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Potential of forest thinning to mitigate drought stress: A meta-analysis

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ABSTRACT

Increasing frequency of extremely dry and hot summers in some regions emphasise the need for silvicultural approaches to increase the drought tolerance of existing forests in the short term, before long-term adaptation through species changes may be possible. The aim of this meta-analysis was to assess the potential of thinning for improving tree performance during and after drought. We used results from 23 experiments that employed different thinning intensities including an unthinned control and focused on the response variables: radial growth, carbon- and oxygen-isotopes in tree-rings and pre-dawn leaf-water potential. We found that thinning effects on the growth response to drought differed between broadleaves and conifers, although these findings are based on few studies only in broadleaved forests. Thinning helped to mitigate growth reductions during drought in broadleaves, most likely via increases of soil water availability. In contrast, in conifers, comparable drought-related growth reductions and increases of water-use efficiency were observed in all treatments but thinning improved the post-drought recovery and resilience of radial growth. Results of meta-regression analysis indicate that benefits of both moderate and heavy thinning for growth performance following drought (recovery and resilience) decrease with time since the last intervention. Further, growth resistance during drought became smaller with stand age while the rate of growth recovery following drought increased over time irrespective of treatment. Heavy but not moderate thinning helped to avoid an age-related decline in medium-term growth resilience to drought. For both closed and very open stands, growth performance during drought improved with increasing site aridity but for the same stands growth recovery and resilience following drought was reduced with increasing site aridity. This synthesis of experiments from a wide geographical range has demonstrated that thinning, in particular heavy thinning, is a suitable approach to improve the growth response of remaining trees to drought in both conifers and broadleaves but the underlying processes differ and need to be considered.

1. Introduction

Forest ecosystems are particularly susceptible to extreme climatic events due to their relatively slow natural adaptation rates (Allen et al., 2010). More chronic water deficits due to increases in the frequency and intensity of extreme drought events have already led to decreases in forest productivity (Ciais et al., 2005; Phillips et al., 2009; Allen et al., 2015), increases of tree mortality and even widespread vegetation die-off in different regions of the world (van Mantgem et al., 2009; Allen et al., 2010; Adams et al., 2012). A higher resistance and resilience of forest ecosystems to extreme climatic events may be achieved through active adaptation strategies that aim to alter the composition of future forest stand; i.e., growing more drought-resistant tree species and converting monocultures into mixed, uneven-aged forests (e.g., Lasch et al., 2002; Bolte and Degen, 2010; Brang et al., 2014). However, for existing forest stands that have not reached economic maturity, suitable short-term adaptation strategies need to be developed (Lindner, 2000; Lasch et al., 2002).

Over the last decades, increasing evidence shows that the maintenance of low stand densities can promote the vigour of individual trees and therefore thinning is suggested as an approach to climate adaptation in the short-term (Spittlehouse and Stewart, 2003; Anderson, 2008; Chmura et al., 2011). The positive impact of thinning on growth performance of trees during or after drought has been demonstrated for a number of genera and regions (Legoff and Ottorini, 1993; Cescatti and Piutti, 1998; Misson et al., 2003; McDowell et al., 2007; Kohler et al., 2010; Brooks and Mitchell, 2011; Giuggiola et al., 2013; Sohn et al., 2013). In addition, it has been shown that the higher resource acquisition capacity per tree with increasing growing space can reduce drought-induced

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mortality (McDowell et al., 2008; Allen et al., 2010), fire risk and predisposition to insects and diseases (e.g., Chmura et al., 2011).

Residual trees become more vigorous after thinning inferior trees of a stand because resource availability increases along with growing space (Aussenac and Granier, 1988; Breda et al., 1995). Studies have revealed that forest stands with less dense canopies following thinning are often characterized by higher soil water availability for the residual trees (e.g., Aussenac and Granier, 1988; Misson et al., 2003; McDowell et al., 2003; Skov et al., 2004; Brooks and Mitchell, 20110). This is commonly attributed to reductions in stand transpiration and interception due to a lower leaf-area index (LAI) in thinned compared to unthinned stands (Breda et al., 1995). In addition, trees promoted through thinning may develop more extensive individual root systems over time, hence, increasing their capacity to extract water from the soil during and after drought periods compared to trees in unthinned stands (Whitehead et al., 1984; Aussenac and Granier, 1988; Misson et al., 2003).

However, thinning may also have negative effects on tree-water relations both in the short- and long-term. In recently thinned stands, higher wind speeds and greater penetration of solar radiation can lead to greater transpiration and evaporative water loss compared to unthinned stands (e.g., Lagergren et al., 2008; Brooks and Mitchell, 2011). Furthermore, the increase in leaf area of promoted trees and of ground vegetation after thinning can result in increases of stand-level transpiration and interception that may compensate or even reverse the previously described positive effects of thinning on water availability (e.g., Anders et al., 2006, for ground vegetation see references in Thomas et al., 1999). How fast and to what extent ground vegetation establishes in the years following thinning depends on a number of factors including thinning intensity and site quality (Nilsen and Strand, 2008).

Thinning intensity seems to be a major determinant of the magnitude and duration of the effects of thinning on growth. After less intense thinning, stand transpiration can return within few years to the pre-thinning level (Breda et al., 1995; Lagergren et al., 2008) while canopy closure proceeds more slowly and stand water use remains low for longer time periods after more intense thinning (Bren et al., 2010). How long stand-level LAI and thus water interception remain lower in thinned compared to unthinned stands should depend not only on how much LAI was reduced (thinning intensity) but also on the species' potential to occupy newly available growing space and on the intervals between thinning interventions (Sohn et al., 2016). Additionally, benefits of thinning for the growth response of trees during and after drought have been found to decrease with stand age due to higher water demands of larger trees in open compared to closed stands (D'Amato et al., 2013).

Drought impacts on tree physiology and growth are more detrimental in areas of limited water availability (Fritts et al., 1965; Hsiao et al., 1976; Ciais et al., 2005; Bréda et al., 2006). Therefore, thinning effects on tree performance are likely more positive on sites where water is the main growth limiting factor.

This brief overview shows that tree growth and vitality may be influenced by thinning in quite different ways. The contrasting results among the studies reported above are likely related to dissimilar site conditions, tree species and thinning regimes. The aim of this paper is to systematically review the effects of thinning interventions on different variables of tree and stand performance during and after drought events through a meta-analysis. Based on results of existing studies, we hypothesize that thinning can help to improve the drought response of trees by mitigating tree performance during drought and by accelerating the recovery of tree performance after the drought. We specifically tested whether potential benefits of thinning for the tree response during and after drought events: (1) increase with thinning intensity, (2) decrease with time elapsed since the first thinning intervention and with stand age, (3) differ between coniferous and broadleaved tree species, and (4) increase with site aridity.

2. Material and methods

2.1. Data compilation

Developing study selection criteria is a crucial first step in meta-analysis for the purpose of robust synthesis (Hungate et al., 2009). To be included in our meta-analysis, studies had to meet the following criteria: (1) they were carried out under field conditions in forests or plantations; (2) they permitted a comparison between at least two treatments, an un-thinned stand as control and at least one thinned stand; (3) a drought event had taken place during the study period (either the event was reported by the study itself or could be derived from data of local weather stations by us); (4) tree performance data were available for a period that spanned at least from one year before to one year after the drought; and (5) studies provided statistical information needed to perform a meta-analysis; i.e., mean, standard deviation of the mean and sample sizes of target variables. We searched the peer-reviewed literature using common databases like ISI Web of Knowledge, Google Scholar and CAB Abstracts for studies that quantified the potential of thinning to mitigate drought stress in trees. We used a factorial combination of search terms such as: "drought", "thinning", "thinning effect", "diameter growth", "height growth", "basal area increment", "leaf-water potential", "stomatal conductance", "sap-flow", and "isotopes". As of April 2016, we had found 158 articles using these keywords/queries. About 35 of these examined the effect of thinning on the drought response of trees but only 23 of these studies met our 5 selection criteria. The datasets included studies from 7 countries referring to temperate and Mediterranean regions and 2 datasets from the subtropics (Table 1, Fig. 1).

2.2. Target variables

We carefully selected target (response) variables that are considered to be suitable proxies for changes of tree vitality and that are sensitive to the combined effects of drought and competition intensity (thinning). Based on these considerations and the studies that fulfilled all selection criteria, 4 response variables were identified for our meta-analysis: (1) radial growth (provided as either tree-ring widths, or basal area increments or dendrometer measurements), (2) and (3) carbon and oxygen isotopic ratios in wood, as well as (4) pre-dawn leaf water potential (Table 1).

Tree ring series are commonly used to quantify tree and stand growth responses to climatic extremes at multiple spatial and temporal scales (Fritts, 1976). Additionally, annual radial growth is affected by neighborhood competition and thus is sensitive to thinning interventions (e.g., Fritts and Swetnam, 1989). Likewise, stable carbon and oxygen isotope ratios ($\delta^{13}C$ and $\delta^{18}O$) in wood are good indicators of meteorological and environmental variations (Farquhar et al., 1989; Saurer et al., 1997; Schleser et al., 1999) and have been reported to be responsive to thinning as well (e.g. McDowell et al., 2006; Sohn et al., 2013). Pre-dawn leaf water potential is one of the most commonly used parameters for determining tree water status (see references in Turner, 1988). For example, elevated pre-dawn leaf potentials in recently thinned stands have been linked with higher relative extractable water in the soil due to lower crown interception and transpiration after canopy opening (e.g., Aussenac and Granier, 1988; Breda et al., 1995).

We extracted mean, standard deviation and number of sampled trees for all four target variables. As not all studies included analyses of all four target variables, the number of studies varied among target variables and thus among meta-analyses (Table 1).