The effects of drought and wildfire on forest structure and carbon storage in a resprouting eucalypt forest

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Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution

Lewis Walden

6 December 2019

Abstract

The frequency and intensity of forest disturbances are projected to increase in many regions as climate changes, with an increased likelihood of multiple disturbance events occurring in short succession. The effects and importance of multiple disturbance events are gaining increasing attention but there is substantial uncertainty regarding the strength of interactions in relation to type, sequence, and relative timing. Forests play an integral role in climate change mitigation efforts, however, multiple disturbances could alter forest carbon dynamics, potentially reducing the storage capacity of impacted stands. Accurate accounting of carbon losses and transformations is thus imperative across forests globally, and particularly in non-conifer dominated types and with different responses such as resprouting.

This study investigated the effects of a global change-type drought (2010-11) and the Waroona Fire (2016), singularly on forest carbon dynamics in the regrowth Northern Jarrah (*Eucalyptus marginata*) Forest of southwestern Australia. This was followed by an investigation of the additive and interactive effects of these two disturbances on forest structure and recruitment. The affected forest stands were assessed using a plot-based forest inventory method combined with allometric equations and remote sensing metrics to determine carbon transformations and fire severity.

Following the drought die-off there was a significant loss of live standing carbon (49.3 t C ha^{-1}), and a corresponding significant increase in the dead standing carbon pool six months after the drought. The Waroona Fire caused pyrogenic carbon emissions of between 10 and 21 t C ha^{-1}, which corresponded to 5.5-12.2% of the mean pre-fire carbon storage, and the conversion of 59.2 – 72.8 t C ha^{-1} from the live to dead standing tree pool. This carbon, which comprises another 30-37% of the pre-fire carbon storage will be susceptible to loss over time both from decomposition and from future fires. Total immediate carbon emissions from the 360 km^2 wildfire were estimated at 723,113 t C. When the disturbances were examined in combination there was no evidence of linked or compounding effects of these disturbances. Instead a strong effect of wildfire on live basal area (-20.7 ± 7.3 m^2 ha^{-1}) overwhelmed pre-existing drought impacts.

Eucalypt resprouting forests are particularly resilient, with focal species able to survive multiple stressors over a short time period. However, the newly regrowing burnt stands are vulnerable to future disturbance until they develop bark thick enough to withstand fire, and carbon stores to maintain resprouts following drought. The drought event preferentially removed large trees and the wildfire smaller trees from the live standing carbon pool. With a continually decreasing rainfall and projections of more frequent and severe fires in this area the trajectory of the regrowth in these stands is likely to be strongly tied to the future disturbance regime. Increases in disturbance frequency and intensity may therefore lessen the chances of these forests recovering to pre-fire structure and therefore carbon storage capacity.

Preface

This thesis consists of three papers that present my PhD research (Chapters 2-4). They are bracketed by an introduction (Chapter 1) and synthesis (Chapter 5), which review the literature, explain links between papers, and place the research in a broader context. The papers were written to stand alone, so this thesis does not contain a chapter describing the study area, study species and common methods. Inevitably there is some degree of overlap, particularly in descriptions of the study area, study design, survey methods and some introductory material.

My project established a network of sites within and near the Waroona Fire boundary. Outside of my three direct supervisors (Prof. Richard Harper, Dr Joe Fontaine, Dr Katinka Ruthrof), Dr. George Matusick, was fundamental in devising the experimental design for Chapters 3 and 4 and has therefore been included as a co-author on the papers derived from those chapters. To complete Chapter 2, I acquired and added to data from long-term plots established to monitor drought induced die-off as part of the State Centre of Excellence for Climate Change Woodland and Forest Health. The project leaders on that team for that initial dataset included Dr George Matusick and Dr Katinka Ruthrof. Prof. Giles Hardy was a key contributor to the experimental design and implementation of the dataset used in the Chapter 2 and was thus included as a co-author in the resultant publication.

One of the papers presented in this thesis has been published, and two are in preparation. The contributions of co-authors, are as follows:

Chapter	Manuscript	Contribution (%)
2	Walden LL, Fontaine JB, Ruthrof KX, Matusick G, Harper RJ, Hardy GESJ (2019) Carbon consequences of drought differ in forests that resprout. *Global Change Biology*, **25**, 1653-1664.	L Walden 80 J Fontaine 5 K Ruthrof 5 G Matusick 5 R Harper 2 G Hardy 3
3	Walden LL, Fontaine JB, Ruthrof KX, Matusick G, Harper RJ (in prep). Above-ground carbon dynamics following wildfire in a eucalypt forest.	L Walden 80 J Fontaine 8 K Ruthrof 8 G Matusick 2 R Harper 2
4	Walden LL, Fontaine JB, Ruthrof KX, Matusick G, Harper RJ (in prep). High severity wildfire overrides drought legacy impact in a resprouting forest.	L Walden 80 J Fontaine 8 K Ruthrof 8 G Matusick 2 R Harper 2

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I would like to thank George Matusick for the time and effort put in to help me establish an experimental method and field sites. Whilst not a supervisor of the project, George's contributions in the early stages of my field work were imperative to the successful commencement and completion of data collection.

I would also like to thank Willa (Billi) Veber who volunteered months of her time to help me for long, hot and challenging days of data collection. Billi also taught me the fine art of databasing and data management. I cannot thank her enough for her support and contribution to my thesis. I thank the many volunteers who contributed their time in the field to collect data, Travis Rasmussen, Jon Nyquist, Phoebe Wester, Corey Boivin, Giles Hardy, Phil Ladd and Christopher Shaw.

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and the lab but also put up with me during the course of the thesis process. Leonnie's unwavering and continual support, patience and encouragement was crucial to the submission of my thesis.

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1 Introduction and aims of the thesis

1.1 Introduction

Forests are a significant store of carbon and are critical for global climate change mitigation efforts, in terms of retaining existing stores, replacing stores through reforestation or afforestation or through management of existing forests (Canadell and Raupach 2008; Smith *et al.* 2013). An estimated 861 ± 66 Gt of carbon is stored in forests, with the majority stored in tropical forests (55%), followed by boreal (32%) and temperate forests (14%) (Pan *et al.* 2011). Carbon stock density is also greatest in tropical and boreal forests with mean values of 242 and 239 t C ha^{-1}, respectively. Temperate forest carbon density is markedly lower with approximately 60% of the carbon density of the other two forest types with 155 t C ha^{-1} (Pan *et al.* 2011).

The land sector plays a major role both in carbon emissions and carbon mitigation strategies. Land-based climate change mitigation is dependent upon the (a) the reduction of atmospheric GHG emissions through carbon sequestration, with the transfer of atmospheric CO_2 into long lived carbon pools (ocean and terrestrial) (Lal 2008), (b) the preservation of existing carbon stocks, such as in forests and peatlands and/or (c) the replacement of fossil fuels with biomass. Globally, forests sequester and store large amounts of carbon, and in recent decades forests have sequestered 30% of the annual anthropogenic CO_2 emissions (Pan *et al.* 2011). Forests thus consistently feature in mitigation strategies (Smith *et al.* 2013) that aim to use these biomes as a major component in global carbon mitigation efforts (Grassi *et al.* 2017).

Climate change will have adverse effects on ecosystems globally (Lenton *et al.* 2008). The changing climate is largely due to an increased concentration of greenhouse gases (GHGs), mainly carbon dioxide (CO_2) (Hartmann *et al.* 2013). Concentrations of CO_2 emissions have increased by 40% since pre-industrial times (Ciais *et al.* 2013) and this has led to an increase in the radiative forcing of the planet, which in turn has increased global mean surface temperatures (Ramaswamy *et al.* 2001; Hartmann *et al.* 2013). There are likely to be many adverse side effects associated with the changing climate, and to limit the impacts of climate change, substantial and sustained reductions of GHGs are needed (Meehl *et al.* 2007; Collins *et al.* 2013).

As the climate changes, it is projected there will be an increased frequency and severity of disturbance events (Hoegh-Guldberg *et al.* 2018) including both abiotic and biotic factors, (Randhir and Erol 2013). These can include deforestation (Canadell and Raupach 2008), drought (Harper *et al.* 2009a), storms (Ziemblińska *et al.* 2018), and insect outbreaks (Kurz *et al.* 2008a). However, whilst the ecological impact of single events has been generally well researched, there is a lack of research on the carbon storage consequences of disturbance events, particularly in the resprouting forest types, such as Australian eucalypt forests.

Multiple disturbance events can cause profound changes to forest composition, structure and function (Buma 2015), and again, the impact of successive interacting disturbance events has been documented across forest types with differing disturbance types and frequencies (Buma and Wessman 2011; Harvey *et al.* 2014b; Fairman *et al.* 2019). There is however a paucity of information on the effect of multiple disturbances on carbon storage, and this situation is particularly apparent for resprouting eucalypt forests.

Disturbances alter the carbon storage and dynamics in a forest stand through mortality, combustion and biogenic decay (Galik and Jackson 2009). Importantly, disturbance events can change forest stands from carbon stores to carbon sinks. For example Kurz *et al.* (2008a) reported that outbreaks of mountain pine beetles (*Dendroctonus ponderosae*) caused forests in Western Canada and the USA to transition from a carbon sink to a carbon source over a 20-

year period; the cumulative impact of the affected regions resulted in a loss of 270 Mt of carbon. Quantifying the carbon consequences of disturbance events is thus imperative to understanding the stability of forest carbon storage and their feasibility as long-term carbon sinks.

With a changing climate it is likely that many systems will be disturbed more frequently, potentially altering stand structure and carbon storage capacity. Therefore, it is important to understand the interaction between forest disturbance and forest carbon storage.

1.2 Literature Review

This literature review will examine the disturbance factors affecting forests globally and how these disturbances affect carbon sequestration and storage.

1.2.1 Forest carbon stores

Forest carbon stores are here split into three different pools, which are live biomass carbon (above and below ground), soil carbon and dead organic matter. The stressors driving changes in carbon dynamics which are discussed will affect each of these stores, so an understanding of this construct is essential as a base for further discussion.

Above ground biomass is the living biomass on the plant above the ground surface and includes, leaves, branches, and stems. Below ground biomass refers to the carbon found in the fine and coarse roots combined, although, roots <2 mm in diameter are included in the soil organic carbon pool as they are difficult to distinguish from the soil organic matter (Paustian et al. 2006). The majority of the stressors mentioned in this chapter affect the carbon stored in the biomass (Aalde et al. 2006). The measurement of the biomass carbon pool can be difficult in large forests as destructive sampling is required, and this particularly applies to roots (Sochacki *et al.* 2017). Instead, default values are often used to estimate below ground biomass (Grierson *et al.* 2000; Mokany *et al.* 2006; Sochacki *et al.* 2012). For example, Mokany *et al.* (2006) assume below ground carbon stores are approximately 20% of the standing above ground carbon. Losses from the biomass carbon store can be associated with anthropogenic and natural factors including roundwood and fuelwood removal, fire, insects, diseases, and storm damage (Aalde *et al.* 2006).

When litter, debris and below ground biomass decompose they transfer into the soil organic matter pool, which is the carbon stored in soil (soil organic carbon) or through the release of carbon dioxide to the atmosphere. Soil organic carbon can then be classified in several ways, depending if it based on physical or chemical analysis. For soil carbon modelling, such as the model RothC, three subgroup pools are used which comprise: particulate organic carbon, humic carbon, and resistant organic carbon (Coleman *et al.* 1997; McKenzie *et al.* 2000; Paul *et al.* 2003) which in forested soils can be comprised of a large proportion of charcoal (Santín *et al.* 2015b).

1.2.2 Disturbance regimes

Resistance and resilience are terms long established in forest ecology (Holling 1973). These terms conceptualise ecological systems as ones that can recover from both biotic and abiotic disturbances (Pimm 1984). A recurring way of visualising resistance and resilience of ecosystems is the ‘ball and cup’ model (Figure 1.1)(Larsen 1995; Gunderson 2000). These two terms of ‘ball’ and ‘cup’ refer to the ability of a system to return to its former state (Larsen 1995) following disturbance. However, multiple disturbance events occurring before ecosystem recovery may push the ecosystem in to a different state (Donato *et al.* 2009b; Fairman *et al.* 2019). It is important to consider these terms when discussing the potential threats to both natural and planted forest ecosystems, as there may be processes that the forests are adapted to, and, in some cases, dependant on. As will be seen, the examples described in this chapter will be of processes which go beyond this natural regime to which the forest is adapted.

Figure 1.1 Schematic representation of ecological resilience based on Gunderson (2000). The ball in the basin represents the 'state' of a system. Resilience is a measure of how much disturbance a system (the ball) can absorb and still remain in the same basin, before it moves into another stable state (different basin). Source: Griffiths and Philippot (2013).

1.2.3 Abiotic disturbances affecting carbon stores

1.2.3.1 Drought and temperature extremes

Climate change will affect a range of variables, including precipitation, evaporation and temperatures (IPCC 2013; Hoegh-Guldberg *et al.* 2018). There are also likely to be changes in the frequency of extreme events, such as temperatures and precipitation (Field *et al.* 2013). Drought occurs due to decreased rainfall over extended periods of time and can often be coupled with higher temperatures during both wet and dry seasons. This increases the stress on large plants and may lead to die off and mortality events. Allen *et al.* (2010b) documented 88 cases of increased mortality due to drought and heat in forests across the globe.

The response of plants to drought will vary depending on the species, as some have the potential to resprout after a substantial loss of biomass (Zeppel *et al.* 2015), which may lead to an increase in the abundance of resprouters rather than reseeding species (Vilagrosa *et al.* 2014). Williams *et al.* (2013) stated that with temperature as a significant driver of drought mortality, the structure and composition of water limited forest across the globe will transition to unfamiliar distributions. Notable changes in forest canopy structure has been observed in the jarrah forest of south-western Australia due to extreme drought and heat conditions, with an estimated 16 515 ha experiencing canopy collapse (Matusick *et al.* 2013). There have also been reports of widespread deaths as a result of drought in *Eucalyptus globulus* plantations (Harper *et al.* 2009a) in this region. Although such events affect significant amounts of biomass, no studies have considered how this will affect the carbon dynamics of these systems.

Drought and fire are interlinked disturbances, as increased drought stress may produce more fuel for wildfire from dead biomass (Dale *et al.* 2000; 2001). Fuel produced through drought-induced mortality, along with the drying of existing fuel, has been shown to increase the wildfire area burned of fires in forested areas of the Western America (Littell *et al.* 2009). Drought induced canopy dieback has also been reported to increase local fuel loads in the resprouting forests of southwestern Australia (Ruthrof *et al.* 2016). It follows that with subsequent fire, areas that have experienced pre-fire drought stress may experience a higher severity of fire than adjacent 'healthy' stands.

Future projections of global climate depict a substantial increase in temperature, along with an increase in rainfall variability for areas currently affected by seasonal drought (Collins *et al.* 2013). Although this trend has not been consistently shown, Greve *et al.* (2014) reported that only 10.8% of land globally follows this pattern (dry gets drier, wet gets wetter) when based on various combinations of hydrological datasets from 1948-2005. Greve *et al.* (2014) also found that 9.5% of global land area shows the opposite pattern, with dry areas becoming wetter. However, an increased prevalence of drought will place further stress on forests and large trees, and therefore increase the incidence of drought induced tree mortality (Zeppel *et al.* 2015). Considering the large documented collapses and potential future events, there is little known about how this type of event will affect the carbon dynamics of forests.

1.2.3.2 Fire

Fire is a process that affects many global forest ecosystems around the world, and is thought to have been a major factor affecting the vegetation composition and structure of these forests (Bond and Keeley 2005; Bond *et al.* 2005; Bowman *et al.* 2009). Distinctive fire regimes, which refers to a specific fire frequency and intensity, have shaped many forest ecosystems into what occurs presently (Gill 1975). For example, many Australian vegetation systems are adapted to frequent fires, and have developed strategies to recolonise after these events (through reseeders and resprouters, Pausas *et al.* 2004). However, many forest ecosystems are not adapted to fire, and this can lead to large mortality events (Campbell *et al.* 2007), with the forests regenerating from seed.

In both types of ecosystem, a fire disturbance leads to a loss of biomass and release of carbon previously stored in the vegetation. The loss of carbon from the system may be incomplete, as some biomass still stands and some material may not have fully combusted (Santín *et al.* 2015a).

A change in fire regime can lead to forest degradation and a severe decline in forest health, and this has led to forest canopy collapses in some instances (Holz *et al.* 2015; Paritsis *et al.* 2015). For example, recurrent fires outside the regular fire cycle has resulted in the loss of the obligate seeder species Alpine ash (*Eucalyptus delegatensis*) in south-eastern Australia, where a second fire occurred before regenerating vegetation was able to produce seed (Bowman *et al.* 2014). Fairman *et al.* (2019) also reported the loss of resprouting ability in the temperate eucalypt forests of Victoria, south-eastern Australia, where repeated fires in short succession resulted in widespread mortality and resprouting failure of the dominant overstory. It follows that these events may have both short- and long-term consequences on carbon storage and dynamics in those stands as lost carbon is sequestered by recruitment of new trees. This concept of increasing fire frequency affecting forest species composition can be extended to a range of ecological communities containing woody species (Enright *et al.* 2015).

Globally, significant amounts of carbon are lost from the terrestrial pool each year with approximately 1.4-3.1 Gt tonnes of carbon emissions each year from wildfire for the period from 1960-2000 (Schultz *et al.* 2008). The carbon emissions from forest wildfire have been estimated in the mixed conifer forests of south western Oregon. Campbell *et al.* (2007) quantified the carbon emissions from a fire that burnt 20,000 ha of mixed conifer forest with an estimated 17-22 Mg C ha^{-1} $^{-}$released from the event. A large wildfire that burnt an area of 450,000 ha of temperate eucalypt forest in Victoria, Australia, emitted an estimated 3.9 Mt C, at an estimated rate of 40-58 t C ha^{-1} (Keith *et al.* 2014). These examples represent large quantities of carbon released from the terrestrial pool into the atmosphere from single events, highlighting the importance of fire in global carbon accounts and climate change mitigation efforts. Kirschbaum (2000) argued that the emissions from wildfires in Australian systems would only be temporary emissions as the carbon is recovered from regeneration starting directly after the event, and this is how they are treated in the Australian National Greenhouse Gas Inventory.

It follows that if fire regimes and climate equilibrate, the carbon emissions from a fire event will be counteracted by the surviving vegetation and regeneration (Bowman *et al.* 2009). Fire intensity is important to the recovery of forest carbon stores following fire (Volkova *et al.* 2014). During low intensity planned fires litter and debris layers may be removed from the forest stand but large mature individuals are typically not killed by these fires, and carbon lost is quickly replenished through resprouting and regrowth (Volkova and Weston 2015). Alternatively severe wildfire can result in mortality of overstorey trees and therefore the transfer of live to dead carbon as well as losses from combustion of material (Keith *et al.* 2014). It follows that as the climate changes and fire severity and frequency increase (Clarke *et al.*

2016), regeneration and persisting vegetation may not be able to counteract carbon lost from fires.

1.2.3.3 Storm damage

Storm damage occurs during a meteorological event and can lead to tree mortality. This type of forest degradation is more pronounced in production forests, as they are usually monocultures. For example, a large storm which affected southern Sweden in 2005 caused widespread damage to the forests with approximately 70 million cubic meters of timber being felled (Valinger and Fridman 2011). There was also a reported decrease in growth in subsequent years after the event, which shows that the effects extend beyond the storm (Valinger *et al.* 2014). Valinger *et al.* (2014) also reported that there was no change in the choice of species used for regeneration, and minimal adaption by forest owners for possible future events. There is a gap in the literature surrounding the effects of storms on the carbon dynamics of affected forests.

1.2.4 Biotic disturbances affecting carbon stores

1.2.4.1 Insect pests

Insect outbreaks can cause widespread damage to forests and ecosystem dynamics by reducing growth and increasing mortality (Mattson and Addy 1975; Kurz *et al.* 2008a). In Canada, the mountain pine beetle (*Dendroctonus ponderosae*) had a record outbreak in 2005, which affected 140 million m^3 of lodgepole pine (*Pinus contorta*) trees. Insect outbreaks are not only focussed on mature trees as some species are known to affect seedlings and juvenile plants. This is the evident in Sweden where the Pine Weevil (*Hylobius abietis*) attacks Norway spruce (*Picea abies*) seedlings, hindering growth and increasing mortality in reforestation activities (örlander and Nilsson 1999). It is important to reiterate that these forests may be adapted to this type of disturbance, and the increase in mortality and general degradation stems from a broadened range or increased prevalence of these insects.

The effect pest outbreaks have on carbon dynamics has been quantified for the ponderosa pine (*Pinus ponderosa*) forests of Canada, along with the potential impact climate change will have on these type of outbreaks. Kurz *et al.* (2008a) estimated the cumulative carbon emissions from mountain pine beetle outbreaks in Canada (British Columbia) from 2000-2020, which equated to 270 Mt of carbon. This led to the forest being converted from a small net carbon sink to a carbon source, during and directly after the outbreak (Kurz *et al.* 2008a; Kurz *et al.* 2008b). Bark beetle outbreaks (*Dendroctonus spp.*) have also been linked to an increase in severity of crown fires in lodgepole pine forests (Turner *et al.* 1999), which would have additional effects on the carbon dynamics of this system. However, debate is ongoing as to whether bark beetle outbreaks actually increase the severity of crown fires in these forests (Simard *et al.* 2010; Black *et al.* 2013).

1.2.4.2 Pathogens

Pathogens are one of the possible causes of tree decline, and they can weaken or kill the infected individual. Pathogens are in the form of microscopic organism such as, bacteria, fungi, phytoplasmas or viruses, and unlike their hosts are usually highly mobile (Hamelin *et al.* 2005). The heightened ability to disperse allows large areas of forest to be affected by the pathogen. For example, Podger (1972) estimated that 80 000 ha of *Eucalyptus* forest in southwestern Australia had been affected by the pathogen *Phytophthora cinnamomi*, a soil borne water mould which causes root rot. This type of mortality has led to a change in the forest structure at the affected sites (Newhook and Podger 1972).

There are many cases of forest pathogen induced mortality across the globe, from a variety of different pathogens and vectors (Allison *et al.* 1986; Rizzo and Garbelotto 2003; Gonthier *et* *al.* 2007). However, the effect these mortality events have on forest carbon dynamics is unstudied, although its significance has been mentioned (Bergot *et al.* 2004). The carbon implications of these events could be significant for terrestrial carbon sinks, not only because of the associated mortality, but also the possible change in forest structure.

The spread and establishment of pathogens has been linked to an increase risk of wildfires in California, where areas which were recently invaded by the pathogen (*Phytophthora ramorum*) had an increased overstory burn severity (Metz *et al.* 2010). Metz *et al.* (2010) also found that in areas with long-term prevalence of the disease the increased log volumes led to increased substrate burn severity, and that the mortality had only a minor effect on the fire severity. Rather the areas of most concern were those recently affected by the disease.

1.2.4.3 Stacked disturbance events

The role of disturbance in ecosystem carbon storage and dynamics has been highlighted for multiple disturbance and forest types. However, as the climate changes and frequency of disturbance increases there is a higher likelihood of multiple, stacked disturbances occurring in short succession. These events can cause abrupt and profound changes to forest composition, structure and function (Buma 2015). Multiple disturbance events can push the ecological resilience of an ecosystem beyond its resistive capacity and therefore push the system to an alternative state. For example Donato *et al.* (2009a) reported that in the mixed conifer forests of Oregon, there was no decline in diversity but a change in forest structure following multiple fires in short succession (15 years). Areas which experienced short burn intervals had a reduced dominance of woody forest components and an increase in shrub cover. It is likely that these changes to forest structure and woody biomass will also have significant effects on carbon dynamics in these forest stands; however, these were not reported.

Repeated disturbance events can either have *linked* or *compound* interactions (Buma 2015). Linked disturbances occur when the first disturbance affects the likelihood, extent, or severity of the second disturbance (Buma 2015). Compound disturbances describe the biotic response (for example, tree recruitment) following a second disturbance event, and how it is altered relative to the individual disturbance event. The interaction between successive disturbance events has been documented across different disturbance types and frequencies (Metz *et al.* 2010; Buma and Wessman 2011; Kulakowski *et al.* 2013; Harvey *et al.* 2014b; Fairman *et al.* 2019). Linked disturbance effects have been reported in the interaction between tree windthrow, and subsequent fire severity by Kulakowski and Veblen (2007). They reported that in the subalpine forests of Colorado stands with severe windthrow (66% of trees) experienced higher wildfire severity compared to those with lower rates of windthrow (Kulakowski and Veblen 2007). Linked disturbance effects have also been reported between intense storms and fire with defoliation leading to higher fuel loads and subsequent fire intensity (Gower *et al.* 2015) as well as pest (*Dendroctonus ponderosae)* outbreaks and subsequent fire (Harvey *et al.* 2014b). Compound disturbance interactions have been reported in a resprouting shrubland system of southwestern Australia (Gower *et al.* 2015). Gower *et al.* (2015) found that areas that experienced hailstorm damage and subsequent planned (prescribed) fire had reduced resprouting vigour and seedling recruitment compared to those that just experienced fire alone. With a projected increase in disturbance frequency and intensity with a changing climate, the complex effects of disturbance types, potential interactions and cumulative effects are key to understanding ecosystem resilience and the stability of global carbon sinks in a changing climate.

1.2.5 Conclusions

Forest are a large store of anthropogenic carbon emissions and thus they play a key role in the mitigation of climate change. However, there are threats to these forest carbon stores which could potentially have significant feedbacks on the global carbon cycle. These threats include both abiotic and biotic processes such as, wildfire, drought, storm damage, insect attack, and pathogens. These threatening processes do not work independently, rather the processes work synergistically and can have a heightened effect on forest ecosystems when they occur before the forest has recovered. The impacts of these disturbance events singularly have on forest mortality and structure have for the most part been thoroughly researched. However, there is a significant lack of research focussed on the implications of these events for carbon storage, particularly in a resprouting forest. There is also a need for more research which investigates the impacts of stacked disturbance. This presents a very large gap in the literature, considering the significant amount of carbon stored in forests globally and the role these are posited in playing in management of global carbon cycles. It is also important to consider the effects climate change will have on these disturbances, as most are expected to worsen over time.

1.3 Thesis questions

The jarrah forest is a 30-40 m tall evergreen forest with a diverse understorey (Dell and Havel 1989b). Harper *et al.* (2019) provide an overview of the jarrah forest and its management. Although there was complete forest cover at the time of European settlement in 1829 there has subsequently been considerable forest harvesting and deforestation for agriculture. The Northern Jarrah Forest comprises 11,276 km^2 of forest, with approximately 81% of this vested with the Western Australian Government (Conservation Commission of Western Australia 2013) and the remainder in private ownership.

Following repeated harvests, the forest is now almost wholly comprised of regrowth of various ages. Low intensity planned fires are used at intervals of 6 to 8 years to reduce the build-up of fuel loads (Burrows and McCaw 2013). Around 62% of the forest is in conservation reserves, with the remainder subject to timber harvest, through selective logging rather than clear-fall

(Conservation Commission of Western Australia 2013). Bauxite mining also occurs across 10 km^2/yr of the forest, with this involving the removal of the surface 2-4 m of regolith and subsequent rehabilitation (Koch and Hobbs 2007).

Southwestern Australia and the Northern Jarrah Forest () has experienced a significant change in climate since the 1970's (Bates *et al.* 2008; Andrys *et al.* 2017), which has been characterised by a reduction in annual rainfall (10-15%) and increase in temperature (0.15°C per decade, Figure 1.3, Andrys *et al.* 2017). Following a global change-type drought (hotter drought) in 2010, and a series of heatwaves in early 2011, the structure of approximately 16 000 ha of the Northern Jarrah Forest was affected by sudden canopy die-off (Matusick *et al.* 2013). The structure of severely affected stands was altered, moving these areas towards shorter, more densely stocked stands (Matusick *et al.* 2016). However, there was no assessment of the carbon storage consequences of this event, and subsequent recovery. Five years after the drought die-off event, a severe wildfire (the Waroona Fire) burnt 36 000 ha of the Northern Jarrah Forest (NJF). Whilst the recovery of the jarrah forest following fire had been well documented (Abbott and Loneragan 1983; Abbott and Loneragan 1986; Burrows *et al.* 2010; Burrows 2013), there had been no accounting of carbon losses associated with wildfire in this forest type.

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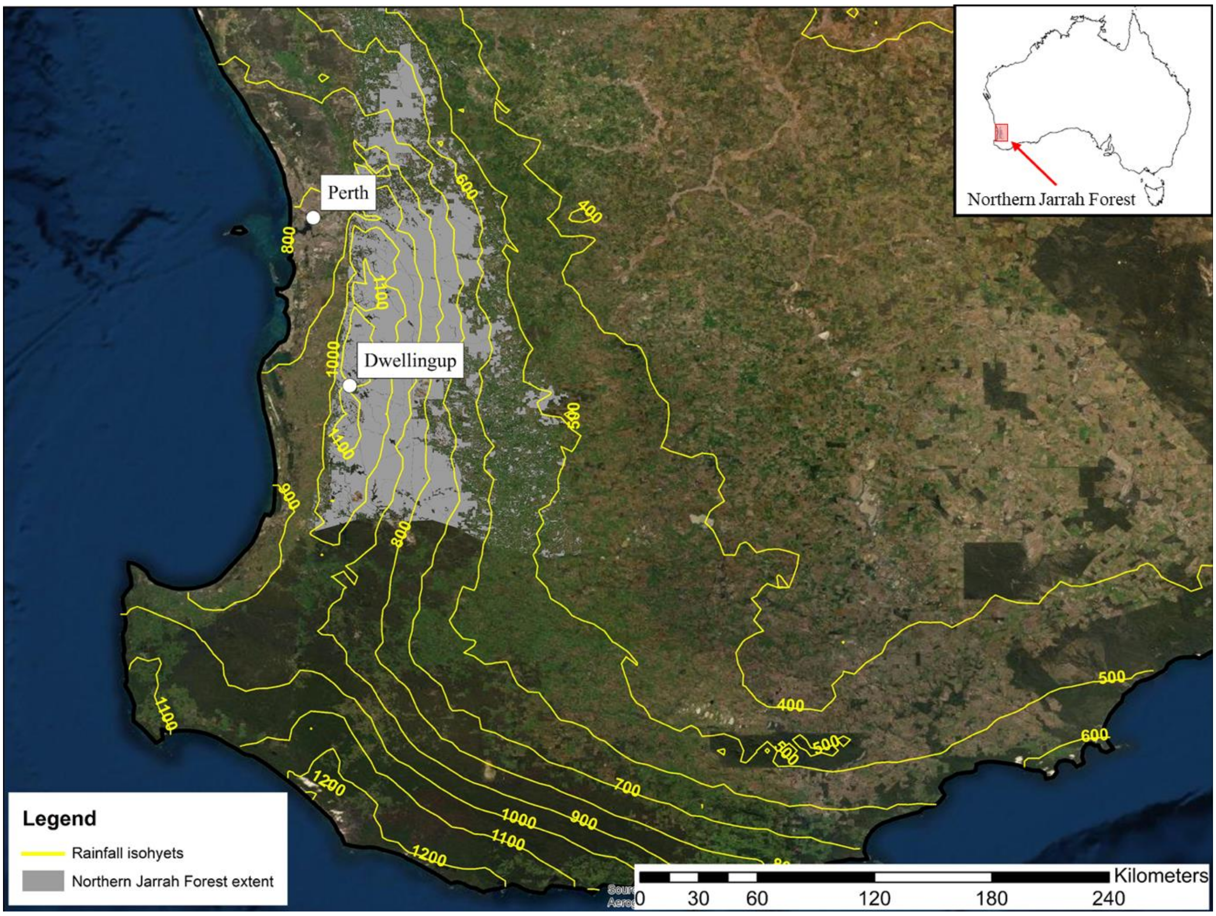

Figure 1.2 Location of the Northern Jarrah Forest (grey shading) in southwestern Australia. Isohyets illustrate the rainfall gradient from east to west. State capital city Perth, and Dwellingup (Station number: 009538) the source of long-term rainfall data is presented. Data source: Australian Bureau of Meteorology

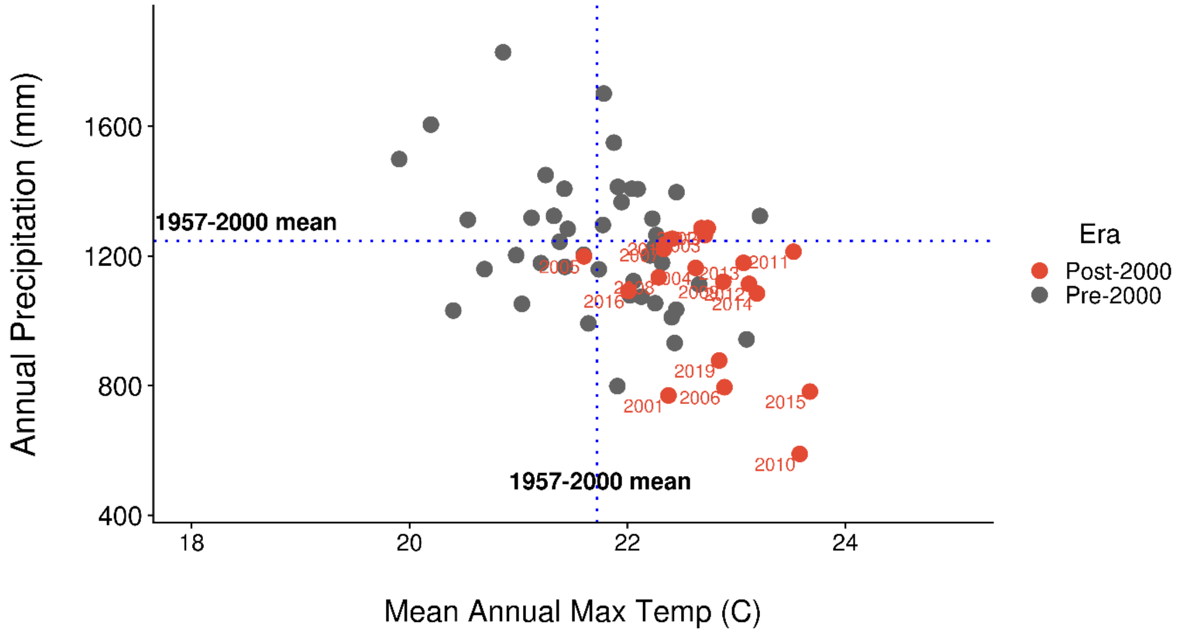

Figure 1.3 Annual precipitation for Dwellingup (Station number: 009538) from 1957 to 2019. Dotted blue lines represent mean (1957-2000) annual rainfall and mean annual maximum temperature. Grey dots indicate years pre-2000 and red dots indicate post-2000 years. Data source: Australian Bureau of Meteorology.

During the Waroona Fire there were areas of forest that burnt which had been previously affected by drought induced die-off. This layering, or stacking, of disturbances presented an opportunity to investigate the potential additive and interacting effects of these disturbance events in a resprouting forest.

Eucalypt forests are already subject to recurrent fire (Bowman *et al.* 2009; Burrows *et al.* 2010) and drought (Brouwers *et al.* 2013a; Matusick *et al.* 2013) and while there are some studies that have examined the impacts of fire on carbon storage (Keith *et al.* 2014; Volkova *et al.* 2014; Volkova and Weston 2015), there is little information on the impacts of drought, or indeed fire and drought in combination on carbon storage. Eucalypt forests differ in their response to non-sprouting coniferous forests, which have been subject to wildfire and drought in the northern hemisphere, in that they have differing mechanisms of resistance and resilience to these events. After both drought and fire, eucalypts can resprout from epicormic buds on their stems and continue growth (Burrows 2013), whereas non-sprouting forests can be killed outright and have to regenerate from seed (Pausas *et al.* 2004).

The objectives of this thesis, therefore for a resprouting eucalypt forest, are to a) quantify the carbon implications of global-change-type drought and recovery, b) quantify the carbon emissions and transformations following severe wildfire and c) investigate the additive and interactive effects of drought plus wildfire on forest structure, mortality and recruitment in a resprouting forest type, such that the future recovery trajectory of the forest can be understood.

This thesis thus explores both the carbon storage and structural consequences of repeated disturbance in a resprouting eucalypt forest. Chapters 2 and 3 investigate the disturbances singularly, then the stacked disturbance event will be examined (Figure 1.4). The thesis will attempt to answer the following questions:

1) *What are the carbon implications of global-change-type drought and recovery?*

   Chapter 2 investigates the carbon consequences of global change-type drought in a resprouting eucalypt forest in south-western Australia. With the use of ecological knowledge, we calculated the estimated carbon transfers (e.g. from live to dead standing carbon) following die-off and early recovery.

2) *What are the carbon emissions and transformations following severe wildfire?*

   Chapter 3 uses a field survey approach to quantify the carbon emissions and structural transformations following a large severe wildfire. Field surveys were also undertaken to examine the structural and carbon transformations following the event.

3) *What are the additive and interacting effects of drought plus wildfire on forest structure and mortality in a resprouting forest type?*

Although there is a body of literature that examines the effect of fire and drought on the Northern Jarrah Forest there are no data on the effect of stacked disturbances on this forest type. Or indeed resprouting forest types in general. To understand the likely trajectory, in terms of forest growth and carbon storage of these stands, Chapter 4 investigates the effects of repeated disturbance on forest structure, mortality and recruitment in a resprouting forest type. This is of interest because as climate changes and disturbance regimes shift there will undoubtedly be more areas of resprouting forest that are subjected to repeated disturbance.

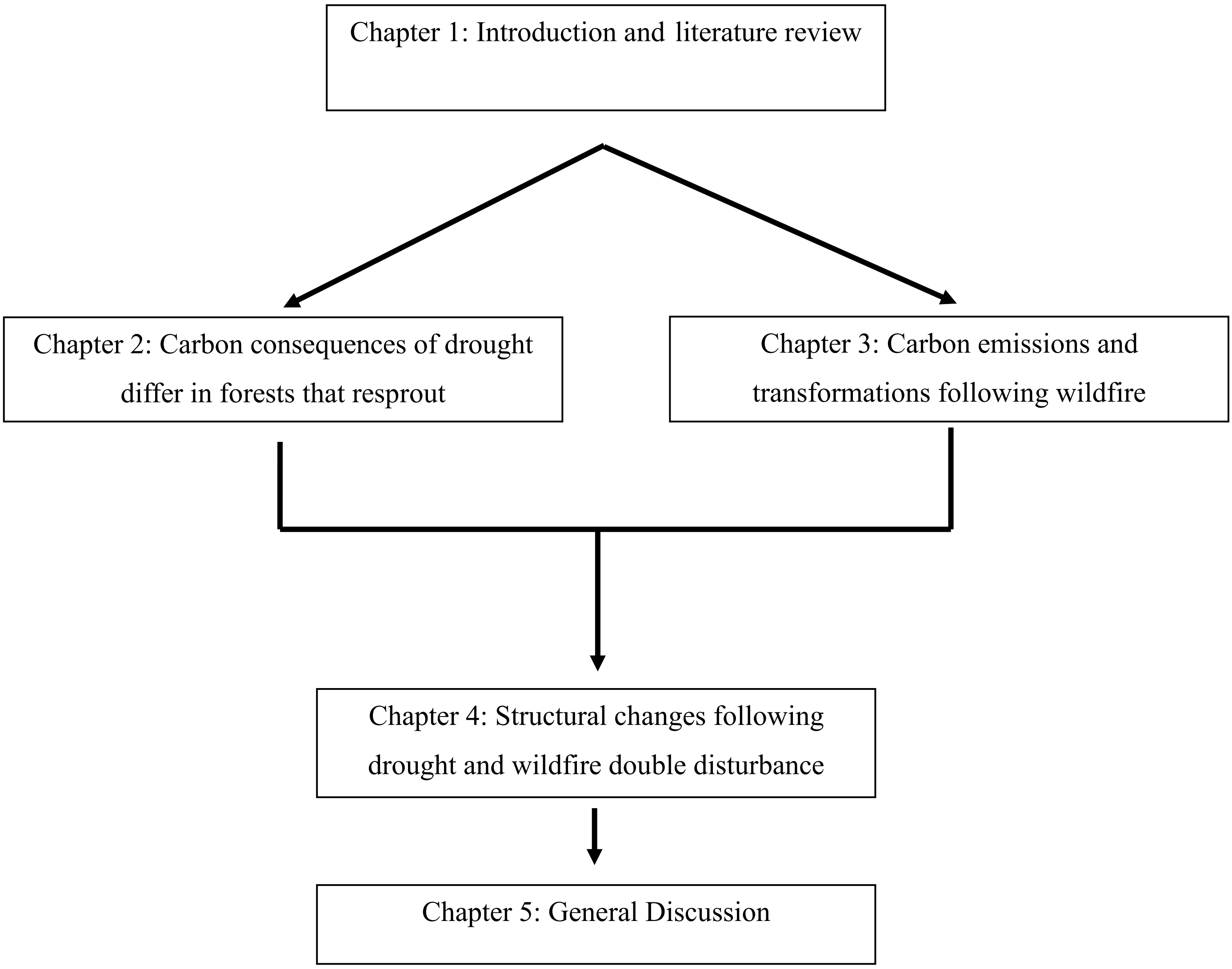

Figure 1.4 Roadmap of thesis chapters and interrelationships of research topics

2 Carbon consequences of drought differ in forests that resprout[1]

2.1 Abstract

Prolonged drought and intense heat-related events trigger sudden forest die-off events and have now been reported from all forested continents. Such die-offs are concerning given that drought and heatwave events are forecast to increase in severity and duration as climate change progresses. Quantifying consequences to carbon dynamics and storage from die-off events is critical for determining the current and future mitigation potential of forests. Stand measurements were taken five times over 2+ years from affected and unaffected plots across the Northern Jarrah Forest, southwestern Australia, following an acute drought/heatwave in 2011. There was a significant loss of live standing carbon (49.3 t C ha^{-1}), and subsequently a significant increase in the dead standing carbon pool by six months post die-off. Of the persisting live trees, 38% experienced partial mortality contributing to rapid regrowth and replenishment (82-88%) of labile carbon pools (foliage, twigs, branch) within 26 months. Such regrowth was not substantial in terms of net carbon changes within the timeframe of the study but does reflect the resprouting resilience of this forest type. Dead carbon generated by the die-off may persist for centuries given low fragmentation and decay rates resulting in low biogenic emission rates relative to other forest types. However, future fire may threaten persistence of

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[1] This chapter has been published as: Walden LL, Fontaine JB, Ruthrof KX, Matusick G, Harper RJ, Hardy GESJ (2019) Carbon consequences of drought differ in forests that resprout. *Global Change Biology,* **25**, 1653-1664.

both dead and live pools via combustion and mortality of live tissue and impaired regrowth capacity. Resprouting forests are commonly regarded as resilient systems, however a changing climate could see vulnerable portions of forests become carbon sources rather than carbon sinks.

2.2 Introduction

Globally, increased heatwave and drought events are leading to elevated rates of forest die-off events (Allen *et al.* 2010a; Hicke *et al.* 2012). There have been at least 88 incidences of drought and heat related die-off events, reported from every forested continent and every major forest type (Allen *et al.* 2010a; Allen *et al.* 2015; Cobb *et al.* 2017). These global change-type droughts (that is, hotter droughts) are predicted to increase in frequency, duration and severity into the future (IPCC 2013). Die-off events may have broad repercussions, impacting the structure, function and biodiversity of ecosystems, with some systems experiencing structural state shifts (Clark *et al.* 2016; Matusick *et al.* 2016). For example, Martínez-Vilalta and Piñol (2002), reported drought-induced mortality in three pine species (*Pinus pinaster, P. nigra,* and *P. sylvestris*) on the north eastern Iberian Peninsula, and suggested that a drier climate may extirpate *P. sylvestris* populations in the region. In the southwestern USA, Breshears *et al.* (2005) reported that a global change-type drought in 2002-2003 led to the die-off of the key overstorey species, *P. edulis,* across over a million hectares. Such impacts have garnered broad and intense interest and while changes in forest structure and composition have been documented, the carbon consequences of drought and heat related forest die-off events remains relatively unreported, leaving substantial uncertainty around drought/heat wave-caused emissions and destabilisation of carbon pools.

Forest carbon sinks and the maintenance of existing forest carbon stocks contribute significantly to the global carbon budget, and are an essential component of climate change mitigation strategies (Le Quéré *et al.* 2013). Indeed, the management of forest carbon sinks to sequester and store carbon emissions was included in the recent Paris Agreement (Schleussner *et al.* 2016; Grassi *et al.* 2017) and forms the basis of the National Determined Contributions (NDCs) of 187 countries (Grassi *et al.* 2017). Forests cover 30% of the earth's land mass and offset approximately 25% of emissions from fossil fuel use, which equates to approximately 2.3 Gt C annually (Pan *et al.* 2011). However, forest disturbance events can have profound effects on forest carbon dynamics (Williams *et al.* 2016). Such events directly emit carbon dioxide into the atmosphere (e.g. via pyrogenic emissions from wildfire) or drive large transformations in the structure of carbon pools (i.e. live to dead) in forest stands, through for example, insect outbreaks, drought, or disease. Harvest, fire, windthrow, bark beetles and drought collectively lead to the gross loss of approximately 200 Mt C yr^{-1} of live biomass annually across the conterminous USA (Williams *et al.* 2016). A large wildfire event in Oregon, USA, for example, was reported to have released 19 t C ha^{-1} of carbon from pyrogenic emissions (3.8 Mt C total fire emissions), which was an estimated 16 times the net annual ecosystem emissions (Campbell *et al.* 2007). Kurz *et al.* (2008a) reported that outbreaks of mountain pine beetles (*Dendroctonus ponderosae*) caused forest of Western Canada to transition from a carbon sink to a carbon source over a 20-year period; the cumulative impact of the affected regions resulted in a loss of 270 Mt of carbon. Quantifying the carbon consequences of disturbance events such as those above is imperative to understanding the stability of forest carbon storage and their feasibility as long-term carbon sinks.

Drought-induced forest mortality events alter the rate at which carbon moves through the carbon cycle (Law and Waring 2015) by reducing the carbon sequestration potential. Given that this type of disturbance can vary in intensity and duration, so do the potential live carbon losses. The magnitude, pace and pattern by which a system responds to drought is determined by the functional traits of the species within the stand. For example, Zeppel *et al.* (2015) suggest that drought stress may have a relatively minor impact on resprouting forest systems, such as eucalypt forests, due to a lack of tree mortality compared with conifer-dominated systems, which do not resprout and require seedling-based regeneration and may experience larger and longer lasting live carbon losses.

Not all drought related die-off events, however, lead to a reduction in carbon storage capacity. For example, Fauset *et al.* (2012) documented drought-induced structural and functional changes (including shifts from shade tolerant, evergreen, wet forest species, to deciduous, dry forest species) in tropical forests of Ghana, which led to an increase in above ground biomass (carbon) following two decades of chronic drought. Contrasting results from the boreal forest of Canada suggest that if climate change-induced drought events continue to intensify, forests could transition from a carbon sink to a carbon source as the climate warms and water deficits lead to a decline in tree growth, a reduction in net primary production and widespread increases in mortality (Ma *et al.* 2012). It is important to quantify the movement of carbon through forest stands, as well as changes in the volume of live and dead carbon, as these may have implications for the response of forests to future disturbance events, for example, fire, windthrow, or insect outbreak.

Quantification of the carbon consequences of a drought-induced die-off event in a resprouting forest type, rather than a coniferous forest, is a pressing yet largely unexplored area of research. Resprouting species can experience partial mortality and may regrow lost biomass quickly, rather than the complete biomass loss that results from tree mortality commonly seen and reported in coniferous forests (Zeppel *et al.* 2015). The effect that this ‘incomplete’ type of disturbance has on forest carbon storage and dynamics is important for carbon accounting and ongoing forest management, as the accumulation of dead material and the reduction of live carbon will impact forest structure, carbon storage and fire risk. The Mediterranean climate-type forest of southwestern Australia is a region dominated by resprouting canopy species (predominantly *Eucalyptus* and *Corymbia* spp.) and has experienced intermittent droughts since the mid 1970s, an acute drought in 2010, and multiple heatwave events in 2011 (Bates *et al.* 2008; Petrone *et al.* 2010; Matusick *et al.* 2018; Ruthrof *et al.* 2018). Mediterranean climate-type ecosystems are considered highly vulnerable to climate change (Klausmeyer and Shaw 2009) because of a retraction in the Mediterranean climate extent and increase in the prevalence of disturbances in these systems (e.g. fire, drought, temperature increase, invasive species; Cheddadi *et al.* 2001; Lenihan *et al.* 2003; Fried *et al.* 2004; Parry *et al.* 2007; Enright *et al.* 2015). Drought and heat events in 2010/2011 impacted multiple forest types in southwestern Australia, driving canopy die-off and tree mortality across at least three forest types Ruthrof *et al.* (2018); Tuart (*Eucalyptus gomphocephala*) woodlands (Matusick *et al.* 2012), the Northern Jarrah (*E. marginata*) Forest (Matusick *et al.* 2013), and Banksia woodland (Bader *et al.* 2014; Challis *et al.* 2016). Although there is the beginning of an understanding of the ecological implications of drought in such forest and woodland systems, the magnitude of live carbon loss, or the effects on live and dead carbon pools within forest stands is unknown. This type of information is critical for carbon mitigation, forest management and climate change adaptation. Therefore, this paper aims to:

a) quantify stand dynamics and carbon consequences of a major drought die-off event in 2011; and,
b) quantify initial regrowth dynamics following the die-off event for all major above-ground biomass pools.

2.3 Methods

2.3.1 Study area

The Northern Jarrah Forest (NJF) is located in southwestern Australia (30.8-33.5 S and 115.8-117.8E) and covers an area of 1,127,600 ha (Havel 1975). The forest ranges from an open dry sclerophyll forest in the north to a tall, closed forest in the south (Dell and Havel 1989a). Deep lateritic weathering profiles cap Archaean granite and metamorphic rocks (Gilkes *et al.* 1973). The NJF has a Mediterranean type climate, with hot dry summers and warm wet winters. Most rainfall occurs between April and October, and a seasonal drought may last between four to seven months (Bates *et al.* 2008). There is a strong rainfall gradient across the forest, which ranges from >1100 mm yr^{-1} on the western edge to approximately 700 mm yr^{-1} in the north east (Gentilli 1989).

Southwestern Australia has experienced a significant change in climate, characterised by a reduction in rainfall (10-15%) and increase in temperature (0.15°C per decade) since the 1970s (Bates *et al.* 2008). During this period of warming and drying, two extreme drought events occurred during the Australian summers of 2006-2007 and 2010-2011. The winter of 2010 was extremely dry, with rainfall 40-50% below the annual average (BOM 2011). In addition, the number of heatwave days in 2011 was the highest on record since 1960 (BOM 2011). Prolonged reduction in rainfall, coupled with a heatwave, triggered significant, abrupt biotic disruptions across the region spanning both the terrestrial and marine ecosystems which included mortality as well as demographic shifts and altered species distributions (Ruthrof *et al.* 2018). During this event, it was estimated that approximately 16,000 ha of the NJF suffered severe canopy die-off (Brouwers *et al.* 2013a; Matusick *et al.* 2013). Areas that were severely affected were those in close proximity to granite outcrops, had soil with a lower water holding capacity compared to surrounding areas (Brouwers *et al.* 2013b), and were more clustered at xeric sites (Andrew *et al.* 2016). Following the die-off, Ruthrof *et al.* (2016) reported that the areas affected by drought had significantly higher amounts of fine fuels, which could elevate fire spread and intensity in subsequent fire events.

Our current study focussed on drought-affected areas that are composed of a *E. marginata* (Jarrah) and *Corymbia calophylla* (Marri) co-dominant overstorey, a midstorey composed of a mixture of *Banksia grandis*, *Allocasuarina fraseriana*, and two *Persoonia* species. The predominant disturbance agent in the NJF has historically been fire (Burrows *et al.* 1995) and the dominant overstorey species both have the ability to resprout from epicormic and lignotuberous buds.

2.3.2 Site selection

Following the 2011 drought-induced die-off event, twenty die-off patches were randomly selected from 236 patches identified during an aerial survey of the drought affected forest (Matusick *et al.* 2013). The 20 patches (Figure 2.1) with survey plots established spanned areas of 0.37 to 16.8 ha. These patches were delineated according to canopy die-off, with >70% of crown die-off considered a drought die-off patch, as outlined in Matusick *et al.* (2013). That is, most tree crowns were dying or recently killed on affected plots, including 74 % (±3 %) (mean [±SE]) of all stems that were living prior to the collapse, as opposed to only 11 % (±2 %) in paired control plots (Matusick *et al.* 2013). The 20 patches initially established were visited four times, and a subset of 12 were visited five times following the initial observations of crown die-off (3, 6, 16, and 26 months post-event). Sampling events were chosen to document the initial damage and response following the first winter rains as well as response following subsequent summer drought periods (Matusick *et al.* 2013; Matusick *et al.* 2016).

At each of the 20 patches, three plots were randomly established within the delineated affected patch and three plots 20 m outside the drought-affected boundary in ‘healthy’ forest (giving a total of 120 plots, 60 inside the drought-affected patches, and 60 outside). The close proximity of plots meant that topography, soil type and fire history did not vary, thereby allowing for direct, straight-forward estimation of impact.

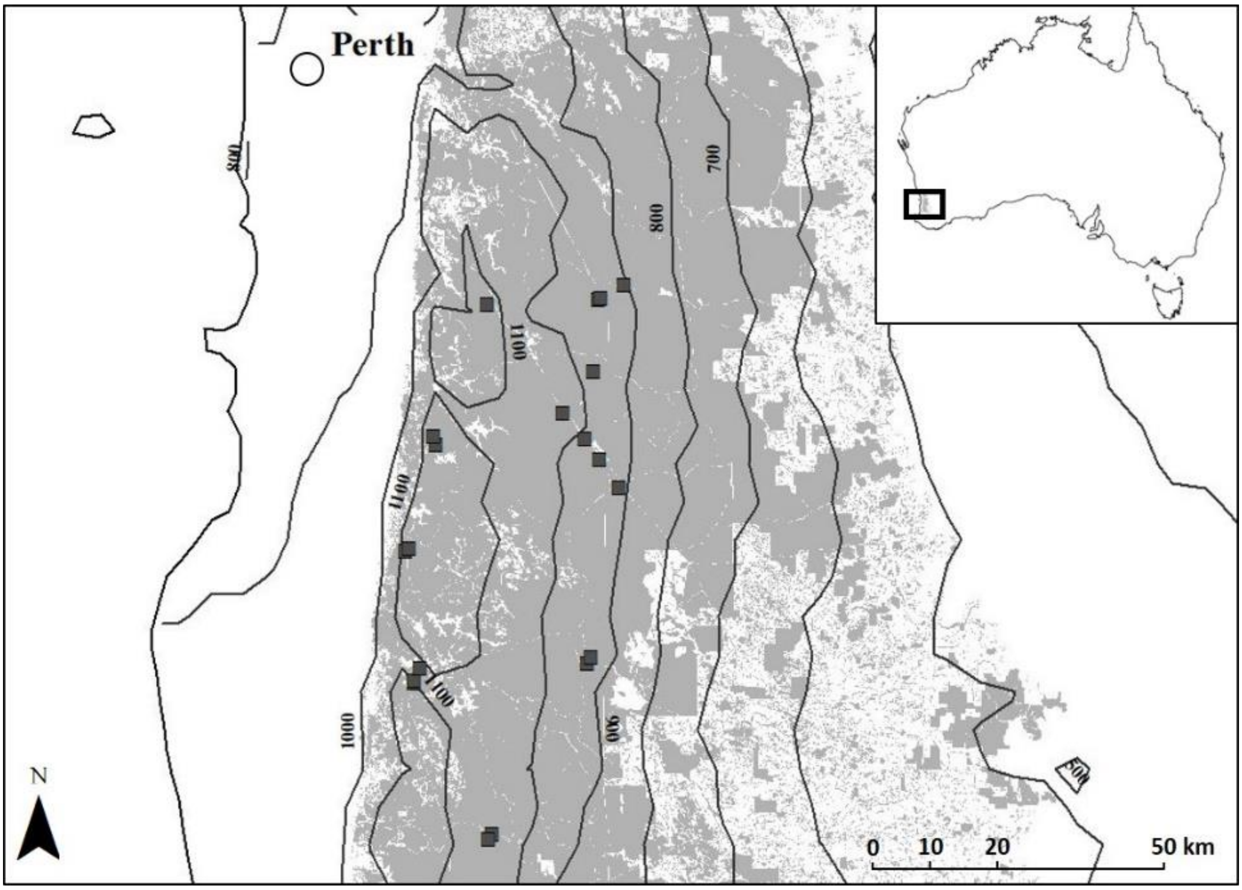

Figure 2.1 Location of the 20 field sites (dark grey squares) in the Northern Jarrah Forest (light grey), southwestern Australia. Isohyets illustrate the rainfall gradient from east to west.

2.3.3 Plot measurements

At each of the 120 plots, a stand assessment was completed of the overstorey, understorey live vegetation and surface fuels. A plot radius of 6 m was used to sample individuals of >1 cm diameter at breast height (DBH). These individuals were identified to species and were measured for DBH, live height and crown health class. The crown health class score, described by Worrall *et al.* (2008), and used by Matusick *et al.* (2013) and (Ruthrof *et al.* 2015), ranged from 1 to 4, with 1 signifying healthy trees, characterised by predominately green turgid foliage, 2 signifying dying trees, characterised by predominately dry and discoloured foliage, 3 signifying recently killed trees, characterised by predominately red and dead foliage, and 4 signifying long dead trees, characterised by a lack of leaves, fine twigs, and the presence of sloughing bark (Matusick *et al.* 2013; Ruthrof *et al.* 2015; Matusick *et al.* 2016). This tree survey method was carried out at 0, 3, 6, 16, and 26 months post drought die-off. Time 0 is a derived measure from the initial measurement at 3 months, given that trees impacted by the drought retained their symptomatic foliage, which was wilted, discoloured and dead (Matusick *et al.* 2016). At 6 and 16 months post-drought die-off, affected trees were assessed for resprouting to assess partial bole mortality. The presence, number, and height of epicormic sprouting was used as an indicator to determine individuals that had suffered partial bole mortality. After 26 months, these measurements were not repeated because vigorous resprouting made tracking individual tree sprouts unreliable (Matusick *et al.* 2016). No effort was made to estimate the proportion of individual stems that were dead in weakly resprouting trees. For the purposes of this study, partial mortality refers to individuals that have suffered severe canopy dieback and have epicormically resprouted on the bole.

2.3.4 Biomass and carbon calculations

Above ground biomass was estimated for each stem using previously published allometric equations (Hingston *et al.* 1980; Grierson *et al.* 2000). These equations relate DBH to dry weight (DW) of that individual (Table 2.1). Carbon content was calculated as 50% of the dry weight (Gifford 2000).

Table 2.1:Species and corresponding allometric equations relating DBH (cm) to dry biomass (kg) for plots in the Northern Jarrah Forest investigating drought-induced forest die-off, southwestern Australia.

Species	Equation	Reference
Eucalyptus marginata	ln(DW) = -3.680 + 2.84 ln(DBH)	Hingston *et al.* (1980)
Corymbia calophylla	ln(DW) = -3.370 +2.74 ln(DBH)	Hingston *et al.* (1980)
Banksia grandis	ln(DW) = -2.26 + 2.5 ln(DBH)	Grierson *et al.* (2000)
Allocasuarina fraseriana	ln(DW) = 3.57 + 2.68 ln(DBH)	Grierson *et al.* (2000)

Total biomass was allocated into the tree components (foliage, twig, branch, bark, and bole) according to published proportions (Hingston *et al.* 1980; Grierson *et al.* 2000). Individual trees measured during the field assessment included both healthy and drought-affected trees which had experienced partial mortality. Partial mortality entailed a spectrum of impacts on trees and tree components; therefore, it was necessary to quantify impacts with field-based techniques (observation of canopy impact, bole death, resprouting extent) as well as literature-supported approaches to fractionate pools (estimation of live and dead fractions from allometric equations and similar studies; i.e. Campbell *et al.* 2007; Gordon *et al.* 2018; Collins *et al.* 2019). To account for loss of foliage, fine branches and aerial decay, each component was adjusted according to its health score (Table 2.2, Equation 1). Dead standing carbon biomass was calculated as the remaining biomass following the live biomass corrections (Table 2.2, Equation 2). It was assumed that there was no substantial fragmentation of dead material, and all dead biomass was retained in the canopy and underwent aerial decay only.

Table 2.2: Biomass corrections for each of the biomass component for trees in the Northern Jarrah Forest study sites, southwestern Australia. Values are presented as a live proportion of each class.

Biomass component	Crown Mortality score			
	1	2	3	4
Foliage	1	0.5	0.15	0
Twig	1	0.6	0.2	0
Branch	1	0.7	0.3	0
Bark	1	1	0.75	0
Bole	1	1	0.75	0

The total live and dead carbon composition of an individual was calculated using the crown health rating, which corresponds to a specific biomass correction (Table 2.2). Summing each component yielded dry weight of biomass. which was reduced by 50% for carbon content (Equation 1; Gifford, 2000).

Equation 1 $$\boldsymbol{T_{liveC}} = \sum(\boldsymbol{L_{corr}} \times \boldsymbol{DW_{comp}}) \times \mathbf{0.5}$$

Where L_{corr} is the correction for the respective biomass component (based on health score) and DW_{comp} is the dry weight for the component derived from Hingston *et al.* (1980) and equations in Table 2.1. Total individual live carbon (T_{liveC}) was calculated by summing each live component dry weight multiplied by its relative correction value, multiplied by 0.5 (Equation 1).

$$\text{Equation 2} \qquad \boldsymbol{T_{deadC} = (\sum\ (1 - L_{corr}\ ) \times DW_{comp})\ ) \times 0.5)}$$

Dead carbon (T_{deadC}) was calculated by using the inverse of the live correction of Equation 1 to determine the weight of biomass to be allocated to the dead carbon pool (Equation 2). Once the individual carbon content was determined, total carbon was calculated for each plot and averaged for condition (die-off vs control) at each site, then scaled to tonnes per hectare.

2.3.5 Statistical analyses

The overarching aims of this study were (1a) to quantify how stand attributes (density, basal area) varied following die-off, and (1b) to quantify the effect of drought on live and dead standing carbon stocks across multiple visits following die-off, (2) quantify initial regrowth across all above ground carbon components. Impact and early response were quantified five times over 26 months, total carbon and basal area was tested using one-way analysis of variance and change over time by pool type using a mixed model analysis. All data analyses were carried out using R (R Core Team 2014) with the lme4 package (Bates *et al.* 2014) and data visualisation with ggplot2 (Wickham 2011). In all cases, means and 95% confidence intervals are reported and a lack of overlap of the mean with adjacent confidence intervals was interpreted as evidence for a statistical difference between groups, while asymmetrical overlap of means (intervals overlap one mean but not the other) was interpreted as suggestive evidence of a statistical difference between groups (Ramsey and Schafer 2012).

Basal area was analysed across visits to detect stand level changes to structure. Changes in basal area were tested with a one-way analysis of variance, with Tukey’s multiple comparison tests used to reveal changes over time. Test assumptions (homogeneity of variance and normality of residuals) were checked visually using histograms and residual plots, and no violations were detected.

Given that the experimental design included repeated measure of plots over time and plots were nested within site, a mixed effects model structure was implemented. Random effects were assigned to plot and site, and stand attributes such as density, basal area and drought impact were fixed effects. The response variable was biomass in tonnes per hectare and was analysed for stem density, live and dead carbon. Model structure consisted of a two-way interaction between time since die-off (TSD) and drought impact (control vs die-off).

Prior to analysis, the covariates were assessed for outliers and collinearity. There were only two covariates (drought impact, and time since die-off) and no issues with collinearity were evident. Model residuals were examined graphically to ensure model assumptions were met; no violations were detected.

The same method was used to analyse differences in proportional mortality at the die-off and control plots over time (that is, time since die-off). However, this model used the binomial distribution given the nature of the data.

2.4 Results

2.4.1 Impact of die-off

The impact of the drought-induced die-off was evident in all stand characteristics six months following the event (six months since die-off, TSD6). Six months following the drought event, live basal area in die-off plots decreased and remained significantly lower than control plots (23.40 vs 41.19 m^2 ha^{-1}, TSD6; $F_{8,483}$= 5.29, p= 0.041, Table 2.3). Approximately 38% (8.97 m^2 ha^{-1}) of the remaining live basal area in die-off plots consisted of individuals that had suffered partial mortality. Live stem density also decreased significantly at six months (t= 3.11, p<0.01,Figure 2.2). Mean proportional stem mortality levels in die-off plots (0.39±0.07) also climbed significantly six months following the event and remained elevated relative to control plots (0.17± 0.06, z = 4.55, p<0.001, Figure 2.3). Within die-off plots, proportional mortality peaked at six months and then declined somewhat at the TSD16 and TSD26 visits ($p = 0.120$; Figure 2.3) as some trees resprouted over the intervening growing season.

The changes found in stand characteristics six months following the event were mirrored in the live and dead carbon pools. Total (live + dead) carbon storage between die-off and control plots was not significantly different at any of the visits following the disturbance ($F_{2,157} = 1.33$ p =0.27). However, the relative size and fluctuations of live and dead pools varied substantially across time and plot type (Figure 2.4). Three months following the disturbance, dead carbon significantly increased in the die off plots compared to the first visit (+20.2 ± 19.33 t ha^{-1}, $t = 2.05$, $p<0.05$, Table 2.4). At six months following the disturbance, dead carbon increased further in the die-off plots compared to the initial visit (+49.3 ± 19.32 t ha^{-1}, $t = 5.01$, $p<0.001$, Table 2.4) and with a corresponding decrease in live carbon (-49.3 ± 25.3 t ha^{-1}, $t = -3.82$, $p<0.001$). Within die-off plots, the largest contributor to the decrease in live carbon of 49.3 t ha^{-1} (95% CI=25.34) six months post drought ($t = -3.82$, $p<0.001$) was from bole-stored carbon (Figure 2.5).

Table 2.3: Mean live basal area ($m^2\ ha^{-1}$) at die-off and control plots in the Northern Jarrah Forest, southwestern Australia across five visits. Ninety-five percent confidence intervals (CI) are presented in brackets after each estimate.

Time Since Die-off (months)	n sites	Live		Partial mortality		Complete mortality	
		Control (CI) $m^2\ ha^{-1}$	Die-off (CI) $m^2\ ha^{-1}$	Control (CI) $m^2\ ha^{-1}$	Die-off (CI) $m^2\ ha^{-1}$	Control (CI) $m^2\ ha^{-1}$	Die-off (CI) $m^2\ ha^{-1}$
0	20	41.46 (5.56)	36.78 (8.73)	-	-	-	-
3	20	41.46 (5.56)	36.78 (8.73)	-	-	-	-
6	20	41.19 (5.46)	23.40 (5.58)	3.58 (2.58)	8.97 (3.48)	3.20 (2.57)	18.81 (6.46)
16	20	41.19 (5.47)	29.48 (6.40)	0	8.85 (3.86)	3.14 (2.53)	12.55 (4.96)
26	12	44.30 (8.28)	28.47 (7.70)	-	-	-	-

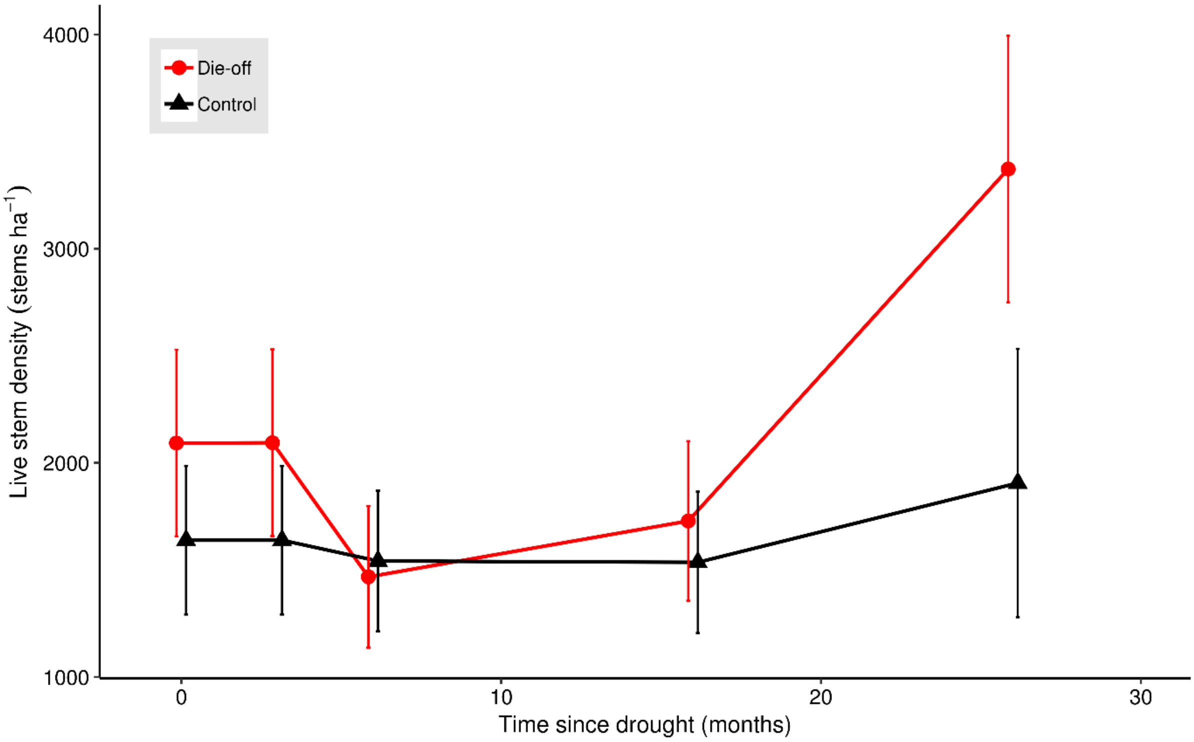

Figure 2.2 Mean live stems per hectare for die-off (circles) and control plots (triangles) in the Northern Jarrah Forest, southwestern Australia across five visits. Error bars represent the 95% CI of the mean

2.4.2 Initial regrowth

In subsequent visits following the significant decline in live carbon, early regrowth response was observed (Figure 2.2). Early regrowth was captured as the live stem density increased in die-off plots to a level that was significantly higher at TSD26 than TSD0 levels (t = 3.77, p<0.001, Figure 2.2). Live stem density did not change across all the visits in the control plots (Figure 2.2) with broad overlap of 95% confidence intervals for all visits.

Live and dead carbon pools were relatively stable from six to 26 months post die-off (Figure 2.4). From six months onwards, regrowth from resprouting trees contributed a small amount to live carbon; however, resprouting of previously ‘dead’ individuals drove an increase in bole live carbon when comparing TSD3 and TSD6 visits (protracted epicormic resprouting above breast height led to an allocation of a proportion of the bole mass the live pool; Figure 2.5). Resprouting and subsequent growth led to the recovery of the more labile pools (foliage, twig, and branch) to close to pre-drought levels by TSD26 (Figure 2.6). At the 6-month visit, the labile biomass components branch, twig, and foliage were reduced to 42%, 53%, and 46% of their initial pre-drought mass, respectively (Figure 2.6). Foliage recovered to 82.4% of its original mass by the 26-month visit, while branch and twig pools recovered to 88% and 82.1% of their first visit carbon mass respectively (Figure 2.6).

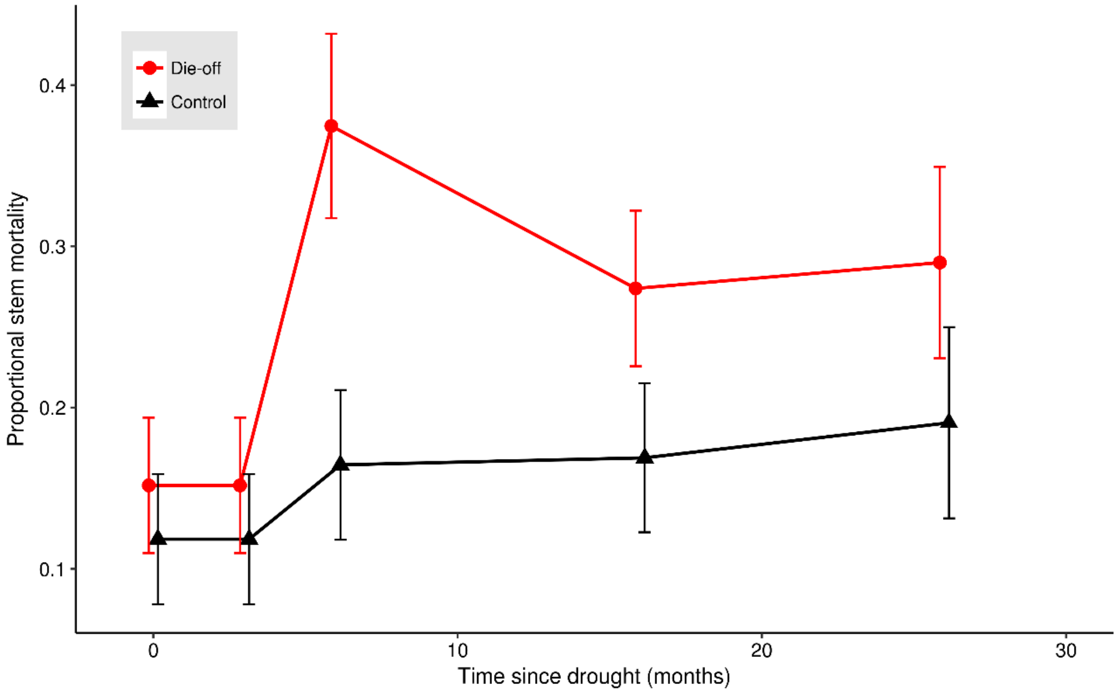

Figure 2.3 Mean proportional mortality of die-off (circles) and control (triangles) plots in the Northern Jarrah Forest, southwestern Australia, across the five visits. Error bars represent the 95% confidence intervals of the mean.

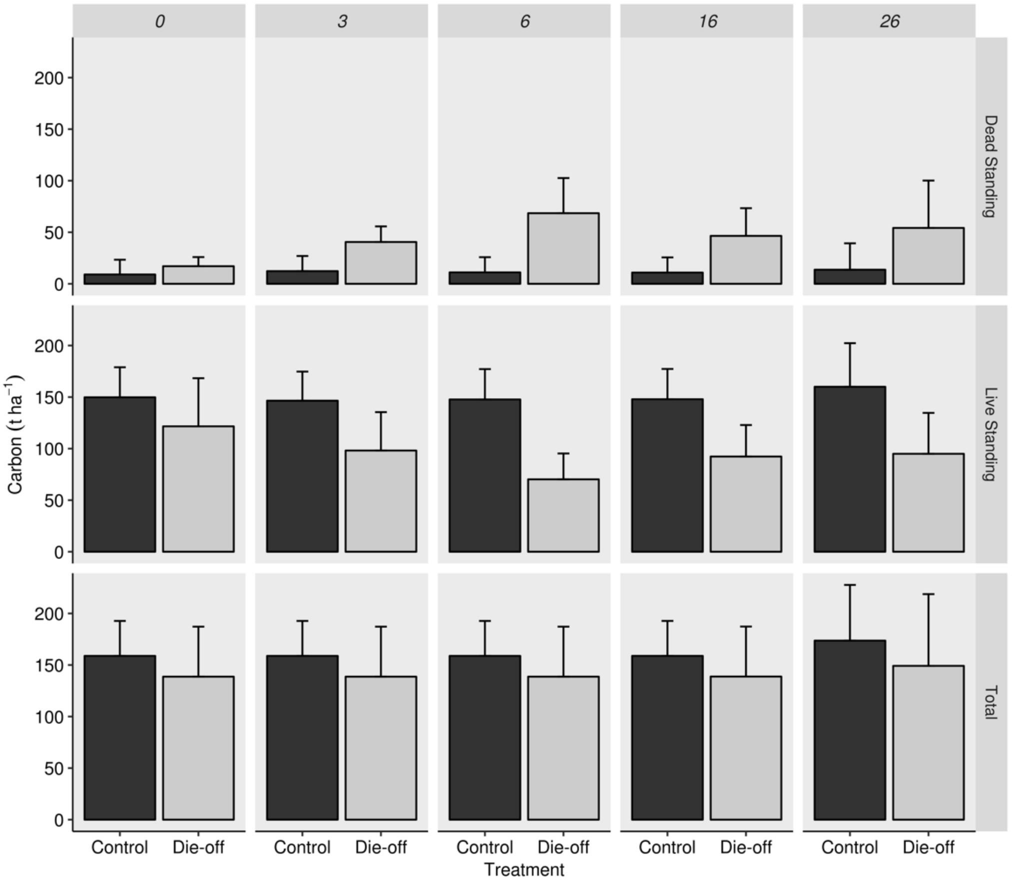

Figure 2.4 Mean dead standing (top) and live standing (middle) and total (bottom) carbon (t C ha^{-1}) for both control and die-off plots across all visit times (months) since die-off (TSD0, 3, 6, 16, 26) in the Northern Jarrah Forest, southwestern Australia. Values represent the means of 120 plots across 20 sites (60 plots per treatment), and bars represents 95% confidence intervals of the mean.

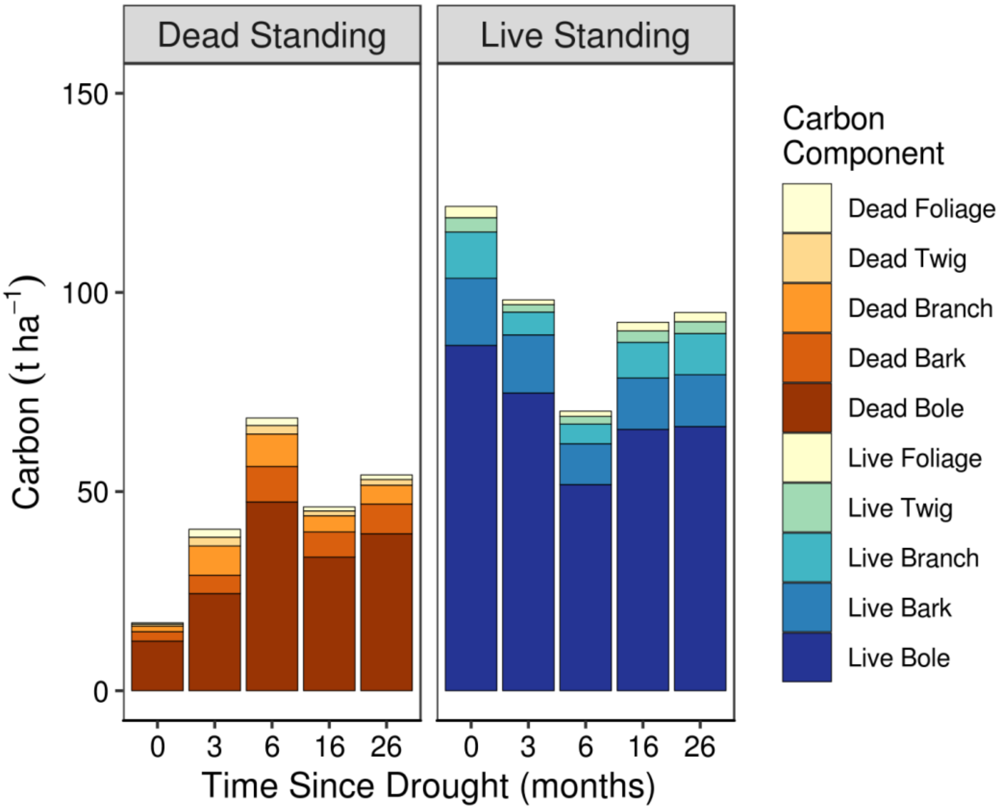

Figure 2.5 Dead and live standing carbon (t C ha^{-1}) for carbon components for drought-induced die-off plots in the Northern Jarrah Forest, southwestern Australia, across all visits (time since die-off).

Table 2.4: Results from a linear mixed effects model used to quantify carbon dynamics following a drought die-off event in the Northern Jarrah Forest, southwestern Australia. Models tested differences in live carbon, dead carbon, stems per hectare and proportional stem mortality in the different treatments (die-off and control plots) and across the visits (time in months since drought, TSD). Estimates are the difference from the initial value at control plots at the first visit (TSD0), with 95% confidence intervals of the estimate in brackets.

Coefficients	*Response*											
	Live carbon (t ha^{-1})			Dead carbon (t ha^{-1})			Stem density (stems ha^{-1})			Proportional stem mortality		
	Estimate (CI)	*t-value*	*p-value*	*Estimate (CI)*	*t-value*	*p-value*	*Estimate (CI)*	*t-value*	*p-value*	*Odds Ratio (CI)*	*z-value*	*p-value*
Intercept	150(29.4)	9.99	**<0.001**	9.02 (17.7)	1.00	0.32	1640 (369)	8.70	**<0.001**	0.07 (0.04)	-11.8	**<0.001**
Die-off	-28.2 (41.5)	-1.33	0.18	8.05 (24.3)	0.65	0.51	453 (513)	1.73	0.08	1.9 (1.18)	2.62	**<0.010**
TSD3	-3.28 (17.9)	-0.36	0.72	3.28 (13.7)	0.47	0.76	0.00 (235)	0.00	1.00	1 (0.35)	0.00	1.00
TSD6	-2.07 (17.9)	-0.23	0.82	2.07 (13.7)	0.30	0.78	-97.3 (361)	-0.81	0.42	1.79 (0.57)	4.09	**<0.001**
TSD16	-1.86 (17.9)	-0.20	0.84	1.88 (13.7)	0.27	0.79	-103 (235)	-0.86	0.39	1.82 (0.58)	4.22	**<0.001**
TSD26	7.45 (21.3)	0.69	0.49	-0.21 (16.2)	0.02	0.99	188 (279)	1.32	0.19	2.2 (0.81)	5.00	**<0.001**
Die-off TSD3	-20.2 (25.3)	-1.56	0.12	20.2 (19.3)	2.05	**<0.05**	1.47 (332)	0.01	0.99	1 (0.46)	0.00	1.00
Die-off TSD6	-49.3 (25.3)	-3.82	**<0.001**	49.3 (19.3)	5.01	**<0.001**	-527 (332)	-3.11	**0.002**	2.26 (0.94)	4.55	**<0.001**
Die-off TSD16	-27.4 (25.3)	-2.12	**<0.05**	27.5 (19.3)	2.79	**0.005**	-260.8 (332)	-1.54	0.12	1.33 (0.56)	1.56	0.120
Die-off TSD26	-53.4 (30.11)	-3.48	**<0.001**	36.1 (22.9)	3.09	**0.002**	1020 (395)	5.07	**<.001**	1.22 (0.58)	1.03	0.300

Model constructed from 552 observations, 20 unique sites, with 120 unique plots over 5 visits

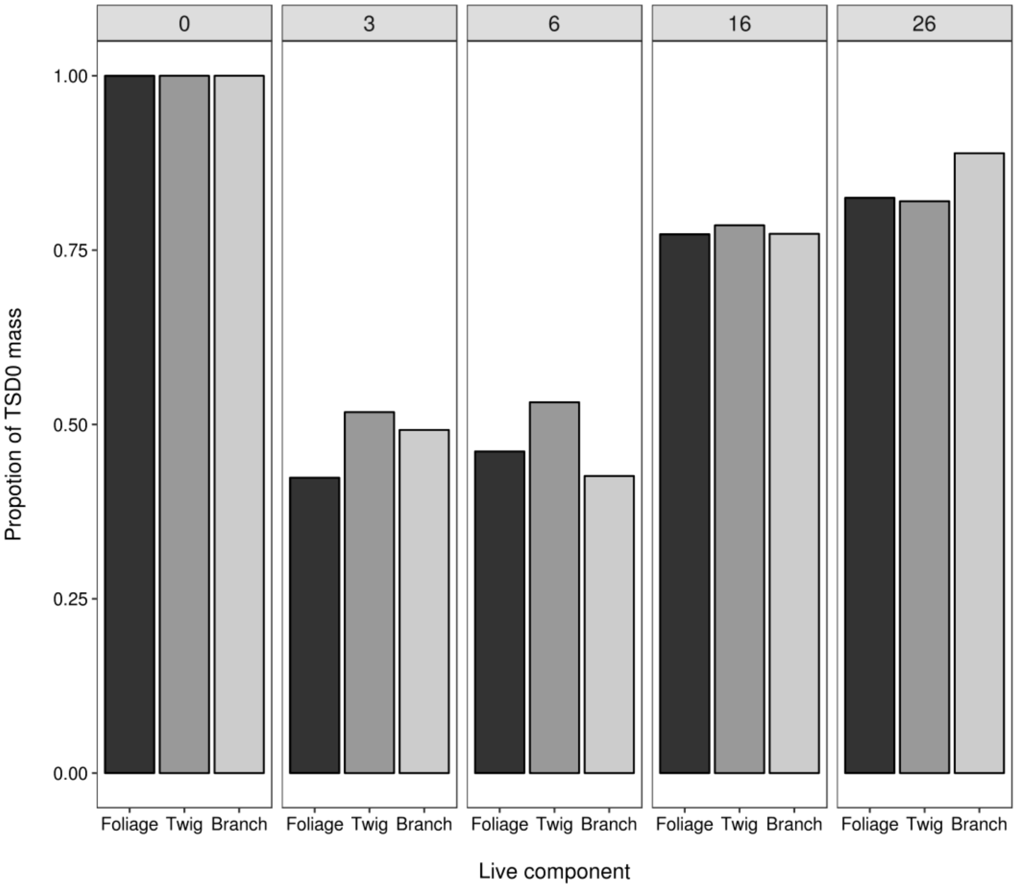

Figure 2.6 Mean proportion of initial live biomass components (foliage, twig, branch) in die-off plots in the period up to 26 months following the drought event in the Northern Jarrah Forest, southwestern Australia. Values are expressed as the proportion of the TSD0 (time in months since die-off) mass. TSD0 is included for reference.

2.5 Discussion

This study quantifies carbon dynamics following a drought-induced forest die-off in a resprouting Australian eucalypt forest. It builds on the work of other drought-induced die-off carbon studies (Fauset *et al.* 2012; Ma *et al.* 2012) by showing that although the total carbon storage did not differ over time following the die-off event, the composition of the carbon pools shifted markedly with substantial dead carbon contained in standing trees suffering complete and partial mortality. Such increases in dead carbon are in contrast to Fauset *et al.* (2012), who reported post-drought increases in above ground biomass (that is, carbon) in a Ghanaian tropical forest due to shifts in tree species. The impacted forest underwent a structural state change, from a tall, open forest to a shorter, denser, closed forest (Matusick *et al.* 2016) but without changes in tree species composition (Ruthrof *et al.* 2015). Stem mortality occurred by six months post die-off and resprouting of these trees ensued with regrowth of both basal and epicormic shoots from six to 26 months post die-off. Overall, the forest transitioned from large trees to short, multi-stemmed individuals, and our study has shown that this is clearly reflected in its carbon sequestration potential.

The die-off driven carbon transformation from live to dead pools was substantial (49.3 t C ha^{-1}). Subsequent biogenic emissions and decay rates (Gunn *et al.* 2012) will be contingent on a range of factors including standing versus down, snag fragmentation rates, climatic setting, material size and wood density, and biotic agents of decay. Suspended, aerial dead wood (dead trees, portions of trees) decays more slowly (lower annual emissions) than downed wood on the forest floor in contact with the soil that experiences greater moisture content and decomposition rates (Harmon *et al.* 2011). The rate of snag fragmentation (recruitment of dead material from suspended to down) is undocumented for the dominant tree species in this study. However, using the knowledge available regarding the mechanisms that influence snag fragmentation rate (climate, wood density, and biotic agents), it can be assumed that snag fragmentation and fall rate will be more gradual than that of tropical and boreal forests. Climate plays a large role in snag decomposition rate, with decay rates decreasing from the equator towards the poles (Cooper 1983). Warm moist environments result in faster rates of wood decay, and the Mediterranean climate (cool wet winters and warm dry summers) of southwestern Australia, therefore, do not provide optimal conditions for wood decay. In general, in a tropical forest almost all the woody material may decay within 10 years (Cooper 1983). In contrast, the turnover time for *Eucalyptus* species in a temperate sclerophyll forest can range from seven (e.g. *E. regnans*) to 375 years (e.g. *E. camaldulensis* and *E. tereticornis)* based on climate setting (Mackensen and Bauhus 1999). The initial wood density of a species will also contribute to decay rate, with higher wood densities decaying slower than lower initial wood densities (Mackensen and Bauhus 1999). Climatic conditions coupled with high wood density of the species in this study, *E. marginata* (0.67g cm^3) and *C. calophylla* (0.65g cm^3), dead individuals may remain standing for decades before being added to the coarse woody debris pool and remain in the stand and ecosystem as decaying wood for a century or more in the absence of fire. This suggests that the loss of carbon (decay and subsequent heterotrophic respiration of dead wood) from the NJF may not translate to total carbon storage loss at the same rate as other forest types more commonly studied. Thus, it follows that in the absence of disturbance the total carbon storage in the die-off sites could increase as new growth counteracts the carbon lost from biogenic emissions of dead material. However, with a drying climate (Bates *et al.* 2008) regrowth is unlikely to grow to the extent of the individuals that died. The post-disturbance regrowth is also more likely to have a severe fire occur within it (Zylstra 2018), further reducing carbon stored in both live and dead pools. A combination of these two factors are likely to prevent these stands from regaining or increasing carbon storage.

Fluctuations in live and dead carbon storage have implications on forest structure and future carbon sequestration capacity by potentially putting an upper limit on the amount of carbon a forest stand can fix (Ma *et al.* 2012). This study quantified live carbon loss and initial regrowth in die-off plots and found significant losses to live carbon occurred six months following the event. However, the resprouting nature of the dominant tree species in this study, *E. marginata* and *C. calophylla,* resulted in many large trees resprouting at 16 months resulting in partial mortality, which permitted rapid regrowth of the same individual and live carbon being ‘regained’ in the system. The loss of canopy also allows plants to compete for available resources, potentially elevating regrowth and subsequently increasing live carbon in smaller stems. These results are consistent with Zeppel *et al.* (2015) who reported the ability of resprouters to avoid complete mortality, through partial mortality, and withstand drought, indicating that the impact of drought stress in resprouting forest systems may be lower than in other forests dominated by nonsprouting species (i.e. conifers).

It has been suggested that even in the most rapidly growing forests, another disturbance (drought or fire) may occur before stands have recovered similar sized individuals and forest structure (Adams *et al.* 2009; Allen *et al.* 2015; Frank *et al.* 2015). Furthermore, post-disturbance regrowth forests have been linked to an increase in the likelihood of occurrence, severity, or extent of another disturbance, particularly fire, as the structure of the regrowing forest is growing closer to the surface and more likely to be ignited (Kitzberger *et al.* 2012; Kitzberger *et al.* 2016; Zylstra 2018). The NJF of southwestern Australia is considered a frequent fire forest, unlike forests that naturally experience infrequent stand replacing disturbances. Many of the stands that experienced drought-induced die-off are likely to be burnt by either wildfire or planned burns before they have completely recovered. Given that the drought- affected patches in this study were comprised of many younger, multiple, resprouting stems (Matusick *et al.* 2016), these younger/shorter individuals are more susceptible to mortality during a fire, or future drought event, as they do not have thick bark to withstand fire events (Abbott and Loneragan 1986; Pausas 2015). Thus, the already stressed and drought affected mature individuals may not have the resilience to resprout again (Galiano *et al.* 2012; Fairman *et al.* 2019) which would result in large losses in carbon storage and future sequestration potential. In a study of *Quercus ilex* forest in Spain, Galiano *et al.* (2012) suggested that progressive depletion of carbon reserves through repeated drought events may lead to loss of resilience in resprouting species. Therefore, these systems may be at an even greater risk of future carbon loss because large trees have undergone canopy retraction (partial mortality) and resprouted epicormically, and resulting new small stems lack the thick bark required to survive even a low intensity fire (Abbott and Loneragan 1986). Thus, it follows that the resilience of these stands has been compromised compared with the surrounding vegetation.

The distribution of carbon (recalcitrant soil fractions or live bole wood versus labile live pools or dead decomposing pools) within a forest stand will influence future carbon storage and sequestration. Partial mortality of large individuals, and the increase in the number of small individuals, may temporarily buffer live carbon loss from the system (Zeppel *et al.* 2015). In our study, six months after the drought event, a reduction in live carbon was recorded, which was attributed to the movement of bole-stored carbon from the live to dead carbon pool. The slight rebound in live carbon following the initial drop can be mainly attributed to the large individuals (DBH>30cm) resprouting in the intervening period of six to 26 months when originally scored as dead at six months. This was also highlighted in the labile pools (foliage, twigs, and branches), which nearly recovered to pre-die-off levels by 26 months after the drought event. Mean foliage, twig and branch biomass were approximately 82.5, 82.0 and 88.9% of pre-drought levels respectively. Fluctuations like this highlight the significance of large trees in this forest ecosystem. Bole-stored carbon, and the transition from dead to live, plays a substantial role in the structure and carbon storage capacity of these stands. However, the rapid return of labile pools in this study highlights that partial bole mortality in resprouting forests may lead to leaf area recovery and return to pre-drought-carbon storage levels in a shorter time scale compared to coniferous forests.

The potential for live carbon recovery is largely dependent on the pattern of disturbance in the future. Given the fire frequency and climatic predictions for southwestern Australia that include an increase in fire risk (Pitman *et al.* 2007), it is likely that subsequent disturbances will occur before complete forest recovery. Indeed, wildfire and planned (prescribed) burning recently have impacted the sites reported in this work. Subsequent disturbances will act to substantially reduce total stand carbon storage in two ways; firstly, the drought affected patches studied here are made up of younger/shorter individuals (Matusick *et al.* 2016) which are more susceptible to mortality during a fire or future drought event than larger, extant individuals. Secondly, once dead trees eventually fall and are converted to coarse woody debris, they are more likely to be consumed by fire, even if it takes multiple fire events to be completely consumed (Abbott and Loneragan 1983; Donato *et al.* 2016). Both pathways transition away from live carbon sequestration as well as an eventual reduction in dead carbon storage of die-off affected stands.

3 Above-ground carbon dynamics following wildfire in a eucalypt forest[2]

3.1 Abstract

Forests are an integral component of the global carbon cycle and climate change mitigation efforts. Fire is a predominant disturbance factor in many forests and is likely to increase in severity with climate change, and thus affect forest carbon storage and dynamics. Whereas wildfire can be stand-replacing in a variety of forest types, eucalypts which typically experience frequent fire (5-20 years), most commonly resprout after fire thereby conserving most of their live carbon stocks. Pyrogenic carbon emissions and carbon pool transformations were quantified following a severe wildfire in a regrowth eucalypt forest in southwestern Australia with mean above ground carbon storage of 69-104 t C ha^{-1}. The wildfire induced pyrogenic carbon emissions of between 10 and 21 t C ha^{-1}, which corresponds to 5.5-12.2% of average pre-fire carbon density. These values were comparable to results from forest with a frequent, low-intensity regime and infrequent high-intensity fire regimes. Crown fire in this study only partially killed many trees, whereas fires in forests that experience infrequent fire high intensity fire have higher rates of live standing carbon loss as they typically do not resprout. This has implications for the recovery of carbon stocks through protection of existing carbon stocks in standing trees, as well as differences in the amounts of dead biomass, and replenishment of carbon through regrowth from existing trees and seedlings, rather than primarily seedlings. Whilst many trees underwent partial mortality, there were high rates of top

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[2] This chapter has been prepared to be submitted to *Journal of Geophysical Research*

kill (individuals resprouting basally or fire killed). The projected increase in fire severity with climate change may lead to permanent reductions in forest carbon storage, particularly when combined with other climate induced forest changes such as an increased incidence of drought and heat-related mortality.

3.2 Introduction

Forests are an integral component of the global carbon cycle and climate change mitigation efforts (Canadell and Raupach 2008). Forests cover nearly 30% of earth's land mass and contribute significantly to the 3.8 Gt C yr^{-1} (for 2017: Le Quéré *et al.* 2018) sequestered by terrestrial ecosystems which in turn equates to ~33% of current anthropogenic emissions (Grassi *et al.* 2017; Keenan and Williams 2018; Kirschbaum *et al.* 2019). Disturbance events, such as deforestation (Canadell and Raupach 2008), drought (Harper *et al.* 2009a), storms (Ziemblińska *et al.* 2018), and insect outbreaks (Kurz *et al.* 2008a), along with decomposition of dead biomass can release previously stored carbon back into the atmosphere (Galik and Jackson 2009).

Fire has been recognised as having a particularly large potential impact on forest carbon stocks (Campbell *et al.* 2007; Bowman *et al.* 2009; Keith *et al.* 2014). Fire as a forest disturbance leads to a loss of biomass and release of carbon previously stored in various forest carbon pools, whether it be in the form of standing trees, debris, litter, or soil organic matter (Bowman *et al.* 2013; Volkova and Weston 2013). Globally, burning of biomass (via wildfire and planned burns) between 1996 and 2016 was estimated as a source of approximately 2.2 Gt C yr^{-1} (Van Der Werf *et al.* 2017), and is therefore a key component of the global carbon cycle (Bowman *et al.* 2009; Pan *et al.* 2011; Zhang *et al.* 2018). However individual wildfire events emit substantial C emissions, regardless of the historical fire regime or forest type. For example Campbell et al. (2007) quantified the carbon emissions from a 200,000 ha wildfire in 2002 in a mixed conifer forest of southwestern Oregon with an estimated 3.8 Mt C (~19 t C ha^{-1}) released. Emissions from a series of wildfires in Portugal that burnt over 286,000 ha in 2003 were estimated to have reached 2.01 Mt C (~7.02 t C ha^{-1}) (Rosa *et al.* 2011; Chiriacò *et al.* 2013) and in Victoria, Australia, 3.9 Mt C (40-58 t C ha^{-1}) was estimated to have been released from a fire that burnt 450 000 ha of temperate, tall wet eucalypt forest (Keith *et al.* 2014). Forest fires are predicted to increase in severity, duration, and frequency for fire prone regions with a changing climate (Moritz *et al.* 2012; Seidl *et al.* 2017; Hoegh-Guldberg *et al.* 2018). Quantifying the effect that fire, and particularly fire in a drier and hotter future, has on forest carbon stores is key to understanding the stability and persistence of forest systems as global carbon sinks (Williams *et al.* 2016).

Although wildfire is considered, apart from deforestation, the most common disturbance factor and a major influence on the vegetation composition and structure of the resprouting eucalyptus forests of Australia (Bond and Keeley 2005; Bond *et al.* 2005; Bowman *et al.* 2009), the implications of wildfire for carbon dynamics are poorly understood in these ecosystems. Resprouting enables large trees to survive fire events throughout their lifespan. It follows that the long-term carbon losses from wildfire events in resprouting forests may not be as substantial as those experienced in other forest types, which typically experience large rates of mortality amongst the mature individuals (Keith *et al.* 2014; Volkova *et al.* 2014). In a system where climate and fire regimes are in equilibrium, the atmospheric carbon emissions of fire and subsequent uptake by surviving vegetation and regeneration are balanced (Bowman *et al.* 2009). However, with a changing climate, drought-induced mortality, a lengthening of fire weather seasons and an increased frequency of long fire weather seasons globally (Jolly *et al.* 2015; Miller *et al.* 2019), these forests may not be able to continually resist carbon losses from wildfire and will undergo changes to structure (Fairman *et al.* 2019), and carbon storage dynamics (Kirschbaum 2000). Fairman *et al.* (2019) reported the loss of resprouting ability in the temperate eucalypt forests of Victoria, south-eastern Australia, where repeated fires in short succession resulted in widespread mortality. It follows that these events may have both short- and long-term consequences on carbon storage and dynamics in those stands.

To help bridge this gap in knowledge regarding carbon dynamics following fire in a resprouting forest ecosystem, this chapter examines the carbon dynamics in a *Eucalyptus marginata* forest in southwestern Australia following a landscape-scale summer wildfire that occurred in January 2016 (Waroona Fire). The aim was to determine the consequences of the wildfire event by:

a) quantifying the pyrogenic carbon emissions from the affected forest,
b) determining the total and pool-specific carbon transformations across forest plots in areas with different wildfire severity.

This study thus quantifies pyrogenic carbon emissions and carbon pool transformations following a severe wildfire in a fire-prone Australian eucalypt forest and builds on previous forest disturbance and carbon studies (Campbell *et al.* 2007; Kurz *et al.* 2008a; Ziemblińska *et al.* 2018).

3.3 Methods

3.3.1 Study area

The Waroona Fire was ignited by lightning on the morning of the 6th January 2016 in open forest subject to bauxite mining. A combination of severe fire weather and steep inaccessible terrain made initial fire suppression unsuccessful. Fire development was further aided through the formation of multiple pyro-cumulonimbus clouds, with extensive spotting and further lightning ignitions (McCaw *et al.* 2016). The Waroona fire burnt an area of 69,165 ha, with 36,000 ha of native vegetation and the remainder including agricultural land, and rehabilitated bauxite mining sites (McCaw *et al.* 2016) (Figure 3.2). Rainfall for the year preceding the fire was 35% below the long-term average (1233 mm year^{-1}) and was the third lowest on record. The fire burnt through jarrah forest stands of varying litter age, these ranging between 6 and 30 years since last burning.

The Northern Jarrah Forest (NJF), the focal area within the Waroona Fire, is located in southwestern Australia (30.75-33.5 S and 115.8-117.8E) and covers an area of 1,127,600 ha (Havel 1975). The forest ranges from an open dry sclerophyll forest in the north to a tall, closed forest in the south (Dell and Havel 1989a). Across the forest system, deep weathering profiles have formed on Archaean granitic and metamorphic rocks (Gilkes *et al.* 1973) with a resultant range of infertile soils. The NJF has a Mediterranean type climate, with hot dry summers and warm wet winters with the majority of rainfall occurring between April and October, and a seasonal drought that may last between four and seven months (Gentilli 1989). There is a strong rainfall gradient across the forest, which ranges from >1100 mm yr^{-1} on the western edge to approximately ~700 mm yr^{-1} in the north east (Gentilli 1989). Since the mid 1970s southwestern Australia has undergone a 15-20% reduction in precipitation and a temperature (increase of 0.15 °C/decade: Liu *et al.* 2019b) It also experienced extremely low rainfall and high temperature events in 2010 and 2011 that impacted on forest survival (Ruthrof *et al.* 2018).

This study focusses on upland areas composed of a forest with *Eucalyptus marginata* Donn ex Sm. and *Corymbia calophylla* R. Br. K.D. Hill and L.A.S. Johnson co-dominant overstorey, and a midstorey composed of a mixture of *Banksia grandis*, and *Allocasuarina fraseriana*. The predominant disturbance agents in the NJF have historically been frequent fire and selective timber harvesting, with forest stands planned burnt on a fire return interval of 5 to 10 years (Burrows *et al.* 1995). The dominant overstorey species are both considered to be adapted to frequent fires via thick bark and the ability to resprout from both epicormic and lignotuberous buds (Abbott and Loneragan 1986; Pausas 2015).

3.3.2 Site selection and plot establishment

Following the fire, burn severity was observed to fall into two main categories; 1) severe surface fire with canopy scorch, and 2) crown fire with complete canopy consumption. Twenty sites were chosen within the forest area that had been burnt, with 17 containing paired plots in the two observed fire severities (a total of 37 plots). If both conditions were not present only a single plot was established (Table 3.1,Figure 3.2). Ten unburnt control plots were also established within 10 km of the fire boundary to ensure soil type, rainfall and stand composition and structure did not vary widely between burnt and unburnt areas.

Plots were established in a modified Forest Inventory and Analysis (FIA) sampling design (Bechtold and Scott 2005). Each plot consisted of four subplots, of variable radius, comprising a central subplot and subplots orientated at 0°, 120°, and 240° from the central subplot. The centre of each subplot was at least 35 m from the middle of the central subplot.

Table 3.1: Count of control (unburnt) and wildfire burnt plots in relation to the respective fire severity category and time since fire.

Time Since Fire (years)	Fire Severity				
	Control (unburnt)	Low	Mixed	Moderate	High
1-5	1	-	-	-	-
5-10	9	-	-	7	10
10-20	-	-	-	1	4
20-30	-	-	-	5	12
>30	-	-	-	-	1
Total	10	-	-	12	27

3.3.3 Plot measurements

At each plot a series of measurements was collected to quantify the pyrogenic carbon emissions from the fire event, as well as the transfer of carbon between the live and dead biomass pools within the stands. A stand survey was conducted 12 months following the fire event, in January 2017. This included a tree survey, an understorey/ shrub assessment, and transect measurements of forest floor fuels.

3.3.3.1 Tree survey

Trees were assessed within each of the subplots. To assess the impact of the fire on live and dead standing carbon pools data were collected from each stem to quantify the degree of mortality each stem had experienced. Individuals fell into categories of complete mortality (lack of resprouting), partial mortality (only bole resprouting), top kill (only basal resprouting), or live (resprouting in the canopy).

Tree size was assessed through diameter at breast height (DBH) and tree height. A rating system was developed to capture the loss of canopy from consumption or fire scorch: individuals that had experienced complete mortality were scored as 100, whereas minimally affected individuals were given lower scores corresponding to the proportion of original canopy that was lost. This measure was used to quantify mortality and the loss of canopy on every individual. Dead portions of the individual were then given a fragmentation score to account for pre-fire death and decomposition. Fragmentation categorisation of the previously dead material in the canopy was ranked from class 1-4 according to Harmon *et al.* (2011), and Woldendorp and Keenan (2005), where newly dead material is ranked 1 and long dead, rotten material is scored a 4.

Regrowth was quantified using a measure of resprouting vigour: individuals that had completely regrown canopy to pre-fire levels were scored 100, and completely dead individuals were scored a 0. To estimate the degree of partial bole mortality in burnt individuals, the presence and height of basal resprouts were recorded, as well as the height of the lowest epicormic sprout. The total height of resprouting was also measured.

The charring of each individual was also recorded and categorised based on a scoring system developed by Ryan (1982) with a 0 being no char, 1 is surface char, and 2 being deep charring. The overstorey species of the NJF do not possess stringy bark, which causes fire to scorch entire boles, thereby rendering scorch height measurements irrelevant.

3.3.3.2 Understorey/shrub assessment

The species, basal diameter of stems, and canopy dimensions of any perennial understory shrubs were recorded in each subplot.

3.3.3.3 Forest floor fuels transects

A planar intersect method was used to determine coarse and fine woody debris (CWD, FWD) loads within each of the plots (Brown 1971). Transects were established along intercardinal directions, originating from the centre subplot (NE, SE, SW, NW). Coarse woody debris (diameter >7.6 cm) was surveyed along four 50 m transects (200 m total per plot), while FWD was recorded on a smaller (15 m) section at the end of the same transect. Fine woody debris transects were further stratified by time-lag size classes (Fosberg 1970): 1h (0-0.6 cm) were recorded on the last 5 m, 10 h (0.61-2.5 cm) fuels on the last 10 m, and 100 h (2.5-7.6 cm) fuels on the last 15 m of each transect. All pieces of CWD and FWD were classified with a burn category, either surface or deep charring, and a decay category following Harmon *et al.* (2011). Decay is rated between 1 and 5. A piece at decay class 1 has all bark still intact with most twigs present and the wood is still hard, while a piece at decay class 5 is almost completely decayed, the sapwood is rotten, and any remaining material is easily broken apart.

To establish the amount of litter accumulation within each unburnt plot, ground sampling was undertaken on each debris transect. Along each transect, two 25 x 25 cm quadrats were used to collect all dead, non-attached material down to mineral earth. Thus, in total eight samples were taken from 10 plots, totalling 80 samples. In burnt plots, all litter was consumed and any material on the ground was considered post fire accumulation of litter. All leaf litter in burnt plots had clearly fallen from the canopy and therefore was allocated to aerial C pools (Figure 3.1).

Figure 3.1 Plot photos highlighting post fire conditions of a) high (canopy consumed) fire severity and b) moderate (canopy scorch) fire severity condition of plots measured in the Northern Jarrah Forest, south western Australia. Litter present in both fire severity categories was considered post fire fall.

3.3.4 Biomass and carbon transfer calculations

Above-ground biomass (AGB) was estimated for each tree and shrub using previously published allometric equations (Hingston *et al.* 1980; Grierson *et al.* 2000; Paul *et al.* 2015) (Table 3.2). These equations relate diameter at breast height (DBH; trees) or diameter 10 cm from the surface (D10; shrubs) to dry weight (DW) of that individual. Carbon content was calculated on the basis of 50% of the dry weight (Gifford 2000).

Table 3.2: Allometric equations for key species in the Northern Jarrah Forest, south western Australia, and associated reference.

Species	**Equation**	**Reference**
Eucalyptus marginata	$\ln(DW) = -3.680 + 2.84 \ln(DBH)$	Hingston *et al.* (1980)
Corymbia calophylla	$\ln(DW) = -3.370 +2.74 \ln(DBH)$	Hingston *et al.* (1980)
Banksia grandis	$\ln(DW) = -2.26 + 2.5 \ln(DBH)$	Grierson *et al.* (2000)
Allocasuarina fraseriana	$\ln(DW) = 3.57 + 2.68 \ln(DBH)$	Grierson *et al.* (2000)
Persoonia longifolia	$\ln(DW) = -2.93 + 2.55 \ln(DBH)$	Grierson *et al.* (2000)
Generalised shrub allometric	$\ln(DW) = 2.428 \ln(D_{10}) – 3.007$	Paul *et al.* (2015)

Total biomass was allocated to the tree components (foliage, twig, branch and bark) according to published proportions (Hingston *et al.* 1980; Grierson *et al.* 2000). Individual trees measured during the field assessment included both burnt and healthy unburnt trees. To avoid overestimation of live carbon and to account for combustion or loss of foliage, twigs, fine branches, each component was adjusted according to its health, fragmentation score, live and dead height measurements, and height of resprouting.

Individual stems were examined for pre-fire stress, which was determined by the presence of severe canopy architectural damage (presence and quantity of large dead wood in the canopy) and/or the presence of large epicormic sprouts. Both states are symptomatic of stress resulting in partial tree mortality (see Chapter 3 for a description of drought mortality in the same forest, but on different plots). These correction values were then applied to the biomass estimates calculated from the allometric equations for the species (Table 3.2).

Bole biomass was classified as live, dead, or suffering partial mortality. These classifications were determined using live height and crown break height. If an individual was epicormically resprouting in the canopy (live height greater than crown break height), the bole was deemed live, and if the individual was only basally resprouting the bole was deemed dead. In these cases, the biomass allocated to the bole was determined using published allometric equations and proportions. However, if the stem was epicormically resprouting on the bole below the crown break the bole was fractionated into live and dead portions using live and dead heights and a taper function determined from literature values to calculate a volume (Innes *et al.* 2007). In these cases, Smalian's formula (Equation 1) was used to calculate the volume of live and dead portions of the bole, rather than the allometrically derived portions of bole biomass. The known wood densities of each tree species were then used to convert volume to mass of live and dead bole portions.

Smalian's formula was used to calculate bole volume

$$V = \frac{A_1 + A_2}{2} \times L \qquad \text{Equation 1}$$

Where V is the volume of the log (m^3), A_1 is the area of the log at the small end, A_2 is the area of the log at the large end, and L is the log length. The large area was calculated using the DBH measured during the field survey and the small area was calculated using the live height/crown break height and taper equation. Once a volume of live and dead biomass was obtained it was converted to mass using the wood density of the given species. These values were taken from Innes *et al.* (2007).

The method of using taper equations and height was used to estimate the biomass stored in stumps throughout the plots. Once a mass was determined the value was corrected to account for the percentage of mass missing and the decay score of the individual. There was no correction made for butt swell.

Unburnt plot surface fuels ages ranged from 2-10 years since the last fire. As noted, the burnt plots had all litter consumed. Therefore to calculate pre-fire surface fuel loads for areas that were unburnt for >15 years published values and equations were used (Gould *et al.* 2011).

3.3.5 Combustion coefficients

Combustion coefficients were calculated using a combination of literature derived values, and data collected in space for time plots. Literature values were used to estimate the mass of bark lost from burnt areas (Burrows 2001). Complete combustion of the litter pool was assumed across all burnt areas (Keith *et al.* 2014). Mass loss of fine woody debris and coarse woody debris were calculated as the average difference between pre-fire and post-fire debris volume. The fraction of foliage reported missing from each tree via ocular assessment was used as an estimate of foliage and twig combustion coefficient for the fire severity categories. Post fire litter values were also used as an indication of foliage combustion. Higher post fire litter values resulted in less canopy foliage consumption as canopy was scorched and not consumed.

3.3.6 Fire severity classification

Fire leads to changes in the reflectance of burnt vegetation. After fire there is an increase in the reflectance of the midinfrared region, with this region sensitive to water content of soil and vegetation, while the reflectance in the near infrared region declines because of the loss of live vegetation and chlorophyll content (Miller and Thode 2007; Lanorte *et al.* 2013; Ghermandi *et al.* 2019). The spectral bands used in the calculation of normalised burn ratio (NBR) have been selected considering these spectral characteristics (Ghermandi *et al.* 2019).

Normalised burn ratio was calculated from Landsat TM, Near Infrared (NIR) and Short-wave infrared (SWIR) bands in pre and post fire images (Equation 2). An image was chosen from within two months pre and post fire to establish the extent of burn severity across the area that had been burnt by the wildfire. The NBR data from these two images was then used to calculate the relative difference normalised burn ratio (RdNBR, Equation 3). The use of RdNBR removes biases occurring from differences in pre-fire vegetation across the fire (Miller *et al.* 2009).

$$NBR = \frac{(\mathrm{NIR{-}SWR})}{(\mathrm{NIR + SWR})} \qquad \text{Equation 2}$$

$$\frac{((preNBR - postNBR)\times 1000)}{\sqrt{abs(preNBR)}} \qquad \text{Equation 3}$$

The RdNBR data were used to classify areas that experienced different fire conditions.

A combination of aerial photography paired with ground-based observations was used to delineate areas of forest with differing fire severities. Twenty polygons were constructed using post-fire aerial imagery to cover the range of fire severities observed in the burn area. Relative difference normalised burn ratio (RdNBR) data were extracted from these polygons and averaged to create the fire severity class cut points, which could be applied to the burnt area. Choosing the threshold values between fire severity categories can be fairly subjective (Miller *et al.* 2009). However, the threshold values for fire severity class were determined following Miller *et al.* (2009), by using the mid-point between aerially delineated and observed fire severities polygons mean RdNBR values. Once burnt areas had been categorised into fire severity class, a combination of field measurements and values from the literature were used to calculate pyrogenic emissions.

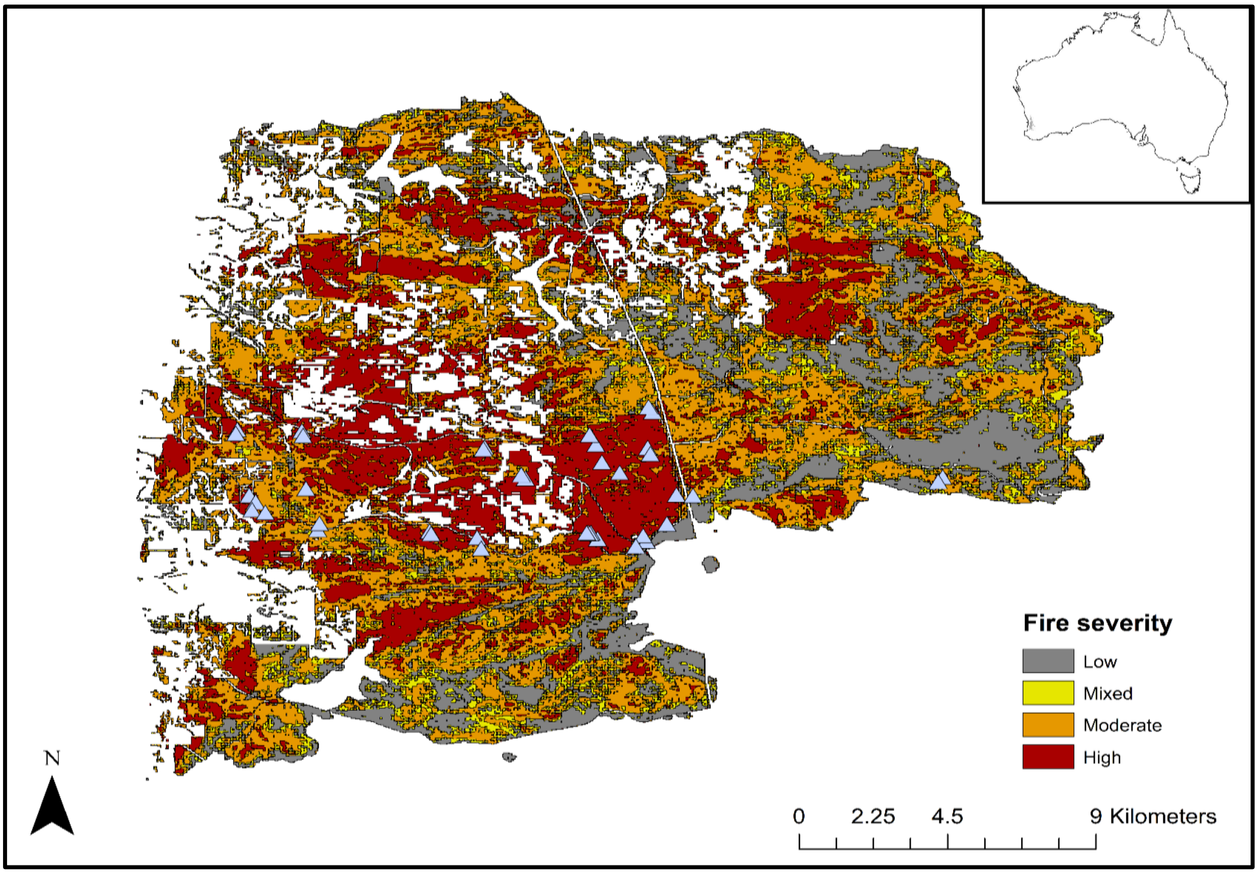

Figure 3.2: Location of 39 burnt plots (triangles) within the moderate and high fire severity classes in native upland Northern Jarrah Forest (NJF), southwestern Australia. Patches of unclassified areas are a combination of farmland, mining and mining rehabilitation. Fire severity by burn area; Low 18%, Mixed 13%, Moderate 43%, High 26%.

3.3.7 Pyrogenic carbon emissions

Pyrogenic carbon emissions for the Waroona Fire were calculated following eq. 1 in Campbell *et al* (2007);

$$PyC = \sum_{i=1,j=1}^{n} A_i \left(D_{ij} * CF_{ij}\right) \qquad \text{Equation 4}$$

Where *PyC* is the pyrogenic emission in mass of carbon, A is the area affected by fire severity class i, *D* is the pre-fire carbon load in mass per unit area of forest carbon pool j, which was averaged across plots of fire severity *i*. The fraction of the pre-fire carbon pool *j* combusted in fire severity *I* is the combustion factor, CF. In this study the forest is separated into 13 carbon pools which were burnt by four fire severity classes

Once severity and pre-fire litter loads were calculated across the fire area, combustion coefficients were applied to each of the fire severities for each of the forest carbon pools. These values were then converted to tonnes for each fire severity class to give an estimate of carbon emissions from the plots.

3.3.8 Statistical analyses

Quantifying pyrogenic carbon emissions of the 2016 wildfire event. Carbon losses across the fire severities (unburnt, moderate, high) were tested using a one-way analysis of variance.

Determining whether wildfire severity had significant effects on forest carbon pools. Changes in each of the carbon pools following the wildfire was also tested using one-way analysis of variance. All data analyses were carried out using R (R Core Team 2014) and data visualisation with ggplot2 (Wickham 2011). In all cases, the means and 95% confidence intervals are presented and a lack of overlap of the mean with adjacent confidence intervals was interpreted as evidence for a statistical difference between groups while asymmetrical overlap of means (intervals overlap one mean but not the other) was interpreted as evidence of a statistical difference between groups (Ramsey and Schafer 2012).

3.4 Results

3.4.1 Pyrogenic emissions

Combustion coefficients showed a uniform increase across all forest carbon pools with increasing fire severity class from low to high burn class. The highest combustion coefficients were in the litter, shrub and tree foliage carbon pools (Table 3.3).

Table 3.3: Combustion coefficients for the forest carbon pools across four fire severities observed in the Waroona Fire of January 2016 in the Northern Jarrah Forest, southwestern Australia.

Forest carbon pool type		Fire severity			
		High	Moderate	Mixed	Low
Foliage		0.95	0.9	0.4	0
Twig *<1 cm diam*		0.2	0.1	0.05	0
Branch		0.01	0.01	0	0
Bark		0.3	0.25	0.2	0.1
Bole		0	0	0	0
Understorey (Shrubs)		0.95	0.92	0.7	0.5
Coarse Woody Debris		0.01	0.01	0	0
Fine Woody Debris	*1hr*	1	1	1	1
	10hr	0.9	0.85	0.7	0.5
	100hr	0.8	0.7	0.6	0.4
Surface Litter		1	1	1	1

The total pyrogenic emissions from the 2016 Waroona Fire are estimated as 723 113 t C emitted from above-ground carbon pools. The highest emissions came from tree biomass from the combustion of foliage, bark, and small twig material (Table 3.4). Surface fuels released the second largest amount of emissions (200 674 t C) as large litter loads (6.6 t C ha^{-1}) in long unburnt stands (>30 years) were severely burnt. A general increase in carbon emissions was recorded with an increase in fire severity category (Table 3.4), with this ranging from 10.0 to 22.1 t C ha^{-1} for the low and severe fire categories, respectively. Much of the carbon loss (3.7 and 13.3 t C ha^{-1}) came from the forest canopy and understory shrubs. Total pyrogenic carbon emissions from low to high severity burn areas were approximately 5.5-12.2% of the initial pre-fire carbon density.

3.4.2 Transfer of carbon

The Waroona Fire affected the total carbon storage and the composition of forest carbon pools in the NJF (Figure 3.3). Total above ground carbon of measured stands ranged from 76.3 t C ha^{-1} to 229.6 t C ha^{-1} and was significantly lower in moderate (-41.8 t C ha^{-1}, $F_{2,44}= 6.19$, $p<0.05$) and high (-48.8 t C ha^{-1}, $F_{2,44}= 6.19$, $p<0.01$) severity burnt stands compared to the unburnt condition (Figure 3.3a). The primary store of carbon in all measured stands was live standing carbon, which on average made up 79%, 62% and 56% of unburnt, moderate and high fire severity class forest stands, respectively (Figure 3.3a).

Table 3.4: Pre-fire forest carbon density (t C ha^{-1}) and pyrogenic carbon emissions (t C ha^{-1}) by carbon pool and fire severity class. Total carbon emissions (t C) area also displayed for each of the above ground forest carbon pools burnt in the Waroona Fire of January 2016 in the Northern Jarrah Forest, southwestern Australia.

		Pre-Fire density (t C ha^{-1})	Combusted carbon (t C ha^{-1})				Fire wide emissions (t C)
			High	Moderate	Mixed	Low	
Trees		156.5	10.2	8.6	5.7	2.1	268 905
Shrubs		3.2	3.1	2.9	2.2	1.6	95 137
Coarse Woody Debris		11.6	0.1	0.1	0.0	0.0	2 873
Fine Woody Debris	10 hr	1.5	1.3	1.3	1.1	0.8	41 971
	100 hr	4.8	3.8	3.4	2.9	1.9	113 553
Litter		0.6-6.6	-	-	-	-	200 674
Total		181.2	22.1	19.9	15.5	10.0	

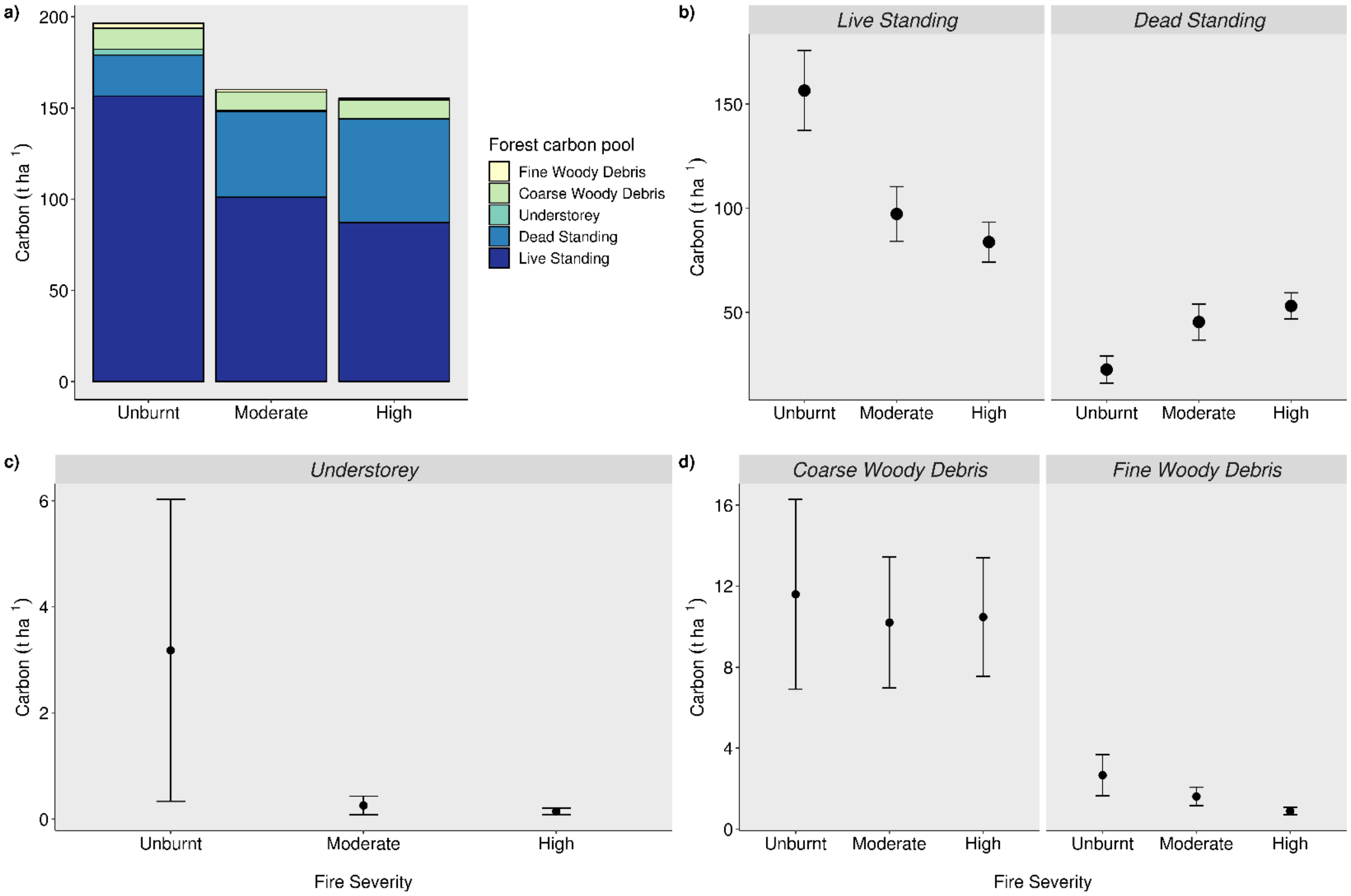

Figure 3.3: Mean total above ground carbon (t ha^{-1}) for above-ground forest carbon pools in unburnt and wildfire-burnt plots. b) Mean live standing and dead standing carbon (t C ha^{-1}) for unburnt, moderate and high fire severity category plots. c) mean carbon in understorey carbon pool for unburnt, moderate and high severity category plots d) Mean carbon content (t C ha^{-1}) in coarse woody debris and fine woody debris for unburnt, moderate and high fire severity category plots in the Northern Jarrah Forest, southwestern Australia. Points represent means and bars represents 95% confidence intervals of the mean.

Live tree carbon in the burnt plots ranged from 39.4±18.3 t C ha^{-1} to 202.4±67.9 t C ha^{-1} with mean values of 97.2±13.1 t C ha^{-1} and 83.7±9.6 t C ha^{-1} for the moderate and high fire severities, respectively. High wildfire severity resulted in the most combustion of canopy stored carbon as well as the largest transfer of live standing carbon to dead standing carbon (Figure 3.3b).

The wildfire thus significantly lowered live carbon storage in both moderate (-59.2 t C ha^{-1}, $F_{2,44}$= 15.53, $p<0.001$) and high (-72.8 t C ha^{-1}, $F_{2,44}$= 15.53, $p<0.001$) fire severity classes compared to the unburnt stands. However, live standing carbon did not differ between the two measured fire severity classes ($F_{2,44}$= 15.53, p= 0.51, Figure 3.3b). The pattern of decrease in standing live carbon was mirrored in the standing dead carbon pools, with an increase in dead standing carbon in the moderate (22.8 t C ha^{-1}, $F_{2,44}$= 6.71, $p<0.05$) and high (30.6 t C ha^{-1}, $F_{2,44}$= 6.71, $p<0.001$) severity classes compared to the unburnt condition, and no difference between measured fire severity classes ($F_{2,44}$= 6.71, p=0.57, Figure 3.3b).

Coarse and Fine Woody Debris

Carbon storage in coarse woody debris decreased slightly following the fire, however this was highly variable across plots and was not significant ($F_{2,44}$= 0.15, p=0.86, Figure 3.3d). Fine woody debris post fire was lower in both moderate (-1.1 t C ha^{-1}, $F_{2,44}$= 15.49, $p<0.05$) and high (-1.8 t C ha^{-1}, $F_{2,44}$= 15.49, $p<0.001$, Figure 3.3d) severity burnt stands. Fine woody debris also varied between the two measured fire severity classes, with the high severity having significantly less debris than the moderate severity class (-0.7 t C ha^{-1}, $F_{2,44}$= 15.49, $p<0.05$, Figure 3.3d).

3.5 Discussion

Wildfire significantly reduced the total carbon storage of the severely burnt stands through combustion of litter, debris, tree and shrub canopies, with this representing a direct emission of between 10 and 21 t C ha^{-1}. The fire also killed trees, which increased the storage of carbon in the dead tree and shrub pools, with this having two consequences. The first is related to the vulnerability of the now dead carbon to tree decay and future fires, and the second to the ability of the forest to sequester carbon. The persisting live trees will resprout and new individuals will germinate, and this will restore some of the carbon lost during the event. However, regrowth and seedlings may be vulnerable to subsequent disturbance events such as drought and fire (Chapter 2).

Pyrogenic carbon emissions were directly related to the severity of wildfire across the burnt area, with higher combustion (and thus emissions) resulting from a higher wildfire severity (Keeley 2009). In this study, plots experiencing high fire severity class released carbon stored in foliage, twigs, and bole bark. The rate of emissions reported here (20.1 t C ha^{-1}) is comparable to other severe wildfires and other forest systems. A large wildfire that burnt an area of 450,000 ha of temperate eucalypt forest in Victoria, Australia, emitted an estimated 3.9 Mt C, at an estimated 40-58 t C ha^{-1} (Keith *et al.* 2014). This corresponded to 6-14% of pre-fire carbon density. In contrast, a stand-replacing wildfire that burnt 200,000 ha of non-sprouting mixed coniferous forest in Oregon, United States, released an estimated 3.8 Mt C, or approximately 19 t C ha^{-1} (Campbell *et al.* 2007).

While the reported rates of pyrogenic carbon emissions are closely aligned between resprouting and non-resprouting forests, the subsequent carbon trajectories may differ. Secondary emissions from biogenic decay could differ between these two systems for two reasons: firstly, resprouting forest results in a lower rate of overstorey mortality, and secondly, the decay rate and subsequent emissions of the dead material can be assumed to be slower in resprouting forests because of climate and a high initial wood density. In addition, tree growth rates will differ between forest types, which are affected by local climate and edaphic conditions. There is clear uncertainty on the impact of climate change on forest growth and survival (Chapter 2; Allen *et al.* 2010)

The regrowth of carbon will differ as well; from forests with stand replacing fires with complete mortality, where carbon will have to be regained through seedlings or advanced regeneration, whereas in a resprouting forests this will come from surviving trees, albeit damaged to different degrees. In the severely burnt trees of this study, not all standing above ground carbon was transferred from the live to dead carbon pools, as the co-dominant overstorey species, *E. marginata* and *C. calophylla* both resprout from lignotuberous buds following disturbance (Abbott and Loneragan 1983). The resilience of the co-dominant overstorey species allows them to quickly regenerate any lost canopy, however this occurs to different degrees in different trees. In some trees there has been partial mortality where trees have suffered severe canopy loss and have epicormically resprouted on the bole but not in the crown (Chapter 2; Walden *et al.* 2019), whereas in other trees there has been bole mortality and regrowth begins from the base. The resprouting ability of the predominant overstorey species has reduced standing live carbon lost from the wildfire event and increased the rate at which carbon will be restored in this system.

Once a tree dies it is subject to biogenic emissions from dead wood decay and the release of carbon back into the atmosphere. The rate of decay (Gunn *et al.* 2012) and subsequent emissions are strongly reliant on climate and wood characteristics of the tree that has died, which include; being standing versus horizontal, rates for snag fragmentation, material size, wood density and biotic agents of decay. Standing, aerial dead wood (dead trees, portions of trees) decays slower (lower annual emissions) than downed wood on the forest floor in contact with the soil, as those pieces experience greater moisture content and therefore higher decomposition rates (Harmon *et al.* 2011). Climate also plays a large role in snag decomposition rate, as decay rates decreases from the equator towards the poles (Cooper 1983). If follows that the Mediterranean climate (cool wet winters and warm dry summers) of southwestern Australia, does not provide ideal conditions for wood decay. In a tropical forest almost all the woody material may decay within 10 years as warm moist environments promote decay (Cooper 1983). The turnover time for eucalyptus species in a temperate sclerophyll forest can range from seven (e.g. *E. regnans*) to 375 years (e.g. *E. camaldulensis* and *E. tereticornis*) based on climate setting (Mackensen and Bauhus 1999). Not only will the amount of material available to biogenic decay be markedly less than the non-sprouting alternative, the rate at which that dead material decays can be assumed to be slower due to the high initial wood density and warm dry conditions of southwestern Australia. Termites are not a major feature of this forest ecosystem.

Ecosystem responses will be determined by the intrinsic ability of species to withstand fire (resistance traits), and respond to fire (resilience traits; Ruthrof *et al.* 2015) . In this study, there was significantly lower mean live standing carbon (-72.8±31.6 t C ha^{-1}) in the higher burn severity plots, and a corresponding significantly higher mean dead standing carbon store (+30.57± 20.25 t C ha^{-1}), when compared to unburnt forest stands. Nonetheless, live carbon loss from these stands will take time to regenerate. The shrub and litter forest carbon pools were uniformly combusted throughout the severely burnt forest area. These pools will quickly regenerate and replenish carbon lost from combustion, however they will not contribute to long-term storage due to the frequent planned burning in these systems. Although coarse woody debris decreased, these changes were not statistically significant. Fire may have consumed some of the CWD, however, with the large increase in dead standing carbon, the CWD pool will likely increase in size as large dead trees fragment and are converted to debris.

Pyrogenic emissions from the Waroona Fire of 0.72 Mt C were equivalent to 3% of Western Australia's total carbon emissions for 2016 (Australia National Greenhouse Gas Inventory Committee 2018). Given the severity of this wildfire, the significant losses of live carbon, and the potential of more frequent severe fires in this area, the stability of these forest carbon stores may be threatened with forest regrowth never restoring carbon lost from combustion and mortality. For example, Fairman *et al.* (2019) reported the loss of resprouting ability of fire tolerant eucalypt species in the temperate eucalypt forests of Victoria, south-eastern Australia, where repeated fires in short succession resulted in resprouting failure and widespread mortality. While the effects of these events on carbon storage were not directly measured, it can be assumed that the loss of large overstorey trees and replacement with ground coppice and seedlings will result in decreased carbon storage in those stands.

3.6 Conclusions

This study quantified the movement of live standing carbon to dead standing carbon in burnt stands in a resprouting eucalypt forest. The significant loss of live carbon from the stand will require long periods of unburnt and undisturbed regrowth if carbon stores are to return to pre-fire levels. Given the projections of hotter and more frequent fires Clarke *et al.* (2016) it is uncertain whether these stands will have the time to recover prior to the next fire event. It follows that the resilient eucalyptus forests of southwestern Australia may not be stable carbon sinks if fire frequency and severity increase substantially with a changing climate.

The total emissions from the fire and rates of emissions allign closely with other forested systems. However, the movement of carbon and loss of live standing carbon may be lower than non-sprouting systems which experience infrequent severe fire. There were significant losses of live standing carbon and increases in dead standing carbon. Individuals that have undergone partial mortality, top-kill and regrowth in this forest are vulnerable to subsequent disturbances as they recover and develop bark thick enough to withstand fire. Studies such as this are important, as they show that even fire-resilient forests cannot withstand large, hot fires without large losses of overstorey individuals and hence carbon.

4 High severity wildfire overrides drought legacy impacts in a resprouting forest[3]

4.1 Abstract

The frequency and intensity of forest disturbances are projected to increase as climate shifts in many regions, with an increased likelihood of multiple disturbance events occurring in short succession. The effects of multiple disturbance events are becoming increasingly important but with substantial uncertainty regarding interaction strength in relation to type, sequence, and relative timing. This chapter examines the effects of wildfire following global change type drought (hotter drought) to quantify linked and compounding effects in a resprouting eucalypt-dominated forest. The impact (mortality) and early response (resprouting, recruitment) in the dominant overstory tree species *Eucalyptus marginata* and *Corymbia calophylla* in south-western Australia were quantified. There was no evidence of linked or compounding effects of these disturbances in combination. Instead a strong effect of wildfire on live basal area (-20.7 ± 7.3 m^2 ha^{-1}) overwhelmed pre-existing drought impacts. Stem size, fire severity, and harvest frequency were found to be the strongest determinants of stem survival. Resprouting eucalypt forests are particularly resilient with focal species able to survive multiple stressors over a short time period. However, the newly regrowing burnt stands are vulnerable to future disturbance as they develop bark thick enough to withstand fire and develop carbon stores to maintain resprouts following drought. With projections of continually decreasing rainfall and more frequent and severe fire in this region the trajectory of the regrowth in these forest stands is strongly tied to the future disturbance regime. Increases in disturbance frequency and intensity

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[3] This chapter has been prepared to be submitted to *Global Change Biology*

may therefore lessen the chances of these stands recovering to pre-fire structure and carbon store.

4.2 Introduction

Forest disturbance frequency and intensity have increased in recent decades and are projected to continue to increase across global forested ecosystems as climate change continues to accelerate (Hoegh-Guldberg *et al.* 2018). Disturbance regimes (composed of frequency, size, season, intensity of events) are often a key driver of ecosystem structure, function and composition (Buma 2015). The capacity of an ecosystem to return to a pre-disturbance state (as measured by cover, composition, or structure) has been defined as the ecological resilience of a population, community, or ecosystem and reflects the frequency and intensity and type of impact the ecosystem can withstand whilst still returning to its ‘original’ state (Gunderson 2000). Increasing attention to the occurrence of disturbances outside a historic regime has openly questioned the capacity of systems to return to their original state and instead shift to alternative states (i.e. phase change from forest to shrubland; Donato *et al.* 2009a; Fairman *et al.* 2019)

Multiple disturbance events can cause profound changes to forest composition, structure and function (Buma 2015). The impact of successive interacting disturbance events has been documented across forest types with differing disturbance types and frequencies (Buma and Wessman 2011; Harvey *et al.* 2014b; Fairman *et al.* 2019). Repeated disturbance events can either have *linked* or *compound* interactions. Linked disturbances occur when the first disturbance affects the likelihood, extent, or severity of the second disturbance (Buma 2015). For example the interaction between tree windthrow, and subsequent fire severity, has been examined by Kulakowski and Veblen (2007) in the subalpine forests of Colorado where stands with severe windthrow (66% of trees) experienced higher wildfire severity compared to those with lower rates of windthrow. Linked disturbance effects have also been reported between intense storms and fire with defoliation leading to higher fuel loads and subsequent fire intensity (Gower *et al.* 2015) as well as pest (*Dendroctonus ponderosae)* outbreaks and subsequent fire (Harvey *et al.* 2014b). Harvey *et al.* (2014b) reported that fire severity was higher in areas with recent outbreak if moderate fire was present. However, once high severity fire (canopy fire) was present there was no link between outbreak age and fire severity (Harvey *et al.* 2014a).

Compound disturbances describe the biotic response (for example, tree recruitment) following a second disturbance event, and how it is altered relative to the individual disturbance event. For example, forest stands experiencing windthrow in the subalpine forests of Colorado, which lost a substantial seed source, and then experienced fire, had reduced recruitment relative to forests which experienced fire alone (Buma and Wessman 2011). In a resprouting shrubland system of southwestern Australia, Gower *et al.* (2015) found that areas that experienced hail storm damage and subsequent planned fire had reduced resprouting vigour and seedling recruitment compared to those that just experienced fire alone. The complex effects of disturbance types, potential interactions and cumulative effects are key to understanding ecosystem resilience particularly in changing climate. Quantifying the impacts of linked and compounding disturbances is critical for forest management, as drought, wildfire, storms and insect outbreaks are predicted to increase with a changing climate (Moritz *et al.* 2012; Allen *et al.* 2015), therefore increasing the frequency of disturbance interactions.

Fire is the dominant natural disturbance factor globally (Bowman *et al.* 2009), and many climate models project the development of more fire-prone systems with a changing climate (Moritz *et al.* 2012; Jolly *et al.* 2015). Fire prone regions may face more frequent, severe and larger wildfires as forest dynamics continue to change and stand characteristics are affected by multiple stressors. The increase in fire frequency has already been reported to cause forest structure collapses and test resilience mechanisms. For example, Fairman *et al.* (2019) reported the loss of resprouting ability in the temperate eucalypt forests of Victoria, south-eastern Australia, where repeated fires in short succession resulted in widespread mortality. An increasing incidence of wildfire has implications on both non-sprouting boreal and resprouting forests and is therefore likely to exert a strong selection force on the species within such fire prone forests.

Drought-induced forest die off as a disturbance factor can also have major implications on forest structure and function. Drought and heatwave related die-off events have been recorded on every forested part of the globe (Allen *et al.* 2015). These die off events may have impacts on the structure, function and biodiversity of ecosystems, with some systems experiencing complete structural state shifts (Clark *et al.* 2016; Matusick *et al.* 2016; Steel *et al.* 2019). These forest stands may experience further stress from other biological stressors (such as pests) as they have weakened resistance and resilience mechanisms (Zeppel *et al.* 2015). The time between disturbances, as well as the type of the disturbance that follows underpins the potential resilience of that system. For example, fire-drought interactions have been shown to reduce seed production and population persistence (Enright *et al.* 2015) with increasing concern as all dimensions of historic disturbance regimes change (i.e. unseasonal fire + increased frequency; Miller *et al.* 2019).

In southwestern Australia the austral summer of 2010/11 was the hottest and driest since records began (BOM 2011) with region wide impacts spanning multiple trophic levels and ecosystems (Ruthrof *et al.* 2018). Approximately 16 000 ha of resprouting forest (The Northern Jarrah Forest) experienced severe canopy collapse and began to regrow from basal and epicormic resprouting (Matusick *et al.* 2013; Steel *et al.* 2019). Five years later in January 2016, areas of forest that had been subject to drought and heatwave related die-off were subject to a lightning-ignited wildfire (The Waroona Fire) (McCaw *et al.* 2016). The wildfire burnt through 65,000 ha of native forest, farmland, and destroyed the small town of Yarloop. This layering of disturbances presented an opportunity to investigate the potential linked and compounding effects of these disturbance events in a resprouting forest. The objectives of this study, therefore, were to examine the additive and interactive impacts of drought and wildfire at the stand and stem level with regards to mortality rates, and recruitment in the Northern Jarrah Forest of south-western Australia.

4.3 Methods

4.3.1 Study area

The Northern Jarrah Forest (NJF) is located in southwestern Australia (30.8-33.5° S and 115.8-117.8°E) and covers an area of 1,127,600 ha (Havel 1975). The forest ranges from an open dry sclerophyll forest in the north to a tall, closed forest in the south (Dell and Havel 1989a). The NJF harbours over 850 described vascular plant species forming a distinct and important component of southwestern Australia’s exceptional plant biodiversity and classification as one of 35 global biodiversity hotspots (Mittermeier *et al.* 2011). Across the NJF, vegetation tends to cluster into woodland/forest, riparian, and heath types; this study focussed on upland sites, which are predominantly *Eucalyptus marginata* (jarrah) and *Corymbia calophylla* (marri) with a midstorey dominated by *Allocasuarina fraseriana*, *Banksia grandis*, and *Persoonia longifolia* (Dell and Havel 1989a). Deep lateritic weathering profiles cap Archaean granite and metamorphic rocks (Gilkes *et al.* 1973). Soils of upland sites in the NJF are characterised by a fissured lateritic caprock overlying a clay profile of depths of up to 30 to >100 m to bedrock (Taylor and Butt 1998). Shallow depths to bedrock have been implicated in drought vulnerability (Harper *et al.* 2009b; Brouwers *et al.* 2013a; Brouwers *et al.* 2015; Steel *et al.* 2019).

The NJF has a Mediterranean type climate, with hot dry summers and mild wet winters. Most rainfall occurs between April and October, and a seasonal drought may last between four to seven months (Bates *et al.* 2008). There is a strong rainfall gradient across the forest, which ranges from >1100 mm yr^{-1} on the western edge to approximately 700 mm yr^{-1} in the north east (Gentilli 1989). Mean annual rainfall for the study area is between 1233 mm (Dwellingup) and 992 mm (Waroona).

Southwestern Australia has experienced a significant change in climate, characterised by an increase in temperature (0.15°C per decade) and a reduction in rainfall (10-15%) since the 1970s (Bates *et al.* 2008). During this period of warming and drying, two extreme drought events occurred during the Australian summers of 2006-2007 and 2010-2011. The winter of 2010 was extremely dry, with rainfall 40-50% below the annual average (BOM 2011). In addition, the number of heatwave days in 2011 was the highest on record since 1960 (BOM 2011). During this event, it was estimated that approximately 16,000 ha of the NJF suffered severe canopy die-off (Brouwers *et al.* 2013a; Matusick *et al.* 2013). Areas that were severely affected were those in close proximity to granite outcrops, had soil with a lower water holding capacity compared to surrounding areas (Brouwers *et al.* 2013b), and were more clustered at xeric sites (Andrew *et al.* 2016).

The Waroona Fire was ignited by lightning on the morning of 6 January 2016 and coincided with hot, dry offshore winds thereby eluding suppression and growing into an area of approximately 69,165 ha, burning both agricultural and native vegetation (McCaw *et al.* 2016). Rainfall for the year preceding the fire was 35% below the long-term average and was the third lowest on record (McCaw *et al.* 2016). The fire burnt through stands previously burned six to 30 years prior (McCaw *et al.* 2016). During the fire event the smoke and heat created by the fire resulted in a pyrocumulus cloud which caused further ignitions and intensified fire behaviour (Peace *et al.* 2017).

There were no planned, prescribed, fuel-reduction burns in the area between the 2010-2011 drought event and the wildfire.

The two co-dominant overstorey eucalypt species show differing life strategies to drought stress with *E. marginata* being more resilient, commonly resprouting lower on the bole, and *C. calophylla* showing a higher resistance with the canopy remaining intact for longer and resprouting less often (Ruthrof *et al.* 2015). Large *E. marginata* trees may be injured by fire but are rarely killed (Abbott and Loneragan 1986). Fire damaged trees typically resprout vigorously from epicormic buds that are well protected in thick bark making them extremely resilient to fire (Burrows 2008; Pausas 2015). Smaller individuals such as seedlings and saplings readily re-coppice from belowground lignotubers (Abbott and Loneragan 1983; Burrows *et al.* 1995). A summer wildfire just north of the study area in 1961 resulted in 11% of mature individuals (~>30 cm DBH) and 76% of younger individuals (~<30 cm DBH) suffering stem mortality (Peet and Williamson 1968). The predominant disturbance agents in the NJF have historically been frequent fire and selective timber harvesting over the past ~200 years, with forest stands treated with planned fire on a 5 to 15 year basis since the 1960s (Burrows *et al.* 1995).

4.3.2 Site selection and plot establishment

To assess the impact of drought and wildfire, sites were selected based on their pre-fire drought stress and wildfire severity. The experimental design followed a factorial design with two pre-fire drought conditions and three burn severities (crown consumption, crown scorch, unburned). Field assessments were undertaken 1-year post fire and involved 30 sites with a complex of 47 plots spread across the fire and drought treatments; sites typically had two plots of differing fire severity spanning one level of drought (Figure 4.1).

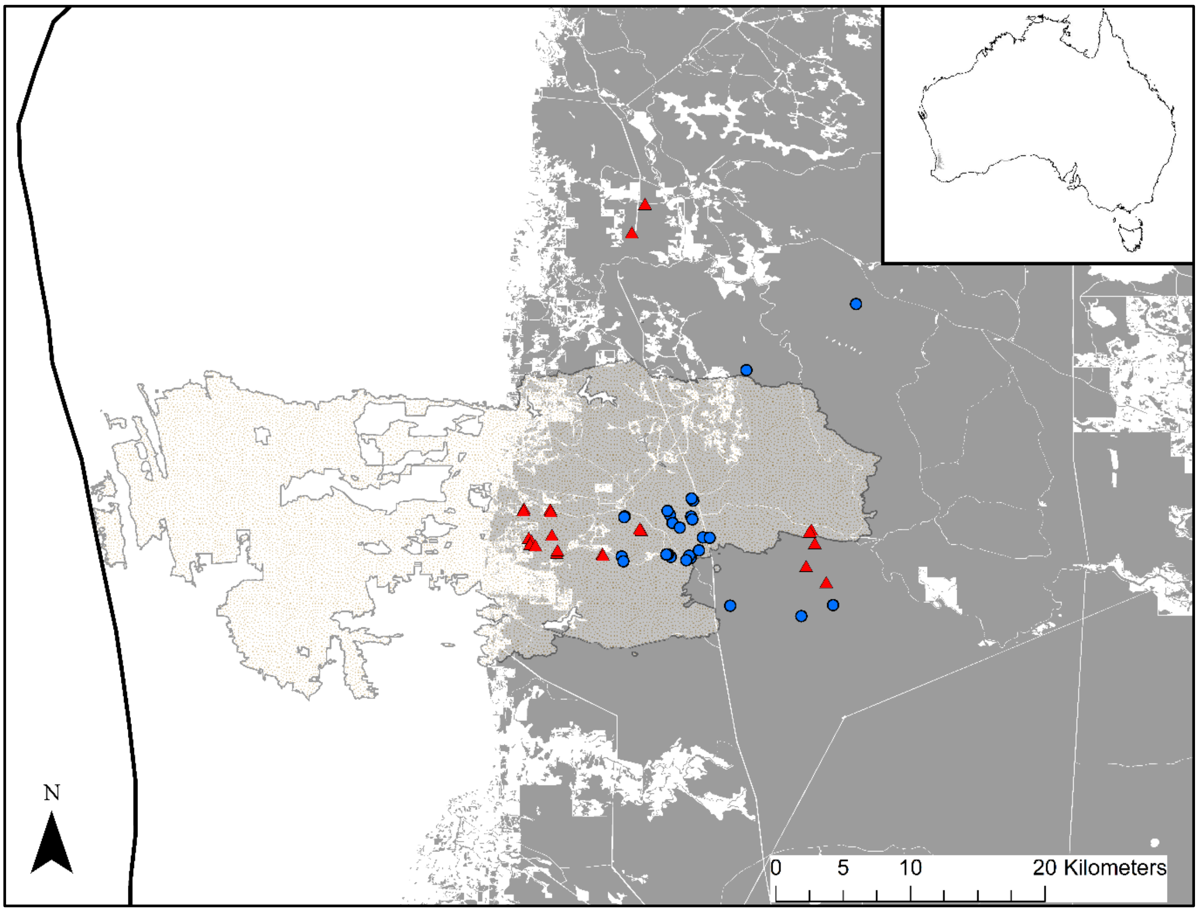

Figure 4.1: Location of 47 burnt and unburnt low drought (blue circles) and high drought (red triangles) native upland Northern Jarrah Forest (grey shaded area), southwestern Australia. Red dotted shaded area indicates Waroona Fire boundary.

A model developed by Brouwers *et al.* (2015) was used to delineate areas of pre-fire drought stress within the burn area. The model uses elevation, slope, distance to rocky-outcrop, rainfall and temperature data to infer drought and heat sensitivity across a landscape. The model was used to nominate stands which were potentially drought stressed pre-fire. These sites were validated by applying on ground selection criteria based on plant species association with drought and the structural indications of drought collapse (Ruthrof *et al.* 2015). For example, *Banksia grandis* rarely occurs in severely heatwave/drought impacted areas as they are more susceptible to drought mortality (Matusick *et al.* 2013; Steel *et al.* 2019). Therefore, sites with an established midstorey of *B. grandis* were not used as high probability drought sites. To validate predicted drought occurrence, high probability drought sites also required structural evidence of the drought collapse reported by Matusick *et al.* (2013), with epicormic sprouts of a size that would have developed following this disturbance event. The size (diameter) of the epicormics determined whether they were 2010-2011 drought-induced epicormics.

Following the fire, burn severity was observed to fall into two main categories; 1) severe surface fire with canopy scorch (moderate severity), 2) crown fire with complete canopy consumption (high severity). Twenty sites (10 high drought, 10 low drought) were chosen within the forest area that had been burnt, with 17 containing paired plots in the two observed fire severities (a total of 37 plots). If both conditions were not present only a single plot was established. Ten unburnt control plots (5 high probability drought, 5 low probability drought) were also established within 10 km of the fire boundary to ensure soil type, rainfall and stand composition and structure did not vary widely between burnt and unburnt areas.

Plots were established in a modified Forest Inventory and Analysis assemblage (Bechtold and Scott 2005). Each plot consisted of four subplots, of variable radius, comprising a central subplot and subplots orientated at 0°, 120°, and 240° from the central subplot. The centre of each subplot was at least 35 m from the middle of the centre subplot. Subplot configuration was altered only if the forest condition changed rapidly or the subplot was situated on a track.

4.3.3 Fire severity assessment

To avoid further repetition, calculation of RdNBR and subsequent fire severity assessment used to determine fire severity categories in this chapter can be found in Section 4.3.6

4.3.4 Stand assessment

4.3.4.1 Tree survey

Trees were surveyed at each of the four subplots at each plot. The plots had a variable radius depending on tree stocking rate. The radii were adjusted to capture a minimum of 60 trees with a diameter at breast height (DBH) >10 cm in each plot. Three radii were established for the different DBH classes; >30 cm, 10-30 cm, and <10 cm. The largest tree radius was not larger than 15 m to avoid overlap of subplots. The radii remained constant across each of the subplots within a plot.

To quantify combustion from wildfire and the portion of a tree killed, stem level measurements included: live and dead height (m), diameter at breast height (DBH), basal sprout height (m), highest and lowest epicormic sprouts point of origin (m), and a canopy health score. The health score rating was developed to capture the loss of canopy from consumption or fire scorch on a scale of 0-100, with 100 being a tree that had completely lost all crown and was dead with no evidence of resprouting, whereas minimally affected individuals were given lower scores corresponding to the proportion of original canopy that was lost. A resprouting vigour rating was also recorded on a scale of 0-100, with 100 being a tree that has its complete canopy resprouting, one-year post fire.

In burnt stands, to capture the effect of the 2011 canopy collapse on tree architecture, a range of measurements were taken that categorised the pre-fire state of the individual, in addition to the measurements capturing fire damage and regrowth. To assess pre-fire architecture and capture any pre-fire canopy retraction evident the number, size and height of epicormic sprouts present on the bole before the wildfire were recorded, as well as a categorisation of the fragmentation of previously dead material in the canopy from class 1-4 according to Harmon *et al.* (2011), and Woldendorp and Keenan (2005). That is, if an individual had experienced obvious pre-fire stress, the snag fragmentation category would be higher compared to ‘healthy’ individual as a significant portion of the canopy material had been lost pre-fire.

The same measurements were taken in unburnt plots, without the need for categorising fire damage, instead to capture information about which trees had been drought-affected and how they had recovered. The height at which drought induced epicormic resprouts were protruding from the tree was recorded, along with the height of resprouts themselves. A count was taken of any epicormic sprouts and grouped according to diameter classes: 0-5 cm, 5-10 cm, 10-12 cm.

Individuals fell in to categories of complete mortality (lack of resprouting), partial mortality (only bole resprouting), top kill (only basal resprouting), or live (resprouting in the canopy). For the purposes of this study, partial mortality refers to individuals that have suffered severe canopy dieback and have only epicormically resprouted on the bole.

4.3.4.2 Regeneration counts

At each of the subplots a count of the tree species germinants, seedlings, saplings and resprouters was conducted. Classification of regeneration followed Abbott and Loneragan (1984) (Table 4.1).

Table 4.1:Classification of regeneration in the Northern Jarrah Forest (reproduced from Abbott & Loneragan, 1984).

Regeneration Type	Description
Seedling	Less than one year old, usually with cotyledons present, without an obvious lignotuber
Lignotuberous seedling	More than one year old, cotyledons absent, and lignotuber obvious
Seedling coppice	Formed from lignotuberous seedling after damage has caused the original shoot to die
Ground coppice	Shoot length up to 1.5m and representing a resprout from the lignotuber after the death of antecedent shoots.
Sapling	Shoot length more than 1.5 m in height but diameter at breast height less than 15 cm.

4.3.5 Fine woody debris survey

To avoid further repetition, collection and calculation of fine woody debris (FWD) loads can be found in section 4.3.3.3.

4.3.6 Statistical analyses

The overarching aims of this study were to investigate the linked and compounding effects of drought plus wildfire as a disturbance iteration. All data analyses were conducted using R (R

Core Team 2014) with the lme4 (Bates *et al.* 2014) package and data visualisation with ggplot (Wickham 2011). In all cases means are reported and 95% confidence intervals and a lack of overlap of the mean with adjacent confidence intervals was interpreted as evidence of a statistical difference between groups, while asymmetrical overlap of means (intervals overlap one mean but not the other) was interpreted as suggestive evidence of a statistical difference between groups (Ramsey and Schafer 2012). Impact and early response were quantified one-year post wildfire.

To investigate the linked effects of the double disturbance of drought and wildfire, the effect of pre-fire stress on two separate measures of fire severity at the stand level was evaluated. This included a remotely sensed index of fire severity (RdNBR), and post fire fine woody debris measurements. Differences in fire severity were analysed between pre-fire drought stress with t-tests.

To evaluate whether drought and wildfire had compounding effects on post fire biotic response differences in mortality at the site and stem scale were investigated. For response measures quantified at the site scale, differences in basal area, stem density, proportional basal area mortality and post fire seedling recruitment were assessed. One-way ANOVA with Tukey's multiple comparison test were used to assess the interaction between pre-fire drought stress and fire-killed individuals.

To evaluate the effects of drought and wildfire on the probability of stem death and early resprouting, the effects of the disturbances individually (separately) or combined (drought + fire) with other variables specific to the site, individual (multiple stems), and stem were evaluated. To test whether a combination of these factors may have predisposed certain stems to *top kill* or a lower resprouting proportion a series of general linear models (GLMs), with the binomial distribution and proportional stem mortality as our response were used. A range of site, individual and stem factors were included to test the *a priori* hypotheses of drought and wildfire disturbance interactions. Given that the experimental design included measures of multiple stems on a single individual, and fire severity plots were nested within drought condition sites, a mixed effects model structure was implemented. Random effects were assigned to a site, plot and tree identifier to account for multiple stems on a single individual. Fixed effects included stand level factors such as, site basal area, time since fire and harvest history (recorded number of times harvested), drought probability, and fire severity experienced. Tree level data included; species, stems per tree, and the tree cross sectional area (area of all stems on the individual combined). Stem level data included diameter at breast height (DBH) of the stem. Interacting variables added to models were; drought condition and fire severity, drought condition and species, fire severity and species, stem size (DBH) and stems per tree.

A set of candidate models were developed which included variables to test the *a priori* hypotheses (drought and wildfire) as well as other site, individual, and stem level variables (harvest and fire history, species and stem size). Akaike's information criterion (AIC) was used to evaluate the model set, and the model with the lowest AIC value was considered the 'best' model. Models that fell within two AIC points of the best model were considered as potential alternatives (Anderson and Burnham 2004; Zuur *et al.* 2009). Prior to analysis covariates were assessed for outliers and collinearity. Model residuals were examined graphically to ensure model assumptions were met and no violations were detected. A natural logarithm was applied to linearize the fit between DBH and probability of top kill. The same method was used to analyse differences in resprouting proportion, which was the ratio of live height to maximum height of that stem resulting in a scale between 0 (dead stem) and 1 (Resprouting at pre-fire height).

4.4 Results

4.4.1 Fire severity and linked disturbance effects

There was no evidence of differences in fire severity across pre-fire drought conditions (Figure 4.2) with a large overlap of 95% confidence intervals for both measures. Pre-fire drought stress did not increase remotely sensed measures of fire severity (Figure 4.2a), or post fire fine debris loads (diameter <7.6cm, Figure 4.2b).

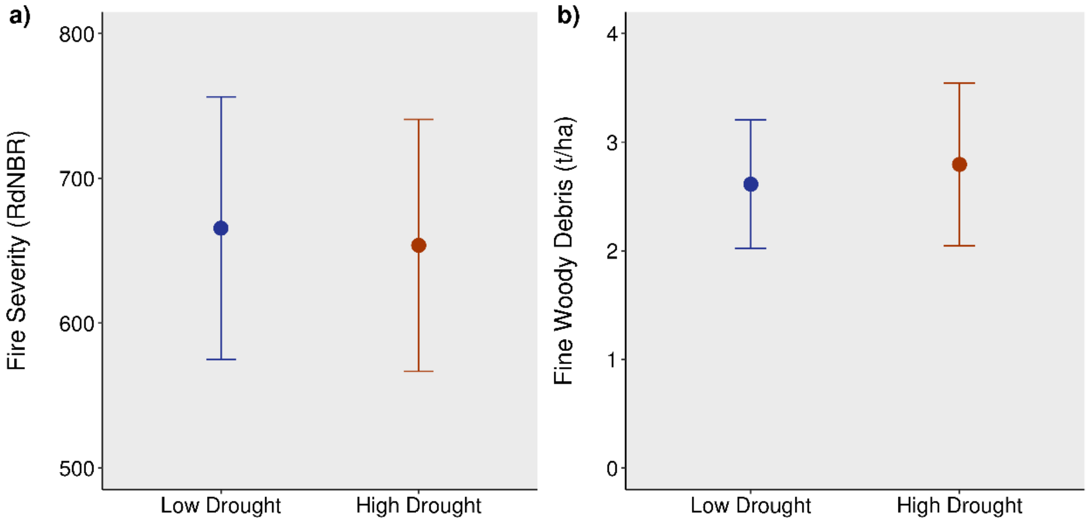

Figure 4.2: Indicators of a linked disturbance interaction between drought and wildfire a) remotely sensed fire severity (RdNBR) and b) post fire fine woody debris (t ha^{-1}) loads in drought and fire affected plots of the Northern Jarrah Forest, southwestern Australia.

4.4.2 Stand structure and compound effects of disturbances

Stem diameter distributions of all individuals (live and dead) for the fire severities within respective drought probability condition were similar in shape (Figure 4.3), and had modal stem diameter categories of 5-10cm DBH. However, high drought sites had a higher relative abundance of smaller stems, and fewer large stems, whereas low drought probability sites had fewer small stems and a higher number of large mature individuals (Figure 4.3). The majority of the small stems (5-10 cm DBH) did not survive wildfire in either pre-fire drought conditions (Figure 4.3). Following wildfire, live stem distributions were similar in shape with modal stem diameter shifting towards larger, more mature individuals (Figure 4.4). However, modal stem diameter was smaller in the high drought probability sites (10-20cm DBH) compared to low drought probability sites (30-40cm DBH).

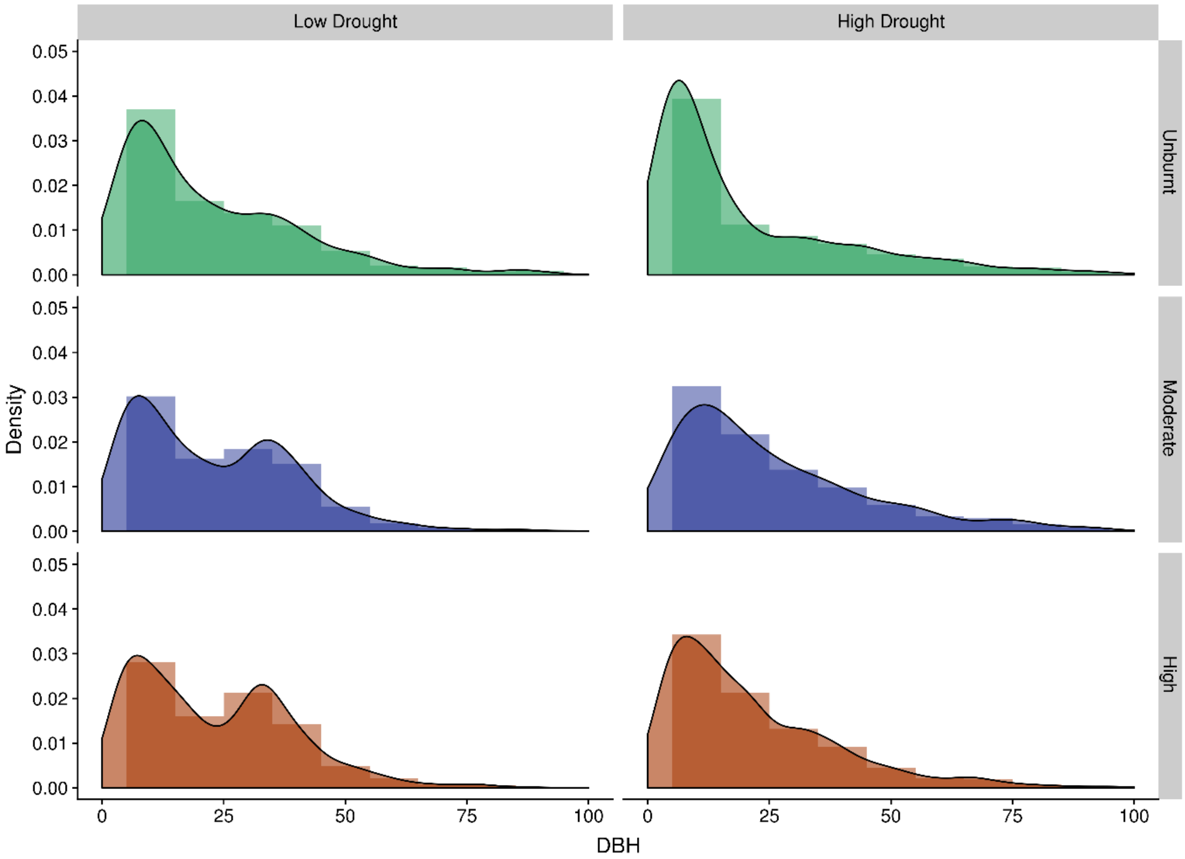

Figure 4.3: Weighted density plot of diameter distributions in drought and fire affected and control plots of the Northern Jarrah Forest, southwestern Australia. Showing all stems measured (live and dead).

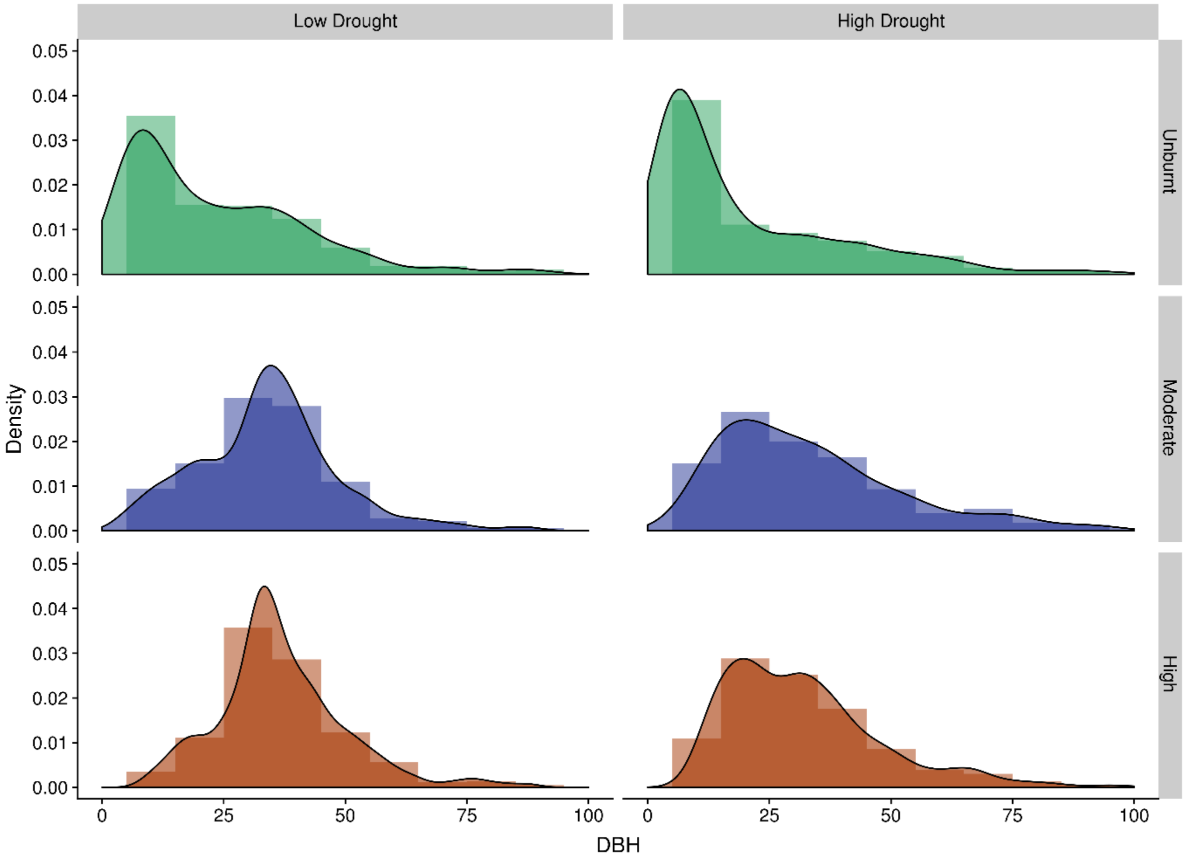

Figure 4.4: Weighted density plot of diameter distributions in low and high drought probability and moderate and high fire affected and unburnt plots of the Northern Jarrah Forest, southwestern Australia (showing only the live stems persisting following the wildfire).

The pre-fire stand conditions of basal area and stem density showed no significant differences amongst fire severity and drought probability combinations (Figure 4.5-Figure 4.6). However, the highest total basal area (56.4 ± 21.4 m^2 ha^{-1}, Figure 4.5) and stem density (2763 ± 934 stems ha^{-1}, Figure 4.4) was recorded in the unburnt high drought plots. There was higher variability in stocking density in the high drought probability sites compared to the low drought probability sites, which was evidenced by larger confidence intervals across all fire severity classes (Figure 4.5).

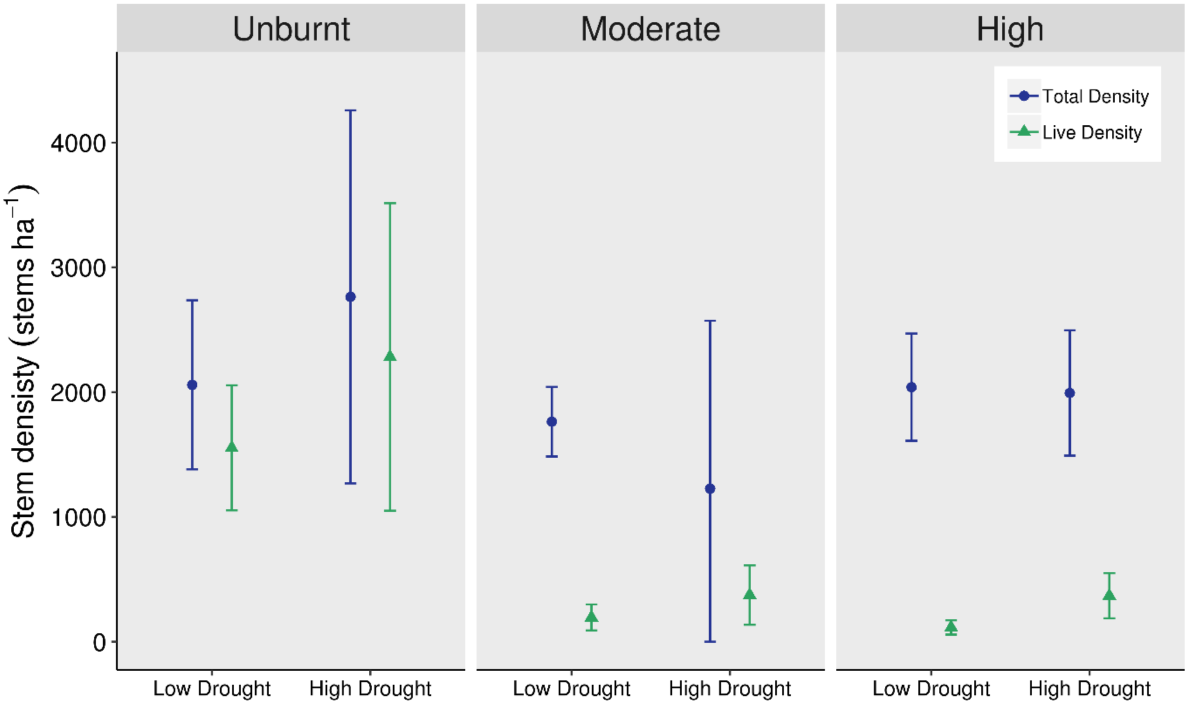

Figure 4.5: Mean total (circles) and live (triangles) stem density in sites with low and high drought probability, moderate and high severity fire-affected, and unburnt control plots of the Northern Jarrah Forest, southwestern Australia. Estimates are means of (±95% CI).

4.4.3 Post-fire stand mortality and compound effects of drought and wildfire

Wildfire strongly reduced live basal area (-20.7 ± 7.3 m^2 ha^{-1}, $F_{(2,36)} = 28.84$, $p < 0.001$, Figure 4.6) and stem density (1654 ± 406 stems ha^{-1}, $F_{(2,36)} = 67.8$, $p < 0.001$, Figure 4.5) compared to the unburnt plots, with no significant difference between the moderate and high fire severities ($F_{(2,36)} = 26.82$, $p = 0.9$, Figure 4.6). The low drought probability plots had consistently smaller live basal areas in respective burn categories compared to the high drought probability plots, however, there was a large overlap of confidence interval bars. There was no evidence of drought legacy interacting with wildfire impacts with the impact of wildfire more apparent in all measures of stand mortality (Figure 4.5 - Figure 4.7). Wildfire preferentially removed smaller stems from the stands (Figure 4.4).

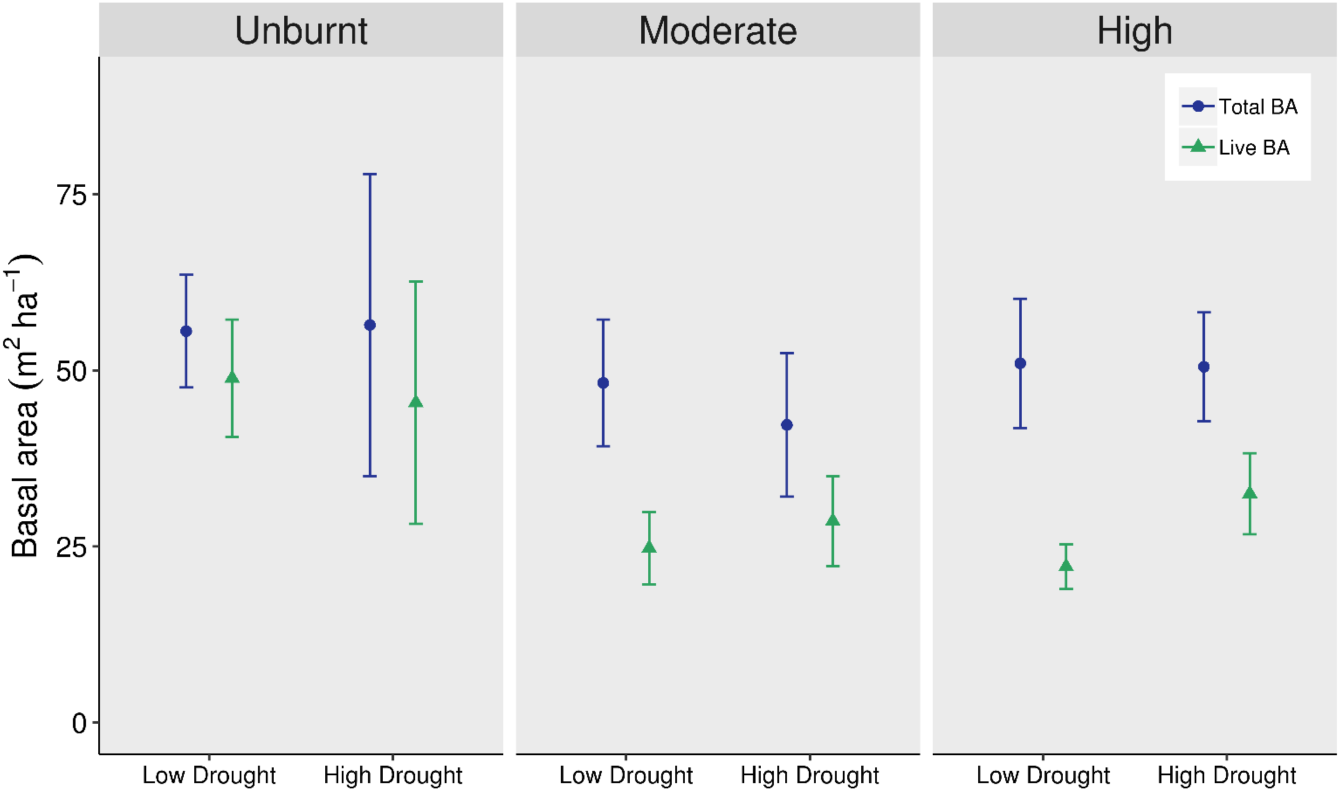

Figure 4.6: Mean total (circles) and live (triangles) basal area (m^2 ha^{-1}) in drought and fire affected and control plots of the Northern Jarrah Forest, southwestern Australia. Estimates are means with 95% CI bars.

Mean proportional basal area (m^2 ha^{-1}) stem mortality increased with fire severity and this was more pronounced in plots with low drought probability (Figure 4.7). There was a strong wildfire effect on proportional basal area mortality, with both drought conditions showing markedly lower live basal area in burnt areas compared to unburnt areas (Figure 4.6, Figure 4.7). Interactions between pre-fire drought stress and post fire mortality were less pronounced, with the low drought probability condition showing consistently higher levels of partial and total stem mortality compared to the high drought probability alternative for the respective burn condition (Figure 4.7). Partial mortality was unchanged in high drought plots between unburnt and moderate fire severity. However, this subsequently increased and was then similar to the low drought probability condition in the high severity wildfire plots (Figure 4.7).

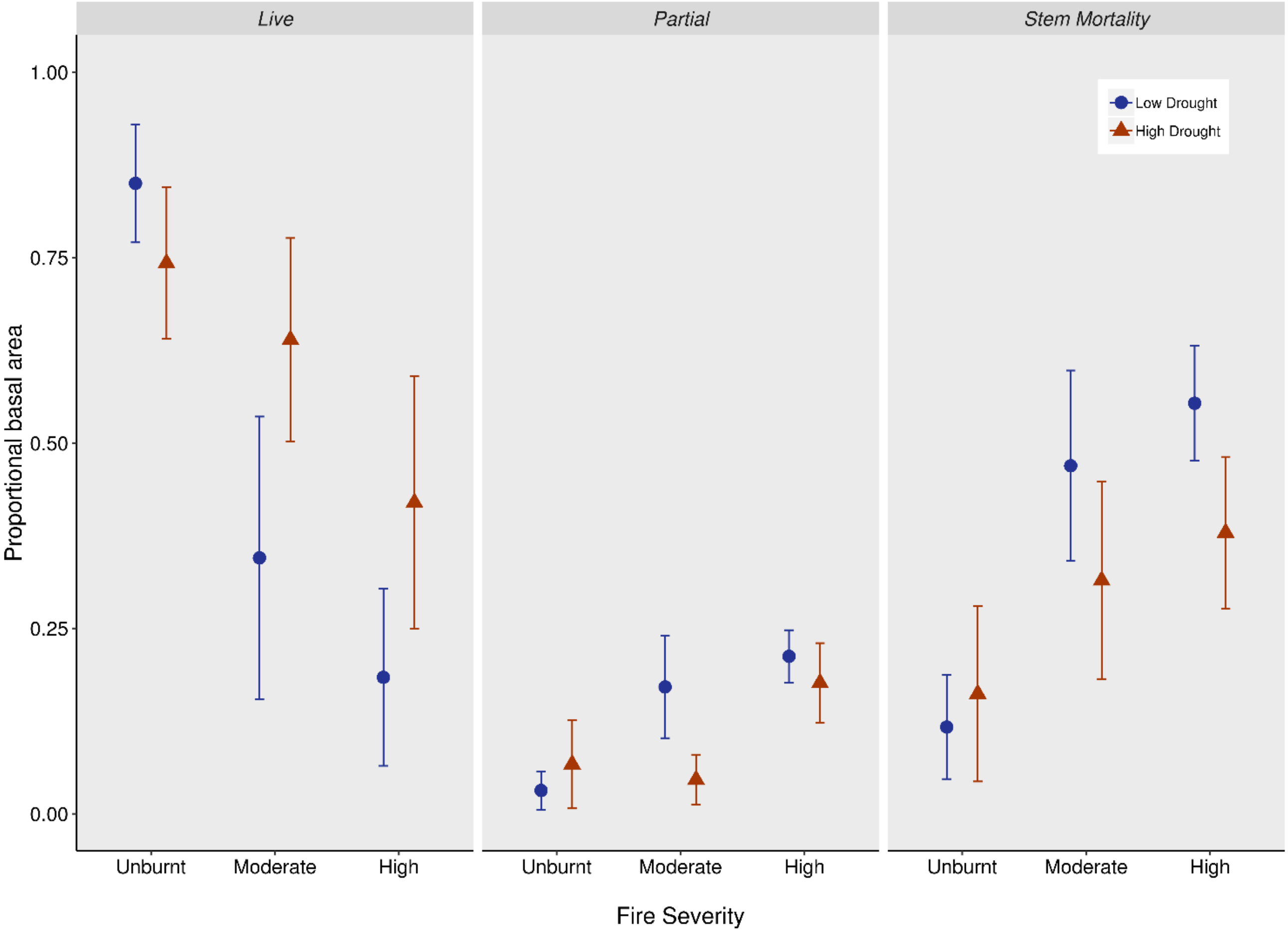

Figure 4.7: Proportional basal area separated by sprouting types (live, partial mortality, stem mortality) in high drought (triangles) and low drought (circles) fire affected and unburnt plots of the Northern Jarrah Forest, southwestern Australia. Estimates are means (±95% CI)

4.4.4 Post fire recruitment

Pre-fire drought condition and fire severity altered post-fire seedling counts of the two overstorey tree species (Figure 4.8). *E. marginata* germination rates were consistently higher than those for *C. calophylla*, for all drought and fire severity combinations (Figure 4.8). High fire severity fire reduced germinant recruitment to the same rate as unburnt control plots ($F_{(1,60)} = 0.15$, $p = 0.70$). Moderate severity wildfire significantly increased post fire seedling counts, with mean germination count of moderate fire severity (7192 ± 3409 germinants ha^{-1}) compared to high severity and unburnt plots (2681±959 germinants ha^{-1}, $F_{(2,83)} = 14.36$ $p<0.001$). Whilst there was an obvious fire effect on post-fire recruitment, the effect of pre-fire drought was less obvious. High drought condition consistently increased post fire seedling count compared with the low drought alternative, however there was large overlap of confidence interval bars (Figure 4.8).

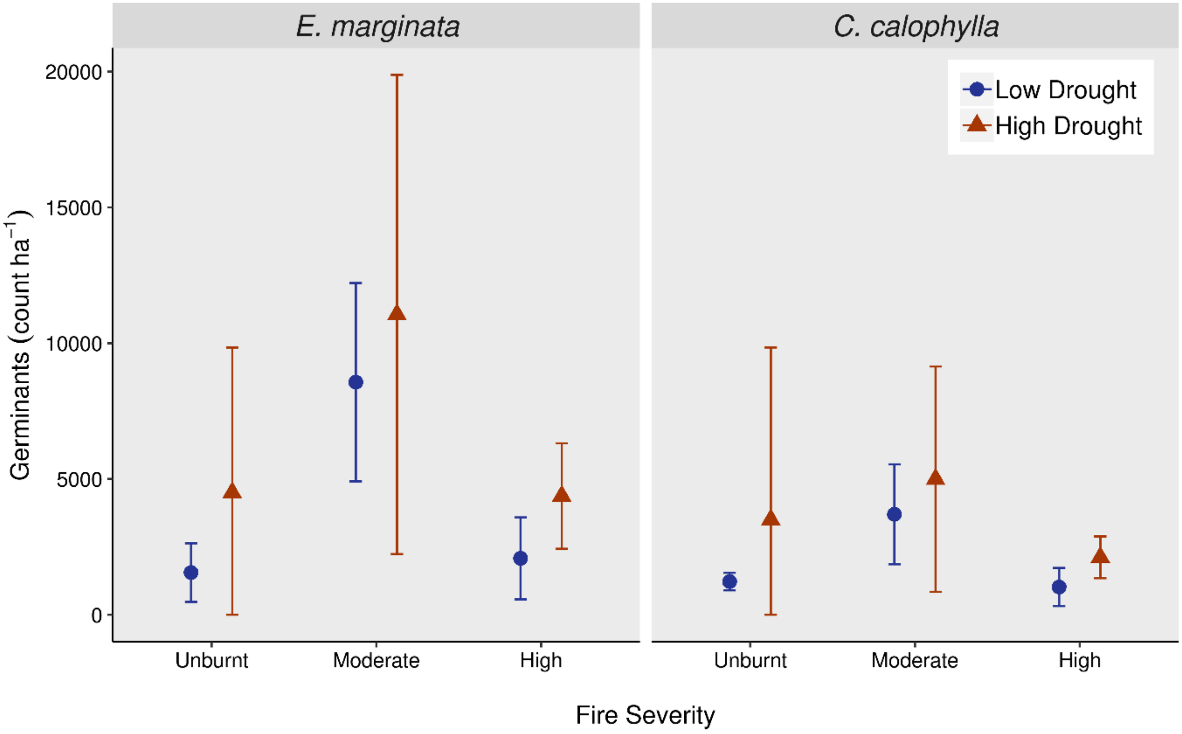

Figure 4.8: Mean recruitment (germinants ha^{-1}) of the co-dominant overstorey tree species (*Eucalyptus marginata* and *Corymbia calophylla*) in drought and fire affected and control plots of the Northern Jarrah Forest, southwestern Australia. Estimates are means (±95% CI).

4.4.5 Stem level response to drought and wildfire

4.4.5.1 Top kill

The best model explaining the probability of stem survival (Model Weight ω_ii = 0.62, Table 4.2) included stem size (log-DBH), cross sectional area of the tree (which includes all stems of that tree), species, site basal area, frequency of harvest, time since last fire, and two-way interactions between drought condition and fire severity, tree species and time since fire, fire severity and previous fire type. Other competitive models included the number of stems per tree, the presence of a stump as part of the tree, and the interaction between log-DBH and stems per tree. Within the best models, stem size (log-DBH), fire severity and harvest frequency were consistently the variables that had the greatest impact (effect size) on stem survival. Larger stems were more likely to survive ($\Delta P_{topkill}$ ~ 0.80, z = 26.98, $p<0.001$, Figure 4.9a) for all combinations of drought and fire severity. The impact of pre-fire drought stress on stem survival was not as obvious as wildfire (Figure 4.9).

Areas with a high probability of drought had a reduced probability of stem survival in the unburnt condition (Figure 4.9). However, in combination with wildfire evidence of pre-fire drought legacy is minimal with large overlap of 95% confidence interval bars between low and high drought probability conditions. A high drought condition increased the probability of survival marginally compared to that in the low drought condition ($\Delta P_{survival}$ ~ 0.64, z = 2.28, $p<0.05$, Figure 4.9a). Harvest frequency also decreased stem survival, with areas experiencing more timber harvests having a decreased probability of stem survival ($\Delta P_{survival}$ -0.44, z= -5.80, $p<0.001$, Table 4.2)

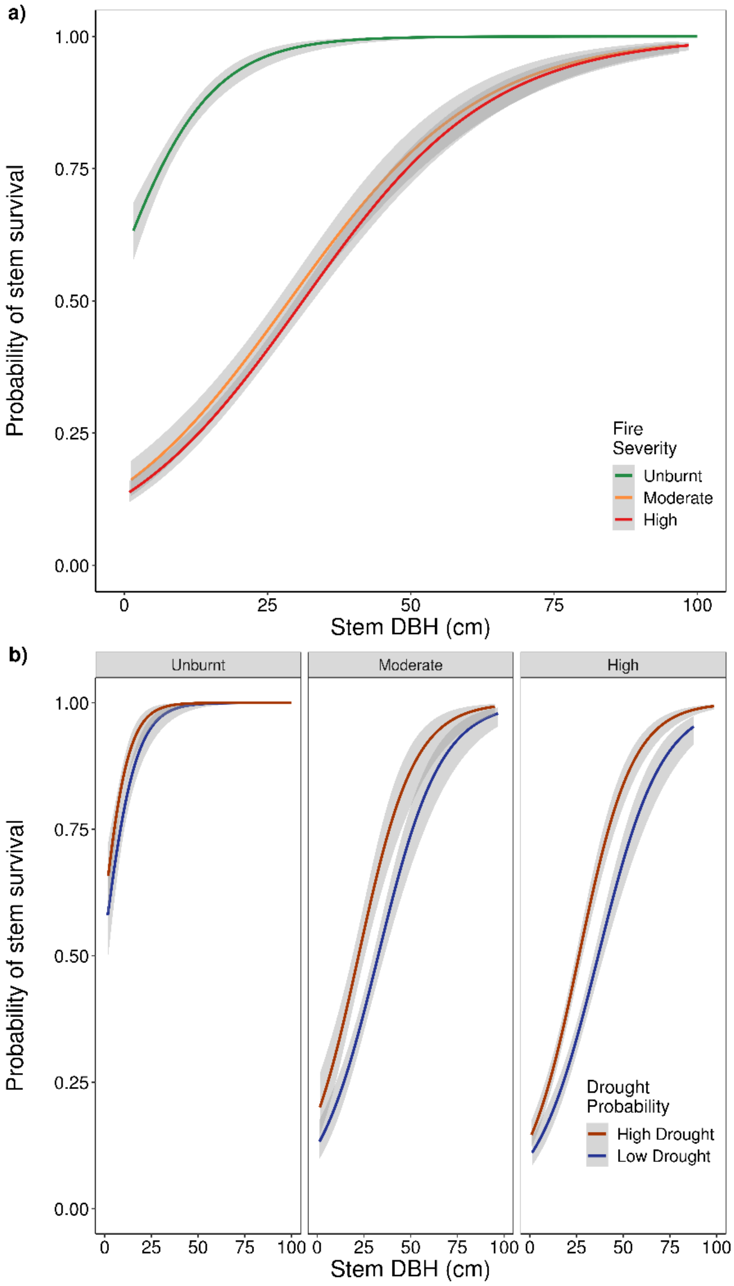

Figure 4.9: Predicted probability of stem survival and diameter at breast height (DBH, cm) in response to a) wildfire severity (unburnt, moderate, and high) and b) and drought probability (low and high drought), in the Northern Jarrah Forest, southwestern Australia. Predictions from the 'best' model. Shaded area indicates the 95% CI of the estimate.

Table 4.2: Results from a linear mixed effects model used to quantify top kill in wildfire burnt plots across differing pre-fire drought probability conditions in the Northern Jarrah Forest. Models tested differences in probability of top kill across fire severity and drought conditions, using covariates from site to stem level. 95% confidence intervals in brackets.

	Top kill			
Coefficients	Estimate	Odds Ratios (±CI)	z-value	p-value
(Intercept)	0.98	62.46 (±30.9)	11.87	**<0.001**
High drought probability	0.64	1.75 (±0.67)	2.28	**0.022**
Fire severity class (Moderate)	-0.03	0.03 (±0.02)	-8.96	**<0.001**
Fire severity class (High)	-0.04	0.04 (±0.02)	-8.26	**<0.001**
Site basal area (m^2 ha^{-1})	-0.47	0.9 (±0.07)	-2.66	**0.008**
Log(DBH (cm))	0.80	4.06 (±0.39)	26.98	**<0.001**
Species (*E. marginata*)	-0.24	0.31 (±0.13)	-4.09	**<0.001**
Time since fire (years)	-0.49	0.96 (±0.01)	-5.22	**<0.001**
Harvest frequency	-0.44	0.8 (±0.06)	-5.80	**<0.001**
High drought probability: Moderate fire severity	-0.38	0.61 (±0.24)	-1.95	0.051
High drought probability: High fire severity	-0.32	0.48 (±0.19)	-2.91	**0.004**
Moderate fire severity: *E. marginata*	0.75	2.98 (±1.35)	3.53	**<0.001**
High fire severity: *E. marginata*	0.76	3.15 (±1.32)	4.12	**<0.001**
High drought probability: *E. marginata*	-0.47	0.87 (±0.27)	-0.79	0.429

Model based on 5069 observations from 47 plots.

4.4.5.2 Resprouting proportion

Eucalyptus marginata and *C. calophylla* stem survival varied based on pre-fire drought stress as well as fire severity. As fire and drought categories changed, the two species changed order thereby reflecting the two-way interaction of species and drought condition. The two dominant overstorey species exhibited differing probabilities of top kill following drought and wildfire overall, with the likelihood of survival decreasing if stems were *E. marginata* ($\Delta P_{\text{resprouting}} \sim -0.31$, z = 4.33, p<0.001, Figure 4.9a) compared to *C. calophylla*. Under high drought probability conditions *C. calophylla* showed higher ratios of stem resprouting compared to a *E. marginata* stem of the same size (Figure 4.10). However, without pre-fire stress *E. marginata* had increased ratios of resprouting compared to *C. calophylla* (Table 4.3,Figure 4.10).

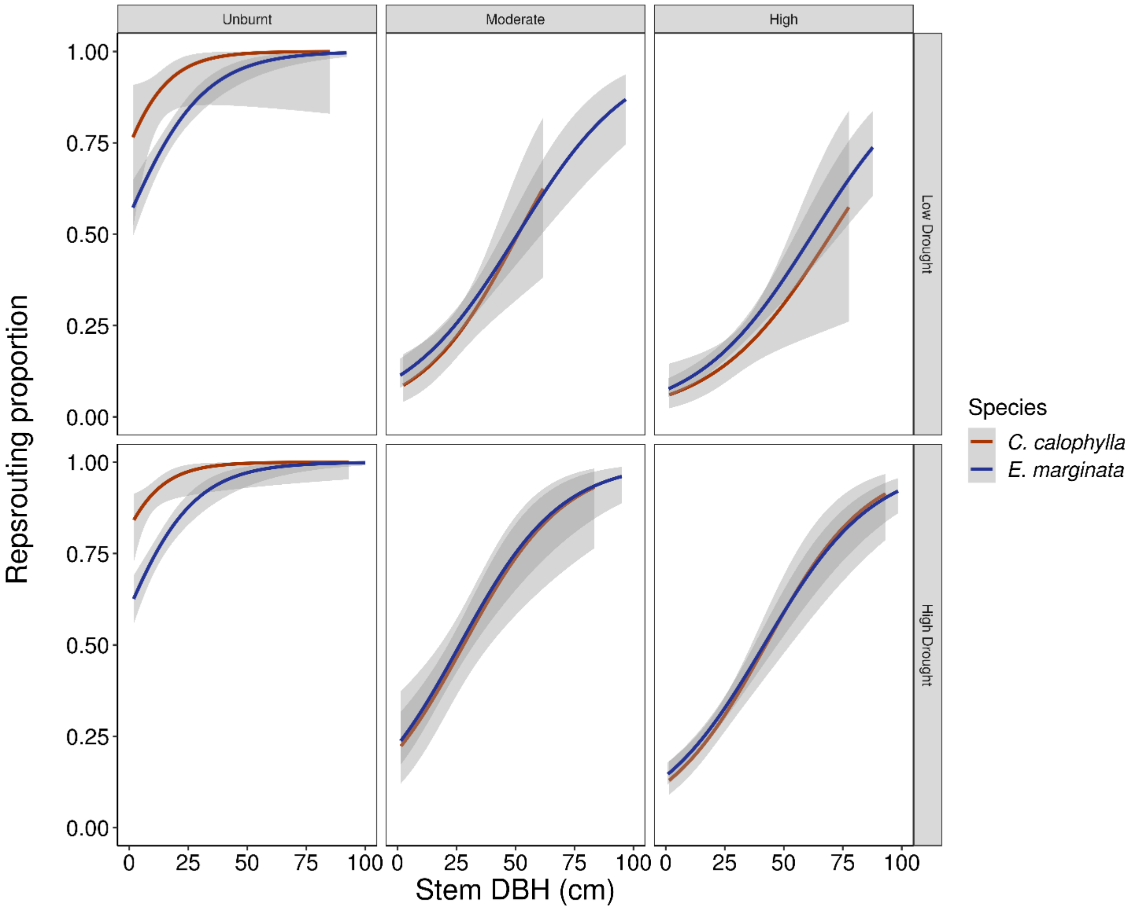

Figure 4.10: Predicted resprouting height proportion of *Eucalyptus marginata* and *Corymbia calophylla* in response to DBH, in the Northern Jarrah Forest, southwestern Australia. Predictions are from the 'best' model and shown for all combinations of fire severity and drought condition measured. Shaded area indicates the 95% CI of the estimate.

Table 4.3: Results from a linear mixed effects model used to quantify the resprouting proportion in wildfire burnt plots across differing pre-fire drought conditions in the Northern Jarrah Forest, southwestern Australia. Models tested differences in probability of top kill across fire severity and drought conditions, using covariates from site to stem level with 95% confidence intervals in brackets.

		Resprouting proportion		
Coefficients	Estimate	Odds Ratios (±CI)	z-value	p-value
Intercept	0.97	33.09 (±13.74)	12.79	**<0.001**
High drought probability	0.63	1.67 (±0.06)	2.24	**0.025**
Fire severity class (Moderate)	-0.04	0.04 (±0.02)	-10.48	**<0.001**
Fire severity class (High)	-0.03	0.03 (±0.01)	-11.2	**<0.001**
Log(DBH (cm))	0.70	2.38 (±0.02)	19.53	**<0.001**
Species (*Eucalyptus marginata*)	-0.24	0.31 (±0.12)	-4.58	**<0.001**
Site basal area (m^2 ha^{-1})	-0.48	0.91 (±0.07)	-2.44	**0.015**
Stems per tree	-0.46	0.86 (±0.07)	-3.86	**<0.001**
Time since fire (years)	-0.49	0.95 (±0.01)	-6.43	**<0.001**
Harvest frequency	-0.43	0.74 (±0.06)	-7.09	**<0.001**
High drought probability: Moderate fire severity	-0.44	0.8 (±0.29)	-0.97	0.33
High drought probability: High fire severity	-0.37	0.58 (±0.21)	-2.37	**0.017**
Moderate fire severity: *Eucalyptus marginata*	0.81	4.21 (±1.79)	5.08	**<0.001**
High fire severity: *Eucalyptus marginata*	0.82	4.68 (±1.83)	6.08	**<0.001**
High drought probability: *Eucalyptus marginata*	-0.48	0.93 (±0.29)	-0.36	0.716

Model based on 5069 observations from 37 plots.

4.5 Discussion

This study has shown that in the resilient resprouting Northern Jarrah Forest of southwestern Australia, pre-fire drought does not seem to increase subsequent fire severity (linked disturbance) experienced or biotic responses (compound disturbance) following a wildfire. Responses to drought and wildfire alone were consistent with other studies from this forest type (Abbott and Loneragan 1983; Matusick *et al.* 2013; Ruthrof *et al.* 2018). When the combined effect of both disturbances was analysed, there was no evidence of any interaction between these two disturbances in impact and early response measures. There was no difference between the impacts of fire severity (i.e. RdNBR) in drought plus wildfire sites, and those with no pre-fire stress, suggesting that any increased fuel loads from drought induced canopy die-off did not alter local fire severity under these high severity conditions experienced at the Waroona Fire.

Evidence of a compound disturbance was not present within the timeframe of this study, with mortality, proportional resprouting and recruitment rates with these not showing evidence of interactions between drought and wildfire thus far. Instead, the plots showed a single strong effect of the wildfire. It thus follows that high severity canopy fire may override pre-fire drought legacy. However, the future trajectory of regrowth and potential for further collapse in these two pre-fire drought conditions (low and high drought probability) may differ as high drought probability sites are more prone to drought induced canopy collapse. Regrowth and stand dynamics will also be heavily dependent upon the future disturbance regime, as new growth and epicormic regrowth begin to reach a size where they can withstand stressors.

4.5.1 Fire severity and linked disturbance effects

Drought induced canopy die-off increases fuel loads as dead standing material is converted to fine woody debris, which may affect fire behaviour, such as fire rate of spread in die-off stands, compared to surrounding ‘healthy’ forest (Ruthrof *et al.* 2016). Evidence of linked disturbance effects between drought and wildfire severity were not present in remotely sensed RdNBR values and post fire FWD loads. A high FWD load post fire may indicate higher fire severity in the canopy, leading to higher canopy dead biomass, and therefore larger post fire woody debris loads. Fire behaviour during the wildfire event in this study was extreme (Peace *et al.* 2017), and many of the forest stands surveyed as part of this study experienced canopy fire. Once canopy fire was present it is likely that fire severity would not be significantly altered by the increased pre-fire litter loads or elevated fuel loads (dead material in the canopy) caused by drought induced canopy die-off. Similar results have been reported in a subalpine forest of Wyoming where beetle (*Dendroctonus ponderosae)* outbreak followed by wildfire occurred. Harvey *et al.* (2014a) reported that the fire severity was higher in areas with a recent beetle outbreak if moderate fire was present. However, once high severity fire (canopy fire) was present there was no link between outbreak age and fire severity (Harvey *et al.* 2014a). Our results indicate that even moderate severity (canopy scorch) fire may diminish the link between drought legacy and subsequent fire severity.

4.5.2 Mortality and compound disturbance impact at the stand scale

Pre-fire forest structure was markedly different between the drought conditions, with the high drought probability condition having a higher abundance of small stems and fewer large stems, compared to the low drought probability condition. The low drought condition had an almost bimodal distribution in stem DBH with peaks between 10-15 cm and 30-40 cm. Drought induced canopy die-off increases the number of small stems in a stand as the individuals regrow from resprouts and new individuals (Nano and Clarke 2011; Matusick *et al.* 2016). Following the wildfire in this current study, the diameter distribution of persisting stems was similar between the two drought conditions, with the smaller stems mostly killed by fire and some larger, potentially pre-fire stressed trees also dying. High rates of regeneration and resprouting, coupled with declining rainfall may see these forest stands more vulnerable to drought collapse continuing towards more densely stocked 'states'. It follows that large individuals are increasingly important for persistence and stand structure. However, the time between disturbances and the next disturbance type is likely to determine the future structure of these stands. For example, fire in all forms preferentially removes small individuals from a stand and large mature individuals persist (Abbott and Loneragan 1986). However, drought and heatwave related die-off thins from above, preferentially affecting large mature individuals and pushing them to shorter multi-stemmed versions of the same tree, or new individuals (Matusick *et al.* 2016). Following the wildfire there has been a significant decrease in the live individuals in these stands and regrowth will be susceptible to high rates of mortality with further disturbance as both new individuals and resprouting mature individuals regenerate the stands.

This study has shown that the resprouting overstorey species of the Northern Jarrah Forest, *E. marginata* and *C. calophylla* are extremely resilient to disturbance, with many individuals surviving both extreme drought and heatwave conditions, as well as a canopy fire. The Northern Jarrah Forest is an ecosystem that does not typically experience stand-replacing fire (Abbott and Loneragan 1986; Burrows 2013). Large mature individuals in this region are typically not killed by fire. However, rates of stem top kill found here were higher than previously recorded following canopy fire with 23.5% of mature (DBH >30 cm) suffering top kill in our study, compared with the 11.7% previously reported for this size class (Peet and Williamson 1968). Furthermore, with 49% of total BA top kill (all individuals), the wildfire studied here was potentially as close as this system gets to 'stand replacing', where many individuals are regrowing from basal resprouts or have died completely. Stand replacing fires are common in mixed conifer forests where most overstorey tree species do not resprout following fire and instead rely on seed stores for regeneration (Wagener 1961). In this study, although not all of the overstorey individuals have suffered stem mortality, a significant portion either suffered partial mortality or stem mortality, clearly illustrating the severity of the fire and its impact on the forest.

4.5.3 Mortality and compound disturbance impact at the stem scale

This study investigated the singular and interactive effects of drought and wildfire on stand and stem level measures of mortality. There was no evidence of an interaction between pre-fire drought condition and mortality, or proportional resprouting height. Larger stems are more likely to survive high severity wildfire, and species behaved differently between the two disturbance factors. Stem size is consistently a determinant of stem survival throughout resprouting (Collins 2019) and non-sprouting forests (Regelbrugge and Conard 1993). Differences between species survival dependant on disturbance types are consistent with other works, which suggest that *E. marginata* and *C. calophylla* have different life strategies to deal with disturbance (Ruthrof *et al.* 2015).

Harvest frequency and time since previous fire also appeared to be an important determinant of stem survival. Individuals located in stands which had higher frequencies of logging were more likely to suffer stem mortality and resprout at lower levels, compared to stems of the same size located in areas harvested fewer times. A higher frequency of timber harvest could increase mortality with further disturbance as harvest removes genetically stronger individuals (large, straight, no bole damage). It follows that after repeated entries the individuals remaining in the stand are mostly made up of damaged (basal scarring) or not merchantable (multi-stemmed). Harvest activity also leads to soil compaction which may reduce the productive capacity (regrowth) of those stands (Whitford and Mellican 2011). It follows that more frequent timber harvest could lead to greater and more widespread compaction. More research is required to understand the effect of timber harvest activities on forest resilience. This highlights the importance of forest management practices on forest resilience to disturbance, particularly under changing conditions.

4.5.4 Initial regrowth and stand trajectory

High severity canopy fire may diminish the legacy effects of a drought disturbance in relation to stand level stem mortality. Lower drought conditions had consistently higher levels of mortality across multiple stand level measures (basal area, stems per hectare) than under high drought probability conditions, potentially suggesting that those individuals that were stressed pre-fire were more capable of withstanding fire effects. Evidence of compound interactions between these disturbances was also not present in the regrowth following fire. Sites that were drought affected before the wildfire showed consistently higher rates of recruitment compared to those that did not have evidence of a drought response. It is likely that once canopy fire is present evidence of interaction between drought and wildfire are diminished. However, post-fire regrowth vulnerable and areas more prone to drought and water stress could be predisposed to further collapse following the wildfire. Therefore, long term germinant and resprouting success may be diminished in high drought stands.

Projections for this region are an increase in fire frequency (Clarke *et al.* 2016) and severity as rainfall continues to decline and temperatures increase (Bates *et al.* 2008; Andrys *et al.* 2017). Eucalypt forests have been reported to have resprouting failure with repeated fire events before recovery from the last fire event (Fairman *et al.* 2019). Given the high proportion of mortality and subsequent regrowth most fire affected stands are vulnerable to further loss with another fire event. The NJF is a resilient system with mature overstorey individuals capable of regrowing following both drought and wildfire conditions. However, with further disturbance and a declining rainfall, some stands could potentially ‘tip over’ with high mortality of persisting individuals. As burnt stands resprout and regrow following these disturbances, affected areas will predominantly be occupied by large dead individuals and regrowth will occur through smaller trees (basal resprouts and new growth). This is a state which will require decades before recovery to a point where stems can survive disturbance. However, with a continual decline of rainfall, and projected increases in frequency and severity of fire these stands are likely to be disturbed before reaching a mature forest structure and will therefore continue to transition towards shorter, smaller, and more densely stocked stands of *E. marginata* and *C. calophylla*.

4.6 Conclusions

This study found that high severity wildfire overrides drought legacy in the resprouting Northern Jarrah Forest. There was no evidence of additive or interactive effects with moderate fire severity in impact (mortality) and early response (resprouting and recruitment). Instead there was a strong impact of wildfire reducing live basal area, and live stem density. Stem survival and resprouting proportion was influenced most by stem size (DBH), fire severity, and the frequency of harvest. With a high proportion of partial death and full stem mortality the affected stands will need decades to regrow in order to be able to withstand further disturbance and potentially return to a pre-fire structure. However, with declining rainfall and projected increases in fire frequency and severity, it may be unlikely that more vulnerable stands will return to pre-fire structural states, instead transitioning towards smaller, shorter and denser stocked stands.

5 General Discussion

5.1 Introduction

Globally, pressure on forest carbon stocks will continue to increase as disturbance regimes shift to more frequent and severe events with a warming and drying climate. The effect of different disturbances on stand structure and carbon balances have been well documented in the non-sprouting forests of the northern hemisphere (Campbell *et al.* 2007; Kurz *et al.* 2008a; Valinger and Fridman 2011; Buma *et al.* 2014). However, there is a distinct lack of knowledge on disturbance effects on forest structure and carbon storage in resprouting forests. Temperate forests make up 767 million ha of global forest area (Pan *et al.* 2011), and native Australian forests make up 132 million ha, which equates to approximately 21,949 Mt C stored in these forests (NFISC 2018). As forests play a significant role in global climate change mitigation efforts an understanding of the dynamics of forests under global change is vital.

As disturbance frequencies increase, there will be an escalating incidence of stacked disturbances, where multiple disturbances occur in short succession within the same forest stand and may interact producing ecological ‘surprises’ (Paine *et al.* 1998). Disruptions to disturbance regimes can cause significant and abrupt changes to forest structure (Buma 2015; Fairman *et al.* 2019). Whilst some effort has been made to document these occurrences in non-sprouting forests (Göthlin *et al.* 2000; Buma and Wessman 2011; Harvey *et al.* 2014b), there have been few reports of the effects of repeated disturbances from resprouting forests. Resprouting forests are thought to be resilient systems, capable of surviving multiple disturbance events in short succession (Bowman *et al.* 2013; Collins 2019). However, recently Fairman *et al.* (2019) reported that even these systems have their limit to disturbance where repeated fire events have led to resprouting failure of dominant overstorey eucalypt species in

Australia. It follows that, resprouting forests may have an upper threshold to disturbance resistance. Disturbance type, frequency, severity and the interplay between multiple disturbance events (of differing types and severities) is likely to affect forest structural responses and resilience in resprouting ecosystems. Multiple disturbance events may cause significant and abrupt changes to resprouting forests structure, carbon storage and resilience not dissimilar to non-sprouting forests.

In this thesis I used the Northern Jarrah Forest of southwestern Australia as a model of a resprouting ecosystem to address three major study questions (page 13). These relate to forest disturbances and their interactions with forest carbon and stand dynamics in a resprouting forest:

1) What are the carbon storage implications and recovery of global-change-type drought (hotter drought, Breshears *et al.* 2005) and recovery?
2) What are the carbon emissions and stand transformations following severe wildfire?
3) What are the additive and interacting effects of drought and wildfire on forest structure and mortality in a resprouting forest?

Although each of these questions has been explored in Chapters 2-4, this Chapter provides an overview that integrates across all chapters, providing an indication of the implications for the Northern Jarrah Forest and suggestions for future research.

5.2 Consequences of drought on carbon storage and dynamics

Prolonged drought coupled with intense heat waves trigger sudden forest die off events (Allen *et al.* 2010b), which have now been reported from all forested parts of the globe (Allen *et al.* 2015). These die-off events cause significant changes to forest structure through mortality of the large overstorey individuals (Breshears *et al.* 2005; Matusick *et al.* 2016) and function by altering soil fungal communities (Oliva *et al.* 2014; Hopkins *et al.* 2018). However, there is little documented knowledge on the consequences to carbon storage and dynamics of these events, particularly in a resprouting forest ecosystem. With a changing climate the incidence of these types of events is expected to increase (IPCC 2013) thus, highlighting the need for accurate estimates of carbon transformations to account for the consequence of drought and heatwave related die-off events. In Chapter 2, I investigated the carbon consequences of drought in a resprouting system and quantified movement of carbon through the forest carbon pools immediately following die-off and up to 26 months after the event.

The die-off event occurred in 2010-2011, and several studies documented the biotic responses to the forest and key species (Matusick *et al.* 2013; Ruthrof *et al.* 2015; Matusick *et al.* 2016; Ruthrof *et al.* 2018). I quantified the carbon dynamics showing how partial and complete mortality in overstorey trees impacted carbon pools for the 2+ years following the die-off event. In contrast to conifer-dominated systems where regeneration occurs solely via seed, trees rapidly resprouted and this buffered live carbon loss (49.3 t ha^{-1} loss of live C), increased stem densities (1020 stems ha^{-1}) and drove recovery of live carbon stocks (82-88% of labile carbon pools within 26 months). Stem mortality and therefore dead carbon remained largely in standing pools with little fragmentation over the measurement period.

Total carbon storage would be expected to increase in stands affected by drought if there were no further disturbance, as sequestration through resprouting and new growth would counteract carbon lost through biogenic decay. However, with a drying climate (Andrys *et al.* 2017) and a projected increased frequency and intensity of fire (Clarke *et al.* 2016), it is unlikely that regrowth will grow to the extent of the individuals that died.

It has been suggested that changes in climate, including a reduction in rainfall, will reduce the potential biomass (carbon) the forests of the southwestern Australia can support as the forest leaf area comes into ecohydrological equilibrium (Liu *et al.* 2019a). This is based on the theoretical framework of ecological optimality of Eagleson (1982), where in water limited environments the natural vegetation comes to a stable equilibrium with the climate and soils. It follows that with a reduction in rainfall, such as has already occurred and is predicted to occur into the future, the level of this stable equilibrium will reduce. The amounts of biomass and thus carbon storage, or carrying capacity, will thus also reduce. The Northern Jarrah Forest is growing on very deep regolithic soils, which contain both soil moisture and groundwater. There is evidence that forest growth has relied on these stores (Smettem *et al.* 2013) and the moisture in the regolith has been depleted (Kinal and Stoneman 2012). This may explain why drought deaths were associated with shallow soils with poor overall water holding capacity. Thus, the forest will readjust to a new hydrologic equilibrium (Harper *et al.* 2019).

Whilst rainfall, and interactions between vegetation and streamflow may prescribe the upper limit of carbon stored in these forests, disturbance will ultimately determine whether that carbon storage potential is achieved. The changes to forest structure following drought die-off reported here may limit the recovery of carbon storage in affected stands. Resprouting of the dominant overstorey species buffered the loss of live carbon as individuals either partially died, or resprouted in the canopy. This resilience to disturbance via resprouting will inevitably determine how long large individuals (DBH >30 cm) persist in these stands as future drought/ heatwave events occur.

Australian resprouting forest ecosystems can experience mixed severity wildfires (Collins *et al.* 2018) as well as planned fires at frequencies between 5-20 years (Murphy *et al.* 2013). Many of the stands that experienced die-off are likely to be burnt before they have completely recovered. The drought die-off affected stands are comprised of many younger, multiple resprouting stems (Matusick *et al.* 2016), and it is unlikely that many of these stems will survive fire, therefore making increases in carbon storage following drought die-off ephemeral. Any additional disturbance prior to these stands completely recovering would further push this system from being dominated by large overstorey trees towards shorter, denser stands. It follows, that resprouting forests, and the carbon stored within them, may be vulnerable to changes in disturbance regime similar to non-sprouting forest types.

5.3 Carbon storage and dynamics following wildfire in a eucalypt forest

Fire has been recognised as having a particularly large potential impact on forest carbon stocks (Campbell *et al.* 2007; Bowman *et al.* 2009; Keith *et al.* 2014) with the consequent critical need to incorporate disturbance into global carbon cycle models (Dixon *et al.* 1994; Hicke *et al.* 2012). Pyrogenic emissions from wildfire differ depending on fire severity, size and forest type it occurs within (pre-fire carbon density), with larger more severe fires typically leading to higher emission. It follows that representative estimates of pyrogenic emissions are required for all forest types.

Fire is the most common mode of disturbance in resprouting forests (Bond and Keeley 2005; Bond *et al.* 2005; Bowman *et al.* 2009). Resprouting enables large trees to quickly regain carbon lost during fire and this may occur multiple times over their lifespan. This mechanism of resprouting may lead to lower carbon losses and more rapid recovery of carbon combusted following fire compared to other forest types, which naturally experience high rates of mortality amongst mature individuals (stand replacing) when high severity fire occurs.

Southwestern Australia has experienced a reduction in rainfall (10-15%) and increase in temperature (0.15°C per decade) since the 1970s (Bates *et al.* 2008) with these drying and warming trends predicted to continue (Andrys *et al.* 2017). Fire frequency and severity is also predicted to increase (Clarke *et al.* 2016), further highlighting the need for accurate carbon accounts for resprouting forest types in this region following, for example, drought and wildfire. Continuing the theme of quantification of carbon transformations and dynamics following forest disturbance, in Chapter 3 I estimated pyrogenic emissions and carbon transformations following an extreme wildfire event in the summer of 2016.

Wildfire caused significant disruptions to the forest carbon pools in the Northern Jarrah Forest (NJF), as reported in Chapter 3. The approximately 35,000 ha of burnt upland NJF sites had total pyrogenic emissions at a rate of between 10 and 21 t C ha^{-1}, or an estimated 723 133 t C in total. This corresponds to approximately 5.5-12.2% of the pre-fire carbon density. Rates of pyrogenic carbon emission were comparable to non-sprouting forests, where Campbell *et al.* (2007) reported combustion of approximately 19 t C ha^{-1} following a severe wildfire that burnt 200,000ha of mixed coniferous forest in Oregon, United States. In areas of high fire severity, the loss of live standing carbon was estimated at 73 t ha^{-1}, significantly higher than the mean rate of pyrogenic emissions from the wildfire, and these represent carbon stores which will be released in the coming years as the dead material decomposes. Although these estimates are for one forest type, they are nonetheless very significant, when extrapolated over whole regions. A key issue for carbon accounting is whether the losses are reversible.

The Waroona Fire in January 2016 emitted significant amounts of pyrogenic carbon and caused changes to the forest carbon pools as stems died, resprouted or were converted from standing to surface carbon pools. Regrowth in the forest after fire was mainly comprised of bole epicormics and basal resprouts (66% of BA in the high severity fire areas) on persisting individuals, and new growth as seedlings. Carbon stored in these stores is vulnerable to further loss with subsequent fires. Carbon lost from the understorey pool, will be quickly replenished as shrubs regrow and regenerate. However, this pool will likely be burnt and lost in subsequent planned fuel reduction burns or wildfire. Moreover, it is relatively small (3.17 t C ha^{-1}) when compared to the forest as a whole. Similarly, litter will be subject to decomposition. Again, this is a relatively small pool (2.62 t C ha^{-1}) but can be regarded as essentially ephemeral.

Similar to the finding on the effects of drought (Chapter 2), and with an increased incidence of disturbance (decreased rainfall and increased frequency and severity of fire) projected with a changing climate, it is likely that moderate and severely burnt stands will not recover total above ground carbon storage to pre-fire levels. Fire could be regarded as a mechanism that reduces the carbon storage capacity in the forests, as climate changes and the equilibrium storage value decreases. If forests are to be maintained as long-term carbon pools, they will require management to retain large individuals within stands and promote the growth of new individuals to the size of pre-disturbance trees.

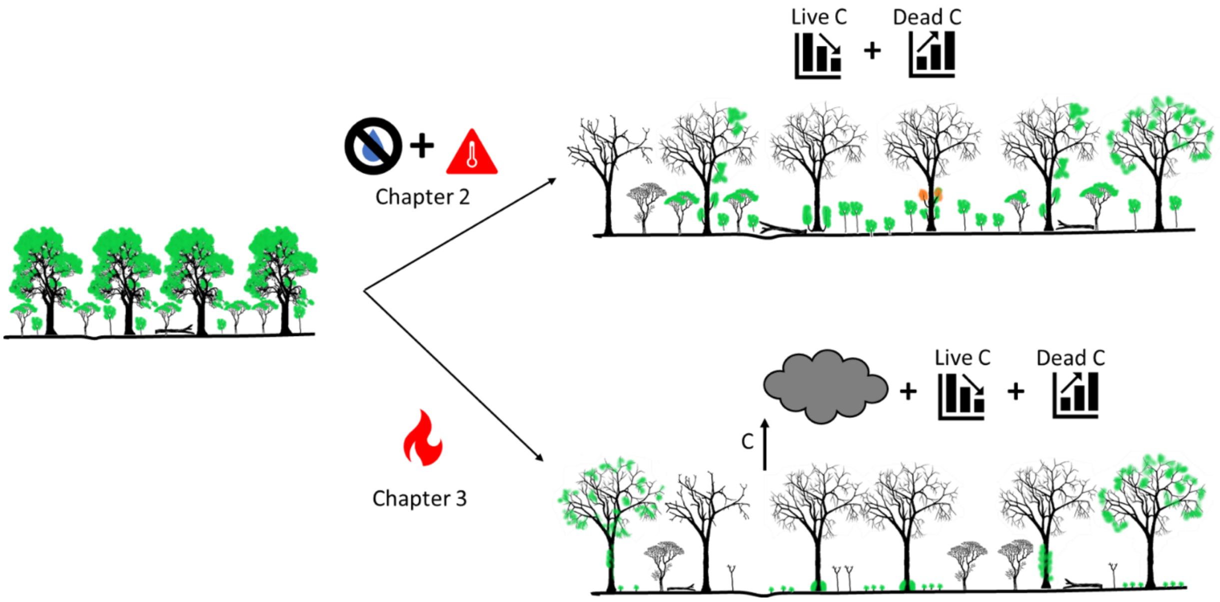

Figure 5.1 Effects of forest carbon storage and structure of areas of the Northern Jarrah Forest affected by drought and severe wildfire

Drought (Chapter 2) and wildfire (Chapter 3) both resulted in changes to the composition of forest carbon pools (Figure 5.1), in terms of total storage, the distribution across the different pools and likely future trajectories of carbon accumulation. Carbon emissions from combustion as well as biogenic decay will not override carbon sequestered in early regrowth in these stands. Drought and wildfire both altered the carbon dynamics of the affected stands with large amounts of dead wood now present. Early regrowth following these events will be similar with large stressed individuals regrowing from epicormic or basal resprouts and new recruitment through seedlings.

Both Chapters 2 and 3 illustrated that following disturbance in a resprouting forest live standing carbon moves to the dead standing carbon pool in a manner like what occurs in a non-sprouting forest. Marked separation between the two forest types occurs after disturbance where rapid regrowth and resprouting of stressed trees buffers live carbon loss and there is a return of labile carbon pools (branch, twig, foliage) to pre-disturbance levels. It is difficult to compare the actual fluxes of carbon between pools in the two forest types, as they will have different growth rates due to a variety of reasons, such as climate, soils and past management.

Dead wood generated from these disturbances will likely remain standing for a considerable period (decades), and once converted to the debris pool, multiple fire events will be required to completely remove carbon stored in these dead individuals (Whitford and McCaw 2019). Thus, although carbon moves from live standing trees to dead standing trees this is unlikely to be lost even after multiple future disturbances. It is likely that dead standing individuals are most likely to be converted to the debris pool as multiple fires burn out the base of the tree, and the individual eventually falls. Whitford and McCaw (2019) found that in the jarrah forest of southwestern Australia coarse woody debris loads were positively correlated with the number of planned burns that each stand had experienced since 1937. They suggested that these fires contribute to the eventual or immediate fall of a tree (dead or damaged) without leading to immediate consumption, thus increasing coarse woody debris loads in the forest. It follows that the individuals that have experienced partial mortality, where the crown is dead but differing amounts of the bole are still live, the live base of the bole will slow the process of snag fall as the base is still protected from future fires. Aerial dead material is likely to primarily fall via fragmentation rather than fire. This process will maintain dead standing carbon within burnt and drought affected stands for a considerable period. There are no reports of the contribution of wind throw of dead standing trees from storm events in this region. Although northern Australia is subject to regular cyclones or hurricanes, the storm tracks of very few of these moves into south-western Australia.

5.4 High severity wildfire overrides drought legacy in a resprouting forest

Disturbance regimes (composed of frequency, size, season, intensity) are often a key driver of ecosystem structure, function and composition (Buma 2015). Ecological resilience is defined as the ability of a population, community, or ecosystem to return to its pre-disturbance state and reflects the frequency, intensity and type of disturbance impacts the ecosystem can tolerate whilst still returning to its ‘original’ state (Gunderson 2000; Enright and Fontaine 2014). The occurrence of disturbances outside a historic regime thus opens the question as to the capacity of systems to return to their original state or instead shift to alternative states (i.e. a phase change from forest to shrubland; Donato *et al.* 2009b; Fairman *et al.* 2019). Climate change will alter the frequency and severity of disturbances within forest systems (Hoegh-Guldberg *et al.* 2018), this therefore increasing the likelihood of multiple disturbance events occurring in short succession. Multiple disturbance events can cause significant and abrupt changes to forest composition, structure and function (Buma 2015). However, the strength of interactions in relation to disturbance type, sequence, and relative timing is uncertain, particularly in a resprouting forest type.

The impact of successive interacting disturbance events has been documented across forest types with differing disturbance types and frequencies (Buma and Wessman 2011; Harvey *et al.* 2014b; Fairman *et al.* 2019). Repeated disturbance events can either have *linked* or *compound* interactions. Linked disturbances occur when the first disturbance affects the likelihood, extent, or severity of the second disturbance (Buma 2015). Compound disturbances describe the biotic response (for example, tree recruitment) following a second disturbance event, and how it is altered relative to the individual disturbance event. Following on from Chapter 2 and Chapter 3, which each investigated the effects of a single disturbance on forest carbon stores, Chapter4 investigated the additive and interactive effects of stacked disturbance (e.g. drought and fire) events on forest structure and recruitment in a resprouting forest.

This analysis found that in the NJF both moderate and severity fires override drought legacy effects, with no evidence of linked or compounding interactions between the two disturbances. High levels of mortality for this forest type across all combinations of drought and wildfire severity were recorded (>30% of BA), with at least half of the basal area experiencing stem mortality in some stands (55.3% of BA in low drought, high severity fire plots). Pre-fire drought stress did not increase subsequent fire severity, and there was no evidence of compounding effects in stem mortality, or early regrowth and recruitment. Models suggested that stem size, fire severity experienced, species, and harvest frequency were the key determinants of stem survival.

The co-dominant overstorey species of the NJF (*Eucalyptus marginata, Corymbia calophylla)* are resilient to disturbance with many individuals surviving both drought and wildfire events. However, mortality following the Waroona Fire (23.5% of DBH>30 cm suffering top kill) was higher than any other recorded fires in this forest type (11.7% of DBH>30cm; Peet and Williamson, 1968), which may suggest that this system is not as resilient as previously thought. Similarly, all areas burnt from the wildfire will be vulnerable to significant mortality and structural changes with further disturbance. New growth will need time to develop bark thick enough to withstand fire, and resprouting mature individuals will need adequate time to recover carbon stores to be able to resprout following further disturbance.

Following the wildfire large structural changes have occurred within the severely burnt stands. On average, only 37% of mature individuals (DBH >30 cm) were resprouting in the canopy. The other 63% either experienced stem mortality (top kill) or partial mortality (only resprouting on the bole). It is likely that basal resprouts will continue to grow and the basal area in these stands will subsequently increase. The NJF does not self-thin and large individuals will have many basal resprouts (>5 basal sprouts) that will persist. It follows, that these impacted forest stands have undergone a structure state-change, from a tall open forest to a shorter, denser, closed forest, but without changes in tree species composition or dominance.

Stands burnt by wildfire are currently regenerating, and the trajectory of the regrowth and live carbon storage is strongly reliant on future disturbance regimes (Figure 5.2a). The relative timing, type and intensity of the next disturbance will determine where pressure is exerted on these stands. Timing of future disturbance will determine the proportion of the stand population that is capable of resisting disturbance as new growth will currently not have bark thick enough to withstand mild fire and resprouting mature trees will not have the capacity to resprout in short succession (Abbott and Loneragan 1986).

As described previously, fire is common feature of this forest with both mild planned burns and stochastic wildfire. Whilst not impossible, it is unlikely that fire would occur within these stands in the coming years as fuel loads may not carry or sustain fire. However, planned (prescribed) fire or wildfire are likely to occur within some of these stands before complete recovery. Planned fire preferentially removes smaller stems from the stand, while large mature individuals are usually not affected by these burns (Figure 5.2b). However, fire in these stands before adequate recovery would result in the loss of smaller stems (basal resprouts and recruitment) and potentially the loss of mature individuals that suffered partial mortality in the wildfire. Assuming the 37% of mature individuals that survived the wildfire would also survive subsequent planned fires, they would be the only remaining overstorey individuals in the stand.

Small individuals and basal resprouts would be lost and would either resprout basally (potentially for the second time) or totally killed and remain as dead standing material. This scenario exerts pressure on smaller individuals but also leads to more densely stocked, shorter stands in these areas.

If the next disturbance to affect the burnt stands is a global change-type drought like the 2010/11 event studied in Chapter 2, initial structural consequences would differ from fire effects. Drought in the NJF preferentially affects large mature individuals (Figure 5.2b), pushing stands towards smaller, denser states as large individuals undergo partial or stem mortality (top kill). A drought and heatwave related die-off event would exert pressure mainly on the remaining 37% of mature basal area (Figure 5.2b). Whilst initial changes and where pressure is applied is different (small individuals vs large individuals preferentially removed), long term structural consequences would be similar. Large overstorey stems will be replaced by multi-stemmed individuals creating a shorter, and denser forest. It is unlikely that the composition of the dominant overstorey species will change with further disturbance, structurally these stands could change 'states' to one that more closely resembles a woodland of shorter, denser *E. marginata* and *C. calophylla*. Importantly, this thesis highlights that resprouting eucalypt forests, in this case, are vulnerable to structural changes from disruptions in disturbance regime from a changing climate.

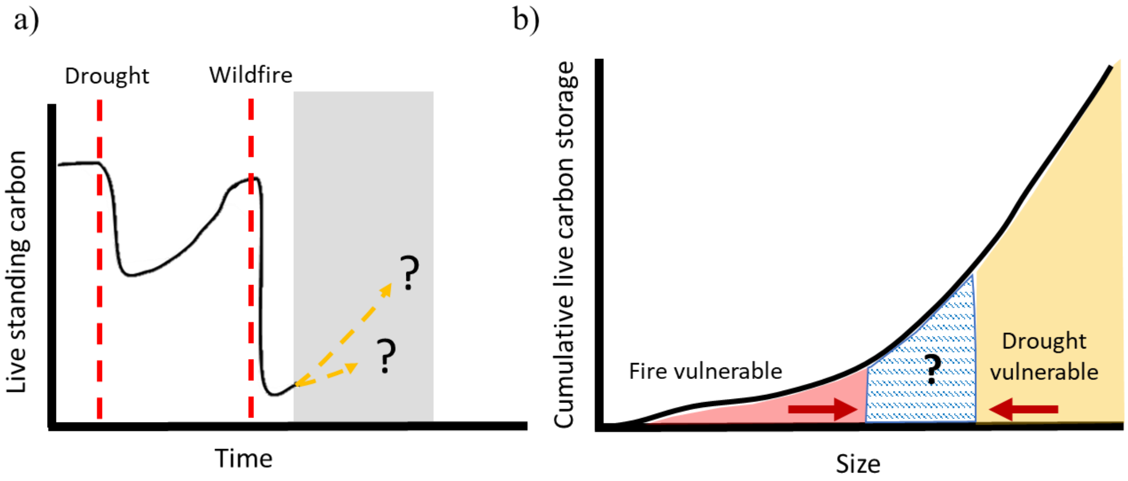

Figure 5.2 Live standing carbon trajectory, storage and vulnerability in the Northern Jarrah Forest a) Live carbon storage across time following drought die-off and wildfire and potential carbon recovery pathways b) cumulative live carbon storage in recovering drought and wildfire affected Northern Jarrah Forest stands. Fire vulnerable size tress shaded red and drought vulnerable size shaded yellow. Red arrows indicate the potential movement of these portions of the stand with a changing climate and altered disturbance regime.

5.5 Future research directions

From this study it is clear that resprouting forests may be vulnerable to disruptions to disturbance regimes with a changing climate. Furthermore, this thesis highlights the role that disturbance frequency, type and severity has played in the changes in carbon storage and forest structure observed in a resprouting Eucalypt-dominated forest of southwestern Australia. Whilst there was no evidence of linked and compounding effects of drought and high severity wildfire, further research should examine additive and interactive effects of global change-type drought and subsequent low intensity planned (prescribed) burns on mortality and fire severity in the NJF.

While all efforts were made to quantify carbon transformations in all forest carbon pools following wildfire, a detailed investigation to the effect of wildfire on carbon stored as black carbon, is necessary. Black carbon is a form of carbon resistant to decay and is a continuum from partially charred organic materials to charcoal and soot (Bird and Ascough 2012; Jones *et al.* 2019). Santín *et al.* (2015b) quantified pyrogenic organic matter (black carbon) in boreal *Pinus banksiana* forest in the Northwest Territories, Canada, following fire and found that 27.6% of the carbon affected by fire was retained in pyrogenic organic matter. If this is a long-term recalcitrant store of carbon generated from fire, in a fire prone system projected to have more frequent fire, it is likely this could become a significant store of forest carbon.

This thesis also examined the impact and early response of upland NJF sites to drought, wildfire and a combination of the two to forest carbon, structure and recruitment. Further research should analyse long term recovery of these sites, as sites with a high probability of drought are likely to experience stress from declining rainfall and heat related events on a more frequent. Continuing to measure regrowth in these stands will also track the replenishment of carbon lost from these disturbances while also documenting delayed mortality in these stands. Repeated measurements will also allow close comparison of forest stand condition, before and after any further disturbance.

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7 Appendix

Table 7.1: Area (ha) and RdNBR range of fire severity classes within the Waroona Fire of January 2016 in the Northern Jarrah Forest, Southwestern Australia.

Fire Severity Class	Area (ha)	RdNBR range
Low	6420.93	<223.91
Mixed	4801.75	223.91-307.14
Moderate	15540.42	307-567.41
High	9236.75	>567.42

Table 7.2: Area (ha) of each time since fire category (years) within the fire area in the Northern Jarrah forest of Southwestern Australia

Time since Fire (years)	Area (ha)
1-5	1648.30
6-10	23685.62
11-15	261.70
16-20	1839.06
21-30	3757.21
>30	4807.96

Table 7.3: Mean basal area (m^2 ha^{-1}) and stem density (stems ha^{-1}) of live tree and dead bole and complete mortality individuals of two wildfire burn severities (canopy scorched, and canopy consumed) and control (unburnt) plots of the Northern Jarrah Forest, southwestern Australia.

		Basal Area (m^2 ha^{-1})			Density (stem ha^{-1})		
		Live (CI)	Mortality (CI)		Live (CI)	Mortality (CI)	
	N (plots)		Bole	Complete		Bole	Complete
Control	10	45.50 (±4.52)	0.58 (±0.68)	9.02 (±2.81)	1780 (±317)	118 (±21.8)	364 (±95.0)
Canopy scorched	20	29.3 (±2.46)	13.3 (±2.24)	8.13 (±1.91)	436 (±63.2)	739 (±116)	568 (±103)
Canopy consumed	17	24.7 (±2.60)	16.8 (±2.59)	9.18 (±2.72)	366 (±62.9)	1098 (±144)	611 (±128)

Table 7.4: Mean Pre-fire carbon mass (t C ha^{-1}) for each fuel category and associated combustion factors (fraction of mass combusted) across the four fire severities experienced during the Waroona Fire of January 2016 in the Northern Jarrah Forest, southwestern Australia.

		Combustion Factors			
Fuel Category	Mass t C ha^{-1}	High	Moderate	Mixed	Low
Trees	156.5	0.12	0.11	0.06	0.02
Shrubs	3.18	0.98	0.92	0.7	0.5
Coarse Woody debris	11.59	0.01	0.01	0	0
10hr	1.49	0.95	0.9	0.7	0.5
100hr	4.79	0.9	0.8	0.6	0.4
Surface litter (incl 1hr)	0.64-6.59	1	1	0.96	0.94
Soil to 10cm	37.03				

Table 7.5: Proportional basal area of resprouting type in fire effected and control plots of the Northern Jarrah Forest, southwestern Australia

Fire severity	Resprouting type	DBH <30cm Proportion (±CI)	DBH >30cm Proportion (±CI)
Unburnt	*Live*	0.81 (±0.10)	0.74 (±0.20)
	Partial	0.05 (±0.03)	0.05 (±0.04)
	Stem Mortality	0.13 (±0.09)	0.04 (±0.01)
Moderate	*Live*	0.25 (±0.15)	0.57 (±0.18)
	Partial	0.13 (±0.05)	0.13 (±0.07)
	Stem Mortality	0.53 (±0.15)	0.19 (±0.11)
High	*Live*	0.12 (±0.09)	0.37 (±0.13)
	Partial	0.16 (±0.03)	0.24 (±0.04)
	Stem Mortality	0.63 (±0.07)	0.24 (±0.08)

Table 7.6: Proportional basal area of resprouting type in drought and fire affected and control plots of the Northern Jarrah Forest, southwestern Australia

Drought probability	Fire severity	Resprouting type	DBH <30cm	DBH >30cm
			Proportion (±CI)	Proportion (±CI)
High Drought	Unburnt	*Live*	0.83 (±0.21)	0.59 (±0.42)
		Partial	0.04 (±0.02)	0.08 (±0.06)
		Stem Mortality	0.11 (±0.19)	0.09 (±0.24)
	Moderate	*Live*	0.42 (±0.30)	0.76 (±0.14)
		Partial	0.10 (±0.08)	0.02 (±0.01)
		Stem Mortality	0.40 (±0.10)	0.12 (±0.21)
	High	*Live*	0.24 (±0.16)	0.45 (±0.21)
		Partial	0.14 (±0.06)	0.21 (±0.07)
		Stem Mortality	0.50 (±0.08)	0.17 (±0.12)
Low Drought	Unburnt	*Live*	0.79 (±0.16)	0.88 (±0.12)
		Partial	0.05 (±0.05)	0.02 (±0.04)
		Stem Mortality	0.16 (±0.15)	0.00
	Moderate	*Live*	0.14 (±0.12)	0.45 (±0.26)
		Partial	0.14 (±0.07)	0.19 (±0.19)
		Stem Mortality	0.61 (±0.24)	0.23 (±0.15)
	High	*Live*	0.00	0.28 (±0.28)
		Partial	0.17 (±0.04)	0.27 (±0.06)
		Stem Mortality	0.76 (±0.06)	0.30 (±0.11)