

The Influence of Changes in Climate and Land-Use on Regeneration Dynamics of Norway Spruce at the Treeline in the Swiss Alps

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Recent changes of climate and land-use are often regarded to affect the European Alpine region substantially and to trigger an increase in the elevation of the upper treeline. The patterns of tree invasion on a subalpine meadow at 1900 m a.s.l. in Sedrun, Canton Grisons, Switzerland, were studied in order 1) to reconstruct the process of tree establishment and tree-growth dynamics in space and time, and 2) to evaluate the influence of site properties, land-use change and climate on these processes. Dendroecological analysis of 105 Norway spruce combined with an assessment of 48 vegetation plots and 17 soil profiles revealed that the trees were established in one main period (1965–1980s), starting 15 years after the abandonment of the agricultural use of the meadow, and that there is a pronounced environmental gradient along the forest-meadow ecotone. Tree establishment and height growth were favoured close to the former forest edge, but all saplings irrespective of their distance to the forest edge and their age showed increased radial growth since 1990, coinciding with a period of higher summer temperatures in the region. Therefore, we conclude that the observed tree-line dynamics in Sedrun are the result of both land-use and climate change: Tree establishment was triggered by the abandonment of the agricultural use of the meadow, and strongly favoured by particularly good growing conditions in a warm decade, which illustrates the sensitivity of conifers near the alpine tree-line to temperature fluctuations.

Keywords dendroecology, microsites, subalpine meadow succession, tree growth, tree invasion

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1 Introduction

Upper tree-lines are part of dynamic landscapes and represent important ecological boundaries. Recently, the European alpine region has started to undergo substantial changes as far as land-use and climate are concerned. These trends are most likely to continue in the future and are expected to have pronounced effects on high-altitude forests and tree-lines. The global mean surface temperature has increased by about 0.6 °C over the 20th century, and the 1990s were the warmest decade of the millennium in the northern hemisphere (IPCC 2001). Since plant growth in high-altitude ecosystems is temperature-limited (Körner 1999, Jobbágy and Jackson 2000, Grace et al. 2002), global warming is expected to have strong effects on plant growth, vegetation composition and tree-line position (Guisan et al. 1995, Theurillat and Guisan 2001).

Tree invasion into previously unforested areas, e.g. increase in tree-lines, and changes in growth dynamics related to climatic changes have been reported widely for the last century and more frequently for the last decades in several high-elevation areas of the world, for instance North America (e.g. Taylor 1995, Weisberg and Baker 1995, Hessler and Baker 1997), Russia (e.g. Shiyatov 2003, Moiseev et al. 2004, Van der Meer et al. 2004), and in the European Alps (e.g. Theurillat and Guisan 2001). In Europe, climatic effects interact strongly with ongoing land-use changes. Natural tree-line has been lowered as a result of century-long mountain pasturing (Kuoch and Amiet 1970, Tessier et al. 1995). In the last few decades, however, a majority of former agriculturally used high-elevation grasslands in the Alps have been abandoned because of decreasing commercial value (Götsch et al. 2004, Leuch 2005). Some of these areas are subject to tree invasion, while other areas are not. The latter phenomenon is often ascribed to unfavourable site properties (Ott et al. 1997).

Nevertheless, it is still not clear which factor is driving the recently widely-observed tree invasions: climate change, land-use change, or changing site properties. We conducted a study near the tree-line in the canton Grison, where a recently abandoned meadow at 1900 m a.s.l. is invaded by trees, with the purpose to investigate

the relative influence of climate change, land-use change and local site properties on the process of tree invasion. Dendroecological analysis and an assessment of vegetation and soil properties were used in order (i) to reconstruct the process of tree establishment and tree growth in space and time, and (ii) to evaluate the influence of climate, land-use change and site properties on these processes.

2 Material and Methods

2.1 Study Site

The study site is located on a south-east facing slope (46°41'27"N; 08°48'08"E) at 1900 m to 1950 m a.s.l. near Sedrun in the northern Central Alps, canton Grisons, Switzerland, approx. 100 m lower than the estimated natural tree-line, i.e. the altitudinal limit of closed forest (Ott et al. 1997). Situated between the Aar massif in the North and the Gotthard massif in the south, the region is characterised by a climate typical for the Central Alps. The annual precipitation is 1500 mm and the mean January and July temperatures are -6.1 °C and 7.9 °C (meteorological station Gütsch, 46°39'14"N; 08°37'59"E, 2280 m a.s.l.). The length of the growing season at this elevation is unlikely to exceed three months (Holtmeier 2003).

The pre-Triassic plutonic rock reaches the surface at this site. Therefore, the bedrock consists of pure granite (Christ and Nabholz 1955). The soil is a Podzol (according to the AG BODEN (1994) classification system) with a thick raw humus layer. The slope of the study area ranges from 78% in the mature forest to 50% in the open meadow, whereas the microtopography is fairly homogeneous without pronounced ridges or depressions. The composition of the forest-meadow ecotone is as follows: The mature forest is dominated by Norway spruce (*Picea abies* L.) reaching a tree height of approx. 30 m and growing in clusters, which is typical for the subalpine zone (Ott et al. 1997). The understory vegetation is a patchy mosaic of dwarf shrubs mainly *Vaccinium myrtillus* L. and *Vaccinium uliginosum* L., graminoids (e.g. *Deschampsia flexuosa* L.



Fig. 1. Picture of the study area. Young Norway spruce invade the abandoned meadow close to the forest edge in Sedrun, Canton Grison, Switzerland.

Parl., *Luzula sylvatica* (Huds.) Gaud.), herbs (e.g. *Melampyrum sylvaticum* L., *Hieracium murorum* L., *Homogyne alpina* L.) and bare ground.

The mature forest is best referred to as *Homogyno-Piceetum vaccinietosum myrtilli* (Ott et al. 1997). Trees have invaded an area along the forest edge approx. 600 m long and 50 to 60 m wide (distance to the outer-most trees). Most of the young Norway spruce saplings occupy the area close to the forest edge (up to 15 m from the edge) growing in clusters, whereas slope-upwards, in the middle-slope area (15–35 m from the forest edge), sapling density is lower (Fig. 1). Further slope upwards, in the upper-slope area (above a distance of 35 m from the forest edge), only a few solitary trees have been able to establish to date. The ground vegetation on the meadow differs from the one in the forest. Dwarf shrubs become more dominant with increasing distance to the former forest edge, while the abundance of herbs and graminoids is decreasing abruptly. In the middle and upper-slope area, *Calluna vulgaris* (L.) Hull. reaches a cover of 80 to 100% with some individuals of *V. uliginosum* intermingled, therefore this area will be referred to as open heath.

The former meadow has been abandoned around 1950. Prior to the 20th century, the area from the forest edge up to the mountain-top (at 1990 m a.s.l.) was used as mountain pasture where cattle were left grazing for the whole growing season. From 1900 until 1950, agricultural use was reduced to the area adjacent to the forest edge at the bottom part of the former meadow. This area was used only as grassland for hay production, not for grazing (Durschei G., Hendry T., community archive, Sedrun, personal communication).

2.2 Field Methods

The research area was stratified into four strata based on tree density. The first stratum encompasses the outermost 10 m of the mature forest; the second stratum encompasses the area of tree invasion close to the forest edge (0 to 15 m from the forest edge), where tree density ranges from 0.29 to 0.61 tree/m²; the third stratum encompasses a smaller, restricted area of tree invasion in the middle slope (15 to 35 m from the forest edge), where tree density is approx. 0.1

tree/m²; and finally the fourth stratum encompasses the upper slope area (above 35 m from the forest edge), where tree density is lower than 0.01 tree/m². Data sampling was conducted along five transects from the mature forest to the upper slope area ending 10 m above the outer-most sapling in the former meadow. The starting point and the angle of the direction of each transect were recorded.

Along the transects, tree data were sampled in plots located in the middle of each stratum. In the 'mature forest', two increment cores per tree of four mature Norway spruce per plot were extracted at breast height (1.3 m) to obtain a reference for typical growth on this site. In the area 'close to the forest edge' and in the 'middle slope', 10 saplings per plot each representing a separate height class, were sampled within a radius of 5 m. If the plot contained less than 20 saplings, the sampling radius was increased to 10 m. In the 'upper slope' area, all saplings within a distance of 10 m on each side of the transect were sampled. Per sapling, two increment cores were extracted on the slope upward, north-west facing side of the stem, one at the stem base above the root collar to determine age, and another one at the lowest point where the stem was growing vertically to analyse growth (height range 0–40 cm above ground). If the stem diameter was too small for coring, stem discs were cut instead. Additionally, vertical tree height, stem diameter at the extraction height and the number of vertical branches (multiple stems) of each sapling were recorded. In total, 95 saplings and 20 mature trees were sampled and permanently labelled for later relocation.

Along three transects, an assessment of the ground vegetation was conducted and soil profiles were dug to describe microenvironmental conditions in each stratum, and to relate patterns of tree establishment and growth to site properties. Each soil profile was located in the centre of a tree-sampling plot except for profiles in the upper slope stratum. There, they were repeated every 10 m along the transects until the area above the uppermost tree was reached. For each soil profile, soil horizons and horizon thickness were documented and classified into the categories L, Of, Oh and Ah according to the German classification system (AG BODEN 1994). L refers to an upland horizon

that consists of relatively fresh plant residuals, Of refers to an horizon that consists largely of poorly decomposed plant residuals, and Oh refers to an horizon that consists of well-decomposed plant residues of which the most part have been transformed into humic materials. Ah, finally, refers to a mineral horizon that is enriched with humified organic matter (Green et al. 1993, AK Bodensystematik 1998).

The assessment of the ground vegetation was conducted in 1 m × 1 m plots whose centre was within a radius of 1 m from the centre of the tree sampling plots. In the upper slope stratum, plots were repeated every 10 m, one being located on each side of the transect at a distance of 1 m until the area above the uppermost tree was reached. In each plot, the percentage cover of ground vegetation and bare ground, and the percentage cover of bryophytes, herbs, graminoids and shrubs were estimated. Each vascular plant species was identified and the percentage cover abundance estimated to the nearest 5%.

2.3 Data Analysis

All increment cores and stem discs were sanded using a belt sander. Tree rings were counted and tree-ring width was measured under a binocular microscope and recorded using the software program TSAP (Time Series Analysis and Presentation Program, Rinn 1996). All ring-width curves were visually cross-dated. If the pith of the tree was not intersected by the increment borer, a pith locator (concentric circles matched to the curvature of the inner rings) was used to estimate the number of missing rings to the pith (Bräker 1981). In some instances, the quality of the base cores was insufficient for exact age determination. In such cases, we estimated the age of the saplings based on the 'age' of the upper core by applying the following formula: $A = D/a + B$, where B is the age of the upper core, D is the distance (cm) between the base core and the upper core, and a is the average height growth per year of all saplings. The ring-width curves of samples from the mature forest were visually cross-dated.

To study the relationship between growth and climate at this site, the samples from the mature forest were standardised (double-detrending)

using the software package ARSTAN, version 6.05P (Cook 1985) to remove the effects of tree aging from the ring width data and to maximize the climatic signal. Subsequently, a correlation analysis was conducted between the detrended master chronology of residuals (samples from the mature forest) and the monthly mean temperatures and precipitation sums (Time period: 1900–2002, meteorological stations: Disentis, 1130 m a.s.l. and Sedrun, 1560 m a.s.l.).

The vegetation surveys were processed as follows: Vegetation structure and species richness were compiled for each plot, and the Evenness (Pielou 1966) was computed according to Eq. 1:

$$J = - \left(\sum_{i=1}^s P_i \ln P_i \right) / \ln S \quad (1)$$

where

J = evenness

S = number of species in the plot

P_i = relative abundance of species i in the plot

To investigate the environmental factors that may contribute to the tree invasion patterns observed, an analysis of plant indicator values (Landolt indicator values: Landolt 1977) was performed. The Landolt indicator values are a special adaptation of the Ellenberg indicator values (Ellenberg 1974) to the Swiss flora. The Landolt indicator values define the ecological range of plant species along environmental gradients on a five point scale and an analysis of these indicator values in the local vegetation can, therefore, provide inference on the prevailing local environmental conditions. We considered the indicator values for light (low values show little necessity of light, high values a great necessity of light), nitrogen (low values indicate nutrient poorness, high values nutrient richness), soil acidity (low values indicate acidic soils, high values base rich soils) and soil moisture (low values indicate low moisture content, high values high moisture content). The mean of each of these Landolt values per vegetation plot was calculated using the unweighted Landolt values of each species per plot applying a software program (D. Ramseier, Geobotanical Institute ETH Zürich).

All statistical analyses were conducted using the software program SYSTAT, version 10.

3 Results

3.1 The Microenvironment: Soil and Ground Vegetation

The topsoil layers throughout the study area are characterized by a thick raw humus layer, but the analysis of the soil profiles revealed distinct changes in horizon thickness with increasing distance from the forest edge (for the pooled soil profiles, see Fig. 2). The organic topsoil layers tended to increase in thickness slope upwards, while the thickness of the humus-mineral horizon decreased. The thickness of the organic topsoil layers for the middle slope area and especially the upper slope area (more than 30 m from the forest edge) was twice as large as that of the organic topsoils in the mature forest and the area close to the forest edge. The humus-mineral horizon is poorly developed in the upper slope region above a distance of 40 m from the forest edge, while it reached a thickness of over 10 cm in the mature forest and in the area close to the forest edge.

Vegetation structure was found to differ between the strata (Table 1). Ground vegetation in the mature forest was characterized by nearly equal proportions of shrub-layer cover, herb-layer cover and bare ground, while the other three strata on the former meadow were dominated strongly by the shrub layer. Bare ground was nearly absent in the middle and upper slope areas. Occasionally, bare-ground patches were found in the area close to the forest edge; in the mature forest, patches of bare ground were frequent. Trees occurred only in vegetation plots in the mature forest and close to the forest edge, while they were absent in vegetation plots in the middle slope and upper slope areas.

Species richness did not differ significantly between the strata, but there was a significant decrease in evenness with increasing distance from the former forest edge (ANOVA, $P < 0.001$) (Table 2). The low evenness in the middle and upper slope areas was due to the vegetation structure presented above. In these areas, *Cal-*

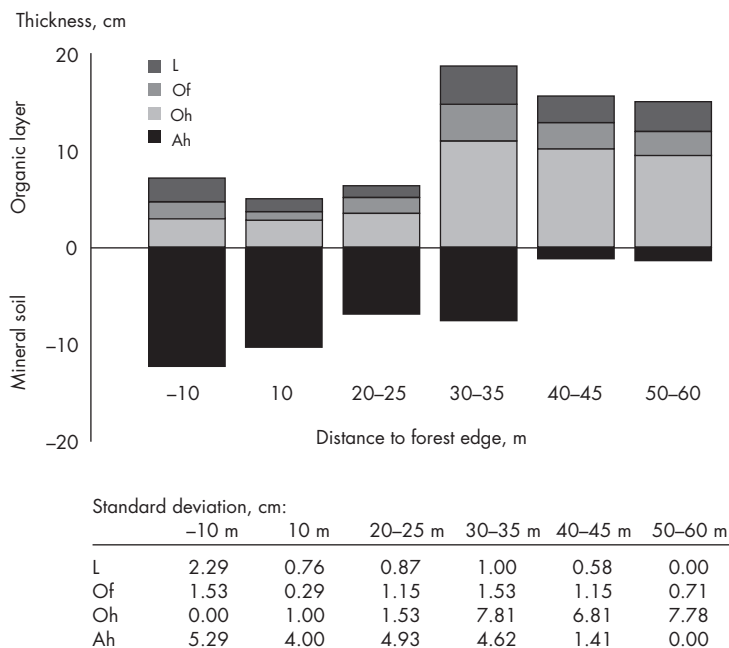


Fig. 2. Pooled soil profiles along the forest-meadow ecotone. The soil profiles show the horizon thickness of the top soil organic layers L, Of and Oh, and the mineral soil horizon Ah with increasing distance to the forest edge. The standard deviation of each value is shown in the table at the bottom right.

Table 1. Vegetation structure. Mean and standard deviation of the percentage cover abundance in each structure layers (ecological groups) per stratum

	Mature forest (n=12)	Close to the forest edge (n=12)	Middle slope (n=4)	Upper slope (n=20)
Tree layer ^{a)}	13.3 ± 25.1	9.2 ± 18.8	0	0
Shrub layer ^{b)}	37.6 ± 30.1	86.7 ± 19.0	91.2 ± 11.1	84.7 ± 14.3
Field layer				
gramineous	26.0 ± 20.4	2.2 ± 3.1	2.7 ± 2.6	2.1 ± 3.7
herbaceous	10.7 ± 1.0	0.7 ± 0.2	3.1 ± 4.6	1.6 ± 2.4
Ground layer ^{c)}	1.2 ± 1.8	0.1 ± 0.2	7.7 ± 9.3	12.9 ± 13.6
Bare ground	23.3 ± 24.8	5.9 ± 11.4	1.6 ± 2.3	0.6 ± 1.5

^{a)} Exclusively Norway spruce saplings exceeding shrub layer height (40 cm)

^{b)} Exclusively dwarf shrubs

^{c)} Exclusively bryophytes and lichens

luna vulgaris reached a dominance of over 60%, whereas in the area close to the forest edge, the dominating shrub layer was composed of the four dwarf shrub species *C. vulgaris*, *Vaccinium uliginosum*, *Vaccinium myrtillus* and *Vaccinium*

vitis-idaea L. with a percentage cover of 38.1%, 24.0%, 19.2% and 12.6%, respectively, which resulted in a higher Evenness.

The occurrence and abundance of some species tended to be characteristic for a single stratum

Table 2. Mean number of species, mean evenness and standard deviation per stratum.

	Mature forest (n=12)	Close to the forest edge (n=12)	Middle slope (n=4)	Upper slope (n=20)
Mean no. of species	8.4 ± 3.4	7.9 ± 2.1	9.2 ± 0.5	8.7 ± 2.05
Evenness	0.7 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1

Table 3. Mean percentage cover abundance and standard deviation of species characteristic for a single stratum

	Mature forest (n=12)	Close to the forest edge (n=12)	Middle slope (n=4)	Upper slope (n=20)
<i>Deschampsia flexuosa</i>	14.2 ± 15.8	3.5 ± 3.8	0.1 ± 0.2	0.6 ± 1.1
<i>Calluna vulgaris</i>	4.2 ± 11.6	35 ± 24.4	66.2 ± 12.5	60.7 ± 21.9
<i>Melampyrum sylvaticum</i>	1.7 ± 2.2	0.6 ± 0.8	0	0 ± 0.1
<i>Vaccinium myrtillus</i>	19.7 ± 21.5	17.7 ± 21.7	2 ± 2.2	3.2 ± 7.7

(Table 3). These were *Deschampsia flexuosa*, *Melampyrum sylvaticum* and *V. myrtillus* for the mature forest, and *C. vulgaris* for the middle and upper slope areas. The area close to the forest edge took an intermediate position regarding the occurrence and abundance of these species.

The analysis of the unweighted, mean Landolt indicator values per vegetation plot revealed a significant difference between the mature forest and all three strata on the former meadow in all Landolt values (Kruskal-Wallis test, $P < 0.001$: e.g. nitrogen, light, reaction (pH) and moisture value: Fig. 3). There is a significant difference between the area close to the forest edge and the upper-slope area in the light value (pairwise Wilcoxon test, $P < 0.05$) and a near-significant difference in the nitrogen value (pairwise Wilcoxon test, $p = 0.057$). Light values were higher, but reaction and nitrogen values tended to be lower in the middle and upper slope area than in the mature forest. Again, the area close to the forest edge takes an intermediate position with respect to the nitrogen and light values.

3.2 Patterns of Tree Invasion

Tree-age analysis (Fig. 4) revealed that there was no significant difference in the mean years of establishment between the three strata (ANOVA,

$F = 0.165$, $P > 0.05$). Tree invasion was a simultaneous process with a main establishment period from 1965 to 1982 in all three strata, irrespective of the distance to the forest edge. This period of enhanced tree invasion began about 15 years after the agricultural use of the meadow had been abandoned. Only in the area close to the forest edge, trees established both before and after this period. It is noteworthy that no tree establishment occurred in the middle and upper slope area since the beginning of the 1980s and close to the forest edge since the beginning of the 1990s.

3.3 Growth Patterns

There was no significant difference in tree height between the three strata. However, maximum tree height tended to decrease with distance from the forest edge. The ratio height /age, a measure of height-growth efficiency, differed significantly between the three strata (ANOVA, $F = 3.686$, $P = 0.029$). Saplings of a given age were smaller in the middle and upper slope than close to the forest edge. We also counted the number of multiple stems and found a striking pattern: There was a highly significant difference in the number of multiple stems between the three strata (Fig. 5; Kruskal-Wallis test, $P < 0.001$). The formation of vertical branches was most frequent in the upper

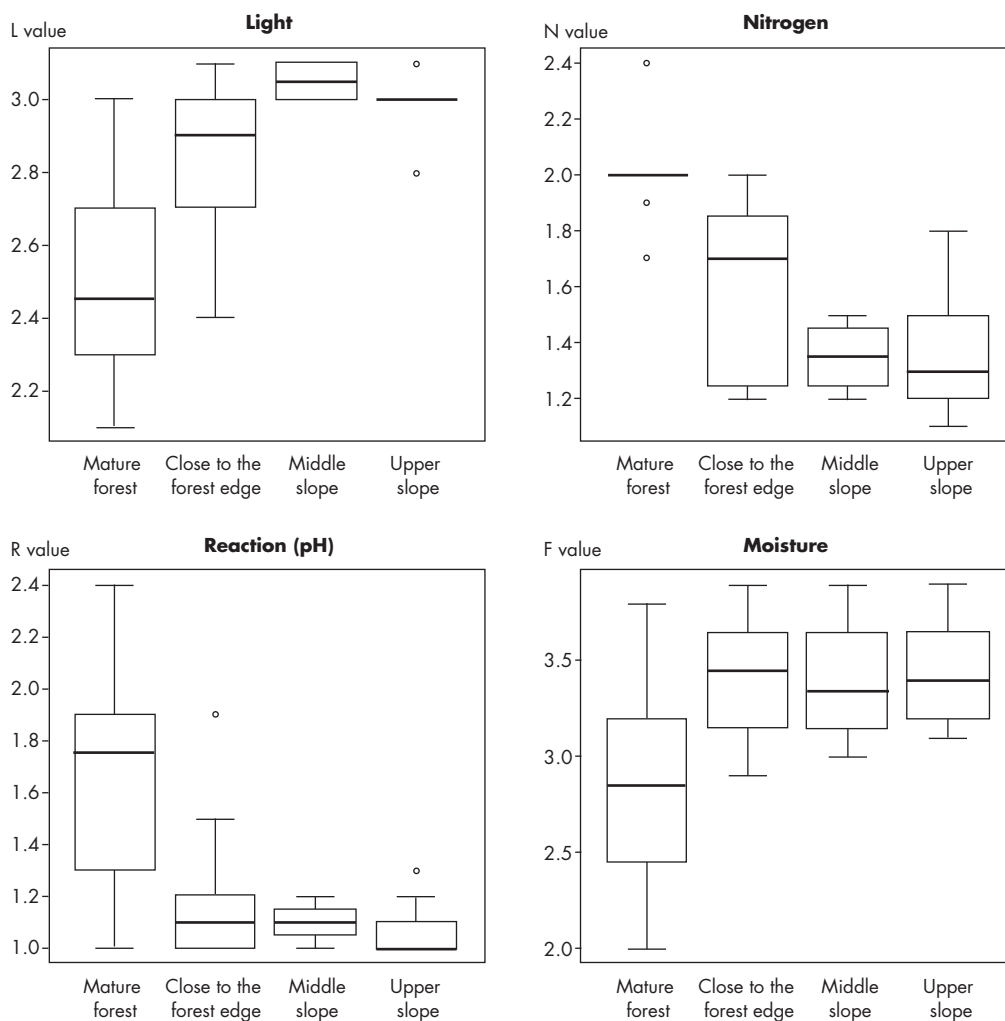


Fig. 3. Landolt indicator values for light, nitrogen, reaction (pH), and moisture. Boxplots show median (central line), 25th and 75th percentiles, and outliers.

slope area, somewhat less frequent in the middle slope area and rare close to the forest edge.

The analysis of the relationship between tree-ring width of the reference trees ($n=20$) in the mature forest (i.e. the detrended master chronology of residuals) and the monthly temperatures and precipitation data revealed that radial growth was correlated with the mean June and significantly correlated with the July temperatures (Correlation analysis (Pearson), $P < 0.05$). No significant correlation was found between radial growth and the precipitation data.

We compared mean radial growth of the sampled saplings but found no obvious difference in growth patterns between the three strata. Striking was the observed increase in radial growth of all saplings irrespectively of slope position and age since 1990 (Fig. 6) while the mature trees in the forest showed no such effect. The analysis of the mean June–July temperatures since 1960 revealed increased summer temperatures for the period between 1990 until 2003 in the study region (Fig. 7). This period coincided exactly with the increase in radial growth of the saplings.

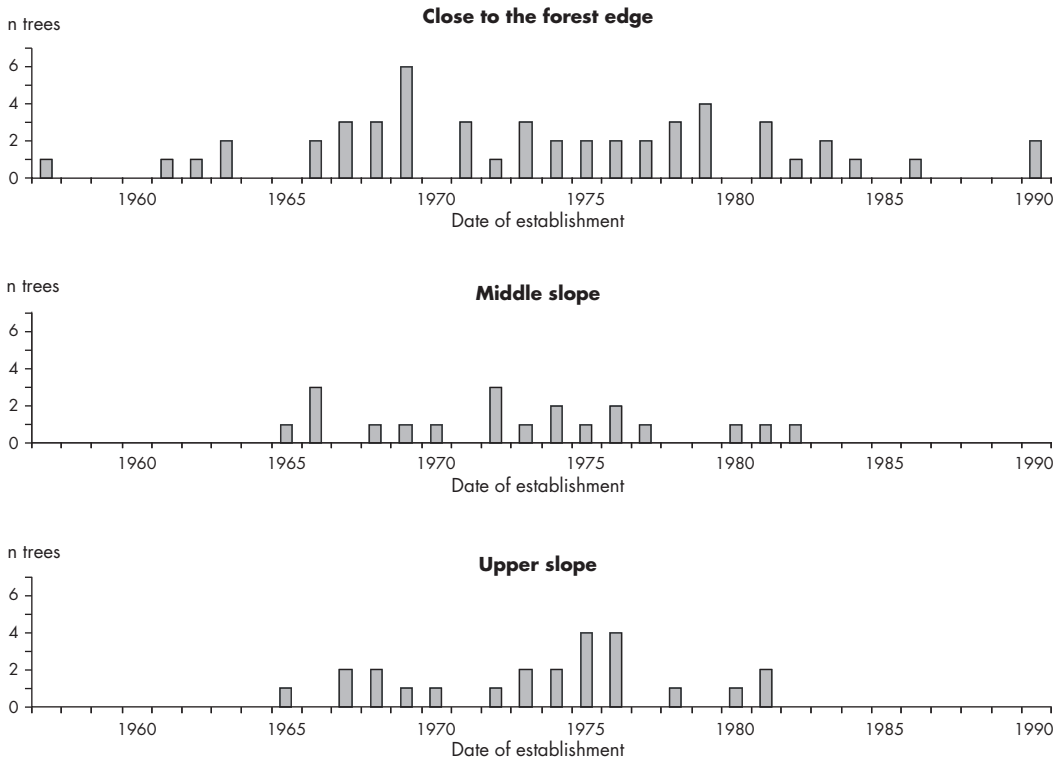


Fig. 4. Date of establishment of the sampled young Norway spruce per stratum. Each bar shows the number of estimated tree establishment events per year.

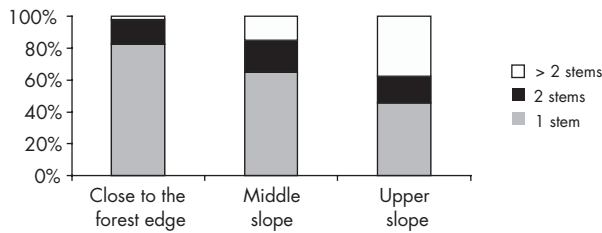


Fig. 5. Growth forms of the sampled young Norway spruce per stratum. The bars show the percentage of trees with multiple stems.

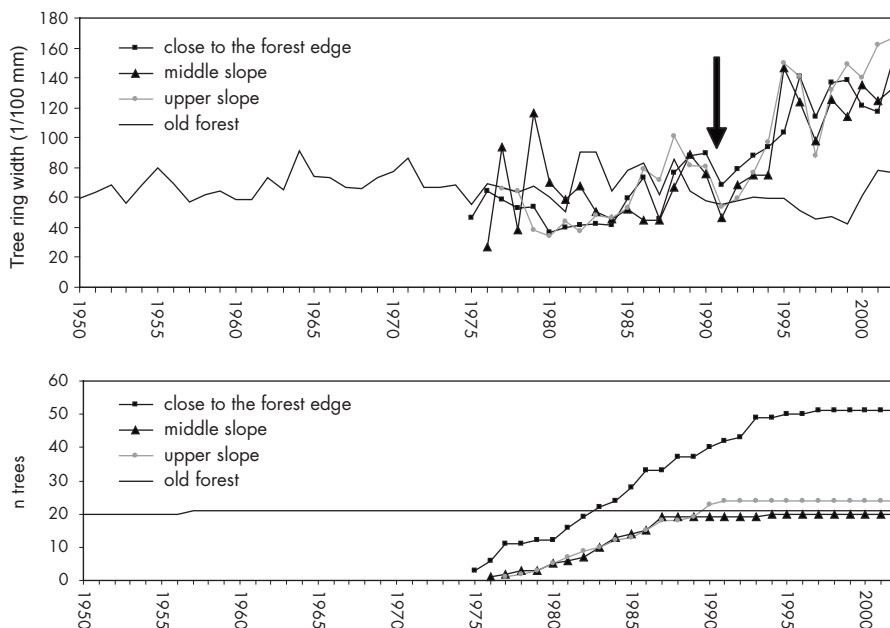


Fig. 6. Average tree-ring width and sample size per year of the sampled young Norway spruce per stratum and for the mature trees in the forest. The arrow points at the synchronous increase in radial growth of the young Norway spruce trees in the 1990s.

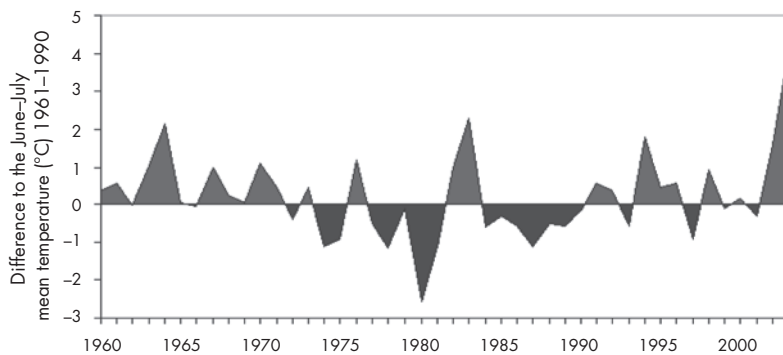


Fig. 7. Temperature anomalies. The graph shows the differences (°C) of the mean June/July-temperatures of the last 40 years to the June/July mean temperature of 1961 to 1990.

4 Discussion

4.1 Tree Establishment

The study area was divided into three strata according to tree density, which reflects the state of forest succession. The number of established saplings is highest in the area close to the forest edge, decreases in the middle slope area and is lowest in the upper slope area, where only some isolated saplings occur. This decrease of sapling density with increasing distance to the forest edge cannot be explained simply by a seed-rain decrease related to the distance to seed trees in the forest, the distance of tree invasion is not exceeding 60 m from the forest edge. This is a distance that the small, light Norway spruce seeds reach easily as was shown in a seed trap experiment conducted in a blowdown area in the Central Alps (Lässig et al. 1995). Furthermore, thermal turbulences and updrafts typical for south-facing slopes might even increase dispersal distances in our study area (Tackenberg et al. 2003). Therefore, microenvironmental factors are more likely to have determined the observed pattern of tree invasion.

The comparison of site properties between the strata exhibited some revealing differences in microenvironmental factors that may help to explain the observed invasion patterns. The thickness of the top organic soil layers increases in the middle slope and upper slope area while the thickness of the humus-mineral layer decreases. A thick organic layer of raw humus is often regarded as unfavourable substrate for germination because of an unsuitable moisture regime and an insufficient nutrient supply (Ott et al. 1997, Hanssen 2003) and might therefore lower establishment success in the middle and upper slope area.

Competition with ground vegetation is often also considered as an important factor limiting seedling establishment (e.g. Franklin et al. 1971, Magee and Antos 1992, Berkowitz et al. 1995, Prach et al. 1996, Jäderlund et al. 1997, Hanssen 2003). These differences in vegetation structure and composition we observed between the strata may have influenced the success of tree invasion.

Competition with ground vegetation (below-ground for water and nutrients, aboveground for

light) can reduce seedling survival and establishment. Additionally, dense vegetation forms a physical barrier for seedling establishment and can damage seedlings through burial by litter (Ott et al. 1997). Dwarf shrubs, although growing slowly, are considered to be more inhibitive to tree-seedling establishment than herbs or grasses since they accumulate a large below- and aboveground biomass (Kuoch and Amiet 1970, Jäderlund et al. 1997, Ott et al. 1997, Hanssen 2003). Furthermore, ericaceous ground vegetation is believed to affect the species composition of the ectamycorrhizal fungal community, which may have consequences for the ability of tree seedlings to acquire nutrients (Jäderlund et al. 1997). Since there is a change in vegetation structure from a patchy mosaic of dwarf shrubs, herbs, grasses and bare ground in the mature forest and close to the forest edge to a dense carpet of heath with hardly any bare ground, we conclude that the area close to the forest edge may have offered more favourable conditions for tree seedling establishment as far as competition by ground vegetation is concerned. Interestingly, the area close to the forest edge consisted of both typical woodland and typical open heath species. This indicates that established saplings already might have changed the microenvironment of the ground vegetation, since woodland ground layer species have been able to establish there.

The analysis of the Landolt indicator values showed a trend to wetter, more acidic and nutrient poorer conditions with increasing distance to the forest edge. Thus, the abrupt decrease in tree density slope upwards may be related to locally harsher environmental conditions.

The age analysis of the invading saplings provided additional information on the patterns of recruitment. Tree invasion was a continuous process from 1965 to 1982 for all three strata, irrespective of the distance to the forest edge. Nevertheless, tree establishment was favoured close to the forest edge since sapling density is higher and some trees established before and after the main establishment period. This might, apart from more favourable vegetation and soil conditions, be due to a shelter effect of the nearby forest edge, which improves microclimate for seedling establishment, e.g. by 1) decreasing the vigour of adjacent meadow vegetation by shading and root

competition (Magee and Antos 1992), 2) protecting the saplings from snow pack movements (Ott et al. 1997), 3) reducing snow loads (Miller and Halpern 1998), 4) accelerating snowmelt and extending the growing season (Franklin et al. 1971), 5) reducing radiative cooling at night time and thus lessening the risk of frost injury (Langvall and Löfvenius 2002), and finally 6) simply offering a larger fraction of bare ground for seed germination (Ott et al. 1997). Once some trees were established, they may again themselves provide shelter for new seedlings to establish. This would explain the spatially clumped distribution of saplings in our study site, which has been described also by other authors for tree regeneration in the subalpine zone (Franklin et al. 1971, Magee and Antos 1992, Miller and Halpern 1998).

Tree invasion, starting 15 years after the agricultural abandonment is likely to have been triggered by this land-use change, since establishment was not hindered mechanically any more and ground vegetation was probably not yet as vigorous. Striking is the absence of tree establishment in the middle and upper slope since the beginning of the 1980s and in the area close to the forest edge since the beginning of the 1990s, in spite of periodical mast fruiting, i.e. periods of simultaneous, massive seed production (1981, 1984, 1985, 1992, 1995, 1999; A. Burkhart, WSL Birmensdorf, personal communication) and generally more favourable weather conditions (Fig. 7). The absence of any establishment during the last two decades in the middle and upper slope region and during the last decade in the area close to the forest edge is likely to be due to a lack of suitable additional microsites. The suitable microsites had already been occupied by saplings during the main establishment period and therefore, their availability decreased. This decrease complies with the hypothesis that secondary succession gradually diminishes with time (Bornkamm 1981, Myster and Pickett 1994) and that the availability of microsites controls early succession (Myster and Pickett 1994). The area close to the forest edge must have offered a larger number of suitable microsites than the middle and upper slope areas, and therefore, experienced a more rapid succession. Varying rates of forest succession over relatively short distances are characteris-

tic for the harsh subalpine zone (Donnegan and Rebertus 1999).

4.2 Tree Growth

We did not find a significant difference in average tree height between the strata. Nevertheless, relatively tall trees (exceeding 5 m up to 6.3 m) occurred only in the area close to the forest edge. The vertical height /age ratio, i.e. height-growth efficiency, was highest close to the forest edge, low in the middle slope area and lowest in the upper slope area. This indicates that conditions allowing relatively rapid vertical growth prevail mainly in the area close to the forest edge, whereas trees in the middle and upper slope areas may experience conditions that reduce height-growth rates, i.e. the trees are forced to invest carbon in stability (diameter) rather than in height growth. Heavy snow loads and snowpack movements, for instance, exert mechanical pressure on the stems and force them to grow thick and concave (Frey 1977, Ott et al. 1997).

Another very pronounced difference in growth forms between the strata was found in the formation of multiple stems. This phenomenon was rare close to the forest edge, occasional in the middle slope area and very frequent in the upper slope area. Several authors have found a similar multiple-stem growth form of conifers near the altitudinal tree-lines (e.g. Marr 1977, Ives and Hansen-Bristow 1983, Weisberg and Baker 1995, Moiseev et al. 2004, Van der Meer et al. 2004). The formation of vertical branches is induced if the main stem axis breaks or dies; subsequently branches start to grow vertically and take over the function of a leader shoot (Schönenberger et al. 1994, Ott et al. 1997). This implies that biotic and abiotic forces that damage the main stem axis were more frequent or more intense in the middle and especially the upper slope area than close to the forest edge, where trees might benefit from the protective influence of the nearby forest edge. Such forces are, for instance, pressure from heavy snow loads, frost, winter desiccation, or snow mold.

In summary, we found pronounced shifts in sapling morphology from the forest edge to the slope top over a distance of merely 60 m. Sur-

prisingly, there is no comparable shift in radial growth. Radial growth of all saplings, irrespective of their position on the slope, their age or vertical height, tends to show similar growth. This implies that in the case of radial growth, the influences of local site conditions, e.g. local abiotic conditions or competition effects with the surrounding vegetation, are overwhelmed by the influence of a common factor, i.e. climate.

4.3 Climate Change

The climate-growth analysis revealed that radial growth at our study site is limited by the mean June and July temperatures. Growth limitation by summer temperatures is a common feature of conifers growing close to altitudinal or boreal tree-lines and has been reported by many authors (Briffa et al. 1996, Waldner and Schweingruber 1996, Desplanque et al. 1999, Körner 1999, Holtmeier 2003, Moiseev et al. 2004). Our dendrochronological analysis showed a pronounced increase in radial growth rates of all saplings, irrespective of their slope position, age or vertical height, coinciding with a period of higher summer temperatures during the last 15 years. However, mature trees inside the forest did not show a similar reaction to the warmer period, which could be explained by a decrease in sensitivity to abiotic conditions often observed with increasing tree age (Schweingruber 1993) or by a strong influence of competition on growth reactions inside the mature forest, which act to reduce climatic signals in tree-ring widths. Nevertheless, the observed increase in radial growth related to warmer temperatures in our study is not a single case. Some researchers have found similar recent increases in growth related to warming in subalpine regions throughout the world during the last century (Neumann and Schadauer 1995) and particularly more pronounced during the last decade (Rolland et al. 1998, Paulsen et al. 2000).

5 Conclusions

Our study provided insights into the role of land-use change, climate change and site properties for

tree invasion in the subalpine region, and therefore, it contributes to a better understanding of tree invasion processes into the alpine tundra. Land-use change, i.e. the abandonment of agricultural use of meadows, can induce tree invasion by rendering tree establishment possible and therefore acting as a trigger. Nevertheless, once tree establishment was possible, it was then highly dependent on the availability of microsites that provided suitable microconditions for seedling establishment and growth. These initial microsites decreased in availability with time, and the rate of tree invasion thus decelerated. However, established trees may, once they have reached a certain height, create new suitable microsites for establishment in their vicinity. Therefore, we predict that future tree invasion at this site will be slow, but it will continue.

As far as climate change is concerned, we were able to show that it exerted a strong stimulation of diameter growth over the past 15 years. However, the limiting factor controlling tree invasion at this site was the availability of suitable microsites, i.e. site properties. Tree-line increase due to higher temperatures at our study site may, therefore, be characterized by a time lag, since suitable microsites must be available first. This indicates that predicting future tree-line dynamics in the light of climate change should also take into account the availability of microsites and the effect of climate change on microsite properties. Therefore, further research on how vegetation, soil and snow patterns are influenced by a changing climate is needed.

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