

Regeneration dynamics of Norway spruce (*Picea abies* L.) on a subalpine meadow near the treeline in Sedrun, Kt. Graubünden, Switzerland

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Introduction

Recently, the European alpine region undergoes substantial changes as far as land-use and climate are concerned and these trends are going to continue. The global average surface temperature has risen by about 0.3 to 0.6 degrees and the mean global temperature of the last decade was the warmest of the last 1000 years (IPCC 2001). Since plant growth in alpine tree-line ecosystems is temperature limited (Körner 1999), global warming is expected to have drastic effects on plant growth, vegetational composition and tree line position in the alpine region (Körner 1998, Rolland et al. 2000, Moiseev et al. 2004). These effects interfere with ongoing land-use changes. In the last few decades a majority of former agriculturally used grasslands in the Swiss mountain areas near the treeline have been abandoned because of decreasing commercial value. Some of these areas undergo a process of tree invasion while others do not. These meadows provide a unique opportunity to study natural regeneration dynamics of Norway spruce near the tree line. We investigated the regeneration patterns on a south-facing, since 1950 abandoned meadow at 1900 m a.s.l. in Sedrun, Kt. Graubünden, Switzerland. Tree establishment and growth dynamics were studied using dendroecological methods and an assessment of vegetation and soil was conducted in order to investigate the relationship between site properties and tree establishment. The following questions were of special interest: 1. Does the regeneration on this site consist of different successional states and is succession moving slope upwards away from the former forest edge? 2. In what dynamics does the process of tree establishment proceed? 3. Do growth patterns depend on the distance from the former forest edge and slope position and what factors control growth at this site?

Materials and methods

Data sampling was conducted along five transects of 60 m length starting in the mature forest and ending in the upper-slope area of the former meadow. Increment cores and stem discs of 95 saplings were sampled. Per tree, two cores or stem discs were extracted; (i) one at the base of the stem above the root collar in order to obtain an accurate age estimation, and (ii) another one at the lowest vertical growing point of the stem in order to analyse radial growth without the interference of reaction wood. Tree height, stem diameter at extraction height and the amount of vertical branches (multiple stems) of each sapling was recorded.

Additionally, 21 mature trees at the former forest edge were cored at breast height to serve as a reference.

The sampled increment cores and stem discs were sanded and digitally measured using the software program TSAP (Rinn (Heidelberg) and subsequently synchronised. All samples of the mature trees of the former forest edge were standardised (double-detrending) applying the software package ARSTAN (Version 6.05P) (Cook 1985). An analysis of simple correlation was conducted between the detrended masterchronology of residuals and the monthly temperatures. Along three transects a vegetation assessment of 48 1x1 m-plots in total was conducted and 17 soil profiles were dug and described.

Results and discussion

Site description

Three different successional states could be identified along the transects using tree density as indicator for the state of regeneration: 1) Close to the forest edge: Up to 15 m distance from the former forest edge tree density varied between 0.3 and 0.6 trees / m². 2) Middle slope: Between 15 m and 35 m distance from the forest edge tree density decreased to approximately 0.1 trees / m². 3) Upper slope: From the distance of more than 35 m to the forest edge on, tree density was lower than 0.025 trees / m².

The soil was characterised as Podzol with a thick raw humus (Gisi 1997). The organic topsoil layers tended to increase slope upwards while the humus-mineral horizon (Ah) decreased in thickness.

There was a significant difference in vegetation structure between the successional stages (for each vegetation layer: Kruskal-Wallis, $p > 0.05$). Vegetation ground cover was increasing with distance from the former forest edge, while bare ground occurred mostly in the old forest and in the area close to the forest edge. The cover of the herb and grass layer was abruptly decreasing slope upwards and dwarf shrubs were dominating middle and upper slope with a cover of about 90%.

An analysis of Ellenberg values (Ellenberg 1974), which are ecological indicator values, revealed an increase in the average moisture value of the assessed species slope upwards, while the average nutrient value and reaction value were decreasing (all Ellenberg values: Kruskal-Wallis, $p > 0.001$). This indicates a change to wetter, more acid and nutrient poorer conditions slope upwards, respectively with distance to the former forest edge. As far as vegetation composition is concerned a change from woodland species (for instance *Avenella flexuosa*, *Melampyrum sylvaticum* and *Vaccinium myrtillus*) to open heath species (for instance *Calluna vulgaris*) was detected with distance from the former forest edge.

The area close to the forest edge seems to be the most advanced state of the three identified successional states. The results above show that there exists a close relationship between the three successional states and vegetation and soil characteristics. The abrupt decrease of tree density could be a consequence of harsher environmental conditions with distance to the former forest edge. The area close to the forest edge takes an intermediate position in

vegetation structure and composition as well as in environmental conditions between the old forest and the open heath of the middle and upper slope.

Regeneration dynamics

The main establishment period took place about 15 years after the abandonment of the agricultural use, from 1965 until the beginning of the 1980's, in the whole study area irrespective of the distance to the former forest edge (Fig. 1). Only in the area close to the forest edge, some trees were established before and after this period. Therefore, tree establishment must be favoured in this area. Tree establishment on this site seems to be a continuous process. However, tree establishment in the middle and upper slope region has ceased since the beginning of the 1980's despite periodical mast fruiting in the region. We conclude that the absence of any regeneration might be due to a lack of suitable microsites, which were already occupied by regeneration during the past decades (Donnegan and Rebertus 1999).

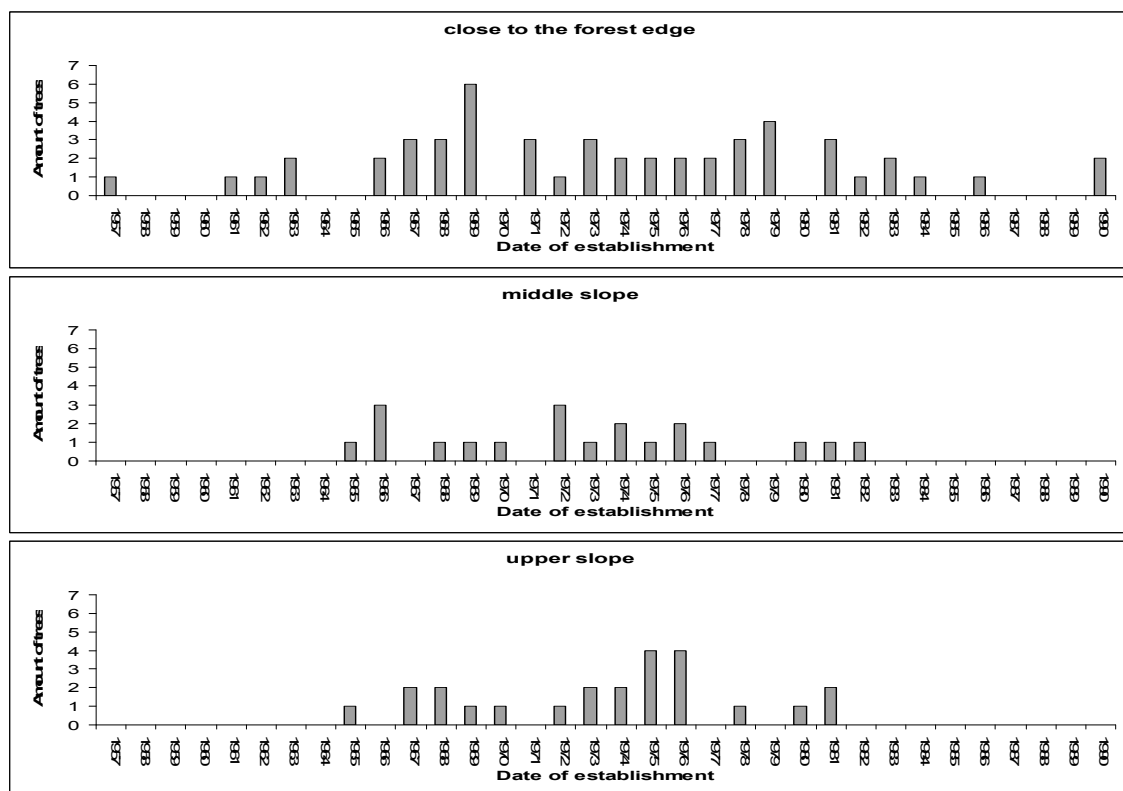


Figure 1: Tree establishment per area.

Growth dynamics

There was no significant difference in tree height between the three areas, but maximum tree height tends to decrease slope upwards. The ratio height / age decreased significantly slope upwards (One-way ANOVA, $p=0.029$). This leads to the conclusion that vertical growth must be favoured close to the forest edge due to better growth conditions.

There was a noticeable difference in growth forms between the three areas (Fig. 2). The forming of vertical branches (multiple stems) became more frequent slope upwards (Kruskal-Wallis, $p=0.001$). Forming of vertical branches is normally induced if the main stem breaks or dies and subsequent branches get upright and overtake the function of a leader shoot (Marr 1977, Schönenberger et al. 1994, Ott et al. 1997). This makes it likely that biotic and abiotic factors which damage the main stem axis, for instance snow pressure, snow mold, frost or winter desiccation, were more frequent or more intense slope upwards with increasing distance to the protective influence of the forest edge.

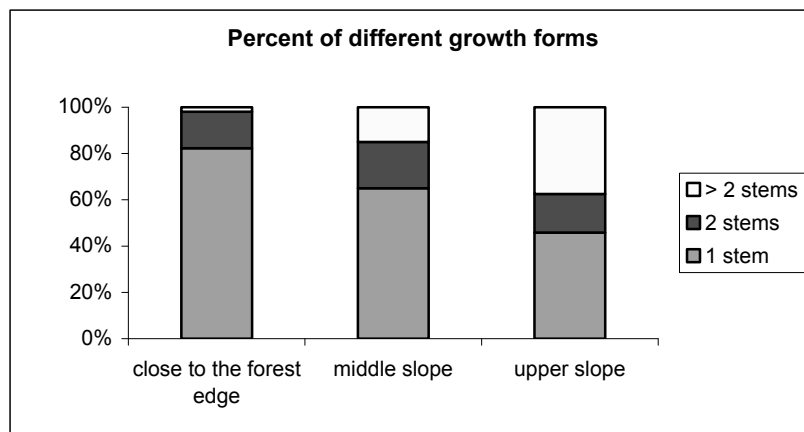


Figure 2: Percent of vertical branches per area.

The comparison of the mean radial growth curves (Fig. 3) revealed no difference in growth patterns between the three different areas of the regeneration, but an enhancement of radial growth since 1990 of all the saplings. Mature trees at the former forest edge showed no such effect. Since all sampled saplings showed this increased radial growth irrespective of their position in the research area or their age (the age of the saplings ranged from 13 to 46 years), we conclude that only a common factor such as climate can act as a trigger.

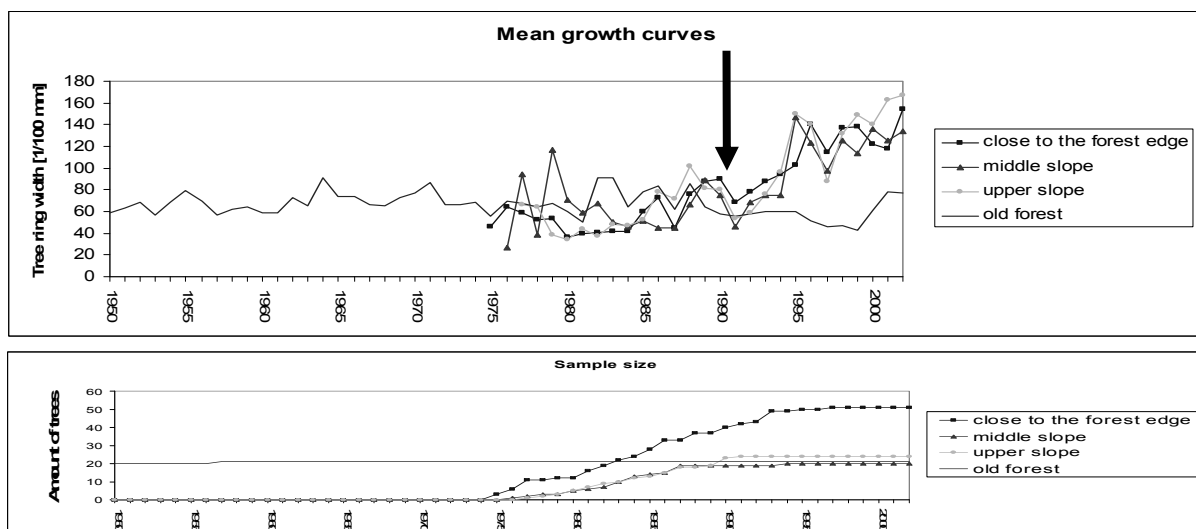


Figure 3: Mean radial growth curves per area and calendar date.

Therefore, a climate-growth analysis was conducted, which revealed that growth at this site is mainly limited by the mean June and especially July temperature (Fig. 4).

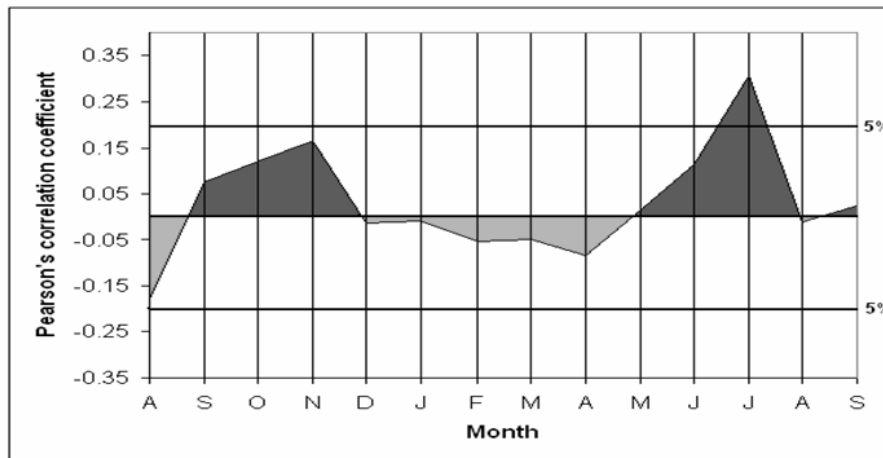


Fig. 4: Correlation between the mean June-July-temperature and the standardised mean radial growth curve of the mature trees in the old forest. The lines indicate the 5%-level of significance.

The analysis of the temperature anomalies for this region (Fig. 5) revealed higher mean June-July temperatures since 1990 compared to the average of the last 40 years. This coincides with the beginning of the period of increased sapling growth rates. A similar growth increase in tree rings of young conifers in the subalpine region related to climate warming has been reported by several authors (Neumann and Schadauer 1995, Jungwirth 1998, Paulsen and Körner 2001).

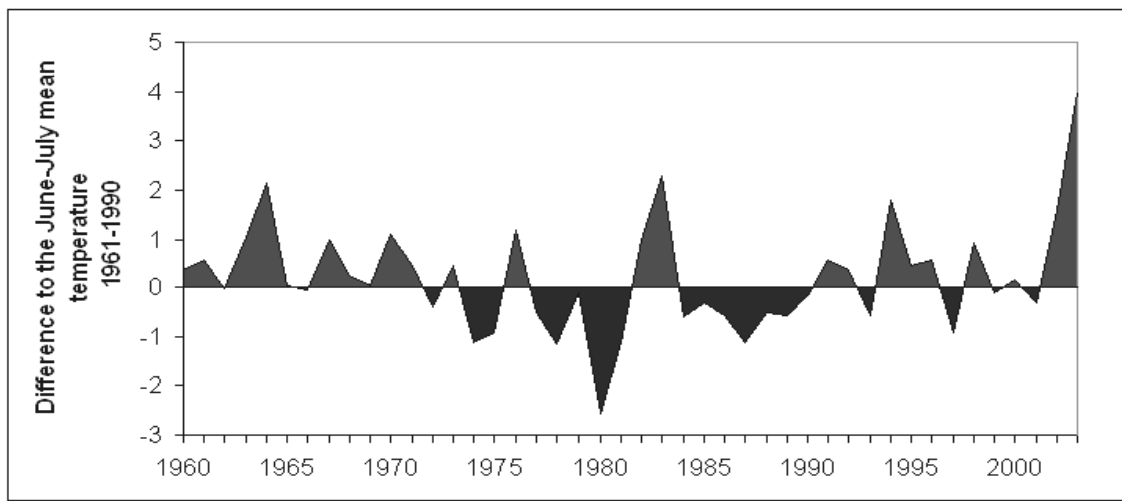


Figure 5: Anomaly of the mean June-July-temperature in the last 40 years.

Conclusions

The here presented results allow the following conclusions:

- Vegetation and soil patterns as well as growth patterns show that environmental factors are changing slope upwards and growing conditions get worse. This indicates a steep environmental gradient on the study site.
- Since the age distribution of the regeneration is not depending on slope position, the process of tree establishment is not a succession moving away from the former forest edge. Most trees were established in the same period. Only close to the former forest edge, regeneration continued after this period. The absence of tree establishment in the middle and upper slope for the last two decades is likely to be a consequence of the lacking in suitable microsites.
- Growth form and height growth depend on the position on the slope. Trees close to the former forest edge are able to grow taller than trees in the middle and upper slope. And trees in the middle and especially in the upper slope form more often multiple stems what indicates harsher conditions slope upwards.
- Therefore, tree establishment and growth patterns on the site are the result of environmental conditions that vary in space and time. Growth and establishment is favoured close to the forest edge.
- Enhanced radial growth rates coinciding with a period of increased summer temperature was detected for all saplings. This suggests that radial growth of young Norway spruce reacts sensitive to warmer summer temperature.
- Our findings underline the importance of available microsites for tree establishment near the tree line, the strong influence of highly variable environmental conditions on growth and establishment and the sensitivity of the tree-line ecotone to increasing summer temperatures.

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