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Drought-induced mortality of Scots pines at the southern limits of its distribution in Europe: causes and consequences

Giuggiola A [1], Kuster TM [1], Saha S [2]

Several severe drought events have been reported in southern Europe during recent decades. Drought has been found to increase the mortality of the southernmost populations of Scots pine forests in Mediterranean countries and in dry inner-alpine valleys. Therefore the ongoing global climate change is likely to endanger Scots pine in future decades. Carbon starvation might be the main cause of the increasing mortality rate due to less carbon uptake and consequently to high susceptibility to biotic attacks. Forest management, in particular, thinning and shrub removal could decrease the intensity of drought stress by decreasing competition for water resources and thus increasing carbon uptake. The ongoing climate change and adaptive forest management will both play an important role for the sustainability of this specie across southern regions of Europe.

Keywords: Scots pine, Drought, Tree mortality, Tree vitality, Europe, Thinning, Shrub removal

Introduction

Global climate change, in particular warming, has been observed in all parts of the world (IPCC 2001), including Europe, where several harmful drought periods have occurred during recent decades (Rebetez et al. 2006). In future, the frequency of drought periods will probably increase as a consequence of global warming (IPCC 2007). Higher temperatures and heat waves will lead to higher evapotranspiration (Schär et al. 2004, Beniston et al. 2007). Prolonged drought periods and concentrations of annual rainfall to heavy precipitations events are both predicted (Frei 2004, Frei et al. 2006, Planton et al. 2008). A decrease in annual rainfall is also expected to take in the western Mediterranean basin (Rambal & Hoff 1998).

Since water is an essential resource for most trees, and since it is also needed for transporting nutrients, drought periods can decrease trees' vigour (Martínez-Vilalta & Piñol 2002), seriously reduce tree growth (Bigler et al. 2006) and ultimately lead to tree death (Rebetez & Dobbertin 2004). Scots pine (*Pinus sylvestris* L.) is one of the most widespread conifer species on earth and is therefore a keystone species. Moreover, Scots pine is widely harvested for wood production in northern Europe and plays an important role in soil protection, recreation, and erosion prevention in mountain areas. Scots pine grows in very different climatic regions, from boreal regions in the north to dryer areas in the south of Europe (Martínez-Vilalta et al. 2009). Even though the mortality of Scots pine shows no clear trend in northern regions (Eid & Tuhus 2001, Langstrom et al. 2001, Jutras et al. 2003, Ozolincius et al. 2005), recent studies indicate that the mortality rate of Scots pine growing at the southernmost limit of its distribution are increasing (Vertui & Tagliaferro 1997, Martínez-Vilalta & Piñol 2002, Rebetez & Dobbertin 2004, Thabeet et al. 2009).

In this article, we will review: (1) the latest findings on the decline of Scots pine currently observed in the southern regions of Europe; (2) the physiological causes of Scots pine mortality during drought; and (3) possible implications for the future and for forest management.

The decline of Scots pine in the southern regions of Europe

In Mediterranean regions and in inner alpine valleys, the yearly precipitation is usually around 600 mm and summer temperatures are high. Scots pines growing in those regions experience water stress during the hottest and driest months. In the late 1980's, decline in Scots pine have been reported in Aosta Valley in Italy, where it was assumed that drought was the triggering factor or at least one of the main factors being involved (Vertui & Tagliaferro 1997). In the north-east of Spain, Martínez-Vilalta & Piñol (2002) report a high mortality rate up to 20% in during the dry years 1994 and 1998. Rebetez & Dobbertin (2004) observed that 43% of Scots pine in the long-term observation plot in Valais, in Switzerland died between March 1996 and June 2002. The year 1998 was very dry and the plot received 397 mm of rainfall. Other studies have reported annual mortality rates higher than 5% in inner-alpine valleys and the Mediterranean basin (Rebetez & Dobbertin 2004, Dieguez-Aranda et al. 2005, Dobbertin et al. 2005). However a steady decline has been recorded since the 1990s up to recent. Bigler et al. (2006) showed that single drought years during the last century considerably slowed down the growth of the Scots pine trees in the Swiss Rhône valley and increased the probability of mortality. A similar pattern was recorded in dry inner-alpine valleys in Austria, where extensive drought limited radial growth and influenced mortality of Scots pine (Oberhuber et al. 1998, Oberhuber 2001, Pichler & Oberhuber 2007). More recently, Scots pine was affected by an extensive drought from 2003 to 2005 in the French Mediterranean region where growth, crown development and cone production decreased (Thabeet et al. 2009, Vennetier et al. 2009). An irrigation experiment in a dry region in Switzerland found that additional water increased growth rate, crown development and needle size (Dobbertin et al. 2010). Even though mortality was not explicitly mentioned, the results suggested that the observed decline in this area was caused by long-term drought.

In contrast, annual mortality in Scots pine forests in northern Europe is reported to be very low and typically stays below 1% (Eid & Tuhus 2001, Langstrom et al. 2001, Jutras et al. 2003, Ozolincius et al. 2005). Those areas might also have low rainfall periods.

(1) WSL Swiss Federal Institute for Forest Snow and Landscape, Zürcherstrasse 111, CH-8903 Birmensdorf (Switzerland); (2) Institute of Silviculture, University of Freiburg, Tennenbacherstrasse 4, D-79085 Freiburg (Germany)

@ Arnaud Giuggiola (arnaud.giuggiola@wsl.ch)

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However, because of the relative low temperatures, trees are less likely to experience severe droughts.

This feed suggests once more that in southern parts of Europe drought is the main factor or at least an important factor responsible for the decline of Scots pine.

The physiological causes of Scots pine mortality during drought

The water ascents under tension from the root to the leaf where loss of water occurs by transpiration. The water vapour deficit of the air is the driving force for water transport while the water in the soil is the source of water supply (Larcher 2003). When an appreciable period without precipitation occurs, water supply in the soil decreases and drought stress for trees increases and causes damage, resulting in either the dehydration of living cells (Larcher 2003) or in cavitation due to overly high tensions in the water columns of the xylem (Tyree & Sperry 1989). Plants show different response strategies to drought. Scots pine has a xylem which is less resistant than some of the other pine species (Cochard 1992, Martínez-Vilalta & Piñol 2002, Martínez-Vilalta et al. 2009). Therefore, trees need mechanisms to keep their water potential gradient within a non-damaging range (Buckley 2005) and to prevent hydraulic failure (McDowell et al. 2008). The most important mechanism is the regulation of the stomatal aperture. Scots pine reacts to drought stress with stomata closure (Martínez-Vilalta & Piñol 2002), in order to reduce water loss and to prevent leaf wilting (Zweifel et al. 2007). During the extreme summer drought of 2003, Scots pine kept the stomata closed during the period June-August, while oaks have kept their stomata open (Zweifel et al. 2007). Tight control of the stomatal aperture is an adaptation to drought stress and helps keeping the trees' cells well watered, but closed stomata also reduce photosynthesis due to a lower carbon uptake (Körner 2003). This means, in periods of drought, Scots pine growth is reduced and can lead to tree death due to carbon starvation (McDowell et al. 2008). The carbon starvation theory claims that stomata closure helps to prevent water loss, but causes photosynthetic carbon to diminish and if the stomata remain closed for too long, the plant starves as a result of the continued metabolic demand for carbohydrates (McDowell et al. 2008). Moreover, Scots pine might have fewer defensive compounds against biotic agents, so that the drought effects could be amplified by pathogens or insect attacks, which could contribute to tree death (McDowell et al. 2008, Adams et al. 2009). In a warmer environment, where respiration rates increase with temperature, carbon starvation should be highly influenced by temperature, whereas hydraulic failure should not (Adams et al. 2009). However, extrapolating this study to future global warming and therefore concluding that carbon starvation is more likely to occur for tall trees than hydraulic failure is contradictory because enhanced leaf respiration is not an evidence of carbon reserve exhaustion at the tree level (Sala 2009, Leuzinger et al. 2009). Moreover, increased temperature may increase insect populations or infections of mistletoes may increase water stress due to high transpiration and thus both contribute to mortality (Dobbertin & Rigling 2006).

Implications for the future and the role of forest management

Drought, pathogen attacks and the lack of appropriate silvicultural management in Scots pine forests in southern Europe could all contribute to the increased mortality of Scots pine in these areas. Reducing stand density increases water resources, nutrients and light for the remaining trees and therefore increase growth rate during the following years (Waring & Schlesinger 1985). Thinning also reduces mortality by decreasing competition and removing suppressed tree, which do not benefit from sufficient light (Aussenac 2000). Related with drought, thinning decreases the interception of precipitation by the canopy (Aussenac 2000) and therefore increases the amount of water reaching the ground. However, microclimatic conditions may change and some reverse effects may appear: increasing light intensity the canopy and may lead to increased temperature at the ground level, which contributes to higher soil water evaporation and development of shrubs. Therefore, it is not clear yet if thinning practice could mitigate drought in those sensitive areas. The literature about the effect of understory vegetation on the water availability of overstory trees is sparse. One study has shown that dense understory vegetation can significantly decrease soil-water availability (Matsushima & Chang 2007). An optimal stand density and removing of shrubs might improve water availability and reduce risks of cavitation for trees and thus have a positive effect on stomatal opening and consequently on carbon uptake. Improving carbon uptake should decrease mortality by allowing the tree to produce enough carbohydrates for the tree's metabolism and defenses against biotic attacks (Kolb et al. 2007)

Conclusion

Scots pine mortality is increasing dramatically at its southern distribution limits, showing that Scots pine grows at its physiological limits. In future decades, it is very likely that mortality rates will further increase as a consequence of global warming in these regions (IPCC 2007, Planton et al. 2008). Therefore, droughts during the upcoming decades might endanger the survival of Scots pine (Rebetez & Dobbertin 2004) and possibly lead to replacement by other, more drought tolerant species.

The impact of the ongoing climate change and adapting forest management will both play an important role for the sustainability of Scots pine across southern regions of Europe. A better understanding of physiological causes of tree death, will also help to predict more precisely the possible shift of vegetation and help to adapt forest practices.

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