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Enhancing pine forests resistance to multiple disturbances through forest management

Lena Vilà Vilardell

Natural disturbances are intensifying because of climate change, pushing forests to unprecedented responses. Forest management treatments aimed at reducing wildfire hazard, have the potential to also increase forest resistance to multiple disturbances. Using simulation modelling, dendrochronology, stable isotopes, and terpene analyses, this thesis examined the physiological responses of *Pinus nigra* and *Pinus ponderosa* to management treatments. High-intensity cutting significantly improved resistance to wildfires, droughts, and insect outbreaks, especially when combined with prescribed burning. However, prescribed burning alone had no effect on pine resistance to insect defoliators. The thesis findings suggest that managing both overstory and understory vegetation holds strong potential for facilitating forests adapt to increasing disturbance pressures.

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ENHANCING PINE FORESTS RESISTANCE TO MULTIPLE DISTURBANCES THROUGH FOREST MANAGEMENT

Enhancing pine forests resistance to multiple disturbances through forest management

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to obtain the degree of Doctor

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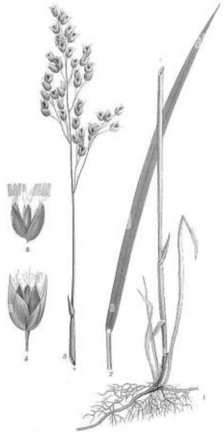
If all the world is a commodity, how poor we grow. When
all the world is a gift in motion, how wealthy become.

Robin Wall Kimmerer



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Preface

The present thesis is the result of the work carried out by Lena Vilà Vilardell between 2020 and 2025. The thesis was developed at the Forest Science and Technology Centre of Catalonia (Solsona, Spain) and includes two research stays at the Institute of Soil Research, University of Natural Resources and Life Sciences, Vienna (BOKU; Vienna, Austria) and at the Missoula Fire Sciences Laboratory of the Rocky Mountain Research Station (Missoula, MT, USA). The following articles have been published or are about to be published in international scientific journals as a result of the work derived from the thesis:

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Abstract

Natural disturbances are intensifying due to climate change, pushing forests to unprecedented responses. While forest management can help mitigate their negative impacts, it is still unknown whether specific treatments can target multiple disturbances impacts, and what are the physiological mechanisms underlying tree responses to these treatments. In this thesis, we explore the potential of forest management strategies primarily aimed at reducing wildfire hazard, to additionally enhance pine forests resistance to multiple interacting disturbances, including wildfires, droughts, and insect outbreaks. Management strategies include different intensities of cutting and prescribed burning, either as stand-alone treatments or combined. We used simulation modelling, dendrochronology, stable isotopes, and terpene content analyses to assess the short-, mid-, and long-term responses to treatments of two ecologically and economically important pine species from the Mediterranean region and western North America: *Pinus nigra* and *Pinus ponderosa*. High intensity cutting treatments, by substantially reducing stand density, improved forest resistance to wildfires, droughts, and insect outbreaks, especially when combined with prescribed burning. The increased resistance was largely driven by improved physiological performance of the residual pines, likely due to reduced competition for resources with overstory and understory vegetation. However, prescribed burning as a stand-alone treatment had no effect on pine resistance to insect defoliators. Our findings suggest that forest management strategies addressing both the overstory and understory vegetation have a great potential to assist forest adaptation to novel disturbance regimes. The integration of this thesis' insights with existing research will help guide sound management decisions.

Resum

Les pertorbacions naturals s'estan intensificant com a conseqüència del canvi climàtic, forçant els ecosistemes forestals a adoptar respostes sense precedents. Tot i que la gestió forestal pot contribuir a mitigar aquests impactes, encara es desconeix quins tractaments poden incidir de manera efectiva sobre diverses pertorbacions alhora, així com els mecanismes fisiològics que expliquen la resposta dels arbres a aquests tractaments. Aquesta tesi explora el potencial de diferents estratègies de gestió forestal, concebudes inicialment per reduir el risc d'incendi, per tal d'augmentar també la resistència de les pinedes davant de pertorbacions com els incendis, les sequeres i les plagues. Els tractaments avaluats inclouen diferents intensitats d'aclarida, seguides o no de cremes prescrites, així com cremes prescrites sense intervenció prèvia. La resposta als tractaments a curt, mitjà i llarg termini s'ha avaluat a través de models de simulació, dendrocronologia i anàlisis d'isòtops estables i de contingut de terpens, en dues espècies de pi d'alta importància ecològica i econòmica de la regió mediterrània i de l'oest de Nord-amèrica: *Pinus nigra* i *Pinus ponderosa*. Els resultats mostren que les aclarides d'alta intensitat, que comporten una reducció substancial de la densitat forestal, milloren la resistència dels boscos a incendis, sequeres i plagues, especialment quan es combinen amb cremes prescrites. Aquest augment de resistència s'associa a una millora del rendiment fisiològic dels arbres romanents, probablement com a resultat d'una menor competència pels recursos amb la vegetació del sotabosc i l'estrat arbori. En canvi, la crema prescrita aplicada de directament sense intervenció prèvia no té efectes significatius sobre la resistència dels pins als insectes defoliadors. En conjunt, els resultats d'aquesta tesi suggereixen que les estratègies de gestió que actuen simultàniament sobre la vegetació arbòria i del sotabosc poden jugar un paper clau en l'adaptació dels boscos als nous règims de pertorbacions. La integració d'aquestes evidències amb el coneixement científic existent pot contribuir a orientar pràctiques de gestió forestal més eficaces.

List of acronyms

A	Net photosynthetic CO_2 assimilation
AIC	Akaike's information criteria
ANOVA	Analysis of variance
BAI	Basal area increment
CBH	Canopy base height
DBH	Diameter at breast height
EW	Earlywood
FCCS	Fuel characteristics classification System
GDBH	Growth-differentiation balance hypothesis
GLMM	Generalized linear mixed-effects model
GRAF	Forest Action Support Group of the Government of Catalonia
g_s	Stomatal conductance
ICC	Intraclass correlation
iWUE	Intrinsic water use efficiency
LAI	Leaf area index
LMM	Linear mixed-effects model
LW	Latewood
MT	Monoterpene
PAR	Photosynthetic active radiation
PDSI	Palmer drought severity index
PET	Potential evapotranspiration
PLC	Percent loss conductivity
PPM	Pine processionary moth
SPEI	Standardised precipitation-evapotranspiration index
sPLS-DA	Sparse partial least-squares discriminant analysis
SQT	Sesquiterpene
VPD	Vapour pressure deficit

CHAPTER 1

Introduction

Introduction

Disturbance regimes are shifting with climate change and land-use changes. As forest continuity increases due to rural abandonment and natural disturbances become more frequent and severe, novel disturbance interactions may lead to unexpected effects on the ecosystem (Buma, 2015) and forests may not adapt quickly enough to resist the new conditions and recover (Seidl et al., 2017). Given that dense forests are highly susceptible to intense disturbances, forest management provides an opportunity to assist adaptation to more frequent and severe disturbance regimes (Davis et al., 2024; Sohn et al., 2016), potentially reducing their vulnerability to multiple interacting disturbances. This thesis explores the potential of different forest management strategies initially designed to reduce wildfire hazard, to additionally enhance resistance to other common natural disturbances, such as droughts and insect outbreaks.

The concepts of resistance, resilience, susceptibility, and vulnerability are often used inconsistently in the literature. However, to incorporate them into management objectives and stimulate informed debates, these concepts must be clearly defined and properly framed. Thus, this thesis defines the concepts as follows (Lecina-Diaz et al., 2024): *resistance* is the ability of the ecological system to persist through the disturbance event; *resilience* is the capacity of the ecological system to absorb or withstand a disturbance event such that the system maintains its structure and functions and does not shift to an alternate state; *susceptibility* refers to the system structural and functional characteristics that modulate the immediate effects of the disturbance; *vulnerability* is the predisposition of the system to be adversely affected by a hazard.

1.1. Natural disturbances as drivers of forest dynamics

Water-limited ecosystems are present around the globe, representing more than 50% of the continental land (Schulze et al., 2019). Forests in these areas experience natural disturbances, such as wildfires, droughts, and insect outbreaks, that drive changes in their structure and composition at both stand and landscape level. While natural disturbances are intrinsic components of ecosystems, and forests are well adapted to their prevailing disturbance regimes, climate change and human activities are modifying their frequency and severity, leading to shifts in disturbance regimes (Seidl and Turner, 2022). These changes can disrupt forest responses, potentially reducing resistance and resilience or triggering permanent shifts in forest ecosystems.

Natural disturbances are mainly driven by climate, but vegetation structure (density, size, and spatial distribution) and composition (identity and diversity of species) are also key factors (Seidl et al., 2011). By creating gaps and fostering heterogeneity, natural disturbances shape the structure and composition of the forest and modify resources availability. This is known as the legacy effect of the disturbance and is an essential element in disturbance interactions. Disturbances can amplify or dampen the intensity and severity of a subsequent disturbance, depending on the impact caused by the previous disturbance and the time elapsed between disturbances (Buma, 2015). For example, drought events weaken trees and predispose them to insect attacks (Gaylord et al., 2013).

As the climate becomes warmer and drier, disturbances such as wildfires, extreme droughts, and insect outbreaks are expected to increase (Seidl et al., 2017), and forest management may be crucial in both reducing forest vulnerability to undesirable disturbances impacts (Hood et al., 2016; Sohn et al., 2016) and supporting forest adaption to novel disturbance regimes (Turner and Seidl, 2023). The following sections present each of these three disturbances, providing examples of tree adaptation mechanisms to them, the influence of forest structure on their prevalence, and their expected future trends.

Drought events

Drought events are intrinsic to many ecosystems worldwide, yet when prolonged in time, they can cause extensive forest die-off (Allen et al., 2010). Plants exhibit a wide range of adaptations to drought. One of the primary mechanisms is through stomatal regulation, which reduces water loss during periods of water deficit. Other adaptation mechanisms include the reduction of leaf area relative to biomass, minimizing water loss at expenses of growing, and the development of deeper root systems, stimulating hydraulic redistribution by mobilizing water from deep to shallow soil layers (Nardini et al., 2014; Schulze et al., 2019). However, despite being adapted to water-limited habitats, increasingly frequent extreme drought events may exceed trees tolerance capacity, leading to widespread tree mortality (Figure 1.1; Allen et al., 2015).

In addition to physiological adaptations, forest structure and composition are crucial factors affecting the response of trees to water deficit as they influence competition for water and other resources as well as tree vigour (Sohn et al., 2016). A better understanding of the mechanisms that enhance tree resistance and resilience to drought will enable the development of effective mitigation and adaptation management strategies in the face of climate change (Field et al., 2020).

Drought pressure is intensifying worldwide due to rising temperatures and prolonged periods with no rain (Cook et al., 2018). Longer and more frequent extreme droughts are expected to impact forests in multiple ways, including shifts in species structure and composition, reduced growth and net primary production, hindered regeneration, increased mortality, and changes in the prevalence of other disturbances. Droughts are the main driver of wildfires (Pausas, 2004) and, by weaking trees, may also trigger insect outbreaks (Anderegg et al., 2015; Gaylord et al., 2013).

Wildfires

Wildfires are a natural disturbance of many ecosystems. Fire-prone ecosystems are dominated by plants well adapted to the fire regime of the region, which have evolved traits such as thick bark, resprouting ability, or keeping a canopy seed bank within serotinous cones (Fernandes et al., 2008). These traits ensure that plants can survive or recover from the fire regime they are adapted to, but not any fire regime (Keeley et al., 2011). For example, trees adapted to a low-intensity frequent fire regime tend to invest in a thick bark, while trees adapted to a high-intensity infrequent fire regime tend to invest in a canopy seed bank. Resprouting species can survive both low- and high-intensity fires but need sufficient time between fires to restore their energy reserves.

Forest structure and composition influence tree mortality after fire, as they affect tree vigour before the fire through resource competition and fire behaviour during the fire (Hood et al., 2018). Thus, understanding the mechanisms that reduce fire-induced tree mortality is crucial to implement forest management strategies that promote forest adaptation to the changing climate. Trees may die immediately during the fire due to the consumption of tissues exposed to lethal temperatures or later, as a result of physiological constraints caused by the high temperatures (Bär et al., 2019; Nolan et al., 2024), and may happen in concert with other stressors such as droughts and insect attacks (Hood et al., 2018). Delayed tree mortality usually occurs in low- to moderate-intensity fire regimes, as high-intensity fires tend to immediately kill the trees.

Fire is intensifying in many ecosystems worldwide as a consequence of an increase in drought pressure (Seidl et al., 2017) and is even expanding to areas that were not historically fire prone (Figure 1.1; Dupire et al., 2017). Although climate and the preceding drought conditions are among the main drivers of fire, human actions play a crucial role: the intensity and severity of a fire is strongly determined by the heterogeneity of the landscape and the structure and composition of the forest. Past and still ongoing out-migration from rural to urban areas leads to expanding forests and changes in the land-use cover types, altering fire regimes (Mantero et al., 2020). Lack of forest management stimulates fuel build-up and increases competition for resources with neighbouring trees and understory vegetation, leading to higher vulnerability to both drought events (Giuggiola et al., 2018) and high-intensity fires (Duane et al., 2021). Indeed, high-intensity and extreme wildfire events are becoming more prevalent due to greater landscape connectivity and increased fuel accumulation, vertical continuity of vegetation strata, and fuel availability, resulting in intense and uncertain fire behaviour that overwhelms suppression capacity (Tedim et al., 2018). These landscapes are much more vulnerable to severe wildfires than mosaic landscapes that mix forests with agricultural areas. However, despite the high mortality caused by a high-intensity fire, low-intensity fires can also injure and weaken trees, causing a decline in photosynthesis and growth and making them more susceptible to insect attacks (Fettig et al., 2022).

Insect outbreaks

Insect pests are an integral part of forests, altering their dynamics, driving succession processes, and eventually shaping their structure and composition. Their severity and impact are often exacerbated by wildfire (Lombardero and Ayres, 2011) and preceding drought conditions, that weaken trees and make them more vulnerable to attack (Anderegg et al., 2015; Netherer et al., 2015). Co-evolution of plant-insect species has led to the development of specific traits that confer certain level of equilibrium between host and pest: trees have evolved complex physical and chemical defence mechanisms to protect themselves against insect pests. Pine trees, for example, have large amounts of resin that serve as both a physical barrier trapping insects and a chemical defence deterring them. Resin-based defences reduce tree mortality after a bark beetle attack (Hood et al., 2015; Kane and Kolb, 2010) and can also deter oviposition of defoliators like the pine processionary moth (PPM; *Thaumetopoea pityocampa* Den. & Schiff; Panzavolta et al., 2015), both of which are main biotic disturbance agents in pine forests.

Bark beetles are phloem feeding insects whose attacks typically occur as population eruptions and generally cause widespread tree mortality. By causing extensive tree death, bark beetles are an active agent of forest dynamics, altering forest structure and composition (Figure 1.1; Raffa et al., 2008) and adding up large quantities of dead wood into the system that may exacerbate a subsequent wildfire (Fettig et al., 2022). Unlike bark beetles, defoliators like PPM are needle feeding insects that generally do not cause tree death (Battisti, 1988), unless defoliation occurs over multiple years (Anderegg et al., 2015). Because they are not eruptive and trees generally recover from the defoliation, their effect on forest structure and composition as well as on subsequent disturbances is more subtle (Fettig et al., 2022).

However, although trees have evolved an efficient defence mechanism to overcome insect attacks, the extend and intensity of an insect outbreak are mostly driven by the prevailing climatic conditions as well as by the host and insect species climatic niche (Jaime et al., 2022), with forest structure and composition also playing a significant role (Fettig et al., 2007; Régolini et al., 2014). For example, dense forests, where trees may experience more stress, are more susceptible to a bark beetle attack (Tepley et al., 2020), while open forests are more susceptible to PPM incidence as they provide optimal conditions for pupation (Azcárate et al., 2023). Understanding the mechanisms that confer resistance and resilience to specific insect attacks will aid in the development of forest management strategies that improve forest health and mitigate damage of insects in a context of climate change.

Insect outbreaks are becoming increasingly prevalent with climate change (Seidl et al., 2017). Additionally, milder winters are contributing to the expansion of bark beetles and PPM beyond their historical limits of distribution (Hódar and Zamora, 2004; Jönsson et al., 2009). Because insects are sensitive to climate, changes in temperature and periods of drought may alter their population dynamics, including their dispersal, reproduction, development, and mortality, as well as associated outbreaks (Harrington et al., 2001; Netherer and Schopf, 2010). The anticipated rise in temperature and increased frequency of drought events are likely to create favourable conditions for insect outbreaks. Additionally, trees that survive insect attacks are more likely to succumb to subsequent drought events (Canelles et al., 2021). Indeed, similar to the effects of a drought or a low-intensity fire, the loss of foliage caused by an insect attack reduces carbon assimilation, leading to a decline in photosynthesis and growth.

Figure 1.1. Natural disturbances in forest ecosystems: top left, mortality due to severe drought in a *Pinus sylvestris* forest (credit: Pere Casals); bottom left, wildfire in the Pyrenees, a new fire area (credit: Jordi Oliveres); right, tree mortality following a bark beetle outbreak in a *Pinus albicaulis* forest.

1.2. Forest management to increase resistance to multiple disturbances

Forest structure (density, size, and spatial distribution of vegetation) and composition (identity and diversity of species) are key drivers of natural disturbance regimes. The intensity and severity of a disturbance agent depend on multiple factors, including climate, topography, landscape heterogeneity, and vegetation structure and composition. Disturbances impacts can be addressed at both the landscape level, increasing landscape compartmentalisation and spatial heterogeneity (Keane et al., 2015; Moreira et al., 2011), and the stand level, modifying the structure and composition of the forest (Jactel et al., 2009). As disturbances intensify with climate change (Seidl et al., 2017), developing effective management strategies is essential to promote both short- and long-term adaptation strategies to increase forest and landscape resistance and resilience to climate change (Bernal et al., 2025; Vilà-Cabrera et al., 2018).

Forest management treatments such as thinning, shelterwood cutting, prescribed burning, or understory clearing are often used to increase tree growth, promote natural regeneration, reduce fire hazard, or restore and improve pasturelands. Yet, their ecological impacts are manifold and may extend beyond their initial objectives (Hood et al., 2016). By modifying forest structure and enhancing tree vigour, these treatments are key in shaping how trees respond (resist and recover) to multiple disturbances, including wildfires, droughts, and insect outbreaks (Jactel et al., 2009; Sohn et al., 2016; Tepley et al., 2020).

In many regions worldwide, forests are expanding due to rural outmigration and land-use cover changes and, without associated management interventions, they grow into dense forests with abundant understory where competition for resources is high and trees are more susceptible to water stress (Giuggiola et al., 2018; Sohn et al., 2016), decline (Vilà-Cabrera et al., 2013), high-intensity fire (Duane et al., 2021), and pest outbreaks (Fettig et al., 2007).

Both the intensity and periodicity of the treatment are key factors to consider when defining a management intervention. Generally, the goal is to minimize the number of interventions while maximizing their long-term effectiveness; however, the duration and effectiveness of the treatment depend not only on the treatment itself but also on other factors such as vegetation species, stand condition, soil type, site characteristics, or climate. A recent meta-analysis found that thinning and prescribed burning significantly reduce wildfire severity for up to 10 years, after which follow-up treatments are needed to maintain effectiveness (Davis et al., 2024). Similarly, tree drought resistance declines over time following thinning (Sohn et al., 2016).

Stand density reduction

Silvicultural treatments such as thinning and shelterwood cutting reduce stand density and tree competition for resources, yet they differ in their primary silvicultural goal and thus, in the final structure of the forest. For example, thinning promotes growth and vigour of the remaining trees by removing the smallest and less vigorous trees, whereas shelterwood promotes natural regeneration by retaining enough mature trees to protect the seedlings. Thus, forest structure after thinning tends to be more uniform while after shelterwood, more heterogeneous (Smith and Arno, 1999).

By reducing density and competition for resources while retaining the most vigorous trees, cutting treatments reduce wildfire severity (Davis et al., 2024) and enhance the resistance of trees to drought events (Sohn et al., 2016) and to certain insect outbreaks such as bark beetles (Anderegg et al., 2015). Following cutting treatments, the reduction in crown density and foliar biomass results in reduced stand transpiration and canopy rainfall interception (Breda et al., 1995), generally increasing stand water availability, growth rate, and overall tree vigour (Sohn et al., 2016; Tepley et al., 2020; Zald et al., 2022).

Cutting intensity determines the amount of radiation and wind that penetrates through the canopy and reaches the soil and the understory vegetation. High-intensity cutting treatments increase both radiation and wind, potentially resulting in a few unintended implications: first, it may increase potential fire behaviour by drying surface fuels (Agee and Skinner, 2005) and promoting a fast regrowth of the understory vegetation (Casals and Rios, 2018), thereby leading to greater fuel accumulation and ladder fuels, reducing the gap to the overstory layer, and facilitating crown fires (Keane, 2015); then, it may increase tree water stress during drought because, on one hand, the regrown understory vegetation increases transpiration due to the high vapor-pressure deficit (Giuggiola et al., 2018; Simonin et al., 2007) and, on the other hand, soil water evaporates faster, potentially leading to soil water depletion (Raz-Yaseef et al., 2010).

In contrast, light-intensity thinning treatments maintain a rather closed canopy cover that prevents the fast regrowth of understory vegetation, thus reducing fire hazard while improving water balance of residual trees. Yet, under a closed canopy it is essential to maintain a low fuel load, as prolonged extreme drought conditions make such structures more susceptible to high-intensity crown fires that can spread rapidly and suppose a great challenge to control (Agee and Skinner, 2005).

Stand density reduction treatments modify both the vigour of trees and the microclimate within the stand, influencing the development of pest outbreaks.

Higher temperatures and wind speeds after thinning may stimulate certain bark beetles (Fettig et al., 2007); however, by enhancing tree vigour and reducing drought stress, cutting treatments may boost resin duct production (Hood et al., 2016) and reduce bark beetles related mortality (Tepley et al., 2020). On the other hand, the incidence of other insect pests, such as the pine processionary moth, is greater in stands with low tree density (Régolini et al., 2014) and abundant open spaces (Azcárate et al., 2023).

In sum, all collateral effects of cutting treatments need to be carefully considered, since they may limit the benefits and duration of the treatment effects. Moreover, the benefits may be specific to one type of disturbance and may not apply to others.

Understory treatments

Managing understory vegetation is crucial for reducing wildfire hazard, as it is the primary carrier of high-intensity surface fires and serves as the medium through which fire can jump into the canopy, becoming a crown fire. By reducing the biomass of understory vegetation, which competes with trees for resources (Riegel et al., 1992), understory management practices can also mitigate the likelihood of trees suffering from drought stress (Giuggiola et al., 2018).

As with silvicultural treatments, the periodicity of understory treatments is also a key factor to consider. Maintaining a low amount of understory vegetation can be achieved by treating the stand at regular intervals, introducing herbivory to convert or restore a silvopastoral system, or maintaining a closed canopy cover to prevent rapid understory regeneration.

Following thinning, cutting, or understory treatments, the resulting slash should be managed to reduce short-term fire hazard (Piqué and Domènech, 2018). Among the various approaches to understory treatments and slash management, this thesis focuses on understory clearing, lop and scatter, and prescribed burning (applied both to live vegetation and slash). The recovery of the vegetation following understory treatments depends on the species composition as well as on the type and intensity of the clearing and burning treatment. In some cases, it may recover more quickly after clearing using mechanical tools than after prescribed burning (Casals and Rios, 2018) or at a similar rate (Fernández et al., 2015).

Understory clearing

Understory clearing involves the partial or complete removal of understory vegetation using mechanical tools such as chainsaws or mulchers. Unlike prescribed burning, it can be implemented under a wide range of weather conditions. By removing understory vegetation and competition for resources, mechanical clearing enhances the physiological performance of the residual trees, boosting growth and improving their water balance (Giuggiola et al., 2018). However, understory clearing may increase short-term fire hazard due to the accumulation of residues left on-site (Piqué and Domènech, 2018). Post-treatment fire hazard reduction can be achieved through lop and scatter –which involves cutting residues to a predefined length and distributing them on the ground– or slash burning –i.e., prescribed burning of the slash generated. Since lop and scatter leaves residues on-site, it helps to reduce soil water evaporation.

Prescribed burning

Prescribed burning is applied in a wide range of fire-adapted grasslands, shrublands, and forests worldwide (e.g., Bradshaw et al., 2018; Davis et al., 2024; Fernandes et al., 2022; Nieman et al., 2021). In the Mediterranean region, it is implemented in strategic areas to reduce wildfire hazard or to maintain or restore habitats for grazing and wildlife (Fernandes et al., 2022).

Prescribed burning in forests can be implemented directly to understory vegetation (Figure 1.2; referred to as underburning) or to woody debris from vegetation treatments (referred to as slash burning), yet it can only be carried out under certain climatic conditions, known as the burning window. This window is defined by specific thresholds of weather conditions and fuel moisture levels that determine the optimal time for burning. It is usually implemented in fall or spring. Fall burns are generally more intense because fuels are drier and more readily available to ignite. However, spring burns are associated with higher mortality since they are often implemented during periods of active growth (Valor et al., 2017a). Understory recover after fall burns is generally slower (Casals et al., 2018).

Prescribed burning modifies forest structure and composition, reducing not only wildfire hazard but also helping to mitigate the negative impact of other disturbances, such as droughts and bark beetles. On one hand, as it removes understory vegetation, prescribed burning reduces competition for resources with the residual trees, and, on the other hand, the ash deposition induces a short-term flush of soil nitrogen availability (DeLuca and Zouhar, 2000; Romanya et al., 2001).

Direct and indirect effects of prescribed fire on trees depend on many factors that can be broadly classified into management-related (type of management prior to burning, time since last management), fire-related (intensity, frequency, seasonality, severity), and vegetation-related factors (species identity, density) (Bottero et al., 2017; Schwilk et al., 2006; Valor et al., 2017a). Fire severity -i.e., the aboveground and belowground organic matter consumed from fire (Keeley, 2009)- can be assessed after prescribed burning by measuring crown damage (percent crown scorch), stem damage (bole scorch height, bark char codes), and root damage (burned litter and duff depth).

Prescribed burning of forest understory vegetation is typically a low- to moderate-intensity fire; yet, it can be challenging in areas with great fuel accumulation, as it may be difficult to burn safely due to abundant surface and ladder fuels (Prichard et al., 2021). Despite its usual low intensity, it may damage tree crown, stem, and roots (Bär et al., 2019). When either of these components are severely damaged, trees may eventually die. Suppressed trees are especially vulnerable and may perish within months or years after prescribed burning (Valor et al., 2017a). Delayed mortality following prescribed burning can result from limited photosynthetic capacity due to severe crown damage, impairment of xylem functionality due to stem girdling, reduced water uptake due to root damage, or indirectly due to increased vulnerability to insect attack or drought stress.

Additionally, heat stress from prescribed burning may trigger changes in the composition of a tree's secondary metabolites. The effects of prescribed burning on resin flow in the phloem or xylem, an effective defence mechanism against woodboring beetles, are known (Lombardero et al., 2006); however, its effects on needle chemical composition, which may affect needle palatability and defoliators impact, remains largely unexplored. Indeed, prescribed burning can potentially modify foliar composition (Lavoir et al., 2013; Rieske et al., 2002; Valor et al., 2017b) and palatability through changes in nitrogen content (Hódar et al., 2002). While direct prescribed burning (i.e., underburning) affects tree defence investment (Valor et al., 2017b), slash burning has shown no effect on tree growth (Bernal et al., 2023; Hood et al., 2016) or tree water balance (Sala et al., 2005), yet it can sometimes stimulate a further increase in the production of resin-based defences (Bernal et al., 2023). Furthermore, slash burning may negatively impact the physical and chemical properties of the soil due to the excessive heat generated by the high concentration of fuels, which is transferred directly to the soil via conduction (Mott et al., 2021). Excessive heat compromises soil fertility due to loss of organic horizons (Certini, 2005) and may damage tree roots (Bär et al., 2019).

Despite being widely implemented in North America and increasingly supported by policies and land managers in southern Europe, it is important to understand the ecological impacts of prescribed burning on forests and its potential to enhance forests resistance to multiple disturbances to accurately inform effective adaptive management strategies (Bernal et al., 2025).

Figure 1.2. Direct prescribed burning in a *Pinus nigra* forest.

1.3. Tree responses to forest management and natural disturbances

To be able to design effective management strategies that foster forest adaptation to changing climate and reduce vulnerability to multiple disturbances, it is essential to understand the physiological mechanisms that drive tree responses to forest management. Tree species have co-evolved with certain disturbance regimes, developing adaptive traits and defensive strategies that enable them to survive as sessile organisms to that particular regime, but not any disturbance regime (Johnstone et al., 2016). Thus, a shift in disturbance patterns caused by a changing climate may threaten the ability of trees to withstand the new conditions (Turner and Seidl, 2023). Forest management treatments may assist in the adaptation of forests to novel disturbance regimes through changes in their physiological response.

Tree growth

Plants grow in height and diameter through the meristematic tissues. Diameter growth occurs in the vascular cambium, located between the xylem and phloem of stem, branches, and woody roots. In temperate and boreal zones, cambial activity resumes after winter and produces new xylem and phloem, forming the annual tree rings, which are extensively used to precisely date events in the past and study environmental factors that influence physiological processes such as tree growth. The wood produced early in the growing season is called earlywood, and is a low-density wood formed by large, thin-wall cells, while the wood produced later in the season is called latewood, which is a higher density wood formed by small, thick-wall cells. Cambial activity is not always uniform around the tree circumference. During certain periods, such as drought events, it may become localized, leading to the formation of discontinuous rings, known as *missing rings*, that do not fully encircle the tree. Additionally, if an environmental stressor occurs during the growth period but then ceases -such as an intense but brief drought followed by rainfall- trees may resume growth within the same year, resulting in the formation of *false rings*. Furthermore, within a given locality, the growth patterns of dominant and suppressed trees may differ considerably due to their different access to resources (Pallardy, 2008).

Plants take up the CO_2 they need to grow through specialized pores that facilitate diffusion called stomata. Stomata allow gas exchange by letting CO_2 diffuse into the leaves or needles for photosynthesis while also permitting water loss as vapour. The photosynthetic rate of trees can be studied using carbon stable isotope composition ($\delta^{13}C$) in needles or tree rings. The analysis of needle $\delta^{13}C$ provides insight into the physiological state of the tree at the time the needles grew, while the analysis of $\delta^{13}C$ in tree rings serves as a retrospective record of the physiological state of the tree throughout its lifetime. Carbon isotope discrimination (Δ) refers to the degree of depletion of ^{13}C in plants and is determined by the fractionation due to diffusion through stomata ($^{12}CO_2$ diffuses easier), the fractionation during carboxylation by Rubisco (the enzyme has greater affinity to ^{12}C), and the ratio of internal to external CO_2 concentrations. As a result, the ratio $^{13}C/^{12}C$ within the leaves is lower than that in the atmosphere. The isotope delta (δ) of a sample is the relative isotope-ratio difference between the sample isotope ratio and a standard reference material isotope ratio. The $\delta^{13}C$ signature can be used to assess the intrinsic water use efficiency (iWUE) of a plant, which refers to the amount of water loss during CO_2 fixation and is defined as the ratio between net photosynthetic CO_2 assimilation and stomatal conductance (Farquhar et al., 1989). However, an increase in $\delta^{13}C$ or iWUE may be related to either lower stomatal conductance or increased CO_2 assimilation. To distinguish whether it is one case or another, the analysis of the oxygen isotope composition ($\delta^{18}O$) can be included (Scheidegger et al., 2000). The $\delta^{18}O$ signature in plant tissues is related to the stomatal aperture, as leaf water becomes enriched in ^{18}O during transpiration because ^{16}O evaporates more quickly. An increase in $\delta^{18}O$ in plant material is associated with increased evaporation rate due to higher vapour pressure deficit (VPD), and stomatal closure is common as VPD increases (Pallardy, 2008).

Photosynthesis is affected by environmental factors such as water deficit, temperature, or soil fertility. Thus, forest management practices influence the photosynthetic rate of plants by altering environmental factors such as changes in density, light, and water availability, and their impact on trees can be assessed through the analysis of $\delta^{13}C$ and $\delta^{18}O$ in needles and tree rings.

Water balance

Trees control on water balance is regulated via transpiration through the stomata. Transpiration creates the energy gradient needed to move water through the plant by pulling water from the soil to the leaves through the xylem, creating a gradually decreasing gradient of water potential along the tree (Bréda et al., 2006). Transpiration is driven by both physical factors such as VPD, radiation, air temperature, and wind speed, and physiological factors such as stomatal aperture control, leaf area index, and leaf morphology (Pallardy, 2008), all of which can be modulated by silvicultural treatments via changes in forest structure and composition.

Under water stress conditions, when VPD is high and soil water availability is low, trees close their stomata to prevent, on one hand, losing water and, on the other hand, an excessive water tension in the xylem that leads to cavitation and the formation of gas bubbles (i.e., embolism). Embolism reduces the xylem's ability to conduct water and, unless refilled, can eventually lead to hydraulic failure (Lambers and Oliveira, 2019). Closing the stomata happens at the cost of reduced

CO_2 assimilation, limiting the carbon available for growth and maintenance, which could eventually lead to carbon starvation (McDowell et al., 2008). Hydraulic failure can happen rapidly, while carbon starvation is a slower process (Sevanto et al., 2014). Indeed, under severe drought conditions, trees are more likely to die from hydraulic failure than carbon starvation (McDowell et al., 2008). However, while hydraulic failure has been recognised as a plausible mechanism of drought-induced mortality, the carbon starvation hypothesis is challenged and actively discussed due to a lack of direct evidence (McDowell et al., 2022; Sala et al., 2010).

The vulnerability of plants to embolism and hydraulic failure is typically assessed through the percent loss of xylem conductivity (PLC) and depends on plant's adaptation mechanisms. When trees experience a sustained stem PLC of 60% or higher, the probability of mortality increases (Adams et al., 2017).

Water balance of trees can be studied using physiological methods such as carbon and oxygen stable isotope composition in plant material (providing a snapshot through needles or a retrospective view through tree rings, e.g., Moreno-Gutiérrez et al., 2012; Shestakova and Martínez-Sancho, 2021) or using simulation models (e.g., De Cáceres et al., 2021). Despite their assumptions and limitations, simulation models are a useful tool to study how forest management practices affect water balance at both tree and stand level while controlling for other influential factors such as soil properties and weather.

Defence investment

Trees have evolved an array of physical and chemical defensive mechanisms to protect themselves from native insects and pathogens. Two types of defence strategies exist: constitutive defences, which are genetically determined, always present, and impose a fixed metabolic cost on the plant, and inducible defences, which are generated upon perception of a foreign challenge, are energetically costly, and may involve structural modifications or the synthesis of chemical defences (Franceschi et al., 2005).

Resin-based defences are the main constitutive and inducible defence mechanisms of conifers. Resin is composed of a mixture of terpenes and is synthesized and stored in a network of resin ducts in needles and stem (Langenheim, 2003). Terpenes, or terpenoids, are formed by a varying number of 5-carbon isoprene units (C_5H_8), including the volatile monoterpenes (10 carbon) and sesquiterpenes

(15 carbon) and the non-volatile diterpenes (20 carbon). Terpenes are important physiological and ecological compounds, protecting plants against phytophagous insect (Pallardy, 2008), but their effect on insect performance varies greatly depending on the specific host-plant pairing and their developmental stage (Mumm and Hilker, 2006). For example, the performance of adult pine processionary moths (PPM, *Thaumetopoea pityocampa*) is influenced by needle terpene content (Niccoli et al., 2008; Panzavolta et al., 2015; Tiberi et al., 1999), yet it remains unclear whether larval performance and survival are similarly affected (Achotegui-Castells et al., 2015; Hódar et al., 2004). On the other hand, while primarily serving as defensive compounds that can deter herbivory, volatile terpenes also play a communicative role by acting as pheromone signals that attract bark beetles (Raffa et al., 2016).

The resin ducts produced from the vascular cambium remain functional for several years and serve as a retrospective record of interannual variation of tree defence investment. The analysis of resin ducts in the secondary xylem allows to infer the environmental factors that have influenced alterations in defence investment over time. They are produced in both the earlywood and latewood, but in the latewood their density is higher. There is substantial evidence indicating that resin duct investment is closely linked to a tree's likelihood of surviving a bark beetle attack (Hood et al., 2015; Valor et al., 2021).

Maintaining defences and producing new ones requires energy and resources, making defence investment a costly process for plants. As a result, there is a trade-off in carbon allocation, where resources invested in defences may come at the expense of growth. Typically, carbohydrates produced by photosynthesis are mostly used in growth, with a smaller portion allocated to defensive mechanisms. However, when resources are limited, the carbon allocation ratio between growth and defence might change. The growth-differentiation balance hypothesis (GDBH) predicts that under limited resources, growth is initially more limited than photosynthesis. As carbon assimilation continues, the excess of carbohydrates is allocated to defence, resulting in a larger relative allocation of carbon to defence than when resources are abundant (Herms and Mattson, 1992). This holds true until resources become severely limited, at which point the carbohydrates produced through photosynthesis are insufficient to meet both growth and defence demand (McDowell et al., 2011).

Similar to growth, terpene content and resin duct production are controlled genetically but are sensitive to biotic and abiotic stressors and environmental factors that impact resource availability. Indeed, tree susceptibility to a bark beetle attack is directly linked to stress factors such as drought (Netherer et al., 2015), fire injury (Powell and Raffa, 2011), or defoliation (Wallin and Raffa, 2001). Following GDBH, alterations in resource availability caused by severe droughts or changes in forest structure may influence the carbon allocation strategy of trees. Thus, understanding how forest management strategies enhance tree vigour, reducing susceptibility to water stress and, in turn, insect attacks, is essential for adapting forests to evolving climatic and social conditions.

Pines as case studies

Pine species are the most widespread conifer species in the world (Farjon, 2008) and are important habitats for biodiversity and sources of people livelihoods. The present thesis studies the responses to forest management of two ecologically and economically important pine species from the Mediterranean region and western North America: black pine (*Pinus nigra* spp. *salzmannii* (Dunal) Franco) and ponderosa pine (*Pinus ponderosa* var. *ponderosa* Dougl. ex Laws.).

Black pine is native to the Mediterranean region and central Europe (Figure 1.3). It grows at elevations ranging from 350 m to 2200 m and it is an important timber source in southern Europe (Vacek et al., 2023). Ponderosa pine is native to western North America (Figure 1.4). It grows at elevations ranging from sea level to up to 3050 m in the southernmost regions and it is a major source of timber within its distributional range (Oliver and Ryker, 1990).

Both pine species are adapted to a frequent, low-intensity surface fire regime, as they have developed a thick bark, high crown base height, and a self-pruning strategy. High-intensity crown fires might threaten the regeneration of these pines, as they rely on seeds of unburned pines to recover after fire, given their inability to resprout and lack of a canopy seed bank (Korb et al., 2019; Martín-Alcón and Coll, 2016).

Both black pine and ponderosa pine are relatively drought-sensitive species (McDowell et al., 2010; Savi et al., 2019). In black pines, the likelihood of drought-induced mortality depends on their water-use strategies, which vary with tree vigour (Petrucco et al., 2017) and crown class: suppressed pines are more vulnerable to drought than dominant pines (Martín-Benito et al., 2008). In ponderosa pines, different water-use strategies have been observed among populations, reflecting local-scale adaptations to different climatic conditions (Kerr et al., 2015; Kolb et al., 2016).

Regarding insect pests, the pine processionary moth is a major pest of black pine (Netherer and Schopf, 2010), though affected pines rarely die (Linares et al., 2014). In contrast, bark beetles are among the primary pests of ponderosa pine, often causing widespread tree mortality (Kolb et al., 2007).

Figure 1.3. *Pinus nigra* forest with no treatment (left) and five years after heavy thinning and slash burning (right).

Figure 1.4. *Pinus ponderosa* forest prior to treatment (top left), immediately after shelterwood cutting and slash burning (top right), 13 years (bottom left), and 23 years after treatments (bottom right).

1.4. Objectives and structure

The overall aim of this thesis is to understand how forest management strategies primarily aimed at increasing tree growth and vigour and reducing wildfire hazard influence pine forests resistance to multiple disturbances, at short-, mid-, and long-term. We hypothesized that by reducing competition for resources, forest management treatments such as thinning, shelterwood cutting, and prescribed burning, increase the resistance of dominant pines to drought and insect outbreaks. We used simulation modelling, dendrochronology, stable isotopes, and terpene content analyses to assess pine responses to treatments (Figure 1.5). The specific objectives are addressed in each of the four chapters introduced below:

Chapter 2 explores how different combinations of overstory and understory management strategies, including two thinning intensities, understory clearing, and slash burning, affect black pine forests resistance to wildfire hazard and water stress at mid-term. To do so, we used simulation models to assess both the potential fire behaviour at stand level and the water balance of dominant black pines five years after treatments. We leveraged simulation models to assess fire behaviour and water balance in virtual forest stands without understory treatment, allowing us to isolate the role of understory vegetation in fire propagation and plant water stress. We hypothesized that (i) heavy-intensity thinning induces a fast understory regrowth that results in higher fire hazard but lower drought stress at mid-term compared to light-intensity thinning, and (ii) prescribed burning after thinning provides additional benefits by enhancing forest resistance to wildfires and drought.

Chapter 3 builds on the knowledge gained from Chapter 2 and aims to further explore the physiological mechanisms underlying the increased resistance to drought events of dominant black pines at mid-term. For that, in the same study area as in Chapter 2, we used dendrochronological and stable isotope techniques to evaluate pine growth and water use efficiency before and after treatments, inferring photosynthetic rate and stomatal conductance from the carbon and oxygen isotope composition of tree rings from specific drought years. We hypothesized that the reduction in competition after thinning enhances growth, water use efficiency, and resilience to drought of dominant pines at mid-term, particularly when followed by slash burning.

Chapter 4 focuses on the effect of prescribed burning on terpene production of dominant black pines at short-term and further investigates how needle terpene content affects pine processionary moth (PPM) larval survival. To this end, we measured needle terpene (monoterpenes and sesquiterpenes) concentrations in current-year and mature needles of dominant black pines before and one year after prescribed burning was implemented. We also conducted a bioassay with first-instar PPM larvae to assess their survival rate as a function of needle terpene and nitrogen concentrations. We hypothesized that (i) prescribed burning reduces needle terpene content at short-term, and (ii) the lower terpene content enhances the survival of first-instar PPM larvae.

Chapter 5 examines the long-term effect of forest restoration treatments, including two cutting treatments with and without subsequent slash burning, on resin ducts production of ponderosa pine, as a proxy for bark beetle resistance. For that, we used dendrochronological techniques to evaluate changes in resin ducts in both earlywood and latewood over 20 years following the treatments. We hypothesized that (i) cutting treatments enhance resin duct defences in pine trees at long-term, and (ii) burning after cutting further amplifies the defensive response.

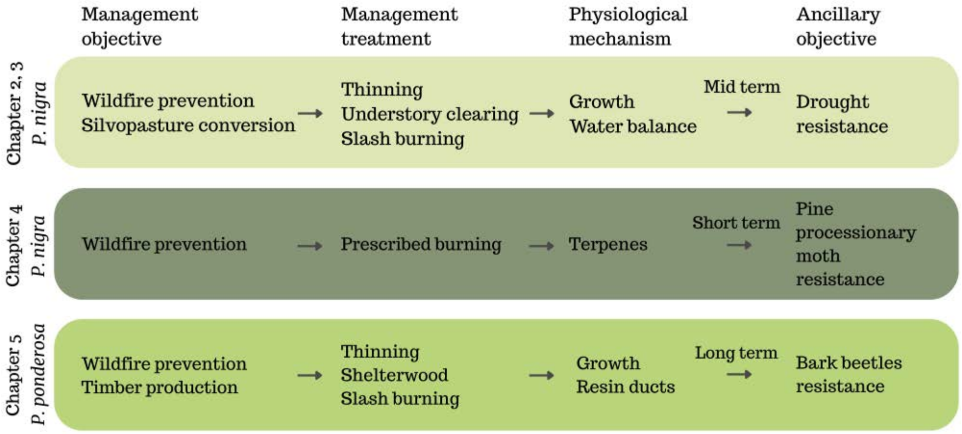

Figure 1.5. Structure of the thesis by chapter, including management objectives and treatments, studied physiological mechanisms, and addressed ancillary objectives.

CHAPTER 2

Prescribed fire after thinning increased resistance of sub-Mediterranean pine forests to drought events and wildfires

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Abstract

Vegetation structure affects the vulnerability of a forest to drought events and wildfires. Management decisions, such as thinning intensity and type of understory treatment, influence competition for water resources and amount of fuel available. While heavy thinning effectively reduces tree water stress and intensity of a crown fire, the duration of these benefits may be limited by a fast growth response of the understory. Our aim was to study the effect of forest structure on pine forests vulnerability to extreme drought events and on the potential wildfire behaviour after management, with a special focus on the role of the understory. In three sub-Mediterranean sites of NE Spain dominated by *Pinus nigra*, two intensities of thinning (light: aiming at 70−75% canopy cover; and heavy: aiming at 50−60% canopy cover) followed by two understory treatments (mechanical only and mechanical plus prescribed burning) were applied, resulting in four differently managed stands plus an untreated control per site. Four to five years after management, we measured forest structure (overstory in one 314 m2 circular plot and understory in 20 quadrats of 1 m2 per treatment unit) and fuel load (in two 10 m transects per treatment unit) and simulated water balance and fire behaviour under extreme weather conditions. Understory contribution was assessed comparing the real structure with a virtual forest stand where understory vegetation equalled the one of the untreated control. Our results suggest that the resulting mid-term structure following treatments effectively reduced water stress and fire behaviour compared with untreated control, and that the most effective treatments were the ones where prescribed burning was applied after light or heavy thinning. While understory clearing contributes to increase the resistance to both disturbances, an additive effect of burning the debris reduced the vulnerability to drought and wildfires after treatments. Our study highlights the importance of managing the understory to further increase forest resistance to both disturbances.

Keywords: drought stress; FCCS; fire behaviour; forest management; medfate; *Pinus nigra*; simulation

2.1. Introduction

Mediterranean forests are water-limited ecosystems where droughts are frequent, intense, and sometimes prolonged in time (Cook et al., 2016). Extreme droughts pave the way for forest fires (Pausas, 2004) and may trigger a forest to die-off (Allen et al., 2010). The intensity and severity of a wildfire depend on preceding drought conditions, terrain characteristics, and structure and composition of the forest. Due to the ongoing out-migration from rural to urban areas, forests are expanding by taking over the abandoned rural land in many areas of the North Mediterranean Basin. Lack of management in these new forest areas promote tree competition and fuel build-up, leading to higher vulnerability to drought events and fire hazard (Mantero et al., 2020). With climate change, an increase in the frequency and intensity of disturbances such as drought and fires is expected globally (Seidl et al., 2017). It is thus essential to understand how different management options contribute to increase forest resistance to severe drought events and wildfires. Thinning is widely applied to reduce competition and promote trees stability, improve growth, and increase revenue, though it may also serve to reduce wildfire hazard (Agee and Skinner, 2005) and improve overall vigour of dominant trees (Sohn et al., 2016). By decreasing crown density and foliar biomass (and thus, available canopy fuel), thinning treatments contribute to reduce stand transpiration and the intensity and severity of a potential crown fire (Prichard et al., 2020; Tepley et al., 2020). While heavy thinning decreases canopy fuel loading and connectivity, it may increase short-term available surface fuel if debris is left on site. Open canopies resulting from thinning allow the wind to penetrate easier to the understory and, together with solar radiation, they contribute to dry the surface fuels: given an ignition, the wind will carry the fire faster and increase its intensity (Agee and Skinner, 2005; Banerjee, 2020). Understory vegetation grows at a faster rate when the intensity of thinning is high: the more trees are removed, the more light goes through the canopy (Casals and Rios, 2018) and the less competition for resources (Riegel et al., 1992). A fast recovery of the understory after heavy thinning might be undesirable as: (i) it increases the risk of high intensity surface fire and the chances of a fire to jump to the canopy layer (Keane, 2015); (ii) it contributes to stand water loss through increased transpiration (Gebhardt et al., 2014; Simonin et al., 2007); and (iii) it competes with overstory vegetation leading to increased water stress and reduced growth of dominant trees (Giuggiola et al., 2018; Tepley et al., 2020). Contrarily, light thinning keeps a more continuous canopy cover, impeding light to go through the canopy and therefore preventing a fast development of the understory. Light thinning prioritizes the removal of overtopped and intermediate trees -the so-called ladder fuels- and although it is primarily applied to reduce fire hazard, it might also serve to increase tree resistance to drought events. Previous studies have proven that when understory is kept at low levels, water balance of trees is particularly benefited during dry periods (Giuggiola et al., 2018; Simonin et al., 2007). Understory vegetation is typically reduced mechanically or via prescribed burning. When mechanical operations are applied, resprouting species (which make up most of the sub-Mediterranean shrub species) grow faster than when controlled burning is applied (Casals and Rios, 2018). Mechanical operations leave residues on site increasing fire hazard at short-term (Keane, 2015; Stephens et al., 2009), while prescribed burning eliminates them. The combination of mechanical thinning and prescribed burning appears to be a potential good management approach for fire risk and drought stress mitigation. Previous studies have experimentally proved short-term benefits of combining prescribed burning with thinning in reducing potential fire hazard (Piqué and Domènech, 2018; Schwilk et al., 2009). Hood et al. (2020a) reported absence of long-term benefits after treatments in terms of fuel reduction, but they described a long-lasting change in species composition towards less flammable mixtures. Prescribed burning can only be applied under certain weather conditions, requires a rather big, specialized team, and emits CO_2 into the atmosphere. It is thus crucial to determine the efficiency of these management approaches in reducing forest vulnerability to drought events and wildfires to help inform management decisions. Forest management effects on water stress and fire behaviour have been usually studied separately (see Castagneri et al., 2021; Fernandes and Botelho, 2003; Fulé et al., 2012; Sohn et al., 2016 for reviews). Besides, only few studies address the role of understory on overstory water balance (e.g., Gebhardt et al., 2014; Giuggiola et al., 2018; Riegel et al., 1992; Tepley et al., 2020). Despite their assumptions and limitations, simulation models are a very useful tool to study water balance of dominant trees while controlling for influential factors such as soil properties and weather, or to study how different fuel treatments affect potential fire behaviour, otherwise extremely difficult to quantify (e.g., Ameztegui et al., 2017; Banerjee, 2020; Rolo and Moreno, 2019; Waldrop et al., 2010). Simulation models can also serve to explore the combined effect of different treatments on forest resistance to both disturbances, and to isolate the treatment which confers greatest resistance. Our aim was to study the effect of forest management, four to five years after silvicultural treatments, on pine forests vulnerability to extreme drought events and potential wildfire behaviour, using simulation models and putting the role of understory vegetation in the spotlight. We expected that (i) heavy thinning would result in forests less vulnerable to drought stress but more prone to wildfire due to fast understory regrowth, and (ii) prescribed burning after thinning would result in forests more resistant to both disturbances.

2.2. Materials and methods

Study area and treatments

The study area is located at the southern foothills of the Pyrenees, in NE Spain (Figure 2.1). Landscape in the area is hilly and dominated by Spanish black pine (*Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco) mixed with scattered Scots pine (*Pinus sylvestris* L.) and downy oak (*Quercus pubescens* Mill.). The understory is dominated by European box (*Buxus sempervirens* L.) with *Amelanchier ovalis* Medik., *Viburnum lantana* L., *Crataegus monogyna* Jacq., and *Q. pubescens*. Climate is sub- Mediterranean, with 13.2 ◦C mean annual temperature and 614 mm mean annual precipitation, with 88 mm falling during summer (July and August). In three different sites (Llobera, Madrona, and Secanella), two intensities of thinning from below followed by understory clearing and residues chopping were applied in 2015 and 2016 (Figure 2.1, Table 2.1). Heavy thinning (Ht) aimed to keep canopy cover at 50−60%, which meant a reduction of tree basal area by 40%, while light thinning (Lt) aimed to keep canopy cover at 70−75%, which meant a reduction of tree basal area by 10%. Trees to cut were selected and marked beforehand by specialists in silviculture and forest management. Understory and ladder fuels were removed in both thinning intensities. In light-thinned stands, suppressed trees were cut, while in heavy-thinned stands, suppressed, dominant, and co-dominant trees were cut (

Table S2.1, Figure S2.2). In one half of each thinned treatment, prescribed burning (underburning) was applied to eliminate residues left by mechanical treatments (Figure S2.1). In each site, treatment combinations were the following: heavy thinning plus understory clearing and residues not burned (HtNB) or burned (HtPB), and light thinning plus understory clearing and residues not burned (LtNB) or burned (LtPB). An untreated stand per site was left as control (Cont). Prescribed burnings were carried out at a temperature between 19 and 23 ◦C and at a relative humidity between 41 and 50% by the Forest Action Support Group of the Government of Catalonia (GRAF). Fire temperature was recorded every 10 s on top of the litter layer using thermocouples (type K, 3 mm diameter) connected to a Testo 175 datalogger, scattered across the entire stand (Table 2.3). Although 3 mm thermocouples cannot detect a fast temperature peak, they cool down slower than thinner ones and thus they reflect better the combustion residence time, which can be used as a proxy of fire severity. See Casals and Rios (2018) for a description of the prescribed burning treatments in Llobera and Madrona).

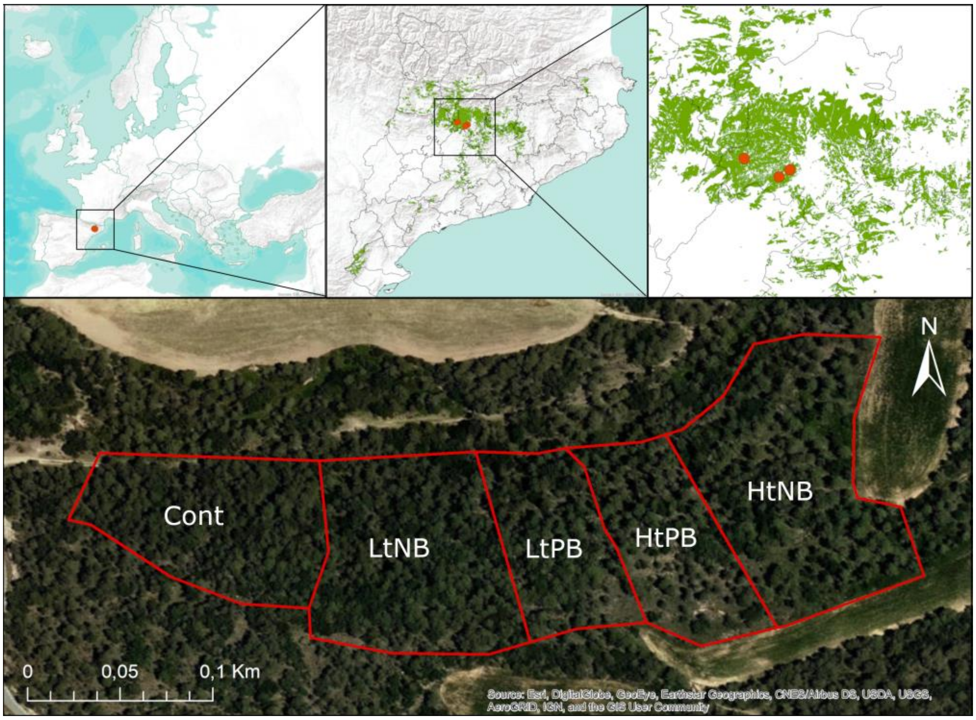

Figure 2.1. On the upper panels, location of the three study sites (orange dots) in north-eastern Iberian Peninsula (left panel), *Pinus nigra* distribution in Catalonia (green shaded, middle panel), and zoom of the study area (right panel). On the lower panel, treatment layout of one site (Madrona). Cont, untreated control; LtNB, light-thinned, not burned,

LtPB: light-thinned, burned, HtPB: heavy-thinned, burned, HtNB: heavy-thinned, not burned.

Data collection

Four to five years after treatments, we inventoried diameter at breast height (DBH), height, and canopy base height (CBH) of trees bigger than 7.5 cm DBH in one 314 m^2 circular plot per treatment unit. Forest inventory plots were placed strategically to ensure a good representation of the treatment. Canopy cover was measured using a spherical convex densiometer from the centre of the plot (Forestry Suppliers, Inc). We measured cover, height, and crown diameter of understory vegetation along two 50 m transects (50 m apart from each other), randomly placed within each treatment in order to account for vegetation variability. These measurements were taken in 20 quadrats of 1 m^2 evenly spread along the transects. In these quadrats we also estimated leaf area index (LAI) of overstory and understory vegetation from measurements of photosynthetic active radiation (PAR) taken with an AccuPAR LP-80 ceptometer and an external radiation sensor. LP-80 determines LAI from PAR measurements using the equation given by Norman and Campbell (1989). LAI understory was directly estimated from simultaneous PAR measurements below and above the understory layer; LAI overstory was estimated applying the Norman and Campbell (1989) equation using the above understory vegetation PAR measurements of the ceptometer and the PAR measurements obtained by a sensor located in the adjacent open forest area. Dead fuel loading (1 h, 10 h, 100 h fuels) was sampled along two 10 m transects (20 m apart from each other) randomly placed within each treatment following the line intersect method (Van Wagner, 1982). The litter and moss fraction were collected using a 24.5 cm diameter cylinder in 16 points laid on a 20 × 20 m square grid placed in the centre of the forest inventory plot, dried at 60 $\circ$C for 48 h and weighted. In each treatment per site, we sampled one soil core below 30 cm and one above 30 cm to analyse soil texture and organic matter content. Soil moisture content was recorded at the centre of each forest inventory plot at 20 cm depth during 2020 using four EC-5 sensors per treatment in two of the three sites (Llobera and Madrona).

Table 2.1. Site characteristics and vegetation structure per treatment and site, four to five years after treatments (mean values and standard deviation in brackets). Cont, untreated control; HtNB, heavy-thinned, not burned; HtPB, heavy-thinned, burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Locality	Llobera				
Treatment	Cont	HtNB	HtPB	LtNB	LtPB
Latitude (º)	41.953	41.952	41.952	41.954	41.953
Longitude (º)	1.465	1.465	1.466	1.466	1.466
Elevation (m.a.s.l.)	816	850	837	843	833
Slope (%)	26	18	21	21	18
Aspect (º)	325	260	290	335	270
Treatment unit size (ha)		0.4	1.1	1.4	0.7
Mechanical treatm. date		Apr '15	Apr '15	Apr '15	Apr '15
Prescribed burning date			May '15		May '15
Tree density (n ha^{-1})	1560	732	637	1273	1401
Basal area (m^2 ha^{-1})	39.7	28.0	24.5	32.1	40.5
QMD (cm)	18.0	22.1	22.2	17.9	19.2
Stand height (m)	9.0 (2.8)	11.9 (1.9)	12.3 (2.1)	10.2 (2.4)	10.5 (2.2)
Canopy base height (m)	5.3 (1.7)	6.7 (1.2)	7.1 (1.6)	5.9 (1.3)	6.1 (1.4)
Canopy cover (%)	89	63	52	85	76
Shrub cover (%)	84	37	13	52	16
Herbaceous cover (%)	0	25	6	25	0
CFFL (Mg ha^{-1})	7.26	5.59	5.17	6.64	7.38
CBD (kg m^{-3})	0.25	0.10	0.09	0.17	0.18
SFFL (Mg ha^{-1})	5.83	1.39	0.48	1.67	0.52
Shrub total load (Mg ha^{-1})	18.41	4.52	1.28	5.62	1.77
Shrub height (m)	2.73 (1.8)	0.83 (0.5)	0.73 (0.3)	0.62 (0.2)	0.62 (0.2)
Herbaceous height (cm)	0 (0)	15 (0)	15 (0)	15 (0)	15 (0)
LAI overstory (m^2 m^{-2})	2.5 (0.7)	1.4 (0.5)	1.3 (0.4)	2.0 (0.5)	2.1 (0.3)
LAI understory (m^2 m^{-2})	1.6 (0.6)	1.1 (0.5)	0.2 (0.2)	0.7 (0.4)	0.2 (0.2)
Load LM (Mg ha^{-1})	3.95	4.68	4.58	5.91	4.45
Load 1h fuels (Mg ha^{-1})	1.41	1.46	0.34	1.12	1.33
Load 10h fuels (Mg ha^{-1})	1.58	2.49	0.76	2.03	1.08
Load 100h fuels (Mg ha^{-1})	6.65	20.29	4.49	7.19	10.61

Notes: QMD: Quadratic mean diameter; CFFL: Canopy fine fuel load; CBD: Canopy bulk density, SFFL: Shrub fine fuel load; Load LM: Load litter + moss.

Table 2.1. (cont.). Site characteristics and vegetation structure per treatment and site, four to five years after treatments (mean values and standard deviation in brackets). Cont, untreated control; HtNB, heavy-thinned, not burned; HtPB, heavy-thinned, burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Locality	Madrona				
Treatment	Cont	HtNB	HtPB	LtNB	LtPB
Latitude (º)	41.972	41.972	41.972	41.971	41.972
Longitude (º)	1.352	1.355	1.354	1.353	1.353
Elevation (m.a.s.l.)	528	538	574	552	543
Slope (%)	31	11	28	15	25
Aspect (º)	340	340	340	355	350
Treatment unit size (ha)		1.1	0.5	0.8	0.4
Mechanical treatm. date		Jul '15	Jul '15	Jul '15	Jul '15
Prescribed burning date			Sep '15		Sep '15
Tree density (n ha^{-1})	1560	446	573	1194	987
Basal area (m^2 ha^{-1})	33.3	23.4	21.7	28.4	26.8
QMD (cm)	16.5	25.8	22.0	17.4	18.6
Stand height (m)	8.9 (2.5)	14.4 (4.3)	11.7 (2.0)	9.1 (3.4)	9.7 (2.9)
Canopy base height (m)	5.2 (1.3)	8.1 (3.2)	6.9 (1.1)	5.4 (2.1)	5.7 (1.8)
Canopy cover (%)	66	50	50	67	64
Shrub cover (%)	71	40	65	49	28
Herbaceous cover (%)	9	26	14	30	28
CFFL (Mg ha^{-1})	6.75	5.07	4.86	6.22	5.57
CBD (kg m^{-3})	0.13	0.06	0.06	0.14	0.12
SFFL (Mg ha^{-1})	3.51	2.22	4.82	2.22	1.10
Shrub total load (Mg ha^{-1})	11.09	4.91	8.90	6.06	2.69
Shrub height (m)	1.6 (0.9)	1.0 (0.6)	1.0 (0.5)	0.9 (0.4)	0.7 (0.4)
Herbaceous height (cm)	14 (3)	15 (4)	18 (6)	15 (7)	19 (9)
LAI overstory (m^2 m^{-2})	1.3 (0.3)	1.0 (0.3)	0.8 (0.2)	1.5 (0.2)	1.4 (0.3)
LAI understory (m^2 m^{-2})	1.3 (0.6)	1.0 (0.7)	1.0 (0.6)	1.0 (0.5)	0.4 (0.3)
Load LM (Mg ha^{-1})	6.16	4.80	5.85	5.26	5.29
Load 1h fuels (Mg ha^{-1})	0.50	0.90	0.61	0.78	0.46
Load 10h fuels (Mg ha^{-1})	0.56	1.63	1.44	1.22	0.80
Load 100h fuels (Mg ha^{-1})	1.96	7.72	2.88	6.04	4.74

Notes: QMD: Quadratic mean diameter; CFFL: Canopy fine fuel load; CBD: Canopy bulk density, SFFL: Shrub fine fuel load; Load LM: Load litter + moss.

Table 2.1. (cont.). Site characteristics and vegetation structure per treatment and site, four to five years after treatments (mean values and standard deviation in brackets). Cont, untreated control; HtNB, heavy-thinned, not burned; HtPB, heavy-thinned, burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Locality	Secanella				
Treatment	Cont	HtNB	HtPB	LtNB	LtPB
Latitude (º)	41.939	41.938	41.937	41.936	41.936
Longitude (º)	1.439	1.435	1.435	1.434	1.435
Elevation (m.a.s.l.)	728	701	705	688	707
Slope (%)	35	13	21	13	22
Aspect (º)	250	270	275	310	300
Treatment unit size (ha)		2.0	0.9	1.1	1.2
Mechanical treatm. date		Apr '16	Apr '16	Apr '16	Apr '16
Prescribed burning date			Apr '17		Apr '17
Tree density (n ha^{-1})	1496	748	668	1369	1305
Basal area (m^2 ha^{-1})	30.4	21.8	18.1	33.0	28.9
QMD (cm)	16.1	19.3	18.6	17.5	16.8
Stand height (m)	8.0 (3.2)	10.2 (2.8)	10.7 (2.8)	9.9 (2.9)	9.3 (1.8)
Canopy base height (m)	4.7 (1.5)	5.9 (1.4)	6.1 (1.4)	5.8 (1.9)	5.5 (0.8)
Canopy cover (%)	72	66	42	67	73
Shrub cover (%)	76	34	16	22	16
Herbaceous cover (%)	13	67	64	24	19
CFFL (Mg ha^{-1})	7.58	5.54	4.57	7.76	7.34
CBD (kg m^{-3})	0.14	0.10	0.09	0.10	0.15
SFFL (Mg ha^{-1})	4.48	1.47	0.68	1.15	0.75
Shrub total load (Mg ha^{-1})	13.29	3.42	1.71	2.87	1.97
Shrub height (m)	1.9 (1.0)	1.1 (0.5)	1.1 (0.5)	0.9 (0.4)	0.7 (0.3)
Herbaceous height (cm)	10 (2)	24 (6)	17 (3)	14 (4)	14 (6)
LAI overstory (m^2 m^{-2})	1.3 (0.3)	1.2 (0.2)	1.2 (0.2)	1.1 (0.1)	1.6 (0.3)
LAI understory (m^2 m^{-2})	1.2 (0.6)	0.5 (0.3)	0.3 (0.3)	0.4 (0.2)	0.2 (0.2)
Load LM (Mg ha^{-1})	4.22	2.72	2.79	4.29	3.20
Load 1h fuels (Mg ha^{-1})	1.50	1.38	0.18	1.62	1.04
Load 10h fuels (Mg ha^{-1})	1.93	3.64	0.93	2.22	2.30
Load 100h fuels (Mg ha^{-1})	6.14	21.75	13.49	11.47	12.65

Notes: QMD: Quadratic mean diameter; CFFL: Canopy fine fuel load; CBD: Canopy bulk density, SFFL: Shrub fine fuel load; Load LM: Load litter + moss.

Water stress and fire behaviour modelling

We used *medfate* R package version 2.2.3 (De Cáceres et al., 2021) to simulate stand water balance from soil, vegetation, and daily weather data. Soil was represented using three layers (0−30 cm, 30−100 cm, and 100−200 cm). Because differences in soil characteristics among treatment units may mask the treatment effect, we used mean values of soil texture and organic matter to represent a typical soil of the region. Based on field observations, we assumed that the deepest soil layer is mostly composed by rocks (Table 3). As vegetation input, *medfate* requires height, DBH, and density of tree cohorts (mean values of inventory plots per treatment unit), and height and percent cover of shrubs (mean values of vegetation transects per treatment unit). Tree diameter classes were used to build tree cohorts (below and above 20 cm DBH; Figure S2.2). Species functional parameters were taken from the available plant trait database in *medfate* (Table S2.2). As weather input, we used daily weather records from the driest years between 1990 and 2020. We used *meteoland* R package v1.0.2 (De Cáceres et al., 2018) to interpolate weather data on our sites from surface stations of the Spanish National Meteorology Agency (AEMET) and calculated SPEI drought index using *SPEI* R package v1.7 (Vicente-Serrano et al., 2010) to identify the driest hydrological years (1st October to 31st September). SPEI calculates a monthly difference between temperature and potential evapotranspiration. The driest years were selected as those hydrological years with SPEI value below the 25th percentile of the series (n = 8). Prior to modelling water flow between vegetation and soil compartments, *medfate* estimates leaf area index (LAI) for each vegetation cohort using site-specific allometries of tree foliar biomass depending on tree DBH and competition (De Cáceres et al., 2015). We used our overstory and understory field LAI estimates to correct modelled LAI values, keeping the proportion between cohorts as estimated by the model (Figure 2.2). We used *medfate* built-in fire behaviour model to simulate potential surface and crown fire behaviour. The model is a modification of the Fuel Characteristics Classification System (FCCS, Prichard et al., 2013), because ground fuels are not included in *medfate*. We derived fuel loading (shrub and canopy fine fuel) from our field data and fuel average physical properties (heat content, surface-area-to-volume ratio, tissue density) from the database available in *medfate.* Shrub total and fine fuel load was estimated from our transect understory measurements (2 × 50 m) using the allometric equations in *medfuels* R package v0.1.1 (De Cáceres et al., 2019). Fine fuels corresponded to leaves and branches with a diameter below 6 mm. Canopy fine fuel load was calculated from our field LAI estimates and *medfate* database values of specific leaf area and the ratio of needles to branches below 6 mm. Canopy bulk density was calculated following the approach in Cruz et al. (2003), which assumes that fuel is uniformly vertically distributed within the canopy layer. The remaining canopy metrics (canopy cover, total height, and canopy base height) were taken from field measurements (Table 2.1). Canopy live fuel moisture content was derived from data obtained from *P. nigra* in August in Spain (Yebra et al., 2019), and minimum moisture content of shrubs was derived from field measurements of *B. sempervirens* done in August 2016 by our team in two of the three study sites (Llobera and Madrona; Table 2.2). Live herbaceous moisture content was assumed at 30% (Burgan, 1979) and dead fuel moisture content at 8% (Aguado et al., 2007). We simulated fire behaviour using the 97th percentile wind conditions registered by a meteorological station in the 1998 wildfire that burned 23,940 ha next to our study area (ICGC, 2018; Table 2.2). We used the function *fire_FCCS()* to simulate several fire behaviour indicators; here we report the results of surface fireline intensity (kW m^{-1}) and crown fire initiation potential [0−9], which is calculated as a function of surface fireline intensity and Van Wagner, 1977 critical fireline intensity (minimum fireline intensity for initiating a crown fire).

Table 2.2. Slope, wind, and fuel moisture data used in fire behaviour simulation.

Slope	Wind	Live fuel moisture content (%)			Dead fuel moisture content (%)				
(%)	(km h^{-1})	Cnpy	Shr	Hrb	Cnpy	Shr	Hrb	Wdy	Ltr
21	24	94	56	30	8	8	8	8	8

Notes: Cnpy, canopy; Shr, shrubs; Hrb, herbs; Wdy, woody; Ltr, litter

Understory contribution to water balance and fire behaviour

To isolate the role of understory vegetation in fire propagation and plant water stress we defined a scenario with virtual forest stands, where we assumed that the two intensities of thinning were applied but the understory vegetation was not managed. Understory structure of these virtual stands was calculated using mean values of each control stand per site; that is, we run again water balance and fire behaviour simulations using as understory vegetation values, the values of the control stand at each site. By defining a new scenario, we were able to distinguish the effect of understory and overstory management on the forest resistance to droughts and wildfires. This scenario of virtual stands will be referred from here on to as *UntreatUnd*; the original stands will be referred to as *TreatUnd.*

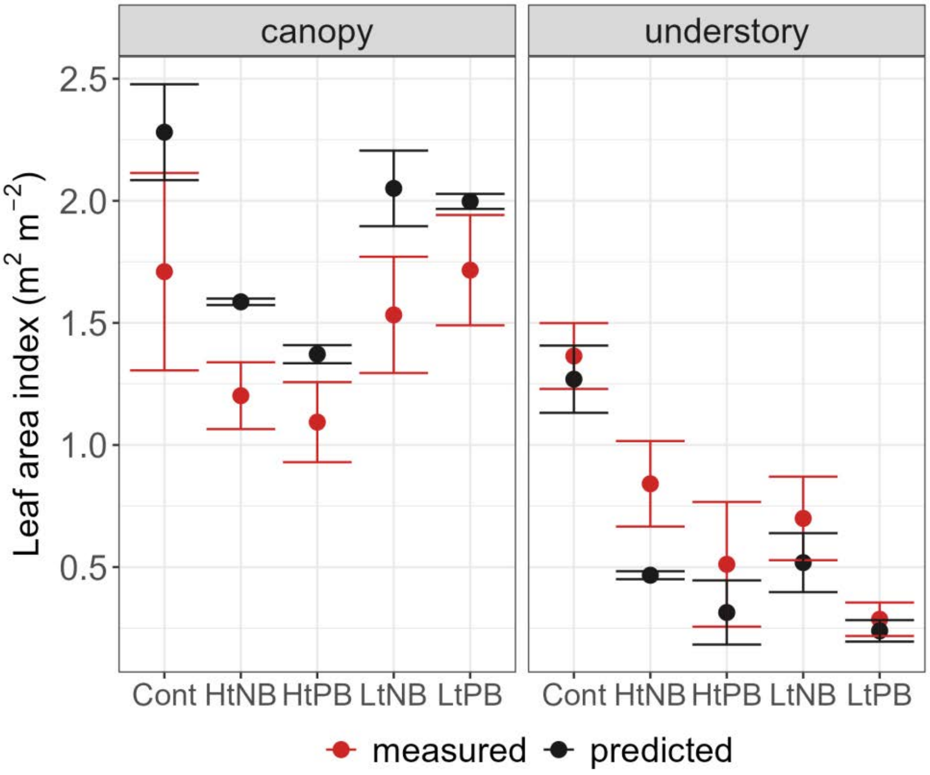

Figure 2.2. Leaf area index (LAI) of overstory and understory vegetation per treatment estimated from field PAR measurements (mean values and standard error, n = 60) and predicted from medfate tree and shrub allometries (mean values and standard error, n = 3).

Data analysis

Differences in forest structure among treatments were assessed using analysis of variance tests (2-way ANOVA: thinning intensity and type of understory management). To assess differences in tree water balance and fire behaviour indicators among treatments, we used maximum annual percent loss of hydraulic conductance in stem and minimum midday annual leaf water potential as a proxy of water stress of dominant trees, and surface fire intensity and crown fire ignition potential as a proxy to study potential fire behaviour. To model loss of hydraulic conductance in stem as a function of treatment we fitted generalized linear mixed-effects models (GLMMs) using a beta distribution with a logit link function. Beta distribution ensures that fitted values will range from 0 to 1. Leaf water potential and fire behaviour indicators were modelled fitting linear mixed-effects models (LMMs). To assess differences among treatments (including managed and control stands), we first fitted the models using only *TreatUnd* scenario values with *treatment* (categorical with five levels) as fixed factor and *site* as random intercept (Gelman and Hill, 2007). Additionally, *year* was used as a random intercept besides *site* for water balance models. Since the control effect was always significant, to better discern the differences between thinning intensity and understory treatment, new models were fitted using a subset of data without the control stands. This new set of models used *thinning* intensity (categorical with two levels) and *understory treatment* (categorical with two levels) as fixed factors. When the focus was on the contribution of understory management, the new models also included *understory scenario* (categorical with two levels: *TreatUnd* and *UntreatUnd*) as fixed factor. The Akaike's Information Criteria (AIC) was used to select the best final models. All model assumptions were verified ensuring absence of residual patterns by plotting residuals versus fitted values and versus each covariate in the model and not in the model (Zuur and Ieno, 2016). All simulations and data analysis were done using R software (R Core Team, 2021); including *glmmTMB* R package v1.1.3 (Brooks et al., 2017) and *lme4* R package v1.1-28 (Bates et al., 2015). Linear regression was used to compare measured to simulated soil moisture content during the summer precipitation-free period of 2020 that lasted 38 days. During this period there were only two small rainfall events of less than 4 mm, which did not show any response in the measurements or the simulations.

2.3. Results

Stand structure after treatments

Four to five years after treatments, forest structure in managed stands was different than in controls (Table 2.1). Differences between thinning intensities in forest structure were also apparent (Table S2.3). Understory shrub total fuel load of non-burned stands was on average about 1.5 Mg ha^{-1} higher than their paired burned ones, but still 3 times lower than in untreated controls. This was also reflected in LAI understory: non-burned stands had on average 0.37 m^{2} m^{-2} higher LAI than burned ones, and 0.51 m^{2} m^{-2} lower than controls (Figure 2.2). LAI canopy estimated from field PAR measurements was lower than LAI estimated using allometric relationships (average difference of 0.41 m^2 m^{-2}), while both LAI estimates were similar for the understory (average difference of 0.17 m^2 m^{-2}). Fine fuel load derived from shrub allometries was also lower in treated stands than in control. While no clear differences were found in total or fine shrub fuel load between heavy-and light-thinned stands, fuel load in burned stands was lower than in non-burned stands, except for HtPB stand of Madrona, where the development of *A. ovalis* resulted in a fine fuel load similar to the control (Table 2.1). No clear patterns were apparent in dead fuel and litter load among treatments and controls, although burned stands tended to have less amount of 1 h fuels.

Table 2.3. Burning characteristics per stand (mean values, and minimum and maximum range in brackets), measured on top of the litter using thermocouples (type K, 3 mm diameter). Temperature was recorded every 10 s by dataloggers (Testo 175).

Locality	Llobera		Madrona		Secanella	
Thinning intensity	Heavy	Light	Heavy	Light	Heavy	Ligth
Number of thermocouples	14	15	8	12	7	15
Max fire temperature (ºC)	546 (244-871)	502 (300-676)	435 (157-778)	314 (59-633)	438 (60-735)	356 (60-840)
Residence time T>60 ºC (minutes)	91 (21-272)	112 (23-495)	28 (12-48)	9 (1-24)	7 (0-14)	6 (0-18)
Residence time T>120 ºC (minutes)	43 (4-241)	69 (6-263)	12 (4-31)	4 (0-12)	4 (0-8)	3 (0-11)
Temperature-Time integral (ºC x minutes)	14407 (2052-58722)	20691 (3062-87801)	3936 (1533-9183)	1271 (0-3182)	1435 (0-2845)	1253 (0-4589)

Notes: Residence time (in minutes) with treatment above 60 ºC and 120 ºC respectively. Time integral, integral of the curve between the time and the temperature above 60 ºC.

Stand water balance

Soil water holding capacity estimated by *medfate* was 193 mm and amount of extractable water between field capacity (-0.033 MPa) and Psi -5 MPa was 104 mm (Table 2.4). During the 2020 summer precipitation-free period, simulated soil moisture content relative to field capacity across all treatments was on average 0.16 higher than values measured by the sensors, in a 0−1 scale (Figure S2.3). Measured and simulated values were correlated in all treatments during the summer drought (r = 0.95).

Table 2.4. Soil characteristics used to model water balance.

Layer depth (cm)	Texture (%) Clay	Silt	Sand	Organic matter (%)	Rock fragment content (%)
0-30	19	29	48	3	17
31-100	29	29	40	2	50
101-200	26	44	29	1	95
Water holding capacity (mm)			193		
Extractable water (mm)			104		

Notes: Extractable water between field capacity (-0.033 MPa) and Psi -5 MPa

Water stress and fire behaviour simulations

Forest structure four to five years after treatments resulted in lower water stress (loss of hydraulic conductance and minimum midday leaf water potential) and milder fire behaviour (surface fire intensity and crown fire ignition potential) compared to untreated control stands (Figure 2.3, Table S2.4). Hydraulic conductance of trees in light-thinned stands was lower (i.e., higher loss of conductance) compared with trees of heavy-thinned ones. Yet, although prescribed burning after thinning increased hydraulic conductance of trees, we found that the increase was more evident in trees of light-thinned stands (Lt × PB interaction, Table S2.5). No differences were found between both thinning intensities on minimum leaf water potential, surface fire intensity, and crown fire ignition. Prescribed burning reduced both water stress and fire behaviour compared with stands where debris was not burned (Table S2.5): maximum loss of conductance and surface fire intensity were about two- fold higher, minimum leaf water potential was about 1.5 times higher, and crown fire ignition potential was about 1.1 times lower in non-burned stands than in burned ones (Figure 2.3, Table S2.5).

Water stress and fire behaviour simulations using the UntreatUnd scenario

When the understory was considered unmanaged, equalling the mean values of each control plot (*UntreatUnd* scenario), all water stress and fire behaviour indicators performed clearly worse than in *TreatUnd* scenario (Table S2.6). The difference between *TreatUnd* and *UntreatUnd* for each treatment is associated to the effect of understory management, while the difference between treatments and control under *UntreatUnd* scenario is associated to the effect of overstory management (Figure 2.3). Thus, fire behaviour and water stress indicators in the *UntreatUnd* scenario were similar in control and light-thinned stands. Heavy thinning in *UntreatUnd* scenario reduced loss of conductance and increased minimum leaf water potential of dominant trees, and reduced potential crown fire ignition of the stand. Surface fire intensity was similar in all stands (heavy-thinned, light-thinned, and control; Figure 2.3, Table S2.6).

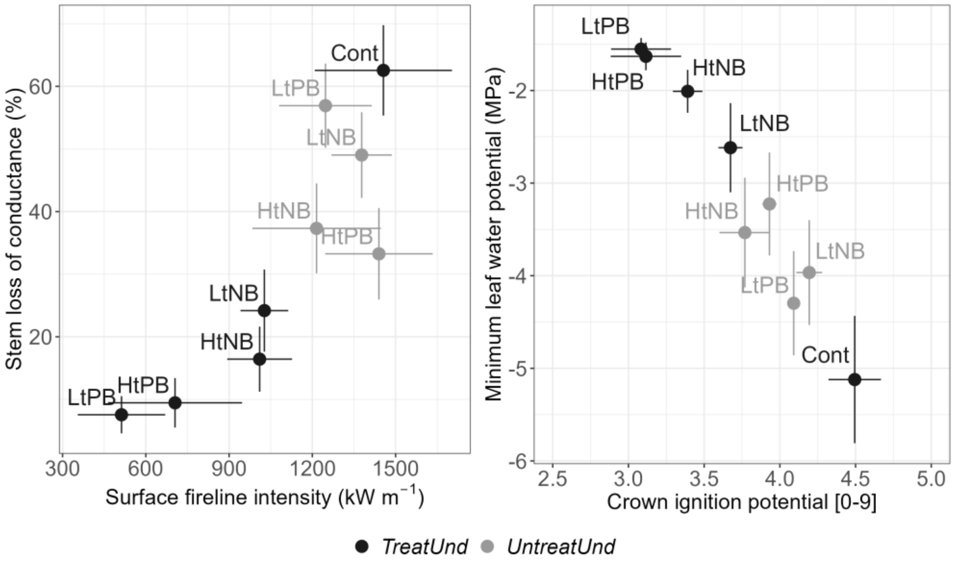

Figure 2.3. Simulated stem loss of hydraulic conductance and potential surface fireline intensity (left panel) and simulated minimum leaf water potential and crown ignition potential (right panel) for two understory scenarios: measured after treatments (*TreatUnd*) and using understory values of control stands (*UntreatUnd*) (mean values and standard errors, n = 3). Differences between *TreatUnd* and *UntreatUnd* stands show the understory management effect. Differences between treated stands and control in the *UntreatUnd* scenario show the thinning effect. Cont, untreated; HtPB, heavy-thinned, burned; HtNB, heavy-thinned, not burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

2.4. Discussion

Lack of management of Sub-Mediterranean pine forests resulted in stands susceptible to drought stress and wildfires. Management of both overstory and understory vegetation increased forest resistance to both stresses by reducing amount of fuel available, increasing the distance between surface and canopy layer, and eliminating competition for available soil water. Dominant trees of all managed stands lost less than 50% of their hydraulic conductance ability, a threshold that, when surpassed (as it was the case for trees of untreated stands), conventionally indicates an elevated risk of cavitation-induced mortality in conifers. Under drought conditions, in untreated stands where competition is high, trees are more prone to water stress because there is limited water in the soil and the transpiration rates are high, which induces an increase in the tension of the water column in the xylem that results in cavitation and the formation of gas bubbles, leading to a reduction of the hydraulic conductance (Lambers and Oliveira, 2019). A similar pattern was detected with midday leaf water potential, where only untreated stands exceeded the threshold at which leaves start to close their stomata and lose turgor (Figure 2.3b). This threshold depends on the drought tolerance of the species, from below -2.7 for less tolerant species to -3.5 MPa to relative drought-tolerant species, and, when surpassed, the photosynthetic activity of the plant is compromised (Lambers and Oliveira, 2019). The amount of fine fuel load (including canopy and understory fuels) above which fire suppression capacity is compromised under extreme weather conditions is estimated between 9 and 12 Mg ha^{-1} (Burrows, 2000; P. M. Fernandes et al., 2016). Although untreated stands were the only ones that exceeded this threshold, light-thinned non-burned stands (LtNB) were close to surpass it (Table 2.1). As expected, forest management contributed to increase the resistance to drought events and wildfires under extreme conditions, yet nuances between different overstory and understory management options were apparent and are discussed below.

Overstory management effects

Both thinning treatments reduced tree competition for water in comparison to untreated stands. We expected that dominant trees of heavy-thinned stands would show lower levels of water stress than trees of light-thinned ones; yet that was only true for hydraulic conductance when understory vegetation had not been burned (Table S2.5). Even though heavy-thinned stands had overall lower overstory LAI (Figure 2.2, Table S2.3), we could not see differences between thinning intensities in hydraulic conductance in burned stands, neither in leaf water potential in burned or non-burned stands, likely because dominant trees face significant competition for soil water from understory plants (Giuggiola et al., 2018; Simonin et al., 2007). Thinning decreases wildfire risk by reducing crown density and continuity (i.e., canopy bulk density; Agee and Skinner, 2005), but vigorous understory resprout may counteract increasing surface fire intensity and the probability of torching.

Although in a previous study we showed that the resprouting vigour of understory (i.e., growth in volume or length) was directly related to light availability (Casals and Rios, 2018), here we did not detect clear patterns in total or fine understory fuel load at stand level between both overstory thinning intensities of non-burned stands. Differences in fuel load between thinning intensities were apparent within burned stands, but these differences were attributed to one stand that had an above-average shrub fuel load (HtPB in Madrona), similar to the one of untreated stands. Accordingly, and contrary to our hypothesis, we did not detect differences in stand vulnerability to wildfires between thinning intensities in burned and non-burned stands. Fire behaviour simulation models use the critical minimum surface fireline intensity, calculated as a function of canopy base height and fuel moisture content, to set a threshold to initiate a crown fire. When surface fire intensity exceeds this threshold, fire jumps into the canopy (Scott and Reinhardt, 2001). Because heavy thinning highly reduces canopy cover and the amount of canopy fuel load, a surface fire has less chances to become a crown fire, and even if a tree torches, it has less fuel to burn and the fire will be less intense (Banerjee, 2020). Yet, in our stands, the potential crown ignition was not significantly affected by thinning intensity, likely because surface fire intensity was also not influenced by type of thinning treatment (Table S2.5). This could be attributed to low level of replication, yet similar results were found by Piqué and Domènech (2018). Our set of environmental inputs might have also played a role in failing to find differences between thinning intensities, as varying results can be expected depending on how realistic the assumptions made are (Cruz et al., 2014). Higher canopy base height in heavy-thinned stands was also not enough to reduce crown ignition potential (Table 2.1, Figure 2.3). Overstory thinning serves as a management tool to reduce active crown fire spread by decreasing canopy bulk density (Agee and Skinner, 2005). In our stands, a reduction in canopy cover and basal area in light-thinned and heavy-thinned stands did not seem to impact crown fire intensity or crown flame length compared to untreated stands (Table S2.4). In contrast, previous studies have found a reduction in crown fire activity in treated compared to untreated sites (Fulé et al., 2012; Piqué and Domènech, 2018). These differences might be attributed to the different calculation methods or models used (Fulé et al., 2012).

Understory management effects

Differences in simulation results between *TreatUnd* and *UntreatUnd* understory scenarios suggested an important role of understory treatments irrespective of thinning intensity (Figure 2.3, Table S2.6). In a previous study, we showed that burning the understory, in comparison to treating it only mechanically, increased mortality and reduced resprouting vigour of European box tree, the dominant understory species of these stands (Casals and Rios, 2018). Accordingly, here we detected that four-to-five years after burning, shrub understory biomass, and LAI were still lower in burned stands than in non-burned ones, with the exception of HtPB in Madrona. These differences resulted in significant lower levels of simulated water stress and milder wildfire behaviour in burned stands (Figure 2.3, Table S2.5). Thinning decreases water stress of dominant pines by reducing tree competition for water. Our results showed that, while competition among trees is crucial, understory vegetation also has a significant impact. Trees of non-burned stands lost to a greater extent their ability to carry water through the xylem than trees of burned stands (Figure 2.3a). This may be attributed to higher understory biomass: when understory transpiration and contributes to deplete soil water pools faster (Gebhardt et al., 2014; Giuggiola et al., 2018; Simonin et al., 2007). Simulations comparing both understory scenarios (*TreatUnd* and *UntreatUnd*) highlighted the benefits of applying prescribed burning after thinning. Especially when light thinning is applied, debris burning plays a key role in reducing forest vulnerability to both disturbances (Figure 2.3), and particularly in reducing xylem cavitation that causes loss of hydraulic conductance (Lt × PB interaction, Table S2.5). While this is consistent with our second hypothesis, it is worth noting that prescribed burning may impact xylem hydraulic functionality through cambium necrosis or xylem embolism, depending on the intensity of the fire, its residence time, and the species affected (Bär et al., 2019). Although we may expect that severity of prescribed burning on xylem of adult Mediterranean pines protected by thick barks is low (Battipaglia et al., 2016; Valor et al., 2015, 2020), further studies should address the potential effect of prescribed fire on tree physiology and growth. Surface fire intensity and potential crown fire ignition were also more influenced by understory treatment than by thinning intensity: non-burned stands had higher chances of experiencing a crown fire (Figure 2.3b, Table S2.5). When surface fuels are abundant, both in height and in cover, chances that a crown fire starts are higher. A crown fire will only be sustained if crown density and understory fuel load are sufficiently high (Van Wagner, 1977). Within non-burned stands, heavy-thinned ones had slightly lower chances to experience a crown fire than light-thinned ones, likely because of the higher amount of understory fuel load, yet these differences were not significant. Within burned stands, crown fire ignition potential was similar between both thinning intensities.

Study limitations

It is worth to note the low level of replication of this experimental study (n = 3) and to highlight that simulation results should be interpreted with caution, and rather as comparative between treatments than as absolute values. Varying results might be expected depending on the model used, the indicator chosen, how environmental factors are input (Cruz et al., 2014; De Cáceres et al., 2021), or on the sampling method used (Keane and Gray, 2013). The water balance model used in this study is a very detailed process-based model that incorporates many recent research findings, yet it assumes certain factors and processes that need to be considered (De Cáceres et al., 2021). For example, tree crown position within the canopy is not considered when simulating energy balance of the canopy, which may result in biased estimations of transpiration and drought stress. Also, FCCS, the fire behaviour model used in this study, is a semi-empirical model that has been calibrated assuming homogeneously scattered fuels. Yet, the use of average fuel values is not entirely correct, since fire spread is rather influenced by the packing ratio of the fuel bed and the most flammable species of the community (De Magalhaes and Schwilk, 2012; Scarff and Westoby, 2006). Acknowledging that fuels structural complexity and composition influences spread and intensity of fires, efforts have been made in developing 3-D physics based models (Linn et al., 2002; Mell et al., 2010). Despite the uncertainties associated with models used in this study, we believe that our results are robust and may be taken into account when considering treatment alternatives.

2.5. Conclusions

Our study illustrates the potential of forest management to increase forest resistance to the two main disturbances of the Mediterranean region, drought events and wildfires, and shows that its benefits persist four to five years after treatments. It also stresses the importance of managing the understory to further increase the resistance ability of the forests, especially when the understory is burned under controlled conditions, since shrub load is kept at lower levels for a longer period. Thus, even though the forest management plan does not consider a thinning intervention for some years, an active management of the understory might be desired (and if appropriate, with prescribed burns) to boost forest resistance to drought events and wildfires. When understory vegetation is actively managed, the choice between thinning intensities may be subject to the management goal (i.e., wood production, biodiversity, carbon sequestration, hazard reduction, etc.).

Acknowledgements

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2.6. Supplementary material

Figure S2.1. Treatment LtPB (light-thinned, burned) in the foreground and LtNB (light-thinned, not burned) in the background (Llobera site).

Table S2.1. Vegetation structure per treatment and site, before and four to five years after the treatments. Cont, untreated control; HtNB, heavy-thinned, not burned; HtPB, heavy-thinned, burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Locality		Llobera				
Treatment		Cont	HtNB	HtPB	LtNB	LtPB
Tree density (n ha^{-1})	Pre	1591	2132	1687	1352	1782
	Post	1560	732	637	1273	1401
Basal area (m^2 ha^{-1})	Pre	40.0	45.4	38.4	32.1	39.5
	Post	39.7	28.0	24.5	32.1	40.5
Quadratic mean diameter (cm)	Pre	17.9	16.4	17.0	17.4	16.8
	Post	18.0	22.1	22.2	17.9	19.2
Stand height (m)	Pre	12.8 (2.1)	11.6 (2.3)	10.6 (2.9)	12.3 (1.8)	13.4 (1.0)
	Post	9.0 (2.8)	11.9 (1.9)	12.3 (2.1)	10.2 (2.4)	10.5 (2.2)
Canopy base height (m)	Pre	7.0 (0.3)	7.9 (1.5)	6.9 (1.7)	6.1 (1.1)	8.4 (0.7)
	Post	5.3 (1.7)	6.7 (1.2)	7.1 (1.6)	5.9 (1.3)	6.1 (1.4)
Canopy cover (%)	Pre	87	87	91	80	83
	Post	89	63	52	85	76
Shrub total load (Mg ha^{-1})	Pre	12.14	12.69	12.71	16.47	22.14
	Post	18.41	4.52	1.28	5.62	1.77

Table S2.1. (cont.). Vegetation structure per treatment and site, before and four to five years after the treatments. Cont, untreated control; HtNB, heavy-thinned, not burned; HtPB, heavy-thinned, burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Locality		Madrona				
Treatment		Cont	HtNB	HtPB	LtNB	LtPB
Tree density (n ha^{-1})	Pre	1273	907	955	1066	955
	Post	1560	446	573	1194	987
Basal area (m^2 ha^{-1})	Pre	28.2	30.7	28.1	28.5	25.8
	Post	33.3	23.4	21.7	28.4	26.8
Quadratic mean diameter (cm)	Pre	16.8	20.9	19.4	18.4	18.5
	Post	16.5	25.8	22.0	17.4	18.6
Stand height (m)	Pre	11.0 (2.2)	15.1 (4.0)	11.4 (1.6)	13.4 (4.7)	11.4 (3.6)
	Post	8.9 (2.5)	14.4 (4.3)	11.7 (2.0)	9.1 (3.4)	9.7 (2.9)
Canopy base height (m)	Pre	8.4 (1.2)	9.8 (2.2)	6.8 (1.1)	7.9 (3.1)	7.5 (2.1)
	Post	5.2 (1.3)	8.1 (3.2)	6.9 (1.1)	5.4 (2.1)	5.7 (1.8)
Canopy cover (%)	Pre	76	79	80	77	76
	Post	66	50	50	67	64
Shrub total load (Mg ha^{-1})	Pre	19.27	13.33	14.92	16.91	12.05
	Post	11.09	4.91	8.90	6.06	2.69

Table S2.1. (cont.). Vegetation structure per treatment and site, before and four to five years after the treatments. Cont, untreated control; HtNB, heavy-thinned, not burned; HtPB, heavy-thinned, burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Locality		Secanella				
Treatment		Cont	HtNB	HtPB	LtNB	LtPB
Tree density (n ha^{-1})	Pre	1592	1623	1846	1703	2356
	Post	1496	748	668	1369	1305
Basal area (m^2 ha^{-1})	Pre	31.6	31.4	31.0	40.4	32.9
	Post	30.4	21.8	18.1	33.0	28.9
Quadratic mean diameter (cm)	Pre	15.9	15.7	14.6	17.4	13.3
	Post	16.1	19.3	18.6	17.5	16.8
Stand height (m)	Pre	14.1 (2.3)	12.8 (1.6)	11.3 (2.3)	15.3 (3.4)	11.7 (0.8)
	Post	8.0 (3.2)	10.2 (2.8)	10.7 (2.8)	9.9 (2.9)	9.3 (1.8)
Canopy base height (m)	Pre	6.7 (1.4)	6.5 (1.2)	5.2 (0.5)	9.4 (1.7)	6.3 (0.4)
	Post	4.7 (1.5)	5.9 (1.4)	6.1 (1.4)	5.8 (1.9)	5.5 (0.8)
Canopy cover (%)	Pre	71	73	77	77	77
	Post	72	66	42	67	73
Shrub total load (Mg ha^{-1})	Pre	16.07	13.28	8.83	15.27	15.20
	Post	13.29	3.42	1.71	2.87	1.97

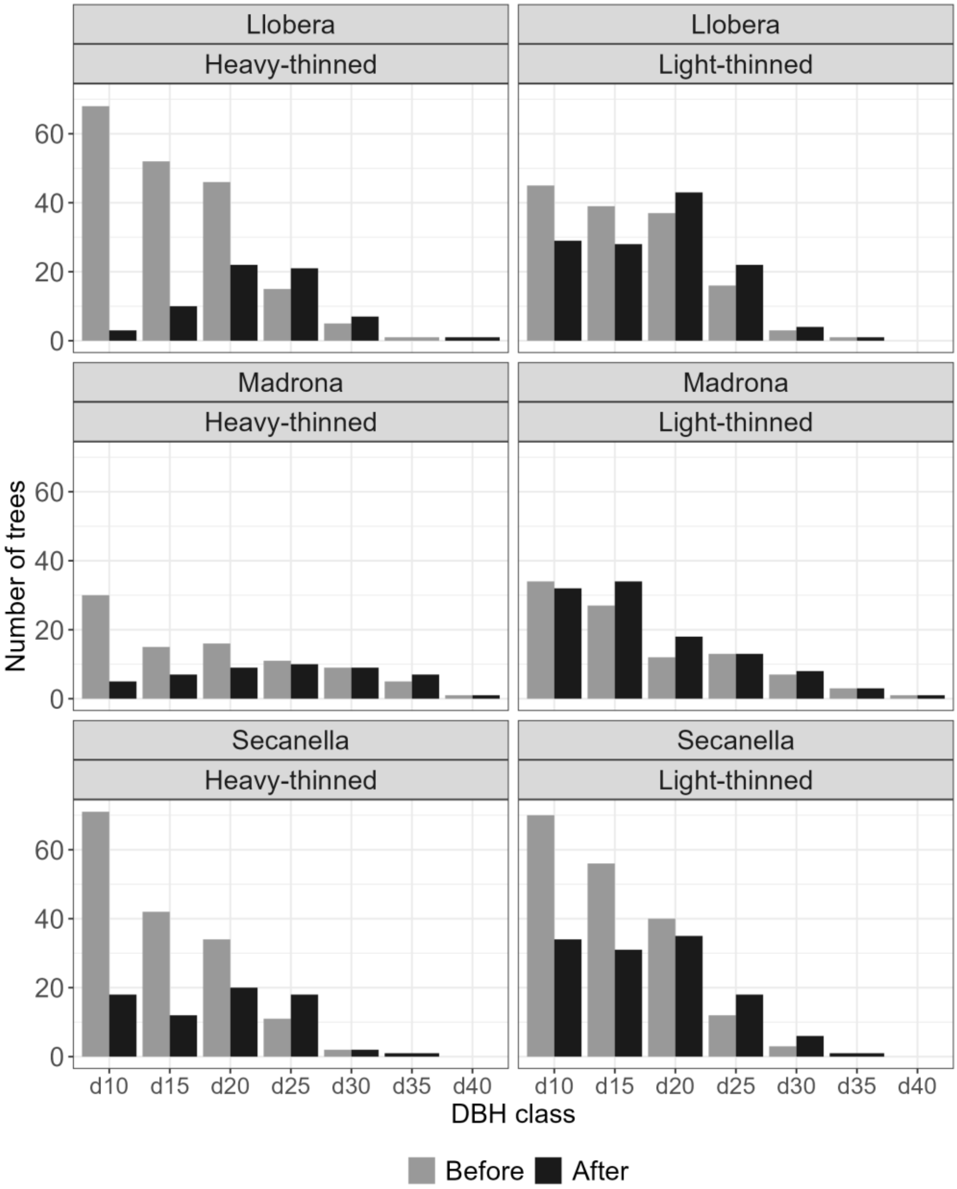

Figure S2.2. Number of trees per diameter class before and after treatments (four to five years) by locality and thinning intensity applied. The number of trees represents all trees inventoried in two 314 m^2 plots per thinning treatment and site (one plot in non-burned and another in burned stands per treatment).

Table S2.2. Species parameters used as input for the water balance model. Gswmin, minimum stomatal conductance to water vapor per leaf area unit (mol s^{-1} m^{-2}); Gswmax, maximum stomatal conductance to water vapor per leaf area unit (mol s^{-1} m^{-2}); Kmax_stemxylem, sapwood-specific hydraulic conductivity of stem xylem (kg H_2O s^{-1} m^{-1} MPa^{-1}); Kmax_rootxylem, sapwood-specific hydraulic conductivity of root xylem (kg H_2O s^{-1} m^{-1} MPa^{-1}); VCleaf_kmax, leaf hydraulic conductance (mol H_2O s-1 m-2 MPa^{-1}); Plant_kmax, maximum whole-plant conductance (mol H_2O s^{-1} m^{-2} MPa^{-1}).

Species	Gsw min	Gsw max	Kmax_ stemxylem	Kmax_ rootxylem	VCleaf_ kmax	Plant_ kmax
Acer monspessulanum	0.005	0.452	0.54	1.1	8	1.26
Acer opalus	0.005	0.452	0.18	0.7	8	0.44
Amelanchier ovalis	0.004	0.291	1.57	6.3	4	2.00
Buxus sempervirens	0.005	0.052	0.15	0.6	3	0.53
Crataegus spp.	0.004	0.291	1.57	6.3	4	1.74/1.98[1]
Ligustrum vulgare	0.005	0.291	1.57	6.3	4	2.19
Pinus nigra	0.003	0.220	0.41	1.6	4	1.07
Pinus sylvestris	0.003	0.220	0.45	1.8	4	0.97
Quercus faginea	0.004	0.261	0.7	2.8	5	1.30
Quercus pubescens	0.004	0.289	0.7	2.8	3	0.92 / 1.30[1]
Sorbus spp.	0.004	0.452	0.28	5	8	0.70
Viburnum spp.	0.005	0.291	1.57	6.3	4	2.12

[1] First value of Plant_kmax belongs to individuals treated as tree, second value to individuals treated as shrub.

Table S2.3. Forest structure characteristics by treatment four to five years after management (mean values and standard deviation between brackets, n = 3 localities), and p-values of a two-way ANOVA test. The interaction thinning intensity and understory management was not significant for any variable. In bold, significant differences between treatments. HtPB, heavy-thinned, burned; HtNB, heavy-thinned, not burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Treatment	**HtNB**	**HtPB**	**LtNB**	**LtPB**	p-values	
Thinning intensity	Ht	Ht	Lt	Lt		
Understory management	NB	PB	NB	PB	Thinning intensity	Understory management
Tree density (n ha^{-1})	642 (170)	626 (48)	1279 (88)	1231 (217)	**< 0.005**	0.700
Basal area (m^{2} ha^{-1})	24.4 (3.3)	21.4 (3.3)	31.2 (2.4)	32.1 (7.4)	**0.007**	0.691
Quadratic mean diameter (cm)	22.4 (3.3)	20.9 (2.0)	17.6 (0.3)	18.2 (1.2)	**0.011**	0.699
Stand height (m)	12.2 (2.1)	11.6 (0.8)	9.7 (0.6)	9.8 (0.6)	**0.012**	0.716
Canopy base height (m)	6.9 (1.1)	6.7 (0.5)	5.7 (0.3)	5.8 (0.3)	**0.015**	0.856
Canopy bulk density (kg m^{-3})	0.09 (0.02)	0.08 (0.02)	0.14 (0.04)	0.15 (0.03)	**< 0.005**	0.831
Shrub height (m)	1.0 (0.1)	0.9 (0.2)	0.8 (0.2)	0.7 (0.04)	**0.023**	0.327
LAI overstory (m^{2} m^{-2})	1.2 (0.2)	1.1 (0.3)	1.5 (0.5)	1.7 (0.4)	**0.033**	0.862
LAI understory (m^{2} m^{-2})	0.9 (0.3)	0.5 (0.4)	0.7 (0.3)	0.3 (0.1)	0.274	**0.045**
Load 1h fuels (Mg ha^{-1})	1.3 (0.3)	0.4 (0.2)	1.2 (0.4)	0.9 (0.4)	0.300	**0.036**

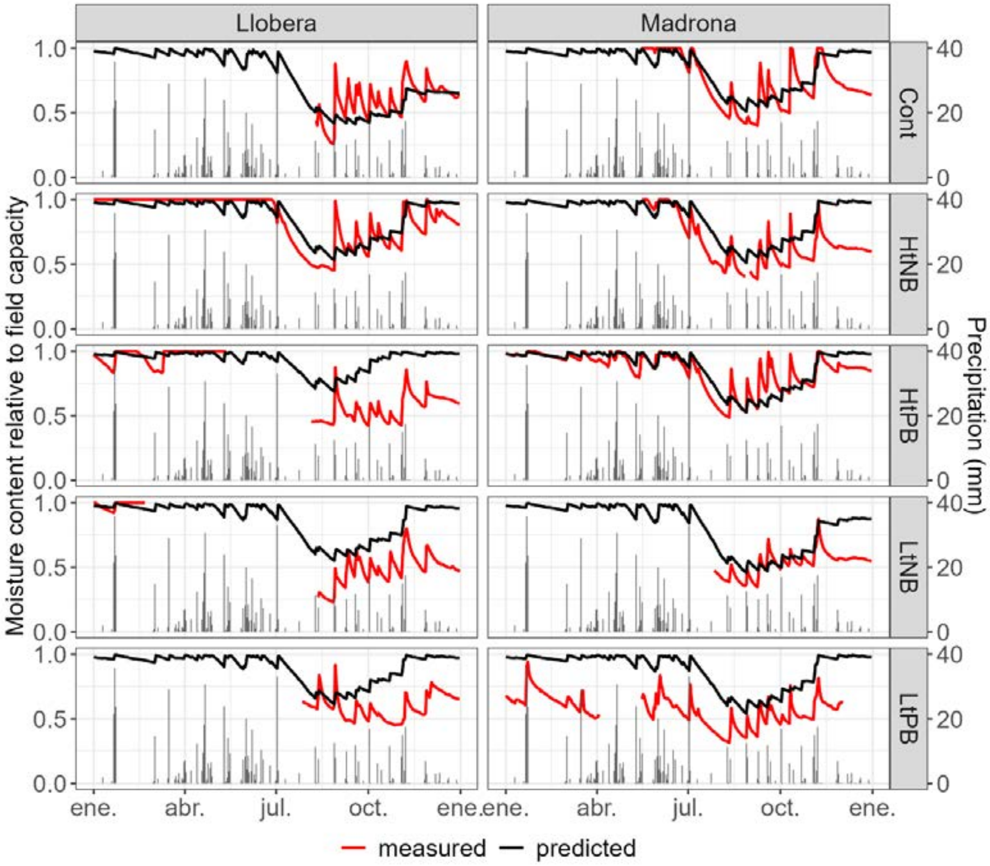

Figure S2.3. Measured (at 20 cm depth) and simulated (0-30 cm depth) soil moisture content in 2020 by treatment and site. Bars represent precipitation amount. Cont, untreated; HtPB, heavy-thinned, burned; HtNB, heavy-thinned, not burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Table S2.4. Water balance and all fire behaviour simulation results (mean values and standard error in brackets, n= 3). Cont, untreated; HtPB, heavy-thinned, burned; HtNB, heavy-thinned, not burned; LtNB, light-thinned, not burned; LtPB, light-thinned, burned.

Variable	Cont	HtNB	HtPB	LtNB	LtPB
Loss of hydraulic conductance (%)	62.5 (7.2)	16.4 (5.1)	9.5 (4.0)	24.2 (6.6)	7.6 (3.0)
Minimum leaf water potential (MPa)	-5.1 (0.7)	-2.0 (0.2)	-1.6 (0.2)	-2.6 (0.5)	-1.6 (0.1)
Surface fire intensity (kW m^{-1})	1456 (247)	1010 (117)	705 (242)	1027 (86)	512 (158)
Flame length (m)	2.2 (0.2)	1.9 (0.1)	1.5 (0.2)	1.9 (0.1)	1.3 (0.2)
Rate of spread (m min^{-1})	9.8 (1.9)	6.5 (1.2)	7.2 (1.1)	6.7 (0.3)	5.5 (0.9)
Potential crown ignition [0-9]	4.5 (0.2)	3.4 (0.1)	3.1 (0.2)	3.7 (0.1)	3.1 (0.2)
Crown fire intensity (kW m^{-1})	5948 (1899)	5776 (2091)	2394 (854)	6243 (1695)	3952 (255)
Crown flame length (m)	8.4 (0.7)	10.1 (0.2)	8.5 (0.2)	9.1 (0.6)	8.4 (0.1)
Crown rate of spread (m min^{-1})	20.3 (4.2)	18.5 (3.8)	10.4 (1.5)	21.0 (3.8)	16.5 (0.1)

Table S2.5. Water balance and fire behaviour mixed-effects models among treatments for the *TreatUnd* scenario, control stand was excluded. Bold Confidence Intervals (CI) indicate a significant difference with the intercept. Ht, heavy-thinned; Lt, light-thinned; NB, not burned; PB, burned.

Response	R^2c	R^2m	ICC	Fixed effects	Estimate	Std. Error	95% CI lower	95% CI upper
Loss hydraulic conductance	0.946	0.117	0.939	(Intercept)	-2.43	0.94	-4.28	-0.58
(Beta)				Lt	0.77	0.17	**0.44**	**1.10**
				PB	-0.80	0.19	**-1.17**	**-0.42**
				Lt x PB	-0.93	0.27	**-1.45**	**-0.40**
Minimum leaf water potential	0.571	0.062	0.542	(Intercept)	-2.18	0.60	-3.35	-1.01
(Gaussian)				Lt	-0.27	0.21	-0.67	0.14
				PB	0.72	0.21	**0.32**	**1.13**
Surface fire intensity	0.56	0.388	0.281	(Intercept)	1062.6	143.7	781.0	1344.2
(Gaussian)				Lt	-87.9	134.5	-351.6	175.8
				PB	-409.8	134.5	**-673.5**	**-146.2**
Potential crown ignition	0.479	0.403	0.127	(Intercept)	3.47	0.15	3.18	3.76
(Gaussian)				Lt	0.13	0.15	-0.18	0.43
				PB	-0.43	0.15	**-0.74**	**-0.13**

Notes: Intercept equals Ht, NB.

Table S2.6. Water balance and fire behaviour mixed-effects models among treatments for *TreatUnd* and *UntreatUnd* scenarios, control stand was excluded. Bold CI intervals indicate a significant difference with the intercept. Ht, heavy-thinned; Lt, light-thinned; NB, not burned; PB, burned; UntreatUnd, *UntreatUnd* scenario.

Response	R^{2}c	R^{2}m	ICC	Fixed effects	Estimate	Std. Error	95% CI lower	95% CI upper
Loss hydraulic conductance (Beta)	0.776	0.387	0.634	(Intercept)	-1.56	0.32	-2.19	-0.93
				Lt	0.41	0.16	**0.10**	**0.71**
				PB	-0.25	0.16	-0.55	0.06
				UntreatUnd	1.31	0.17	**0.97**	**1.65**
Minimum leaf water potential (Gaussian)	0.492	0.153	0.401	(Intercept)	-1.88	0.58	-3.01	-0.74
				Lt	-0.51	0.25	**-1.00**	**-0.02**
				PB	0.36	0.25	-0.14	0.85
				UntreatUnd	-1.80	0.25	**-2.30**	**-1.31**
Surface fire intensity (Gaussian)	0.694	0.683	0.034	(Intercept)	1044.4	145.6	759.0	1329.7
				Lt	-51.4	98.8	-245.1	142.2
				PB	-409.8	139.7	**-683.7**	**-135.9**
				UntreatUnd	277.8	139.7	**3.9**	**551.7**
				PB x UntreatUnd	457.0	197.6	**69.6**	**844.3**
Potential crown ignition[1] (Gaussian)		0.79		(Intercept)	3.43	0.11	3.22	3.64
				Lt	0.21	0.10	**0.02**	**0.40**
				PB	-0.43	0.14	**-0.70**	**-0.17**
				UntreatUnd	0.45	0.14	**0.18**	**0.72**
				PB x UntreatUnd	0.46	0.19	**0.09**	**0.84**

Notes: Intercept equals Ht, NB, *TreatUnd*

[1] The model resulted in singular fits (variance estimated as zero)

CHAPTER 3

Thinning followed by slash burning enhances growth and reduces vulnerability to drought for *Pinus nigra*

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Abstract

Increasingly frequent severe drought events are pushing Mediterranean forests to unprecedented responses. Lack of management leads to dense forests that are highly susceptible to drought stress, potentially resulting in extensive dieback and increased vulnerability to other disturbances. Forest treatments like thinning and slash burning reduce competition for resources and have to potential to enhance tree growth and vigour and minimize tree vulnerability to drought. Here, we used tree rings to study the growth and physiological response of black pine (*Pinus nigra*) to drought in northeastern Spain under different treatments, including two thinning intensities (light and heavy, with 10% and 40% basal area reduction, respectively) followed by two understory treatments (clearing alone and in combination with slash burning), resulting in a research design of four treatments plus an untreated control with three replicates. Specifically, we studied basal area increment (BAI), resilience indices, and intrinsic water use efficiency (iWUE) using carbon and oxygen isotope composition (δ^{13}C and δ^{18}O in tree-ring cellulose) before and after treatments. Our results showed that BAI and resistance to drought increased in the heavy-thin (burned and unburned) and light-thin burned units. Resilience increased in the burned units regardless of the thinning intensity, while recovery was not affected by treatment. Slash burning additionally increased BAI in the light-thin and resistance and resilience in the heavy-thin units compared to clearing alone. The stable isotope analysis revealed a minor effect of treatments on δ^{13}C and δ^{18}O. No change in iWUE among treatments was presumably linked to a proportional increase in both net CO_2 assimilation and stomatal conductance, which particularly increased in the heavy-thin (burned and unburned) and light-thin burned units, indicating that these trees were the least affected by drought. This study shows that management approaches aimed at reducing wildfire hazard can also increase vigour of dominant trees under drought stress. By reducing competition both from the overstory and the understory, thinning followed by clearing alone or in combination with slash burning promotes tree growth and vigour and increases its resistance and resilience to drought.

Keywords: basal area increment, carbon and oxygen stable isotopes, dendroecology, prescribed burning, resilience indices, tree-ring, water stress, water-use efficiency.

3.1. Introduction

Mediterranean forests are experiencing growing pressure due to the increasingly frequent occurrence of severe drought events (Cook et al., 2018; Gazol et al., 2020). Severe droughts affect forests by altering tree physiological functions such as stomatal regulation and carbon assimilation, while recurrent droughts can result in widespread tree dieback when the time to recover is compromised (Gessler et al., 2020). Besides the intensity and frequency of the drought itself, the structure of the forest is also crucial in determining how trees respond to a drought event. Lack of management leads to dense forests with abundant understory where competition for resources is high and trees are more vulnerable to drought stress (Giuggiola et al., 2018), drought-induced die-off (Field et al., 2020; Sánchez-Salguero et al., 2013), and wildfires (Mantero et al., 2020). As drought events are becoming more common with climate change, forest treatments such as thinning and prescribed burning might offer an opportunity to promote tree growth and minimize tree vulnerability to drought (e.g., Tepley et al., 2020; Sohn et al., 2016).

Thinning increases water, nutrient, and light availability by reducing tree competition and canopy rainfall interception (Breda et al., 1995). Prescribed burning in the Mediterranean region is applied with the aim to reduce wildfire hazard or to maintain or restore habitats for grazing and wildlife (Fernandes et al., 2022). It can be implemented either directly on live vegetation (commonly referred to as underburning) or on thinning or mechanical clearing residues (commonly referred to as slash burning), which is typically more severe (Carter and Foster, 2004). Prescribed burning can contribute to increasing tree resilience to drought (Valor et al., 2020; 2018) by limiting the resprouting ability of the understory and thus, its competition for resources (Casals and Rios, 2018). However, medium to high-intensity prescribed burning can damage tree cambium and roots (Bär, et al., 2019), compromising tree vigour and potentially causing delayed tree mortality of suppressed or intermediate trees (Valor et al. 2017a; Kobziar et al., 2006). Additionally, treatments like thinning and prescribed burning lead to an increase in soil temperature and soil water evaporation because more radiation penetrates into the soil (Giuggiola et al., 2018; Raz-Yaseef et al., 2010), with the potential to negatively impact tree water balance and limit the benefits of the treatment.

Tree rings provide information on how trees respond to environmental or density changes such as drought events or forest treatments. Resilience indices (i.e., resistance, recovery, and resilience) are commonly used to measure the relative changes in tree radial growth resulting from a disturbance event by quantifying growth before, during, and after the event, and are often used to assess tree vulnerability to drought (Lloret et al., 2011). While we must be cautious when interpreting tree responses to drought using these indices because they depend on factors such as the climatic conditions before and after the drought, the definition of the drought event itself, and the length of the reference period used to calculate them (Schwarz et al., 2020), they still provide valuable information and are widely used. Indeed, a sensible workaround is to interpret them in combination with other analyses. For example, combining tree ring widths with carbon and oxygen stable isotope data provides more informative insights into the physiological mechanisms driving growth and promoting resilience to drought events (Tepley et al., 2020; Valor et al., 2018).

The carbon isotope composition ($\delta^{13}C$) in tree rings serves as a long-term proxy of the intrinsic water-use efficiency (iWUE) during ring formation. iWUE is the ratio between net photosynthetic CO_2 assimilation (A) and stomatal conductance (g_s) (Farquhar et al., 1989), and by estimating iWUE following a drought event we can gain insights into the physiological mechanisms that trees employ to sustain growth under drought stress. No change in iWUE (or $\delta^{13}C$) could indicate no change in A and g_s or a change in both factors but with equal magnitude. To distinguish if it is one case or the other, we can adopt the dual-isotope approach and include oxygen isotope composition ($\delta^{18}O$) in the analysis (Scheidegger et al., 2000). The $\delta^{18}O$ signature in plant tissues is related to the isotopic signature of source water and the stomatal response to vapour-pressure deficit and thus, it can be used to differentiate the role of g_s on iWUE. The dual-isotope analysis may therefore yield information on which physiological process (A or g_s) is more affected by thinning and prescribed burning. Previous studies analysing tree growth and both $\delta^{13}C$ and $\delta^{18}O$ have focused solely on either thinning (Giuggiola et al., 2016; Martín-Benito et al., 2010; Sohn et al., 2014; Manrique-Alba et al., 2020; Moreno-Gutiérrez et al., 2011; T. Fernandes et al., 2016) or prescribed burning (Valor et al., 2018), and have yielded divergent results, presumably due to differences in thinning intensities, climate, region, site conditions, species, and the plant tissues analysed.

In a previous simulation study in the same sites, we found that thinning followed by mechanical clearing of the understory higher than 1.3 m efficiently reduced the loss of hydraulic conductance of dominant black pines (*Pinus nigra* Arn. spp. *salzmannii* (Dunal) Franco) during drought years, particularly when slash burning was implemented (Vilà-Vilardell et al., 2023). Water balance simulations indicated that forest treatments improved the resistance of trees to drought; here, we examined the underlying physiological mechanisms driving their vulnerability to drought. Black pine is a widely distributed species across the drought-prone Mediterranean basin (Figure 3.1) that is well adapted to surface fires due to its thick bark (Fernandes et al., 2008). To understand how thinning and slash burning influence the response of dominant black pines to drought, we combined data on basal area increment (BAI), resilience indices, and C and O stable isotopes. We hypothesized that reduced competition due to thinning and mechanical clearing of the understory would improve growth, water balance of trees (reduce iWUE), and resilience to drought, especially when combined with slash burning.

3.2. Materials and methods

Study area and treatments

This study took place in sub-Mediterranean forests located in north-eastern Spain, at the southern foothills of the Pyrenees (Figure 3.1). Forests in this area are dominated by Spanish black pine (*Pinus nigra* spp. *salzmannii*) with scattered Scots pine (*Pinus sylvestris* L.) and downy oak (*Quercus pubescens* Mill.). The understory is mainly composed of European box (*Buxus sempervirens* L.) with snowy mespilus (*Amelanchier ovalis* Medik.), wayfarer (*Viburnum lantana* L.), common hawthorn (*Crataegus monogyna* Jacq.), and downy oak seedlings. The mean annual temperature is 13.1 ºC and the mean annual precipitation is 592 mm (period 1976 – 2021; De Cáceres et al., 2018).

The study was established in a block design of four treatments units plus an untreated control replicated in three sites (Llobera, Madrona, and Secanella) between 2015 and 2017. Treatments included two intensities of thinning from below (heavy and light) followed by mechanical clearing of understory vegetation higher than 1.3 m (hereafter referred to as clearing), along with chopping and scattering of the resulting slash. Light thinning treatments aimed to keep a canopy cover of 70-75%, which required removing only suppressed trees, while heavy thinning treatments aimed for a canopy cover of 50-60%, which required removing not only suppressed trees but also a few dominant and co-dominant ones. Prior to treatments, all trees to be cut were selected and marked by experienced forest managers. Thinning treatments were assigned randomly in each site. In half of each thinning treatment, prescribed burning of the slash and of the remaining understory vegetation lower than 1.3 m was implemented (hereafter referred to as slash burning). Burning treatments were systematically placed in the middle of the block between thinning intensities to ease its implementation. Thus, the resulting treatment units were: heavy thinning plus clearing and slash burning (heavy-thin burned, HB), heavy thinning plus clearing (heavy-thin unburned, HU), light thinning plus clearing and slash burning (light-thin burned, LB), light thinning plus clearing (light-thin unburned, LU), and untreated control (C). Treatment units ranged from 0.4 to 2.0 ha. Site characteristics and forest structure per treatment and site are presented in Table S3.1. Thinning and clearing treatments were carried out manually using a chainsaw in 2015 in two sites (Llobera and Madrona) and 2016 in the other (Secanella). Once trees were lopped, commercial boles (> 20 cm in diameter 1.3 above ground) were removed from the stand and tree crowns and cleared shrubs were left on site and chopped and scattered (and burned in half of the area). Slash burning was implemented using a strip head fire ignition pattern by the Forest Action Support Group of the Government of Catalonia (GRAF) at air temperature between 19 and 23 ºC and at a relative humidity between 41 and 50% in spring 2015 in Llobera, autumn 2015 in Madrona, and spring 2017 in Secanella. When slash burning was conducted, fuels were drier in Llobera and Madrona than in Secanella (Table S3.1). Fire temperature was recorded every 10 seconds on top of the litter layer using thermocouples (type K, 3 mm diameter) connected to a Testo 175 datalogger that were scattered across the entire stand (see details in Casals and Rios, 2018; Vilà-Vilardell et al., 2023). Total fine woody fuel load immediately after treatments was on average 72 and 57 Mg ha^{-1} in unburned units (HU and LU, respectively) and 34 and 23 Mg ha^{-1} in burned units (HB and LB, respectively). In the untreated control units, it was around 40 Mg ha^{-1} (Piqué and Domènech, 2018). Diameter at breast height (DBH), tree height, and canopy base height of trees bigger than 7.5 cm DBH were surveyed in one 314 m^2 circular plot per treatment unit. Canopy cover was measured with a spherical convex densiometer at plot centre (Forestry Suppliers, Inc). Shrub cover, height, and crown diameter as well as herb cover were surveyed in 20 quadrats of 1 m^2 evenly spread along two 50 m transects. Shrub biomass was estimated with regional allometries using the *medfuels* R package v.0.1.1 (De Cáceres and Casals, 2023; Table 3.1, Table S3.1). All these variables were measured right before and five years after treatments.

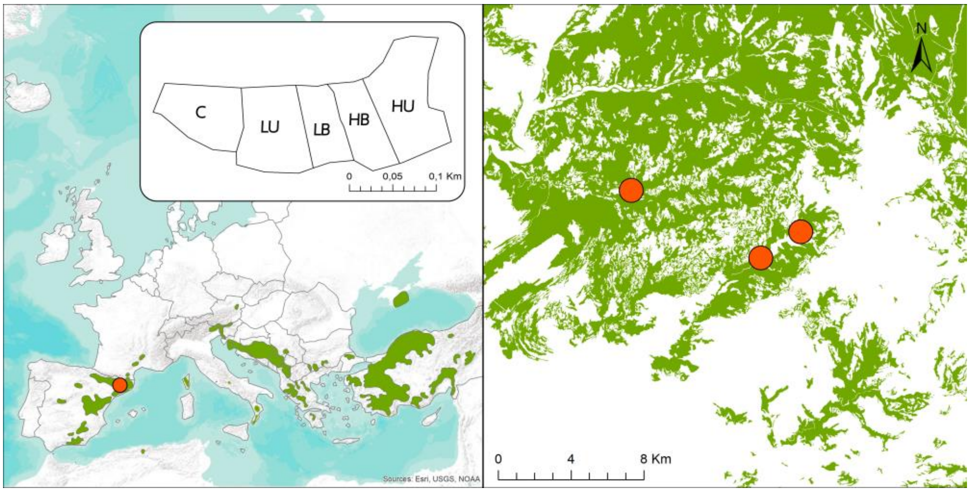

Figure 3.1. Location of the study sites (orange circles) and *Pinus nigra* distribution (green areas) in Europe (left panel), and zoom of the three study sites (right panel). The inset shows an example of the treatment layout of one of the sites. C, untreated control; HB, heavy-thin burned; HU, heavy-thin unburned; LB, light-thin burned; LU, light-thin unburned.

Table 3.1. Mean (SE) of site characteristics and vegetation structure per treatment unit, four to five years after treatments (n = 3).

	C	HB	HU	LB	LU
Elevation (m.a.s.l.)	691 (85)	706 (132)	694 (156)	688 (145)	698 (146)
Slope (%)	31 (3)	23 (2)	14 (2)	22 (2)	16 (2)
Tree density (n ha^{-1})	1539 (21)a	626 (28)b	642 (98)b	1231 (125)a	1279 (51)a
Basal area (m^2 ha^{-1})	34.5 (2.7)	21.4 (1.9)	24.4 (1.9)	32.1 (4.2)	31.2 (1.4)
QMD (cm)	16.9 (0.6)a	20.9 (1.2)ab	22.4 (1.9)b	18.2 (0.7)ab	17.6 (0.2)ab
Stand height (m)	8.7 (0.3)a	11.6 (0.5)ab	12.1 (1.2)b	9.8 (0.3)ab	9.7 (0.3)ab
Canopy base height (m)	5.1 (0.2)a	6.7 (0.3)ab	6.9 (0.6)b	5.7 (0.2)ab	5.7 (0.2)ab
Canopy cover (%)	76 (7)a	48 (3)b	60 (5)ab	71 (4)ab	73 (6)ab
Shrub cover (%)	77 (4)a	31 (17)ab	37 (2)ab	20 (4)b	41 (10)ab
Shrub biomass (Mg ha^{-1})	14.1 (2.1)a	3.9 (2.4)b	4.2 (0.4)b	2.1 (0.3)b	4.8 (1.0)b
Herb cover (%)	7 (1)	28 (3)	42 (2)	16 (2)	26 (2)

Notes: QMD, quadratic mean diameter. Letters within a row denote significant treatment differences (α = 0.05, Bonferroni adjustment). Treatment types include untreated control (C), heavy- thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB). See Table S3.1 for the detailed characteristics per site.

Tree-ring data

In 2021, we cored to pith 15 dominant and co-dominant black pines per treatment unit with DBH ranging from 20 to 35 cm (n = 225 trees). We measured DBH and collected two cores per tree at 1.3 m height with a Pressler increment borer of 4.3 mm diameter, one perpendicular to the slope and the other at 120º upslope. Tree cores were sanded, scanned at 1200 dpi, and visually cross-dated following standard dendrochronological methods (Stokes and Smiley, 1968). Tree-ring widths were measured to the nearest 0.001 mm using CooRecorder v.9.6 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden) and visual cross-dating was assessed using COFECHA (Holmes, 1983). Common dendrochronological statistics (mean inter-series correlation and first-order autocorrelation) were derived from the raw series until 2015 to avoid treatment effects. Tree chronologies spanned from 44 to 154 years; the oldest trees were from Madrona. Mean inter-series correlation was higher in Llobera and lower in Secanella, while mean first-order autocorrelation was higher in Madrona and lower in Secanella (Table 3.2). We removed age-related growth trends by detrending the tree-ring series with a cubic smoothing spline with a 50% frequency cut-off at 38 years (two-thirds of the whole series mean length) (Klesse, 2021), using *dplR* R package v.1.7.4 (Bunn, 2008). The detrended series were used to assess climate-growth relationships, using correlation functions between tree-ring chronologies and monthly precipitation, temperature, and the difference between precipitation and potential evapotranspiration (P-PET; see details in Appendix S3.2Appendix S3.2. Climate-growth relationships). Climate data were obtained from surface stations of the Catalan Meteorology Service (SMC) and the Spanish National Meteorology Agency (AEMET). The R package *meteoland* v.1.0.3 (De Cáceres et al., 2018) was used to interpolate station data to our study area and to estimate potential evapotranspiration (PET) using Penman (1948) method. Climate-growth relationships showed that May and June were the months that correlated most to growth in our study area (Figure S3.4). We used hydrological years (October of the previous year to September) to assess the climate-growth relationships (Table 3.3).

Table 3.2. Median (IQR) of dendrochronological characteristics of tree-ring chronologies per site.

	Llobera	Madrona	Secanella
n trees	72	74	75
Age	63 (56-68)	92 (74-98)	60 (54-72)
Rbar	0.73 (0.72-0.73)	0.68 (0.68-0.69)	0.65 (0.64-0.67)
AR1	0.59 (0.58-0.65)	0.69 (0.63-0.70)	0.57 (0.53-0.62)

Notes: Rbar, inter-series correlation; AR1, first-order autocorrelation

Drought effect on growth

We calculated basal area increment (BAI) starting from the outer ring (DBH minus bark thickness) and moving towards the pith of the tree with *dplR* R package. Mean bark thickness of *P. nigra* from the same region was taken from Valor et al. (2021). Drought was characterized using only climate data, as growth-dependent definitions of drought are likely to show biased results (Schwarz et al. 2020). To identify drought years before and after treatments, we calculated SPEI drought index (Vicente-Serrano, Beguería, and López-Moreno 2010) using *SPEI* R package v.1.7 (Beguería and Vicente-Serrano 2017). Specifically, we calculated a

2-month SPEI from June, since May and June were the months that correlated most to growth (Table 3.3, Figure S3.4). For this study, a drought event was defined as those years with SPEI-2 values of June below the 25th percentile of the series (-0.73; minimum -1.87, maximum 2.08). Because we wanted to avoid any age-related response to drought, we selected as pre-treatment drought, the closest year to treatments possible (2012) and as post-treatment drought, the year with the most negative SPEI value (2017). We also selected a moderately wet year post-treatment (2018) to compare the physiological response to drought between a dry and a wet year (Table 3.3).

Table 3.3. Annual precipitation and meteorological variables for May and June of the selected years, in which resilience indices and stable isotopes were analysed.

	2012	2017	2018
Annual precipitation (mm)	514	546	726
Precipitation (mm, May-June)	69	65	169
P-PET (mm, May-June)	-248	-277	-134
Mean temperature (ºC, May-June)	19.5	19.8	17.2
Maximum temperature (ºC, May-June)	25.0	25.8	22.0
SPEI-2 (June)	-0.90	-1.28	0.63

Notes: Annual precipitation of the hydrological year (previous October through current September). P-PET, precipitation minus potential evapotranspiration

We used the concept of engineering resilience, understood as the capacity of the system to return to pre-disturbance performance levels (Pimm, 1991), to study the response of black pine forests to the identified drought years (2012 and 2017) by measuring BAI before, during, and after the drought. We calculated the resilience indices of Lloret et al. (2011) using *pointRes* R package v.2.0.1 (van der Maaten-Theunissen et al., 2015):

$$Resistance = \frac{BAI_D}{BAI_{preD}} \quad [1]$$

$$Recovery = \frac{BAI_{postD}}{BAI_D} \quad [2]$$

$$Resilience = \frac{BAI_{postD}}{BAI_{preD}} = Resistance\ x\ Recovery\ [3]$$

where BAI_D is the basal area increment (BAI) during the drought year, and BAI_{preD} and BAI_{postD} are the average 3-year BAI before or after the drought year, respectively. At first, we estimated resilience indices using reference periods ranging from 1 to 10 years to assess the performance of the indices based on the length of the reference period. Since we were interested in the response of trees after treatments, and treatments were imposed towards the end of the series length, we continued all analysis using a 3-year reference period. We omitted the use of one and two years as reference periods because one year alone does not account for the legacy effect (Schwarz et al., 2020) and a two-year span may not adequately smooth out years with a strong signal, be it very wet or very dry (Figure S3.1).

Carbon and oxygen stable isotope data

We selected the five trees per treatment unit with the highest inter-series correlation to study carbon and oxygen stable isotopes (n = 75 trees). For each selected tree, we collected one extra core perpendicular to the slope at 1.3 m height with a Pressler increment borer of 10 mm diameter. These new cores were not sanded to prevent any cross-year contamination. Since we wanted to study the treatment effect on tree physiological response to drought, we analysed $\delta^{13}C$ and $\delta^{18}O$ of two drought years (2012 and 2017, before and after treatments, respectively) and a wet year (2018), to account for response differences between a dry and a wet year. We used a scalpel to isolate rings of selected years and extracted alpha-cellulose from whole tree rings. Whole tree ring was chosen over separating earlywood and latewood because conifers mainly use photosynthates from the current year, so earlywood is not influenced by previous year photosynthates (Kress et al.. 2009; Treydte et al., 2007), and sometimes rings were so narrow that such a precise cut was not possible. Alpha-cellulose was extracted using a modified version of the Jayme-Wise method based on Loader et al. (1997) and Boettger et al. (2007), as we did not apply the initial solvent extraction step. Whenever there was not enough sample, we pooled tree rings from different trees of the same treatment unit together ($n_{2012} = 19$; $n_{2017} = 48$; $n_{2018} = 65$; Table S3.2). We measured $\delta^{13}C$ (1 mg of cellulose in tin capsules) using an elemental analyser (organic EA, Flash 2000; Thermo Fischer Scientific Inc., Bremen, Germany) connected to an isotope ratio mass spectrometer (Delta V Advantage; Thermo Fisher Scientific Inc., Bremen, Germany) and $\delta^{18}O$ (0.4 mg of cellulose in silver capsules) using a continuous flow isotope ratio mass spectrometry (CF-IRMS; Thermo Finnigan ConFlo III, Thermo Finnigan Delta XP, Bremen, Germany) at the Stable Isotope Lab of the Institute of Soil Research of BOKU University, Austria. All results are expressed as per mil (‰) deviations relative to reference standards (VPDB for $\delta^{13}C$ and VSMOW for $\delta^{18}O$).

Intrinsic water-use efficiency (iWUE) was calculated assuming that mesophyll conductance is finite and limits carbon flux into chloroplasts, thus limiting photosynthesis. The iWUE approach used accounts for fractionation in CO_2 diffusion through the stomata and across the leaf mesophyll into chloroplasts, in carbon fixation by Rubisco, and in photorespiratory processes. Carbon isotope discrimination ($\Delta^{13}C$) was internally calculated assuming post-photosynthetic fractionation, i.e. from leaf photoassimilates to wood alpha-cellulose, at -2.1‰ (Frank et al., 2015). We chose the mesophyll model over the widely used simplified one of Farquhar et al. (1982) because iWUE estimates are more accurate (Ma et al., 2021; Gong et al., 2022), using the functions implemented in *isocalcR* R package v.0.1.0 (Mathias and Hudiburg, 2022).

Data analysis

We used analysis of variance (ANOVA) to test the differences in forest structure four to five years after treatments, with treatment type as a factor.

We fitted three sets of mixed-effects models to analyse variation due to treatments in (1) BAI and resilience indices, (2) stable isotope composition, and (3) the relation between BAI and stable isotope composition. (1) BAI was modelled using a 20-year time span to avoid age-related growth trends, from 2001 to 2020. Mean BAI before and after treatments was modelled fitting a Gamma generalized linear mixed-effect model (GLMM) with a log link function, with *treatment type* (categorical with 5 levels) and *time* (categorical with two levels: pre (2001-2015) and post (2016-2020)) as fixed factors and *site* and *tree* as random intercepts, to account for dependency among observations of the same site and repeated measures from the same tree. Resilience indices were modelled individually by year (2012 as drought before treatments and 2017 as drought after treatments) fitting linear mixed-effects models (LMMs), with *treatment type* (categorical with 5 levels) as fixed factor and *site* as random intercept. We modelled these indices separately for each year to prevent any confounding effect of weather or treatments over the 3-year period analysed. (2) LMMs were also used to model $\delta^{13}C$, $\delta^{18}O$, and iWUE measurements, with *treatment type* (categorical with 5 levels) and *year* (categorical with 3 levels: drought-pre, 2012; drought-post, 2017; wet-post, 2018) as fixed factors and *site* and *tree* as random intercepts. Additionally, individual LMMs by year were fitted to assess differences among treatments for each year. Pooled rings were treated as single trees and were given a unique identity code (Martin et al., 2011). Finally, (3) to assess the difference in $\delta^{13}C$ and $\delta^{18}O$ between post-treatment (2017 and 2018) and pre-treatment year (2012) we fitted LMMs with *BAIdifference* (continuous) and *treatment type* (categorical with 5 levels) as fixed factors and *site* as random intercept.

In those sets of models where covariates interaction had to be tested, Akaike's Information Criteria (AIC) was used to select the best models. For all sets of models, we verified the assumptions ensuring the absence of residual patterns by plotting residuals versus fitted values and each covariate (Zuur and Ieno, 2016). Pairwise differences among treatments were tested using a Bonferroni correction factor to account for multiple comparisons and reduce the risk of Type I errors ($\alpha = 0.05$). All analyses were done using R v.4.1.3 (R Core Team, 2022), including *lme4* package v.1.1-28 (Bates et al., 2015), *glmmTMB* package v.1.1.3 (Brooks et al., 2017), and *emmeans* package v.1.8.6 (Lenth, 2023).

3.3. Results

Stand characteristics

Site characteristics and forest structure 4 to 5 years after treatments are shown in Table 3.1. Basal area was reduced by approximately 40% and 10% and tree density was significantly reduced from around 1500 trees per hectare to 1250 and 630 in the heavy and light thinning treatments, respectively (Table S3.1). Canopy cover in the heavy-thin was 55% on average, while in the control and light-thin units was around 75%. Shrub biomass was about 3 times lower in all treated units than in control. The unburned units (HU, LU) had on average 1.5 Mg ha^{-1} more shrub biomass than their paired burned ones (HB, LB), yet this difference was not significant. Slash burning was applied under drier fuel moisture conditions in Llobera and Madrona than in Secanella (Table S3.1). The highest fire intensity was recorded in Llobera, with temperatures above 60 ºC lasting an average of 102 minutes, in contrast to 19 minutes in Madrona and 7 minutes in Secanella. Further details of slash burning characteristics and treatment effects on forest composition and structure are described in Vilà-Vilardell et al. (2023).

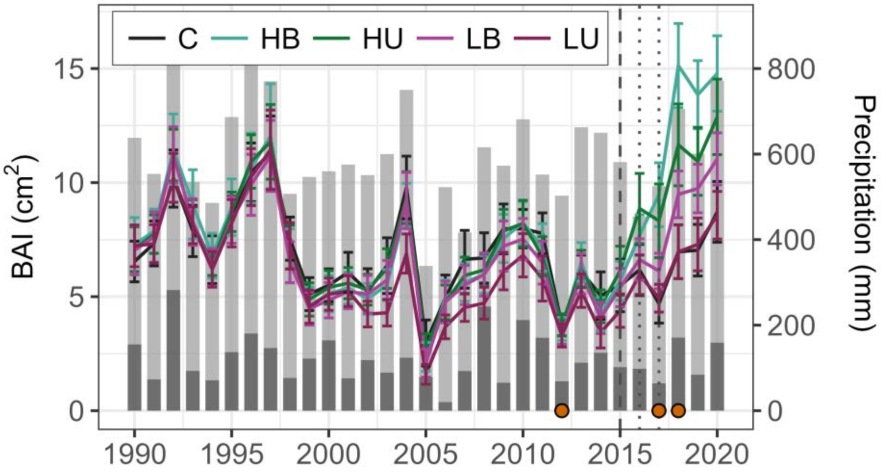

Figure 3.2. Mean (SE) of basal area increment (BAI) per treatment unit, mean total annual (hydrological year) precipitation in light gray, and total precipitation of May and June in dark gray. The dashed line indicates the treatment year (thinning and slash burning) in two localities (Llobera and Madrona). Dotted lines indicate mechanical thinning (2016) and slash burning (2017) in Secanella. Orange circles indicate years where the isotope signature was analyzed. C, untreated control; HB, heavy-thin burned; HU, heavy-thin unburned; LB, light-thin burned; LU, light-thin unburned.

Tree growth and its effect on resistance, recovery, and resilience to drought

Before treatments, trees of all stands grew at a similar rate except for those of the light-thin unburned (LU) units, which consistently had lower basal area increment (BAI) from 2002 until treatments (Figure 3.2, Table S3.3). After treatments, trees of both heavy-thin (HU, HB) and the light-thin burned units (LB) grew significantly more than those of the control and the light-thin unburned units (LU; $P < 0.01$; Table S3.4). Heavy thinning followed by clearing led to the greatest growth release and, although not significant, trees of the burned units (HB) tended to grow more than those of the unburned (HU; $P = 0.13$; Table S3.4): BAI increased by 1.9 in HB and by 1.6 in HU from 2017 to 2020 relative to control. Trees of the light-thin burned unit (LB) grew 1.3 times more than the control and their paired unburned trees (LU). Under the same understory vegetation treatment (clearing alone or clearing plus slash burning), heavy thinning led to the greatest growth release (HB > LB, HU > LU; $P < 0.001$; Table S3.4). Trees of the heavy-thin unburned (HU) and the light-thin burned (LB) units had a similar growth rate after treatments ($P = 0.83$). Trees of the light-thin unburned units (LU) grew at a similar rate as the control trees following treatments, yet they still increased their growth relative to the average growth before treatments (Figure S3.3).

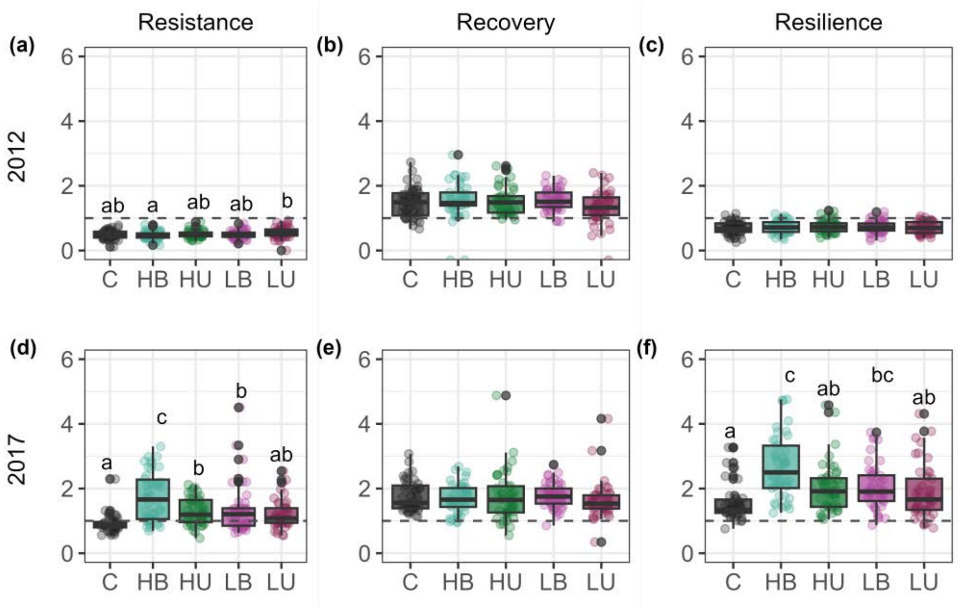

Figure 3.3. Resistance, recovery, and resilience indices for a drought year before (2012) and after (2017) treatments (3 years used as reference period). Letters denote significant treatment differences ($\alpha = 0.05$, Bonferroni adjustment). C, untreated control; HB, heavy-thin burned; HU, heavy-thin unburned; LB, light-thin burned; LU, light-thin unburned.

Tree resilience indices were similar in virtually all units before treatments but differed after (Figure 3.3), with the exception of the recovery index ($P > 0.05$). Resistance improved in both heavy-thin units regardless of the understory treatment (HB, HU) and in light-thin units only when slash burning was implemented (LB) compared to control ($P < 0.05$; Figure 3.3d). Instead, resilience, which includes both resistance and recovery components, increased in both burned units regardless of the thinning intensity (HB, LB) relative to control ($P < 0.01$; Figure 3.3f). Heavy-thin burned units (HB) had higher resistance and resilience than their paired unburned (HU). This pattern, though, was not observed in the light-thin units (Figure 3.3, Table S3.4).

Table 3.4. Mean (SE) of basal area increment (BAI), resilience indices, stable isotopes of extracted cellulose, and water use efficiency (iWUE).

		C	HB	HU	LB	LU
BAI (cm^2)	pre$_{01\text{-}15}$	6.19 (0.15)b	5.78 (0.12)ab	5.97 (0.12)b	5.58 (0.13)ab	4.68 (0.10)a
	post$_{16\text{-}20}$	6.72 (0.26)a	12.2 (0.39)c	10.5 (0.38)bc	8.60 (0.25)b	6.75 (0.32)a
Resistance	pre$_{12}$	0.49 (0.02)ab	0.47 (0.02)a	0.50 (0.02)ab	0.49 (0.02)ab	0.55 (0.03)b
	post$_{17}$	0.91 (0.05)a	1.84 (0.15)c	1.29 (0.06)b	1.35 (0.11)b	1.20 (0.07)ab
Recovery	pre$_{12}$	1.47 (0.07)	1.52 (0.08)	1.54 (0.07)	1.54 (0.05)	1.33 (0.07)
	post$_{17}$	1.76 (0.07)	1.69 (0.07)	1.74 (0.12)	1.78 (0.06)	1.62 (0.08)
Resilience	pre$_{12}$	0.69 (0.03)	0.72 (0.03)	0.74 (0.03)	0.73 (0.03)	0.71 (0.03)
	post$_{17}$	1.54 (0.08)a	2.97 (0.28)c	2.03 (0.12)ab	2.35 (0.24)bc	1.88 (0.12)ab
δ^{13}C (‰)	pre$_{12}$	22.0 (0.18)	21.9 (0.38)	21.6 (0.31)	21.9 (0.17)	21.8 (0.39)
	post$_{17}$	22.5 (0.25)	22.4 (0.30)	22.1 (0.40)	22.4 (0.15)	22.9 (0.30)
	post$_{18}$	23.2 (0.27)	23.5 (0.30)	23.1 (0.29)	23.3 (0.16)	23.2 (0.24)
δ^{18}O (‰)	pre$_{12}$	31.6 (0.46)	30.5 (0.35)	30.8 (0.38)	30.9 (0.69)	30.1 (0.38)
	post$_{17}$	30.8 (0.43)	31.3 (0.26)	31.7 (0.27)	31.5 (0.58)	30.2 (0.54)
	post$_{18}$	30.6 (0.28)ab	30.4 (0.37)ab	31.1 (0.19)b	31.1 (0.27)b	29.8 (0.32)a
iWUE (μmol mol^{-1})	pre$_{12}$	82.7 (0.99)	83.5 (2.11)	85.1 (1.70)	83.1 (0.93)	84.0 (2.13)
	post$_{17}$	83.8 (1.39)	84.1 (1.70)	85.7 (2.26)	84.3 (0.87)	81.2 (1.70)
	post$_{18}$	80.6 (1.53)	78.7 (1.70)	81.0 (1.66)	79.6 (0.90)	80.6 (1.38)

Notes: Letters within a row denote significant treatment differences (α = 0.05, Bonferroni adjustment)

Stable isotopes and iWUE

No differences in δ^{13}C, δ^{18}O, and water use efficiency (iWUE) among treatments for a given year were observed (Table 3.4). The carbon isotope composition of tree rings was sensitive to year: after treatments, all units including the control showed significantly more negative δ^{13}C than before treatments, particularly during the wet year (Table S3.5). There was no year or treatment effect on the oxygen isotope composition of tree rings, yet the lowest δ^{18}O was consistently found in trees of the light-thin unburned units (LU). Additionally, a positive relation between δ^{13}C and δ^{18}O was observed in the drought year following treatments (Figure 3.4a). iWUE of all stands was very similar in both drought years but decreased in 2018, the wet year (Figure 3.5, Table S3.5). There was a strong effect of the site on both carbon and oxygen isotope composition (Figure S3.2), particularly for carbon, as indicated by the high intraclass correlation (ICC = 0.74; Table S3.5). While both light-thin units (LB, LU) showed the lowest variability of δ^{13}C between sites, they were among the treatments with the highest δ^{18}O variability. iWUE variability was particularly high in both heavy-thin units (HU, HB) after treatments (Figure 3.5).

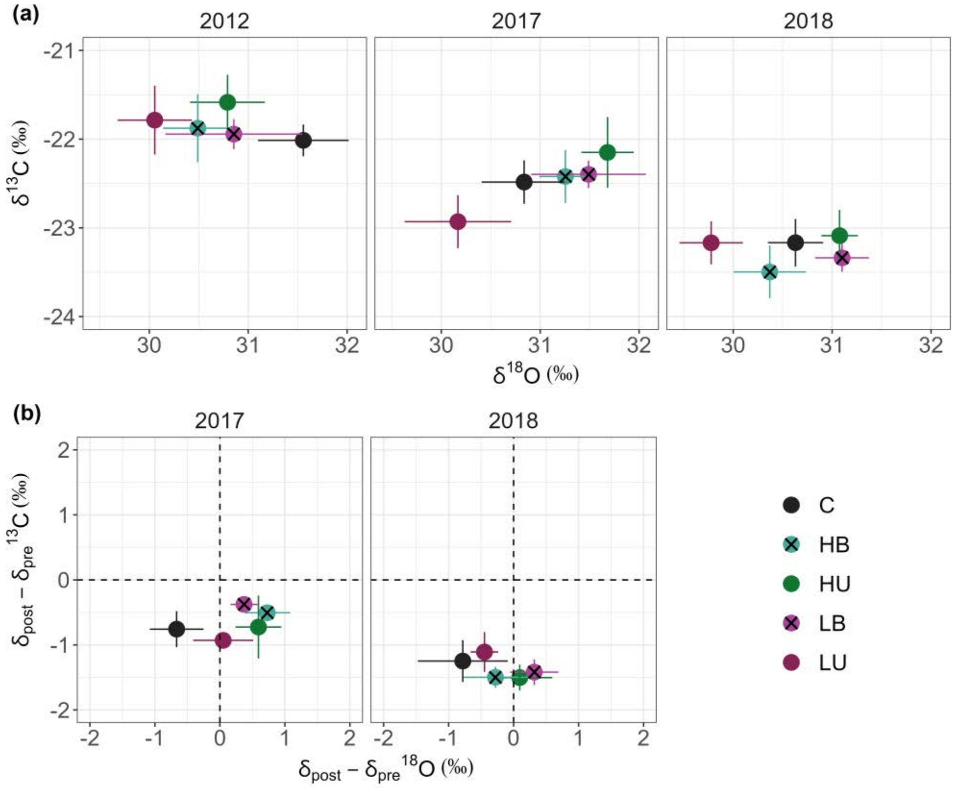

Figure 3.4. (a) Mean (SE) of δ^{13}C and δ^{18}O per treatment and year, and (b) difference in mean δ^{13}C and δ^{18}O between post-treatment years (2017 or 2018) and pre-treatment year (2012). C, untreated control; HB, heavy-thin burned; HU, heavy-thin unburned; LB, light-thin burned; LU, light-thin unburned.

Relationship between tree growth and stable isotopes

No pattern was detected between tree growth and $\delta^{13}C$ after treatments (Figure 3.6). While not significant, a positive trend between growth and $\delta^{18}O$ was observed in all treated units in 2017, since the units with the highest growth release showed higher $\delta^{18}O$ (HB, HU, LB; Figure 3.6). This pattern was not detected in 2018. Although trees of the heavy-thin burned units (HB) grew the most in 2018, they experienced a similar reduction in $\delta^{18}O$ as trees of the light-thin unburned units (LU), the trees that had the most modest growth release (Figure 3.6).

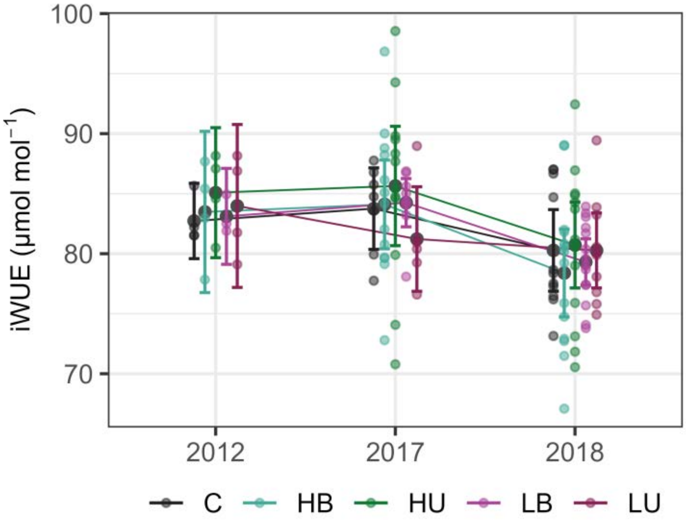

Figure 3.5. Intrinsic water use efficiency (iWUE) assuming finite mesophyll conductance per treatment and year. C, untreated control; HB, heavy-thin burned; HU, heavy-thin unburned; LB, light-thin burned; LU, light-thin unburned.

3.4. Discussion

Forest treatments aimed at reducing wildfire hazard proved to be also valuable in boosting tree growth and reducing tree vulnerability to drought stress for at least five years following the treatments. Tree growth and resistance to drought increased in both heavy-thin units (burned and unburned) and in the light-thin burned units (Table 3.4). Tree resilience to drought improved only when slash burning was applied, either after heavy or light thinning followed by understory clearing. The underlying physiological mechanisms were, though, less conclusive as virtually no differences among treatments were detected. Instead, iWUE appeared to be dependent on the drought intensity of the year (Figure 3.5).

Treatments increased growth and boosted resistance and resilience to drought

Tree ring analysis revealed the benefits of thinning and understory management on dominant trees facing a drought event, illustrated by the increase in growth, resistance, and resilience after treatments. By removing competition both from the overstory and the understory, treatments substantially increased tree vigour and reduced drought stress (Giuggiola et al., 2018; Sohn et al., 2016). As thinning was always applied in combination with mechanical clearing of understory higher than 1.3 m, we cannot completely isolate the specific impacts of thinning alone on tree growth. Yet, by comparing light-thin with heavy-thin units, we can infer that the intensity of thinning was a crucial factor in determining how trees respond to drought. While thinning intensity was key in the response of trees, the use or not of subsequent slash burning also had a substantial impact. Slash burning enhanced tree growth after light thinning and increased tree resistance and resilience to drought after heavy thinning relative to control (Table 3.4). Accordingly, prescribed burning has been previously described to increase resistance and resilience of *P. nigra* to drought (Valor et al., 2020). This can be explained by the lower shrub cover and biomass in burned stands compared to unburned ones (Table 3.1), likely because slash burning hampers the resprouting ability and vigour of the dominant understory species, as it was previously described in these sites (Casals and Rios, 2018) as well as in other Mediterranean forests (Knapp et al., 2013). In a simulation study carried out in the same sites (Vilà-Vilardell et al., 2023), we showed the importance of understory competition in mitigating the loss of hydraulic conductance of dominant trees under drought stress, which was attributed to the higher availability of soil water resulting from the reduced understory biomass after slash burning (Giuggiola et al., 2018). In addition, while not specifically quantified in this study, slash burning is also known to induce a short-term soil nutrient flush as a result of the ash deposition and the mineralization of soil organic matter, which could also contribute to stimulate tree growth (Carter and Foster, 2004) by increasing tree C net assimilation (Guerrieri et al., 2011). In the heavy-thin units, where basal area was considerably reduced, slash burning had little effect on tree growth in addition to thinning and clearing, in agreement with

Zald et al. (2022), Bernal et al. (2023), and Hood et al. (2016). This can be explained because the effect of substantially reducing overstory competition after heavy thinning masks the effect of both reducing the understory and increasing nutrient availability as a result of slash burning. In the light-thin units, where basal area was modestly reduced, we found that slash burning had a positive impact on tree growth. This finding contrasts with the above-mentioned studies, which did not observe any effect of slash burning on tree growth. However, it emphasizes the importance of understory competition and the fertilizer effect of fire on tree growth and vigour when the competition for resources from the overstory persists. The fact that treatments did not affect growth recovery from drought could be explained by a quicker and more plastic response of dominant trees (Martín-Benito et al., 2008), or by the minor role that competition plays on the growth of dominant trees when water is not limiting. In our case, the years following the drought after treatments were not particularly dry, since out of the three years considered to calculate the recovery index after treatments, precipitation exceeded the 75th percentile of the entire series in two of them, and in the third-year precipitation was above the average (Figure 3.2).

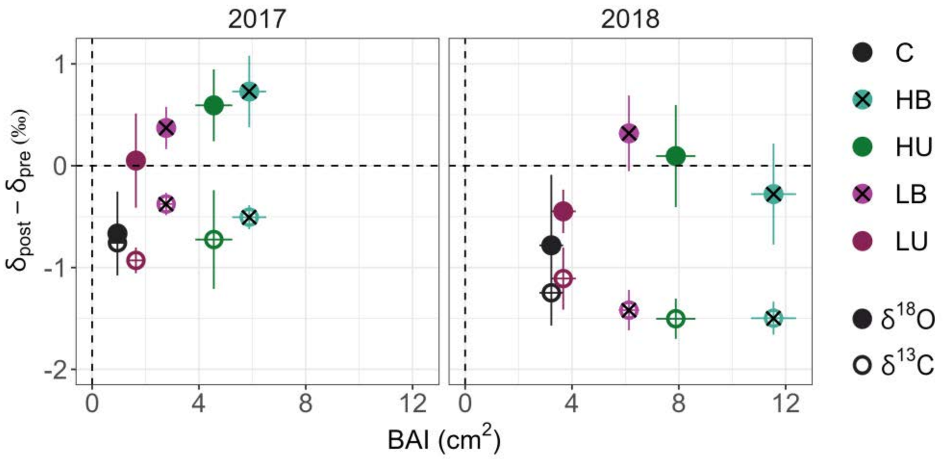

Figure 3.6. Difference in mean $\delta^{13}C$ (empty circles) and $\delta^{18}O$ (filled circles) and in basal area increment (BAI) between post-treatment years (2017 or 2018) and pre-treatment year (2012), and SE. C, untreated control; HB, heavy-thin burned; HU, heavy-thin unburned; LB, light-thin burned; LU, light-thin unburned.

Physiological mechanisms underlying tree response to drought

Treatments did not change iWUE (or $\delta^{13}C$) for a given year in agreement with Martín-Benito et al. (2010), indicating that either there was no effect of treatment in net photosynthetic CO_2 assimilation (*A*) and stomatal conductance (g_s) for that year, or that they changed with equal magnitude. Because treatments enhanced the growth of dominant trees, we can infer that *A* increased, and thus g_s increased proportionally. Consistently, Sala et al. (2005) found that thinning with or without subsequent prescribed burning resulted in higher *A* and g_s. An increase in *A* could be explained by an increase in nitrogen availability due to competition release after treatments, since nitrogen content drives Rubisco content, and thus *A* (Luo et al., 2021). According to the dual-isotope approach, an increase in *A* is reflected either with increased or constant $\delta^{13}C$, while an increase in g_s is reflected with decreased $\delta^{18}O$ (Scheidegger et al., 2000). In this study, an increase in *A* across all treatments was related to constant $\delta^{13}C$. Actually, the high intra-class correlation (ICC; Table S3.5) of the $\delta^{13}C$ model indicated that observations within the same site were similar and most of the variability in $\delta^{13}C$ was explained by between-site rather than among-treatment differences. This could be linked to the different timing of the treatments, as Secanella was thinned in 2016 and burned in 2017 (one and two years after the other sites, respectively).

Our study sites did not entirely fulfil the premises assumed by the dual-isotope approach (Barnard et al., 2012; Roden and Siegwolf, 2012), which is why, presumably, we could not explain the lack of treatment effect on both $\delta^{13}C$ and $\delta^{18}O$ using the model. First, the model was developed using leaf material and, although it has been widely applied in tree ring cellulose, controlled experiments have proved that the model does not always predict the right cause of variation in wood cellulose (Roden and Farquhar, 2012). Also, the model assumes that $\delta^{18}O$ of source water is constant over time. Yet, thinning followed by clearing treatments increased the radiation that penetrates through the canopy, particularly in the heavy-thin units, resulting in an increase on the transpirative demand driven by higher vapour-pressure deficit (VPD) and an increase on soil water evaporation. Moreover, slash burning in addition to clearing left the soil uncovered, leading to a further increase in soil temperature and soil water evaporation (Raz-Yaseef et al., 2010). Both processes, increased VPD-driven transpirative demand and soil water evaporation, resulted in an enrichment of ^{18}O in leaf and soil surface water. At leaf level, though, the enrichment was likely diminished due to the Péclet effect, which explains why bulk leaf water is less enriched in ^{18}O than water at the evaporating surface, especially at high transpiration rates (Barbour et al., 2000). On the other hand, thinning followed by clearing alone or with subsequent slash burning led to increased water availability, enabling trees to take up more accessible water from the ^{18}O enriched soil surface water. The lack of treatment effect on $\delta^{18}O$ was presumably due to the interaction of all these factors that affect oxygen isotope composition in different directions and dampen the ^{18}O signal in tree ring cellulose, namely the increase in VPD-driven transpirative demand, in $\delta^{18}O$ of source water, in soil water availability, and in stomatal conductance. Other studies that previously reported thinning effects on $\delta^{13}C$ and $\delta^{18}O$ have shown divergent findings (see Giuggiola et al., 2016 for a summary). We did not observe any additional effect of slash burning on the physiological response of trees, in agreement with Sala et al. (2005) but contrary to our previous simulation study, wherein we showed that slash burning further promoted the maintenance of hydraulic conductance under drought stress (Vilà-Vilardell et al., 2023). Additionally, although it was not the objective of this study, we did not detect any pattern associated to the season of burning: spring in Llobera and Secanella and autumn in Madrona. Differences could be expected due to the physiological status of the vegetation in spring or autumn (Valor et al., 2017a), yet other factors such as fire intensity might be relevant (Schwilk et al., 2006). Fuel moisture content was similar in Llobera and Madrona and higher in Secanella (Table S3.1), yet burning intensity was much higher in Llobera than in the other two sites (Vilà-Vilardell et al., 2023). Despite the different burning conditions, no differences in the physiological response were observed.

Our findings, though not significant, revealed a higher $\delta^{18}O$ in both heavy-thin units and in the light-thin burned units (Figure 3.4b) as well as a positive relation between $\delta^{18}O$ and tree growth (Figure 3.6) during the drought year after treatments. These findings suggest that the increase in VPD-driven transpirative demand as a consequence of thinning, and in $\delta^{18}O$ of source water as a consequence of thinning followed by clearing alone or with subsequent slash burning, outweighed the increase in g_s (Giuggiola et al., 2016). In addition, according to the dual-isotope model, the positive relation between $\delta^{18}O$ and $\delta^{13}C$ during the drought year after treatments (Figure 3.4a) suggests that changes in g_s across treatments are responsible for the observed iWUE (Battipaglia et al., 2014).

We found consistently lower $\delta^{18}O$ in trees of the light-thin unburned units (LU; Figure 3.4a), which seemed to be related to the intrinsic low growth of these trees (Figure 3.2). This could be explained by the denser canopy and minimal soil water evaporation in the light-thin unburned units, which result in a constant VPD-driven transpirative demand and $\delta^{18}O$ of source water. During the wet year following treatments, the lack of treatment effect could be related to the minor role that competition plays when water is not limiting (Martín-Benito et al., 2010). However, since a wet year before treatments was not analysed, general inferences cannot be drawn.

3.5. Conclusion

The findings of this study emphasize the importance of reducing competition in both the overstory and understory to alleviate drought stress in the face of climate change. Tree growth and resistance to drought increased in both heavy-thin units and in the light-thin burned ones, while resilience increased only when slash burning was applied, regardless of the thinning intensity. Forest treatments did not influence carbon isotope composition and water-use efficiency (iWUE), which appeared to be more influenced by the drought intensity of the year. During the drought year after treatments, similar iWUE among treatments was presumably linked to a proportional increase in both the net CO_2 assimilation and stomatal conductance of dominant trees. These processes were particularly enhanced in both heavy-thin and in the light-thin burned units, as indicated by the greater growth of these trees. No differences among treatments were found in the oxygen isotope composition. Although thinning followed by clearing alone or in combination with slash burning treatments were first aimed at reducing wildfire hazard, we showed that they can also be beneficial to promote tree growth and vigour and reduce its vulnerability to drought stress.

Acknowledgements

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3.6. Supplementary material

Appendix S3.1.

Table S3.1. Mean (SE) of site characteristics and vegetation structure per treatment and site, four to five years after treatments. C, untreated control; HU, heavy-thin unburned; HB, heavy-thin burned; LU, light-thin unburned; LB, light-thin burned.

Locality	Llobera				
Treatment	C	HU	HB	LU	LB
Latitude (º)	41.953	41.952	41.952	41.954	41.953
Longitude (º)	1.4648	1.4651	1.4657	1.4658	1.4661
Elevation (m.a.s.l.)	816	850	837	843	833
Slope (%)	26	18	21	21	18
Aspect (º)	325	260	290	335	270
Treatment unit size (ha)	0.5	0.4	1.1	1.4	0.7
Mechanical treatm. date		Apr '15	Apr '15	Apr '15	Apr '15
Slash burning date			May '15		May '15
Moisture content (%)					
Litter			19.9 (0.8)		19.9 (0.8)
Moss			41.3 (12.4)		41.3 (12.4)
1h fuels			23.8 (2.8)		23.8 (2.8)
Duff			41.2 (5.6)		41.2 (5.6)
Tree density (n ha^{-1}) PRE	1591	2132	1687	1352	1782
Tree density (n ha^{-1})	1560	732	637	1273	1401
Basal area (m^2 ha^{-1}) PRE	40.0	45.4	38.4	32.1	39.5
Basal area (m^2 ha^{-1})	39.7	28.0	24.5	32.1	40.5
Quadratic mean diameter (cm)	18.0	22.1	22.2	17.9	19.2
Stand height (m)	9.8 (0.4)	12.0 (0.3)	11.6 (0.5)	10.0 (0.3)	10.6 (0.3)
Canopy base height (m)	5.8 (0.2)	6.9 (0.2)	7.0 (0.3)	5.9 (0.1)	6.3 (0.2)
Canopy cover (%)	89	63	52	85	76
Understory woody cover (%)	84	37	13	52	16
Shrub biomass (Mg ha^{-1}) PRE	12.14	12.69	12.71	16.47	22.14
Shrub biomass (Mg ha^{-1})	18.41	4.52	1.28	5.62	1.77
Herb cover (%)	0	25	6	25	0

Notes: Moisture content measured right before slash burning (samples oven-dried at 60º C for 48 h; n = 5); PRE, measured before treatments.

Table S3.1. (cont.). Mean (SE) of site characteristics and vegetation structure per treatment and site, four to five years after treatments. C, untreated control; HU, heavy-thin unburned; HB, heavy-thin burned; LU, light-thin unburned; LB, light-thin burned.

Locality	Madrona				
Treatment	C	HU	HB	LU	LB
Latitude (º)	41.972	41.972	41.972	41.971	41.972
Longitude (º)	1.3519	1.3545	1.3539	1.3527	1.3534
Elevation (m.a.s.l.)	528	538	574	552	543
Slope (%)	31	11	28	15	25
Aspect (º)	340	340	340	355	350
Treatment unit size (ha)	0.8	1.1	0.5	0.8	0.4
Mechanical treatm. date		Jul '15	Jul '15	Jul '15	Jul '15
Slash burning date			Sep '15		Sep '15
Moisture content (%)					
Litter			n.a.		n.a.
Moss			51.5 (0.1)		51.5 (0.1)
1h fuels			14.3 (0.6)		14.3 (0.6)
Duff			n.a.		n.a.
Tree density (n ha^{-1}) PRE	1273	907	955	1066	955
Tree density (n ha^{-1})	1560	446	573	1194	987
Basal area (m^2 ha^{-1}) PRE	28.2	30.7	28.1	28.5	25.8
Basal area (m^2 ha^{-1})	33.3	23.4	21.7	28.4	26.8
Quadratic mean diameter (cm)	16.5	25.8	22.0	17.4	18.6
Stand height (m)	9.1 (0.4)	14.2 (0.8)	11.8 (0.5)	9.9 (0.4)	10.3 (0.5)
Canopy base height (m)	5.4 (0.2)	8.7 (0.6)	6.9 (0.3)	5.8 (0.2)	6.0 (0.3)
Canopy cover (%)	66	50	50	67	64
Understory woody cover (%)	71	40	65	49	28
Shrub biomass (Mg ha^{-1}) PRE	19.27	13.33	14.92	16.91	12.05
Shrub biomass (Mg ha^{-1})	11.09	4.91	8.90	6.06	2.69
Herb cover (%)	9	26	14	30	28

Notes: Moisture content measured right before slash burning (samples oven-dried at 60º C for 48 h; n = 5); PRE, measured before treatments.

Table S3.1. (cont.). Mean (SE) of site characteristics and vegetation structure per treatment and site, four to five years after treatments. C, untreated control; HU, heavy-thin unburned; HB, heavy-thin burned; LU, light-thin unburned; LB, light-thin burned.

Locality	Secanella				
Treatment	C	HU	HB	LU	LB
Latitude (º)	41.939	41.9380	41.937	41.936	41.936
Longitude (º)	1.4386	1.4349	1.4351	1.4339	1.4347
Elevation (m.a.s.l.)	728	701	705	688	707
Slope (%)	35	13	21	13	22
Aspect (º)	250	270	275	310	300
Treatment unit size (ha)	0.3	2.0	0.9	1.1	1.2
Mechanical treatm. date		Apr '16	Apr '16	Apr '16	Apr '16
Slash burning date			Apr '17		Apr '17
Moisture content (%)					
Litter			43.1 (1.7)		43.1 (1.7)
Moss			116 (10.5)		116 (10.5)
1h fuels			n.a.		n.a.
Duff			118.6 (5.8)		118.6 (5.8)
Tree density (n ha^{-1}) PRE	1592	1623	1846	1703	2356
Tree density (n ha^{-1})	1496	748	668	1369	1305
Basal area (m^2 ha^{-1}) PRE	31.6	31.4	31.0	40.4	32.9
Basal area (m^2 ha^{-1})	30.4	21.8	18.1	33.0	28.9
Quadratic mean diameter (cm)	16.1	19.3	18.6	17.5	16.8
Stand height (m)	9.2 (0.5)	10.5 (0.4)	10.4 (0.6)	10.1 (0.3)	9.3 (0.3)
Canopy base height (m)	5.2 (0.2)	5.9 (0.2)	5.7 (0.3)	6.0 (0.2)	5.4 (0.1)
Canopy cover (%)	72	66	42	67	73
Understory woody cover (%)	76	34	16	22	16
Shrub biomass (Mg ha^{-1}) PRE	16.07	13.28	8.83	15.27	15.20
Shrub biomass (Mg ha^{-1})	13.29	3.42	1.71	2.87	1.97
Herb cover (%)	13	67	64	24	19

Notes: Moisture content measured right before slash burning (samples oven-dried at 60º C for 48 h; n = 5); PRE, measured before treatments.

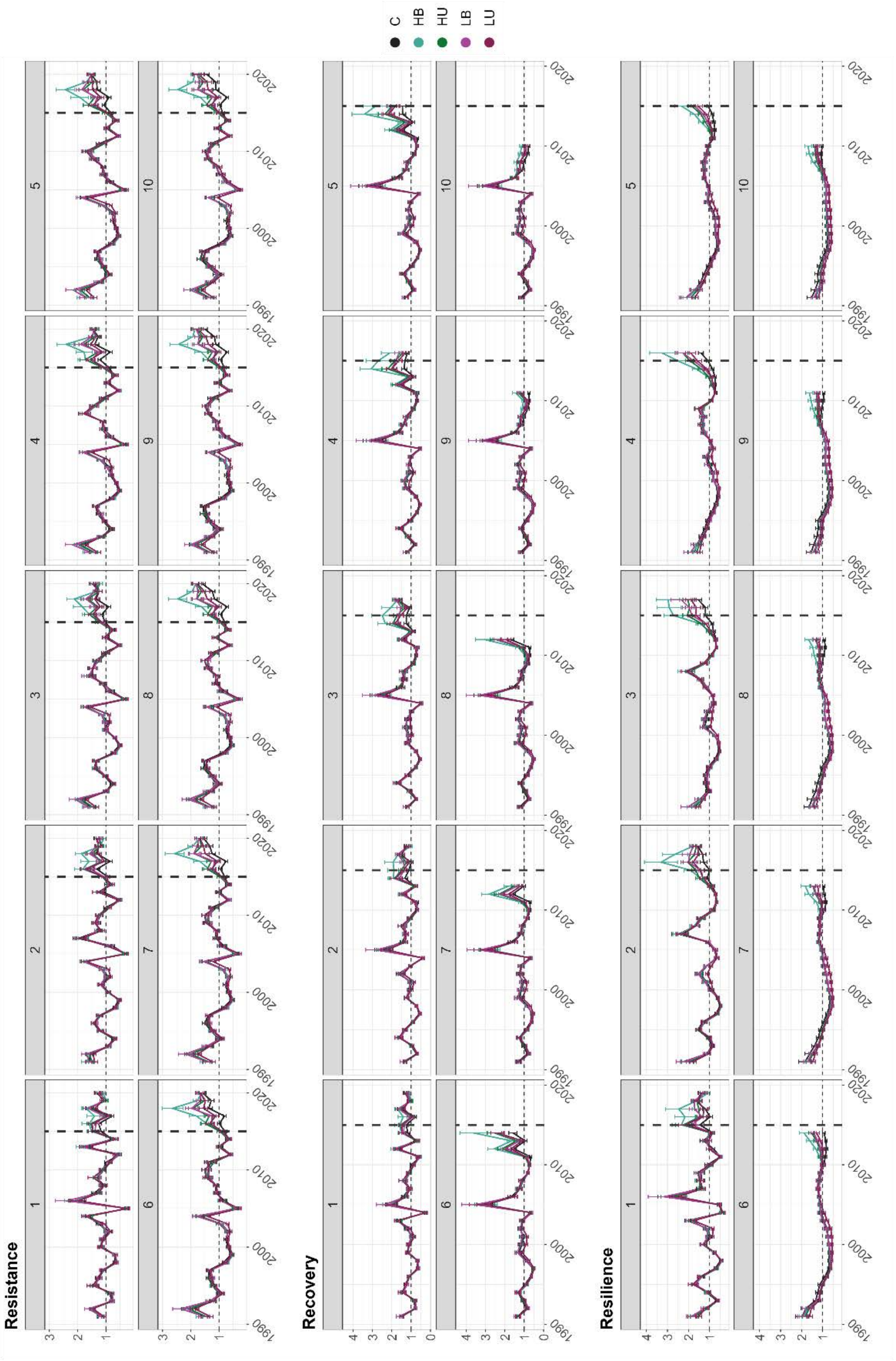

Figure S3.1. Resilience indices as a function of the reference period (from 1 to 10 years). Treatment types include untreated control (C), heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Table S3.2. Number of cellulose extraction samples per treatment and year.

Year	C	HU	HB	LU	LB	Total
2012	4	4	4	4	3	19
2017	7	12	13	7	9	48
2018	11	14	14	11	15	65

Notes: Treatment types include untreated control (C), heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

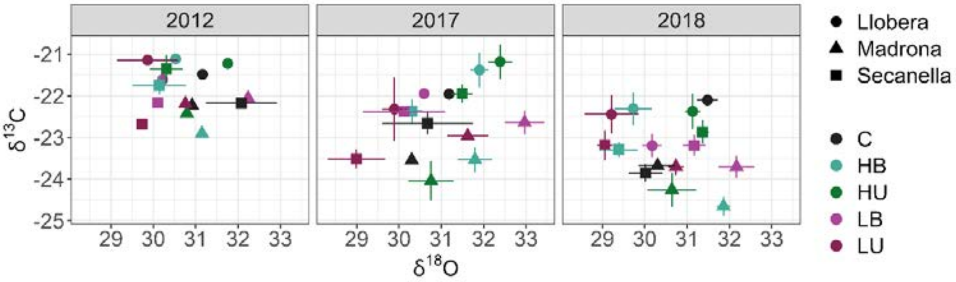

Figure S3.2. Mean (SE) of $\delta^{13}C$ and $\delta^{18}O$ per treatment, site, and year. Treatment types include untreated control (C), heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

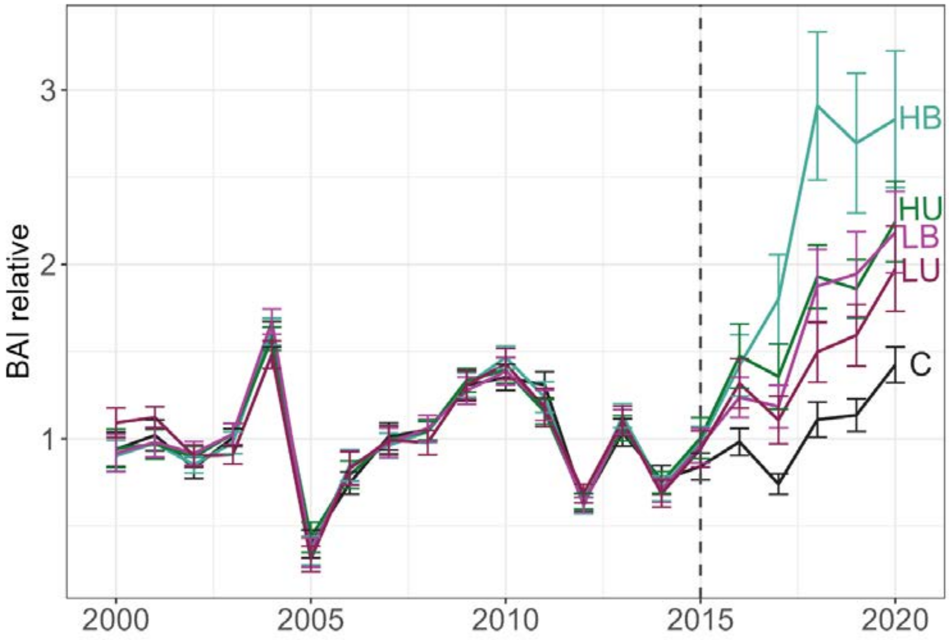

Figure S3.3. Mean (SE) of relative basal area increment (BAI) per treatment unit. The dashed line indicates the thinning year. Relative BAI was calculated for each tree as the ratio between the annual growth and the 2000 to 2014 core average growth. Treatment types include untreated control (C), heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Appendix S3.2. Climate-growth relationships

To assess climate-growth relationships we first removed age-related growth trends by detrending the tree-ring series with a cubic smoothing spline with a 50% frequency cut-off at 38 years (two-thirds of the whole series mean length) (Klesse, 2021), using *dplR* R package v.1.7.4 (Bunn, 2008), and then estimated residual chronologies for each site by removing the autocorrelation from previous year growth using autoregressive models and averaging the series with a robust estimation of the mean (Cook and Peters, 1997). These residual chronologies were correlated to monthly precipitation, temperature, and the difference between precipitation and potential evapotranspiration (P-PET) with the *treeclim* R package v.2.0.6.0 (Zang and Biondi, 2015), using Pearson's linear correlations and regular bootstrapped confidence intervals to estimate the significance of the correlation coefficients ($\alpha = 0.05$) (Biondi and Waikul, 2004). We used hydrological years (October of the previous year to September) to assess the climate-growth relationships. Climate data was obtained from surface stations of the Catalan Meteorology Service (SMC) and the Spanish National Meteorology Agency (AEMET) using *meteoland* R package v.1.0.3 (De Cáceres et al., 2018) to interpolate station data to our study area and to estimate potential evapotranspiration using Penman (1948) method.

Climate-growth relationships showed that May and June were the months that correlated most to growth in our study area (Figure S3.4), in agreement with Valor et al. (2020). Correlation between climatic variables and growth was similar across all three sites before treatments were applied. Winter, early-, and late-spring precipitation and P-PET were positively correlated to growth, while temperatures in October, late-spring, and early-summer were negatively correlated (Figure S3.4). Considering the three climate variables, late-spring (May and June) climatic conditions appeared to be the most strongly correlated to *P. nigra* growth: precipitation 0.44, P-PET 0.44, and temperature -0.49. Drought years in which resilience indices and stable isotopes were analysed had similar total and accumulated May and June precipitation (Table 3.3).

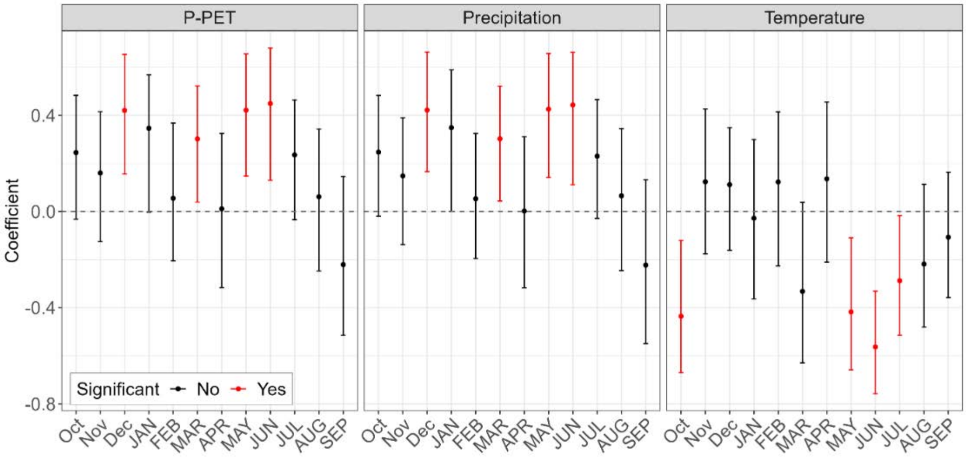

Figure S3.4. Correlation coefficients from tree-ring chronologies of all sites and monthly mean P-PET, precipitation, and temperature. Lowercase months correspond to previous year, uppercase months correspond to current year.

Appendix S3.3. Model statistics of BAI, resilience indices, stable isotopes, and iWUE

Table S3.3. Mixed-effects models results of basal area increment (BAI) and resilience indices.

Response	R^2c	R^2m	ICC	Fixed effects	Estimate	Std. Error	Lower CI	Upper CI
BAI	0.549	0.161	0.462	(Intercept)	1.734	0.073	**1.59**	**1.88**
Pre*Post				HU	-0.001	0.083	-0.16	0.16
(Gamma)				HB	-0.027	0.083	-0.19	0.14
				LU	-0.245	0.082	**-0.41**	**-0.08**
				LB	-0.088	0.082	-0.25	0.07
				Post	0.077	0.033	**0.01**	**0.14**
				HU*Post	0.485	0.047	**0.39**	**0.58**
				HB*Post	0.737	0.047	**0.64**	**0.83**
				LU*Post	0.287	0.046	**0.20**	**0.38**
				LB*Post	0.416	0.046	**0.32**	**0.51**
Resistance	0.078	0.04	0.04	(Intercept)	0.489	0.025	**0.44**	**0.54**
Pre				HU	0.012	0.028	-0.04	0.07
(Gaussian)				HB	-0.021	0.028	-0.08	0.03
				LU	0.060	0.028	**0.01**	**0.11**
				LB	-0.002	0.028	-0.06	0.05
Resistance	0.389	0.171	0.263	(Intercept)	0.906	0.214	**0.49**	**1.33**
Post				HU	0.388	0.122	**0.15**	**0.63**
(Gaussian)				HB	0.932	0.122	**0.69**	**1.17**
				LU	0.294	0.120	**0.06**	**0.53**
				LB	0.443	0.120	**0.21**	**0.68**
Recovery	0.359	0.026	0.341	(Intercept)	1.475	0.174	**1.13**	**1.82**
Pre				HU	0.063	0.084	-0.10	0.23
(Gaussian)				HB	0.058	0.084	-0.11	0.22
				LU	-0.143	0.083	-0.31	0.02
				LB	0.066	0.083	-0.10	0.23

Notes: In BAI model, intercept equals Control, pre-treatments (2001-2015); in resistance, recovery, and resilience models intercept equals Control.

Confidence intervals (95% CI) in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Treatment types include heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Table S3.3. (cont.). Mixed-effects models results of basal area increment (BAI) and resilience indices.

Response	R^2c	R^2m	ICC	Fixed effects	Estimate	Std. Error	Lower CI	Upper CI
Recovery	0.164	0.011	0.155	(Intercept)	1.756	0.148	**1.47**	**2.05**
Post				HU	-0.020	0.110	-0.23	0.19
(Gaussian)				HB	-0.076	0.110	-0.29	0.14
				LU	-0.135	0.108	-0.35	0.08
				LB	0.027	0.108	-0.19	0.24
Resilience	0.278	0.008	0.272	(Intercept)	0.687	0.067	**0.56**	**0.82**
Pre				HU	0.055	0.037	-0.02	0.13
(Gaussian)				HB	0.038	0.037	-0.03	0.11
				LU	0.025	0.037	-0.05	0.10
				LB	0.042	0.037	-0.03	0.11
Resilience	0.301	0.128	0.198	(Intercept)	1.540	0.361	**0.83**	**2.25**
Post				HU	0.499	0.238	**0.03**	**0.96**
(Gaussian)				HB	1.414	0.238	**0.95**	**1.88**
				LU	0.344	0.235	-0.12	0.80
				LB	0.815	0.235	**0.35**	**1.28**

Notes: In BAI model, intercept equals Control, pre-treatments (2001-2015); in resistance, recovery, and resilience models intercept equals Control.

Confidence intervals (95% CI) in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Treatment types include heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Table S3.4. Pairwise comparisons among treatments of BAI and resilience indices.

		Pre			**Post**		
Response		df	t.ratio	p-value	df	t.ratio	p-value
BAI	C / HU	4375	0.02	1.00	4375	-5.39	**<.001**
	C / HB	4375	0.32	1.00	4375	-7.90	**<.001**
	C / LU	4375	2.99	**0.03**	4375	-0.47	1.00
	C / LB	4375	1.07	1.00	4375	-3.69	**<.001**
	HU / HB	4375	0.30	1.00	4375	-2.49	0.13
	HU / LU	4375	2.94	**0.03**	4375	4.92	**<.001**
	HU / LB	4375	1.04	1.00	4375	1.74	0.83
	HB / LU	4375	2.63	0.08	4375	7.44	**<.001**
	HB / LB	4375	0.74	1.00	4375	4.25	**<.001**
	LU / LB	4375	-1.92	0.55	4375	-3.23	**0.01**
Resistance	C / HU	214	-0.41	1.00	214	-3.19	**0.02**
	C / HB	214	0.75	1.00	214	-7.66	**<.001**
	C / LU	214	-2.17	0.32	214	-2.44	0.15
	C / LB	214	0.06	1.00	214	-3.69	**0.001**
	HU / HB	214	1.15	1.00	214	-4.42	**<.001**
	HU / LU	214	-1.73	0.85	214	0.78	1.00
	HU / LB	214	0.47	1.00	214	-0.45	1.00
	HB / LU	214	-2.89	**0.04**	214	5.25	**<.001**
	HB / LB	214	-0.69	1.00	214	4.02	**0.001**
	LU / LB	214	2.22	0.27	214	-1.24	1.00
Resilience	C / HU	214	-1.48	1.00	214	-2.10	0.37
	C / HB	214	-1.02	1.00	214	-5.95	**<.001**
	C / LU	214	-0.68	1.00	214	-1.46	1.00
	C / LB	214	-1.15	1.00	214	-3.47	**0.01**
	HU / HB	214	0.46	1.00	214	-3.81	**0.002**
	HU / LU	214	0.81	1.00	214	0.65	1.00
	HU / LB	214	0.35	1.00	214	-1.33	1.00
	HB / LU	214	0.35	1.00	214	4.50	**<.001**
	HB / LB	214	-0.12	1.00	214	2.52	0.12
	LU / LB	214	-0.47	1.00	214	-2.01	0.46

Notes: In BAI model, Pre includes 2001-2015 and Post 2016-2020; in resistance and resilience models, Pre includes 2012 and Post 2017.

P-values are adjusted after Bonferroni method (α = 0.05).

Treatment types include untreated control (C), heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Table S3.5. Mixed-effects models results of stable isotopes (δ13C, δ18O) and water use efficiency (iWUE).

Response	R^2c	R^2m	ICC	Fixed effects	Estimate	Std. Error	Lower CI	Upper CI
δ^{13}C	0.803	0.236	0.742	(Intercept)	-21.889	0.472	**-22.81**	**-20.96**
(Gaussian)				HU	0.187	0.200	-0.21	0.58
				HB	-0.018	0.202	-0.41	0.38
				LU	0.013	0.214	-0.41	0.43
				LB	0.018	0.202	-0.38	0.41
				2017	-0.641	0.170	**-0.97**	**-0.31**
				2018	-1.458	0.166	**-1.78**	**-1.13**
δ^{18}O	0.476	0.184	0.358	(Intercept)	31.014	0.409	**30.21**	**31.82**
(Gaussian)				HU	0.273	0.289	-0.29	0.84
				HB	-0.221	0.290	-0.79	0.35
				LU	-1.036	0.313	**-1.65**	**-0.42**
				LB	0.190	0.295	-0.39	0.77
				2017	0.311	0.264	-0.21	0.83
				2018	-0.280	0.255	-0.78	0.22
iWUE	0.771	0.116	0.741	(Intercept)	83.403	2.678	**78.15**	**88.65**
(Gaussian)				HU	1.043	1.141	-1.19	3.28
				HB	-0.118	1.150	-2.37	2.13
				LU	0.072	1.216	-2.31	2.46
				LB	0.099	1.149	-2.15	2.35
				2017	0.122	0.968	-1.78	2.02
				2018	-3.852	0.944	**-5.70**	**-2.00**

Notes: Intercept equals Control, 2012.
Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.
R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.
Treatment types include heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Table S3.6. Pairwise comparisons among treatments of stable isotopes (δ13C, δ18O) and water use efficiency (iWUE).

	2012			2017			2018		
δ^{13}C	df	t.ratio	p-value	df	t.ratio	p-value	df	t.ratio	p-value
C / HU	12	-1.49	1.00	40	-1.28	1.00	56	-0.35	1.00
C / HB	12	-0.47	1.00	40	-0.90	1.00	56	0.77	1.00
C / LU	12	-0.26	1.00	40	0.52	1.00	56	-0.48	1.00
C / LB	12	-0.16	1.00	40	-1.40	1.00	56	0.58	1.00
HU / HB	12	1.01	1.00	40	0.47	1.00	56	1.19	1.00
HU / LU	12	1.19	1.00	40	1.81	0.78	56	-0.17	1.00
HU / LB	12	1.21	1.00	40	-0.24	1.00	56	0.98	1.00
HB / LU	12	0.20	1.00	40	1.45	1.00	56	-1.26	1.00
HB / LB	12	0.27	1.00	40	-0.68	1.00	56	-0.21	1.00
LU / LB	12	0.08	1.00	40	-1.91	0.63	56	1.07	1.00

	2012			2017			2018		
δ^{18}O	df	t.ratio	p-value	df	t.ratio	p-value	df	t.ratio	p-value
C / HU	12	1.27	1.00	40	-1.44	1.00	56	-1.15	1.00
C / HB	12	1.76	1.00	40	-0.68	1.00	56	0.86	1.00
C / LU	13	2.36	0.35	40	1.32	1.00	56	2.32	0.24
C / LB	12	1.06	1.00	41	-0.91	1.00	56	-1.22	1.00
HU / HB	12	0.50	1.00	40	0.91	1.00	56	2.14	0.37
HU / LU	13	1.16	1.00	40	2.85	0.07	56	3.57	**<0.01**
HU / LB	12	-0.10	1.00	40	0.49	1.00	56	-0.07	1.00
HB / LU	13	0.68	1.00	40	2.15	0.38	56	1.62	1.00
HB / LB	12	-0.55	1.00	40	-0.34	1.00	56	-2.21	0.31
LU / LB	12	-1.21	1.00	40	-2.29	0.27	56	-3.63	**<0.01**

	2012			2017			2018		
iWUE	df	t.ratio	p-value	df	t.ratio	p-value	df	t.ratio	p-value
C / HU	12	-1.48	1.00	40	-1.28	1.00	56	-0.35	1.00
C / HB	12	-0.47	1.00	40	-0.89	1.00	56	0.78	1.00
C / LU	12	-0.26	1.00	40	0.52	1.00	56	-0.48	1.00
C / LB	12	-0.16	1.00	40	-1.40	1.00	56	0.58	1.00
HU / HB	12	1.01	1.00	40	0.47	1.00	56	1.19	1.00
HU / LU	12	1.19	1.00	40	1.80	0.79	56	-0.17	1.00
HU / LB	12	1.20	1.00	40	-0.24	1.00	56	0.98	1.00
HB / LU	12	0.20	1.00	40	1.45	1.00	56	-1.26	1.00
HB / LB	12	0.27	1.00	40	-0.68	1.00	56	-0.22	1.00
LU / LB	12	0.08	1.00	40	-1.91	0.63	56	1.07	1.00

Notes: P-values are adjusted after Bonferroni method ($\alpha = 0.05$).

Treatment types include untreated control (C), heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Table S3.7. Mixed-effects models results of the difference in stable isotopes (δ13C, δ18O) between post-treatment years (2017, 2018) and pre-treatment (2012).

Response	R^2c	R^2m	ICC	Fixed effects	Estimate	Std. Error	Lower CI	Upper CI
δ^{13}C diff	0.654	0.351	0.466	(Intercept)	-0.804	0.144	**-1.09**	**-0.52**
2017-2012				BAIdiff^2	0.049	0.022	**0.01**	**0.09**
(Gaussian)				HU	-0.272	0.071	**-0.41**	**-0.13**
				HB	0.153	0.082	-0.01	0.31
				LU	-0.079	0.069	-0.21	0.06
				LB	0.418	0.082	**0.26**	**0.58**
				BAIdiff*HU	0.028	0.024	-0.02	0.07
				BAIdiff*HB	-0.025	0.025	-0.07	0.02
				BAIdiff*LU	-0.078	0.032	**-0.14**	**-0.02**
				BAIdiff*LB	-0.045	0.031	-0.11	0.02
δ^{13}C diff	0.567	0.174	0.476	(Intercept)	-1.061	0.166	**-1.39**	**-0.74**
2018-2012				BAIdiff^2	-0.058	0.015	**-0.09**	**-0.03**
(Gaussian)				HU	-0.494	0.104	**-0.70**	**-0.29**
				HB	-0.567	0.124	**-0.81**	**-0.32**
				LU	-0.049	0.090	-0.23	0.13
				LB	-0.339	0.128	**-0.59**	**-0.09**
				BAIdiff*HU	0.064	0.017	**0.03**	**0.10**
				BAIdiff*HB	0.069	0.017	**0.04**	**0.10**
				BAIdiff*LU	0.059	0.020	**0.02**	**0.10**
				BAIdiff*LB	0.055	0.023	**0.01**	**0.10**
δ^{18}O diff	0.638	0.444	0.349	(Intercept)	-0.664	0.202	**-1.06**	**-0.27**
2017-2012				BAIdiff^2	-0.002	0.011	-0.02	0.02
(Gaussian)				HU	1.290	0.103	**1.09**	**1.49**
				HB	1.388	0.109	**1.17**	**1.60**
				LU	0.718	0.095	**0.53**	**0.90**
				LB	1.041	0.097	**0.85**	**1.23**

Notes: Intercept equals Control, 2012. BAIdiff corresponds to the difference between BAI post-treatment (2017, 2018) and pre-treatment (2012).

Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Treatment types include heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

Table S3.7. (cont.) Mixed-effects models results of the difference in stable isotopes (δ13C, δ18O) between post-treatment years (2017, 2018) and pre-treatment (2012).

Response	R^2c	R^2m	ICC	Fixed effects	Estimate	Std. Error	Lower CI	Upper CI
δ^{18}O diff	0.365	0.352	0.02	(Intercept)	-0.368	0.152	**-0.67**	**-0.07**
2018-2012				BAIdiff^2	-0.128	0.033	**-0.19**	**-0.06**
(Gaussian)				HU	0.604	0.237	**0.14**	**1.07**
				HB	-0.772	0.277	**-1.32**	**-0.23**
				LU	-0.145	0.205	-0.55	0.26
				LB	1.077	0.290	**0.51**	**1.65**
				BAIdiff*HU	0.113	0.039	**0.04**	**0.19**
				BAIdiff*HB	0.205	0.038	**0.13**	**0.28**
				BAIdiff*LU	0.146	0.045	**0.06**	**0.23**
				BAIdiff*LB	0.065	0.051	-0.03	0.16

Notes: Intercept equals Control, 2012. BAIdiff corresponds to the difference between BAI post-treatment (2017, 2018) and pre-treatment (2012).
Confidence intervals (95% CI) in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient. Treatment types include heavy-thin unburned (HU), heavy-thin burned (HB), light-thin unburned (LU), light-thin burned (LB).

CHAPTER 4

No evidence of prescribed burning effects on needle terpene content of *Pinus nigra* spp. *salzmannii* and larvae survival of pine processionary moth (*Thaumetopoea pityocampa*)

In preparation

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Abstract

Prescribed burning treatments, initially designed to mitigate wildfire risk, may have broader ecological consequences by enhancing forest resilience to various disturbances. Prescribed burning can alter tree defences both directly, through thermal stress, and indirectly, by modifying soil nutrient availability and forest structure. Such changes may affect defoliator species like the pine processionary moth (PPM). With the increasing severity of PPM defoliation associated to warmer winters, it is crucial to investigate how prescribed burning affects tree defences against PPM. We quantified terpene composition and concentration in current-year and mature needles of dominant black pines before and one year after prescribed burning across burned and unburned sites in three sub-Mediterranean forests, coinciding with the period when early-instar PPM larvae feed. Additionally, we assessed needle nitrogen content, $\delta^{13}C$ and $\delta^{18}O$ composition, and fire severity parameters. A bioassay was also conducted to evaluate how needle terpene and nitrogen content influence the survival rate of first-instar PPM larvae. Prescribed burning had no effect on needle terpene content one year after treatments. Terpene concentration was neither explained by fire severity, nitrogen content, or isotope composition. Instead, drought conditions likely contributed to the increased terpene concentrations in current-year needles of both burned and unburned pines one year after treatments. Prescribed burning had a minor impact on PPM larvae, whose survival appears to be complex and shaped by multiple interacting factors including treatment, needle age, and terpene and nitrogen content. Notably, a higher survival rate was observed in mature needles of burned pines as terpene and nitrogen content increased. Yet, the lack of differences in terpene concentration following treatments suggests that prescribed burning in sub-Mediterranean pine forests does not have adverse effects on potential future PPM outbreaks.

Keywords: bioassay, defence mechanisms, defoliator, larval mortality, monoterpenes, sesquiterpenes, stable isotopes.

4.1. Introduction

Prescribed burning, widely used to mitigate wildfire hazards, often generates collateral effects that extend beyond its primary goal. As a low- to moderate-intensity fire, prescribed burning may influence the physiological performance of trees (Battipaglia et al., 2016; Reed and Hood, 2024), including their defence mechanisms (Cannac et al., 2009a; Valor et al., 2017b; Vilà-Vilardell et al., 2024a). With rising temperatures predicted to intensify pest outbreaks (De Boer and Harvey, 2020; Seidl et al., 2017), understanding the effects of prescribed burning on tree defences is crucial for designing effective forest management strategies that support adaptation to changing climatic conditions.

Resin-based defences are a fundamental component of conifer defence mechanism. Resin is composed of a complex mixture of terpenes, the most diverse class of secondary metabolites, which include volatile compounds, such as mono- and sesquiterpenes, stored in resin ducts in needles, xylem, and phloem, that serve essential ecological roles such as deterring herbivores and reducing plant palatability (Langenheim, 2003). Terpene content (i.e., composition and concentration) varies between different components of a tree, among trees within a population, and across populations (Langenheim, 2003), and is influenced by both biotic and abiotic factors, including defoliator pressure, drought stress, and temperature changes (Kopaczyk et al., 2020). For instance, while high temperatures up to 40 ºC enhance enzyme activity and terpene synthesis, these processes decline with higher temperatures, and cell necrosis begins above 60 ºC (Dickinson and Johnson, 2004; Guenther et al., 1993).

Prescribed burning can directly affect resin-based defences of pines through heat stress (Hood et al., 2015) and indirectly via changes in forest structure (Vilà-Vilardell et al., 2024a). However, the direction and magnitude of these effects remain unclear, particularly concerning needle terpenes. While extensive research has explored how prescribed burning affects resin flow in the phloem or xylem, an important defence against woodboring beetles (Hood et al., 2016; Santoro et al., 2001), its impact on needle terpene content, which may affect needle palatability and defoliators impact, is less understood.

Studies on *Pinus* species suggest that heat initially triggers an increase in needle terpene emissions (Zhao et al., 2012), but they cease within 24 hours post-burning

(Alessio et al., 2004). At this stage, terpene content may vary by species and as a function of time since burning or the number of times burned (Lavoir et al., 2013; Valor et al., 2017b), with higher concentrations in pines experiencing higher crown scorch and lower concentrations in pines with improved physiological performance following fire (Valor et al., 2017b). These differences are likely influenced by variations in prescribed burning conditions. However, no studies have yet examined how fire-induced changes in needle terpene content might affect resistance or vulnerability to defoliating insects. This is relevant because alterations in terpene composition and concentration may influence the behaviour of defoliator species such as the pine processionary moth (PPM; *Thaumetopoea pityocampa* Den. & Schiff), whose defoliation impact is expected to intensify with increasingly frequent warmer winters (Hódar and Zamora, 2004).

The pine processionary moth (PPM) is an endemic univoltine moth (Lepidoptera: Notodontidae) native to the northern Mediterranean basin. It exhibits a non-selective oviposition pattern (Hódar et al., 2002) and a life cycle comprising five stages. Larvae are gregarious and feed on needles during autumn and winter (Hódar et al., 2002). Early-instar larval mortality within the colony is generally high but variable (Zalucki et al., 2002) and plays a crucial role in their overall survival, as larger colonies are more likely to endure winter due to their ability to build better-insulated nests that facilitate thermoregulation (Breuer and Devkota, 1990). Once the larvae complete the fifth developmental stage, they descend to the ground and burrow into the mineral soil to pupate, where they can remain in diapause for up to 9 years. However, since they pupate at an average depth of 6-8 cm (Torres-Muros et al., 2016), they are unlikely to be affected by prescribed burning treatments.

PPM incidence has been linked to lower concentrations of needle terpenes (Achotegui-Castells et al., 2013); however, PPM larval survival shows weak (Hódar et al., 2004) or no correlation (Achotegui-Castells et al., 2015) with needle terpene composition. Some terpenes, such as limonene and β-pinene, deter PPM oviposition (Niccoli et al., 2008; Panzavolta et al., 2015; Tiberi et al., 1999). Additionally, early-instar PPM larval survival increases with higher needle nitrogen concentrations (Hódar et al., 2002). The short-term excess of soil nitrogen following prescribed burning (DeLuca and Zouhar, 2000; Romanya et al., 2001) may accumulate in leaves, enhancing tree photosynthetic rates and plant growth (Reich et al., 1995), which could ultimately boost larval survival rates.

Although limited, previous studies indicate that open and grazed forests with sparse understory are more susceptible to PPM infestation, due to greater soil exposure to sunlight, creating optimal conditions for pupation (Azcárate et al., 2023; Dulaurent et al., 2011a; Torres-Muros et al., 2016). Such conditions are likely to occur following prescribed burning, as understory recovers slowly (Casals and Rios, 2018), reducing shading. Moreover, PPM egg parasitoids, key predators and regulators of the PPM population, may also be impacted by the reduction in vegetation after burning, as they may lose their main source of carbohydrates (Dulaurent et al., 2011b), thus compromising their role in regulating PPM incidence. Despite existing studies on the impact of prescribed burning on phytochemicals and defoliator performance (Rieske et al., 2002), the cascading effects of burning on needle terpene content and PPM survival remain largely unexplored.

Here, we measured the terpene content (composition and concentration) in current-year and mature needles of dominant black pines (*Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco) both before and one year after prescribed burning, coinciding with the period when early-instar PPM larvae feed. We examined terpene content in relation to needle nitrogen content, $\delta^{13}C$ and $\delta^{18}O$ composition, and fire severity parameters, which provide insights into the physiological state and potential palatability of needle throughout their lifespan. Additionally, we conducted a bioassay to evaluate how changes in needle terpene or nitrogen content affect the survival of first-instar PPM larvae. Black pine is one of the primary host species for PPM (Hódar et al., 2004) and is highly sensitive to its impact (Azcárate et al., 2023).

Given that temperature influences needle terpene content (Guenther et al., 1993; Kopaczyk et al., 2020) and that terpene and nitrogen levels affect PPM larval performance (Achotegui-Castells et al., 2013; Hódar et al., 2002), we hypothesized that (i) prescribed burning would reduce needle terpene concentration in black pines one year after implementation, and (ii) the combined effect of lower terpene and higher nitrogen concentration following burning would increase the survival of first-instar PPM larvae.

4.2. Materials and methods

Study area

The study was conducted in three sub-Mediterranean forests at the southern foothills of the Pyrenees, northeastern Spain (Figure 4.1). These south-facing slopes, at elevations ranging from 570 to 670 meters above sea level, are dominated by Spanish black pine (*Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco), with scattered Aleppo pines (*Pinus halepensis* Mill.) and downy oaks (*Quercus humilis* Mill.). The understory vegetation primarily consists of European box (*Buxus sempervirens* L.), kermes oak (*Quercus coccifera* L.), rosemary (*Salvia rosmarinus* Spenn.), and cade juniper (*Juniperus oxycedrus* L.). The mean annual temperature is 14.3 ºC with total annual precipitation of 591 mm (1996-2024). Notably, in 2020, the treatment year, precipitation was 787 mm, while in 2021, it dropped to 487 mm.

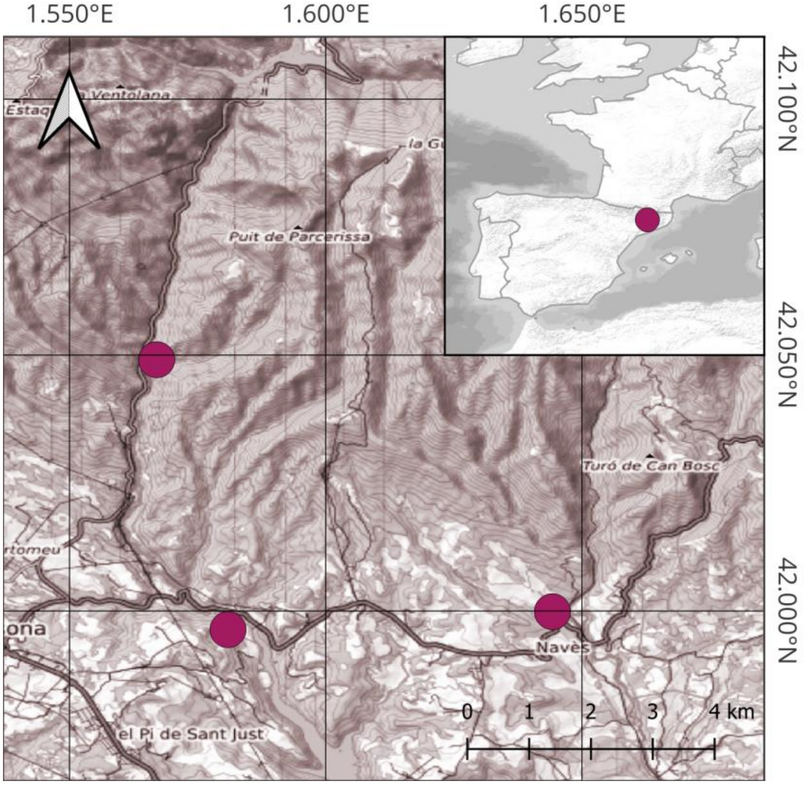

Figure 4.1. Location of the study sites in northeastern Iberian Peninsula and zoom of the three sites.

In autumn 2020, prescribed burning was implemented in three sites (Can Feliu, 8.2 ha; Lloreda, 10.6 ha; Puiggalí, 8.7 ha) by the Forest Action Support Group of the Government of Catalonia (GRAF). The burns were implemented using a strip-head fire ignition pattern as a direct underburn, meaning that no prior thinning or harvesting treatments had been conducted for at least the last ten years. Air temperature during prescribed burning ranged from 12 ºC to 24 ºC, relative humidity varied between 40% and 70%, an average windspeed of 2.6 km h^{-1}. Each of the three burned units had a paired unburned control unit, established adjacent to the burn treatment. Fire temperature was recorded every 10 seconds below the litter layer using thermocouples (type K, 3 mm diameter) connected to a Testo 175 datalogger in 15 to 20 pines per burned unit. Two thermocouples were used per pine, one on the leeward (uphill) side and one on the windward (downhill) side.

To estimate fuel moisture content at the time of burning, we sampled live fine fuels (<6 mm) from pines, main understory shrub species, and herbs, as well as from duff, litter, and mineral soil. Sampling was conducted at six randomly selected points per treatment unit. Samples were weighted, dried at 60 ºC for 48 hours, and reweighted. To measure the depth of the burned litter and duff layers, two nails were buried next to both thermocouples per pine.

Data collection

Prior to the prescribed burning treatments, we inventoried the forest structure in two 452 m^2 circular plots per treatment unit. We measured diameter at breast height (dbh), height, and canopy base height of all pines larger than 7.5 cm dbh, as well as canopy cover at the plot centre using a spherical convex densiometer (Forestry Suppliers, Inc.). Shrub cover, height, and crown diameter were surveyed in 20 quadrats of 1 m^2 along two 10 m transects. Regional allometries were used to estimate the mean shrub biomass per treatment unit, using *medfuels* R package v.0.1.1 (De Cáceres et al., 2019).

We selected and tagged 15 to 20 dominant, vigorous black pines with similar dbh (average dbh of 17 cm) per treatment unit, hereafter referred to as *selected trees*, and sampled needles before and after prescribed burning in both burned and unburned units, following a before-after-control-impact (BACI) design. In the burned units, *selected trees* were those where fire temperature had been recorded. Needles were sampled from the upper, south-facing portion of the crown due to their larger photosynthetic capacity and greater nitrogen content (Camm, 1993;

Leuning et al., 1991), as nitrogen levels influence pine processionary moth (PPM) larval performance (Hódar et al., 2002). They were consistently collected from the same position within the crown to minimize differences in needle chemical composition due to their location (Gomez-Gallego et al., 2020), during the morning hours to minimize terpene fluctuations as a function of the time of day (Riba et al., 1987), and at the same time each year to minimize differences in terpene concentration caused by seasonal changes (Llusià et al., 2006), in late September to early October 2020 and 2021, before and after treatments, respectively. We sampled needles during this period because it is when early-instar larvae are feeding. Before treatments, we sampled current-year needles (Pre-y1), while one year after, we sampled mature needles (Post-y2: needles that were Pre-y1 before treatments) and current-year needles (Post y1: needles that grew after treatments). Needles were preserved in liquid nitrogen until laboratory processing. Needles used for the PPM larval bioassay were collected in October 2021 from the upper, south-facing portion of the crown of eight additional black pines, referred to as *larvae trees*, from the Lloreda site. In the lab, part of the needles from both *selected* and *larvae trees* were stored at -20 ºC for terpene analysis; the remainder were scanned, dried at 60 ºC for 48 hours, and processed for $\delta^{13}C$ and $\delta^{18}O$ composition and nitrogen content analyses.

Fire severity parameters, such as maximum scorch height, bark char codes, percent crown scorch, and burned litter and duff depth, were measured one week after burning for all *selected trees*. The bark char codes were assessed visually at the lower 10 cm around the stem, following Ryan (1982), and serve as a measure of stem damage after the fire. They were transformed into a continuous stem damage index ranging from 0 (completely unburned) to 1 (severely burned). Percent crown scorch was visually assessed. The depth of the burned litter and duff layers was estimated by measuring the exposed portion of the nails placed above the litter layer prior to the fire.

Terpene content

Monoterpene and sesquiterpene content in the needles was analysed both before and after prescribed burning (Pre-y1, Post-y1, Post-y2) from *selected* and *larvae trees*. Fresh needles (0.35 g) were manually ground 0.35 g in 50 mL Teflon tubes (filled with liquid nitrogen, then mixed with 2 mL of a daily-prepared dodecane:pentane solution (1:2000, with dodecane as an internal standard). Teflon tubes were shaken for 20 minutes, and the extract was transferred into a 2 mL glass vial, sealed and frozen. The ground needles in Teflon tubes were dried at 60 ºC for 24 hours and weighted.

Samples were analysed using a Gas Chromatograph (GC; 7890A, Agilent Technologies) coupled with a mass spectrometer (MS; 5975C inert MSD with Triple-Axis Detector, Agilent Technologies), using helium as the carrier gas at a flow rate of 1 ml min-1. Two µl of samples were injected into the column, initially set at 35 ºC for 2 minutes, then heated at a rate of 15 ºC per minute to 150 ºC, held for 5 minutes. The temperature was then raised at 20 ºC per minute to 250 ºC, held for 5 minutes, and finally raised at 20 ºC per minute to 280 ºC, where it was held for 10 minutes, resulting in a total run time of 36 minutes. Commercial standards at different dilutions (1:1000, 1:10000, 1:100000) were used to prepare calibration curves to quantify terpene content, which included six monoterpenes (α-pinene, 3-carene, p-cymene, eucalyptol, γ-terpinene, linalool) and one sesquiterpene (α-caryophyllene). All terpene calibration curves were highly significant ($R^2 \geq 0.95$). Terpene quantification was performed using the fractionation product with an ion mass of 93. Terpene concentration was calculated on a needle dry mass basis. Monoterpene and sesquiterpene identification were based on the comparison of each terpene mass spectra with published spectra (NIST 05 and Wiley275 libraries).

Stable isotope composition and nitrogen content

Needle $\delta^{13}C$ and $\delta^{18}O$ composition, along with nitrogen content, were analysed in samples from *selected trees* collected both before and after prescribed burning (Pre-y1, Post-y1, Post-y2). Additionally, nitrogen content was measured in samples from *larvae trees*. The samples were ground to a powder at a frequency of 24 s^{-1} for 70 seconds, and 4 mg were weighted into tin capsules for $\delta^{13}C$ and nitrogen content analyses, and 0.5 mg into silver capsules for $\delta^{18}O$ analysis. The $\delta^{13}C$ and nitrogen content were measured using an elemental analyzer (organic EA, Flash 2000; Thermo Fischer Scientific Inc.) connected to an isotope ratio mass spectrometer (Delta V Advantage; Thermo Fisher Scientific Inc.). The $\delta^{18}O$ was measured using a continuous-flow isotope ratio mass spectrometry (CF-IRMS; Thermo Finnigan ConFlo III, Thermo Finnigan Delta XP) at the Stable Isotope Facility of UC Davis, CA, USA (Pre-y1), and at the Stable Isotope Lab of the Institute of Soil Research, BOKU University, Austria (Post-y1 and Post-y2). The stable isotope results are expressed as per mil (‰) deviations relative to reference standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and Vienna Standard Mean Ocean Water for $\delta^{18}O$), while nitrogen content results are expressed in mg g^{-1} of dry needle.

Pine processionary moth larvae survival

Pine processionary moth (PPM) egg batches were collected in August 2022 from black pines near the Lloreda site. Needles for feeding the larvae were sampled in October 2021, shortly after needles of *selected trees* were collected. Needles of *larvae trees* were collected from eight pines at the Lloreda site, with four from burned units and four from unburned units. Collected needles were frozen with liquid nitrogen in the field and later stored at -20 ºC until analysis for terpenes and nitrogen content. Needles sourced from *larvae trees* were also taken from the upper, south-facing portion of the crown; however, these pines were intermediate, rather than dominant. We selected intermediate pines because we assumed that they would be more affected by prescribed burning, potentially having a greater impact on larvae survival. The bioassay began in August and concluded in September 2022. The bioassay protocol involved placing 30 first-instar larvae in Petri dishes, where they were fed a specific needle age from one of the four pines per treatment (Post-y1 or Post-y2, either burned or unburned). Each treatment had five sets of Petri dishes, totalling 80 dishes with 2400 larvae. Any larvae that died immediately after being placed in a Petri dish were replaced. If they survived beyond one day, the experiment began. Each Petri dish contained larvae from two different egg batches were transferred to mitigate batch effects. Larvae were fed fresh, unfrozen needles daily. Petri dishes were kept at room temperature, with a daily drop of water added to maintain moisture (Figure S4.4). The bioassay concluded once all larvae either died or transitioned to the second instar, following the method outlined by Hódar et al. (2002).

Data analysis

To evaluate variations in terpene concentration following treatments, we fitted a linear mixed-effects model (LMM) to total terpenes, monoterpenes, and sesquiterpenes as a function of *treatment* (categorical with two levels: burn and control) and *needle age* (categorical with three levels: Pre-y1, Post-y1, and Post-y2), using *tree j* as a random intercept to account for the repeated measures of the same pine (Eq. 1). The factor site was removed as a random intercept because the initial model exhibited in singular fit; likewise, the interaction between *treatment* and *needle age* was excluded due to non-significance. This model was applied separately for both *selected* and *larvae trees*.

$$TerpeneConcentration_{ij} = Treatment_{ij} + NeedleAge_{ij} + Tree_j \ [4]$$

To assess variation in terpene concentration as a function of fire severity in the burned units, we fitted a LMM, using *crown scorch, stem damage, minutes above 60 ºC*, and *depth of litter and duff burned* (all standardized continuous variables), and *needle age* as fixed covariates, with *tree j* as a random intercept (Eq. 2). The factor *site* was removed as a random intercept because the model was overfitted.

$$\begin{aligned} TerpeneConcentration_{ij} \\ &= CrownScorch_{ij} + StemDamage_{ij} + Min60_{ij} \\ &+ LitterDuffBurned_{ij} + NeedleAge_{ij} + Tree_j \ [5] \end{aligned}$$

We fitted a LMM to assess variation in terpene concentration as a function of δ^{13}C composition, δ^{18}O composition and nitrogen (N) content (all standardized continuous variables) as fixed covariates, with *tree j* as a random intercept (Eq. 3). The factor site was removed as a random intercept because the model was overfitted.

$$TerpeneConcentration_{ij} = \delta^{13}\mathrm{C}_{ij} + \delta^{18}\mathrm{O}_{ij} + \mathrm{Ncontent}_{ij} + \mathrm{Tree}_j \ [6]$$

We applied a multivariate sparse partial least-squares discriminant analysis (sPLS-DA) to identify a set of terpenes associated with either burned or unburned pines to assess changes in terpene composition following prescribed burning using *mixOmics* v.6.25.1 R package (Rohart et al., 2017). sPLS-DA is a supervised technique that selects the most relevant predictors that contribute to discriminate between classes (burned vs. unburned). We applied the sPLS-DA separately by needle age (Pre-y1, Post-y1, and Post-y2) and removed terpenes that were identified in less than 90% of all pines, resulting in a total of 28 terpenes.

Differences in δ^{13}C, δ^{18}O, and needle nitrogen content of selected trees between burned and unburned units were assessed using LMMs as a function of the interaction between *treatment* and *needle age*, with *tree j* as a random intercept to account for the dependency from repeated measures of the same tree (Eq. 4). The factor site was removed as a random intercept to simplify the model, as it explained less than 10% of the total variance.

$$Response_{ij} = Treatment_{ij} + NeedleAge_{ij} + Treatment_{ij}\ x\ NeedleAge_{ij} + Tree_j \text{ [7]}$$

Differences in needle nitrogen content of *larvae trees* between burned and unburned pines were assessed using LMMs as a function of *treatment* and *needle age*, with *tree j* as random intercept (Eq. 5). The interaction between *treatment* and *needle age* was excluded from the initial model due to non-significance.

$$Ncontent_{ij} = Treatment_{ij} + NeedleAge_{ij} + Tree_j \text{ [8]}$$

Finally, to assess potential factors affecting first-instar larvae survival, we fit a zero-inflated binomial generalized linear mixed-effects model (GLMM), with *treatment*, *needle age*, *terpene concentration*, and *N content* as fixed covariates and *tree j* as a random intercept (Eq. 6 and Eq. 7). We chose a zero-inflated model because initial results indicated zero-inflation caused by a large number of zeros (60%). The interactions between *Ncontent* and *treatment*, *Ncontent* and *needle age*, and *treatment* and *needle age* were excluded due to non-significance.

$$\begin{aligned} logit(LarvaeSurvival_{ij}) &= Treatment_{ij} + NeedleAge_{ij} + TerpeneConcentration_{ij} \\ &+ Ncontent_{ij} + TerpeneConcentration_{ij}\ x\ Treatment_{ij} \\ &+ TerpeneConcentration_{ij}\ x\ NeedleAge_{ij} + Tree_j \text{ [9]} \end{aligned}$$

$$logit(\pi_j) = \gamma \text{ [10]}$$

where $LarvaeSurvival_{ij}$ is the proportion of larvae alive per Petri dish and γ is the intercept for the Bernoulli part of the model. The probability (π_i) of finding all larvae dead was assumed to be constant.

Akaike's Information Criterion (AIC) was used to select the best models, with a preference for the most parsimonious model when AIC difference was < 2. Pairwise differences among treatment units and needle ages were determined using least-square means, with a Holm correction factor to adjust the significance level ($\alpha = 0.05$) for multiple comparisons, thereby reducing the risk of Type I errors. Model assumptions were verified by checking for residual patterns using *DHARMa* v.0.4.6 package (Hartig, 2022) and by plotting residuals against fitted values and each covariate (Zuur and Ieno, 2016). All analyses were conducted using R v.4.3.1 (R Core Team, 2023), including packages *lme4* v.1.1-34 (Bates et al., 2015), *glmmTMB* v.1.1.7 (Brooks et al., 2017), and *emmeans* v.1.8.8 (Lenth, 2023).

4.3. Results

Stand characteristics and fire behaviour

Forest structure before prescribed burning treatments is summarized in Table 4.1. After burning, we observed a significant reduction in understory biomass and cover. Fire severity on dominant black pines showed no clear correlation with fire temperature or fuel moisture content (Table 4.2). Burning intensity was notably higher on the east-facing slope of Puiggalí, where maximum temperatures averaged 541 ºC, and exceeded 60 ºC at the stem base for an average of 215 minutes. Greater crown scorch was also recorded in Puiggalí. Moisture content of live overstory fuels prior to burning was lower in Puiggalí and Lloreda, while understory woody fuel moisture content was lowest in Puiggalí. In contrast, herbs, litter, and duff layers were significantly drier in Lloreda compared to the other sites; however, the depth of litter and duff burned was, on average, greater in Puiggalí. Milder burning conditions were recorded on the southeast-facing slope of Can Feliu, where temperatures averaged 487 ºC, and exceeded 60 ºC for 103 minutes.

Needle terpene concentrations

We identified a total of 32 terpenes, including 14 monoterpenes (MT) and 18 sesquiterpenes (SQT). The total terpene concentration ranged from 50.4 to 74.0 mg g^{-1} of dry weight, with the highest concentration found in Post-y1 needles of control units and the lowest in Pre-y1 needles of burned units (i.e., before burning; Figure 4.2, Table S4.1). Overall, Post-y1 needles had the highest concentrations in both burned and unburned units. The most abundant terpenes were α-pinene (MT, 25.9%), β-caryophyllene (SQT, 19.0%), α-caryophyllene (SQT, 13.0%), germacrene-D (SQT, 12.2%), β-pinene (MT, 8.4%), and limonene (MT, 4.4%), cumulatively accounting for 83% of the total terpene concentrations.

Prescribed burning had no effect on terpene concentration one year after treatment ($p > 0.05$, Figure 4.2). Terpene concentrations were consistently lower in burned units, both before and after treatments. The various fire severity parameters assessed at tree level failed to explain variability in terpene concentration as well. The observed variability in terpene concentration was attributed primarily to needle age (Figure 4.3A). Monoterpene concentrations were positively related with $\delta^{13}C$ composition ($p < 0.05$, Figure 4.3B). Consistent with the lack of treatment effects, the sPLS-DA analysis did not identify any terpenes that discriminated between the burned and unburned classes (Figure S4.1).

Table 4.1. Site characteristics and vegetation structure per treatment unit and site right before prescribed burning (mean values and SE in brackets).

	Can Feliu		**Lloreda**		**Puiggalí**	
	Control	**Burn**	**Control**	**Burn**	**Control**	**Burn**
Latitude (º)	42.000	41.999	42.048	42.049	41.995	41.996
Longitude (º)	1.641	1.584	1.567	1.567	1.579	1.581
Elevation (m)	605	609	660	670	600	601
Aspect	SW	SE	S	W	SE	E
Slope (%)	10	27	14	20	25	27
Stand basal area (m^2 ha^{-1})	29.2	34.8	19.9	16.6	24.6	24.6
Stand density (trees ha^{-1})	928.4	1790.5	618.9	751.6	906.3	1182.6
DBH (cm)	18 (1.4)	14.5 (0.5)	19.6 (1)	16 (0.6)	16.9 (1.2)	14.9 (0.6)
Stand height (m)	14 (0.2)	9.7 (0.3)	10.3 (0.1)	10 (0.2)	14.7 (0.3)	9.6 (0.2)
Canopy base height (m)	8.4 (0.3)	4.7 (0.2)	5.7 (0.2)	4.9 (0.1)	8.3 (0.2)	4.6 (0.1)
Canopy cover (%)	60	52.6	45	60.8	65	58.5
Shrub cover (%)	-	35.5	-	29.7	-	40.5
Shrub biomass (Mg ha^{-1})	-	6.8	-	4.3	-	4.7
Herb cover (%)	-	39.4	-	65.1	-	65.8

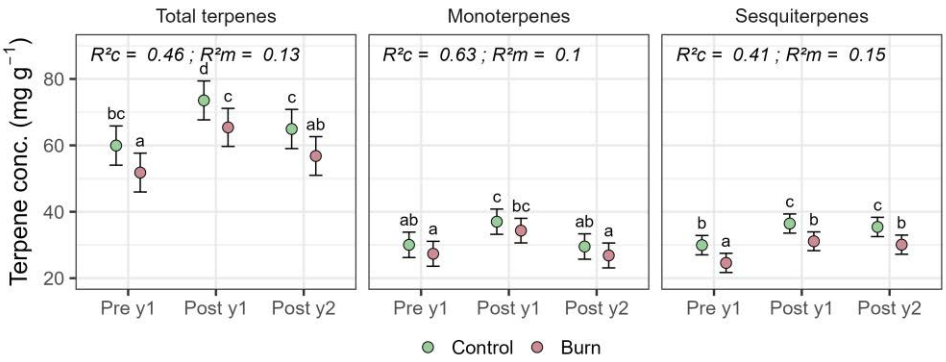

Figure 4.2. Estimated marginal means and confidence intervals (95%) of the mixed-effects models for total terpene, monoterpene, and sesquiterpene concentration (mg g^{-1} of dry weight) in Control and Burn treatments before (Pre) and one year after prescribed fire (Post) of current-year (y1) and mature (y2) needles (n = 54). Marginal (R^2m) and conditional (R^2c) variance of the models. Letters denote differences among treatments and needle age levels ($\alpha = 0.05$, Holm adjustment). Coefficient estimates of the models are in Table S4.2.

Stable isotopes and nitrogen content

Post-y1 needle $\delta^{13}C$ and Post-y2 needle $\delta^{18}O$ compositions exhibited different responses following treatments ($p < 0.001$; Figure 4.4). Specifically, Post-y1 needles in unburned units exhibited 2.5% higher $\delta^{13}C$ values compared to those in burned units, while $\delta^{18}O$ vales remained similar. Conversely, Post-y2 needles in unburned units showed 3.3% lower $\delta^{18}O$ values than burned units, while $\delta^{13}C$ remained similar. Nitrogen content was significantly higher in Post-y1 needles of both burned and unburned units and in Post-y2 needles of burned units compared to pre-treatment levels.

Pine processionary moth larvae survival

Survival of first-instar larvae ranged from 1% to 20%, primarily influenced by nitrogen content and the interaction of terpene concentration with treatment and needle age (Figure 4.5A, Figure S4.3). Larvae fed on mature needles (Post-y2) demonstrated a 9.5% higher survival probability compared to those fed on current-year needles (Post-y1; $p < 0.001$). Interestingly, higher terpene concentrations increased survival for larvae fed on burned pine needles, whereas the opposite trend was observed for larvae fed on unburned needles (indicated by the *terpene concentration* x *treatment interaction*; Table 4.3, Figure S4.3). Furthermore, the relationship between terpene concentration and survival also varied by needle age (denoted by the *terpene concentration* x *needle age* interaction). Additionally, higher survival probabilities were observed with increasing nitrogen content in both needle age classes of burned and unburned pines (Table 4.3, Figure S4.3). Terpene concentrations in current-year needles were consistently higher than in mature needles from both burned and unburned *larvae trees* (Figure 4.5B, Table S4.6), which was also seen in *selected trees* (Figure 4.2). However, no significant differences in nitrogen content were observed between treatments or needle age classes for the *larvae trees* (Figure 4.5C, Table S4.7), contrasting with findings from *selected trees* (Figure 4.4).

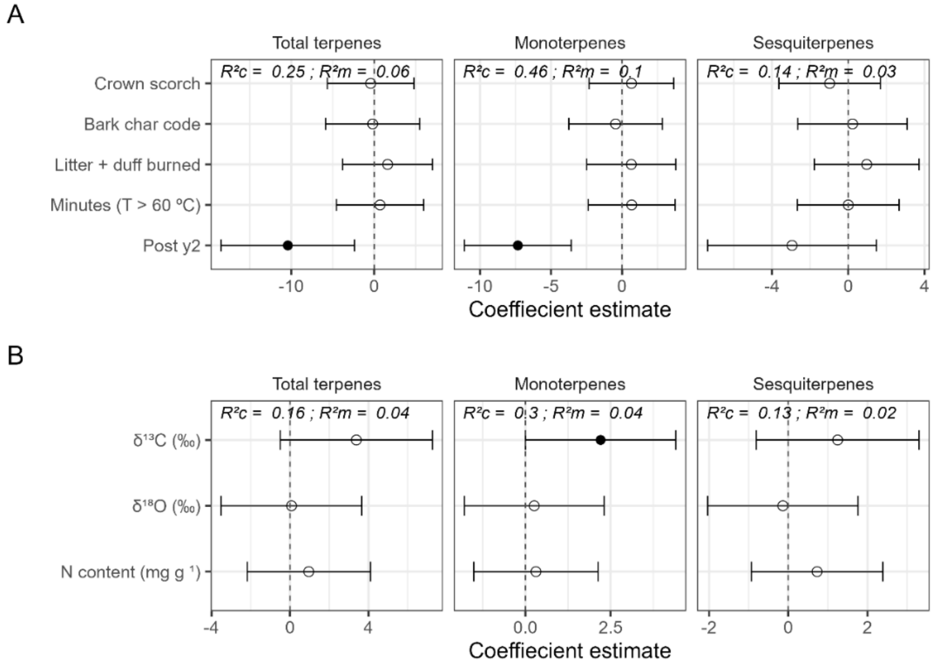

Figure 4.3. Model coefficient estimates and confidence intervals (95%) of total terpene, monoterpene, and sesquiterpene concentration (A) in burned units as a function of fire severity parameters and needle age and (B) in both burned and unburned units as a function of isotope composition and N content. Intercept of (A) equals Post-y1 (current-year) measurements; intercept of (B) equals average concentration across Pre-y1 (current-year), Post-y1 (current-year), and Post-y2 (mature needles) measurements. Coefficients are standardized. Filled points denote significant coefficients ($p < 0.05$). Marginal (R^2m) and conditional (R^2c) variance of the models.

Table 4.2. Median (IQR) of prescribed burning characteristics and fuel moisture content per site.

	CanFeliu	**Lloreda**	**Puiggali**
Burning characteristics			
Burning date	28/09/2020	30/09/2020	08/10/2020
n thermocouples	38	40	40
Maximum temperature (ºC)	487 (216 - 610)	552 (475 - 620)	541 (503 - 586)
n thermocouples (T > 60 ºC)	27	32	36
Minutes (T > 60 ºC)	103 (11 - 187)	113 (45 - 201)	215 (61 - 304)
Minutes (T > 120 ºC)	34 (3 - 88)	45 (20 - 140)	111 (26 - 149)
Crown scorch (%)	3 (0 - 35)	26 (7.6 - 51.9)	35 (10 - 60)
Maximum scorch height (m)	0.7 (0.3 - 1.1)	2.3 (1.8 - 2.9)	1.6 (1.1 - 2.1)
Bark char code [0-1]	0.6 (0.5 - 0.7)	0.7 (0.7 - 0.8)	0.7 (0.6 - 0.7)
Litter + duff burned depth (cm)	2 (0 - 3.8)	1.4 (0.7 - 1.9)	3.8 (0.8 - 5.1)
Moisture content (% dry weight)			
Pine 1h fuels	104.6 (101.1 - 107)	95.5 (92.5 - 96.7)	97.3 (93.6 - 100.3)
Pine needles	117.9 (113.7 - 133.8)	116.3 (112.2 - 120.9)	113.1 (109.2 - 116.5)
Shrubs 1h fuels	84.1 (80.6 - 91.4)	90.1 (79.8 - 103.7)	80 (67 - 94.2)
Herbs	71.2 (68.6 - 79.8)	63 (58.9 - 79.7)	69.9 (62 - 73.5)
Litter	29.2 (23.9 - 35.3)	5.6 (4.2 - 6.9)	34.6 (27.3 - 36.9)
Duff	57.9 (39.2 - 59.3)	15.9 (9.4 - 25.2)	57 (48.1 - 67.7)
Mineral soil (0-5 cm)	11.8 (11.5 - 13.6)	10.4 (8.4 - 11.5)	15 (14.2 - 16.9)

4.4. Discussion

Needle terpene concentration and composition did not differ between burned and unburned pines one year after prescribed burning, when PPM larvae are in the early stages of development. While terpene concentrations of both current-year (Post-y1) and mature needles (Post-y2) increased one year after burning, similar trends in unburned units suggest that this increase was unrelated to burning (Figure 4.2), refuting our first hypothesis. Neither did fire severity parameters explain the variability in terpene content of burned pines (Figure 4.3A). Instead, a considerable amount of variability was attributed to differences among individual pines, as indicated by a relatively high intraclass correlation coefficient (ICC) in the monoterpene model. These intrinsic differences likely influenced the observed survival trends of first-instar PPM larvae. Specifically, larvae feeding on burned pine needles had higher survival probability when terpene concentrations were lower (Figure 4.5A, B). Interestingly, larvae feeding on mature needles, regardless of burning treatment, showed higher survival probabilities, likely due to the consistently lower terpene concentrations in these needles. This provides partial support for our second hypothesis: needle terpene content affects larvae survival, but the relationship is neither linear nor universal.

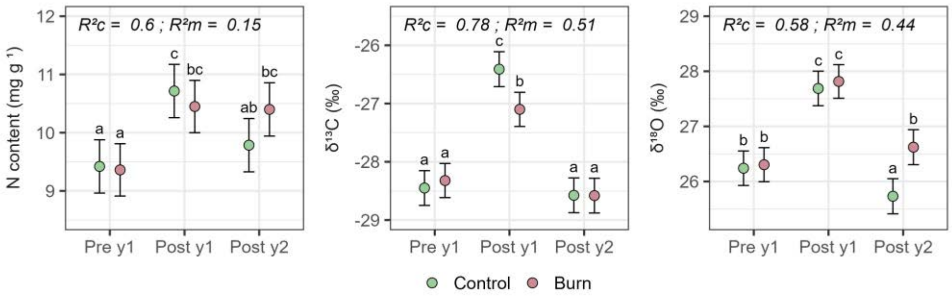

Figure 4.4. Estimated marginal means and confidence intervals (95%) of the mixed-effects models for nitrogen (N) content (mg g^{-1}) and $\delta^{13}C$ and $\delta^{18}O$ composition (‰) in Control and Burn treatments before (Pre) and one year after prescribed fire (Post) of current-year (y1) and mature (y2) needles (n = 54). Marginal (R^2m) and conditional (R^2c) variance of the models. Letters denote differences among treatments and needle age levels ($\alpha = 0.05$, Holm adjustment). Coefficient estimates of the models are in Table S4.5.

No effect in terpene content one year after burning

Prescribed burning did not lead to changes in needle terpene concentration one year after its implementation. This finding aligns with previous studies showing a lack of persistent effects on needle terpene content (Lavoir et al., 2013; Valor et al., 2017b) or other leaf chemical components (Cannac et al., 2009b; Rieske et al., 2002) following prescribed burning. Similar transient responses in needle terpene concentration have been observed following other stressors such as drought (Llusià and Peñuelas, 1998). While resin flow, a related defence mechanism, may increase temporarily after burning (Cannac et al., 2009a; Knebel and Wentworth, 2007), needle terpene concentration appeared unaffected by fire, even under the wide range of observed fire severity levels (Table 4.2). However, needle terpene concentration 24 h post-burning may be positively correlated to crown scorch (Valor et al., 2017b), whereas phloem terpene concentration may decline as fire injury increases (Powell and Raffa, 2011).

Consistent with the lack of differences in terpene concentration, we observed no effect of burning treatments on terpene composition. Findings of earlier work are mixed, with some reporting changes in needle terpene composition after prescribed burning (Lavoir et al., 2013; Valor et al., 2017b), PPM defoliation (Achotegui-Castells et al., 2013; Hódar et al., 2004; Lombardero et al., 2013), or drought (Blanch et al., 2009; Llusià and Peñuelas, 1998), and others reporting no changes after PPM defoliation (Hódar et al., 2015) or drought (Kleiber et al., 2017).

Our results, along with those of others who observed no terpene response after a stress factor appears or ceases, support the hypothesis that terpenes in pines serve primarily as constitutive defences rather than induced responses to stressors (Haukioja et al., 1998; Lewinsohn et al., 1991). Needle terpene content is highly variable as a function of climate (Kleiber et al., 2017), species (Lavoir et al., 2013; Valor et al., 2017b), or even subspecies growing at the same site (Achotegui-Castells et al., 2015), but the mechanisms underlying this variation remain unclear (Malone et al., 2024).

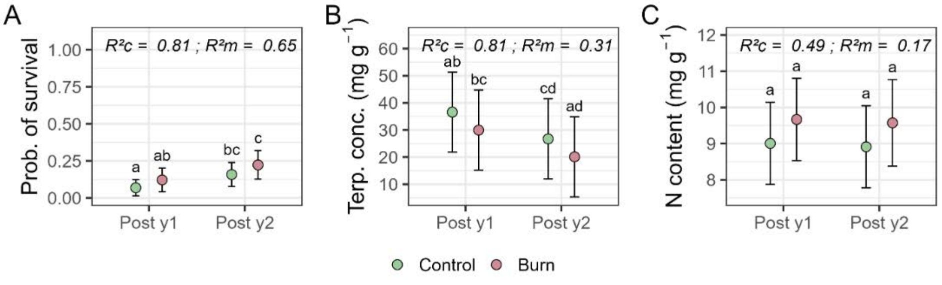

Figure 4.5. Estimated marginal means and confidence intervals (95%) of (A) the predicted probability of survival of first-instar larvae as a function of treatment, needle age, total terpene concentration, and nitrogen (N) content (mg g^{-1} of dry weight), (B) total terpene concentration and (C) N content of the needles used to feed larvae as a function of treatment and needle age, one year after Control and Burn treatments of current-year (y1) and mature (y2) needles. Marginal (R^2m) and conditional (R^2c) variance of the mixed-effects models. Letters denote differences among treatments and needle age levels ($\alpha = 0.05$, Holm adjustment). Coefficient estimates of (A) model are in Table 4.3, (B) model in Table S4.6, and (D) model in Table S4.7.

Drought effects on terpene content

The higher terpene concentrations observed in Post-y1 needles of both burned and unburned units compared to pre-burning levels were likely driven by the drought conditions during needle growth (Blanch et al., 2009; Llusià and Peñuelas, 1998; Turtola et al., 2003). This result aligns with the growth-differentiation balance hypothesis (GDBH), which posits that limited resources –in this case, water deficit– constrain growth more than carbon fixation, leading to a larger relative allocation of carbon to defences (Herms and Mattson, 1992). However, this interpretation is not universal: some studies challenge the GDBH noting that terpenes and proteins do not share biosynthetic pathways, thus questioning the idea of a direct trade-off between growth and carbon-based secondary compounds such as terpenes (Haukioja et al., 1998; Malone et al., 2024). Additionally, the concurrent increase in nitrogen content observed in Post-y1 needles (Figure 4.4) may reflect broader physiological responses to drought rather than a direct link between nutrient availability and terpene production, as terpenes do not respond to fertilization (Haukioja et al., 1998).

We expected burned pines to be less affected by drought conditions and exhibit an enhanced water balance, owing to the reduced competition from understory vegetation following prescribed burning (Vilà-Vilardell et al., 2024b), and, consequently, to follow a different defence investment strategy than unburned pines. The dual-isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) revealed physiological differences between burned and unburned pines, suggesting variations in their performance one year after burning. For instance, in burned pines, the lower $\delta^{13}C$ in Post-y1 needles suggests reduced photosynthetic rates, while the higher $\delta^{18}O$ in Post-y2 needles points to lower stomatal conductance (Scheidegger et al., 2000), likely reflecting a response to drought conditions. However, despite the physiological differences, we found no relationship between terpene concentration and isotope composition (Figure 4.3B). In contrast, previous research has found a decrease in needle terpene content in pines that showed physiological improvement one year after prescribed burning (Valor et al., 2017b).

Table 4.3. Coefficient estimate, standard error (SE), and confidence intervals (CI, 95%) of the zero-inflated mixed-effects model for the probability of survival of first-instar larvae as a function of needle terpene concentration, treatment, and needle age. The conditional component of the model explains the factors influencing the survival of larvae; intercept equals Control, Post-y1. The zero-inflated component (Bernoulli part) of the model indicates that the probability of finding a larva as either dead or alive is constant across different concentration of terpenes and different levels of treatment and needle age. CI in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Parameter	**Coefficient**	**SE**	**CI Low**	**CI High**	**R^2c**	**R^2m**	**ICC**
Prob. of survival (Conditional)					0.81	0.65	0.44
(Intercept)	-3.06	0.98	-4.99	-1.13			
Terpenes	-3.01	1.39	**-5.73**	**-0.28**			
Burn	2.53	1.31	-0.03	5.09			
Post y2	3.32	0.52	**2.3**	**4.34**			
N content	0.58	0.23	**0.12**	**1.04**			
Terpenes x Burn	4.66	1.43	**1.86**	**7.46**			
Terpenes x Post y2	1.34	0.47	**0.42**	**2.26**			
Prob. of survival (Zero inflated)							
(Intercept)	0.9	0.27	0.37	1.42			

Note: Post-y2, mature-needles post-treatment

PPM larvae survival is influenced by multiple factors

PPM larvae survival was shaped by multiple interacting factors rather than by prescribed burning alone, as observed with other phytophagous insects (Land and Rieske, 2006; Rieske et al., 2002). The interaction between burning treatment and needle terpene concentration underscores the role of chemical defences in modulating the effects of burning. Needle age and nitrogen content further influenced survival, emphasizing the multifaceted nature of these dynamics.

Larvae survival was higher on mature needles (Post-y2), which consistently had lower terpene concentrations (Figure 4.5B). While this aligns with prior studies (Šmits and Larsson, 1999), other factors, such as needle toughness or defoliation status, could also have contributed to the observed survival patterns (Hódar et al., 2004; Zovi et al., 2008). The literature reports a weak or non-existent relationship between PPM larvae performance and needle terpene levels (Achotegui-Castells et al., 2015; Hódar et al., 2004, 2015; Lombardero et al., 2013). As such, our study failed to find a conclusive result. The significant variation in terpene concentrations among individual trees (ICC = 0.72) suggests that tree-specific traits play a key role in shaping the environment for larvae.

The positive relation between needle nitrogen content and larvae survival further emphasizes the importance of host plant quality. Nitrogen supports the synthesis of structural proteins critical for larval development (Hódar et al., 2002; Mattson, 1980). However, the absence of differences in nitrogen content between burned and unburned pines, despite transient increase in soil nitrogen following burning (DeLuca and Zouhar, 2000; Romanya et al., 2001), suggests that these changes may not translate directly into foliar nitrogen content.

Implications and future directions

The survival rates observed in our bioassay (1-20%) are lower than in other studies (Achotegui-Castells et al., 2015; Hódar et al., 2004, 2015) and may reflect unmeasured factors, such as behavioural or developmental dynamics. While we controlled environmental factors affecting larvae performance, such as temperature and moisture, and manipulated only the type of food provided (burned vs. unburned, current-year vs. mature needles), the overall low survival rate could indicate that we overlooked important, yet not entirely understood, factors (Zalucki et al., 2002). For example, larvae reared in small groups may experience different survival outcomes compared to their natural gregarious behaviour in communal settings. Mixing larvae from different egg batches might also introduce variability. Future studies could address these limitations by standardizing larvae sources and incorporating behavioural observations.

Our findings demonstrate that, under the conditions studied, prescribed burning does not affect needle terpene concentration or composition, nor does it negatively affect PPM larvae survival. These results emphasize the need to consider both biotic and abiotic factors, as well as individual tree variation, when evaluating the ecological impacts of prescribed burning and other forest management practices.

4.5. Conclusions

Forest management treatments initially designed to reduce wildfire risk, may have broader ecological implications by potentially enhancing forest resistance to subsequent disturbances (Hood et al., 2016; Vilà-Vilardell et al., 2024a, 2024b), yet when prescribed burning is implemented without prior cutting treatments, our findings indicate that this does not always hold true. We found no evidence that prescribed burning affected needle terpene content in dominant black pines one year after its implementation, a period when pine processionary moth (PPM) larvae are in their early developmental stages. This suggests that any defensive response to heat stress, if present, does not persist. Instead, the increased terpene concentrations observed in current-year needles of both burned and unburned pines likely relate to the prevailing drought conditions during their growth. Furthermore, one year after prescribed burning, the effect on PPM larvae survival was minimal, with variations in survival primarily attributed to differences in terpene concentration across needle age classes. These results indicate that the survival patterns of PPM larvae are complex, influenced by multiple factors, yet highlight that prescribed burning in these sub-Mediterranean forests does not lead to undesirable negative impacts on subsequent PPM incidence or performance.

Acknowledgements

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4.6. Supplementary material

Table S4.1. Mean (SE) of needle terpene concentration (µg g^{-1} of dry weight) of *Pinus nigra* spp. *salzmannii* in Control and Burn treatments before (Pre) and one year after prescribed fire (Post) of current-year (y1) and mature (y2) needles.

	Pre y1		**Post y1**		**Post y2**	
	Burn	**Control**	**Burn**	**Control**	**Burn**	**Control**
Monoterpenes						
tricyclene	48.1 (4.1)	55.5 (5.1)	70.1 (6.4)	76.7 (6.7)	49.8 (5.5)	49.5 (3.6)
α-pinene	13823.1 (729.6)	16536.1 (580.4)	16330.2 (731.8)	18568.1 (526.1)	14821.6 (784.3)	16738.3 (521.4)
camphene	243 (18.1)	290.3 (21.3)	354 (25.6)	420.1 (28.8)	208 (20.5)	215 (17.6)
sabinene	76 (15.3)	84.4 (11.3)	114.4 (18.6)	163.3 (27.1)	45.8 (9.3)	51.3 (5.8)
β-pinene	4573 (625.6)	5174.2 (810.6)	6632.1 (740)	5777.3 (760.8)	5119.6 (649.8)	4128.3 (608.8)
β-myrcene	1772.7 (304.6)	2989.4 (349.8)	3307.3 (562.5)	4418.3 (404.7)	2039.8 (390.6)	2397.6 (250.5)
α-phellandrene	148 (19.7)	200.9 (20.1)	199.2 (24.2)	283.8 (24.7)	165.3 (23.1)	203.3 (19.8)
3-carene	1220.4 (469)	1657.5 (489.7)	1749.4 (495.9)	2267.5 (667)	1198.5 (410.9)	1294.9 (390.5)
limonene	2456.6 (231.9)	2517.8 (192.4)	3328 (262.9)	3289 (211.8)	2607.3 (258.4)	2435.3 (150.6)
cis-β-ocimene	257.5 (34.1)	424.9 (51.7)	498.6 (65.2)	709.1 (94.4)	213.5 (43.2)	228.8 (27.7)
terpinolene	119.5 (31.7)	157.2 (35.6)	194.7 (43.6)	256 (64)	134.9 (36.8)	127.1 (23.6)
linalool	233 (31.1)	263.9 (38.4)	156.2 (30.1)	310 (60.5)	116.3 (23.8)	250.9 (49.4)
linalyl anthranilate	1257.4 (264.5)	1379.6 (338.4)	2008.5 (480.5)	1547.7 (408.2)	1070.1 (297)	861.6 (237.3)
L-bornyl acetate	61.2 (6.5)	72.4 (6)	113.3 (10.1)	146.7 (13.4)	38.9 (6)	38.4 (3.6)
Sesquiterpenes						
γ-pyronene	48.1 (5.2)	53.9 (5.7)	69 (6.4)	79.4 (15)	55.9 (6.4)	64.3 (7.3)
α-cubebene	135.4 (24.2)	179.8 (45.2)	335.8 (123.8)	339 (104.4)	193 (36)	236.7 (42.5)
ylangene	26.4 (2.2)	35.5 (2.9)	36.1 (2.9)	41.4 (3.4)	82.2 (8.1)	116.2 (10.3)
α-copaene	103.5 (6.4)	124.4 (6.8)	140.9 (7.6)	154.4 (8.6)	205.2 (16.2)	255.2 (16.7)
β-elemene	285.1 (29.7)	362.6 (28.6)	354.1 (30.5)	383.6 (31)	214.8 (25)	314.9 (34.1)

Table S4.1. (cont.). Mean (SE) of needle terpene concentration (μg g^{-1} of dry weight) of *Pinus nigra* spp. *salzmannii* in Control and Burn treatments before (Pre) and one year after prescribed fire (Post) of current-year (y1) and mature (y2) needles.

	Pre y1		**Post y1**		**Post y2**	
	Burn	**Control**	**Burn**	**Control**	**Burn**	**Control**
β-caryophyllene	9555 (496.5)	11565 (347.1)	12273 (489.2)	13591 (327.4)	11283 (636.8)	12889 (361.3)
α-caryophyllene	6413.4 (390.9)	7597.7 (307)	8733 (407.6)	9700.6 (339)	7646.2 (511.2)	8729.9 (355.9)
isocaryophyllene	62.9 (4.2)	74.4 (3.5)	90.5 (5)	101.8 (4.5)	75.4 (5.2)	89 (4.3)
γ-muurolene	376.2 (30.8)	446.7 (34.8)	491.4 (36.9)	492 (41.1)	1123.5 (103.9)	1406.5 (109.6)
germacrene D	5744 (356.2)	8175.5 (344.1)	7522.2 (413.6)	9024.9 (312.4)	6407.9 (459.2)	8925.6 (356.7)
α-muurolene	294.4 (27.4)	340.7 (25.3)	372.5 (27.9)	384.7 (29)	479.9 (46.9)	597.1 (38)
γ-cadinene	227.5 (18.7)	269.4 (20.8)	299.8 (23.5)	305.1 (24.6)	554.9 (51.7)	687.4 (51.7)
δ-cadinene	216 (17.2)	261.2 (19.5)	293 (21.9)	296.7 (22.9)	549.8 (48.8)	691.7 (50.5)
α-cadinene	65.3 (14.9)	62.7 (5.4)	119.5 (45.1)	82.7 (9)	122.6 (13.2)	200.7 (18.6)
germacrene D-4-ol	375.3 (52.3)	454.7 (43.3)	476.1 (49.3)	548.8 (49.5)	197.6 (28.2)	287.5 (33)
caryophyllene oxide	78.9 (7.8)	88.2 (12.4)	79.8 (6.7)	86.4 (6)	220.3 (20.7)	225.6 (15.7)
τ-cadinol	45.9 (3.6)	52.2 (3.1)	56.8 (4.6)	64 (4.2)	80.9 (7.3)	102.6 (5.8)
α-cadinol	36.9 (3.5)	44.3 (2.8)	47.5 (4)	55.8 (4)	64 (6.9)	86.3 (6.1)
Total terpenes	50379 (4277)	61992 (4208)	66846 (5203)	73965 (4634)	57386 (4991)	64926 (3828)

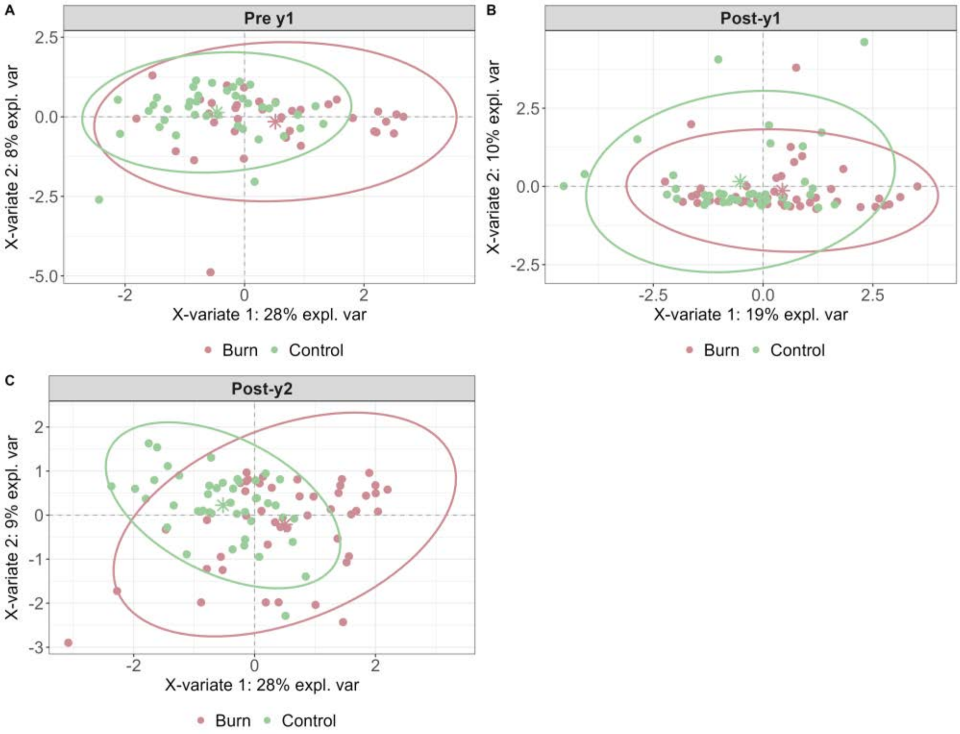

Figure S4.1. Sample plot of the sparse partial least-square discriminant analysis (sPLS-DA) showing terpene concentration by needle age projected into the space spanned by the two components in Control and Burn treatments before (Pre) and one year after prescribed fire (Post) of current-year (y1) and mature (y2) needles. Ellipses represent 95% confidence intervals around each treatment (Burn and Control); the star represents the centroid of each treatment.

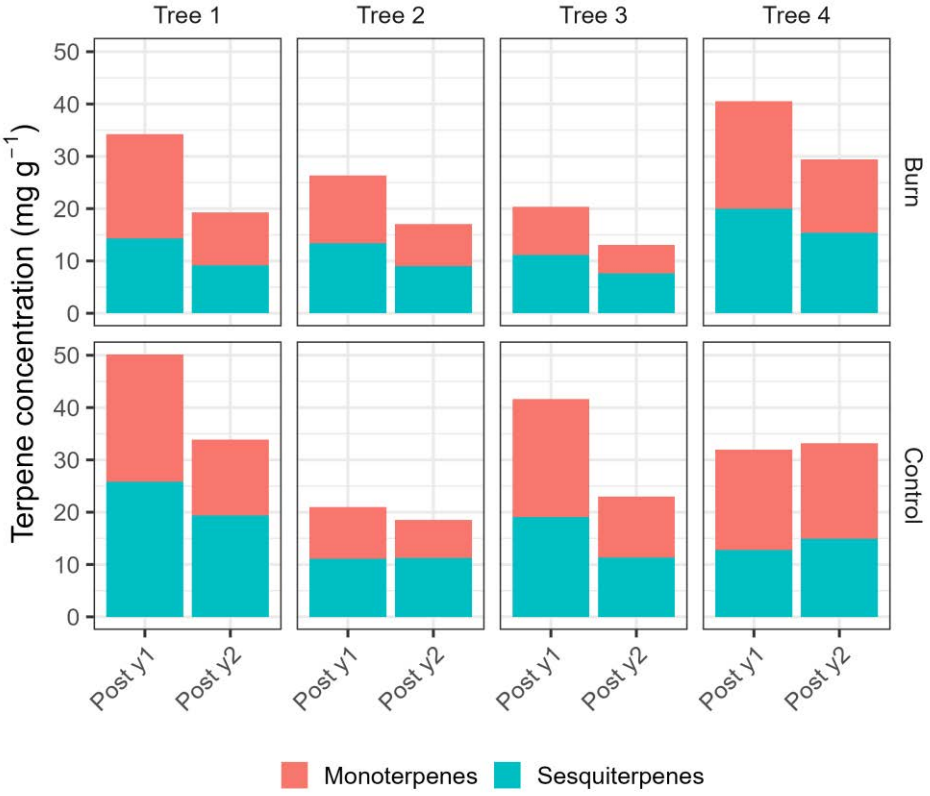

Figure S4.2. Terpene concentration (mg g^{-1} of dry weight) of the needles used in the bioassay to feed larvae by tree and treatment, divided by monoterpene and sesquiterpene concentration of current-year (y1) and mature (y2) needles.

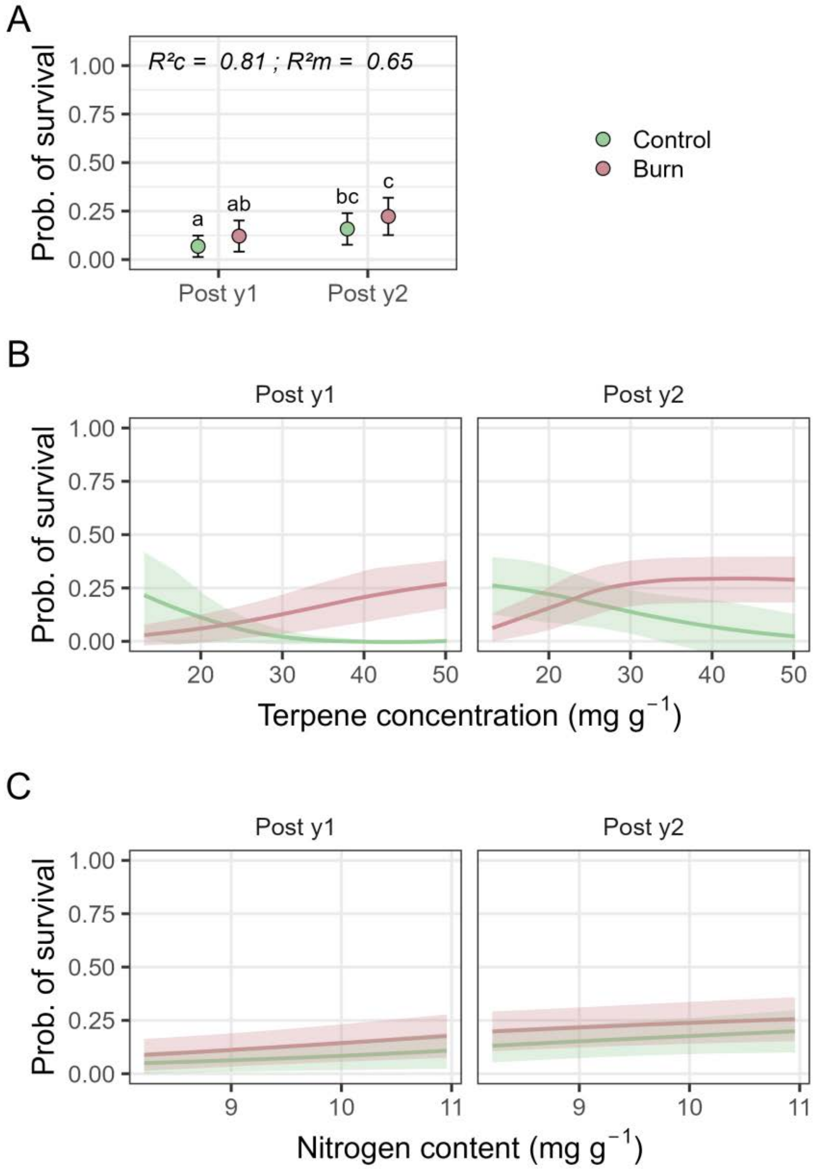

Figure S4.3. Predicted probability of survival of first-instar larvae as a function of treatment, needle age, total terpene concentration, and N content (mg g^{-1} of dry weight) in Control and Burn treatments of current-year (y1) and mature (y2) needles. (A) Estimated marginal means and confidence intervals (95%); (B) predicted response as a function of terpene concentration, treatment, and needle age (N content is marginalized over); (C) predicted response as a function of N content, treatment, and needle age (terpene concentration is marginalized over). Shaded areas represent the 95% confidence intervals. Marginal (R^2m) and conditional (R^2c) variance of the mixed-effects models. Letters denote differences among treatments and needle age levels ($\alpha = 0.05$, Holm adjustment). Coefficient estimates of the model are in Table S4.6.

Figure S4.4. Collection of *Pinus nigra* needles for the bioassay (left); first-instar larvae feeding on *Pinus nigra* needles (right).

Table S4.2. Coefficient estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for needle total terpene, monoterpene, and sesquiterpene concentration (mg g^{-1} of dry weight) as a function of treatment and needle age. Intercept equals Control, Pre-y1. CI in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Parameter	**Coefficient**	**SE**	**CI Low**	**CI High**	**R^2c**	**R^2m**	**ICC**
Total terpenes					0.46	0.13	0.38
(Intercept)	59.94	2.21	55.58	64.3			
Burn	-8.13	2.65	**-13.35**	**-2.92**			
Post y1	13.6	1.96	**9.74**	**17.46**			
Post y2	4.99	1.99	**1.08**	**8.9**			
Monoterpenes					0.63	0.1	0.59
(Intercept)	30.04	1.43	27.22	32.85			
Burn	-2.69	1.82	-6.27	0.89			
Post y1	6.98	1	**5**	**8.95**			
Post y2	-0.5	1.02	-2.5	1.5			
Sesquiterpenes					0.41	0.15	0.3
(Intercept)	29.94	1.09	27.79	32.09			
Burn	-5.34	1.27	**-7.84**	**-2.84**			
Post y1	6.51	1.05	**4.45**	**8.57**			
Post y2	5.49	1.06	**3.4**	**7.58**			

Notes: The interaction *treatment x needle age* was removed from the model as it was not significant. Post y1, current-year needles post-treatment; Post-y2, mature-needles post-treatment.

Table S4.3. Coefficient estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for needle total terpene, monoterpene, and sesquiterpene concentration (mg g^{-1} of dry weight) of pines growing in burned units one year after prescribed fire as a function of fire severity. Intercept equals Post-y1. CI in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Parameter	**Coefficient**	**SE**	**CI Low**	**CI High**	**R^2c**	**R^2m**	**ICC**
Total terpenes					0.25	0.06	0.2
(Intercept)	64.86	3.13	58.65	71.07			
Crown scorch	-0.42	2.62	-5.63	4.79			
Bark char code	-0.19	2.85	-5.85	5.48			
Minutes (T > 60 ºC)	0.7	2.65	-4.56	5.96			
Litter + duff burned	1.62	2.72	-3.79	7.02			
Post y2	-10.41	4.05	**-18.45**	**-2.37**			
Monoterpenes					0.46	0.1	0.4
(Intercept)	33	1.68	29.66	36.34			
Crown scorch	0.66	1.5	-2.32	3.64			
Bark char code	-0.45	1.65	-3.74	2.83			
Minutes (T > 60 ºC)	0.68	1.54	-2.38	3.73			
Litter + duff burned	0.65	1.58	-2.48	3.78			
Post y2	-7.34	1.9	**-11.1**	**-3.57**			
Sesquiterpenes					0.14	0.03	0.12
(Intercept)	31.83	1.64	28.57	35.09			
Crown scorch	-0.97	1.34	-3.63	1.69			
Bark char code	0.23	1.45	-2.64	3.1			
Minutes (T > 60 ºC)	0	1.34	-2.67	2.67			
Litter + duff burned	0.97	1.38	-1.77	3.71			
Post y2	-2.95	2.23	-7.37	1.48			

Note: Post-y2, mature-needles post-treatment.

Table S4.4. Coefficient estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for needle total terpene, monoterpene, and sesquiterpene concentration (mg g^{-1} of dry weight) as a function of needle isotope composition and N content. Intercept equals the average terpene concentration across both Control and Burn treatments before (Pre) and one year after prescribed fire (Post) of current-year (y1) and mature (y2) needles measurements. CI in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Parameter	**Coefficient**	**SE**	**CI Low**	**CI High**	**R^2c**	**R^2m**	**ICC**
Total terpenes					0.16	0.04	0.12
(Intercept)	59.54	1.52	56.54	62.54			
$\delta^{13}C$	3.38	1.96	-0.5	7.26			
$\delta^{18}O$	0.08	1.82	-3.51	3.66			
N content	0.96	1.59	-2.18	4.1			
Monoterpenes					0.3	0.04	0.27
(Intercept)	30.01	0.93	28.17	31.85			
$\delta^{13}C$	2.21	1.11	**0.004**	**4.41**			
$\delta^{18}O$	0.26	1.04	-1.79	2.31			
N content	0.31	0.92	-1.51	2.13			
Sesquiterpenes					0.13	0.02	0.11
(Intercept)	29.6	0.8	28.03	31.18			
$\delta^{13}C$	1.25	1.04	-0.81	3.3			
$\delta^{18}O$	-0.14	0.96	-2.03	1.76			
N content	0.73	0.84	-0.93	2.39			

Table S4.5. Coefficient estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for needle $\delta^{13}C$ (‰), $\delta^{18}O$ (‰), and N content (mg g^{-1} of dry weight) as a function of treatment and needle age. Intercept equals Control, Pre-y1. CI in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

	Parameter	**Coefficient**	**SE**	**CI Low**	**CI High**	**R^2c**	**R^2m**	**ICC**
$\delta^{13}C$						0.78	0.51	0.55
	(Intercept)	-28.45	0.11	-28.67	-28.23			
	Burn	0.13	0.16	-0.18	0.44			
	Post y1	2.04	0.11	**1.83**	**2.25**			
	Post y2	-0.13	0.11	-0.33	0.08			
	Burn x Post y1	-0.82	0.15	**-1.12**	**-0.52**			
	Burn x Post y2	-0.13	0.15	-0.43	0.17			
$\delta^{18}O$						0.58	0.44	0.25
	(Intercept)	26.24	0.12	26.01	26.47			
	Burn	0.06	0.17	-0.26	0.39			
	Post y1	1.45	0.14	**1.16**	**1.73**			
	Post y2	-0.51	0.15	**-0.8**	**-0.22**			
	Burn x Post y1	0.06	0.2	-0.34	0.46			
	Burn x Post y2	0.83	0.21	**0.42**	**1.23**			
N content						0.6	0.15	0.53
	(Intercept)	9.42	0.17	9.08	9.76			
	Burn	-0.06	0.24	-0.53	0.41			
	Post y1	1.29	0.17	**0.97**	**1.62**			
	Post y2	0.36	0.17	**0.04**	**0.69**			
	Burn x Post y1	-0.21	0.23	-0.67	0.25			
	Burn x Post y2	0.67	0.24	**0.21**	**1.14**			

Notes: Post y1, current-year needles post-treatment; Post-y2, mature-needles post-treatment.

Table S4.6. Coefficient estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for total terpene concentration (mg g^{-1} of dry weight) in needles used in the bioassay to feed larvae as a function of treatment and needle age, collected one year after prescribed fire. Intercept equals Control, Post-y1. CI in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Parameter	**Coefficient**	**SE**	**CI Low**	**CI High**	**R^2c**	**R^2m**	**ICC**
Total terpenes					0.81	0.31	0.72
(Intercept)	36.58	4.42	26.86	46.31			
Burn	-6.62	6.01	-19.84	6.6			
Post y2	-9.84	2.43	**-15.19**	**-4.5**			

Note: Post-y2, mature-needles post-treatment

Table S4.7. Coefficient estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for N content (mg g^{-1} of dry weight) in needles used in the bioassay to feed larvae as a function of treatment and needle age, collected one year after prescribed fire. Intercept equals Control, Post-y1. CI in bold indicate a significant difference with the intercept. R^2c, conditional variance; R^2m marginal variance; ICC, intraclass correlation coefficient.

Parameter	Coefficient	SE	CI Low	CI High	R^2c	R^2m	ICC
Nitrogen content					0.49	0.17	0.39
(Intercept)	9	0.35	8.21	9.8			
Burn	0.66	0.46	-0.36	1.69			
Post y2	-0.09	0.31	-0.79	0.61			

Note: Post-y2, mature-needles post-treatment

CHAPTER 5

Prescribed fire after thinning increased resistance of sub-Mediterranean pine forests to drought events and wildfires

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Abstract

Forest restoration treatments aimed primarily at reducing fuel load and preventing high-severity wildfires can also influence resilience to other disturbances. Many pine forests in temperate regions are subject to tree-killing bark beetle outbreaks (e.g., *Dendroctonus*, *Ips*), whose frequency and intensity are expected to increase with future climatic changes. Restoration treatments have potential to increase resistance to bark beetle attacks, yet the underlying mechanisms of this response are still unclear. While the effect of forest restoration treatments on tree growth has been studied, less is known about their impact on resin-based defences. We measured axial resin ducts in the earlywood and latewood of ponderosa pines (*Pinus ponderosa*) in western Montana, USA, 20 years before and after the implementation of restoration treatments, with the aim to elucidate changes in the yearly and interannual investment in resin duct defences following treatments and their sensitivity to climate. Two experiments were established in 1992: a moderate thinning and a retention shelterwood, with 35% and 57% basal area reduction, respectively. Each experiment comprised four treatments with three replicates per treatment: cutting only, cutting followed by prescribed burning in either spring or fall or under wet or dry duff moisture conditions, and an untreated control. Cutting treatments stimulated a long-term, sustained increase in resin duct production, more pronounced in the earlywood, which we attribute to a higher availability of resources due to reduced tree density. Prescribed burning following cutting induced a short-term increase in resin ducts, likely aiding in the compartmentalization of fire-killed cambium and enhancing the resistance of fire-injured trees to bark beetle attack. However, the fire-induced spike in duct production was not related to the degree of crown scorch. Treatments had little effect on climate-defence relationships, as ducts remained positively correlated to winter precipitation and, though less significantly, negatively correlated to spring maximum temperature. Our findings show that by reducing stand density, forest restoration treatments induce the synthesis of resin ducts, which are key in mitigating vulnerability of ponderosa pine to mountain pine beetle (*D. ponderosae*) attacks, thus promoting forest resilience to multiple disturbances.

Keywords: climate-defence relationships, earlywood, latewood, *Pinus ponderosa*, shelterwood, thinning.

5.1. Introduction

Forest management treatments, such as cutting and prescribed burning, are often used to increase timber production, reduce fuels and fire hazard, or restore vegetation and fuel structure associated with historical fire regimes. Yet, their benefits are manifold and often extend beyond their initial objectives. By modifying forest structure and enhancing tree vigour, these treatments are key in shaping how trees respond to various disturbances including pest outbreaks, droughts, and wildfires (Sohn et al., 2016; Vilà-Vilardell et al., 2024b). Bark beetle outbreaks (Coleoptera: Curculionidae, Scolytinae) are the predominant biotic disturbance in conifer forests worldwide and their occurrence is often associated with drought (Gaylord et al., 2013). As drought and bark beetle outbreaks become increasingly prevalent with climate change (Seidl et al., 2017), understanding how tree defence investment, forest structure, and climate are intertwined is essential.

Pine species (*Pinus* spp.) have a network of constitutive and induced resin ducts or canals which remain functional for several years after synthesis. As sites of resin synthesis, storage, and delivery, resin ducts provide conifers a lasting defence mechanism (Hudgins and Franceschi, 2004). Because resin ducts are produced from the vascular cambium as wood develops, they are embedded in the secondary xylem and serve as a retrospective record of the interannual variation of tree defences, allowing the study of the effect of environmental factors on tree defence investment over time (Vázquez-González et al., 2020b). Resin ducts are produced both in the earlywood and latewood, and their relative proportion is under strong genetic control (Vázquez-González et al., 2020a). Duct density is typically greater in the latewood (Saracino et al., 2017), which is formed later in the growing season when competition for resources with other tree functions is presumably lowest (Herms and Mattson, 1992). Consistently, Rigling et al. (2003) showed that management treatments that ameliorate resource availability stimulates the synthesis of resin ducts in the earlywood. More research is needed to understand the different responses of earlywood and latewood ducts to external stimuli.

While a number of studies have shown the efficacy of resin ducts in providing tree resistance to bark beetle-related mortality (e.g., Ferrenberg et al., 2023; Hood et al., 2015; Kane and Kolb, 2010; Sangüesa-Barreda et al., 2015; Valor et al., 2021), relatively few have focused on how forest treatments and forest structure influence the production of resin ducts and several uncertainties remain. First, reported effects of prescribed burning on the production of resin ducts in pines are inconclusive, with some studies reporting a short-term spike when prescribed burning was implemented in combination with thinning (Bernal et al., 2023) or tapping (Rodríguez-García et al., 2018), while others have found no significant effect of prescribed burning alone or combined with thinning (Hood et al., 2016) or even a reduction in resin duct size following smouldering fire (Slack et al., 2016). Secondly, reported effects of thinning treatments followed by prescribed burning are also mixed: while Hood et al. (2016) found that thinning, rather than prescribed burning, promoted the production of new resin ducts, Bernal et al. (2023) found that thinning increased resin duct defences particularly when followed by prescribed burning. These mixed results could reflect the diverse effects of different cutting intensities, burning seasons, or burning under different moisture conditions on resin duct investment, a topic that remains unexplored.

Understanding the sensitivity of resin ducts to forest management treatments helps to elucidate the underlying mechanism that triggers the synthesis of resin-based defences and thus, the resistance to beetle-related mortality. For example, a greater investment in resin ducts after prescribed burning would be related to the role of low-intensity fire in stimulating resin-based defences (Hood et al., 2015), while a greater investment after thinning would be associated with the greater availability of resources due to reduced tree density and competition (Hood et al., 2016). Moreover, the season of burning can affect tree resin defences (Cannac et al., 2009b), either because of the different phenological status of the tree at the time of burning (Valor et al., 2017a) or as a result of the fire intensity and crown scorch derived (Wallin et al., 2003).

Climate is an important driver of physiological processes like tree growth and investment in resin defences (Rigling et al., 2003). Climate influence on resin duct defences is particularly intricate in water-limited environments, where soil-water availability for physiological processes depends not only on precipitation and temperature patterns (Saracino et al., 2017) but also on forest structure and tree vigour (Tepley et al., 2020). In the context of climate change, disentangling the influence of both forest structure and climate on tree resin defences is crucial for anticipating and predicting future responses.

Here, we use tree ring chronologies to examine the sensitivity of resin duct defences in ponderosa pine to forest restoration treatments and climate in western

Montana, USA. Treatments included two independent cutting experiments with and without subsequent prescribed burning (cut-burn and cut-only, respectively), implemented either in spring or fall or under wet or dry duff moisture conditions. Specifically, we study the interannual (whole tree rings) and intra-annual (earlywood vs. latewood) variation in resin duct production along a 40-year period, covering 20 years before and after the treatments. We seek to answer:

(1) How do the different treatments affect the inter- and intra-annual production of resin duct defences? We expect to see (H1.1) higher resin duct defences in treatments relative to control and (H1.2) a relatively higher increase in earlywood than in latewood ducts;

(2) Are resin duct defences sensitive to prescribed burning? (H2.1) We expect a more pronounced response in cut-burn treatments than in cut-only treatments. Further, if the fire effect is mediated via heating stress and fire-caused injury, (H2.2) we expect a greater response in trees with intermediate crown scorch compared to low or no crown scorch;

(3) Do treatments influence the sensitivity of resin ducts to climate? (H3) We expect that treatments will reduce sensitivity of tree resin duct defences to climate by reducing tree competition that lessens drought stress.

5.2. Materials and methods

Study site and treatments

The study took place in the Lick Creek Demonstration-Research Forest, located in the Bitterroot National Forest in southwestern Montana, USA (46º5’N, 114º15’W). The site is a south-facing slope dominated by ponderosa pine (*Pinus ponderosa* var. *ponderosa* Dougl. ex Laws.) with scattered Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and its elevation ranges from 1300 to 1500 m.a.s.l. Mean maximum and minimum temperatures are 13.1 ºC and -2.7 ºC, respectively, and mean annual precipitation is 380 mm (period 1958-2017). Ponderosa pine is a widely distributed species in western North America, ranging from southwestern Canada to northern Mexico, and the primary bark beetles that affect it are western pine beetle (*Dendroctonus brevicomis* LeConte) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Smith and Arno, 1999). These native beetles are commonly associated with virulent blue-stain fungi, a group of unrelated genera of ascomycetes, that play an important role in killing the tree (Franceschi et al., 2005).

The area was first harvested in 1906 and part of it was additionally cut in 1955, 1967, and 1979 (Smith and Arno, 1999). In spring 1992, forest restoration treatments were implemented with the goals of reducing fire hazard and susceptibility to insects and diseases and improving timber production and wildlife habitat. Towards that end, efforts were directed at reducing stand density and fuels, increasing dominance of ponderosa pine, and retaining the largest, most vigorous trees. The treatments consisted of two independent cutting experiments: moderate intensity thinning from below, which promotes tree growth, and retention shelterwood, which promotes tree growth and pine regeneration. The moderate thinning, hereafter referred to as the thinning experiment, reduced basal area by 35% and tree density by 42%, while the retention shelterwood, hereafter referred to as the shelterwood experiment, reduced basal area by 57% and density by 64% (Table 5.1). Part of the thinning experiment had been last harvested in 1979 (Smith and Arno, 1999). Both experiments were divided into 12 management units of 1-2 hectares, allowing the following four treatments to be replicated three times within each experiment: a cut-only treatment, two cutting followed by prescribed burning treatments (cut-burn: spring vs. fall burn in the thinning experiment and burning under moist vs. dry duff in the shelterwood experiment), and an untreated control. Within each of the 12 units, 12 circular plots of 0.04 ha (radius 11.35 m) were established on a systematic grid to measure stand characteristics and assess tree responses.

The treated units were randomly assigned, while the untreated units were placed according to logistical needs for the prescribed burns. In the thinning experiment, prescribed burning was implemented in fall 1993 (fall-burn, 20% duff moisture content) and spring 1994 (spring-burn, 30% duff moisture content). In the shelterwood experiment, units were all burned in spring 1993, either under wet conditions (wet-burn, 50% duff moisture content) or under dry conditions (dry-burn, 16% duff moisture content) (Figure 5.1). Although both cutting experiments are density reduction treatments, they differ in environmental site conditions (the thinning treatment was on the upper slope and the shelterwood on the lower slope) and in their primary objective (promotion of tree growth vs. regeneration); thus, they are considered independent in this study and have been analysed separately. Similarly, burning treatments were implemented under different conditions in each experiment (spring vs. fall, wet vs. dry) and have also been considered separately. Further details on harvesting prescriptions and burning conditions are given in Smith and Arno (1999).

Table 5.1. Mean (SE) of stand and tree characteristics before (Pre), right after (Post-1), and 13 years after treatments (Post-13). Measurements are for all live trees > 15.24 cm dbh. Cont, untreated control.

		Thinning				Shelterwood			
		Cont	Cut-only	Spring-burn	Fall-burn	Cont	Cut-only	Wet-burn	Dry-burn
Stand density (n ha^{-1})	Pre		332 (17)	310 (16)	358 (20)		405 (30)	375 (25)	358 (24)
	Post-1	352 (22)	178 (9)	200 (10)	200 (9)	328 (23)	141 (11)	120 (9)	148 (11)
	Post-13	364 (22)	188 (9)	200 (13)	216 (11)	314 (23)	138 (11)	119 (10)	130 (10)
Stand basal area (m^2 ha^{-1})	Pre		20.6 (0.7)	18.8 (0.9)	22.4 (1.3)		28.1 (1.4)	25.2 (1.1)	25.0 (1.7)
	Post-1	23.6 (1.1)	13.0 (0.6)	13.0 (0.6)	14.2 (0.6)	25.6 (1.4)	11.9 (0.6)	10.1 (0.5)	11.7 (0.6)
	Post-13	29.9 (1.3)	17.4 (0.5)	16.8 (0.7)	18.8 (0.8)	28.5 (1.5)	15.0 (0.7)	12.5 (0.8)	13.3 (0.6)
DBH (cm)	Pre		27.1 (0.3)	26.8 (0.3)	27.2 (0.3)		28.4 (0.4)	27.7 (0.4)	28.4 (0.4)
	Post-1	28.2 (0.3)	29.3 (0.4)	27.8 (0.3)	28.9 (0.3)	30.1 (0.4)	29.5 (0.5)	29.3 (0.5)	29.9 (0.4)
	Post-13	31.0 (0.4)	33.7 (0.5)	31.4 (0.5)	32.1 (0.5)	32.3 (0.5)	35.4 (0.8)	34.4 (0.8)	34.4 (0.7)
Height (m)	Pre		16.3 (0.2)	16.1 (0.2)	16.1 (0.1)		20.3 (0.2)	18.9 (0.2)	18.0 (0.2)
	Post-1	16.2 (0.1)	16.0 (0.1)	15.6 (0.1)	16.0 (0.1)	20.4 (0.2)	21.1 (0.2)	19.7 (0.2)	18.8 (0.2)
	Post-13	18.8 (0.1)	18.7 (0.2)	17.5 (0.2)	18.0 (0.2)	23.2 (0.2)	23.9 (0.4)	21.8 (0.3)	20.8 (0.3)

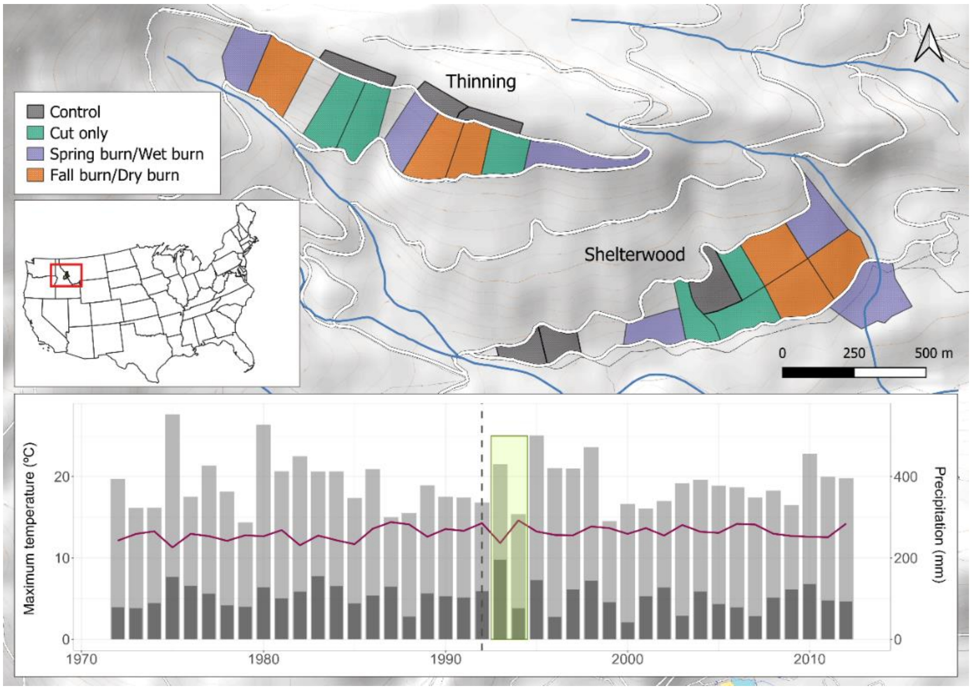


Figure 5.1. Location of the treatment units in the Lick Creek Demonstration-Research Forest in southwestern Montana, USA. The lower inset displays total annual precipitation in light grey overlaid by the total precipitation during the growing season (June through August) in dark grey, and mean annual maximum temperature from 1972 to 2012 (purple line). Vertical dashed line denotes year of cutting treatments (1992). The light-green rectangle highlights the 2 years after cutting treatments, when prescribed burns were implemented.

A number of studies have reported treatment responses at Lick Creek including studies on initial (Ayers et al., 1999; Smith and Arno, 1999) and long-term carbon responses (Clyatt et al., 2017), soil nitrogen dynamics (DeLuca and Zouhar, 2000), tree physiology (Sala et al., 2005), cone production (Peters and Sala, 2008), forest structural and fuel load responses (Hood et al., 2020a), understory vegetation (Jang et al., 2021) and tree growth, physiological activity, and mortality (Tepley et al., 2020).

Data collection

All trees larger than 15.24 cm in diameter at breast height (dbh) inside the 12 circular plots were measured in 1991 (pre-cutting) and in 1993, 2005, and 2015 (post-cutting) to estimate stand basal area and tree density. After the prescribed burning treatments, percent crown scorch was visually assessed. In 2016, 8 of the 12 circular plots per unit were randomly selected for collecting increment cores for dendrochronological analyses. Two ponderosa pine trees from each of the 8 randomly selected plots were chosen for coring: the closest large (> 25.4 cm dbh) and small (15.2 – 25.4 cm dbh) tree to the plot centre, resulting in 16 trees per unit, 48 per treatment within each experiment, and 192 trees per experiment. Two increment cores were collected from each tree on opposite sides perpendicular to the slope at a mean height of 51 cm with an increment borer of 5.15 mm diameter. Basal area increment (BAI) was calculated based on the cross-dated tree-ring width and the distance to the pith. See Tepley et al. (2020), for a detailed description of cross-dating methods and growth characterization. Climatic variables were retrieved at 4-km resolution from the TerraClimate database (Abatzoglou et al., 2018), and included monthly maximum temperature, precipitation, and the Palmer Drought Severity Index (PDSI).

Axial resin ducts

We quantified resin duct metrics on one of the two cored trees per plot, and one of the two increment cores collected from that tree, as a compromise between measurement effort and obtaining a sample size large enough to identify common patterns in resin duct defences, resulting in 8 cores per unit, 24 per treatment within each experiment, and 96 cores per experiment. To quantify resin ducts, cores were sanded using a belt sander with a progression of 120- to 400-grit, then progressively hand-polished with 40- to 9-micron polishing paper, and finally scanned at 1200 dpi. Resin ducts in the earlywood and the latewood were measured in ImageJ (version 1.8.0_112, National Institutes of Health, Bethesda, MD, USA) using the ellipse tool and adding calendar years to the measurements. We measured resin ducts formed between 1972 and 2012, to analyse a 20-year time interval before and after the treatments (1992 was designated as the treatment year since the harvests took place at that time, though the prescribed burns were conducted in 1993 and 1994). We estimated the annual earlywood, latewood, and whole ring investment in resin ducts by calculating absolute and relative to ring area metrics: duct size, duct production, and total duct area as absolute (unstandardized) metrics, and duct density and relative duct area as relative (standardized) metrics following Hood et al. (2020b). Ring area, needed to calculate the standardized resin duct metrics, was calculated as ring width x tree core diameter (5.15 mm). The latest version of the R script used to assign calendar years to ducts in both the earlywood and latewood can be found at https://github.com/jeffkane/resinduct/ (Vilà-Vilardell et al., 2024c).

Data analysis

To study the impact of cutting and prescribed burning on resin ducts, we compared the response over the 20-year intervals before and after treatments. Specifically, we evaluated the changes in duct size, duct production, total duct area, duct density, and relative duct area in response to the treatments. We chose a 20-year interval as a measure of the long-term response to management treatments.

We modelled the effect of treatments on the 20-year mean resin duct values per core of earlywood, latewood, and whole-ring resin ducts using generalized linear mixed-effects models (GLMMs). We fit separate models for both the thinning and shelterwood experiments for all duct metrics, using treatment type (categorical with four levels) and its interaction with treatment period (categorical with two levels: before and after) as fixed factors and tree as random intercept, to account for repeated measures of the same tree.

We also explored the effects of crown scorch and stand structure on whole-ring resin ducts as proxies of prescribed burning and cutting impacts, respectively. Because measures of crown scorch and stand structure were taken only in specific years, we used relative duct measurements to smooth out the extremes of individual trees in those years. Relative duct measurements were calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Crown scorch was modelled using only burned units. To model the crown scorch effect on resin ducts, we fitted models using percent crown scorch (continuous standardized) and year (categorical with two levels: Post-1 and Post-2; see below) as fixed factors and treatment type nested in experiment (thinning and shelterwood) as random intercept. As year, we used the two years following treatments (Post-1 and Post-2: 1993 and 1994, or 1994 and 1995, depending on the treatment completion date). To model the stand structure effect we fit GLMMs on the mean duct metrics per plot using stand basal area of the plot (continuous standardized), tree density of the plot (continuous standardized), and year (categorical with three levels: Pre, Post-1, and Post-13; see below) as fixed factors and treatment unit nested in treatment type and experiment (thinning and shelterwood) as random intercept, to account for dependency among observations of the same treatment unit. As year of the stand structure models, we used a before-treatment year (Pre: 1991) and two after-treatment years (Post-1: 1993 or 1994, depending on the treatment completion date; and Post-13: 2005). These two after-treatment years were the years when plots were resampled. Control plots were not sampled until 1993, but since we assume minimal changes in forest structure over two years, we used data of 1993 structure as the before-treatment structure. Model selection led to models without tree density as a covariate.

Depending on the distribution of the data, we fit Gamma, zero-inflated Gamma, or Conway-Maxwell Poisson (COM-Poisson) GLMMs with a log link function, or Gaussian GLMMs with an identity link function. We used the COM-Poisson distribution to account for underdispersed data. We used Akaike's Information Criteria (AIC) to select the best models, and when AIC < 2 we kept the most parsimonious model. Pairwise differences among treatment units were tested using least-square means, adjusting the significance level ($\alpha = 0.05$) with a Holm correction factor to account for multiple comparisons and reduce the risk of type I errors. The differences between resin duct measurements before and after treatments separately for both earlywood and latewood were also assessed using pairwise comparisons with a Holm correction factor. Model assumptions were verified ensuring the absence of residual patterns by plotting residuals versus fitted values and each covariate (Zuur and Ieno, 2016). All analyses were done using R v.4.3.1 (R Core Team, 2023), including *lme4* v.1.1-34 (Bates et al., 2015), *glmmTMB* v.1.1.7 (Brooks et al., 2017), *DHARMa* v.0.4.6 (Hartig, 2022), and *emmeans* v.1.8.8 packages (Lenth, 2023).

Finally, we explored the sensitivity of resin duct defences to climate before and after treatments. Climate-defence relationships were assessed by treatment unit, treatment period (pre and post), and cutting experiment separately (n = 20) with Pearson's correlation analyses between resin duct measurements and monthly maximum temperature and precipitation, using *treeclim* R package v.2.0.6.0 (Zang and Biondi, 2015). Correlation analyses were conducted separately for earlywood, latewood, and whole ring measurements from September of the previous year to August of the current year. Confidence intervals were bootstrapped to test for significant correlations ($\alpha = 0.05$). Because correlations consisted of a 20-year interval, we relied upon the principle of uniformity, assuming that the statistical relationship between resin duct measurements and the climate variable is stable over time. This principle has been discussed in dendrochronology for many years, particularly in climate reconstruction studies (Peltier and Ogle, 2020; Wilmking et al., 2020), yet the time interval in our analysis is relatively short compared to these studies. In the following sections, the term "treatment year" refers to the year of the harvests (1992) unless explicitly clarified, even though the prescribed burns were conducted over 1993 and 1994. Because duct size and total duct area are correlated with resin flow in ponderosa pine (Hood and Sala, 2015), and the focus of this study is consequences of forest management on resin ducts as a proxy for defence, for simplicity, we chose to focus primarily on these metrics in the results section. Results of the other metrics are reported in Appendix S5.1, S5.2, and S5.3.

5.3. Results

Resin ducts responses to cutting and prescribed burning

After treatments there was an increase in duct production and duct area that lasted throughout the 20-year analysis (Figure 5.2). During this period, both metrics were 2-fold higher in the treated units compared with the control ($p < 0.05$; Figure 5.4, Figure S5.1). In the thinning experiment, ducts of treated trees were on average 27% larger than ducts of control trees, while in the shelterwood experiment, only ducts in the cut-only and wet-burn units were larger, by 17% ($p < 0.01$; Figure 5.4). All unstandardized metrics (i.e., size, total area, and production) tended to decline over time in the control units of both experiments (Figure 5.2). Duct density and relative duct area in the treated units of the shelterwood experiment exhibited a spike following treatments (Figure 5.3), particularly in the earlywood (EW) in the dry-burn units, but also in the wet-burn ones (Figure S5.6, Figure S5.7). Thereafter, they gradually decreased, reaching similar levels to those of the control trees four years after the cutting treatments. A similar, but smaller peak in duct density and relative duct area was observed in the fall-burn units of the thinning experiment (Figure 5.3). The variance explained by fixed factors alone (R^2m) was relatively low, ranging from 3 to 22% (Figure 5.4, Figure S5.1, Table S5.1 to S5.10), indicating that treatments and period contributed moderately to the interannual variation in resin ducts, and that a greater proportion was explained by variation within the tree itself (R^2c, ranging from 37 to 87%).

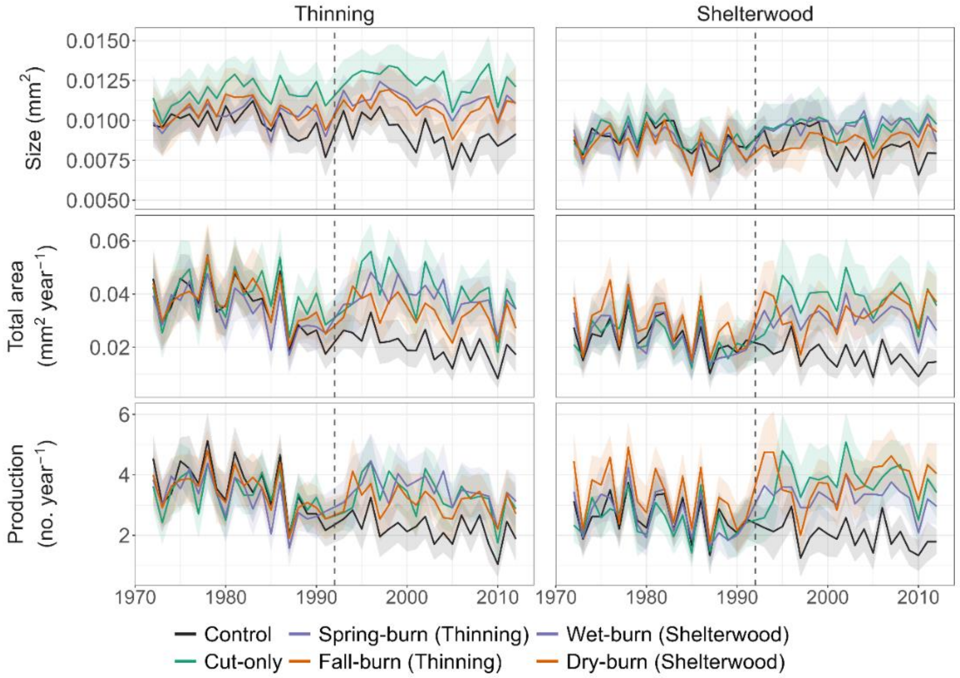


Figure 5.2. Mean annual variation of duct size, total duct area, and duct production in the whole ring by experiment. Shaded areas represent the 95 % confidence interval. N = 192 trees were analysed across the period 1972–2012. The vertical dashed line denotes year of cutting treatments (1992).

Differences between earlywood and latewood duct responses

Treatments had a comparatively smaller effect on latewood (LW) resin ducts compared to EW ducts in the shelterwood experiment for all metrics but size (Figure 5.5, Figure S5.2). Control units had smaller ducts that occupied a smaller portion of the EW and LW after treatments in both experiments. Average EW and LW duct size was larger in the cut-only and in the spring-burn or wet-burn units after treatments ($p < 0.05$; Figure 5.5). Average total duct area did not change after treatments in the thinning experiment, but it increased in the EW of all treated units ($p < 0.05$) and in the LW of the cut-only units ($p < 0.001$) of the shelterwood experiment (Figure 5.5).

Resin duct sensitivity to crown scorch and stand structure

Crown scorch had little impact on resin duct responses, explaining less than 9% of the total variance in relative duct size and total area (Figure 5.6a, Table S5.16).

Stand basal area was negatively related to duct size before and 13 years after treatments (Post-13). Immediately after treatments (Post-1), duct size did not change with basal area. Post-1 ducts were larger than both the pre-treatment and the Post-13 ducts, especially in the units where stand basal area was high ($p < 0.01$; Figure 5.6b). Total duct area was not related to stand basal area before treatments; however, their relationship became increasingly negative over time. Thirteen years after treatments (Post-13), greater duct area was observed in units with lower stand basal area ($p < 0.01$, significant Post-13 x stand basal area interaction; Figure 5.6b). However, the variance in resin ducts explained by stand basal area is relatively small ($R^2c < 0.19$) (Table S5.17).

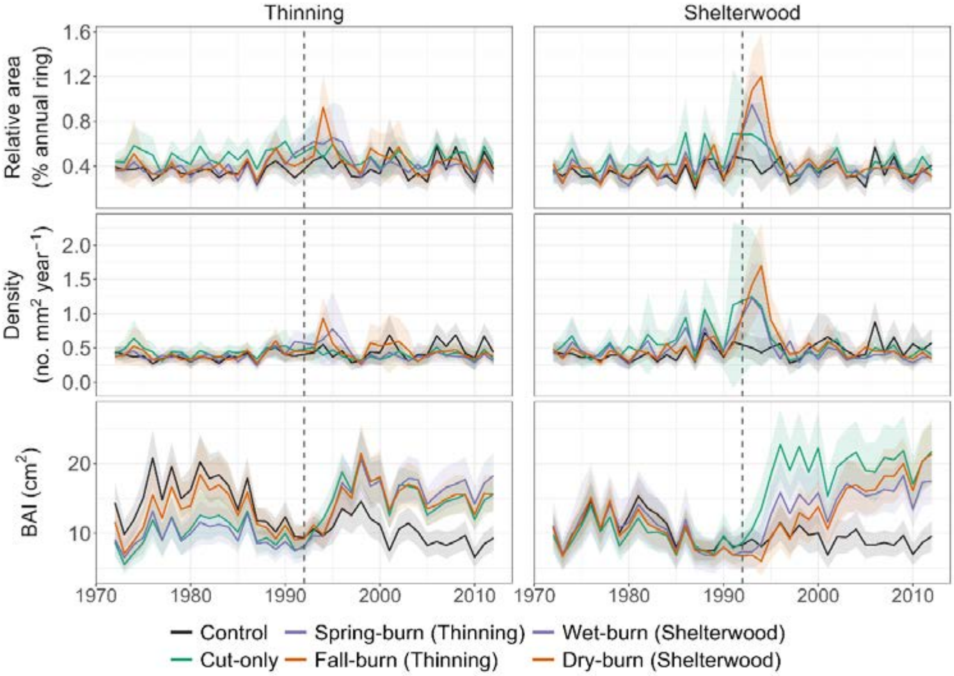


Figure 5.3. Mean annual variation of relative duct area, duct density, and basal area increment (BAI) in the whole ring by experiment. Shaded areas represent the 95 % confidence interval. N = 192 trees were analysed across the period 1972–2012. Vertical dashed line denotes year of cutting treatments (1992).

Relationships between climate and defences

The correlation between duct defences and climate did not show any trend linked to treatment type (Figure 5.7). Winter precipitation was positively correlated with duct size and total duct area before and after treatments in treated and control units of both experiments; yet the correlation with total duct area was weaker in virtually all units during the post-treatment period. Similarly, but in the opposite direction, mid-spring to mid-summer maximum temperature was more strongly negatively correlated with duct defences before than after treatments in treated and control units of both experiments. Additionally, July precipitation and maximum temperature were positively and negatively correlated with duct size, respectively, mostly at the latewood (LW) ducts and weaker after treatments, particularly in the treated units of the shelterwood experiment (Figure S5.8). Similarly, the positive and negative correlation of April precipitation and maximum temperature with total duct area before treatments, respectively, became weaker after treatments (Figure 5.7).

5.4. Discussion

Forest restoration treatments aimed at shifting structure and composition towards historical levels and increasing resistance to high-severity wildfires, may also have the additional benefit of boosting tree resistance to bark beetles. Our findings show that cutting and burning treatments increased resin duct defences and that this response lasted for at least 20 years (H1.1 accepted; Figure 5.2). Thus, they provide insight into the mechanism driving the increased resistance to the mountain pine beetle outbreak that impacted the Lick Crick area from 2011 to 2014 (Martin, 2024), where tree mortality in treated units was less than half that in control units (Tepley et al., 2020). The greatest increase in resin duct defences was observed in the earlywood of the shelterwood experiment (H1.2 accepted; Figure 5.5). Cut-burn and cut-only treatments induced a similar increase in resin duct defences in the long run (H2.1 rejected; Figure 5.4). Yet, the addition of prescribed burning led to a short-term increase in resin duct defences compared with cut-only and control treatments, particularly in the shelterwood experiment (Figure 5.3). However, this increase in the burned units was not associated to the degree of tree crown scorch (H2.2 rejected, Figure 5.6a).

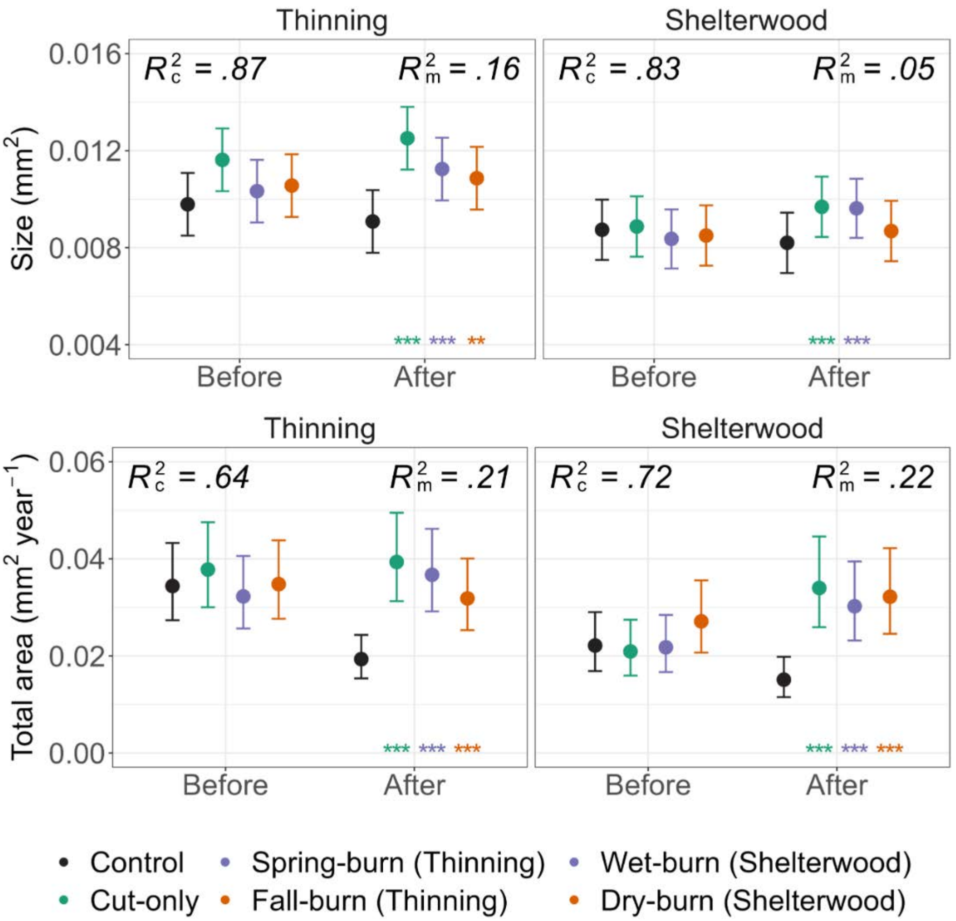


Figure 5.4. Estimated marginal means and confidence intervals (95 %) of the mixed-effects models for duct size and total duct area in the whole ring using the mean value of a 20-year interval before and after treatments. Marginal (R^2m) and conditional (R^2c) variance of the models and significance ($^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$) of the estimated marginal means relative to control units ($\alpha < 0.05$).

Stand density reduction stimulates resin duct investment

Trees in the shelterwood experiment (57% basal area reduction) experienced the greatest increase in resin duct area (Figure 5.2) along with the greatest growth release (Figure 5.3). In the thinning experiment (35% basal area reduction), treatments stabilized duct area, in contrast to the decrease observed in the untreated control units. Greater resin duct defences in treated units relative to control persisted for at least 20 years following treatments in both experiments, in agreement with our hypothesis (H1.1; Figure 5.4). Yet, contrary to our hypothesis

H2.1, no differences in resin duct investment between cut-only and cut-burn units were observed. This result aligns with those reported by Tepley et al. (2020) and Sala et al. (2005) at the same study site in Lick Creek, who found that the physiological differences among treatments were small relative to the physiological differences between treatments and control.

The increase in resin duct investment following cutting with or without subsequent prescribed burning may be attributed to the favourable conditions created by the reduction in stand density and tree competition (Bernal et al., 2023; Hood et al., 2016). The greater availability of resources for trees likely resulted in increased photosynthetic rate and stomatal conductance (Sala et al., 2005) and consequently, in more carbon to invest in both growth (Tepley et al., 2020) and defences (Hood et al., 2016) in the long term. The increase in resin ducts was probably also influenced by the fact that both cutting experiments retained the most vigorous trees. However, resin ducts often show contrasting responses in different studies, including a decline in trees growing under favourable conditions (Vázquez-González et al., 2020a) and a slightly positive correlation between tree competition (i.e., unfavourable conditions) and resin duct area (Slack et al., 2017), suggesting variability in response to site productivity and resource availability in the different studies.

We found a positive response of duct size to treatments, yet in different directions depending on the cutting experiment: ducts became larger in treated units of the thinning experiment, did not change in treated units of the shelterwood, and became smaller in control units of both experiments (Figure 5.2). Smaller ducts in control units may be associated with the long-term, cumulative effect of high competition (Slack et al., 2017). Duct size and duct area are correlated to resin flow (Hood and Sala, 2015), and resin flow is related to the chances of surviving a bark beetle attack (Perrakis et al., 2011). Therefore, changes in duct size and total area after treatments likely explain the observed low mortality rates in the treatments of both experiments relative to the controls during the 2011-2014 mountain pine beetle outbreak, as reported in Tepley et al. (2020) and consistent with Hood et al. (2016), who reported higher total duct area and lower mountain pine beetle-caused mortality in thinned treatments.

Earlywood resin ducts are more sensitive to treatments than latewood ducts

Our findings illustrate the greater sensitivity of earlywood (EW) ducts to treatments, particularly in the shelterwood experiment (Figure 5.5, Figure S5.2), in agreement with our hypothesis (H1.2). These changes may be relevant for increased resistance to bark beetles, as timing of EW xylem production in late-spring through mid-summer (Ziaco et al., 2018) coincide with the timing of western pine beetle (Gaylord et al., 2006) and mountain pine beetle flight (Jackson et al., 2008). However, despite remaining active for years (Hudgins and Franceschi, 2004), it is unknown if recently formed ducts contribute more to resin flow than older ducts or whether there are functional differences between EW and LW ducts. Hood and Sala (2015) found positive, but slightly weaker correlations between resin flow and 10-year average duct size and total duct area than between resin flow and 5-year averages, suggesting a decline in resin flow with resin duct age.

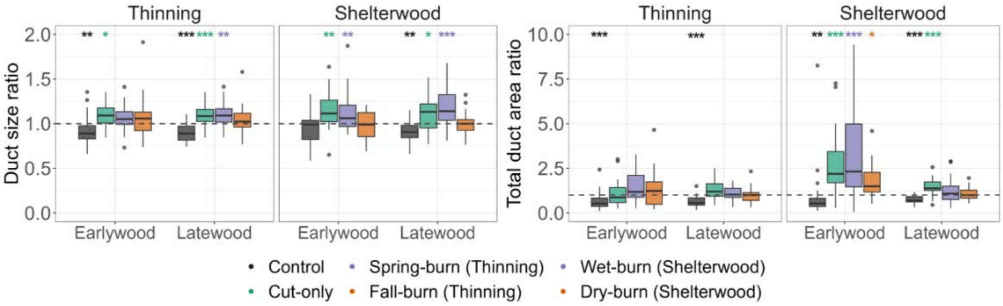


Figure 5.5. Mean departure from average duct size and total duct area in earlywood and latewood, calculated for each tree as the ratio between the 20-year core average after treatments and the 20-year core average before. Significance (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) of the estimated marginal means relative to pre-treatments ($\alpha < 0.05$). The horizontal dashed line denotes no departure from pre-treatments 20-year core average, above denotes increase, and below, decrease.

Although before treatments most of the resin ducts were synthesized in the latewood (LW), treatments led to a shift in the relative proportion between EW and LW ducts, with the exception of duct size, which was the only metric that changed proportionally in both EW and LW following treatments. Prior to treatments, higher density of resin ducts in LW can be explained by the harsher environmental conditions and limited availability of resources experienced by plants during LW formation. According to the growth-differentiation balance hypothesis (GDBH), when resources are limited, growth is more constrained than photosynthesis, leading to a larger relative allocation of carbon to defences than when resources are abundant (Herms and Mattson, 1992). For example, factors such as high vapor pressure deficit and low soil moisture later in the growing season induce water stress and promote differentiation processes, leading to a greater relative investment in defences in LW (Saracino et al., 2017). While we did not explicitly test the GDBH, our results support its predictions, with higher investments in growth and ducts in the EW and increased ducts in the LW in the density reduction treatments. After treatments, higher relative proportion of resin ducts in the EW of the shelterwood experiment may be attributed to an increase in resource availability as suggested by Rigling et al. (2003), who found greater proportion of ducts in the EW of irrigated trees. Our findings are consistent with Tepley et al. (2020) results based on carbon isotope discrimination, who observed that treatments enhanced carbon assimilation in ponderosa pine early in the growing season when water is available, but also allowed continued assimilation late in the growing season under more severe water stress. Higher photosynthesis early in the growing season may allow both growth and resin duct production.

Burning after cutting induces a short-term increase in resin duct investment

Although stand density reduction had a greater effect in resin defences in the long term, prescribed burning stimulated a sharp, but short-term increase in resin ducts. Burning after cutting triggered a short-term increase in earlywood (EW) resin duct density and relative duct area in both experiments, but especially in the shelterwood (Figure 5.3, Figure S5.6, Figure S5.7), where the increase of resin ducts stimulated by the fire preceded the growth release caused by cutting. The increase in resin duct production began immediately after treatments, while the increase in growth rate (i.e., BAI) began two years after and reached its peak at year three or four. An immediate response of resin ducts and delayed response in the growth of ponderosa pine after cutting and burning treatments was also reported by Hood et al. (2016).

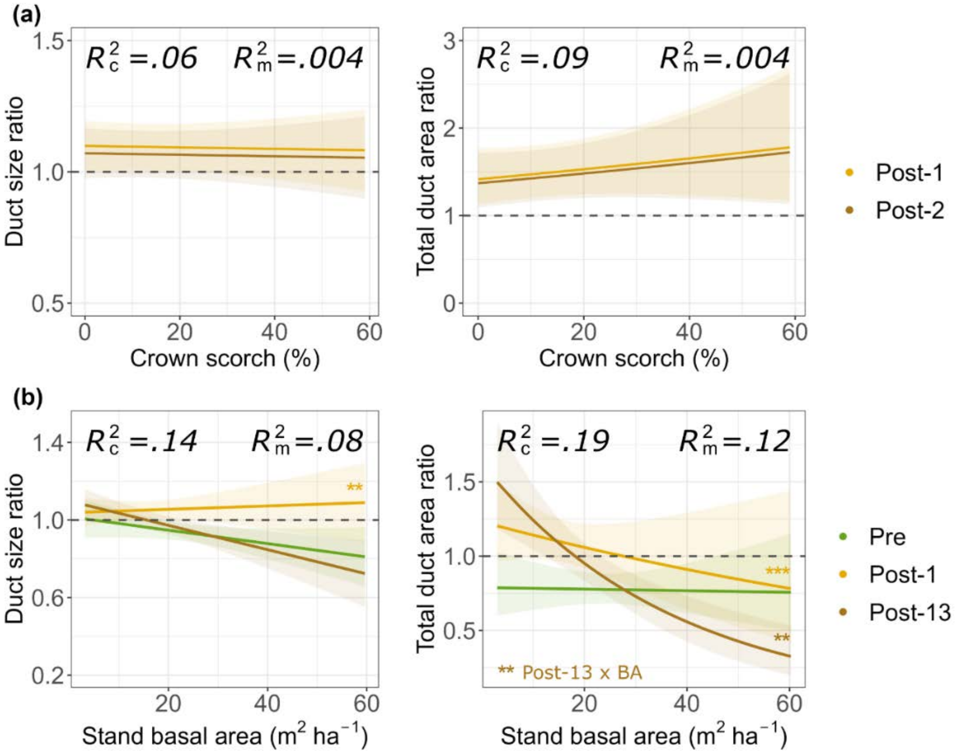


Figure 5.6. Mixed-effects models of whole ring relative duct metrics as a function of (a) crown scorch and (b) stand basal area. Relative duct metrics were calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Crown scorch models were fit using only the burned units for the two years following prescribed burning (Post-1 and Post-2). Stand basal area models were fit in all units before (Pre), right after (Post-1), and 13 years after treatments (Post-13). Shaded areas represent the 95 % confidence interval. Marginal (R^2m) and conditional (R^2c) variance of the models and significance (*p<0.05; **p<0.01; ***p<0.001) of the estimated marginal means comparing resin ducts following treatments to pre-treatments are shown ($\alpha < 0.05$). Horizontal dashed line denotes no departure from pre-treatments 20-year core average, above denotes increase and below, decrease.

Low-intensity fire stimulates resin flow (Cannac et al., 2009b; Knebel and Wentworth, 2007; Lombardero and Ayres, 2011) and the effect can last for up to 4 years (Perrakis et al., 2011). The increase in resin flow occurs within days to weeks, likely via upregulation of resin synthesis in existing ducts, and it persists as new resin ducts are formed and become functional (Hood et al., 2015). However, an increase in the number of ducts after fire does not always translate into higher resin flow (Rodríguez-García et al., 2018), and more research is needed to understand the fire intensity required to elicit resin flow responses. Increases in resin production in pines after low-intensity fire likely aids in compartmentalization of fire-killed cambium (Verrall, 1938; Wallin et al., 2004) and in resisting post-fire bark beetle attacks (Hood et al., 2015; Valor et al., 2021), both of which increase tree survival.

While prescribed fire stimulated resin duct synthesis in the short term, crown scorch explained only a limited amount of the variation in resin ducts (Figure 5.6a), contrary to our hypothesis (H2.2). Our results agree with Sparks et al. (2017), who found no clear correlation between fire intensity and resin duct responses following prescribed burning, with fires of a wide range of intensities increasing duct production, total duct area, and duct size. Resin flow is inversely related to crown scorch after fire (Lombardero and Ayres, 2011), particularly in cases of severe scorch (75%; Wallin et al., 2003) due to a reduction in the photosynthetic capacity of the tree (Valor et al., 2018). In our study area, most trees exhibited < 25% crown scorch, with almost all falling below 50%. Low-intensity fire mostly affects the lower-crown foliage, and these levels of lower foliage loss are likely insufficient to significantly affect the photosynthetic rate (Gomez-Gallego et al., 2020) and, consequently, the synthesis of resin defences. Additionally, ponderosa pine buds can survive if the temperature that reaches the surrounding needles is enough to scorch but not to consume the foliage (Fowler et al., 2010), in which case, the buds flush new needles that contribute to post-fire recovery (Reed and Hood, 2024). The narrow range of observed crown scorch in our study limits our ability to test its effects on resin duct responses and additional research is needed.

The spike in resin duct synthesis was especially evident in the EW of trees in the shelterwood experiment (Figure S5.6, Figure S5.7), particularly within the dry-burn units, which burned under the driest moisture conditions. Prescribed burning in the shelterwood experiment was applied in spring of 1993 (before the second growing season following the cutting treatments), while in the thinning experiment it was applied in fall of 1993 and spring of 1994 (before the third growing season following the cutting treatments). The difference in response to prescribed burning between the two experiments could be partly explained by the substantially different weather patterns during the years following the cutting treatments: 1993 was a notably wet year, particularly during the growing season (PDSI = 3.0), with below-average maximum temperature (Figure 5.1). In 1994, the situation was quite the opposite, as it was a dry year with warm, dry conditions during the growing season (PDSI = -4.9), and the maximum temperature was higher than the average, causing high evaporative demand and stress for the trees. In brief, the growing season following prescribed burning in the shelterwood was an unusually wet season, while in the thinning experiment it was an unusually dry season.

Besides differences in weather conditions, prescribed burning in the thinning experiment was conducted in fall of 1993 and spring of 1994, meaning that the trees had two full growing seasons to respond to the thinning before showing additional responses to the burning treatments. The earlier growth response to reduced competition could have masked the spike in duct density and relative area stimulated by the burning treatments. We observed a delay in tree growth during the two years after the treatments that could be explained because trees first invest in increasing leaf area index with new foliage and buds (i.e., larger crown) and in new roots. A larger crown allows for an increase in the photosynthetic capacity and carbon assimilation that can eventually be allocated to growth (Waring and Pitman, 1985). Yet, immediately after cutting treatments, trees may already benefit from increased resource availability. The unusually wet year that followed cutting might have allowed trees to not only invest in new foliage but also in defences. Additionally, a short-term increase in soil nitrogen content immediately following prescribed burning treatments (DeLuca and Zouhar, 2000) could increase photosynthetic rates and thus, resin duct production (Mason et al., 2019). Considering that resin ducts remain functional for several years after their synthesis (Hudgins and Franceschi, 2004), the current investment in anatomical defences is expected to provide defences in the future. However, for how long and whether older resin ducts can produce the same volume of resin as the new ducts remains uncertain.

Dry-burn and fall-burn units, the units that burned under drier conditions, in the shelterwood and the thinning experiment, respectively, were the ones with the greatest spike in resin ducts. This could indicate a stronger stress response under higher fire intensity, which would be consistent with the increase in resin ducts observed after wildfire but not necessarily after prescribed burning (Hood et al., 2015, 2016). However, the fact that burning treatments were not implemented under consistent conditions (spring vs. fall and moist vs. dry) limits our ability to draw conclusions.

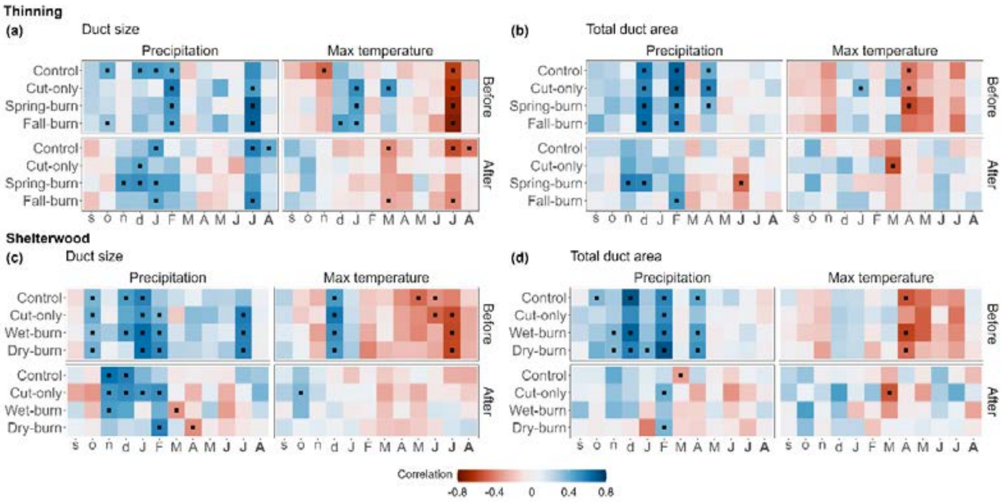


Figure 5.7. Pearson correlation coefficients between monthly precipitation and maximum temperature and duct size (a, c) or total duct area (b, d) in the whole ring, 20 years before and after treatments for the thinning (a, b) and the shelterwood (c, d) experiments. Tiles marked with a dot denote significant correlation (α < 0.05) using regular bootstrapping. Months in lowercase letters correspond to previous year and capital letters to current year (September previous year to August current year); months in bold denote the growing season.

Treatments have a minor impact on climate-defence relationships

Treatments did not influence the sensitivity of resin ducts to climate (Figure 5.7), contrary to our third hypothesis (H3). Resin duct investment seemed to be less sensitive to climate after treatments, yet there was a different range of weather conditions over the 20-year intervals before and after treatments, characterized by a decline in annual precipitation and a rise in temperature, and a 20-year window may be too short to quantify statistically significant changes in the response to climate. Winter precipitation was positively correlated to duct defences. These findings align with those reported for longleaf pine (*Pinus palustris*) (Slack et al., 2016) but differ from those reported for whitebark pine (*Pinus albicaulis*) (Kichas et al., 2020) or Bosnian pine (*Pinus leucodermis*) (Saracino et al., 2017), which might be explained by the different environments in which these pines grow: ponderosa and longleaf pine in moisture-limited environments, while whitebark and Bosnian pine in energy-limited environments near the treeline where precipitation is abundant. In moisture-limited environments, trees use water originating from winter precipitation even in the peak of summer (Martin et al., 2018). The generally positive correlation between winter precipitation and duct defences in all units before and after treatments may be partially explained by the also positive correlation between winter precipitation and latewood (LW) growth found by Tepley et al. (2020), as more LW growth leads to a generally greater investment in duct defences.

The reduced sensitivity following treatments observed in both treated and untreated trees indicates that changes in climate-defence relationships cannot be attributed to the treatments but to weather pattern changes. Trends towards less snowfall and earlier beginning of the growing season have been documented in western United States (Knowles et al., 2006; Stewart et al., 2005). Indeed, we observed that the negative correlation between spring maximum temperature and duct area moved from April, before treatments, to March, after treatments (Figure 5.7), which we attributed to the increasing trend in March maximum temperature over the 40-year period analysed, leading to an earlier snowmelt. We found slightly different responses to climate between EW and LW duct investment (Figure S5.8 to S5.12), which could be explained because they are produced asynchronously, and sensitivity of resin duct production to weather conditions may change.

5.5. Conclusions

Our findings highlight the additional benefits of forest restoration treatments primarily aimed at mitigating high-severity fire in also boosting resistance to bark beetle outbreaks. Previous research showed that cutting with or without subsequent prescribed burning stimulates resistance to drought and reduces tree mortality during a mountain pine beetle outbreak (Tepley et al., 2020). Here, we further established that these restoration treatments increase resistance to bark beetles by inducing the production of resin ducts, providing a mechanism for the observed reductions in beetle-caused mortality during the 2011-2014 mountain pine beetle outbreak. Our results showed that density reduction treatments stimulated a long-term, sustained increase in resin duct production, thereby providing long-term benefits for mitigating future outbreaks (Hood et al., 2016). Additionally, when cutting was followed by prescribed burning it triggered a short-term increase in resin ducts. This spike was especially evident in the lower residual basal area shelterwood treatment, where prescribed burning was implemented right before a particularly wet growing season. Given that these ducts remain functional for several years, the investment likely bolsters the resistance of fire-injured trees to bark beetle pressure, which often temporarily increases after low and mixed-severity fires (Davis et al., 2012; Powell et al., 2012). Overall, our findings confirm that trees are better prepared to resist bark beetle attacks after density reduction treatments when trees experience faster growth rates. Moreover, the short-term positive effect of prescribed burning should be taken into consideration when planning management actions, as prescribed burning is usually repeated at regular intervals to ensure that its primary objective, fire hazard reduction, is maintained. Future climatic changes will likely increase the frequency and intensity of coupled disturbances such as drought episodes and pest outbreaks, and forest treatments that reduce tree density are key in promoting tree adaptation to the anticipated harsher conditions.

Acknowledgments

This work was funded by the European Research Council Horizon 2020 program (DecisionES, 101007950 - H2020-MSCA-RISE-2020) and by the Spanish Ministry of Science and Innovation (FPI to LVV, PRE2019-089518). Funding from the Joint Fire Science Program under project JFSP 15-1-07-30 allowed increment core collection. We would like to thank Charlotte Reed for providing advice on resin duct analysis.

5.6. Supplementary material

Appendix S5.1. Duct production, relative duct area, and duct density estimated marginal means and mean departure from average

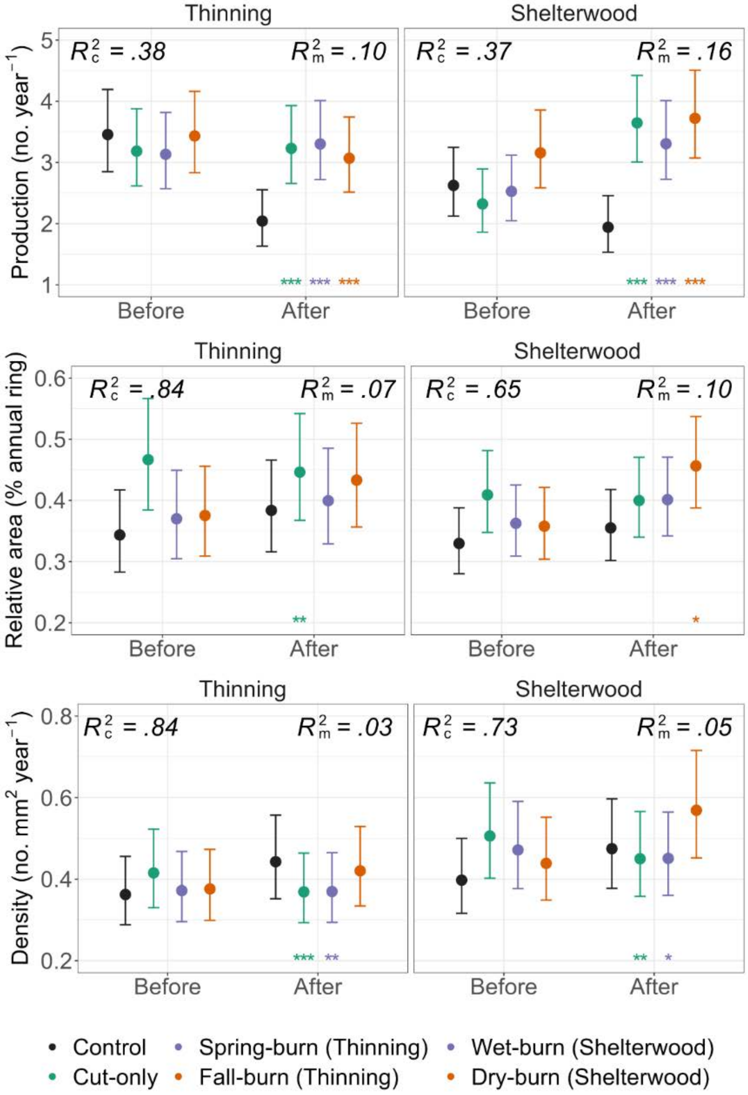


Figure S5.1. Estimated marginal means and confidence intervals (95%) of the mixed-effects models for duct production, relative area, and density in the whole ring using the mean value of a 20-year interval before and after treatments. Marginal (R^2m) and conditional (R^2c) variance of the models and significance (**p*<0.05; ***p*<0.01; ****p*<0.001) of the estimated marginal means relative to control units (α < 0.05).

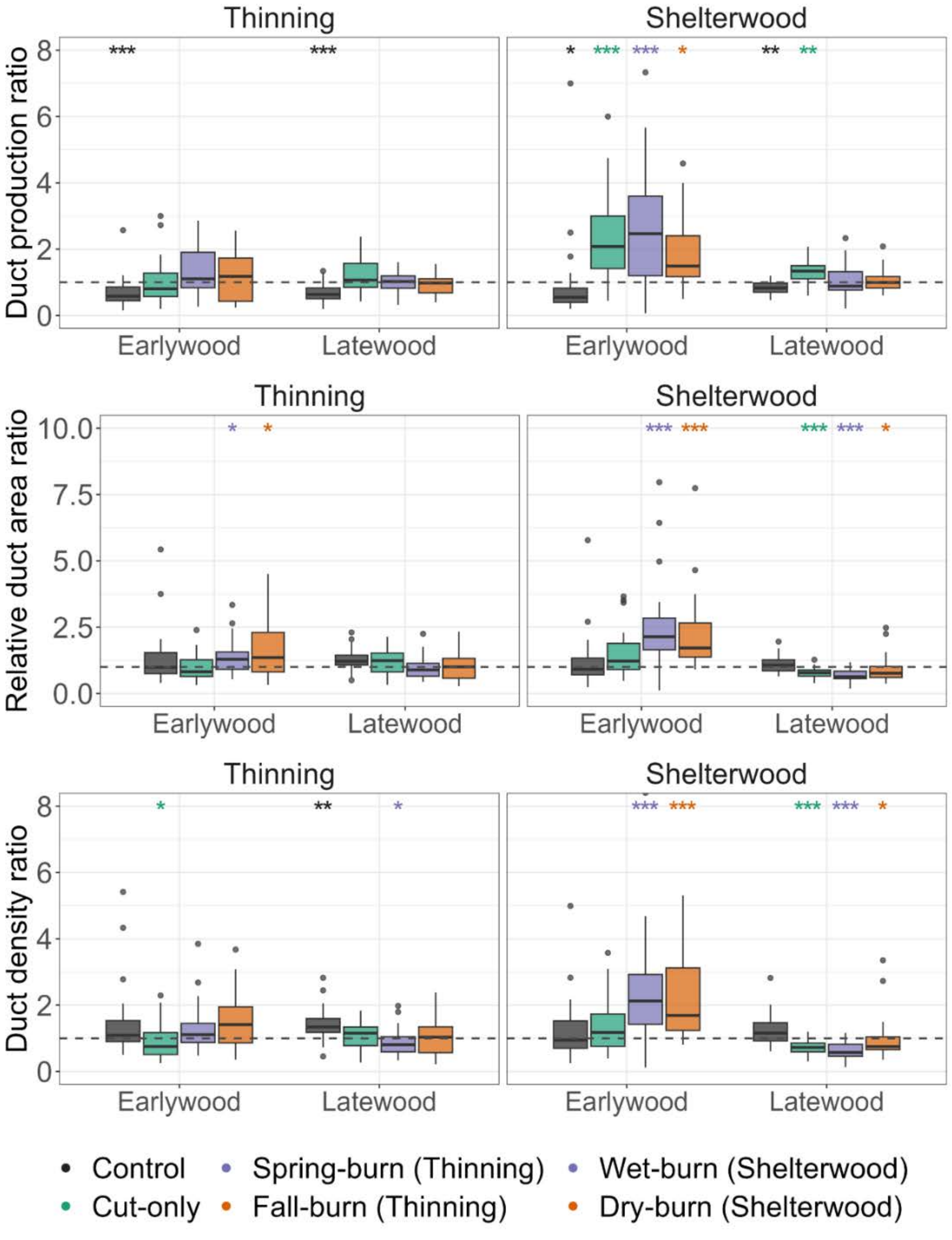


Figure S5.2. Mean departure from average duct production, relative area, and density in earlywood and latewood, calculated for each tree as the ratio between the 20-year core average after treatments and the 20-year core average before. Significance (**p*<0.05; ***p*<0.01; ****p*<0.001) of the estimated marginal means relative to pre-treatments ($\alpha < 0.05$). The horizontal dashed line denotes no departure from pre-treatments 20-year core average, above denotes increase and below, decrease.

Appendix S5.2. Mean annual variation and mean departure from average resin duct metrics and basal area increment

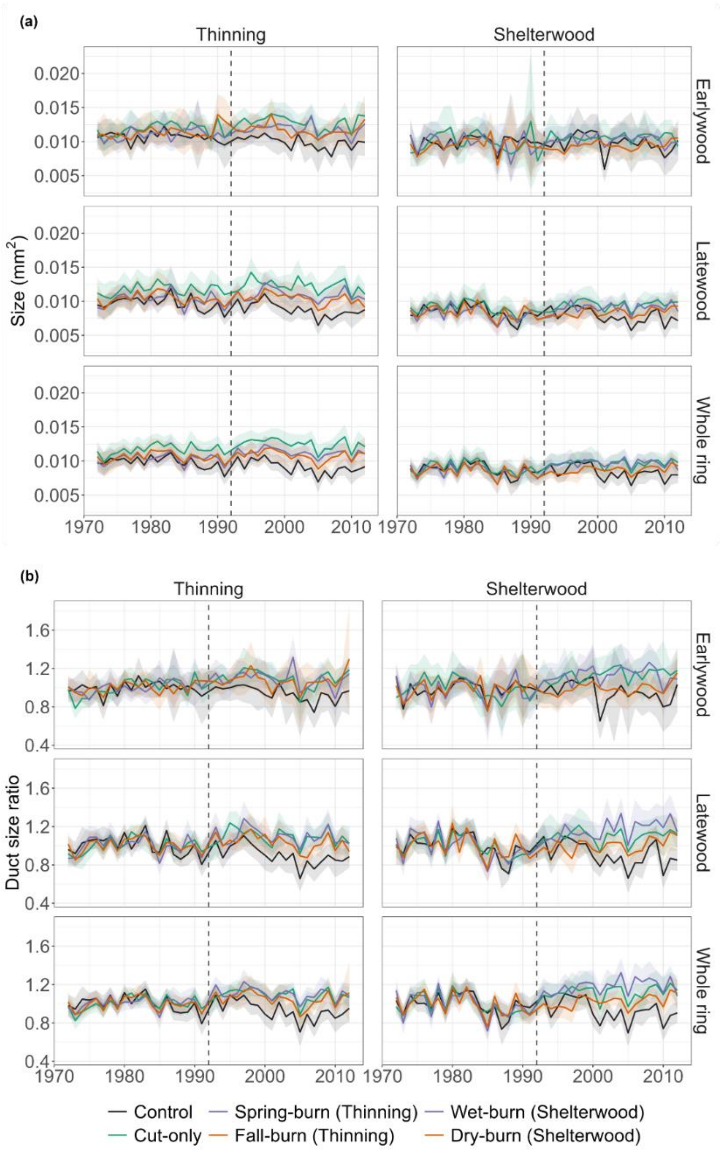


Figure S5.3. (a) Mean annual variation of duct size and (b) mean departure from average duct size in the earlywood, latewood, and whole ring by experiment. Mean departure was calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Shaded areas represent the 95% confidence interval. N = 192 trees were analysed across the period 1972-2012. The vertical dashed line denotes year of cutting treatments (1992). The horizontal dashed line in (b) denotes no departure from 40-year core average, above denotes increase and below, decrease.

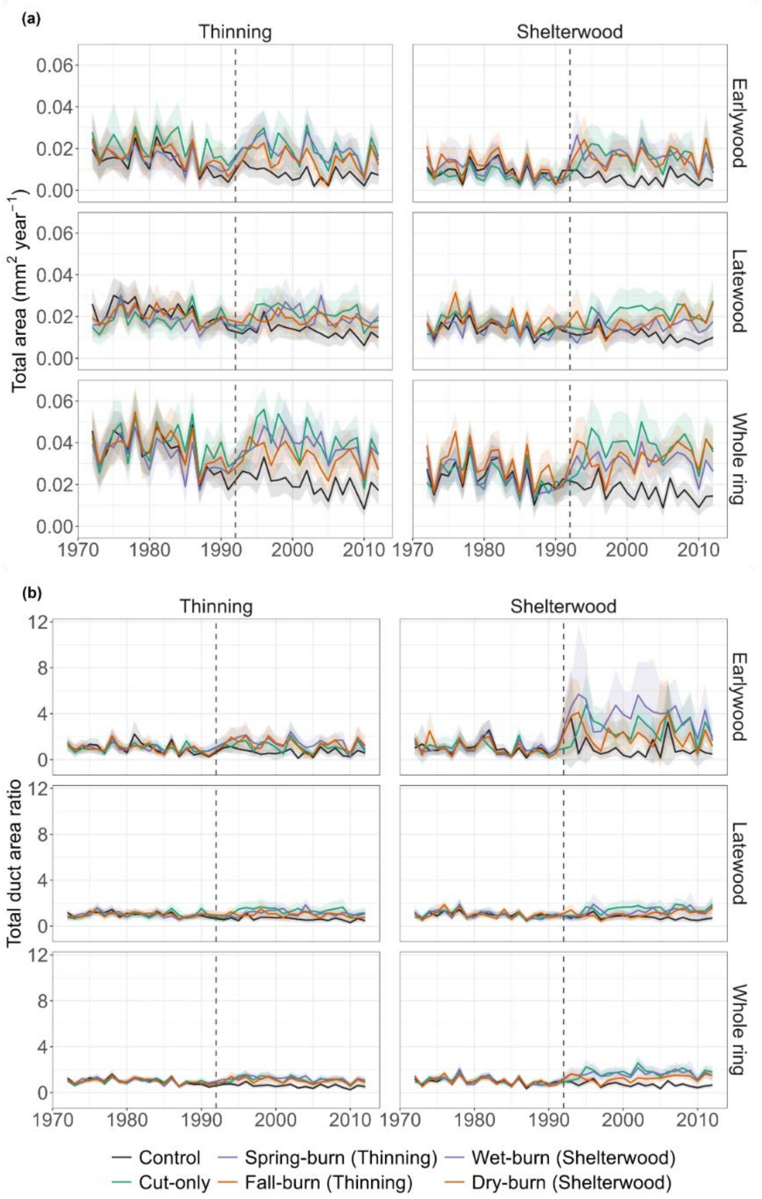


Figure S5.4. (a) Mean annual variation of **total duct area** and (b) mean departure from average duct area in the earlywood, latewood, and whole ring by experiment. Mean departure was calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Shaded areas represent the 95% confidence interval. N = 192 trees were analysed across the period 1972-2012. The vertical dashed line denotes year of cutting treatments (1992). The horizontal dashed line in (b) denotes no departure from 40-year core average, above denotes increase and below, decrease.

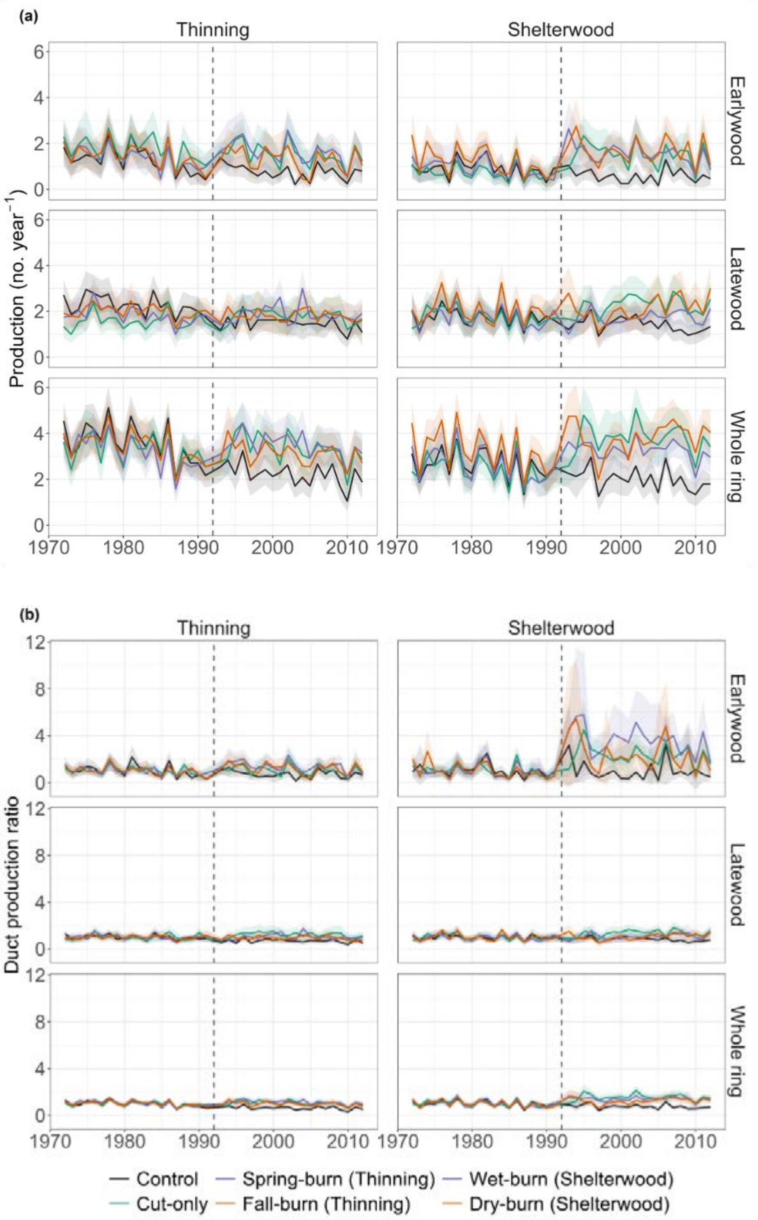


Figure S5.5. (a) Mean annual variation of **duct production** and (b) mean departure from average duct production in the earlywood, latewood, and whole ring by experiment. Mean departure was calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Shaded areas represent the 95% confidence interval. N = 192 trees were analysed across the period 1972-2012. The vertical dashed line denotes year of cutting treatments (1992). The horizontal dashed line in (b) denotes no departure from 40-year core average, above denotes increase and below, decrease.

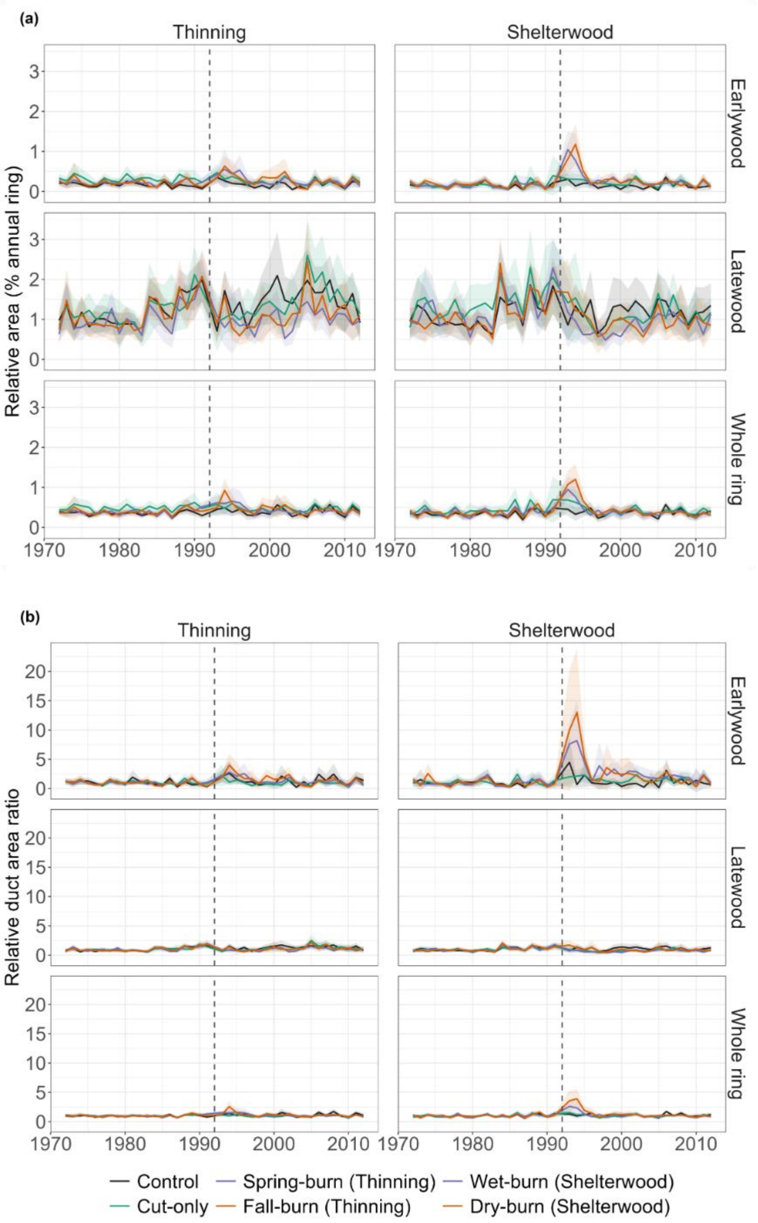


Figure S5.6. (a) Mean annual variation of **relative duct area** and (b) mean departure from average relative duct area in the earlywood, latewood, and whole ring by experiment. Mean departure was calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Shaded areas represent the 95% confidence interval. N = 192 trees were analysed across the period 1972-2012. The vertical dashed line denotes year of cutting treatments (1992). The horizontal dashed line in (b) denotes no departure from 40-year core average, above denotes increase and below, decrease.

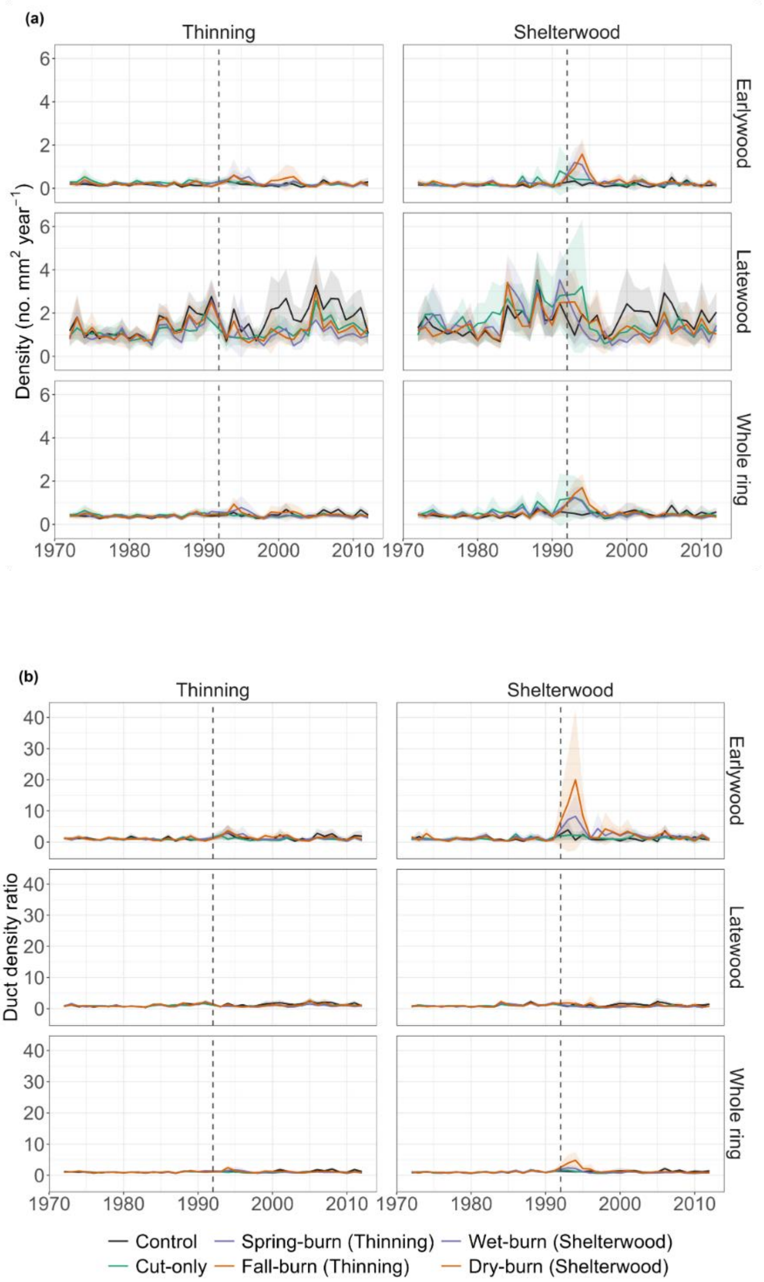


Figure S5.7. (a) Mean annual variation of **duct density** and (b) mean departure from average duct density in the earlywood, latewood, and whole ring by experiment. Mean departure was calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Shaded areas represent the 95% confidence interval. N = 192 trees were analysed across the period 1972-2012. The vertical dashed line denotes year of cutting treatments (1992). The horizontal dashed line in (b) denotes no departure from 40-year core average, above denotes increase and below, decrease.

Appendix S5.3. Climate-defense relationships

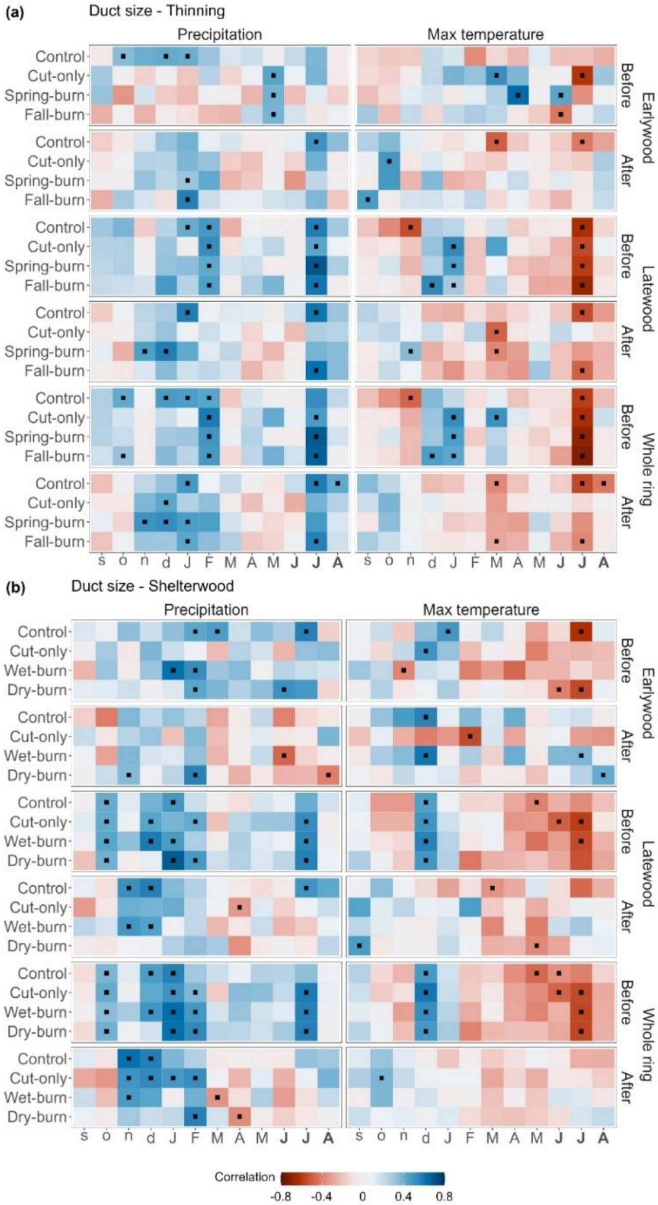


Figure S5.8. Pearson correlation coefficients between monthly precipitation and maximum temperature and **duct size** in the earlywood, latewood, and whole ring, 20 years before and after treatments for the (a) thinning and the (b) shelterwood experiment. Tiles marked with a dot denote significant correlation (α < 0.05) using regular bootstrapping. Months in lowercase letters correspond to previous year and capital letters to current year (September previous year to August current year); months in bold denote the growing season.

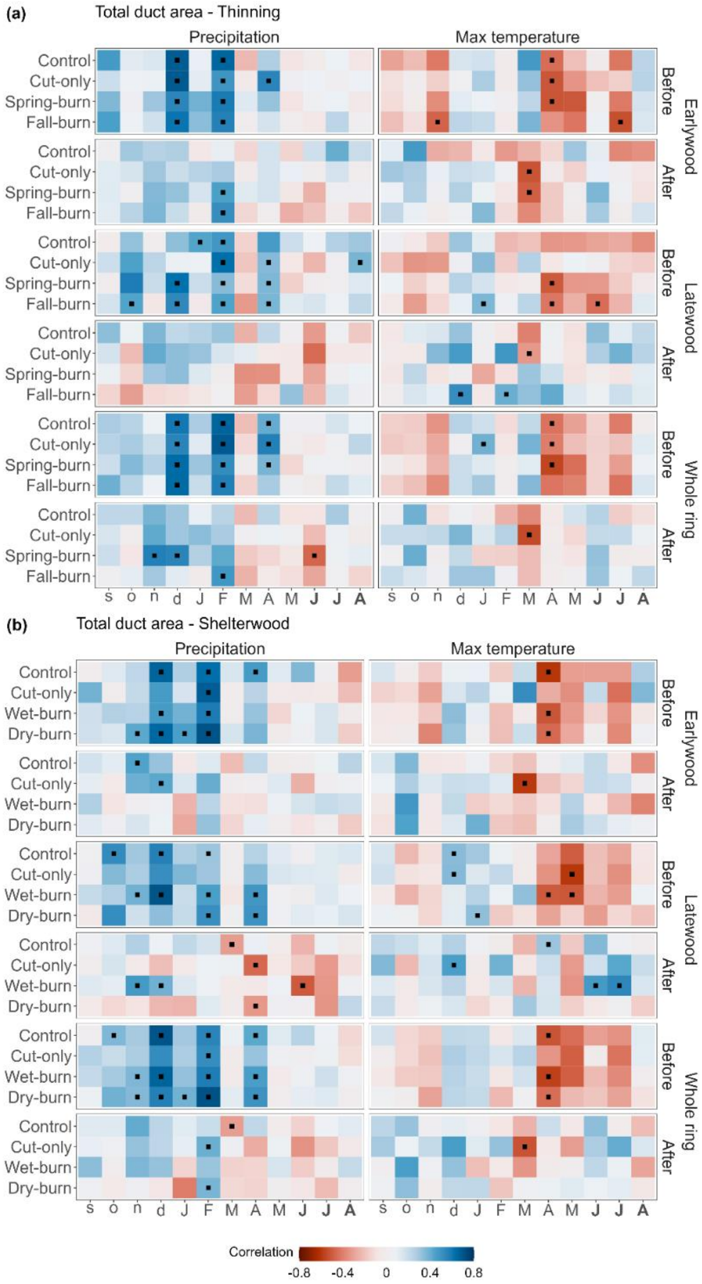


Figure S5.9. Pearson correlation coefficients between monthly precipitation and maximum temperature and **total duct area** in the earlywood, latewood, and whole ring, 20 years before and after treatments for the (a) thinning and the (b) shelterwood experiment. Tiles marked with a dot denote significant correlation (α < 0.05) using regular bootstrapping. Months in lowercase letters correspond to previous year and capital letters to current year (September previous year to August current year); months in bold denote the growing season.

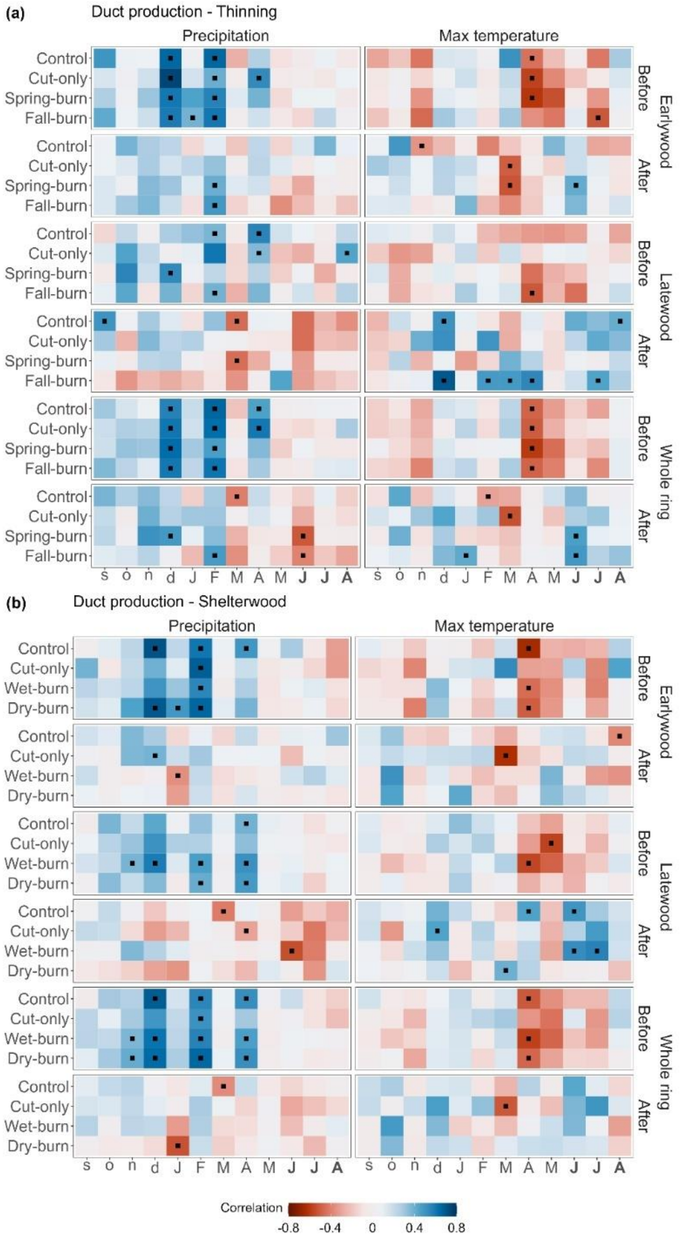
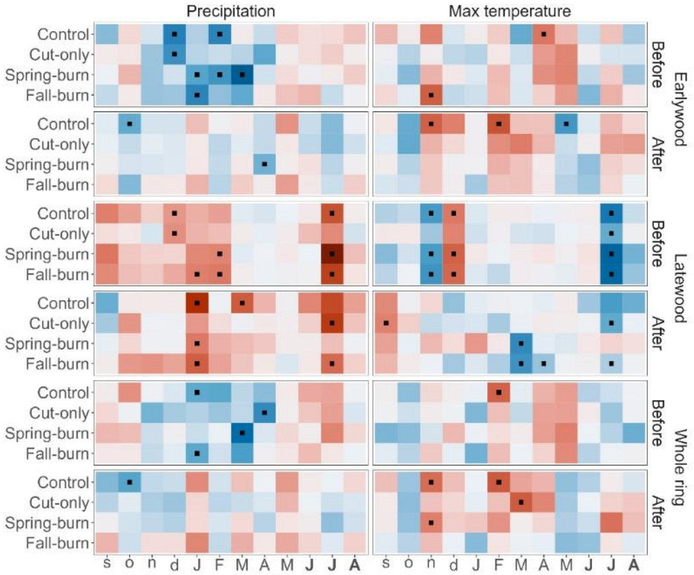


Figure S5.10. Pearson correlation coefficients between monthly precipitation and maximum temperature and **duct production** in the earlywood, latewood, and whole ring, 20 years before and after treatments for the (a) thinning and the (b) shelterwood experiment. Tiles marked with a dot denote significant correlation (α < 0.05) using regular bootstrapping. Months in lowercase letters correspond to previous year and capital letters to current year (September previous year to August current year); months in bold denote the growing season.

(a) Relative duct area - Thinning



(b) Relative duct area - Shelterwood

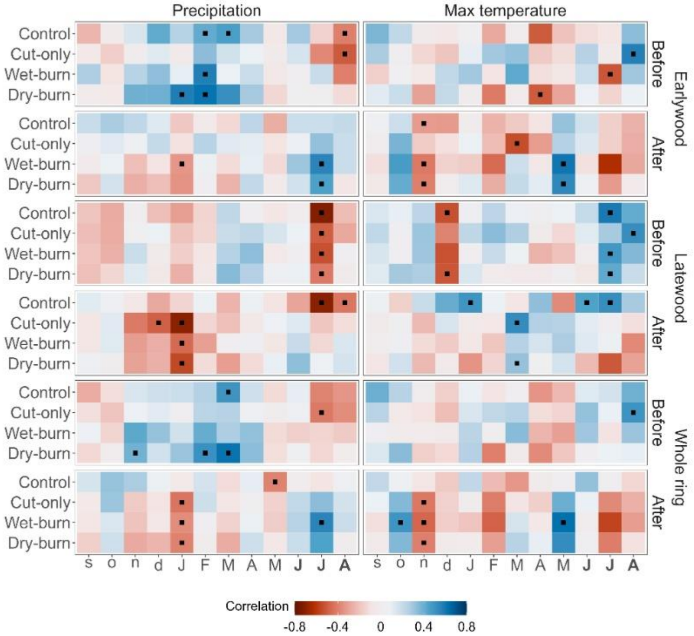


Figure S5.11. Pearson correlation coefficients between monthly precipitation and maximum temperature and **relative duct area** in the earlywood, latewood, and whole ring, 20 years before and after treatments for the (a) thinning and the (b) shelterwood experiment. Tiles marked with a dot denote significant correlation (α < 0.05) using regular bootstrapping. Months in lowercase letters correspond to previous year and capital letters to current year (September previous year to August current year); months in bold denote the growing season.

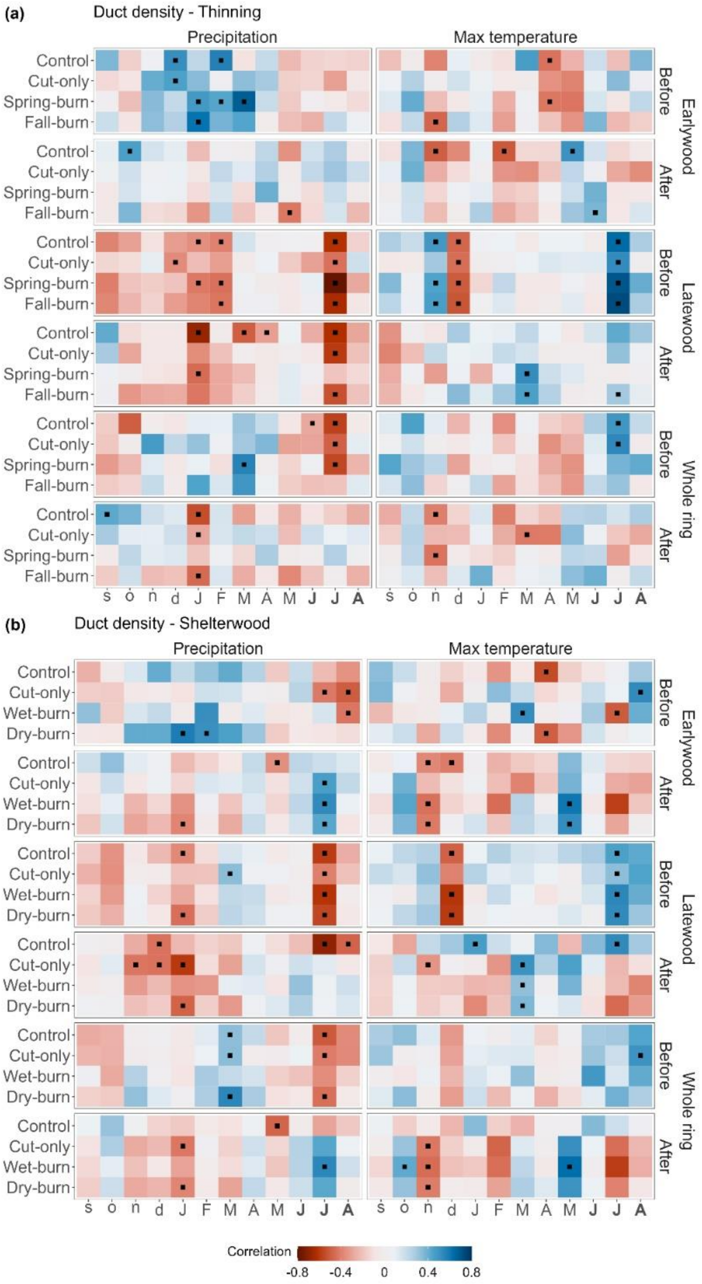


Figure S5.12. Pearson correlation coefficients between monthly precipitation and maximum temperature and **duct density** in the earlywood, latewood, and whole ring, 20 years before and after treatments for the (a) thinning and the (b) shelterwood experiment. Tiles marked with a dot denote significant correlation (α < 0.05) using regular bootstrapping. Months in lowercase letters correspond to previous year and capital letters to current year (September previous year to August current year); months in bold denote the growing season.

Appendix S5.4. Model statistics of resin duct metrics

Table S5.1. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **duct size** of the **thinning** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Duct size					
Thinning					
Earlywood					
	(Intercept)	0.011	4.6E-04	**0.010**	**0.012**
	Cut-only	0.001	6.4E-04	-2.1E-04	0.002
	Spring-burn	2.3E-04	6.4E-04	-0.001	0.002
	Fall-burn	2.3E-04	6.4E-04	-0.001	0.001
	Post	-0.001	3.6E-04	**-0.002**	**-3.4E-04**
	Post*Cut-only	0.002	5.0E-04	**9.7E-04**	**0.003**
	Post*Spring-burn	0.002	5.0E-04	**6.3E-04**	**0.003**
	Post*Fall-burn	0.001	5.0E-04	**4.6E-04**	**0.002**
Latewood					
	(Intercept)	0.010	4.8E-04	**0.009**	**0.011**
	Cut-only	0.002	6.9E-04	**6.2E-04**	**0.003**
	Spring-burn	5.0E-04	6.9E-04	-8.5E-04	0.002
	Fall-burn	7.6E-04	6.9E-04	-6.0E-04	0.002
	Post	-9.7E-04	2.6E-04	**-0.001**	**-4.6E-04**
	Post*Cut-only	0.002	3.7E-04	**0.001**	**0.003**
	Post*Spring-burn	0.002	3.7E-04	**0.001**	**0.003**
	Post*Fall-burn	0.001	3.7E-04	**4.8E-04**	**0.002**
Whole ring					
	(Intercept)	0.010	4.6E-04	**0.009**	**0.011**
	Cut-only	0.002	6.6E-04	**5.4E-04**	**0.003**
	Spring-burn	5.4E-04	6.6E-04	-7.5E-04	0.002
	Fall-burn	7.7E-04	6.6E-04	-5.2E-04	0.002
	Post	-7.1E-04	2.5E-04	**-0.001**	**-2.1E-04**
	Post*Cut-only	0.002	3.6E-04	**8.9E-04**	**0.002**
	Post*Spring-burn	0.002	3.6E-04	**9.1E-04**	**0.002**
	Post*Fall-burn	0.001	3.6E-04	**3.0E-04**	**0.002**

Notes: Gaussian GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.2. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **duct size** of the **shelterwood** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Duct size					
Shelterwood					
Earlywood					
	(Intercept)	0.010	4.9E-04	**0.009**	**0.011**
	Cut-only	-3.3E-04	6.9E-04	-0.002	0.001
	Wet-burn	-4.5E-04	6.8E-04	-0.002	9.0E-04
	Dry-burn	-3.1E-04	6.9E-04	-0.002	0.001
	Post	-3.9E-04	3.4E-04	-0.001	2.8E-04
	Post*Cut-only	0.001	4.8E-04	**5.3E-04**	**0.002**
	Post*Wet-burn	0.001	4.8E-04	**4.4E-04**	**0.002**
	Post*Dry-burn	1.2E-04	4.8E-04	**-8.3E-04**	**0.001**
Latewood					
	(Intercept)	0.008	4.4E-04	**0.008**	**0.009**
	Cut-only	3.5E-04	6.2E-04	-8.7E-04	0.002
	Wet-burn	-3.6E-04	6.1E-04	-0.002	8.4E-04
	Dry-burn	-1.7E-04	6.2E-04	-0.001	0.001
	Post	-8.0E-04	2.7E-04	**-0.001**	**-2.7E-04**
	Post*Cut-only	0.001	3.8E-04	**7.1E-04**	**0.002**
	Post*Wet-burn	0.002	3.7E-04	**0.001**	**0.003**
	Post*Dry-burn	8.1E-04	3.8E-04	**6.6E-05**	**0.002**
Whole ring					
	(Intercept)	0.009	4.5E-04	**0.008**	**0.010**
	Cut-only	1.3E-04	6.3E-04	-0.001	0.001
	Wet-burn	-3.8E-04	6.2E-04	-0.002	8.6E-04
	Dry-burn	-2.4E-04	6.3E-04	-0.001	0.001
	Post	-5.4E-04	2.7E-04	**-0.001**	**-1.1E-05**
	Post*Cut-only	0.001	3.8E-04	**6.0E-04**	**0.002**
	Post*Wet-burn	0.002	3.7E-04	**0.001**	**0.003**
	Post*Dry-burn	7.2E-04	3.8E-04	-2.2E-05	0.001

Notes: Gaussian GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.3. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **duct production** of the **thinning** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Duct production					
Thinning					
Earlywood					
	(Intercept)	0.234	0.149	-0.058	0.526
	Cut-only	0.257	0.200	-0.136	0.649
	Spring-burn	-0.079	0.209	-0.489	0.332
	Fall-burn	-0.062	0.209	-0.472	0.347
	Post	-0.660	0.183	**-1.019**	**-0.302**
	Post*Cut-only	0.428	0.222	-0.007	0.864
	Post*Spring-burn	0.900	0.226	**0.456**	**1.344**
	Post*Fall-burn	0.578	0.235	**0.118**	**1.038**
Latewood					
	(Intercept)	0.810	0.080	**0.653**	**0.967**
	Cut-only	-0.418	0.112	**-0.639**	**-0.198**
	Spring-burn	-0.189	0.116	-0.415	0.038
	Fall-burn	-0.193	0.114	-0.417	0.030
	Post	-0.410	0.080	**-0.566**	**-0.253**
	Post*Cut-only	0.558	0.115	**0.333**	**0.782**
	Post*Spring-burn	0.414	0.115	**0.188**	**0.640**
	Post*Fall-burn	0.351	0.114	**0.128**	**0.573**
Whole ring					
	(Intercept)	1.240	0.071	**1.102**	**1.379**
	Cut-only	-0.082	0.101	-0.279	0.115
	Spring-burn	-0.098	0.101	-0.296	0.099
	Fall-burn	-0.007	0.100	-0.202	0.189
	Post	-0.526	0.076	**-0.675**	**-0.378**
	Post*Cut-only	0.541	0.101	**0.343**	**0.738**
	Post*Spring-burn	0.579	0.101	**0.382**	**0.776**
	Post*Fall-burn	0.414	0.101	**0.217**	**0.611**

Notes: COM-Poisson GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.4. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **duct production** of the **shelterwood** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Duct production					
Shelterwood					
Earlywood					
	(Intercept)	-0.218	0.177	-0.564	0.128
	Cut-only	-0.402	0.278	-0.947	0.143
	Wet-burn	-0.014	0.244	-0.493	0.464
	Dry-burn	0.378	0.225	-0.063	0.818
	Post	-0.698	0.294	**-1.273**	**-0.123**
	Post*Cut-only	1.594	0.371	**0.866**	**2.322**
	Post*Wet-burn	1.325	0.345	**0.648**	**2.002**
	Post*Dry-burn	1.018	0.330	**0.371**	**1.666**
Latewood					
	(Intercept)	0.537	0.081	**0.377**	**0.696**
	Cut-only	-0.007	0.115	-0.232	0.218
	Wet-burn	-0.039	0.114	-0.263	0.185
	Dry-burn	0.186	0.116	-0.040	0.413
	Post	-0.224	0.080	**-0.382**	**-0.066**
	Post*Cut-only	0.455	0.110	**0.240**	**0.670**
	Post*Wet-burn	0.256	0.115	**0.031**	**0.481**
	Post*Dry-burn	0.275	0.111	**0.058**	**0.492**
Whole ring					
	(Intercept)	0.965	0.078	**0.813**	**1.117**
	Cut-only	-0.123	0.112	-0.342	0.096
	Wet-burn	-0.038	0.109	-0.252	0.176
	Dry-burn	0.185	0.106	-0.024	0.393
	Post	-0.302	0.090	**-0.477**	**-0.126**
	Post*Cut-only	0.753	0.118	**0.521**	**0.985**
	Post*Wet-burn	0.570	0.117	**0.340**	**0.800**
	Post*Dry-burn	0.466	0.114	**0.243**	**0.689**

Notes: COM-Poisson GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.5. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **total duct area** of the **thinning** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Total duct area					
Thinning					
Earlywood					
	(Intercept)	-4.388	0.149	**-4.681**	**-4.095**
	Cut-only	0.357	0.211	-0.057	0.770
	Spring-burn	0.001	0.211	-0.413	0.414
	Fall-burn	0.106	0.212	-0.309	0.521
	Post	-0.600	0.136	**-0.866**	**-0.335**
	Post*Cut-only	0.539	0.191	**0.165**	**0.914**
	Post*Spring-burn	0.845	0.192	**0.470**	**1.221**
	Post*Fall-burn	0.577	0.194	**0.197**	**0.957**
Latewood					
	(Intercept)	-3.866	0.097	**-4.057**	**-3.675**
	Cut-only	-0.170	0.138	-0.440	0.101
	Spring-burn	-0.182	0.138	-0.452	0.088
	Fall-burn	-0.086	0.138	-0.356	0.184
	Post	-0.566	0.093	**-0.747**	**-0.385**
	Post*Cut-only	0.722	0.131	**0.465**	**0.979**
	Post*Spring-burn	0.623	0.130	**0.367**	**0.878**
	Post*Fall-burn	0.446	0.131	**0.189**	**0.702**
Whole ring					
	(Intercept)	-3.370	0.084	**-3.534**	**-3.205**
	Cut-only	0.094	0.119	-0.139	0.326
	Spring-burn	-0.064	0.119	-0.297	0.168
	Fall-burn	0.011	0.119	-0.221	0.244
	Post	-0.576	0.080	**-0.733**	**-0.420**
	Post*Cut-only	0.617	0.113	**0.395**	**0.839**
	Post*Spring-burn	0.706	0.113	**0.484**	**0.928**
	Post*Fall-burn	0.488	0.113	**0.265**	**0.710**

Notes: Gamma GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.6. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **total duct area** of the **shelterwood** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Total duct area					
Shelterwood					
Earlywood					
	(Intercept)	-4.881	0.168	**-5.210**	**-4.552**
	Cut-only	-0.163	0.237	-0.627	0.301
	Wet-burn	-0.030	0.237	-0.494	0.434
	Dry-burn	0.244	0.237	-0.221	0.709
	Post	-0.519	0.169	**-0.849**	**-0.188**
	Post*Cut-only	1.290	0.238	**0.825**	**1.756**
	Post*Wet-burn	1.268	0.242	**0.794**	**1.741**
	Post*Dry-burn	0.936	0.238	**0.471**	**1.402**
Latewood					
	(Intercept)	-4.312	0.104	**-4.516**	**-4.108**
	Cut-only	0.053	0.147	-0.235	0.342
	Wet-burn	0.013	0.146	-0.272	0.299
	Dry-burn	0.183	0.147	-0.105	0.471
	Post	-0.311	0.083	**-0.473**	**-0.149**
	Post*Cut-only	0.637	0.117	**0.408**	**0.867**
	Post*Wet-burn	0.380	0.117	**0.151**	**0.609**
	Post*Dry-burn	0.320	0.117	**0.091**	**0.550**
Whole ring					
	(Intercept)	-3.811	0.099	**-4.005**	**-3.616**
	Cut-only	-0.057	0.140	-0.331	0.218
	Wet-burn	-0.017	0.139	-0.289	0.256
	Dry-burn	0.203	0.140	-0.072	0.478
	Post	-0.383	0.084	**-0.547**	**-0.218**
	Post*Cut-only	0.869	0.119	**0.635**	**1.102**
	Post*Wet-burn	0.711	0.119	**0.478**	**0.944**
	Post*Dry-burn	0.554	0.119	**0.321**	**0.787**

Notes: Gamma GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.7. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **duct density** of the **thinning** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Duct density					
Thinning					
Earlywood					
	(Intercept)	-1.939	0.131	**-2.196**	**-1.683**
	Cut-only	0.540	0.185	**0.178**	**0.903**
	Spring-burn	0.175	0.185	-0.187	0.538
	Fall-burn	0.226	0.185	-0.137	0.589
	Post	0.181	0.114	-0.042	0.404
	Post*Cut-only	-0.436	0.161	**-0.751**	**-0.121**
	Post*Spring-burn	-0.013	0.160	-0.328	0.301
	Post*Fall-burn	-0.006	0.163	-0.326	0.314
Latewood					
	(Intercept)	0.255	0.112	**0.036**	**0.475**
	Cut-only	-0.197	0.158	-0.507	0.113
	Spring-burn	-0.184	0.158	-0.494	0.127
	Fall-burn	-0.102	0.159	-0.413	0.209
	Post	0.297	0.098	**0.106**	**0.488**
	Post*Cut-only	-0.261	0.138	-0.531	0.010
	Post*Spring-burn	-0.503	0.138	**-0.774**	**-0.232**
	Post*Fall-burn	-0.366	0.139	**-0.639**	**-0.093**
Whole ring					
	(Intercept)	-1.015	0.084	**-1.179**	**-0.851**
	Cut-only	0.136	0.119	-0.096	0.369
	Spring-burn	0.026	0.119	-0.206	0.259
	Fall-burn	0.037	0.119	-0.195	0.270
	Post	0.200	0.048	**0.106**	**0.295**
	Post*Cut-only	-0.319	0.068	**-0.453**	**-0.185**
	Post*Spring-burn	-0.207	0.069	**-0.341**	**-0.072**
	Post*Fall-burn	-0.089	0.069	-0.223	0.046

Notes: Gamma GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.8. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **duct density** of the **shelterwood** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Duct density					
Shelterwood					
Earlywood					
	(Intercept)	-1.972	0.140	**-2.246**	**-1.698**
	Cut-only	0.284	0.198	-0.104	0.672
	Wet-burn	0.142	0.196	-0.243	0.527
	Dry-burn	0.245	0.198	-0.143	0.633
	Post	0.062	0.145	-0.223	0.346
	Post*Cut-only	0.051	0.205	-0.351	0.453
	Post*Wet-burn	0.585	0.206	**0.182**	**0.988**
	Post*Dry-burn	0.653	0.207	**0.247**	**1.059**
Latewood					
	(Intercept)	0.344	0.105	**0.138**	**0.551**
	Cut-only	0.185	0.149	-0.107	0.476
	Wet-burn	0.193	0.147	-0.095	0.482
	Dry-burn	0.044	0.149	-0.248	0.335
	Post	0.154	0.087	-0.016	0.323
	Post*Cut-only	-0.511	0.122	**-0.751**	**-0.271**
	Post*Wet-burn	-0.725	0.122	**-0.963**	**-0.486**
	Post*Dry-burn	-0.327	0.123	**-0.569**	**-0.086**
Whole ring					
	(Intercept)	-0.922	0.084	**-1.086**	**-0.758**
	Cut-only	0.241	0.118	**0.009**	**0.473**
	Wet-burn	0.171	0.117	-0.059	0.401
	Dry-burn	0.098	0.119	-0.134	0.331
	Post	0.177	0.064	**0.053**	**0.302**
	Post*Cut-only	-0.294	0.090	**-0.471**	**-0.118**
	Post*Wet-burn	-0.222	0.089	**-0.397**	**-0.047**
	Post*Dry-burn	0.083	0.090	-0.095	0.260

Notes: Gamma GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.9. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **relative duct area** of the **thinning** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Relative duct area					
Thinning					
Earlywood					
	(Intercept)	-1.896	0.128	**-2.148**	**-1.645**
	Cut-only	0.612	0.181	**0.257**	**0.968**
	Spring-burn	0.177	0.181	-0.179	0.532
	Fall-burn	0.236	0.182	-0.120	0.592
	Post	0.096	0.112	-0.123	0.314
	Post*Cut-only	-0.249	0.157	-0.557	0.060
	Post*Spring-burn	0.146	0.157	-0.162	0.454
	Post*Fall-burn	0.175	0.158	-0.135	0.486
Latewood					
	(Intercept)	0.210	0.089	**0.035**	**0.386**
	Cut-only	-0.025	0.121	-0.263	0.213
	Spring-burn	-0.273	0.122	**-0.512**	**-0.035**
	Fall-burn	-0.154	0.121	-0.392	0.084
	Post	0.043	0.047	-0.048	0.135
Whole ring					
	(Intercept)	-1.068	0.071	**-1.208**	**-0.929**
	Cut-only	0.306	0.100	0.109	0.503
	Spring-burn	0.074	0.100	-0.123	0.271
	Fall-burn	0.089	0.100	-0.108	0.285
	Post	0.111	0.042	**0.028**	**0.193**
	Post*Cut-only	-0.155	0.060	**-0.273**	**-0.038**
	Post*Spring-burn	-0.034	0.060	-0.151	0.084
	Post*Fall-burn	0.033	0.060	-0.085	0.150

Notes: Gamma GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.10. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for earlywood, latewood, and whole ring **relative duct area** of the **shelterwood** experiment using the mean value of a 20-year interval before and after treatments.

Response	Fixed effects	Estimate	SE	Lower CI	Upper CI
Relative duct area					
Shelterwood					
Earlywood					
	(Intercept)	-2.010	0.129	**-2.263**	**-1.758**
	Cut-only	0.169	0.181	-0.186	0.524
	Wet-burn	0.081	0.180	-0.272	0.434
	Dry-burn	0.164	0.181	-0.191	0.520
	Post	-0.029	0.141	-0.306	0.248
	Post*Cut-only	0.258	0.199	-0.132	0.649
	Post*Wet-burn	0.719	0.200	**0.327**	**1.110**
	Post*Dry-burn	0.689	0.200	**0.296**	**1.082**
Latewood					
	(Intercept)	0.067	0.082	-0.094	0.229
	Cut-only	0.214	0.117	-0.014	0.442
	Wet-burn	0.113	0.115	-0.113	0.339
	Dry-burn	0.042	0.117	-0.186	0.271
	Post	0.065	0.072	-0.077	0.207
	Post*Cut-only	-0.336	0.102	**-0.536**	**-0.136**
	Post*Wet-burn	-0.458	0.101	**-0.657**	**-0.259**
	Post*Dry-burn	-0.251	0.103	**-0.453**	**-0.050**
Whole ring					
	(Intercept)	-1.110	0.059	**-1.226**	**-0.993**
	Cut-only	0.216	0.084	**0.051**	**0.381**
	Wet-burn	0.095	0.083	-0.068	0.258
	Dry-burn	0.082	0.084	-0.083	0.247
	Post	0.074	0.052	-0.028	0.177
	Post*Cut-only	-0.097	0.074	-0.242	0.048
	Post*Wet-burn	0.027	0.073	-0.117	0.171
	Post*Dry-burn	0.169	0.074	**0.023**	**0.315**

Notes: Gamma GLMMs. Intercept equals Control, Pre-treatment. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept.

Table S5.11. Pairwise comparisons for earlywood, latewood, and whole ring **duct size** for each treatment contrasting pre- and post-treatment values.

Response		**Thinning**			**Shelterwood**		
Duct size	Treatment	df	t-value	p-value	df	t-value	p-value
Earlywood							
	Control	92	2.93	**0.004**	93	1.14	0.258
	Cut-only	92	-2.58	**0.012**	93	-3.21	**0.002**
	Spring-burn	92	-1.62	0.108	93	-2.97	**0.004**
	Fall-burn	92	-1.16	0.249	93	0.80	0.428
Latewood							
	Control	92	3.75	**< 0.001**	93	3.00	**0.004**
	Cut-only	92	-3.70	**< 0.001**	93	-2.46	**0.016**
	Spring-burn	92	-3.28	**0.001**	93	-4.16	**< 0.001**
	Fall-burn	92	-0.87	0.384	93	-0.04	0.967
Whole ring							
	Control	92	2.78	**0.007**	93	2.01	**0.047**
	Cut-only	92	-3.50	**< 0.001**	93	-3.04	**0.003**
	Spring-burn	92	-3.57	**< 0.001**	93	-4.82	**< 0.001**
	Fall-burn	92	-1.19	0.237	93	-0.69	0.489

Notes: *p*-values are adjusted after Holm method (α = 0.05)

Table S5.12. Pairwise comparisons for earlywood, latewood, and whole ring **duct production** for each treatment contrasting pre- and post-treatment values.

Response		**Thinning**		**Shelterwood**	
Duct production	Treatment	z-value	p-value	z-value	p-value
Earlywood					
	Control	3.61	**< 0.001**	2.38	**0.017**
	Cut-only	1.84	0.066	-3.93	**< 0.001**
	Spring-burn	-1.80	0.073	-3.45	**0.001**
	Fall-burn	0.56	0.576	-2.12	**0.034**
Latewood					
	Control	5.13	**< 0.001**	2.79	**0.005**
	Cut-only	-1.80	0.072	-3.11	**0.002**
	Spring-burn	-0.05	0.959	-0.39	0.695
	Fall-burn	0.73	0.465	-0.66	0.512
Whole ring					
	Control	6.95	**< 0.001**	3.37	**< 0.001**
	Cut-only	-0.21	0.830	-5.84	**< 0.001**
	Spring-burn	-0.79	0.427	-3.54	**< 0.001**
	Fall-burn	1.70	0.090	-2.35	**0.019**

Notes: *p*-values are adjusted after Holm method ($\alpha = 0.05$)

Table S5.13. Pairwise comparisons for earlywood, latewood, and whole ring **total duct area** for each treatment contrasting pre- and post-treatment values.

Response		**Thinning**		**Shelterwood**	
Total duct area	Treatment	z-value	p-value	z-value	p-value
Earlywood					
	Control	4.43	**< 0.001**	3.08	**0.002**
	Cut-only	0.45	0.652	-4.60	**< 0.001**
	Spring-burn	-1.81	0.071	-4.34	**< 0.001**
	Fall-burn	0.17	0.864	-2.50	**0.012**
Latewood					
	Control	6.12	**< 0.001**	3.77	**< 0.001**
	Cut-only	-1.68	0.093	-3.93	**< 0.001**
	Spring-burn	-0.62	0.538	-0.83	0.405
	Fall-burn	1.30	0.194	-0.11	0.914
Whole ring					
	Control	7.21	**< 0.001**	4.56	**< 0.001**
	Cut-only	-0.50	0.614	-5.75	**< 0.001**
	Spring-burn	-1.61	0.107	-3.91	**< 0.001**
	Fall-burn	1.10	0.272	-2.04	**0.041**

Notes: *p*-values are adjusted after Holm method (α = 0.05)

Table S5.14. Pairwise comparisons for earlywood, latewood, and whole ring **duct density** for each treatment contrasting pre- and post-treatment values.

Response		**Thinning**		**Shelterwood**	
Duct density	Treatment	z-value	p-value	z-value	p-value
Earlywood					
	Control	-1.59	0.111	-0.42	0.672
	Cut-only	2.24	**0.025**	-0.78	0.435
	Spring-burn	-1.49	0.137	-4.46	< **0.001**
	Fall-burn	-1.50	0.134	-4.85	< **0.001**
Latewood					
	Control	-3.04	**0.002**	-1.77	0.076
	Cut-only	-0.37	0.711	4.14	< **0.001**
	Spring-burn	2.11	**0.035**	6.68	< **0.001**
	Fall-burn	0.69	0.489	1.98	**0.048**
Whole ring					
	Control	-4.14	< **0.001**	-2.79	**0.005**
	Cut-only	2.46	**0.014**	1.84	0.066
	Spring-burn	0.13	0.900	0.72	0.473
	Fall-burn	-2.30	**0.021**	-4.04	< **0.001**

Notes: *p*-values are adjusted after Holm method ($\alpha = 0.05$)

Table S5.15. Pairwise comparisons for earlywood, latewood, and whole ring **relative duct area** for each treatment contrasting pre- and post-treatment values.

Response		**Thinning**		**Shelterwood**	
Relative duct area	Treatment	z-value	p-value	z-value	p-value
Earlywood					
	Control	-0.86	0.392	0.21	0.837
	Cut-only	1.38	0.167	-1.63	0.103
	Spring-burn	-2.19	**0.029**	-4.90	< **0.001**
	Fall-burn	-2.41	**0.016**	-4.65	< **0.001**
Latewood					
	Control	-0.93	0.350	-0.90	0.368
	Cut-only	-0.93	0.350	3.75	< **0.001**
	Spring-burn	-0.93	0.350	5.52	< **0.001**
	Fall-burn	-0.93	0.350	2.55	**0.011**
Whole ring					
	Control	-2.61	**0.009**	-1.42	0.156
	Cut-only	1.06	0.291	0.44	0.661
	Spring-burn	-1.80	0.071	-1.97	0.049
	Fall-burn	-3.38	< **0.001**	-4.61	< **0.001**

Notes: *p*-values are adjusted after Holm method (α = 0.05)

Table S5.16. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for whole ring relative **duct size** and **total duct area** of both experiments as a function of **crown scorch**. Relative duct metrics were calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Results of the pairwise comparisons contrasting relative duct metrics one year (Post-1) and two years (Post-2) post-burning.

Fixed effects	Estimate	SE	Lower CI	Upper CI	Pairwise comparisons			
Duct size					Contrast	df	t-value	p-value
(Intercept)	1.095	0.045	**1.006**	**1.184**	Post-1 - Post-2	118.1	0.69	0.493
Crown scorch	-0.004	0.021	-0.046	0.037				
Post-2	-0.028	0.041	-0.109	0.053				
Family: Gaussian GLMM								
Total duct area					Contrast	z-value	p-value	
(Intercept)	0.399	0.101	**0.201**	**0.598**	Post-1 - Post-2	0.29	0.771	
Crown scorch	0.058	0.061	-0.061	0.177				
Post-2	-0.032	0.111	-0.249	0.185				
Family: Zero-inflated Gamma GLMM								

Notes: Intercept equals Post-1 (one year post-burning). Crown scorch is standardized. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept. In pairwise comparisons, *p*-values are adjusted after Holm method ($\alpha = 0.05$).

Table S5.17. Estimate, standard error (SE), and confidence intervals (CI, 95%) of the mixed-effects models for whole ring relative **duct size** and **total duct area** of both experiments as a function of **stand basal area**. Relative duct metrics were calculated for each tree as the ratio between the annual value and the 20-year core average before treatments. Results of the pairwise comparisons contrasting relative duct metrics pre- (Pre), one year post- (Post-1), and 13 years post-burning (Post-13).

Fixed effects	Estimate	SE	Lower CI	Upper CI	Pairwise comparisons			
Duct size					Contrast	df	t-value	p-value
(Intercept)	0.948	0.024	**0.900**	**0.996**	Pre - Post-1	438	-4.12	< **0.001**
Basal area	-0.030	0.018	-0.065	0.005	Pre - Post-13	428	-1.06	0.540
Post-1	0.106	0.026	**0.056**	**0.157**	Post-1 - Post-13	430	3.36	**0.002**
Post-13	0.026	0.024	-0.022	0.073				
Basal area * Post-1	0.037	0.026	-0.015	0.089				
Basal area * Post-13	-0.024	0.025	-0.073	0.025				
Family: Gaussian GLMM								
Total duct area					Contrast	z-value	p-value	
(Intercept)	-0.251	0.070	**-0.389**	**-0.113**	Pre - Post-1	-4.4	< **0.001**	
Basal area	-0.006	0.050	-0.104	0.091	Pre - Post-13	-3.1	**0.005**	
Post-1	0.309	0.070	**0.172**	**0.445**	Post-1 - Post-13	1.6	0.256	
Post-13	0.205	0.065	**0.077**	**0.333**				
Basal area * Post-1	-0.060	0.077	-0.212	0.091				
Basal area * Post-13	-0.229	0.072	**-0.369**	**-0.089**				
Family: Zero-inflated Gamma GLMM								

Notes: Intercept equals Post-1 (one year post-burning). Crown scorch is standardized. Confidence intervals (95% CI) in bold indicate a significant difference with the intercept. In pairwise comparisons, *p*-values are adjusted after Holm method (α = 0.05).

CHAPTER 6

General discussion

General discussion

As natural disturbances increase in frequency and severity with climate change, forest management provides an opportunity to mitigate their negative impacts and support forest adaptation to novel disturbance regimes (Davis et al., 2024; Hood et al., 2016; Sohn et al., 2016). Natural disturbances often occur as concatenate events, whose legacy effects determine the likelihood and intensity of subsequent disturbances (Buma, 2015; Seidl et al., 2017). In this thesis, we have explored the potential of different forest management treatments, primarily designed to reduce wildfire hazard, to increase the resistance of pine forests to multiple interacting disturbances.

As hypothesized, competition for resources is a key factor influencing pine forests resistance to disturbances. However, its effects can sometimes be attributed to both overstory and understory competition (Chapter 2 and 3) and, in other cases, solely to overstory competition (Chapter 5). We provide evidence that cutting treatments that substantially reduce stand density and basal area increase forest resistance to wildfires (Chapter 2), droughts (Chapter 2 and 3), and pest outbreaks (Chapter 5). The implementation of prescribed burning following cutting (i.e., slash burning) offers additional benefits and further enhances forest resistance to these disturbances. However, contrary to our hypothesis, the release from understory competition following direct prescribed burning does not increase pine susceptibility to insect defoliators, as a subsequent drought may offset the potential decrease in needle terpene concentration caused by the burn (Chapter 4). Results of this thesis suggest that forest management treatments that consider both the overstory and understory vegetation have great potential to assist forest adaptation to novel disturbance regimes. Yet, tree and forest responses are dependent on multiple interacting factors that must be considered when designing management plans. These include cutting intensity, prescribed burning type and season, treatment longevity, and weather conditions, among other factors that have not been explored within the scope of this thesis but may also play an important role (e.g., soil organic carbon, Mäkipää et al., 2023, or post-fire regeneration strategies, Vallejo et al., 2012). Moreover, while forest treatments are key in determining resistance to disturbances, weather conditions may emerge as the primary factor driving the prevailing response (Chapter 4).

6.1. Forest management determines resistance to multiple disturbances

Stand density reduction treatments lead to a higher proportion of larger, more vigorous trees at stand level that benefit from reduced competition for resources. The extent of competition reduction depends on the cutting intensity, which is determined by the primary objective of the management intervention as well as the developmental stage of the forest or the site index. Heavy intensity cutting treatments open the canopy cover and induce a significant growth release of residual trees (Chapter 3 and 5) that enhances their resistance to a later drought event (Chapter 2 and 3) and allows trees to invest more in resin duct defences (Chapter 5). However, heavy thinning may also accelerate the recovery of the understory vegetation due to increased radiation (Casals and Rios, 2018), potentially shortening the longevity of treatment benefits by increasing available fuel to burn (Keane, 2015) and contributing to stand water loss through increased transpiration (Simonin et al., 2007). In this thesis, the effects of cutting alone can only be assessed based on the results of Chapter 5, as all other thinning treatments were consistently accompanied by clearing of the understory, thus their effects cannot be solely attributed to overstory management.

Since cutting treatments are implemented at relatively regular intervals, it is important to consider the type and timing of the last intervention, as reducing stand density in a very dense stand differs significantly from doing so in a more open stand (Pretzsch, 2020). This was evident in Chapter 5, where the thinning treatment followed prior active management, resulting in a smaller increase in resin duct investment and growth release compared to the shelterwood experiment. In the latter, the absence of recent previous interventions combined with a greater stand density reduction contributed to a greater investment in resin ducts and growth release. Notably, pines of the unmanaged control units in the thinning experiment exhibited a decline in both defence investment and growth, likely due to the long-term cumulative effect of competition (Slack et al., 2017). Thus, while indirectly, treatments helped alleviate the pressure from resource competition.

When cutting intensity is very mild, such as when the objective is to maintain a closed canopy cover to slow understory regrowth and prevent wildfire hazard (Piqué and Domènech, 2018), the resulting competition release might be too small to significantly impact tree growth or drought resistance, as observed in the light-thin units of Chapter 2 and 3. After such light-intensity thinning, the management of understory vegetation becomes particularly important to relieve competition for resources with the overstory. Indeed, in the light-thinned units of Chapters 2 and 3, tree growth and resistance to wildfires and droughts were greater with slash burning than with clearing alone. This is likely because burning reduced competition from understory vegetation (Giuggiola et al., 2018; Simonin et al., 2007), as reflected in our simulations (Chapter 2) and tree-ring analysis (Chapter 3).

6.2. Prescribed burning modulates tree resistance to multiple disturbances

Prescribed burning implemented directly without a prior management intervention tends to be of high intensity due to the abundance of available fuel to burn, impacting both understory vegetation and suppressed and intermediate pines, that may die due to their thin bark (Valor et al., 2017a). Dominant, vigorous pines, though, are less likely to die due to heat stress, especially if they have invested in a thick bark, as seen in species like black and ponderosa pines. In Chapter 4, we observed that defences of dominant black pines, estimated through needle terpene content, were not affected by direct prescribed burning. This lack of effect suggests that prescribed burning can be successfully implemented to reduce wildfire hazard (Chapter 2) without adversely affecting potential future defoliator outbreaks, such as those caused by the pine processionary moth (PPM; Chapter 4).

Prescribed burning implemented after a cutting treatment (i.e., slash burning) mostly affects the understory vegetation, as suppressed and intermediate trees have already been removed through mechanical means (Davis et al., 2024). Slash burning is an effective treatment to reduce wildfire severity both at short term (Piqué and Domènech, 2018) and at mid-term (Chapter 2), as understory vegetation following burning recovers slowly (Casals and Rios, 2018). Although generally a lower intensity fire, slash burning can have a greater impact on surface fuels and soil, as it may burn at higher temperatures for longer, girdling the stem base of shrubs, killing the basal buds of resprouter species (Clarke et al., 2013), or negatively affecting soil physical and chemical properties (Mott et al., 2021). Additionally, slash burning after a heavy cutting treatment leaves the soil exposed to increased solar radiation, potentially leading to higher soil water evaporation (Raz-Yaseef et al., 2010). This may have been observed in Chapter 3, where changes in $\delta^{18}O$ in tree rings suggested increased soil water evaporation following slash burning. Since cutting treatments of a certain intensity already have a significant impact on residual trees by reducing overstory competition, any further effects of slash burning on trees may be masked by the initial impact of cutting.

In black pine forests, slash burning provides additional benefits in terms of tree growth (Chapter 3) and increased resistance to both wildfires (Chapter 2) and droughts (Chapter 2 and 3), either because of the greater availability of resources due to the slow recovery of the understory vegetation (Casals and Rios, 2018), or because of the short-term increase in soil nitrogen following prescribed burning (DeLuca and Zouhar, 2000). However, the increase in soil nitrogen availability did not translate into higher needle nitrogen levels (Chapter 4). In Chapter 3, the increased resistance to drought was attributed to higher growth rate due to increased net CO_2 assimilation and stomatal conductance. In ponderosa pine forests, slash burning resulted in a short-term increase in resin duct production. This response likely resulted from either the heat stress caused by the low-intensity fire (Hood et al., 2015) or the trees' use of increased post-fire soil nitrogen (DeLuca and Zouhar, 2000), combined with the delayed growth release of the residual pines following cutting (Chapter 5).

The different fire severity levels associated to prescribed burning treatments were not related to defence investment, either in needle terpene content (Chapter 4) or axial resin ducts (Chapter 5). Increased crown scorch has been associated with higher terpene concentrations, but only in certain Mediterranean pine species that do not include black pine (Valor et al., 2017b). Our findings suggest that the usual low-to-moderate intensity of prescribed burns is insufficient to elicit a clear defence response. Additionally, low-intensity fires mostly affect the lower crown foliage, which contributes minimally to photosynthesis (Gomez-Gallego et al., 2020) and thus, to defence investment. On the other hand, while low-intensity fires may scorch foliage, they may not kill the buds (Fowler et al., 2010), allowing new needles to grow in the following season and continue performing photosynthesis. Bud kill is also influenced by burning season: buds are more vulnerable during spring burns prior to bud break, whereas in fall burns, they are better protected by fully developed needles (Knapp et al., 2009). However, despite no direct relation to fire severity, the significant short-term increase in resin duct investment after burning in the units that burned under the drier moisture conditions may have resulted from higher fire intensity (Chapter 5).

Besides the type of prescribed burning, the timing of its implementation is also crucial in determining tree responses (Knapp et al., 2009). Although not the focus of any chapter of this thesis due to lack of replicates, the impact of the burning season may have influenced the observed results by affecting fire intensity variations across sites and studies. Prescribed burning treatments in Chapter 2 and 3 were conducted in spring at two sites and in autumn at another (Casals and Rios, 2018; Tudela-Haberland et al., in prep); in Chapter 4, all sites were burned in autumn, whereas in Chapter 5, one unit was burned in autumn, while all other units were burned in spring, though under different moisture conditions (Smith and Arno, 1999). Trees may be affected differently depending on the burning season due to variations in fire intensity (Schwilk et al., 2006), the crown scorch derived (Wallin et al., 2003), and the phenological state of the tree at different times of the year (Valor et al., 2017a).

6.3. Effectiveness of silvicultural treatments over time

Considering the longevity of silvicultural treatments effectiveness is key when designing a forest management plan, as it determines the frequency of follow-up treatments and the cost-effectiveness of the overall forest model. In this thesis, we have assessed the effects of different forest management treatments across three time scales: short-term (Chapter 4), mid-term (Chapter 2 and 3), and long-term (Chapter 5). Both short- and long-term responses are crucial to evaluate the effectiveness of the treatment, as short-term responses can sometimes be misleading when assessing long-term effects (Pretzsch, 2020). The results from Chapter 4 suggest that, in the short term, prescribed burning does not negatively affect pine chemical defences in a way that would enhance defoliator survival. We did not observe any response in needle terpene content to low-intensity fire one year after, nor do we expect a delayed response (Lavoir et al., 2013). In Chapters 2 and 3, we found that five years after implementing thinning and understory clearing, with or without slash burning, understory vegetation biomass remained low, allowing trees to continue benefiting from the increased resource availability.

Chapter 5 shows that even 20 years after the treatments, pines continued to benefit from enhanced resource access, as reflected in their growth and resin duct investment.

Since we did not assess the same treatment or even the same cutting intensity across studies and time scales, drawing general conclusions on the time-since-treatment effect from our results is not possible. However, growth measurements from Chapter 3 and 5 allow us to infer the effects of slash burning following cutting on two pine species. Our findings suggest that slash burning further enhances black pine growth for at least five years; yet, in contrast, no such effect was observed in ponderosa pine, where growth release appeared to be primarily driven by the cutting treatments, lasting for at least 20 years.

A key factor determining the length of treatment effectiveness is the recovery rate of understory vegetation. Following a wildfire, the regrowth of the understory largely depends on the regeneration strategy of the dominant understory species and fire severity (Vallejo et al., 2012). Since treatment efficacy diminishes over time, vegetation regrowth will determine the frequency at which understory treatments should be applied to achieve management objectives (Davis et al., 2024). In black pine forests, where resprouting species dominate the understory, vegetation tends to grow relatively quickly after fire. However, our findings show that five years after prescribed burning treatments, although the understory vegetation had resprouted, it had not fully recovered (Chapter 2 and 3).

6.4. Post-treatment weather conditions shape treatment effects

Despite we focused on the effects of forest management treatments on tree physiological responses, we observed that both intrinsic water use efficiency (iWUE, Chapter 3) and needle terpene concentrations (Chapter 4) were more sensitive to the weather conditions following treatments than to the treatments themselves. In Chapter 5, resin duct production following treatments also appeared to be strongly influenced by the weather conditions. Despite detecting a higher sensitivity to weather, forest management treatments have long been recognized as a means of modulating tree responses to weather extremes (Sohn et al., 2016)

In Chapter 3, iWUE of dominant pines remained similar during both the pre-treatment and the post-treatment droughts but decreased during the wet year post-treatments. However, despite the lack of iWUE response, isotope analyses and growth measurements suggested an increase in the photosynthetic rate and stomatal conductance during the post-treatment drought compared to untreated units, indicating an improvement in their physiological condition following thinning with or without slash burning (Sala et al., 2005).

Similarly, in Chapter 4, higher terpene concentrations were observed in all needles during the drought year, regardless of treatment. This suggests that drought conditions during needle growth determined needle terpene content (Llusià and Peñuelas, 1998). However, unlike in Chapter 3, stable isotope analysis revealed lower photosynthetic rates and stomatal conductance in burned pines, suggesting that prescribed burning may have reduced pine resistance to the subsequent drought.

The importance of post-treatment weather conditions was also evident in Chapter 5. The sharp increase in resin ducts following treatments was especially apparent in the shelterwood experiment, where prescribed burning was implemented right before a particularly wet season. In contrast, the increase was less pronounced in the thinning experiment, where prescribed burning was followed by a dry season.

6.5. Potentials, limitations, and implications

This thesis results evidence the potential of forest management in assisting forest adaptation to multiple disturbances and novel disturbances regimes. Forest management actions must constantly evolve in response to change, anticipating changes in disturbances regimes and incorporating new knowledge into the planning process (Turner and Seidl, 2023).

In this thesis, we have observed that different combinations of cutting treatments, with or without slash burning, provide ecological benefits beyond reducing wildfire hazard, enhancing forest resistance to droughts and insect outbreaks by influencing different physiological mechanisms (Table 6.1). The thesis' findings suggest that prescribed burning under the forest canopy can be applied either after a cutting treatment or directly to understory vegetation, with minimal impact or even additional benefits for residual trees. Residual trees benefit from increased resource availability, which leads to greater growth, improves their water balance, and increases resin duct production, strengthening their defences against a bark beetle outbreak. Importantly, these advantages do not come at a cost, as trees do not become more palatable to pine processionary moth larvae. However, it is worth noting that these studies primarily focused on the response of dominant pines to management, and different responses may be expected in suppressed pines (Martín-Benito et al., 2008).

Throughout the studies of this thesis, we observed that while the differences in physiological responses among various management treatments were sometimes subtle, the contrast between treated and untreated units was consistently more pronounced, emphasizing the importance of active forest management.

However, effective management decisions require careful consideration not only of the intended objectives but also of the forest structure and composition that will be managed, as the success of management actions strongly depends on the pre-treatment site conditions. The choice of the most appropriate type of treatment for a given location must be site-specific to maximise long-term benefits. Thus, the findings of this thesis should not be considered in isolation but rather as a contribution to the broader body of knowledge on forest management effects on pine resistance to disturbances. The integration of this thesis' insights with existing research will help guide sound management decisions.

Future research should prioritize advancing our understanding of adaptive management strategies to enhance forest resistance and resilience to multiple disturbances and novel disturbances regimes.

Table 6.1. Pine physiological responses to forest management treatment, their key drivers, and resistance to natural disturbances.

Management treatment	Physiological response				Management-related drivers	Other drivers	Resistance to natural disturbances			
	Growth	Water balance / iWUE	Terpenes	Resin ducts			Wildfire	Drought	Bark beetles	PPM
Overstory										
Light thinning	No change	No change or increase	-	-	Competition	Post-treatment weather conditions	Increase	No change	-	-
Heavy thinning	Increase	No change or increase	-	Increase	Competition, forest structure change, retention of most vigorous trees	Post-treatment weather conditions	Increase	Increase	-	-
Shelterwood	Increase	-	-	Increase	Competition, forest structure change, retention of most vigorous trees	Post-treatment weather conditions	Increase	-	Increase	-
Understory										
Prescribed burning	-	-	No change	-	-	Post-treatment weather conditions	Increase	-	-	No change
Slash burning	Increase	Increase	-	Temporary increase	Competition, forest structure change, soil N availability	Post-treatment weather conditions	Increase	Increase	Increase	-

CHAPTER 7

Conclusions

Conclusions

1. Forest management treatments provide ecological benefits beyond their primary objectives, enhancing forest adaptation to multiple interacting disturbances.

2. Competition for resources with overstory and understory vegetation is a key driver of forest resistance to multiple disturbances. When overstory competition persists, effective understory management becomes increasingly critical for further enhancing forest resistance.

3. Cutting treatments enhance forest resistance to wildfires, droughts, and insect outbreaks by reducing combustible fuels and improving the physiological condition of residual pines -increasing net CO_2 assimilation and stomatal conductance-, which enable greater investment in both growth and defence mechanisms.

4. Prescribed burning following cutting treatments (i.e., slash burning) further increases pine resistance to wildfires, drought, and bark beetle outbreaks by keeping understory vegetation at low levels over time, which supports increased growth, improved water balance, and greater resin duct production.

5. Prescribed burning as a stand-alone intervention does not increase pine susceptibility to pine processionary moth (PPM), as it neither affects needle terpene concentrations nor influences the survival of early-instar PPM larvae.

6. Pine responses to treatments, as well as treatment longevity, are determined by multiple interacting factors, including treatment type, pre- and post-treatment forest structure and composition, competition for resources, and post-treatment weather conditions.

References

Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data,* 5(1), 1–12. https://doi.org/10.1038/sdata.2017.191

Achotegui-Castells, A., Llusià, J., Hódar, J. A., & Peñuelas, J. (2013). Needle terpene concentrations and emissions of two coexisting subspecies of Scots pine attacked by the pine processionary moth (Thaumetopoea pityocampa). *Acta Physiologiae Plantarum*, 35(10), 3047–3058. https://doi.org/10.1007/S11738-013-1337-3/FIGURES/6

Achotegui-Castells, A., Peñuelas, J., & Llusià, J. (2015). The role of terpenes in the defensive responses of conifers against herbivores and pathogens. Autonomous University of Barcelona (UAB).

Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., Huxman, T. E., Hudson, P. J., Franz, T. E., Allen, C. D., Anderegg, L. D. L., Barron-Gafford, G. A., Beerling, D. J., Breshears, D. D., Brodribb, T. J., Bugmann, H., Cobb, R. C., Collins, A. D., Dickman, L. T., … McDowell, N. G. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution,* 1(9), 1285–1291. https://doi.org/10.1038/s41559-017-0248-x

Agee, J. K., & Skinner, C. N. (2005). Basic principles of forest fuel reduction treatments. *Forest Ecology and Management*, 211(1−2), 83−96. https://doi.org/10.1016/j.foreco.2005.01.034

Alessio, G. A., De Lillis, M., Fanelli, M., Pinelli, P., & Loreto, F. (2004). Direct and indirect impacts of fire on isoprenoid emissions from Mediterranean vegetation. *Functional Ecology*, 18(3), 357–364. https://doi.org/10.1111/J.0269-8463.2004.00833.X

Aguado, I., Chuvieco, E., Borén, R., Nieto, H., 2007. Estimation of dead fuel moisture content from meteorological data in Mediterranean areas. Applications in fire danger assessment. *International. Journal of. Wildland Fire,* 16 (4), 390−397. https://doi.org/10.1071/WF06136

Allen, C. D., Macalady, A. K., Chechouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted., Gonzalez, P., Fensham, R., Zhang, Castro, J., Demidova, N., Lim, J. H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660−684.

Allen, C. D., Breshears, D. D., McDowell, N. G., Allen, C., Breshears, D. D., & Mcdowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), 1–55. https://doi.org/10.1890/ES15-00203.1

Ameztegui, A., Cabon, A., De Cáceres, M., & Coll, L. (2017). Managing stand density to enhance the adaptability of Scots pine stands to climate change: A modelling approach. *Ecological Modelling*, 356, 141−150. https://doi.org/10.1016/j.ecolmodel.2017.04.006

Anderegg, W. R. L., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., Hood, S. M., Lichstein, J. W., Macalady, A. K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J. D., Stephenson, N. L., Tague, C., & Zeppel, M. (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, 208(3), 674–683. https://doi.org/10.1111/NPH.13477

Ayers, D. M., Bedunah, D. J., & Harrington, M. G. (1999). Antelope Bitterbrush and Scouler's Willow Response to a Shelterwood Harvest and Prescribed Burn in Western Montana. *Western Journal of Applied Forestry*, 14(3), 137–143. https://doi.org/10.1093/WJAF/14.3.137

Azcárate, F. M., Seoane, J., & Silvestre, M. (2023). Factors affecting pine processionary moth (Thaumetopoea pityocampa) incidence in Mediterranean pine stands: A multiscale approach. *Forest Ecology and Management*, 529, 120728. https://doi.org/10.1016/J.FORECO.2022.120728

Banerjee, T. (2020). Impacts of Forest Thinning on Wildland Fire Behavior. *Forests* 11(9), 918. https://doi.org/10.3390/F11090918

Bär, A., Michaletz, S. T., & Mayr, S. (2019). Fire effects on tree physiology. *New Phytologist*, 223(4), 1728−1741. https://doi.org/10.1111/NPH.15871

Barbour, M. M., R. Anthony Fischer, Ken D. Sayre, & Graham D. Farquhar. (2000). Oxygen Isotope Ratio of Leaf and Grain Material Correlates with Stomatal Conductance and Grain Yield in Irrigated Wheat. *Functional Plant Biology,* 27(7), 625−637. https://doi.org/10.1071/PP99041

Barnard, H. R., Brooks, J. R., & Bond, B. J. (2012). Applying the Dual-Isotope Conceptual Model to Interpret Physiological Trends under Uncontrolled Conditions. *Tree Physiology* 32 (10), 1183−98. https://doi.org/10.1093/TREEPHYS/TPS078

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1−48. https://doi.org/10.18637/JSS.V067.I01

Battipaglia, G., Strumia, S., Esposito, A., Giuditta, E., Sirignano, C., Altieri, S., & Rutigliano, F. A. (2014). The Effects of Prescribed Burning on Pinus Halepensis Mill. as Revealed by Dendrochronological and Isotopic Analyses. *Forest Ecology and Management*, 334, 201−208. https://doi.org/10.1016/J.FORECO.2014.09.010

Battipaglia, G., Savi, T., Ascoli, D., Castagneri, D., Esposito, A., Mayr, S., & Nardini, A. (2016). Effects of prescribed burning on ecophysiological, anatomical and stem hydraulic properties in Pinus pinea L. *Tree Physiology*, 36(8), 1019−1031. https://doi.org/10.1093/treephys/tpw034

Battisti, A. (1988). Host-plant relationships and population dynamics of the Pine Processionary Caterpillar Thaumetopoea pityocampa (Denis & Schiffermuller). *Journal of Applied Entomology*, 105(1–5), 393–402. https://doi.org/10.1111/J.1439-0418.1988.TB00202.X

Beguería, S., & Vicente-Serrano, S. M. (2017). SPEI: Calculation of the Standardised Precipitation-Evapotranspiration. https://CRAN.R-project.org/package=SPEI

Bernal, A. A., Kane, J. M., Knapp, E. E., & Zald, H. S. J. (2023). Tree resistance to drought and bark beetle-associated mortality following thinning and prescribed fire treatments. *Forest Ecology and Management*, 530, 120758. https://doi.org/10.1016/J.FORECO.2022.120758

Bernal, A. A., Stephens, S. L., Callaham, M. A., Collins, B. M., Crotteau, J. S., Dickinson, M. B., Hagan, D. L., Hedges, R., Hood, S. M., Hutchinson, T. F., Taylor, M. K., Adam Coates, T., & Alexis Bernal, C. A. (2025). The national Fire and Fire Surrogate study: Effects of fuel treatments in the Western and Eastern United States after 20 years. *Ecological Applications*, 35(1), e70003. https://doi.org/10.1002/EAP.70003

Biondi, Franco, and Kishor Waikul. 2004. “DENDROCLIM2002: A C++ Program for Statistical Calibration of Climate Signals in Tree-Ring Chronologies.” *Computers & Geosciences*, 30 (3), 303–11. https://doi.org/10.1016/J.CAGEO.2003.11.004

Blanch, J. S., Peñuelas, J., Sardans, J., & Llusià, J. (2009). Drought, warming and soil fertilization effects on leaf volatile terpene concentrations in Pinus halepensis and Quercus ilex. *Acta Physiologiae Plantarum*, 31(1), 207–218. https://doi.org/10.1007/S11738-008-0221-Z/METRICS

Boettger, T., Haupt, M., Knöller, K., Weise, S. M., Waterhouse, J. S., Rinne, K. T., Loader, N. J. Sonninen, E., Jungner, H., Masson-Delmotte, V., Stievenard, M., Guillemin, M. T., Pierre, M., Pazdur, A., Leuenberger, M., Filot, M., Saurer, M., Reynolds, C. E., Helle, G., & Schleser, G. H. (2007). Wood Cellulose Preparation Methods and Mass Spectrometric Analyses of ∆13C, ∆18O, and Nonexchangeable ∆2H Values in Cellulose, Sugar, and Starch: An Interlaboratory Comparison. *Analytical Chemistry,* 79(12), 4603−4612. https://pubs.acs.org/doi/full/10.1021/ac0700023

Bottero, A., D'Amato, A. W., Palik, B. J., Kern, C. C., Bradford, J. B., & Scherer, S. S. (2017). Influence of Repeated Prescribed Fire on Tree Growth and Mortality in Pinus resinosa Forests, Northern Minnesota. *Forest Science*, 63(1), 94–100. https://doi.org/10.5849/FORSCI.16-035

Bradshaw, S. D., Dixon, K. W., Lambers, H., Cross, A. T., Bailey, J., & Hopper, S. D. (2018). Understanding the long-term impact of prescribed burning in mediterranean-climate biodiversity hotspots, with a focus on south-western Australia. *International Journal of Wildland Fire*, 27(10), 643–657. https://doi.org/10.1071/WF18067

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63(6), 625–644. https://doi.org/10.1051/FOREST:2006042

Breda, N., Granier, A., & Aussenac, G. (1995). Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (Quercus petraea (Matt.) Liebl.). *Tree Physiology*, 15(5), 295–306. https://doi.org/10.1093/TREEPHYS/15.5.295

Breuer, M., & Devkota, B. (1990). Studies on the importance of nest temperature of Thaumetopoea pityocampa (Den. & Schiff.) (Lep., Thaumetopoeidae). *Journal of Applied Entomology*, 109(1–5), 331–335. https://doi.org/10.1111/J.1439-0418.1990.TB00060.X

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). {glmmTMB} Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2), 378−400. https://journal.r-project.org/archive/2017/RJ-2017-066/index.html

Buma, B. (2015). Disturbance interactions: Characterization, prediction, and the potential for cascading effects. *Ecosphere*, 6(4), 1–15. https://doi.org/10.1890/ES15-00058.1

Bunn, A. G. (2008). A Dendrochronology Program Library in R (DplR). *Dendrochronologia,* 26(2), 115−124. https://doi.org/10.1016/J.DENDRO.2008.01.002

Burgan, R.E., (1979). Estimating live fuel moisture for the 1978 National Fire Danger Rating System. Vol. 226. Intermountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture.

Burrows, N. (2000). Behaviour and some impacts of a large wildfire in the Gnangara maritime pine (*Pinus pinaster*) plantation, Western Australia. *CALMScience*, 3(2), 251−260.

Camm, E. (1993). Photosynthetic responses in developing and year-old Douglas-fir needles during new shoot development. *Trees*, 8(1), 61–66. https://doi.org/10.1007/BF00240983/METRICS

Canelles, Q., Aquilué, N., James, P. M. A., Lawler, J., & Brotons, L. (2021). Global review on interactions between insect pests and other forest disturbances. *Landscape Ecology*, 36(4), 945–972. https://doi.org/10.1007/S10980-021-01209-7/TABLES/2

Cannac, M., Barboni, T., Ferrat, L., Bighelli, A., Castola, V., Costa, J., Trecul, D., Morandini, F., & Pasqualini, V. (2009a). Oleoresin flow and chemical composition of Corsican pine (Pinus nigra subsp. laricio) in response to prescribed burnings. *Forest Ecology and Management*, 257(4), 1247–1254. https://doi.org/10.1016/J.FORECO.2008.11.017

Cannac, M., Pasqualini, V., Barboni, T., Morandini, F., & Ferrat, L. (2009b). Phenolic compounds of Pinus laricio needles: A bioindicator of the effects of prescribed burning in function of season. *Science of the Total Environment*, 407, 4542–4548.

Carter, M.C., & Foster, C. D. (2004). Prescribed Burning and Productivity in Southern Pine Forests: A Review. *Forest Ecology and Management*, 191(1-3), 93-109. https://doi.org/10.1016/j.foreco.2003.11.006

Casals, P., & Rios, A. I. (2018). Burning intensity and low light availability reduce resprouting ability and vigor of Buxus sempervirens L. after clearing. *Science of the Total Environment*, 627, 403−416. https://doi.org/10.1016/j.scitotenv.2018.01.227

Casals, P., Valor, T., Rios, A. I., & Shipley, B. (2018). Leaf and bark functional traits predict resprouting strategies of understory woody species after prescribed fires. *Forest Ecology and Management*, 429, 158–174. https://doi.org/10.1016/j.foreco.2018.07.002

Castagneri, D., Vacchiano, G., Hacket-Pain, A., DeRose, R. J., Klein, T., & Bottero, A. (2021). Meta-analysis Reveals Different Competition Effects on Tree Growth Resistance and Resilience to Drought. *Ecosystems* 25(1), 30-43. https://doi.org/10.1007/s10021-021-00638-4

Certini, G. (2005). Effects of fire on properties of forest soils: A review. *Oecologia*, 143(1), 1–10. https://doi.org/10.1007/S00442-004-1788-8/TABLES/2

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright, N. J., & Knox, K. J. E. (2013). Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist*, 197(1), 19–35. https://doi.org/10.1111/NPH.12001

Clyatt, K. A., Keyes, C. R., & Hood, S. M. (2017). Long-term effects of fuel treatments on aboveground biomass accumulation in ponderosa pine forests of the northern Rocky Mountains. *Forest Ecology and Management*, 400, 587–599. https://doi.org/10.1016/J.FORECO.2017.06.021

Cook, E. R., and Kenneth P. (1997). Calculating Unbiased Tree-Ring Indices for the Study of Climatic and Environmental Change. *Holocene,* 7(3), 361–70. https://doi.org/10.1177/095968369700700314

Cook, B. I., Anchukaitis, K. J., Touchan, R., Meko, D. M., & Cook, E. R. (2016). Spatiotemporal drought variability in the mediterranean over the last 900 years. *Journal of Geophysical Research*, 121(5), 2060−2074. https://doi.org/10.1002/2015JD023929

Cook, B. I., Mankin, J. S., & Anchukaitis, K. J. (2018). Climate Change and Drought: From Past to Future. *Current Climate Change Reports*, 4(2): 164−179. https://doi.org/10.1007/S40641-018-0093-2

Cruz, M. G., Alexander, M. E., & Dam, J. E. (2014). Using Modeled Surface and Crown Fire Behavior Characteristics to Evaluate Fuel Treatment Effectiveness: A Caution. *Forest Science*, 60(5), 1000−1004. https://doi.org/10.5849/FORSCI.13-719

Cruz, M. G., Alexander, M. E., & Wakimoto, R. H. (2003). Assessing canopy fuel stratum characteristics in crown fire prone fuel types of western North America. *International Journal of Wildland Fire*, 12(1), 39−50. https://doi.org/10.1071/WF02024

Davis, R. S., Hood, S. M., & Bentz, B. J. (2012). Fire-injured ponderosa pine provide a pulsed resource for bark beetles. *Canadian Journal of Forest Research*, 42(12), 2022–2036. https://doi.org/10.1139/x2012-147

Davis, K. T., Peeler, J., Fargione, J., Haugo, R. D., Metlen, K. L., Robles, M. D., & Woolley, T. (2024). Tamm review: A meta-analysis of thinning, prescribed fire, and wildfire effects on subsequent wildfire severity in conifer dominated forests of the Western US. *Forest Ecology and*

Management, 561, 121885. https://doi.org/10.1016/J.FORECO.2024.121885

De Boer, J. G., & Harvey, J. A. (2020). Range-Expansion in Processionary Moths and Biological Control. *Insects* 11(5), 267. https://doi.org/10.3390/INSECTS11050267

De Cáceres, M., Martínez-Vilalta, J., Coll, L., Llorens, P., Casals, P., Poyatos, R., Pausas, J. G., Brotons, L., De Cáceres, M., Martínez-Vilalta, J., Coll, L., Llorens, P., Casals, P., Poyatos, R., Pausas, J. G., & Brotons, L. (2015). Coupling a water balance model with forest inventory data to predict drought stress: The role of forest structural changes vs. climate changes. *Agricultural and Forest Meteorology*, 213, 77−90. https://doi.org/10.1016/j.agrformet.2015.06.012

De Cáceres, M., Martin-StPaul, N., Turco, M., Cabon, A., & Granda, V. (2018). Estimating daily meteorological data and downscaling climate models over landscapes. *Environmental Modelling and Software*, 108, 186−196. https://doi.org/10.1016/j.envsoft.2018.08.003

De Cáceres, M., Casals, P., Gabriel, E., & Castro, X. (2019). Scaling-up individual-level allometric equations to predict stand-level fuel loading in Mediterranean shrublands. *Annals of Forest Science*, 76(3), 1-17. https://doi.org/10.1007/s13595-019-0873-4

De Cáceres, M., Mencuccini, M., Martin-StPaul, N., Limousin, J. M., Coll, L., Poyatos, R., Cabon, A., Granda, V., Forner, A., Valladares, F., & Martínez-Vilalta, J. (2021). Unravelling the effect of species mixing on water use and drought stress in Mediterranean forests: A modelling approach. *Agricultural and Forest Meteorology*, 296, 108233. https://doi.org/10.1016/j.agrformet.2020.108233

De Cáceres, M., and Casals, P. (2023). Medfuels: Fuels of Mediterranean Forests and Shrublands.

De Magalhaes, R.M.Q., Schwilk, D.W., 2012. Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology*. 100 (5), 1153−1163. https://doi.org/10.1111/J.1365-2745.2012.01987.X

DeLuca, T. H., & Zouhar, K. L. (2000). Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. *Forest Ecology and Management*, 138(1–3), 263–271. https://doi.org/10.1016/S0378-1127(00)00401-1

Dickinson, M. B., & Johnson, E. A. (2004). Temperature-dependent rate models of vascular cambium cell mortality. *Canadian Journal of Forest Research*, 34(3), 546–559. https://doi.org/10.1139/X03-223

Duane, A., Castellnou, M., & Brotons, L. (2021). Towards a comprehensive look at global drivers of novel extreme wildfire events. *Climatic Change*, 165(3), 1–21. https://doi.org/10.1007/S10584-021-03066-4

Dulaurent, A.-M., Porté, A. J., Van Halder, I., Vétillard, F., Menassieu, P., & Jactel, H. (2011a). A case of habitat complementation in forest pests: Pine processionary moth pupae survive better in open areas. *Forest Ecology and Management*, 261, 1069–1076. https://doi.org/10.1016/j.foreco.2010.12.029

Dulaurent, A. M., Rossi, J. P., Deborde, C., Moing, A., Menassieu, P., & Jactel, H. (2011b). Honeydew feeding increased the longevity of two egg parasitoids of the pine processionary moth. *Journal of Applied Entomology*, 135(3), 184–194. https://doi.org/10.1111/J.1439-0418.2010.01547.X

Dupire, S., Curt, T., & Bigot, S. (2017). Spatio-temporal trends in fire weather in the French Alps. *Science of the Total Environment*, 595, 801–817. https://doi.org/10.1016/j.scitotenv.2017.04.027

Farjon, A. (2008). A natural history of conifers. Timber Press.

Farquhar, G. D., O'Leary, M. H., & Berry, J. A. (1982). On the Relationship Between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. *Australian Journal of Plant Physiology,* 9(2): 121−137. https://doi.org/10.1071/PP9820121

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon Isotope Discrimination and Photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology,* 40(1), 503−537. https://doi.org/10.1146/ANNUREV.PP.40.060189.002443

Fernandes, P. M., & Botelho, H. S. (2003). A review of prescribed burning effectiveness in fire hazard reduction. *International Journal of Wildland Fire*, 12(2), 117−128. https://doi.org/10.1071/WF02042

Fernandes, P. M., Vega, J. A., Jiménez, E., & Rigolot, E. (2008). Fire Resistance of European Pines. *Forest Ecology and Management,* 256(3), 246−55. https://doi.org/10.1016/j.foreco.2008.04.032

Fernandes, P. M., Barros, A. M. G., Pinto, A., & Santos, J. A. (2016). Characteristics and controls of extremely large wildfires in the western Mediterranean Basin. *Journal of Geophysical Research: Biogeosciences*, 121, 2141−2157. https://doi.org/10.1002/2016JG003389

Fernandes, P. M., Rossa, C., Madrigal, J., Rigolot, E., Ascoli, D., Hernando, C., Guimar, N., & Guijarro, M. (2022). Prescribed burning in the European Mediterranean Basin. In: Global Application of Prescribed Fire, CRC Press, Boca Raton, Florida, United States, 230-248.

Fernandes, T., Del Campo, A. D., Herrera, R., & Molina, A. J. (2016). Simultaneous Assessment, through Sap Flow and Stable Isotopes, of Water Use Efficiency (WUE) in Thinned Pines Shows Improvement in Growth, Tree-Climate Sensitivity and WUE, but Not in WUEi. *Forest Ecology and Management,* 361, 298−308. https://doi.org/10.1016/J.FORECO.2015.11.029

Fernández, C., Vega, J. A., & Fonturbel, T. (2015). Does shrub recovery differ after prescribed burning, clearing and mastication in a Spanish heathland? Plant Ecology, 216(3), 429–437. https://doi.org/10.1007/S11258-015-0447-Y/FIGURES/4

Ferrenberg, S., Vázquez-González, C., Lee, S. R., & Kristupaitis, M. (2023). Divergent growth-differentiation balance strategies and resource competition shape mortality patterns in ponderosa pine. *Ecosphere*, 14(1), e4349. https://doi.org/10.1002/ECS2.4349

Fettig, C. J., Klepzig, K. D., Billings, R. F., Munson, A. S., Nebeker, T. E., Negrón, J. F., & Nowak, J. T. (2007). The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management*, 238, 24–53. https://doi.org/10.1016/j.foreco.2006.10.011

Fettig, C. J., Runyon, J. B., Homicz, C. S., James, P. M. A., & Ulyshen, M. D. (2022). Fire and Insect Interactions in North American Forests. *Current Forestry Reports*, 8(4), 301–316. https://doi.org/10.1007/S40725-022-00170-1/FIGURES/2

Field, J. P., Breshears, D. D., Bradford, J. B., Law, D. J., Feng, X., & Allen, C. D. (2020). Forest Management Under Megadrought: Urgent Needs at Finer Scale and Higher Intensity. *Frontiers in Forests and Global Change,* 3, 140. https://doi.org/10.3389/FFGC.2020.502669/BIBTEX

Fowler, J. F., Sieg, C. H., McMillin, J., Allen, K. K., Negrón, J. F., Wadleigh, L. L., Anhold, J. A., & Gibson, K. E. (2010). Development of post-fire crown damage mortality thresholds in ponderosa pine. *International Journal of Wildland Fire*, 19(5), 583–588. https://doi.org/10.1071/WF08193

Franceschi, V. R., Krokene, P., Christiansen, E., & Krekling, T. (2005). Anatomical and chemical defenses of conifer bark against bark beetles and other pests.

New Phytologist, 167(2), 353–376. https://doi.org/10.1111/J.1469-8137.2005.01436.X

Frank, D. C., Poulter, B., Saurer, M., Esper, J., Huntingford, C., Helle, G., Treydte, K., Zimmermann, N. E., Schleser, G. H., Ahlström, A., Ciais, P., Friedlingstein, P., Levis, S., Lomas, M., Sitch, S., Viovy, N., Andreu-Hayles, L., Bednarz, Z., Berninger, F., Boettger, T., D'Alessandro, C.M., Daux, V., Filot, M., Grabner, M., Gutierrez, E., Haupt, M., Hilasvuori, E., Jungner, H., Kalela-Brundin, M., Krapiec, M., Leuenberger, M., Loader, N. J., Marah, H., Masson-Delmotte, V., Pazdur, A., Pawelczyk, S., Pierre, M., Planells, O., Pukiene, R., Reynolds-Henne, C. E., Rinne, K. T., Saracino, A., Sonninen, E., Stievenard, M., Switsur, V. R., Szczepanek, M., Szychowska-Krapiec, E., Todaro, L., Waterhouse, J. S., & Weigl, M. (2015). Water-Use Efficiency and Transpiration across European Forests during the Anthropocene. *Nature Climate Change,* 5(6), 579−583. https://doi.org/10.1038/nclimate2614

Fulé, P. Z., Crouse, J. E., Roccaforte, J. P., & Kalies, E. L. (2012). Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management*, 269, 68−81. https://doi.org/10.1016/J.FORECO.2011.12.025

Gaylord, M. L., Kolb, T. E., Pockman, W. T., Plaut, J. A., Yepez, E. A., Macalady, A. K., Pangle, R. E., & Mcdowell, N. G. (2013). Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytologist*, 198(2), 567–578. https://doi.org/10.1111/NPH.12174

Gaylord, M. L., Kolb, T. E., Wallin, K. F., & Wagner, M. R. (2006). Seasonality and Lure Preference of Bark Beetles (Curculionidae: Scolytinae) and Associates in a Northern Arizona Ponderosa Pine Forest. *Environmental Entomology*, 35(1), 37–47. https://doi.org/10.1603/0046-225X-35.1.37

Gazol, A, Camarero, J. J., Sangüesa-Barreda, G., Serra-Maluquer, X., Sánchez-Salguero, R., Coll, L., & Casals, P. (2020). Tree Species Are Differently Impacted by Cumulative Drought Stress and Present Higher Growth Synchrony in Dry Places. *Frontiers in Forests and Global Change,* 3, 128. https://doi.org/10.3389/FFGC.2020.573346/BIBTEXGebhardt, T., Haeberle, K. H., Matyssek, R., Schulz, C., Ammer, C., Häberle, K. H., Matyssek, R., Schulz, C., & Ammer, C. (2014). The more, the better? Water relations of Norway spruce stands after progressive thinning. *Agricultural and Forest Meteorology*, 197, 235−243. https://doi.org/10.1016/J.AGRFORMET.2014.05.013

Gelman, A., & Hill, J. (2007). Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press.

Gessler, A., Bottero, A., Marshall, J., & Arend, M. (2020). The Way Back: Recovery of Trees from Drought and Its Implication for Acclimation. *New Phytologist* 228(6), 1704−1709. https://doi.org/10.1111/NPH.16703

Giuggiola, A., Ogée, J., Rigling, A., Gessler, A., Bugmann, H., & Treydte, K. (2016). Improvement of Water and Light Availability after Thinning at a Xeric Site: Which Matters More? A Dual Isotope Approach. *New Phytologist,* 210(1), 108−121. https://doi.org/10.1111/NPH.13748

Giuggiola, A., Zweifel, R., Feichtinger, L. M., Vollenweider, P., Bugmann, H., Haeni, M., & Rigling, A. (2018). Competition for water in a xeric forest ecosystem − Effects of understory removal on soil micro-climate, growth and physiology of dominant Scots pine trees. *Forest Ecology and Management*, 409, 241−249. https://doi.org/10.1016/j.foreco.2017.11.002

Gomez-Gallego, M., Williams, N., Leuzinger, S., Scott, P. M., & Bader, M. K. F. (2020). No carbon limitation after lower crown loss in Pinus radiata. *Annals of Botany*, 125(6), 955–967. https://doi.org/10.1093/AOB/MCAA013

Gong, X. Y., Ma, W. T., Yu, Y. Z., Fang, K., Yang, Y., Tcherkez, G., & Adams, M. A. (2022). Overestimated Gains in Water-Use Efficiency by Global Forests. *Global Change Biology,* 28(16), 4923−4934. https://doi.org/10.1111/GCB.16221

Guenther, A. B., Zimmerman, P. R., Harley, P. C., Monson, R. K., & Fall, R. (1993). Isoprene and monoterpene emission rate variability: Model evaluations and sensitivity analyses. *Journal of Geophysical Research: Atmospheres*, 98(D7), 12609–12617. https://doi.org/10.1029/93JD00527

Guerrieri, R., Mencuccini, M., Sheppard, L. J., Saurer, M., Perks, M. P., Levy, P., Sutton, M. A., Borghetti, M., & Grace, J. (2011). The Legacy of Enhanced N and S Deposition as Revealed by the Combined Analysis of ∆13C, ∆18O and ∆15N in Tree Rings. *Global Change Biology*, 17(5), 1946−1962. https://doi.org/10.1111/J.1365-2486.2010.02362.X

Harrington, R., Fleming, R. A., & Woiwod, I. P. (2001). Climate change impacts on insect management and conservation in temperate regions: can they be predicted? *Agricultural and Forest Entomology*, 3(4), 233–240. https://doi.org/10.1046/J.1461-9555.2001.00120.X

Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. https://cran.r-project.org/package=DHARMa

Haukioja, E., Ossipov, V., Koricheva, J., Honkanen, T., Larsson, S., & Lempa, K. (1998). Biosynthetic origin of carbon-based secondary compounds: Cause of variable responses of woody plants to fertilization? *Chemoecology*, 8(3), 133–139. https://doi.org/10.1007/S000490050018/METRICS

Herms, D. A., & Mattson, W. J. (1992). The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology*, 67(3), 283–335. https://doi.org/10.1086/417659

Hódar, J. A., Zamora, R., & Castro, J. (2002). Host utilisation by moth and larval survival of pine processionary caterpillar Thaumetopoea pityocampa in relation to food quality in three Pinus species. *Ecological Entomology*, 27(3), 292–301. https://doi.org/10.1046/J.1365-2311.2002.00415.X

Hódar, J. A., & Zamora, R. (2004). Herbivory and climatic warming: A Mediterranean outbreaking caterpillar attacks a relict, boreal pine species. *Biodiversity and Conservation*, 13(3), 493–500. https://doi.org/10.1023/B:BIOC.0000009495.95589.A7/METRICS

Hódar, J. A., Zamora, R., Castro, J., & Baraza, E. (2004). Feast and famine: previous defoliation limiting survival of pine processionary caterpillar Thaumetopoea pityocampa in Scots pine Pinus sylvestris. *Acta Oecologica*, 26(3), 203–210. https://doi.org/10.1016/J.ACTAO.2004.05.004

Hódar, J. A., Torres-Muros, L., Zamora, R., Pérez-Luque, A. J., & Senhadji, K. (2015). No evidence of induced defence after defoliation in three pine species against an expanding pest, the pine processionary moth. *Forest Ecology and Management*, 356, 166–172. https://doi.org/10.1016/J.FORECO.2015.07.022

Holmes, R. L. (1983). Computer-Assisted Quality Control in Tree-Ring Dating & Measurement. *Tree-Ring Bulletin,* 43, 69−75. http://hdl.handle.net/10150/261223

Hood, S. M., & Sala, A. (2015). Ponderosa pine resin defenses and growth: metrics matter. *Tree Physiology*, 35(11), 1223–1235. https://doi.org/10.1093/TREEPHYS/TPV098

Hood, S. M., Sala, A., Heyerdahl, E. K., Boutin, M., & Raffa, K. F. (2015). Low-severity fire increases tree defense against bark beetle attacks. *Ecology*, 96(7), 1846–1855. https://doi.org/10.1890/14-0487.1

Hood, S. M., Baker, S., & Sala, A. (2016). Fortifying the forest: Thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. *Ecological Applications*, 26(7), 1984–2000. https://doi.org/10.2737/RDS-2016-0010

Hood, S. M., Varner, J. M., Van Mantgem, P., & Cansler, C. A. (2018). Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters*, 13(11), 113004. https://doi.org/10.1088/1748-9326/AAE934

Hood, S. M., Keyes, C. R., Bowen, K. J., Lutes, D. C., & Seielstad, C. (2020a). Fuel treatment longevity in ponderosa pine-dominated forest 24 years after cutting and prescribed burning. *Frontiers in Forests and Global Change*, 3. https://doi.org/10.3389/ffgc.2020.00078

Hood, S. M., Reed, C. C., & Kane, J. M. (2020b). Axial resin duct quantification in tree rings: A functional defense trait. *MethodsX*, 7, 101035. https://doi.org/10.1016/J.MEX.2020.101035

Hudgins, J. W., & Franceschi, V. R. (2004). Methyl Jasmonate-Induced Ethylene Production Is Responsible for Conifer Phloem Defense Responses and Reprogramming of Stem Cambial Zone for Traumatic Resin Duct Formation. *Plant Physiology*, 135(4), 2134–2149. https://doi.org/10.1104/PP.103.037929

ICGC, 2018. Foc al Bosc: Visor incendis forestals Catalunya 1986-2017. Institut Cartogràfic i Geològic de Catalunya. https://visors.icgc.cat/focalbosc/

Jackson, P. L., Straussfogel, D., Lindgren, B. S., Mitchell, S., & Murphy, B. (2008). Radar observation and aerial capture of mountain pine beetle, Dendroctonus ponderosae Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Canadian Journal of Forest Research*, 38(8), 2313–2327. https://doi.org/10.1139/X08-066/ASSET/IMAGES/LARGE/X08-066F7.JPEG

Jactel, H., Nicoll, B. C., Branco, M., Gonzalez-Olabarria, J. R., Grodzki, W., Långström, B., Moreira, F., Netherer, S., Christophe Orazio, C., Piou, D., Santos, H., Schelhaas, M. J., Tojic, K., & Vodde, F. (2009). The influences of forest stand management on biotic and abiotic risks of damage. *Annals of Forest Science*, 66(7), 701–701. https://doi.org/10.1051/FOREST/2009054

Jaime, L., Batllori, E., Ferretti, M., & Lloret, F. (2022). Climatic and stand drivers of forest resistance to recent bark beetle disturbance in European coniferous forests. *Global Change Biology*, 28(8), 2830–2841. https://doi.org/10.1111/GCB.16106

Jang, W., Crotteau, J. S., Ortega, Y. K., Hood, S. M., Keyes, C. R., Pearson, D. E., Lutes, D. C., & Sala, A. (2021). Native and non-native understory vegetation responses to restoration treatments in a dry conifer forest over 23 years. *Forest Ecology and Management*, 481, 118684. https://doi.org/10.1016/J.FORECO.2020.118684

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L. W., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14(7), 369–378. https://doi.org/10.1002/FEE.1311

Jönsson, A. M., Appelberg, G., Harding, S., & Bärring, L. (2009). Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, Ips typographus. *Global Change Biology*, 15(2), 486–499. https://doi.org/10.1111/J.1365-2486.2008.01742.X

Kane, J. M., & Kolb, T. E. (2010). Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia*, 164(3), 601–609. https://doi.org/10.1007/S00442-010-1683-4/FIGURES/2

Keane, R.E., Gray, K., (2013). Comparing three sampling techniques for estimating fine woody down dead biomass. *International Journal of Wildland Fire,* 22, 1093−1107. https://doi.org/10.1071/WF13038

Keane, R. E. (2015). Wildland Fuel Fundamentals and Application. Springer International Publishing Switzerland.

Keane, R. E., Mckenzie, D., Falk, D. A., Smithwick, E. A. H., Miller, C., & Kellogg, L.-K. B. (2015). Representing climate, disturbance, and vegetation interactions in landscape models. *Ecological Modelling*, 309, 33–47. https://doi.org/10.1016/j.ecolmodel.2015.04.009

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire*, 18(1), 116–126. https://doi.org/10.1071/WF07049

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16(8), 406–411. https://doi.org/10.1016/j.tplants.2011.04.002

Kerr, K. L., Meinzer, F. C., Mcculloh, K. A., Woodruff, D. R., & Marias, D. E. (2015). Expression of functional traits during seedling establishment in two populations of Pinus ponderosa from contrasting climates. *Tree Physiology*, 35(5), 535–548. https://doi.org/10.1093/TREEPHYS/TPV034

Kichas, N. E., Hood, S. M., Pederson, G. T., Everett, R. G., & McWethy, D. B. (2020). Whitebark pine (Pinus albicaulis) growth and defense in response to mountain pine beetle outbreaks. *Forest Ecology and Management*, 457, 117736. https://doi.org/10.1016/J.FORECO.2019.117736

Kleiber, A., Duan, Q., Jansen, K., Junker, L. V., Kammerer, B., Rennenberg, H., Ensminger, I., Gessler, A., & Kreuzwieser, J. (2017). Drought effects on root and needle terpenoid content of a coastal and an interior Douglas fir provenance. *Tree Physiology*, 37(12), 1648–1658. https://doi.org/10.1093/TREEPHYS/TPX113

Klesse, S. (2021). Critical Note on the Application of the 'Two-Third' Spline. *Dendrochronologia*, 65, 125786. https://doi.org/10.1016/J.DENDRO.2020.125786

Knapp, E., Estes, B., & Skinner, C. (2009). Ecological Effects of Prescribed Fire Season: A Literature Review and Synthesis for Managers. In Joint Fire Science Program Synthesis Reports. https://digitalcommons.unl.edu/jfspsynthesis/4

Knapp, E. E., Skinner, C. N., North, M. P., & Estes, B. L. (2013). Long-Term Overstory and Understory Change Following Logging and Fire Exclusion in a Sierra Nevada Mixed-Conifer Forest. *Forest Ecology and Management,* 310, 903−914. https://doi.org/10.1016/j.foreco.2013.09.041

Knebel, L., & Wentworth, T. R. (2007). Influence of Fire and Southern Pine Beetle on Pine-Dominated Forests in The Linville Gorge Wilderness, North Carolina. *Castanea*, 72(4), 214–225. https://doi.org/10.2179/06-18.1

Knowles, N., Dettinger, M. D., & Cayan, D. R. (2006). Trends in Snowfall versus Rainfall in the Western United States. *Journal of Climate*, 19(18), 4545–4559. https://doi.org/10.1175/JCLI3850.1

Kobziar, L., Moghaddas, J., & Stephens, S. L. (2006). Tree Mortality Patterns Following Prescribed Fires in a Mixed Conifer Forest. *Canadian Journal of Forest Research,* 36(12), 3222−3238. https://doi.org/10.1139/X06-183

Kolb, T. E., Agee, J. K., Fulé, P. Z., McDowell, N. G., Pearson, K., Sala, A., & Waring, R. H. (2007). Perpetuating old ponderosa pine. *Forest Ecology and Management*, 249(3), 141–157. https://doi.org/10.1016/J.FORECO.2007.06.002

Kolb, T. E., Grady, K. C., McEttrick, M. P., & Herrero, A. (2016). Local-Scale Drought Adaptation of Ponderosa Pine Seedlings at Habitat Ecotones. *Forest Science*, 62(6), 641–651. https://doi.org/10.5849/FORSCI.16-049

Korb, J. E., Fornwalt, P. J., & Stevens-Rumann, C. S. (2019). What drives ponderosa pine regeneration following wildfire in the western United States? *Forest Ecology and Management,* 454, 117663. https://doi.org/10.1016/j.foreco.2019.117663

Kopaczyk, J. M., Warguła, J., & Jelonek, T. (2020). The variability of terpenes in conifers under developmental and environmental stimuli. *Environmental and Experimental Botany*, 180, 104197. https://doi.org/10.1016/J.ENVEXPBOT.2020.104197

Kress, A., Young, G. H. F., Saurer, M., Loader, N. J., Siegwolf, R. T. W., & McCarroll, D. (2009). Stable Isotope Coherence in the Earlywood and Latewood of Tree-Line Conifers. *Chemical Geology,* 268(1−2), 52−57. https://doi.org/10.1016/J.CHEMGEO.2009.07.008

Lambers, H., & Oliveira, R. S. (2019). Plant Physiological Ecology. Springer Nature Switzerland AG. https://doi.org/10.1016/B978-008045405-4.00819-3

Land, A. D., & Rieske, L. K. (2006). Interactions among prescribed fire, herbivore pressure and shortleaf pine (Pinus echinata) regeneration following southern pine beetle (Dendroctonus frontalis) mortality. *Forest Ecology and Management*, 235, 260–269. https://doi.org/10.1016/j.foreco.2006.08.336

Langenheim, J. H. (2003). Plant Resins: Chemistry, Evolution, Ecology, and Ethnobotany. Timber Press.

Lavoir, A. V., Ormeño, E., Pasqualini, V., Ferrat, L., Greff, S., Lecareux, C., Vila, B., Mévy, J. P., & Fernandez, C. (2013). Does Prescribed Burning Affect Leaf Secondary Metabolites in Pine Stands? *Journal of Chemical Ecology*, 39(3), 398–412. https://doi.org/10.1007/S10886-013-0256-5

Lecina-Diaz, J., Martínez-Vilalta, J., Lloret, F., & Seidl, R. (2024). Resilience and vulnerability: distinct concepts to address global change in forests. *Trends in Ecology & Evolution*, 39(8), 706–715. https://doi.org/10.1016/j.tree.2024.03.003

Lenth, R. V. (2023). Emmeans: Estimated Marginal Means, Aka Least-Squares Means. https://CRAN.R-project.org/package=emmeans

Leuning, R., Cromer, R. N., & Rance, S. (1991). Spatial distributions of foliar nitrogen and phosphorus in crowns of Eucalyptus grandis. *Oecologia*, 88(4), 504–510. https://doi.org/10.1007/BF00317712/METRICS

Lewinsohn, E., Gijzen, M., & Croteau, R. (1991). Defense Mechanisms of Conifers Differences in Constitutive and Wound-Induced Monoterpene Biosynthesis Among Species. *Plant Physiology*, 96(1), 44–49. https://doi.org/10.1104/PP.96.1.44

Linares, J. C., Senhadji, K., Herrero, A., & Hódar, J. A. (2014). Growth patterns at the southern range edge of Scots pine: Disentangling the effects of drought and defoliation by the pine processionary caterpillar. *Forest Ecology and Management*, 315, 129–137. https://doi.org/10.1016/J.FORECO.2013.12.029

Linn, R., Reisner, J., Colman, J.J., Winterkamp, J., 2002. Studying wildfire behavior using FIRETEC. *International Journal of Wildland Fire,* 11 (4), 233−246. https://doi.org/10.1071/WF02007

Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of Tree Resilience: Effects of Successive Low-Growth Episodes in Old Ponderosa Pine Forests. *Oikos,* 120, 1909−1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x

Llusià, J., & Peñuelas, J. (1998). Changes in terpene content and emission in potted Mediterranean woody plants under severe drought. *Canadian Journal of Botany*, 76(8), 1366–1373. https://doi.org/10.1139/B98-141

Llusià, J., Peñuelas, J., Alessio, G. A., & Estiarte, M. (2006). Seasonal contrasting changes of foliar concentrations of terpenes and other volatile organic compound in four dominant species of a Mediterranean shrubland submitted to a field experimental drought and warming. *Physiologia Plantarum*, 127(4), 632–649. https://doi.org/10.1111/J.1399-3054.2006.00693.X

Loader, N. J., Robertson, I., Barker, A. C., Switsur, V.R., & Waterhouse, J. S. (1997). An Improved Technique for the Batch Processing of Small Wholewood Samples to α-Cellulose. *Chemical Geology,* 136(3−4), 313−317. https://doi.org/10.1016/S0009-2541(96)00133-7

Lombardero, M. J., Ayres, M. P., & Ayres, B. D. (2006). Effects of fire and mechanical wounding on Pinus resinosa resin defenses, beetle attacks, and pathogens. *Forest Ecology and Management*, 225(1–3), 349–358. https://doi.org/10.1016/J.FORECO.2006.01.010

Lombardero, M. J., & Ayres, M. P. (2011). Factors Influencing Bark Beetle Outbreaks After Forest Fires on the Iberian Peninsula. *Environmental Entomology*, 40(5), 1007–1018. https://doi.org/10.1603/EN11022

Lombardero, M. J., Pereira-Espinel, J., & Ayres, M. P. (2013). Foliar terpene chemistry of Pinus pinaster and P. radiata responds differently to Methyl Jasmonate and feeding by larvae of the pine processionary moth. *Forest Ecology and Management*, 310, 935–943. https://doi.org/10.1016/J.FORECO.2013.09.048

Luo, X., Keenan, T. F., Chen, J. M., Croft, H., Prentice, I. C., Smith, N. G., Walker, A. P., Wang, H., Wang, R., Xu, C & Zhang, Y. (2021). Global Variation in the Fraction of Leaf Nitrogen Allocated to Photosynthesis. *Nature Communications,* 12(1), 1−10. https://doi.org/10.1038/s41467-021-25163-9

Ma, W. T., Tcherkez, G., Wang, X. M., Schäufele, R., Schnyder, H., Yang, Y., & Gong, X. Y. (2021). Accounting for Mesophyll Conductance Substantially Improves 13 C-Based Estimates of Intrinsic Water-Use Efficiency. *The New Phytologist,* 229(3), 1326−1338. https://doi.org/10.1111/NPH.16958

Mäkipää, R., Abramoff, R., Adamczyk, B., Baldy, V., Biryol, C., Bosela, M., Casals, P., Curiel Yuste, J., Dondini, M., Filipek, S., Garcia-Pausas, J., Gros, R., Gömöryová, E., Hashimoto, S., Hassegawa, M., Immonen, P., Laiho, R., Li, H., Li, Q., … Lehtonen, A. (2023). How does management affect soil C sequestration and greenhouse gas fluxes in boreal and temperate forests? – A review. *Forest Ecology and Management*, 529, 120637. https://doi.org/10.1016/J.FORECO.2022.120637

Malone, S. C., Thompson, R. A., Chow, P. S., de Oliveira, C. R., Landhäusser, S. M., Six, D. L., McCulloh, K. A., Adams, H. D., & Trowbridge, A. M. (2024). Water, not carbon, drives drought-constraints on stem terpene defense against simulated bark beetle attack in Pinus edulis. *New Phytologist*, 341(1), 318-331. https://doi.org/10.1111/NPH.20218

Manrique-Alba, A., Beguería, S., Molina, A. J., González-Sanchis, M., Tomàs-Burguera, M., del Campo, A. D., Colangelo, M., & Camarero, J. J. (2020). Long-Term Thinning Effects on Tree Growth, Drought Response and Water Use Efficiency at Two Aleppo Pine Plantations in Spain. *Science of the Total Environment,* 728, 138536. https://doi.org/10.1016/j.scitotenv.2020.138536

Mantero, G., Morresi, D., Marzano, R., Motta, R., Mladenoff, D. J., & Garbarino, M. (2020). The influence of land abandonment on forest disturbance regimes: a global review. *Landscape Ecology*, 35, 2723−2744. https://doi.org/10.1007/s10980-020-01147-w

Martin, J. G. A., Nussey, D. H., Wilson, A. J., & Réale, D. (2011). Measuring Individual Differences in Reaction Norms in Field and Experimental Studies: A Power Analysis of Random Regression Models. *Methods in Ecology and Evolution,* 2(4), 362−374. https://doi.org/10.1111/J.2041-210X.2010.00084.X

Martin, J., Looker, N., Hoylman, Z., Jencso, K., & Hu, J. (2018). Differential use of winter precipitation by upper and lower elevation Douglas fir in the Northern Rockies. *Global Change Biology*, 24(12), 5607–5621. https://doi.org/10.1111/GCB.14435

Martin, L. (2024). Aerial Insect and Disease Detection Survey. USFS Aerial Detection Survey. https://www.fs.usda.gov/detail/r1/forest-grasslandhealth/?cid=stelprdb5410518

Martín-Alcón, S., & Coll, L. (2016). Unraveling the relative importance of factors driving post-fire regeneration trajectories in non-serotinous Pinus nigra forests. *Forest Ecology and Management*, 361, 13–22. https://doi.org/10.1016/j.foreco.2015.11.006

Martín-Benito, D., Cherubini, P., del Río, M., & Cañellas, I. (2008). Growth Response to Climate and Drought in Pinus Nigra Arn. Trees of Different Crown Classes. *Trees,* 22(3), 363−373. https://doi.org/10.1007/S00468-007-0191-6

Martín-Benito, D., del Río, M., Heinrich, I., Helle, G., & Cañellas, I. (2010). Response of climate-growth relationships and water use efficiency to thinning in a Pinus nigra afforestation. *Forest Ecology and Management,* 259(5), 967−975. https://doi.org/10.1016/J.FORECO.2009.12.001

Mason, C. J., Keefover-Ring, K., Villari, C., Klutsch, J. G., Cook, S., Bonello, P., Erbilgin, N., Raffa, K. F., & Townsend, P. A. (2019). Anatomical defences against bark beetles relate to degree of historical exposure between species and are allocated independently of chemical defences within trees. *Plant, Cell & Environment*, 42(2), 633–646. https://doi.org/10.1111/PCE.13449

Mathias, J. M., & Hudiburg, T. W. (2022). IsocalcR: An R package to streamline and standardize stable isotope calculations in ecological research. *Global Change Biology,* 28(24), 7428−7436. https://doi.org/10.1111/GCB.16407

Mattson, W. J. (1980). Herbivory in Relation to Plant Nitrogen Content. *Annual Review of Ecology, Evolution, and Systematics*, 11, 119–161. https://doi.org/10.1146/ANNUREV.ES.11.110180.001003

McDowell, N. G., Allen, C. D., & Marshall, L. (2010). Growth, carbon-isotope discrimination, and drought-associated mortality across a Pinus ponderosa elevational transect. *Global Change Biology*, 16(1), 399–415. https://doi.org/10.1111/J.1365-2486.2009.01994.X

McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*, 26(10), 523–532. https://doi.org/10.1016/J.TREE.2011.06.003

McDowell, N. G., Sapes, G., Pivovaroff, A., Adams, H. D., Allen, C. D., Anderegg, W. R. L., Arend, M., Breshears, D. D., Brodribb, T., Choat, B., Cochard, H., De Cáceres, M., De Kauwe, M. G., Grossiord, C., Hammond, W. M., Hartmann, H., Hoch, G., Kahmen, A., Klein, T., … Xu, C. (2022). Mechanisms of woody-plant mortality under rising drought, CO2 and vapour pressure deficit. *Nature Reviews Earth & Environment*, 3(5), 294–308. https://doi.org/10.1038/s43017-022-00272-1

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Mell, W., McDermott, R., Forney, G., 2010. Wildland fire behavior modeling: perspectives, new approaches and applications. Proceedings of 3rd Fire Behavior and Fuels Conference, 2010, Spokane, Washington, USA

Moreira, F., Viedma, O., Arianoutsou, M., Curt, T., Koutsias, N., Rigolot, E., Barbati, A., Corona, P., Vaz, P., Xanthopoulos, G., Mouillot, F., & Bilgili, E. (2011). Landscape - wildfire interactions in southern Europe: Implications for landscape management. *Journal of Environmental Management,* 92, 2389–2402, https://doi.org/10.1016/j.jenvman.2011.06.028

Moreno-Gutiérrez, C., Barberá, G. G., Nicolás, E., De Luis, M., Castillo, V. M., Martínez-Fernández, F., & Querejeta, J. I. (2011). Leaf ∆18O of remaining trees is affected by thinning intensity in a semiarid pine forest. *Plant, Cell & Environment,* 34(6), 1009−1019. https://doi.org/10.1111/J.1365-3040.2011.02300.X

Moreno-Gutiérrez, C., Dawson, T. E., Nicolás, E., & Querejeta, J. I. (2012). Isotopes reveal contrasting water use strategies among coexisting plant species in a Mediterranean ecosystem. *New Phytologist*, 196(2), 489–496. https://doi.org/10.1111/J.1469-8137.2012.04276.X

Mott, C. M., Hofstetter, R. W., & Antoninka, A. J. (2021). Post-harvest slash burning in coniferous forests in North America: A review of ecological impacts. *Forest Ecology and Management*, 493, 119251. https://doi.org/10.1016/j.foreco.2021.119251

Mumm, R., & Hilker, M. (2006). Direct and indirect chemical defence of pine against folivorous insects. *Trends in Plant Science*, 11(7), 351–358. https://doi.org/10.1016/J.TPLANTS.2006.05.007

Nardini, A., Lo Gullo, M. A., Trifilò, P., & Salleo, S. (2014). The challenge of the Mediterranean climate to plant hydraulics: Responses and adaptations. *Environmental and Experimental Botany*, 103, 68–79. https://doi.org/10.1016/J.ENVEXPBOT.2013.09.018

Netherer, S., Matthews, B., Katzensteiner, K., Blackwell, E., Henschke, P., Hietz, P., Pennerstorfer, J., Rosner, S., Kikuta, S., Schume, H., & Schopf, A. (2015). Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist*, 205(3), 1128–1141. https://doi.org/10.1111/NPH.13166

Netherer, S., & Schopf, A. (2010). Potential effects of climate change on insect herbivores in European forests-General aspects and the pine processionary moth as specific example. *Forest Ecology and Management*, 259, 831–838. https://doi.org/10.1016/j.foreco.2009.07.034

Niccoli, A., Panzavolta, T., Marziali, L., Sabbatini Peverieri, G., Florenzano, G. T., & Tiberi, R. (2008). Further studies on the role of monoterpenes in pine host selection and oviposition of Thaumetopoea pityocampa. *Phytoparasitica*, 36(4), 313–321. https://doi.org/10.1007/BF02980810/METRICS

Nieman, W. A., Van Wilgen, B. W., & Leslie1, A. J. (2021). A review of fire management practices in African savanna-protected areas. *Koedoe*, 63(1), 13. https://doi.org/10.4102/KOEDOE.V63I1.1655

Nolan, R. H., Reed, C. C., & Hood, S. M. (2024). Mechanisms of fire-caused tree death are far from resolved. *Tree Physiology*, 44(7). https://doi.org/10.1093/TREEPHYS/TPAE073

Norman, J. M., & Campbell, G. S. (1989). Canopy Structure. In R. E. Percy, J. R. Ehleringer, H. A. Mooney, & P. W. Rundel (Eds.), Plant Physiological Ecology: Field methods and instrumentation (pp. 301−325). Springer.

Oliver, W. W., & Ryker, R. A. (1990). Pinus ponderosa Dougl. ex Laws. ponderosa pine. In Silvics of North America (Vol. 654, p. 413).

Pallardy, S. G. (2008). Physiology of Woody Plants.

Panzavolta, T., Tellini Florenzano, G., & Tiberi, R. (2015). Pine monoterpene deterrence of pine processionary moth oviposition. *Urban Forestry & Urban Greening*, 14(3), 538–543. https://doi.org/10.1016/J.UFUG.2015.05.004

Pausas, J. G. (2004). Changes in fire and climate in the Eastern Iberian Peninsula (Mediterranean Basin). *Climatic Change*, 63, 337−350.

Peltier, D. M. P., & Ogle, K. (2020). Tree growth sensitivity to climate is temporally variable. *Ecology Letters*, 23(11), 1561–1572. https://doi.org/10.1111/ELE.13575

Penman, H. L. (1948). Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of London. Series A. Mathematical and Physical Sciences,* 193(1032), 120−145. https://doi.org/10.1098/RSPA.1948.0037

Perrakis, D. D. B., Agee, J. K., & Eglitis, A. (2011). Effects of prescribed burning on mortality and resin defenses in old growth ponderosa pine (Crater Lake, Oregon): Four years of post-fire monitoring. *Natural Areas Journal*, 31(1), 14–25. https://doi.org/10.3375/043.031.0103

Peters, G., & Sala, A. (2008). Reproductive output of ponderosa pine in response to thinning and prescribed burning in western Montana. *Canadian Journal of Forest Research*, 38(4), 844–850. https://doi.org/10.1139/X07-203/ASSET/IMAGES/X07-203T2H.GIF

Petrucco, L., Nardini, A., von Arx, G., Saurer, M., & Cherubini, P. (2017). Isotope signals and anatomical features in tree rings suggest a role for hydraulic strategies in diffuse drought-induced die-back of Pinus nigra. *Tree Physiology*, 37(4), 523–535. https://doi.org/10.1093/TREEPHYS/TPX031

Pimm, S. L. (1991). The balance of nature? ecological issues in the conservation of species and communities. University of Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/B/bo3684491.html

Piqué, M., & Domènech, R. (2018). Effectiveness of mechanical thinning and prescribed burning on fire behavior in Pinus nigra forests in NE Spain. *Science of the Total Environment*, 618, 1539−1546. https://doi.org/10.1016/j.scitotenv.2017.09.316

Powell, E. N., & Raffa, K. F. (2011). Fire Injury Reduces Inducible Defenses of Lodgepole Pine against Mountain Pine Beetle. *Journal of Chemical Ecology*, 37(11), 1184–1192. https://doi.org/10.1007/S10886-011-0031-4/METRICS

Powell, E. N., Townsend, P. A., & Raffa, K. F. (2012). Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. *Ecological Monographs*, 82(1), 69–84. https://doi.org/10.1890/11-0607.1

Pretzsch, H. (2020). Density and growth of forest stands revisited. Effect of the temporal scale of observation, site quality, and thinning. *Forest Ecology and Management*, 460, 117879. https://doi.org/10.1016/J.FORECO.2020.117879

Prichard, S. J., Andreu, A., Eagle, P., Swedin, K., Sandberg, D. V., Ottmar, R. D., & Eberhardt, E. (2013). Fuel characteristic classification system version 3.0: Technical documentation. USDA Forest Service - General Technical Report PNW-GTR, 887 GTR, 1−79.

Prichard, S.J., Povak, N.A., Kennedy, M.C., & Peterson, D.W., (2020). Fuel treatment effectiveness in the context of landform, vegetation, and large, wind-driven wildfires. *Ecological Applications*, 30 (5), 1−22. https://doi.org/10.1002/eap.2104

Prichard, S. J., Hessburg, P. F., Hagmann, R. K., Povak, N. A., Dobrowski, S. Z., Hurteau, M. D., Kane, V. R., Keane, R. E., Kobziar, L. N., Kolden, C. A., North, M., Parks, S. A., Safford, H. D., Stevens, J. T., Yocom, L. L., Churchill, D. J., Gray, R. W., Huffman, D. W., Lake, F. K., & Khatri-Chhetri, P. (2021). Adapting western North American forests to climate change and wildfires: 10 common questions. *Ecological Applications*, 31(8), e02433. https://doi.org/10.1002/EAP.2433

R Core Team. (2021). R: A Language and Environment for Statistical Computing. https://www.r-project.org/

R Core Team. (2022). R: A language and environment for statistical computing. Vienna, Austria. https://www.R-project.org/

R Core Team. (2023). R: A Language and Environment for Statistical Computing. https://www.r-project.org/

Raffa, K. F., Andersson, M. N., & Schlyter, F. (2016). Host Selection by Bark Beetles: Playing the Odds in a High-Stakes Game. In Advances in Insect Physiology (Vol. 50, pp. 1–74). Academic Press. https://doi.org/10.1016/BS.AIIP.2016.02.001

Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., & Romme, W. H. (2008). Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. *BioScience*, 58(6), 501–517. https://doi.org/10.1641/B580607

Raz-Yaseef, N., Rotenberg, E., & Yakir, D. (2010). Effects of spatial variations in soil evaporation caused by tree shading on water flux partitioning in a semi-arid pine forest. *Agricultural and Forest Meteorology,* 150(3), 454–62. https://doi.org/10.1016/J.AGRFORMET.2010.01.010

Reed, C. C., & Hood, S. M. (2024). Nonstructural carbohydrates explain post-fire tree mortality and recovery patterns. *Tree Physiology*, 44(2), tpad155. https://doi.org/10.1093/treephys/tpad155

Régolini, M., Castagneyrol, B., Dulaurent-Mercadal, A. M., Piou, D., Samalens, J. C., & Jactel, H. (2014). Effect of host tree density and apparency on the probability of attack by the pine processionary moth. *Forest Ecology and Management*, 334, 185–192. https://doi.org/10.1016/J.FORECO.2014.08.038

Reich, P. B., Walters, M. B., Kloeppel, B. D., & Ellsworth, D. S. (1995). Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia*, 104(1), 24–30. https://doi.org/10.1007/BF00365558/METRICS

Riba, M. L., Tathy, J. P., Tsiropoulos, N., Monsarrat, B., & Torres, L. (1987). Diurnal variation in the concentration of α- and β-pinene in the landes forest (France). *Atmospheric Environment,* 21(1), 191–193. https://doi.org/10.1016/0004-6981(87)90285-X

Riegel, G.., Miller, F. ., & Krueger, W. . (1992). Competition for Resources Between Understory Vegetation and Overstory Pinus Ponderosa in Northeastern Oregon. *Ecological Applications*, 2(1), 71−85.

Rieske, L. K., Housman, H. H., & Arthur, M. A. (2002). Effects of prescribed fire on canopy foliar chemistry and suitability for an insect herbivore. *Forest Ecology and Management*, 160, 177–187.

Rigling, A., Brühlhart, H., Bräker, O. U., Forster, T., & Schweingruber, F. H. (2003). Effects of irrigation on diameter growth and vertical resin duct production in Pinus sylvestris L. on dry sites in the central Alps, Switzerland. *Forest Ecology and Management*, 175(1–3), 285–296. https://doi.org/10.1016/S0378-1127(02)00136-6

Roden, J. S., & Farquhar, G. D. (2012). A controlled test of the dual-isotope approach for the interpretation of stable carbon and oxygen isotope ratio variation in tree rings. *Tree Physiology,* 32(4), 490−503. https://doi.org/10.1093/TREEPHYS/TPS019

Roden, J., & Siegwolf, R. (2012). Is the dual-isotope conceptual model fully operational? *Tree Physiology,* 32, 1179−1182. https://doi.org/10.1093/treephys/tps099

Rodríguez-García, A., Madrigal, J., González-Sancho, D., Gil, L., Guijarro, M., & Hernando, C. (2018). Can prescribed burning improve resin yield in a tapped Pinus pinaster stand? *Industrial Crops and Products*, 124, 91–98. https://doi.org/10.1016/J.INDCROP.2018.07.049

Rolo, V., & Moreno, G. (2019). Shrub encroachment and climate change increase the exposure to drought of Mediterranean wood-pastures. *Science of the Total Environment*, 660, 550−558. https://doi.org/10.1016/j.scitotenv.2019.01.029

Romanya, J., Casals, P., & Vallejo, V. R. (2001). Short-term effects of fire on soil nitrogen availability in Mediterranean grasslands and shrublands growing in old fields. *Forest Ecology and Management*, 147, 39–53.

Ryan, K. (1982). Techniques for assessing fire damage to trees. In J. Lotan (Ed.), Proceedings of the symposium: Fire, its field effects (pp. 1–11). Intermountain Fire Council, Missoula, MT.

Sala, A., Peters, G. D., McIntyre, L. R., & Harrington, M. G. (2005). Physiological responses of ponderosa pine in western montana to thinning, prescribed fire and burning season. *Tree Physiology,* 25(3), 339−348. https://doi.org/10.1093/TREEPHYS/25.3.339

Sala, A., Piper, F., & Hoch, G. (2010). Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist*, 186(2), 274–281. https://doi.org/10.1111/J.1469-8137.2009.03167.X

Sánchez-Salguero, R., Camarero, J. J., Dobbertin, M., Fernández-Cancio, A., Vilà-Cabrera, A., Manzanedo, R. D., Zavala, M. A., & Navarro-Cerrillo, R. M. (2013). Contrasting vulnerability and resilience to drought-induced decline of densely planted vs. natural rear-edge Pinus nigra forests. *Forest Ecology and Management,* 310, 956−967. https://doi.org/10.1016/J.FORECO.2013.09.050

Sangüesa-Barreda, G., Linares, J. C., & Camarero, J. J. (2015). Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: Connecting climatic and biotic drivers of forest dieback. *Forest Ecology and Management*, 357, 126–137. https://doi.org/10.1016/J.FORECO.2015.08.017

Santoro, A. E., Lombardero, M. J., Ayres, M. P., & Ruel, J. J. (2001). Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management*, 144(1–3), 245–254. https://doi.org/10.1016/S0378-1127(00)00389-3

Saracino, A., Rita, A., Rossi, S., Andreu-Hayles, L., Helle, G., & Todaro, L. (2017). Climatic signal from Pinus leucodermis axial resin ducts: a tree-ring time series approach. *European Journal of Forest Research*, 136(1), 27–36. https://doi.org/10.1007/S10342-016-1005-4/FIGURES/5

Savi, T., Casolo, V., Dal Borgo, A., Rosner, S., Torboli, V., Stenni, B., Bertoncin, P., Martellos, S., Pallavicini, A., & Nardini, A. (2019). Drought-induced dieback of Pinus nigra: a tale of hydraulic failure and carbon starvation. *Conservation Physiology*, 7(1). https://doi.org/10.1093/CONPHYS/COZ012

Scarff, F.R., Westoby, M., 2006. Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology*, 20 (5), 745−752. https://doi.org/10.1111/J.1365- 2435.2006.01174.X

Scheidegger, Y., M. Saurer, M. B., & Siegwolf, R. (2000). Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. *Oecologia,* 125(3), 350−357. https://doi.org/10.1007/S004420000466

Schulze, E.-D., Beck, E., Bhuchmann, N., Clemens, S., Müller-Hohenstein, K., & Scherer-Lorenzen, M. (2019). Plant Ecology. Springer-Verlag GmbH Germany.

Schwarz, J., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., & Bauhus, J. (2020). Quantifying growth responses of trees to drought—a critique of commonly used resilience indices and recommendations for future studies. *Current Forestry Reports,* 6(3), 185−200. https://doi.org/10.1007/S40725-020-00119-2/FIGURES/8

Schwilk, D. W., Knapp, E. E., Ferrenberg, S. M., Keeley, J. E., & Caprio, A. C. (2006). Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management,* 232(1−3), 36−45. https://doi.org/10.1016/j.foreco.2006.05.036

Schwilk, D. W., Keeley, J. E., Knapp, E. E., Mciver, J., Bailey, J. D., Fettig, C. J., Fiedler, C. E., Harrod, R. J., Moghaddas, J. J., Outcalt, K. W., Skinner, C. N., Stephens, S. L., Waldrop, T. A., Yaussy, D. A., & Youngblood, A. (2009). The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. *Ecological Applications*, 19(2), 285−304. https://doi.org/10.1890/07-1747.1

Scott, J. H., & Reinhardt, E. D. (2001). Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service - Research Paper RMRS-RP, 29 RMRS-RP, 1−62. https://doi.org/10.2737/RMRS-RP-29

Seidl, R., Schelhaas, M. J., & Lexer, M. J. (2011). Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology*, 17(9), 2842–2852. https://doi.org/10.1111/J.1365-2486.2011.02452.X

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395−402. https://doi.org/10.1038/nclimate3303

Seidl, R., & Turner, M. G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world. *Proceedings of the National Academy of Sciences*, 119(28). https://doi.org/10.1073/PNAS.2202190119

Sevanto, S., Mcdowell, N. G., Dickman, L. T., Pangle, R., & Pockman, W. T. (2014). How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell and Environment*, 37(1), 153–161. https://doi.org/10.1111/PCE.12141/SUPPINFO

Shestakova, T. A., & Martínez-Sancho, E. (2021). Stories hidden in tree rings: A review on the application of stable carbon isotopes to dendrosciences. *Dendrochronologia*, 65, 125789. https://doi.org/10.1016/j.dendro.2020.125789

Simonin, K., Kolb, T. E., Montes-Helu, M., & Koch, G. W. (2007). The influence of thinning on components of stand water balance in a ponderosa pine forest stand during and after extreme drought. *Agricultural and Forest Meteorology*, 143, 266−276. https://doi.org/10.1016/j.agrformet.2007.01.003

Slack, A. W., Kane, J. M., Knapp, E. E., & Sherriff, R. L. (2017). Contrasting Impacts of Climate and Competition on Large Sugar Pine Growth and Defense in a Fire-Excluded Forest of the Central Sierra Nevada. *Forests*, 8(7), 244. https://doi.org/10.3390/F8070244

Slack, A. W., Zeibig-Kichas, N. E., Kane, J. M., & Varner, J. M. (2016). Contingent resistance in longleaf pine (Pinus palustris) growth and defense 10 years following smoldering fires. *Forest Ecology and Management*, 364, 130–138. https://doi.org/10.1016/J.FORECO.2016.01.014

Smith, H. Y., & Arno, S. F. (1999). Eighty-eight years of change in a managed ponderosa pine forest. US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Šmits, A., & Larsson, S. (1999). Effects of previous defoliation on pine looper larval performance. *Agricultural and Forest Entomology*, 1(1), 19–26. https://doi.org/10.1046/J.1461-9563.1999.00004.X

Sohn, J. A., Brooks, J. R., Bauhus, J., Kohler, M., Kolb, T. E., & McDowell, N. G. (2014). Unthinned slow-growing ponderosa pine (Pinus ponderosa) trees contain muted isotopic signals in tree rings as compared to thinned trees. *Trees - Structure and Function,* 28(4), 1035−51. https://doi.org/10.1007/S00468-014-1016-Z/FIGURES/8

Sohn, J. A., Saha, S., & Bauhus, J. (2016). Potential of forest thinning to mitigate drought stress: A meta-analysis. *Forest Ecology and Management*, 380, 261−273. https://doi.org/10.1016/J.FORECO.2016.07.046

Sparks, A. M., Smith, A. M. S., Talhelm, A. F., Kolden, C. A., Yedinak, K. M., & Johnson, D. M. (2017). Impacts of fire radiative flux on mature Pinus ponderosa growth and vulnerability to secondary mortality agents. *International Journal of Wildland Fire*, 26(1), 95–106. https://doi.org/10.1071/WF16139

Stephens, S. L., Moghaddas, J. J., Edminster, C., Fiedler, C. E., Haase, S., Harrington, M., Keeley, J. E., Knapp, E. E., Mciver, J. D., Metlen, K., Skinner, C. N., & Youngblood, A. (2009). Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecological Applications*, 19(2), 305−320. https://doi.org/10.1890/07-1755.1

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2005). Changes toward Earlier Streamflow Timing across Western North America. *Journal of Climate*, 18(8), 1136–1155. https://doi.org/10.1175/JCLI3321.1

Stokes, M. A., & Smiley, T. L. (1968). An introduction to tree-ring dating. Chicago, IL: University of Chicago Press.

Tedim, F., Leone, V., Amraoui, M., Bouillon, C., Coughlan, M. R., Delogu, G. M., Fernandes, P., Ferreira, C., McCaffrey, S., McGee, T. K., Parente, J., Paton, D., Pereira, M. G., Ribeiro, L. M., Viegas, D. X., & Xanthopoulos, G. (2018). Defining Extreme Wildfire Events: Difficulties, Challenges, and Impacts. *Fire*, 1(1), 9. https://doi.org/10.3390/FIRE1010009

Tepley, A. J., Hood, S. M., Keyes, C. R., & Sala, A. (2020). Forest restoration treatments in a ponderosa pine forest enhance physiological activity and growth under climatic stress. *Ecological Applications*, 30(8), 1−18. https://doi.org/10.1002/eap.2188

Tiberi, R., Niccoli, A., Curini, M., Epifano, F., Marcotullio, M. C., & Rosati, O. (1999). The role of the monoterpene composition inPinus spp. needles, in host selection by the pine processionary caterpillar, Thaumetopoea pityocampa. *Phytoparasitica,* 27(4), 263–272. https://doi.org/10.1007/BF02981482

Torres-Muros, L., Hódar, J. A., & Zamora, R. (2016). Effect of habitat type and soil moisture on pupal stage of a Mediterranean forest pest (Thaumetopoea pityocampa). *Agricultural and Forest Entomology*, 19(2), 130–138. https://doi.org/10.1111/AFE.12188

Treydte, K., Frank, D., Esper, J., Andreu, L., Bednarz, Z., Berninger, F., Boettger, T., D'Alessandro, C. M., Etien, N., Filot, M., Grabner, M., Guillemin, M. T., Gutierrez, E., Haupt, M., Helle, G., Hilasvuori, E., Jungner, H., Kalela-Brundin, M., Krapiec, M., Leuenberger, M., Loader, N. J., Masson-Delmotte, V., Pazdur, A., Pawelczyk, S., Pierre, M., Planells, O., Pukiene, R., Reynolds-Henne, C. E., Rinne, K. T., Saracino, A., Saurer, M., Sonninen, E., Stievenard, M., Switsur, V. R., Szczepanek, M., Szychowska-Krapiec, E., Todaro, L., Waterhouse, J. S., Weigl, M., & Schleser, G. H. (2007). Signal strength and climate calibration of a European tree-ring isotope network. *Geophysical Research Letters,* 34(24). https://doi.org/10.1029/2007GL031106

Tudela-Haberland, G., Garcia-Pausas, J., Rovira, P., & Casals, P. Soil organic carbon and functionality 5 years after lop-and-scatter slash burning. In preparation.

Turner, M. G., & Seidl, R. (2023). Novel Disturbance Regimes and Ecological Responses. *Annual Review of Ecology, Evolution, and Systematics*, 54, 63–83. https://doi.org/10.1146/ANNUREV-ECOLSYS-110421-101120/1

Turtola, S., Manninen, A.-M., Rikala, R., & Kainulainen, P. (2003). Drought stress alters the concentration of wood terpenoids in Scots pine and Norway spruce seedlings. *Journal of Chemical Ecology*, 29, 1981–1995.

Vacek, Z., Cukor, J., Vacek, S., Gallo, J., Bažant, V., & Zeidler, A. (2023). Role of black pine (Pinus nigra J. F. Arnold) in European forests modified by climate change. In European Journal of Forest Research (Vol. 142, Issue 6, pp. 1239–1258). Springer Science and Business Media Deutschland GmbH. https://doi.org/10.1007/s10342-023-01605-5

Vallejo, V. R., Arianoutsou, M., & Moreira, F. (2012). Fire Ecology and Post-Fire Restoration Approaches in Southern European Forest Types. In F. Moreira, M. Arianoutsou, P. Corona, & J. De Las Hera (Eds.), Post-fire management and restoration of southern European forests (pp. 93–119). Springer Science+Business Media B.V. https://doi.org/10.1007/978-94-007-2208-8_5

Valor, T., González-Olabarria, J. R., & Piqué, M. (2015). Assessing the impact of prescribed burning on the growth of European pines. *Forest Ecology and Management*, 343, 101-109. https://doi.org/10.1016/j.foreco.2015.02.002

Valor, T., González-Olabarria, J. R., Piqué, M., & Casals, P. (2017a). The effects of burning season and severity on the mortality over time of Pinus nigra spp. salzmannii (Dunal) Franco and P. sylvestris L. *Forest Ecology and Management,* 406, 172−183. https://doi.org/10.1016/j.foreco.2017.08.027

Valor, T., Ormeño, E., & Casals, P. (2017b). Temporal effects of prescribed burning on terpene production in Mediterranean pines. *Tree Physiology*, 37(12), 1622–1636. https://doi.org/10.1093/treephys/tpx069

Valor, T., Casals, P., Altieri, S., González-Olabarria, J. R., Piqué, M., & Battipaglia, G. (2018). Disentangling the effects of crown scorch and competition release on the physiological and growth response of Pinus halepensis Mill. using δ 13 C and δ 18 O isotopes. *Forest Ecology and Management,* 424, 276−287. https://doi.org/10.1016/j.foreco.2018.04.056

Valor, T., Battipaglia, G., Piqué, M., Altieri, S., González-Olabarria, J. R., & Casals, P. (2020). The effect of prescribed burning on the drought resilience of Pinus nigra ssp. salzmannii Dunal (Franco) and P. sylvestris L. *Annals of Forest Science*, 77(1), 1−16. https://doi.org/10.1007/S13595-019-0912-1/FIGURES/7

Valor, T., Hood, S. M., Piqué, M., Larrañaga, A., & Casals, P. (2021). Resin ducts and bark thickness influence pine resistance to bark beetles after prescribed fire. *Forest Ecology and Management,* 494, 119322. https://doi.org/10.1016/J.FORECO.2021.119322

Van der Maaten-Theunissen, M., van der Maaten, E., & Bouriaud, O. (2015). PointRes: An R Package to Analyze Pointer Years and Components of Resilience. *Dendrochronologia,* 35, 34–38. https://doi.org/10.1016/J.DENDRO.2015.05.006

Van Wagner, C. E. (1982). Practical Aspects of the Line Intersect Method. (Vol. 12). Chalk River, Canada: Petawawa National Forestry Institute.

Van Wagner, C.E., 1977. Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research*, 7 (1), 23–34. https://doi.org/10.1139/x77-004

Vázquez-González, C., Sampedro, L., Rozas, V., & Zas, R. (2020a). Climate drives intraspecific differentiation in the expression of growth-defence trade-offs in a long-lived pine species. *Scientific Reports*, 1–10. https://doi.org/10.1038/s41598-020-67158-4

Vázquez-González, C., Zas, R., Erbilgin, N., Ferrenberg, S., Rozas, V., & Sampedro, L. (2020b). Resin ducts as resistance traits in conifers: linking dendrochronology and resin-based defences. *Tree Physiology*, 40(10), 1313–1326. https://doi.org/10.1093/TREEPHYS/TPAA064

Verrall, A. F. (1938). The Probable Mechanism of the Protective Action of Resin in Fire Wounds on Red Pine. *Journal of Forestry*, 36(12), 1231–1233. https://doi.org/10.1093/JOF/36.12.1231

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, 23(7), 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Vilà-Cabrera, A., Coll, L., Martínez-Vilalta, J., & Retana, J. (2018). Forest management for adaptation to climate change in the Mediterranean basin: A synthesis of evidence. *Forest Ecology and Management*, 407, 16–22. https://doi.org/10.1016/j.foreco.2017.10.021

Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L., & Retana, J. (2013). Patterns of Forest Decline and Regeneration Across Scots Pine Populations. *Ecosystems*, 16(2), 323–335. https://doi.org/10.1007/S10021-012-9615-2/TABLES/4

Vilà-Vilardell, L., De Cáceres, M., Piqué, M., & Casals, P. (2023). Prescribed fire after thinning increased resistance of sub-mediterranean pine forests to drought events and wildfires. *Forest Ecology and Management,* 527, 120602. https://doi.org/10.1016/J.FORECO.2022.120602

Vilà-Vilardell, L., Tepley, A. J., Sala, A., Casals, P., & Hood, S. M. (2024a). Long-term sensitivity of ponderosa pine axial resin ducts to harvesting and prescribed burning. *Forest Ecology and Management*, 572, 122301. https://doi.org/10.1016/J.FORECO.2024.122301

Vilà-Vilardell, L., Valor, T., Hood-Nowotny, R., Schott, K., Piqué, M., & Casals, P. (2024b). Thinning followed by slash burning enhances growth and reduces vulnerability to drought for Pinus nigra. *Ecological Applications*, 34(7), e3030. https://doi.org/10.1002/EAP.3030

Vilà-Vilardell, L., Tepley, A. J., Sala, A., Casals, P., & Hood, S. M. (2024c). Code from: Long-term sensitivity of ponderosa pine axial resin ducts to harvesting and prescribed burning, v1.0, Figshare. https://doi.org/10.6084/m9.figshare.25764306.v1

Vilà-Vilardell, L., Valor, T., Hood-Nowotny, R, Schott, K., Pique, M., & Casals, P. (2024d). Data from: Thinning followed by slash burning enhances growth and reduces vulnerability to drought of Pinus nigra. Figshare. https://doi.org/10.6084/m9.figshare.25054235.v1

Waldrop, T., Phillips, R. J., & Simon, D. A. (2010). Fuels and predicted fire behavior in the southern Appalachian Mountains and fire and fire surrogate treatments. *Forest Science* 56(1):32-45, 56(1), 32–45. https://www.srs.fs.usda.gov/pubs/36361

Wallin, K. F., & Raffa, K. F. (2001). Effects of folivory on subcortical plant defenses: Can defense theories predict interguild processes? *Ecology*, 82(5), 1387–1400. https://doi.org/10.1890/0012-9658(2001)082[1387:EOFOSP]2.0.CO;2

Wallin, K. F., Kolb, T. E., Skov, K. R., & Wagner, M. R. (2003). Effects of Crown Scorch on Ponderosa Pine Resistance to Bark Beetles in Northern Arizona. *Environmental Entomology*, 32(3), 652–661. https://doi.org/10.1603/0046-225X-32.3.652

Wallin, K. F., Kolb, T. E., Skov, K. R., & Wagner, M. R. (2004). Seven-year results of thinning and burning restoration treatments on old ponderosa pines at the Gus Pearson Natural Area. *Restoration Ecology*, 12(2), 239–247. https://doi.org/10.1111/J.1061-2971.2004.00278.X

Waring, R. H., & Pitman, G. B. (1985). Modifying Lodgepole Pine Stands to Change Susceptibility to Mountain Pine Beetle Attack. *Ecology*, 66(3), 889–897. https://doi.org/10.2307/1940551

Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., Gurskaya, M., Hallinger, M., Lange, J., Shetti, R., Smiljanic, M., & Trouillier, M. (2020). Global assessment of relationships between climate and tree growth. *Global Change Biology*, 26(6), 3212–3220. https://doi.org/10.1111/GCB.15057

Yebra, M., Scortechini, G., Badi, A., Beget, M. E., Boer, M. M., Bradstock, R., Chuvieco, E., Danson, F. M., Dennison, P., Resco de Dios, V., Di Bella, C. M., Forsyth, G., Frost, P., Garcia, M., Hamdi, A., He, B., Jolly, M., Kraaij, T., Martín, M. P., … Ustin, S. (2019). Globe-LFMC, a global plant water status database for vegetation ecophysiology and wildfire applications. *Scientific Data* 6(1), 1−8. https://doi.org/10.1038/s41597-019-0164-9

Zald, H. S. J., Callahan, C. C., Hurteau, M. D., Goodwin, M. J., & North, M. P. (2022). Tree growth responses to extreme drought after mechanical thinning and prescribed fire in a Sierra Nevada mixed-conifer forest, USA. *Forest Ecology and Management,* 510, 120107. https://doi.org/10.1016/J.FORECO.2022.120107

Zalucki, M. P., Clarke, A. R., & Malcolm, S. B. (2002). Ecology and behavior of first instar larval Lepidoptera. *Annual Review of Entomology*, 47, 361–393. https://doi.org/10.1146/ANNUREV.ENTO.47.091201.145220/1

Zang, C., & Biondi, F. (2015). Treeclim: An R package for the numerical calibration of proxy-climate relationships. *Ecography*, 38(4), 431–436. https://doi.org/10.1111/ECOG.01335

Zhao, F.-J., Shu, L.-F., & Wang, Q.-H. (2012). Terpenoid emissions from heated needles of Pinus sylvestris and their potential influences on forest fires. *Acta Ecologica Sinica*, 32(1), 33–37. https://doi.org/10.1016/j.chnaes.2011.06.002

Ziaco, E., Truettner, C., Biondi, F., & Bullock, S. (2018). Moisture-driven xylogenesis in Pinus ponderosa from a Mojave Desert mountain reveals high phenological plasticity. *Plant, Cell & Environment*, 41(4), 823–836. https://doi.org/10.1111/PCE.13152

Zovi, D., Stastny, M., Battisti, A., & Larsson, S. (2008). Ecological costs on local adaptation of an insect herbivore imposed by host plants and enemies. *Ecology*, 89(5), 1388–1398. https://doi.org/10.1890/07-0883.1

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, 7(6), 636−645. https://doi.org/10.1111/2041-210X.12577