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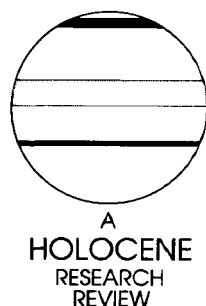
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Changes in sub-alpine tree distribution in western North America: a review of climatic and other causal factors

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Abstract: Changes in the distribution of sub-alpine tree species in western North America have been attributed to climatic change and other environmental stresses. These changes include tree-line fluctuations throughout the Holocene and recent invasion of sub-alpine meadows by forest. Most palaeoecological studies suggest that the tree-line was higher during a period of warmer climate approximately 9000 to 5000 BP and lower during the last 5000 years, with short periods of local tree-line advance. Recent advances in sub-alpine tree distribution can be compared with weather records, allowing an examination of relationships between tree advance and climate at a finer resolution. In general, recent sub-alpine forest advances in western North America, based on studies representing three climatic zones (maritime, Mediterranean and continental), have been associated with climatic periods favouring tree germination and growth, although factors such as fire and grazing by domestic livestock have had an impact in some areas. Limitations to tree establishment (e.g., winter snow accumulation, summer drought) vary in relative importance within each climate zone, as do predicted consequences of anthropogenic climatic change. Recent increases in establishment of sub-alpine trees may continue if climatic change alleviates the limitations to tree establishment important in each climatic zone. However, factors such as topography and disturbance may modify tree establishment on a local scale.

Key words: climatic change, meadow invasion, sub-alpine forest, tree establishment, tree-line, Holocene, North America.

Introduction

Climate change, sub-alpine forests and ecotones

Most general circulation models predict an increase in mean annual temperature of 1–5°C during the next century as the result of increased levels of atmospheric CO₂ and other greenhouse gases (Schneider, 1989). Climatological evidence indicates that mean annual air temperature at the earth's surface has already increased approximately 0.6°C since AD 1880 (Jones *et al.*, 1986; Hansen and Lebedeff, 1988). Even small changes in temperature, such as the 1–1.5°C cooler period of the 'Little Ice Age' (c. AD 1650 to 1850; Porter, 1981), can cause significant changes in vegetation (Lamb, 1982; Brubaker, 1988; Sprugel, 1991). Future precipitation patterns are also predicted to change, but existing models predict changes in only magnitude and/or seasonal pattern (e.g., wetter winters with drier summers – Kellogg and Zhao, 1988; Silver and DeFries, 1990). Even small changes in

global temperature or precipitation patterns are likely to alter conditions affecting earth's ecosystems (Houghton and Woodwell, 1989), resulting in changes in vegetation patterns.

Linking the response of vegetation to future changes in climate is a major challenge facing ecologists. Detecting initial effects of environmental change on vegetation may be difficult due to the high variability within most biological systems. One promising approach is to focus on ecotones – transitions between adjacent communities. Ecotones resulting from environmental gradients (as opposed to disturbances such as fire) may be particularly responsive to climatic changes because organisms are already at some limit to their existence. Ecotones at the sub-alpine/alpine boundary may be particularly relevant to studies of climatic change because the physiognomy of the dominant vegetation changes from trees to shrubs and herbs (Peterson, 1991; Rochefort and Peterson, 1991; Woodward *et al.*, 1991). Tree distribution at high elevation is at least partially limited by temperature and

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snowpack (Wardle, 1974; Tranquillini, 1979; Stevens and Fox, 1991), factors certain to change if temperatures rise in the future.

Palaeoecological studies indicate that altitudinal tree-line has fluctuated in response to climate throughout the Holocene (Pears, 1968; Markgraf and Scott, 1981; Luckman and Kearney, 1986; COHMAP, 1988), and that expanding ranges of tree species are often associated with periods of warmer climate (LaMarche, 1973; Kearney and Luckman, 1983; Grace, 1989; Kullman, 1991). Recent studies provide the opportunity to discover local factors, in addition to climate, responsible for enhancing or preventing tree establishment. Studies in western North America suggest recent expansions in the spatial distribution of sub-alpine tree species at many locations.

Terminology and scope

Many different terms are used to describe ecotonal relationships of high-altitude tree species (Love, 1970; Douglas, 1972; Wardle, 1974; Tranquillini, 1979). We use the following terminology in this discussion. The *sub-alpine park land* is the highest-elevation belt that contains tree species, consisting of a mosaic of individual trees, tree clumps, and meadows that extend from closed forest to alpine (treeless) vegetation (Figure 1 – Henderson, 1974; Franklin and Dyrness, 1987). The lower boundary of the sub-alpine park land is indicated by the upper limit of closed contiguous forest or *forest line*. *Tree-line* indicates the highest elevation at which erect trees are found within the sub-alpine park land. *Tree-limit* indicates the highest elevation at which any trees are found, including prostrate or krummholz growth forms. This paper focuses on altitudinal species distribution, although 'tree-line' and 'tree-limit' can also be used to describe latitudinal, edaphic and maritime tree species limits (Hustich, 1983; Payette, 1983).

Information is available on worldwide tree-line dynamics

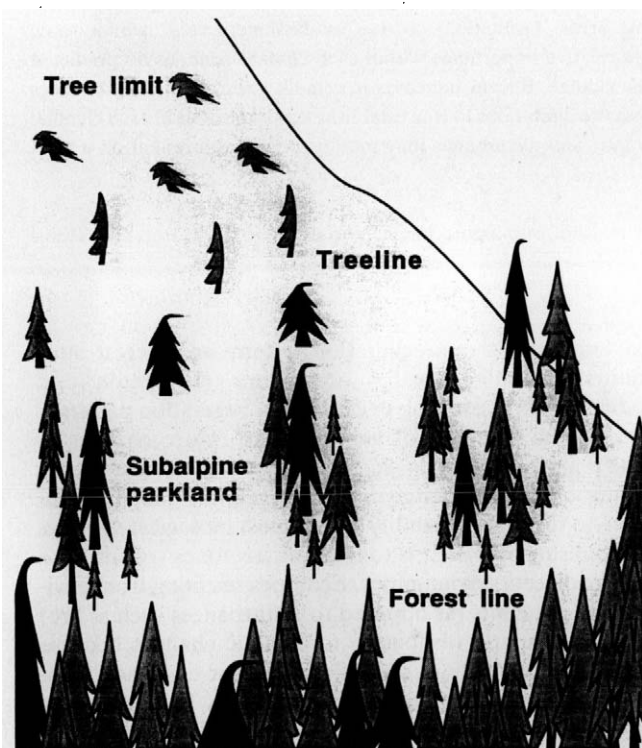


Figure 1 Diagrammatic representation of sub-alpine conifer distribution. A mosaic of trees and meadows dominates the ecotone between the continuous forest below and the treeless alpine above.

and on factors limiting sub-alpine forest distribution (Daubenmire, 1954; Zimina, 1973; Wardle, 1977; Gorchakovskiy and Shiyatov, 1978; Payette and Gagnon, 1979; Tranquillini, 1979; Kullman, 1986). We focus on western North America because: (1) many data exist on recent changes in sub-alpine forest distribution; and (2) many sub-alpine mountain locations in this area lie within protected areas relatively free of human influence (Billings, 1969; Holtmeier, 1989). The impacts of woodcutting, grazing and other activities more common in eastern North America and Europe make it difficult to interpret the influence of climate and other 'natural' environmental forces on sub-alpine vegetation (Holtmeier, 1973; Ives and Hansen-Bristow, 1983; Helms, 1987).

Climatic regimes in western North America are highly varied, and ecosystems range from temperate rainforest to desert. However, climatic regimes in mountainous areas can be classified by their dominant weather patterns and geographic location into: maritime, continental and Mediterranean zones (Schroeder and Buck, 1970; Trewartha, 1980; Critchfield, 1983). Figure 2 indicates the location of the climatic zones and principal mountain ranges discussed in this paper. Alaska and Mexico are not included because we have found no published reports of recent altitudinal changes in the distribution of sub-alpine forests in these areas (Griggs, 1937; Beaman, 1962; Lauer, 1978). The climatic zones are not intended to correspond exactly with macroscale or synoptic climatic classifications.

Characteristics of the three climatic regimes differ substantially. *Maritime climate* – predominant in the northwestern portion of the continental United States and southwestern Canada – is characterized by high coastal rainfall, a long winter period of rain and snow, and extensive cloud cover. Winter temperatures are cool, summer temperatures are mild, and summer precipitation is low. *Continental climate* prevails in the western interiors of the continental United States and Canada. Much of the winter precipitation is snow, and summer precipitation occurs as thunderstorms in the central and southern part of the range. Winter temperatures are cold; summer temperatures vary from cool in the north to warm in the south. *Mediterranean climate* is predominant in the far southwestern continental United States. Annual precipitation is low, and most of it falls during winter. Summers are hot and dry, with persistent droughts in many years, and winter temperatures are mild.

Several authors have reviewed the causes of tree-line and tree species limit (Griggs, 1946; Daubenmire, 1954; Wardle, 1971; Tranquillini, 1979; Arno and Hammerly, 1984; Innes, 1991; Stevens and Fox, 1991); however, these reviews emphasize environmental impacts on growth and survival of mature trees rather than on seedling establishment. In this paper, we focus on the effects of environmental factors on sub-alpine tree establishment and initial survival, because this early stage of forest development determines tree-line advance and meadow invasion. We discuss changes in tree establishment with respect to fluctuations in altitudinal tree-line and tree-limit, and forest advance into sub-alpine meadows. Although most of the literature cited in this paper is from North America, general concepts may be applicable to sub-alpine forests in other areas of the world, especially the temperate zone of Europe (Troll, 1973). In order to evaluate the effects of climate on the distribution of sub-alpine species, we discuss how weather components (e.g., snow, wind and temperature), as well as natural disturbance, limit the distribution of sub-alpine trees. We then review palaeoecological and modern evidence for sub-alpine vegetation changes during the Holocene, and we infer the relative importance of environmental variables associated with these changes. Finally, we project

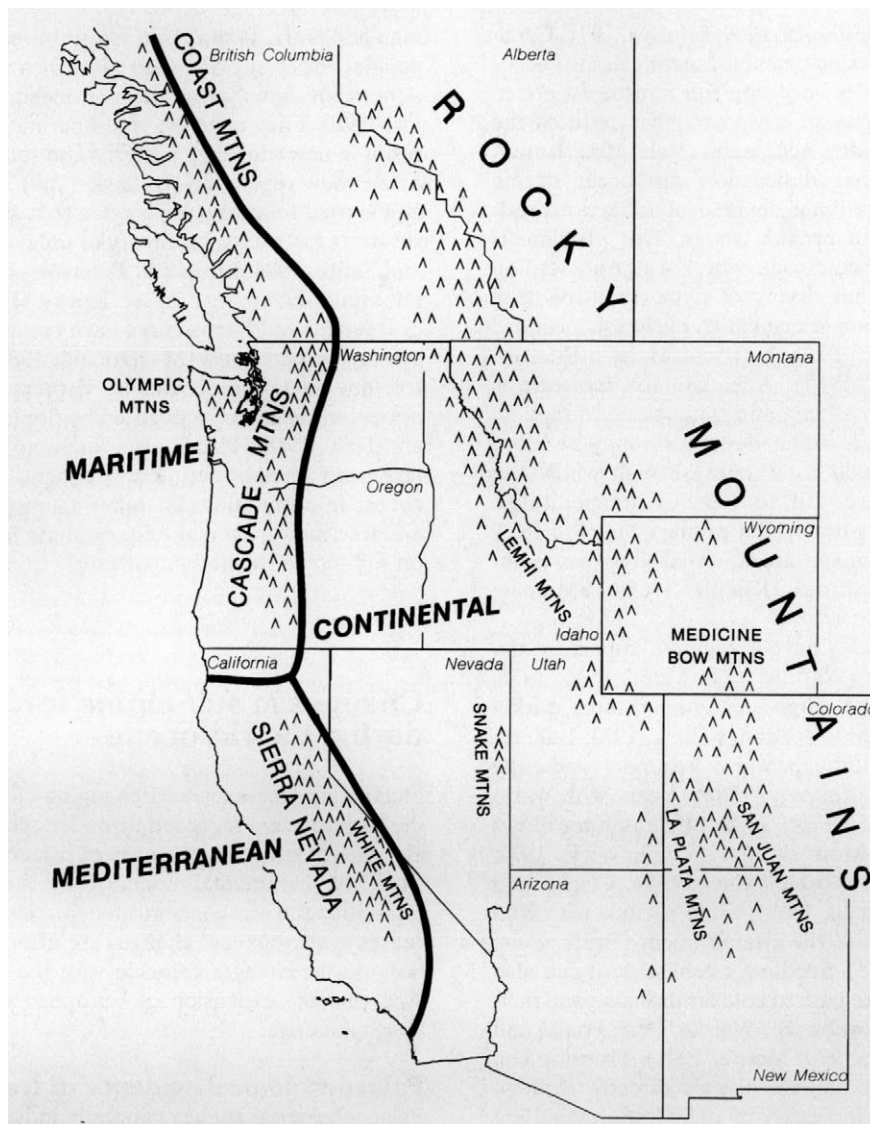


Figure 2 Location of climatic zones (maritime, continental, Mediterranean) and major mountain ranges of western North America.

how potential climatic change could affect sub-alpine forests in the future.

Environmental influences on seedling establishment and survival

Patterns of snow accumulation and snowmelt either promote or hinder seedling establishment and survival. Snowpack shields conifer needles from the desiccating winter winds common at upper elevations (Wardle, 1968; Lindsay, 1971; Hadley and Smith, 1983; Minnich, 1984) and insulates seedling roots and foliage from lethal cold temperatures (Kuramoto and Bliss, 1970). Snowmelt delays summer drought and provides increased soil moisture early in the growing season when tree seeds germinate (Evans and Fonda, 1990). Snowpack may be especially beneficial to seedling establishment in the windswept continental regions and dry Mediterranean mountains. On the other hand, heavy snow accumulation that remains on the ground until midsummer results in a shorter growing season and reduced seedling establishment (Brink, 1959; Fonda and Bliss, 1969; Kuramoto and Bliss, 1970; Douglas, 1972; Heikkinen, 1984; Butler, 1986; Armstrong *et al.*, 1988; Hansen-Bristow *et al.*, 1988). Pro-

longed snow cover also promotes infection by brown felt fungi (*Herpotrichia* spp.), which can damage and kill foliage (Donaubauer, 1963; Simms, 1967; Holtmeier, 1987). Although some tree seeds can germinate directly on snow, they generally have a low survival rate (Franklin and Krueger, 1968; Brooke *et al.*, 1970), and even established seedlings can be physically crushed or uprooted by the weight and movement of snow (Ives and Hansen-Bristow, 1983). The majority of these negative effects of snow on establishment are reported for maritime regions, where deep snowpacks develop. The effect of both snowdrift and wind patterns on tree survival in the Rocky Mountains is demonstrated by the creation of gradually moving ribbon forests aligned perpendicular to westerly winds (Billings, 1969; Benedict, 1984; Holtmeier, 1987).

Availability of soil moisture is critical for seedling germination and survival, particularly during the first year (Cui and Smith, 1991). Soil moisture depends on rainfall and snowmelt, as modified by soil properties, aspect, microtopography and evapotranspiration (Fonda, 1976; Sawyer and Kinraide, 1980). Periods of above average summer precipitation can enhance tree establishment (Agee and Smith, 1984; Allen, 1984; Taylor, 1990), and increased water availability from a melting snowpack can be important for seedling survival

during summer droughts (Billings, 1969; Lindsay, 1971; Canaday and Fonda, 1974). Seedling establishment can also occur when a wet period provides adequate soil moisture for tree seedlings following a series of dry years that reduces the competitive ability of meadow vegetation (Vale, 1981; Butler, 1986; Taylor, 1990). Foliar desiccation can occur during winter when the transpirational demand of foliage exceeds the ability of the roots to provide water. This problem is exacerbated by frozen or cold soils, where water absorption by roots is reduced. Winter drying of tissues controls tree morphology and distribution at many high-elevation locations (Marr, 1977; Tranquillini, 1979; Ives and Hansen-Bristow, 1983; Bella and Navratil, 1987). Adequate soil moisture is important for seedlings in all climatic zones because they all have dry periods; however, winter desiccation may be more prevalent in the continental zone, because high winds can remove snow and expose soil to freezing temperatures. Summer moisture stress is one of the primary limits to tree-line advance in Mediterranean areas, especially when combined with warm temperatures (Klikoff, 1965; LaMarche, 1973).

Extreme soil temperatures have a negative impact on the survival of tree seedlings (Wardle, 1968; Munn *et al.*, 1978; DeLucia and Smith, 1987). High soil temperatures during early summer can be lethal to seedlings (Baig, 1972; Ballard, 1972; Douglas, 1972), although warm summers generally benefit seedling survival (Kearney, 1982). Years with warm air temperatures can promote tree establishment in meadows (Brink, 1959; Franklin, Moir *et al.*, 1971; Lowery, 1972; Kearney and Luckman, 1983; Heikkinen, 1984; Clague and Mathewes, 1989; MacDonald, 1989), while periods with cold air temperatures can inhibit tree establishment (Brink, 1964; Daly and Shankman, 1985). Seedling establishment can also be limited in the immediate path of cold air drainage and melt water originating from snow banks (Wardle, 1968; Fonda and Bliss, 1969; Brooke *et al.*, 1970; Moore, 1991). Freezing soil and air temperature can damage tissues directly through intercellular freezing and indirectly by dehydration resulting from extracellular freezing (Kramer and Kozłowski, 1979; Tranquillini, 1979). Early autumn freezes and late spring freezes may be especially deleterious to seedling tissues that are not cold-hardened (Lindsay, 1971; Ives and Hansen-Bristow, 1983). Seedlings are more sensitive than mature trees to frost heaving caused by differential freezing of soil layers because their shallow roots break or are exposed to desiccation (Brink, 1964; Kramer and Kozłowski, 1979). In general, seedlings in continental and Mediterranean regions are exposed to extreme cold temperatures, while seedlings in maritime regions are protected by deep snow. In continental regions, consistent cold temperatures during summer in combination with desiccating winds may result in inadequate maturation of new tissue, which is subsequently killed during winter (Hadley and Smith, 1986).

Disturbances such as avalanches and fire strongly affect sub-alpine vegetation patterns. Species composition after a physical disturbance often depends on the type, extent and intensity of disturbance (Oliver *et al.*, 1985). For example, a snow avalanche can produce a gradient of disturbance conditions within its path, allowing various regeneration mechanisms to occur, such as advance regeneration, resprouting, or establishment of species with light seeds (Cushman, 1981). Frequent avalanches (15–20 years apart) in the Alberta Rocky Mountains cause trees to be replaced by shrubs in avalanche paths (Johnson, 1987). The role of natural fires in maintaining sub-alpine meadow communities has been shown in many studies (Kuramoto and Bliss, 1970; De-Benedetti and Parson, 1979; Vale, 1981; Butler, 1986; Helms, 1987; Shank-

man and Daly, 1988). Both natural fires and those caused by people, especially by early European settlers and Native Americans, have favoured open meadows (Vankat and Major, 1978). Fires near the tree-line are usually small but can result in new snowdrift patterns and long-lasting replacement by meadow vegetation (Billings, 1969). Establishment of sub-alpine trees following fire is often slow because of snow creep, substrate instability, herbivory or unfavourable climate (Agee and Smith, 1984; Little and Peterson, 1991). Fire is the most important disturbance in the Rocky Mountains, and periods of frequent and intense fires have created open forests in the sub-alpine park land (MacDonald, 1989; Moore, 1991). The tree-line in Colorado can be depressed below its climatic upper limit in areas frequented by fire (Peet, 1981; Shankman and Daly, 1988). Fire is also common in regions with Mediterranean climate but less frequent in maritime climatic zones. Interpretations of other factors controlling tree-line and tree-limit must carefully examine impacts of disturbance on sub-alpine vegetation patterns.

Changes in sub-alpine forest distribution during the Holocene

Fluctuating tree-lines and changing climatic regimes during the Holocene are recorded by pollen records, wood fragments and macrofossils. The majority of palaeoecological studies are from the continental zone, while studies of recent tree establishment are concentrated in the maritime zone. The causes of these recent changes are often difficult to ascertain, because the changes coincide with the end of the 'Little Ice Age' and the expansion of European settlement in western North America.

Palaeoecological evidence of tree-line dynamics

Palaeoecological studies generally indicate a warmer climate during the early to mid-Holocene (9000 to 5000 BP) with tree-line advances (Table 1 – Andrews *et al.*, 1975; Petersen and Mehringer, 1976; Carrara *et al.*, 1984; Luckman and Kearney, 1986; Clague and Mathewes, 1989; Clague *et al.*, 1992). Cooler climates since 5000 BP have generally resulted in stable or lower-elevation tree-lines. Detailed reconstructions of past precipitation patterns and temperature regimes are based on pollen analysis (Maher, 1972; Luckman and Kearney, 1986; Clague and Mathewes, 1989), isotope analysis (Carrara *et al.*, 1984; Friedman *et al.*, 1988; Carrara *et al.*, 1991) and tree-ring growth patterns (LaMarche and Mooney, 1972; Payette *et al.*, 1989). These reconstructions describe a warm/dry early Holocene in the maritime and Mediterranean areas (LaMarche and Mooney, 1972; LaMarche, 1973; Clague and Mathewes, 1989), but a warm/moist early period in the continental zone (Markgraf and Scott, 1981; Friedman *et al.*, 1988; Carrara *et al.*, 1991).

Maritime

Tree-lines in southwestern British Columbia 9100–8200 BP were approximately 60–130 m higher than today (Clague and Mathewes, 1989; Clague *et al.*, 1992). Using adiabatic lapse rates (6.5°C per 1000 m), the authors estimated that temperature was 0.4–0.8°C warmer at this time. Wood fragments from colluvial and alluvial sediments and pollen collected from a bog above the present tree-line were identified as *Pinus albicaulis* and *Abies lasiocarpa*, species still present in the area today. These fragments had wider annual rings than living krummholz from the same site, indicating that condi-

Table 1 Summary of palaeoecological studies that have documented changes in tree-line. Studies are from the United States except as indicated. (T = temperature, P = precipitation)

Date	Comments	Location	Author(s)
Maritime			
9100–8200 BP	Treeline 60–130 m higher; T 0.4–0.8°C higher, P lower	Coast Range, British Columbia (Canada)	Clague and Mathewes, 1989; Clague <i>et al.</i> , 1992
9100–7600 BP	Tree-line higher		
6600–5100 BP	Tree-line higher		
Mediterranean			
7400–4200 BP	Oldest trees 150 m higher; T 3.5°C higher	White Mountains, California	LaMarche, 1973
4000–2000 BP	Tree-line 100 m higher	Snake Mountains, Nevada	LaMarche and Mooney, 1972
3500–2500 BP	T lower, P higher	White Mountains, California	LaMarche, 1973
870–470 BP	Tree-line 50–70 m lower; T lower, P lower		
6300–3500 BP	Tree-line 68 m higher	Sierra Nevada, California	Scuderi, 1987
3200–2800 BP	Tree-line 32 m higher		
1400–1300 BP	Tree-line 10 m higher		
950–850 BP	Tree-line similar to present		
Continental (grouped by study sites)			
10000–7600 BP	Tree-line lower; T lower, P higher	Rocky Mountains, Colo- rado	Maher, 1972
7600–6700 BP	Similar to present		
6700–3000 BP	Tree-line lower; T lower, P higher		
9800 BP	Tree-line lower	La Plata Mountains, Colorado	Petersen and Mehringer, 1976
8500 BP	Tree-line higher		
6700 BP	Tree-line higher		
4000 BP	Tree-line lower		
2500 BP	Tree-line higher		
9600–7800 BP	Tree-line 80 m higher	San Juan Mountains, Colorado	Combined results from studies of: Andrews <i>et al.</i> , 1975
8000 BP	Tree-line 140 m higher		
6700–5400 BP	Tree-line 80 m higher; T 0.5–0.9°C higher, P higher		Carrara, Mode, Rubin and Robinson, 1984
5400–3500 BP	Tree-line lowered to present level		Carrara, Trimble and Ru- bin, 1991
3100 BP	Tree-line higher		
After 3100 BP	Tree-line lower; T lower, P higher		
6500–3500 BP	Period of maximum tree- line advance	Colorado	Short, 1984
8800–7500 BP	Tree-line higher; T 1.0°C higher	Rocky Mountains, Alberta (Canada)	Combined results from studies of:
8300–8000 BP	Tree-line higher		Kearney and Luckman, 1983
7400–7300 BP	Tree-line same as present		
7200–5200 BP	Tree-line higher; T 1.0°C higher		Luckman and Kearney, 1986
4500 BP	Tree-line same as or lower than present		Luckman, 1988
500 BP	Lowest depression of tree- line		
8500–3000 BP	Tree-line higher	Rocky Mountains, British Columbia (Canada)	Reasoner and Hickman, 1989
50–70 BP	Tree-line higher	Lemhi Mountains, Idaho	Winter, 1984

tions favourable for tree growth were present at high-elevation sites during the early Holocene. Wood fragments from additional sites in southern British Columbia and Alberta represent two periods of higher tree-line: 9100–7600 BP, and 6600–5100 BP (Clague and Mathewes, 1989). Wood fragments from the earlier period indicate the early Holocene may have been warmer than the mid-Holocene. Pollen deposited in the upper part of the core contained high percentages of *Cyperaceae*, *Salix* and other wet-habitat species, indicating a recent change to wetter conditions.

Continental

Studies in the continental zone reveal a similar but more detailed record of tree-line movement. Analysis of pollen, macrofossils and oxygen-isotope data from tree-rings from alpine bogs in the Canadian Rocky Mountains indicate a fluctuating tree-line over the last 8800 years (Kearney and Luckman, 1983; Luckman and Kearney, 1986). Pollen ratios (*Abies/Pinus*) and macrofossils indicate two periods of elevated tree-line: 8800–7500 BP and 7200–5200 BP. Wood fragments from a site 100 km south of the bogs also provide evidence of a higher tree-line 8300–8000 BP (Luckman, 1988). The climate was warmer and drier during these periods, and the tree-line was at least 100 m higher. Oxygen-isotope analysis of buried logs suggests temperatures were at least 0.5°C warmer 8770–8060 BP and 1.2–1.6°C warmer 6000–5300 BP (Luckman and Kearney, 1986). Tree-lines have been similar to or lower than present levels since 4500 BP, with minimum levels during the last 500 years. An additional study in Yoho National Park, British Columbia, used pollen and macrofossil data to show that the tree-line was at least 90 m above the modern tree-line during the period 8500–3000 BP, in response to warmer climatic conditions (Reasoner and Hickman, 1989). Tree-lines declined to current levels during cooler climates after 3000 BP.

Studies in southwestern Colorado indicate tree-line and tree-limit were depressed prior to 9800 BP, advanced upward at least twice between 9800 and 5400 BP, and have generally been lower than or equal to present elevations since 3500 BP (Petersen and Mehringer, 1976; Carrara *et al.*, 1984; 1991). Petersen and Mehringer (1976) used *Pinus/Picea* pollen ratios and *Picea* macrofossils to identify three periods of tree-line advance in the La Plata Mountains: 8500, 6700 and 2500 BP. Studies in the San Juan Mountains of Colorado show patterns similar to those described by Petersen and Mehringer (1976) (Andrews *et al.*, 1975; Carrara *et al.*, 1984; 1991). Pollen, wood fragments and macrofossils indicate three periods of tree-line and tree-limit advance of at least 80 m: 9600–7800 BP, 6700–5400 BP, and 3100 BP. The tree-line may have been 140 m higher than at present c. 8000 BP. Mid-Holocene July temperatures were estimated at 0.5–0.9°C higher than today. The tree-line declined to present-day elevations 5400–3500 BP and again after a short upward advance around 3100 BP, when tree species may have been 70 m higher than today (Andrews *et al.*, 1975; Carrara *et al.*, 1984; 1991).

Two studies from the Colorado Rocky Mountains describe contrasting climates in the early to mid-Holocene. Maher (1972) used *Picea/Pinus* pollen ratios to infer that climates from 10000 to 7600 BP and from 6700 to 3000 BP were cooler and/or wetter than today and tree-lines were lower. Warming trends from 7600 to 6700 BP, and since 3000 BP, resulted in higher tree-lines. Conversely, Short (1984) used pollen ratios to show that the tree-line reached a maximum altitude 6500–3000 BP and that it has since lowered in response to climatic cooling.

Mediterranean

Studies of *Pinus longaeva* in the White Mountains, California (LaMarche, 1973), and Snake Mountains, Nevada (LaMarche and Mooney, 1972), indicate higher tree-lines during the early to mid-Holocene. Wood fragments above the current tree-line at the California sites dated 7400 BP indicate that the tree-line was 100 to 200 m above modern levels until 4200–2000 BP. This was a relatively warm period, with estimated mean temperatures 3.5°C higher than today. Tree-line elevation became lower 870–470 BP. Analysis of site conditions and tree growth/climate relationships (in tree-rings) showed that the tree-line was controlled by precipitation as well as temperature. Current *P. longaeva* distribution in the Snake Mountains, Nevada, shows a progressive dwarfing with increasing altitude as follows: erect, tall-dwarf, short-dwarf and krummholz (LaMarche and Mooney, 1972). The authors suggest that the past forest included only erect and tall-dwarf trees. The upper boundary of erect trees was at least 100 m higher than today, and tall-dwarf trees extended to the summit (3559 m) of Mount Washington.

Surveys conducted in the southern Sierra Nevada reconstructed similar Holocene tree-line fluctuations for *Pinus balfouriana* (Scuderi, 1987). Relict wood samples collected 68 m above the present tree-line were dated to 6300 BP. Wide growth rings indicate warm, favourable growing conditions. Samples collected at 65 m above the present tree-line were dated to 3530 BP, suggesting that the tree-line was maintained at this elevated position for about 3000 years. Tree mortality at 20 m above the present tree-line and decreased growth between 2500 and 2300 BP indicate a colder climate. The tree-line declined to 10 m below the present level between 1400 and 1300 BP, and increased to the present level between 950 and 850 BP; a few trees established 5 to 10 m above the present tree-line about 100 years ago.

Summary of tree-line fluctuation

Palaeoecological studies provide a fairly uniform scenario of climatic change and tree response to a changing environment. The Holocene from 10 000 to 3500 BP was generally a warmer period with several periods of tree-line advance, and it was followed by a cooler period with tree-lines lower than or equal to those of today. The climate in the maritime and Mediterranean zones was generally warm and dry during the early Holocene and became cooler and more moist c. 3500 BP (LaMarche, 1973; Clague and Mathewes, 1989). Conversely, precipitation in the continental zone has decreased since the early Holocene (Andrews *et al.*, 1975; Petersen and Mehringer, 1976; Markgraf and Scott, 1981; Carrara *et al.*, 1984). In addition, precipitation patterns have influenced tree growth form, as well as the magnitude and timing of tree-line movement at some locations (LaMarche, 1973). However, the generally synchronous reconstruction of past tree-line fluctuations indicates that temperature is the predominant force determining tree-line location on a broad geographic scale.

Recent tree establishment in sub-alpine meadows

Increases in tree establishment in sub-alpine meadows have been documented in mountainous areas throughout western North America (Table 2). Most areas show initial forest-margin expansion after AD 1890 and significant establishment peaks between 1920 and 1950. Additional peaks of establishment have also been identified in some areas. Most studies conclude that recent increases in tree establishment are the result of a warmer, drier climate following the 'Little Ice Age' (Franklin *et al.*, 1971; Kearney, 1982; Heikkinen, 1984; Butler, 1986). Although most studies conclude that

Table 2 Summary of recent sub-alpine tree invasion attributed to climate. Studies are from the United States except as indicated.

Species	Location	Period of invasion	Author(s)
<u>Maritime</u>			
<i>Abies lasiocarpa</i> <i>Tsuga mertensiana</i>	Coast Mountains, British Columbia (Canada)	1919–1939	Brink, 1959
<i>Abies lasiocarpa</i> <i>Larix lyallii</i> <i>Tsuga mertensiana</i>	Cascade Mountains, Washington	1919–1937	Arno, 1970
<i>Abies amabilis</i> <i>Abies lasiocarpa</i> <i>Chamaecyparis nootkatensis</i> <i>Tsuga mertensiana</i>	Cascade Mountains, Washington	1920–1950	Lowery, 1972
<i>Abies amabilis</i> <i>Tsuga mertensiana</i>	Cascade Mountains, Washington	1923–1943	Douglas, 1972
<i>Abies amabilis</i> <i>Abies lasiocarpa</i> <i>Tsuga mertensiana</i>	Cascade Mountains, Washington	1925–1934 1940–1944	Heikkinen, 1984
<i>Abies lasiocarpa</i> <i>Larix lyallii</i> <i>Tsuga mertensiana</i>	Cascade Mountains, Oregon and Washington	1894–1920 1925–1950	Franklin, Moir <i>et al.</i> , 1971
<i>Tsuga mertensiana</i>	Olympic Mountains, Washington	1920–1950	Agee and Smith, 1984
<i>Abies lasiocarpa</i> <i>Tsuga mertensiana</i>	Olympic Mountains, Washington	1923–1933 1943–1948 1953–1960	Fonda and Bliss, 1969
<u>Mediterranean</u>			
<i>Pinus balfouriana</i>	Sierra Nevada, California	1890–1895 1897–1987	Vankat and Major, 1978 Scuderi, 1987
<i>Pinus contorta</i> var. <i>murrayana</i>	Sierra Nevada, California	1905–1936 1948–1973	Helms, 1987
<i>Pinus longaeva</i>	White Mountains, California	1850–1940	LaMarche, 1973
<u>Continental</u>			
<i>Abies lasiocarpa</i> <i>Picea engelmannii</i>	Rocky Mountains, Alberta (Canada)	1940–1960 1965–1973	Kearney, 1982
<i>Abies lasiocarpa</i> <i>Picea engelmannii</i> <i>Pinus contorta</i> <i>Pseudotsuga menziesii</i>	Lemhi Mountains, Idaho	1895–1915 1925–1950	Butler, 1986
<i>Picea engelmannii</i> <i>Pinus flexilis</i>	Rocky Mountains, Colorado	1957–1979	Daly and Shankman, 1985

these increases were caused by warming trends, it is uncertain whether this is a long-term directional change or a short-term variation in relatively stable ecotones.

Maritime

In one of the first studies on recent increases of tree establishment in sub-alpine meadows, Brink (1959) documented establishment of *Abies lasiocarpa* and *Tsuga mertensiana* between 1919 and 1939 in heather communities (*Phyllodoce* spp./*Cassiope mertensiana*) of the Coast Range, British Columbia. Heather communities were on topographic convexities, with earlier snowmelt and a longer growing season. Soils were also more xeric than surrounding depressions, but not as dry as south-facing forb meadows without trees. Climatic warming during this period is supported by evidence

of decreased glacial volumes.

Arno (1970) noted massive invasions of heather communities by *Larix lyallii*, *T. mertensiana* and *A. lasiocarpa* in the northern Cascade Mountains of Washington. Most of the establishment occurred from 1919 to 1937, although about half of the *L. lyallii* had invaded the area between 1885 and 1910. Douglas (1972) also documented meadow invasion by *T. mertensiana* and *A. amabilis* in heather communities in the northern Cascades. He attributed establishment to several consecutive years of low snow accumulation, moderate spring and early summer temperatures, and the black-body effect of tree clumps that caused faster snowmelt around trees. Tree establishment had been occurring for 120 years in his study area, with peak establishment from 1920 to 1940.

Franklin *et al.* (1971) surveyed six areas in the Cascade

Mountains of Washington and Oregon and documented meadow invasion by *A. lasiocarpa*, *T. mertensiana* and *L. lyallii* (one site in the northern Cascades). Most invasion occurred between 1925 and 1950, predominantly by *A. lasiocarpa*. Seedling density and growth rates varied with vegetation type, with highest densities in heather communities and lowest densities in *Festuca* communities. Invasion was attributed to a series of warm, dry years with low snowpack and the possible influence of large seed crops. Henderson (1974) suggested that periods of establishment in this area occurred during warm periods with average or above average precipitation, which reduced moisture stress on seedlings.

Heikkinen (1984) found that tree advance in the northern Cascades followed the same temporal patterns as noted by Franklin *et al.* (1971) and Brink (1959). The oldest trees dated back to 1886, and tree establishment continued until 1944, with invasion peaks during 1925–1934 and 1940–1944. *Tsuga mertensiana* predominated at the highest elevations, *A. lasiocarpa* at mid-elevations, and *A. amabilis* at low elevations.

In a study of stand dynamics in the northern Cascades, Lowery (1972) found that invasion throughout the meadows started about 1920, coinciding with the expansion of older tree clumps, warmer weather and glacial retreat. *Abies lasiocarpa* was the most abundant species, especially at xeric sites such as the centre of heather-dominated mounds. *Tsuga mertensiana* grew on wet, cool sites, while *A. amabilis* and *Chamaecyparis nootkatensis* established on moist, lower-elevation sites and the exterior of tree clumps. Tree invasion and enlargement of tree clumps continued until the 1950s, when a cooler, wetter climate prevailed and glacial recession ceased.

Studies in the Olympic Mountains of Washington documented tree invasions in meadow basins with normally heavy winter snowpack (Fonda and Bliss, 1969; Kuramoto and Bliss, 1970). These studies inferred that tree establishment occurred during periods of warm, dry weather. There were several discrete peaks of establishment: 1923–1933, 1943–1948 and 1953–1960. These studies also found that establishment was highest in heather communities, and that tree height increased with distance from melting snow.

Agee and Smith (1984) studied tree establishment on three sub-alpine fire sites in the Olympics. Fire removed all vegetation and therefore reduced protection from sun, drought and browsing ungulates, resulting in a time lag of 40–70 years before seedlings could germinate and survive. Burned sites had peak establishment during wet periods (1950s), while unburned heather sites had establishment peaks during both dry periods (1920–1950) and wet periods (1950s). The authors concluded that mesic conditions were optimal for tree establishment; therefore, drier, burned sites required wet periods for establishment, and wetter, unburned areas required warm, dry periods.

Continental

Kearney (1982) noted invasions of *Abies lasiocarpa* and *Picea engelmannii* at three locations in the Rocky Mountains of southern Alberta. Invasion occurred during 1940–1960 and was especially prominent from 1965 to 1973. Both invasion periods were correlated with warm, dry summers. In addition, growth rates of trees on heather hummocks were often twice those of trees in the hollows between hummocks.

Tree invasion in the Lemhi Mountains of Idaho began in the 1890s and continued until the 1950s (Butler, 1986). Invasion peaks occurred in 1905–1919 and 1925–1945, corresponding with warm, dry periods with decreased snowpack. Tree establishment patterns varied slightly among the three meadows studied, indicating some variation in the causal

agent (climate) or site conditions. Invasion peaks in the lowest-elevation meadow were earlier than in the other two by about ten years. Charcoal in the lowest meadow suggests that frequent fire could have limited tree establishment.

Daly and Shankman (1985) found high densities of *Picea engelmannii* and *Pinus flexilis* seedlings (5–27 years old) above the tree-limit in the Colorado Rocky Mountains. The high ratio of seedlings to trees was interpreted as an increase in seedling establishment, which could produce an advance of the tree-limit.

Mediterranean

Establishment above the tree-limit was also documented at one site in the Sierra Nevada (Scuderi, 1987) and two sites in the White Mountains of California (LaMarche, 1973). Small, erect seedlings of *Pinus balfouriana* have established 5–10 m above the present tree-line at Cirque Peak, Sierra Nevada, over the last 100 years. Large numbers of *P. longaeva* have established above the tree limit in the White Mountains since 1850. Few trees established between 1450 and 1850 at one site, and no trees established between 1250 and 1850 at the other site.

In summary, the literature indicates that climatic warming since 1850 has resulted in periods of increased tree establishment in sub-alpine park lands. Studies of recent tree establishment are concentrated in the maritime zone, so it is difficult to determine the geographic extent and variation of tree establishment in western North America. Modern studies demonstrate a more complex climate/site interaction than can be inferred from palaeoecological studies of tree-line fluctuations.

Effect of potential global climate change on tree establishment

Our review indicates that weather components frequently limit establishment of trees in sub-alpine and alpine meadows in the maritime, Mediterranean and continental climatic zones of western North America. A comparison between climatic variables and limits to tree establishment (Table 3) shows that the most extreme characteristic of each zone is often the most limiting factor, specifically: (1) winter precipitation (snowpack) in maritime climates, (2) cold soil temperatures and high winds in continental climates, and (3) summer drought in Mediterranean climates. Our review suggests that tree establishment occurs in any of these climates when these extreme conditions are alleviated. Predictions of tree establishment on a fine scale are difficult, however, because establishment patterns are influenced by local variations such as microtopography and disturbance frequency.

Predictions of future climate are based on numerical models limited by incomplete understanding of atmospheric and oceanic processes, interactions and feedbacks. Furthermore, current computer capacities limit spatial resolution and restrict the coupling of climate system components whose timescales differ by fourteen orders of magnitude (Schlesinger and Mitchell, 1987; Cubash and Cess, 1990). Models predict temperature changes most accurately and are less able to predict changes in precipitation and soil moisture, which are products of complex interactions within the hydrologic cycle. Models also have difficulty in resolving subcontinental variation. Despite weaknesses, climate predictions generated by general circulation models (GCMs) provide the best available description of future climate. We have summarized

Table 3 Levels of climate variables characteristic of three climate zones, with the extremes for each climate indicated by bold type. These extremes are also the limiting factors for tree establishment for each zone.

Climate zone	Summer		Winter	
	Temperature	Precipitation	Temperature	Precipitation
Maritime	Mild	Low	Cool	High
Continental	Cool-warm	Dry	Cold	Low
Mediterranean	Hot	Very low	Mild	Low

Table 4 Range of changes in climate variables predicted by three general circulation models at equilibrium with doubled atmospheric CO₂. Values indicate change from present. Models were developed by the Canadian Climate Centre, the Geophysical Fluid Dynamics Laboratory and the United Kingdom Meteorological Office (Mitchell *et al.*, 1990).

Season	Climate zone	Temperature (°C)	Precipitation (mm/day)	Soil moisture ¹ (cm)
Winter	Maritime	2-6	1-2+	0-2
	Mediterranean	2-6	(-1)-1	0-2
	Continental	2-8	(-1)-1	>2
Summer	Maritime	2-6	(-1)-0	<(-2)-0
	Mediterranean	4-6	(-1)-1	(-1)-1
	Continental	2-8	(-1)-1	<(-2)-0

Note:

¹Represents the available water in the upper layers of soil having field capacity of 15 cm.

the range of changes predicted for several climate variables for the three climate zones based on predictions of response to doubled CO₂ from three of the highest-resolution models (Table 4 – Mitchell *et al.*, 1990).

The most consistent conclusions of the models are: (1) winter soil moisture will increase in all three climates; (2) winter and summer temperatures will increase in all three climates, but especially in the continental climate; (3) summer soil moisture will decline in maritime and continental climates; and (4) distribution of precipitation in the maritime climate will be skewed even more heavily towards winter. Predictions for winter and summer precipitation and summer soil moisture in the Mediterranean climate vary, although two of the three models predict an increase in each case.

Climate model predictions also provide a basis for speculation about future distribution of vegetation, particularly trees. The predicted changes for all three climates should alleviate the identified constraint to tree establishment (Table 3). Winter precipitation is predicted to increase in the maritime climate, but warmer temperatures are expected to cause more to fall as rain at higher elevations, resulting in less snowpack. Summer drought is predicted to lessen in Mediterranean climates. Models predict increased winter temperatures and precipitation in continental areas, although temperatures will still be low enough to produce snow. This may provide greater wind and cold protection than current conditions. However, changes that favour sub-alpine establishment may be negated by other changes such as summer drought, which is predicted to intensify in maritime and continental zones, possibly preventing tree establishment. There is, of course, a high degree of uncertainty about how changes in different combinations of climatic variables might affect future patterns of sub-alpine tree establishment. Moreover, changes in other factors influenced by climate, such as fire frequency, may also affect tree establishment (Franklin *et al.*, 1991).

In summary, we expect an increase in tree establishment (i.e., higher tree-lines, increased meadow invasion) in all

three climate zones. Tree-lines may be similar to those of the early Holocene, when the climate was similar to the predicted future climate. A similar prediction has been made from a landscape model for a single site in the continental zone (Romme and Turner, 1991). Moreover, we may be observing the beginning of a trend in response to the warmer climates of this century (Brink, 1959; Butler, 1986; Franklin *et al.*, 1971; LaMarche, 1973; Kearney, 1982; Rochefort and Peterson, 1991; Woodward *et al.*, 1991). This very general conclusion must be qualified because (1) small-scale variability, disturbance, availability of suitable substrate, and other variables not directly related to climate make it difficult to specify precise situations in which establishment will occur; (2) loss of potential invasion sites due to the imposition of new constraints by changing climate has not been described; and (3) the predictions of GCMs are uncertain. Therefore, we predict that vegetation zones will not simply migrate up in elevation and latitude (Dale and Franklin, 1989; Peters, 1990), but that sub-alpine species may be distributed differently in the future than in the past (Brubaker, 1988; Davis, 1989). Detailed study of site conditions and tree regeneration requirements will help refine predictions of the effects of climate on forest establishment. Long-term monitoring at several sites will determine whether recently observed patterns of sub-alpine tree establishment will continue.

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