Forest Ecology and Management 369 (2016) 74–88

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Climate extremes during high competition contribute to mortality in unmanaged self-thinning Norway spruce stands in Bulgaria

Momchil Panayotov [a,*], Dominik Kulakowski [b,c], Nickolay Tsvetanov [a], Frank Krumm [d], Ignacio Barbeito [e], Peter Bebi [c]

[a] University of Forestry, Kliment Ohridski 10 Blvd., 1797 Sofia, Bulgaria
[b] Graduate School of Geography, Clark University, Worcester, MA 01610, USA
[c] WSL Institute for Snow and Avalanche Research, SLF, Davos, Switzerland
[d] European Forest Institute (EFICENT), Wonnhaldestrasse 3, Freiburg, Germany
[e] INRA, UMR1092, Laboratoire d'Etude des Ressources Forêt Bois (LERFoB), Centre INRA de Nancy, Champenoux, France

ARTICLE INFO

Article history:
Received 24 November 2015
Received in revised form 25 February 2016
Accepted 26 February 2016
Available online 21 March 2016

Keywords:
Tree mortality
Competition
Climate extremes
Tree rings
Norway spruce (*Picea abies* [L. (Karst)]

ABSTRACT

Climatic variability often is thought to be most important for ecosystem development at ecotones, while competition is thought to be most important farther from ecotones, where neighboring plants compete for scarce resources. However, climatic variability may also modulate consequences of competition, especially under recent and future climate change. Norway spruce (*Picea abies*) forests are among the most important ecosystems in the mountain regions of Europe and provide various ecosystem services. Many of these forests are currently in a self-thinning, stem-exclusion phase. Understanding processes governing forest dynamics during this phase is necessary for understanding future forest structure and processes as well as effects of climatic variability on ongoing forest development. We studied growth and mortality patterns in unmanaged 100–150 years-old Norway spruce forests that originated after stand-replacing disturbances in the Parangalitsa Reserve in Bulgaria. We collected data on forest structure and tree ring samples from 648 live and dead trees (DBH >4 cm) to analyze onset, pattern and duration of mortality, as well as contributing factors.

We found that climate extremes acted together with competition to cause sharp growth declines lasting from a few years to several decades and, in some cases, eventually led to death. The majority of dead trees had one to several consecutive growth declines, most of which initiated in response to extreme summer droughts during periods of high within-stand competition (after trees were 40–50 years old). Our tree-ring analysis revealed that some suppressed trees that died were more drought-sensitive than living trees. Other climate extremes such as unusually cold winters or summers also contributed to sharp growth reductions in some cases. Trees that died had significantly lower initial radial growth, which suggests that in the absence of external disturbances, the outcome of mortality in the stem-exclusion stage may be pre-determined from factors that determine initial growth rates. Spatial distribution data showed that there was no significant aggregation of dead and live trees and that in almost all cases, neither live nor dead trees were clustered.

Our findings contribute to understanding mortality processes in self-thinning subalpine Norway spruce forests in Europe and show that under climate change scenarios that include more frequent future droughts, even forests in which competition is thought to be the main driver of dynamics, may experience higher rates of mortality.

1. Introduction

Tree mortality is one of the main driving factors of forest dynamics (Franklin et al., 1987). There are numerous reasons why trees die but essentially, mortality is the ultimate outcome of the inability of trees to cope with unfavorable growing conditions (Schulze et al., 2005). Numerous interacting factors can cause

* Corresponding author.
E-mail addresses: mp2@abv.bg (M. Panayotov), DKulakowski@clarku.edu (D. Kulakowski), frank.krumm@efi.int (F. Krumm), ibarbeito@nancy.inra.fr (I. Barbeito), bebi@slf.ch (P. Bebi).

http://dx.doi.org/10.1016/j.foreco.2016.02.033
0378-1127/

stress to an individual tree, which may lead to reduced growth and eventually to death. These can include various abiotic factors such as extreme temperatures, drought, mechanical injury, wind, fire, rockfall, avalanches and landslides as well as biotic factors related to pathogen fungi, insect attacks or animal and human activities. Abiotic and biotic factors often act together to cause sudden death, or contribute to prolonged stress, which can gradually lead to death (Waring, 1987). Intense competition for resources between trees has traditionally been considered as one of the main factors driving mortality (Mitchell, 1943). Such high mortality is characteristic during the phase of forest development, classically called the "stem-exclusion" or "self-thinning" stage (following Oliver and Larson, 1996). Numerous theoretical models have been developed to describe self-thinning mortality over time (for a review please see Zeide, 2010). While competition is normally thought to drive mortality during the stem-exclusion phase, climatic variability is classically thought to be of predominant importance near ecotones, where species live close to the extreme of their climatic envelope. However, while recent research has focused on how climatic variability affects tree mortality in the context of climate change (Allen et al., 2010), less attention has been given to how climate may be affecting tree mortality in dense forest stands under high competition. Because mortality during the phase of high inter-tree competition is important for future structure, dynamics, and ecological and economical values, understanding factors driving this process is crucially important, especially in the context of climatic variability.

Self-thinning is prevalent in European subalpine forests, yet drivers of mortality in these forests are not completely understood. The patterns and dynamics of European mountain forest ecosystems have changed dramatically during the 20th century. Important drivers of these changes have included modified land-use due mostly to reduced grazing of domestic animals and decreased tree felling for use of wood as fuel or for construction (Gellrich et al., 2007) as well as the interactions of changing land use, changing climate, and suppression of disturbances (Kulakowski et al., 2011). In many mountain areas this has led to increased tree density and filling in of gaps with new establishment (Bebi and Baur, 2002). As a result, numerous European mountain forests are composed of one to two cohorts dominated mostly by Norway spruce (*Picea abies* Karst) trees that established 100–150 years ago. Recent studies have shown that many of the subalpine spruce forests in the European Alps are characterized by a very high number of dead or dying trees and increasing accumulation of volume of dead wood due to self-thinning (e.g., Krumm et al., 2011). The accumulation of dead wood poses numerous management challenges and requires an understanding of past and on-going forest dynamics. Studies that have spatially analyzed mortality in European subalpine coniferous forests suggest that in the absence of exogenous disturbances, tree mortality is often a density-dependent process, implying competition as the major driver (Castagneri et al., 2010). Research on individual tree growth and mortality has shown that in high-elevation Norway spruce forests, many trees die after prolonged decreased growth, which may be attributed to competition (Bigler and Bugmann, 2003). At the same time, other trees may die after short, sharp growth declines. If there are no dramatic changes in growth conditions (e.g. caused by natural disturbances), such sharp growth declines might be associated with climate extremes. For example, Bigler et al. (2007) showed that even in relatively mesic subalpine forests of the U.S. Rocky Mountains, drought can be the triggering factor for mortality of spruce and fir trees. Aakala and Kuuluvainen (2011) came to similar conclusions for old-growth Norway spruce forest in northwestern Europe. Indeed, drought and warmer summer temperatures globally are considered to be related to documented cases of mass tree mortality (for a review see Allen et al., 2010), including in the subalpine and boreal zones of Europe and North America. Despite the fact that trees occupying higher elevations are well adapted to cold temperatures, there is evidence that unusually cold springs or summers may affect tree mortality by promoting pathogen attacks in some regions (Barbeito et al., 2012). In addition, controlled experiments have shown that under a warmer and carbon-enriched environment, which is expected in the subalpine and treeline zone in future, trees might be more susceptible to damages from frost events (Martin et al., 2010; Rixen et al., 2012).

The understanding that climate extremes may contribute to tree mortality in subalpine forests raises additional questions given observed and expected changes in climate in many mountain ranges. Data from climate stations across European mountains provide evidence of observed trends of increasing temperature as well as changes in precipitation amounts and distribution (Lindner et al., 2010). Climatic change is especially pronounced in the mountains of southern Europe, including the Balkan Peninsula (Christensen et al., 2007). For example, over the last two decades climate in Bulgaria has been marked by decreased winter and summer precipitation (Panayotov and Yurukov, 2007; Grunewald et al., 2009) and warmer winter and summer temperatures with frequent heat waves (Gocheva et al., 2006; Grunewald and Scheithauer, 2011; Nojarov, 2012). These climatic trends increase the likelihood of drought stress and improve conditions for insect outbreaks in various subalpine forests (Temperli et al., 2013; Thom et al., 2013; Berg et al., 2006; Hart et al., 2013). Finally, more severe weather with frequent and stronger storms, can also profoundly affect mountain forests (Milad et al., 2011).

Additional challenges in subalpine forests are associated with management issues that are also dynamic and subject of much debate. Many European mountain forests protect settlements and important infrastructure from rockfall, avalanches, and other natural hazards, and therefore are managed to optimize their protective capacity (Brang et al., 2006; Dorren et al., 2004; Teich et al., 2012). At the same time there are increasing demands for management that more closely emulates natural processes and promotes and protects biodiversity (Kraus and Krumm, 2013). This, coupled with high costs of intensive management and harvesting, as well as decreased human populations in high mountain areas, has already led to modified socio-economic conditions in many subalpine forests that have decreased active management over past decades (Krumm et al., 2011). This trend is expected to further increase the role of natural mortality and dynamics in future (Krumm et al., 2012).

The changing drivers and dynamics in European subalpine forests highlight the need to thorough understand tree mortality processes in these forests, especially during the self-thinning phase of forest development that is widespread throughout Europe. Despite the importance of such knowledge, several factors have hindered studies on the topic. Among them are a general insufficiency of long-term monitoring plots in non-managed forests and scarcity of naturally developed subalpine forests in Europe. While many European countries have started periodic national forest inventories, only a few of these include repeated measurements that allow long-term analysis of mortality in subalpine forests (Krumm et al., 2011, 2012). One option to overcome these obstacles is to study forests in reserves or unmanaged Norway spruce forests in mountain areas in Central (Svoboda et al., 2010; Szewczyk et al., 2011) and Eastern Europe. For example, remnants of such forests still exist in Bulgaria (Panayotov et al., 2011b, 2015) and Romania (Svoboda et al., 2013). Here we present a study in one of the few old and unmanaged Norway spruce forests in Bulgaria – the Parangalitsa Forest Reserve (Panayotov et al., 2011b).

The aim of the current study was to study growth and mortality dynamics in an unmanaged 100–150 years old Norway spruce