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Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances

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Abstract

Natural disturbances have been among the most important driving factors in many ecosystems. Anthropogenic suppression of various disturbances has led to documented changes in ecosystem structure and function. Avalanche disturbances are one of the most important processes in many subalpine ecosystems world-wide and avalanche tracks provide unique habitat for various animal and plant species. Over the past decades the natural avalanche regime in the Alps has been disrupted by snow-supporting structures and other measures intended to prevent the occurrence of avalanches. We hypothesized that suppression of avalanche disturbances changes stand structure and composition and increases the relative importance of climatic stress (the degree to which climatic conditions limit the growth of vegetation).

We analyzed stand structure and tree growth at high and low elevations in pairs of active avalanche tracks and tracks from which avalanches have been excluded in the Swiss Alps. Data on density and size of all tree species were collected in the field to analyze stand structure and increment core samples were collected to analyze tree growth.

In tracks from which avalanches have been excluded, dbh (diameter at breast height), tree height, annual tree-ring widths, correlation of ring widths between trees, and correlation of ring-width indices with growing-season temperature were all greater than in active tracks, indicating an acceleration of ecosystem development and an increase in the relative importance of climatic stress. Within tracks from which avalanches have been excluded, increases in tree size and ring width were more pronounced at lower elevations while correlation of ring-width indices with growing-season temperature was more pronounced at higher elevations.

The anthropogenic alteration of the natural avalanche regime is beginning to cause changes in the structure and function of some subalpine forests. The continued suppression of avalanches, while valuable for social reasons, is likely to eventually lead to the decline of certain ecological communities and may alter subsequent forest dynamics. In addition to changing forest structure, the suppression of avalanche disturbances is also changing the relative importance of the factors that are controlling ecosystem development by increasing the role of climatic stress in ecosystem development. We suggest that, in general, the suppression of disturbances predictably changes the relative importance of stress and competition along existing environmental gradients. Such changes represent a major alteration of ecosystem structure and function.

Keywords: C–S–R theory; Grime's triangle; *Picea*; *Larix*; Snow; Subalpine forest

1. Introduction

The C–S–R theory (Grime, 1977) describes a three-way trade off between plant adaptations to sites that are primarily shaped by competition (C), environmental stress (S), and disturbance (R). While the theory is certainly a simplification of ecological systems, it remains one of the most comprehensive theories for community ecology (Wilson and Lee, 2000). This model has generally been used to predict or describe the species composition that develops at a particular site. However, this theory may also describe the performance of the same species. Specifically, changes in natural disturbance regimes can be predicted to alter the relative importance of stress and competition along existing environmental gradients (Fig. 1).

Natural disturbances have been among the most important factors driving the development of ecosystems (White, 1979; Oliver, 1981; Attiwill, 1994; Veblen, 2000; Frelich, 2002). Relatively recent anthropogenic suppression of disturbances has led to documented changes in structure, composition, and processes (Baker, 1992; Swetnam and Lynch, 1993; Fule and

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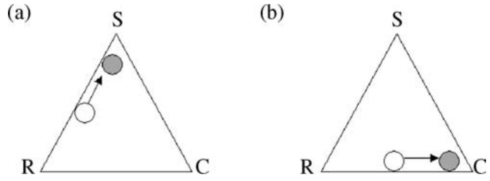

Fig. 1. The theoretical relative importance of stress (S), competition (C), and disturbance (R) at: (a) high- and (b) low-elevation sites. Empty circles represent disturbed sites, arrows represent change in relative importance following suppression of disturbances, and filled circles represent undisturbed sites. When disturbance is removed, the relative importance of stress is predicted to increase at high-elevation sites and the relative importance of competition is predicted to increase at low-elevation sites.

Covington, 1994; Mast et al., 1998; Veblen et al., 2000; Allen et al., 2002; Taylor, 2004). Underlying these changes, the suppression of disturbances is also likely to be altering the relative importance of other driving factors to ecosystem development. In the present study, we examined how the suppression of avalanche disturbances in the Swiss Alps changes forest structure and the relative importance of climatic stress (the degree to which climatic conditions limit the growth of vegetation).

Understanding natural disturbances is fundamental to the contemporary understanding of vegetation ecology. Disturbances can exert a major influence on ecosystem composition and structure and can strongly influence subsequent dynamics (White, 1979; Oliver, 1981; Frelich, 2002; Kulakowski and Veblen, 2002; Bebi et al., 2003). While infrequent disturbances can result in a broad range of natural ecological conditions (Kulakowski et al., 2004), frequent disturbances can often maintain a relatively narrow range of species assemblages, structures, and processes. In such ecosystems, the biota is in a relatively perpetual state of responding to the disturbance regime. Thus, disturbance is most likely to be the primary factor that controls ecosystem development and other potentially important factors, such as stress or competition, are likely to have a smaller relative effect. Especially, in such frequently disturbed systems, disruption of the disturbance regime can lead to unprecedented changes in ecosystem structure and function.

Examples of frequently disturbed ecosystems include those in avalanche tracks. In affected areas, avalanche disturbances can exert the most important influence on ecosystem development by generally reducing tree growth, size, and density (Major, 1977; Butler, 1979; Johnson, 1987; Patten and Knight, 1994). Avalanche tracks are an important component of the subalpine forests in the Swiss Alps, which are primarily dominated by Norway spruce (*Picea abies*) and European larch (*Larix decidua*) and occur over steep environmental gradients that exist in this mountain environment. Avalanches are frequent in these forests and can occur numerous times per year in the same track (Laternser and Schneebeli, 2002). In the Swiss Alps, avalanches maintain frequently disturbed communities that are characterized by small and damaged trees and a higher proportion of shade-intolerant tree species than undisturbed stands (Bebi et al., 2001). These communities provide unique habitat for various animal and plant species (Erschbamer, 1989; Mace et al., 1996; Krajick, 1998).

In addition to shaping ecosystems, avalanches also pose a substantial hazard to human settlements and infrastructures (Burton et al., 1993; Fuchs et al., 2004). Therefore, there has been a major effort in the Alps to construct snow-supporting structures in order to prevent avalanches in areas where their occurrence may be especially costly (SLF, 2000). The snow supporting structures have been quite successful and avalanches have been excluded from many ecological communities in which they once shaped the ecosystems (SLF, 2000). This alteration of the natural disturbance regime is likely to be leading to changes in structure and composition. It is also likely to increase the relative importance of formerly secondary factors such as climatic stress to tree growth and ecosystem development (Fig. 1). Because strong environmental gradients exist in mountain environments, any changes in structure and in the relative importance of climatic stress are likely to be governed by those existing gradients. As high-elevation sites are generally more stressful to tree growth in subalpine forests, climatic stress should be more reflected in tree growth following the suppression of avalanche disturbances at such sites. In contrast, changes in tree growth and stand structure are expected to be more rapid at low elevations.

While in principle, to maximize a desired environmental signal, other factors should be minimized, to our knowledge no study has directly considered how the suppression of disturbances influences the effect of climate on plant growth. Furthermore, no study has investigated changes in tree growth and forest structure as a result of avalanche suppression. In the present study, we examined changes in forest structure and in the relative importance of climatic stress as a result of the suppression of avalanche disturbances in the Swiss Alps by studying tree growth at high and low elevations in avalanche tracks with and without avalanche suppression. We hypothesized that suppression of avalanches will lead to changes in stand structure and composition and in the degree to which climatic conditions limit annual tree growth. Specific hypotheses included that following avalanche exclusion: (1) absolute tree density will increase, (2) dominance will change from *Larix* to the more shade-tolerant *Picea*, (3) tree dbh (diameter at breast height) and height will increase, (4) mean annual ring widths will increase, (5) correlation of ring-width indices between trees will increase, and (6) correlation of ring-width indices with growing season temperatures will increase.

2. Study areas

Five pairs of avalanche tracks were located across the subalpine forests of the Swiss Alps (Fig. 2; Table 1). Using a digital elevation model, aerial photographs, and a complete database of avalanche tracks and snow-supporting structures, pairs of active and inactive tracks were identified that were near each other and that were topographically similar. Prior to sampling, sites were visited in the field to verify that the pairs of tracks were indeed similar with the exception of the presence or absence of snow-supporting structures above the tracks. Sampling sites were located at five areas with four types of sites at each area, for a total of 20 sites: high elevation active

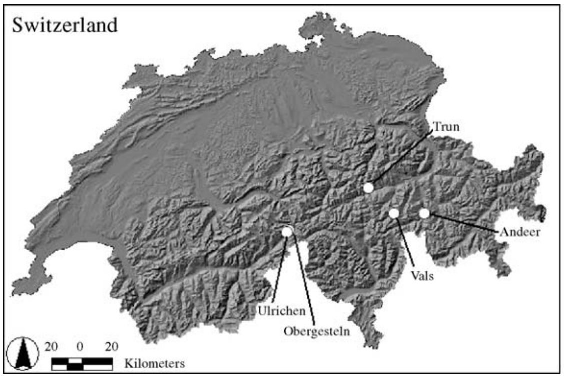

Fig. 2. Location of study areas in the Swiss Alps.

avalanche site (AH) paired with a high elevation inactive (suppressed avalanches) site (IH); a low elevation active avalanche site (AL) paired with a low elevation inactive (suppressed avalanches) site (IL).

3. Methods

A 100-m long point-centered quarter transect was located at each sampling site with points 20 m apart. Data collection began at 20 m, instead of 0 m, to eliminate subjective bias associated with the location of the transect's origin. In each quarter, we recorded the distance to and the species of the closest seedling (0.3–1.4 m tall) and sapling (>1.4 m tall but <4 cm dbh) and the distance to and the species, height, and dbh (diameter at breast height) of the closest tree ($\geq$4 cm dbh). Increment cores were collected perpendicular to the slope from the closest tree in each quarter. Trees were cored perpendicular to the slope, as opposed to on the uphill or downhill side of the tree, in order to minimize the influence of reaction or compression wood on ring width. Additional cores were collected from adjacent stands outside of the tracks to produce master chronologies to aid in crossdating the cores from the tracks.

Absolute and relative densities of tree species were calculated for each site using a correction factor for missing quarter data (Warde and Petranka, 1981). The height diversity index (HDI, Macarthur and Macarthur, 1961) was calculated based on three height categories (seedlings, saplings, and trees) for each site. Overall effects of avalanche activity on dbh, height, and mean annual ring width were analyzed by nested mixed model ANOVA separately for high and low sites with area as a random effect. The effect of avalanche activity was, thus, tested against the interaction of avalanche activity and area following standard rules for nested models (Steel and Torrie, 1980). Density, HDI, and correlation between trees were analyzed by fixed factor ANOVA. Dbh, height, mean annual ring width, and densities were log- and HDI arcsin-transformed to meet the assumptions of normality and homogeneity of variances prior to the two latter analyses. Dunn's test was used for post hoc pairwise comparisons for each site separately and for mean values of all sites.

Cores were processed using standard dendrochronological methods (Stokes and Smiley, 1968) and annual ring widths of all cores were measured. Cores were crossdated against master chronologies using marker years and the program COFECHA

Table 1
Description of sampling sites and climate over the analysis period

Site name	Latitude, longitude	Analysis period	Type[a]	Elev. (m)	Aspect	Steepness (°)	Climate station, elev.	Mean T (°C)		Annual precip. (mm)
								January	July	
Andeer	46°37′N, 9°28′E	1981–2003	AH	1995	NW	35	Davos, 1590 m	−4.7	12.3	1112
			IH	2140	SW	25				
			AL	1671	NW	30				
			IL	1380	SW	35				
Obergesteln	46°32′N, 8°19′E	1984–2003	AH	1888	SE	25	Ulrichen, 1345 m	−7.5	13.9	1241
			IH	2040	SE	25				
			AL	1448	SE	25				
			IL	1656	SE	20				
Trun	46°46′N, 8°59′E	1979–2003	AH	1889	S	25	Disentis, 1190 m	−1.4	15.1	1136
			IH	1900	S	15				
			AL	1620	S	15				
			IL	1496	S	10				
Ulrichen	46°31′N, 8°18′E	1984–2003	AH	1880	SE	25	Ulrichen, 1345 m	−7.5	13.9	1241
			IH	2046	SE	30				
			AL	1585	SE	25				
			IL	1678	SE	25				
Vals	46°36′N, 9°12′E	1986–2003	AH	2066	WSW	30	Disentis, 1190 m	−0.8	15.1	1153
			IH	2032	NW	25				
			AL	1712	SW	40				
			IL	1697	NW	20				

The analysis period began the year that construction of avalanche barriers was completed at each respective area.

[a] A, active; I, inactive; H, high elevation; L, low elevation.

(Holmes, 1983). Cores that could not be crossdated were excluded from subsequent analysis. All ring-width measurements were detrended using a linear regression or negative exponential function. The use of this single detrending was intended to remove trends associated with biological growth but retain the influences of disturbance and climate. Standard chronologies were developed for all sites using the program ARSTAN (Cook and Holmes, 1986). Bootstrapped correlation function analysis was performed between tree-ring indices and growing season temperatures of the current and previous spring (March–May) and summer (June–August) based on temperatures from the closest climate stations (MeteoSwiss, 2004). The analysis period varied across sampling areas and began the year that construction of avalanche barriers was completed at each respective area (Table 1). Fixed-factor ANOVA was used to compare maximum correlation coefficients among the four categories of sites.

4. Results

The differences in density of stems varied among size classes between active and inactive tracks (Fig. 3). Among all sites, absolute density of trees was higher at low elevations ($F_{(1,16)} = 67.6$, $P < 0.001$), but was not consistently associated with avalanche activity ($F_{(1,16)} = 0.68$, $P = 0.42$). Absolute density of saplings was higher in active tracks than in tracks from which avalanches have been excluded ($F_{(1,16)} = 5.63$, $P < 0.05$). Among trees, the relative dominance of spruce was not higher than of larch in inactive tracks ($P = 0.62$). Among seedlings, the relative dominance of spruce was on average greater than that of larch in all categories of sites but this difference was not significant ($P = 0.30$).

The dbh, height, and HDI differed among active and inactive tracks, and these differences varied with elevation (Fig. 4). At high elevations, dbh and height of trees was greater in inactive tracks by a small and insignificant margin (mean dbh at all sites: $F_{(1,4)} = 0.029$, $P = 0.87$; height: $F_{(1,4)} = 1.97$, $P = 0.23$). At low elevations, dbh and height of trees was greater in inactive tracks by a larger and significant margin (mean dbh at all sites: $F_{(1,4)} = 12.75$, $P < 0.05$; mean height at all sites: $F_{(1,4)} = 14.49$, $P < 0.05$). HDI was lowest in inactive low-elevation sites ($P < 0.05$).

A total of 401 cores from 20 sites were successfully crossdated (Table 2). At high elevations, mean ring width was greater in inactive tracks by a small but significant margin (mean ring width at all sites: $F_{(1,4)} = 17.31$, $P = 0.014$). At low elevations, mean ring width was greater in inactive tracks by a larger and significant margin (mean ring width at all sites: $F_{(1,4)} = 10.35$, $P = 0.032$). Correlation of ring-width indices between trees was higher at inactive sites than at active sites ($F_{(1,16)} = 7.90$, $P < 0.05$).

At high elevations, tree growth at inactive sites was strongly and positively correlated with growing season temperatures of the current and preceding year (Fig. 5) (effect of avalanche activity on maximum correlation coefficient: $F_{(1,16)} = 24.36$, $P < 0.001$; effect of elevation on maximum correlation coefficient: $F_{(1,16)} = 23.37$, $P < 0.001$). Tree growth at active high-elevation and inactive low-elevation sites showed lower and sporadic correlation with growing season temperatures. Tree growth at active low-elevation sites was not significantly correlated with growing season temperatures.

5. Discussion

The present study indicates three main points. First of all, the rate of ecosystem development and the relative importance of climate to ecosystem development increases after the limiting effect of disturbance is removed. Second, this increase is a function of existing environmental gradients. And third, changes resulting from the anthropogenic suppression of avalanches are likely to lead to a decline of the natural communities that have been shaped by these frequent disturbances.

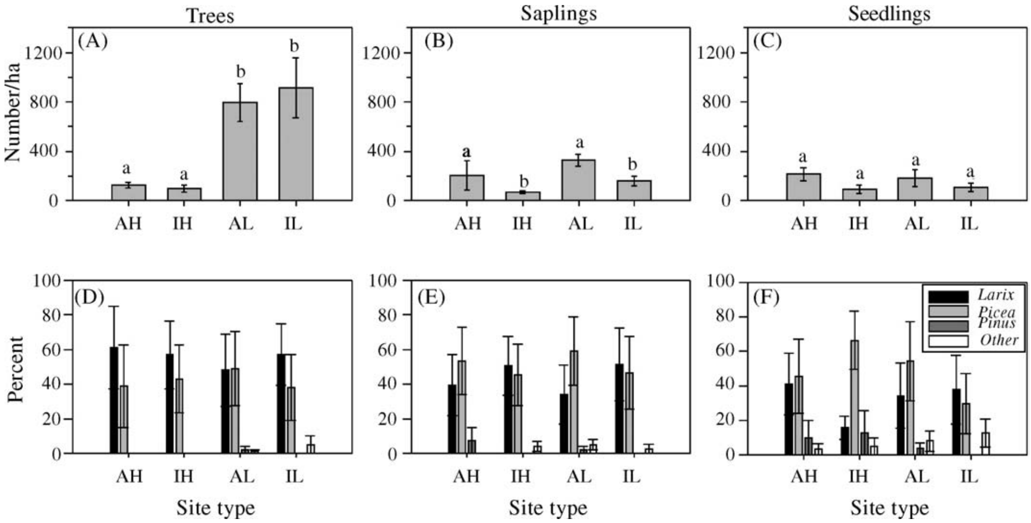

Fig. 3. Mean absolute (A–C) and relative (D–F) density of all sampled sites. Trees are ≥4 cm dbh, saplings are >1.4 m tall but <4 cm dbh and seedling are 0.3–1.4 m tall. For absolute densities, same letters above bars indicate no significant difference in post hoc tests ($P > 0.05$).

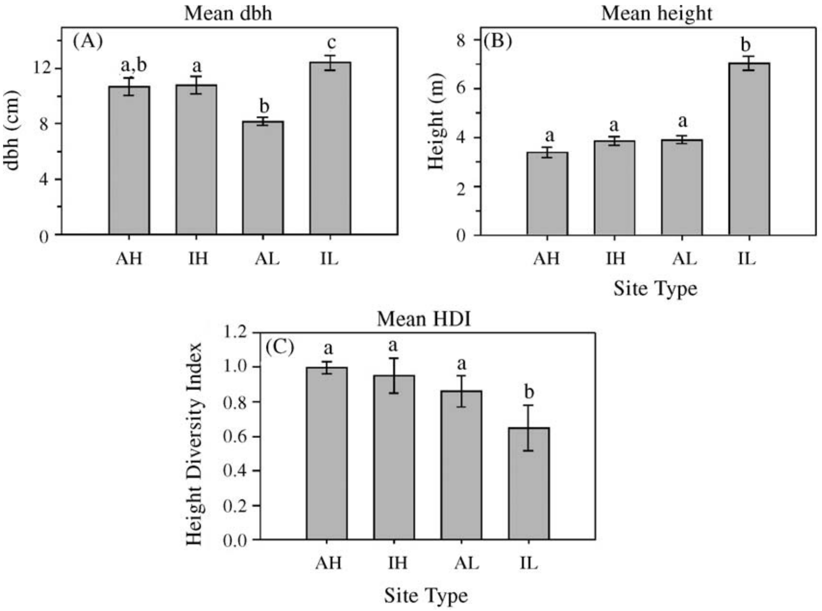

Fig. 4. Mean dbh (A), height (B), and height diversity index (HDI) (C) of all sampled sites. Same letters above bars indicate no significant difference in post hoc tests ($P > 0.05$).

5.1. Changes in forest structure

The present study documents the initial stages of changes in forest structure as a result of avalanche suppression. The effect of avalanche suppression on the density of conifers depends on the size of the stem (Fig. 3). The high density of trees at low elevations, regardless of avalanche activity, suggests that growing conditions associated with elevation over-ride the effects of avalanches on tree density. While we used standard size designations for the categories of trees, saplings, and

Table 2
Summary statistics of tree ring widths and standard chronologies

Site	Type[a]	No. cores	Mean ring width (mm)	Mean sensitivity	Correlation between trees
Andeer	AH	17	1.64_a	0.194	0.201
	IH	16	1.89_a	0.222	0.212
	AL	24	1.64_a	0.151	0.131
	IL	10	4.24_b	0.171	0.544
Obergesteln	AH	14	2.46_a	0.159	0.123
	IH	12	2.52_a	0.150	0.178
	AL	19	2.29_a	0.157	−0.265
	IL	15	2.96_a	0.139	0.278
Trun	AH	24	0.96_a	0.172	0.091
	IH	25	1.43_a	0.117	0.129
	AL	22	1.52_a	0.158	0.122
	IL	25	4.99_b	0.148	0.368
Ulrichen	AH	18	1.72_a	0.109	0.133
	IH	13	2.37_a	0.172	0.316
	AL	19	2.12_a	0.132	0.050
	IL	23	2.39_a	0.116	0.069
Vals	AH	27	1.17_a	0.090	0.013
	IH	27	1.02_b	0.136	0.198
	AL	25	1.52_b	0.130	0.027
	IL	26	3.56_c	0.082	0.073
All sites (means)	AH	100	1.48_b	0.140	0.101
	IH	93	1.89_a	0.153	0.196
	AL	109	1.79_a	0.145	0.022
	IL	99	3.57_c	0.124	0.225

For ring-width measurements, same subscript letters indicate no significant difference ($P > 0.05$) among values for a given site.

[a] A, active; I, inactive; H, high elevation; L, low elevation.

seedlings, we recognize that these categories are indicative of size and not necessarily age, especially at disturbed or high-elevation sites. The unfavorable growing conditions at high elevations reduce the rate of growth and consequent size of conifers. This likely resulted in a number of relatively old individuals being classified as saplings. The density of these smaller individuals was more clearly affected by avalanche activity. In active tracks, it is likely that the high density of stems in the sapling classes may represent relatively old individuals, whose small size is a result of avalanche activity. Avalanches can reduce growth rates and sizes of conifers and, furthermore, the susceptibility of conifers to avalanche damage is lower among smaller individuals (Butler and Malanson, 1985; Johnson, 1987; Patten and Knight, 1994). Thus, there is a feedback loop in which avalanches contribute to smaller stem sizes and smaller stems, in turn, are less likely to be damaged by avalanches.

We observed neither increases in absolute density nor successional changes in relative density from larch to the shade-tolerant spruce as a result of exclusion of avalanches, even though avalanches favor shade-intolerant species. Previous studies have documented lower densities of trees in frequently disturbed avalanche tracks (Butler, 1979; Johnson, 1987) and other studies have found changes in tree composition following the suppression of disturbances. However, such differences usually become detectable only

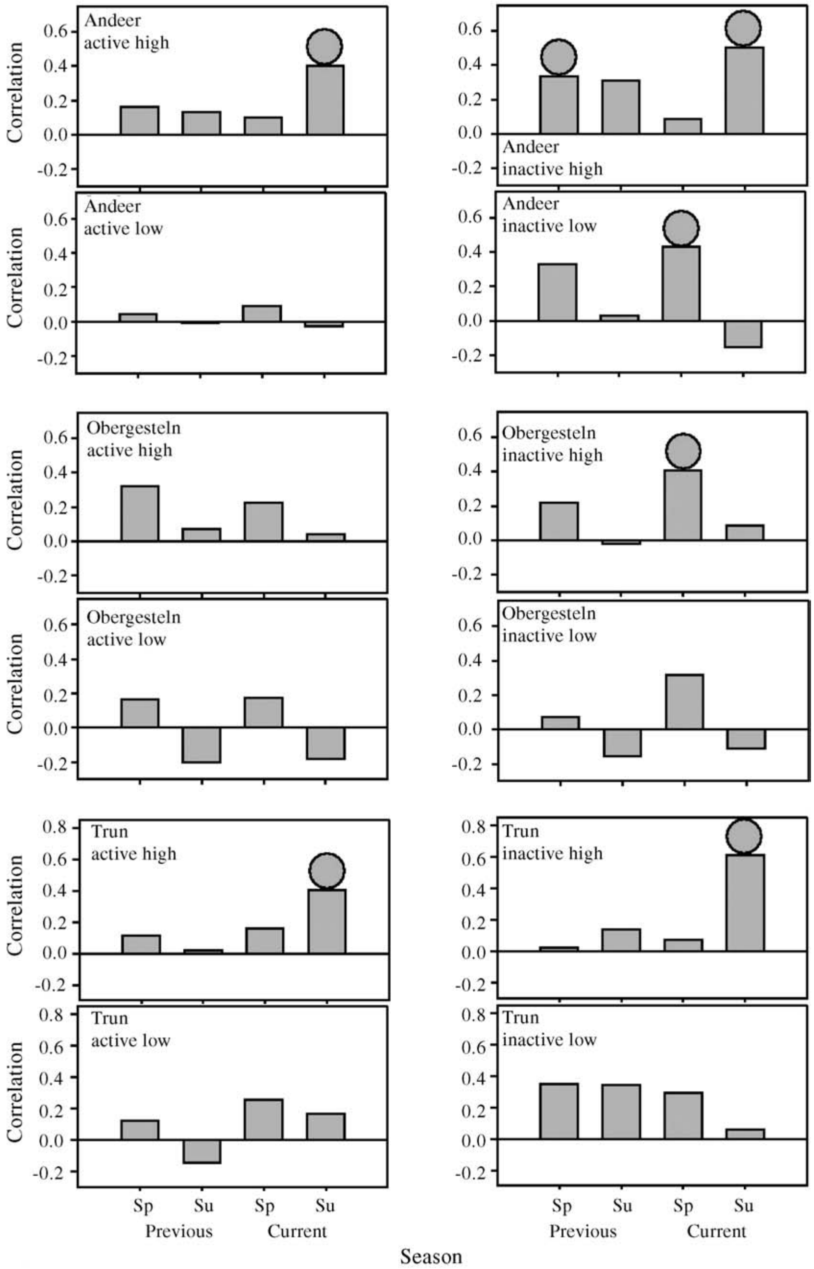

Fig. 5. Median correlation coefficients between annual ring-width indices from standard chronologies and spring and summer temperatures of the current and previous year. Analysis began the year that construction of avalanche barriers was completed. Dots above bars indicate significant correlations ($P < 0.05$).

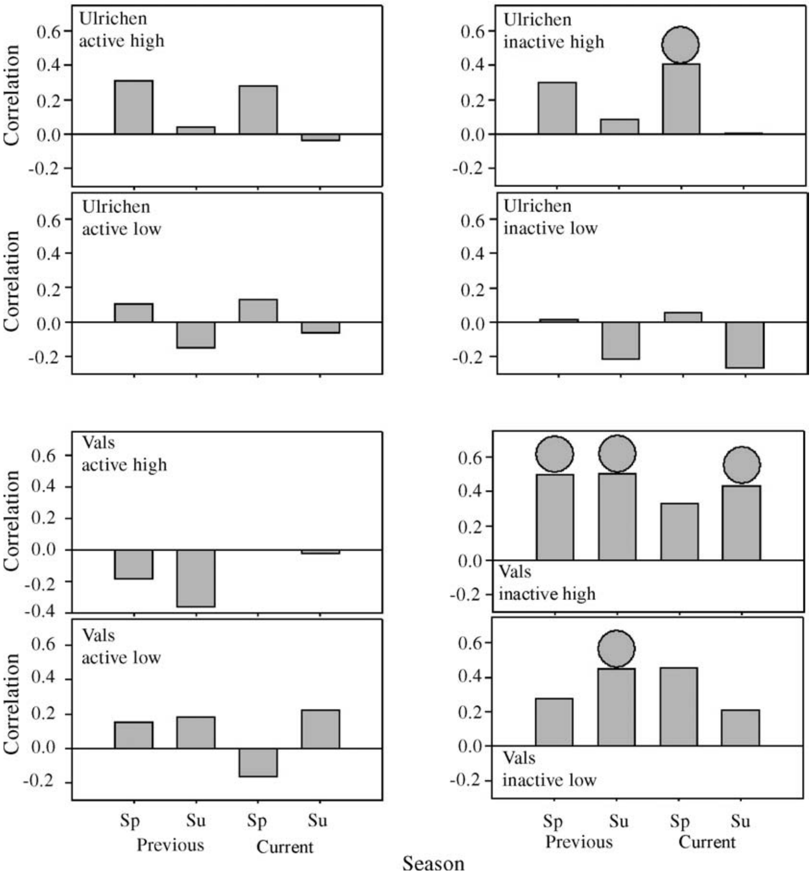

Fig. 5. (*Continued*).

after the new disturbance regime operates over relatively long time periods in contrast to the period considered in the present study. Thus, a likely explanation for the lack of hypothesized change in absolute and relative densities in the present study is that the time since exclusion of avalanches has not been sufficiently long given the relatively slow development in these high-elevation forests.

While the effect of avalanche suppression on tree density and composition has been negligible, we did observe more subtle differences that consistently indicate changes are occurring in structure and function following exclusion of avalanches (Fig. 4 and Table 2). First of all, the suppression of avalanches has resulted in the development of trees with greater diameters and heights, especially at lower elevations. These inactive stands at low-elevation are also the most structurally homogenous. The observed changes in tree size are mechanistically explained by the greater annual tree ring widths in inactive tracks, especially at lower elevations. This indicates that the rates of tree growth and ecosystem development have increased following the suppression of avalanches. Furthermore, all of these increases in development were most pronounced at low elevations, where climatic conditions are less stressful to tree growth. Thus, when the limiting influence of avalanche disturbance is removed, the rate of ecosystem development increases, but is governed by the limiting factors associated with existing environmental gradients.

5.2. Changes in driving factors

In addition to changing forest structure, the suppression of avalanche disturbances is also changing the relative importance of the factors that are controlling ecosystem development. The differences in the correlation between trees' annual growth (Table 2) and in the influence of climate on tree growth (Fig. 5) indicate a distinct change in the relative importance of climate to tree growth. Avalanches exert a heterogeneous influence on tree growth, even in the same track. As a result of the same avalanche, some trees may suffer broken limbs or other loss of biomass resulting in a reduction in tree growth, other trees may be killed, and others may escape injury and/or benefit from the mortality of neighboring trees. This phenomenon is responsible for the low correlation between trees in active tracks. In contrast, correlation between trees is substantially higher in inactive tracks. This indicates that once avalanche disturbance is suppressed, tree growth, and ecosystem development, is controlled more homogenously by the same broad-scale influence. The widespread and high correlations of ring-width indices with growing season temperatures at inactive sites, especially at high elevations, confirms that this broad-scale influence is climatic. Correlation analysis clearly shows that the degree to which climatic conditions limit tree growth is higher in inactive avalanche tracks, especially at high elevations. As with the stand structure data, this demonstrates that following the suppression of the dominant disturbances, there is an increase in the degree to which climatic conditions limit the growth of vegetation, indicating that climatic stress has a greater relative influence on ecosystem development. While the absolute effect of climate is the same at active and inactive avalanche tracks, climate becomes clearly more limiting to tree growth after the limiting effect of disturbances is excluded from the ecosystem.

In mountainous areas, as with other systems, stress is associated with existing environmental gradients. Following the suppression of disturbances in areas of high climatic stress (in this case at high elevations), ecosystem development will be more strongly influenced by climatic conditions. In contrast, in areas of low climatic stress (in this case at low elevations), climatic conditions are apparently less important, tree growth is more rapid, and competition among trees will likely become the dominant factor that will eventually most significantly control tree growth and stand development.

6. Conclusions and synthesis

A central theme in ecology is how organisms respond to changing environmental conditions. The suppression of natural disturbances is occurring in numerous ecosystems world-wide. For example, the suppression of formerly frequent fires has been shown to increase stand density, affect forest composition, and sometimes alter natural forest dynamics (e.g. Allen et al., 2002; Taylor, 2004). Likewise, the suppression of floods through dam construction has been found to change forest structure and composition in riparian areas (Cordes et al., 1997; Nislow et al., 2002; Shafroth et al., 2002; Azami et al., 2004). Similarly, our data indicate that the suppression of the natural avalanche regime is beginning to change forest structure in some communities in the Alps. The beginning of this change is reflected in greater growth rates of trees and in larger tree heights and diameters. In other ecosystems, avalanche tracks have been shown to influence the spread of other natural disturbances such as fires (Veblen et al., 1994). Furthermore, the structure and composition of avalanche tracks provides unique habitat for animal and plant species (Erschbamer, 1989; Mace et al., 1996; Krajick, 1998). The continued suppression of avalanches, while valuable for social reasons, is likely to eventually lead to the decline of these communities and may alter subsequent forest dynamics.

Furthermore, the suppression of avalanche disturbances can also increase the relative importance of climatic stress to ecosystem development. Following avalanche suppression, annual tree growth is more highly correlated among trees at a given site and tree growth is more highly correlated with growing season temperatures, especially at higher elevations. These changes amounts to a categorical shift from R communities to S or C communities along existing environmental gradients (Fig. 1). Suppression of various disturbances such as avalanches, fires, and floods is occurring in numerous ecosystems worldwide. We suggest that, in general, the suppression of disturbances predictably changes the relative importance of stress and competition along existing environmental gradients. Such a change in the driving ecological factors represents a major alteration of ecosystem function.

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