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Impacts of climate change on the establishment, distribution, growth and mortality of Swiss stone pine (*Pinus cembra* L.)

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Anticipated future climate changes are expected to significantly influence forest ecosystems, particularly in treeline ecotones. Climate change will have both direct and indirect effects on the future distribution of alpine tree species, some of which will be positive and others negative. Although increased temperatures are on the whole likely to have a positive impact on growth and distribution of Swiss stone pine (*Pinus cembra* L.), indirect effects that influence seed dispersal may threaten the population viability of species. The complexity of the interrelations between climatic and non-climatic factors demands further research, which should include long-term monitoring.

Keywords: Swiss stone pine, Treeline, Climate change, Distribution shift, Tree growth, Mortality

Introduction

Future impacts of global climate change such as predicted increases in annual air and surface temperatures and variations in precipitation will cause significant alterations in forest ecosystems (Eastaugh 2008). Impacts of these changes will be proportionally more perceptible at high elevations (Bensiton et al. 1997).

In timberline ecotones near the upper limit of closed forests tree growth, forest structure and forest dynamics are mainly temperature-driven (Tranquillini 1979, Innes 1991, Körner 1998). The sensitivity of these biomes to climate variability is high and thus of special interest for understanding the effects of global change.

Swiss stone pine (*Pinus cembra* L.) is distributed in timberline ecotones across Europe from the Carpathian Mountains to the French Alps (Polunin & Walters 1986, Ulber et al. 2004). During several hundred years of human activities such as alpine farming or timber extraction Swiss stone pine was often eliminated and therefore restricted to stands on inaccessible slopes exposed to the North (Holtmeier 1966, Motta & Nola 2001, Höhn et al. 2009). In recent decades, socio-economic and silvicultural changes have favoured the establishment of Swiss stone pine (Motta et al. 2006). This five-needled conifer tree is well adapted to the harsh subalpine climate conditions in the Central European Alps (Ulber et al. 2004) and is often associated with mountain pine (*Pinus montana* Miller), Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Miller) and Norway spruce (*Picea abies* L. Karst). In the continental subalpine forests of the Central Alps with relatively low rainfall and mean annual temperatures below 1.5 °C (Ellenberg 1996), stands develop from early-successional stages dominated by mountain pine to a late-successional stage dominated by Swiss stone pine and European Larch (Risch et al. 2003, Höhn et al. 2009).

This review will summarize the evidence of Swiss stone pine responses to climate change at the timberline ecotone. The review will consider all life stages, and possible distribution shifts of Swiss stone pine populations in the future will be discussed.

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Seedling establishment

Swiss stone pine is a monoecious, wind pollinated species which reaches reproductive maturity at 40-60 years of age (Ulber et al. 2004) with good seed production years occurring on average twice in ten years (Mattes 1982). Seed production is especially sensitive to climate because important developmental processes such as the initiation of flower and cone primordia, meiosis and the release of pollen depend to a large degree on climatic variables (Pigott 1992). The temporal dynamics of seed production and the influence of climate change on seed production of Swiss stone pine have however not been comprehensively investigated to date.

The wingless Swiss stone pine seeds are mainly dispersed by the European nutcracker bird (*Nucifraga caryocatactes* L.). Swiss stone pine seeds are the main food source for European nutcrackers, and those birds are capable of gathering and transporting a large amount of seeds for storage in their own territory. Nutcrackers hide the seeds on the ground and prefer sites under sheltering trees or stumps, ridges or rock ledges in open areas (Mattes 1982), which in turn places Swiss stone pine seeds into microsites favourable for germination and seedling establishment. Gregory et al. (2009) determined that variation in observed population trend among European bird species is significantly linked with model projections of change in the extent of the species' potential geographical range associated with climate change. Their results show that the European nutcracker is one of the ten bird species to have most declined with global warming during the period 1980-2005.

Swiss stone pine germinates well on organic soils with an accumulated layer of litter and moss, but it can also germinate and establish itself on mineral soils or even rocky surfaces (Ulber et al. 2004). Seedlings profit from large endosperm reserves, are shade tolerant and therefore able to persist as understorey saplings (Hättenschwiler & Körner 1995). Seedling survival is enhanced by early snow melt in warm spring months and early snow falls at the beginning of winter that limit deep freezing of the soil (Vittoz et al. 2008). Increased soil warming is favourable for cell activity and cell differentiation and thus for further root establishment (Gruber et al. 2009). Particularly at mountain sites tree seedlings are likely to benefit from microclimates created by dwarf shrubs, but as they grow taller, there may be a microclimatological bottleneck in the development of the seedlings to mature tress (Grace et al. 2002).

Growth

The growing season at the timberline is very short and any extensions of the season due to small temperature differences at the beginning and the end of the snow-free period have a large effect on the annual carbon gain of evergreen conifers (Wieser et al. 2009). The maturation and hardening of tissues, needles, shoots and buds are positively influenced by an extended growing season (Baig & Tanquillini 1980), as is resilience against winter stress (e.g. frost desiccation) in combination with the climate conditions during winter of the current year (Tranquillini 1963, Tranquillini 1979). Swiss stone pine has a relative low photosynthetic capacity and a low daily and seasonal carbon gain (Wieser et al. 2009), the length of the active growing period is thus of special importance for further growth increase. Motta & Nola (2001) detected a distinct increasing trend in growth rates of Swiss stone pine over the last century in the Eastern Italian Alps. The radial growth of several Swiss stone pine stands in the Central Swiss Alps has increased with increasing summer temperatures and longer growing seasons since 1980 (Vittoz et al. 2008), although continuing periods of drought may have limited radial growth (Oberhuber 2004, Vittoz et al. 2008). Pietsch & Hasenauer (2005) show that stomatal conductance in Swiss stone pine (necessary for CO_2 uptake and tree growth) is correlated to stem temperature, which provides a physiological explanation for these recent increasing growth rates. An early initiation of growth may, however, increase trees' susceptibility to late frost events (Cannell & Smith 1986). Radial growth of Swiss stone pine at the timber line is negatively correlated with cool summer (June-August) and previous autumn (September-October) temperatures and low precipitation in late winter (Pfeifer et al. 2005). Several other authors also mention a similar influence of precipitation in the previous autumn and winter as well as current summer temperatures (Carrer et al. 1998, Oberhuber 2004, Carrer et al. 2007, Oberhuber et al. 2008, Gruber et al. 2009, Leonelli et al. 2009).

Non-climatic aspects of global change such as higher nitrogen deposition and the rise in atmospheric CO_2 concentration may also be considered as enhancing growth simulators (Nicolussi et al. 1995, Wieser et al. 2009). Other non-climatic aspects such as tropospheric ozone are suspected on the other hand as contributing factors for growth decline of Swiss stone pine (Dalstein et al. 2002).

Mortality

At high elevations, the survival of trees is mainly affected by environmental factors (Tranquillini 1979). In the context of climate change several factors are worth mentioning, besides drought periods. Long-lasting snow cover may stress trees by significantly reducing the length of the growing period, but snow also has mechanical effects on trees (snowbreak damage). The branches of Swiss stone pine are relatively short and elastic, therefore the crowns of adult Swiss stone pine trees are less prone to snowbreak damage from overloading than for example the crowns of Scots pine with less elastic branches (McKinney et al. 2009).

The occurrence of the ascomycete *Gremmeniella abietina*, the main pathogenic fungus for Swiss stone pine, is positively related to the mean duration of snow cover in spring (Senn 1999). Prolonged snow cover allows the fungus to grow for a longer time under favourably moist conditions. Infections of Swiss stone pine with *Phacadium infestans,* the second most important pathogenic fungus, are governed more by stand density-dependent interactions (Burdon et al. 1992).

Insects are the most important seed predators during the predispersal phase of seed development (Turgeon et al. 1994). Dormont & Roques (1999) speculate that the limited colonization of Swiss stone pine seeds by insects may also be due to the behaviour of the European nutcracker. The bird harvests most of the mature cones by the end of the summer (Mattes 1982) before the completion of insect larval development within the cone, which may help to limit seed damage by insects.

Discussion

An understanding of seedling recruitment dynamics and their climatic controls is indispensable for predicting likely future changes in the distribution of Swiss stone pine in response to climate change. The quantity and quality of seed production, dispersal, establishment and subsequent growth after establishment are essential for the formation of new subalpine forest areas at higher altitudes.

Swiss stone pine may reestablish in alpine areas even long after the reduction or cessation of farming or other human activities, due to the seed dispersal accomplished by the European nutcracker (Mattes 1982). Climate change may have a deleterious effect on Swiss stone pine establishment due to added pressures on this seed dispersal vector. Although a further increase in summer temperatures might shorten the interval between good seed years (Holtmeier & Broll 2007), the recruitment of Swiss stone pine populations is likely to be reduced if the population of the European nutcracker is significantly impacted (Mattes 1982).

The Alpine climate system is very complex, with complex patterns of variation and dynamics on interannual and decadal time scales. Besides local microclimates (Daniels & Veblen 2003), the primary climatic limitation on vegetation establishment is the combined effects of growing-season length, seasonal temperatures and the duration of the snowpack (e.g. Tranquillini 1979, Körner 1998). Several studies (e.g. Innes 1991, Pauli et al. 1996, Walther et al. 2002, Pauli et al. 2003, Daniels & Veblen 2003) have assessed that the lengthening of the growing season, higher spring and summer temperatures and an earlier melting of the snowpack will lead to an altitudinal upward movement of high mountain vegetation and a consistent upslope advance of altitudinal timberlines. This may be the case as well for Swiss stone pine in the timberline ecotone and possibly lead to an upward distribution of this species, although in some cases soil water conditions may be a limiting factor (Anfodillo et al. 1998). The upper tree line is the preferred territory of the European nutcracker, and thus possible altitudinal expansion of Swiss stone pine populations at the treeline ecotone will depend in part on the response of nutcrackers to environmental change (Motta & Nola 2001).

Variations in altitudinal timberline positions and tree growth are explained by a combination of a general thermal boundary for tree growth and regional edaphic properties and disturbances (Körner 1998). These regional to local scale factors may obscure or reverse vegetation patterns and trends expected from global climate change (Daniels & Veblen 2003). Anfodillo et al. (1998) for example reported for the Eastern Italian Alps that soils at the timberline could become physiologically dry during the growing period and that high temperatures and vapour pressure deficits limit the radial growth of Swiss stone pine. Severe climatic events such as drought or severe frost during the growing season are more likely than temperature changes to control tree population dynamics in timberline ecotones (Wieser et al. 2009). An increase in stochastic disturbances due to for example fire or windthrow may diminish the regeneration of the shade tolerant Swiss stone pine and may give pioneer species the chance to establish (Hättenschwiler & Körner 1995). Vegetation changes at the timberline ecotone may rather occur abruptly, therefore long-term trends on large spatial distribution scales of Swiss stone pine due to global climate change may be difficult to detect or predict.

Besides the possible upward shift Hättenschwiler & Körner (1995) considered that in recent decades reduced forest pasturing and increased nitrogen input may have led to denser ground and understorey vegetation in some parts of Central Switzerland, which may result in a possible downward movement of Swiss stone pine due to its shade tolerance as a climax species. Under predicted warmer climatic conditions however this downward shift of Swiss stone pine is likely to be limited by the competitive advantage of other tree species. Anfodillo et al. (1998) speculate that for example European larch is favoured in competition against Swiss stone pine in the case of an increase of air temperature due to a higher water uptake capacity.

Although tree mortality is a highly random process that is difficult to predict (Monserud 1976), it seems that environmental factors such as snowbreak or pathogenic insects and fungi are not the major influences on large tree mortality of Swiss stone pine. Frequent drought periods or late frost events however may be more significant drivers of mortality rates.

Longer observation periods will be necessary to confirm and predict distribution shifts, growth increase and mortality of Swiss stone pine in the Central Alps, and long-term data collection of multiple parameters will be necessary to distinguish the relative influence of climate on the development of Swiss stone pine.

Conclusions

Climatic influences on treeline ecosystems are a complex mix of direct and indirect effects, which individually may either positively or negatively influence tree growth and distribution. Although individual aspects of these effects have been studied, the overall likely consequences of new climatic conditions for the establishment, distribution, growth and mortality of Swiss stone pine are still poorly understood. Continued warming is likely to lead to an altitudinal or latitudinal population shift and increased growth, but extreme events such as drought or wildfires may however cause growth declines or mortality. The distribution of Swiss stone pine populations in the future is however inescapably related to the adaptability of the primary seed dispersal vector (the European nutcracker bird) to environmental change. Future research on Swiss stone pine should use long-term monitoring on large spatial scales to better understand the ongoing changing dynamic processes during the lifespan of Swiss stone pine in the timberline ecotone and the contributing factors that influence the dynamics. Combined studies involving both forest growth researchers and avian ecologists would help to better understand seed dispersal and seedling establishment processes.

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