ENVIRONMENTAL DETERMINANTS OF SUBALPINE TREELINES IN THE VALLES CALDERA, NEW MEXICO

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Abstract

Environmental determinants of subalpine treelines in the Valles Caldera, New Mexico

Subalpine grasslands are prominent but poorly understood features of the southern Rocky Mountains. Grasslands frequently occur in broad valleys, forming abrupt subalpine treelines where they abut forested mountain slopes. Nearly 10,000 ha of such grasslands occur in the Valles Caldera National Preserve (VCNP) in the Jemez Mountains of northern New Mexico. To assess the causes of this pattern I conducted gradient analyses, observations on adult tree growth and moisture relations, experimental tests of tree seedling establishment, and a reconstruction of historic landscape dynamics using aerial photographs and tree establishment dates from increment cores.

Gradient analysis revealed that the position of subalpine treelines in the VCNP was most strongly associated with spatially coupled shifts in the thermal regime due to cold air drainage and pooling in the valleys (partial Mantel $r = 0.76$, $P < 0.001$) and edaphic factors, particularly increased % sand on the forested slopes and increased % clay in the valleys (partial Mantel $r = 0.12$, $P < 0.05$). Adult ponderosa pine (*Pinus ponderosa* var. *scopulorum*) trees growing at the inverted valley bottom treelines did not show decreased growth relative to trees on forested slopes above, as would be expected if these treelines were analogous to alpine treelines. In fact, adult trees exhibited greater rates of radial growth and lower moisture stress at treeline.

Ponderosa seedlings transplanted into 32 sites in valley bottoms and mountain slopes showed very strong decreases in growth at sites experiencing lower minimum temperatures and greater incidence of growing-season frosts. Measurements of chlorophyll fluorescence suggested that cold-induced photoinhibition in tree seedlings was frequent in grassland sites. Transplanted seedling survival was greatest on sandy soils and at warmer sites, though this pattern was substantially weakened by high mortality from golden-mantled ground squirrels (*Spermophilus lateralis*) on warmer sites in forest clearings.

Between 1935 and 1996, the area of grasslands in the Valles Caldera declined by 18%. Tree invasion was most pronounced, and more continuous, on high, steep, south-facing slopes where grassland maintenance was most dependent on frequent ground fires. Tree invasion in valley bottoms was relatively less severe, and increased during periods of higher temperatures.

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Introduction

Environmental determinants of subalpine treelines in the Valles Caldera, New Mexico

Subalpine grasslands in the Rocky Mountains

Subalpine grasslands are prominent but poorly understood features of otherwise forested landscapes in the southern Rocky Mountain region of the United States (Dick-Peddie 1993; Brown 1994; Peet 2000). These communities are commonly known as meadows or parks, and by the Spanish terms *vegas* and *valles* where they occur in the mountain valleys of northern New Mexico. They are dominated by graminoids and forbs in an otherwise wooded landscape, and as such contribute importantly to floristic diversity (Ramaley 1927; Peet 1981; Stohlgren et al. 1997), provide critical habitat for animals ranging from butterflies (Scott 1986; Holland and Cary 1996; Simonson et al. 2001) to elk (*Cervus elaphus* L.)(Boyce and Hayden-Wing 1979), and often provide substantial benefit to local economies through livestock grazing and recreation (Turner and Paulsen 1976).

Such grasslands have, however, received little scientific attention. Their herbaceous vegetation has been the focus of few quantitative studies, except for early descriptions of Boulder Park in Colorado (Ramaley 1910, 1915, 1916; Rydberg 1913; Reed 1917; Robbins 1918) and more recent work by Moir (1967) and Allen (1984) on high-elevation, grassy "balds" in the Sierra Blanca and Jemez Mountains of New Mexico. Moreover, the causes of the treeline ecotones that define these grasslands - and to which these grasslands owe their existence in an otherwise forested landscape - are unknown, although they have been the subject of considerable discussion.

Possible causes of subalpine treelines

Throughout the southern Rocky Mountain region, grasslands often occur on level or shallowly-sloping topography in valley bottoms (Ramaley 1927; Turner and Paulsen 1976; Brown 1994; Peet 2000), and form abrupt treeline ecotones where they abut forested mountain slopes. This pattern can be observed across a wide range of elevations, on different geologic substrates, and with different tree and grass species abutting at the treeline ecotone. Surprisingly, little quantitative study has focused on the shift from forested slopes to grassy valleys in the southern Rockies. However, numerous hypotheses have been proposed to account for this pattern in the southern Rockies, and for similar treelines elsewhere. These include the effects of spatially structured gradients in **(1) edaphic factors**, **(2) moisture shortage or excess**, **(3) thermal conditions**, and **(4) disturbance** on tree establishment, growth, and survival.

Additionally, **(5) positive feedbacks** may stabilize forest and grassland communities once established, or foster a dynamic balance based on the mutual tendencies of each to expand once present (see Wilson and Agnew 1992). Each of these hypotheses is developed below.

1. Edaphic factors

The occurrence of meadows and parks in the mountain valleys of the Rocky Mountain region is most frequently tied to finer-texture soils (Ramaley 1910, 1927; Daubenmire 1943; Peet 1981, 2000; Veblen and Lorenz 1986, but see Pearson 1913; Koterba and Habeck 1971). Perhaps the most commonly given hypothesis for treeless parks in the southern Rockies is that the increased moisture-holding capacity and nutrient availability of fine-textured soils promotes such a dense growth of grasses that tree seedling establishment is prevented by competition (Ramaley 1910, 1927; Peet 1981, 2000). Fine textured soils are often more productive in semi-arid grasslands elsewhere in the western U.S. (Sala et al. 1988; Singh et al. 1998), which may also result in increased grass competition with tree seedlings. A large body of literature documents the negative effects of herbaceous competition on tree seedling establishment for tree species of Rocky Mountain region (e.g. references cited in Stewart et al. 1984; Burns and Honkala 1990). Alternatively, heavy soils may directly impede tree seedling root penetrance, as proposed by Daubenmire (1943). However, Pearson (1913) and Koterba and Habeck (1971) suggested that grassy montane parks in Arizona and Montana occurred on sandier soils, and that the treeless condition at these sites was related to soil moisture deficits.

Fine-textured soils on lower slopes and flats might also decrease adult tree growth by reducing the availability of moisture to trees vs. grasses, which root at different depths (Walter 1971; Walker and Noy-Meir 1982). Walter (1971) proposed a two-layer soil system for semi-arid subtropical savannas, in which grasses outcompete woody plants for shallow soil moisture, but woody plants have exclusive access to deep moisture. Knoop and Walker (1985) found that the increased water-holding capacity of fine-textured topsoils in a subtropical savanna supported a dense growth of grasses that depleted the moisture available to deeply rooted woody plants, and resulted in decreased woody plant growth; however, they found no such effect on sandy soils.

2. Moisture shortage or excess

Some researchers have proposed that soil drought (Koterba and Habeck 1971; Doering and Reider 1992; Rhemtulla et al. 2002) or, conversely, waterlogging (Rydberg 1913; Ives 1942) may maintain montane and subalpine grasslands in valleys in the Rockies. Doering and Reider (1992) hypothesized that soil moisture deficits resulting from the soil-texture discontinuity of a 3-10 cm layer of gravel in Cinnabar Park in Wyoming prevented tree growth there. Grassy openings in the Rockies also occur on steep, south-facing ridgetops or mountaintops, where reduced soil depth and limited moisture availability have been proposed to prevent tree establishment (Rydberg 1913; Moir 1967, Daubenmire 1968). Alternatively, Rydberg (1913) and Ives (1942) have both proposed that treeless parks may occur on sites where saturated, anoxic soils inhibit conifer establishment or growth.

3. Cold-air drainage

Ramaley (1910) proposed that the treeless valley bottoms of Boulder Park, in Colorado, might be due in part to the pooling of cold air, though he also advanced soil texture and competition as causes of this park. The deleterious effects of cold-air drainage on tree growth and survival has been the favored explanation for analogous subalpine grasslands in concave

basins in the mountains of Australia and New Zealand (Wardle 1971; Smith 1975; Moore and Williams 1976; Paton 1988), where the term "inverted treeline" or "inverted timberline" is widely used to describe the shift from grassy basins to forested slopes. However, grass competition (Fensham and Kirkpatrick 1992) and waterlogged soils (Gilfedder 1988) have also been proposed as causes of treelines in these systems.

Low nightly minimum temperatures in valley bottoms followed by daily high insolation might cause cold-temperature photoinhibition, which has been demonstrated to adversely affect tree seedling growth and survival at or near alpine treelines (Ball et al. 1991; Germino and Smith 1999). Growing season frosts are known to damage to growing conifer tissues, especially needles. Schubert and Adams (1971) reported that unhardened needles of ponderosa pine exposed to temperatures < -3° C experienced substantial injury. Similarly, Tranquillini (1987) found that Norway spruce required at least 50 consecutive days without frosts = -3° C to avoid damage to growing needles, and a total of 90 days without frosts = -3° C for needle cuticles to become adequately developed to avoid winter desiccation. Frost-heaving of soils has been reported to result in extensive root damage to young ponderosa seedlings (Larson 1960; Heidmann and Thorud 1976).

Cold temperatures in valley bottoms may also reduce adult tree growth via mechanisms similar to those proposed to cause alpine treelines. These include (1) reduced photosynthetic period (Tranquillini 1979); (2) decreased photosynthetic capacity due to frost damage, especially for taller plants unsheltered by snow or the ground boundary layer (Tranquillini 1979; Grace 1988); (3) desiccation resulting from frozen soils (Tranquillini 1979; Sowell et al. 1982); and (4) cold-temperature photoinhibition (e.g. Ball 1991). Any or all of these factors may make it impossible for tall woody plants to maintain a positive carbon balance, given the necessary allocation to wood production (e.g. Daubenmire 1954) and the increasing fraction of annual production allocated to wood as plant height increases (Givnish 1995). Alternatively, cold temperatures in low-lying sites may (5) reduce tree growth by impeding cell division and differentiation as has been proposed to occur at alpine treelines by Körner (1998).

4. Disturbance

Fire is often considered an important factor in the generation or maintenance of grassy openings in the Rockies on the steep, south-facing slopes of high mountains (Langenheim 1962; Moir 1967; Allen 1984, 1989). However, it may be much less important in maintaining the subalpine treeline ecotones that border broad valley bottoms, given the many other factors (discussed above) that could potentially limit tree seedling establishment or growth at these sites, and given the cool and often relatively moist conditions in these grasslands. In fact, Ramaley (1926), Despain (1973), and Doering and Reider (1992) explicitly dismissed fire as causes of treeless parks, noting that after fires had burned across subalpine parks or adjacent forests, trees only became re-established on the previously forested side of former treeline ecotones. Doering and Reider (1992) and Schauer et al. (1998) also noted that trees quickly became reestablished in logged areas immediately adjacent to treeless parks in Colorado and Wyoming, but not in the parks themselves. Ramaley (1926) also pointed out that fires usually burn in an uphill direction, rather than proceeding from a mountain slope down into an open basin.

However, at lower elevations in the semi-arid western U.S., fire has in been invoked as the primary mechanism by which trees were excluded from gentle topography and restricted to steeper terrain (Wells 1965; Burkhardt and Tisdale 1976; Miller and Rose 1995). These authors proposed that the greater continuity of grassy fine fuels on flat or gently rolling topography,

perhaps combined with greater grass production on finer-textured, more nutrient rich soils, supported a fire regime inimical to the survival of tree seedlings. Tree seedlings were likely to escape fire only on thin and rocky soils of steep slopes, or where rocky firebreaks of cliffs and bluffs decreased the quantity and continuity of grassy fuels. Under this hypothesis, treeline ecotones correspond to the position on a topographically-mediated gradient of grassy fuel continuity and increasing fire frequency beyond which trees or their seedlings are unable to escape being killed by fire. Such a gradient in fire frequency could be further reinforced or even stabilized by resultant differences in vegetation and fuel dynamics. Recent fire histories from forest-grassland ecotones in the Black Hills (Brown and Sieg 1999) and woodland-grassland ecotones of the Colorado Front Range (Weider and Bower 2004) have higher fire frequencies at stands bordering the grasslands of the Great Plains than at more interior stands. However, it is not clear to what extent these differences in fire frequency were driven by a topographically-mediated gradient in fine-fuel continuity, as opposed to the divergent fuel dynamics of grassy vs. forested vegetation, or dissimilarities in elevation, precipitation, or other abiotic factors.

Herbivory is another type of disturbance that may form subalpine treelines, or otherwise affect their position on the landscape. Cantor and Whitham (1989) found that pocket gophers (*Thomomys bottae*) caused extensive aspen (*Populus tremuloides*) mortality on the deep soils of montane meadows in Arizona, but not on thin-soiled rock outcrops. They proposed that these outcrops served as refugia for aspen, and that aspen invasion of the montane meadows they studied was largely limited by the belowground herbivory of pocket gophers. High levels of Rocky Mountain elk (*Cervus elaphus*) browsing has nearly eliminated aspen reproduction, especially in the winter ranges of large herds in the western U.S. (e.g. Hessl et al. 2002; Kaye et al. 2003). Palmer et al. (2003) found that ungulate effects on non-preferred food sources increased as a function of proximity to preferred resources. Hence, even though aspen and conifer seedlings may not be the preferred food source for ungulates in the Rockies (including elk, domestic cattle, and sheep), the detrimental impacts of these herbivores on tree seedlings are likely to increase as a function of proximity to preferred grassy vegetation of subalpine parks and meadows.

5. Positive feedbacks

Positive feedbacks may further influence the stability, sharpness, and position of treelines generated by any of the processes described above. Given the apparent consistency of the association between subalpine treelines and shifts from steep to level slopes in the southern Rockies, it is unlikely that positive feedbacks alone generate or maintain these treelines. However, once formed, trees may create conditions favorable to their own establishment or growth in cool-temperate or boreal areas by reducing wind speeds and associated mechanical stresses and evaporation (Billings 1969, Alftine and Malanson 2004); increasing soil moisture, temperature, and nitrogen availability (Belsky et al.1989; Li and Wilson 1998; Siemann and Rogers 2003); and suppressing shade-intolerant grasses and thereby reducing the competition faced by their own seedlings, and the frequency and intensity of fire and grazing/browsing subsidized by the grasses (Bird 1930; Wilson and Agnew 1992; Li and Wilson 1998). In addition, tree seedlings and saplings may experience photoinhibition or other photodamage as a result of heavy re-radiative heat loss at night in the absence of a protective tree canopy (Jordan and Smith 1995; Germino and Smith 1999; Germino et al. 2002; Davidson et al. 2004; Johnson et al. 2004). Grasses may favor their own spread by interfering with the establishment of tree

seedlings or (less plausibly in subalpine ecosystems of the southern Rockies) increasing fire frequency or intensity (see above).

Study area

Subalpine grasslands in the Valles Caldera National Preserve

In the newly established Valles Caldera National Preserve (VCNP; 35°50'-36°00'N; 106°24'-106°37'W) in the Jemez Mountains of northern New Mexico, approximately 10,000 ha of grasslands occur in a vast basin between 2575 and 2730 m elevation (Figure 1). Grasslands primarily occupy the expansive valley bottoms of the caldera floor. Several smaller meadows occur in minor valleys and drainages scattered over a wider range of elevations in the caldera. These grasslands occupy gently-sloping to level terrain, and form abrupt ecotones with forested stands dominated by ponderosa pine (*Pinus ponderosa* var. *scopulorum* Douglas ex. P.& C. Lawson) and Colorado blue spruce (*Picea pungens* Engelm.) on the surrounding mountain slopes. Smaller grassy openings also occur in minor drainages, and on south-facing slopes and mountain tops above ca. 3000 m. All of the grasslands and treeline ecotones under study fall well below alpine treeline (ca. 3500 m). We therefore refer to these communities and ecotones as *subalpine treelines* and *subalpine grasslands*. Given that these subalpine grasslands occur primarily above 2500 m, this terminology also agrees with the nomenclatural convention of Brown (1994), though the surrounding matrix of intermediate-elevation ponderosa pine and mixed-conifer forests are widely referred to as *montane* forests, as originally defined by Ramaley (1907).

Physiographic setting

The Valles Caldera is a 24 km-wide basin formed by explosive volcanic eruptions and the subsequent collapse of the underlying magma chamber ca. 1.22 Ma. (Smith and Bailey 1966, 1968; Izett and Obradovich 1994). The mountainous rim of the caldera reaches elevations ranging from 2850 to 3150m; the basin floor lies between 2575 and 2730 m. Within the caldera, resurgence and post-collapse ring-fracture volcanism have formed several secondary domes (Smith et al. 1970); the highest of these is Redondo Peak at 3370 m. The primary rock types of the mountain slopes are ignimbrite and rhyolite, with some pumice deposits. The caldera floor is underlain by a combination of Quaternary alluvium, fan deposits, and lacustrine sediments deposited by Pleistocene lakes (Smith et al. 1970). Soils include alfisols and inceptisols beneath forested vegetation on the slopes, and well-developed mollisols in the grassy valley bottoms (USDA Soil Conservation Service 1987).

The climate in the VCNP is semi-arid and continental. No long-term climatological data exist for the VCNP. At the nearest climate station in the interior of the Jemez Mountains (Wolf Canyon; 35°57'N, 106°45'W, 2505.5m), the 50-year mean total annual precipitation is 57.6 cm (years 1954-2004). Summers are generally characterized by severe drought in May and June followed by monsoonal, convective showers, which occur almost daily during July and August. Fifty-year mean monthly high and low temperatures at Wolf Canyon are 3.4° and -13.5° C in January, 24.9° and 5.7° C in July. Additional climatic data from Wolf Canyon are listed in Table 1.

Holocene dynamics of montane and subalpine vegetation in the Jemez Mountains

Relatively little is known about Holocene ecological changes in the Jemez Mountains region. Palynological analysis has been conducted on sediment cores collected at two sites in the Jemez Mountains, at Alamo Bog (2630 m, in the VCNP, see Figure 1) (Stearns 1980; Brunner-Jass 1999) and at Chihuahueños Bog (2930 m, northern rim of Valles Caldera: Brunner-Jass 1999). Stearns (1980) obtained basal radiocarbon date of 4595 ± 105 BP from a single core in Alamo Bog; Brunner-Jass (1999) obtained basal radiocarbon dates of 7940 ± 80 BP at Alamo Bog and 11, 850 ± 80 BP at Chihuahueños Bog. Both authors reported that the modern dominant plant species at both of these sites are well-represented throughout the length of their cores, suggesting relatively little overall vegetation change at either site over most of the Holocene.

Human land use history and recent ecological changes in the Valles Caldera

Human occupation in surrounding areas of New Mexico has been documented to date back to at least 11 Ka with early Paleoindian era sites; however, the earliest dates of human use of the Valles Caldera are poorly known (Baker and Winter 1981; Acklen 1997; Chomko 2005). Human use throughout prehistory probably focused primarily on obsidian procurement along the periphery of Cerro del Medio (Figure 1), in the center of the Valles Caldera. The earliest evidence of extensive human use of the caldera is in the Archaic period (5500 B.C. – 400 A.D.), particularly after 1800 B.C. in the Late Archaic. Archaic sites precede the development of large pueblos across mesas and plateaus at lower elevations in the Jemez Mountains during the Ancestral Pueblo period (A.D. 400 – 1600). Seasonal agricultural use probably after A.D. 900 is indicated on the Banco Bonito in the southwest corner of the study area (Figure 1) where numerous small stone structures known as field houses are documented (Kulisheck 2003). While the ecological impacts of Puebloan use of the Valles Caldera are unknown, it is unlikely that native people in this region substantially increased fire regimes, given the very high frequency of natural ignition from lightning strikes (Swetnam and Baisan 1996; Allen 2002).

While Spanish settlement of the upper Rio Grande valley began in the late 16th century, livestock grazing in interior of the Jemez Mountains probably did not begin until the early-mid 1800's (Martin 2003; Anschuetz and Merlan 2004 and sources therein). Unfortunately, documentation of livestock numbers and grazing practices in the Valles Caldera is very scarce. Early livestock grazing in the Valles Caldera appears to have been limited to minor sheep grazing by Hispanic shepherds and pasturing of horses by Jemez Pueblo members, and was mostly limited to the Sulfur Canyon drainage and in some of the northern valles (Martin 2003; Anschuetz and Merlan 2004). However, it was not until the Navajo and Apache were forcibly removed in 1860's and a nearby railroad terminal completed at Española in 1881 that large-scale, seasonal grazing became economically viable in the interior of the Jemez Mountains (Martin 2003). In 1860, as part of settlement of a land dispute, the United States granted 40,470 ha of the Valles Caldera to the heirs of Luis Maria Cabeza de Vaca; this area thus became known as Baca Location No. 1. Rothman (1989) documented the presence of herds of sheep in the Valles Caldera in summer by the late 1880's. Estimates of sheep numbers on Baca Location No. 1 in 1918 range from 20,000 to over 100,000 (Anschuetz and Merlan 2004).

The transition from sheep to cattle grazing on the Baca Location occurred during the 1940's and 1950's. A brief decline in wool prices from 1939-1940 probably marked the initiation of the shift away from sheep, and toward cattle grazing on the Baca Location No. 1 (Anschuetz and Merlan 2004). However, wool prices rose again during the 1940's, due to a demand for uniforms in World War II, and it was not until after the war, as newly-developed

synthetic fibers became available, that sheep grazing became entirely uneconomical (Martin 2003). In the early 1950's, 30,000 sheep and 5,000 cattle grazed on the property. By the end of the decade, sheep grazing had ceased, and cattle numbers had increased to 12,000 (Martin 2003). Cattle grazing practices may not have changed substantially until 2000, when the Baca Location No. 1 was publicly acquired through the Valles Caldera National Preservation and Federal Land Transaction Facilitation Act. The VCNP now occupies 35,560 ha of the former Baca Location (Figure 1). In addition to livestock, the Valles Caldera forms the core range of a large elk population, estimated between 4000 and 8000 (Martin 2003). Elk were extirpated from the Jemez early in the 20th century, but were reintroduced in 1947 and again in 1961. The herd grew slowly at first, but expanded rapidly after the La Mesa fire of 1977 opened up considerable winter range at lower elevations in Bandelier National Monument and the Santa Fe National Forest in the southeastern Jemez Mountains (Martin 2003).

Additional recent human impacts to the vegetation of the Valles Caldera include logging, geothermal exploration, and the general development of ranch infrastructure (e.g. roads, fences, stock tanks). Of these, only logging had the potential to substantially affect the dynamics of treeline ecotones. Logging practices from 1935 to 1962 involved the selective harvest of accessible, economically valuable old growth, primarily from forest margins along the valley bottom grasslands; from 1963 through 1972 extensive clearcutting occurred on the steep slopes and upper elevations of many of the secondary domes and mountain rims of the Valles Caldera (Balmat 2004). Logging activities ceased until 1980, but then resumed at moderate levels until the public acquisition of the VCNP in 2000 (Balmat 2004).

Changes in the fire regime in the Jemez Mountains

Several studies have documented fairly high pre-settlement frequencies of widespread, synchronous fire over a range of elevations in the Jemez Mountains, followed by a near complete cessation of fire throughout the region in the 1890's (Swetnam and Baisin 1996; Allen et al. 1996; Morino et al. 1998). Fire histories have been reconstructed from fire scars at three locations in the VCNP (Morino et al. 1998) and at numerous nearby locations in the Jemez Mountains (Allen 1989; Swetnam and Baisin 1996; Allen et al. 1996; Morino et al. 1998). Of four trees sampled in a relict stand of old growth ponderosa near the forest-grassland ecotone (ca. 2700 m) in the Valle Grande, only two recorded more than a single fire between the mid-1600's and the late 1800's; the mean fire intervals (MFI) calculated for these two trees were 27 and 29 years (Morino et al. 1998). Fire scar data collected from five ponderosa pine stumps on a southwest aspect ca. 200 m from the forest-grassland ecotone at the base of Cerros del Abrigo (ca. 2700m, Figure 1) suggest a MFI of ca. 5-15 years (C.D. Allen, unpublished data). These studies provide some evidence that trees adjacent to forest-grassland ecotones in the VCNP did not experience more frequent fires than at other sites supporting continuous ponderosa pine forests in the Jemez, where reported MFI's range between ca. 3 and 20 years (Allen et al. 1996, Morino et al. 1998). Reconstructed fire histories based on scars sampled from 32 trees from ponderosa, limber pine, Douglas fir, and white fir near Alamo Bog (ca. 2650 m) reveal a MFI of ca. 15 years (Morino 1998). MFI's at all three sites are similar to those collected at similar elevations and vegetation types throughout the Jemez (Allen et al. 1996) and at other sites in the southwestern U.S. (e.g. Brown et al. 2001). Two-thirds of these fires occurred in the late spring or early summer, before the onset of monsoon rains in July. Several of the fire years found by these studies were common to more than one of these sites (separated by 5-15 km of

mountainous terrain), and to sites sampled elsewhere in the Jemez (Allen 1989; Allen et al. 1996). Across the almost the entire Jemez Mountains, the regime of fairly frequent fire came to an abrupt end in the late 1800's (Allen et al. 1996). The last fire scar occurred in 1861 at the Valle Grande site and in 1896 at both Cerros del Abrigo and Alamo Bog. The end of frequent fires in this period is attributed to the onset of large-scale livestock grazing (Allen et al. 1996), which removed the fine, grassy fuels necessary to support low-intensity ground fires.

Changes in the position of subalpine treelines in the VCNP

A recent ground-based photographic study (Hogan and Allen 1999) compared three photographs taken in valleys of the VCNP in 1907 by members of Vernon Bailey's Bureau of Biological Science expedition with photographs taken from the same locations in 1997. This study revealed that substantial forest encroachment had occurred at the inverted treelines along the margins of the broad, lower elevation valley bottoms. Tree invasion of grasslands on high-elevation mountaintops and south-facing slopes along the southeastern rim of the Valles Caldera has also been documented using aerial photography. Based on a comparison of photos taken in 1935 and 1981, Allen (1984, 1989) found that grasslands in the area he examined declined by nearly 55%, from 554 to 250 ha., which he attributed primarily to fire suppression and release from sheep grazing pressures in the 1930's.

Elsewhere in the Rocky Mountain region, tree invasion of montane and subalpine grasslands has been attributed to both changes in climate and changes in the disturbance regime, particularly fire suppression and grazing practices. Dyer and Moffett (1999) suggested a linkage between tree invasion of subalpine grasslands in southern New Mexico and warmer temperatures and increased precipitation. However, forest invasion of subalpine grasslands elsewhere has also been linked to periods of drier than normal climates (Franklin et al. 1971; Ostler et al. 1982; Butler 1986), presumably where moist soils or summer snowpack prevented tree seedling establishment. Several studies have tied woody encroachment with fire suppression (Koterba and Habeck 1971; Burkhart and Tisdale 1976) on sites where tree establishment may have been precluded by frequent fire lethal to tree seedlings. However, other researchers in this region have also connected specific episodes of tree invasion with the occurrence of fire (Butler 1986; Mast et al. 1998), which may have temporarily exposed a bare mineral seedbed, and decreased competition from grasses. Increased livestock grazing is often implicated as a trigger for forest invasion by decreasing grass competition (Dunwiddie 1977; Madanay and West 1983; Butler 1986; Miller and Wigland 1994), though other research has tied tree invasion in these systems to releases from heavy livestock grazing pressure (Vale 1981 a,b; Mast 1998).

Research Objectives

The purpose of this research is to evaluate the environmental determinants of subalpine treelines in the Valles Caldera. What environmental factors are responsible for the presence of these grasslands in an otherwise forested landscape? How do these factors give rise to subalpine treelines, and what processes underlie recent changes in the position of these ecotones? To answer these questions I have conducted an integrated series of (i) gradient analyses, (ii) observations on adult tree growth and moisture relations, (iii) experimental tests of tree seedling establishment, and (iv) a reconstruction of historic landscape dynamics using aerial photographs and tree establishment dates from increment cores.

In the first chapter (I), I present the results of a gradient analysis of 200 100-m^2 samples of vegetation and abiotic variables across multiple subalpine treelines in the VCNP. This

gradient analysis was designed to quantify the relationship between subalpine treelines in the VCNP and edaphic and thermal factors that have been proposed as potential causes of similar treelines elsewhere. I also address the potential problem of spatial autocorrelation, expected in ecological research in general, but especially in this case, where strong positive feedbacks may substantially influence treeline position independent of underlying abiotic gradients

In general, treeline ecotones may be caused by context-dependent restrictions on **adult tree growth** (Daubenmire 1954; Givnish 1995; Körner 1998, Li et al. 2002) and/or **tree seedling establishment** (Wardle 1971; Tranquillini 1979; Cuevas 2000). Given the correlations between treeline position, edaphic factors, and the thermal regime uncovered in the gradient analysis (Chapter I), the next two studies were designed to test for the effects of these factors on adult tree growth and tree seedling establishment. In the study outlined in chapter II, I tested the hypothesis that subalpine treelines in the VCNP are related to increasing constraints on adult tree growth with increasing proximity to treeline. I present findings on the factors that affected radial growth rates and moisture relations of adult ponderosa pine trees in a drought year (2002) and a more normal year (2003). In the research described in chapter III, I experimentally tested the effects of thermal conditions, soil texture, competition, and ungulate damage on ponderosa pine germination, seedling growth, and seedling survival across subalpine treelines.

To examine possible causes of recent treeline advances, and to further clarify the possible role of thermal constraints vs. disturbance on tree seedling establishment or survival in the VCNP, in the final chapter (IV), I reconstructed historic landscape dynamics between 1935 and 1996 using aerial photos and tree establishment dates estimated from increment cores. I present findings on the spatial and temporal patterns of tree invasion of subalpine grasslands in the Valles Caldera, and relate these patterns to changes in climate and human land use, in the context of my previous findings on the constraints on tree establishment in this system.

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Figures and Tables

Figure 1. The location of the Valles Caldera National Preserve (VCNP) in the Jemez Mountains, NM. The 1996 aerial phots used in this image clearly show the locations of large grasslands (uniform grey color) in the otherwise forested (darker vegetation) landscape.

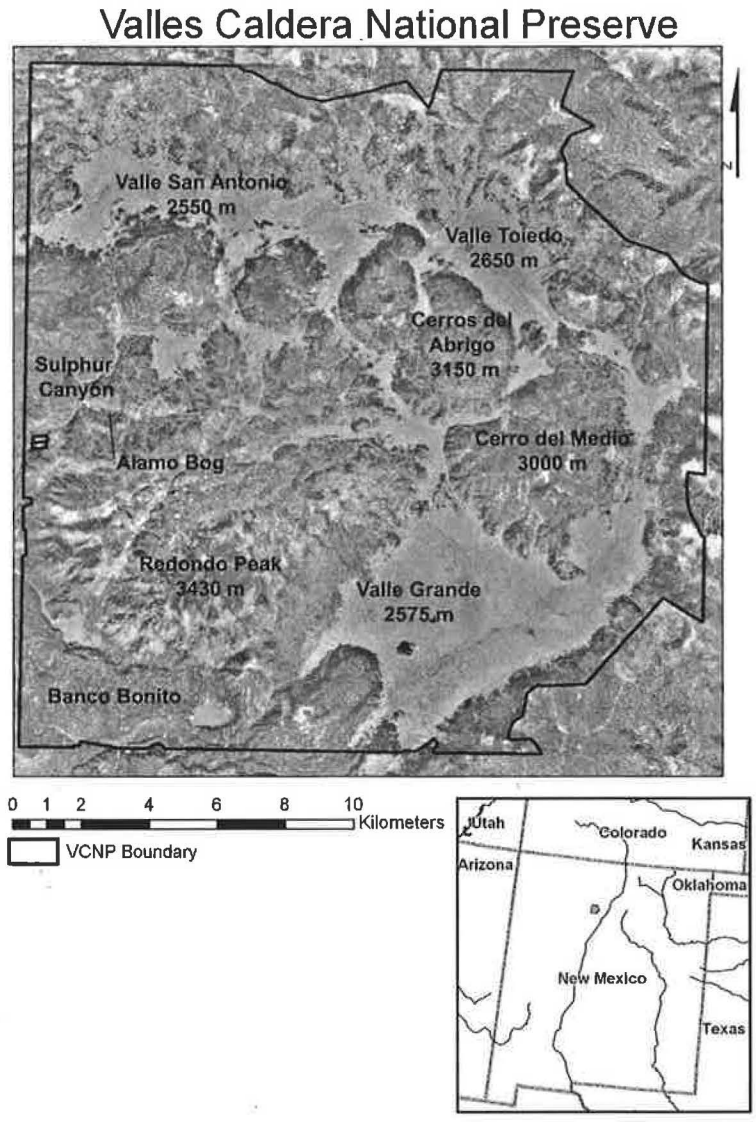


Table 1. Summary of monthly climate means (1 = January, 2 = February,...) for Wolf Canyon, New Mexico, since the beginning of record keeping in August 1912, through August 2004.

	1	2	3	4	5	6	7	8	9	10	11	12	Annual
Mean Temp. (C)	-5.8	-4.1	-0.7	3.8	7.9	12.5	15.4	14.5	10.9	5.6	-0.6	-4.6	4.6
Maximum Temp. (C)	3.5	4.8	7.8	12.9	18.1	23.8	25.3	23.9	21.0	15.3	8.6	4.7	14.2
Minimum Temp. (C)	-15.2	-13.0	-9.3	-5.3	-2.2	1.1	5.4	5.0	0.8	-4.2	-9.7	-13.8	-5.0
Total Precip. (cm)	4.2	4.3	4.6	3.6	3.4	3.0	8.6	8.6	5.1	4.3	3.4	3.8	56.9
Total Snowfall (cm)	55.8	55.3	56.2	27.7	7.2	0.1	0.0	0.0	1.1	8.9	28.7	50.0	290.9

Chapter I

Gradient Analysis of Subalpine Treelines and Grasslands of the Valles Caldera, Jemez Mountains, New Mexico

Abstract

Meadows and parks are poorly understood features of the mountains of the western U.S. Frequently these communities occupy valley bottoms, forming subalpine treelines where they adjoin forested slopes; however, this pattern has received little quantitative study. In the Jemez Mountains of New Mexico, 10,000 ha of subalpine grasslands occupy flats and gentle slopes within the Valles Caldera, shifting abruptly to forests of ponderosa pine and Colorado blue spruce on the surrounding mountain slopes. To assess the environmental determinants of these treelines, and elucidate patterns in diversity, compositional turnover, and their correlates in the caldera grasslands, we conducted a gradient analysis of this vegetation, based on 200 nested quadrats spanning the compositional heterogeneity of the grasslands and crossing treeline ecotones. We used non-metric multidimensional scaling, and simple- and partial- Mantel tests that control for spatial autocorrelation, to assess the relationship between plant compositional variation and measured environmental variables. Both methods reveal strong, highly significant relationships of the vegetation to gradients in slope, soil texture, moisture, nutrient availability, and thermal factors. Treeline position is most strongly associated with shifts in the thermal regime (partial Mantel $r = 0.76$, $P < 0.001$) and soil texture (partial Mantel $r = 0.12$, $P < 0.05$). Lower nightly minimum temperatures (and fewer consecutive frost-free days) results from cold air drainage into valley bottoms, and may prohibit tree seedling establishment via photoinhibition, tissue damage, or frost heaving. Fine-textured soils in valley bottoms may also impede tree seedling establishment directly, enhance the relative competitive ability of grasses. These findings lay the groundwork for further experimental and observational studies designed to test contrasting hypotheses for the causes of subalpine treelines.

Key words: ecotone, inverted treeline, timberline, park, ordination, gradient analysis, Mantel test, ponderosa pine

Introduction

Montane and subalpine grasslands are important features of the southern Rocky Mountain region of the United States, though the causes of their occurrence in an otherwise forested landscapes are not well known (Dick-Peddie 1993; Brown 1994; Peet 2000). These communities are commonly known as meadows or parks, and by the Spanish terms *vegas* and *valles* where they occur in the mountain valleys of northern New Mexico. They are dominated by graminoids and forbs in an otherwise wooded landscape, and as such contribute importantly to floristic diversity (Ramaley 1927; Peet 1981; Stohlgren et al. 1997), provide critical habitat for animals ranging from butterflies (Scott 1986; Holland and Cary 1996; Simonson et al. 2001) to elk (*Cervus elaphus* L.) (Boyce and Hayden-Wing 1979) and often benefit local economies through livestock grazing and recreation (Turner and Paulsen 1976).

Such grasslands have, however, received scientific attention. Their herbaceous vegetation has been the focus of few quantitative studies, except for early descriptions of Boulder Park in Colorado (Ramaley 1910, 1915, 1916; Rydberg 1913; Reed 1917; Robbins 1918) and more recent work by Moir (1967) and Allen (1984) on high-elevation, grassy "balds" in the Sierra Blanca and Jemez Mountains of New Mexico. Moreover, the causes of the treeline ecotones that define these grasslands - and to which these grasslands owe their existence in an otherwise forested landscape - are unknown, although they have been the subject of considerably more discussion.

Throughout the southern Rocky Mountain region, grasslands often occur on level or

shallowly-sloping topography in valley bottoms (Ramaley 1927; Turner and Paulsen 1976; Brown 1994; Peet 2000), and form abrupt treeline ecotones where they abut forested mountain slopes. Numerous hypotheses have been proposed to account for this pattern in the southern Rockies, and similar treelines elsewhere, including the effects of **edaphic factors**, **moisture limitations or excesses**, and **thermal conditions** on tree establishment or growth. The occurrence of meadows and parks in the southern Rocky Mountain region is frequently tied to fine-textured soils (Ramaley 1910, 1927; Daubenmire 1943; Peet 1981, 2000; Veblen and Lorenz 1986). Heavy soils may directly impede tree seedling root penetrance (Daubenmire 1943). Alternatively, the increased moisture-holding capacity and nutrient availability of fine-textured soils may promote such a dense growth of grasses that tree seedling establishment is prevented by competition (Ramaley 1910, 1927; Peet 1981, 2000). Fine-textured soils on lower slopes and flats might also decrease adult tree growth by reducing the availability of moisture to trees vs. grasses, which root at different depths (Walter 1971; Walker and Noy-Meir 1982). Some researchers have proposed that soil drought (Koterba and Habeck 1971; Doering and Reider 1992) or, conversely, waterlogging (Ives 1942, Rydberg 1913) maintains montane and subalpine grasslands in valleys in the Rockies. Ramaley (1910) also proposed that treeless valley bottoms may be due partly to the pooling of cold air. The deleterious effects of cold-air drainage on tree growth and survival has been the favored explanation for analogous subalpine grasslands in concave basins in the mountains of Australia and New Zealand (Wardle 1971; Smith 1975; Moore and Williams 1976; Paton 1988), where the term "inverted treeline" or "inverted timberline" is widely used to describe the shift from grassy basins to forested slopes. However, grass competition (Fensham and Kirkpatrick 1992) and waterlogged soils (Gilfedder 1988) have also been proposed as causes of treelines in these systems. Grassy openings in the Rockies also occur on steep, south-facing ridgetops or mountaintops, where fire (Langenheim 1962; Allen 1984) or reduced soil depth and moisture availability (Rydberg 1913; Moir 1967, Daubenmire 1968) is likely to be responsible.

Subalpine grasslands and the treeline ecotones that define them may also be independent of current ecological gradients, reflecting historic disturbances by fire or other agents. Once formed, positive feedbacks may stabilize forest and grassland communities once established or foster a dynamic balance based on mutual tendencies to expand (see Wilson and Agnew 1992). Trees may create conditions favorable to their own establishment or growth in cool-temperate or boreal areas by reducing wind speeds and associated mechanical stresses and evaporation (Billings 1969, Alftine and Malanson 2004); increasing soil moisture, temperature, and nitrogen availability (Belsky et al.1989; Li and Wilson 1998; Siemann and Rogers 2003); and suppressing shade-intolerant grasses and thereby reducing the competition faced by their own seedlings and the frequency and intensity of fire and grazing/browsing subsidized by the grasses (Bird 1930; Wilson and Agnew 1992; Li and Wilson 1998). In addition, tree seedlings and saplings may experience photoinhibition or other photodamage as a result of heavy re-radiative heat loss at night in the absence of a protective tree canopy (Jordan and Smith 1995; Germino et al. 2002; Davidson et al. 2004; Johnson et al. 2004).

The Valles Caldera National Preserve (VCNP), in the Jemez Mountains of northern New Mexico, contains ca. 10,000 ha. of subalpine grasslands, primarily in the expansive valley bottoms of the caldera floor at elevations ranging between 2575 and 2700 m (see Fig.1). Several smaller meadows occur in minor valleys and drainages scattered over a wider range of elevations in the caldera. These grasslands occupy gently-sloping to level terrain, and form abrupt ecotones with forested stands on steeper mountain slopes (Fig. 2). Meadows also occur on some upper

mountain slopes, on flat sites and south-facing slopes above ca. 3000 m. All of these grasslands, and treeline ecotones that define them, occur well below the elevation of alpine treeline (ca. 3500 m at this latitude in the southern Rockies). As these grasslands also occur primarily above 2500 m, we adopt the nomenclatural convention of Brown (1994) in referring to them as *subalpine grasslands*, though we recognize that ponderosa pine and mixed-conifer forests at these elevations are widely referred to as *montane* forests, as originally defined by Ramaley (1907). The caldera itself is a 24 km-wide basin formed by volcanic eruptions and the subsequent collapse of the underlying magma chamber ca. 1.22 Ma (Smith and Bailey 1966, 1968; Izett and Obradovich 1994). Until recently, most of the Valles Caldera was held as a privately-owned ranch and off-limits to most biological investigations. In 2000, most of the area was transferred to public ownership, primarily in the 36,000-ha VCNP.

Our primary objectives in this report are to (1) characterize the previously undescribed subalpine grasslands and forest-grassland ecotones in the Valles Caldera National Preserve; (2) relate variation in grassland and forest edge composition to environmental factors; and (3) determine whether the position of the subalpine treelines can best be predicted from soil texture, soil moisture, temperature, or other variables. We focus especially on the abiotic factors that may determine treeline position, but also examine ecological correlates of diversity, dominance, and compositional variation within both forests and grasslands. Given that positive feedbacks may affect the position of treelines or other shifts in vegetation composition and structure, it is quite possible that the positions of these ecotones may in some cases be more a result of spatial context, in terms of the environment or community composition of nearby sites. To analyze the role of spatial context and examine the possibility of type I error due to spatial autocorrelation in vegetation or the environment – a possibility inherent in any community study (e.g., Legendre et al. 2002), we employ simple and partial Mantel tests, as well as more traditional analytical approaches that ignore spatial autocorrelation.

Methods

Study area

All measurements were made within the Valles Caldera (35°50'-36°00'N, 106°24'-106°37'W) (Fig. 1). The mountainous rim of the caldera reaches elevations of 2850-3150 m; the basin floor lies between 2575 and 2750 m. Within the caldera, resurgence and post-collapse ring-fracture volcanism have formed several secondary domes (Smith et al. 1970); the highest of these is Redondo Peak at 3370 m. The primary rock types of the mountain slopes are ignimbrite and rhyolite; the caldera floor is underlain by a combination of Quaternary alluvium, fan deposits, and lacustrine sediments (Smith et al. 1970). Soils include alfisols and inceptisols beneath forested vegetation on the slopes, and well-developed mollisols in the grassy valley bottoms (USDA Soil Conservation Service 1987). The climate is semi-arid and continental. No long-term climatological data exist for the Valles Caldera, but mean annual precipitation is probably slightly higher than the 57.6 cm recorded at the nearest climate station at Wolf Canyon, NM (35°57'N, 106°45'W; 2506 m elevation, 50-yr mean 1954-2004). May and June are the driest months (3.4 and 3.0 cm precipitation), and July and August are the wettest (8.6 cm for both months), reflecting the importance of summer convective storms triggered by southerly, monsoonal flow throughout this region. At the Wolf Canyon station, mean monthly high and low temperatures for January are 3.4° and -13.5° C; for July, they are 24.9° and 5.7° C. During the years that this study was conducted (2001 and 2002), yearly precipitation at Wolf Canyon was 16% and 18% below the 50-year mean.

Pre-Columbian use of the Valles Caldera was limited primarily to obsidian collection (Chomko 2005). Spanish settlement of the upper Rio Grande valley came in the late 16th century; but intensive livestock grazing in the caldera did not begin until the late 1800's, when the Navajo and Apache were forcibly removed from the area by the U.S. Cavalry and nearby rail lines gave stockmen access to distant markets (Martin 2003 and sources cited therein). The area occupied by the VCNP was a privately-owned ranch from 1860 until 2000, and subjected to periods of intensive grazing and logging operations, as has occurred throughout much of the southern Rocky Mountains (Martin 2003). Elk, which were extirpated from the Jemez Mountains toward the end of the 19th century, were reintroduced in 1947; the population is currently estimated between 4,000 and 8,000. These factors, as well as fire suppression both direct and indirect [e.g., the cessation of frequent ground fires ca. 1890 due to removal of grassy fuels by livestock grazing (Allen et al. 1996)], have certainly resulted in some changes in composition, structure, and functioning of ecological communities, but the extent of these changes is uncertain. Historic photos (Hogan and Allen 1999) indicate recent encroachment of forests into grasslands at many locations in the Valles Caldera, though this encroachment has occurred at different rates in different sites (see Chapter IV for an analysis of historic treeline dynamics).

Sampling methodology

Data on plant community composition, community structure, and environmental factors were collected during 2002-2004 in 200 quadrats dispersed in a spatially stratified, hierarchical design. Each quadrat was 100 m^2 in area, and 5 m x 20 m. Because our main objective was to characterize vegetation-environment relationships across treeline ecotones, most quadrats were placed along transects crossing forest-grassland ecotones. To efficiently achieve a broad, unbiased sample, these transects were stratified spatially as follows. First, boundaries between forest and subalpine grassland were identified on the 7.5' USGS topographic quadrangles that cover the VCNP. Second, these treeline boundaries were divided into 20 sections of roughly equal length, and one transect was randomly located in each section; 18 of these transects were ultimately sampled. Third, on each side of the treeline (defined by a generally abrupt shift from open communities to those with >50% cover by trees), equal numbers of quadrats were placed at exponentially increasing distances from the ecotone. The long axis of each quadrat was perpendicular to the transect. On 12 transects, eight quadrats were placed at 5, 20, 50, and 110 m on either side of the ecotone; on six transects, only four quadrats were sampled, at 20 and 110 m from the ecotone. Finally, to sample the compositional heterogeneity of subalpine grasslands more completely, we extended sampling further into the valleys. We added 40 quadrats by lengthening several transects, sampling additional areas at horizontal increments of 60 m. Another 40 quadrats were subjectively located in infrequently-encountered plant assemblages along transects that would otherwise not have been sampled.

In each quadrat, the total basal area, density, and mean and maximum height of each tree species were tallied, including all individuals = 2.5 cm dbh. Percent cover of tree seedlings (< 2.5 cm dbh) and shrubs was visually estimated for each woody species in five 9-m^2 (3 m x 3 m) subquadrats spaced at regular intervals inside each quadrat. Cover of herbaceous species was visually estimated in five 1-m^2 plots nested in the center of each 9-m^2 subquadrat, using the following classes: 0% (absent), 1%, 2-3%, 3-6%, 6-10%, 10-15%, 15-20%, 20-30%, 30-40%, 40-50%, 50-60%, 60-70%, 70-80%, 80-90%, 90-100%. Mean cover of each tree-seedling, shrub, and herbaceous species was calculated across the samples within each quadrat.

Herbaceous and shrubby species present within the 100-m^2 quadrat but occurring outside of the sampled subquadrats and plots was scored as 0.2% for the quadrat as a whole. To control for seasonal shifts in leafing, herbaceous cover at each quadrat was censused in August, towards the end of the summer monsoon, when most species reached their maximum coverage. Vouchers for all species of shrubs and herbs were collected and deposited at WIS. Tree canopy cover was estimated above the center of each subquadrat using a concave spherical densiometer. To estimate the percent cover by each tree species for a given quadrat, we multiplied the mean percent canopy cover by the proportions of the total basal area accounted for by each tree species present.

Environmental data sampled in the center of each quadrat included slope inclination and aspect (using a compass and a clinometer), and spatial position (UTM x, UTM y, and elevation, using a handheld GPS unit with 15-m resolution [Garmin, Olathe, KS]). Limitations imposed by time, money, and in some cases quadrat inaccessibility, made it impossible to measure in every quadrat all of the remaining environmental variables – including soil texture, nutrient concentrations, temperature, and moisture content, and time courses of air temperature. Hence, these variables were sampled in partially overlapping subsets of the 200 quadrats (Table 1). Three soil cores (2.5 cm diameter, 0-15 cm depth) collected from the center and both ends of each quadrat were pooled for texture analysis using a modified hydrometer method (Bouyoucos 1962; Day 1965) for 150 quadrats. For 32 of these quadrats, a series of macronutrient concentrations (available P; exchangeable K, Ca, and Mg; total N), pH, and % organic matter were measured by the University of Wisconsin Soils and Plant Tissue Analysis Laboratory, using techniques summarized in Table 1. Soil temperatures at 50-cm depth were sampled at the center of 60 quadrats during August 2001. Soil moisture was measured at three-week intervals during the 2002 growing season, between 1 June and 1 September 1, using gravimetric analysis of soil cores collected to a depth of 15 cm, as above. Soil moisture was sampled at 64 sites corresponding to quadrats at 20 and 110 m from the ecotone on 13 of the most accessible transects (52 sites); at five other locations in valley bottom meadows chosen to include a broader range of grassland compositional variation; and seven additional backslope locations where timber-harvest units and large canopy gaps adjacent to sampled quadrats would allow some examination of the effect of landform position on soil moisture independent of the potentially confounding effects of the forest canopy itself. Growing-season air temperatures in 2002 were measured from 1 June to 1 September, using a combination of max/min thermometers (reset weekly) and thermistor readings at 0.5 hour intervals using twelve single channel dataloggers (Hobo Pro Temp, Microdaq.com, Ltd., Warner, NH) at 15 cm above the ground surface at 28 sites. Twenty-one of these were quadrats (paired across the subalpine treeline except in one instance) at 20 or 110 m from the ecotone. To assess the thermal regimes of backslopes independent of forest cover, the remaining seven sites were in the adjacent, natural or logged canopy openings just described. Data logging of air temperatures continued through 1 July 2003. All environmental measurements were transformed as needed to approximate normal distributions for the purposes of standard parametric tests of significance (Table 1).

Statistical analysis

We characterized the overall variation in plant community composition in subalpine grasslands and adjacent forest borders using cluster analysis, indicator species analysis, ordination with overlays of environmental variables, and simple and partial Mantel tests. We first conducted a hierarchical, agglomerative cluster analysis using the flexible beta linkage method

with ß = -0.25 implemented by PC-Ord 3.0 (McCune and Mefford 1997). We generated the compositional dissimilarity matrix using Sørensen pairwise distances between all 200 quadrats, based on the square-root coverages by all 204 species. Square-root transformation decreased skewness and kurtosis for each species and increased the effect of sub-dominant species on the dissimilarity matrix. In effect, this transformation was a compromise between using raw percent cover and simple presence/absence data. To determine the most ecologically meaningful number of groups for cluster analysis, we used the indicator species analysis method suggested by McCune and Grace (2002). We plotted the number of groups against both the average indicator species p-value and the number of indicators with $p < 0.05$. Using this method, the ideal number of groups minimizes indicator species p-values and maximizes the number of significant (at a = 0.05) indicators.

Using the compositional dissimilarity matrix described above, we conducted an ordination of plot data in species space using global non-metric multi-dimensional scaling (NMS) as implemented by PC-ORD 3.0 (McCune and Mefford 1997). To ensure the appropriate dimensionality of the final ordination, we assessed declines in the reduction in stress with increasing dimensionality. To ensure that we found the best solution, we ran the ordination 100 times using random starting coordinates, with a stability criterion of 0.0001. The best (least-stress) solution emerging from this analysis was then used to provide starting coordinates for an additional 100 runs. To explore relationships between ordination axes and measured environmental variables, we used joint plots (PC-Ord Method, see McCune and Grace 2002). Vectors representing the strength and direction of correlation between each environmental variable and sample composition (as reflected by ordination-axis scores) were drawn from the centroid of the ordination, with the components of each vector corresponding to the correlation coefficients between the environmental variable and the samples scores on each ordination axis. Only those environmental variables with a total $r^2 > 0.15$ were plotted.

To complement the traditional gradient analysis just described, we conducted Mantel tests to quantify relationships between sample compositional dissimilarity and environmental distance, using a randomization approach to assess the significance of such relationships when spatial structure and different levels of resolution in vegetation composition are taken into account. Correlations between composition and environmental variables may reflect (i) shifts from forest to grassland, but not variation within either type; (ii) vegetation-environment relationships within grasslands alone; or (iii) similar relationships within forests alone. To test each of these possibilities, we partitioned the vegetation data into three components. To test for significance of the first component – involving determinants of the forest-grassland ecotone – we constructed a "type" matrix, categorizing sites as forest or grassland: all grassland-grassland and forest-forest pairwise distances were set to 0, and grassland-forest pairwise distances to 1. To test significance of the second and third components, we used Sørensen dissimilarity matrices of square-root transformed cover by all species for the 60 forest samples alone, and for the 140 grassland samples alone. Euclidean distances for each transformed environmental variable for each pair of quadrats were used to build environmental dissimilarity matrices.

Simple Mantel tests offer a straightforward approach to test for sample spatial dependence (using a geographic distance matrix), while partial Mantel tests can control for spatial autocorrelation in testing composition-environment relationships (Legendre and Trousselier 1988, Urban et al. 2002). Spatial dependence of community composition may result both from broad-scale spatial structure in sampled (and unsampled) environmental gradients and finer scale patchiness attributable to spatially contagious processes (e.g., fire) or spatially

restricted processes (e.g., seed dispersal). In this study, we envisioned the possibility of patchiness resulting from positive feedbacks that might reinforce, accentuate, or indeed generate treelines independent of any significant, present-day abiotic differences among sites. Such feedbacks would be likely, among other things, to generate spatial contagion in vegetation type (forest vs. grassland). Because spatial autocorrelation in either vegetation response or predictor variables can lead to an increased probability of type I error (Legendre et al. 2002), we conducted both simple and partial Mantel tests to examine the relationship between vegetation composition and each measured variable, controlling for geographic distance and spatial autocorrelation. In addition, we ran partial Mantel tests controlling for temperature while examining the effect of soil texture on the shift from forest to grassland, and vice versa, to analyze whether soil texture (a proxy for grass competition) or temperature (a proxy for adverse impacts via photoinhibition, photodamage, and frost heaving) had more support as potential determinants based on vegetation-environment correlations. All Mantel tests were implemented using the R package v. 4.0 (Casgrain and Legendre 2001).

Lastly, to evaluate the validity of several key hypotheses regarding the determinants of subalpine treeline position – involving soil texture (and grass competition), soil moisture, and air or soil temperature – we used simple and backwards-elimination multiple regression to test for significant relationships between predictor variables (soil texture, soil moisture, thermal data, distance from ecotone, and slope aspect) and measures of tree vigor and abundance (mean and maximum height and basal area of each species, total basal area, stand density, and seedling abundance). All regressions were conducted using S-Plus (Insightful Corp, 2001 release).

Results

Vegetation composition

We encountered 204 vascular plant species in 200 quadrats (total sample area of 2 ha) in subalpine grasslands and adjacent forests in the Valles Caldera National Preserve. Species are listed in Appendix I in order of decreasing abundance; nomenclature and authorities follow Hartman and Nelson (2005). Of these, 160 species occurred in the 140 grassland quadrats, and 141 species occurred in the 60 forest samples. Plant species richness per quadrat ranged from 2 to 45, with a mean of 22.2 ± 6.7 species for grassland samples, 18.0 ± 7.3 for forest samples, and 20.9 ± 7.2 for all quadrats together. Grassland quadrats had significantly more species per 100 m^2 ($P < 0.0005$, 2-tailed t-test for 198 d.f.). Richness in 1-m^2 subquadrats ranged between 0 and 23 species, with a mean value of 10.4 ± 5.0 for all quadrats. The difference between grasslands and forests was even more pronounced at the 1-m^2 level, with 12.3 ± 4.2 species in grasslands and 6.5 ± 4.3 in forests ($P << 0.0001$, 2-tailed t-test with 9998 d.f.).

Only 10 of the 204 taxa encountered were exotic to the region; however, two of these, Kentucky bluegrass (*Poa pratensis*) and common dandelion (*Taraxacum officinale*) were exceptionally abundant, with mean coverages across the gradient of 8.8% and 2.5%, respectively. Forest edges were generally dominated by ponderosa pine (*Pinus ponderosa*, the most abundant tree sampled, with mean cover of 11.0%), or by Colorado blue spruce (*Picea pungens*, with mean cover of 4.6%). After Kentucky bluegrass, the most abundant grassland species based on coverage were Parry's oatgrass (*Danthonia parryi*) (6.3%) and Arizona fescue (*Festuca arizonica*) (4.4%). The five most frequent species encountered were western yarrow (*Achillea millefolium* var. *occidentalis*, occurring in 78% of quadrats), Kentucky bluegrass (75%), common dandelion (74%), wooly cinquefoil (*Potentilla hippiana*) (71%), and beautiful

fleabane (*Erigeron formosissimus*) (58%).

Community classification

Beta-linkage cluster analysis and indicator-species analysis identified nine groups of samples that resulted in the lowest average indicator-species *p*-value and the greatest number of significant indicators. For convenience, in the following we use names for these vegetation-types based on the dominant species (e.g., *Ponderosa Pine*) or, where no species exhibited consistent dominance, we labeled groups based on general composition or position in the landscape (e.g., *Mixed Conifer*, *Wet Meadows*). Three groups (*Ponderosa Pine, Blue Spruce,* and *Mixed Conifer*) reflect forested communities of mountain backslopes. One group (*Aspen Groves and Subalpine Balds*) combines some forested and some grassy communities generally found at higher elevations on mountain slopes. Five groups (*Arizona Fescue*, *Parry's Oatgrass, Mesic Grasslands*, *Wet Meadows*, and *Sedge Meadows*) represent graminoid-dominated communities of valley bottoms. The three most abundant species and strongest indicators for each group, as well as measures of species diversity and richness for each group, are listed in Table 2. Table 3 presents the mean values of several environmental variables for each group, including slope, soil texture, moisture, and summer minimum temperatures.

Ordination and gradient analysis

Non-metric multidimensional scaling produced a 3-dimensional solution, with additional dimensions resulting in little further decrease in stress. The final ordination had a stress value of 14.27 (p <0.01 based on 100 runs with randomized data), and a final instability of 6×10^{-5}. Axes were rotated to maximize the variance explained by the first axis. The ordination explained 83% of the variance in the original dissimilarity matrix, with axes 1 and 2 accounting for 38% and 25% of the total, respectively. Groupings identified by cluster analysis segregate well along both axes 1 and 2 (Figure 2). Axis 1 clearly separates forest from grassland types, and correlates strongly with measures relating to **cold-air drainage** (consecutive days between minimum temperatures below 0° C [r = 0.92] or -5° C [r = 0.97], mean **minimum growing-season temperature** [r = 0.85]) and less strongly with shifts in **soil texture and cation availability** (% sand [r = 0.46]), % clay [r = -0.59], soil [Ca^{++}] [r = -0.70], and soil [Mg^{++}] (r = -0.57]), as well as % **slope** (r = 0.66), which correlates with both cold-air drainage and soil texture along the catenas on concave mountain slopes. Several groupings within forests and grasslands segregate along axis 2, which correlates well with **aspect** (r = 0.40), **soil moisture** (r = 0.51), and **annual mean temperature** (r = 0.43), as well as soil [K] (r = -0.53). Axis 3 accounts for 19.8% of the variance in vegetation dissimilarity but is more difficult to interpret, with weak relationships to most environmental variables and ecological communities, except for *Sedge Meadows*, which segregate well on axis 3 but poorly on axes 1 and 2. Because axis 3 added little additional understanding of compositional and structural variation, we do not discuss it further.

As is visually evident (e.g., Figure 2), forest types are generally found on steeper slopes and sandier (and rockier) soils above grassland communities. However, grassy balds dominated by Thurber's fescue (*Festuca thurberi*) and Parry's oatgrass (*Danthonia parryi*) occur also at the highest elevations sampled, both on flat mountaintops and also on steeper, south-facing slopes. Our cluster analysis did not separate these sites from groves of trembling aspen (*Populus trembloides*), which often occur adjacent to these subalpine balds or interspersed within them. Subalpine forests on cooler, north-facing slopes at higher elevations are dominated by

Engelmann spruce (*Picea engelmannii*), occasionally with corkbark fir (*Abies arizonica*). Cluster analysis included these stands with samples from slopes at somewhat lower elevations, and across a range of aspects, which included a mixture of Engelmann spruce, white fir (*Abies concolor*), and Douglas fir (*Pseudotsuga menziesii*). At the lowest elevations, and on footslopes adjacent to the vast grassy basins of the VCNP, Colorado blue spruce dominates stands on north and east aspects and ponderosa pine dominates those of south and west aspects (Tables 2 and 3).

Grassland types appear to sort primarily along catenas of soil moisture, texture, and nutrient availability. Arizona Fescue (*Festuca arizonica*) dominates driest, loamy soils on gentle slopes with a southwest aspect; Parry's oatgrass dominates similar landforms on sites with cooler, moister northeast aspects. Increasingly mesic, clay-rich and organic soils on level sites are dominated by pine dropseed (*Blepharoneuron tricholepis*) and Idaho fescue (*Festuca idahoensis*) in mesic grasslands; then by tufted hairgrass (*Deschampsia caespitosa*) and wooly sedge (*Carex pellita*) in wet meadows; and finally by water sedge *(Carex aquatilis)* on the wettest, lowest, flattest sites (Tables 2 and 3).

Mantel tests

Mantel tests corroborate many of the vegetation-environment correlations identified by NMS, and confirm spatial structure in community composition and several environmental factors (Table 4). The presence of forest vs. grassland was most strongly correlated with **thermal regime** (June-August mean weekly minimum temperature, consecutive days between 0° and -5° C), and was also significantly related to **edaphic factors** (percent sand, clay, and Ca) but not soil moisture. Forest composition was strongly related to several edaphic factors (Ca, % organic matter, total N), elevation, moisture, and aspect, which probably reflect the expected shifts in these factors with increasing elevation as one moves from relatively dry, fertile ponderosa pine and blue spruce forests fringing the exposed, grassy lower slopes to moister, less fertile sites at higher elevations dominated by Douglas fir, white fir, and Englemann spruce, and aspen. Within this range of habitats on forested slope at higher elevations, however, none of the seven thermal variables examined had an effect (Table 4). Grassland composition was strongly related to % organic matter, soil moisture, pH, total N, slope, and % clay, reflecting the array of plant community types along catenas ranging from dry, gently-sloping sites on loamy soils to mesic sites on level ground with finer-textured soils, to the waterlogged and highly organic soils dominated by *Carex* spp. along watercourses in the valley bottoms.

In no case did we find a substantial effect of spatial position on the relationships of vegetation type, forest composition, or grassland composition to underlying environmental variables using partial Mantel tests (Table 4). In most cases, partial Mantel tests yielded results identical to those obtained using simple tests, and in all other cases the difference between partial and simple Mantel correlations was trivial. We did not find a significant Mantel correlation between the binary vegetation type matrix and the spatial distance matrix. These surprising results most likely reflect the spatial stratification of our sampling design, with widely spaced transects repeatedly sampling large changes in vegetation and environmental factors over short distances in the middle of each transect. The lack of a partial-Mantel effect of spatial position on vegetation-environment relationships indicates that such relationships were relatively consistent across transects, and robust to any effects of spatial autocorrelation at the distances involved among transects. It is important to note, however, that we did find significant *direct* effects of spatial position on forest composition and grassland composition using simple Mantel tests, although the magnitude of correlations is substantially less than that for almost all other

environmental factors with significant effect (Table 4). This suggests that there is significant spatial autocorrelation within portions of transects, but that its effect is small relative to other environmental factors, and that – based on the partial Mantel tests – spatial autocorrelation hardly interferes with the direct relationships of those factors themselves to vegetation composition.

Simple Mantel tests of the correlation between **vegetation type** (forest vs. grassland) and three variables associated with key hypotheses of forest/grassland ecotone maintenance (**% clay**, a proxy for soil texture and grass competition; mean **soil moisture**, an indicator of waterlogging or soil drought; and **June-August mean minimum weekly temperature**, a proxy for physiological damage by cold temperatures) at the 22 sites where we measured all of these factors showed a much stronger relationship of vegetation type to temperature ($r = 0.77$) than to soil texture ($r = 0.25$), and no correlation to soil moisture (Table 5). Furthermore, partial Mantel tests showed a substantially greater weakening of the vegetation-soil texture relationship when temperature is controlled ($r = 0.12$ vs. 0.25, a 50% decline) than the vegetation-temperature relationship did when soil texture was controlled ($r = 0.74$ vs. 0.77, a 4% decline) (Table 5). Taken together, these results identify a much stronger relationship of the transition from forest to grassland with temperature than with soil texture, although both sets of factors have highly significant correlations with vegetation type. Soil moisture content – in terms of both its mean value and seasonal variation – had no significant correlation with the transition from forest to grassland (Table 5), confirming our qualitative observation that subalpine treelines occur in and around well-drained sites and that increased soil drought or waterlogging has nothing to do with the location of such treelines (see Figure 2).

Univariate predictors of treeline stand structure and seedling abundance

Treeline ecotones in the Valles Caldera are generally marked by an abrupt shift from completely open herbaceous communities to fairly dense forests. Across the narrowest sampling interval of 10 meters, average tree density jumped from <1 to 8.5 stems per 100 m^2 quadrat (850 stems/ha) where ponderosa pine formed the forest boundary, and from <1 to 12 stems per quadrat (1200 stems/ha) for stands dominated by Colorado blue spruce. The abruptness of the shift from grassland to forest is further highlighted by the lack of a significant positive relationship of stand density or total basal area to distance from the ecotone. Based on regression analysis, mean tree height, girth, and basal area showed no systematic increase with distance from the ecotone, for individual species or all species in a stand combined. Mean tree height and girth 5 m from the ecotone were not significantly different from those 110 m into the forest. At 5 m from the treeline, mean tree height was 12.4 m (11.3 m for ponderosa forests, and 14.5 m for forests of Colorado blue spruce or mixed conifers) vs. 12.3 m for stands 20-110 m into the forest. Mean basal area per individual at 5 m from the ecotone was 5.6 dm^2, vs. 6.3 dm^2 for 20-110 m, a small and non-significant increase. Maximum tree height within stands did show a significant increase with distance from the ecotone (regression $r^2 = 0.12$, $P = 0.017$ for 48 d.f.). However, these results are likely to have been impacted both by historic logging along forest-grassland edges and encroachment of treelines into grasslands that were previously more heavily grazed, and may not reflect natural patterns of stand structure near treelines.

Tree seedling density was very low, with most sampled quadrats having no seedlings present. Across the entire gradient, there was a striking sigmoid shift in tree seedling density based on distance from treeline, increasing from nearly zero in or immediately adjacent to grasslands to over 200 seedlings/ha at more than 100 m from the ecotone (Figure 4, regression r^2

= 0.13, $P < 0.0001$ for 198 d.f.). Multiple regression models that included distance from treeline as a predictor of tree seedling density retained no other significant predictor variables. Mean seedling density in forested quadrats was 7.2 seedlings in each 45-m^2 sample (159 seedlings/ha), but only 1.1 seedlings per 45-m^2 sample (25 seedlings/ha, two-tailed t-test $P < 0.0001$).

To account for the potential effects of forest canopy cover and proximity of seed sources on establishment, we separated grassland samples and forest samples in testing for relationships between seedling abundance, herbaceous cover, and environmental variables. The abundance of tree seedlings on forested sites showed no relationship to canopy cover, thermal variables, soil texture, or distance from the treeline ecotone. Interestingly, tree seedling abundance in forests did show a strong positive relationship to soil moisture ($r^2 = 0.30$, $p < 0.005$ for 23 d.f.). This may suggest that during the drought years we sampled (2001 and 2002), seedling survival was constrained to more mesic microsites. In the grasslands, tree seedling abundance was most strongly positively related to % sand (regression $r^2 = 0.11$, $p < 0.001$ for 95 d.f.) and conversely, negatively related to % clay ($r^2 = 0.09$, $p < 0.005$ for 95 d.f.). Too few grassland samples contained tree seedlings to test for relationships with either thermal conditions or soil moisture. Seedling abundance in grasslands was not related to aboveground cover by grasses, or to total herbaceous cover, as might be expected if grass or herb competition were limiting tree establishment in the grasslands. Additionally, neither grass cover nor total herbaceous cover exhibited a significant relationship with percent sand or clay *within* the grasslands. In fact, grass cover was slightly positively correlated with percent sand ($r^2 = 0.05$, $p < 0.02$ for 96 d.f.). Total herbaceous cover in grasslands was positively related to soil moisture ($R^2 = 0.18$, $p = 0.015$ on 30 d.f.).

We also examined the potentially confounding effect of forest canopy cover on the apparent relationships between topography and both soil moisture and air temperature by sampling these factors in logged openings on backslopes adjacent to sampled forested quadrats. Mean soil moisture beneath closed forest canopies was only 0.6 % greater than that beneath adjacent openings (11.4% vs. 10.8%; two-tailed paired t-test on ln-transformed soil moisture $P = 0.70$ on 6 d.f.). Closed canopies and adjacent openings did exhibit a 1.4° C difference in minimum temperature (4.6° vs. 3.2°; two-tailed $P = 0.03$ on 6 d.f.). In both cases, the difference between open- and closed-canopy backslope sites was dwarfed by differences due other factors; especially topography in the case of the thermal regime (Figure 5); however, the slightly warmer conditions beneath forested canopies suggest decreased re-radiative cooling relative to adjacent openings. The 1.4° C difference is 25% of the 5.4-degree difference between forested slopes and open valley bottoms.

Discussion

Forests and grasslands of the Valles Caldera

Not unexpectedly, cluster analysis, indicator species analysis, NMS ordination, and Mantel tests clearly separated grassland and forest communities in the VCNP (Figure 2; Tables 2-5). Cluster analysis identified three forest types (*Ponderosa Pine, Colorado Blue Spruce,* and *Mixed Conifers*), five grassland types (*Arizona Fescue, Parry's Oatgrass, Mesic Grasslands, Wet Meadows,* and *Sedge Meadows*), and – at elevations fairly close to the alpine treeline – one heterogeneous type containing a mix of both tree- and grass-dominated stands (*Aspen Groves and Subalpine Balds*).

The three forest types found in this study are similar to the broad groupings and, to a lesser extent, the finer-scale associations among tree species previously observed in other

mountain ranges of the American Southwest (Moir and Ludwig 1979; Alexander 1985; DeVelice et al. 1986; Dick-Peddie 1993; Brown 1994). Our findings offer less support for other proposed groupings of montane grassland communities (e.g., Dick-Peddie 1993; Brown 1994), undoubtedly because there have been almost no detailed analyses of such grassland communities in the Southwest previously.

The separation of forest communities from each other corresponds primarily to aspect and elevation and correlated shifts in soil moisture and soil cations, based on the balance of results from NMS and Mantel tests (Figure 3; Tables 3 and 4). *Ponderosa Pine* and *Colorado Blue Spruce* communities occur on southwest vs. northeast exposures near 2650 m elevation, with dominance shifting to white fir, Engelmann spruce, and/or Douglas fir in stands of *Mixed Conifers* over a wide range of aspects at about 200 m higher elevation. NMS and Mantel tests differ somewhat in the factors they identify as being important correlates of forest composition, with the former pointing toward decreasing levels of exchangeable soil K with elevation, and the latter not and instead highlighting decreases in % clay and other major cations, as well as increases in % soil organic matter. Correlations of forest composition with % clay content and exchangeable [Ca] are highly significant, and unreported previously for forests in the southern Rocky Mountains. Correlations of forest composition with % organic matter and total [N] are weaker, probably reflecting differences in vegetation driving these parameters, rather than differences in % OM and [N] driving vegetation.

The five grassland community types appear to be distributed along soil catenas of decreasing slope and increasing % silt, % clay, and % OM below where they usually abut forests at a topographic break from slopes usually at least twice as steep (Figure 3; Tables 3 and 4). The *Arizona Fescue* community dominates on south and west aspects of gentle foot- and toeslopes immediately below treeline stands of ponderosa pine, while *Parry's Oatgrass* dominates the same kinds of sites on more mesic, east- and north-facing slopes, generally beneath treelines comprised of blue spruce. *Mesic Grasslands* occur further downslope. *Wet Meadows* and *Sedge Meadows* occur in the lowest, flattest sites with the most clay-rich soils and greatest cold-air drainage. Note that NMS axis 1 plays a much greater role in differentiating among grassland communities than among forest communities, implying a more 2-dimensional structure of variation in grasslands vs. forests (Figure 3). As with forest communities, the correlation of grassland composition with % soil organic matter and available N should probably be discounted as potential causes of grassland differentiation and instead seen as likely consequences of such differentiation.

The transition from *Arizona Fescue* and *Parry's Oatgrass* into the floristically more heterogeneous *Mesic Grasslands* and *Wet Meadows* is often marked by the replacement of several species by others in the same genera. The most striking cases involve Arizona fescue being replaced by Idaho Fescue (*Festuca idahoensis*) toward more mesic sites, and Parry's oatgrass being replaced by timber oatgrass (*Danthonia intermedia*). A similar pattern is shown in several other genera, including *Agoseris, Allium, Campanula,* and *Muhlenbergia.*

Sedge Meadows, occur in areas that are seasonally or perennially flooded. This community is frequently dominated by only one species, water sedge (*Carex aquatilis*). However at some sites dominance is by Northwest territory sedge (*Carex utriculata*), while at others dominance is by common spikerush (*Eleocharis palustris*).

Only one community type identified by cluster analysis, *Aspen Groves and Subalpine Balds*, contains a mix of grass- and tree-dominated stands. Tree canopy cover, primarily *Populus tremuloides*, ranged from 0 - 72 % at these sites. These quadrats all come from higher-

elevation forests and grasslands (mean elevation of 2940 m, compared with a mean of 2652 m for all other samples; see Table 2), and often from south-facing slopes, but with a fairly wide and generally lower range of slope inclination and variety of soil textural classes. At these elevations, meadows and grassy openings occur not only in flat areas and concave depressions, but also on south-facing slopes. Unlike the sharply defined treelines associated with the valley bottoms, treelines on these south-facing slopes tended to be more diffuse and savanna-like, with solitary ponderosa pines and Douglas firs, and groves of aspen, often scattered in grassy openings. The elevation, topographic position, and more diffuse nature of treelines on these south-facing slopes suggest that the limit of tree growth there may be determined by processes different from those that determine treelines adjacent to valley bottoms further downslope. Allen (1984, 1989) documented very high rates of tree invasion in nearby subalpine grasslands on south-facing slopes in the Jemez, which he attributed to fire suppression. Langenheim (1962) also attributed the occurrence of high-elevation grasslands dominated by Thurber's fescue on south-facing slopes in Colorado to recent fires. Other researchers (Rydberg 1913; Daubenmire 1968) have attributed grasslands on steep, south-facing slopes and ridges to shallow soils with insufficient moisture-holding capacity. However, stresses due to interaction between high irradiance and thermal conditions (such as winter desiccation or cold-induced photoinhibition) could be important both in valley bottoms and on high-elevation, south-facing slopes. The more diffuse treelines on these south-facing slopes may reflect a shallower gradient in minimum temperatures driven by aspect and elevation, in comparison to steeper gradients generated by concave topography.

As a practical matter, the placement of such a heterogeneous collection of grasslands and open woodlands in a single community type reflects the presence of Thurber's fescue (*Festuca thurberi*) and Parry's oatgrass at sites with a substantial aspen cover. A similar association between aspen and Thurber's fescue has been reported from the mountains of northern Colorado (Hess 1981), which may suggest that a deciduous, rather open canopy of aspen does not produce enough shade to limit the growth of bunchgrasses usually restricted to entirely open habitats. Several other graminoids and forbs that are generally confined to open areas at lower elevations can be found beneath the aspen canopy at high elevations, including yarrow (*Achillea millefolium* var. *occidentalis*) and Nevada pea (*Lathyrus lanszwertii*). Alternatively, the occurrence of these species beneath aspen may also indicate recent tree invasion into grassland vegetation and the persistence of long-lived herbs in spite of increasing shade.

Causes of subalpine treelines

In the Valles Caldera, abrupt topographic shifts from steep mountain slopes to gently inclined valley bottoms consistently result in subalpine treelines (Figure 2). The sharp transitions from forested slopes to grassy valleys are strongly related to both thermal and edaphic gradients. NMS ordination indicates that the shift from forests to grasslands is most strongly related to lower nighttime temperatures ($r = 0.97$ for number of consecutive nights below $-5°C$), but also shows significant relationships to gentler slopes, lower elevations, and heavier, less rocky soils with lower total N, % organic matter (to which [N] is often tied), and the concentrations of several major cations (Figure 3). Our data provide no evidence that excessively dry or excessively wet soils determine the position of these treelines (Figure 3; Tables 3 and 4). While a few low-lying riparian areas are almost certainly too wet to support growth by conifers or aspen, all of the subalpine treelines we observed were on well-drained sites where both slopes and valley bottoms were likely never inundated. Based on experience obtained while obtaining soil

cores, we can also say that treeline ecotones do not correspond to a shift to exceptionally thin soils. This suggests that neither waterlogging nor excessive drought determines the position of subalpine treelines in the Valles Caldera, acting alone or in concert with other factors.

We also found no evidence to support the hypothesis that treelines in the Valles Caldera might be caused by positive feedbacks alone, given strong and consistent relationships between treeline position, topography and underlying gradients in soil texture and thermal regime, and the robustness of these relationships to partial Mantel tests that control for spatial autocorrelation (Figure 2; Tables 2-4). The possibility can not be excluded that positive feedbacks might nevertheless influence the position of ecotones, or the composition of adjoining forests and grasslands, while acting in concert with other processes. The pattern of spatial autocorrelation within forests and grasslands near subalpine treelines (Table 4) is consistent with the operation of positive feedbacks.

This study uncovered circumstantial evidence for two mechanisms by which positive feedbacks might act. First, we observed a small but significant drop in nighttime air temperatures near the ground under experimentally opened vs. naturally closed canopies on otherwise equivalent microsites, presumably reflecting a greater level of re-radiative heat loss below open canopies, which might adversely affect photosynthesis by tree seedlings via photoinhibition or other kinds of photodamage (Chapter III), or via frost-heaving. The presence of a woody canopy in sites near treeline has been shown to reduce re-radiative cooling and elevate minimum nighttime temperatures in Wyoming and Tasmania, resulting in reduced photoinhibition or photodamage during ensuing light periods (Davidson et al. 2004; Johnson et al. 2004). Germino et al. (2002) showed that Engelmann spruce seedlings near alpine treelines in Wyoming showed a 70% increase in survival with tree cover overhead present vs. absent. In our study, the depression of nighttime minimum temperatures by canopy absence vs. presence on comparable sites was relatively small, ca. 25 % of that between forest and grassland sites generally, suggesting that topographic determinants of nighttime temperature are likely to be more important than temperature-related positive feedbacks in determining the position of subalpine treelines in the Valles Caldera.

Second, we found a regular, strong drop in tree seedling density from high values (ca. 200/ha) to essentially zero in moving from forests to grasslands through treelines in VCNP (Figure 4). Whatever its cause, this finding is consistent with positive feedback, with the presence of trees favoring further reproduction by trees. However, we currently lack data to demonstrate positive feedback in this case, because tree adults and seedlings may both simply be favored by the same abiotic conditions, independent of the presence of either. Recent forest encroachment into Australian subalpine grasslands in Victoria involves sapling regeneration within 5 m of the forest-grassland ecotone, and is strongly associated with the amount of overhanging tree cover (Wearne and Morgan 2001). We note that this pattern of regeneration is similar to that observed in the Valles Caldera, and that both are consistent with the possibility of positive feedback based on reduction of nightly frosts, perhaps coupled with local climatic warming. In the case of Valles Caldera, however, some additional factors can not be excluded as the bases for potential positive feedbacks, notably the possibility of elk browsing concentrated primarily at the grassy edges of forests. Krantz (2001) found that the greatest levels of elk browse, and damage due to antler rubbing, occurred at forest/grassland ecotones in the VCNP.

Taken together, our observational data strongly support minimum nighttime temperatures – and thus, presumably, cold-air drainage – as at least one cause of the position of subalpine

treelines in the Valles Caldera. Tree seedlings may be damaged or killed by frost heaving, cold-temperature photoinhibition, or some other factor. For ponderosa pine, frosts have been demonstrated to be a large source of seedling mortality via frost heaving (Larson 1960, 1961), and drops in growing-season temperatures below –3°C are detrimental to seedling growth and survival (Schubert and Adams 1971). Ball et al. (1991), Germino and Smith (1999), and Germino et al. (2002) have all demonstrated that tree seedling growth and survival are adversely affected by photoinhibition in areas of cold-air drainage or locally severe re-radiative cooling. Consistently cold nightly minimum temperatures may also limit conifer seedling growth by maintaining seedlings in a prolonged state of winter dormancy.

However, our data also provide substantial support for the effects of edaphic factors – especially total N, greater exchangeable [Ca], and heavier soil texture – for the exclusion of trees from valley bottoms. The fact that soil texture and minimum nighttime temperature both exhibit moderate to strong to moderate correlations with the presence/absence of tree cover even when we control for variation in the other factor (Table 5) strongly suggests that both factors are significant – and may indeed interact – in setting the position of subalpine treelines. An abiotic mechanism through which soil texture and temperature might interact is frost heaving and consequent effects on seedling mortality, which have been shown to be much greater on fine-textured and/or moister soils (Heidmann 1975, 1985; Heidmann and Thorud 1975, 1976). The absence within grasslands of a significant negative relation of seedling density to grass cover, or of a significant positive relation of grass cover to increased nutrient concentrations, offers no support for the prevailing hypothesis that subalpine treelines in the southern Rockies are caused by increased grass competition with tree seedlings on finer-grained, richer soils on flats below mountain slopes (see Ramaley 1910, 1927; Peet 1981, 2000). The detrimental effect of herbaceous competition on seedling establishment by conifers, especially ponderosa pine, is well-known (e.g., Pearson 1942; Schubert 1974; Stewart et al. 1984; Burns and Honkala 1990; Kolb and Robberecht 1996), and so cannot be dismissed by a purely observational study like ours. Experiments to explore the roles of grass competition vs. other factors correlated with topographic position in determining seedling survival and growth are presented in chapter III.

In general, treeline ecotones may be caused by context-dependent restrictions on **tree seedling establishment** (Wardle 1971; Tranquillini 1979; Cuevas 2000) or **adult tree growth** (Daubenmire 1954; Givnish 1995; Körner 1998, Li et al. 2002). In the Valles Caldera, the low density of tree seedlings overall and their extremely low abundance on grassland sites argue for the importance of demographic bottlenecks at early life stages as the most likely cause of subalpine treelines. This result agrees with Schauer et al. (1998), who found that Engelmann spruce seed germination and seedling survival were much higher in subalpine forests than in adjacent grassy parks in Colorado. Adult tree radial growth rates in the Colorado study were actually higher at the subalpine treeline ecotone than in the forest interior, indicating that constraints on adult tree growth were not likely to maintain the treeline ecotones at this site (Schauer et al. 1998). While we did not examine radial tree growth rates (see Chapter II), we found no tendency for mean or maximum tree basal area to decrease with increasing proximity to subalpine treelines in the VCNP. However, maximum tree height did show a systematic decrease from forest interiors toward the treeline ecotone, as expected if treeline formation is driven by limitations of growth by tall woody plants imposed by a gradient of increasing environmental severity (e.g., see Givnish 1995). An alternative explanation for this pattern in the VCNP is that it reflects a progressive advance of trees into grasslands over recent decades, with the shortest, youngest plants at the ecotone itself, and older, taller trees limited to more distant

sites in the forest interior. Photographs taken by members of Vernon Bailey's 1907 U. S. Bureau of Biological Science expedition (Hogan and Allen 1999) do indeed suggest that subalpine treelines in the Valles Caldera were located slightly further upslope in many areas, suggesting that location-specific constraints on tree establishment have been relaxed over that period (see Chapter IV).

Elsewhere in the southern Rockies, shifts in the position of montane and subalpine treelines have been attributed to climatic changes (Dyer and Moffett 1999) and to changing human land use, especially livestock grazing and fire suppression (Allen 1984, 1989; Mast et al. 1997). Any of these processes may be relevant, but their relevance depends strongly on the hypothesized mechanism that best explains the occurrence of these treeline ecotones. If subalpine treelines in the Valles Caldera are maintained solely by the adverse effects of cold-air drainage in valley bottoms on tree seedling establishment or growth, then climatic warming could clearly shift treelines down-slope. Alternatively, if increased competition with grasses on fine-textured soils prevents tree seedling establishment, then reductions in grass cover by grazing livestock or elk may explain tree invasion of former grasslands. Lastly, prior to ca. 1890, any of the spatially-structured constraints on tree seedling establishment or growth discussed above operated in conjunction with frequent, low-intensity fire. Alone, these constraints on seedling establishment or growth may not have precluded the eventual development of forests in the valley bottoms of the VCNP, but may simply have increased the interval of time required for seedlings to reach sufficient size to survive low-intensity fire. As such, the required fire-free interval in valley bottoms may have greatly exceeded the short fire-return intervals (< 5-15 years; Swetnam and Baisan 1994; Allen et al. 1996; Brown et al. 2001) that characterized the ponderosa pine and mixed-conifer forests of the southwestern U.S. prior to the initiation of large-scale livestock grazing in the late 19th century. Continued fire suppression may allow a gradual encroachment by trees into sites even where tree establishment is infrequent and/or growth is slow.

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Figures and Tables

Figure 1. The Valles Caldera National Preserve (VCNP) in the Jemez Mountains, New Mexico. White indicates grassland vegetation, grey indicates forest.

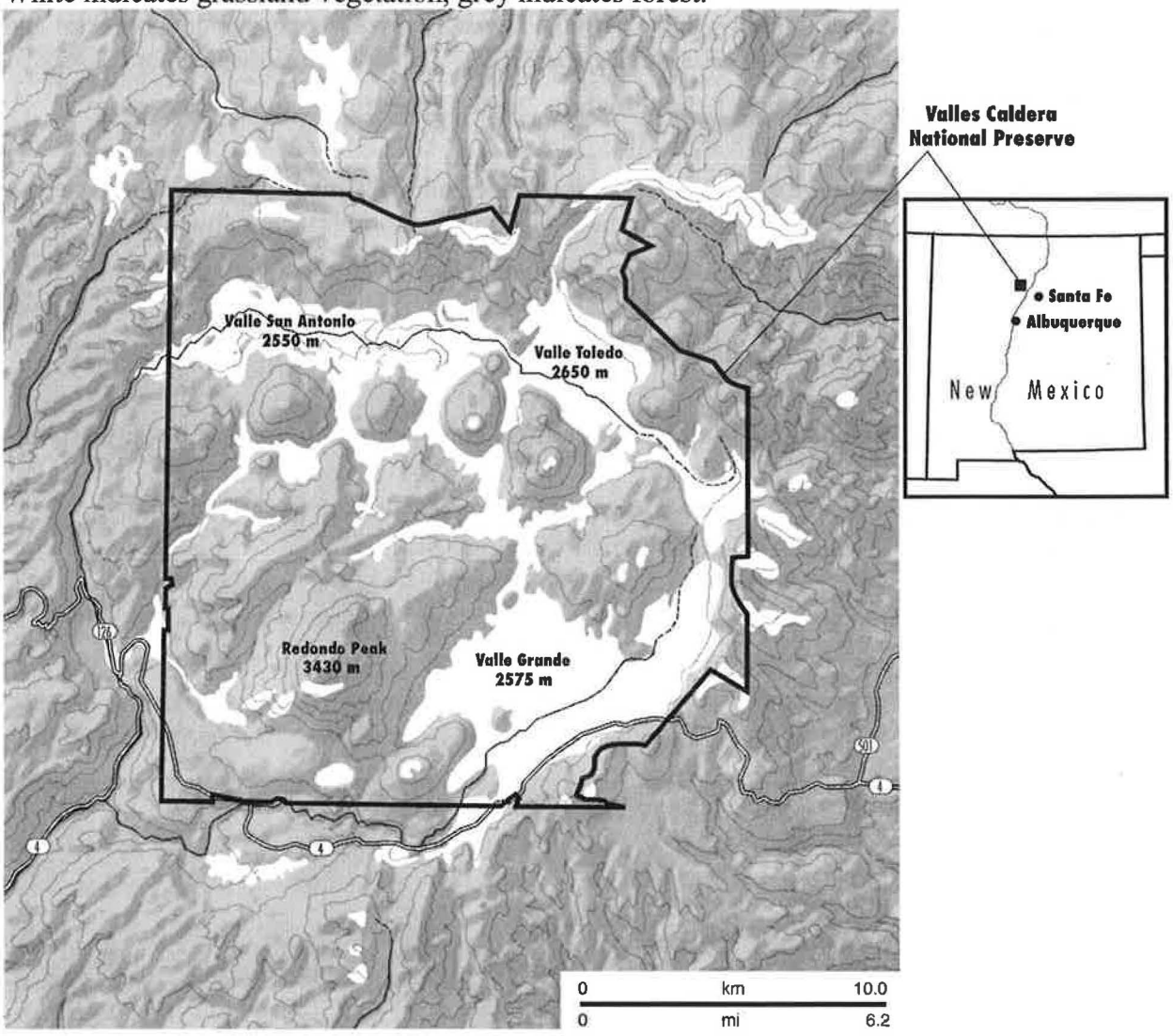


Figure 2. Cerro la Jara, a small volcanic dome in the Valle Grande, exhibiting the abrupt, subalpine treeline ecotones that characterize the shift from steeper mountain slopes to gentle valley bottoms in the Valles Caldera.



Figure 3. Ordination joint plot, showing the position of sites on the first and second NMS axes and vectors representing the correlation between ordination axes and measured environmental variables. Axes 1 and 2 accounted for 38.0% and 25.3% of the original variance in dissimilarity. Sites are highlighted by symbols corresponding to the nine vegetation types identified by cluster and indicator-species analyses. Filled symbols identify forest types, found primarily to the right on steeper slopes and sandier/rockier soils, and differing among each other primarily along axis 2 in factors relating to aspect, coolness, moisture, and exchangeable [K^+]. Hollow symbols signify grassland types, found mainly to the left at lower elevations and sorting along catenas of decreasing slope, and increasing coolness, moisture, and percent clay and organic soil content (see text).

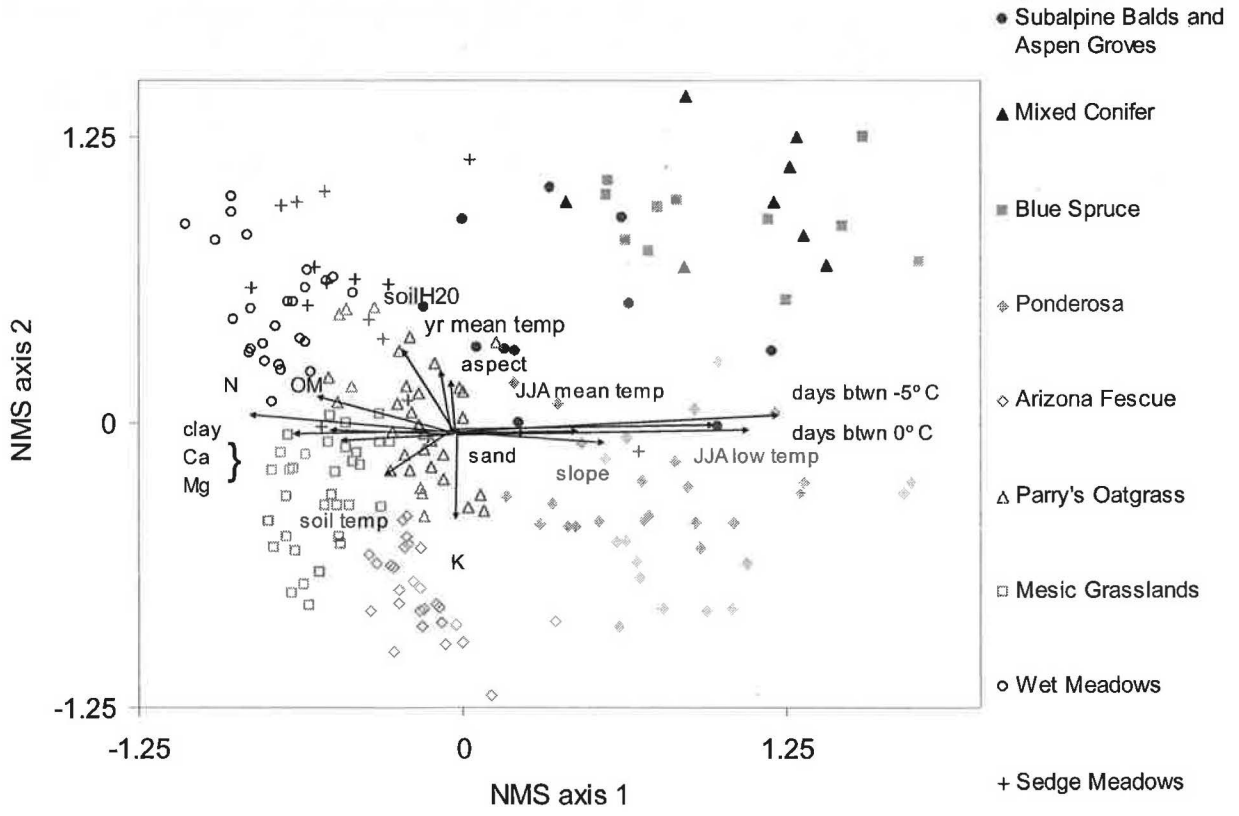


Figure 4. Tree seedling density (all species) and distance from subalpine treeline ecotones in sampled quadrats. Tree seedlings were categorized by a dbh of less than 2.5 cm, and include aspen root sucker shoots. Most tree seedlings were found in forested sites above the treeline ecotone.

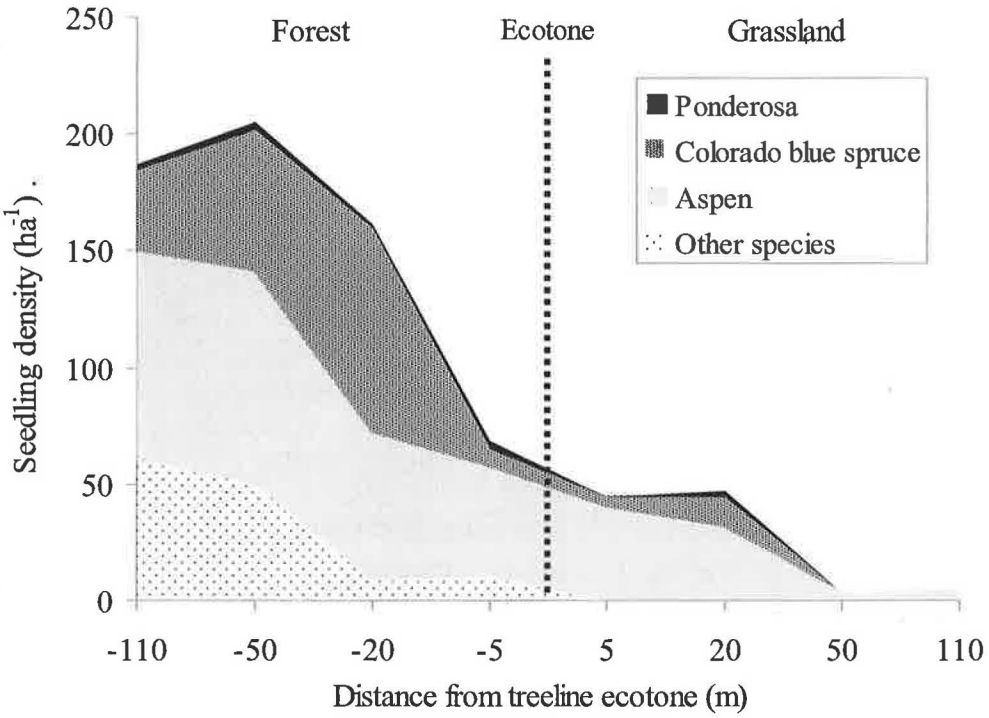


Figure 5. The relationship between topography and minimum growing season temperatures in the Valles Caldera (simple linear regression between log-transformed percent slope and mean weekly minimum temperature $r^2 = 0.53$, $P < 0.001$, on 30 d.f.). To account for the potentially confounding effects of the forest canopy on thermal conditions, we sampled temperature on both forested backslopes and adjacent, logged openings. There was a minor difference between these closed-canopy and open-canopy sites; however, this difference is dwarfed by the effect of cold air pooling within the shallowly-sloping valley bottoms.

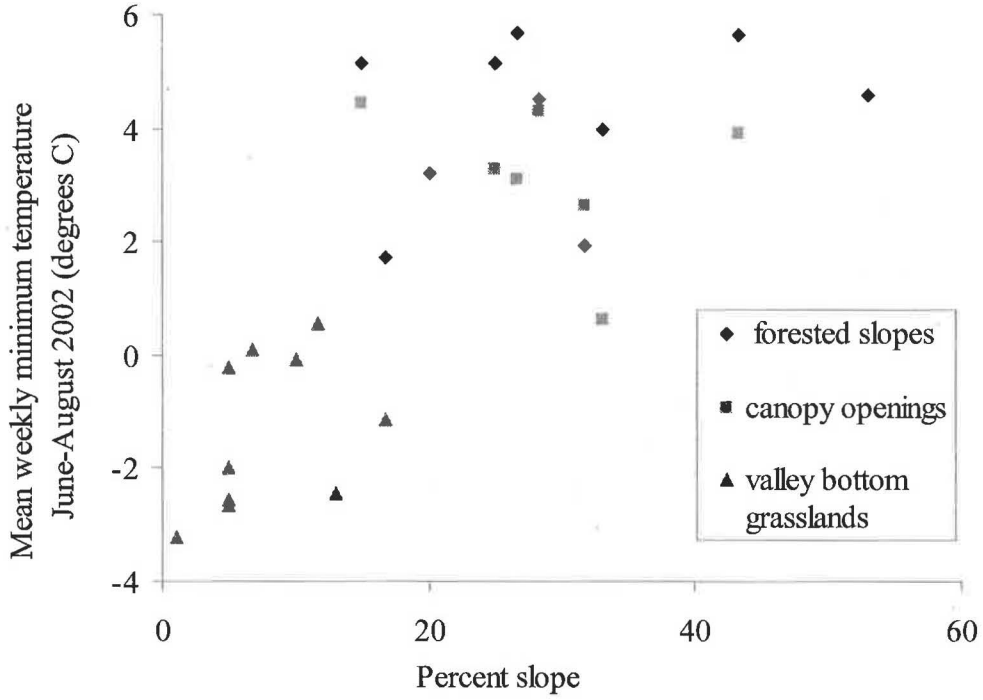


Table 1. Environmental variables measured at sampled quadrats.

Variable	code	N	Sampling methodology	Transformation
Spatial location (*x,y*)	Space	200	UTM x,y GPS reading (meters)	none
Elevation	Elev	200	GPS reading (meters)	none
Slope	Slope	200	clinometer reading across steepest reach of quadrat (proportion)	ln
Aspect	Aspect	200	compass bearing (degrees)	-cos(degrees-45°)
Coarse fraction	Coarse	150	oven dry mass coarse fraction/ oven dry mass sand + silt + clay (proportion)	ln
Sand	Sand	150	modified hydrometer method (proportion dry mass)	2/p * arcsin(squareroot)
Silt	Silt	150	modified hydrometer method (proportion dry mass)	2/p * arcsin(squareroot)
Clay	Clay	150	modified hydrometer method (proportion dry mass)	2/p * arcsin(squareroot)
pH	pH	32	pH meter; soil pH in water using a 1:1.3 soil:solution ratio (-log[H^+])	none
Organic matter	OM	32	loss-on-ignition (360° C for 2 hours) (proportion dry mass)	ln
Available P	P	32	acid extraction (0.002 M sulfuric acid) (ppm)	ln
Exchangeable K	K	32	extracted in 1 M NH_4OAc at pH 7.0 (ppm)	ln
Exchangeable Ca	Ca	32	extracted in 1 M NH_4OAc at pH 7.0 (ppm)	none
Exchangeable Mg	Mg	32	extracted in 1 M NH_4OAc at pH 7.0 (ppm)	none
Total N	N	32	(Org N + NH_4-N + NO_3-N, NO_2-N) digested with sulfuric acid, metal catalyst, salicylic acid (ppm)	ln
Soil moisture	SoilH_20	64	mean value of gravimetric moisture content; sampled every 3 weeks June-August 2002 (proportion dry mass)	ln
Soil moisture Standard deviation	SDH_20	64	standard deviation of gravimetric moisture content, 3 soil cores 15 cm depth pooled for each quadrat; sampled every 3 weeks June-August 2002 (proportion dry mass)	ln
Soil temperature	Soiltemp	60	50 cm depth at center of quadrat, August 2001 (degrees C)	none
Weekly minimum air temperature (June-Aug)	JJA lowtemp	28	mean of minimum air temperatures recorded each week June-August 2002, 15 cm above ground surface, using a combination of max/min thermometers (16) and dataloggers (12) (degrees C)	none
Mean air temperature (June-Aug)	JJA meantemp	12	mean air temperature, 15 cm height, June-August 2002, using dataloggers (degrees C)	none
Annual mean air temperature	Yr meantemp	12	mean air temperature, 15 cm height, June 2001-June 2002, using dataloggers (degrees C)	none
Days between 0° C	Days btwn 0°C	12	longest period between air temperatures of 0° C, June 2001-June 2002 (days)	none
Days between -5° C	Days btwn -5°C	12	longest period between air temperatures of -5° C, June 2001-June 2002 (days)	none

Table 2. Groups identified by cluster analysis, with the three most abundant species in each group, the strongest indicator species, and mean ± s.d. values for species richness and diversity. Subplot richness is measured in 1 m^2 subquadrats and does not include the tree layer; total plot richness includes all plant species occurring in each 100 m^2 sample.

Group	Dominant species (mean percent cover)	Indicator species (indicator species value)	Subplot richness	Total plot richness	Simpson diversity index
Communities of Mountain Slopes					
Subalpine Balds and Aspen Groves	*Festuca thurberi* (36) *Populus tremuloides* (19) *Danthonia parryi* (19)	*Festuca thurberi* (65) *Lathyrus lanszwertii* (51) *Vicia americana* (36)	8.3 ± 3.2	17.7 ± 5.7	0.58 ± 0.19
Mixed Conifer	*Pseudotsuga menziesii* (63) *Abies concolor* (23) *Picea engelmannii* (4)	*Pseudotsuga menziesii* (68) *Abies concolor* (44) *Viola canadensis* (30)	5.3 ± 5.6	18.8 ±10.8	0.54 ± 0.20
Blue Spruce	*Picea pungens* (63) *Populus tremuloides* (5) *Carex siccata* (3)	*Picea pungens* (82) *Carex siccata* (44) *Trisetum montanum* (43)	5.9 ± 4.6	18.3 ± 8.3	0.60 ± 0.20
Ponderosa	*Pinus ponderosa* (57) *Poa pratensis* (9) *Danthonia parryi* (6)	*Pinus ponderosa* (85) *Geranium caespitosum* (15) *Festuca arizonica* (13)	6.1 ± 3.7	17.1 ± 5.7	0.55 ± 0.19
Communities of Valley Bottoms					
Arizona Fescue	*Festuca arizonica* (20) *Muhlenbergia montana* (9) *Blepharoneuron tricholepis* (7)	*Festuca arizonica* (51) *Muhlenbergia montana* (48) *Bouteloua gracilis* (46)	13.1 ± 2.8	22.4 ± 3.6	0.88 ± 0.03
Parry's Oatgrass	*Danthonia parryi* (22) *Poa pratensis* (19) *Taraxacum officinale* (5)	*Campanula rotundifolia* (33) *Trifolium repens* (28) *Danthonia parryi* (27)	13.2 ± 3.4	26.5 ± 5.8	0.77 ± 0.17
Mesic Grasslands	*Blepharoneuron tricholepis* (11) *Festuca idahoensis* (10) *Poa pratensis* (8)	*Blepharoneuron tricholepis* (41) *Festuca idahoensis* (39) *Muhlenbergia wrightii* (39)	12.9 ± 3.5	22.2 ± 4.4	0.86 ± 0.09
Wet Meadows	*Poa pratensis* (12) *Deschampsia caespitosa* (11) *Carex pellita* (10)	*Carex pellita* (47) *Deschampsia caespitosa* (45) *Carex microptera* (39)	11.6 ± 4.5	20.7 ± 6.4	0.82 ± 0.06
Sedge Meadows	*Carex aquatilis* (20) *Deschampsia caespitosa* (12) *Carex pellita* (9)	*Carex utriculata* (79) *Carex aquatilis* (71) *Eleocharis palustris* (43)	8.0 ± 5.0	17.3 ± 9.8	0.69 ± 0.25

Table 3. Average elevation, slope, soil texture, summer soil moisture, and summer minimum temperatures in each of the nine vegetation groups.

Group	N	Mean elevation (meters)	Mean % slope	Soil textural classes	Mean June-August % soil moisture (mass basis)	Mean June-August weekly minimum temperature (degrees C)
Communities of Mountain Slopes						
Subalpine Balds and Aspen Groves	12	2943	14.5	sandy loam, loam, sandy clay loam	9.6	N/A
Mixed Conifer	9	2874	25.8	loam	17.1	4.6
Blue Spruce	12	2657	27.0	sandy loam, loam	13.6	4.9
Ponderosa	36	2660	26.2	sandy loam, loam	10.5	4.1
Communities of Valley Bottoms						
Arizona Fescue	29	2625	15.7	loam	10.7	0.3
Parry's Oatgrass	36	2651	12.0	loam	16.0	-1.0
Mesic Grasslands	34	2624	5.2	clay loam	14.2	-1.4
Wet Meadows	26	2658	3.7	clay loam, clay	21.9	-1.9
Sedge Meadows	16	2615	1.8	clay loam	65.5	-0.2

Table 4. Simple Mantel correlations between environmental dissimilarity, spatial distance, and vegetation compositional dissimilarity, and partial Mantel correlations between environment and vegetation controlling for spatial location. Three components of compositional dissimilarity were examined – type, forest composition, and grassland composition – through a binary coding of the entire dissimilarity matrix or a focus on forest or grassland samples alone. For each, we tested the simple Mantel correlation (left subcolumn) and the partial Mantel correlation controlling for relationships with a spatial dissimilarity matrix (right subcolumn). ns = $p > 0.05$, * = $0.05 > p > 0.01$, ** = $0.01 > p > 0.001$, *** = $p < 0.001$.

Variable	Space	Vegetation type		Forest composition		Grassland composition	
	simple Mantel *r*	simple Mantel *r*	partial Mantel *r* controlling for space	simple Mantel *r*	partial Mantel *r* controlling for space	simple Mantel *r*	partial Mantel *r* controlling for space
Space	na	ns		0.09*		0.10**	
Elev	0.17****	0.08*	0.07*	0.36***	0.36***	0.26**	0.25**
Slope	0.05*	0.22***	0.22***	ns	ns	0.30***	0.30***
Aspect	0.07****	ns	ns	0.30***	0.29**	0.05*	0.05*
Coarse	ns	0.12***	0.12***	0.22**	0.22**	ns	ns
Sand	0.06*	0.14***	0.14***	ns	ns	0.17**	0.16**
Silt	0.06*	ns	ns	ns	ns	0.08*	0.08*
Clay	ns	0.24***	0.24***	0.21***	0.21***	0.33***	0.33***
pH	ns	ns	ns	ns	ns	0.35**	0.34**
OM	ns	ns	ns	0.37*	0.38*	0.54***	0.53**
P	0.20*	ns	ns	ns	ns	ns	ns
K	ns	ns	ns	ns	ns	ns	ns
Ca	ns	0.26**	0.25**	0.49**	0.50**	ns	ns
Mg	ns	ns	ns	ns	ns	ns	ns
N	ns	0.31***	0.31***	0.36*	0.36*	0.34***	0.36***
SoilH_20	ns	ns	ns	0.33***	0.33***	0.52***	0.50***
SDH_20	ns	ns	ns	ns	ns	0.32*	0.29*
Soiltemp	0.11**	0.21**	0.21**	ns	ns	ns	ns
JJA lowtemp	ns	0.77***	0.77***	ns	ns	ns	ns
JJA meantemp	ns	ns	ns	ns	ns	ns	ns
Yr meantemp	ns	ns	ns	ns	ns	ns	ns
Days btwn 0° C	ns	0.66*	0.64*	ns	ns	ns	ns
Days btwn -5° C	ns	0.89*	0.89*	ns	ns	ns	ns

Table 5. Simple and partial Mantel correlations between the type (forest vs. grassland binary dissimilarity matrix) and dissimilarity matrices based on % sand, soil moisture, and June-August mean weekly minimum temperatures, viewed as direct effects or controlling for variation in the other predictors. Note the much stronger relationship of vegetation type to temperature than soil texture, and the larger impact of controlling for temperature on the apparent correlation based on soil texture. ns = $p > 0.05$, * = $0.05 > p > 0.01$, ** = $0.01 > p > 0.001$, *** = $p < 0.001$.

Variable	Type simple Mantel *r*	Type partial Mantel *r* controlling for clay	Type partial Mantel *r* controlling for soilH_20	Type partial Mantel *r* controlling for JJA lowtemp
Clay	0.25***		0.25***	0.12*
SoilH_20	ns	ns		ns
JJA lowtemp	0.77***	0.74****	0.77***	

Appendices

Appendix I. List of 206 taxa sampled in 200 (5 x 20m^2) quadrats in mountain grasslands and forest edges in the Valles Caldera National Preserve. Nomenclature follows USDA Plants database and Flora of North America. Species pairs that could not be consistently distinguished in the field were included together (e.g. *Antennaria parvifolia* and *A. marginata*); for several taxa, no determination beyond genus was possible (e.g. *Stellaria* spp.). Taxa are listed in order of abundance (percent cover on all quadrats); percent frequency is also given. Group occurrences are also noted as follows: 1, Aspen Groves and Subalpine Balds; 2, Mixed Conifer; 3, Blue Spruce; 4, Ponderosa Pine; 5, Arizona Fescue; 6, Parry's Oatgrass; 7, Mesic Grasslands; 8, Wet Meadows; 9, Sedge Meadows.

Binomial	Common Name	Percent Cover	Percent Frequency	Groups
Pinus ponderosa Douglas ex P. & C. Lawson var. *scopulorum* Engelm.	ponderosa pine	11.049	19.5	1,3,4,5
Poa pratensis L	Kentucky bluegrass	8.829	75.0	1,2,3,4,5,6,7,8,9
Danthonia parryi Scribn.	Parry's oatgrass	6.25	35.5	1,2,3,4,5,6,7,8
Picea pungens Englem.	Colorado blue spruce	4.578	10.5	1,2,3,4,6
Festuca arizonica Vasey	Arizona fescue	4.38	47.5	1,3,4,5,6,7
Blepharoneuron tricholepis (Torr.) Nash	pine dropseed	3.177	44.5	1,2,4,5,6,7,8,9
Potentilla hippiana Lehm.	wooly cinquefoil	2.97	71.0	1,2,3,4,5,6,7,8,9
Festuca thurberi Vasey	Thurber's fescue	2.899	17.0	1,2,3,4,6,7,8
Taraxacum officinale G.H. Weber ex Wiggers	common dandelion	2.492	73.5	1,2,3,4,5,6,7,8,9
Festuca idahoensis Romer	Idaho fescue	2.467	27.5	4,5,6,7,8,9
Muhlenbergia montana (Nutt.) Hitchc.	mountain muhly	2.379	39.0	4,5,6,7,9
Deschampsia caespitosa (L.) Beauv.	tufted hairgrass	2.262	18.0	6,7,8,9
Carex pellita Willd.	wooly sedge	2.055	21.5	4,5,6,7,8,9
Achillea millefolium L. var. *occidentalis* DC.	western yarrow	1.934	78.0	1,2,3,4,5,6,7,8,9
Koeleria macrantha (Lebed.) Schult.	Junegrass	1.795	50.5	1,4,5,6,7,8,9
Pseudotsuga menziesii (Mirb.) Franco var *glauca* (Beiss.) Franco	Douglas fir	1.758	5.5	2,3,4
Juncus balticus Willd. var. *montanus* Engelm.	Baltic rush	1.621	56.5	4,5,6,7,8,9
Antennaria parivifolia Nutt./*A. marginata* Greene	small-leaf pussytoes, white margin pussytoes	1.584	39.5	1,2,3,4,5,6,7
Carex aquatilis Wahlenb.	water sedge	1.511	7.0	8,9
Muhlenbergia wrightii Vasey ex Coult.	spike muhly	1.37	16.5	5,6,7,8,9
Abies concolor (Gord. & Glend.) Hildebr.	white fir	1.35	6.5	1,2,3,4
Trifolium repens L.	white clover	1.347	31.5	2,3,4,5,6,7,8,9
Populus tremuloides Michx.	quaking aspen	1.309	4.5	1,2,3
Danthonia intermedia Vasey	timber oatgrass	1.09	9.5	6,7,8

Erigeron formosissimus Greene	beautiful fleabane	1.082	57.5	1,2,3,4,5,6,7,8,9
Symphyotrichum adscendens (Lindl.) Nesom.	western aster	1.053	27.0	1,4,5,6,7,8,9
Carex praegracilis W. Boott	clustered field sedge	0.984	36.5	2,4,5,6,7,8,9
Arenaria fendleri Gray	Fendler's sandwort	0.871	29.5	1,4,5,6,7
Bouteloua gracilis (Kunth) Lag.	blue grama	0.858	13.0	4,5,6
Erigeron flagellaris A. Gray	trailing fleabane	0.84	41.0	2,3,4,5,6,7,8
Carex utriculata Boott.	Northwest territory sedge	0.729	8.0	8,9
Iris missouriensis Nutt.	Rocky Mountain iris	0.718	23.5	1,2,4,6,7,8,9
Carex microptera Mack.	smallwing sedge	0.697	19.5	3,6,7,8,9
Eleocharis palustris (L.) Roemer & J.A. Schultes	common spikerush	0.667	5.0	7,8,9
Carex inops Bailey ssp. *heliophila* (Mackenzie) Crins	sun sedge	0.663	29.5	1,2,4,5,6,7,8
Argentina answerina (L.) Rydb.	silverweed cinquefoil	0.636	10.5	6,7,8,9
Carex rossii Boott.	Ross' sedge	0.625	18.0	1,2,3,4
Ranunculus cardiophyllus Hook	heart-leaf buttercup	0.574	36.5	4,5,6,7,8,9
Agrostis scabra Willd.	rough bentgrass	0.546	24.5	2,3,4,5,6,7,8,9
Muhlenbergia richardsonis (Trin.) Rydb.	mat muhly	0.472	26.0	5,6,7,8,9
Elymus ×pseudorepens (Scribn. & J.G. Sm.) Barkworth & D.R. Dewey	hybrid wheatgrass	0.462	35.5	1,3,4,5,6,7,8,9
Poa fendleriana (Steud.) Vasey	muttongrass	0.459	27.0	1,3,4,5,6,7
Carex siccata Dewey (*C. foenea* Willd. var. *foenea*)	dryspike sedge	0.441	16.0	1,2,3,4,6
Penstemon rydbergii A. Nelson	Rydberg's penstemon	0.437	9.5	5,6,7,8
Carex obtusata Lilj.	obtuse sedge	0.429	28.0	1,3,4,5,6,7,8
Antennaria rosulata Rydb.	Kaibab pussytoes	0.417	8.0	4,5,6,7
Heterotheca villosa (Pursh) Shinners	hairy false goldenaster	0.401	11.0	4,5,6
Elymus elymoides (Raf.) Swezey ssp. *brevifolius* (J.G. Sm.) Barkworth	squirreltail	0.385	31.0	1,3,4,5,6,7
Carex simulata Mack.	analogue sedge	0.334	4.0	7,9
Campanula rotundifolia L.	Parry's bellflower	0.299	34.0	1,3,4,5,6,7,8
Carex petasata Dewey	Liddon sedge	0.296	33.5	1,5,6,7,8
Juniperus communis L.	common juniper	0.267	9.0	2,3,4,6
Dodecatheon pulchellum (Raff.) Merr.	darkthroat shootingstar	0.265	4.5	6,8,9
Bromus porteri (Coult.) Nash	Porter brome	0.261	26.0	1,4,5,6,7
Dasiphora floribunda (Pursch) Kartesz	shrubby cinquefoil	0.216	11.5	6,7,8,9
Fragaria virginiana Duchesne ssp. *glauca* (S. Wats.) Staudt	Virginia strawberry	0.214	13.0	1,2,3,4,6
Vicia americana Muhl. ex Willd.	American vetch	0.209	31.0	1,3,4,5,6,7,8,9
Phleum pratense L.	timothy	0.203	11.5	4,5,6,7,8,9
Cerastium arvense L.	field chickweed	0.201	20.0	1,2,3,4,5,6,7,8,9
Artemisia carruthii Wood ex Carruth.	Caruth's sagewort	0.2	15.0	4,5,7
Picea engelmannii Parry ex. Englm.	Engelmann spruce	0.198	1.5	2,3
Fragaria vesca L. ssp. Americana (Porter) Staudt	woodland strawberry	0.197	9.0	1,2,3,4,6
Hordeum brachyantherum Nevski	meadow barley	0.195	5.5	7,8,9

Symphiotrichum Nees sp.	aster	0.178	7.0	7,8,9
Elymus L. sp.	wheatgrass	0.175	5.0	1,3,4,6
Abies arizonica Merriam	corkbark fir	0.172	1.0	2
Lathyrus lanszwertii Kellogg	Nevada pea	0.16	20.0	1,2,3,4,5,6,7
Potentilla pulcherrima Lehm.	beautiful cinquefoil	0.154	15.0	1,2,3,4,6,7,8,9
Phleum alpinum L.	alpine timothy	0.154	8.5	6,8,9
Geranium richardsonii Fisch. & Trautv.	Richardson's geranium	0.153	8.0	1,2,3,4,6
Trifolium longipes Nutt.	longstalk clover	0.147	10.0	6,7,8,9
Viola adunca Sm.	hookspur violet	0.144	15.0	1,3,4,5,6,8,9
Allium geyeri S. Wats.	Geyer's onion	0.143	20.5	6,7,8,9
Erigeron eximius Greene	sprucefir fleabane	0.129	4.5	2,3
Bromus ciliatus L. var. *richardsonii* (Link) Boivin	fringed brome	0.128	9.0	1,2,3,4
Pascopyrum smithii (Rydb.) A. Löve	western wheatgrass	0.116	5.0	4,5,6,7,8
Poa palustris L.	fowl bluegrass	0.112	4.0	8,9
Prunella vulgaris L.	self-heal	0.112	4.5	5,6,8
Trisetum montanum Vasey	spike trisetum	0.093	7.0	1,2,3,4
Calamagrostis canadensis (Michx.) P. Beauv. var. *canadensis*	bluejoint	0.091	3.5	6,8,9
Agoseris glauca (Pursh) Raf.	pale agoseris	0.086	13.0	5,6,7,8,9
Carex douglasii Boott.	Douglas' sedge	0.079	6.0	4,5,6,7,8
Pseudocymopterus montanus (Gray) Coult. & Rose	alpine false springparsley	0.076	19.5	1,2,3,4,6,7
Vaccinium myrtillus L.	whortleberry	0.076	1.0	2,3
Hypericum scouleri Hook.	Scouler's St. Johnswort	0.074	3.0	6,8,9
Mertensia oblongifolia (Nutt.)G.Don	oblongleaf bluebells	0.069	8.5	1,3,4,5,6
Geranium caespitosum James	James geranium	0.069	6.5	1,4,5
Orthocarpus luteus Nutt.	yellow owl's clover	0.068	9.0	1,4,5,6,8
Solidago missouriensis Nutt.	Missouri goldenrod	0.066	3.0	5,6,7
Hymenoxys hoopesii (Gray) Bierner	sneezeweed	0.063	3.0	1,6,8
Veratrum viride Ait.	false hellebore	0.062	0.5	8
Viola canadensis L.	Canadian white violet	0.062	3.5	2,3,4
Geum triflorum Pursh	prairiesmoke	0.061	9.0	1,4,5,6,7
Crepis runcinata (James) Torr. & Gray	fiddleleaf hawksbeard	0.056	4.0	1,6,8,9
Campanula parryi A. Gray	bluebell bellflower	0.052	10.5	1,4,5,6,7,8,9
Hierochloë odorata (L.) P. Beauv.	sweetgrass	0.052	3.0	8,9
Rumex acetosella L.	sheep sorrel	0.05	4.0	3,6,8,9
Galium aparine L.	bedstraw	0.046	5.0	1,2,3,4,6
Gentiana affinis Griseb.	pleated gentian	0.045	10.0	5,6,7
Agoseris aurantica (Hook.) Greene	orange agoseris	0.044	10.0	1,5,6,7,8
Artemisia ludoviciana Nutt.	white sagebrush	0.044	13.0	2,4,5,6,7
Galium boreale L.	northern bedstraw	0.044	6.0	4,3,6,8
Krigia biflora (Walt.) Blake	twoflower dwarfdandelion	0.043	1.5	8,9
Schizachyrium scoparium (Michx.) Nash	little bluestem	0.043	0.5	5
Thermopsis divaricarpa A. Nels.	spreadfruit	0.043	1.0	1,6

	goldenbanner			
Carex duriuscula C.A. Mey	needleleaf sedge	0.042	3.5	5,6,8
Erigeron subtrinervis Rydb. ex Porter and Britton	threenerve fleabane	0.041	1.5	8
Osmorhiza depauperata Phil.	sweet cicely	0.039	3.0	2,3
Besseya plantaginea (James) Rydb.	White River coraldrops	0.034	4.5	3,5,6
Tragopogon dubius Scop.	yellow salsify	0.033	2.0	1,2,5,6
Erigeron speciosus (Lindl.) DC.	aspen fleabane	0.032	5.5	2,3,4
Festuca saximontana Rydb.	Rocky Mountain fescue	0.031	1.0	6
Packera neomexicana (Gray) W.A. Weber & A. Löve	New Mexico groundsel	0.03	6.0	5,6,7
Caltha leptosepala DC.	white marsh marigold	0.028	2.5	8,9
Oxalis violacea L.	violet woodsorrel	0.026	3.5	2,3,4
Cicuta maculata L.	spotted water hemlock	0.025	1.0	8,9
Carex occidentalis Bailey	western sedge	0.024	3.5	2,4,6
Allium cernuum Roth	nodding onion	0.023	7.5	2,4,5,6,7,8
Pyrrochoma Hook sp.	goldenweed	0.023	3.0	6,8
Polygonum douglasii Greene ssp. *johnstonii* (Munz) Hickman	Johnston's knotweed	0.022	5.5	4,5,6
Eleocharis quinqueflora (F.X. Hartmann) Schwarz	fewflower spikerush	0.021	1.0	8,9
Acer glabrum Torr.	mountain maple	0.019	0.5	2
Lupinus argenteus Pursh	silvery lupine	0.018	2.0	5
Paxistima myrsinites (Pursh) Raf.	mountain-lover	0.018	2.5	2,3
Rorippa sphaerocarpa (Gray) Britt.	roundfruit yellowcress	0.018	3.5	7,8,9
Silene drummondii Hook./*S. scouleri* Hooker	Drummond's campion/simple campion	0.017	8.0	1,2,3,5,6,7,8
Sisyrinchium montanum Greene	blue-eyed grass	0.017	5.0	6,7,8
Heuchera parvifolia Nutt. ex Torr. & A. Gray	littleleaf alumroot	0.016	4.0	1,3,4,6
Thalictrum fendleri Engelm. ex A. Gray	Fendler's meadowrue	0.016	1.0	1,2
Juncus saximontanus A. Nels.	Rocky Mountain rush	0.015	1.5	8,9
Cyperus fendlerianus Boeckl.	Fendler's flatsedge	0.014	1.5	4
Mirabilis comata (Small) Standl.	hairy-tuft four o'clock	0.014	2.0	4,5
Saxifraga rhomboidea Greene	diamondleaf saxifrage	0.013	4.5	4,6,7,8
Descurainia sophia (L.) Webb ex Prantl.	sophia tansymustard	0.013	2.0	3,5
Erigeron lonchophyllus Hook.	shortray fleabane	0.013	2.0	8,9
Androsace septentrionalis L.	rockjasmine	0.012	5.0	2,4,6,7,9
Chamaesyce serpyllifolia (Pers.) Small	thymeleaf sandwort	0.012	1.0	7
Cystopteris fragilis (L.) Bernh.	brittle bladderfern	0.011	1.0	2
Hymenopappus newberryi (Gray) I.M.	Newberry's	0.01	2.0	4,5

Johnston	hymenopappus			
Ribes inerme Rydb.	whitestem gooseberry	0.01	2.5	2,4
Artemisia franserioides Greene	ragweed sagebrush	0.01	1.0	2
Carex conoidea Schkuhr ex Willd.	openfield sedge	0.01	0.5	8
Madia glomerata Hook	mountain tarweed	0.01	0.5	9
Mahonia repens (Lindl.) G. Don	creeping barberry	0.01	1.0	4
Veronica peregrina L.	neckweed	0.01	3.0	7,8,9
Oenothera flava (A. Nels.) Garrett	yellow evening primrose	0.01	1.0	7
Arabis drummondii Gray	Drumond's rockcress	0.009	3.0	5,6,7
Gentianella amarella (L.) Boerner	autumn dwarf gentian	0.009	4.0	1,6,7,8
Plantago major L.	common plantain	0.009	2.5	6,7,8
Mentha arvensis L.	wild mint	0.008	2.0	8,9
Rubus ideas L.	American red rasberry	0.008	2.0	2,3
Solidago simplex Kunth ssp. *simplex*	Mt. Albert goldenrod	0.008	1.0	1
Elymus trachycaulus (Link) Gould ex Shinners ssp. *trachycaulus*	slender wheatgrass	0.007	1.0	7,8
Hieracium fendleri Schultz-Bip.	Fendler's hawkweed	0.007	2.5	4,3
Ranunculus aquatilis L.	whitewater crowfoot	0.007	0.5	9
Torreyochloa pallida (Torr.) Church var. *pauciflora* (J. Presl) J.I. Davis	pale false mannagrass	0.007	1.0	8,9
Calochortus gunnisonii S. Wats.	Gunnison's mariposa lily	0.006	3.0	6,8
Castilleja. Mutis ex. L.f. sp	sulfur Indian paintbrush	0.006	2.0	5
Clematis columbiana (Nutt.) Torr. & A. Gray	rock clematis	0.006	0.5	2
Juncus longistylis Torr.	longstyle rush	0.006	1.5	8,9
Linum lewisii Pursh	prairie flax	0.006	1.0	1
Packera fendleri (Gray) W.A. Weber & A. Löve	Fendler's ragwort	0.006	0.5	4
Penstemon barbatus (Cav.) Roth	beardlip penstemon	0.006	2.0	5
Quercus gambelii Nutt.	Gambel's oak	0.006	2.0	4,6,8
Stellaria L. sp.	starwort	0.006	2.0	2,3,4,8
Carex deweyana Schwein.	Dewey sedge	0.005	1.5	2,3
Epilobium leptophyllum Raf.	bog willowherb	0.005	2.5	9
Pinus strobiformis Englm.	southwestern white pine	0.005	1.0	2,4
Galium trifidum L.	threepetal bedstraw	0.005	1.5	7,8,9
Gentianopsis detonosa (Rottb.) Ma	windmill fringed gentian	0.005	0.5	9
Lappula occidentalis (S.Wats.) Greene	flatspine stickseed	0.005	1.0	5
Lepidium virginicum L. var. *pubescens* (Greene) Thellung	hairy pepperweed	0.005	1.0	5
Ranunculus inamoenus Greene	graceful buttercup	0.005	2.0	2,3
Cerastium brachypodum (Engelm. Ex Gray) B.L. Robins.	shortstalk chickweed	0.004	0.5	9

Oreochrysum parryi (Gray) Rydb.	Parry's goldenrod	0.004	1.0	1
Ranunculus macounii Britt.	Macoun's buttercup	0.004	1.0	8
Rosa nutkana C. Presl.	Nootka rose	0.004	1.0	4,3
Triglochin palustre L.	marsh arrowgrass	0.004	1.0	8,9
Veronica americana Schwein. ex Benth. in DC.	American speedwell	0.004	1.0	9
Artemisia frigida Willd.	fringed sage	0.003	1.5	5
Chenopodium fremontii S. Wats.	Fremont's goosefoot	0.003	1.5	4,3,6
Conioselinum scopulorum (A.Gray) J.M. Coult. & Rose	Rocky Mountain hemlockparsley	0.003	0.5	2
Festuca sororia Piper	ravine fescue	0.003	1.5	1,3,4
Polygonum aviculare L.	prostrate knotweed	0.003	0.5	9
Rudbeckia hirta L.	blackeyed Susan	0.003	0.5	1
Aquilegia elegantula Greene	western red columbine	0.002	0.5	2
Cirsium parryi (Gray) Petrak	Parry's thistle	0.002	1.0	6,9
Draba aurea Vahl. ex Hornem.	golden draba	0.002	1.0	5,6
Linnaea borealis L.	twinflower	0.002	1.0	2,3
Maianthemum racemosum (L.) Link. var. *amplexicaule* (nutt.) Dorn	false lily-of-the-valley	0.002	1.0	2
Poa compressa L.	Canada bluegrass	0.002	1.0	2,7
Sambucus racemosa L.	red elderberry	0.002	0.5	3
Spiranthes romanzoffiana	ladies tresses	0.002	1.0	8
Urtica dioica L. var. *procera* (Muhl. ex. Willd.) Wedd.	stinging nettle	0.002	1.0	2,3
Zigadenus elegans Pursch	mountain deathcamus	0.002	1.0	6
Juniperus scopulorum Sarg.	Rocky Mountain juniper	0.001	0.5	4
Bromus carinatus Hook. & Arn.	California brome	0.001	0.5	9
Corydalis aurea Willd.	golden smoke	0.001	0.5	2
Draba rectifructa C.L. Hitchc.	mountain draba	0.001	0.5	6
Erysimum capitatum (Douglas ex. Hook.) Greene	sanddune wallflower	0.001	0.5	5
Gentiana fremontii Torr.	moss gentian	0.001	0.5	9
Hymenoxys richardsonii (Hook.) Cockerell var. *floribunda* (A.Gray) Bierner	pingue rubberweed	0.001	0.5	4
Mimulus guttatus DC.	seep monkeyflower	0.001	0.5	9
Senecio eremophilus Richardson	desert ragwort	0.001	0.5	2
Senecio wootonii Greene	Wooton's ragwort	0.001	0.5	4
Shepherdia canadensis (L.) Nutt.	buffaloberry	0.001	0.5	3

Chapter II

Ponderosa pine adult tree growth and moisture stress at subalpine treelines in the Valles Caldera National Preserve, New Mexico

Abstract

The causes of subalpine treelines – including the shift from forested mountain slopes to grassy valley bottoms in semi-arid ranges of the western United States – are not well known. Here we test the hypothesis that such ecotones in the Valles Caldera are caused by declines in adult tree growth toward treeline, and may reflect declines in moisture availability due to finer-grained soils and/or increased competition from grasses. We measured predawn xylem water potential (ψ_L), height growth, radial growth, and stand density of ponderosa pine (*Pinus ponderosa* var. *scopulorum*), as well as coverage by grasses and forbs, at 20 sites spanning the topographic gradient from steep, forested slopes on coarse soils to flat, grassy valley bottoms with loamy soils. We found no evidence that adult tree growth was limited at the subalpine treelines; in fact, trees growing at the forest-grassland ecotone on fine-grained soils grew at higher rates and experienced less water stress than trees growing further upslope. Summer water stress exerted a strong negative effect on adult tree growth in both 2002 (a drought year) and 2003, but water stress tended to be greater upslope in heavily forested areas. We conclude that constraints on adult tree growth are not responsible for the exclusion of trees from valley bottoms in the Valles Caldera, and that the mechanism underlying exclusion must be sought elsewhere is more likely some constraint on tree seedling establishment.

Key words: meadow, park, pine-grassland ecotone, Jemez Mountains, montane grasslands, *Pinus ponderosa*, species distributions, water status

Introduction

Grassy meadows and parks are common features in the otherwise forested landscapes of the southern Rockies and the southwestern United States generally (Dick-Peddie 1993; Brown 1994; Peet 2000). Subalpine treeline ecotones frequently occur on the transition from forested slopes to shallowly-sloping or level sites, especially at the margins of broad valley bottoms and drainages (Ramaley 1927; Turner and Paulsen 1976; Brown 1994). Numerous environmental factors have been proposed as possible explanations for the treeless conditions on these sites, including **adverse soil chemistry/texture** Ramaley 1910, 1927; Peet 1989, 2001), **soil drought** (Koterba and Habeck 1971), **waterlogging** (Ives 1942), and **cold-air drainage** (Ramaley 1910) via their effects on adult or juvenile tree growth and survival. In the newly established Valles Caldera National Preserve (VCNP) of the Jemez Mountains, New Mexico, approximately 10,000 ha of grasslands occur in a vast volcanic basin between 2575 and 2730 m elevation (Fig. 1). These communities (subalpine grasslands *sensu* Brown 1994) primarily occur on flats and gentle slopes within the central topographical concavities of the caldera, and form abrupt, inverted treeline ecotones with stands dominated by ponderosa pine (*Pinus ponderosa* Douglas ex. P.& C. Lawson) and Colorado blue spruce (*Picea pungens* Engelm.) on the surrounding mountain slopes. A gradient analysis of these grasslands, adjacent forests, and inverted treelines in the VCNP (Chapter I; Coop and Givnish, unpubl. data) showed that shifts from forested slopes to grassy valley bottoms were strongly correlated with both edaphic and thermal conditions. Soils were generally finer-textured in the grassy valley bottoms (38.9 ± 14.3 % sand [mean ± s.d.]) than on the adjacent forested slopes (50.0 ± 12.6 %). Valley bottoms also experienced substantial cold-air drainage and pooling, resulting in dramatically lower minimum temperatures - ca. 5.8° ± 1.4°C lower in valley bottoms than on adjacent forested slopes - and many fewer frost-free days. Minimum temperatures across the VCNP increased strongly with slope inclination, independent of the relatively minor positive effects of the tree canopy alone (openings were 1.4°C cooler than closed-canopy sites on slopes).

While any ecotone likely reflects the response of several species to a complex, site-specific set of environmental factors, the actual *processes* that favor the formation and maintenance of treelines are likely to be general. Persistent treeline ecotones may be caused by context-dependent, spatially localized restrictions on **adult tree growth** (Daubenmire 1954; Givnish 1995; Körner 1998, Li et al. 2002) or **tree seedling establishment and growth** (Wardle 1971; Tranquillini 1979; Cuevas 2000). This paper tests the hypothesis that subalpine treeline ecotones in the VCNP are caused by spatially localized constraints on adult tree growth. The potential relevance of environmental spatial variation in the growth and survival of tree seedlings is examined in a companion study (Chapter III; Coop and Givnish unpublished data).

The primary physiological constraints on adult tree growth near subalpine ecotones in the southern Rockies are likely to involve (i) the effects of fine soil texture on trees, including direct effects on moisture supply and indirect effects of increased competition with grasses; (ii) adverse impacts of cold-air drainage on adult tree growth; or (iii) both. Fine-textured soils on lower slopes and flats might decrease tree growth by decreasing the availability of moisture to trees vs. grasses, which root at different depths (Walter 1971; Walker and Noy-Meir 1982). To explain patterns of competition and resource partitioning between trees and grasses in semi-arid subtropical savannas, Walter (1971) proposed a two-layer soil system, in which grasses outcompete woody plants for shallow soil moisture, but woody plants have exclusive access to deep moisture. Knoop and Walker (1985) found that the increased water-holding capacity of

fine-textured topsoils in a subtropical savanna supported a dense growth of grasses that depleted the moisture available to deeply rooted woody plants, and resulted in decreased woody plant growth; however, they found no such effect on sandy soils. They also found that competition between trees and grasses on fine-textured soils was more pronounced during a year when rainfall was relatively high. Based on these findings, we might expect that finer-textured soils in the valley bottoms of the VCNP should increase moisture availability to shallow-rooted grasses and decrease moisture availability to deep-rooted trees, by decreasing the rates of water infiltration and percolation and (perhaps) by providing more nutrients to support a more lush growth of grasses. Trees growing on finer-textured soils might also show little or slow response to summer precipitation, which would be absorbed rapidly by shallowly rooted grasses reaching their peak growth rates during the summer monsoons; trees on sandier soils should show a much greater and more rapid response to summer precipitation.

Cold temperatures in the valley bottoms of the VCNP may reduce tree growth via mechanisms similar to those proposed to form alpine treelines. These include (1) reduced photosynthetic period (Tranquillini 1979); (2) reductions in photosynthetic capacity due to frost damage, especially for taller plants unsheltered by snow or the ground boundary layer (Grace 1988); desiccation due to frozen soils (Tranquillini 1979; Sowell et al. 1982); and (4) cold-temperature photoinhibition (e.g. Ball 1991). Any or all of these factors may make it impossible for tall woody plants to maintain a positive carbon balance, given the necessary allocation to wood production (e.g. Daubenmire 1954) and – most importantly – the increasing fraction of annual production allocated to wood as plant height increases (Givnish 1995). Alternatively, cold temperatures in low-lying sites in the VCNP may (5) reduce tree growth by impeding cell division and differentiation as has been proposed to occur at alpine treelines by Körner (1998).

Here we test the hypothesis that adult tree growth decreases with proximity to subalpine treelines in the Valles Caldera, reflecting decreased water availability and/or increased competition with grasses on loamier soils on flatter microsites. We examine the correlations of height and radial growth of ponderosa pine to predawn xylem water potential (ψ_L), slope inclination (a proxy for air temperature; see Chapter I), soil texture, tree density, and coverage by graminoids and by other herbs. Water stress (measured as (ψ_L) was measured over two summers, including periods of pre-monsoon drought and monsoonal rainfall, during a drought year (2002) and a year of more typical rainfall (2003).

Methods

Study area

The study was conducted entirely within the Valles Caldera National Preserve (VCNP; 35°50'-36°00'N, 106°24'-106°37'W), in the Jemez Mountains of north-central New Mexico (Fig. 1). The Valles Caldera is a 24 km-wide basin formed by explosive volcanic eruptions and the subsequent collapse of the underlying magma chamber ca. 1.22 Ma. (Smith and Bailey 1966, 1968; Izett and Obradovich 1994). The mountainous rim of the caldera reaches elevations ranging from 2850 to 3150m; the basin floor lies between 2575 and 2750 m. Within the caldera, resurgence and post-collapse ring-fracture volcanism have formed several secondary domes (Smith et al. 1970), the highest of which is Redondo Peak at 3370 m. The primary rock types of the mountain slopes are ignimbrite and rhyolite; the caldera floor is underlain by alluvium, fan deposits, and lacustrine sediments (Smith et al. 1970). Soils include alfisols and inceptisols beneath forested vegetation on the slopes, and well-developed mollisols in the grassy valley bottoms (USDA Soil Conservation Service 1987).

The area occupied by the VCNP was a privately owned ranch from 1860 until 2000, and was subjected to periods of intensive grazing and logging operations, as has occurred throughout much of the southern Rocky Mountains. Such practices, together with fire suppression - both direct and indirect (e.g., removal of grassy fuels by livestock grazing and fairly large herds of elk in VCNP in recent times) – have undoubtedly resulted in some changes in the composition, structure, and dynamics of ecological communities, but the extent of these changes is unknown. A comparison of several historic vs. current photographs at ground level indicates some recent encroachment of forests into grasslands at some locations in the Valles Caldera (Hogan and Allen 1989), though this encroachment has not been uniform and occurred at different rates in different sites.

Climate during study

The climate in the VCNP is semi-arid and continental. Monthly high and low temperatures at the nearest climate station in the interior of the Jemez Mountains (Wolf Canyon; 35°57'N, 106°45'W, 2505.5m) are 3.4° and -13.5° C in January, 24.9° and 5.7° C in July. Total annual precipitation at Wolf Canyon has averaged 57.6 cm over the last 50 years (1954-2004). Summers are characterized by severe drought in May and June followed by monsoonal, convective rains, which occur almost daily during July and August. Precipitation during the two years of this study was conducted was markedly different. Throughout northern New Mexico, 2002 was a very dry year, while 2003 was closer to normal. During 2002, annual precipitation at Wolf Canyon was only 400 mm, or 69% of the 50-year mean, and in 2003, it was 551 mm, or 96% of the 50-year mean. Differences in winter precipitation were even more pronounced. From November 2001 through May 2002, Wolf Canyon recorded only 110 mm of precipitation, 40% of the 50-year mean and the second lowest total in the 89 years for which complete records exist. Winter precipitation for the same period the following year was 278 mm, 102% of the 50-year mean.

No winter precipitation data in the VCNP exists for the period of this study. Summer precipitation data measured from a rain gage at the VCNP headquarters (35°52'N, 106°31'W, 2711 m) in 2002 and 2003 was kindly provided by K Bealey of the USGS Jemez Mountains Field Station. Unfortunately, data collection in 2002 did not begin until June 26, after summer storms had already occurred across the entire Jemez Mountains. From June 20-22, Wolf Canyon recorded 13.97 mm of rain. We use this measurement, and other measurements of trace precipitation at Wolf Canyon between May 15 and June 26, as an estimate of the precipitation in the VCNP during the same period. Given the ca. 200 m lower elevation of the Wolf Canyon rain gage, this is likely to be a conservative estimate.

Sample design

Twenty sites were chosen for more intensive study from a larger set of 200 100-m^2 sites sampled in 2001 as part of our earlier research; greater detail on sampling methods and sample stratification beyond what is described below is contained therein (Chapter I; Coop and Givnish unpublished data). For this study, we chose sites that were readily accessible, included as great a range of soil texture and slope inclination as possible, and were dominated by ponderosa pine of roughly similar dbh- and height-class distributions. Locations for the twenty sites used are listed in Appendix I.

At each site, species identity, basal area, and height for all trees < 2.5 cm dbh were recorded in a 5 m x 20 m quadrat, with the long axis running parallel to the slope contour.

Percent cover by herbaceous species in five 1-m^2 subquadrats within each quadrat was visually estimated. Coverage data were summed in each subquadrat and then averaged to produce an estimate of understory percent cover for each quadrat. We also separately summed and averaged coverage by graminoids alone. Slope inclination was measured across each quadrat along the steepest axis, and soil samples from the upper 15 cm of the soil profile were collected at three locations corresponding to center of three subquadrats at each site (at the periphery and center of the 5 x 20 m quadrat). Soil texture was measured using a modified hydrometer method (Bouyocous 1962; Day 1968). Distance from the treeline was measured as the horizontal space between the treeline and the sampled quadrat. Greater positive distances indicate samples were located farther into the forest interior, and farther away from the open grasslands.

Tree moisture status (ψ_L)

Predawn xylem water potential was measured regularly during the summer of 2002 and 2003 on three trees randomly selected at each site. Sampling was conducted six times over 3-week intervals in 2002, and four times, over 4- to 5-week intervals in 2003. The time required to complete each sampling episode was three days, and all samples were collected before sunrise. Three small branchlets (ca. 0.3-0.5 m in length, diameter < 2 cm, and containing abundant fascicles of needles at the end) from each tree were cut from branches 2 – 5 m high using pole-pruners, labeled, and packed in bags in a cooler. Xylem potential measurements on needle fascicles were made using a Scholander pressure bomb within 3 hours of collection. We returned to the same three trees at each site for all measurements (60 trees in all x 10 censuses = 600 data points), with two exceptions. At one site, a tree died early in the summer of 2002, after maintaining quite low ψ_L (-3.05 to -3.75 Mpa) during the previous two sampling periods. Data from this tree were not used in subsequent analyses. This same site also had the unfortunate distinction of being adjacent to a small forest fire in early 2003. No trees were visibly damaged by the fire, but one was felled by a fire crew in the creation of a fire break.

Growth rates of ponderosa pine

In 2004, we collected increment cores from each of the 58 surviving trees from which we had made the water potential measurements the preceding two years. Seven of these cores were later judged not usable due to problems reading rings, cross-dating, or poor estimates of tree age because of the distance from the end of the core to the pith. To allow for an estimate of radial growth rates over the entire lifespan of the tree, and also an estimate of the age of the tree, cores were collected at the base of each tree. To collect these basal cores, we mounted an increment borer on the end of a ratchet, so the borer could be easily rotated, perpendicular to the axes of tree growth, even close to the ground surface.

Increment cores were mounted and sanded using standard dendroecological methods (Stokes and Smiley 1996). Rings were counted and measured using a sliding bench micrometer (Velmex, Inc., Bloomfield, NY) coupled with a Metronics QC-1000 digital readout (Metronics, Inc., Bedford, NH) and the software Measure J2X (Voortech Consulting, 2000). Thirty-six of these cores contained the pith. To estimate the distance from the last ring measured to the pith for thirteen cores other cores, we overlayed the core with a clear plastic template with concentric circles printed at radial increments of 1 mm. This distance (radius) could then be used to estimate the number of missing years based on the relationship between growth rate and age. This method is described in more detail in a separate study (Chapter IV; Coop and Givnish unpublished data). Cores were cross-dated using skeleton plots (Stokes and Smiley 1996).

In our analyses of 2002 and 2003 radial growth we used both the raw increment data and also a relativized increment growth index that was adjusted for tree age by fitting the mean growth increment (from all trees, for each year age 1, 2,…,*n*) to a polynomial function [radial increment = $0.00002*age^3 - 0.0031*age^2 + 0.1251*age + 1.1197$; $r^2 = 0.86$, $P << 0.00001$ for 81 d.f.]. The relativized radial growth index for a given year is the difference between the observed growth increment and that predicted by the model based on the mean increment growth of all trees sampled at that age. We generated a similar index for height growth by fitting a second order polynomial curve to the relationship between tree height and age [height = $0.0016*age^2 + 3.28*age - 0.1463$; a much poorer-fitting model with $r^2 = 0.38$, $P = 0.00001$ on 48 d.f.] and subtracting modeled height from actual height for each tree. Tree ages ranged from 19-68 years, and height from 5-19.5 m.

Statistical analysis

To test for relationships between response variables (relativized and absolute increment growth for 2002 and 2003, relative height growth, predawn xylem potential) and predictor variables (including predawn xylem potential, percent sand, slope, graminoid/herbaceous cover, and tree density) we used backwards-elimination stepwise multiple linear regression models, as implemented by S-plus 6.0 (Insightful Corp., 2001). Because predawn xylem potential could be considered both a measure of environmental conditions (as a proxy for soil water potential, but perhaps also related to atmospheric moisture [e.g. Stone 1957; Boucher et al. 1995; but see Rundel 1982]) and also a measure of tree physiological performance (related to root water uptake, rooting depth and extent, water storage in sapwood, xylem hydraulic conductance, and factors relating to water use efficiency) we separately examined the relationships between tree growth and xylem potential, between tree growth and all other predictor variables, and between xylem potential and all other predictor variables. Model fit was assessed using Akaike's Information Criterion (AIC). Stand density, basal area, and slope were log-transformed; soil sand fraction was arcsine-squareroot-transformed to increase normality.

Results

Relativized radial increment growth for 2002 and 2003 exhibited moderately strong positive relationships to predawn xylem potential ($r^2 = 0.33$, $P < 0.0001$ and $r^2 = 0.21$, $P < 0.001$ for 49 d.f. for each year; Fig. 2). The relationship between relativized radial growth and predawn xylem potential ($ß_1 = 3.32$ in 2002, 2.16 in 2003) was not significantly different between years (two-tailed t-test $P > 0.20$ for 98 d.f.). Absolute radial increment for 2002 and 2003 exhibited only slightly weaker relationships to predawn xylem potential ($ß_1 = 3.03$ $r^2 = 0.30$, $P < 0.0001$ and $ß_1 = 2.05$, $r^2 = 0.18$, $P < 0.005$ for 49 d.f., regression slopes were also not significantly different).

In multiple regression models that included xylem potential, no other variables were retained as significant predictors of radial growth. We also ran multiple regressions for relative and absolute radial increment growth in 2002 and 2003 that did not include xylem potential as a predictor variable. In 2002, both relative and absolute radial growth were showed a negative relationship to log-transformed percent sand ($ß_1 = -4.39$, $r^2 = 0.15$, $P < 0.005$ for 49 d.f.; $ß_1 = -3.48$, $r^2 = 0.10$, $P < 0.05$ for 49 d.f.); no other predictors were retained as significant terms in these models. In 2003, both relative and absolute radial growth showed moderate negative relationships to log-transformed total stand basal area ($ß_1 = -0.33$, $r^2 = 0.09$, $P < 0.05$ for 49 d.f.; $ß_1 = -0.38$, $r^2 = 0.11$, $P < 0.05$ for 49 d.f.); no other predictors were retained as significant terms

in these models. Radial growth did not show a systematic increase with distance from treeline, slope, graminoid cover or total understory cover, counter to trends expected if constraints on tree growth maintain subalpine treeline ecotones.

Relative height growth was weakly positively related to graminoid cover ($r^2 = 0.01$, $P < 0.05$ for 49 d.f.), but not to any other environmental predictor variables including xylem potential or distance from the treeline ecotone. Unrelativized tree height data showed no significant relationships to any measured environmental variable. The absence of any relationships between tree height growth and distance from treeline, slope, or sand, further indicates that constraints on adult tree growth do not occur at subalpine treeline ecotones of the VCNP.

Surprisingly, during the exceptionally dry year of 2002, the best-fitting multiple regression model for mean predawn xylem potential showed ψ_L to be strongly positively related to herbaceous cover ($ß_1 = 0.003$, $r^2 = 0.25$, $P < 0.0005$ for 49 d.f.). The best fitting model for the wetter year of 2003 (multiple $r^2 = 0.31$, $P < 0.0005$ for 48 d.f.) showed xylem potential to be strongly negatively related to both log-transformed total stand density ($ß_1 = -0.10$, $P < 0.0005$) and distance from treeline ($ß_1 = -0.001$, $P < 0.05$).

Tree density at the 20 sites used in this study was positively correlated to total stand basal area, % sand, and slope inclination, and negatively correlated to graminoid and total herbaceous understory cover (Table 1). Graminoid and total herbaceous cover (themselves strongly positively correlated) were negatively correlated with % sand, slope inclination, and distance from treeline.

The temporal progression of predawn xylem potential during the summers of 2002 and 2003 shows a correspondence to summer (Figures 3 and 4). Predawn xylem potential was very low during the early summer of 2002, presumably due to poor snowfall the previous winter, and trees growing on sandy sites showed the greatest moisture stress. At the onset of summer rains in early June, tree water balance overall showed rapid increases, especially on sandy sites. Interestingly, xylem potential exhibited decreases from mid-July through the end of August, even though rains continued throughout this period. In 2003, water balance was much higher early in the summer due to much higher snowfall during the winter of 2003-2003, but it decreased into the summer, even after rains began. Xylem potential did not increase until somewhat later in the summer, and trees growing on siltier soils experienced a greater increase.

Discussion

The subalpine treelines we examined in the VCNP do not appear to be maintained by any processes potentially hindering adult tree growth near the treeline. We found no support for the hypothesis that the growth of mature trees decreases as a function of decreasing distance to forest-grassland ecotones in the VCNP. Likewise, tree growth showed no decrease on finer-textured soils, where grass cover was higher, or on shallowly sloping sites prone to cold-air drainage and increased frosts. If anything, tree growth appears to be greater, and tree moisture balance better, on fine-textured soils and shallowly sloping sites in the grassy valley bottoms of the VCNP. These results parallel a similar finding in northern Arizona by Cantor and Whitham (1989), who found greater radial growth by aspens on deeper meadow soils than on the rock outcrops, though aspen occurrence was primarily limited to rock outcrops. Our findings are also similar to those of Schauer et al. (1998), who found that Engelmann spruce (*Picea engelmannii*) in Colorado exhibited greater rates of tree radial growth adjacent to park boundaries than in the forest interior.

The overwhelming determinant of ponderosa pine radial growth in our study was plant water status (Fig. 2), which was linked to many of the other environmental factors we examined (Table 1). However, the controls on predawn xylem appear mainly to run counter to Walter's (1971) hypothesis that grass competition, facilitated by increased moisture-holding capacity of the topsoil, will decrease the water available to more deeply rooted trees. In fact, during the drought year of 2002, predawn xylem potential was strongly positively related to herbaceous cover (including grasses and forbs). Interestingly, tree height was also positively related to total herb cover. Because herbaceous cover in this study was negatively associated with tree density, it is thus an indicator of decreased intraspecific competition (Table 1). Herbaceous cover was also associated with finer soil texture and lower landform position in this study (Table 1).

In regression models that did not include xylem potential, tree growth in 2002 showed a strong negative relationship with sand. In 2002, trees growing on fine-textured soils showed a better water balance overall than trees on sandier soils (Fig. 4a.), especially during the rainless early summer. The most likely explanation for this is that finer-textured soils in the study area invariably occur where slopes are shallower, and on lower-lying topographic positions where soil moisture may be more abundant due to both increased runoff from adjacent slopes and groundwater flow (e.g. Kirkby and Charley 1967; Knapp 1978). Fine-textured valley bottom soils are also much deeper than soils on adjacent mountain slopes (USDA Soil Conservation Service 1987; C. Hibner, Santa Fe Soil Survey, pers. com.) and may thus hold much greater reservoirs of soil moisture, which may become especially important during drought years. During the wetter year of 2003, xylem potential was most strongly negatively related to total stand basal area, an indicator of intraspecific competition. Likewise, multiple regression models that did not include xylem potential showed that radial growth was strongly negatively related to stand density, also indicative of competition. Given these differences between 2002 and 2003, it appears that site location and access to deep soil moisture were stronger determinants of tree growth during an extremely dry year, and that intraspecific competition for soil moisture was a stronger determinant of tree growth during a wetter year.

Temporal patterns of xylem potential across all sites also show substantial differences between the drought year of 2002 and the more normal year of 2003, including a very rapid response to summer precipitation patterns in 2002, but a much weaker response in 2003 (Figures 4 and 5). The extremely low values in early summer of 2002 (Figure 4) suggest that poor winter snowfall in 2001-2002 had strong negative consequences on tree moisture relations, whereas xylem potential appears to be declining well into the rainy season of 2003 (Figure 5), probably as trees continued to utilize deep moisture recharged by adequate winter snowfall. Given the extreme level of moisture stress across all sites in early 2002, a rapid response to summer precipitation should not be entirely surprising. However, the magnitude of this response suggests that 1) ponderosa pines are able to quickly utilize shallow soil moisture, or 2) the generally rapid and intense summer convective showers resulted in substantially more recharge to deep soil moisture than we would have expected. Both may be the case. Though ponderosa pines generally may be extremely deeply rooted (ca. 24 m; Stone and Kalisz 1991), trees growing on finer-textured soils are reported to have an increased density of shallow roots, and open-grown trees may exhibit substantial lateral root growth (Curtis and Lynch 1965). It may thus be that the trees we sampled at the forest margins, occurring on fine-textured, valley bottom soils, are more reliant on shallow soil moisture; trees growing in dense stands on the sandier soils of upper mountain slopes may be more dependent on deep soil moisture. Conversely, the response to rainfall we saw was most rapid for trees growing on sandy soils, where infiltration

and percolation were more rapid and likely not impeded by the low coverage of herbaceous plants at these sites, suggestive of similar findings of Knoop and Walker (1985).

In our data, adult tree growth shows no tendency to decline near subalpine treeline ecotones. We suggest that in the VCNP the shift from forested mountain slopes with coarser soils to gently-sloping, grassy valley bottoms with loamy soil is linked to constraints on establishment, in agreement with the finding of Schauer et al. (1998). In fact, the positive correlations between tree density and both sand and slope inclination (themselves positively correlated) suggest that either or both factors exert substantial influence on tree seedling establishment or subsequent survival.

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Figures and Tables

Figure 1. The location of the Valles Caldera National Preserve (VCNP) in the Jemez Mountains, NM. The 1996 aerial phots used in this image clearly show the locations of large grasslands (uniform grey color) in the otherwise forested (darker vegetation) landscape.

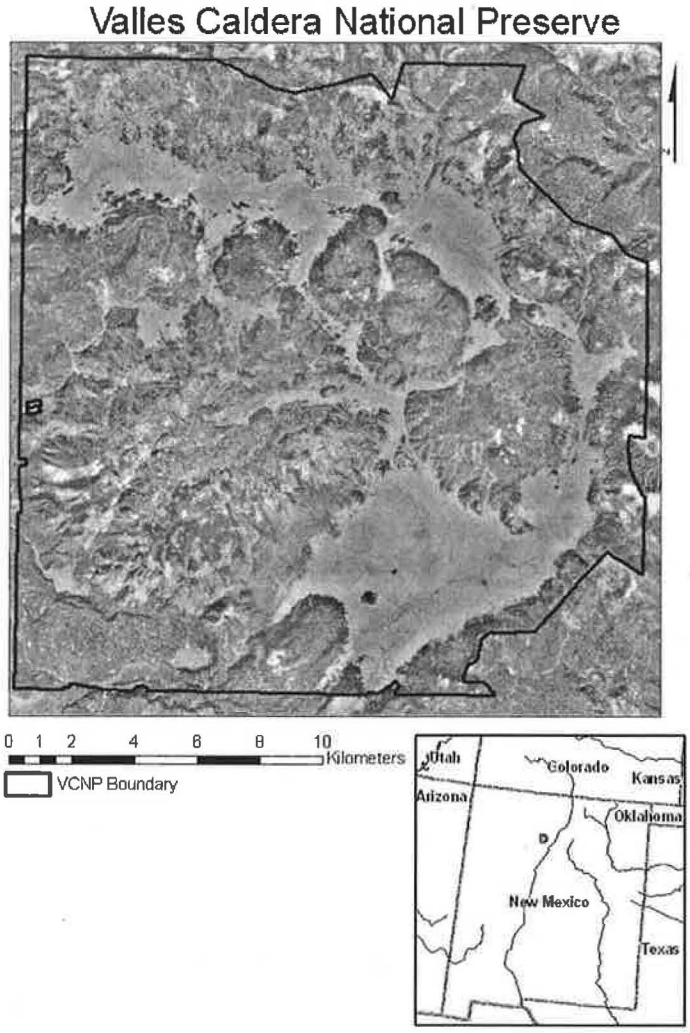


Figure 2. The relationship between increment growth and mean predawn needle xylem potential for 2002 and 2003.

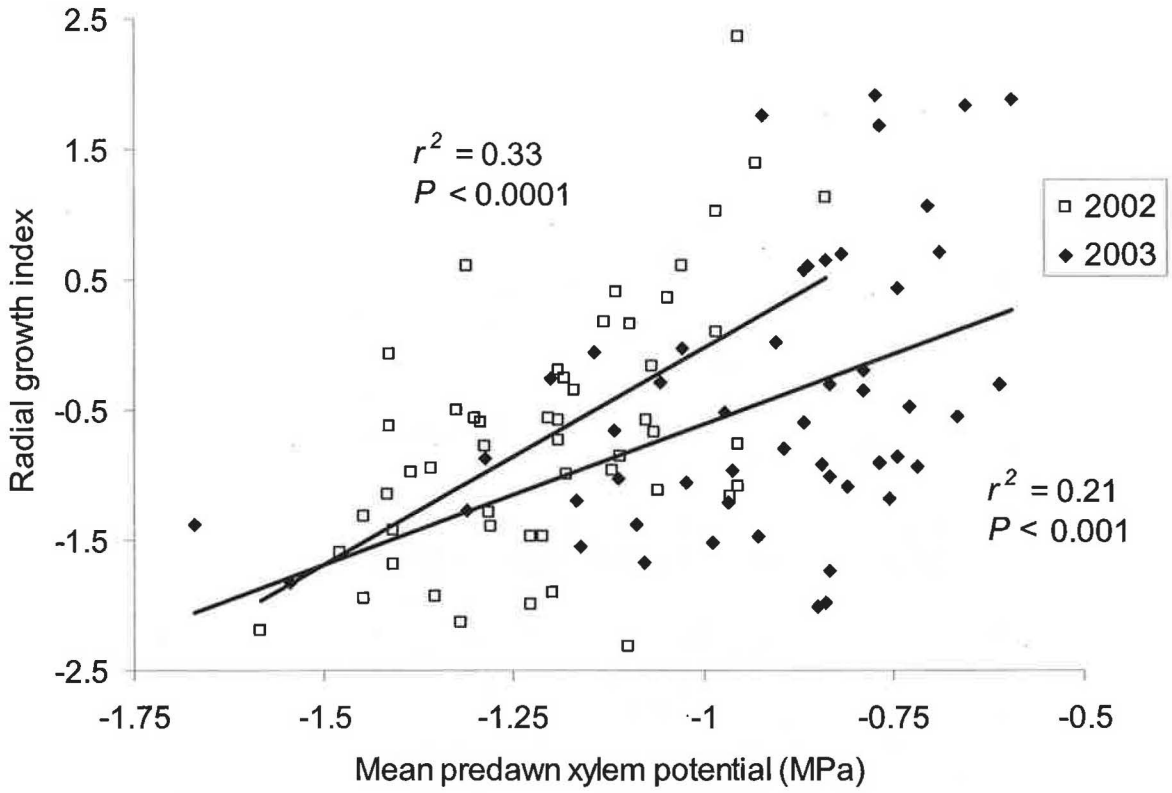
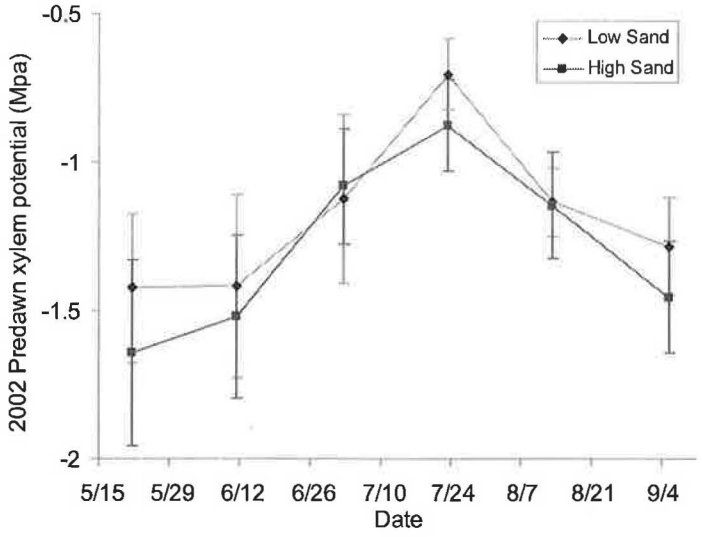
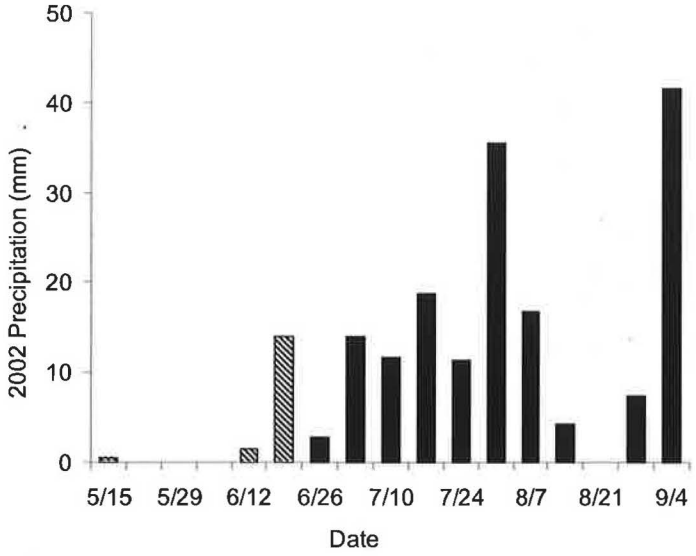


Figure 3. The temporal progression of predawn xylem potential (a) and precipitation (b) in 2002. Solid bars in (b) are data collected at the VCNP; hatched are precipitation data from Wolf Canyon. Precipitation in the VCNP was probably somewhat greater due to its 200 m higher elevation.

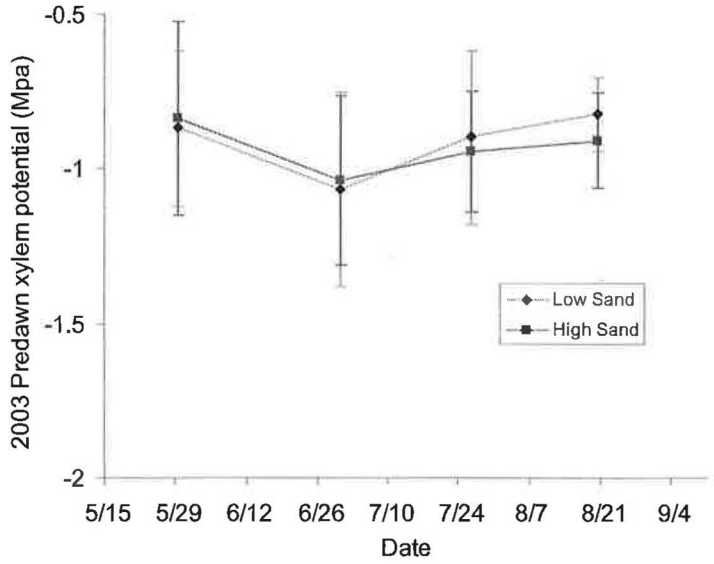


a.

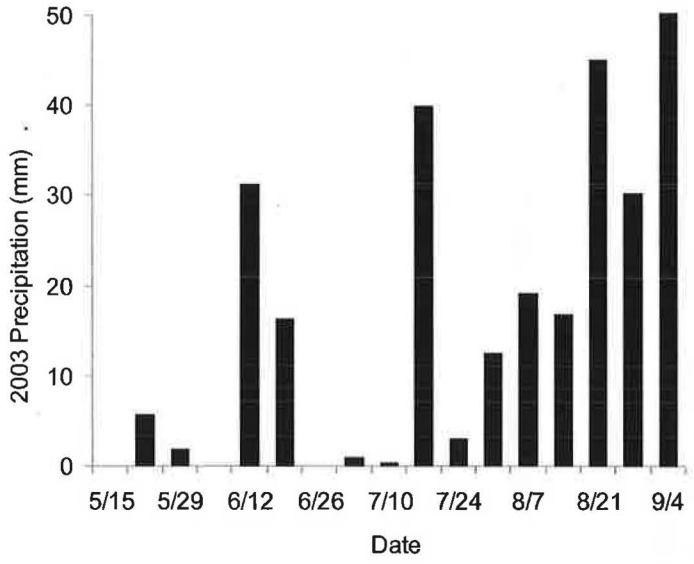


b.

Figure 4. The temporal progression of predawn xylem potential (a) and precipitation (b) in the VCNP in 2003.


-0.5
-1
-1.5
-2
2003 Predawn xylem potential (Mpa)
Low Sand
High Sand
5/15
5/29
6/12
6/26
7/10
7/24
8/7
8/21
9/4
Date

a.


50
40
30
20
10
0
2003 Precipitation (mm)
5/15
5/29
6/12
6/26
7/10
7/24
8/7
8/21
9/4
Date

b.

Table 1. Correlation matrix for environmental variables sampled at each site.

	Ln tree density (ha^{-1})	Ln total BA (dm^2/ha)	Distance from treeline	Ln sand (%)	Ln slope (%)	Graminoid cover	Total cover	2002 $?_L$	2003 $?_L$
Ln tree density (ha^{-1})	1								
Ln total BA (dm^2/ha)	0.73	1							
Distance from treeline	0.09	0.22	1						
Ln sand (%)	0.50	0.33	0.14	1					
Ln slope (%)	0.52	0.56	0.31	0.66	1				
Graminoid cover	-0.60	-0.52	-0.23	-0.58	-0.83	1			
Total cover	-0.63	-0.52	-0.26	-0.64	-0.83	0.98	1		
2002 $?_L$	-0.29	-0.22	-0.43	-0.36	-0.54	0.65	0.64	1	
2003 $?_L$	-0.69	-0.48	-0.37	-0.20	-0.38	0.57	0.55	0.48	1

Appendices

Appendix I. Locations of sites used in this study.

Site name	Elev. (m)	Location (UTM 13 S, NAD 83) Meters E-W	Meters N-S
01A	2640	365456	3972746
01D	2636	365489	3972711
04A	2685	359676	3966618
04D	2640	359616	3966737
05A	2677	367955	3971901
05D	2640	367896	3971840
08A	2749	372213	3976688
08D	2736	372211	3976596
11B	2611	355594	3983269
11D	2597	355615	3983193
12A	2646	361691	3982213
12D	2605	361720	3982141
14A	2701	367271	3975822
14D	2692	367280	3975735
15C	2638	365741	3973521
CAJ	2635	359500	3967118
COR	2668	362396	3969193
P	2795	361126	3967774
R	2677	371424	3974255
Y	2645	366122	3973687

Chapter III

Constraints on ponderosa pine establishment in subalpine grasslands of the Valles Caldera National Preserve, New Mexico

Abstract

Subalpine grasslands are prominent yet poorly understood features of the otherwise forested landscapes of the southern Rocky Mountains. These communities commonly occur on valley floors where fine-textured soils are often spatially coupled with temperature extremes caused by nightly cold air drainage and pooling. We experimentally assessed the roles of fine-textured soils, cold air drainage, herbaceous competition, and elk (*Cervus elaphus*) browsing on ponderosa pine (*Pinus ponderosa*) establishment at 32 sites positioned across multiple subalpine treeline ecotones in the 35,000 ha. Valles Caldera National Preserve (VCNP) in the Jemez Mountains. We found extremely poor germination and subsequent survival of seeds planted between 2002 and 2004, indicating severe bottlenecks to establishment from seed across all sites. Growth of transplanted seedlings was very strongly positively related to minimum temperatures; seedlings experiencing the coldest temperatures in valley bottoms exhibited stunted needles and often no measurable height growth. We found moderate evidence of cold-temperature photoinhibition as measured using the chlorophyll fluorescence ratios F_{PSII} [$(F_m' - F_t)/F_m'$ or $(F_m' - F_s)/F_m'$] and F_v/F_m during 2004 but also evidence that soil texture and moisture content contributed to photosynthetic performance. The large decreases in growth we observed at cold sites are more likely caused by freezing damage to developing tissues than to energetic limitations imposed by photoinhibition alone. Herbaceous competition had only minor effects on ponderosa establishment, and we found no effect of browsing. However, substantial seedling mortality was incurred by golden-mantled ground squirrels, *Spermophilus lateralis*. Rodent damage was greatest on slopes above the temperature inversion, which negated an opposing trend towards increased seedling mortality in the colder valley bottoms due to physiological stress. Overall, first year survival of transplanted seedlings was highest on sandy soils, and second year survival was highest at warm sites. While recognizing that other factors, climatic interactions, and multiple feedbacks may also affect tree seedling establishment in valley bottoms, we propose that differential tree seedling growth and survival imposed by cold air drainage, are primarily responsible for the maintenance of subalpine grasslands in the valleys of the VCNP.

Keywords: pine/grassland ecotone, timberline, meadow, park, species distribution, conifer

Introduction

Grassland plant communities in the southern Rocky Mountains frequently occur on level surfaces in valley bottoms, and form abrupt, subalpine treeline ecotones where they abut forested mountain slopes (Ramaley 1927, Turner and Paulsen 1976, Brown 1994). These grasslands are commonly known as *valles* or parks in northern New Mexico. Despite the prevalence and biological importance of these herbaceous communities in an otherwise forested landscape (Dick-Peddie 1993; Brown 1994), their occurrence remains the subject of considerable speculation and surprisingly little empirical research. Proposed causes mainly invoke either **edaphic** or **thermal** factors in limiting tree establishment or growth in valley bottoms. **Edaphic** hypotheses have generally focused on the effects of soil texture - the favored explanation by researchers working in the Rocky Mountain region is that fine-textured soils in valley bottoms promote such dense grass growth that tree seedlings cannot become established (Ramaley 1910, 1927; Peet 1981, 2000). Alternatively, fine-textured soil may impede conifer establishment directly by slowing root growth and limiting access to soil moisture (Daubenmire 1943; Patten 1963). Other researchers in the Rockies have proposed that soil moisture limitations (Koterba and Habeck 1971; Doering and Reider 1992) or excessive soil moisture (Ives 1942; Rydberg 1913) limit tree growth in these communities. **Thermal** explanations recognize the potentially damaging effects of cold-air drainage and pooling in valley bottoms on tree establishment or growth, as first suggested by Ramaley (1910), to account in part for the treelessness of Boulder Park, Colorado. While this explanation has gained little acceptance in the southern Rockies, it has long been favored by researchers working in seemingly analogous treeless communities in the mountains of Australia and New Zealand (Wardle 1971; Smith 1975; Moore and Williams 1976; Paton 1988), where transitions from subalpine, grassy basins to forested slopes are widely known as "inverted timberlines" (Wardle 1971) or "inverted treelines" (Moore and Williams 1976). However, grass competition (Fensham and Kirkpatrick 1992) and waterlogged soils (Gilfedder 1988) have also been proposed as explanations for these communities.

Despite widespread interest and speculation on the causes of montane and subalpine grasslands and inverted treelines, only two previous studies (Wardle 1971 and Schauer et al. 1998) have experimentally tested for the presence of edaphic or thermal constraints on tree establishment in these systems, and the results of these studies are ambiguous as to which predominate. In the Craigieburn Range of New Zealand, Wardle (1971) planted seeds and seedlings of several tree species under four light regimes in a cold, treeless basin at 900 m. Though this study did not test for effects due to soil texture or competition with grasses, Wardle did find that the only seedlings of the native mountain beech (*Nothofagus solandri* var. *cliffordiodes* (Hook. f.) Poole) that survived in the basin were those grown beneath the darkest shadecloth (ca. 27% full sun). While Wardle ascribed seedling mortality in this study to winter dessication due to the combination of nightly frozen soils followed by rapid daytime heating, his results also suggest effects due to cold-temperature photoinhibition, which has since been demonstrated to adversely affect tree seedling growth and survival at or near alpine treelines (Ball et al. 1991; Germino and Smith 1999). Interestingly, Wardle found that seedlings of three conifers native to high elevations in North America, including Engelmann spruce (*Picea engelmannii* Parry ex. Engelmann), performed much better in the cold basin than mountain beech, which "seems to agree with timberline patterns in western North America, where evidence that temperature inversion is a direct cause of inverted timberlines is less compelling" (1971: 396). However, these observations contrast with the findings of Schauer et al. (1998), who planted seeds and seedlings of Engelmann spruce at three locations across a subalpine

forest-grassland ecotone in Willow Park, in the San Juan Mountains of Colorado. They found the highest germination of seeds and survival of transplanted seedlings occurred in the forest interior and at the treeline ecotone, and was greatly decreased within the subalpine park, where nightly minimum temperatures were much lower. Given that shading was also presumably far less in the open, treeless park, these results may also suggest the effects of low temperatures in combination with light stress in limiting tree establishment. However, Schauer et al. (1998) did not account for potentially confounding effects of soil texture and herbaceous vegetation, which also differed across the treeline ecotone, and they provide additional observations suggesting these differences may in fact be more important in limiting tree establishment than the thermal regime.

In the newly established Valles Caldera National Preserve (VCNP) of the Jemez Mountains, New Mexico, approximately 10,000 ha of grasslands occur in a vast basin between 2575 and 2730 m elevation. These grasslands primarily occupy flats and gentle slopes within the central topographical concavities of the caldera and form sharp treeline ecotones with stands dominated by ponderosa pine (*Pinus ponderosa* var. *scopulorum* Douglas ex. P.& C. Lawson) and Colorado blue spruce (*Picea pungens* Engelm.) on the surrounding mountain slopes (Fig. 1). Smaller grassy openings also occur in minor drainages, and on south-facing slopes and mountain tops above ca. 3000 m. All of the grasslands and treeline ecotones under study fall well below alpine treeline (ca. 3500 m). We therefore refer to these communities and the ecotones that define them as *subalpine grasslands* and *subalpine treelines*. Given that these subalpine grasslands occur primarily above 2500 m, this terminology also agrees with the nomenclatural convention of Brown (1994), though the surrounding matrix of intermediate-elevation ponderosa pine and mixed-conifer forests are widely referred to as *montane* forests, as originally defined by Ramaley (1907). A gradient analysis of these grasslands and the treeline ecotones that define them (Chapter I; Coop and Givnish unpublished data) found that valley bottom grasslands were strongly associated with both richer and finer-textured soils, and were also characterized by nightly cold-air pooling resulting in minimum temperatures up to 10° C colder than on adjacent slopes, independent of effects of the tree canopy. However, edaphic and thermal gradients were generally spatially coupled in this study, and their separate effects on treeline position – as inferred from environmental correlations - were not discernable.

Tree establishment in the VCNP, especially at the margins of grasslands, is also likely to be impacted by browsing and damage by elk or cattle. Krantz (2001) documented very high levels of recent elk browse on all woody species in the VCNP, and found that antler rubbing scars and resultant mortality to conifer saplings was more frequent at the forest-grassland ecotones than in the forest interior. The area occupied by the VCNP has long been used for cattle grazing (Martin 2003), which may both facilitate - by reducing the density of herbaceous competition - or impede - through physical damage - conifer seedling establishment, depending on stocking intensity (Pearson 1934; Burns and Honkala 1990 and references therein).

The objective of this paper is to assess via experiments the effects of competition, browsing, and abiotic environmental stresses on the establishment of ponderosa pine seedlings across gradients of edaphic and thermal conditions. Here we test four distinct hypotheses for the occurrence of inverted, subalpine treelines in the VCNP:

> ***Hypothesis 1)*** *Nightly cold-air drainage and pooling on flat or gently-sloping topography results in decreased germination, seedling growth, and/or seedling survival of ponderosa pine.* Seed germination may be inhibited by cold temperatures, and

seedlings may be damaged or killed by freezing or frost-heaving. In addition, cold-temperature photoinhibition may reduce tree seedling growth/survival below the inverted treeline.

Hypothesis 2) *Edaphic factors directly impede seedling germination, growth, and/or survival on the fine-textured soils that characterize valley bottoms in the VCNP.* Finer-textured soils in valleys may inhibit root penetrance, become seasonally waterlogged or, alternatively, exhibit lower water potentials.

Hypothesis 3) *Edaphically-mediated competition with grasses reduces seedling establishment.* Finer-textured soils produce a greater growth by herbaceous (especially graminoid) competitors, which may then exclude tree seedlings. On sandy soils, herb competition may not be sufficient to preclude tree seedling establishment.

Hypothesis 4) *Browsing and other damage by elk or cattle reduces tree seedling survival at and below inverted treelines.* Seedlings may exhibit increased mortality where they are readily accessible to ungulates active in grasslands.

If each of these hypotheses are rejected, this would suggest some other process (e.g. differential mortality induced by varying fire regimes) is responsible for generating or maintaining montane forest-grassland ecotones in the VCNP. Here we present data bearing on the operation of each of these hypotheses - based on cold-air drainage, direct edaphic effects, indirect edaphic effects on seedling competition, and browsing - from field experiments conducted at the Valles Caldera National Preserve from 2002 to 2004. Other studies excluding shifts in adult tree survival and growth as causes of inverted treelines will be reported elsewhere (see Chapters II and IV).

Methods

Study location

The study was conducted entirely within the Valles Caldera National Preserve (VCNP; 35°50'-36°00'N, 106°24'-106°37'W), in the Jemez Mountains of north-central New Mexico (Fig. 1.). The Valles Caldera is a 24 km-wide basin formed by explosive volcanic eruptions and the subsequent collapse of the underlying magma chamber ca. 1.22 Ma. (Smith and Bailey 1966, 1968; Izett and Obradovich 1994). The mountainous rim of the caldera reaches elevations ranging from 2850 to 3150m; the basin floor lies between 2575 and 2750 m. Within the caldera, resurgence and post-collapse ring-fracture volcanism have formed several secondary domes (Smith et al. 1970), the highest of which is Redondo Peak at 3370 m. The primary rock types of the mountain slopes are ignimbrite and rhyolite; the caldera floor is underlain by alluvium, fan deposits, and lacustrine sediments (Smith et al. 1970). The climate in the VCNP is semi-arid and continental. Total annual precipitation at the nearest climate station in the interior of the Jemez Mountains (Wolf Canyon; 35°57'N, 106°45'W, 2505.5m) is 57.6 cm (50-yr mean, 1954-2004). Summers are characterized by severe drought in May and June followed by monsoonal, convective rains, which occur almost daily during July and August. During the three years of this study, annual precipitation at Wolf Canyon was 70.6% of normal (2002), 97.2% (2003) and 101.7% (2004). Monthly high and low temperatures at Wolf Canyon are 3.4° and -13.5° C in January, 24.9° and 5.7° C in July.

Spatial and environmental stratification of experimental sites

Our primary objective in this study is to assess constraints on seedling establishment by ponderosa pine imposed by fine soil texture and/or cold air drainage. To facilitate an analysis of both the individual and combined effects of edaphic and thermal factors, eight experiments were located at each of four kinds of sites within the VCNP. These included (***a***) *silty valley bottoms* - cold, low-lying areas in the valles with loam or silty loam soils and grassy cover, and (***b***) *sandy backslopes* – warmer mountain slopes with gravelly, sandy loam soils and forested cover. Across these two kinds of sites, thermal and edaphic gradients are coupled to each other and to shifts from grassland to forest, in a manner representative of the general condition across treelines the study area. We also sought out sites where thermal and edaphic gradients were naturally decoupled, including: (***c***) *silty backslopes* – shallow benches on mountain slopes with loam or silt loam soils that are located above the temperature inversion layer, and (***d***) *sandy valley bottoms* - cold, low-lying valley bottoms with gravelly, sandy loam soils such as may occur on recent fluvial deposits.

Thermal conditions at each site were sampled with single channel dataloggers (Hobo Pro Temp, Microdaq.com, Ltd., Warner, NH) placed at 15 cm above ground level at each site beginning in early summer of 2003. Soil texture, macronutrient concentrations (available P; exchangeable K, Ca, and Mg; total N), pH, and % organic matter were measured by the University of Wisconsin Soils and Plant Tissue Analysis Laboratory for three soil cores (2.5 cm diameter, 0-15 cm depth) at three of the corners, randomly selected at each site. We initially sampled site soil water potential using two gypsum blocks buried at 15 cm at each site beginning in early summer 2003, but this system gave unreliable and often uninterpretable results, and the blocks were frequently dug up and the cords cut by rodents. In the summer of 2004, we measured gravimetric soil moisture from soil cores collected from three randomly-selected locations at the border of each site. Soil moisture was thus sampled seven times at each plot during 2004, on the same days that we sampled tree seedling growth and photosynthetic stress (*see below*).

Because we used only ponderosa pine in our planting experiments, we chose sites on south or west aspects, near naturally occurring ponderosa treeline ecotones. Given that ponderosa pine is shade-intolerant and seedling establishment under dense canopies is thus likely to be nil (Pearson 1940; Schubert 1974), we had to minimize the confounding effects of shading on seedling establishment. Hence, all transplant experiments were conducted where there was no forest canopy present, either in the open valley bottoms, or on backslope forest sites where the canopy was removed. In the latter case, we were generally able to utilize pre-existing canopy openings caused by recent logging or blowdown; however, at several sites we cut a number of young trees to enlarge openings such that there were no trees within 20 meters - or a distance equal to the height of the adjacent forested stands - of the actual experimental plots.

Many locations that met the above criteria were identified across the 35,560-ha VCNP, and we selected sites spread widely across the preserve to maximize the spatial coverage of our experiments and minimize the confounding effect of any spatially patchy factors (e.g., disturbance history). Due to management considerations, we did not conduct any experiments in the most publicly visible valley, the Valle Grande and, where possible, we located sites away from access roads or where they were screened from view by vegetation or topography.

Plot design

At each experimental plot, ponderosa seeds and seedlings were planted under four browsing *x* competition treatments. Plot design (described below) is depicted in Figure 2a; the treatments applied to seeds and seedlings within each plot are listed in Figure 2b. To test for an effect of browsing or other damage by elk or livestock on tree seedling success, and to protect germinating seeds from possible damage, each experimental plot consisted of both a fenced portion ("- browsing": 3.4 m x 4.4 m plots enclosed with barbed-wire fences 2 m high) and an unfenced portion ("+ browsing"). Exclosures contained two strips (0.3 m x 3.6 m) for seeds and a grid of 10 cells (each 0.4 m x 0.4 m) for seedlings. Each strip and cell was separated by a 0.4-m mowed buffer zone. Ten seedling cells were located outside each exclosure. To test for an effect of competition by herbaceous vegetation on both seed germination and establishment, and on the growth and survival of transplanted seedlings, herbaceous cover was removed ("- competition") from one of the two seeded strips and from 10 seedling cells (5 fenced, 5 unfenced) at each site. Herbaceous cover was left intact on the remaining 10 seedling cells ("+ competition"). Vegetation removed included the aboveground parts as well as the upper 15 cm of fine graminoid and forb roots; the edges of each strip and cell were sliced with a spade to cut roots originating externally in the "- competition" treatment. To quantify the competitive environment, cover by herbaceous species was visually estimated using the method described in Chapter I at three randomly-placed, 1-m^2 samples at the periphery of each site. Aboveground herbaceous biomass (clipped at each 1-m^2 sample) and below-ground root biomass (from a soil sample 100-cm^2 x 15 cm deep at the center of each 1-m^2 clip-plot) were collected, dried and weighed at the end of the growing season in 2004.

Seed and seedling plantings and monitoring

Twenty of the 32 experimental plots were established and planted in the summer of 2002. In the summer of 2003, we enlarged these plots to accommodate an additional set of two seeded strips and ten seedling cells within the fenced exclosure, and ten seedling cells outside the exclosure. In addition, we established and planted 12 more plots in 2003, for a total of 32 plots, with eight in each thermal x edaphic regimen. In 2003, 2004, and 2005, strips were seeded with 20 cold-stratified, locally collected seeds of ponderosa pine in early summer, planted at a depth of 1 cm at an 8-cm spacing under each competition treatment. This planting ("spring") was timed to coincide with the onset of monsoonal convective showers at the beginning of July, and to simulate natural germination of over-wintered seeds at the onset of the summer rainy season. For the first two years we also planted a set of 20 seeds at the end of the summer field season ("fall"), in early September, at the time that ponderosa cones would be naturally maturing and releasing their seeds. These seeds were not cold stratified prior to planting. In 2003, a total of 1600 seeds were sown during spring and fall plantings at 20 experimental sites; 2560 seeds were sown in spring and fall plantings during 2003, and 1260 seeds were sown during only a spring planting in 2004. During each summer, germination and survival of both early- and late-summer plantings was monitored at 2- to 3-week intervals.

Ponderosa pine seedlings (1-yr old) grown from a local seed source were transplanted into cells in the early summers of 2002 and 2003. In 2002, we planted 15 seedlings (5 under the – browsing/– competition treatment, 5 under – browsing/+ competition, and 5 under + browsing/– competition) at each of 20 sites, for a total of 300 seedlings. In 2003, we planted the full set of 20 seedlings at each of 32 sites, for a total of 640 additional seedlings. Transplanted seedlings that died or were killed within two weeks of planting were replaced. During 2003, summer rainfall arrived later than expected, and we supplemented recently planted seedlings by

hand watering them for the first two weeks of July. Survival and bud elongation were measured at 2- to 3- week intervals during each of the three summers of the experiment. The length of needles produced during 2003 and 2004 was measured in late September by measuring three randomly-selected needles on each surviving seedling.

Photoinhibitory stress was assessed using fluorescence measurements, twice during August 2003, and seven times during the summer of 2004 at 2- to 3-week intervals from May 31 to September 25. We used a portable chlorophyll fluorometer (Mini-PAM, Walz, Germany)) to sample both the light-adapted quantum yield of photosystem II, [F_{PSII}, $(F'_m - F_t)/F'_m$] and the dark-adapted maximum quantum yield (F_v/F_m). Both measurements were made on new needles of seedlings of each cohort at each site; all sites were sampled within four days of each other during each sampling period. All measurements were conducted between 9 am and 4 pm; light-adapted F_{PSII} was sampled under ambient sunlight on each surviving seedling at each site. Dark-adapted F_v/F_m was measured on needles that had been held in darkness for 15 minutes of darkness on three seedlings randomly selected from each cohort at each site.

Analyses

We used linear mixed-effects models to assess the effects of treatment factors on normally-distributed response variables (seedling growth and photosynthetic stress), and generalized linear mixed-effects models to test for the effects of factors on binomial response variables (seed germination emergence and seedling survival). Mixed-effects models can include both fixed and random effects, and can parameterize the covariance structure imposed by the clustering of observations (Pinheiro and Bates 2000), such as individuals grouped in sites, or repeated measurements on individuals, as a random variable. Mixed-effects models are also less sensitive to missing observations than ANOVA, because variance parameters are modeled using maximum likelihood instead of a sum-of-squares approach. In our analyses, observations on seeds and seedlings were grouped by 32 locations of experimental sites; location was included in all models as a random effect. For the mixed-effects model of predictors of fluorescence ratios, sampled at seven intervals over the summer 2004, we also included seedling ID as a random variable. Competition and browsing (two-level categorical variables), and edaphic and thermal factors (continuous variables) were modeled as fixed effects. To facilitate comparisons among the effects of different treatments, all predictor variables were rescaled between 0 and 1. Variables measured as a proportion (i.e. percent sand) were arcsine-squareroot transformed prior to rescaling to increase normality.

Treatment effects on each cohort of seeds and seedlings were tested separately, to account for interannual climatic variation and varying seedling establishment, as well as the expansion of the study in 2003. To limit the number of explanatory variables in each model in addition to competition and browsing, we used measurements of the two most relevant edaphic factors (sand and 2004 mean June-August soil moisture) and one thermal factor (2004 mean June-August daily minimum temperature), and included only first-order interaction terms. Model selection was conducted using the same procedure for each hypothesis tested as follows. First, we found the best linear- or generalized linear model not including random effects using the backwards-elimination stepwise model selection procedure of S-plus 6.0 (Insightful Corp., 2001). We then experimental site location as a random effect to this model, and tested it as a mixed-effects model. We then eliminated non-significant terms in the mixed-effects model as needed to minimize the Akaike Information Criterion (AIC) to find the best-fitting mixed-effects

model. Linear mixed-effects models were implemented with the lme command in S-plus. Generalized mixed-effects models were implemented using the glmmPQL function.

For statistical tests where response and predictor variables were not subject to grouping within sites or repeated measures on individual seedlings we used linear and generalized linear models, also selected using the stepwise procedure implemented in S-plus. We tested for the effects of edaphic and thermal factors on the cover and biomass of herbaceous competitors using backwards elimination multiple regression. We also tested for relationships between growth in 2003 and growth and survival in 2004 using regression and logistic regression, and for relationships between mean fluorescence ratios and 2004 growth rates using simple linear regression.

Results

Site-level factors and herbaceous biomass

Across all sites, herbaceous plant cover and above- and belowground biomass were all strongly related to edaphic factors. Herb cover increased with percent soil moisture [% cover = 35.2* ln (% soil moisture) – 19.5, $r^2 = 0.52$, $P < 0.0001$ for 30 d.f.], but not with soil texture. Aboveground biomass was also not related to soil texture, but was positively related to percent soil moisture and to daily maximum temperature [biomass (g/m^2) = 183.7* ln (% soil moisture) + 19.8*mean T_{max} – 776.1, $r^2 = 0.43$, $P = 0.0003$ for 29 d.f.). Belowground biomass was strongly negatively related to percent sand [biomass(g/m^3) = 11565.8*$\sin^{-1}$ v(sand) – 16433.6, $r^2 = 0.42$, $P < 0.0001$ for 30 d.f), but was not significantly related to soil moisture or thermal variables.

Overall we were able to stratify our experiments broadly across the coupled edaphic and thermal gradients, and also where sandy soils occurred in cold, valley bottom locations. However, we were somewhat less successful in finding sites with both silty soils and warm nighttime temperatures (*c*) in the VCNP (see Appendix I). At many of the sites we chose, minimum temperatures at 15 cm above the surface were still fairly low, suggesting that cold-air pooling occurred at a much finer topographic scale than we had expected, and that the decrease in slope inclination necessary for the production or retention of finer-textured upper-horizon soils is usually enough to also result in substantially increased cold-air pooling.

Establishment from seed

Ponderosa seed germination and emergence was extremely low. Only 96 of 6400 planted seeds (1.5%) germinated and emerged over the three years of this study. All germinants but one were dead by the end of the study; most survived at most a few weeks. Germination in our study was associated on the initiation of summer rains in early July 2002, mid-July 2003, and mid-July 2004. The subsequent mortality of germinants was associated with short, rainless periods each summer, in mid-August 2002, late July 2003, and early August 2004. Seeds planted in the early spring of 2002 showed the greatest percent germination and emergence (5.53%) during August of 2002 (Figure 3). Seeds planted in fall 2002 exhibited the lowest germination (0.06%) during the following summer. Emergence of seeds planted in 2002 and 2003 showed no relationship to any experimental treatment. Emergence of seeds planted in spring 2004 was positively related to both percent sand (GLMM coefficient 24.12, $P = 0.002$) and soil moisture (GLMM coefficient 20.47, $P = 0.013$). Competition was not a significant predictor of emergence for any single cohort of seeds; however, across years a slightly greater percentage (1.81% vs. 1.22%) of seeds emerged where grassy competition had been removed.

Seedling survival

Transplanted seedlings exhibited fairly high rates of survival, and much of the seedling mortality was not linked directly to experimental treatments but was instead imposed by unexpected rodent damage. Rodent mortality was primarily due to clipping at the base, apparently by golden-mantled ground squirrels (*Spermophilus lateralis*), though we also noted cases in which seedlings had been uprooted, tunneled beneath, or buried by pocket gophers (*Thomomys* spp.) At the end of the experiment in September 2004, survival across all experimental sites was 28.67% for seedlings planted in 2002 (cohort 1) and for 30.15% for seedlings planted in 2003 (cohort 2). For both cohorts, seedling survival during the first year was higher on sandy soils and lower on fine-textured soils (Table 1), but showed no relationship to thermal factors. Seedling survival for cohort 1 in 2003 was also lower where grassy competition was present, although the effect was only about half as strong as that for % sand (Table 1). During the second year, cohort 1 survival was not related to soil texture or competition, but showed a significant decrease with lower minimum temperatures (Table 1).

We divided seedling mortality into three classes: **physiological stress** (37.66% of transplanted seedlings: seedlings exhibited poor growth, a gradual browning out and dropping of needles, and no apparent physical damage by insects or animal herbivores), **rodent activity** (29.68%: seedlings were clearly uprooted or clipped at the base by rodents, probably almost all by golden-mantled ground squirrels), and **other** (2.87%; this includes seedlings that were trampled, defoliated by grasshoppers, or vanished without a trace). Mortality caused by rodents and physiological stress was roughly equal on silty and sandy soils (Figure 4). However, on cold sites mortality was primarily caused by stress, while on warm sites it was caused mainly by rodents.

Seedling growth and photoinhibition

Ponderosa seedling growth was strongly positively related to minimum temperatures experienced during the growing season. Both cohorts of seedlings showed increased height growth with increasing mean minimum temperature, though this effect was less strong for cohort 2 (Table 2a, Figures 5 and 6) The relationship between needle growth and minimum temperature was even stronger (Table 2b, Figures 5 and 6). Competition had no effect in most models, and only minor effects where it was a significant factor (Table 2a, b), and no other experimental factor significantly affected growth. Seedlings experiencing the lowest minimum temperatures in the valley bottoms generally exhibited stunted, reddish needles, and very little (< 5mm) or no measurable height growth even after two years. Needle growth in 2003 was also a strong predictor of height growth in 2004 (height growth (cm) = 0.53*needle growth (cm) + 1.09, r^2 = 0.52, $P < 0.0001$ for 87 d.f.) and subsequent mortality (logistic regression, probability of survival = 0.04*needle growth (cm) - 0.44, $P < 0.0001$ for 116 d.f.), suggesting cumulative effects of poor needle growth on later growth and survival

Seedling growth itself was related strongly related to the chlorophyll fluorescence ratio F_{PSII} (F_v'/F_m'), but less so to F_v/F_m. Both height and needle growth for cohort 1 increased with increasing F_{PSII} (height growth (mm) = 135.20*F_{PSII} – 38.0, r^2 = 0.23; needle growth (mm) = 164.4* F_{PSII} – 23.4, r^2 = 0.24, for both $P < 0.0001$ for 89 d.f., Figure 7) and with increasing F_v/F_m (height growth (mm) = 221.5* F_v/F_m – 137.5, r^2 = 0.20, $P < 0.0001$; needle growth (mm) = 135.3* F_v/F_m – 74.4, r^2 = 0.09, $P = 0.006$ for 87 d.f.). Height and needle growth for cohort 2 also both increased moderately with F_{PSII} (height growth (mm) = 45.1*F_{PSII} – 1.3, r^2 = 0.12;

needle growth (mm) = 118.2* F_{PSII} – 13.1, r^2 = 0.25, for both $P < 0.0001$ for 194 d.f., Figure 7) and showed a weaker positive relationship with F_v/F_m (height growth (mm) = 21.7*F_v/F_m + 2.0, r^2 = 0.03, P = 0.01 for 188 d.f.; needle(mm) = 60.5* F_v/F_m – 7.0, r^2 = 0.08, P = 0.0001 for 188 d.f.). These relationships indicate an effect of photoinhibition, but both fluorescence ratios and their components were correlated with several environmental variables (Table 3), including percent sand, soil moisture at the time fluorescence was measured, the minimum temperature recorded within five days preceding fluorescence measurement, and seedling age – younger seedlings (cohort 2, 2 year old seedlings) exhibited overall lower values for both ratios.

Discussion

Overall, we found the strongest support for our first hypothesis, that cold-air drainage limits seedling establishment in ponderosa pine on flat or gently sloping sites below inverted subalpine treelines (Figures 5-7; Table 2). Minimum temperature during the growing season was consistently positively linked with seedling growth. At sites experiencing colder nighttime temperatures, seedlings exhibited substantially decreased height growth, and needles were stunted, often curled, and appeared physically damaged. Needle growth was also the single best predictor of both height growth and seedling survival the following year, suggesting compounding effects – decreased needle growth undoubtedly limits energetic returns during subsequent years, limiting growth and increasing the vulnerability to other sources of mortality. However, we did not find any direct effect of thermal regime on the germination and emergence of ponderosa pine, and only moderate effects on the survival of transplanted seedlings, though this may be due in large part to climatic factors and confounding and uncontrolled factors, particularly rodent damage (discussed in detail below) and the small number of germinants in this study.

We found less support for our second hypothesis, that edaphic factors directly impede seedling germination, growth, or survival on finer-textured soils. Although both percent sand and soil moisture had significant positive effects of seed germination and emergence during one of seven seeding trials, and percent sand was a significant predictor of first year transplanted seedling mortality, the magnitude of these effects was substantially less than that of temperature on seedling growth (see Tables 1 and 2, Figure 6).

Likewise, our results offer little support for our third hypothesis, that grass competition reduces ponderosa pine seedling establishment on fine-grained valley soils (Tables 1 and 2). While we found very strong support for the edaphic controls on herbaceous plant cover and biomass (see Results and Chapter 1) – as has been seen for semi-arid grasslands elsewhere in the western U.S. (Sala et al. 1988; Singh et al. 1998) – we found less support for any subsequent effect on ponderosa pine establishment (i.e., a competition x sand interaction term, significant in only one model), beyond relatively minor effects of competition occurring across all sites (a competition term alone). Competition resulted in only minor and inconsistent decreases in seedling survival, growth, and photosynthetic performance relative to other variables (Tables 1-3), results that were somewhat surprising given a large body of literature on the negative effects of herbaceous competition on ponderosa pine seedling establishment (Pearson 1942; Tackle and Roy 1953; Larson and Schubert 1969; Kolb and Robberecht 1996, but see Pearson 1934).

Finally, our results do not support our fourth hypothesis, that browsing or other damage by elk or cattle reduces seedling growth/survival below the inverted treeline. We found no measurable effect of our fencing treatment on seedling growth or survival, despite evident grazing by both elk and cattle surrounding our experimental sites. This result was surprising

given the high levels of elk damage to woody plants, including ponderosa pine, at forest-grassland ecotones in the VCNP reported by Krantz (2001). We suggest that browsing damage to ponderosa pine by elk may not occur except when winter snowpack decreases the availability of preferred forage, and conifer seedlings may not be particularly susceptible to such damage until they are tall enough to emerge above the snowpack. Hence it may be that an effect of elk browse will not become apparent until somewhat later stages in the tree life cycle, and certainly damage due to antler-rubbing only occurs on larger seedlings and saplings. Interestingly, we noted abundant growth by aspen shoots within several exclosures (all at openings on backslopes where mature aspens were present nearby) after only one or two years, in stark contrast with their near total absence from surrounding, unenclosed areas, suggesting that herbivory on aspen saplings may be important *above* the inverted treeline; such a pattern clearly would not help to generate the observed ecotone.

Though we found some evidence for cold-temperature photoinhibition in the relationship between fluorescence ratios and minimum temperature (Table 3) and strong relationships between fluorescence ratios and seedling growth (Figure 7), decreased photosynthetic performance associated with colder temperatures in this study can not wholly account for the relationship between thermal conditions and growth, given the equally strong relationships between fluorescence ratios and percent sand and soil moisture, which themselves were not good predictors of seedling growth. Growth in our study was more strongly related to the light-adapted fluorescence ratio F_{PSII} than to the dark-adapted F_v/F_m, though the latter is more commonly used as a measure of photoinhibition (Ball et al. 1995, Maxwell and Johnson 2000). However, both ratios and their components generally showed similar relationships to environmental variables (Table 3). In our study, reductions in both F_{PSII} and F_v/F_m with low temperatures were accompanied by decreases in minimum fluorescence levels (F_t and F_o). Several researchers have suggested that decreases in fluorescence ratios associated with decreases in minimum fluorescence indicate the operation of regulated, reversible photoprotective quenching mechanisms as opposed to damage to photosystem II, which is associated with increases in F_o (Demmig and Björkman 1987, Osmond et al. 1993). Ball et al. (1991) also reported that the pattern of decreases in photosynthetic performance of *Eucalpytus pauciflora* seedlings near alpine treeline was also suggestive of photoprotective mechanisms as opposed to photodamage. In ponderosa pine, winter reductions in photosynthetic capacity are correlated with an increase in xanthophyll cycle pigments (zeaxanthin + antheraxanthin)-dependent energy dissipation (Verhoeven et al. 1999), which may be the same mechanism employed to dissipate excess light energy by seedlings experiencing environmental stress during summer months in our study. However, the source of this stress was not limited to cold temperatures, but also appears to be related to soil moisture, soil texture, and to a lesser extent to competition. Decreases in F_t have also been shown to be a predictor of water stress (Flexas et al. 2000), which is congruent with our findings. However, the fact that F_t increased with soil moisture content while F_o decreased remains somewhat inexplicable. Younger seedlings (cohort 2) also exhibited lower levels of both F_{PSII} and F_v/F_m, and the negative interaction term seedling age x soil moisture (Table 4.) suggests that the effect of moisture stress was more pronounced in younger seedlings, with presumably less root growth.

Cold temperatures may decrease tree seedling growth through mechanisms other than photoinhibition, and it is quite possible that the reductions in growth we observed were linked more closely to direct tissue damage. Growing season frosts are known to damage to growing conifer tissues, especially needles. Shubert and Adams (1971) reported that unhardened needles

of ponderosa pine exposed to temperatures < -3° C experienced substantial injury. Similarly, Tranquillini (1987) found that Norway spruce required at least consecutive 50 days without frosts of -3° C to avoid damage to growing needles, and a total of 90 days without frosts of -3° C for needle cuticles to become adequately developed to avoid winter desiccation. The unseasonable frosts experienced by seedlings in the valley bottoms of the VCNP may thus have directly injured growing needles, or resulted in unhardened needles susceptible to later damage via winter cuticular water loss.

Frost heaving of soils has been reported to result in extensive root damage to young ponderosa seedlings (Larson 1960; Heidmann and Thorud 1976), and it likely damaged seedlings in the valleys of the VCNP. Many sites in our study exhibited evidence of frost heaving, in the form of raised and broken soil surfaces, which seemed to have taken place during late winter or early spring, probably after snows melted and resulted in exposed and saturated soils that then experienced numerous freeze-thaw cycles. While this process generally did not fully uproot our transplanted seedlings, it may have injured roots near the soil surface.

Given the robust relationship between thermal conditions and growth of transplanted seedlings (Figures 5 and 6, Tables 2 and 3), it seems likely that minimum temperatures have equally strong effects on recently germinated seedlings. It may be that we did not find such a relationship only because region-wide precipitation patterns resulted in near-total mortality of germinants each year of our study. Given the toll imposed by rodents, especially golden-mantled ground squirrels, on transplanted seedlings, it is also possible that the low rates of germination and emergence we observed may have been due at least in part to seed predation. Ponderosa pine seeds are known to be consumed by a wide variety of birds and mammals (Larson 1961; Hooven 1970), including golden-mantled ground squirrels (Taylor and Gorsuch 1932). Survival of seeds that did germinate in our study was also very poor, and in all cases except one, germinants died within only one or three weeks. McKeever (1964) reported that golden-mantled ground squirrels also occasionally consumed newly emerged cotyledons of recently-germinated seeds. However, mortality in the VCNP was consistently associated with brief, dry episodes during otherwise rainy summer monsoons. These results are also in agreement with previous research on ponderosa pine regeneration, which suggests that drought is the major cause of mortality for newly germinated seedlings (Larson 1961). While we found little difference in germination as a function of site-specific environmental factors, this may be because region-wide precipitation patterns are simply more potent. During the period of 2002-2004 we also observed no natural ponderosa pine establishment across the VCNP. Site-specific differences may only become relevant in years where climatic constraints are lifted.

While seedling mortality did not vary with thermal conditions, the apparent sources of mortality shifted from physiological damage on cold, low-lying sites to rodent damage on warmer sites on slopes (Figure 4). Golden-mantled ground squirrels, which were responsible for most of this mortality, are most common in open ponderosa pine forests (McKeever 1976), perhaps especially in openings formed by logging (Tevis 1955), such as the forest clearings on sunny slopes where we located half of our experiments. Pocket gophers, which favor deeper, finer textured soils, also appear to have been responsible for some seedling mortality in our study, and it may be that the slight, but significant, decrease in seedling survival on silty soils (Table 1.) is related to their activity. Cantor and Whitham (1989) found that pocket gophers (*Thomomys bottae*) caused extensive aspen mortality on the deep soils of montane meadows in Arizona, but not on thin-soiled rock outcrops. They proposed that these outcrops served as

refugia for aspen, and that aspen invasion of the montane meadows they studied was limited in large part by the belowground herbivory of pocket gophers.

By itself, the reduction in seedling growth we found along thermal gradients in the VCNP (Figures 5 and 6) cannot explain the persistence of subalpine grasslands and the origin of inverted treelines. However, the relationship we found between needle growth and mortality the following year does suggest the longer-term effects of poor growth on seedling/sapling survival in the frosty valley bottoms. While overall seedling mortality during the first year was uncorrelated to the thermal conditions, low minimum temperatures clearly increased mortality during the second year (Table 1). We believe that as seedlings on warmer sites continue to grow, rodent-imposed mortality is likely to become unimportant, leaving much lower rates of seedling/sapling mortality on elevated sites on coarse soils above the inverted treeline, a spatial pattern that could help generate that ecotone. It will be important to determine, therefore, whether the relationship between thermal conditions and seedling survival becomes sharper during future recensuses of our sites.

We recognize that several factors not addressed in this study may also affect tree seedling survival and growth along valley-slope gradients in the VCNP and elsewhere in the montane and subalpine zone of the southern Rockies. Given the extremely low germination rate and subsequent survival we observed in our experiments, and the clearly episodic nature of establishment by only a few seedling cohorts (see Chapter IV), we cannot exclude the possibility that intense grass competition on loamy, low-lying sites decreases germination and/or seedling survival soon after germination. Furthermore, possible shifts along valley-slope gradients in pathogens, insect herbivores, or mycorrhizae may reduce tree establishment, as may feedbacks caused by increased shading by trees leading to decreased reradiative heat loss leading to increasing seedling establishment, or increased dominance by grasses leading to increased fire leading to increased dominance by grasses. We do know, however, that adult tree survival and growth *increase* with proximity to the subalpine treeline, excluding spatial shifts in these processes as causes of that inverted ecotone (see Chapter II).

Finally, while the constraints on growth we identified are alone not enough to preclude eventual forest encroachment into grasslands, historically these constraints have worked in combination with frequent, low-intensity fire. Several studies have documented high pre-settlement frequencies of widespread, synchronous fires over a range of elevations in the Jemez Mountains, followed by a near complete cessation of fire regimes throughout the region coincident with the initiation of livestock grazing 1890's (Allen et al. 1996; Morino et al. 1998). Fire scar data collected from ponderosa pine trees and stumps bordering VCNP grasslands suggest a mean fire return interval of ca. 5-15 years (Morino et al. 1998; C.D. Allen, unpublished data). This fire frequency would require tree seedlings to achieve sufficient size to withstand fire within that same short interval. Decreased seedling growth in stressful environments including the cold valley bottoms we studied undoubtedly increased the length of time required to achieve this size, and increased the period when ponderosa seedlings were vulnerable to fire. Hence, the interaction of infrequent establishment and reduced seedling growth imposed by cold-air drainage, and frequent, low-intensity ground fires across the entire landscape may have historically maintained the open grassland communities in the valleys of the VCNP. Recent expansion of forests into montane grasslands in the VCNP and elsewhere in this region may thus be attributable to fire suppression, as proposed by Allen (1984), as well as global warming, as suggested by Dyer and Moffet (1999). Records from the nearby Wolf Canyon station suggest an increase of ca. 1.5 °C in summer minimum temperatures since record keeping began in 1912;

there is evidence of a substantial downward movement of subalpine treelines in the VCNP during that time interval (Chapter IV; Hogan and Allen 1999).

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Figures and Tables

Figure 1. Location of the Valles Caldera National Preserve in the center of the Jemez Mountains. White indicates montane and subalpine grasslands; grey represents forest vegetation. Grasslands primarily occupy on gentle surfaces within the central topographic concavity of the caldera, though smaller patches also occur on south-facing slopes and mountaintops above ca. 3000m.

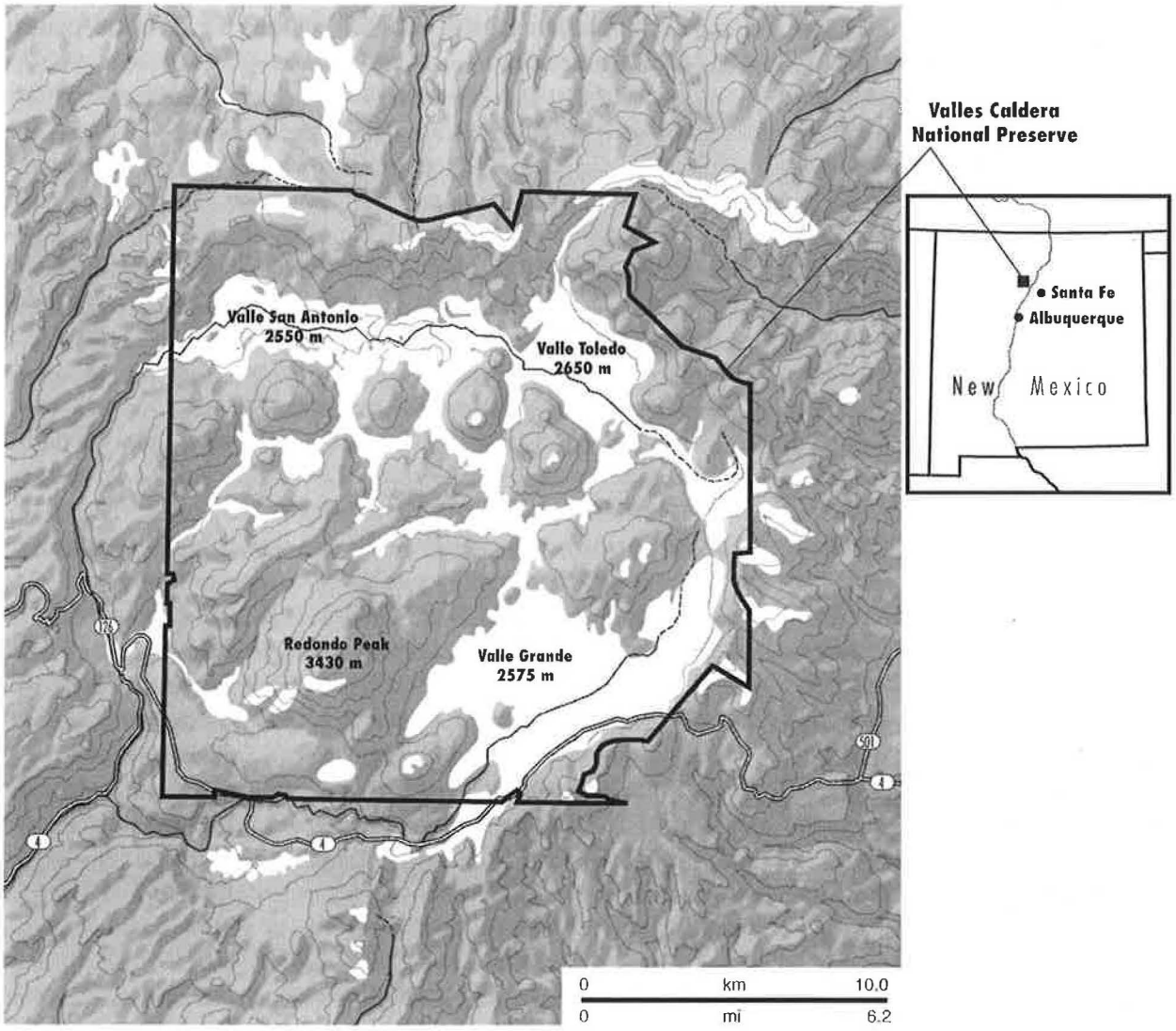
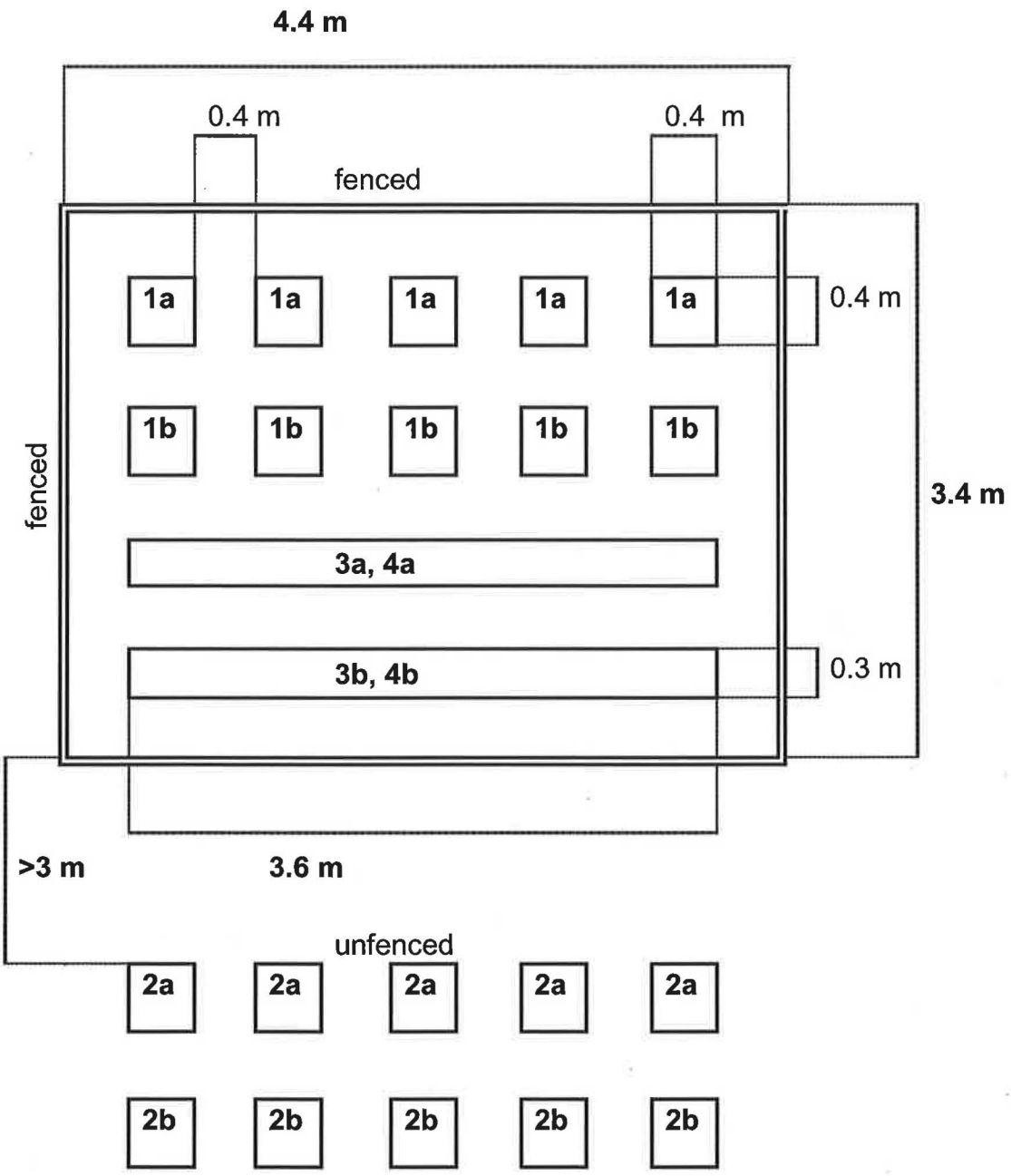


Figure 2. Experimental site layout (a) and a matrix showing treatment combinations (b). Twenty 0.4 x 0.4 m cells were planted with ponderosa seedlings (five under each competition x grazing treatment); each cell was surrounded by a 0.4 m mowed buffer strip. The two strips were 0.3 x 3.6 m (one under each competition treatment). Half of each strip was planted with 20 seeds in early summer; the other half was planted in the fall. Competition treatments were applied to cells and strips at random. The twenty sites established in 2002 were expanded in 2003 to accommodate an additional full set of plantings: the fenced area was increased to 4.4 x 7.4 m to add two seedling strips and twenty seedling cells plus the necessary buffers; twenty cells were also added to the array outside the exclosure.

a. Experimental site design



b. Treatment combinations.

	+ competition Intact herbaceous vegetation	**- competition** Herbaceous vegetation removed
- browsing Within fenced exclosure	**1a)** 5 cells planted with ponderosa seedlings **3a)** 20 ponderosa seeds planted early summer **4a)** 20 ponderosa seeds planted early fall	**1b)** 5 cells planted with ponderosa seedlings **3b)** 20 ponderosa seeds planted early summer **4b)** 20 ponderosa seeds planted early fall
+ browsing Outside exclosure	**2a)** 5 cells planted with ponderosa seedlings	**2b)** 5 cells planted with ponderosa seedlings

Figure 3. Seed germination and emergence for spring and fall plantings between 2002 and 2004.

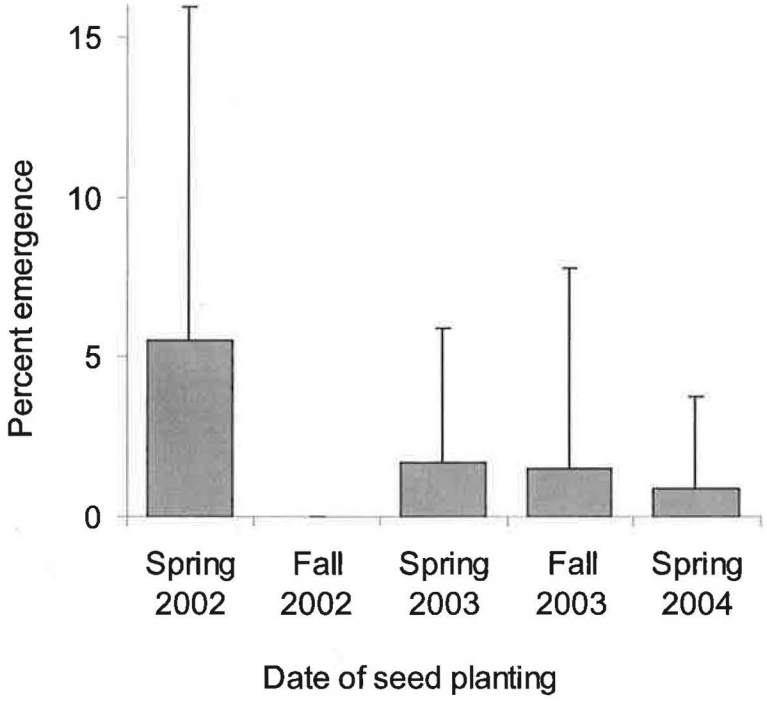


Figure 4. Sources of mortality for all transplanted ponderosa seedlings grouped by site-level factors. Mortality resulting from stress (an admittedly nebulous term) was distinguished by poor growth, a gradual browning out and loss of needles, and a lack of apparent animal damage. Mortality was ascribed to rodents when seedlings were clearly clipped at the base (apparently by golden-mantled ground squirrels, *Spermophilus lateralis,* or possibly pocket gophers, *Thomomys* spp.), or uprooted, tunneled beneath, or buried by pocket gophers.

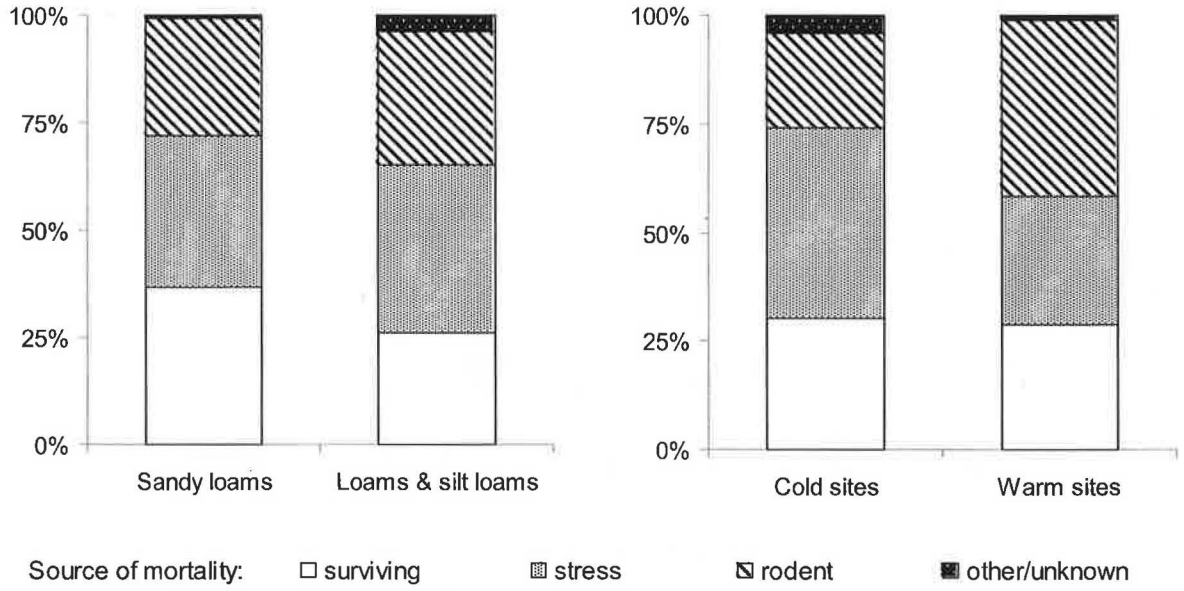
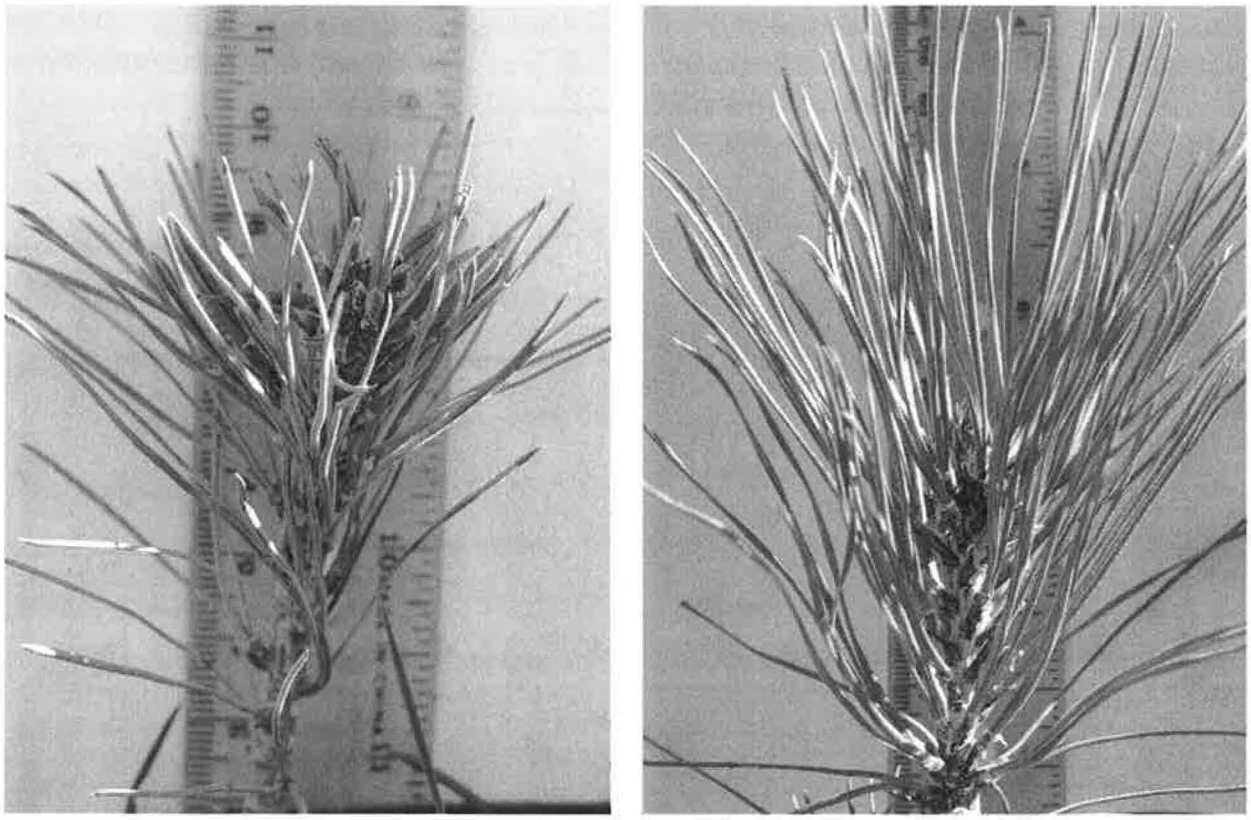
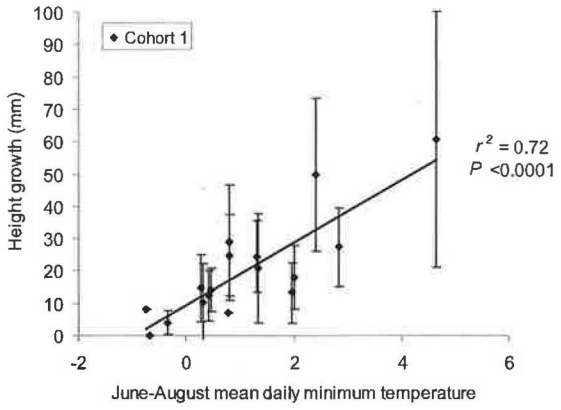


Figure 5. Typical seedling height and needle growth at (a) a cold site (LSAM2, mean summer minimum temperature -0.67° C) and (b) a warm site (LSAF; mean summer minimum temperature 2.14° C) Seedlings grown at sites experiencing lower nighttime temperatures generally exhibited minimal growth from the terminal bud, and stunted, reddish needles.

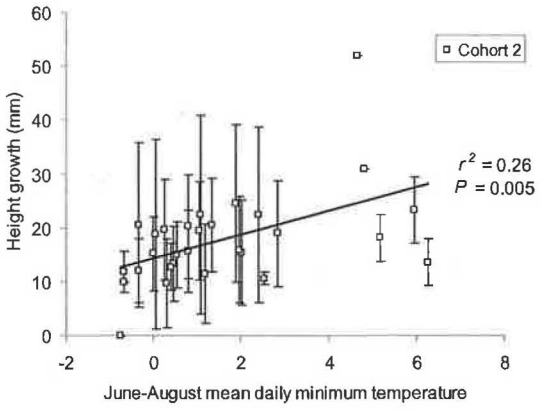


a. **b.**

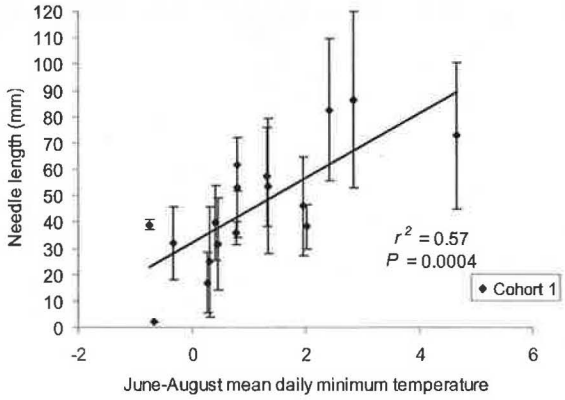
Figure 6. Mean height (a, b) and needle (c, d) growth for transplanted seedlings at each site plotted against the mean daily minimum temperature from June-August 2004.



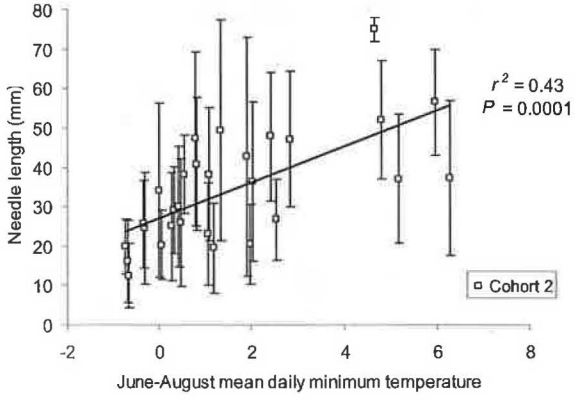
a.



b.

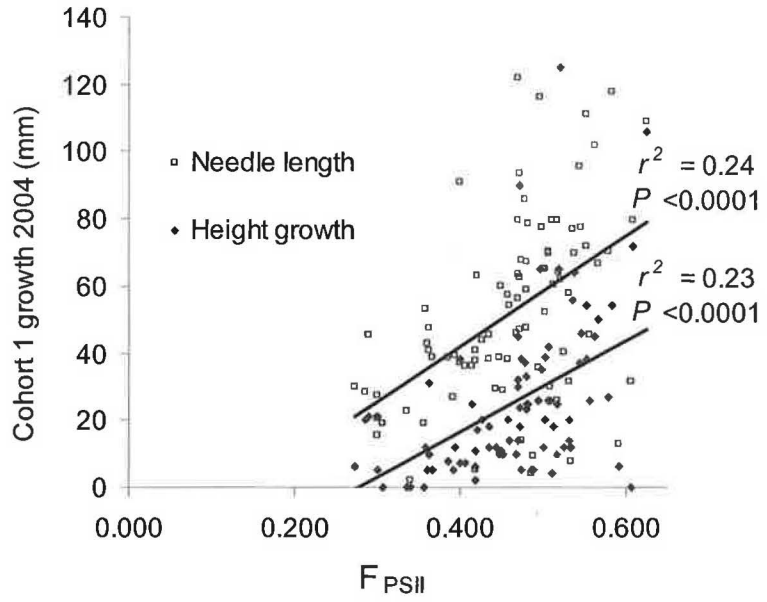


c.

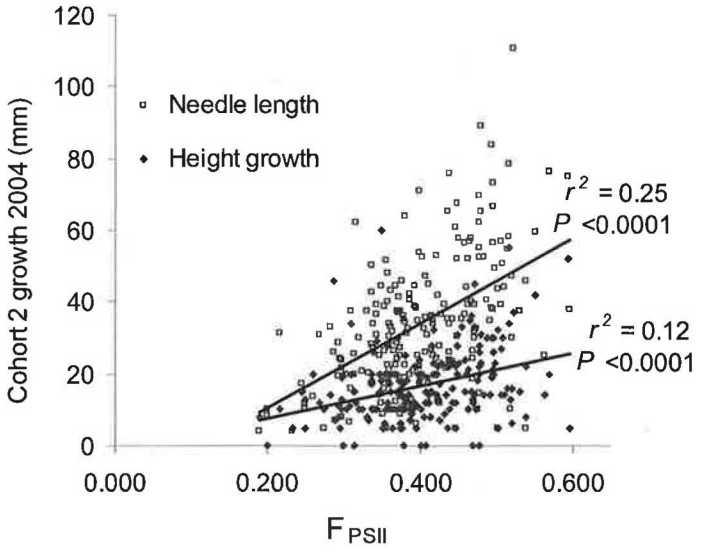


d.

Figure 7. Seedling growth and the quantum yield of PSII [F_{PSII} or $(F'_m - F_t)/F'_m$] for seedling cohort 1 (3-year old seedlings) and cohort 2 (2-year old seedlings).



a.



b.

Table 1. Generalized linear mixed-effects model (GLMM) for survival of transplanted seedlings after year 1 (cohort 1 2002-2003 and cohort 2 2003-2004) and year 2 (cohort 1 2003-2004). For all tables showing results of mixed-effects models, competition was included as a binomial variable, 0 (absent) or 1 (present), while other experimental factors were rescaled as continuous variables between 0 and 1; coefficients (partial linear regression slopes) are thus directly comparable. Only those predictor variables included in the best-fitting model are shown.

Parameter	Cohort 1 2002-2003		Cohort 1 2003-2004		Cohort 2 2003-2004	
	coefficient	*p-value*	coefficient	*p-value*	coefficient	*p-value*
Intercept	**-4.56**	*0.0122*	0.59	*NS*	**-3.89**	*0.0021*
Competition	**-2.36**	*0.0138*				
Sand	**8.51**	*0.0355*			**5.93**	*0.0272*
Mean minimum temperature			**0.58**	*0.0345*		
Competition x sand	**4.62**	*0.0181*				

Table 2. Mixed-effects model for height growth (a) and needle growth (b) of transplanted seedlings after 1 year (cohort 1 2003 and cohort 2 2004) and 2 years (cohort 2 2004). Height and needle growth showed significant increases with increasing minimum temperature, in both cohorts and in both years. Competition had minor effects in both models.

a. Height growth

Parameter	Cohort 1 2003 coefficient	*p-value*	Cohort 1 2004 coefficient	*p-value*	Cohort 2 2004 coefficient	*p-value*
Intercept	**10.68**	*<0.0001*	0.57	*NS*	**14.33**	*<0.0001*
Competition			**-5.15**	*0.0156*		
Mean minimum temperature	**25.31**	*<0.0001*	**70.18**	*<0.0001*	**5.61**	*0.0365*

b. Needle length.

Parameter	Cohort 1 2003 coefficient	*p-value*	Cohort 1 2004 coefficient	*p-value*	Cohort 2 2004 coefficient	*p-value*
Intercept	**14.59**	*0.0053*	**25.39**	*0.0003*	**25.82**	*<0.0001*
Competition					**-2.82**	*0.0176*
Mean minimum temperature	**72.52**	*<0.0001*	**81.80**	*<0.0001*	**25.27**	*0.0015*

Table 3. Mixed-effects models of predictors of light-adapted (a.) and dark-adapted (b.) chlorophyll fluorescence ratios and their components, minimum and maximum fluorescence, for seedling ponderosa pine needles during the summer of 2004.

a. Light-adapted chlorophyll fluorescence ratios.

Parameter	F_{PSII} coefficient	*p-value*	*Ft* coefficient	*p-value*	*Fm'* coefficient	*p-value*
Intercept	-0.002	*NS*	**152.23**	*<0.0001*	53.66	*NS*
Competition	**-0.018**	*0.0001*	**-4.21**	*0.0415*	**-23.14**	*0.0014*
Sand	**0.318**	*<0.0001*	**70.71**	*0.0231*	**259.65**	*0.0164*
Soil Moisture	**0.334**	*<0.0001*	**45.01**	*0.0003*	**284.91**	*<0.0001*
5 Day Minimum temperature	**0.160**	*<0.0001*	**25.66**	*0.0079*	**205.20**	*<0.0001*
Seedling age	**0.147**	*<0.0001*	**48.38**	*<0.0001*	**155.13**	*<0.0001*
Seedling age x soil moisture	**-0.173**	*0.0001*	**-91.27**	*<0.0001*	**-228.23**	*0.0010*

b. Dark-adapted chlorophyll fluorescence ratios.

Parameter	*Fv/Fm* coefficient	*p-value*	*Fo* coefficient	*p-value*	*Fm* coefficient	*p-value*
Intercept	**0.510**	*<0.0001*	**405.32**	*<0.0001*	**699.96**	*0.0001*
Sand	**0.257**	*0.0055*			**931.95**	*0.0088*
Soil Moisture	**0.061**	*0.0318*	**-108.37**	*<0.0001*		
5 Day Minimum temperature	**0.066**	*0.0018*	**59.39**	*0.0079*	**675.56**	*<0.0001*
Seedling age	**0.052**	*0.0002*			**57.24**	*0.0019*

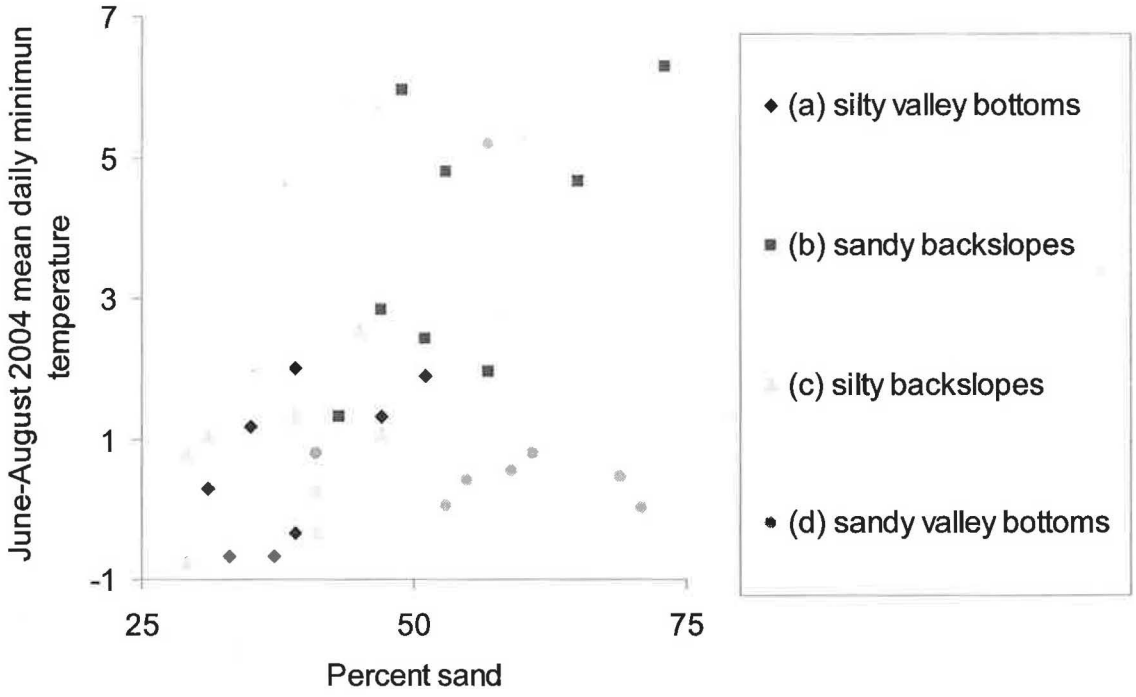
Appendices

Appendix I. List of experimental sites, locations in the VCNP, percent sand and mean nightly minimum temperature from 01 June- 01 September 2004. Site categories are as follows: (***a***) *silty valley bottoms* - cold, low-lying areas in the valles with loams or silty loams, (***b***) *sandy backslopes* – warmer mountain slopes with gravelly, sandy loams, (***c***) *silty backslopes* – shallow benches on mountain slopes with loams or silt loams that are located above the temperature inversion layer, and (***d***) *sandy valley bottoms* - cold, low-lying valley bottoms with gravelly, sandy loams such as may occur on fluvial and erosional deposits. While we were able to stratify our experiments broadly across the coupled edaphic and thermal gradients, and also where sandy soils occurred in cold, valley bottom locations (***d***), we were generally unsuccessful in finding sites with both silty soils and warm nighttime temperatures (***c***) in the VCNP. The silty sites we selected, located on slight benches on mountain slopes well above the valley bottoms, generally experienced thermal regimes very similar to the valley bottom sites. Cold-air pooling occured at a much finer topographic scale than we had expected, and the decrease in slope inclination necessary for the production or retention of finer-textured upper-horizon soils is usually enough to also result in substantially increased cold-air pooling.

a. Site locations, percent sand and mean minimum temperature.

Site Name	Site Category	Elevation (Meters)	Location (UTM 13 S) Meters E-W	Meters N-S	% Sand	J-A 2004 Mean Minimum Temperature (°C)
14F	*B*	2725	367296	3975910	65	4.65
14M	*A*	2685	367315	3975642	31	0.31
BBOSA	*B*	2544	354555	3966896	73	6.27
BBOSI	*C*	2566	355776	3966692	39	1.33
JARF	*B*	2722	363636	3975385	53	4.78
JARM	*A*	2687	363791	3975185	47	1.33
LSAE	*D*	2679	356084	3981098	69	0.46
LSAF	*B*	2617	355935	3983483	51	2.41
LSAF2	*C*	2644	355608	3983641	31	1.05
LSAF3	*C*	2624	354360	3981290	41	-0.33
LSAM	*D*	2583	356038	3983369	53	0.05
LSAM2	*A*	2579	355938	3983330	33	-0.67
LSAM3	*D*	2538	354011	3980952	59	0.54
LTOE	*D*	2635	365891	3980808	55	0.41
REDSA	*D*	2461	355096	3969552	57	5.17
REDSI	*A*	2618	355916	3968751	51	1.89
RINM	*A*	2657	370636	3972552	39	2.01
RINS	*C*	2701	371613	3974328	41	0.27
RITF	*B*	2695	365889	3982174	43	1.32
RITM	*C*	2671	366169	3982031	29	-0.74
SECF	*B*	2710	358438	3978162	47	2.84
SECM	*A*	2683	358430	3977966	39	-0.34
SLUE	*D*	2626	360337	3978238	71	0.01
SLUF	*B*	2731	359207	3977742	49	5.95
SLUS	*C*	2686	360395	3977620	45	2.53
SULE	*D*	2662	356441	3978348	61	0.79
SULS	*C*	2728	356544	3978826	47	1.08
TOLM	*A*	2659	369114	3978980	37	-0.68
TOLS	*C*	2694	369367	3978993	29	0.78
USAF	*B*	2633	359760	3982673	57	1.96
USAM	*A*	2603	359870	3982549	35	1.19
UTOE	*D*	2677	369660	3978430	41	0.80

b. Percent sand plotted against mean daily minimum temperature for each site



Chapter IV

Spatial and temporal dynamics of tree invasion of subalpine grasslands in the Valles Caldera, New Mexico

Abstract

Recent tree forest encroachment into montane and subalpine grasslands has been widely documented in the southern Rocky Mountain region, as well as in many other mountain ranges globally. The timing of tree invasion is often linked to shifts in climate, grazing, and fire regimes, while the spatial extent of tree invasion may depend on complex interactions between these temporally variable factors, spatially-structured environmental gradients, and positive feedbacks. Here we examine both spatial and temporal patterns of tree invasion of subalpine grasslands within the Valles Caldera, in the Jemez Mountains of New Mexico. We used a GIS analysis of aerial photos taken in 1935 and 1996 covering a 40,000-ha study area to assess the spatial pattern and extent of tree invasion. We obtained dates of establishment from 299 tree ring series collected from increment cores and basal disks at 50 sites in the Valles Caldera National Preserve (VCNP) to reconstruct temporal patterns of tree invasion. Overall, the area of subalpine grasslands declined by nearly 18% between 1935 and 1996, from 11,747 to 9336 ha. The extent of tree invasion depended on spatial factors: smaller, higher elevation grasslands that occupied steeper slopes experienced disproportionately high rates of tree invasion; larger grasslands in the cold-air drainage basins of the caldera experienced lower rates of invasion. Tree invasion has been more continuous on upper mountain slopes, consistent with the hypothesis that the maintenance of grasslands on these steep, high elevation sites was dependent on frequent fire. Tree invasion at the margins of the basins has been more episodic, and appears to track summer minimum temperatures, consistent with the hypothesis that these valley bottom grasslands are largely maintained by summer frosts damaging to tree seedlings. The initiation of substantial tree invasion across all sites coincided with the transition from sheep to cattle grazing in the 1940's, and the rates of tree invasion declined during droughts in the early 1950's and from 1995 to present. Further research to separate the effects of grazing and fire on forest-grassland dynamics should be a priority in the VCNP, in addition to long-term monitoring of treeline fluctuations in response to climatic variation. We encourage the use of prescribed fire for grassland restoration efforts.

Keywords: ecotone, park, meadow, montane grassland, ponderosa pine, fire, herbivory

Introduction

Recent tree invasions of montane and subalpine grasslands have been widely reported in the southern Rocky Mountain region (Allen 1984, 1989; Savage 1991; Mast et al. 1997,1998; Miller 1999; Dyer and Moffett 1999). Advances by trees or shrubs into subalpine grasslands have occurred elsewhere in western North America (Brink 1959; Dunwiddie 1977; Franklin et al. 1971; Vale 1981a, b; Butler 1986; Helms 1987; Berlow et al. 2002, Rhemtulla et al. 2002), Australia (Wearne and Morgan 2001; McDougal 2003), and Europe (Didier 2001; Dullinger et al. 2003), and also across many other grassland and savanna systems globally (e.g., Burkhart and Tisdale 1976; Miller and Wigland 1994; Bowman et al.1995; Silva et al. 2001). While the direction of recent changes in these systems, from herbaceous to woody, is a general phenomenon, underlying processes are much more variable. Woody plant establishment and growth in herbaceous vegetation depends upon a complex set of interactions between spatially-structured environmental gradients, temporally-variable climatic factors and/or land use practices, and positive feedbacks (Wilson and Agnew 1992; Hofgaard 1997; Malanson 1997; Dullinger et al. 2004; Daniels and Veblen 2004).

The tempo of woody invasion in western North America is often attributed to anthropogenic changes in disturbance regime, but the actual triggers of invasion appear somewhat variable. While several studies in have linked woody encroachment with direct or inadvertent fire suppression (Koterba and Habeck 1971; Burkhart and Tisdale 1976; Allen 1984, 1989) on sites where tree establishment may have been precluded by frequent fire lethal to tree seedlings, other researchers in this region have also linked specific episodes of tree invasion with the recent occurrence of fire (Butler 1986; Mast et al. 1998), which may have temporarily exposed a bare mineral seedbed, and decreased competition from grasses. Likewise, while increased livestock grazing is often implicated as a cause of forest invasion and increases in tree density by decreasing grass competition (Dunwiddie 1977; Madanay and West 1983; Butler 1986; Miller and Wigland 1994), other research has suggested that tree invasion can be triggered by release from heavy livestock grazing pressure (Vale 1981; Allen 1984, 1989; Mast 1998).

Climatic factors have also been widely associated with episodes of tree invasion, especially at typical, high-altitude and high-latitude treelines. It is widely accepted that the position of alpine and arctic treelines is largely determined by cold temperatures, though the exact mechanisms by which cold temperatures constrain tree growth remains the subject of some debate (e.g. Tranquillini 1979; Stevens and Fox 1991; Körner 1998). Recent advances of such temperature-dependent treelines have frequently been tied to local and global warming (e.g. Lescop-Sinclair and Payette 1995; Lloyd and Fastie 2003; Walther 2004). However, the pattern of change at such treelines also appears to be modulated by numerous other factors, including precipitation (Daniels and Veblen 2004), land use history (Hofgaard 1997), and propagule availability and the nature of competing vegetation (Dullinger et al. 2003). The timing of forest invasion of subalpine grasslands below atypical, inverted treelines may also be associated with periods of drier than normal climates (Franklin et al. 1971; Ostler et al. 1982; Butler 1986), presumably where moist soils or summer snowpack may have previously prevented tree seedling establishment. However, increased precipitation (Mast et al. 1998; Dyer and Moffett 1999) may result in forest invasion of dry grasslands. Lynch (1998) reconstructed the prehistoric dynamics of subalpine grasslands using pollen extracted from sediment cores around Fish Creek Park in northern Wyoming; she concluded that stand-removing disturbance, coupled with the onset of regionally cooler or possibly more moist conditions, gave rise to the conditions in the park that prevented conifer establishment therein.

Discerning among changes in grazing, fire, and climate as possible triggers of tree invasion in the mountains of the western U.S. is often difficult due to a combination of (1) poor resolution in dendrochronological reconstructions of tree establishment dates, (2) lack of detailed documentation of site-specific changes in land use history, and (3) the paucity of precise climatic data available for both the location and time period of interest. Given these limitations, and a lack of appropriate controls, rigorous testing between causal hypotheses is usually not possible. Additionally, relevant changes in livestock grazing regimes, fire frequency, precipitation patterns and temperature are often synchronous in this region, further obfuscating the bases of spatial and temporal patterns of tree establishment. The initiation of large-scale livestock grazing at intermediate elevations in the southwestern U.S. in the 19th century resulted in a near total cessation of fire due to removal of grassy fuels by grazing sheep and cattle (Savage and Swetnam 1990; Swetnam and Baisan 1996; Allen et al. 1996). Historic patterns of livestock grazing in this region were themselves susceptible to climatic influences; both extreme drought and cold, snowy winters often resulted in widespread livestock death (Denevan 1967), resulting in temporary decreases in grazing pressure.

An examination of the spatial pattern and extent of tree invasion may provide important insights into the processes underlying the observed shifts (Mast et al. 1997; Bai et al 2004; Daniels and Veblen 2004). Topographic factors that decrease soil moisture availability may result in decreased invasibility of grasslands. Mast et al. (1997) found that ponderosa pine (*Pinus ponderosa* var. *scopulorum*) invasion at lower timberlines along the Colorado Front Range occurred primarily on north-facing slopes; south-facing slopes showed little change. This pattern of invasion was attributed to more severe spring drought conditions on south-facing slopes; which agrees with their later findings (Mast et al. 1998) that the timing of ponderosa pine invasion was associated with periods of above-normal spring precipitation, in addition to changes in grazing practices and fire. White spruce establishment in prairie vegetation in Manitoba was also confined primarily to mesic, north aspects, and the likelihood of successful establishment was negatively related to July temperature (Chhin and Wang 2002). Bai et al. (2004) reported that conifer invasion of grasslands in interior British Columbia was negatively related to slope inclination, which the authors attributed to moisture limitations on steeper slopes.

Another spatially-structured factor that may facilitate or inhibit woody invasion is competition, which may depend on interspecific differences in physiology or growth form (Dullinger et al. 2003) and variation in disturbance or edaphic factors (Berlow et al. 2002). Berlow et al. (2002) found that disturbances that exposed bare soil were most critical for sagebrush invasion of montane meadows only on moist sites that supported a dense growth of herbaceous plants. In addition to these factors, proximity to seed source is also likely to be important. Several studies also found woody invasion to be confined largely to areas immediately adjacent to previously forested or shrub-dominated vegetation (Didier 2001; Wearne and Morgan 2001; Dullinger et al. 2003), indicative of dispersal limitations or other positive feedbacks (e,g., reduction of night-time reradiative heat losses, reductions in herbaceous competition due to shading) whereby the presence of nearby trees otherwise enhances the probability of seedling establishment.

The Valles Caldera, in the Jemez Mountains of northern New Mexico, contains ca. 10,000 ha. of subalpine grasslands, primarily in the expansive valley bottoms of the caldera floor at elevations ranging between 2575 and 2700 m (see Fig. 1). Grassy openings also occupy smaller drainages and topographic concavities across a wider range of elevations. Where these grasslands adjoin forested mountain slopes, they form abrupt, inverted treeline ecotones. Such

treelines elsewhere in the southern Rockies are commonly hypothesized to result from increased competition with grasses on the moist, fine-textured, and nutrient-rich soils characteristic of valley bottom locations (e.g. Ramaley 1927; Peet 2001). Other factors that have been proposed as causes of valley bottom grasslands in the Rockies include soil moisture shortage (Koterba and Habeck 1971) or excess (Ives 1942) and cold-air drainage (Ramaley 1910). Grasslands in the valley bottoms of the Valles Caldera are most strongly associated with very low nightly temperatures resulting from cold-air drainage and pooling (Chapter I) and previous experimental research in this system (Chapter III) revealed strong constraints on the growth of transplanted ponderosa pine seedlings in valley bottoms due to the deleterious effects of low minimum temperatures. Grassy openings also occupy mountaintops and south-facing slopes at higher elevations (above ca. 2800 m). Grasslands occurring at such sites in the Rockies are thought to result from soil drought (Rydberg 1913; Daubenmire 1968), but may also be due to fire (Langenheim 1962; Allen 1989) or some combination of those factors (Moir 1967).

A recent ground-based photographic study (Hogan and Allen 1999) compared three photographs taken in valleys of the VCNP in 1907 by members of Vernon Bailey's Bureau of Biological Science expedition with photographs taken from the same locations in 1997. This study revealed that substantial forest encroachment had occurred at the inverted treelines along the margins of the broad, lower elevation valley bottoms. Tree invasion of grasslands on high-elevation mountaintops and south-facing slopes along the southeastern rim of the Valles Caldera has also been documented using aerial photography. Based on a comparison of photos taken in 1935 and 1981, Allen (1984, 1989) found that grasslands in the area he examined declined by nearly 55%, from 554 to 250 ha., which he attributed primarily to fire suppression and release from sheep grazing pressures in the 1930's.

The objectives of this study are (1) to quantify the historic loss of subalpine grasslands in the Valles Caldera between aerial photographic surveys in 1935 and 1996; and (2) to assess spatial and temporal patterns of tree invasion using a GIS analysis and dendrochronological reconstruction of the timing of tree establishment at different elevations, on different slope inclinations and aspects, and at different distances from pre-existing wooded stands. Given the relationships between subalpine grasslands and landform position in the Valles Caldera (Introduction and Chapter I), we expect both the extent and timing of tree invasion to be modulated by topographic factors. Temperature-dependent, inverted treelines adjacent to valley bottoms should be especially susceptible to shifts toward a warmer climate. Invasion of high-elevation grasslands of steeper slopes and mountaintops may be more dependent on increased precipitation, if soil drought limits tree seedling establishment at these sites, as has been hypothesized by other authors (see above). If this is true, we would expect tree invasion to be more extensive on more mesic sites (such as north-facing slopes) or on shallower slopes that might be less excessively drained. If high-elevation grasslands have instead been maintained largely by frequent fire, tree invasion may have proceeded independently of other factors since the nearly total collapse of the surface-fire regime since late 19th century (Allen et al. 1996). Finally, tree invasion should also be affected by the proximity of wooded stands, via their effects on propagule availability (Malanson 1997).

Methods

Physiographic setting

This study was conducted within the Valles Caldera National Preserve (Fig. 1; 35°50'-36°00'N; 106°24'-106°37'W) in the Jemez Mountains of northern New Mexico. The Valles

Caldera is a 24 km-wide basin formed by explosive volcanic eruptions and the subsequent collapse of the underlying magma chamber ca. 1.22 Ma. (Smith and Bailey 1966, 1968; Izett and Obradovich 1994). The mountainous rim of the caldera reaches elevations ranging from 2850 to 3150m; the basin floor lies between 2575 and 2750 m. Within the caldera, resurgence and post-collapse ring-fracture volcanism have formed several secondary domes (Smith et al. 1970); the highest of these is Redondo Peak at 3370 m. The primary rock types of the mountain slopes are ignimbrite and rhyolite, with some pumice deposits. The caldera floor is underlain by a combination of Quaternary alluvium, fan deposits, and lacustrine sediments deposited by Pleistocene lakes (Smith et al. 1970). Soils include alfisols and inceptisols beneath forested vegetation on the slopes, and well-developed mollisols in the grassy valley bottoms (USDA Soil Conservation Service 1987).

The climate in the VCNP is semi-arid and continental. No long-term climatological data exist for the Valles Caldera. At the nearest climate station in the interior of the Jemez Mountains (Wolf Canyon; 35°57'N, 106°45'W, 2505.5m), the 50-year mean (1954-2004) total annual precipitation is 57.6 cm. Summers are generally characterized by severe drought in May and June followed by monsoonal, convective showers, which occur almost daily during July and August. Fifty-year mean monthly high and low temperatures at Wolf Canyon are 3.4° and -13.5° C in January, 24.9° and 5.7° C in July.

Vegetation

All of the grasslands and treeline ecotones under study fall well below alpine treeline (ca. 3500 m). We therefore refer to these communities and ecotones as *subalpine treelines* and *subalpine grasslands*. Given that these subalpine grasslands occur primarily above 2500 m, this terminology also agrees with the nomenclatural convention of Brown (1994), though the surrounding matrix of intermediate-elevation ponderosa pine and mixed-conifer forests are widely referred to as *montane* forests, as originally defined by Ramaley (1907).

The composition of subalpine grasslands in the Valles Caldera is strongly related to edaphic gradients, soil moisture, elevation, slope inclination, and aspect (Chapter I). The most widespread communities, occurring on loamy, well-drained soils on gently-sloping topography in the valleys, are dominated by Arizona Fescue (*Festuca arizonica*; botanical nomenclature follows Hartman and Nelson 2005) on south and west aspects, and Parry's oatgrass (*Danthonia parryi*) on north and east aspects. Downhill from these communities, on flatter, more mesic, and finer-textured substrates, dominance shifts to pine dropseed (*Blepharoneuron tricholepis*), then to Idaho fescue (*Festuca idahoensis*), and finally to tufted hairgrass (*Deschampsia caespitosa*) and wooly sedge (*Carex pellita*). Waterlogged sites with highly organic soils are dominated by water sedge (*Carex aquatilis*) and northwest territory sedge (*Carex utriculata*). At higher elevations, grassy balds on mountaintops and south-facing slopes are frequently dominated by Thurber's fescue (*Festuca thurberi*) and Parry's oatgrass. Subalpine grasslands in the Valles Caldera are generally quite species rich, containing 12.3 ± 4.2 (s.d.) species per square meter. (Chapter I; Coop and Givnish unpublished data). While the subalpine grassland flora of the Valles Caldera contains a low proportion of exotics (Hartman and Nelson 2005), the high abundance and frequency of species such as Kentucky bluegrass (*Poa pratensis*), western yarrow (*Achillea millefolium* var. *occidentalis*) and common dandelion (*Taraxacum officinale*) indicate widespread effects of over a century of livestock grazing (Chapter I).

Forested stands at treeline ecotones across the Valles Caldera are dominated primarily by ponderosa pine on south and west aspects, and Colorado blue spruce (*Picea pungens*) on north

and east aspects. While forests composed entirely of ponderosa pine also occur across a broad elevational band (from ca. 2000 to 2800 m) in the Jemez Mountains, dominance by Colorado blue spruce in the southern Rockies is generally restricted to the edges of stream corridors and meadows (Fechner 1990), as is the case in our study area. Less commonly, treeline ecotones in the Valles Caldera may be formed by quaking aspen (*Populus tremuloides*). Stands at the subalpine treeline may also include Douglas fir (*Pseudotsuga menziesii* var. *glauca*), white fir (*Abies concolor*), and Engelmann spruce (*Picea engelmannii*), especially at higher elevations (Chapter I).

Forest composition in the Valles Caldera generally follows the elevational zonation general to the southern Rocky Mountain region (Brown 1994; Peet 2000). Higher elevations (above ca. 3200 m) in the Valles Caldera are dominated by Englemann spruce, occasionally with corkbark fir (*Abies arizonica*) codominant. At intermediate elevations (ca. 2800-3200 m), forests are composed of a mixed conifer assemblage, which includes Engelmann spruce, Douglas fir, white fir, and southwestern white pine (*Pinus strobiformis*). At lower elevations (below ca. 2800 m), ponderosa pine becomes dominant. Quaking aspen occurs across the elevational gradient, often at sites that have experienced stand-replacing disturbances such as crown fires or clear cutting.

Human land use history and ecological change in the Valles Caldera

Human occupation in surrounding areas of New Mexico has been documented to date back to at least 11 Ka with early Paleoindian era sites; however, the earliest dates of human use of the Valles Caldera are poorly known (Baker and Winter 1981; Acklen 1997; Chomko 2005). Human use throughout prehistory probably focused primarily on obsidian procurement along the periphery of Cerro del Medio, in the center of the Valles Caldera. The earliest evidence of extensive human use of the caldera is in the Archaic period (5500 B.C. – 400 A.D.), particularly after 1800 B.C. in the Late Archaic. Archaic sites precede the development of large pueblos across mesas and plateaus at lower elevations in the Jemez Mountains during the Ancestral Pueblo period (A.D. 400 – 1600). Seasonal agricultural use probably after A.D. 900 is indicated on the Banco Bonito in the southwest corner of the study area where numerous small stone structures known as field houses are documented (Kulisheck 2003). While the ecological impacts of Puebloan use of the Valles Caldera are unknown, it is unlikely that native people in this region substantially increased fire regimes, given the very high frequency of natural ignition from lightning strikes (Swetnam and Baisan 1996; Allen 2002).

While Spanish settlement of the upper Rio Grande valley began in the late 16th century, livestock grazing in interior of the Jemez Mountains probably did not begin until the early-mid 1800's (Martin 2003; Anschuetz and Merlan 2004 and sources therein). Unfortunately, documentation of livestock numbers and grazing practices in the Valles Caldera is very scarce. Early livestock grazing in the Valles Caldera appears to have been limited to minor sheep grazing by Hispanic shepherds and pasturing of horses by Jemez Pueblo members, and was mostly limited to the Sulfur Canyon drainage and in some of the northern valles (Martin 2003; Anschuetz and Merlan 2004). In 1860, as part of settlement of a land dispute, the United States granted 40,470 ha of the Valles Caldera to the heirs of Luis Maria Cabeza de Vaca; this area thus became known as Baca Location No. 1 (Figure 1). However, it was not until Navajo and Apache were forcibly removed from the area in the 1860's and a nearby railroad terminal was completed at Española in 1881 that large-scale, seasonal grazing became economically viable in the interior of the Jemez Mountains (Martin 2003). Rothman (1989) documented the presence of herds of

sheep in the Valles Caldera in summer by the late 1880's. In 1917, grazing rights on Baca Location No. 1 were leased to the Bond brothers, a pair of Española businessmen, who purchased the entire property in 1918 (Martin 2003). The Bonds used the Baca Location No. 1 for summer sheep grazing; flocks wintered on Ramon Vigil Grant (now Los Alamos County). Estimates of sheep numbers on Baca Location No. 1 around 1918 range from 20,000 to over 100,000 (Anschuetz and Merlan 2004).

The transition from sheep to cattle grazing on the Baca Location occurred during the 1940's and 1950's. A brief decline in wool prices from 1939-1940 probably initiated the shift away from sheep, and toward cattle grazing on the Baca Location No. 1 (Anschuetz and Merlan 2004). However, wool prices rose again during the 1940's, due to a demand for uniforms in World War II, and it was not until after the war, as newly-developed synthetic fibers became available, that sheep grazing became entirely uneconomical (Martin 2003). In the early 1950's, 30,000 sheep and 5,000 cattle grazed on the property. By the end of the decade, sheep grazing had ceased, and cattle numbers had increased to 12,000 (Martin 2003). In 1963 the Baca Location No. 1 was purchased by James Dunnigan, a Texas oilman who gradually decreased the grazing intensity on the ranch to an estimated 7,000 head of cattle (Martin 2003), but also increased its spatial extent, by building numerous stock tanks, especially in higher-elevation grasslands that had not previously been utilized by cattle (Anschuetz and Merlan 2004). Livestock grazing practices are unlikely to have changed substantially until 2000, when the Baca Location No. 1 was publicly acquired through the Valles Caldera National Preservation and Federal Land Transaction Facilitation Act. The VCNP now occupies 35,560 ha of the former Baca Location. Currently, cattle grazing in the VCNP is in flux; after two years without grazing in 2000 and 2001, smaller numbers (ca. 1000-2000) grazed in the VCNP during the summer months of 2002-2004. In addition to livestock, the Valles Caldera forms the core range of a large elk population, estimated between 4000 and 8000 (Martin 2003). Elk were extirpated from the Jemez early in the 20th century, but were reintroduced in 1947 and again in 1961. The herd grew slowly at first, but expanded rapidly after the La Mesa fire of 1977 opened up considerable winter range at lower elevations on the outer slopes of the caldera (outside the range considered in this study) (Martin 2003).

The initiation of large-scale livestock grazing in the Southern Rockies has generally been linked to the cessation of frequent, low-intensity fires, due to the removal of fine, grassy fuels by grazing livestock (Savage and Swetnam 1990; Allen et al. 1996; Swetnam and Baisin 1996). Prior to the late 19th century, low-intensity fires occurred across intermediate elevations throughout much of the Jemez Mountains at intervals of < 5 - 20 years (Allen et al. 1996). Fire scar data collected from ponderosa pine, Douglas fir, southwestern white pine, and white fir at three sites in the Valles Caldera show a similarly high frequency, between 5 and 20 years (Morino et al. 1998; C.D. Allen, USGS, pers. com.). However, this fire regime collapsed throughout the Jemez by the beginning of the 20th century. The last fire scars in the Valles Caldera occurred in 1861at one site and in 1896 at two other sites.

Other recent human impacts to the vegetation of the Valles Caldera include logging, geothermal exploration, and the general development of ranch infrastructure (e.g. roads, fences, stock tanks). Of these, only logging had the potential to substantially affect treelines. Logging practices from 1935 to 1962 involved the selective harvest of accessible, economically valuable old growth, primarily from forest margins along the valley bottom grasslands; from 1963 through 1972 extensive clearcutting occurred on the steep slopes and upper elevations of many of the secondary domes and mountain rims of the Valles Caldera (Balmat 2004). Logging activities

ceased until 1980, but then resumed at moderate levels until the public acquisition of the VCNP in 2000 (Balmat 2004).

Spatial pattern and extent of forest encroachment

The area included in this study is a square of 40,700 ha, roughly 20.2 km on a side (Fig. 1). We includes the entire area occupied by the Baca Location in 1935, as well as an inholding at Sulphur Springs near its western margin, and the entirety of the 35,560-ha Valles Caldera National Preserve.

To assess the spatial dynamics of treeline ecotones, we conducted a GIS analysis of changes in the position of forest-grassland boundaries, and in the location and extent of patches of grassland vegetation, based on aerial photographs taken in 1935 and 1996. Aerial photo coverage for 1935 was kindly loaned to us by Karen Lee of the Valles Caldera Trust. We digitally scanned 22 of these 1:24,000, gray-scale photos at a resolution of 600 dpi (ca. 1 m/pixel); the set of photographs chosen was sufficient to cover the entire study area with substantial overlap. Georectification of these photos to the UTM projection of 1996 orthophoto quarter quads (DOQQ's; 1:12,000 scale) and the digital elevation model (DEM, 30 m x 20 m horizontal resolution) obtained from the USGS was done with Orthomapper software (Image Processing Software, Inc., Madison, WI). To orthorectify each 1935 image, we identified and manually entered between 8 and 16 tie points that could be accurately visually located in both the 1935 and 1996 coverage. Such tie points, which were spaced widely across each 1935 photo, included prominent, permanent landscape features such as large rocks, rocky outcrops and points, stable hydrologic features (i.e. springs, old oxbows) and, where possible, historic ranch buildings. The standard deviation of model fit ranged between 4.8 and 20.5 m for the orthorectified 1935 photos, with a mean deviation of 10.2 m. We judged this fit to be adequate given the size of the study area, the extent of forest encroachment, and the coarse 30-m resolution of the digital elevation model we used. Georectified photos were trimmed to remove their borders, and stitched into mosaics for both 1935 and 1996.

The locations of forest-grassland treeline ecotones on the photomosaic were used to digitize polygons of grassland vegetation from both photo coverages using ArcGIS 9.0 (ESRI, Redlands, CA). Due to variable levels of grey-scale contrast between the two photo sets, and between patches of grassland at different elevations and aspects within photos, and because photos also contained unvegetated rockfields that could be mistaken for grasslands without prior knowledge of the study area, we chose to manually digitize forest-grassland boundaries instead of using automated procedures. We used a threshold of 10 % tree cover distinguish forests from grasslands. Transitions between forest and grassland vegetation in the study area are generally very abrupt; tree densities often shift from < 1/ha to 800 – 1200/ha over a distance of 10 m (see Chapter I). Treelines occurring where forests bordered unvegetated sites, primarily felsenmeer rock fields, were not digitized and were excluded in this study.

To test for a relationship between topographic predictor variables and forest invasion, we first developed a grid of 10,000 regularly spaced points that uniformly covered the entire 40,700 ha. study area using the HawthTools extension (Beyers 2004). We intersected these points with the 1935 and 1996 grassland coverages to generate a binary response variable for forest invasion of former grasslands (i.e., 0 = 1935 grassland-to-1996 grassland and 1 = 1935 grassland-to-1996 forest). A total of 2810 points fell within 1935 grasslands and were used in subsequent analyses; 2305 of these points remained grassland in 1996 and 505 points were invaded by forest. To generate topographic predictor variables, we intersected this point coverage with coverages of

elevation, slope, and aspect derived from the DEM. Slope values (measured in degrees) were log-transformed to increase normality. We used three different transformations for aspect: (1) a north-south variable (-cosine(?)), a proxy for insolation, (2) a northeast-southwest variable (-cosine (?-45°)), a proxy for heat load, and (3) an east-west variable (-cosine (?-90°)), which could approximate increased exposure to wind, predominantly from the west in this region, and account for potential rainshadow effects on leeward slopes. To test for an effect of spatial proximity to treeline ecotones on subsequent encroachment, we developed a 30 x 30 m raster coverage of linear distances to the closest forest edge for the 1935 grassland polygons, which we also intersected with the point layer. We used logistic regression to test for relationships between these topographic and spatial predictor variables and forest invasion. We used a stepwise backwards elimination of the full model including all six predictor variables and all first-order interaction terms. Model selection was based on minimizing Akaike's Information Criterion (AIC), and was implemented by S-plus 6.0 (Insightful Corp, 2001 release).

To quantify the extent of grassland encroachment for both photo coverages, we calculated the total area of grassland. We also calculated the area of grassland occurring within five discrete bands of elevation (2400-2599 m, 2600-2799 m, 2800-2999m, 3000-3200m, and > 3200m) and six categories of slope inclination (0-4.99°, 5-9.99°, 10-14.99°, 14-19.99°, 20-14.99°, and > 25°) derived in each case from the 30-m resolution DEM.

Tempo of forest invasion

Based on the comparison of 1935 and 1996 aerial photo coverages of the study area, we identified fifty locations for field sampling in areas where trees had encroached into former grasslands during 60 year period. Unfortunately, time constraints necessitated field sampling prior to the completion of the above GIS analysis, and the selection of stands for sampling was subjectively based on maximizing the spatial extent of our sampling across the study area, including stands across a wide range of elevations, and accessibility. The UTM location, elevation, and dominant species at each sample site are listed in Appendix I.

At each site, we established a 200-m^2 quadrat of 10 x 20 m for sampling the species identity and basal area (at a 1.5 m height) of all saplings and trees present. Because tree seedling densities are generally exceptionally low (ca. 160 /ha. in forested stands 5-110 meters from treeline ecotones; see Chapter I) across the study area, it was also feasible for us to tally all seedlings within each 200 m^2 quadrat. We divided the tree population into quintiles based on dbh, and collected increment cores or basal disks from 1 or 2 stems randomly selected from each quintile. At the first 15 sites sampled, we collected cores or disks from 2 stems in each quintile; to increase our efficiency we sampled only one stem in each quintile at the remaining 35 sites.

Increment cores and basal disks were collected as close to the ground surface as possible, in an effort to increase the accuracy of estimates of establishment dates. To collect cores at this level, we mounted an increment borer on the end of a ratchet, so the borer could be easily rotated perpendicular to the axes of tree growth, even close to the ground surface; a total of 214 cores were collected using this method. Basal disks were cut from 111 smaller trees, saplings and seedlings; the smallest seedlings were collected whole and sliced with a razor in the lab.

Increment cores and basal disks were mounted and sanded using standard dendroecological methods (Stokes and Smiley 1996). Rings were counted and measured using a sliding bench micrometer (Velmex, Inc., Bloomfield, NY) coupled with a Metronics QC-1000 digital readout (Metronics, Inc., Bedford, NH) and the software Measure J2X (Voortech Consulting, 2000). We were able to obtain ring series from 299 samples; 26 of 325 cores/disks

could not be reliably read and were discarded. Eighteen of these discarded cores were collected from aspen; hence, with the exception of aspen the number of ring series used in our final analysis is proportional to the number of individuals of each species encountered during stand sampling (Appendix II). A total of 211 of these 299 series contained the pith. To estimate tree ages from series that did not include the pith, we overlayed the core with a clear plastic template with concentric circles printed at radial increments of 1 mm. This distance (radius) could then be used to estimate the number of missing years based on the relationship between age and the ratio of radius/increment growth for following ten years. We modeled this relationship from the series that did contain the pith (separate models for each species) with a second order polynomial function, where y = age, and x = radius/mean annual increment for the following ten years. This function has the advantage of including the changing growth rate with age (increasing annular increment at young ages) as well as incorporating variation due to growth rate of individual trees. Models for aspen, blue spruce, Douglas fir, and ponderosa pine are presented in Appendix III. We had a total of only eight series from the three other tree species (Engelmann spruce, southwestern white pine, and white fir), all of which contained the pith.

Where possible, tree ring series were visually cross-dated using skeleton plots (Stokes and Smiley 1996). However; most of the series we obtained showed little correspondence to annual regional precipitation patterns (e.g., a *complacent* growth series [Stokes and Smiley 1996]), undoubtedly due to the location of many invading trees on the deep and well-watered soils of valley bottoms. Hence, cross-dating became increasingly unreliable on ring series from trees at lower landform positions. For this reason, we decided to use 5-year classes of establishment dates in our subsequent analyses.

To assess whether forest encroachment corresponded to periods of favorable climate, we obtained daily records for the three nearest climate stations, including Los Alamos (35°52'N, 106°19'W, 2263 m), Jemez Springs (35°47'N, 106°41'W, 1909 m) and Wolf Canyon (35°57'N, 106°45'W, 2506 m). All climatic data were downloaded from the National Climatic Data Center climate data online (http://www.ncdc.noaa.gov). Unfortunately, these climate stations are all at low elevations relative to the Valles Caldera (2400 – 3150 m), and may not be adequate proxies for conditions across the study area, especially at higher elevations. Much more problematic, however, are numerous missing data and substantial changes in station locations during the 1935-1996 period. In some cases, data were missing for days or weeks, in other cases, entire years were not available (e.g. the Manhattan Project era and slightly beyond, from 1942 – 1947, in Los Alamos). To account for the potential effect of missing daily values on monthly and yearly temperature means and precipitation totals, we discarded records for months with fewer than 25 recorded values, and for years with fewer than 330 values. When we plotted these data (Figure 3) we also plotted 5-year running averages. The problem of changing station locations is more difficult to address, and of much greater concern. Tables showing the location of stations (also available online from the National Climatic Data Center) are given in Appendix IV. Given the strong dependence of precipitation and temperature on topographic location and site elevation, apparent trends in long-term climatic patterns recorded from these stations should be treated with profound caution.

Despite these problems, we sampled the climatic records to generate five parameters from each station that we expected could be correlated with tree invasion. These include three precipitation totals: annual (November-October, a measure of total yearly moisture availability), spring (April-June, a measure of the extent of spring drought), and summer monsoon (July and August, necessary for germination and early growth). We also generated two averages of

thermal conditions from each station: yearly mean temperature (January-December) and summer mean daily minimum (June-August, proportional to nocturnal temperature inversions in Valles Caldera during the growing season, [Coop and Givnish, unpublished data]).

To visually assess patterns between the timing of tree invasion, and known changes in land use history, precipitation patterns, and thermal conditions, we plotted the frequency of tree establishment (in a total sample area of 1 ha.) against time from 1925 to 2003 (Figure 2). Because tree seedlings ca. 1-15 years old are not discernable from grassland vegetation in the aerial photos, and because seedling establishment continued after 1996, our field sampling captured tree invasion over a somewhat greater period than the 61-year photo interval (the earliest dates of tree establishment we recorded are 1907 and 1915). We also plotted a regional mean value for each climatic parameter its 5-year running average. To generate the regional mean we averaged the values for each parameter from all three stations for each year. Where we encountered missing values from one or two, but not all three stations, we used the 50-year mean value for that station. Out of 1170 total values, we were required to substitute the 50-year mean for missing values in 60 cases. We refrained from further statistical analysis for three reasons. First, the poor quality of the climate data would make any results suspect. Secondly, we would be reluctant to assign p-values to correlation or regression coefficients because of the strong likelihood of type I error likely to arise from temporal autocorrelation in both establishment dates and climatic parameters. Third, while the climatic data are amenable to statistical analysis, we lack comparable data on land use history; hence further analysis would be inherently biased towards accepting (or rejecting) one set of explanations, and then rejecting (or accepting) the other only as a matter of default.

Results

Spatial pattern and extent of treeline change

We found a very strong topographic dependence of forest invasion, as well as a negative relationship between the probability of invasion and distance from treeline (Table 1). We found no significant effect of slope aspect in the best-fitting multiple logistic regression model, but a strong positive relationship between invasion and both elevation and slope inclination. These relationships were very strong, even when distance from treeline was accounted for in the model (Table 1). Grasslands at higher elevations and on steeper slopes were much more likely to be invaded by trees, and the probability of invasion was much lower for grasslands in the shallowly-sloping bottoms of the major valles. The negative interaction term between slope and elevation included in this model also reveals that at higher elevations the dependence on slope inclination is slightly weaker, and conversely, on steeper sites, elevation is less important.

Not surprisingly, forest invasion between 1935 and 1996 was much more likely to occur closer to forests present in 1935, indicating a strong dependence on propagule availability and/or other positive feedbacks by which the presence of a forest canopy may facilitate tree seedling establishment. Intriguingly, the best-fitting logistic regression model also retained a positive interaction term between distance from treeline and slope. The positive sign of the interaction term indicates that the negative effect of distance from treeline on tree invasion is weaker on steep slopes, and slope inclination is a stronger predictor of invasion farther from treeline.

Between 1935 and 1996, the total area of subalpine grasslands in the Valles Caldera study area decreased by nearly 18%, from 11,747 to 9336 ha. (Fig. 2). Forest encroachment was most severe at higher elevations and on steeper slopes (Tables 2 and 3). Above 2800 m, the area of grassland decreased by 62.5%, from 1297 to 498 ha.; below 2800 m the area of grassland

dropped by 12.4 %, from 10,449 to 9152 ha. Grasslands on steeper slopes showed similarly disproportionate declines (Table 2). Grasslands at sites steeper than 10 degrees (17% slope) declined by 51.4%; grasslands on shallower slopes declined by 13.9% (Table 3).

Regional climatic record

Temporal patterns of annual precipitation (Figure 4a) exhibit both short-term (1-5 year) fluctuations, often associated with the El Niño Southern Oscillation (ENSO), and multidecadal variation, probably due largely to shifts in the Pacific Decadal Oscillation (PDO). El Niño winters generally produce above average snowfall, evident in such years as 1957-1959, 1968-1970, and 1986-1987; La Niña years are associated with dry winters such as 1954-1957, 1973-1976, and 1998-2002. ENSO fluctuations are enhanced by the PDO, and the dry years of the early 1950's, the wet years of the 1980's, and the drought from 1995 though the present probably reflect the interactions of ENSO and the PDO. While these oscillations exert strong controls on winter and early spring precipitation, controls on summer monsoonal rainfall (only included as July and August precipitation here, the blue line in Figure 4a) in the southwestern U.S. are less well understood (Sheppard et al. 2002).

While patterns of precipitation are fairly straightforward, the progression of annual mean and summer minimum temperature we derived from the three climate stations (Fig. 4b) is somewhat less clear. Overall, the long-term fluctuations exhibited in both annual mean and summer minimum temperatures show a strong correspondence to documented patterns in temperature in this region (Bradley et al. 1982; Briffa et al. 1992; Sheppard et al. 2002). Briffa et al. (1992) used tree-ring densities to reconstruct summer temperatures in from 1600 to 1982 and reported very high temperatures in the southwestern United States and Rocky Mountains in 1935, a drop around 1940, a smaller rise in the 1950's and the early 1960's, and a decline ca. 1970; all of these trends show a clear correspondence to the mean trend in our region (Fig. 4a). A more recent summary of climatic trends in the southwestern U.S. (Sheppard et al. 2002) also documents an overall increase in temperatures since ca. 1975, which is also reflected in our data. However, in addition to these oscillations, our data exhibit a very unusual pattern over the period 1935-2003, which is the tendency for minimum temperatures to increase while annual means decrease, with the net effect being a convergence from an original difference of ca. 2° C. This strange pattern may result partly or wholly from changes in the locations of climate stations between 1952 and 1972. During this time all stations appear to have been moved to slightly higher elevations, Jemez Springs from 1861 to 1905 m in 1962, Los Alamos from 2230 to 2260 in 1956, and Wolf Canyon from 2439 to 2485 m in 1952, and then to 2507 m in 1975 (Appendix IV). Taken together these changes result in a mean increase of 46 m; given a lapse rate of 6.4° C/1000 m, the expected net decrease in temperature should be only 0.3° C, and we would expect a decrease in minimum temperatures as well as means. Given the location of Jemez Springs and Wolf Canyon in canyons, it may be that the increase in elevation moved the stations out of an inversion layer, with resultant increases in summer minimum temperatures. While we cannot rule out the possibility that these trends reflect actual changes in temperature across the Jemez Mountain region; we likewise cannot rule out the possibility that long-term decreases in annual means and increases in summer minimums are entirely due to changing climate station locations.

Timing of forest encroachment

While tree invasion of subalpine grasslands in the Valles Caldera appears to have been ongoing over the duration of our study (Fig. 3a), it is marked by a dramatic 30-year pulse beginning around 1940 and ending around 1970. A second, smaller episode of encroachment began around 1975 and ended around 1995. The major burst of tree invasion occurred at the same time as increases in yearly mean temperature and summer minimum temperature (Fig. 3b) and was coincident with the shift from sheep to cattle grazing. A small decline in the early 1950's may be linked with severe regional drought (Fig. 3a). The decline in tree establishment between 1970 and 1975 corresponds with decreases in minimum temperatures (Fig. 3b, c), but does not correspond with a change in precipitation (Fig. 3a) or any known changes in land use. Likewise, an increase in tree establishment beginning in 1975 also corresponds only with increasing temperature. Recent declines from ca. 1995 to the present, exhibit little correspondence to trends in temperature.

Most of the temporal variation in establishment is due to ponderosa pine, with relatively minor contributions by blue spruce and aspen (Fig. 4 and Table 4). These three species make up nearly all of the trees encountered during our field sampling, and we believe that this pattern is fairly representative of the pattern of tree invasion across the entire study area. However, above 3000 m ponderosa pine becomes less important, and forest encroachment was primarily by aspen, Douglas fir, and other conifer species. Given the bias in our field sampling toward lower elevation sites uncovered following the completion of the GIS analysis, it is likely that aspen and possibly Douglas fir make up a slightly greater proportion of tree invasion, and ponderosa slightly less, across the study site. Even given this bias, it is clear that ponderosa pine was by far the most invasive species across a very broad elevational range of Valles Caldera grasslands.

The ponderosa establishment we recorded may be attributable to only a few episodes of reproduction and subsequent treeline advance. Individual years showing peaks in ponderosa establishment occurred in 1946 (7 trees), 1957-1958 (11 and 7 trees), 1961-1965 (5 trees each year), 1980 (5) and 1987 (7). Blue spruce exhibits a more continuous pattern of encroachment, with no year showing > 3 trees. Because fewer aspen were sampled, and many of these could not be reasonably accurately dated, temporal patterns of aspen establishment are less clear. Most sampled aspen encroachment occurred between 1957 and 1969. While we also encountered some aspen establishment that we dated between 1990 and 1999, these shoots were all heavily browsed, and appeared unlikely to achieve canopy stature. We have too little information by which to assess patterns of establishment for the remainder of the tree species we encountered (Douglas fir, Engelmann spruce, southwestern white pine, and white fir).

A comparison (Fig. 5) of temporal patterns of tree invasion at low elevations (< 2700 m) where treelines border the grasslands of the major valley bottoms, and high elevations (> 2700 m), where grasslands occur in both smaller drainages and also on steep, south facing slopes, reveals both similarities and differences. The overall pattern is more suggestive of an association with temperature at lower elevations, and less so at higher elevations. Invasion is more episodic, due primarily to greater fluctuations in ponderosa pine establishment, at lower elevations and more continuous at higher elevations (Fig. 5). Across elevations, tree establishment is infrequent between 1925 and 1940, and occurs at a much higher rate between 1940 and 1970 followed by a decline from 1970 to 1975. Both low and high elevations show a secondary peak, though this occurred in the 1980's at lower elevations and in the 1990's at higher elevations. Both elevations also exhibit a recent decline in tree establishment, though this decline is much more pronounced at lower elevation sites (Fig. 5).

Discussion

The spatial pattern of tree invasion indicates that the constraints on tree establishment that originally maintained the grasslands of the Valles Caldera have been substantially lifted, and more so on steeper slopes at high elevation than at the inverted treelines of the valley bottoms. Overall, subalpine grasslands of the Valles Caldera have experienced widespread recent tree invasion (Figs. 2 and 3), but tree invasion has not been uniform, and has occurred predominantly at higher elevations, on steeper slopes, and proximal to the previous location of treeline ecotones (Table 1). While the grasslands of the major valleys (Figs. 1 and 2) were relatively resilient to tree invasion, smaller, steeper grasslands at higher elevation sites decreased substantially. Many small pockets of high-elevation grassland disappeared altogether between 1935 and 1996 (Figs. 2 and 3).

If higher elevation grasslands on upper mountain slopes were originally maintained by soil drought (e.g. Rydberg 1913; Daubenmire 1968) we would expect to see increased invasion on more mesic, north-facing slopes or on concave topography, and lower rates of invasion on dry, steep, south-facing slopes; in fact we found no effect of aspect on the probability of tree invasion, and a much greater extent of invasion on steeper slopes. Likewise, the temporal pattern of tree invasion at higher elevations (Fig. 5b) is not clearly associated with regional precipitation patterns, though declines in the early- to mid- 1950's, and since 1995 (occurring across the entire elevational gradient), may be associated with regional drought. Overall, the pattern of tree invasion on high-elevation, upper slope grasslands is much more consistent with the hypothesis that the maintenance of these grasslands was originally dependent on frequent fire, as suggested by Allen (1989), and we agree with his conclusions that the cessation of frequent fire in this region is the single most important cause of tree invasion of high elevation subalpine grasslands in this region.

Grasslands of the extensive valley bottoms of the Valles Caldera also experienced substantial recent tree invasion, though to a lesser extent than those at higher elevations. The maintenance of the inverted treelines that define these lower-elevation grasslands appears to have been less dependent on frequent fire, and much more dependent on thermal conditions in the cold-air drainage basin. Tree invasion along the margins of the valley bottoms, especially by ponderosa pine (Fig. 5a), increased in association with increasing temperatures (Fig. 4b), especially June-August mean regional daily minimum temperatures, which are strongly correlated to minimum temperatures in the valley bottoms of the Valles Caldera (unpublished data). This association is particularly strong between ca. 1940 and 1995, suggesting that tree seedling establishment at these treelines is in large part dependent on warmer summer temperatures. This interpretation is supported by previous experimental research (Chapter III) on ponderosa pine establishment at these ecotones, as well as earlier research, which has demonstrated the deleterious effects of growing season frosts (Pearson 1923; Schubert 1970, 1974) on seedling establishment by ponderosa pine. However, low temperatures may also limit ponderosa pine reproduction by imposing constraints on fruiting and cone development (Macguire 1956; Schubert 1974).

The probability of tree invasion showed a strong negative relationship to distance from 1935 forest edge. Dispersal limitations may explain why invasion is less likely farther from treeline (Malanson 1997); however, numerous other positive feedbacks may enhance seedling establishment near forest canopies, including reduced wind speeds and associated mechanical stresses and evaporation (Billings 1969, Alftine and Malanson 2004), increased soil moisture, temperature, and nitrogen availability (Belsky et al. 1989; Li and Wilson 1998; Siemann and

Rogers 2003), and reduced grass competition (Wilson and Agnew 1992; Li and Wilson 1998; Siemann and Rogers 2003). Another interpretation of the increased probability of tree invasion close to the 1935 treeline in our logistic regression model is that it represents spatial autocorrelation in unsampled environmental factors favorable to tree establishment. Lastly, we cannot rule out the possibility that some of the negative relationship between invasion and distance to forest edge may be an artifact induced by orthorectification error. Given the mean 10-m standard deviation of fit between the orthorectified 1935 and 1996 photos, we might expect a slightly inflated estimate of the amount of encroachment that occurred within ten meters of the former treeline. However, orthorectification error could just as likely result in artifactual treeline retreat as advance. The mean distance from treeline of sampled points where invasion occurred was 53.26; even plus or minus 10 meters, tree invasion unarguably occurred proximal to the previous forest boundary.

The two interaction terms retained in our logistic regression model (distance to treeline x slope and elevation x slope) also indicate compounding effects of elevation, slope, and the distance to treeline. The positive effect of elevation on invasion was enhanced on steep slopes, and the positive effect of slope inclination on invasion was enhanced at higher elevations. This finding may also reflect a shift in the relative importance of constraints on tree seedling establishment due to fire vs. cold air drainage across the elevational gradient from the depths of the basin to higher elevation slopes. The interaction term between distance to treeline and slope indicates that the negative effect of distance from treeline (alternatively, the positive effect of nearby trees) in facilitating tree seedling establishment is weaker on steeper slopes. While the decreased effect of distance on steeper slopes may simply reflect increased seed dispersal distance by gravity, it may also point at the greater relative importance of other positive feedbacks at the temperature-dependent forest margins along drainages and valley bottoms, such as the amelioration of thermal conditions and high insolation, with commensurate reductions in seedling photodamage resulting from re-radiative heat loss at night and high insolation by day (Jordan and Smith 1995; Germino et al. 2002; Davidson et al. 2004; Johnson et al. 2004).

Taken as a whole, the temporal pattern of tree invasion (Figures 4 and 5) suggests that both changing disturbance regimes and climatic factors were linked to tree establishment. Though frequent fires ceased burning in the late 19th century across the study area, tree invasion occurred at only minor levels prior to 1940-1945 (Figure 4), coincident with the shift from sheep to cattle grazing. Though we cannot exclude earlier episodes of tree invasion between ca. 1890 and 1945, our data should reflect patterns of invasion going back to at least 1925. Two other lines of evidence suggest that major earlier invasion did not occur. First, Allen (1984; 1989), working along the eastern rim of the Valles Caldera, also found only sparse tree invasion occurred prior to the 1930's, which coincided with declines in sheep grazing across the Santa Fe National Forest. Secondly, three historic photos taken by members of Vernon Bailey's 1907 expedition through the northern valleys of the Valles Caldera, and another photo taken in 1935 farther south in the Valle Grande, show a clear absence of tree seedlings and saplings near treeline ecotones. Repeat photos from 1997 show not only trees in formerly grassy vegetation, indicative that invasion had occurred, but also numerous seedlings and saplings, suggesting ongoing invasion. The visible presence of young trees in these photos suggests that they should have been visible if they were present when the historic photos were taken, and that their absence indicates a lack of substantial encroachment up to 1907 in the northern valles, and 1935 in the Valle Grande Location.

Following release from sheep grazing, tree invasion occurred at different tempos at low- and high-elevation sites, as discussed above, showing more continuous establishment at highelevations, and more episodic establishment in the lower valley bottoms, which appeared to track summer minimum temperatures until the 1990's (Figures 4 and 5). Additionally, both high- and low- elevation sites show declines in total tree seedling establishment in the early 1950's and also the period from 1995 to present, which correspond with severe regional droughts.

We cannot rule out possible effects of fluctuations in cattle grazing on tree invasion over the time series, because we have no data to bear on this point, and also the effects of rapidly increasing elk populations in the Jemez since the second reintroduction in 1961. Elk populations probably peaked in the study area in the mid- to late- 1990's at 6000-8000, and have since declined to ca. 4000 (New Mexico Division of Game and Fish). Krantz (2001) in the found high levels of browse to woody plants, especially concentrated in the grasslands and forest margins VCNP. Nearly all of the younger trees sampled in this study showed evidence of browsing, and many saplings had been damaged or killed antler rubs (Krantz 2001). In particular, aspen reproduction and growth has been shown to be severely limited by high elk populations in numerous other studies in the western U.S. (e.g. Hessl et al. 2002; Kaye et al. 2003) and we suspect that elk in the Valles Caldera are having similar effects. Aspen invasion has been restricted since the 1950's and 60's, and the recent dates recorded in Figures 4 and 5 were all sucker shoots that exhibited strong evidence of elk browsing. These shoots are unlikely to achieve substantially greater height growth. While such high levels of elk browsing may be detrimental to aspen populations in the long term, the effect appears to be positive in slowing encroachment by aspens, and possibly other species, into subalpine grasslands. These results parallel findings of Cairns and Moen (2004) who found that treelines in Sweden had advanced only at sites where reindeer herbivory was low, and showed little change at sites where reindeer herbivory was high.

Fluctuations in ponderosa pine establishment account for much of the temporal trend in tree invasion, especially the recent drop off, which is of an even greater magnitude than the decline of the 1950's. Recent experimental research on the germination and survival of ponderosa pine (Chapter II) in 2002 and 2003 found poor germination and no survival of germinants across the entire VCNP. Ponderosa pine cone crops have also been exceptionally low across the almost the entire southwestern region during the period from the late 1990's through present (D. Swift, Dean Swift Seed Company), suggesting region-wide constraints on seed production in addition to subsequent limitations to germination and establishment. Interestingly, ponderosa pine invasion in the Valles Caldera peaked immediately following the 1950's drought, when warm temperatures coincided with the return of wet conditions across the region. In fact, the peak episode of ponderosa establishment in our study (1957-1958) was also noted by Cooper (1960) to be an banner year for ponderosa establishment in the White Mountains of Arizona, who recorded that "in September, 1957, as many as 30 to 40 seedlings per square foot could be counted in parts of the White Mountains" (Cooper 1960:133). Another year of high establishment in the Valles Caldera was 1980, which was also noted to be a year of abundant seed germination nearby in Bandelier National Monument, by Potter et al. (1982), though these authors suggested that "the possibility of the hundreds of 1980 seedlings surviving the winter of 1980-1981 is small" (Potter et al. 1982: 23) due to warm and dry conditions.

In summary, we found extensive recent tree invasion of subalpine grasslands of the Valles Caldera, which exhibited strong spatial and temporal patterns. Smaller, high elevation

meadows on steeper slopes are particularly susceptible to invasion, and are rapidly disappearing from the landscape. While the larger grasslands of the valley bottoms may be buffered against invasion by their size and by thermal conditions that inhibit seedling establishment in the valley bottoms, the greatest areal losses of grasslands have occurred along the margins of these valley bottom grasslands. Further research that separately examines the effects of cattle- and elk-grazing and fire, on forest-grassland dynamics should be a priority in the VCNP, in addition to long-term monitoring of treeline fluctuations in response to climatic variation. We also encourage the utilization of prescribed fire for grassland restoration efforts, especially at higher elevations and on south-facing slopes, where the maintenance of subalpine grasslands was most dependent on fire, and where most of the greatest losses in grasslands have occurred since 1935.

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Figures and Tables

Figure 1. Location of the Valles Caldera study area in the Jemez Mountains of northern New Mexico. The area of our GIS analysis incorporated the 40,700 ha. square, which formerly bounded the Baca Location No. 1. The boundary of the newly-designated Valles Caldera National Preserve (VCNP) is shown by the red line, and excludes portions of the northeast and southeast corners of the Baca Location.

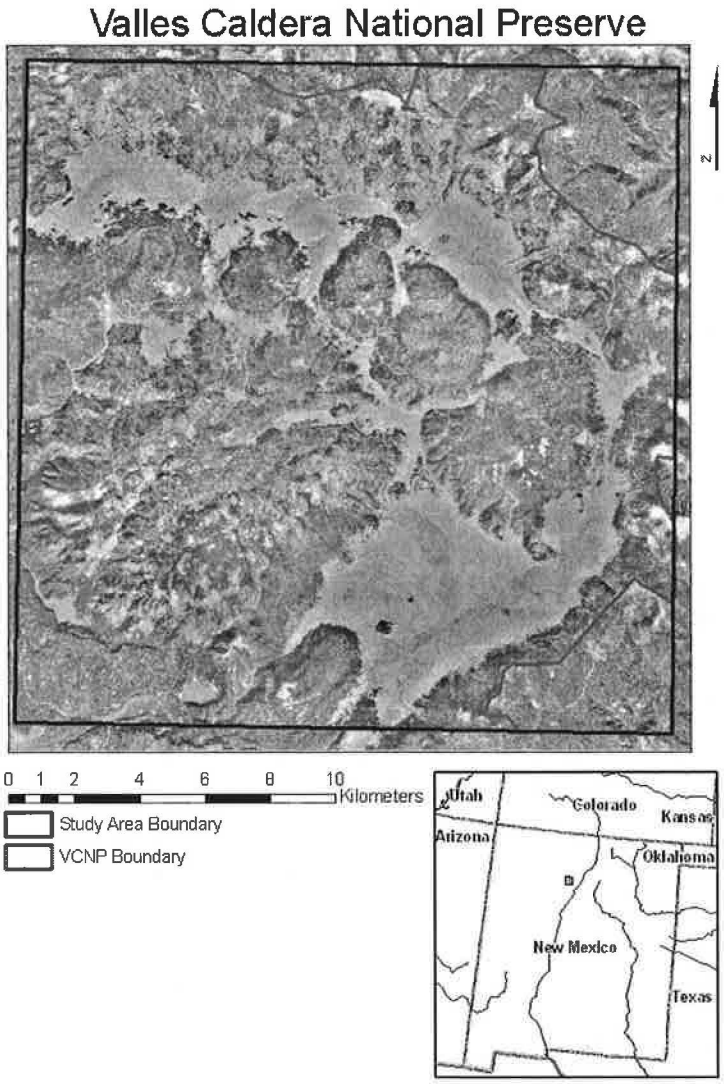


Figure 2. The area occupied by grasslands in 1996 (yellow) and the area that has experienced tree invasion since 1935 (red).

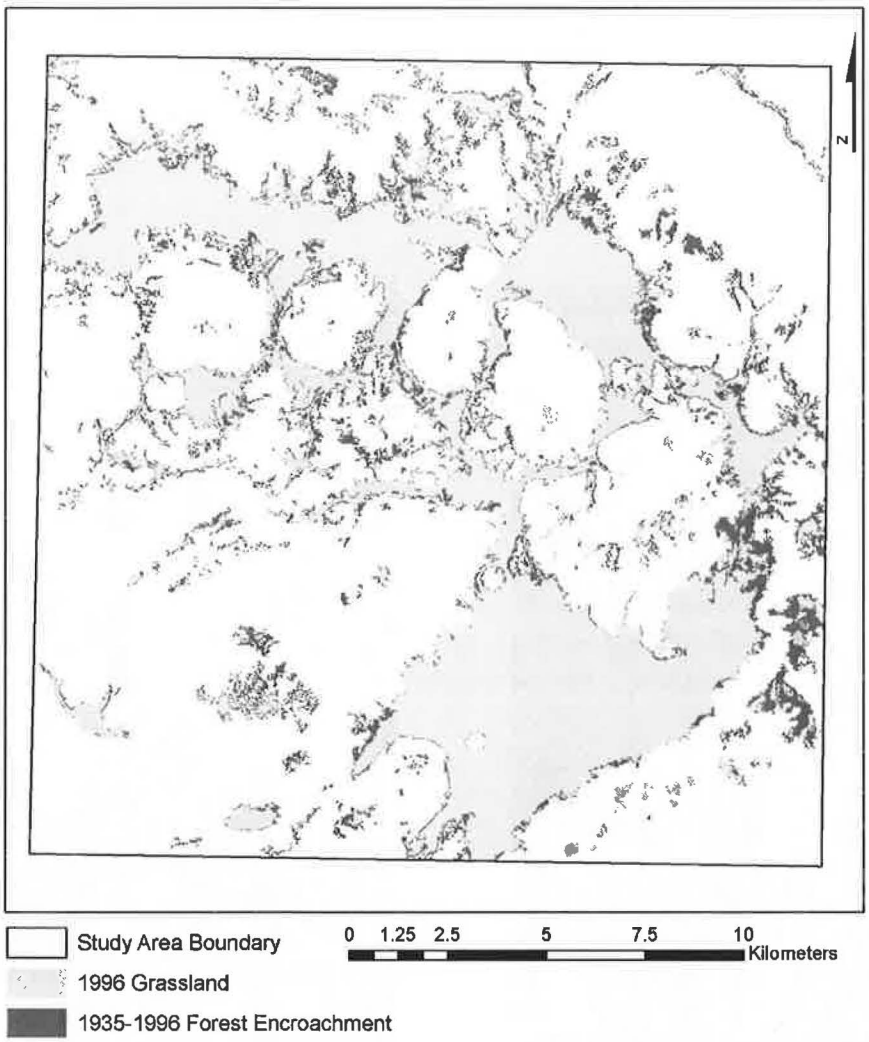
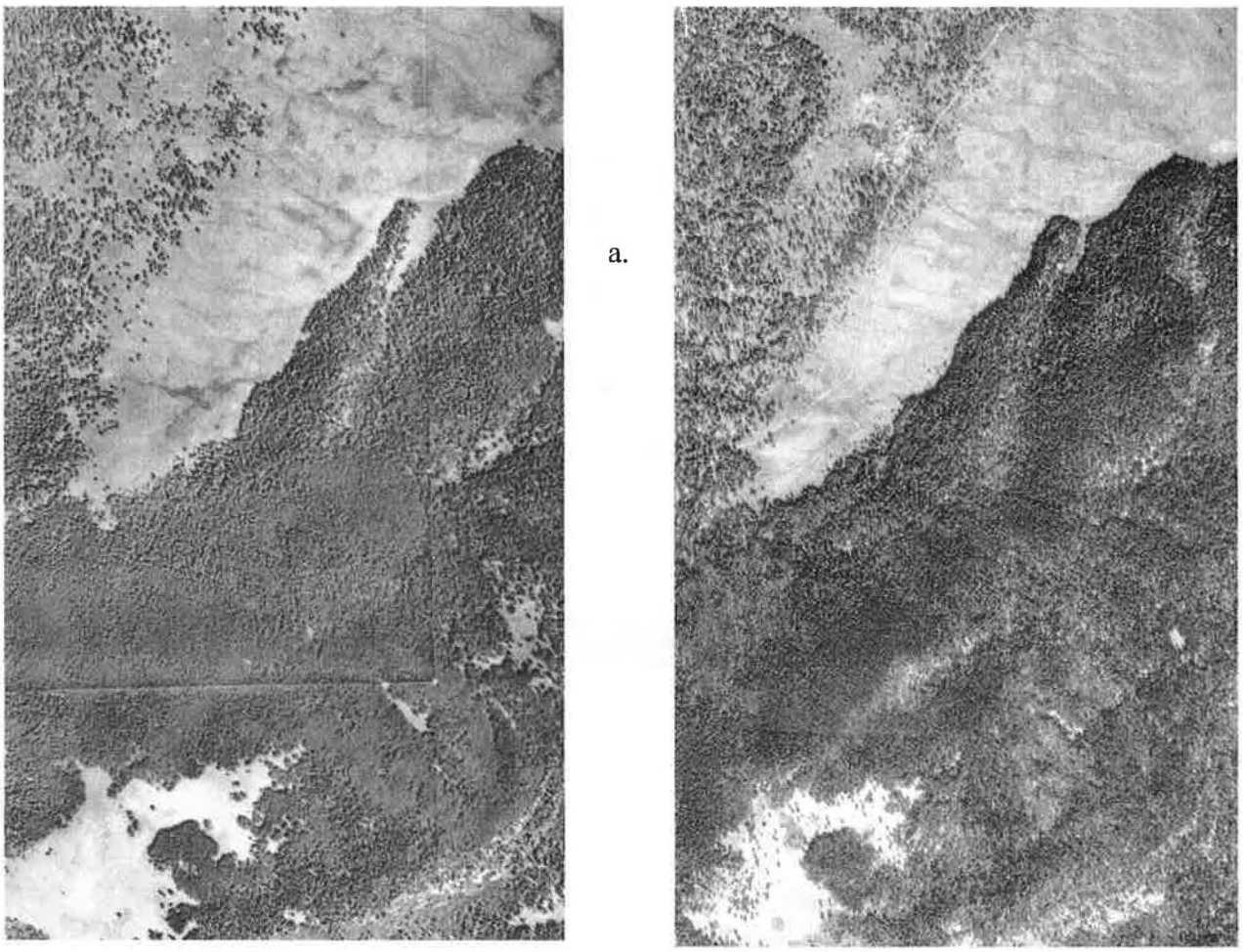


Figure 3. Aerial photo imagery from 1935 (a) and 1996 (b) showing a variable pattern of tree invasion of grasslands in the Valle Grande (top half of photos) and a higher elevation grassy bald on top of South Mountain (bottom of photos). In these photos ponderosa pine encroachment along the western margin of the Valle Grande, and ponderosa and aspen expansion on South Mountain are quite pronounced. However, blue spruce encroachment along the edge of South Mountain (upper right of photos) has been relatively minor by comparison. Several small meadows on South Mountain (right, center) have been completely filled in.



a.

b.

Figure 4. Temporal patterns of regional precipitation (a) and temperature (b), and tree establishment in the grasslands of the Valles Caldera (c), between 1925 and 2003. Tree establishment, especially ponderosa pine, appears to track summer minimum temperatures between 1935 and 1990, though a drop in establishment between 1950 and 1954 is probably associated with severe regional drought. The transition from sheep to cattle grazing occurred sometime in the 1940's to early 50's; the lack of substantial invasion prior to the 1940's may be related to extremely high levels of sheep grazing. The decline in establishment beginning ca. 1995 may be associated with decreased precipitation, elk, or other factors.

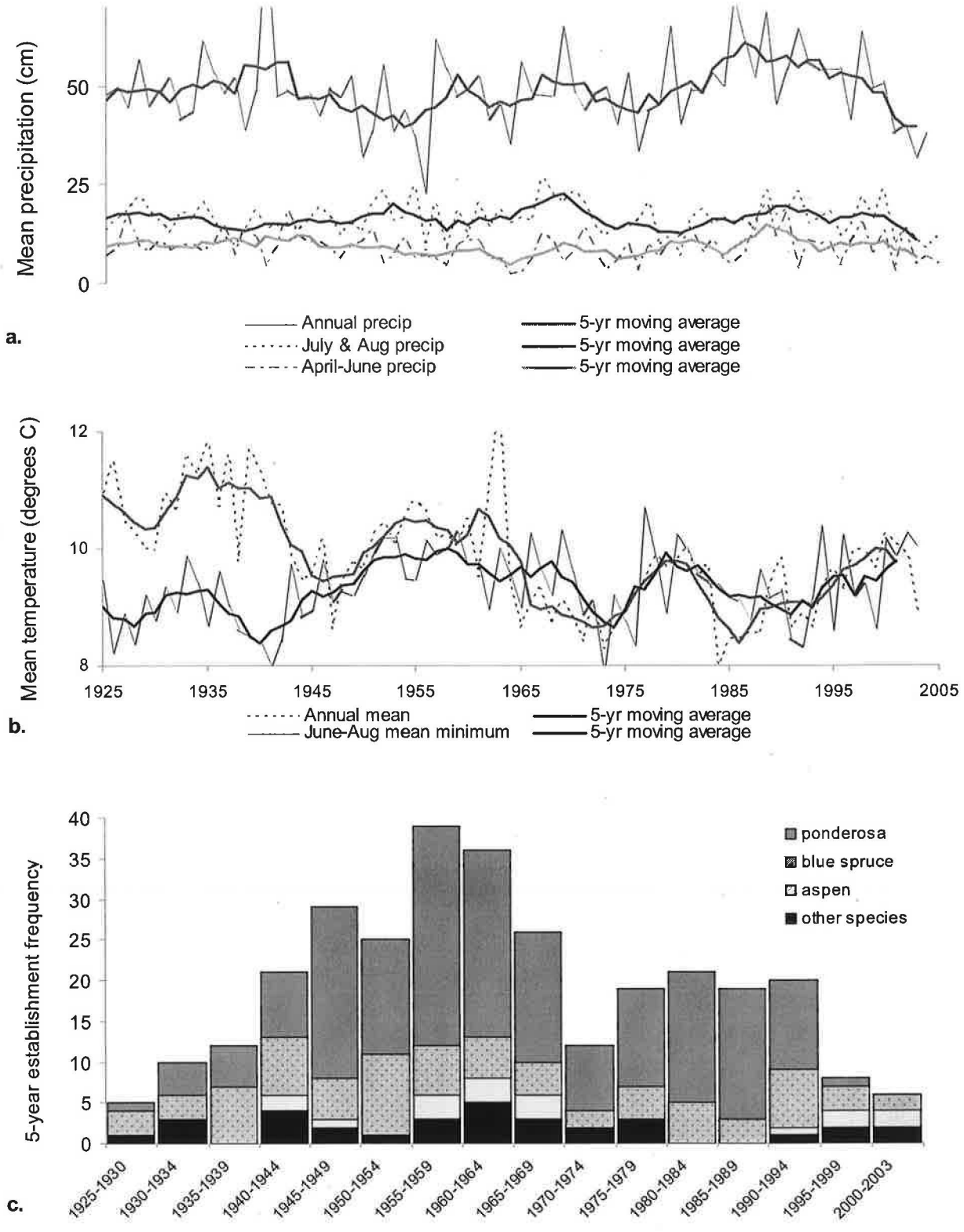


Figure 5. Establishment frequency below 2700 m (a) and above 2700 m (b).

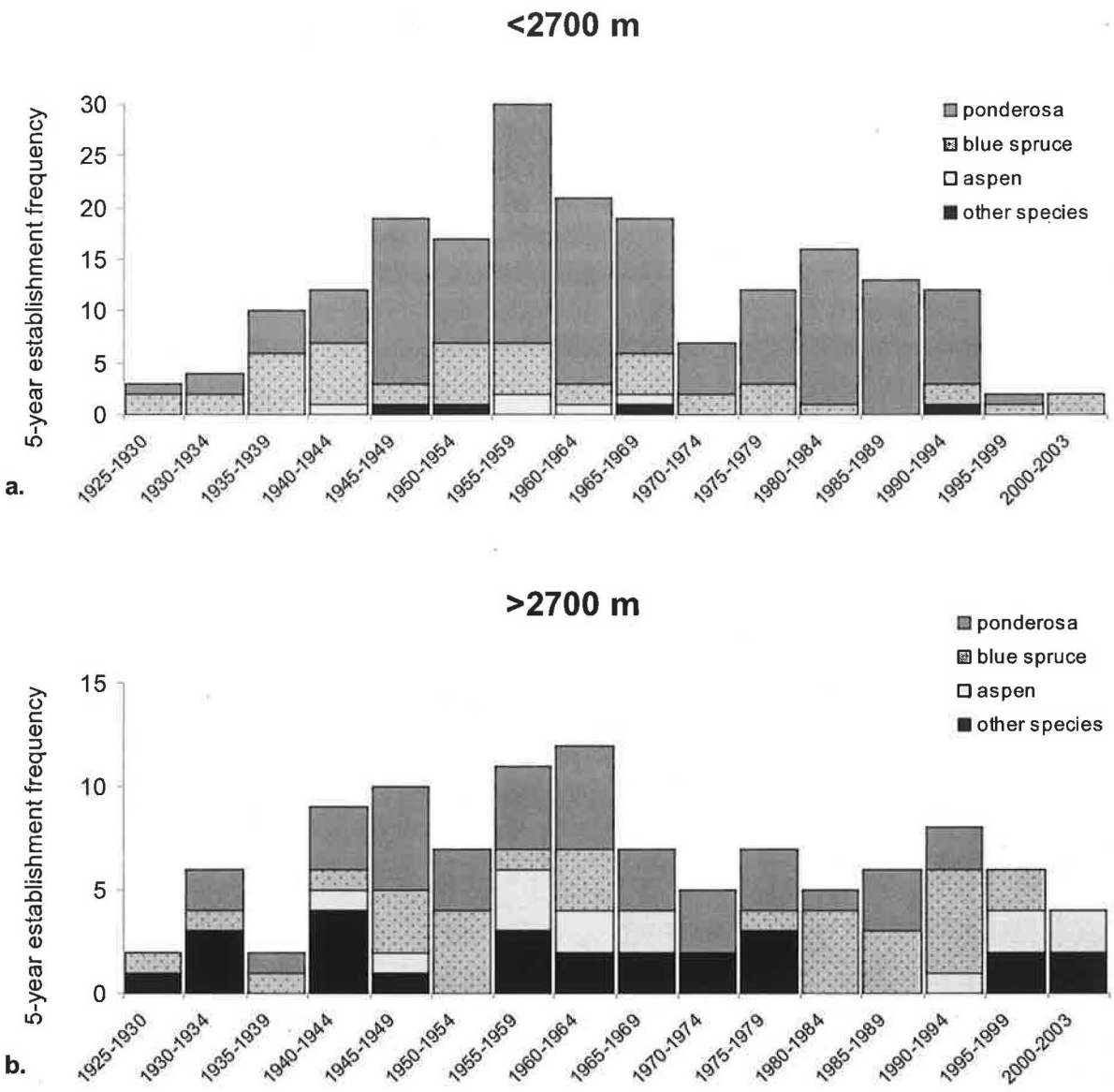

<2700 m
5-year establishment frequency
30
25
20
15
10
5
0
ponderosa
blue spruce
aspen
other species
1925-1930
1930-1934
1935-1939
1940-1944
1945-1949
1950-1954
1955-1959
1960-1964
1965-1969
1970-1974
1975-1979
1980-1984
1985-1989
1990-1994
1995-1999
2000-2003
a.
>2700 m
5-year establishment frequency
15
10
5
0
ponderosa
blue spruce
aspen
other species
1925-1930
1930-1934
1935-1939
1940-1944
1945-1949
1950-1954
1955-1959
1960-1964
1965-1969
1970-1974
1975-1979
1980-1984
1985-1989
1990-1994
1995-1999
2000-2003
b.

Table 1. Partial logistic regression coefficients for spatial predictors of forest encroachment in the Valles Caldera between 1935 and 1996.

Factor	Value	*P*
distance from treeline [meters from 1935 ecotone]	-0.024	<<0.0001
elevation	0.009	<<0.0001
slope [ln (° slope)]	7.751	<<0.0001
distance to treeline *x* slope	0.006	<<0.0001
elevation *x* slope	-0.003	<<0.0001

residual deviance 1853.89 null deviance 3061.10 2809 d.f.

Table 2. Areal loss of grasslands in the 40,700 ha. study area in the Valles Caldera, by elevation.

Elevation	Area in 1935 (ha.)	Area in 1996 (ha.)	Areal change (ha.)	% change
> 3200 m	177.75	70.83	-106.92	-60.15
3000-3199 m	582.12	199.17	-382.95	-65.79
2800-2999 m	537.39	216.09	-321.30	-59.79
2600-2799 m	8918.28	7835.40	-1082.88	-12.14
2400-2599 m	1531.08	1316.70	-214.38	-14.00
Total all elevations	11746.62	9638.19	-2108.43	-17.95

Table 3. Areal loss of grasslands in the Valles Caldera by slope inclination.

Slope	Area in 1935 (ha.)	Area in 1996 (ha.)	Areal change (ha.)	% change
> 25°	8.46	5.58	-2.88	-34.04
20-25°	103.14	61.02	-42.12	-40.84
15-20°	469.26	164.7	-304.56	-64.90
10-15°	691.83	386.55	-305.28	-44.12
5-10°	8172.00	6787.62	-1384.38	-16.94
0-5°	2301.93	2232.72	-69.21	-3.01
Total all slopes	11746.62	9638.19	-2108.43	-17.95

Table 4. The proportion of grasslands by elevation in the two photo coverages, the proportion of total forest encroachment (out of 2108 ha. that were invaded between 1935 and 1996), and the proportion of our 50 samples that fell within each elevational band. While our sampling was roughly proportional to the total area of grasslands in each elevational band, we over-sampled encroachment at lower elevations, and under-sampled encroachment above 2800 m.

Elevation	Proportion of total forest	Proportion of grasslands in	Proportion of grasslands in	Number of sites

	encroachment (%)	1935 (%)	1996 (%)	sampled
> 3200 m	5.07	1.51	0.73	0
3000-3199 m	18.16	4.96	2.07	2
2800-2999 m	15.24	4.57	2.24	5
2600-2799 m	51.36	75.92	81.30	33
2400-2599 m	10.17	13.03	13.03	10

Appendices

Appendix I. UTM locations (NAD 83, Zone 13 N), elevations, and dominant tree species at 50 sites sampled in the VCNP for tree establishment dates. Mixed conifer assemblages were dominated by a combination of Douglas fir, white fir, and often ponderosa, Engelmann spruce, or southwestern white pine.

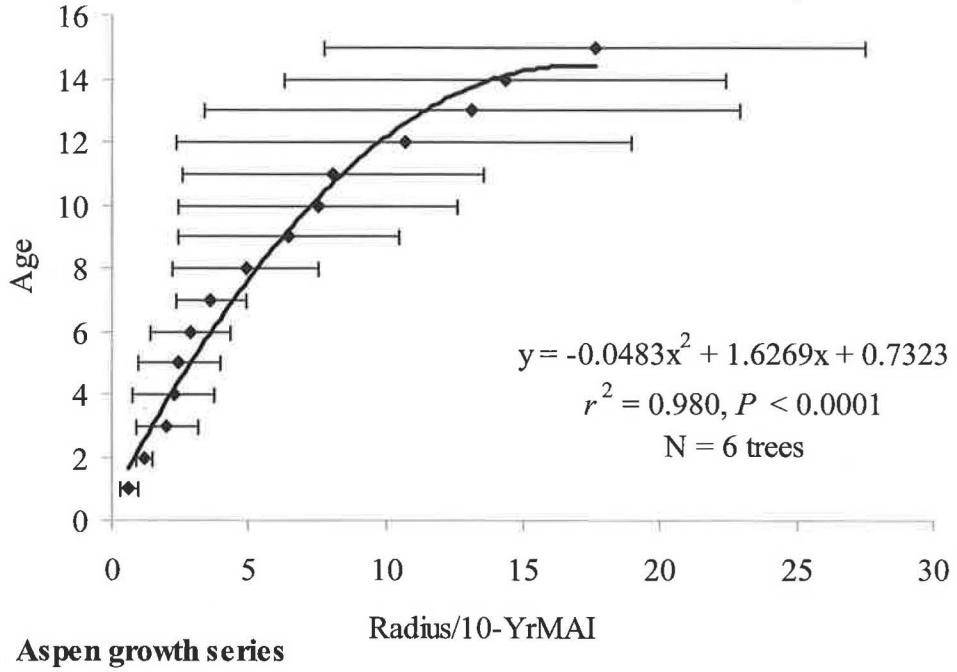
Site	UTM EW	UTM NS	Elev. (m)	dominant tree species
1	353946	3984585	2726	mixed conifer
2	354021	3981006	2562	ponderosa
3	354120	3980788	2546	ponderosa
4	354123	3984604	2800	blue spruce
5	354766	3981100	2573	ponderosa
6	355594	3983269	2611	ponderosa
7	355615	3983193	2597	ponderosa
8	355875	3980469	2584	blue spruce
9	356650	3981888	2587	blue spruce
10	357810	3982383	2612	mixed conifer
11	358513	3977881	2702	ponderosa
12	359297	3966974	2651	ponderosa
13	359500	3967118	2635	ponderosa
14	359524	3966973	2591	ponderosa
15	359615	3967022	2671	ponderosa
16	359616	3966737	2640	ponderosa
17	359676	3966618	2685	ponderosa
18	360255	3977817	2678	blue spruce
19	360875	3977534	2677	ponderosa
20	361126	3967774	2845	ponderosa
21	361691	3982213	2646	ponderosa
22	361720	3982141	2594	ponderosa
23	361775	3966684	2976	mixed conifer
24	361883	3966647	2959	aspen
25	362301	3968676	2669	ponderosa
26	362396	3969193	2668	ponderosa
27	363001	3981415	2595	ponderosa
28	363866	3970580	2643	aspen
29	364104	3975034	2678	blue spruce
30	364704	3975397	2673	ponderosa
31	364721	3981130	2598	blue spruce
32	365456	3972746	2640	ponderosa
33	365489	3972711	2636	ponderosa
34	365741	3973521	2638	blue spruce
35	366752	3981666	2665	ponderosa
36	367271	3975822	2701	ponderosa
37	367280	3975735	2692	ponderosa
38	367633	3981882	2728	ponderosa
39	367759	3967661	2686	aspen
40	367896	3971840	2640	ponderosa
41	367955	3971901	2677	ponderosa
42	368917	3978583	2672	ponderosa
43	369025	3973704	3011	aspen

44	369138	3973714	3011	mixed conifer
45	371145	3972383	2631	ponderosa
46	371391	3976520	2715	blue spruce
47	371550	3974011	2694	ponderosa
48	371664	3976772	2801	blue spruce
49	372211	3976596	2736	ponderosa
50	372213	3976688	2749	ponderosa

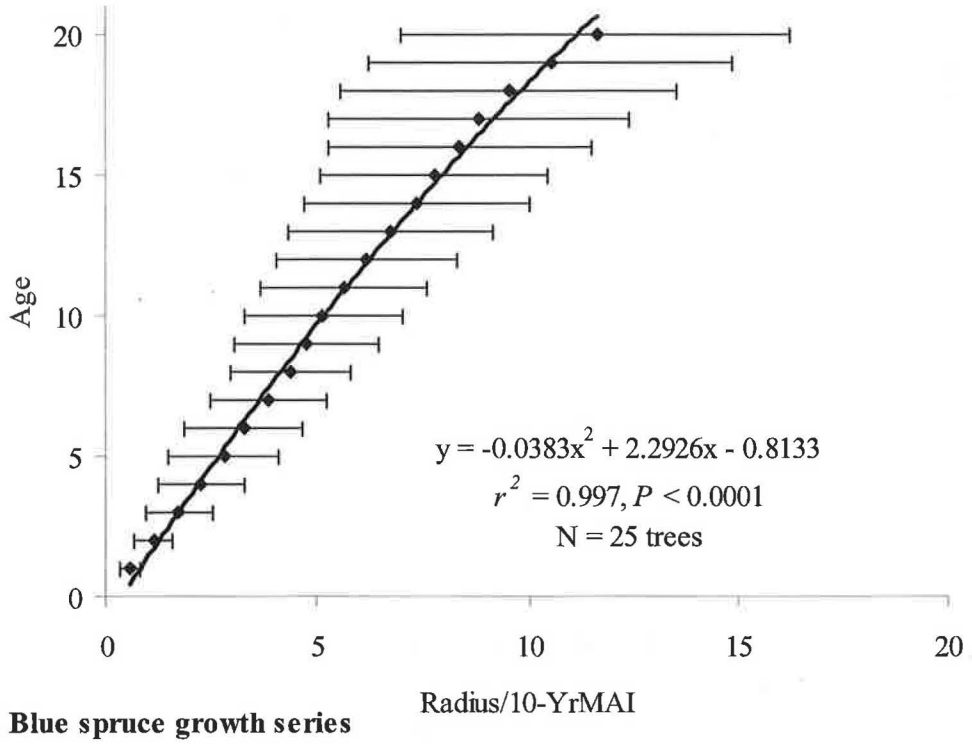
Appendix II. Total number of individuals by species in all stands sampled, and the number of increment cores or basal disks used in our analyses. Eighteen of the thirty five cores collected from aspens could not be dated, and only 17 could be used in our analyses.

Species	Total stems encountered in field sampling		Increment cores and disks analyzed	
	Number	%	Number	%
White fir	26	1.8	5	1.7
Engelmann spruce	4	0.3	1	0.3
Colorado blue spruce	371	26.0	79	26.4
Ponderosa pine	805	56.3	186	62.2
Southwestern white pine	11	0.8	1	0.3
Trembling aspen	160	11.2	17	5.7
Douglas fir	52	3.6	10	3.3

Appendix III. Modeled relationships between tree age and the ratio of radius/mean increment growth for the following ten years [abbreviated as 10-yr MAI]) derived for (a) aspen, (b) blue spruce, (c) ponderosa pine. The equation derived from each model was used to estimate the ages of cores for each species that did not contain the pith, but where the distance from the last measured ring to the pith could be estimated. The resulting estimates have the advantage of incorporating both variation in the growth rates of individual trees as well as the increasing annular increment growth rates exhibited over the first 15 - 20 years of tree seedling growth.

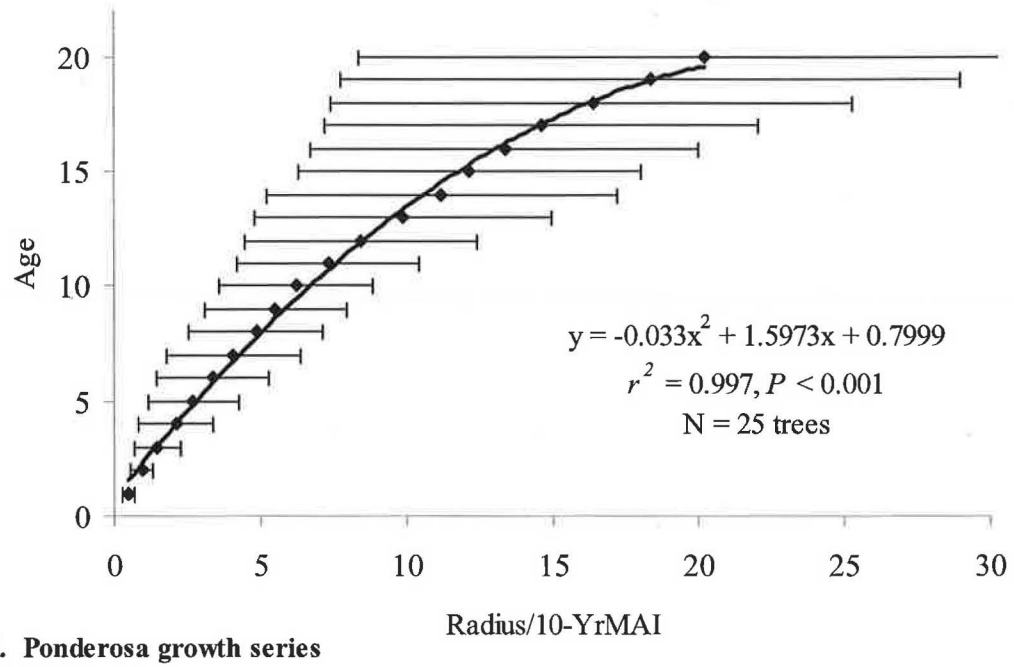


a. Aspen growth series



b. Blue spruce growth series

-+0



d. Ponderosa growth series

Appendix IV. Climate stations used in this study, and locations from the beginning of record-keeping through the present. Selsor Ranch is the former name for the station located in Wolf Canyon.

Station	from	to	Latitude	Longitude	elevation	Station ID
Jemez Springs	14 October 2004	Present	35°47'N	106°41'W	1908.7m	294369
	25 May 2000	13 October 2004	35°47'N	106°41'W	1908.7m	294369
	20 August 1984	25 May 2000	35°46'N	106°41'W	1909.0m	294369
	01 July 1975	20 August 1984	35°46'N	106°41'W	1900.1m	294369
	01 May 1962	01 July 1975	35°47'N	106°41'W	1905.9m	294369
	01 July 1946	01 May 1962	35°47'N	106°41'W	1861.1m	294369
	01 May 1911	31 June 1946	unknown	unknown	unknown	294369
Los Alamos	12 May 2004	Present	35°52'N	106°19'W	2262.8m	295084
	07 March 2002	11 May 2004	35°52'N	106°19'W	2262.8m	295084
	01 January 1990	07 March 2002	35°52'N	106°19'W	2262.8m	295084
	08 November 1978	01 January 1990	35°52'N	106°19'W	2242.4m	295084
	01 January 1976	08 November 1978	35°52'N	106°19'W	2244.9m	295084
	01 August 1956	31 January 1976	35°52'N	106°19'W	2260.1m	295084
	01 July 1946	01 August 1956	35°53'N	106°18'W	2233.0m	295084
	01 November 1910	30 June 1946	unknown	unknown	unknown	295084
Wolf Canyon	09 September 1996	Present	35°57'N	106°45'W	2505.5m	299820
	25 July 1990	09 September1996	35°57'N	106°45'W	2505.5m	299820
	01 Dec 1975	25 July 1990	35°57'N	106°45'W	2506.1m	299820
	01 October 1975	01 December 1975	35°58'N	106°46'W	2507.0m	299820
	01 July 1966	01 October 1975	35°58'N	106°46'W	2482.9m	299820
	28 July 1952	01 July 1966	35°58'N	106°46'W	2485.9m	299820
Selsor Ranch	01 July 1946	28 July 1952	35°58'N	106°47'W	2439.9m	298192
	01 August 1912	31 June 1945	unknown	unknown	unknown	298192