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Short-term regeneration dynamics after windstorm: interaction between disturbance legacies, management strategies and restoration practices.

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Dinamiche di rinnovazione a breve termine a seguito di tempeste da vento: interazioni con biological legacies, strategie di gestione e pratiche di riforestazione.

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Summary

Abstract

The following thesis investigates the roles of disturbance legacies and management strategies on forest regeneration dynamics after windstorms. As the first step, I conducted a systematic literature review that aims to identify and analyze the effect of deadwood on regeneration. It underlines quite a good literature about direct effects, mostly about seedbed functions, but a scarcity about indirect effects. Nevertheless, indirect effects are the most versatile effects and do not rely exclusively on deadwood decay.

The second step was to analyze the effect of different post-disturbance management strategies on natural regeneration. Firstly, we established and monitored two permanent areas within each two different sites with different management strategies to compare the effect of salvage logging and no-intervention strategies on seedlings' establishment and growth. Then we sampled 148 areas in the forests damaged by the storm Vaia and salvaged logged to research the natural regeneration dynamics after intervention. The data analysis suggests that short-term regeneration occurrence is higher in no-intervention areas. Moreover, the distance from windthrown edges and green islands significantly decreases seedlings' density for all species surveyed. Future stand species composition is driven by the previous stand species composition, except for bird seed dispersal species. Deadwood helps in creating favorable regeneration microsites and conditions and different harvesting systems influenced regeneration occurrence.

The last step was to understand the role of deadwood in creating favorable microsites by mitigating environmental drought stress and protecting from browsing planted seedlings. In this case, I planted 450 seedlings of five different species within a windthrown area, both near deadwood elements and both in sites without the influence of deadwood. It emerged that deadwood creates favorable microsites, decreasing significantly the temperature on the microsites with an anisotropic relation. Moreover, the presence of deadwood decreases deer browsing.

In conclusion, deadwood demonstrates a clear role in seedling protection and microsite amelioration, increasing seedling establishment and growing probability. After large or stand-replacing disturbance deadwood can help reduce environmental stressors, so it is important to

consider and take advantage of deadwood in the post-disturbance and regeneration management planning.

Sommario

Questa tesi ha come obiettivo l’analisi del ruolo delle *disturbance legacies* e delle strategie di gestione nei confronti delle dinamiche di rinnovazione in seguito a schianti da vento. in primo luogo, ho effettuato una revisione sistematica della letteratura scientifica, con lo scopo di indentificare ed analizzare gli effetti della necromassa legnosa nei confronti della rinnovazione. Questa analisi ha portato alla luce una discreta quantità di articoli inerenti agli effetti diretti, in particolar modo a proposito della funzione di substrato per la rinnovazione, ma una scarsità di articoli riguardanti gli effetti indiretti. A dispetto di ciò, gli effetti indiretti sono i più versatili e non dipendono strettamente dallo stato di decomposizione della necromassa legnosa.

In secondo luogo ho analizzato gli effetti di due differenti strategie gestionali post-disturbo sulla rinnovazione naturale. In primo luogo, sono state individuate due diverse aree di monitoraggio permanente al cui interno sono presenti due siti con trattamenti differenti, per confrontare gli effetti del *salvage logging* totale rispetto ad una strategia di non intervento. Dopo di che, sono stati effettuati rilievi sulla rinnovazione naturale in 148 aree danneggiate dalla tempesta Vaia ed in seguito esboscate, per analizzare le dinamiche di rinnovazione naturale dopo l’esbosco. In tale rilievi sono stati valutati anche gli effetti della distanza dal margine dello schianto e dalle *green islands* sulla densità di rinnovazione. Dai risultati è emerso che la composizione specifica della rinnovazione dipende dalla composizione del popolamento preesistente, ma fanno eccezione alcune specie con disseminazione zoocora ad opera degli uccelli. La necromassa legnosa contribuisce a creare micrositi favorevoli all’insediamento della rinnovazione e differenti sistemi di esbosco influenzano le dinamiche di rinnovazione.

Infine l’ultima analisi è stata condotta sul contributo del legno morto nel creare micrositi favorevoli alla rinnovazione artificiale, mitigando gli stress ambientali e proteggendo i semenzali dal brucamento. In questo caso sono stati messi a dimora 450 semenzali di cinque specie differenti all’interno di un’area schiantata non esboscata, sia nei pressi della necromassa sia in un sito di controllo lontano da essa. I risultati mostrano che la necromassa crea micrositi favorevoli alla rinnovazione, diminuendo significativamente la temperatura nei micrositi vicini al legno morto e di conseguenza la mortalità, con una relazione anisotropica. Infine la presenza di legno morto a terra diminuisce i danni da brucamento sulle piantine.

In conclusione è possibile affermare che la necromassa ha un chiaro ruolo nella protezione dei semenzali e nel miglioramento dei micrositi di rinnovazione, aumentando significativamente la probabilità di insediamento e sopravvivenza della rinnovazione. In seguito a disturbi vasti ed ad elevata severità, la necromassa può aiutare nel mitigare i fattori di stress, di conseguenza è necessario considerare questa funzione nelle strategie di gestione e di pianificazione post-disturbo, cercando di trarre vantaggio e sfruttare a nostro favore la presenza del legno morto.

Introduction

Forest regeneration is a critical stage in forest development. During the first stages of seed dispersal, seedling establishment, and growth, the basements are laid for the future forest structure and composition, as well as for the future functions and ecosystem services (ES) provided by the forest ecosystem (Lindenmayer et al. 2008). Forest regeneration is a spontaneous process occurring within naturally regenerated and old-growth forests, that take advantage of protection from mature trees and the availability of regeneration niches in the environment to establish and growth, with the purpose to reach the dominant layer and maintain the forest cover. Such process at the landscape level is in equilibrium with all the other processes of natural forest ecosystems, but can be altered and modified in disturbed environments (e.g., after wildfires, windstorms, human intervention, etc.…). After a disturbance, a huge amount of resources are available in the environment, but at the same time, also the limiting factors increase (Franklin et al. 2000). In these situations regeneration plays an even more critical role to restore forest cover, especially natural regeneration (Taeroe et al. 2019). If natural regeneration is not enough to support some functions or ES that a precise stand is managed for then artificial regeneration and other restoration practices are needed.

Forest ecosystems are dynamic and heterogenous environments, both in space and time. Disturbances are natural components of those ecosystems and are defined as: "relatively discrete events in time that disrupt the ecosystem, community, or population structure and change resource or substrate availability or the physical environment” (Pickett and White 1985). Disturbances drive the evolutions and changes of the ecosystems, modifying the growing space by killing living plants or changing the environment (Chadwick 1980). Each disturbance event is characterized by intensity and severity, which determine the impact and the damages of the event on a given ecosystem. The return period, i.e. the time between two events of the same magnitude over the same area, is strictly related to those two concepts: disturbances with lower magnitude are more frequent than disturbances with higher magnitude (White and Jentsch 2001). Despite disturbances being a natural part of ecosystem dynamics, in the latest half-century, we are facing an increasing of extreme events related to climate changes (Wastl et al. 2013; IPCC 2014; Seidl et al. 2014), causing a higher impact of extreme disturbances on forest ecosystems.

There can be different disturbances, with different consequences on forest ecosystem dynamics: biotic and abiotic ones. Biotic disturbances, like pest outbreaks or damages by herbivores, have a longer duration than abiotic ones, and often are endogenous of the system and triggered by some external factor. For example, bark beetle outbreaks in Norway spruce stands can be triggered by previous disturbances, or very intense drought stress (Marini et al. 2017; Grodzki and Fronek 2019). After pest outbreaks, the structure of the forest is not altered substantially in the short term, so regeneration dynamics don’t change abruptly (Bottero et al. 2013). Among abiotic disturbances, wildfire is one of the most common disturbances in Mediterranean and arid or semi-arid environments (Forzieri et al. 2021), ranging from really low severity as ground fire to a stand-replacing disturbance in very intense canopy fire. Due to high temperatures and depending on the time of permanence of the fire on the stand, it can disrupt and modify heavily the environment and the availability of water and nutrient (Marcolin et al. 2019), leading to the mineralization of organic matter and changing soil properties. Gravitative hazards like rockfalls influenced less the whole stand but can heavily damage single trees. Avalanches can destroy a vast proportion of forest stands, but the damages and the behavior of the forest during recovery processes could be likened to that of windthrows.

Windstorms are recognized as the most important disturbance for European forests, and the first responsible for forests damages (Seidl et al. 2014; Gregow et al. 2017). Small windstorms create small gaps that increase forest structure diversity and determine openings in the forest canopy that allows the light to reach the ground, making these clearings preferential sites for natural regeneration, especially for light-demanding species (Kuuluvainen and Kalmari 2003a; Kramer et al. 2014). Large windthrows, on the other hand, could represent an obstacle to regeneration. The high distance from the edges and the seed trees does not allow seed dispersion (Kramer et al. 2006; Gratzer and Waagepetersen 2018); too much light and nutrients can favor competitive species, e.g. shrubs or herbs, and obstacle regeneration establishment and survival (Bellingham and Richardson 2006); too much deadwood can have a mulching effect and do not allow seeds to reach the ground (Leverkus et al. 2021a). Except for regeneration issues, windthrows and their management in the alpine landscape can be complex and it is necessary to consider the function of the damaged stand to decide how to manage the windstorm. In protective forests, for example, is better to release the deadwood on the ground or to manipulate it to create obstacles along the maximum slope angle against rockfall (Costa et al. 2021), or just leave it there to create a complex terrain to prevent avalanches (Cordonnier et al. 2008). Subsequent disturbance and cascading effects must be taken into account, for example leaving high amounts of deadwood on the ground in spruce-dominated forests can lead to bark beetle outbreaks, thereby increasing the damages (Leverkus et al. 2021a).

The strategies in post-disturbance management could be summed up in these three cases: total salvage logging, salvage logging and alternative measures, and no-intervention. As widely discussed in the last years, salvage logging could cause additional damages (Lindenmayer et al. 2008; Jonášová et al. 2010; Waldron et al. 2014; Leverkus et al. 2018; Morimoto et al. 2019). During salvage logging operations is necessary to keep in mind the importance of the dynamic equilibrium between the different components of forests ecosystem (Lindner et al. 2010), releasing an appropriate amount of legacies like living trees, broken stems, logs, snags, or coarse woody debris (CWD) in general (Thorn et al. 2014). Deadwood and CWD are very important to guarantee protection against different natural hazards (e.g. rockfall, avalanches, etc.) and also to facilitate the regeneration after many disturbances directly and indirectly (Lingua et al. 2008; UFAM 2008; Rost et al. 2009; Castro et al. 2011; Marzano et al. 2013; Wohlgemuth et al. 2017). While direct facilitation (e.g. substrate function) has been widely illustrated in literature, indirect functions such as microsite amelioration or browsing protection are still not fully investigated.

According to the literature, overall the negative effects of complete salvage logging are greater than the beneficial ones. It has an undisputed positive effect as sanitary logging in preventing pest outbreaks in certain cases (e.g. bark beetle and spruce forest) (Marini et al. 2017). At the same time, it can add damage to disturbance legacies, already recognized to be really important in forest regeneration after disturbance. Moreover, it can lead to an increase in the frequency and magnitude of other disturbances (Leverkus et al. 2021a). In areas with a high danger of forest fires (e.g. lower elevation with southern exposure or Mediterranean forest), salvage logging reduces total ecosystem fuel, but increases small ground fuels and consequently the short-term risk of fire spread (Leverkus et al. 2020). It increases the erosion impact of the flood at the catchment scale and It removes the protective effect of deadwood against rockfall and avalanches due to the increased roughness (Costa et al. 2021; Brožová et al. 2021). In the end, in unsalvaged areas biological legacies protect seedlings from browsing and maintain buffered conditions on microsites, avoiding extreme peaks in environmental factors like temperature, humidity, and light

(Leverkus et al. 2021a). Partial salvage logging or deadwood manipulation seems to be the best options to adopt, but so far they have been poorly investigated, especially after wind disturbances in the southern Alps.

Planting and restoration practices are strictly correlated with salvage logging and post-disturbance management strategies. Adopting artificial restoration is a valid option in a context where there is the need to restore as soon as possible forest cover, and maybe try to change forest stands structure and composition. Usually, plantation is a process that follows clear-cuts or areas affected by stand-replacing disturbance after total salvage logging. Few studies have been done about planting after a disturbance exploiting the role of disturbance and biological legacies to ameliorate microsites and protect seedlings, mainly after fires in the Mediterranean area (Castro et al. 2002; Leverkus et al. 2015; Valenzuela et al. 2016). At the moment is not well studied the effect of restoration practices in unsalvaged or only partially harvested areas, nor the exploitation of disturbance legacies to facilitate regeneration.

Objectives and thesis structure

This thesis aims to analyze what are the regeneration dynamics after large disturbances considering the influence of environmental factors and management strategies on forest regeneration dynamics after a disturbance. As case study I considered the storm VAIA, which stroke in the north-east Italian alpine range at the end of October 2018, the first large windstorm in the southern Alps in the last century. To answer this main research question, I followed a workflow (fig.1) focusing on three main aspects:

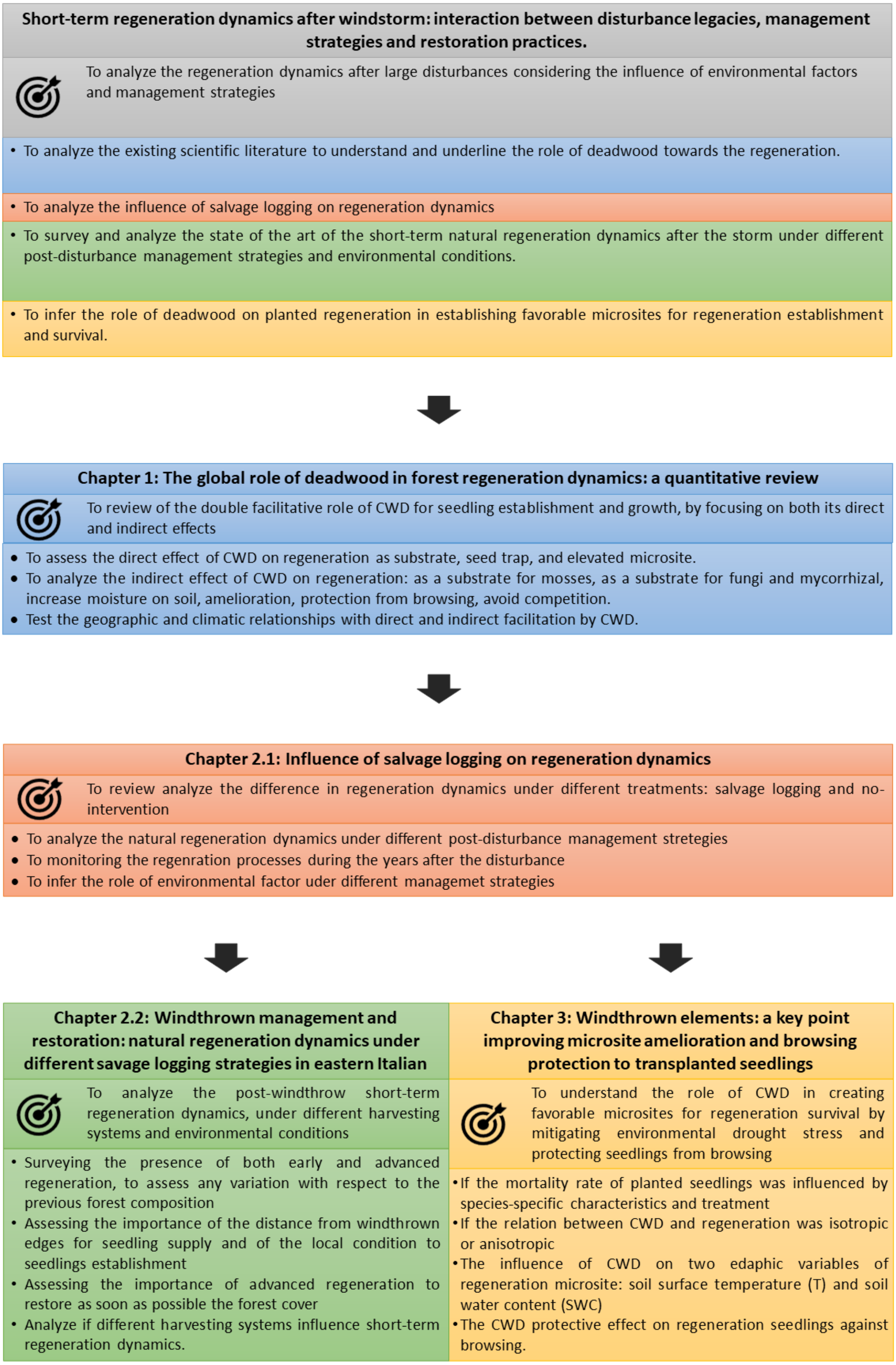
1. Analyze the existing scientific literature to understand and underline the role of deadwood towards regeneration. To better analyze the effects of deadwood on regeneration, in this literature review I decide to divide these interaction effects into two main categories: direct effects if the effect of deadwood is directly on the seed or seedlings (e.g. substrate or trap); indirect effects if deadwood conditions another environmental element, or process or factor the influence in a second moment the seed or seedlings (e.g. elevated site to escape competition, microsite amelioration).

The results of the review gave really important information and the key point to interpret the results of the natural regeneration sampling campaign and to decide the protocol to infer the role of deadwood on planted seedlings.

2. Survey and analyze the current situation of the short-term natural regeneration dynamics after the storm under different post-disturbance management strategies:
    - 2.1 Compare and monitor the natural regeneration dynamics under opposite management strategies: complete salvage logging and no-intervention.
    - 2.2 Analyze the short-term natural regeneration dynamics in salvaged areas in relation to environmental conditions, focusing on different harvesting systems, gap dimensions, and the importance of different regeneration ages (early or new regeneration).
3. Infer the role of deadwood on planted regeneration in establishing favorable microsites for regeneration establishment and survival by mitigating environmental stressors and protecting seedlings from deer browsing.

Considering the importance of deadwood towards regeneration establishment and survival the last two objectives lead to two different studies, focusing on the two different main options for regeneration strategies: the first one is focused on natural regeneration, the most convenient solution in case of large damaged areas since it is the cheapest and allows to obtain a high amount of seedlings that would be otherwise impossible to produce in plant nurseries; the second one on planted artificial regeneration, the most convenient strategy to restore specific sites with particular needs, in areas not too large, giving the chance to better control and shape the future stand composition and structure.

In both the experimental studies field surveyed data and remote sensing data have been used together to analyze natural regeneration dynamics. In particular, Lidar data have been used to quantify the roughness of the deadwood at ground level, and orthophoto and photo-interpretation have been used to assess the distance from green islands, windthrown edges, and surveyed plots.



Short-term regeneration dynamics after windstorm: interaction between disturbance legacies, management strategies and restoration practices.

To analyze the regeneration dynamics after large disturbances considering the influence of environmental factors and management strategies

- To analyze the existing scientific literature to understand and underline the role of deadwood towards the regeneration.
- To analyze the influence of salvage logging on regeneration dynamics
- To survey and analyze the state of the art of the short-term natural regeneration dynamics after the storm under different post-disturbance management strategies and environmental conditions.
- To infer the role of deadwood on planted regeneration in establishing favorable microsites for regeneration establishment and survival.

Chapter 1: The global role of deadwood in forest regeneration dynamics: a quantitative review

To review of the double facilitative role of CWD for seedling establishment and growth, by focusing on both its direct and indirect effects

- To assess the direct effect of CWD on regeneration as substrate, seed trap, and elevated microsite.
- To analyze the indirect effect of CWD on regeneration: as a substrate for mosses, as a substrate for fungi and mycorrhizal, increase moisture on soil, amelioration, protection from browsing, avoid competition.
- Test the geographic and climatic relationships with direct and indirect facilitation by CWD.

Chapter 2.1: Influence of salvage logging on regeneration dynamics

To review analyze the difference in regeneration dynamics under different treatments: salvage logging and no-intervention

- To analyze the natural regeneration dynamics under different post-disturbance management stretegies
- To monitoring the regenration processes during the years after the disturbance
- To infer the role of environmental factor uder different managemet strategies

Chapter 2.2: Windthrown management and restoration: natural regeneration dynamics under different savage logging strategies in eastern Italian

To analyze the post-windthrow short-term regeneration dynamics, under different harvesting systems and environmental conditions

- Surveying the presence of both early and advanced regeneration, to assess any variation with respect to the previous forest composition
- Assessing the importance of the distance from windthrown edges for seedling supply and of the local condition to seedlings establishment
- Assessing the importance of advanced regeneration to restore as soon as possible the forest cover
- Analyze if different harvesting systems influence short-term regeneration dynamics.

Chapter 3: Windthrown elements: a key point improving microsite amelioration and browsing protection to transplanted seedlings

To understand the role of CWD in creating favorable microsites for regeneration survival by mitigating environmental drought stress and protecting seedlings from browsing

- If the mortality rate of planted seedlings was influenced by species-specific characteristics and treatment
- If the relation between CWD and regeneration was isotropic or anisotropic
- The influence of CWD on two edaphic variables of regeneration microsite: soil surface temperature (T) and soil water content (SWC)
- The CWD protective effect on regeneration seedlings against browsing.

Figure 1 Workflow of the thesis

Chapter 1: The global role of deadwood in forest regeneration dynamics: a quantitative review

Based on a paper in preparation

Abstract

Deadwood is a fundamental component of forest ecosystem. It derives from many different sources, starting from natural senescence processed of mature trees, to small disturbances like sporadic wind damages or heavy snow breakages, to big disturbances that disrupt large parts of the forest, or even stand-replacing disturbances. Another crucial component of forest ecosystem dynamics shaping future forest composition and structure is forest regeneration. It is therefore crucial to identify the relationship that occurs between these two components of forest ecosystem, especially in harsh climates or after severe stand-replacing disturbance. In this review, we aim to identify and analyze the effects of deadwood toward regeneration by analyzing 63 different papers. We divide the effects into two main different categories: direct effects, when deadwood affects the regeneration directly, and indirect effects when deadwood affects another element that affects regeneration a second time. Among all the effects, direct effects are the most studied, with a clear prevalence of the substrate effect. The indirect effects are less studied, even if certain protective effect, ameliorative effect, shadowing effect, elevated site effect and competition effect can be traced in literature, especially after disturbance and more likely after wildfires. In conclusion, there still is a lack of information about deadwood effects on regeneration, in particular about indirect effects, and more long-term studies are needed. Under future climate change scenarios, exploiting deadwood to facilitate recovery and forest regeneration should play an important role in forest management and recovery planning.

Introduction

Regeneration plays a fundamental and unique role to determine the future development of a forest stand. Usually, the success of seedlings' establishment is defined by more restrictive microenvironmental conditions than those requested for adult stage survival (Bell et al. 2014; Marcolin et al. 2019), and so in juvenile stages the regeneration niche is narrower and for this reason, seedlings are less tolerant to liming factors (Jackson et al. 2009).

Regeneration can be natural, based on the environmental conditions and stand composition, or artificial when planted with specific purposes (e.g. timber production, restoring protection forests, etc.…). Natural regeneration is considered one of the dominant recovery processes in forest ecosystems after a disturbance (e.g. Taeroe et al., 2019). This process is essential to re-establish forest and soil cover, and to minimize post-disturbance losses of ecosystem services (ES). The type of regeneration, from seeds or sprouting, and environmental conditions are key elements for seedling establishment and survival. Tree species are recognized to be particularly vulnerable in early life stages due to biotic and abiotic conditions (Muhamed et al. 2013).

The establishment and juvenile growth depend on the availability of different resources, like water, light, nutrients, temperature, space, and proper substrate. Those ecological factors are strictly related to climatic conditions, topography, soil type, and humus layer and could be even more constraining under future climate change scenarios (Vodde et al. 2011; Matías et al. 2011; Dobrowski et al. 2015). For example, the conifer seedling establishment can be strongly limited by the combination of a dry climate and poor soil. Under the same site conditions instead, mature trees can properly survive, thanks to the already developed root system that allows better water retention. Drought and high temperatures are recognized as the first cause of mortality in conifer plantations, but as reported by Hogg & Schwarz (1997), mortality usually decreases with increasing age. Light is considered one of the main factors influencing trees in the early stages. Direct solar radiation increases soil and microsite temperature causing a decrease in soil water content (Matías et al. 2011). During dry and hot summers, water availability is recognized as the main limiting factor for seeds' survival. Then, in warmer climates, regeneration failure is more common during the juvenile stages. The early post-disturbance regeneration phase is crucial to maintaining ecosystem resilience (Kuuluvainen and Gauthier 2018), and also has a key role in ecosystem biodiversity richness and dynamics supporting a wide range of rare species during early successional stages (Lindenmayer et al. 2019).

Deadwood is considered a key element in forest ecosystem structure and stand function. It has a central role in maintaining biodiversity, in forest biogeochemical processes, in promoting regeneration, and in carbon sequestration (Parisi et al. 2018). The role of coarse woody debris (CWD) in forests is nowadays quite well defined: increase tree productivity, provide structures and substrate to increase species diversity, store carbon in the long-medium term, mitigate the hydrological risk in steep slopes controlling the runoff and contribute to forest protection function (Wohlgemuth et al. 2017; Parisi et al. 2018). CWD could also have many different functions towards regeneration establishment and growth and is positively associated with tree establishment, protecting saplings from stress, unfavorable climate conditions, and predation (Taeroe et al. 2019). As well documented in the literature, CWD is widely recognized as a relevant regeneration substrate, mainly in coniferous forests (Bolton and D'Amato 2011). CWD supplies habitats for many birds and mammals and is essential for many saproxylic organisms, which need woody resources to complete their life cycle (Parisi et al. 2018). Moreover, the biodiversity related to deadwood is around 20% of both animal and plant central European forest biodiversity (Bütler et al. 2006). Deadwood with its different sizes, shapes, and decay stages is a heterogeneous element at the microsite level contributing to increase the number of ecological niches. Substrate-dependent taxa of lichens, fungi, and beetles show a reduction in managed forests, due to the reduction in dead trees, both standing and lying on the ground (snags and logs) in different decay stages (Paillet et al. 2010). The slow decay rate of logs and snags allows the coexistence of successions and a larger number of species. CWD in advanced decay stages is important especially for red-list species (Parisi et al. 2018). Downed woody debris accounts up to 20% of total ecosystem C in old-growth forests. To preserve the stocked carbon and to favor the biogeochemical cycles, many local forest guidelines suggest maintaining and increasing the abundance of CWD (Russell et al. 2015). On the contrary, removing CWD by salvage logging and by common forest practices influence the stand composition and dynamics, slowing down the regeneration processes compared to non-salvaged areas (Taeroe et al. 2019). Under future scenarios of increasing disturbance and extreme meteorological conditions, like drought and fires (Seidl et al. 2017), CWD will be a key element in creating favorable microsites, both to increase biodiversity and to support forest regeneration.

CWD can have different origins. Stumps are created when a standing tree snaps, or as a result of forest operations like thinning or logging. The uprooting of living trees creates pits and adjacent mounds made by the radical plate. Falling of either living or dead tree or branches contribute to creating decaying logs (Cornett et al. 1997). More in general senescence and the consequence dead and collapsing of mature trees is the mechanism responsible for the constant supply of deadwood in forests. The main drivers in producing a large amount of deadwood, instead, are forest disturbances, which can be small-scale disturbances, like small and isolated windthrows due to local turbulences, or stand-replacing disturbances, like extended crown fires. Wind, fire, and pest outbreaks are the major disturbances affecting forests (Seidl et al. 2014). Wind disturbances are more stochastic and less influenced by stand and site properties (Vodde et al. 2011) than wildfire, and gravitative disturbances. Wildfires are the disturbances that caused the highest modification of the environment, due to the burning of living stands, understory, duff, and organic matter in the soil. Those modifications change significantly the nutrient availability and the total amount of solar radiation on the grounds. Insect and pest outbreaks (e.g. bark beetles) could cause heavy damage to forests and are quite difficult to manage, in particular under the ongoing scenario of global warming. Snow-related disturbances, like avalanches, are less frequent and most of the time occur at high altitudes and their effects are quite similar to windstorm damages. On a local scale, the impact of forest operations can be compared to disturbances. The removal of all dead wood during logging and salvage logging operations reduces site heterogeneity and can inhibit tree regeneration (Vodde et al. 2011). There are three main types of disturbance legacies in a forest stand: trees and patches of standing untouched and intact forest, damaged trees and advanced regeneration (including sprouting), disturbance related microsites like pit and mounds, and Coarse Woody Debris (CWD) (Vodde et al. 2011). As a result of a disturbance, there is a sudden variation in surface topography, solar radiation, and nutrient availability, which is critical in creating different microsite conditions. Stand-replacing disturbances affect a large portion of the forest canopy, promoting the regeneration of pioneer species and releasing advanced regeneration and sprouts. Minor disturbances instead, generally favor shade-tolerant species. After a stand-replacing disturbance, where full-light conditions are stable for long periods, the availability of favorable microsites is critical in forest regeneration establishment and growth (Vodde et al. 2011). It has been widely recognized the high ecological importance of young forests, which provides an opportunity for ecosystem adaptation in changing environments. In young forests, a lot of different species benefit from a complex mosaic of canopy openings, high structural diversity, post-disturbance legacies like deadwood, and aboveground structures left by disturbances (Kuuluvainen and Gauthier 2018). While the general role of deadwood in forest ecosystem dynamics and the key role of natural regeneration for the future of the forests stands have been widely recognized, less is known about the indirect effect of deadwood on seedlings' establishment and growth, and how to determine and distinguish them. Furthermore, not only the direct effect of deadwood as a substrate is important but also other direct effects and indirect effects like shadowing and microsite amelioration play an important role in early regeneration dynamics.

In this paper, we review the double facilitative role of CWD for seedling establishment and growth, by focusing on both its direct and indirect effects. The direct effects are intended when the CWD acts directly on the seedling influencing the seedling itself. The indirect effects are when the influence of the CWD is directly on something else (the environment, some limiting factor) and then such interaction has a direct impact on the seedling. In particular, we aim to:

- assess the direct effect of CWD on regeneration as substrate, seed trap, and elevated microsite.
- analyze the indirect effect of CWD on regeneration: as a substrate for mosses, as a substrate for fungi and mycorrhizal, increase moisture on soil, amelioration, protection from browsing, and avoid competition.
- test the geographic and climatic relationships with direct and indirect facilitation by CWD.

Material and methods

PRISMA review

In this review, we adopt the PRISMA statement which improves the reporting of systematic reviews and meta-analysis papers (Moher et al. 2009; Page et al. 2021). To collect the articles of this review paper we used the Scopus, Web of science, and Tree Search databases (https://www.scopus.com/home.uri, https://www.webofknowledge.com, https://www.fs.usda.gov/treesearch/). We used a combination of the terms “coarse wood* debris”, “log*”, “snag*”, “stump*”, “deadwood*” to detect papers about deadwood and CWD and the words “forest” and “regeneration*” to focus the research on forest regeneration. We used just these few words to try to have the wider range of climate and forest ecosystems possible and also try to include in the analysis every possible type of interaction between deadwood and regeneration.

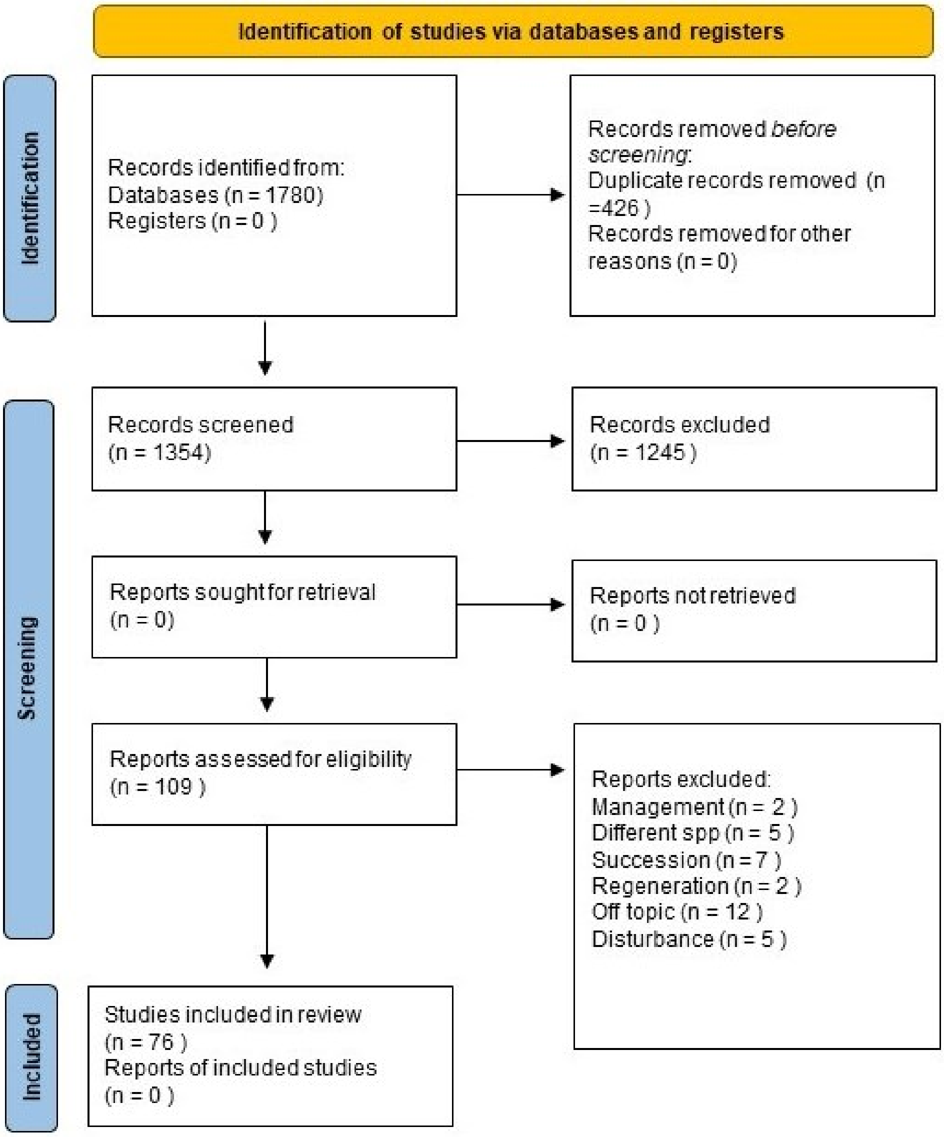


Figure 1.1 Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) diagram. Here are reported the number of publications found during the literature research and the number of excluded papers in each step. The report excluded during the last screening phase were classified like that: i) management: the paper is about forest management in general but not specifically about CWD-regeneration interaction; ii) different spp: the paper about the interaction between CWD and other species of plant or animal, not tree seedlings (ex. Saproxylic fungi); iii) succession: the paper is about ecological succession in the forest ecosystems, but not highlight any relations between CWD and regeneration; iv) regeneration: the paper about regeneration dynamics but does not mention any interaction with CWD; v) off-topic: the paper is off topic, is not about regeneration (ex. Dynamics of deadwood in forest); vi) disturbance: the paper is about post-disturbance recovery or disturbance ecology, but does not highlight any CWD-regeneration interaction. Diagram adapted from (Page et al. 2021)

We obtained 1780 papers and after duplicate removal, the total amount of papers was 1354. The first step in this review was the screening phase (see the PRISMA flow diagram fig. 1.1), where we focused on paper titles. According to the titles, the criteria used for screening were: the article topic must regard the regeneration and/or the deadwood processes in forests; the articles must take into account the interaction between deadwood and regeneration. In case of doubt, the article was included until the next step. In the second phase of screening, we went deeper into the article analysis focusing on their abstracts. The criteria adopted in this step are the same as the previous one, but we classified also six different exclusion causes, based on the main focus of the paper: management (focused on management practices and not on interaction CWD-seedling), different species (focusing on a different animal or plant species like fungi or bryophyte community), succession processes (focusing on general succession processes of stands and not on interaction CWD-seedlings), regeneration only (focusing only on regeneration of particular species and not considering interaction with CWD), disturbance (disturbance management and post-disturbance practices or disturbance influence on ecosystems in general) and off-topic. As before the uncertain articles were deeply investigated in the next step. To make a paper eligible for the analysis it was screened by reading the full-text articles. The articles were analyzed and excluded with the same criteria as the screening phase. At the end of the analysis, 76 articles have been considered eligible for this systematic review.

Types of analysis

Using high-resolution climate data (Karger et al. 2017), we extrapolate the reference biome for each paper based on the position of the study areas, and then we look for relations between the deadwood functions found in the reviewing process and the biome.

Results

Fig. 1.2 World distribution of the paper included in the final analysis.

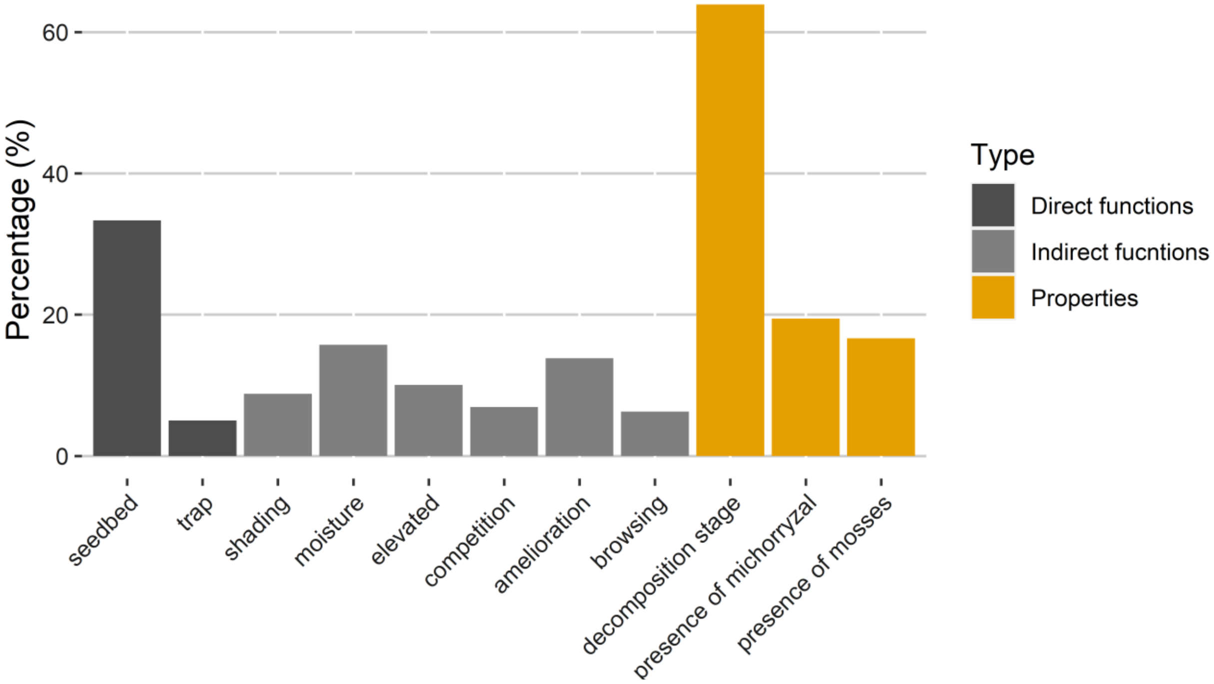


Figure 1.2 occurance of different categories of effect of CWD that emerged from the analysis.

As reported in figure 2 during the reviewing process we were able to identify eight functions and three properties that deadwood has towards regeneration: we intended properties as the intrinsic characteristic of CWD that influences regeneration (e.g. decomposition rate), while function as the interactions between the CWD and regeneration (e.g. shading of the regeneration microsite). Functions can be divided into two different main categories: direct influence and indirect influence on regeneration. Direct influence on regeneration is considered when CWD has a direct impact on saplings, influencing directly the tree regeneration dynamics. Direct functions are considered:

- Substrate: the deadwood act as a preferred substrate for regeneration, which can have different properties. The most important was recognized to be the decomposition stage, estimated using different scales proposed by different authors (Maser et al. 1979; Hunter 1990; Nakagawa et al. 2003; Orman et al. 2016; Ulyshen et al. 2018). The softness and the capacity to be penetrated by the roots are strictly correlated and they are a consequence of the decomposition stage. For this reason, these properties are not included in the list. Also, being a suitable substrate for mycorrhizal fungi can enhance the chances of successful establishment and survival due to the positive plant-fungus interactions. This relation is often species-specific. The role of CWD as a substrate was the first function recognized. Thus, the bigger part of the papers reviewed is about this topic.
- Trap: the CWD act as a physical trap for the seeds, in particular the smallest ones. That forces the seeds to establish on CWD or near them. The CWD acts as an obstacle and traps the seeds during flood events, snowmelt, or wind transportation. Moreover, bark cracks and decomposition crevices trap the seeds during the seed dispersal processes.

Indirect function towards regeneration instead, is considered when the CWD alters conditions for the establishment, growth, or survival of seeds and juvenile stages. CWD as a substrate can have also an indirect function. In particular when deadwood becomes a suitable substrate for mosses creating better conditions in terms of moisture retention and trapping capacity, due to the presence of mosses. The main indirect function of CWD on seedlings is the amelioration of microsites. The amelioration of the microsite can produce a better environment in general, where the sapling establishes and grow better than elsewhere, or contribute in some specific situations.

- Shadowing: the shadow of the CWD contributes to decreasing the temperature in the soil and avoiding direct solar radiation. This protects seedlings from extreme temperatures and extreme solar radiation in particular in warm climates or slopes directly exposed to the sun (e.g. southern slopes in northern hemisphere). The shadowing effect of CWD can decrease up to 10°C the microsite surface temperature, by increasing at the same time soil moisture content (Gray and A. 1997).

- Increase moisture content: the presence of CWD thanks to the shadowing, lower temperature, and less direct solar radiation contribute to maintaining a higher soil moisture content, favorable to seedling establishment and growth, especially during the first years. Also, the soil, duff, or litter accumulation close to the CWD, mainly on the upper side of a slope, contributes to creating a microsite with a higher moisture and nutrient content.

- Elevated site: deadwood, in particular stump and logs, create elevated microsites suitable for tree regeneration. In boreal and alpine areas elevated sites are favorable because of early emergence from the snow cover and so seedlings can receive more and sooner light. That gives them the chance to start slightly earlier the vegetative period, having a competitive advantage over other seedlings. Further, elevated sites allow escaping sites too humid at the base of the CWD, sites that could favor fungi or other diseases. Elevated sites can also give advantages in both intraspecific and interspecific competition against regeneration, herbaceous layer, and understory in general.

- Competition: CWD helps seedlings and early growth stages to escape competition and take advantage of it. As said before as elevated sites allow one to escape competition, but also create favorable conditions to favor some species over another. Creating particular microsites, deadwood determines better conditions to avoid diseases and stressful situations. Such amelioration can create slightly favorable conditions for a single seedling, to overcome competitors. The presence of CWD and species-specific relations can also influence the successional dynamics in a forest stand.

- protection effect: CWD can protect the seedlings from mechanical damages, like snow gliding or rock falls, especially at tree-line altitude or at the edges of forest stands.

- Browsing: the role of CWD against the browsing pressure can be positive or negative, depending on the species of animal. CWD presence and chaotic disposition are very effective in protecting regeneration from ungulates browsing (deer in particular), making it difficult for animals to move between the CWD. Quite the opposite, the presence of CWD increases the browsing damage (especially seeds and acorns) from rodents because of the disposition of debris to create a favorable and protective environment from predators.

Spatial and climatic (köppen) patterns

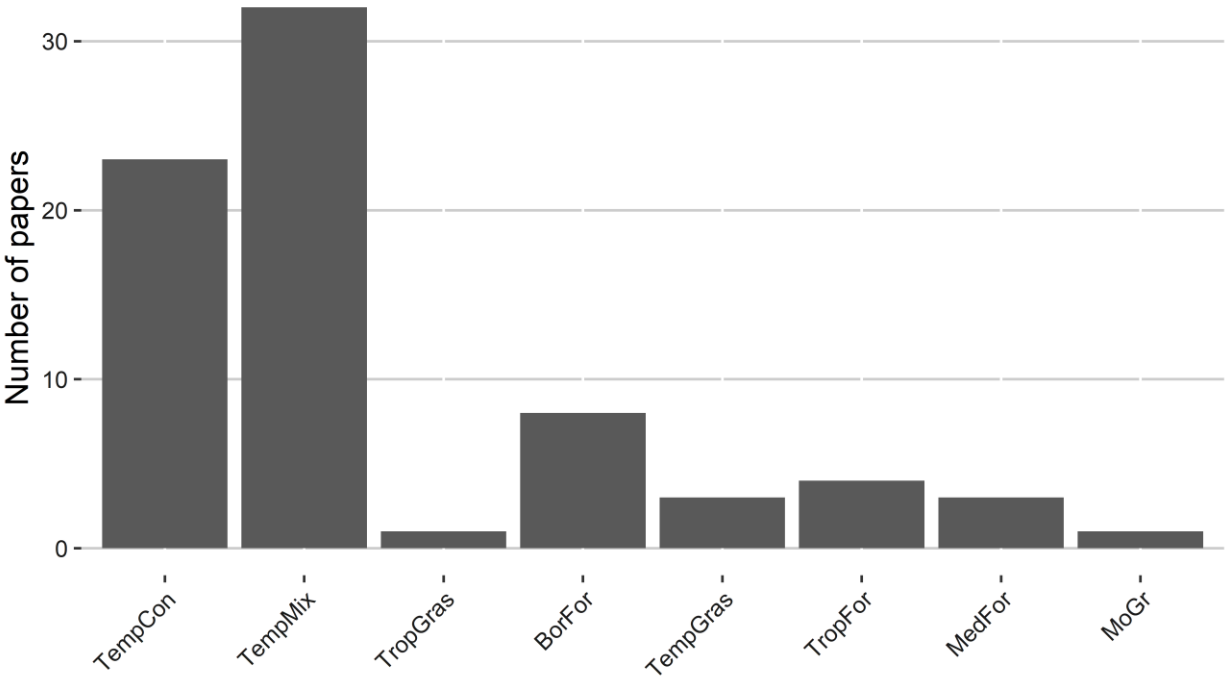


Figure 1.3 Number of article per biome

Table 1.1 Legend of biome adopted in the paper

Biome	**code**
Temperate Conifer Forests	TempCon
Temperate Broadleaf & Mixed Forests	TempMix
Tropical & Subtropical Grasslands, Savannas & Shrublands	TropGras
Boreal Forests/Taiga	BorFor
Temperate Grasslands, Savannas & Shrublands	TempGras
Tropical & Subtropical Moist Broadleaf Forests	TropFor
Mediterranean Forests, Woodlands & Scrub	MedFor
Montane Grasslands & Shrublands	MoGr

There is no significant evidence of a correlation between the global location of the study sites and the function of CWD towards regeneration. Most of the studies took place in the northern hemisphere, clustered in the USA-Canada border, in Europe, and Japan. In the southern hemisphere, articles are clustered in Patagonia, the southeast part of Australia, and New Zealand. Most of the correlations are found in Europe and North America. The trap function is recorded only in central Europe and in the northwest of the USA.

According to figure 1.3, most of the studies took place in the temperate broadleaf and mixed forest or the temperate conifer forest. The third most represented biome is the boreal forest/taiga, followed by tropical forest, montane grasslands and shrublands, and Mediterranean forest, woodlands, and scrubs.

About the function identified during the analysis, most of them are correlated to the temperate coniferous forests and the temperate mixed forest, which are by the way the most represented biome in the paper analysis. Other relevant correlations are between amelioration and more extreme bioma, like warm Mediterranean forests and cold boreal forests. Tropical forest shows a high number of papers about deadwood as an elevated microsite for establishment. Grasslands are the third most represented biome in the browsing protection function. Boreal forests in the ends are also quite well correlated to the increase in soil moisture.

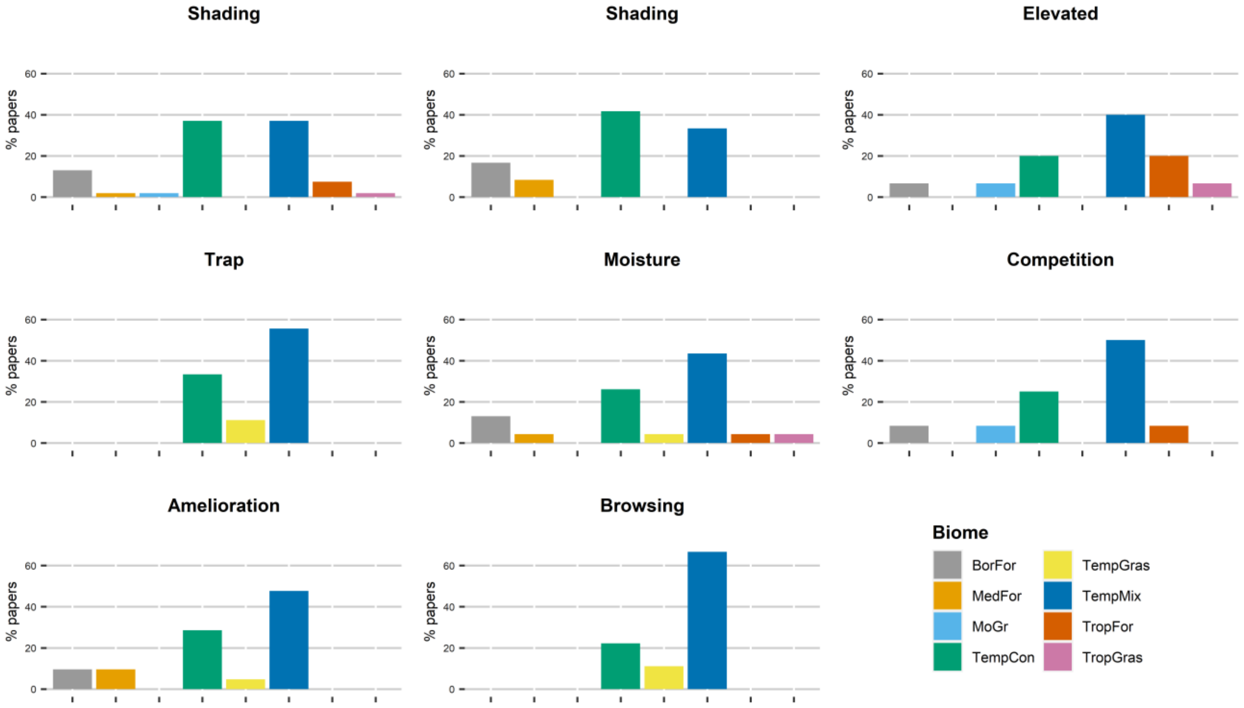


Figure 1.4. Distribution of bioma relatively of each function, indicated by the percentage of studies which underlined the given functions that have been conducted on forests classified under the indicated biome (tab. 1.1).

Figure 1.4 illustrates the characteristic of the deadwood that influenced the regeneration dynamics, that emerged during the analysis. As with the function, also in this case most of the characteristics show a correlation with the temperate forests, both mixed and coniferous ones, due to the high amount of paper which has the study area classified under these bioma.

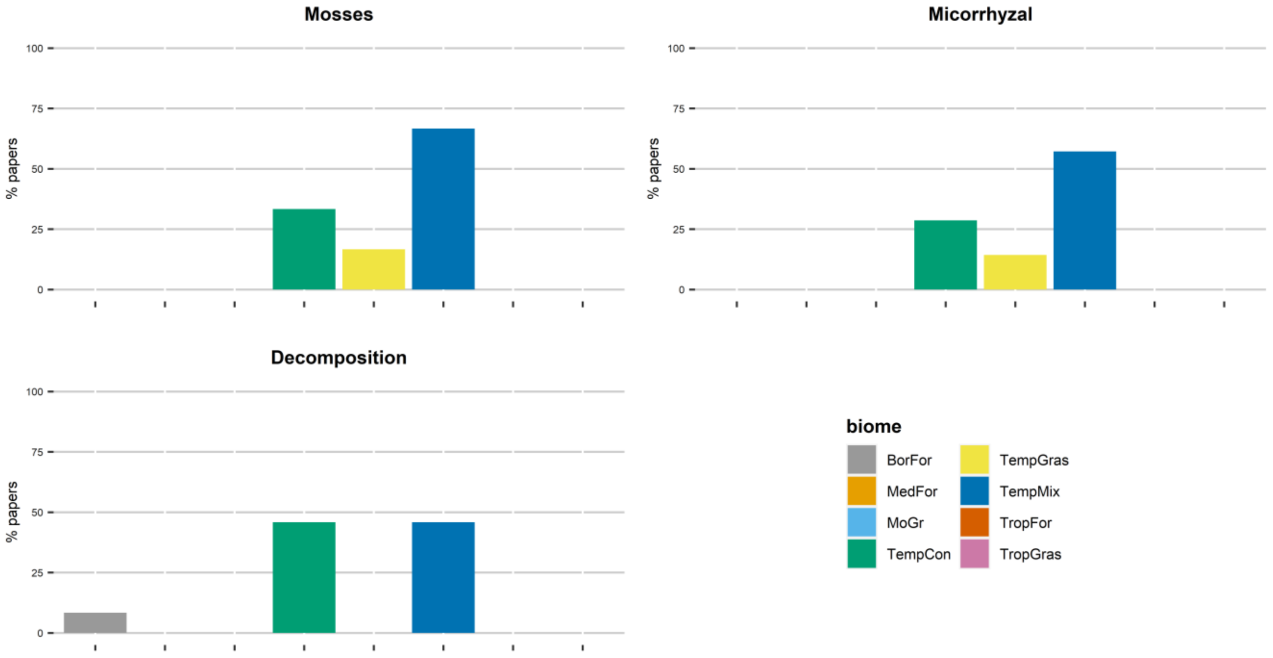


Figure 1.5 Distribution of bioma relatively of each characteristic of the deadwood, indicated by the percentage of studies that underline the given characteristic that has been found in forests classified under the indicated biome (fig. 1.4b)

Discussion

Direct

Soil should be the most preferred substrate for seedling germination, but it has some limitations: it is more susceptible to nutrient leaching; there can be high competition against nemoral species; there can be a lack of niches for germination (Kern et al. 2019). CWD instead, can provide alternatives to these limitations, playing many different roles in forest regeneration dynamics. As nurse logs, they have a positive influence both in seedling establishment and in seedling growth. This positive influence must take into account also some species-specific relations between different types of substrate and different tree species, that are influenced by growing behavior (e.g. shade-tolerant species, root system type, and root system development pattern) (Anderson and Winterton 1996; Orman et al. 2016). CWD can be a safe site for seedlings establishment but not safe for germination (Szewczyk and Szwagrzyk 1996; Simard et al. 2003; Holeksa et al. 2021). This is particularly true after the first growing season because recent deadwood is not decayed and not soft enough to allow root penetration (Ježek 2004; Robert et al. 2012), a situation that could take place after more than 40 years, according to Konôpka et al. (2021). CWD as a favorable substrate is proved by the evidence that the seedlings establish preferably on a woody substrate, better if well decayed, even though CWD doesn't occupy the largest part of the surface (often between 5% and 20%) (Bace et al., 2011; Beach & Halpern, 2001; Cornett et al., 1997; Hornberg et al., 1997; Kuuluvainen & Kalmari, 2003; Lusk, 1995; Mori et al., 2004; Motta et al., 2006; Nakagawa et al., 2001; Peterson & Haines, 2000; Robert et al., 2012; Scott & Murphy, 1987; Scowcroft, 1992; Szewczyk & Szwagrzyk, 1996, Morimoto et al., 2021). As a substrate, the total volume of CWD is positively correlated with the total number of saplings (Lampainen et al. 2004). Moreover, the role of CWD becomes crucial in the secondary post-disturbance regeneration, 10-20 years after the disturbance (Tsvetanov et al. 2018), especially in canopy gaps created by large disturbances or as a consequence of a single tree falling (Scott and Murphy 1987; Sanchez et al. 2009; Holeksa et al. 2012). Post-disturbance management practices, like salvage logging or deadwood manipulations, resulted in a greater growing rate on sites with manipulated logs than on sites with no intervention. Under these scenarios, logs have the main function of substrate (Cornett et al. 2001).

To act as a favorable substrate, the CWD (especially logs and stumps) must be in middle to advanced decomposition stage, allowing nutrient and moisture retention, and better root penetration (Bače et al., 2012; Brang et al., 2003; Bujoczek et al., 2015; Chećko et al., 2015; Heinemann et al., 2000; Hofgaard, 1993; Johnson & Yeakley, 2013; Lambert et al., 2015; Motta et al., 2006; Nakagawa et al., 2003; Orman et al., 2016; Orman & Szewczyk, 2015; Robert et al., 2012; Santiago, 2000; Stroheker et al., 2018; Zielonka & Piątek, 2001, Fukasawa et al., 2019). To evaluate this decomposition stage several scales have been proposed (Maser et al. 1979; Sollins 1982; Sippola and Renvall 1999; Holeksa et al. 2012). Most of the saplings were found on CWD in a quite advanced decomposition stage, but young seedlings are present also in the middle decomposition stages. If the decomposition stage is to advance, it can lead to an increase in sapling mortality due to mechanical failure of the substrate and the consequent falling of trees (Holeksa et al. 2021). CWD with a DBH between 20 cm and 50 cm are the most suitable for regeneration and, anyway, a positive correlation between CWD diameter and regeneration presence was found (Holeksa et al. 2012; Bače et al. 2012; Johnson and Yeakley 2013; Bujoczek et al. 2015; Stroheker et al. 2018; Khanina and Bobrovsky 2021). After falling, logs could be accessible for regeneration in 50-100 years (Zielonka and Piątek 2001; Narukawa et al. 2003). Some studies report that stumps are better than logs for the establishment because they are better shaped (horizontal) and better linked to the soil (Nakagawa et al. 2003; Motta et al. 2006; Bace et al. 2011; Bujoczek et al. 2015; Orman et al. 2016). CWD are substrates with higher moisture content and with less competition from surrounding vegetation (Lusk 1995). The moisture on decayed wood is elevated and that makes CWD more favorable germination sites (Scowcroft 1992; Lusk 1995; Anderson and Winterton 1996; Cornett et al. 2001; Mori et al. 2004; Sanchez et al. 2009; Johnson and Yeakley 2013). Moreover, decayed wood contributes to keep the moisture level, resulting in greater water availability also in late summer (Heinemann et al. 2000; Fukasawa et al. 2020). Therefore in very xeric environments, CWD could not be safe sites for regeneration, because direct solar radiation dried them up faster (Heinemann and Kitzberger 2006). Among the various species, CWD are particularly relevant for coniferous regeneration, in particular for *Abies spp.*, *Picea spp.* (Hofgaard 1993; Anderson and Winterton 1996; Nakagawa et al. 2001; Brang et al. 2003; Lampainen et al. 2004; Ježek 2004; Holeksa et al. 2012, 2021; Bujoczek et al. 2015; Orman and Szewczyk 2015; Stroheker et al. 2018; Tsvetanov et al. 2018; Hotta et al. 2021) and *Tujia spp., Tsuga spp.* and *Cupressus spp.*(Liao et al. 2003). Coniferous wood is recognized also as a better substrate for regeneration (Cornett et al. 2001; Lambert et al. 2015).

Another important direct function of CWD is to act as a trap for seeds. Bark, cracks, and crevices on decaying woods act as a trap for light and small seeds, enlarging the variety of micro-topographical conditions favorable to seedling establishment (McGee and Birmingham 1997; Sanchez et al. 2009; Marzano et al. 2013; Logan et al. 2020), e.g. spruce and white cedar, during mast years and also during snowmelt period (Bače et al. 2012). The trap function of CWD towards small seedlings can perform also as a filter for species capable of regenerating on deadwood (Chećko et al. 2015). This trap function seems to be clustered only in central Europe and the northwest of the USA. This spatial distribution is probably correlated with the aim of the paper talking about it. In most of the paper underlining the trap function, the main species involved are spruce and other conifers. Spruce has very light seeds and so this function is underlined. But spruce and conifer are also the most widespread species in Europe, both naturally and artificially, due to the climatic conditions and their high economic value. Therefore, a lot of studies focused on these species, considering only marginally other light seed species.

Indirect

CWD laying on forest ground can act as a suitable substrate for mosses, having thus an indirect substrate function. In this case, they can be a suitable substrate for other ecosystem components which effect directly regeneration, like mosses or fungi. Mosses can influence positively the regeneration dynamics because their high fog-absorbing capacity help in maintaining a good moisture level on the germination substrate (Liao et al. 2003; Lambert et al. 2015; Stroheker et al. 2018; Fukasawa et al. 2019). At the same time, deadwood is the most important substrate for many types of fungi, which can have both positive and negative interactions with saplings. Fungal and other diseases could be avoided by growing on elevated CWD microsites. The environmental conditions of growing on a collar at ground level (e.g. elevated moisture, less solar radiation, etc…), could be unfavorable due to the higher probability to suffer fungal disease (Nakagawa et al. 2003). Positive interactions have been underlined between seedlings and mycorrhizal, thanks to the positive mutual interactions that enhance seedlings' survival, often species-specific (Fukasawa et al. 2020). Moreover, deadwood can help in maintaining such interaction also after disturbances (e.g. wildfires) protecting mycorrhizal from damages (Logan et al. 2020). Interactions between trees and fungi or trees and deadwood are most of the time species-specific (Nakagawa et al. 2001; Mori et al. 2004; Štícha et al. 2010; Orman et al. 2016; Macek et al. 2017). Trees killed by fungal pathogens result to be better for future colonization by seeds. This process has been recognized as species-specific, depending also on the interaction between tree species and fungi (Debeljak et al. 2019).

CWD creates elevated microsites, which are particularly favorable as a seedbed for seedling establishment. As reported by several authors, elevated woody microsites contribute to increase the substrate moisture content and favor exposure to solar radiation. This larger exposure, contributes to increasing local temperature, which is important, especially in cold climates (Scowcroft 1992; Hornberg et al. 1997; Motta et al. 2006; Štícha et al. 2010; Johnson and Yeakley 2013). Elevated microsites that imply more light are also important in very dense stands, like tropical forests, where understory competition is a limiting factor (Bellingham and Richardson 2006).

CWD as an elevated microsite allows the seedlings to avoid interspecific competition. On one side elevated microsites move away saplings from the competition with shrubs and herbaceous ground cover, e.g. really strong competition of dwarf bamboo understory in Japanese forests (Narukawa and Yamamoto 2002), but also create different regeneration niches for different tree species (McGee and Birmingham 1997; Beach and Halpern 2001; Sanchez et al. 2009; Khanina and Bobrovsky 2021). Intraspecific competition could be a limiting factor and responsible for density-dependent mortality on CWD (Liao et al. 2003; Bellingham and Richardson 2006). In dense understory stands, elevated microsites, often associated with gaps, can be more favorable due to the higher amount of light available for seedlings and saplings (Heinemann et al. 2000; Santiago 2000; Nakagawa et al. 2001). A higher microsite with more light could favor mainly shade-intolerant species (Peterson and Haines 2000; Christie and Armesto 2003), and the presence of CWD has been recorded to influence the relative abundance of a species (Simard et al. 2003). Moreover, slow-growth species seem to be facilitated by deadwood, mainly when they grow at a similar rate as wood decay (Sanchez et al. 2009). In these cases, particularly appropriate is the CWD originated at different times by repeated disturbance, which creates a complex pattern of regeneration, generating several cohorts within the stands (Vodde et al. 2010a). Deadwood presence can have a diverse influence on different species' attitudes. CWD can favor particular pioneer species, acting as substrate, creating favorable microsites, and originating particular microtopography like pit and mounds (Vodde et al. 2010a; Holeksa et al. 2012).

Amelioration of microsite

Among indirect functions, a special focus should be on how CWD creates favorable microclimatic conditions for seedling establishment and germination (Logan et al. 2020; Hotta et al. 2021). CWD is the most common and convenient shelter object for saplings (Bailey et al., 2012), resulting to be the most suitable regeneration microsite for more than 70% of seedlings (Smit et al. 2012). These “safe microsites” are very important in post disturbances regeneration dynamics, such as post-fire (Pausas et al. 2004; Castro et al. 2011; Marzano et al. 2013; Bailey et al. 2015) and post-windthrow restoration (Tsvetanov et al. 2018) and after bark beetles outbreak (Macek et al. 2017). Also, CWD is an important protective object in reforestation practices, both natural and artificial, sometimes associated also with plastic shelters (Valenzuela et al. 2016). This use of CWD in reforestation plans can be the best strategy since seedlings establish and grow better on favorable sites near CWD (Castro, Allen, Molina-Morales, Marañón-Jiménez, Sánchez-Miranda, Zamora, et al., 2011; Kuuluvainen & Kalmari, 2003; Minore, 1986; Wild et al., 2014). Up to ~25% of total regeneration is besides CWD (Lampainen et al. 2004). CWD-related microsites show lower mortality compared to other microsites (e.g. graminoid, litter, pit, and mounds, etc.), mainly because of lower stress-induced mortality (Macek et al. 2017). A possible explanation is that the shadow provided by CWD increases the local soil moisture content, and avoids excessive desiccation by direct solar radiation (De Chantal et al. 2005; Castro et al. 2011; Smit et al. 2012; Marzano et al. 2013; Goldin and Brookhouse 2015; Bailey et al. 2015; Valenzuela et al. 2016; Macek et al. 2017; Marcolin et al. 2019) and/or by wind blow (Bailey et al. 2012). CWD presence and its consequent shadow, influence the water soil moisture both in distance and in depth (Bailey et al. 2015). This shadowing effect and the microsite amelioration are so relevant because heat and desiccation are one of the major causes of death for young seedlings due to high temperatures and direct solar radiation during hot and dry summers (Gray and A. 1997; Castro et al. 2011; Marzano et al. 2013; Stroheker et al. 2018; Marcolin et al. 2019). The shadowing effect contributes substantially to reducing soil temperature (Marcolin et al. 2019), especially under future scenarios of climate change and warming temperatures (Lindner et al. 2010). In colder regions on contrary, CWD can create a local warmer microsite beside them (Castro et al. 2011).

There can be opposite functions of deadwood depending on climate. According to Johnson & Yeakley, (2019), elevated convex sites and/or decayed wood facilitate earlier snowmelt for seedlings located in cold and wet climates with abundant snowfall, depressions or concave sites both enhance moisture and protect seedlings from wind chill exposure for seedlings growing in cold and dry locations, and objects protect seedlings from excessive radiation in warm& dry high locations. Small CWD, in particular branches and crowns of lying trees, helps better the regeneration in the first years. They could provide the necessary shadowing and protection, but after a few years, seedlings can overcome them and take advantage of light in the gaps (Castro et al. 2011). The CWD protection effect is species-specific and can influence the competition's dynamics among different species and different phenological phases (Goldin and Brookhouse 2015). The relationship between deadwood and seedlings is often anisotropic (Marzano et al. 2013; Marcolin et al. 2019). In alpine and boreal regions, in particular, elevated microsites are favorable regeneration spots, because they are some of the first sites emerging the snow cover during the snowmelt period, so the vegetative season can potentially start sooner (Štícha et al. 2010; Wild et al. 2014; Macek et al. 2017; Johnson and Yeakley 2019). Moreover, CWD absorbs short-wave radiations, contributing to accelerate the snowmelt process (Marcolin et al. 2019). At treeline altitude CWD protects against snow gliding, a process happening commonly on steep slopes, acting as a safe substrate or as a physical barrier (Johnson and Yeakley 2013). At treeline edges, CWD contributes to the successful regeneration and expansion/maintenance of treeline ecotone (Johnson and Yeakley 2013). Raftoyannis & Spanos, (2005) by manipulating CWD, find out that branches and logs have no effect on coniferous regeneration and can have a negative effect on re-sprouting species, like *Quercus*. CWD instead, is helpful in the protection and control of soil degradation and erosion.

The CWD disposition and spatial pattern help to protect the regeneration from deer browsing, being difficult for those animals to move within the regeneration areas (Minore 1986; Bailey et al. 2012; Smit et al. 2012; van Ginkel et al. 2013; Whyte and Lusk 2019; Hagge et al. 2019; Puig-Gironès et al. 2020). The ability of CWD to avoid browsing from ungulates depends on the species of animal, the geometry, and the disposition of woody debris on the ground (Whyte and Lusk 2019), in particular branching has resulted as an effective tool for reducing seedlings browsing than logging (Neilly and Cale 2020). On contrary, Szwagrzyk et al., (2020) suggest a positive correlation between browsing and a moderate presence of CWD (25 m^3/ha), then such correlation decreases indicating how only above that threshold there is an effective protective function. On the other side, CWD creates a favorable environment for rodents increasing predation and damages of seeds and acorns (van Ginkel et al. 2013; Hagge et al. 2019; Puig-Gironès et al. 2020).

Management implication

As reported by many papers, coarse woody debris should not be considered only as process waste, but they have a critical role in the ecological processes in the forests. They are important not only as a regeneration microsite but they are key elements in many ecosystem components, like nutrient cycle, water retention, and soil stabilizing structures. CWD should be left on the ground after the forest utilization processes (Scowcroft 1992; Lambert et al. 2015). The presence of CWD in management sites is lower than in old-growth ones, and that can have a great influence on regeneration and ecosystem dynamics. It is recommended tough, to conserve old senescent trees that can serve as nurse logs (Hornberg et al. 1997).

Cut and release in salvage logging operations increase the microsites heterogeneity, increase surface roughness and contribute to smoothing the extreme temperature values (Marcolin et al.

2019). Moreover, leaving CWD on the ground during salvage logging and reforestation practices can reduce the browsing damage by ungulate, but can increase the damage from rodents (Hagge et al. 2019). In conclusion, during restoration or reforestation processes, management strategies of assisting species or providing migration can be enhanced by leaving in situ natural legacies that could enhance tree regeneration (Kuuluvainen and Gauthier 2018).

Conclusions

CWD can influence the seedling establishment probability and growth patterns. The direct effect of CWD on regeneration is well reported in the literature, like the positive role of CWD as substrate, especially for conifers if it is well decomposed since it results softer and wetter than the surroundings. Usually, deadwood covers a small part of the ground but hosts a high number of individuals. For this reason, a higher percentage of CWD in forests, similar to the percentage of old-growth forests (Christie and Armesto 2003), is positively associated with regeneration.

Fewer studies were found about the indirect roles of CWD. The most studied indirect functions of CWD include creating elevated microsites and acting as hosts for mosses and fungi that can favor and enhance seed germination and seedling growth. Mycorrhizal associations are species-specific and often favorable, but other forms of fungal interaction can be negative and cause disease. In general, the presence of CWD leads to an amelioration of regeneration microsite, making it more suitable for regeneration establishment. In future scenarios of warmer and drier conditions the presence of deadwood act as a buffer, avoiding direct solar radiation, decreasing the soil surface temperature, and increasing the soil moisture content, creating particularly favorable microsites for seed establishment. In the end, CWD distribution and disposition contribute to protecting saplings from ungulates browsing but result to favor rodents predation of seeds.

According to what is stated in literature nowadays, there are still open questions for future research. Regeneration dynamics after different disturbances can lead to very different regeneration processes and scenarios. In particular, natural structures and processes after windthrows are less frequently investigated (Taeroe et al. 2019). Moreover, under future climate change scenarios, natural disturbances are increasing and so is the role of CWD in post-disturbance recovery. A limitation of this review paper could be the lack of long-term studies regarding the effect of CWD on regeneration, especially the indirect effect. It is also complicated to find a unique interpretation and a separation of different effects of CWD on seedlings because, frequently, these effects are multiple and deeply interconnected. More studies are needed to understand how CWD can facilitate recovery under different salvage logging management strategies. Since the influence of a changing climate in reshaping species ranges, the role of deadwood in forest recovery or species migration assistance will be critical in the future. In conclusion, there is still a gap of knowledge in the role of CWD in influencing and ameliorating the regeneration microsite. Since the lack of long-term studies will be essential to analyze how the role of CWD changes over time and if the same CWD changes its role and function in facilitating the various steps of tree and forest regeneration and growth.

Chapter 2: Windthrown management and restoration: natural regeneration dynamics under different savage logging strategies in eastern Italian Alps.

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Under submission

Abstract

Wind disturbances are the main driver of forest dynamics in Europe, shaping forest stands and modifying the ecosystem services (ES) provisioning. Salvage logging is the most common strategy adopted in post-disturbance management. Understanding natural regeneration dynamics, and their interaction with the logging strategies, is crucial to understand how forests are changing under CC and what are the best post-disturbance management strategy. In this study we analyze: I) the natural regeneration dynamics under different management strategies to compare the effect of salvage logging and no-intervention measures on seedlings establishment and growth in two study areas with both measures applied one net to the other; II) the natural regeneration dynamics in 148 areas damaged by storm Vaia, the biggest windstorm of the last century in the southern alps. The aim was to analyze natural regeneration dynamics under different logging systems and what are the influences of site characteristics and disturbance legacies on seedlings and seed dispersal. The sampling protocol consists of one transect per area, perpendicular to one of the windthrown edges, and with a length of 80m. Along the transect, we collect soil cover, and we establish four sample plots, 3m radius at 0, 20, 40, and 80 meters from the edges within which we collect data about natural regeneration and deadwood. Results show that regeneration composition is driven mainly by previous stand composition, with some exceptions depending on seed dispersal strategy. Distance from the edge significantly influences the regeneration occurrence in large gaps and affects the browsing damage percentage, together with deadwood presence. According to GLM's models, distance from the edge, soil as a substrate, edge structure, and logging methods influenced regeneration establishment, while elevation, species characteristics, and logging damages influenced mostly early regeneration. In conclusion site factors, disturbance legacies, and logging methods reveal to be key-points to consider in post-disturbance management strategies to re-establish the soil cover as fast and efficiently as possible.

Introduction

Disturbances are one of the most important factors influencing forest ecosystem dynamics and shaping forest stands. Under the ongoing climate change (CC), disturbances have become more and more frequent, and windstorms, in particular, have been recognized as the most important disturbance affecting European forests, becoming the first responsible for forest cover loss and stand damages (Seidl et al. 2014; Gregow et al. 2017), as well as they can have negative influences on Ecosystem Services (ES) provision (Fleischer et al. 2017). Climate modifications make the forests more vulnerable to disturbances, and in particular to subsequent disturbances: one disturbance can lead to another one (e.g. large windows could lead to massive insect outbreaks), and these disturbances' interactions can be amplified by climate changes leading to a cascading process (Seidl et al. 2017; Leverkus et al. 2021a). Focusing on mountain forests, such disturbance interactions could result in long-term effects, with partly dramatic consequences for ecosystem services. For example, windthrow followed by bark beetle outbreak and amplified by exceptionally warm summer conditions can reduce the protection function in mountain forests for decades due to slow regeneration processes at higher elevations... Natural regeneration and seed establishment and survival have been described for long as crucial for the restoration of mountain forests, especially after a disturbance (Taeroe et al. 2019). Awareness rose that climate warming in forest openings may produce serious threats to regeneration processes (von Arx et al. 2014, Zellweger et al. 2020). Under the ongoing and future climate scenarios, the regeneration of forests stands severely damaged by disturbances plays a key role to define the future forest composition and structure, and their ability to face environmental modifications. The increase in temperatures is one of the biggest threats to European forests, especially in very sensitive ecosystems like alpine forests (Gobiet et al. 2014; Obojes et al. 2022). A closed canopy mitigates, to some extent, the effect of temperature increase (Dietz et al. 2020), instead, the lack of forest cover leads to a thermophilization of understory and forest species, especially in more sensitive ecosystems like mountain areas (Von Arx et al. 2013; Brice et al. 2019). After a disturbance, the new regeneration consisting of different and better-adapted species could grow in damaged areas, and these modifications in species composition can persist after the disturbance (Dietz et al. 2020). Wind disturbances can therefore potentially help in the adaptation of mountain forests to CC (Thom et al. 2020).

Since most of the forests in Europe are actively managed for various purposes after large windthrows salvage logging operations are often performed. The goals can be different: to reduce the economic losses selling merchantable timber (Slyder et al. 2020), to protect infrastructures from unstable material (Motta et al. 2006), to prevent pest outbreaks by performing sanitary loggings (Schroeder and Lindelöw 2002), and to manage the landscape, especially in touristic areas. Three different management strategies can be adopted after windthrows: I) no intervention: leaving all the deadwood and the damaged area as they are after the storm, without any intervention II) salvage logging: the total removal of damaged or uprooted trees; III) partial salvage logging and/or deadwood manipulation: removing only a certain percentage of damaged or uprooted trees and modify the disposition of deadwood for a different purpose (e.g. protecting from gravitative hazard) (Taeroe et al. 2019; Leverkus et al. 2021a). Different management strategies have shown different influences on forest regeneration. In particular, releasing a certain amount of deadwood help in creating favorable regeneration conditions and microsites (Leverkus et al. 2021b; Marangon et al. 2022). Different management strategies influence also ecosystem dynamics, modifying the biological legacies in forest stands (Morimoto et al. 2019), and, as a consequence, influencing forest regeneration structure and composition (Jonášová et al. 2010; Vodde et al. 2011).

Salvage logging operations can be executed using different systems: highly mechanized systems, cable yarding systems, and skidder and tractor systems. One system is preferable to another depending on site conditions, costs, safety, and impact on the forest ecosystem. Nevertheless, salvage logging operations have a negative impact on regeneration sites, damaging saplings and regeneration microsites (Waldron et al. 2014). On the other hand, too much deadwood or wood debris covering the soil can reduce the available regeneration niches for seedlings, slowing the regeneration processes and leading to a lower recovery rate in unsalvaged areas (Senf et al. 2019).

In the management of large windthrow areas, also the dimension of the gaps is a crucial variable for the timing and the dynamics of forest regeneration. It is well known the role of the gaps in natural regeneration dynamics (Holeksa et al. 2012; Allen et al. 2012; Filicetti and Nielsen 2022), making available higher quantities of light, water, and nutrients for the seedlings (Van Couwenberghe et al. 2011). Nevertheless, if the gap is too large, that can heavily affect seedling recruitment delaying the gap closing and triggering many different questions (e.g., soil erosion, landslides, avalanche risk, etc.…) (Cordonnier et al. 2008).

Together with gap-induced dynamics, site factors play a central role in regeneration establishment and growth. Slope aspect, temperature, water availability, and light intensity on the site are critical factors for forest regeneration dynamics (Taylor et al. 2017; Marangon et al. 2022). These factors can be heavily influenced by a disturbance's large variety of biological legacies. As reported before, deadwood and windthrown edges can strongly influence the solar radiation reaching the ground, modifying consequently temperature, humidity, transpiration, and nutrient availability (Saxton and Rawls 2006; Štícha et al. 2010; Marzano et al. 2013). Such modifications in the environmental conditions could lead to a change in the species composition, but at the same time make available for the already established regeneration lot of new growing space (Dietz et al. 2020).

The main objective of this paper is to analyze the post-windthrow short-term regeneration dynamics, under different harvesting systems and environmental conditions. We focused in particular on I) surveying the presence of regeneration, both early and advanced regeneration, to assess any variation from the previous forest composition; II) assessing the importance of the distance from windthrown edges for seedling supply and of the local condition to seedlings establishment; III) assessing the importance of advanced regeneration to restore possible the forest cover; IV) analyze if different harvesting systems influence short-term regeneration dynamics.

Chapter 2.1: Management strategies

Material and methods

Study area

The two study areas are located in the Eastern Italian alps, within the municipality of Cortina d’Ampezzo (BL). They have been damaged by the storm Vaia in late October 2018. Two different sites have been chosen for this experiment: Valbona (VB) located at 1350 m a.s.l. characterized by the presence of a mixed forest composed of Norway spruce (*Picea abies* (L.) H. Karst), beech (*Fagus sylvatica* L.), and silver fir (*Abies alba* Mill.), uneven-age structure with the dominant layer represented by coniferous trees and the dominated ones by broadleaves; Ospitale (OS) located at 1550 m a.s.l. characterized by the presence of a pure Norway spruce (*Picea abies* (L.) H. Karst) forest with the presence of sporadic Scots pine (*Pinus sylvestris* L.), even-age structure. In each site two areas have been established: one where total salvaged logging has been performed (SL), and the other one where no intervention has been performed (NI). The four areas from here on will be defined as: Ospitale salvage logging (OSSL), Ospitale no-intervention (OSNI), Valbona salvage logging (VBSL), Valbona no-intervention (VBNI). Within each area, 25 plots have been established (fig. 2.1.1), surveying the center of the plot with a GNSS receiver (multi-band RTK GNSS receiver

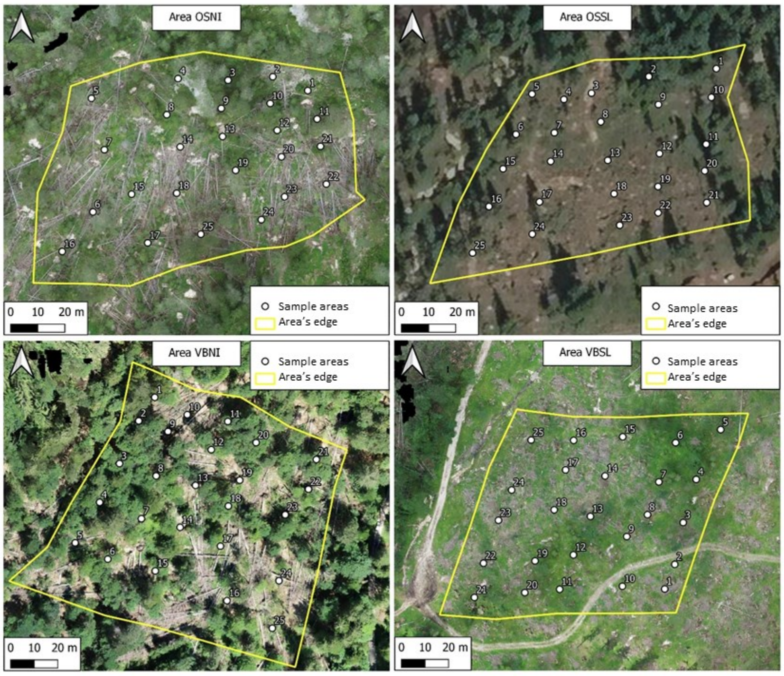

Figure 2.1.1 The four areas Ospitale salvage logging (OSSL), Ospitale no-intervention (OSNI), Valbona salvage logging (VBSL), Valbona no-intervention (VBNI). In yellow are represented the area’s edges, in white the sample plots.

EMLID Reach RS2, precision PPK H:5mm+0.5ppm, V:8mm+1ppm, recording period: 1s). Each sample plot was circular, with 4 m radius. Within the plot we sampled all the tree presents, reporting species, height, browsing damages, and other types of damages (e.g., mechanical damages, drought damages, etc….). By photo-interpretation of the images acquired by UAVs (Unnamed Aerial Vehicles), we identify the shortest distance from each plot to the nearest windthrown edge or green island. We sample the same areas three times since the storm in October 2018: in summer 2019, in summer 2021, and in summer 2022. This monitoring is still ongoing.

To analyze the statistical differences between different treatments and different years we adopted Chi-squared test, ANOVA type 3, and Tuckey post-hoc test. We applied Pearson correlation to test any correlation between the number of regeneration individuals and distance from the edge, and GLM's models to identify the influence of treatment, age, area, and year on the number of regeneration individuals.

Results

The number of seedlings sampled during the first survey campaign in 2019 was 1338, during the second survey campaign in 2021 was 3218, and during the third survey campaign in 2020 was 2618 (tab. 2.1.1). There is a significant difference in seedlings numbers over the three sampling years (Student's t test, p<0.05). The most represented species were Norway spruce, followed by silver fir, beech, sycamore maple, scots pine, mugo pine, and rowan. During the last survey campaign in 2022 also some individuals of larch have been found (fig. 2.1.2).

Table 2.1.1 Number of seedlings surveyed in the two different areas, Ospitale and Valbone, under two different measures: salvage logging (SL) and no-intervention (NI).

	Ospitale (OS)		Valbona (VB)	
Species	SL	NI	SL	NI
Abies alba	0	1	727	150
Larix decidua	7	14	5	3
Piacea abies	859	1001	2098	1373
Pinus mugo	2	9	0	0
Pinus sylvestris	13	70	0	0
Sorbus aucuparia	17	10	18	172
Acer pseudoplatanus	0	0	171	220
Fagus sylvatica	0	0	452	91

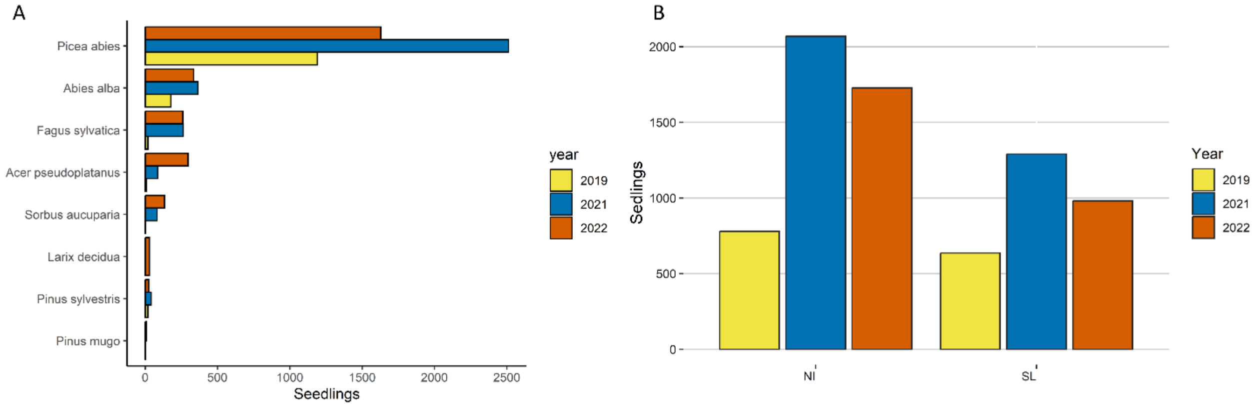

Figure 2.1.2 A) Seedlings surveyed grouped by species and year. B) Seedlings number sampled every year divided according to treatment (NI=non intervention, SL=salvage logging).

Significant differences have been found also in the number of seedlings between salvage logging areas and no-intervention areas (Student's t-test, p<0.05), where the trend during the three years of sampling is the same, but they registered different values overall. The peak in seedling number was registered in 2021. According to the post-hoc Tuckey test (p<0.05) the difference between salvage logging and no-intervention areas are significantly different. There is a negative significative correlation between the number of seedlings and distance from the edge or green islands (Pearson p=-0.30, p<0.05). This relation is significant also for seedlings both in salvaged logged areas (Pearson p=-0.19, p<0.05) and both in unsalvaged ones (Pearson p=-0.30, p<0.05) (fig. 2.1.3A).

ANOVA type 3 and Tuckey post-hoc test shows significant differences in the seedling number under salvage logging or no-intervention (p<0.05, fig. 2.1.3B) every year of sampling. According to linear models, age of the seedlings, treatment, and year after disturbance are significant variables influencing natural regeneration. New regeneration, year after disturbance, and local characteristics influence positively the regeneration number, while salvage logging influence negatively salvage logging (mod1 p<0.05, tab 2.1.1). Mod2 shows instead the influence of distance. Distance influence negatively the seedling occurrence, together with the site characteristics (mod2 p<0.05, tab 2.1.1).

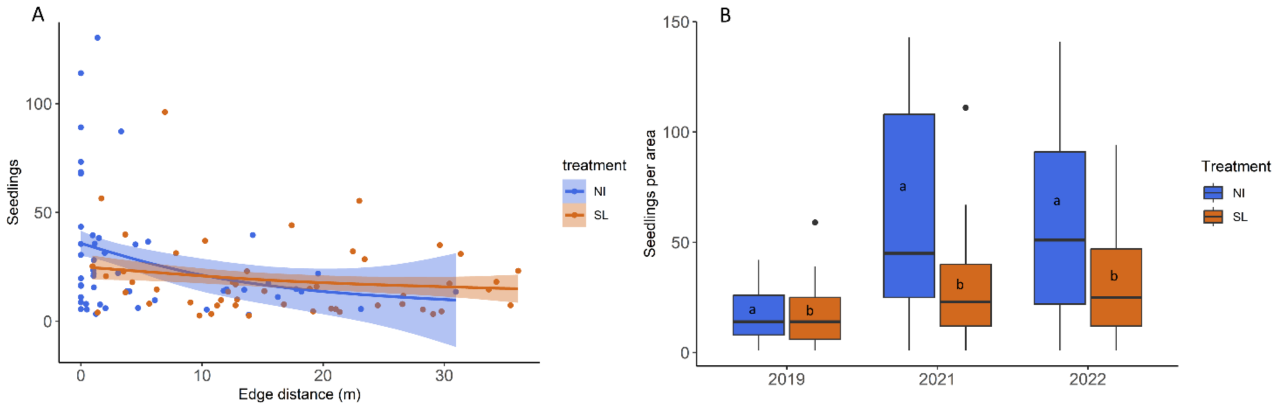

Figure 2.1.3 A) Correlation between seedling numbers per plot and distance from the edge divided per treatment (NI=non intervention, SL=salvage logging). B) Differences between seedlings' number under different treatments every year of samplings. The different letters indicate statistically significant differences according to Tuckey post-hoc test

Table 2.1.1 Results of the LM (mod1) and LMER (mod2). Bold font indicates significant values (p<0.05)

mod1						
Dependent variable		**Estimate**		**Std. Error**	**t value**	**Pr(>|t|)**
Trees	**(Intercept)**	**-4.6433**	**±**	**1.1819**	**-3.929**	**8.62E-05**
	agenew	**22.1902**	**±**	**0.873**	**25.417**	**2.00E-16**
	areaVB	**30.3189**	**±**	**0.8985**	**33.745**	**2.00E-16**
	treatmentSL	**-20.3997**	**±**	**0.7852**	**-25.981**	**2.00E-16**
	year2021	**24.9632**	**±**	**1.0649**	**23.443**	**2.00E-16**
	year2022	**18.9979**	**±**	**1.1045**	**17.201**	**2.00E-16**
mod2						
Dependent variable		**Estimate**		**Std. Error**	**t value**	**Pr(>|t|)**
Trees	**(Intercept)**	**19.7461**	**±**	**2.8555**	**6.915**	**3.17E-11**
	areaVB	**22.9391**	**±**	**2.4139**	**9.503**	**2.00E-16**
	treatmentSL	-4.6477	±	2.8805	-1.613	0.107764
	year2021	-0.1039	±	2.9409	-0.035	0.971855
	year2022	0.2307	±	2.9764	0.078	0.938271
	edge_dist	**-0.472**	**±**	**0.1366**	**-3.455**	**0.000637**

Discussion

The early results of the monitoring in these two sites affected by the storm Vaia indicate differences in short-term regeneration dynamics under different management strategies. The data shows a higher number of regeneration seedlings in the areas with no-intervention, in agreement with the data found in literature (Lindenmayer et al. 2008; Morimoto et al. 2019; Leverkus et al. 2021b). The lower regeneration density in salvaged logged areas can be attributed to the damages of heavy machinery and other harvesting methods (Waldron et al. 2014). Both areas have been harvested using heavy machinery that can have an elevated impact on the ecosystem. Have been reported in literature (Slyder et al. 2020; Konôpka et al. 2021) that the use of heavy machinery contributes to disrupt the ground surface, helping in seed establishment. This can be an advantage in sites with a low environmental stressor, but in the case of the southern Alps with high temperatures and shallow soil, the damages appear to be too serious making soil unavailable for seed germination and survival. Moreover, mechanical damages on advanced regeneration can further affect regeneration dynamics that after disturbance rely a lot on advanced regeneration (Taylor et al. 2017). Even if a lot of deadwood on the ground can be an obstacle for the seedling acting as a mulching layer (Leverkus et al. 2021a), if the damaged stand is not too dense the deadwood on the ground helps to mitigate environmental conditions (Marcolin et al. 2019; Oreja et al. 2020) and creating a buffered microsite favorable to regeneration establishment and growth. Moreover, the chaotic distribution of deadwood in a windthrown area is a serious obstacle for deer browsing (Doris Kupferschmid et al. n.d.; Whyte and Lusk 2019), increasing the seedling's protection effect.

Another important aspect that combined with the management strategies has a big impact on regeneration is the distance from the nearest green island, whether it is the edge of the windthrow or a surviving tree (Kramer et al. 2014). Most of the species in mature forest stands have heavy seeds, that allow short dissemination distances. It is important therefore to preserve standing tress or partially damaged trees that could help to speed up the regeneration processes, especially resprouting from broadleaves (Vodde et al. 2010a; Frischbier et al. 2019), plants that are usually harvested together with deadwood. Regeneration occurrence appears to be much higher near the disturbance legacies than far from them in unsalvaged areas, whereas in salvaged logged areas this difference is reduced and smoothed. This difference in regeneration density creates also more heterogeneity in the forest composition and structure, which is very important to make the future stand more resistant and resilient.

Chapter 2.2: Natural regeneration

Materials and methods

Study areas and field sampling

The study areas are in the north-eastern Italian Alps, in the gaps and windthrown areas created by the storm Vaia in late October 2018, which struck the southern Alps, from the outer to the inner alpine range. The elevation ranges between 900 m a.s.l and 1942 m a.s.l. and the precipitation ranges between 600 mm in dry areas and 3000 mm per year in the rainiest upper zones. In the upper areas above 1500 m a.s.l., snow cover is continuous at least during the winter months, with some exceptions on southern slopes. According to the Köppen system the climate ranges from oceanic (Cfb)/humid continental climate (Dfb) at lower elevations (1300m a.s.l.) to subarctic (Dfc)/alpine (ET) at higher elevations (up to 2000m a.s.l.) (Beck, H.E., N.E. Zimmermann, T.R. McVicar, N. Vergopolan, A. Berg 2018).

Forests damaged by the storm Vaia are composed mainly of *Picea abies* (L.) H. Karst (PA), mixed with *Abies alba* Mill. (AA) and *Fagus sylvatica* L. (FS) in particular at lower elevations. At higher elevations, *Larix decidua* Mill. (LD) and *Sorbus aucuparia* L. (SAu) are more abundant. Other species present in the areas are: *Acer pseudoplatanus* L. (APs), *Alnus incana (L.)* Moench (ALi), *Ailanthus altissima* (Mill.) Wsingle (AIa), *Alnus alnobetula (Ehrh.)* K. Koch (ALv), *Sorbus aria (L.)* Crantz (SAr), *Fraxinus excelsior* L. (FE), *Pinus silvestris* L. (PS), *Betula pendula* Roth (BPe), *Betulla Pubescens* Ehrh. (BPu), *Salix caprea* L. (SCa), *Corylus avellana* L. (CA), *Ostrya carpinifolia* Scop. (OC), *Populus tremula* L. (PT), *Quercus pubescens* Willd. (QPu), *Quercus petraea* (Matt.) Liebl. (QPe), *Sorbus domestica* L. (SDo), *Sambucus nigra* L. (SN).

A total of 148 windthrow areas were established in the north-eastern Italian Alps (fig. 2.2.1), located in the regions of Friuli Venezia-Giulia (20), Lombardia (11), Veneto (25), and the Autonomous Provinces of Trento (60), and Bolzano (32).

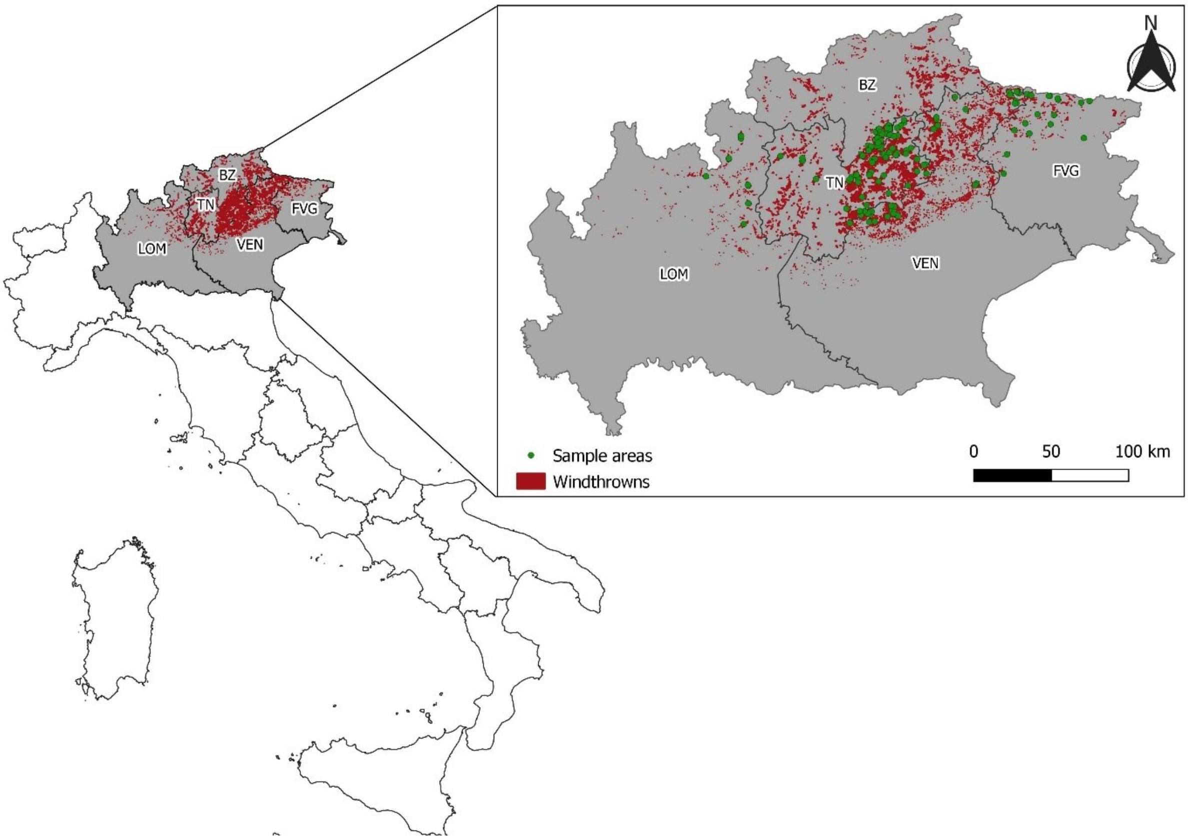

Figure 2.2.1. Distribution of the study areas in the northeastern regions of Italy (Regions of Friuli Venezia-Giulia, Lombardia, Veneto, and Autonomous provinces of Bolzano and Trento), in red the areas damaged by storm Vaia*. Data have been collected in four plots (0,20,40,80) positioned along a transect perpendicular to the windthrown edge. Soil cover was sampled every two meters along the transect.*

To establish the sampling protocol, reference was made to previous studies conducted in Switzerland after storm Vivian (2000) and Lothar (1999) (Kramer et al., 2014). These protocols were adapted to the local conditions and the objectives of this monitoring.

Following conditions served as selection criteria: savaged sites should be located at a regular slope having the same aspect across the windthrow area and the salvage logging operation must be concluded to avoid successive modifications to the environment. Areas that present sharp ridges, high cliffs, or overly complex terrain morphology were excluded. Areas including stabilized road networks or other infrastructures were avoided, and areas with exclusively logging corridors were accepted. (Tab. 1)

Table 2.2.1. Variables recorded for each sample area.

id_area	Identification code for each area
forest_type	Type of forest according to the classification of Del Favero, 2004
elevation	Elevation above sea level
structure	Even or uneven-aged forest
h_edge	Mean height of the standing trees in the windthrow edge
slope	
exposition	Exposition of the slope, based on the digital terrain model ….
treatment	Harvesting systems: Cable yarding systems (cy); winch tractor (wt); highly mechanized systems, e.g., harvester and forwarder (hf); both of previous systems have been used (mix).

Data collection

In each windthrown area, we defined four different circular plots along a transect, starting from the edge of the windthrown area and following a perpendicular direction (fig. 2.2.2). The first plot is placed on the windthrown edge (p0), and the other ones are placed at 20, 40, and 80 meters along the transect (p20, p40, p80). The cleared areas must have a minimum radius of 80m to be sure that each plot along the transect is far enough from other edges or green islands to avoid bias. The transect must start from a well-defined edge, large enough to provide seeds for the regeneration processes (Kathrin Kramer et al., 2014; Priewasser et al., 2013). Two types of transects are distinguished: horizontal transect (H) parallel to the contour lines, which can be on the left (HL) or the right (HR) to the edge; vertical transect (V), perpendicular to the contour lines, that can run uphill (VU) or downhill (VD). GPS position of the center of each plot has been surveyed using a GNSS receiver (multi-band RTK GNSS receiver EMLID Reach RS2, precision PPK H:5mm+0.5ppm, V:8mm+1ppm, recording period: 1s).

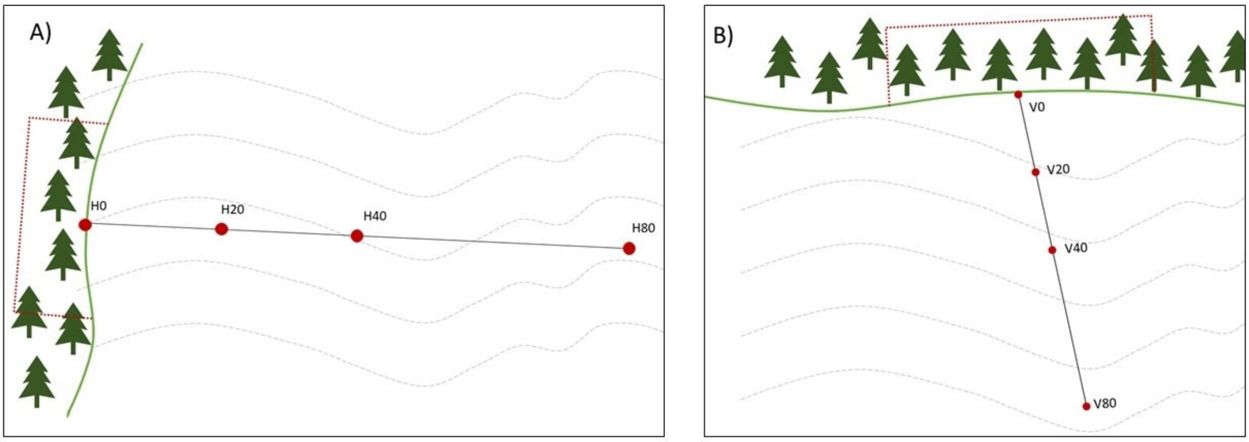

Figure 2.2.2. The two types of transect: A) horizontal transect (H), parallel to the contour lines, that can be on the left (HL) or on the right (HR) of the edge; B) vertical transect (V), perpendicular to the contour lines, that can run uphill (VU) or downhill (VD). On each transect, we set center points for four circle plots at distances of 0, 20, 40, and 80 meters from the edge. The red dotted lines represent the area where to estimate the previous stand characteristics (mean height, species composition, structure, forest type).

Along the transect every two meters we sampled the soil cover, considering the highest and the most present category of soil cover within an area of 50 cm around the point (tab. 2.2.2)

Table 2.2.2 Soil cover categories adopted and their description.

id	**soil cover**	**description**
1	Forest trees	species
2	Forest shrubs	species
3	Pteridium spp.	
4	Other ferns	other species of fern
5	Rubus spp.	e.g., raspberry
6	Ericaceae	e.g., blackberry, rhododendron ...
7	Graminoids	e.g., *poa* spp.
8	Carex, Juncaceae spp.	
9	Herbs	all the herbs with large leaves, growing on the ground
10	High herbs	the taller herbs. e.g., Verbascum, Urtica spp.
11	Bryophytes	
12	Bare soil	also with thin branches
13	Compacted soil	bare soil with compaction e.g., logging corridors
14	Branches	branches or deadwood below 15cm of diameter
15	Deadwood	deadwood above 15cm of diameter
16	Rocks	

In the circle plot (p0, p20, p40, p80) with a radius of 3 m, the following parameters were assessed: presence of regeneration and trees divided into three categories depending on height: trees below 20 cm (class 1), trees between 20 cm and 150 cm (class 2), and trees above 150 cm (class 3). Regeneration in class 1 (<20 cm) was counted in a subplot with a diameter of 100 cm tangent to the main plot, positioned on the right along the transect direction, with the center located 3.5 m from the center of the plot. The regeneration of class 2 (between 20 cm and 150 cm) and the trees in class 3 (<150 cm) were sampled within the 3 m radius plot. Deadwood within the plot with a diameter larger than 15 cm and length more than 50 cm was recorded only for its part laying within the sample area (Table 2.2.3).

Table 2.2.3. Variables assessed for trees and deadwood.

Variable	**Description**	**Below 20 cm**	**Between 20 and 150 cm**	**Taller than 150 cm**	**Deadwood**
species	The tree species	name	name	name	name
dbh	Diameter at 1.30m			cm	cm
height	Height of the tree			m	
length	Length of deadwood				cm
age_class	New regeneration, three years old or younger, post-storm; advanced regeneration, older than 3 years, pre-storm.	yes/no	yes/no	yes/no	
substrate	The growing substrate: deadwood or soil	soil/ deadwood	soil/ deadwood	soil/ deadwood	
trees	Number of trees counted	n	n	n	
damages	Any damage to the tree		yes/no	yes/no	
apex_brow	Apex of the tree with browsing damages		yes/no	yes/no	
lateral_brow	Lateral branches with browsing damages		yes/no	yes/no	
note	Additional information	string	string	string	
type_tree	Coniferous or deciduous				coniferous/ deciduous
type	Type of deadwood: stump (ST), uprooted stump (STs), log (LG), snag (SN)				ST, STs, LG, SN
Decay	Decay stage: 1 = no decay, 2 =initial stage of decay, 3= advanced decay stage				1,2,3

All the data were organized in datasets, with specific IDs for the area, plot, and single trees. To perform the analysis on regeneration of different ages, a subset of the main dataset was defined by height classes: regeneration below 20 cm as seedlings and regeneration between 20 cm and 150 cm as established saplings. We only considered regeneration up to 150 cm height in the analysis; taller trees were considered as stand initiation stage. The data served to a general description of the regeneration status.

Linear models, ANOVA, and post-hoc Tuckey test were used to test differences in the regeneration density regarding different treatments, distance to the edge, and new/advanced regeneration. T-test and Wilcoxon test were performed to test any significant difference in tree density regarding new or advanced regeneration, treatment, and distance from the edge. Chi-squared test were performed to test significant differences in regeneration density between different plots (i.e., distance from the edge), substrate, height class, age class, and treatment.

To evaluate the influence of explanatory variables on regeneration density and regeneration, both advanced and new, we employed Generalized Linear Models, including aspect as a random factor (GLM, using packages lm and lme4 on Rstudio Bates, 2015). We excluded the models with highly intercorrelated variables. Models were ranked according to the Akaike Information Criterion (AIC) for the goodness of fit. Operations between datasets and statistical analysis were performed using the software R (RStudio team, 2022).

Table 2.2.3 Dependent and explanatory variables adopted in the models

DEPENDENT VARIABLE	EXPLANATORY VARIABLE
Density (n/ha, n)	Distance from edge/**plot** (m, 0,20,40,80)
Browsed (n/ha, n)	**Elevation** (m a.s.l.)
	Exposition (N, S, E, W)
	Slope? (°, yes/no)
	Treatment (cy, hf, mix, wt)
	Deadwood (m^3/ha, plot)
	Structure (even/uneven)
	Edge height (m)
	Soil cover (type) only for total transect, not for a single plot

Results

General data

During the 2021 field campaign, 148 different areas were sampled, with a total amount of 3134 trees sampled: 693 were in class 1 (<20 cm tall), 2126 were class 2 (between 20 and 150 cm tall), and only 315 were in class 3 (<150 cm tall). Most of the trees have been found in p0 (1114 individuals, min=0 max=50 stems/plot) but the number decreases as the plot distance from the edge increases with 800 (min=0 max=38 seedlings/plot), 612 (min=0 max=50 seedlings/plot), and 608 (min=0 max=27 seedlings/plot) trees respectively. Norway spruce was the most counted tree species (1151 individuals), followed by rowan (768), silver fir (335), beech (314), larch (111), goat willow (69), silver birch (59), hazel (52), sycamore maple (42), and aspen (34). For the other species, we found less than 19 individuals per species (the total number of trees per species is less than 1% of overall trees surveyed) (fig. 2.2.3).

A large part of the areas (46) is characterized by a northern aspect, followed by south (42), west (39), and eastern (29) aspect. Slope ranks from flat areas (slope angle=0°) to steeper areas with a slope angle of 55°; the mean slope is 8.52°, with most of the areas below the third quartile (14.75°). Browsing damages have been found in 392 trees over 3134 (13% of the trees have been browsed on the apex or lateral branches). Most of the trees damaged were in the height class between 20 cm and 150 cm (fig 2.2.5a). Among different species, green alden, downy birch, aspen

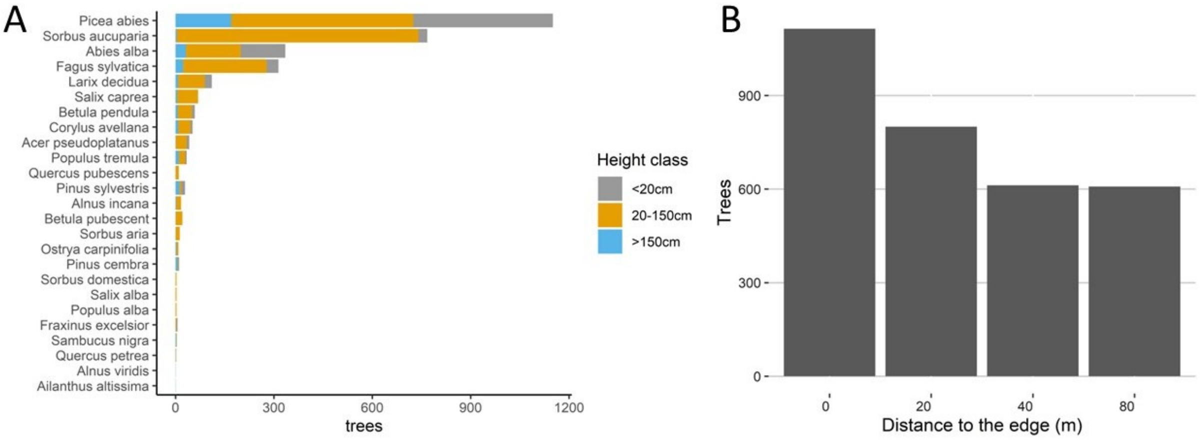

Figure 2.2.3 A) Number of trees sampled per species, considering all plots, stacked by height classes. B) Number of trees arranged by distance to the forest edge (p0 = 0m from the edge, p20 = 20m, p40 = 40m, p80 = 80m edge, respectively.)

spp., rowan spp., and willow emerged as the most appetible species since more than 25% of the individuals surveyed present browsing damages (fig. 2.2.5b). Elevation influenced overall regeneration occurrence since the number of individuals is negatively correlated with elevation (Pearson correlation P = -0.12, p<0.05).

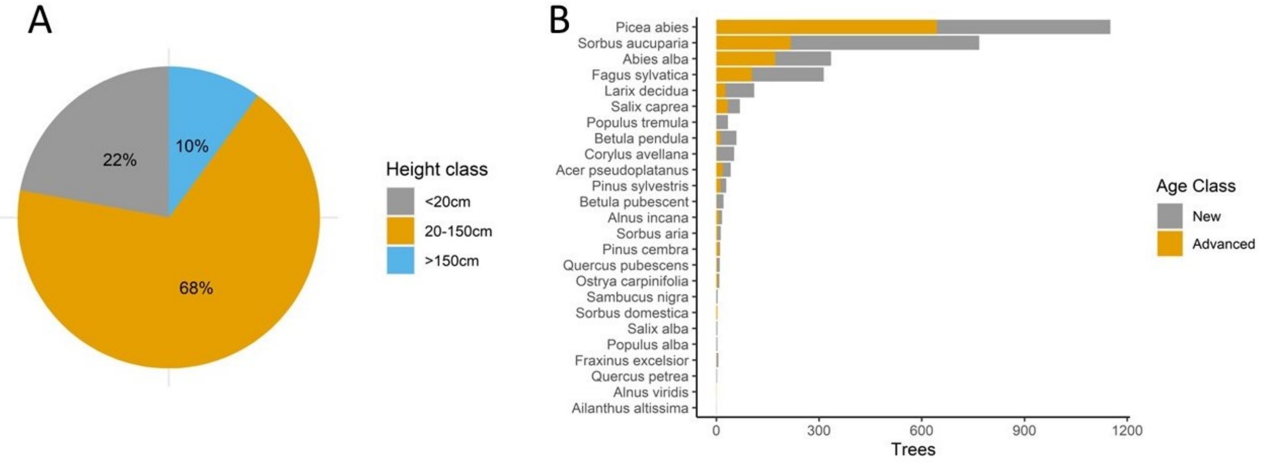

Figure 2.2.4 A) proportion of surveyed trees divided according to the height class. B) Trees per height class divided per species

Class 1: seedlings < 20 cm

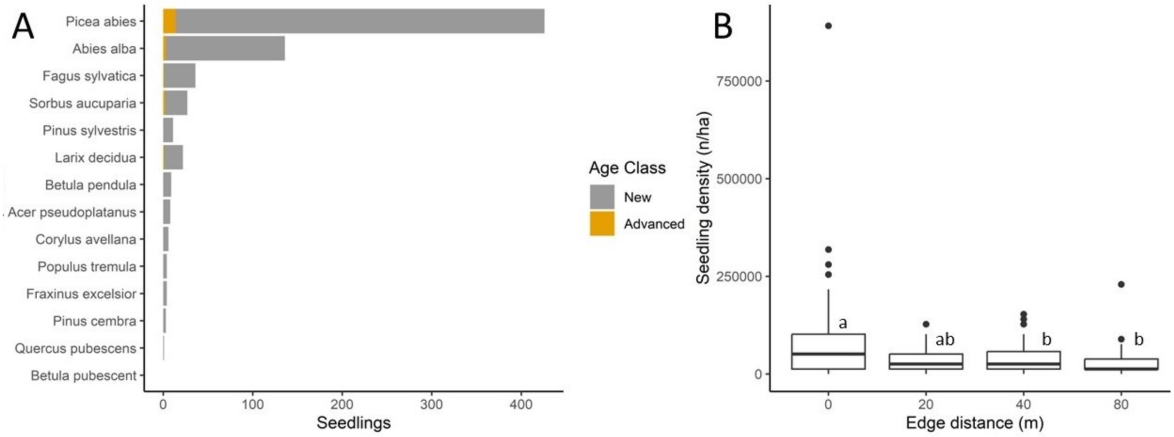

Fig. 2Figure 2.2.5 A) Trees per species and divided into seedlings born before the storm (pre-storm) or after the storm(post-storm). B) Different seedling densities at different distances from the windthrown edge. The letters refer to post-hoc Tuckey test.

Seedling number, density, and species distribution are different considering only the new regeneration. In this case, we found 693 trees, with an average density of 142.296 stems/ha. The highest stem density was found in p0 (212.178 stems/ha, min=0 max=50 seedlings/plot), followed by p40 (112.005 stems/ha, min=0 max=11 seedlings/plot), p20 (85.387 stems/ha, min=0 max=8 seedlings/plot), and p80 (79.748 stems/ha, min=0 max=12 seedlings/plot). Norway spruce is the species that occurs more frequently (426 individuals), followed by silver fir (136), beech (36), rowan (27), larch (22), Scot's pine (11), silver birch (9), and sycamore maple (8). For the other species, the stems per each species are less than 1% of the total. Regeneration density shows significant differences between the different age classes (t-test, p<0.05), i.e., between seedlings established before or after the storm (end of October 2018), where most of the seedlings were established after the storm. Significant differences have been found in seedlings density between seedlings established on soil or on deadwood (chi-squared test, p<0.05), with most of the seedlings established on soil. Significant differences have been found in seedling density grown on slopes with different aspects (chi-squared test, p<0.05). About the influence of distance on seedling density, it emerged to be significantly different between the four groups of plot distances from the forest edge (p0, p20, p40, p80, chi-squared test, p<0.05) with a decreasing density from the plot nearest to the windthrown edge to the furthest. For seedlings < 20 cm, elevation is not a significant factor, apart from beech, which is negatively correlated with elevation (Pearson correlation P = -0.031, p<0.05). The two-way ANOVA and the Tuckey post-hoc test both confirmed such a significant difference (p<0.05) (fig. 5). A significant difference in seedling density was found also under different treatments (cy, hf, mix, wt, tab 2.2.1; chi-squared test, p<0.05). However, the two-way ANOVA and the Tuckey post-hoc test both do not confirm such a significant difference (p>0.05) (fig. 2.2.6b).

The GLMs showed that the only significant factor influencing seedling density is the distance from the edge (ANOVA type 3, p<0.05; mod1, tab. 2.2.1). If aspect was considered as a random factor (mod2, tab. 2.2.1), the elevation, treatment hf (harvester and forwarder), and treatment wt (winch and tractor) emerged to positively influence the regeneration, beyond distance from the edge with a negative influence (p<0.05). According to ANOVA type 3 analysis treatment, the distance of the plots from the edges and elevation influenced significantly regeneration (p<0.05).

Table 2.2.1 Results of the GLM (mod1) and GLMER (mod2). Bold font indicates significant values (p<0.05)

mod1						
Dependent variable		**estimate**		**Std. Error**	**t value**	**Pr(>|t|)**
	(Intercept)	1.153031	±	3.135396	0.368	0.71348
	structurecoetanea	0.635998	±	0.858646	0.741	0.4598
	elevation	0.000353	±	0.001751	0.202	0.84048
	id_plotPL2	**-2.57419**	**±**	**0.901164**	**-2.857**	**0.00477**
	id_plotPL3	-1.69402	±	1.072418	-1.58	0.11587
	id_plotPL4	**-2.81496**	**±**	**1.078669**	**-2.61**	**0.00979**
	h_edge	0.089819	±	0.058433	1.537	0.12594
	substratesoil	0.651151	±	1.198607	0.543	0.5876
	age_classpre	-1.93515	±	1.314278	-1.472	0.14258
mod2						
Dependent variable		**estimate**		**Std. Error**	**t value**	**Pr(>|t|)**
	(Intercept)	**0.91025**	**±**	**0.361749**	**2.516**	**0.011861**
	elevation	**0.000547**	**±**	**0.000208**	**2.632**	**0.008481**
	treatmenthf	**0.400271**	**±**	**0.112927**	**3.545**	**0.000393**
	treatmentmix	0.071346	±	0.183774	0.388	0.697846
	treatmentwt	**0.419362**	**±**	**0.195669**	**2.143**	**0.032095**
	deadwood	-0.00203	±	0.002539	-0.799	0.424106
	id_plotPL2	**-1.07164**	**±**	**0.118001**	**-9.082**	**2.00E-16**
	id_plotPL3	**-0.9161**	**±**	**0.133625**	**-6.856**	**7.09E-12**
	id_plotPL4	**-1.18485**	**±**	**0.144626**	**-8.193**	**2.56E-16**

Class 2: seedlings 20 - 150 cm

Considering advanced regeneration, plot density and species abundancy is different than the total. In this case, we counted 2126 tree individuals in total, with an average density of 2638 stems/ha. The highest tree density is in p20 (3089 stems/ha), followed by p40 (2655 stems/ha), p80 (2466 trees/ha), and p0 (2315 stems/ha). Rowan is the species that occurs most frequently (737 individuals), followed by Norway spruce (555), beech (255), silver fir (167), larch (81), goat willow (64), silver birch (43), hazel (38), sycamore maple (33). For the other species, numbers of individuals per species were less than 1% of the total.

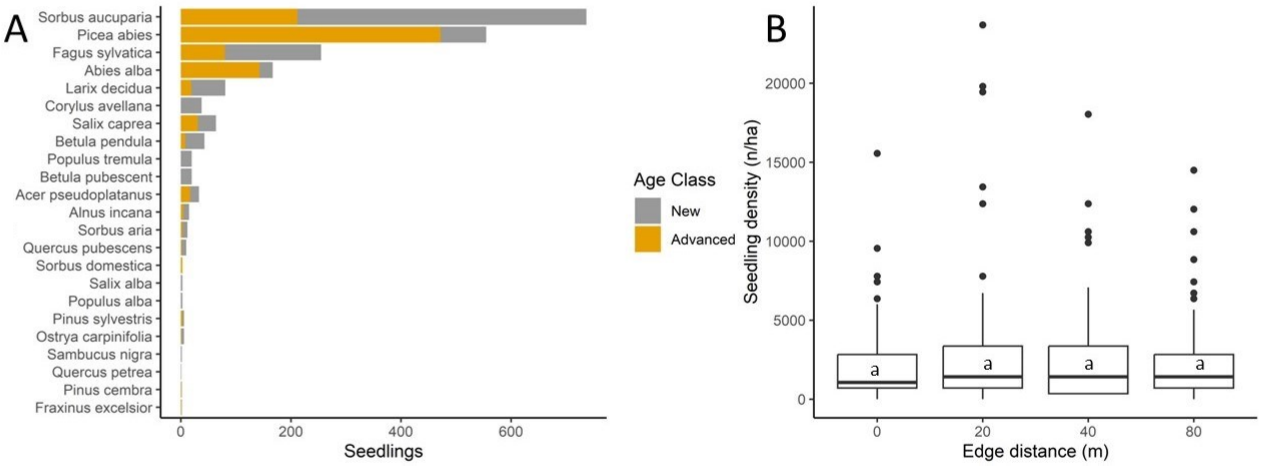

Figure 2.2.6 A) Trees per species, and divided into seedlings born before the storm (pre-storm) or after the storm(post-storm). B) Different seedling densities at different distances from the windthrown edge. The letters refer to post-hoc Tuckey test.

or seedlings of class 2, regeneration density doesn't show any significant difference between seedlings established pre vs post the storm Vaia (end of October 2018). In contrast, stem densities of seedlings established in pre-storm uneven-aged forests were significantly higher than those in even-aged forests (Wilcoxon test, $p<0.05$). Significant differences in stem densities were also found regarding substrate (more abundant on soil than on deadwood; Chi-squared test, $p<0.05$), regarding different slope aspects (Chi-squared test, $p<0.05$), and distance to the edge (decreasing from p20 to p80; Chi-squared test, $p<0.05$). This distance decay in regeneration density was not confirmed by both a two-way ANOVA and a Tuckey post-hoc test both ($p>0.05$) (Fig. 6). Individuals of class 2 are overall negatively correlated with elevation (Pearson correlation, P = -0.14, $p<0.05$). Regarding single species correlation only that for beech was significantly and negatively correlated with elevation (Pearson correlation, P = -0.35, $p<0.05$).

In GLM models, even-aged structure of the windthrown forest and elevation emerged to be the significant factors influencing advanced regeneration (mod3 tab. 2.2.2, ANOVA type3, $p<0.05$). Considering aspect as a random factor, elevation, treatment, presence of deadwood, and distance from the edges resulted in significant effect on regeneration density (mod4, tab. 2.2.2). Shorter distance from the edge influences positively regeneration ($p<0.05$)while elevation and deadwood influenced negatively stem density ($p<0.05$ and $p<0.05$, respectively). Mixed treatment affected densities positively. According to ANOVA type 3 analysis, elevation, deadwood and treatment significatively influence regeneration (p<0.05).

Table 2.2.2 Results of the GLM (mod3) and GLMER (mod4). Bold font indicates significant values (p<0.05)

mod3						
Dependent variable		**estimate**		**Std. Error**	**t value**	**Pr(>|t|)**
Trees	**(Intercept)**	**4.529948**	**±**	**1.033854**	**4.382**	**1.31E-05**
	structurecoetanea	**-1.45729**	**±**	**0.254105**	**-5.735**	**1.30E-08**
	elevation	**-0.00155**	**±**	**0.000613**	**-2.522**	**0.0118**
	id_plotPL2	0.618913	±	0.347009	1.784	0.0748
	id_plotPL3	0.276776	±	0.355168	0.779	0.436
	id_plotPL4	0.094066	±	0.345498	0.272	0.7855
	h_edge	-0.00103	±	0.002677	-0.385	0.7006
	substratesoil	0.458764	±	0.485065	0.946	0.3445
	age_classpre	0.199624	±	0.246414	0.81	0.4181

mod4						
Dependent variable		**estimate**		**Std. Error**	**t value**	**Pr(>|t|)**
trees	**(Intercept)**	**2.885281**	**±**	**0.205329**	**14.052**	**2.00E-16**
	elevation	**-0.00076**	**±**	**0.000131**	**-5.814**	**6.09E-09**
	treatmenthf	0.025007	±	0.063987	0.391	0.695937
	treatmentmix	**0.269776**	**±**	**0.078025**	**3.458**	**0.000545**
	treatmentwt	-0.32196	±	0.199384	-1.615	0.106363
	deadwood	**-0.00283**	**±**	**0.001066**	**-2.657**	**0.007873**
	id_plotPL2	**0.203589**	**±**	**0.076895**	**2.648**	**0.008106**
	id_plotPL3	0.103959	±	0.080757	1.287	0.197987
	id_plotPL4	0.093306	±	0.077536	1.203	0.228829

Discussion

Species and stand structure

After large disturbances and under ongoing climate changes scenario, species composition plays an important role in defining the future shape of a forest and its resistance and resilience to future disturbances (Nagel et al. 2006; Cerioni et al. 2022). One of the most important drivers in determining the species composition in regenerating forest is the composition of the previous forest (Manso et al. 2019). After the storm Vaia (2018) in the north Italian Alps at elevations from 1200 to 1700 m asl, Norway spruce is the most abundant tree species, which mirrors the vast availability of seeds of the most widespread stand-forming tree species in the region of the windthrown areas. The seed supply is provided by intact trees forming the standing windthrown edge and survived trees inside the windthrown areas. Even uprooted trees served for the first year as seed sources. Dissemination from the green islands is a crucial element of post-disturbance regeneration dynamics in the few years after the disturbance(Fidej et al. 2016; North et al. 2019), but at the same time, it is strongly limited by the extension of damaged areas. According to literature, the maximum seed dispersal distance for Norway spruce is between 30 and 60 meters (Kramer et al. 2006; Gratzer and Waagepetersen 2018). In central areas of large windthrow patches, where seed spread by wind is impossible, the presence of young seedlings of anemochorous species with relatively heavy seeds such as Norway spruce and autochorous species, can be explained by dissemination by trees that have been fully or completely damaged by the windthrow and still serving as seed source until the eventually die from disturbance interactions. Zoochorous species such as rowan depend on e.g. the presence of perches (Milne-Rostkowska et al. 2020),are unlimited regarding seed spread though need mineral soil for germination. Plant functional types and habitat preferences are the main reasons why after windthrows a typical series of successional stages certain sporadic species can be observed, like the early presence of bird-spread rowan in mountain forests (Fidej et al. 2018) or the rapid spread of pioneer species like aspen, birch (*Betula pendula*) and willow (*Salix* spp.) especially in central Alpine valleys (Moser et al. 2010; Vodde et al. 2010a) Similarly, resprouting can be also an optimal strategy for some species that profit from higher light transmission (e.g., beech or willow) and eventually escape from the competition with shrubs and herbaceous layers. Nevertheless, young resprouts can be heavily damaged by logging operations and forced to resprout again after the intervention (Leverkus et al. 2021b), and in the case of resprouting shrubs, they can attract herbivores that lead to an increase in browsing damages (Foster et al. 2016).Furthermore, in large gaps, there is more light so young seedling escapes browsing earlier (Holmes and Webster 2010; Walters et al. 2016).

Aspect, slope, and elevation

Seedlings' presence can be strongly influenced by site conditions, like aspect, slope, and elevation. Most of the areas in our study have a northern exposure, which creates better conditions for shade-tolerant species regeneration, with lower temperatures and higher moisture. Overall natural regeneration, considering both class 2 (between 20 and 150 cm) and class 1 (below 20 cm), becomes less abundant with at higher elevation due to harsher environmental conditions (e.g. shorter vegetation time) and narrower regeneration niches (Wohlgemuth et al. 2008; Kramer et al. 2014; Stroheker et al. 2018). More light and less competition with other trees increase in general the seedling density at the elevation optimum. (Vodde et al. 2011). Moreover, since most of the species surveyed are in their elevation optimum (especially Norway spruce, larch, fir, and beech), elevation itself is not a significant factor in determining the seedling density for new regeneration.

Substrate and facilitation

After a disturbance like stand-replacing windthrows and subsequent salvage logging, soil is the most represented substrate for seedlings establishing and growing, as widely discussed (Taylor et al. 2017; Kern et al. 2019). New deadwood is too fresh and not decayed enough to become a suitable substrate for seed germination. Depending on climatic conditions lying logs start becoming suitable for regeneration after twenty or forty years after tree death (Robert et al. 2012; Konôpka et al. 2021). The pit and mound morphology represent a suitable substrate since most of the seedlings established on bare soil in the pit (Ulanova 2000; Vodde et al. 2015; Macek et al. 2017), taking advantage of the exposed mineral soil and nutrients released by the logging waste. Very few seedlings have been found on logging tracks where compacted soil doesn’t allow seedlings’ establishment and root penetration (Ampoorter et al. 2011).More in general, regeneration was clustered around deadwood (Wild et al. 2014) and biological legacies in general (Holeksa et al. 2012).

Distance from the edges

Distance from the edge is another significant parameter to consider after such large disturbances. Wind-dispersed tree species with heavy seeds (i.e. conifers) are not able to reach large distances from the edge or green island, and in particular, the maximum distances ranged from 20 m for pine species and silver fir to a maximum of 40 m for Norway spruce and other coniferous species (Kramer et al. 2006; Gratzer and Waagepetersen 2018). In this case, the regeneration dynamics could be slower for dominant species, while bird-dispersed species (e.g. rowan) seedling density increases in the short term right after the disturbance (Wagner et al. 2010; Szwagrzyk et al. 2021). In our study distance influenced seedling density significantly, but at the same time, there is still a good density of Norway spruce in the far (40 m, 80 m) plots, indicating that the seeds recruited during the tree falling is still an important resource for seedling establishment.

Age classes

After large highly severe disturbances like windstorms or forest fires, intact seed trees are rare, and younger trees would still need a few years until maturation and first dissemination. In our windthrow areas we hardly found established individuals (> 150 cm; 315 trees, 10% of the total). Moreover, within this group of trees, only few were already mature. Most of the trees were between 20 cm and 150 cm tall (2126 trees, 68 % of the total), so regeneration could have been established right after the storm (mainly broadleaves) or a few years before the storm (coniferous species). These trees usually survived disturbance and parts of them also logging. They took advantage of the protection of the laying logs as a favorable microsite to adapt to the new bright conditions and start with amplified growth in the next season (De Chantal et al. 2005; Marzano et al. 2013; Thom et al. 2022). Individuals less than 20 cm tall accounted for 22% of the regeneration (693 trees), and consisted mainly of Norway spruce with slow growth rates compared to other species, with equal shares of both advanced and new regeneration (Fig. 2.2.4b). Fast-growing broadleaves like rowan and other pioneer species like larch take advantage of higher light transmission post disturbance and escape from the competition of herbs and shrubs (Vodde et al. 2010b), which is why there are few individuals smaller than 20 cm but half of the regeneration is still new regeneration. Since severe disturbances widely reduce dominance of mature trees (Scheidegger et al. 2002), the future forest strongly depends on survived regeneration and new arriving seedlings (Bače et al. 2012; Wild et al. 2014).

Treatment

Different salvage logging approaches and strategies seem to influence regeneration dynamics (Li et al. 2023), in particular short-term regeneration establishment and survival. The damage to soil cover produced by logging systems (skidder or harvester track, soil exposure due to erosion or heavy machinery passages, etc.…) exposes a higher portion of bare ground, which emerged to be a favorable substrate for regeneration establishment, if not highly compacted. Salvage logging operations conducted with harvester and forwarder or skidder tractors, disrupt ground surface and early regeneration leading to an increase in tree species regeneration in the understory a few years after the disturbance (Michalová et al. 2017; Slyder et al. 2020; Konôpka et al. 2021). In unsalvaged areas regeneration could be difficult because of the mulching effect of deadwood (Leverkus et al. 2021a). In large areas highly damaged by salvage logging operations and with no deadwood or other legacies able to favor seedlings' establishment and survival (Marangon et al. 2022), regeneration is partially lacking because of the higher shrub density, greater vegetation cover, and higher above-ground biomass, since soil is not covered by CWD (Konôpka et al. 2021). Using mixed salvage logging methods in one area can negatively affect the regeneration establishment in the short-term, since the heavy damages are widespread due to the sum of the disadvantages of different logging strategies.

Conclusion

Forest regeneration dynamics after severe and extensive disturbances is a key process to be analyzed and monitored in order to evaluate best post-disturbance management strategies for optimum forest regeneration. Emphasis should be put on the protection and facilitation of early regeneration – be it advanced or new – as an element of resilience-. In this regard, choosing the logging or post-disturbance management strategy is crucial. Short-terms regeneration dynamics are influenced also by distance from the forest edge or green islands of survived seed trees, especially in a damaged area larger than 2 ha. In this case, active restoration practices are a valid option, especially in very productive stands, for landscape purposes or in protection forests. Particularly in this last case, restoration practices such as deadwood manipulation (shelter and long-term substrate) can be very useful, as well as increase of soil roughness to transiently create favorable microsites especially for coniferous species. Crucial all these considerations is the main purpose of the future forest stand, since wood in intact forests represents basically either incomes for forest stakeholders or protection against natural hazards in mountain forests, the ratio between managed and unmanaged forest (i.e., salvage logging and no intervention) also depends on the main purposes (Konôpka et al. 2021). Even so, a mixture of these two strategies should be taken into account, diversifying the management locally, and making sure to not add up the negative impacts of each strategy. In conclusion, adopting cluster regeneration patterns, taking advantage of microtopography and biological legacies to enhance species characteristics, could represent a winning strategy to maximize restoration success by adopting a closer-to-nature approach.

Chapter 3: Windthrown elements: a key point improving microsite amelioration and browsing protection to transplanted seedlings

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HIGHLIGHTS

- Deadwood helps in creating favorable regeneration microsites, mitigating soil surface temperature and reducing drought stress for the juvenile stage.
- Deadwood contributes efficiently to protecting seedlings from browsing.

Deadwood protection effect can be isotropic or anisotropic depending on the season.

KEYWORDS

Deadwood

Post-disturbance regeneration

Forest regeneration dynamics

Coarse wood debris

Browsing

Environmental predictors

ABSTRACT

Mountain forest dynamics and ecosystems services are critically influenced by disturbances, in particular storm events. After extensive disturbance, a large amount of deadwood lying on the ground and the necessity for restoring the forest cover with natural regeneration are two critical issues to be dealt with. Salvage logging is the most common post-disturbance management strategy, but it does not consider the strategic role of coarse woody debris (CWD) in favoring regeneration establishment and survival. The aim of this study is to analyze how CWD contributes to creating favorable microsites for regeneration, increasing seedling establishment probability, after a large windthrow in the eastern Italian Alps. We focused on two different facilitative mechanisms provided by CWD, microsite amelioration and seedling protection, by planting a set of seedlings in the surroundings of deadwood elements. The former mechanism was analyzed by measuring temperature and SWC (Soil Water Content) locally, while for the latter we recorded evidence of browsing at the end of the season. For each trial, we established control sites in empty areas nearby with no CWD presence in order to infer its contribution. The results show that north-facing microsites have significantly lower temperature, decreasing water stress for saplings located on south-exposed slopes. More in general, the presence of logs and CWD has an ameliorative function that contributes to decreasing the transplanting shock and increasing the establishment probability for saplings. Moreover, the presence of lying deadwood increases roughness and, as a consequence, the cost for browsers to reach the seedlings. Using a coefficient expressing this increment, we underline the significant protective effect of CWD against deer browsing. The results of our study highlight the importance of deadwood in providing favorable regeneration microsites, enhancing saplings' establishment and their survival probability, and protecting them from deer browsing.

INTRODUCTION

Forest ecosystems are an important component of mountain landscapes, providing many different ecosystem services (ES) and largely contributing to landscape equilibrium (Lindenmayer et al. 2008). The main drivers of forest stand dynamics are disturbances, which can be defined as discrete events that disrupt the ecosystem's structure and functions, changing resource availability and the physical environment (White & Pickett, 1985). Due to climate change, disturbances are getting more severe and more frequent and forests are becoming more vulnerable as a consequence of the alteration of disturbance regimes and the increasing growing stock (Seidl et al. 2014, 2017). This is particularly relevant in the Alpine region, where forests have multiple functions (i.e. productive, recreational, and protective). Natural disturbances like windthrows can alter forest composition and structure, affecting the provision of forest ecosystem services. As reported by Forzieri et al. (2021), Alpine forests are more vulnerable to disturbance due to the intensification of climate change and, in this scenario, wind represents the major disturbance threatening forest stands. When wind-disturbance severity is high (i.e. stand-replacing disturbance), a wide range of biological legacies remain in place (Franklin et al. 2000), especially a large amount of deadwood lying on the ground. Moreover, the sudden extensive loss of forest cover can substantially change the functionality of the forests and their capacity to provide ecosystem services (Bebi et al., 2017; Fleischer et al., 2017; Kuuluvainen & Gauthier, 2018; Wohlgemuth et al., 2017). Many strategies can be adopted to manage the large amount of deadwood in windthrown areas, among which the most common are partial or total salvage logging or non-intervention. Salvage logging is a common practice to reduce economic losses (Leverkus et al. 2018), nevertheless, as widely discussed in the last years, it may cause additional damage to forests themselves (Leverkus et al. 2021a). Indeed, it can lower regeneration site heterogeneity and cause direct damage to saplings (Waldron et al. 2014), it can change regeneration dynamics and composition (Jonášová et al. 2010; Vodde et al. 2011) and generally reduce the amount of biological legacies like deadwood (Morimoto et al. 2019). More in general it reduces the regeneration occurrence in the short term. During salvage logging operations, it is necessary to keep in mind the importance of the dynamic equilibrium of the forest ecosystem (Lindner et al. 2010), releasing an appropriate amount of biological legacies like living trees, logs, snags, or coarse woody debris (CWD) in general (Thorn et al., 2014). Biological legacies and CWD in particular can be necessary to guarantee the provision of some ecosystem services (e.g. soil cover, protection against natural hazards) after different disturbance events (Castro et al., 2011; Costa et al., 2021; Lingua et al., 2008; Marzano et al., 2013; Rost et al., 2009). In the complex landscape of the Alps, considering the high amount of human activities depending directly or indirectly on forests, it is crucial to regenerate the forest ecosystems as soon as possible to ensure the durability of ES (Wang et al. 2014; Thom and Seidl 2016; Senf et al. 2019). Many different reforestation patterns and strategies can be adopted for small areas but, after large disturbances, in the steep Alpine environment, promoting natural regeneration is the most convenient management strategy. Furthermore, natural regeneration can provide a wide range of variability both in stand composition and structure (Senf et al. 2019). Stand structure is one of the factors influencing the resistance and resilience of forests to windthrows and other disturbances. Mixed and uneven-aged forests are in general more resistant and resilient than pure even-aged stands (Cordonnier et al. 2008; Schindler et al. 2012; Taylor et al. 2017).

Under this scenario, dealing with regeneration and deadwood is a critical matter. The role of deadwood as a substrate for natural regeneration is well known (Kuuluvainen & Kalmari, 2003; Robert et al., 2012; Stroheker et al., 2018) especially when highly-decayed (Brang et al. 2003; Motta et al. 2006; Bače et al. 2012; Priewasser et al. 2013). On the other hand, the role of CWD in microsite amelioration and in creating favorable microsites for seedling establishment is only partially studied, mainly in relation to other disturbances like wildfires (Marzano et al. 2013; Marcolin et al. 2019). Microsite amelioration could be anisotropic, when deadwood elements are enhancing site conditions only on definite direction (e.g. protecting against snow-gliding, wind-shield effect) or isotropic, when the facilitation is provided in all directions (Haase 2001). Moreover, as reported in the literature, site factors (e.g. soil moisture content, soil temperature, soil texture ecc…) have a stronger influence on regeneration dynamics than salvage logging (Kramer et al. 2014; Taylor et al. 2017). The large amount of deadwood on the ground and the need for quick and efficient recovery of forest coverage in large, severely damaged post-windthrown areas, makes it necessary to deepen our understanding of the dynamics that occur between natural regeneration and CWD, since there is a scarcity of case studies reporting such interaction (Taeroe et al. 2019).

The main objective of this study is to understand the role of CWD in creating favorable microsites for regeneration survival by mitigating environmental drought stress and protecting seedlings from browsing. In particular, we analyzed: i) if the mortality rate of planted seedlings was influenced by species-specific characteristics and treatment; ii) if the relation between CWD and regeneration was isotropic or anisotropic; iii) the influence of CWD on two edaphic variables of regeneration microsite: soil surface temperature (T) and soil water content (SWC); iiii) the CWD protective effect on regeneration seedlings against browsing.

METHODS

Study area

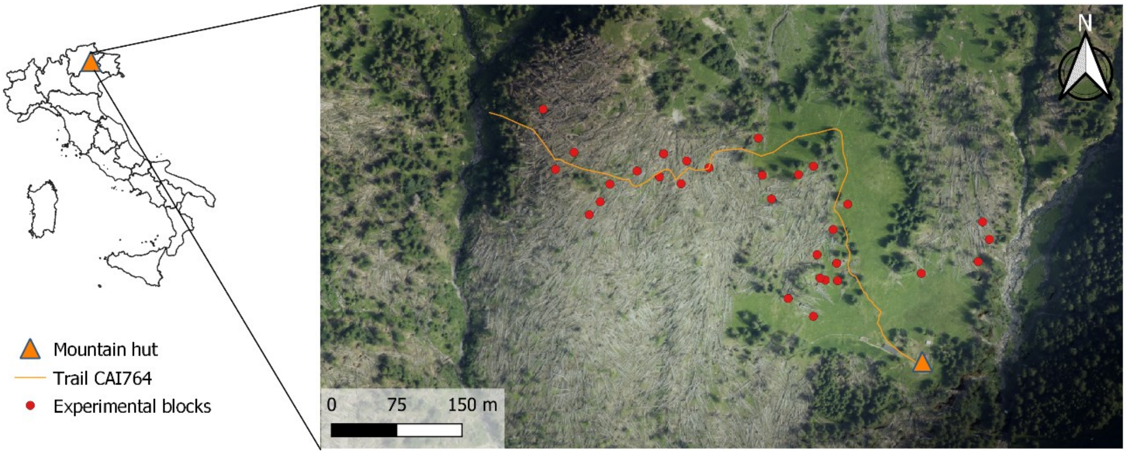

Figure 3.3. Location of study area Malgonera in the north eastern part of the Italian Alps. On the map the position of the 30 blocks in the windthrown area is indicated by the red dots.

The study area is located in the upper part of the San Lucano valley (municipality of Taibon Agordino, NE Italy) in the Malgonera forest (1500-1900 m a.s.l.; 46°18’52’’N, 11°55’37’’E). The area has an average slope of 20° and the aspect is mainly south and southeast. The Malgonera forest is mainly dominated by Norway spruce (*Picea abies* (L.) Karst.), forming mixed stands with beech (*Fagus sylvatica* L.) at lower elevation*,* and with European larch (*Larix decidua* Mill.) at upper elevation. The climate is characterized by continental to alpine climate (8.5°C mean annual temperature, 25.7 °C maximal mean annual temperature in July and -2.7 minimum mean annual temperature in January) with an annual cumulative rainfall of 1630 mm (2001-2020, Col di Prà meteo station, 2 km from the study site), with a precipitation peak between October and November. Snow cover lasts from late November to early May. Between the 27th and 30th of October 2018 in the eastern Alps a strong depression called “Vaia”, originated between the Balearic Islands and Sardinia (ARPAV 2018) triggered very strong southerly winds and heavy rains.

During the storm precipitations peaked at rates of 30-50 mm/h (more than 700 mm of cumulated rainfall) and measured wind gust speeds of up to 200 km/h (Pellegrini et al. 2021). This extreme event caused massive windthrows in the north-east Italian Alps, with more than 50,000 ha of forests affected and about 9 million cubic meters of wood left on the ground (Udali et al., 2021; Giannetti et al., 2021).

Planting protocol and data sampling

In July 2020 we planted seedlings in 30 established blocks within the windthrown area of Malgonera forest. Each block had its center on a log, which may lie on the ground or could be lifted up. The GPS position of the log chosen as center of the block was recorded. Each block was divided into three specific microsites, defined as “treatments” (figure 3.2):

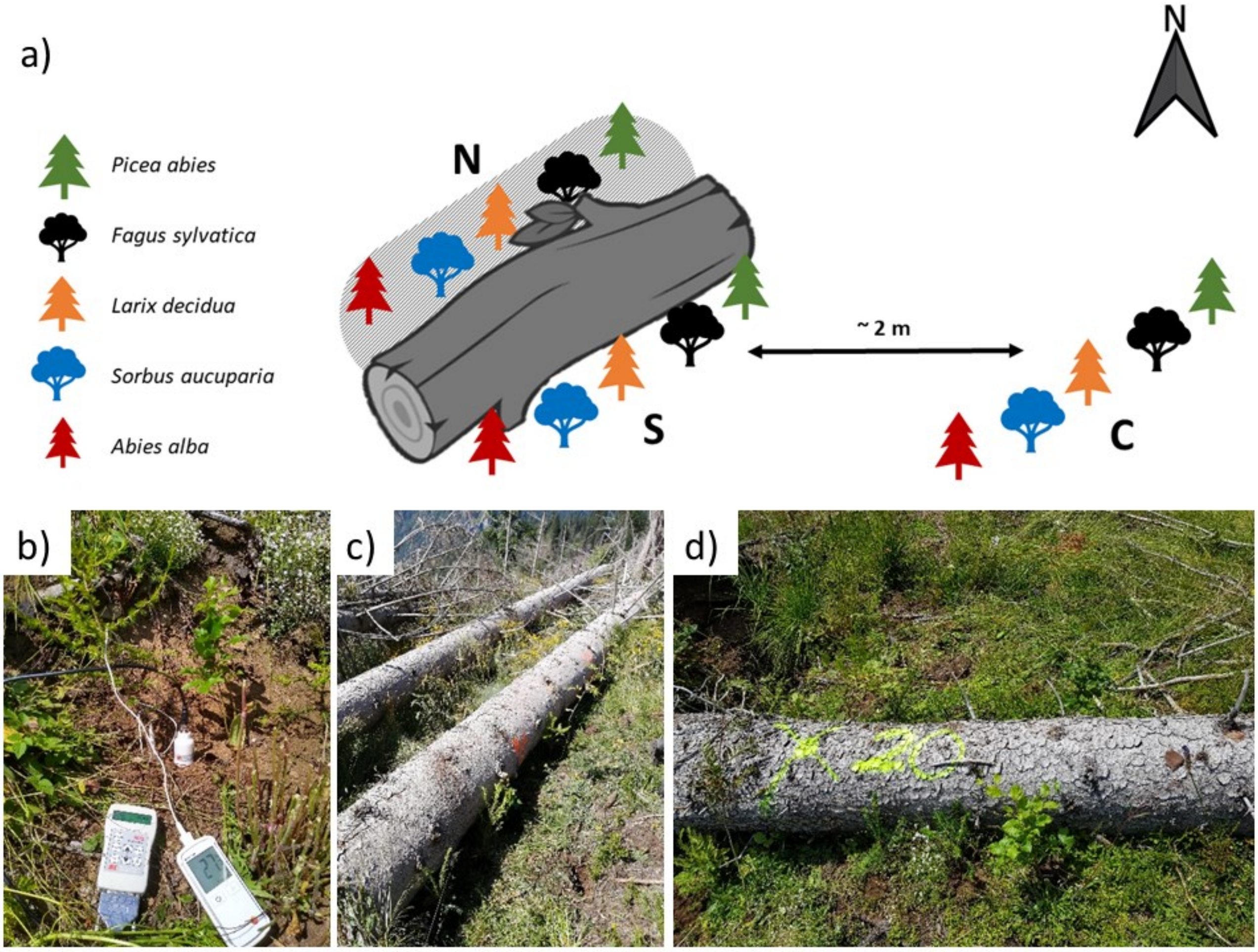

Figure 3.4. (a) Block structure and disposition of microsites. Three microsite have been identified: north (N) to CWD , south (C) to the element of CWD and control (C) in open field around 2 m from CWD element and with negligible effect of CWD. (b) temperature and soil water content collection. (c – d)

- One microsite near the log, on the north side (N)
- One microsite near the log, on the south side (S)
- One microsite far from the log, in the open field where the effect of deadwood is negligible as control (C)

In each microsite five different species were planted: Norway spruce (PA), silver fir (*Abies alba* Mill.; AA), larch (LD), beech (FS), and rowan (*Sorbus aucuparia* L.; SA). Containerized seedlings were provided by the tree nursery of Veneto Region. Seedlings were well developed, with no evidence of diseases or stress. Their age ranged between 5 and 8 years. Seedlings were planted following the same position scheme within the block, but the plantation scheme changed randomly between different blocks, in order to increase the variability of site conditions. Seedlings were planted less than 20 cm from the CWD element and at least 20 cm apart from one another, depending on the microsite micro-topography. No modification of the microenvironment was performed.

After plantation, the height of each plant was measured along with height from the ground of the logs. We measured soil surface temperature (T, °C) and surface soil water content (SWC, %/V_{soil}) using a Testo108 thermometer from Testo and a SM150T moisture sensor from Delta-T Devices Ltd. In order to record the most water-stressed period of the year, we collected data six times between July and September, approximately every two weeks, waiting one or two days after intense precipitation events (>10 mm). To obtain a mean representative value of the two variables for each microsite, three measures were performed per microsite, and then averaged. Soil superficial temperature and SWC were sampled starting every time from a different block, selected randomly. To record the higher variability of the two variables of T and SWC, we sampled each block randomly, at different hours. Mortality and height data were recorded in the middle of August and at the end of September. The rate of browsing damage and related mortality were also recorded at the end of September. Lastly, data of mortality and browsing were collected after the winter at the beginning of the third growing season (June 2021).

General descriptive statistics were performed to analyze mortality observations and trends, from July to September 2020, in SWC and T throughout all microsites and blocks. We performed linear regression to analyze the response of the environmental variables to different treatments. We applied logistic regression, using generalized linear models (GLMs), to analyze the influence of microsite properties on seedlings' survival. Soil moisture content (SMC), surface soil temperature (T), species and treatment were considered as independent variables. Interactions between factors were also tested in the models, especially between sites and physical characteristics. We applied ANOVA type 3 to assess the significance of the models.

To infer the influence of CWD on browsing pressure we calculated two different distances from each block and the nearest open areas: euclidean-distance and cost-distance. Euclidean-distance is the shorter distance between a block and the limit of the windthrown areas. Cost-distance is the shorter distance between a block and the limit of the windthrown areas, calculated considering the roughness of CWD, on a digital surface model (DSM). The DSM (resolution 0.5 x 0.5 m) was extracted from LiDAR data collected by Veneto Region after the storm, in July 2019. The difference between cost distance and euclidean distance was calculated. Cost to distance rate (CDR), the coefficient that represents the difference between distances, was used as an indicator of the effort that an animal needs to make to reach the target seedlings (3.1).

$$\text{CDR} = d_{cost} - d_{euclidean} \tag{3.1}$$

Linear regression was used to analyze the relation between browsing pressure and distance from open areas. Moreover, we applied logistic regression and GLMs to analyze further relationships between browsing and other variables, such as cost-distance, euclidean-distance, CDR, species, and edaphic variables.

RESULTS

Seedlings characteristics and mortality

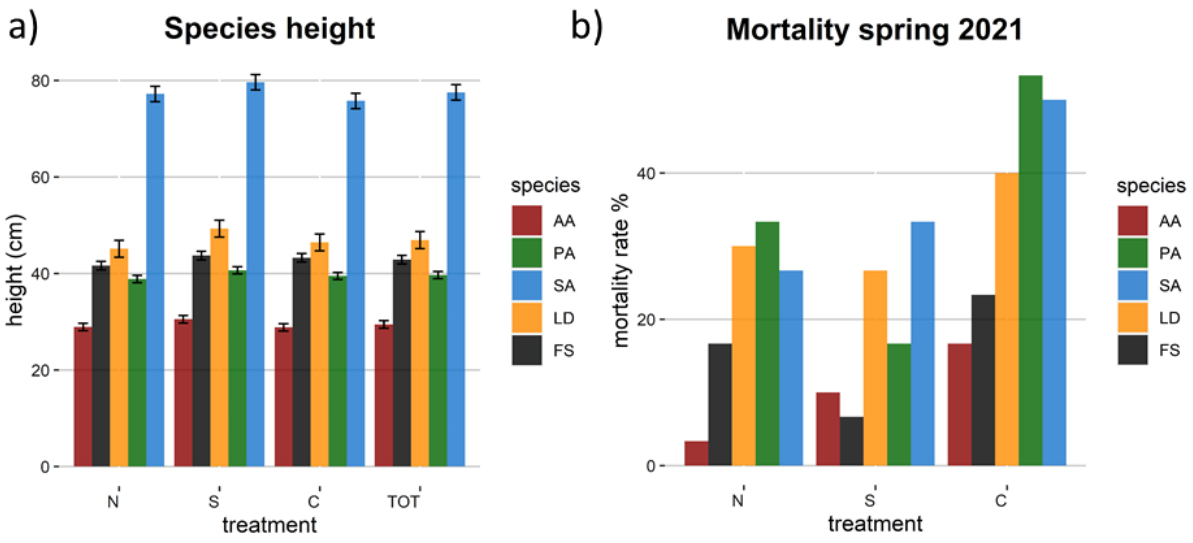

Figure 3.5. a) Mean height (cm) of transplanted seedlings, classified per species (AA= Silver fir, PA= Norway spruce, SA= Rowan, LD= Larch, FS= Beech) and divided by treatment N (North), S (South), C (Control) and the mean (TOT) of all seedlings. B) Mortality rate of seedlings, classified per species and divided by microsite position (N, S, C).

The transplanted seedlings were of different sizes. Rowan (SA) was the tallest species with a mean height of 77.5±1.6 cm. Beech (FS), larch (LD) and spruce (PA) had a similar height, 42.9±0.9 cm, 46.9±1.6 cm, and 39.7±0.7 cm, respectively. Fir (AA) was the shortest species, with an average height of 29.4±0.8 cm. There were no significant differences in the same species seedlings height between the three different treatments at transplanting (ANOVA p>0.05) (figure 3.3).

Table 3.1. Cumulated dead seedlings per treatment N (North), S (South), C (Control) and species (AA= Silver fir, PA= Norway spruce, SA= Rowan, LD= Larch, FS= Beech): after the first growing season recorded in fall 2020, and after the first winter record

Site	**Dead by fall 2020**						**Dead by spring 2021**					
	AA	FS	LD	PA	SA	TOT	AA	FS	LD	PA	SA	TOT
N	0	0	2	0	3	5	1	5	9	10	8	33
S	1	2	4	3	4	14	3	2	8	5	10	28
C	2	2	5	4	10	23	5	7	12	16	15	55
TOT	3	4	11	7	17	42	9	14	29	31	33	116

Mortality in fall 2020 was distributed differently both per species and per microsite (table 1). Numbers of dead seedlings resulted positively correlated (r Pearson = 0.15 and $p<0.005$) with the height of seedlings. Average mortality was 9.9%, 42 dead seedlings out of 450 transplanted seedlings. More than 50% of the dead plants were found on site C (χ^2 test; $p < 0.01$). In the treatments close to deadwood the mortality was lower, 33.3% and 11.9% respectively on site S and site N (table 3.1). Mortality after the first winter recorded in spring 2021 was higher than that recorded in fall 2020, with 116 dead seedlings out of 450 transplanted seedlings, for an overall increase of 25.8%. Mortality increased almost equally on all the microsites, but was lower on site S and N compared to site C, as in fall 2020 (figure 4). There was a significant increase in mortality of larch (29 dead in spring 2021 versus 11 in fall 2020; χ^2 test, $p < 0.01$) and Norway spruce (31 dead in spring 2021 versus 7 in fall 2020; χ^2 test, $p < 0.01$).

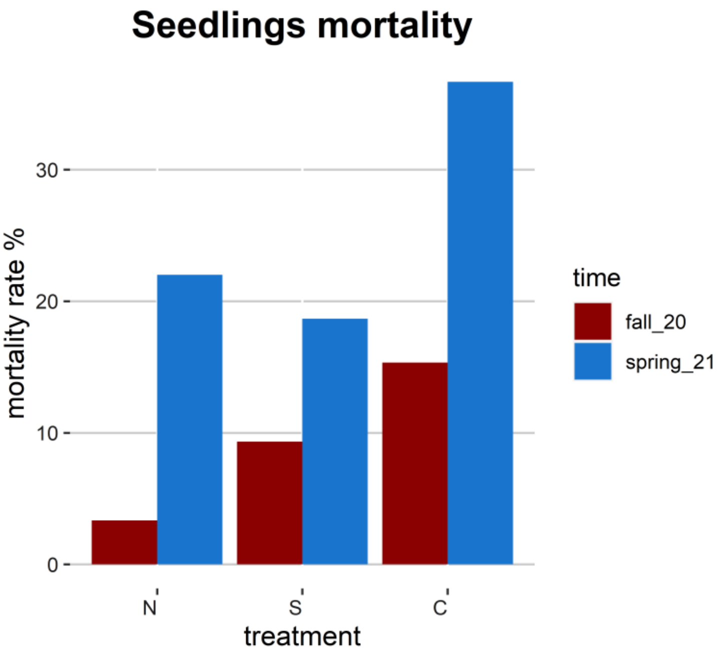

Figure 3.6 Comparison of mortality rate in the three different treatments (C, N, S), between the data recorded in fall 2020 and spring 2021

Microsite characteristics

A significant effect of deadwood on regeneration microsites emerged from the data analysis. Temperature had a quite variable trend during the monitored period, increasing at the end of July and decreasing until mid-September (figure 3.5a). There was a similar trend between the three microsites: the highest temperature was registered in site C, then in site S and was lowest in site N. Significant differences in temperature were found between site N and sites S and C (figure 3.5b). SWC had an opposite trend compared to T. The SWC was increasing in late summer, according to the temperature decrease. In late summer, the value of SWC in the microsites converged to similar values and no differences were found (figure 5c). SWC value was higher in N microsites, but no significant differences between the three different microsites was found, according to Tukey's Post Hoc test (figure 3.5d).

Influence of SWC and T on microsites

Significant relationships between the presence of CWD and temperature on the microsites were found (tab. 3.2), while no significant ones were found between SWC and the presence of CWD. Generalized linear models were used to analyze which factors most influenced mortality. According to logistic regression, mod1 is the best GLM explaining total mortality in function of the following variables: treatment (sites N, S, C), species (AA, PA, LD, FS, SA), mean T on microsite, mean SWC on microsite, height of log from the ground and seedlings browsed. Block was used as a random factor in every analysis. Mod1 had the lowest AIC (142.58) and the variables of site S and species LD and SA are significant ($p<0.05$). Type 3 ANOVA indicates treatment as the significant factor influencing mortality ($p<0.05$).

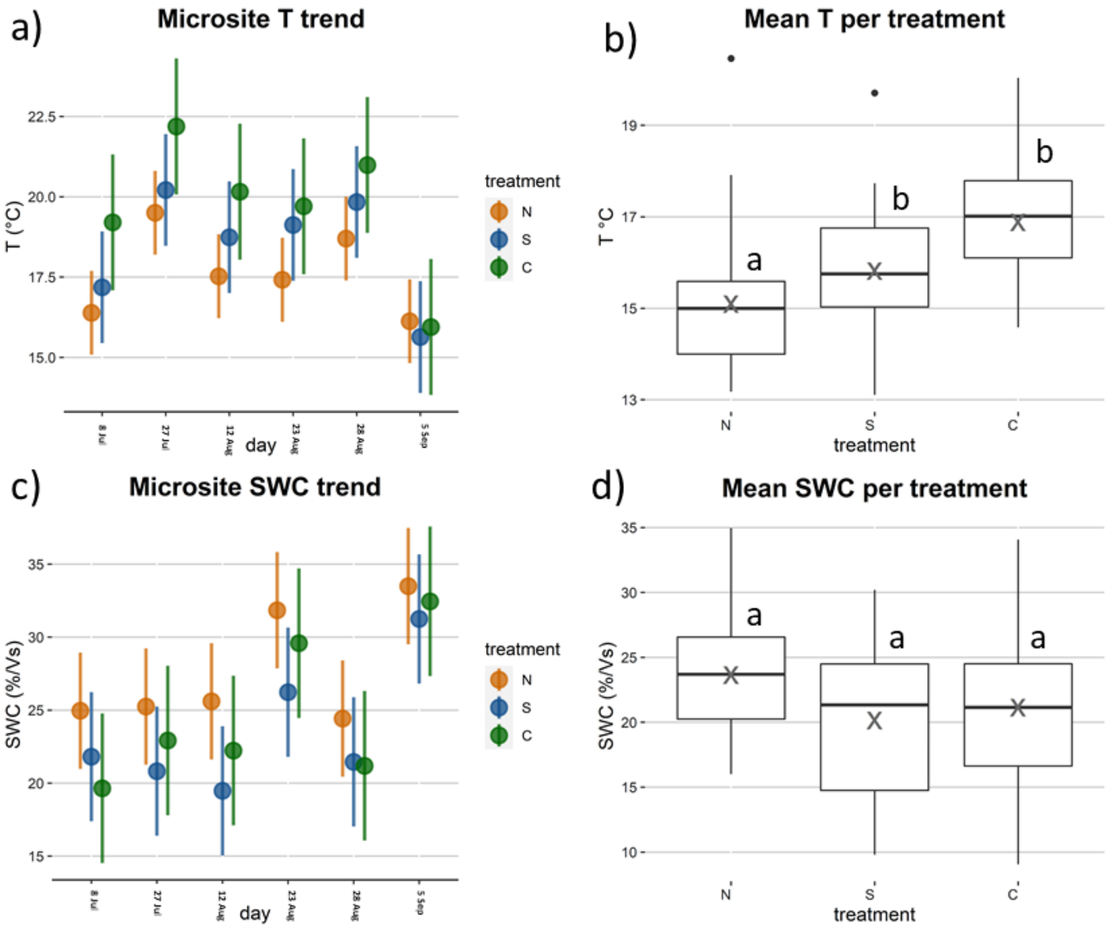

Figure 3.7. Mean values and trend of T and SWC during the summer. a) trend of temperature T (°C) during summer period. b) boxplot of mean temperature in the three different microsites. The mean temperature (indicated by the grey x) in site C is significantly different from site N and S as shown by Tukey's Post Hoc. c) trend of SWC (%/V_{soil}) during summer period. d) boxplot of mean temperature (indicated by the grey x) in the three microsite. There is no significant difference as shown by Tukey's Post Hoc.

Table 3.2 Summary of the GLMs for seedling mortality in 2020 with (mortality_20) and without browsing effect (mortality_20_NB), and mortality in spring 2021. N, microsite located north; S, microsite located south; C, control microsite. (AA= Silver fir, PA= Norway spruce, SA= Rowan, LD= Larch, FS= Beech) represent the species of seedlings. T and SWC are the environmental variable, soil superficial temperature and soil water content respectively. "browsed" represent the number of seedling damaged by browsing and h_ground represent the deadwood height from the ground. . Variables with postscript "" are significant (p<0.05).*

mod1						
Response variable	Explanatory variable	Estimate		SE	z	p
mortality_20						
	N	-5.103	±	7.27	-0.7	0.483
	S*	**-1.834**	**±**	**0.77**	**-2.38**	**0.018**
	FS	1.506	±	1.3	1.16	0.246
	LD*	**2.68**	**±**	**1.27**	**2.11**	**0.035**
	PA	1.112	±	1.37	0.81	0.417
	SA*	**2.835**	**±**	**1.25**	**2.26**	**0.024**
	T	0.14	±	0.38	0.36	0.716
	SWC	-0.083	±	0.1	-0.79	0.428
	browsed	-0.945	±	0.88	-1.08	0.282
	h_ground	-0.022	±	0.02	-1.2	0.232

mod2						
Response variable	Explanatory variable	Estimate		SE	z	p
mortality_20_NB						
	N	-0.524	±	0.54	-0.97	0.331
	S*	**-1.318**	**±**	**0.6**	**-2.3**	**0.022**
	FS	17.424	±	2,723.24	0.01	0.995
	LD	18.115	±	2,737.24	0.01	0.995
	PA	16.428	±	2,737.24	0.01	0.996
	SA	18.956	±	2,737.24	0.01	0.994
	T	0.166	±	0.18	0.93	0.353
	SWC	0.025	±	0.05	0.53	0.596

mod3						
Response variable	Explanatory variable	Estimate		SE	z	p
mortality_21						
	N*	**-0.9466**	**±**	**0.2872**	**-3.296**	**<0.0001**
	S*	**-1.1832**	**±**	**0.2975**	**-3.977**	**<0.0001**
	FS	0.5521	±	0.4729	1.167	0.243026
	LD*	**1.6279**	**±**	**0.4394**	**3.705**	**0.000212**
	PA*	**1.7442**	**±**	**0.4383**	**3.98**	**<0.0001**
	SA*	**1.8574**	**±**	**0.4375**	**4.246**	**<0.0001**

A second GLM model (mod2) was built using as response variable the death of seedlings without considering browsing as cause of death. In this case, the predictors are treatment (sites N, S, C), species (AA, PA, LD, FS, SA), mean T on microsite, mean SWC on microsite. In mod2 the S microsite is the only significant variable (p<0.05). Analysis of variance (ANOVA) indicates species as a significant variable influencing mortality without browsed seedlings (p<0.05).

Using mortality data from spring 2021, we built a third model, mod3, using as response variable treatment (sites N, C, S), and species (AA, PA, LD, FS, SA). Results of mod3 show that both microsites N and C are significant (p<0.05) in reducing seedlings mortality (estimate<0), while larch, fir and rowan result significant in increasing it (p<0.05). We also tested other models including browsing as a variable, but mod3 resulted the best one (AIC=468.9). We tested mod3 with type 3 ANOVA and both treatment and species resulted significant (p<0.05).

Browsing and browsing mortality

Logistic regression (modb) was also performed to analyze which variables influence browsing of seedlings in the three different treatments. In modb browsing was the dependent variable and the predictive variables were treatment, species and height of deadwood from the ground. C treatment results in significantly influencing browsing damage (p<0.05). Among the five different species, only PA, LD, and SA were significant (p<0.05). To analyze the influence of deadwood in protecting seedlings from browsing, we tested different distances from the borders of the windthrown area: euclidean distance, cost distance and CDR. CDR (1) gave the best response on linear model (lower AIC, p<0.05).

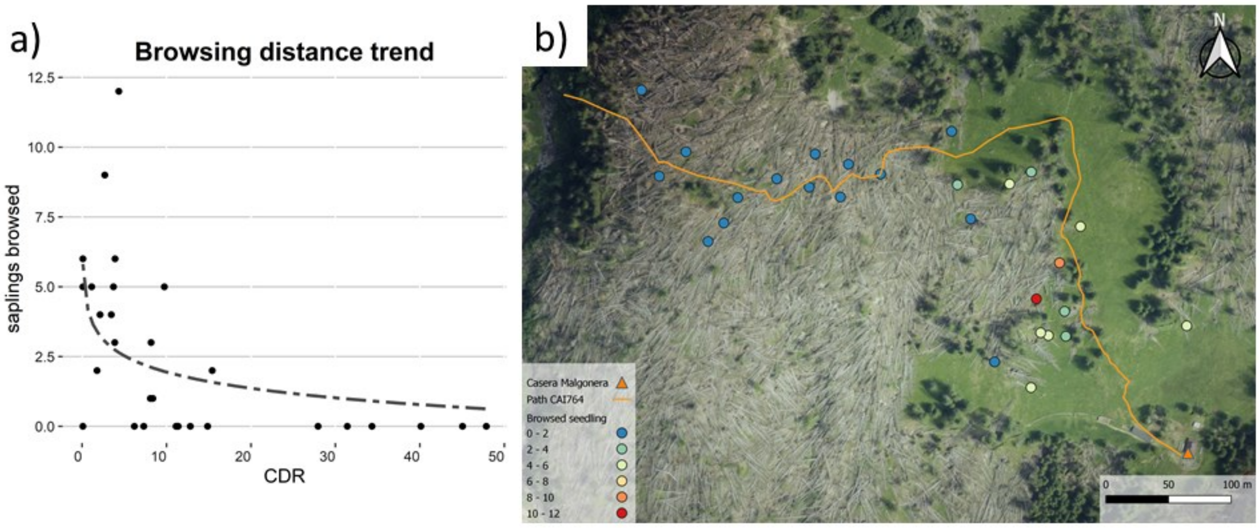

Figure 3.8 a) Trend representing the reduction in number of saplings browsed per block depending on the CDR index. b) Disposition of blocks and number of seedlings browsed per block.

DISCUSSION

Characteristics and mortality of seedlings

CWD combined with other environmental variables can substantially influence microsites' conditions and, as a consequence, regeneration establishment and survival. Overall, seedling's traits appeared to be one of the most important causes of death, and in case of artificial regeneration quality of seedlings can be relevant (Grossnickle 2012). Among species characteristics, stem height seems to be the most relevant. In our study case, rowan was the tallest species and it registered the highest mortality rate, both in sites with the influence of CWD and sites without. More in general, the critical moment when seedlings become taller than CWD can be a very important stage because it could lead to a sensible reduction in the protective effect of CWD. In these situations, seedlings are more exposed to stress factors, like wind and solar radiation, for example increasing drought stress (Castro et al. 2011). Furthermore, the tallest seedlings can be more visible and can result attractive for browsers (Smit et al. 2012).

In drought-stressed environments, e.g. southern exposure in Alpine stands, the conditions in microsites are mitigated by the presence of deadwood. Nevertheless, in microsites that are directly exposed to solar radiation, the contribution of deadwood to reduce drought stress might not be enough to guarantee a large survival of seedlings. The higher mortality rate in sites with no deadwood influence indicates a strong effect of CWD in creating better conditions for seedling survival. The significantly lower mortality in sites on the north side of CWD can be associated to a more intense shading effect. This mechanism stresses the point that CWD contribute to mitigating the microsite conditions in sites shaded by deadwood, identifying the relation between CWD and seedlings survival as anisotropic (Marzano et al. 2013; Marcolin et al. 2019). The position of seedlings relative to deadwood is therefore a very important factor influencing the mortality of tree seedlings. All these results support the hypothesis that CWD has a protective and ameliorating function on microsite regeneration (Matías et al. 2011; Valenzuela et al. 2016; Oreja et al. 2020). Moreover, the fact that mortality rates on control sites were significantly higher than on sites next to CWD, highlights the favorable conditions of deadwood structures for tree regeneration.

In drought conditions, e.g. south-facing slopes, where heat and desiccation could be a critical stress factor, CWD acts as a barrier and can have a really important shading effect, reducing soil surface temperature and increasing soil moisture content (Bailey et al. 2015; Macek et al. 2017; Marcolin et al. 2019). Since the incoming direct solar radiation is the main factor responsible for the soil superficial temperature increase, the shading effect of deadwood contributed to reduce soil surface temperature in sites close to CWD. This effect is anisotropic: stronger on the microsites located north of CWD, and moderately on southern located microsites. This reduction in soil surface temperature can contribute to decreasing soil evapotranspiration, increasing water availability and reducing the drought stress for seedlings, as described in previous studies (De Chantal et al. 2005; Castro et al. 2011; Smit et al. 2012; Goldin and Brookhouse 2015; Valenzuela et al. 2016).

A slightly different situation emerged instead from winter mortality. Environmental variables have a very complex interaction with regeneration, and their influence on regeneration can differ a lot depending on season (Tegelmark 1998; Rodriguez-Garcia et al. 2011). In the Alpine ecosystem for example, solar radiation can be a limiting factor during summer, e.g. on southern slopes, but during winter switches to an important favorable factor, mitigating microsite temperature and accelerating the snowmelt by quickly releasing the seedlings from snow cover. Consequently, the effect on regeneration changes from anisotropic to isotropic. The presence of CWD contributes to mitigating environmental conditions, protecting saplings from snow-gliding and other damage (Johnson and Yeakley 2013; Macek et al. 2017), capturing more radiation and creating warmer microclimatic condition (Štícha et al. 2010), and contributing to speeding up the melting process, prolonging the growing season. At the same time, such an ameliorative effect may not be enough for some more sensitive species, especially with the increase of extreme events due to climate change (Seidl et al. 2014).

Deadwood mitigation effect on SWC had a different trend than soil surface temperature. In our study case deadwood influence on SWC had an opposite trend than T. No significant relations were found between the three microsites with a different position as regards deadwood, so SWC did not seem to be influenced by the presence of CWD. This supports the hypothesis that the presence of CWD alone is not sufficient to influence the SWC on microsites, since the SWC depends on many other factors such as soil composition, soil structure, precipitation regime, temperature and slope (Saxton and Rawls 2006). Moreover, suspended logs can sometimes act as a barrier, intercepting precipitation. As reported by Brais et al. (2005), downed logs can intercept a significant portion of rainfall to the ground (2-5%). In microsites located below a suspended log, this can lead to a reduction in SWC in the root reaching zone, causing drought stress for seedlings. Despite this, the presence of CWD remains a key factor in creating favorable microsites for seedlings' survival. CWD contributes to mitigate the extreme values of limiting environmental variables and, even if deadwood does not significantly influence every single variable, the overall mitigation effect on microsites surrounding CWD can be decisive for regeneration establishment or survival. As emerged both in the literature and from our analysis, the mortality rate is lower in microsites near CWD compared to those in an open field, with no influence of deadwood. Therefore, the presence of CWD results to be important for seedling and regeneration survival (Kuuluvainen & Kalmari, 2003; Tsvetanov et al., 2018; White et al., 2014).

Browsing and browsing mortality

In the context of reforestation dynamics, the importance of deadwood is not only related to microsite amelioration, but also to sapling protection from browsing. The presence of CWD lying on the ground makes it more difficult for browsers to move, potentially lowering the browsing pressure on regeneration (van Ginkel et al. 2013; Hagge et al. 2019; Milne-Rostkowska et al. 2020; Konôpka et al. 2021), depending on browsers species. In fact, if on the one hand CWD has a positive effect in reducing deer browsing pressure, on the other it has no effect on more agile species like chamois (Kupferschmid and Bugmann 2005). The capacity to avoid browsing is also strictly correlated with the spatial distribution and spatial pattern of CWD (Whyte and Lusk 2019). Especially in a windthrown area, the distribution of deadwood is chaotic and represents a serious obstacle for browsers. Therefore, increasing the travel distance within the windthrown area, the cost of reaching seedlings increases and makes them less appetizing (Moriya et al. 2012; Milne-Rostkowska et al. 2020) For this reason, an increasing amount of CWD can significantly protect seedlings from browsing. This protective effect can be explained using equation (1) which allows us to maximize the difference between euclidean distance and real distance on the ground, highlighting the obstruction role of CWD. The greater this difference is, the higher is the soil roughness, and so the greater the cumulative protective effect of CWD on regeneration within windthrown areas. Higher values of CDR correspond to a more complex and rugged terrain morphology, which can be caused by microtopography modification or by deadwood accumulation. Such a complex surface profile is common after windthrows and other disturbances and requires a correct choice among the available tools for proper assessment. High resolution DSMs can be obtained using different technologies, e.g. LiDAR data or photogrammetry applied to UAV-based images in a framework of "*precision forest restoration*" (PFR) (Castro et al. 2021). As reported in (Toth and Jóźków 2016) UAV platforms, and hence UAV-borne sensors, are a fast growing sector of remote sensing applications in forestry, progressively helping to lower prices related to small-scale surveys. Nevertheless, in complex situations like windthrows, photogrammetry reconstructions can be highly limited by the draping effect which would affect the assessment of small areas located among logs, often overlapped. Using remote sensing, it could be possible to estimate a coefficient, CDR index, that gives information about the cost for browsers to reach regeneration seedlings. So higher values of CDR correspond to a lower probability of being damaged by browsers. This coefficient could be adopted to estimate areas of vulnerability to browsing within the windthrown areas, in order to identify potentially safe microsites for regeneration. Moreover, considering this coefficient during salvage logging operations could help to release an appropriate amount of unsalvaged logs, to create a sort of "protection belt" from browsers (Moriya et al. 2012). Browsing rates are also strictly correlated with tree species. First of all, some species are more appetizing to browsers, like rowan, larch or beech (Kupferschmid and Bugmann 2005; Konôpka et al. 2021). Second, if the seedlings are taller than CWD, the protective effect is significantly lower. In our case, SA was significantly taller than the other species and, therefore, the most browsed one. As reported by Castro et al. (2011), once seedlings are taller than the nurse CWD, the protective effect decreases and the microsite influence is most likely reduced too.

CONCLUSIONS

Restoring forest cover after large disturbances like windthrows can be a priority, especially in complex landscapes such as those of the Alpine region, where a large amount of deadwood lying on the ground can be a reliable ally to favor and support forest regeneration. CWD helps in creating favorable regeneration microsites, shading the ground and maintaining a lower soil surface temperature. This mitigation effect can help in reducing drought stress for the juvenile stage. Additionally, CWD contributes efficiently to protecting seedlings from browsing. This protective effect is often anisotropic but, especially during the winter period, the sole presence of CWD can help seedlings' survival, making the protective effect isotropic. The contribution of CWD in protecting seedlings and ameliorating regeneration microsites could last at least for the first critical years, as long as the regeneration is better established and becomes taller than CWD. Despite the greater complexity of reforestation operations within windthrown areas, taking advantage of favorable regeneration microsites and the protective effects provided by CWD can be a valuable option in many situations. In mountain protection forests, where it is crucial to reduce the protection gap (Wohlgemuth et al. 2017), the use of favorable regeneration microsites created by CWD can allow forest cover to regenerate with artificial reforestation and at the same time take advantage of the protective effect of the increased roughness provided by CWD. To make better use of microsite amelioration, a lower seedling height makes the influence of deadwood on sapling survival higher after transplantation. Furthermore, given the ability of CWD to decrease temperature and drought stress, on southern slopes or relatively dry sites, favorable microsites created by CWD can significantly increase the survival probability of both natural and artificial regeneration.

Lastly, LiDAR or photogrammetry applied to UAV-based images are valuable tools to identify and assess the role of deadwood and implement related management strategies for enhancing regeneration establishment and survival, in a framework of precision restoration forestry.

Declaration of Competing Interest: The authors declare no known financial or personal conflict of interest that could have appeared to influence the content of this paper.

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Discussion and conclusions

Deadwood has many different effects on regeneration and depending on the amount, the position, and the dimension such effects could be positive, negative or even change over time. Chapter 1 underlines these different effects, showing how they could change over the years. It is important to clarify and better define the different roles that deadwood can have towards regeneration, so it is possible in a second step to define a temporal sequence in the role played by deadwood. At the moment studies focusing on how the effects of deadwood change over time are missing, like studies underlying the changing role of deadwood. Among all the different effects, direct effects, like substrate, are the most studied. They are important especially for natural regeneration in undisturbed or moderately disturbed forests since affect almost only natural regeneration processes. Most of the direct effects depend on the wood decay stage, so they need quite a long time (more than 20 years, depending on species and climate) to start interacting with regeneration dynamics after deadwood has been created from natural senesce processes or from disturbances. Indirect effects are less studied and more complex to identify, but at the same time, they influence regeneration even more than direct ones. Many of the indirect effects do not strictly depend on decay time to start interacting with regeneration dynamics, so their influence can start sooner and have a longer duration on regeneration. An important aspect to consider in post-disturbance management is that these indirect effects can be manipulated and artificially recreated on regeneration sites, exploiting the existing deadwood on the ground or manipulating the woody debris in order to place them in such a way as to influence seedling establishment and survival. On the contrary, it can be possible to manipulate artificial regeneration and plant them to take advantage of deadwood in the area. Cluster the planted seedlings near CWD to exploit the microsite amelioration and/or cover fresh-planted seedlings with branches or fine CWD to mitigate the extremes and protect them from browsing are just examples of these profitable practices. These practices have been adopted especially after wildfires and in arid climates, but under ongoing climate changes should be taken into account in management strategies at all latitudes and climates, not only after disturbances but also in ordinary management practices after harvesting.

The management of a damaged forest stand is always complex. Many different interests must be taken into account: from securing the area and securing the infrastructures connected to the damaged forest stand to reducing economic losses and restoring previous functions. Regeneration and restoration processes have therefore a central role in post-disturbance management. These management strategies have different influences on regeneration and can influence short-term regeneration dynamics, so it is necessary to adopt strategies that enhance the regeneration process and that damage as less as possible the ecosystem. The most studied management strategies are salvage logging or no-intervention, recognizing some negative impacts of salve logging. No-intervention can be an option to adopt, but not everywhere and not in all conditions. The results of this thesis suggest that probably a mixed approach can be the most appropriate: releasing a certain amount of deadwood on the ground can contribute to maintaining the protective function of the forest, avoid excessive soil erosion, and can favor regeneration processes. This approach can have some limitations in the costs of the operation, and the feasibility of the manipulation depending on terrain morphology. In easy terrain can be an option to release a certain percentage of deadwood consisting of high-cut stumps, highly damaged trees, and processing leftovers; while in more complex terrain, the same result can be reached alternating patches of salvaged and unsalvaged sites. Stated the importance of deadwood, one of the future challenges will be to define thresholds of deadwood percentage releasing, depending on different forest functions and consequent management.

In damaged areas, regeneration species composition is mainly driven by previous stand composition. Most of the time in pure Norway spruce stands in the Italian alps, Norway spruce is at its optimum so the future stand will be a Norway spruce-dominated forest. Therefore, there is the opportunity to increase composition and species diversity, favoring species like beech, larch, silver fir, and other sporadic species depending on local conditions. The aim can be to reach a Norway spruce forest, but with a higher percentage of other species within the forest, to give more resistance and resilience to the stand increasing the diversity (e.g., 80% of Norway spruce and 20% of other species like larch and Swiss stone pine at higher elevation, or beech and fir at lower elevation).

In damaged areas, gap dimensions are a critical factor for seed availability and microclimate mitigation and protection of regeneration. If the maximum seed dispersal distance is shorter than the gap radius, in the middle of the gap there can be problems in seed recruitment for certain species, which do not rely on zoochory dispersal strategy. Distance from the edge and green islands thus represents a critical factor for seed dispersal and subsequent seedlings establishment, moreover, local microclimate can have harsher extremes threatening the shorter regeneration niche of certain species. The protective function of deadwood and other disturbance legacies play in this case a fundamental role to restore forest cover in a relatively short time. As said before, if gaps are larger than the maximum seed dispersal capacity for stand species, planting artificial regeneration exploiting deadwood and disturbance legacies must be taken into account in restoration planning to make the recovery process faster and more effective. Dissemination strategies influenced short-term regeneration structure and composition, increasing significantly the presence of some species, often sporadic species. In unsalvaged areas, it can also be traced back to the perching effect of deadwood, and that suggests similar dynamics can be replicated in the case of partial salvage logging by releasing high-cut stumps and snags. The faster growth of these species can help restore soil cover faster, mitigating the climatic conditions in the area and creating more favorable conditions for regeneration establishment, especially for shade-tolerant species.

Deadwood influences short-term regeneration in different ways depending on shape, dimension, position, and quantity. It can protect seedlings from mechanical damages, like rockfall and snow gliding, creating a barrier that protects the seedling. Moreover, according to the results of this thesis, it is effective also in protecting seedlings and saplings from deer browsing. This protective effects rely mainly on two different mechanisms: the hiding effect of deadwood; the obstacle effect when the presence of deadwood increment the surface roughness increasing the cost to reach the seedling, making the plants less appetible to the browsers. A very important effect not yet thoroughly studied, is the microsite amelioration effect, buffering the extremes in temperature or solar radiation and contributing to retaining more humidity on the regeneration microsite. Moreover, deadwood can create better conditions on the microsites by soil accumulation and nutrient concentration, deriving both from deadwood degradation (with the progress of the decaying processes) and from accumulation near deadwood due to soil erosion and soil nutrient transport processes. Deadwood can also have negative effects on regeneration: in presence of a high amount of deadwood on the ground when its coverage is too dense and uniform, deadwood can act as mulching materials making it hard for seedlings to reach the ground and to germinate.

In post-disturbance management planning, it is more convenient to shift our point of view, considering restoring the whole forest ecosystem not simply by planting individual trees. Focusing on obtaining a new forest with a structure and composition as close as we want to the management objectives we aim for and as close to nature as possible. Under this framework, it can be useful to integrate clusters of planted seedlings and clusters of natural regeneration, step on disturbance legacies to increase seedling establishment and survival probability in restoration practices.

In conclusion, some open question arises. First of all long-term studies on the effect of different management and harvesting practices on regeneration are needed. In general, there is a lack of long-term studies about the influence of deadwood and disturbance legacies on regeneration and future forest stand composition, in particular about the indirect effects of legacies on regeneration. The time it is also crucial to analyze and study if there is a change in the effect of quantity and quality towards regeneration over time, especially as the wood decay processes proceed. Also, the combination of artificial restoration practices and disturbance legacies needs to be explored more in-depth and in different climates. In the end, under the climate changes that are leading to a deep modification in disturbance regimes, it can be really interesting to analyze both natural and artificial regeneration dynamics after different disturbances, that impact differently the same ecosystems.

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