
Depth [cm]	2 - 0	0 - 12	12 - 18	18 - 50	50 - 77	77 - 100+
Color moist		10YR 3/2	10YR 3/4	10YR 4/4	10YR 4/4	10YR 4/4
Color dry		10YR 4/3	10YR 5/4	10YR 6/4	10YR 6/4	10YR 6/4
Skeletal [%]		15	25	35	50	70
Texture		sandy loam	sandy loam	sandy loam	sandy loam	sandy loam
Clay [%]		7.9	10.7	7.0	5.1	6.1
Silt [%]		14.7	14.3	20.1	18.0	16.4
Fine Sand [%]		34.5	37.7	41.7	40.0	37.8
Coarse Sand [%]		42.9	37.4	31.3	36.9	39.7
pH in H_2O	6.3	5.6	5.5	5.3	5.3	5.4
pH in $CaCl_2$	5.0	4.4	4.3	4.0	4.0	4.1
C_{org} [%]		2.0	1.1	0.4	0.2	0.2
N [%]		0.17	0.09	0.04	0.03	0.03
C/N		11.8	11.8	10.1	7.6	8.5
Org. Matter [%]		3.5	1.8	0.7	0.3	0.4

Table 9.18: *Soil profile on site R1 — Typic Dystrocryept, loamy-skeletal, mixed*

Horizon	**A**	**B_w**	**B/C**	**C**
Depth [cm]	0 - 7	7 - 17	17 - 38	38 - 60+
Color moist	10YR 2/1	10YR 3/3	10YR 4/4	10YR 4/4
Color dry	10YR 3/2	10YR 5/4	10YR 6/4	10YR 6/4
Skeletal [%]	40	50	50	80
Texture	loamy sand	loamy sand	sandy loam	sandy loam
Clay [%]	7.8	3.8	5.1	4.8
Silt [%]	8.1	9.3	16.8	14.0
Fine Sand [%]	19.8	29.0	35.3	34.7
Coarse Sand [%]	64.3	58.0	42.8	46.5
pH in H_2O	5.9	5.9	5.7	5.8
pH in $CaCl_2$	4.9	4.6	4.4	4.3
C_{org} [%]	2.0	0.6	0.4	0.1
N [%]	0.13	0.04	0.04	0.02
C/N	15.6	15.0	9.0	6.1
Org. Matter [%]	3.4	1.0	0.6	0.2

* Organic layer ($O_{e/a}$) patchy, up to 1 cm thick, mainly accumulated under *Dryas* mats, not sampled.

Table 9.19: *Soil profile on site R2 — Typic Dystrocryept, loamy-skeletal, mixed*

Horizon	$O_{e/a}$*	**A**	B_{w1}	B_{w2}	**B/C**	**C**
Depth [cm]	2 - 0	0 - 6	6 - 15	15 - 25	25 - 50	50 - 80+
Color moist		10YR 3/2	10YR 3/3	10YR 3/4	10YR 4/4	10YR 5/4
Color dry		10 YR 3/3	10 YR 5/4	10YR 5/4	10YR 6/4	10YR 6/4
Skeletal [%]		30	40	65	70	80
Texture		loamy sand	loamy sand	sandy loam	sandy loam	sandy loam
Clay [%]		7.1	4.4	2.5	4.1	4.1
Silt [%]		8.6	8.7	13.7	20.9	12.3
Fine Sand [%]		21.5	25.9	31.7	29.6	31.4
Coarse Sand [%]		62.9	61.0	52.1	45.4	52.2
pH in H_2O	5.8	5.7	6.0	6.1	6.1	6.1
pH in $CaCl_2$	5.0	4.8	4.8	4.9	4.9	4.9
C_{org} [%]		2.5	1.3	0.8	0.6	0.5
N [%]		0.18	0.11	0.09	0.07	0.04
C/N		14.3	11.6	8.1	7.9	11.6
Org. Matter [%]		4.3	2.2	1.3	1.0	0.8

*O_i horizon above $O_{e/a}$, 0.5 cm thick, patchy, not sampled

Table 9.20: *Soil profile on site R5 — Humic Dystrocryept, loamy-skeletal, mixed*

Horizon	O_a*	A_1	A_2	B_w	A_b	B_{wb}	**C/B**	**C**
Depth [cm]	2.5 - 0	0 - 17	17 - 23	23 - 39	39 - 48	48 - 73	73 - 85	85 - 120+
Color moist		10YR 2/2	10YR 2/2	10YR 3/3	10YR 3/2	10YR 3/4	10YR 4/3	10YR 4/3
Color dry		10YR 3/3	10YR 3/3	10YR 5/4	10YR 4/3	10YR 5/3	10YR 5/4	10YR 6/4
Skeletal [%]		10	10	40	15	30	35	45
Texture		sandy loam	sandy loam	sandy loam	sandy loam	sandy loam	loamy sand	sand
Clay [%]		15.2	12.0	7.7	14.4	3.7	4.1	2.6
Silt [%]		13.3	17.5	8.6	11.7	14.0	7.7	2.9
Fine Sand [%]		34.9	36.7	30.7	31.2	35.0	34.7	30.2
Coarse Sand [%]		36.6	33.8	53.0	42.7	47.3	53.5	64.2
pH in H_2O	5.6	5.2	5.3	5.3	5.4	5.3	5.6	5.6
pH in $CaCl_2$	4.7	4.2	4.1	4.0	4.0	4.0	4.0	4.1
C_{org} [%]		3.6	2.3	0.8	1.2	0.5	0.1	0.1
N [%]		0.32	0.20	0.06	0.12	0.05	0.04	0.03
C/N		11.5	11.7	12.5	10.4	9.2	4.0	2.5
Org. Matter [%]		6.3	4.0	1.3	2.1	0.8	0.2	0.1

*herbaceous $O_{i/e}$ horizon above O_a, 0.5 cm thick, not sampled

9.3 Soil temperatures on Wyoming Creek and Tibbs Butte

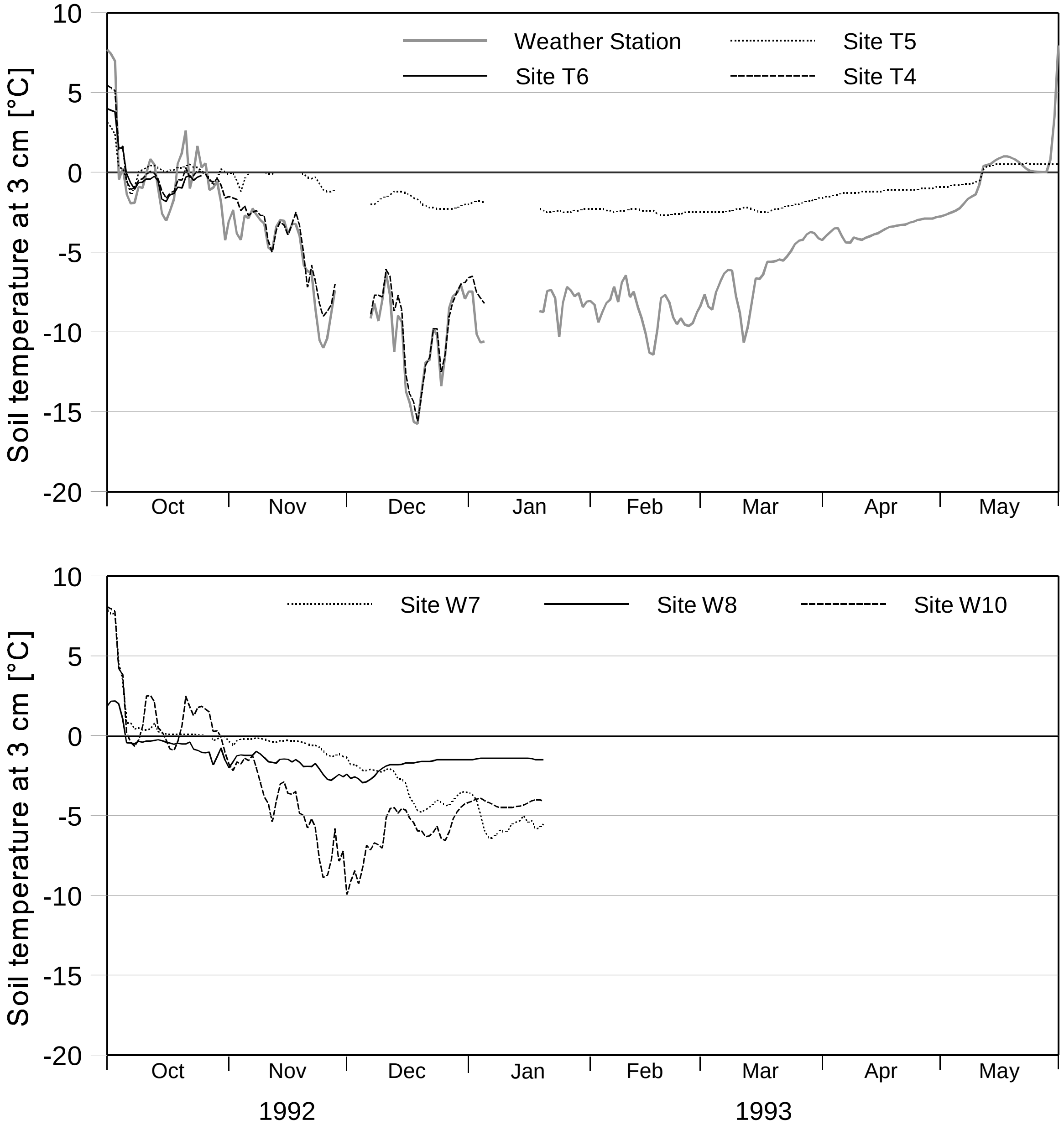

Fig. 9.1: *Daily average soil temperatures at 3 cm depth on selected Tibbs Butte and Wyoming Creek sites during the winter 1992-1993.*

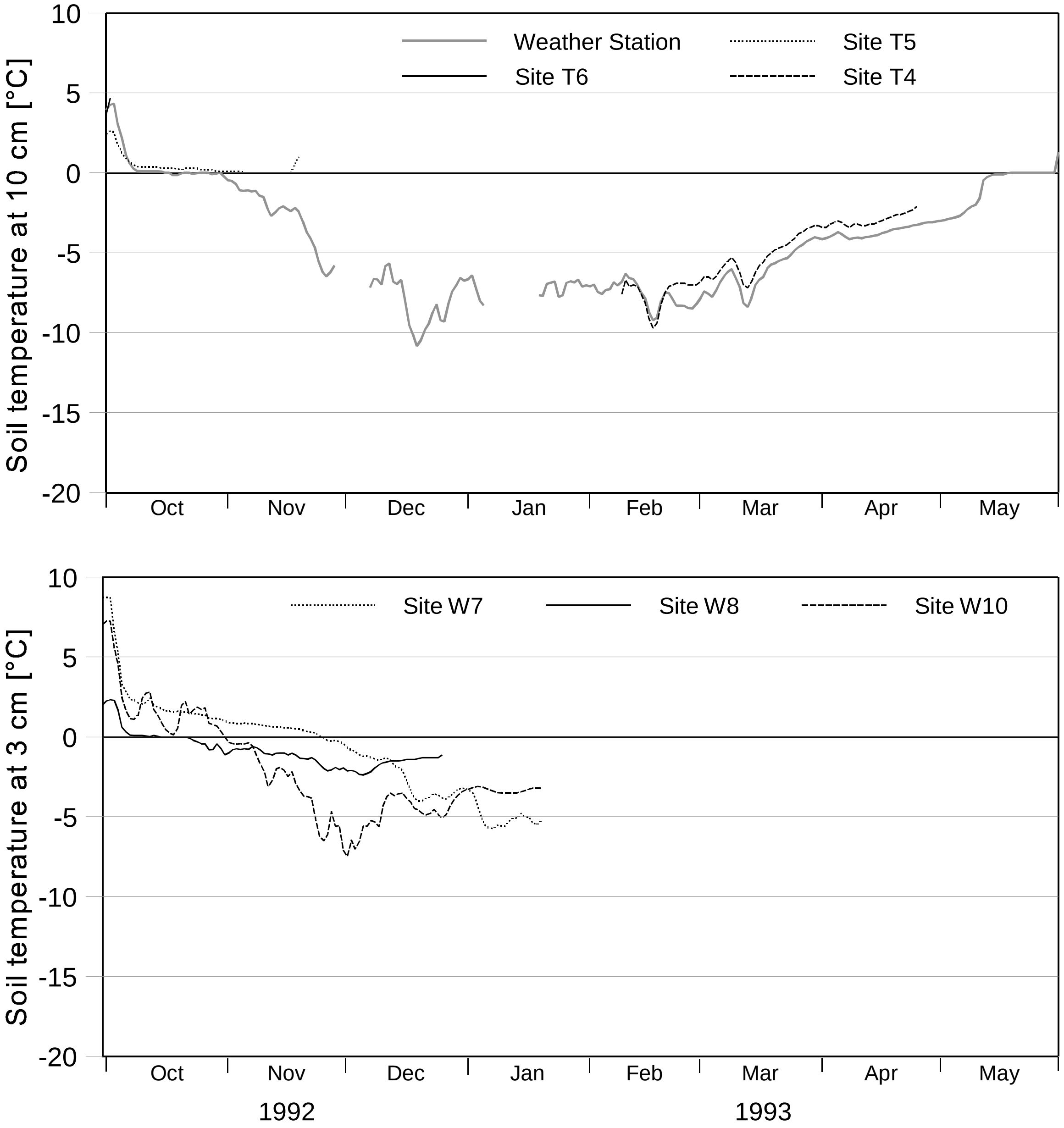

Fig. 9.2: Daily average soil temperatures at 10 cm depth on selected Tibbs Butte and Wyoming Creek sites during the winter 1992-1993.

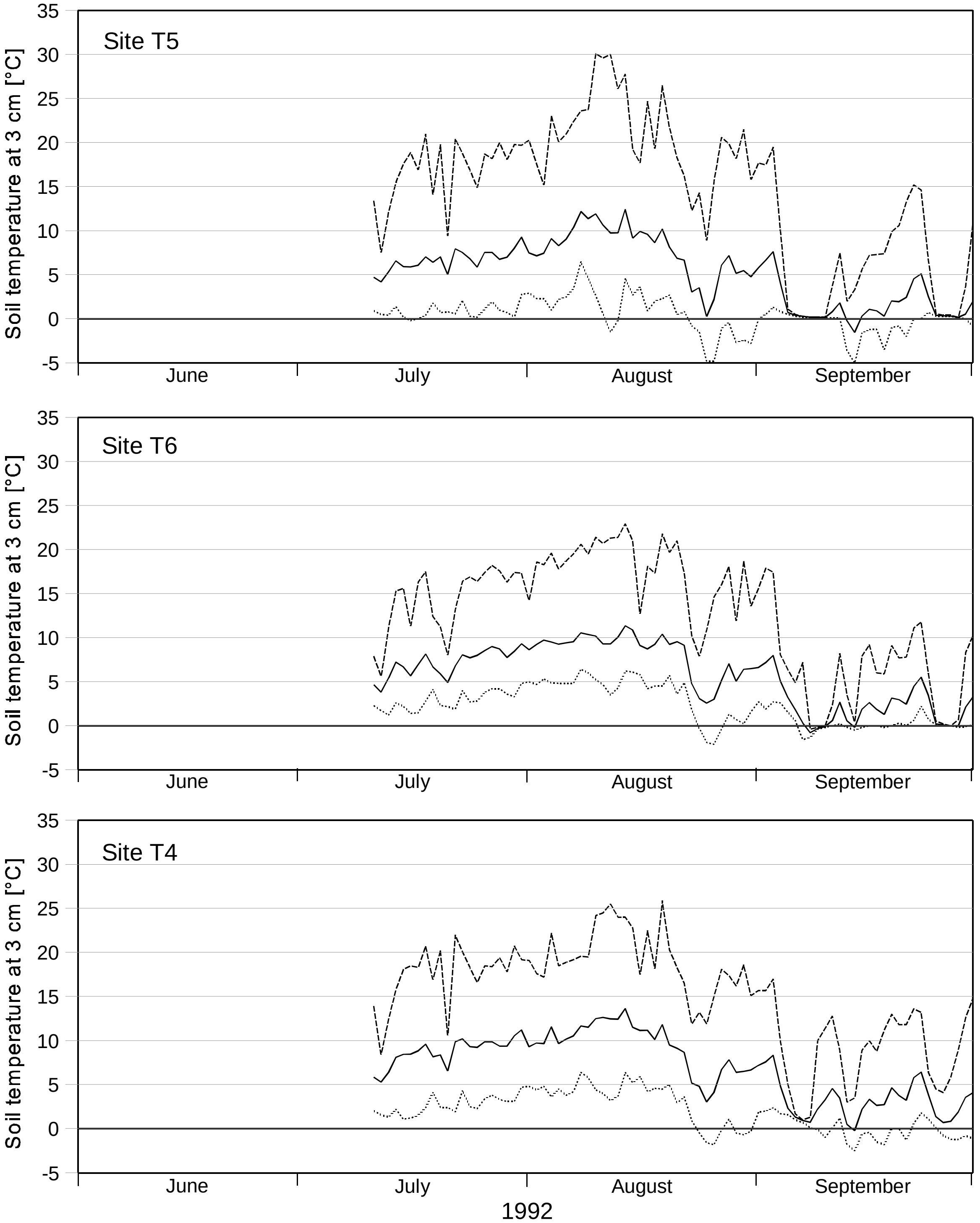

Fig. 9.3: *Soil temperatures at 3 cm depth on Tibbs Butte, summer 1992. Dashed lines represent daily maxima, solid lines daily averages, and dotted lines daily minima.*

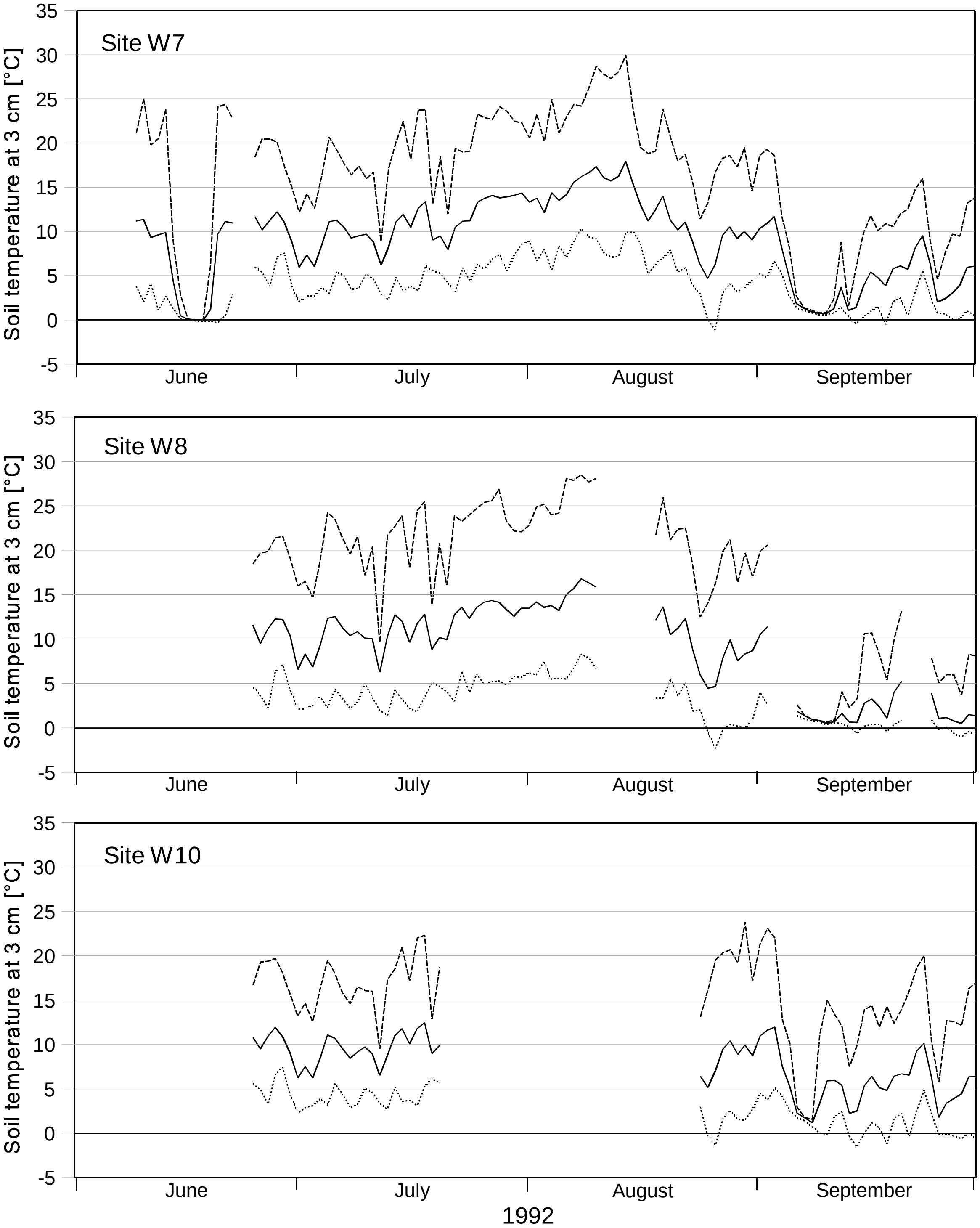

***Fig. 9.4:** Soil temperatures at 3 cm depth on Wyoming Creek, summer 1992. Dashed lines repre-sent daily maxima, solid lines daily averages, and dotted lines daily minima.*

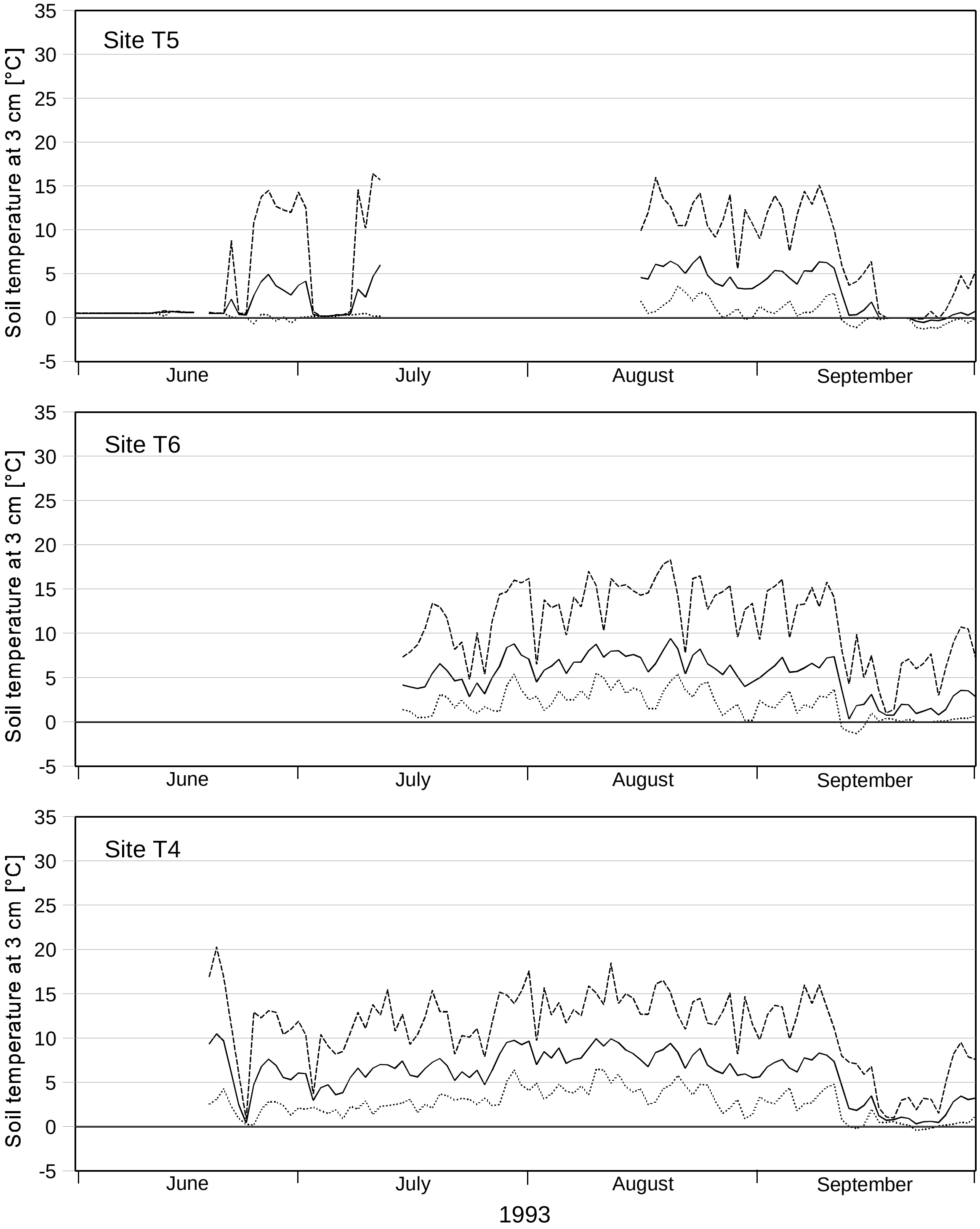

Fig. 9.5: *Soil temperatures at 3 cm depth on Tibbs Butte, summer 1993. Dashed lines represent daily maxima, solid lines daily averages, and dotted lines daily minima.*

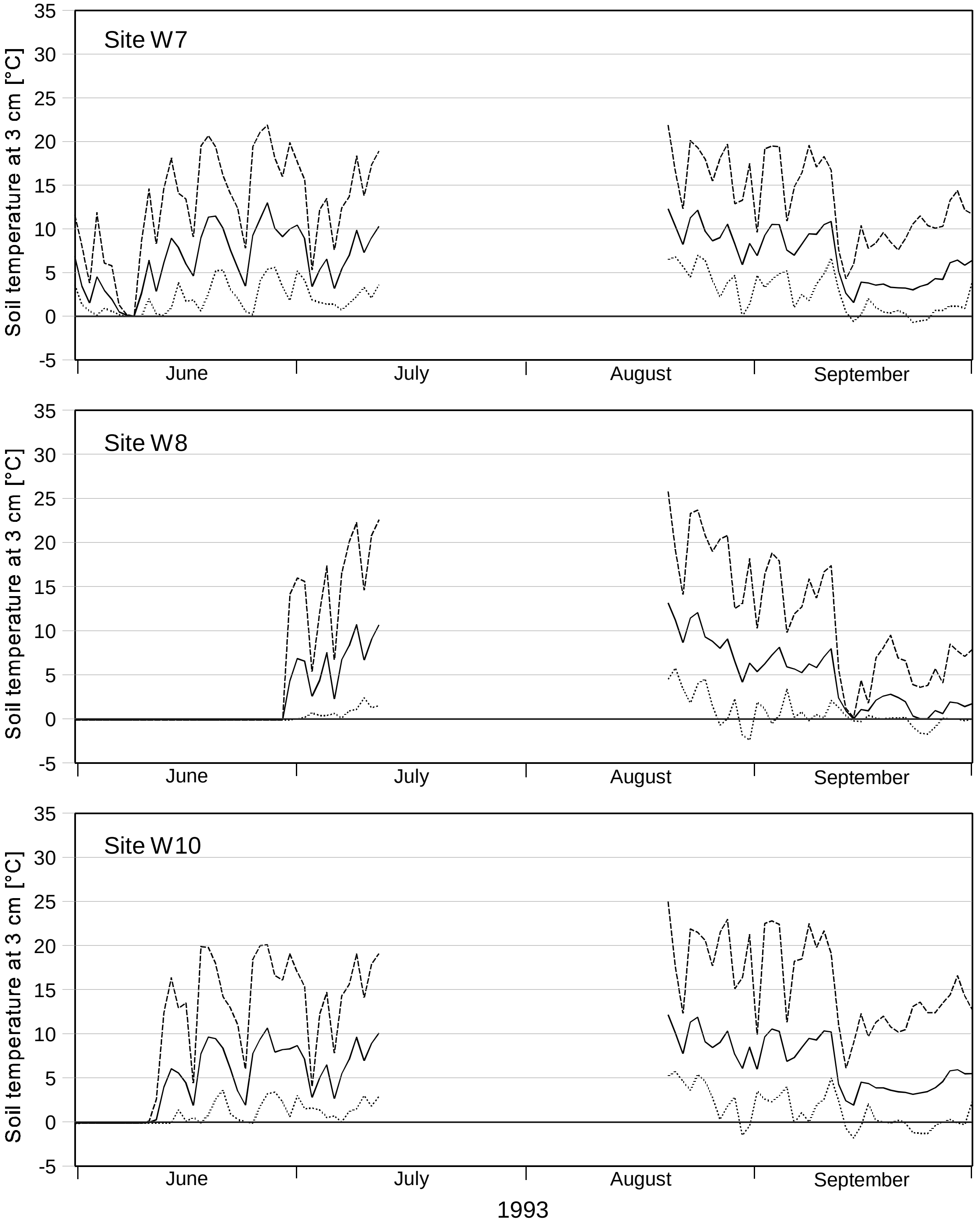

Fig. 9.6: *Soil temperatures at 3 cm depth on Wyoming Creek, summer 1993. Dashed lines repre-sent daily maxima, solid lines daily averages, and dotted lines daily minima.*

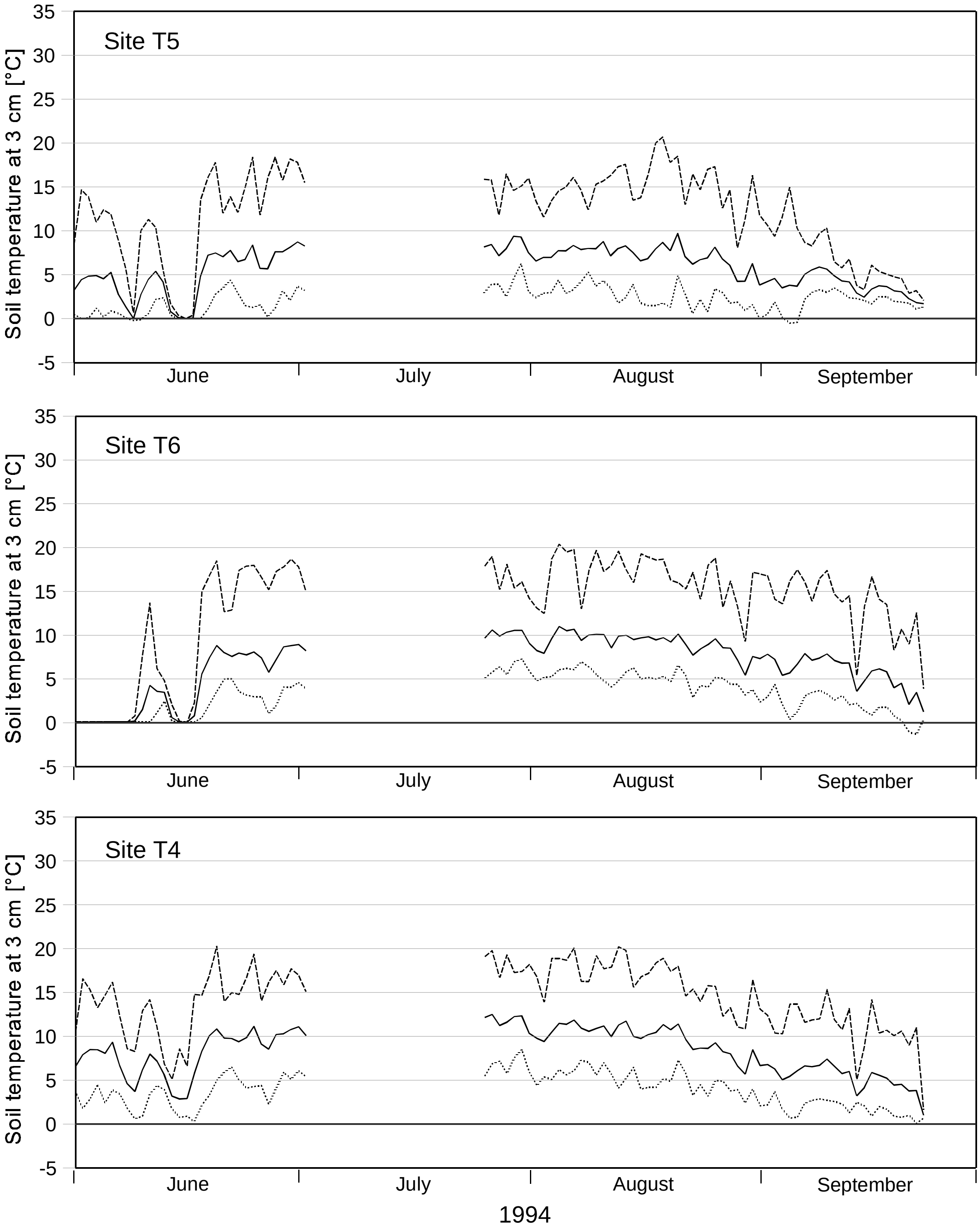

Fig. 9.7: *Soil temperatures at 3 cm depth on Tibbs Butte, summer 1994. Dashed lines represent daily maxima, solid lines daily averages, and dotted lines daily minima.*

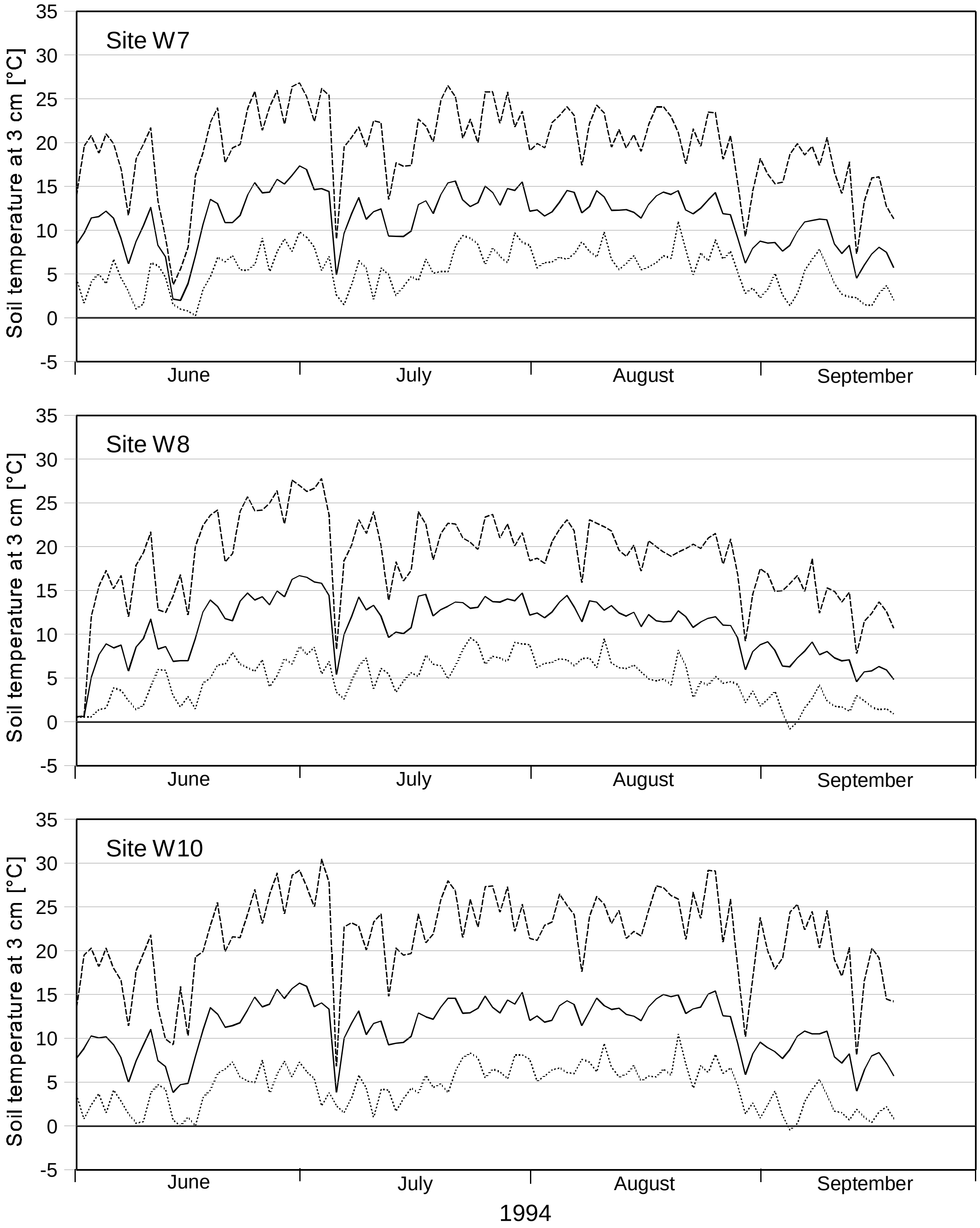

***Fig. 9.8:** Soil temperatures at 3 cm depth on Wyoming Creek, summer 1994. Dashed lines repre-sent daily maxima, solid lines daily averages, and dotted lines daily minima.*

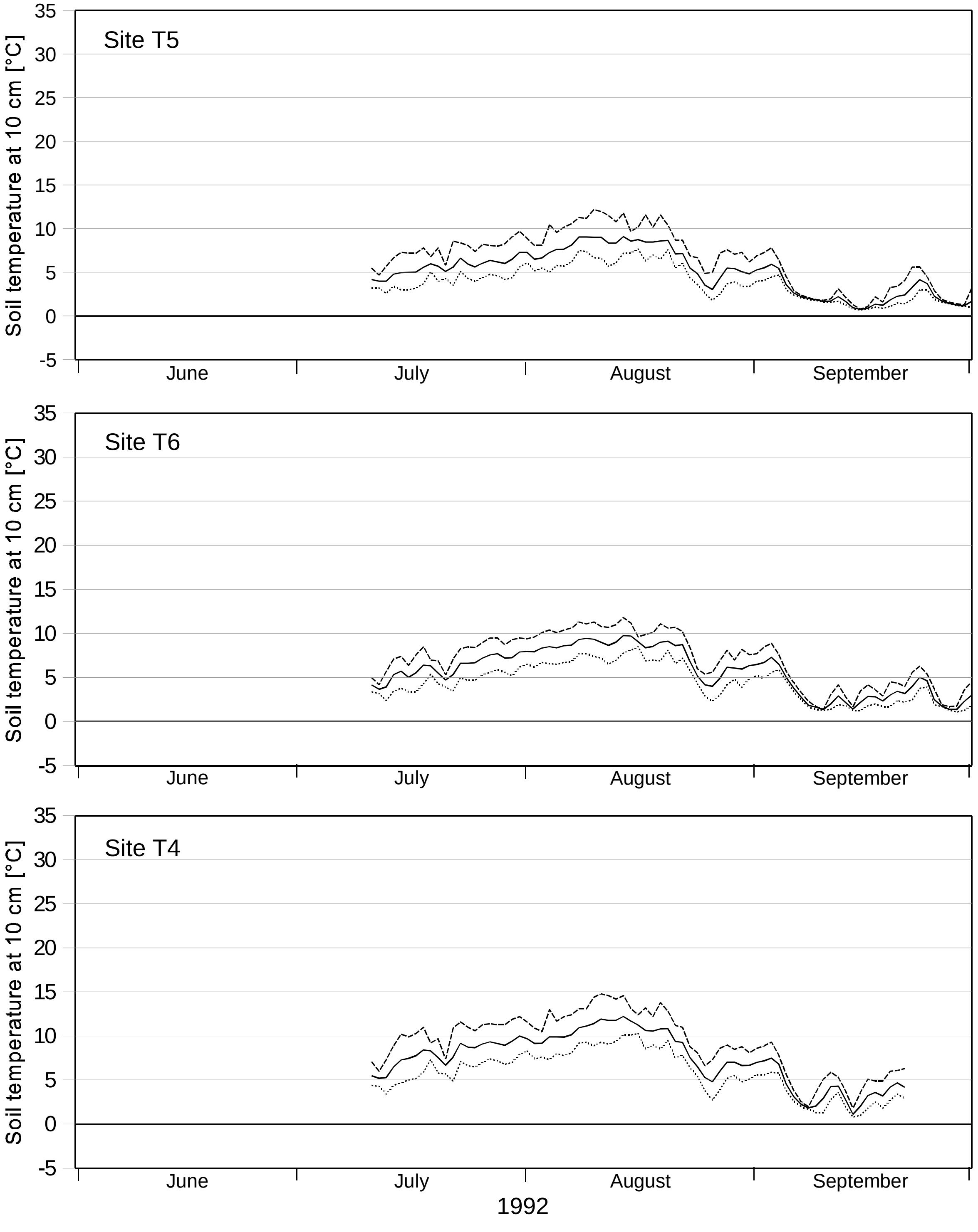

Fig. 9.9: Soil temperatures at 10 cm depth on Tibbs Butte, summer 1992. Dashed lines represent daily maxima, solid lines daily averages, and dotted lines daily minima.

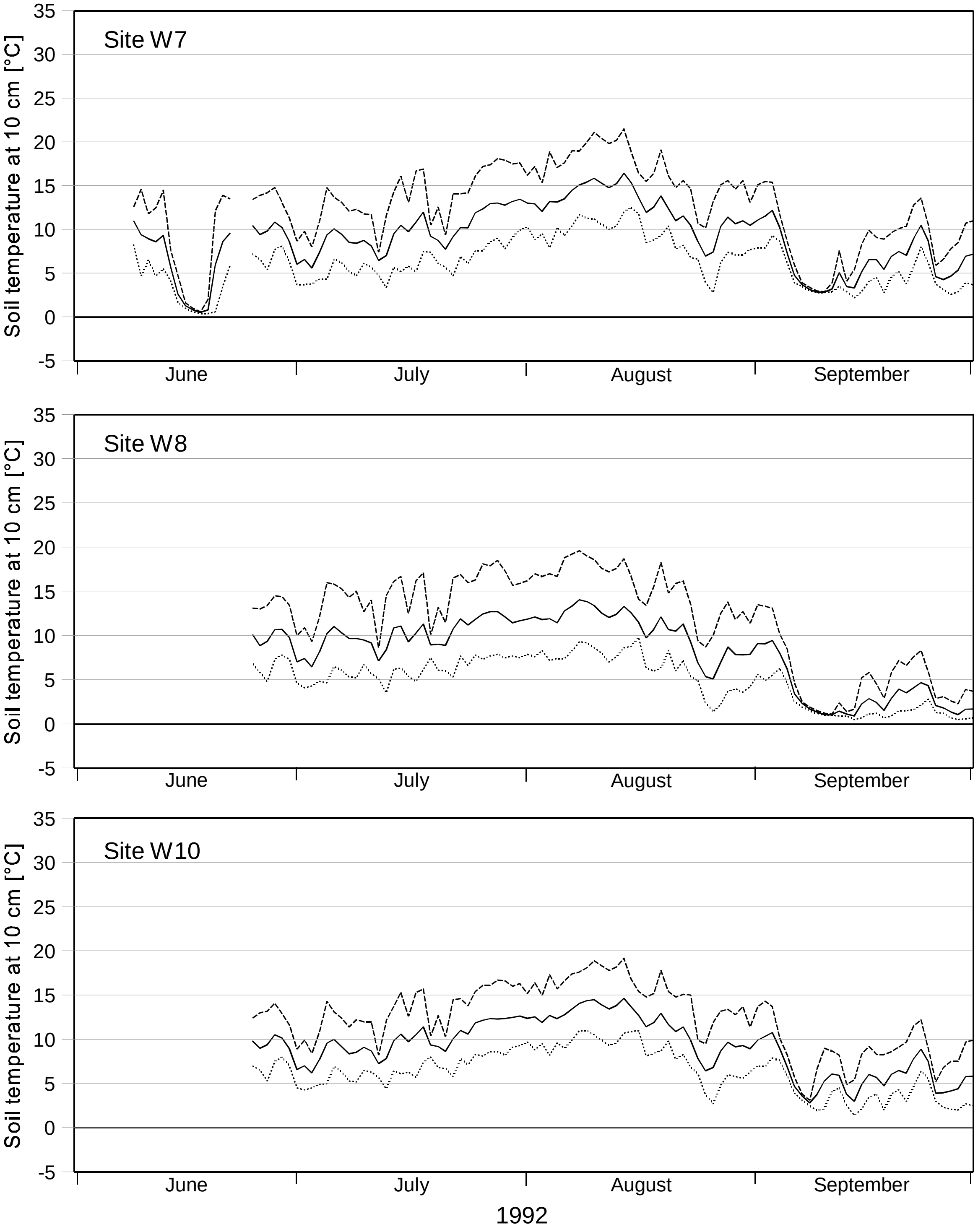

***Fig. 9.10:** Soil temperatures at 10 cm depth on Wyoming Creek, summer 1992. Dashed lines repre-sent daily maxima, solid lines daily averages, and dotted lines daily minima.*

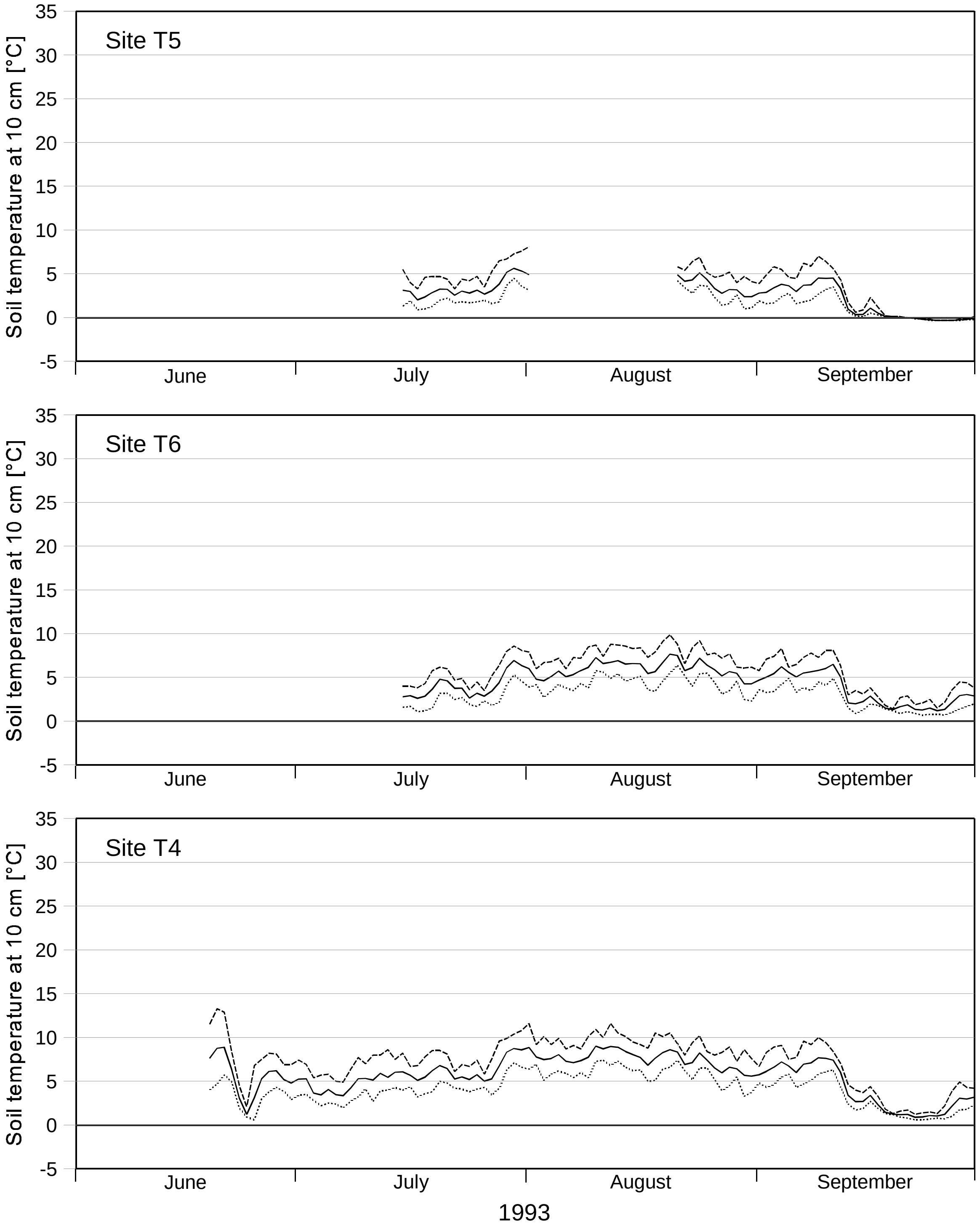

Fig. 9.11: *Soil temperatures at 10 cm depth on Tibbs Butte, summer 1993. Dashed lines represent daily maxima, solid lines daily averages, and dotted lines daily minima.*

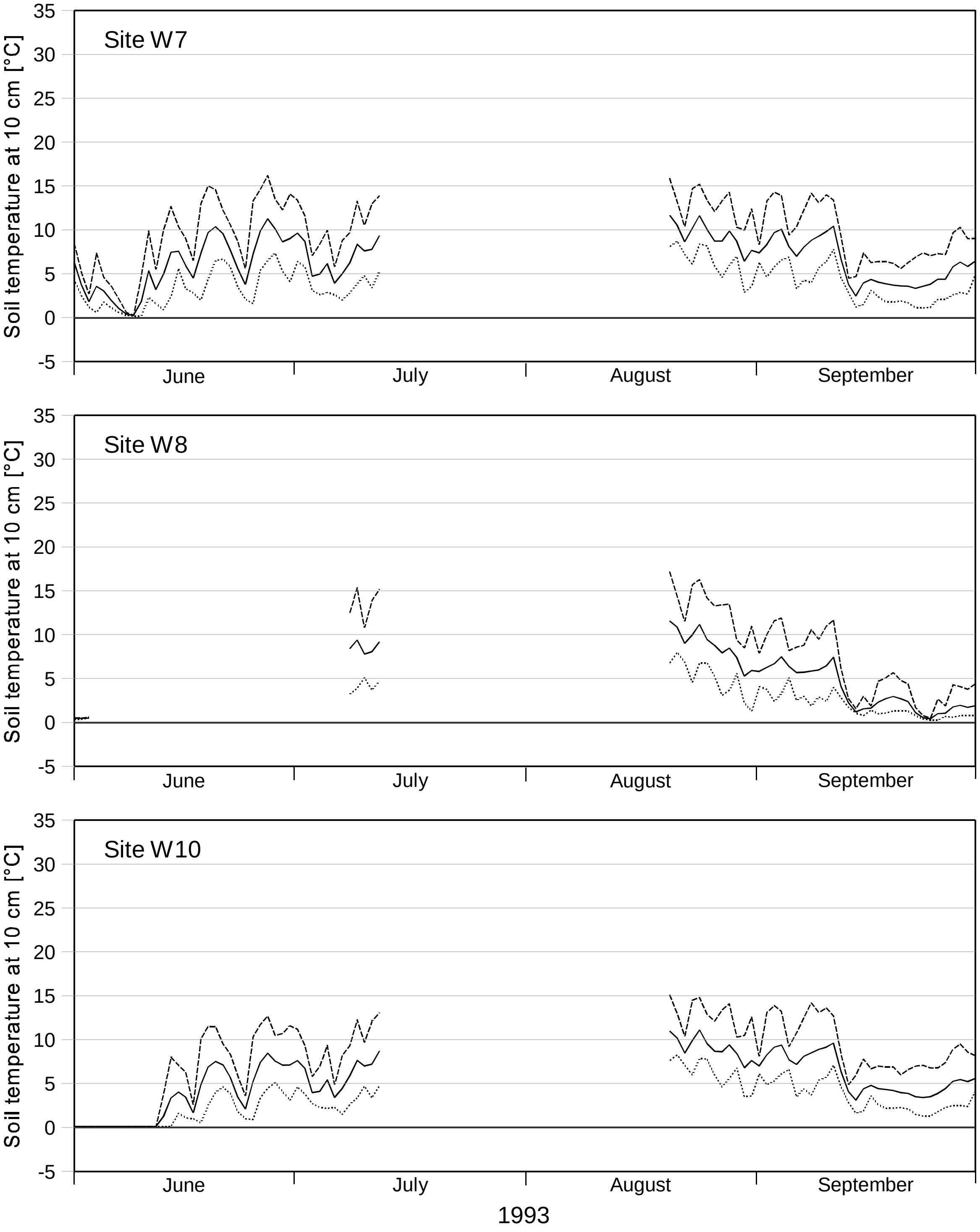

***Fig. 9.12:** Soil temperatures at 10 cm depth on Wyoming Creek, summer 1993. Dashed lines repre-sent daily maxima, solid lines daily averages, and dotted lines daily minima.*

Site T5

No data at 10 cm for 1994

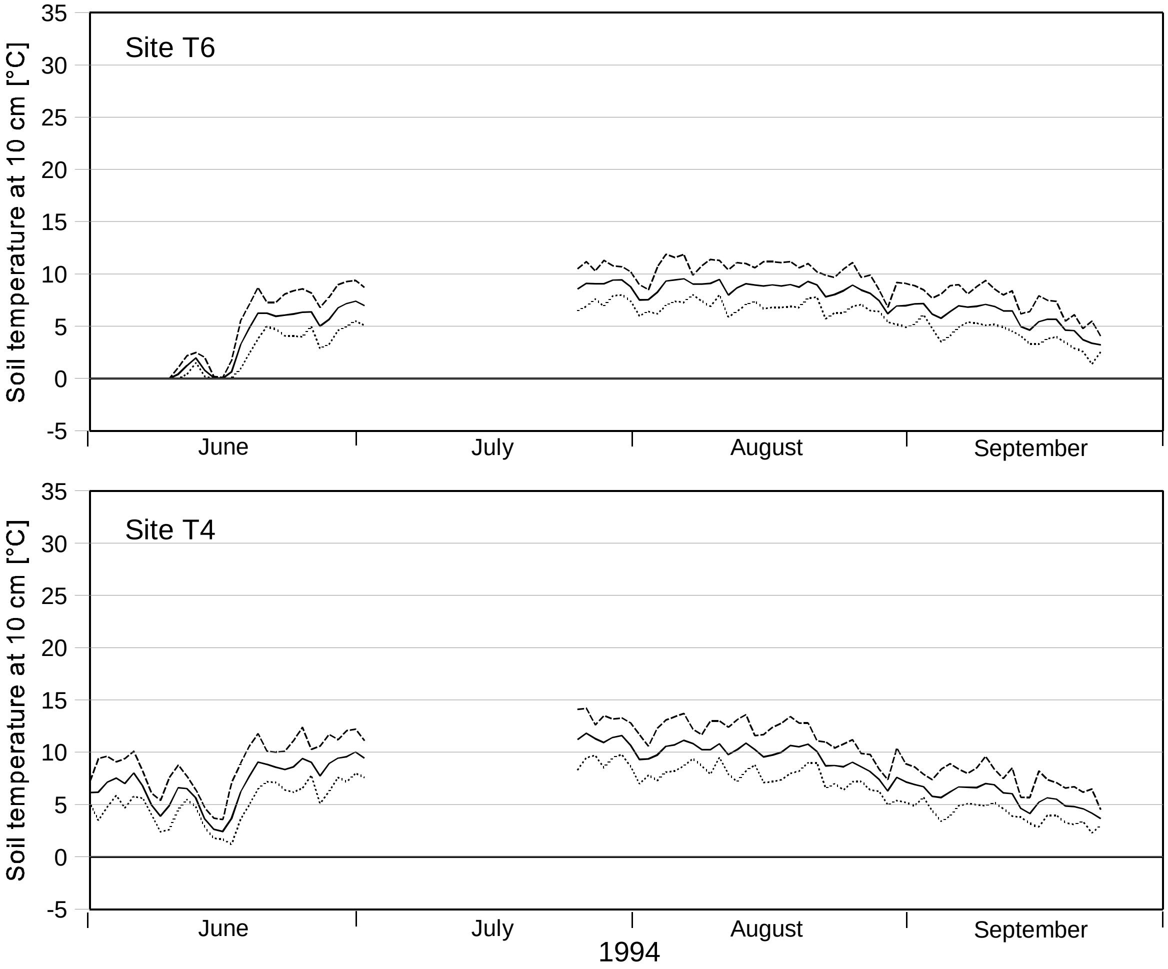

Fig. 9.13: *Soil temperatures at 10 cm depth on Tibbs Butte, summer 1994. Dashed lines represent daily maxima, solid lines daily averages, and dotted lines daily minima.*

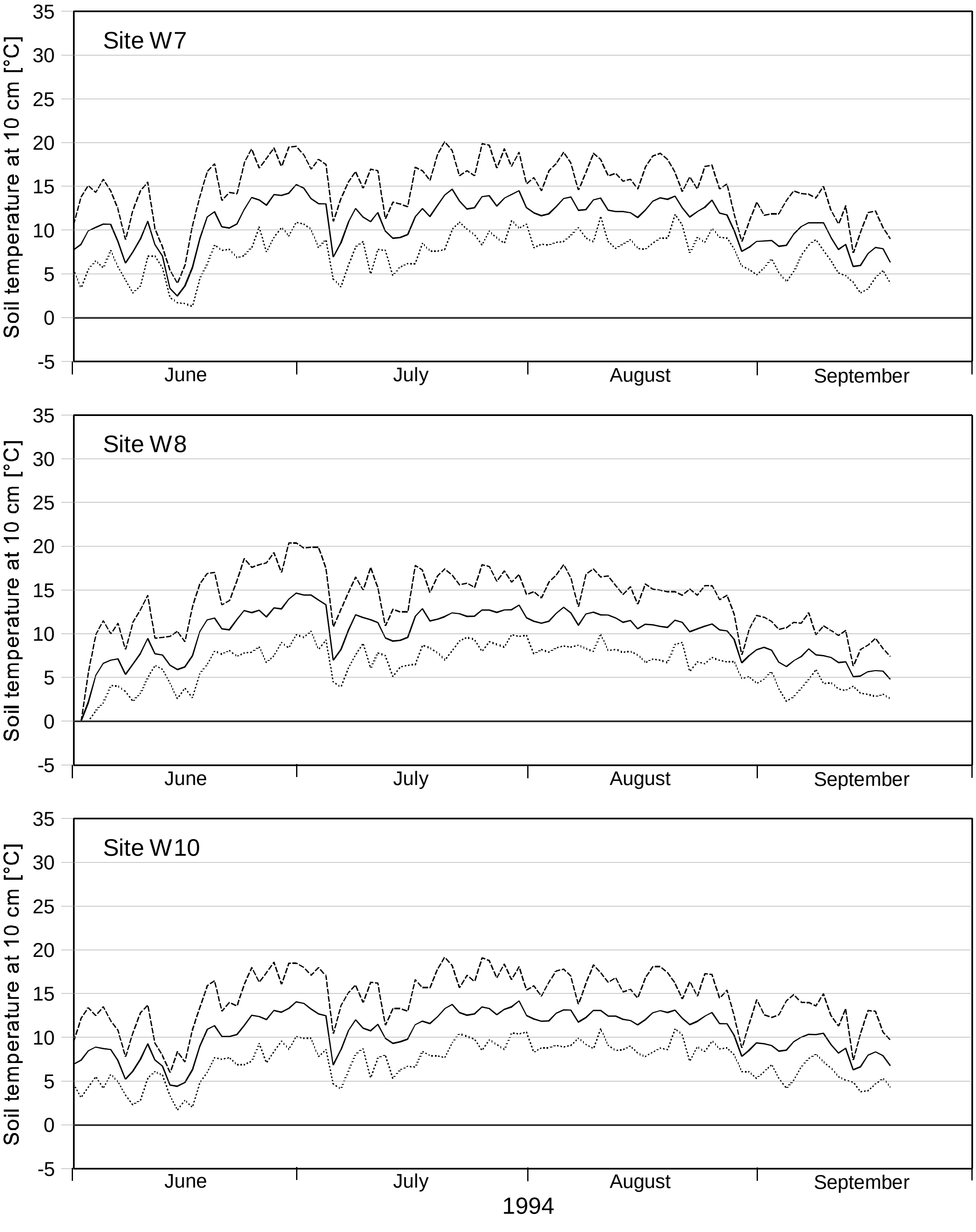

Fig. 9.14: Soil temperatures at 10cm depth on Wyoming Creek, summer 1994. Dashed lines repre-sent daily maxima, solid lines daily averages, and dotted lines daily minima.

9.4 Results of the germination experiment

Table 9.21: *Germination and survival of whitebark pine seedlings in 19 experiment sites. Sites with no germination are omitted from table. Survival data were collected between September 15 and October 7 of each year.*

	Germination			**Survival**							
Site	**1992**	**1993**	**1994**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2001**
L3	0	4	0	4	0	0	0	0	0	0	0
L6	0	4	0	2	0	0	0	0	0	0	0
L7	0	28	0	10	0	0	0	0	0	0	0
L8	0	22	0	16	6	3	2	2	2	2	2
W1	0	63	0	52	45	42	36	22	22	21	21
W2	0	34	0	26	13	11	10	9	9	8	6
W3	0	30	0	22	10	8	7	7	6	6	6
W4	0	31	0	18	3	2	1	0	0	0	0
W5	0	42	0	22	18	11	3	0	0	0	0
W6	0	24	0	22	21	21	21	21	21	21	21
W7	0	26	0	20	11	11	11	10	10	10	10
W8	0	60	0	27	9	5	1	0	0	0	0
W9	4	32	9	19	10	8	4	0	0	0	0
W10	0	46	0	40	21	15	12	12	11	11	10
R1	0	24	0	21	12	11	6	2	2	2	2
R2	0	44	0	30	17	12	4	2	1	1	1
R3	0	19	0	16	11	10	5	0	0	0	0
R4	0	1	0	1	0	0	0	0	0	0	0
R5	0	9	0	8	0	0	0	0	0	0	0
Total	4	543	9	376	207	170	123	87	84	82	79

Table 9.22: *Germination and survival of whitebark pine clusters (planting locations with germination) in 19 experiment sites. Sites with no germination are omitted from table. Survival data were collected between September 15 and October 7 of each year.*

	Germination			**Survival**							
Site	**1992**	**1993**	**1994**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2001**
L3	0	1	0	1	0	0	0	0	0	0	0
L6	0	2	0	2	0	0	0	0	0	0	0
L7	0	12	0	6	0	0	0	0	0	0	0
L8	0	7	0	7	4	2	1	1	1	1	1
W1	0	15	0	13	13	12	12	7	7	7	7
W2	0	12	0	11	6	5	5	5	5	5	5
W3	0	8	0	7	4	4	4	4	3	3	3
W4	0	13	0	9	2	2	1	0	0	0	0
W5	0	15	0	11	9	5	1	0	0	0	0
W6	0	7	0	7	7	7	7	7	7	7	7
W7	0	8	0	7	4	4	4	4	4	4	4
W8	0	15	0	10	5	4	1	0	0	0	0
W9	1	11	2	11	7	6	3	0	0	0	0
W10	0	13	0	13	12	10	7	7	7	7	6
R1	0	10	0	9	6	6	5	2	2	2	2
R2	0	14	0	11	6	5	2	2	1	1	1
R3	0	7	0	7	6	5	2	0	0	0	0
R4	0	1	0	1	0	0	0	0	0	0	0
R5	0	4	0	4	0	0	0	0	0	0	0
Total	1	175	2	147	91	77	55	39	37	37	36

Table 9.23: *Height of 1993 whitebark pine seedling clusters that survived to 2001, in cm. Clusters are represented by their largest healthy seedling.*

Site	Cache	1994	1995	1996	1997	1998	1999	2001
W1	1.3	2.4	2.8	3.4	3.6	3.8	4.2	7.6
W1	2.1	2.4	2.6	3.0	3.3	4.8	6.1	9.8
W1	2.3	2.0	2.7	3.2	3.5	4.2	5.5	10.2
W1	3.3	1.8	2.7	3.0	3.5	3.7	4.2	4.9
W1	5.1	3.3	3.7	4.2	5.0	6.4	9.1	13.2
W1	5.2	2.7	3.4	3.8	4.8	5.8	9.0	15.3
W1	5.3	2.1	2.7	2.9	3.5	4.0	4.5	6.6
W2	1.3	2.4	2.6	3.1	3.5	3.7	4.3	5.5
W2	3.1	1.5	1.6	1.9	2.2	2.7	3.3	4.3
W2	4.2	2.2	2.6	2.7	3.0	3.3	3.9	5.6
W2	5.2	2.6	2.6	3.0	3.7	3.7	4.5	5.1
W2	5.3	2.2	2.4	2.2	2.8	2.7	2.7	3.1
W3	1.1	2.9	3.8	4.5	5.2	6.2	8.7	15.0
W3	2.1	2.1	2.8	3.0	4.1	4.6	5.6	7.2
W3	4.2	1.7	2.5	2.6	3.2	3.6	3.9	4.6
W6	1.3	2.3	2.9	3.2	4.1	4.8	7.2	12.0
W6	2.2	2.5	2.9	3.6	4.2	4.8	5.5	7.8
W6	2.3	2.2	2.7	3.0	4.4	5.7	7.4	11.5
W6	3.2	2.8	3.2	4.1	5.0	5.7	8.9	13.1
W6	3.3	2.9	3.7	4.2	5.2	5.4	5.9	10.4
W6	4.3	2.0	2.5	3.2	4.0	5.2	5.9	9.2
W6	5.1	2.8	3.6	4.9	5.3	6.5	7.5	12.3
W7	1.3	3.0	3.8	4.6	5.1	5.5		7.6
W7	2.1	1.8	1.7	2.3	2.4	2.6		3.2
W7	3.3	2.9	3.2	3.4	4.1	5.0		7.2
W7	4.1	2.6	2.9	3.4	3.7	3.9		6.9
W10	1.1	2.2	2.2	2.3	2.8	3.2	3.4	4.9
W10	1.2	3.1	3.2	3.7	4.2	5.0	5.3	7.8
W10	1.3	3.1	3.0	3.7	4.4	5.2	6.2	9.2
W10	2.1	2.2	2.6	2.9	3.5	4.0	5.0	8.1
W10	2.3	1.6	1.7	1.9	2.5	2.8	3.5	4.2
W10	3.2	2.3	2.1	2.4	2.5	2.8	3.0	4.8
R1	1.1	1.7	2.2	2.5	2.9	3.0	3.0	3.2
R1	2.1	1.7	2.3	1.9	1.8	1.7	1.9	2.6
R2	2.3	2.2	2.7	2.5	2.8	3.4	3.0	3.8
L8	5.2	3.2	3.8	4.0	4.0	4.7		6.5
min		1.5	1.6	1.9	1.8	1.7	1.9	2.6
max		3.3	3.8	4.9	5.3	6.5	9.1	15.3
avg		2.4	2.8	3.2	3.7	4.3	5.2	7.6
std		0.49	0.59	0.78	0.93	1.21	2.01	3.49

Table 9.24: *Diameters of 1993 whitebark pine seedling clusters that survived to 2001, in cm. Clusters are represented by their largest healthy seedling, and were measured approx. 1 cm above ground.*

Site	Cache	1994	1995	1996	1997	1998	1999	2001
W1	1.3	0.17	0.18	0.18	0.20	0.21	0.25	0.36
W1	2.1	0.16	0.16	0.16	0.19	0.22	0.28	0.35
W1	2.3	0.17	0.18	0.18	0.19	0.20	0.28	0.38
W1	3.3	0.15	0.17	0.12	0.17	0.19	0.18	0.21
W1	5.1	0.16	0.17	0.17	0.19	0.21	0.31	0.44
W1	5.2	0.18	0.18	0.19	0.23	0.26	0.34	0.48
W1	5.3	0.15	0.14	0.14	0.17	0.16	0.20	0.27
W2	1.3	0.17	0.17	0.17	0.18	0.18	0.22	0.30
W2	3.1		0.14	0.15	0.16	0.19	0.29	0.38
W2	4.2	0.14	0.14	0.13	0.15	0.17	0.20	0.29
W2	5.2	0.16	0.15	0.14	0.18	0.23	0.27	0.32
W2	5.3	0.17	0.14	0.14	0.15	0.15	0.19	0.20
W3	1.1	0.17	0.16	0.16	0.21	0.23	0.33	0.44
W3	2.1	0.14	0.16	0.17	0.18	0.22	0.32	0.39
W3	4.2	0.21	0.16	0.16	0.20	0.22	0.24	0.36
W6	1.3	0.17	0.21	0.19	0.23	0.23	0.34	0.42
W6	2.2	0.17	0.18	0.19	0.24	0.23	0.28	0.40
W6	2.3	0.15	0.18	0.20	0.23	0.23	0.26	0.35
W6	3.2	0.17	0.19	0.20	0.22	0.26	0.33	0.45
W6	3.3	0.18	0.24	0.25	0.28	0.30	0.34	0.39
W6	4.3	0.16	0.18	0.17	0.22	0.23	0.24	0.33
W6	5.1	0.18		0.21	0.25	0.28	0.37	0.38
W7	1.3	0.14	0.17	0.18	0.21	0.22		0.24
W7	2.1	0.13	0.12	0.14	0.16	0.23		0.24
W7	3.3	0.17	0.18	0.18	0.21	0.23		0.26
W7	4.1	0.15	0.17	0.14	0.19	0.23		0.34
W10	1.1	0.14	0.16	0.15	0.18	0.20	0.19	0.27
W10	1.2	0.13	0.16	0.16	0.15	0.19	0.20	0.35
W10	1.3	0.16	0.17	0.16	0.17	0.20	0.25	0.32
W10	2.1	0.14	0.15	0.14	0.16	0.24	0.24	0.39
W10	2.3	0.12	0.14	0.12	0.16	0.17	0.19	0.26
W10	3.2	0.16	0.14	0.16	0.18	0.20	0.24	0.33
R1	1.1	0.15	0.14	0.14	0.14	0.18	0.17	0.20
R1	2.1	0.12	0.14	0.14	0.14	0.15	0.15	0.16
R2	2.3	0.18	0.16	0.15	0.20	0.20	0.20	0.29
L8	5.2	0.16	0.16	0.15	0.19	0.20		0.33
min		0.12	0.12	0.12	0.14	0.15	0.15	0.16
max		0.21	0.24	0.25	0.28	0.30	0.37	0.48
avg		0.16	0.16	0.16	0.19	0.21	0.25	0.33
std		0.019	0.023	0.027	0.033	0.033	0.060	0.077

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