Case Study at Hinewai-Reserve: Post-fire assessment of the resprouting ability of some New Zealand native woody plants

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By

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Abstract

The ability to resprout after a fire enables plants to persist in their environment. Research on this topic often is conducted in fire-prone areas of the world. As this study demonstrates also plants in more humid regions of the world, like New Zealand, have the ability to resprout. 15 native New Zealand plants (*Aristotelia serrata, Carpodetus serratus, Coprosma dumosa, Fuchsia excorticata, Griselinia littoralis, Melicytus ramiflorus, Pittosporum eugenioides, Pittosporum spp., Podocarpus totara, Pseudopanax arboreus, Pseudopanax crassifolius, Pseudowintera colorata, Rubus cissoides, Schefflera digitata, Teucridium parvifolium*) have been observed being able to resprout after a fire.

Results show that individuals of the same species resprout in a similar way, but that the factor species is no sufficient indicator for determining whether an individual resprouts in the first place. By inducing some general rules this study also would be consistent with the assumptions that: plants that are known to be browsed by animals could be expected to resprout more likely also after a fire; early successional species may resprout more likely than later successional ones; smaller plants could be expected to resprout more likely than bigger ones; individuals of the same species might show a more similar resprouting response; specialist species could be expected to show a more similar resprouting response whereas generalist species could be expected to show more variability; less competitive species could be expected to resprout more likely from higher positions on the stem compared to more competitive species that are shade tolerant and can also afford to resprout from the base.

Keywords: fire – fire ecology – plant functional traits – resprouting – sprouting ability – disturbance – persistence – regeneration – woody plants – topkill – basal sprouting – New Zealand

Kurzfassung

Die Fähigkeit von Gehölzen nach einem Feuer neue Triebe zu bilden sichert ihr Bestehen nach einer Störung im Ökosystem. Forschung die gezielt diese Fähigkeit untersucht wird oft in trockenen und feuergefährdeten Gebieten durchgeführt. Diese Studie zeigt dass auch Pflanzen in einer humiden Region wie Neuseeland dazu imstande sind. 15 heimische Gehölze wurden hierfür untersucht.

Die Ergebnisse lassen einige Rückschlüsse zu: Individuen der gleichen Art bilden Triebe an vergleichbaren Stellen aber die Zugehörigkeit zu einer Art erlaubt es nicht vorherzusagen ob ein Individuum austreibt da die Pflanzengröße vor dem Feuer oder zB das Brandverhalten einen Einfluss haben. In verallgemeinerter Form ist diese Studie auch konsistent mit mehreren Annahmen: Pflanzen die regelmäßig von Tieren als Futterquelle genutzt werden und danach wiederaustreiben, könnten dies auch nach einem Feuer tun; frühsukzessionale Arten könnten eher neue Triebe bilden als spätsukzessionale; kleinere Pflanzen bilden eher neue Triebe als größere; Individuen der gleichen Art bilden neue Triebe an vergleichbaren Stellen; Spezialisten zeigen weniger Variabilität in der Positionierung neuer Triebe während bei Generalisten eine höhere Variabilität erwartet werden könnte; weniger konkurrenzfähige Arten könnten eher von höheren Stellen am Stamm austreiben verglichen mit zB schattentoleranten Arten die es sich auch leisten können an der Basis neue Triebe zu bilden.

Schlagwörter: Feuer – Feuerökologie – Störung – Regeneration – Gehölz - Neuseeland

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CHAPTER 1: Introduction

1.1 Current knowledge

1.1.1 Ecological impacts of fire

Fire is considered as a disturbance that is "*any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment*" (White & Pickett 1985). White & Pickett (1985) also proposed the idea of patch dynamics as fire does not burn homogenously but depending on available fuel might differ significantly on a small scale resulting in different *patches* or *patch mosaic burning* (Allen 2008). Fire has impacts on vegetation dynamics, succession and favours recruitment of pioneer-species whereas the probability of mortality depends on species-specific responses to fire (Balch et al. 2011).

Traits that enable plants to survive fire, such as bark thickness; bark specific gravity, bark moisture content; average plant height; or average plant diameter can differ significantly among species (Vanderweide & Hartnett 2011). Perry et al. (2012) conclude that the response of individual species represents a combination of all its attributes and that grouping species based on a single functional trait is insufficient for understanding the complex dynamics and interactions with fire. Also Klimešová et al. (2008) who investigated plant functional traits regarding grazing and mowing concluded that a single trait cannot be the only basis for predicting vegetation changes and hence a trade-off between key traits is needed.

Topkill can be defined *as* complete death of the aerial biomass, regardless of whether the plant recovers by resprouting and rate of growth of resprouts. It is sometimes also referred to as "stem mortality" (Hoffmann et al. 2009; Hoffmann & Solbrig 2003). In another formulation Balfour & Midgley (2006) describe topkill as death of the aboveground stem but not plant death. Repeated topkill maintains woody plants in smaller size classes and can prevent them turning into reproductive adult size classes, termed "fire trap". This has important implications for vegetation dynamics (Hoffmann et al. 2009). Fire also kills woody plants and has an important role in savannahs as it maintains grasslands and impedes a development to forests (Hoffmann et al. 2009). A differentiation of mortality and topkill is used as topkill is an important measure to understand changes in vegetation cover (Hoffmann & Solbrig 2003). Second, mortality not occurs instantly but delayed as a result of fire damage and secondary agents (e.g. pathogens, insect manifestations) to which damaged plants are more susceptible (Regelbrugge & Conard 2009). Hence classifying plants as “topkilled” is also pragmatic as it can be easily observed in the field.

The question by which mechanisms fire kills trees still remains uncertain. Midgley et al. (2011) differentiate between hydraulic death (damages of the xylem); stem-girdling death (damages of the phloem); and meristematic death (damages of the cambium and buds). Michaletz & Johnson (2007) add that a cambium necrosis is always accompanied by phloem necrosis because the phloem is external to the cambium. To have some concepts of how fire kills trees is considered necessary for studying fire ecology as postfire plant responses are often described by using regression approaches that do not consider the causal processes linking them to fire behavior (Michaletz & Johnson 2007). This is why explanations are often reduced to: “death through heat stress”, “water stress”, “injury”, “fire-induced mortality”, “post-fire mortality”, “necrosis”, “crown-scorch”, “bole-damage” or “cambial damage” for example.

O’Brien et al. (2010) found that in their study plant mortality occurred up to 3 years after the fire and described it as “*cascade of physiological stresses*” of damaged roots that are not able to provide water for the crown resulting in a closure of stomata, vascular embolism and a decline in transpiration. In this case the photosynthetic capacity was restricted by the ability of roots to provide water whereas a damage of roots close beneath the surface also implies that all roots below this position, although not directly damaged, are not available for providing water and nutrients. This example illustrates that how mortality occurs in woody plants also depends on the type of the fire (ground,- surface, or- canopy), which plant tissue in what position is mainly damaged and hence can be quite variable in different fires and fire regimes. Hood & Bentz (2007) similarly find that death can be delayed as long as 4 years post-fire whereas in comparison Midgley et al. (2011) found in their study that most post-fire mortality occurred within days.

Woody species survive wildfires through a combination of features with resprouting ability, bark thickness and height considered to be key adaptions (Nefabas & Gambiza 2007). Such plant functional traits could be described as those that provide a fitness advantage in a given environment (Keeley et al. 2011).

1.1.2 Resprouting capacity and resprouting ability

Resprouting can be defined as production of secondary trunks as an induced response to injury or to profound changes in growing conditions (Bond & Midgley 2003). Clarke et al. (2012) explain sprouting as the initiation of growth from buds, not necessarily requiring a disturbance, whereas resprouting is the initiation of growth from protected buds as response to a disturbance. Resprouting is important as it restores photosynthetic capacity after a loss of aerial biomass. Comparative studies in fire ecology showed that a higher resprouting ability of the savannah species compared to forest species result in a higher fire resistance (Hoffmann et al. 2003). The comparative advantage of different resprouting strategies depends on the time that is required to restore photosynthetic capacity which is restored more rapidly by epicormic rather than basal resprouting or by seedlings (Lawes et al. 2011a; Bond & Midgley 2001).

Depending on the position of resprouts (fig. 1) axillary, branch epicormic, stem epicormic and basal resprouting can be distinguished (Bellingham & Sparrow 2000). Additionally sprouts can grow from underground stems such as lignotubers, rhizomes or roots, also termed “root suckering” (Del Tredici 2001). Lignotubers are genetically fixed swollen structures which are developed as normal part of plant growth (Llorett et al. 1999). A certain position of resprouts not necessarily implies an advantage although one study found that stem epicormic resprouting was a less successful strategy than from the root crown (Bond & Midgley 2003, Neke et al. 2006).

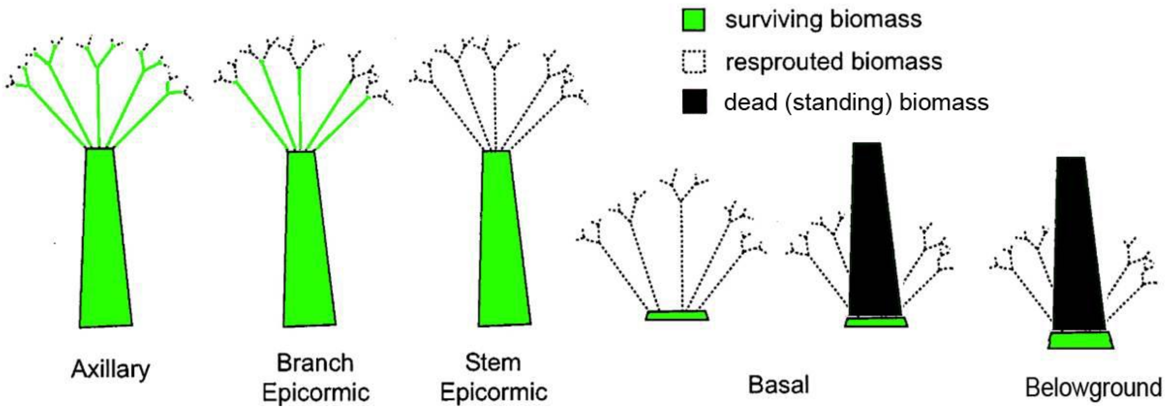


Fig. 1 Patterns of biomass loss and regeneration **(Bellingham & Sparrow 2000, modified)**

Species having a low frequency disturbance regime can lose their ability to resprout (Bellingham & Sparrow 2000). However, the ability to resprout is considered to be the ancestral trait in a wide range of plant taxa while its loss might be the derived development (Wells 1969, Llorett et al. 1999; Waters et al. 2010). Resprouting might also be considered as specialized trait, evolved as a response to periodic fires and "*paradoxically*" the loss of ability to resprout is also a specialized trait (Wells 1969). Hence the ability to resprout, its evolutionary development and a comprehensive understanding of variation in resprouting still remains unclear (Vesk 2006; Ryan & Frandsen 1991). New insights from research could also suggest the evolution from "*obligate resprouters (ancestral state) to facultative resprouters, and then to obligate seeders*" (Keeley 2011 cited in Pausas & Schwilk 2012). Obligate resprouters solely rely on their ability to resprout. Vice versa obligate seeders lack the ability to resprout and facultative resprouters are able to resprout but also produce seeds that might survive fires.

Different factors like a persistent infection with fungi might have been a selective force for the evolution of resprouting but also fire has been of global importance for several hundred million years (Woolley et al. 2008; Keeley et al. 2011). As resprouting enables plants to regain biomass lost during a disturbance wind damage, browsing by animals or snapping and uprooting of trunks can stimulate shoots to grow (Lamont et al. 2011; Curran et al. 2008; Van Bloem et al. 2005). Therefore it is likely that resprouting has evolved independently in different places due to different evolutionary pressures and fire alone might only be one selective force amongst others (Bond & Midgley 2003; Llorett et al. 1999).

Topkill can also be caused by damages to the stem or the xylem and not necessarily the canopy. Studies have shown that clipping aboveground biomass as well as damaging the stem can initiate a resprouting behaviour (Moreira et al. 2012; Balfour & Midgley 2006, Michaletz et al. 2012). But those scenarios of biomass loss lack the heat-component of fire and far fewer plants are capable of resprouting after applying heat to the stem compared to those being clipped only (Lamont et al. 2011; Vesk 2006). In case plants were able to resprout after a fire the resprouting success and survivorship among both groups (clipped only; exposed to heat) were equal (Llorett et al. 1999).

Resprouting branches grow from epicormic buds which are protected from the heat of the fire by the bark. One of the simplest definitions could be that a bud is a structure that contains meristematic cells; whereas meristematic cells could be defined as undifferentiated cells that are able to produce new plant-tissue (Meier et al. 2012). The capacity to produce epicormic buds is likely to be genetically fixed, shaped by the environment and correlated with the length of one growth-unit (Collet et al. 1997 cited in Meier et al. 2012). Although every resprouting branch increases the epicormic potential, a higher ratio of dying to new formed buds might result in a net decline over time (Morisett et al. 2012). Hence it has to be considered that epicormic buds also have a limited longevity and might not be beneficial if a disturbance that requires resprouting fails to appear within the longevity of epicormic buds (Vesk 2006). The resprouting capacity can vary within species (size classes, age classes) and between species and is suggested to be seen as ecosystem response variable rather than a measure for fire intensity (Keeley 2009, Bond & Wilgen 1996, Vivian et al. 2010, Reyes et al. 2009, Keeley et al. 2008). In comparison, some authors assume that the mode of recovery by seed, resprouting or underground rhizomes reflects different impacts from the fire (Timmins 1992; Lamont et al. 2011). Fire intensity has impacts on,- and influences the resprouting response but the resprouting response must not be used as measure, indicator for measuring or drawing conclusions on the fire-intensity.

Resprouting as an ecosystem response is triggered by fire that releases dormant buds and initiates a growth but it is also reported that plants may sprout continuously, with or without disturbance, making classifications more fuzzy (Bond & Midgley 2001). Epicormic branch formation has also been found common in completely closed, undisturbed forests (Meier et al. 2012). Besides the traditional assumptions of a light-triggered or hormonal regulation of resprouting Morisset et al. (2012) found that there is increasing evidence that sprout formation is also controlled by water–carbohydrate supplies. Thus defining resprouting as a response to a disturbance would also require a practical definition of "disturbance" in the context of a specific research question.

Depending on the growth-form "*ground plants"* may be dependent on the ability to resprout throughout their lifetime whereas it can diminish with increasing size. Ground plants cannot avoid damage through size compared to taller species for which resprouting becomes less important (Vesk 2006). Small plants are also more likely to die after a fire even if resprouting is initiated (Moreno & Oechel 1990, Llorett et al. 1999). As resprouting per se does not guarantee post-fire survival a differentiation between initial resprouting ability, resprouting vigor and post resprout survival is suggested as the overall sprouting success depends also on the supply of nutrients, carbohydrates and water after the fire (Moreira et al. 2011; Hodgkinson 1998).

Besides resprouting, reseeding is a second strategy that allows plants to persist in an area after a fire whereas a trade-off between these two strategies might lead to a dominant one. An advantage of resprouting is that sprouts grow faster than seedlings, can reoccupy their own gaps more quickly and a more rapid canopy-closure could inhibit the establishment and development of seeds (Bond & Midgley 2001). Indirect evidence for this trade-off is the smaller number of seeds, seedbanks, seedlings and poorer seedling survival (Bond & Midgley 2001). Contrary to the described trade-off Lamont et al. (2011) conclude that there is little evidence that resprouting is at the expense of sexual reproduction as a vast majority of resprouters also produces seeds. A potential reason for the lower number of seeds and the lower viability might be explained by a high genetic load that is accumulated by resprouters over their long live-time resulting in a poor fruit and seed set (Lamont & Wiens 2003).

This genetic load and somatic mutations that may occur in meristematic tissues can produce genetically novel branches and fruits and be a source for speciation within sprouting species (Lamont & Wiens 2003). While a final answer to whether the speciation rate is higher amongst sprouters or seeders still is missing in some genera weak support for a more than three times greater speciation rate of non-sprouting species has been shown (Bond & Midgley 2003).

Sprouters are also often multi-stemmed and shorter and might be favored where disturbance regimes are frequent and severe whereas they might be outcompeted by non-sprouters if a disturbance fails to appear (Bond & Midgley 2001). Nevertheless a binary classification into sprouters (R+) and non-sprouters (R-) does not always encompass the variation that is found in nature and hence to distinguish plants that mostly seed or mostly resprout may be more likely appropriate (Bellingham & Sparrow 2000). These differences might be dictated by site-productivity, with reseeding in more moist sites and resprouting on drier, less fertile sites for example (Wells 1969; Iwasa & Kubo 1997; Vesk 2006, Read & Brown 1996). But those observations also cannot be generalized as both, an increase and decrease in sprouting ability with increased productivity have been reported (Vesk 2006). The allocation of resources for reproduction and vegetative growth may also vary spatially and temporary within species what enables them to adapt to different environments (Groom & Lamont 2011). Nzunda & Lawes (2011) suggest that intense disturbance favours reproduction and intense stress might favour resprouting. In this context stress is defined as conditions that restrict production such as shortages of light; water; mineral nutrients or suboptimal temperatures (Grime 1977).

The spatial dimension of disturbances as well as the plant responses can be viewed on different scales, such as individual plants, populations, species, communities or landscapes. Plant-specific traits might be well suited for predicting a species-persistence at the scale of an entire landscape but on smaller scales stochastic properties and heterogeneity of fire might mask the effects of species functional traits (Allen 2008; Perry et al. 2012). Understanding the basic mechanisms would be considered necessary in order to "*interpret the exceptions to the patterns as well as those that conform*" (Lamont & Wiens 2003).

1.1.3 Bark thickness

Both, sprouting and non-sprouting species are dependent on a thick bark to protect plant tissue. The function of the bark is to protect epicormic buds of sprouting species and likely, protect stem hydraulic structures of non-sprouting species (Lawes et al 2011, Midgley et al. 2011). The heat of fire causes a thermal softening of viscoelastic polymers resulting in a deformation of conduit walls and a reduced xylem conductivity that might lead to mortality (Michaletz et al. 2011). Bark protects also other plant tissues from a heat pulse that is required to kill cambial tissue of about 60-65 degrees Celsius (Chatto et al. 2003). Vanderweide & Hartnett (2011) found that in their study the likelihood of mortality decreased for 43% for each mm of bark-thickness and calculated a minimum bark-thickness of 8.57 mm (Confidence Interval 7.57mm - 9.62mm) that would be necessary in order to keep the temperature of the vascular cambium below a lethal temperature threshold of 60 degrees Celsius. Hoffmann et al. (2012) calculated a bark-thickness of 9.1mm as necessary to have a 50% chance to survive even high intensity fires with a flame length > 2m.

Bark-thickness and stem diameter can be positively correlated among and within species but not necessarily have to be (Nefabas & Gambiza 2007; Brando et al. 2012, Ryan & Frandsen 1991). Bark thickness as a single predictor can be used to estimate the effects of wildfires whereas the importance of absolute bark thickness or relative bark thickness (bark-thickness divided by stem radius) has recently been recognized (Lawes et al. 2011a, Chatto et al. 2003; Midgley et al 2010; Hoffmann et al. 2009). Lawes et al. (2012) argue that absolute bark thickness is dependent on a measured plant individual and therefore not a species specific trait. Absolute bark thickness seems to be a reliable predictor but there are also examples that a special plant-anatomy and positioning of buds does not necessarily require a thick bark (Lawes et al. 2011). Hence bark thickness is a practicable measure but should not be the only variable to assess fire tolerance (Nefabas & Gambiza 2007). Bark thickness as a measurement can be described as “soft trait” that is easy to measure and might be a good surrogate or correlate for “hard traits” (Cornellissen et al. 2003). For instance, the hard trait “photosynthetic capacity” is harder to measure compared to the “specific leaf area” (Wright et al. 2004).

The best argument for the dominant role of absolute bark-thickness is that bark of all species is primarily made of cellulose and hence the thermal conductivity is approximately constant among species while the maximum cambial temperature has been shown to decline with increasing bark thickness (Martin 1963 cited in Michaletz & Johnson 2007; Lawes et al. 2011). Thermal conductivity is defined as the amount of heat transported through a unit area of the conducting matter in a unit time under a unit temperature gradient (Michaletz & Johnson 2007).

1.1.4 Plant size (height, diameter)

Non-sprouting species usually have one single stem and are taller compared to multi-stemmed sprouting species (Bond & Midgley 2003). The crowns of taller trees are less likely to be damaged and hence might survive fires more easily even at the same diameter (Brando et al. 2012). Another suggestion is that larger trees might also be less susceptible to indirect fire damage caused by falling trees and branches that were killed by the fire (Brando et al. 2012). An “escape height” enables trees to have a lower likelihood of being topkilled or being susceptible to secondary damage but only growing tall is not a sufficient strategy because despite being shortest some species were shown to survive fire best (Bond 2008; Lawes et al. 2011, Midgley et al. 2010). “Escape height” can be interpreted in different ways as it can be a) the height at which the canopy is not damaged or scorched; b) the height at which epicormic buds are beyond the reach of the fire; c) the height at which the bark is thick enough to protect the stem (Lawes et al. 2011). As sometimes an escape height is assumed looking at “plant functional types” could also be justified as responses to fire can be species-specific but in other cases not confined to specific taxa (Balch et al. 2011; Lawes et al. 2011). To explain species intraspecific variability plant functional types might be helpful as individuals of the same species may belong to different plant functional types (Pillar & Sosinki 2003). Plant functional types are defined as groups of (individual) plants that regardless of the species can be grouped according to their approximately similar traits (e.g. height, bark-thickness or wood density) and responses to environmental influences (Müller et al. 2006). As Gutsell & Johnson (1996) found that smaller stems are more likely being heated around the entire bole, larger stems regardless of the species could suffer less damage during a fire based on geometric considerations. Llorett et al. (1999) in comparison found no relationship between the an increasing size of plants and survivorship. A higher mortality of bigger plants could result from an increasing cambium injury with increasing stem diameter. This might be a consequence of a higher fuel accumulation of bigger plants with the potential of a fire to burn longer and more intense. Summarizing, there are two “opposing factors”, namely an increase of a potential cambium injury through a higher fuel accumulation with increasing diameter on the one hand and a higher bark-thickness with increasing diameter protecting the cambium, on the other (Ryan & Frandsen 1991). Prior et al. (2010) also found that small saplings can be defoliated or killed by grassfires hence also the relative distance between the understorey and the canopy of trees could have an influence.

1.1.5 The interaction of determining factors that influence plant responses after fire

As bark thickness, height and diameter are related to one another it is difficult to separate their single contribution to fire resistance (Lawes et al. 2011). An interaction of factors determines the fire-tolerance of species whereas different strategies can be observed, depending on the costs of investing into height, - or bark growth (Nefabas & Gambiza 2007; Hoffmann et al. 2003). Additionally fire-induced tree mortality has been shown to decrease significantly also as a function of increasing wood density although this effect can vary spatially, taxonomically and temporally (Brando et al. 2012; Kraft et al. 2010). A fire-resistance per se does not exist but plants should be more likely seen adapted to a certain fire-regime. Resprouting and reseeding are two types of plant responses that enable them to persist in a fire-disturbed environment whereas those two strategies do not necessarily have to be mutually exclusive. Lamont et al. (2011) conclude that plants that are capable of both, resprouting and reseeding after a fire, have a superior fitness advantage. *Ulex europaeus* for example has been classified as “*strong resprouter*” and produces a large amount of seeds that can remain in the soil for decades (Hill et al. 2001, Reyes et al. 2009). The main advantage of resprouting is that resprouts grow faster and can reoccupy gaps faster than by reseeding. Resprouters might be of shorter statue as a limited amount of resources has to be allocated to multiple stems whereas some authors assume that a multi-stemmed habit is not a species trait but derive from interactions with the disturbance regime (Nzunda et al. 2007, Allen 2008). One advantage of this multi-stemmed habit could be that the plant covers a larger area and hence might be able to capture a larger amount of resources (Nzunda et al. 2007). But it is also reported that woody plants might pass through a multi-stemmed juvenile stage before thinning to single stemmed adults (Bond & Midgley 2001).

As currently observable fire-adaptions are a product of a past fire regime a evolutionary perspective is always implied. Phylogenies can be drawn to show in which branches resprouting is common also because it might be "*genetically fixed*" as sprouting variants of some species have been shown to store starch and sugars while non-sprouting variants do not (Meier et al. 2012; Verdaguer & Ojeda 1999 cited in Bond & Midgley 2003; Schwilk 2002 cited in Bond & Midgley 2003). But an initial growth of new plant tissue could also be achieved by a re-mobilization of stored resources and a refixation of respired CO_2 within the stem if no leaves remain, termed "*corticular photosynthesis*" or from a storage in their xylem parenchyma tissues (Teskey et al. 2007; Kozlowski 1992 cited in Clarke et al. 2012; Lamont et al. 2004 cited in Clarke et al. 2012). A major constraint in using phylogenies is the assumption that resprouting might have evolved and been lost repeatedly within some lineages of genera and the varying degrees of resprouting ability are unlikely being preserved in the fossil record (Pausas & Verdu 2005; Bond & Midgley 2003, Del Tredici 2001 cited in Bond & Midgley 2003). For example Nzunda et al. (2007) found in their study no obvious phylogenetic pattern in the expression of resprouting. Barraclough (2006) states that there might always be a bias towards the interpretation of patterns. Vesk (2006) found that resprouting is a phylogenetically widespread but labile trait across broad phylogenetic trees. Bond & Midgley (2003) additionally conclude that for most ecosystems the disturbance history is not sufficiently enough documented in order to make generalized assessments on the interaction of reseeding, resprouting and the disturbance regime. On the other hand a general tendency for generality in ecology sometimes restricts to account for the variation that occurs in studies and also produces "*conflicting patterns*" (Lawes et al. 2011; Bond & Midgley 2003).

1.1.6 Fire history and fire regime

Fire adapted species should be more likely seen as adapted to a certain fire regime as traits that are adaptive under a particular fire regime can be threatened when that regime changes. Hence it is not correct to equate adaptation to fire as adaptation to frequent fires (Keeley et al. 2011). The necessity to develop a fire resistance can be seen as a product of the past fire history and the fire regime that is composed of: type (ground,- surface,- and crown-fire), frequency (return interval), intensity and seasonality of fires. Fire intensity is:

- a physical combustion process of energy release from organic matter (Keeley 2009).
- the physical force of the event per area per time (White & Pickett 1985).

Another measure is fire-severity that describes the impact of this energy release as:

- the loss or decomposition of organic matter aboveground and belowground (Keeley 2009).
- a measure of the plant’s perception of a disturbance event (Bellingham & Sparrow 2000).
- the impact on the organism, community or ecosystem (White & Pickett 1985).

As in post-fire assessments no direct information on fire intensity is possible, fire severity is used to draw a conclusion on the fire-intensity and can be indicated by bark char height on tree boles as a proxy of flame length (Brando et al. 2012); or indicated by the remaining twig diameter after the fire as, compared to non-sprouting individuals, the skeletons of resprouting plants have shown to be significantly taller, indicating a lower loss of biomass and a higher resprouting success (Keeley 2006).

1.1.7 Fire tolerance and resprouting of New Zealand plants

A study measuring the amount of serotiny in *Leptospermum scoparium* on the South Island of New Zealand as an indicator for a long fire history came to the conclusion that fires have been present for about 50.000 years (Bond et al. 2004). Serotiny was measured as it is not assumed to be randomly distributed within species but a direct reaction of plants to fire but not necessarily to “highly frequent” fires (Bond et al. 2004). Studies of charcoal showed that fires have been a regular but not frequent event with a return interval of hundreds up to 2000 years (Ogden et al. 1998). Burrows (1994) published a paper that discusses resprouting of New Zealand’s taxa. He concluded that in all Banks Peninsula forest remnants evidence for burning and resprouting can be found. The resprouting success is considered to be constrained as feral goats, possums and domestic stock might feed on resprouts (Burrows 1994). Fire may have shaped some properties of New Zealand’s woody plants as Burrows (1994) states that in total there is evidence for a fire history for at least 2.5 million years. Although some New Zealand plants can recover by resprouting lignotubers are not common (Burrows 1994). Table 1 shows a list of species that are known to produce basal resprouts. These are compared to those species that are expected to be found in the study area and therefore potentially can be expected to resprout after a fire. A differentiation between the types of resprouting (fig. 1) is not available, hence the potential capacity of those plants to produce also epicormic branches is uncertain.

Table 1: New Zealand tree species that are capable of producing basal sprouts

Species capable of basal resprouting	Abundant in the study area
Alectryon excelsum	unknown
Aristotelia serrata	yes
Carpodetus serratus	yes
Cordyline australis	unknown
Corynocarpus laevigatus	unknown
Fuchsia excorticata	yes
Griselinia littoralis	yes
Hoheria sexstylosa	unknown
Melicytus ramiflorus	yes
Myrsine australis	unknown
Pittosporum eugenioides	yes
Pseudopanax arboreus	yes
Pseudopanax crassifolius	yes
Schefflera digitata	yes
Sophora microphylla	yes

Source: Burrows 1994; modified

1.1.8 Summary

Resprouting remains an interesting phenomenon for different disciplines. An evolutionary perspective tries to understand the development of resprouting as a product of a past disturbance history. Plant-physiology might try to explain resprouting ability and variation in resprouting by anatomical features. Ecology might try to understand and predict the impact of different disturbances, changes in plant-community composition and ecological impacts. Nature conservation might be interested in which desired plants are capable of surviving wildfires and other disturbances. Research on climate change could ask if resprouting might have an influence or be an important factor in carbon sequestration. The capacity of resprouting plants to sequestrate carbon is also of interest for the Hinewai-Reserve as voluntary carbon credits have been sold in the past.

1.2 Justification for the research

The 2011 fire in the Hinewai-Reserve offers the opportunity to study and document plant-responses to fire. Besides experimental burns investigating past fires is the only opportunity to increase the knowledge in the intended field of research. The research addresses a research-need explicitly mentioned by the Department of Conservation fire research needs analysis Report from 2007, namely to "*Investigate how indigenous species and ecosystems respond to fire for ecosystem management*" (Hunt 2007).

Brando et al. (2012) also conclude that a better understanding of mechanisms that drive fire-induced tree mortality is needed in order to make predictions of the impacts of fire and potential changes in plant cover. Although the importance of understanding plant community responses to fire is considered important little scientific information on the effects of fire on plants and plant-communities is available and fire-induced tree mortality still remains poorly understood (Allen 1996; Brando et al. 2012).

1.3 Research conception

1.3.1 Research questions

The research questions are divided into two categories:

1.3.1.1 Descriptive research questions

1.) How do woody plants at the Hinewai Reserve respond to the fire in 2011?

2.) Which species do resprout and where do they resprout?

1.3.1.2 Explanatory research questions

3.) Which functional traits might explain the capability to resprout?

4.) Are there differences within/between species?

5.) What factors might explain those differences?

1.3.2 Research Objectives

i) Record the resprouting ability of as many native woody plant-species in the Hinewai-Reserve as possible. This is the first step in the proposed framework that consists of: Resprouting ability – Resprouting vigor and post-resprout survival (Moreira et al. 2012).

ii) Measure bark-thickness, plant size (height, diameter), char-height of woody plants in the Hinewai-Reserve. Besides the resprouting ability bark-thickness and plant size are considered to be key adaptions to survive wildfires (Nefabas & Gambiza 2007).

iii) Record the positions of resprouts (base, stem) as the type of resprouting may provide competitive advantages. Branch or stem epicormic resprouting restores the photosynthetic capacity faster than basal resprouting (Lawes et al. 2011a; Bond & Midgley 2001).

iv) Analyse the distribution of height and dbh classes of resprouting plants. According to Vesk (2006) smaller plants might be more dependent on the ability to resprout as they cannot avoid damages and hence might be more likely to resprout.

To narrow the scope this work focuses only on the resprouting response of woody plants, hence a measurement of reseeding as well as non-woody plants are excluded. The main interest lies in the resprouting ability of New Zealand native woody plants, not exotic or invasive species.

CHAPTER 2: Description of the study site

2.1 The Hinewai Reserve

The Hinewai Reserve was established in 1987 and occupies more than 1000 ha of 53% *Ulex europaeus (gorse)*, 30% closed canopy regenerating native forest, 13% pasture, fernland or native tussock land and 4% old-growth forest (Wilson 1994). It is owned and managed by the Maurice White Native Forest Trust aiming at the protection and restoration of native vegetation and wildlife. The area was formerly used as farmland between the 1850s and 1980s. In the absence of fire the landscape is assumed to return to native forest as shade tolerant native species can grow under a gorse-canopy while gorse acts as a “nurse-plant” (Wilson 1994). As long as those natives are not grazed by stock or wild animals they should be able to outcompete gorse in the long run (app. 20 years). Hence grazing animals have been excluded and a control program for possums has been conducted.

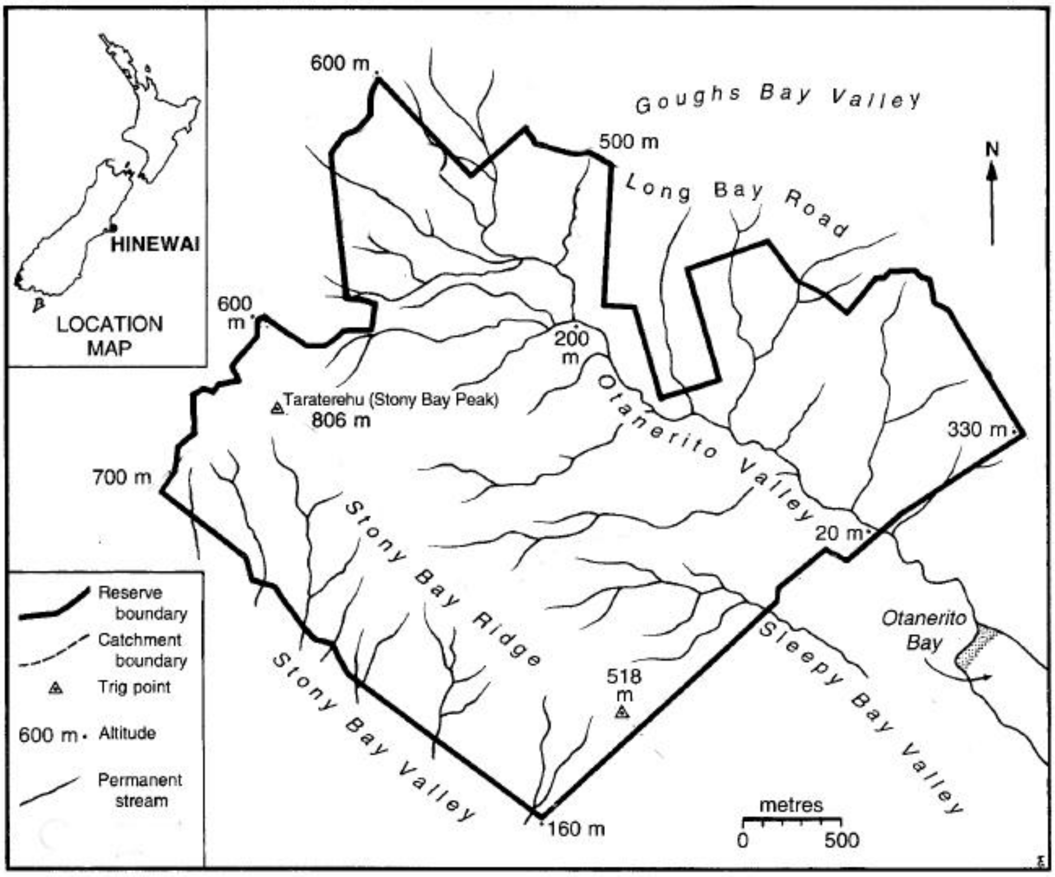


Fig. 2 Location and boundaries of the Hinewai-Reserve **(Wilson 1994, modified)**

2.2 Description of the vegetation

According to Wilson (2012, pers.comm.) the vegetation cover of the Hinewai-Reserve can be divided into:

1. **Exotic scrub** *(Ulex europaeus, Cytisus scoparium)*
2. **Kanuka Forest**
3. **Second growth mixed hardwood forest**
   (*Melicytus ramiflorus, Fuchsia excorticata, Pseudopanax arboreus, Pittosporum eugenioides, Griselinia littoralis, Schefflera digitata, Carpodetus serratus, Pennantia corymbosa, Coprosma spp., Pseudowintera colorata, Muehlenbeckia astonii, Rubus cissoides,* and others.)
4. **Beech forest** (*Nothofagus fusca* with scattered *Nothofagus solandri*)
5. **Fernland**
6. **Pasture**

Plant descriptions are compiled from different sources and hence the given information varies depending on what information was found in the literature.

- ***Ulex europaeus* (gorse):**

Gorse is an invasive spiny shrub in New Zealand and covers large parts of the Hinewai-Reserve. The highly flammable shrub can get up to 4m tall and re-invade burned sites from fire-triggered germination of long-lasting soil-seed banks that may remain in the ground for decades (Hill et al. 2001, Reyes et al. 2009). The flammability of gorse might derive from the emission of volatile organic compounds (Boissard et al. 2001).

A dispersal of seeds up to 50 m from the nearest parent plant by wind is reported (Johnson 2001). Gorse is also able to resprout and was even classified as "*strong resprouter*" based on the probability, number and length of resprouts (Reyes et al. 2009). The capability of resprouting from root shoots remains uncertain as the literature shows conflicting results (Zouhar 2005). Gorse might be considered as a pioneer species that can become highly abundant after a disturbance but is shade-intolerant and hence impedes or delays succession. Laboratory experiments occasionally classified gorse also as shade tolerant but it can be also prone to self-shading (Zouhar 2005; Wilson 2012 pers. comm.). The time required for native broadleaved forest to outcompete gorse is assumed to be about 30 years (Sullivan et al. 2007).

- ***Aristotelia serrata* (Wineberry):**

Altitude:	up to 1050m (Salmon 1980)
Height:	up to 10m
Trunk:	up to 30cm
Flowers:	late spring
Fruits:	in late summer on female trees only. Fruits are small, dark-red to black.
Abundance:	most common in regrowth forest (Crowe 1992)

	forest, forest-margins, roadsides; often occurs as first tree after clearing or felling (Salmon 1980).
Leaves:	sometimes deciduous (Salmon 1980)
Bark:	red bark; juveniles and also adults sometimes have a black bark (Salmon 1980).
Abundance at Hinewai:	quite common; potentially located at the Stones Track (Wilson 2012 pers. comm.).

- ***Carmichaelia australis:***

Abundance at Hinewai:	abundant on Banks Peninsula; rare in the Hinewai .
Other:	resprouts from the base (Wilson 2012 pers. comm.).

- ***Carpodetus serratus* (Marble leaf):**

Altitude:	up to 1000m (Williams & Buxton 1989)
Height:	8-12m
Trunk:	up to 20cm or more (Dawson & Lucas 2000)
Browsing:	Fruits are eaten by Kokako and Possums, leaves by dear and goats (Leathwick et al. 1983).
Leaves:	small sharp teeth (Crowe 1992) 6cm long 3cm wide (Salmon 1980)
Abundance:	Forest-margin, stream banks (Salmon 1980); gap-colonizer (Enright & Cameron 1988)
Wood:	sappy wood which is difficult to burn (Salmon 1980)
Flowers:	early summer with small, “star-like”, white flowers that grow in clusters.
Fruits:	early autumn; fruits are round, small, black capsules (Crowe 1992)
Other:	Holes in the trunk can be caused by the Püriri moth caterpillar (Crowe 1992); seed dispersal by birds (Enright & Cameron 1988)

Abundance at Hinewai: quite common; potentially located at the Stones Track and along other tracks
Other: potentially resprouting (Wilson 2012 pers. comm.).

- ***Coprosma crassifolia:***

Abundance at Hinewai: abundant; potentially located at “Tada Track”;
Other: resprouting species (Wilson 2012 pers. comm.).

- ***Coprosma lucida:***

Abundance at Hinewai: abundant in Hinewai but mostly in bush, that has not been burned; potentially located at Lothlorien and Lisburn track (Wilson 2012 pers. comm.).

- ***Coprosma propinqua:***

Abundance at Hinewai: not quite common; potentially found near Lisburn spur track;
Other: potentially resprouting (Wilson 2012 pers. comm.).

- ***Coprosma rhamnoides:***

Abundance at Hinewai: abundant; most common *Coprosma* species in the Hinewai Reserve but potentially not in the burned area (Wilson 2012 pers. comm.).

- ***Coprosma rotundifolia:***

Abundance at Hinewai: abundant but under the bush; hard to find burned individuals (Wilson 2012 pers. comm.).

- ***Discaria toumatou:***

Abundance at Hinewai: not common at Hinewai; 1 individual plant right by the track Lothlorien side of Lisburn track
Other: resprouting species (Wilson 2012 pers. comm.).

- ***Fuchsia excorticata* (Tree fuchsia):**

Altitude: up to 1060m
Growth form: tree; sometimes shrub (Salmon 1980)

Height:	12m -14m
Trunk:	60-80cm; up to 1m in old trees (Salmon 1980)
Leaves:	few or no teeth; deciduous
Flowers:	dark-purple flowers in late spring
Fruits:	dark-purple to black, narrow fruits that are app. 1cm long (Crowe 1994)
Bark:	loose and papery
Wood:	“*almost impossible to burn*” (Crowe 1994)
Reproduction:	from seeds and cuttings (Crowe 1994)
Bark:	reddish; papery; yellowish-green/brown inner bark (Salmon 1980)
Abundance:	common in second growth areas and along stream banks (Salmon 1980)
Abundance at Hinewai:	quite common; located alongside tracks;
Other:	resprouting species (Wilson 2012 pers. comm.).

- ***Griselinia littoralis*** **(Broadleaf/Kapuka):**

Height:	10-15m (Williams & Buxton 1989)
Altitude:	up to 900m (Crowe 1994)
Leaves:	5-10 cm long 2-5 cm wide (Salmon 1980) appear dark-green on top and are unlike Karaka never shiny below (Crowe 1994)
Browsing:	leaves, buds and fruits are browsed by Kokako; leaves and fruits by possums; leaves by deer and goats (Leathwick et al. 1983)
Fruits:	very small purple-black fruits are produced in autumn by female trees (Crowe 1994).
Other.	can be mistaken for *Griselinia lucida* (Dawson & Lucas 2000)
Abundance at Hinewai:	abundant; potentially near the Tada-Track (Wilson 2012 pers. comm.).

- ***Kunzea ericoides* (Kanuka):**

Altitude:	up to 900m (Salmon 1980, Crowe 1994)
Growth-form:	shrub / tree (Dawson & Lucas 2000)
Height:	up to 15m
Trunk:	up to 60cm (Salmon 1980)
Leaves:	12-15mm long 2mm wide (Salmon 1980)
Potential Age:	100-150 years
Successional status:	pioneer-species
Seeds:	small wind-dispersed seeds; capsules are easily destroyed by fire (Atkinson 2004) seed dispersal up to 62m; soil seedbank (Enright & Cameron 1988)
Leaves:	app. 1cm long and white; clustered flowers of less than 6mm are produced in summer (Crowe 1994).
Seeds:	seeds are “narrower” and in larger capsules compared to Manuka seeds.
Bark:	thin peeling bark (Crowe 1994)
Other:	resprouting species; pioneer species; flammable but not as flammable as *Ulex europaeus* (Wilson 2012 pers. comm.).

- ***Leptospermum scoparium* (Manuka):**

Height:	up to 8m
Altitude:	up to 1000m (Crowe 1994)
Successional status:	pioneer-species
Seeds:	small wind-dispersed seeds; fire can trigger the capsules to open (Atkinson 2004) The viability for Manuka and Kanuka seeds ranges from 6 weeks up to 2 years (Burrows 1973 cited in Atkinson 2004; Enright and Cameron 1988 cited in Atkinson 2004).

Flowers:	in late spring with usually white, sometimes pink flowers
Seeds:	> 6mm. Seeds are in hard, “broad” seed capsules compared to Kanuka
Other:	Manuka beetles can occur in early summer (Crowe 1994).

- ***Melicytus ramiflorus* (Mahoe):**

Altitude:	up to 1000m (Williams & Buxton 1989)
Height:	8-12m
Trunk:	up to 60 cm (Salmon 1980); smooth white lichen patches (Crowe 1994)
Seed dispersal:	by birds (Atkinson 2004)
Shade-tolerance:	seedlings are shade-tolerant (Atkinson 2004)
Browsing:	leaves, flowers and fruits are browsed by Kokako and possums; leaves only by deer and goats (Leathwick et al. 1983)
Flowers:	early summer with small greenish-yellow flowers that grow directly from branches (Crowe 1994)
Fruits:	late summer on female trees
Growth-form:	often short trunk and branches close above the ground
Abundance:	common in regrowth forests and coastal bush; often on partially-cleared land (Crowe 1994; Salmon 1980)
Abundance at Hinewai:	common; resprouting species (Wilson 2012 pers. comm.).

Fig. 3 Epicormic bud and shoot formation of Melicytus ramiflorus (Wabnig 2012)

- ***Muehlenbeckia astonii:***

  Other: resprouting species (Wilson 2012 pers. comm.).

- ***Nothofagus solandri* (Black beech):**

  Altitude: up to 750m

  Height: up to 25m

  Trunk: up to 1m

  Abundance: mountain slopes

  Bark: sometimes covered with black fungus (Salmon 1980)

  Abundance at Hinewai: potentially at “Waterfall gully”; burned individuals in Whakarere Forest.

  Other: resprouts from the top, potentially also from the base (Wilson 2012 pers. comm.).

- ***Pittosporum eugenioides* (Lemonwood/Tarata):**

  Altitude: up to 600m (Crowe 1992)

  up to 1000m (Williams & Buxton 1989)

Growth form:	tree; juvenile trees have a “pyramidal form” (Salmon 1980)
Height:	8-12m
Leaves:	7-15cm long
Flowers:	in bunches; in late spring (Crowe 1992)
Reproduction:	from seed (Crowe 1992)
Trunk :	up to 60cm (Salmon 1980)
Leaves:	10-15cm long (Salmon 1980) 2-4cm wide (Salmon 1980)
Abundance:	forest clearings, forest margins, stream banks; regenerating forests (Salmon 1980); alongside streams; open forests (Crowe 1992)

- ***Pseudowintera colorata* (Pepper tree/Horopito):**

Altitude:	up to 1500 m
Growth form:	shrub, tree
Height:	shrub (1 - 2.5m); tree (up to 10m)
Abundance:	forest edges, in deep shade (Salmon 1980)
Leaves:	1-1.5cm, leaves have a spicy taste and are covered with red blotches which are a visual warning of unpalatable compounds resulting in a potentially reduced herbivory by insects and larvae (Cooney et al. 2012). Leaves have a terpene content of approximately 9% of the weight what contributes to a defense against herbivory and possums (Crowe 1994).
Bark:	dark-greenish-grey, often appearing black through the growth of fungus (Salmon 1980).
Flowers:	greenish-yellow (in spring)
Fruits:	orange-red or black (in summer and autumn)
Other:	*Alseuosmia pusilla* is often mistaken for *P.colorata* (Dawson & Lucas 2000). A hybridization of *P.*

colorata and *P. axillaris* is assumed common (Salmon 1980).

Abundance at Hinewai: quite common; rare in lower altitudes; abundant above 200m; resprouting species (Wilson 2012 pers. comm.).

- ***Pseudopanax arboreus & Pseudopanax colensoi* (Five-Finger):**

Height: 8-10m
Altitude: up to 500m (Williams & Buxton 1989)
up to 760m (Crowe 1992)
Leaves: 5-7 leaflets (Crowe 1992, Salmon 1980)
Flowers and fruits: only on female trees in spring
Browsing: possums; fruits by Kokako; leaves by deer and goats (Leathwick et al. 1983)
Abundance: forests, open scrub (Salmon 1980)
Other: Fivefinger can also grow as an epiphyte on tree fern trunks (Salmon 1980)

- ***Pseudopanax crassifolius* (Lancewood/Horoeka):**

Altitude: up to 760 m (Crowe 1994)
Height: up to 10m (Gould 1993)
up to 15m (Crowe 1994; Williams & Buxton 1989)
Trunk: up to 50cm (Salmon 1980)
Fruits: Female trees fruit in autumn and winter. Fruits are 4-5mm and purplish-black.
Browsing: The caterpillar of the “leaf miner” feeds on leaves of Horoeka (Crowe 1994). Fruits are predated by Kokao and possums, the leaves by deer and goats (Leathwick et al. 1983).
Abundance: disturbed sites, open shrublands, forest edges and forests (Clearwater & Gould 1995); forests and shrubland (Salmon 1980)

Wood: "*one of the toughest woods of native timbers*" (Salmon 1980)

Other: Horoeka is a heteroblastic plant that has a different phenotype in juvenile and adult stages. Gould (1993) found that the leaf-growth can be subdivided into 4 phases (seedling, juvenile, transitional, adult) of which each has unique leaf forms. Clearwater & Gould (1995) found that a steeply declined leaf-orientation increases the interception of diffuse light under a dense canopy. As described in Dawson & Lucas (2000) it was also observed in the Hinewai that some shoots that grow from adult Horoeka have the juvenile leave form.

- ***Podocarpus totara* (Tötara):**

Height: up to 30m
Altitude: up to 600m
Fruits: in autumn on female trees
Bark and trunks: red-brown (Crowe 1994)
Age: up to 800 years (Salmon 1980)
Leaves: deciduous (Salmon 1980)

- ***Rubus cissoides* (Bush-Lawyer, Climbing Thorn):**

Altitude: up to 1000m
Other: climbs to patchy canopy sunlight (Crowe 1994); resprouting species (Wilson 2012 pers. comm.).

- ***Schefflera digitata* (Sevenfinger/Pate):**

Altitude: up to 1200m
Height: up to 8m (Crowe 1992, Salmon 1980)
Leaves: 7-9 leaflets, which are fine-toothed.
Abundance: mainly at forest-edges „with some shade"; damp

	parts of forests and stream banks (Salmon 1980)
Propagation:	from seed or cuttings
Other:	plant for attracting birds

- ***Sophora microphylla*:**

Abundance at Hinewai:	potentially found between Lothlorien and Lisburn Track (Wilson 2012 pers. comm.).

- ***Urtica ferox* (Nettle-tree):**

Altitude:	up to 1000m
Height:	up to 3m (Salmon 1980)
Trunk:	up to 12cm (Salmon 1980)
Leaves	5-12cm long
Abundance:	grows at edges of forests and scrubs (Crowe 1994)

2.3 The Hinewai Fire

On 14th July 2011, during a winter drought, a bush fire started with a lightning strike near Stony Bay Ridge and burned an area of approximately 300 hectares. The burned area covers a height difference from close above sea-level up to 806m. 2011 was a dry winter that set the record for the last 24 years with 530mm precipitation with an average of 832.2mm and the wettest with 1247.7mm in 1995. Below average rainfall continued until mid-October. After 27 hours most of the fire-fronts had burned out against green forest edges and tracks acted as fire-breaks (Wilson 2011). The predicted successional return of the landscapes' cover to mainly second-growth native forest has been set back by the fire that burnt mainly gorse dominated vegetation with varying amounts of native plants regenerating through it leading to a differently aged forest (Wilson 1994, Wilson 2011).

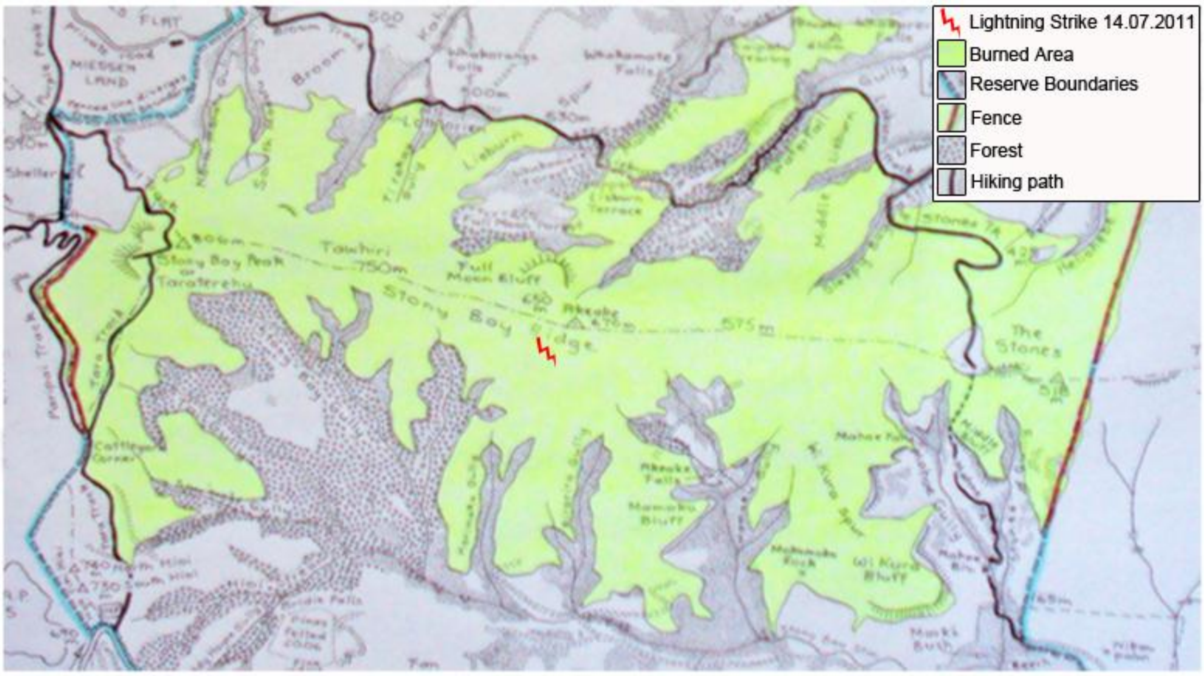


Fig. 4 Burned Area of the Hinewai-Reserve and position of the lightning strike **(Wilson 2011 modified)**

The fire was not the only disturbance. A polar blast in October 2011 defoliated some plants and induced also a resprouting of *Schefflera digitata* for example and defoliated *Hoheria angustifolia* which is an evergreen tree (Wilson 2012 pers. comm.). Additionally earthquakes in December 2011 caused some damages and uprooting of trees (Wilson 2012 pers. comm.). As the fire burned out against the forest edges there are also some individuals (potentially beeches) that are approximately 50% burned on the side facing the fire front. Some areas should be accessible due to corridors that were established for fire-fighting measures and will not be kept open in the future (Wilson 2012 pers. comm.).

CHAPTER 3: Methods

3.1 Field measurements and primary data collection

Fieldwork was carried out between July and October 2012. After an onsite-inspection 181 plants were sampled. Species were identified and plants were tagged with a metal plate and a continuous number. Heights were measured with a telescope-bole. The effective height from the center of the base of the plant up to the highest point was measured. The circumference was measured at 30 cm and 130 cm (dbh). Smaller individuals were measured 2 times with a calliper and averaged whereas a measuring tape was used for larger circumferences. If a plant showed multiple stems the biggest one was recorded as “main stem”. The position of resprouts were recorded with the categories: <30 cm; 30 cm – 130 cm; >130 cm. Resprouting was considered as binary trait with 1=resprouting and 0=no resprouting. Plants that resprouted from the base only (<30cm) or did not resprout at all were considered “topkilled”. The position of the plants were recorded with a GPS-device (accuracy ranged between +/- 1-30m). Charheight was not identifiable in most cases otherwise measured in cm from the ground. Bark-thickness measurements were carried out by using a Haglöf bark-gauge at breast height (1.3m). When measured, bark-thickness was measured at 2-3 points around the bole that seemed to be most representative for the bark at a given height or accounted for more than 50% of the circumference of a plant. Sample sites were chosen according to their accessibility but also based on the suggestions of Manager Hugh Wilson where species might be most likely found. As *Ulex europaeus* is declared as invasive pest species that covers a large area of the Hinewai Reserve a plot-based approach was not chosen as most plots would contain mainly only *Ulex europaeus* and some ferns and grasses. The edges of gullies were inspected anti-clockwise as the fire usually did not penetrate into the closed forest of the gullies.

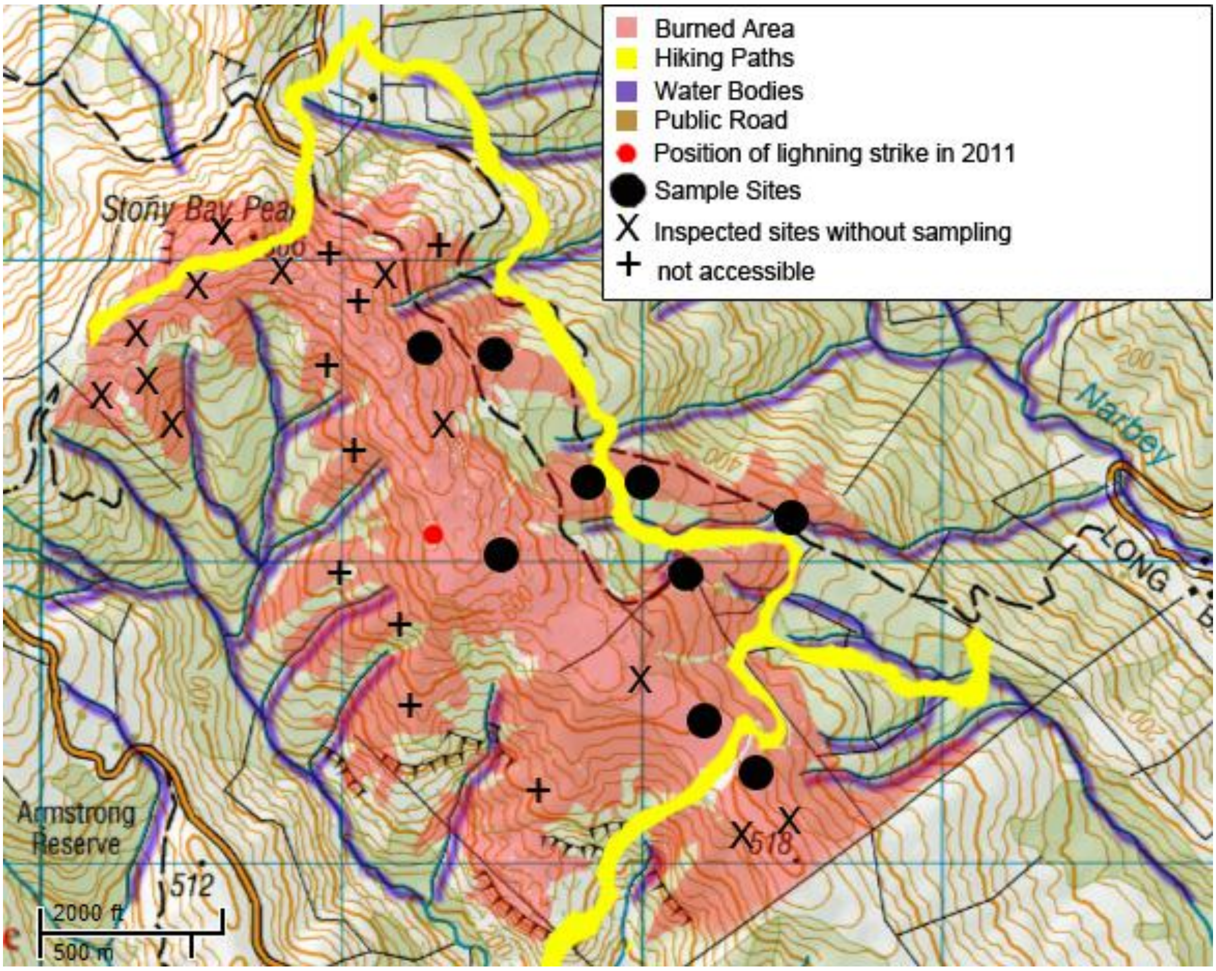


Fig 5. Sampling-sites of the fieldwork

3.2 Data Analysis

To analyse the data the statistic program “R” was used to perform a logistic-regression with the package “lme4”. The binary resprouting response (yes/no) were modeled to be the dependent variable and the factors: species, height and diameter the independent variables. The R-Code had the form: summary(null <- lmer(resprout ~ 1 + (1|species), data=observations)); summary(m1 <- lmer(resprout ~ height + (1|species), data=observations))

This analysis provides AIC-values (Akaike Information Criterion) and takes into account model fit and model simplicity, based on the principle of parsimony (fewer parameters in the model) (Lawes et al. 2011). The model with the lowest AIC value is selected as best for the empirical data at hand (Burnham & Anderson 2001). By using a logistic regression analysis and AIC-values different factors (e.g. species, height, diameter) can be tested for their influence on a dependent binary variable (e.g. resprouting, not resprouting). This approach also allows a ranking of models by looking at the differences (Δ) of the calculated values:

$\Delta \leq 2$ substantial support (evidence),
$4 \leq \Delta \leq 7$ considerably less support
$\Delta > 10$ essentially no support (Burnham & Anderson 2001).

CHAPTER 4: Results

Table 2 shows the 17 species that were found in the field and which of them were capable of resprouting. Additionally the proportion of resprouting individuals is subdivided in the proportions of individuals that resprouted from the base only (<30 cm) and hence can be considered topkilled, those that resprouted from the base and from positions higher on the stem (<30cm and 30cm-130cm) and those that resprouted from the stem only (>130cm).

Table 2: Resprouting species of the Hinewai-Reserve and position of resprouts

	Total	**not resprouted**	**resprouted**	resprouting individuals		
				base only	**base and stem**	**stem only**
Aristotelia serrata	9	-	100%	-	89%	11%
Carpodetus serratus	10	10%	90%	-	33%	67%
Coprosma dumosa	1	-	100%	-	100%	
Fuchsia excorticata	9	-	100%	12%	55%	33%
Griselinia littoralis	4	-	100%	-	75%	25%
(Kunzea ericoides)	6	100%	-	-	-	-
Melicytus ramiflorus	29	6.9%	93.1%	56%	37%	7%
Pittosporum eugenioides	16	12.5%	87.5%	-	93%	7%
Pittosporum spp.	2	-	100%	-	100%	-
Podocarpus totara	7	28.6%	71.4%	20%	40%	40%
Pseudopanax arboreus	7	-	100%	-	85.7%	14.3%
Pseudopanax crassifolius	15	6.7%	93.3%	36%	7.00%	57%
Pseudowintera colorata	57	22.8%	77.2%	25%	63.7%	11.3%
Rubus cissoides	1	-	100%	-	-	100%
Schefflera digitata	1	-	100%	-	-	100%
Teucridum parvifolium	5	-	100%	40%	60%	-
Ulex europaeus	2	50%	50%	-	100%	-
∑	**181**	**14.3%**	**85.7%**			
				23%	**56%**	**21%**

Fig. 6 gives a graphical overview whereas the green color indicates from which positions woody plants resprouted.

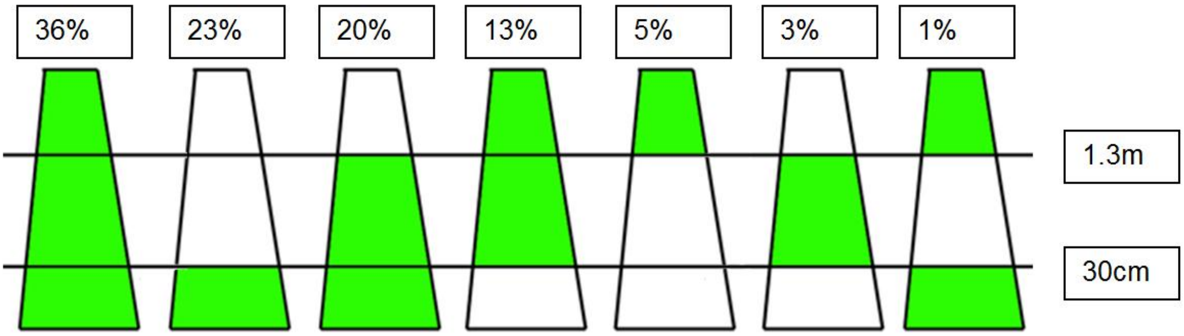


Fig. 6 Position of resprouts and proportions of plants

The histograms in fig.7 and fig.8 give an overview of the size of resprouting individuals. Size is described by the two measures height and diameter.

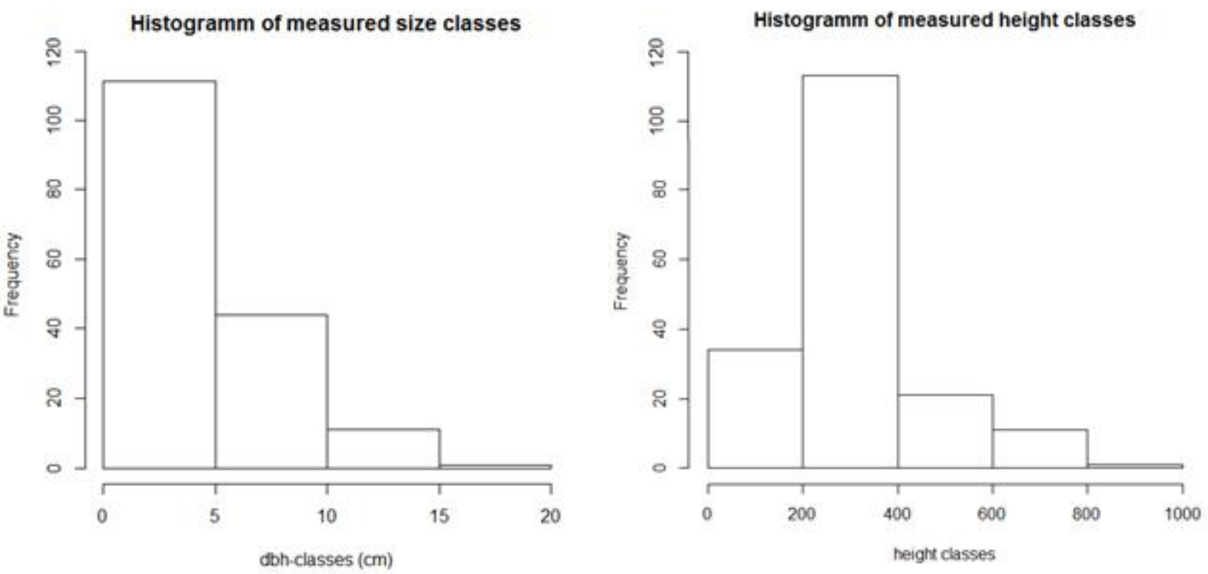


Fig. 7 Distribution of measured dbh-classes (5 cm steps) and height-classes (2m steps)

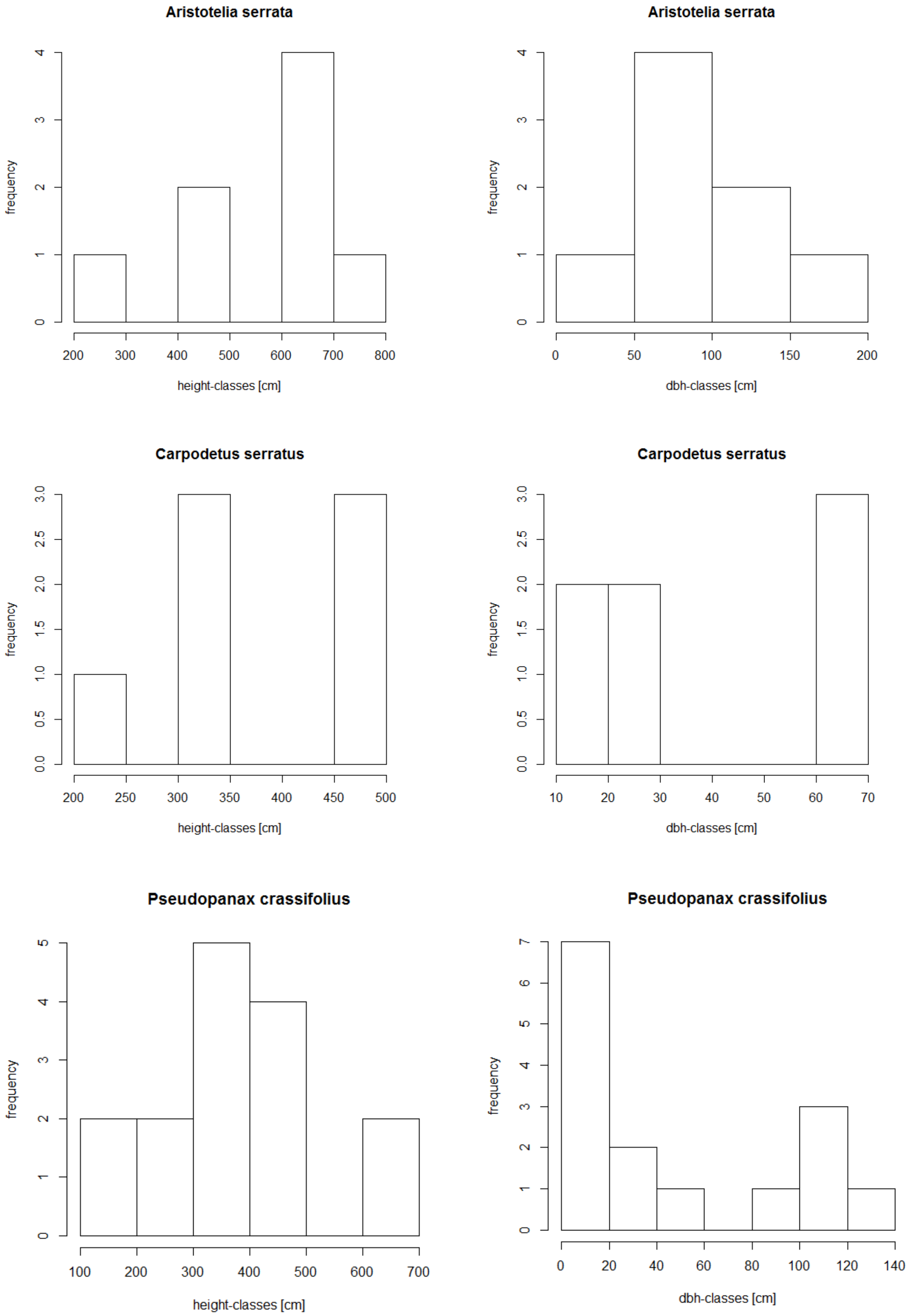
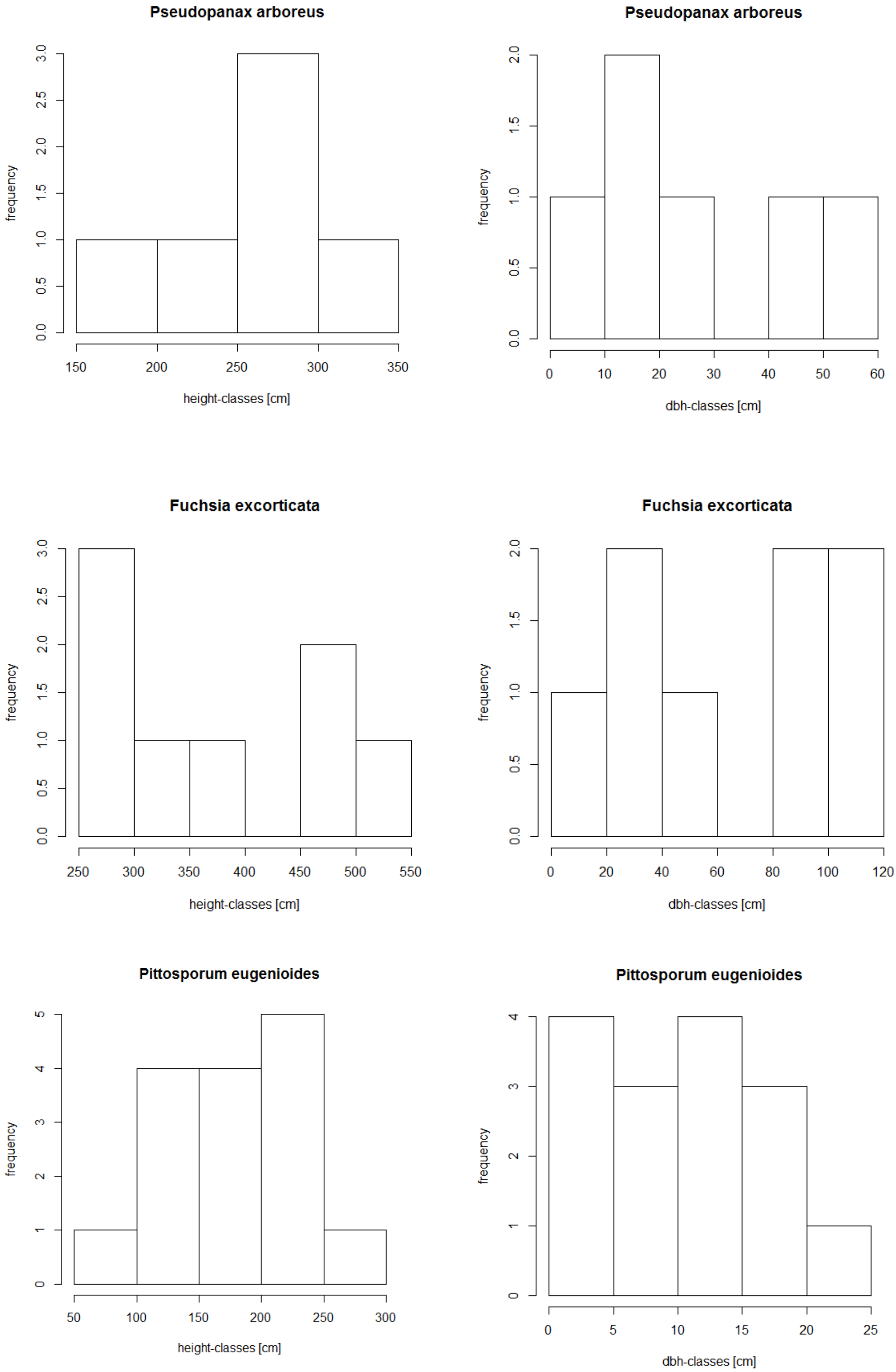
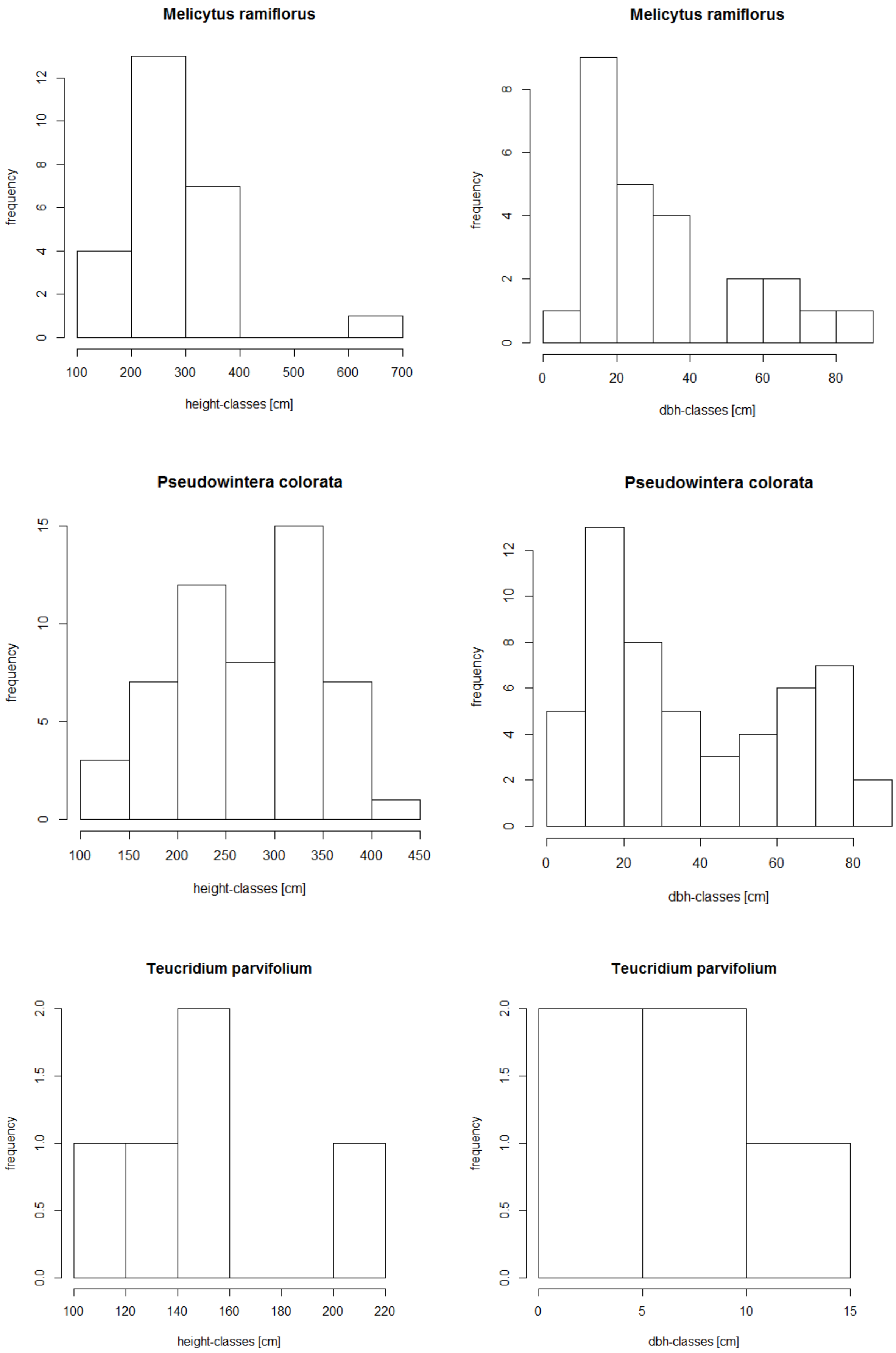


Fig. 8 Distribution of measured dbh-classes and height-classes per species



(Fig. 8 continued) Distribution of measured dbh-classes and height-classes per species



(Fig. 8 continued) Distribution of measured dbh-classes and height-classes per species

The average size and average height of the measured resprouting individuals is shown in fig. 9 and fig. 10.

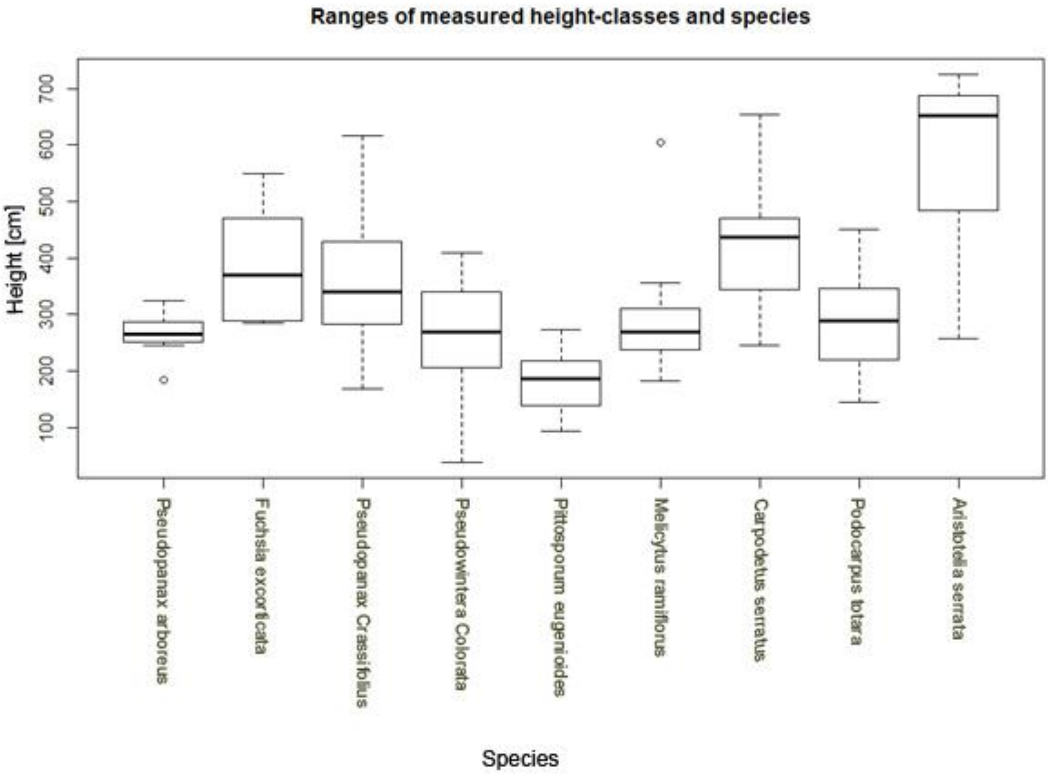


Fig. 9 Heights of resprouting species with n ≥ 5

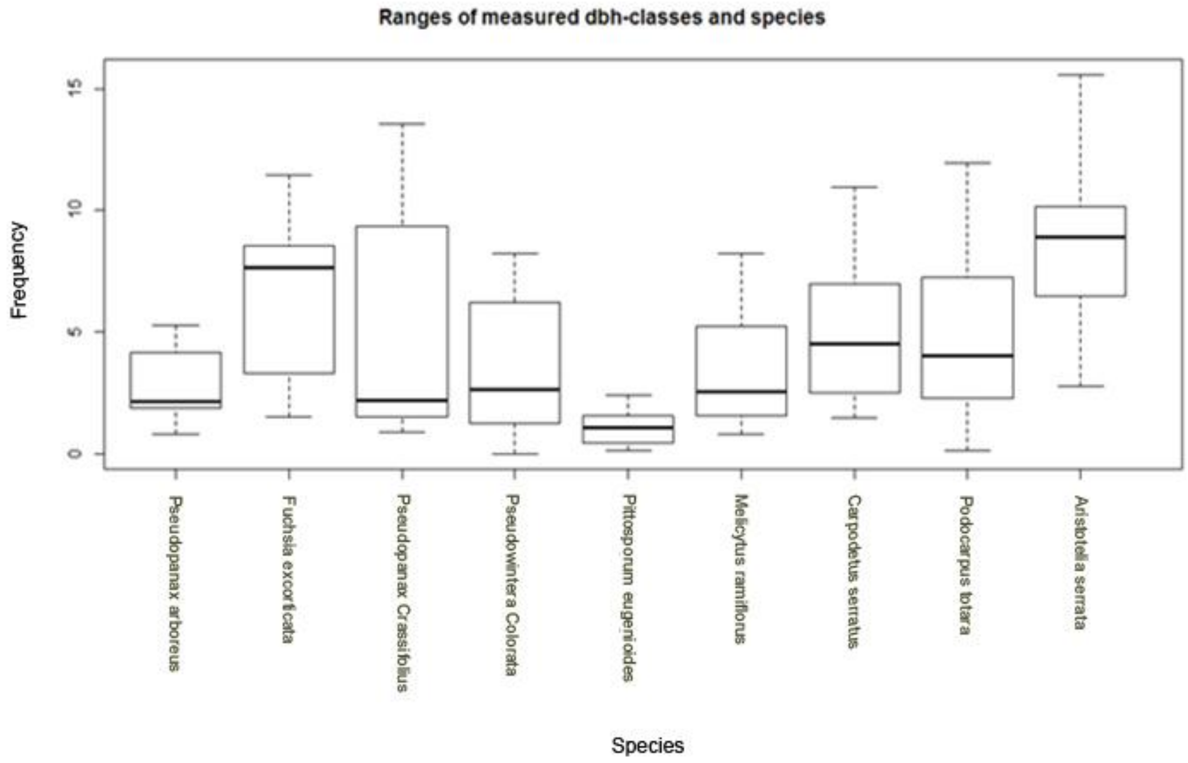


Fig. 10 Diameters of resprouting species with n ≥ 5

Table 3: Differences of AIC-Values for models explaining topkill and resprouting of species

Dependent variable	**topkill**	**resprout**	**resprout <30cm**	**resprout 30cm-130cm**	**resprout >130cm**
Explanatory variable					
species	**216.4**	**120.7**	**219.6**	**237.6**	**249.5**
height	16.2	0.3	4.3	8.9	6.3
dbh	16.9	1.9	10.2	10.1	6.8
species + height	15.8	16.9	15.2	16.1	5.4
species + dbh	8.3	0.6	4.9	8.5	3.3
species + diameter at the base	9.7	7	7.8	9.8	8.9

Legend

🟩	Δ < 2	substantial support to the model "species only"
🟨	Δ 4-7	considerably less support to the model "species only"
🟧	Δ 7-<10	barely support to the model "species only"
🟥	Δ >10	no support to the model "species only"

Table 4: AIC-Values for models explaining topkill and resprouting of *Pseudowintera colorata*

Dependent variable	topkill	resprout	resprouting < 30cm	resprout 30cm-130cm	resprouting >130cm
Independent variable					
diameter at the base	84.49	64.67	77.56	85.58	84.8
height	86.46	67.12	79.85	87.15	86.06
bark thickness (dbh)	86.74 (86.74)	68.35 (68.35)	80.09 (80.09)	87.61 (87.61)	86 (86)

CHAPTER 5: Discussion

Research question 1: How do woody plants at the Hinewai Reserve respond to the fire in 2011?; Research question 4: Are there differences within/between species?

Species differed in their capacity for resprouting. When looking at the position of resprouts with approximately one third the most common response of plants is to resprout from all positions of the stem. A quarter of the plants resprouted from the base only. Stem epicormic or axillary resprouting alone was found to be less common. Evidence for resprouting from belowground was only found for one single individual of *P. colorata.*

Fig. 11 An individual of *P. colorata* resprouting from the roots

P. colorata was the species with the biggest sample size and the variation of resprouting showed that three quarters of the recorded individuals resprouted while one quarter did not. This could a result of a different fire behavior as for example some individuals were severely burned as a result of the surrounding vegetation that likely acted as fire-ladder enabling the fire to climb up and cause a bigger damage.

Fig. 12 Topkilled *Pseudowintera colorata* covered with potential fire-ladders

As Cooney et al. (2012) found that *P. colorata* has a spicy taste and reddish leaves as visual warning against predators, its capacity to resprout may derive from browsing but also be beneficial in case of fires. The observation that resprouting from belowground is in principle possible but not quite common could mean that there is still some variation and possibilities for adaptions in case fire might become more frequent. Although the distribution of the size classes of *P. colorata* are hardly showing a tendency for smaller plants to resprout more likely, the overall right-skewed distribution of all resprouting species may suggest that smaller plants resprout more likely after a disturbance. Of the other 3 species with bigger sample sizes *Melicytus ramiflorus*, *Pittosporum eugenioides* and *Pseudopanax crassifolius* also approximately 9 in 10 plants did resprout after the fire. Together with *P. colorata* also *M. ramiflorus* and *P. crassifolius* are browsed by animals. The leaves, flowers and fruits of *M. ramiflorus* and *P. crassifolius are* browsed by Kokako, possums, deer and goats (Leathwick et al. 1983). The fact that these three species which are browsed by animals are also able to resprout after a fire could be indicative that the ability to resprout may have different origins but be beneficial in any case of biomass loss. When comparing *M. ramiflorus* and *P. eugenioides,* 56% of *M. ramiflorus* did resprout from the base while *P. eugenioides* did not. *M. ramiflorus* seedlings are considered to be shade-tolerant and can also grow under a canopy or coastal bush (Atkinson 2004, Crowe 1994). In comparison *P. eugenioides* occurs on forest clearings, forest margins and regenerating forest (Salmon 1980, Crowe 1992). *P. eugenioides* might be a more pioneer-like species which is a weak competitor. Therefor the photosynthetic capacity is restored more rapidly by resprouting axillary,- branch,- or stem epicormic compared to resprouting from the base and hence might be the better strategy (Lawes et al. 2011a; Bond & Midgley 2001). Applying the same logic on *P. crassifolius* shows another picture. P. crassifolius occurs as well on open sites and forest edges but also in closed forests. The black color of leaves and the downward orientation of leaves is beneficial under a closed canopy (Clearwater & Gould 1995). While again 9 out of 10 individuals of *P. crassifolius* resprouted, one third resprouted from the base and two thirds from higher positions. This might indicate that *P. crassifolius* is a more generalist species able to grow in different environments. Besides *P. eugenioides* also 2 thirds of *Carpodetus serratus* tended to resprout from higher positions while none was found resprouting only from the base. Also *C. serratus* is described as gap-colonizer and growing on forest margins (Salmon 1980, Enright & Cameron 1988). *Aristotelia serrata* might also be considered as generalist. *P. crassifolius* tends to occur in closed and open forests but seems to be more fitted for closed forests. *A. serrata* is „*most common*“ (Crowe 1992) in regrowth forests and closed forests but also grows on forest margins and „*often occurs as first tree after clearing or felling“* (Salmon 1980).

Although the evidence is not definite, it seems reasonably to assume that the less competitive a plant is the more likely it will resprout from higher positions on the stem. Later successional species that are shade tolerant are more likely to resprout from the base. Generalist species might show a higher variation of the resprouting response. These findings are consistent with the results.

Although the sample size is small and induce a general rule is critical a weak support for the findings of Vesk (2006) that smaller size classes are more dependent on the ability to resprout can at least be argumented. The histograms of resprouting individuals summed over all species shows that smaller individuals tend to resprout more likely and resprouting might decrease with increasing size. When plant-size is divided into height and diameter (dbh) it seems that the diameter has a bigger influence than the plant height. Also Lawes et al. (2011) found that some species despite being shortest survived fire best. As Midgley et al. (2011) found that post-fire mortality decreases with diameter rather than height also the resprouting ability might increase with stem diameter rather than height. This is easy to understand if resprouting is interpreted as “absence of mortality”. Although this study provides no definite evidence that height is less important than the diameter it at least suggests that it might be reasonable to assume in the case of the Hinewai fire. But ranking the importance of traits might be critical as already Perry et al. (2012), Klimešová et al. (2008) pointed out that a combination of traits is necessary to explain plant specific responses to disturbances. The separation of the importance of single factors like „height alone“ or „dbh alone“ is also critical as Lawes et al. (2011) found that those measures are often positively correlated, meaning that a higher plant might also tend to have a larger dbh or plants with a bigger dbh tend to be higher.

The average dbh of resprouting species (Fig. 10) also shows that the average diameter of resprouting species is under 10cm. This could also indicate the importance for smaller plants being able to resprout and a decreasing need for bigger plants that can avoid damages, proposed by Vesk (2006). But the question remains whether bigger plants have not resprouted and therefor were not recorded or if it just happened to be that the Hinewai-Reserve as a regenerating forest predominantly consists of smaller sized plants and therefor bigger plants although they might or might not be able to resprout are simply underrepresented in the collected dataset.

Moreira et al. (2012) proposed to separate between resprouting ability, resprouting vigor and post-resprout survival. *P.eugenioides* and *M.ramiflorus* are examples of species that would have to be monitored in the future to see whether the initial resprouting is successful, as some individuals have resprouted but the leaves of resprouts were dry and discolored. Hence the overall resprouting success might not be indicative of longer-term survival.

Fig. 13 Resprouting *Pittosporum eugenioides*

Fig. 14 Resprouting *Melicytus ramiflorus* with infested leaves

As the resprouting vigor has not been measured and post-resprout survival has to be assessed in the future at least the resprouting ability of some woody plants could be recorded.

Research question 2: Which species do resprout and where do they resprout?

The first group of plants was found capable of resprouting from the stem: *Aristotelia serrata, Carpodetus serratus, Fuchsia excorticata, Griselinia littoralis, Pittosporum eugenioides, Pseudopanax arboraeus* and Ulex europaeus. The second group, although also capable of resprouting from the stem showed a higher variance and proportions of individuals that resprouted from the base only. Those species also are those with the largest sample sizes resulting in more variation that has been recorded: *Melicytus ramiflorus, Podocarpus totara, Pseudowintera colorata, Pseudopanax crassifolius and Teucridium parvifolium.*

Fig. 15 Pseudowintera colorata resprouting from the base

Fig. 16 Pseudowintera colorata resprouting from the stem

Fig. 17 Carpodetus serratus resprouting from the stem

Additional categories are those species that were found to be resprouting, although the small sample size did not allow drawing a qualitative conclusion: *Coprosma dumosa, Pittosporum spp*. and *Schefflera digitata.* No sprouting individuals were found for *Kunzea ericoides.* When compared to the findings of Burrows (1994) *Aristotelia serrata, Carpodetus serratus, Fuchsia excorticata, Griselinia littoralis, Melicytus ramiflorus, Pittosporum eugenioides, Pseudopanax arboreus* and *Pseudopanax crassifolius* were also capable of branch- and stem epicormic resprouting in addition to the production of basal sprouts. Besides the species in Burrows' list that are capable of producing basal sprouts also *Coprosma dumosa, Podocarpus totara* and *Pseudowintera colorata* can be added to this list. *Kunzea ericoides* might be considered as "non-sprouter" and has been killed by the fire. *Ulex europaeus is capable of* resprouting and regrowing from a soil seedbank.

Fig. 18 Resprouting *Ulex europaeus*

Fig. 19 Ulex europaeus regrowing from seed

Research question 3: Which functional traits might explain the capability to resprout?

The data suggests that plant-responses to fire, topkill and the position of resprouts are mainly a species-specific trait. However, the results for whether a plant resprouts at all are not as clear. In case species do resprout they behave similarly but the importance of the factor "species" for initiating resprouting in the first place is not evident. This is puzzling as it would contradict the last paragraph. In case the resprouting ability is not a species specific trait it would make no sense to list species that are capable of resprouting. As the results also show that size does matter for resprouting, with smaller plants more likely to resprout, there might be another hidden variable that is decisive for the initiation of resprouting. This could be site productivity (Vesk 2006), stress (Nzunda & Lawes 2011), water-carbohydrate supply (Morisset et al. 2012) or the post-fire state of plants (Moreira et al. 2012). It seems that classifying species into resprouters and non-sprouters is not sufficient as for example also Moreira et al. (2012) pointed out that not all individuals of the same species initiated resprouting. From this perspective it is not surprising that resprouting is more complex than a simple dichotomy of sprouters and non-sprouters.

A preliminary phylogeny shows that although some of the species that are capable of resprouting are closely related in their history (e.g. the genus *Pseudopanax* including the species *Pseudopanax crassifolius* and *Pseudopanax arboreus* with the genus

Schefflera including the species *Schefflera digitata*) an overall pattern is not obvious. To answer questions on speciation and evolution in more detail a study that focuses explicitly on this topic would be required.

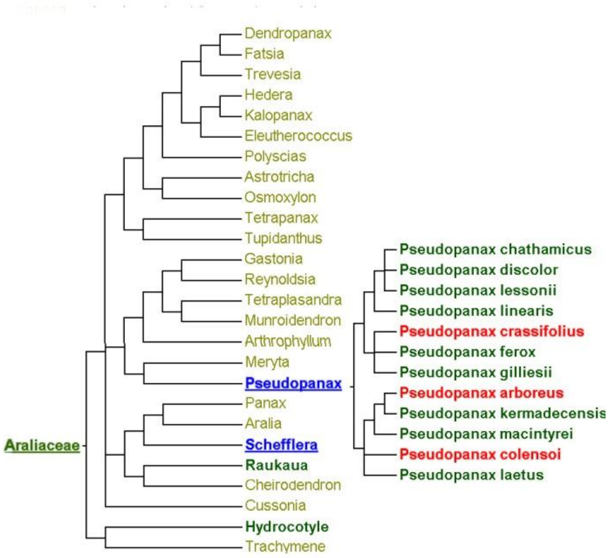


Fig. 20 Partial Phylogeny

CHAPTER 6: Conclusions

This study showed that resprouting enables plants to survive wildfires. The ability to resprout may be a trait that has evolved through fire and has been preserved over millions of years. But it is also possible that the ability to resprout of the observed species in the Hinewai-Reserve may also have different origins. This may derive from the fact that species that are known to be browsed by animals also can resprout after a biomass loss in a fire. The collected data shows that resprouting individuals of the same species resprout in a similar way but that the factor “species” alone is not a good factor to predict whether a plant resprouts in the first place. This weakens the artificial dichotomy in sprouters and non-sprouters and shows its’ limited applicability to certain research-questions. Site productivity, fire behavior and intensity and pre-fire state of the plant are only a few parameters that might have an impact and lead to different outcomes. Considering the results, it is also plausible to assume that the position of resprouts depend on the competitive strength of plants, with less competitive ones resprouting more likely from the top compared to competitive, shade-tolerant plants that can also afford to resprout from the base. Expanding on that argumentation it might be the case that early-successional species are also more likely to resprout than later-successional ones. Also plant-size seems to have an impact with smaller plants more likely resprouting after a fire. This would be also consistent with some literature as bigger plants are more likely able to avoid damages and hence the ability to resprout becomes less important for survival. As an educated guess it could also be assumed that specialized species will show on average a similar resprouting response compared to more generalist species that might show a higher variance. The determining rule of thumb would be that species that grow under different circumstances such as a closed canopy forest or more open types of habitats are more likely to differ in their resprouting response compared to species that are known to grow solely on forest-margins for example.

REFERENCES

Allen H.D. (2008) Fire: plant functional types and patch mosaic burning in fire-prone ecosystems. Prog. Phys. Geog., 2008, 32(4):421–437.

Ashton P.M.S., Lowe J.S., Larson B.C. (1990) Some evidence for the cause of epicormic sprouting in Blue Mahoe (Hibiscus elatus sw.) in the moist limestone region of Puerto Rico. J. Trop. For. Sc.3 (2) 123 – 130.

Atkinson I.A.E. (2004) Successional processes induced by fires on the northern offshore islands of New Zealand. NZ J. Ecol., 2004, 28(2): 181-193.

Balch J.K, Nepstad D.C., Curran L.M., Brando P.M., Portela O., Guilherme P., Reuning-Scherer J.D., DeCarvalho O.jr (2011) Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon.

Balfour D.A. & Midgley J.J. (2006) Fire induced stem death in an African acacia is not caused by canopy scorching. Austr. Ecol., 2006, 31:892–896.

Barraclough T.G. (2006) What can phylogenetics tell us about speciation in the Cape flora? Div. and Distr., 2006, 12:21–26.

Bellingham P.J. & Sparrow A.D. (2000) Resprouting as a life history strategy in woody plant communities. Oikos, 2000, 89:2 .

Bergström R., Skarpe C., Danell K. (2000) Plant responses and herbivory following simulated browsing and stem cutting of Combretum apiculatum. J. Veg. Sc., 2000, 11: 409-414.

Boissard C., Cao X.L., Juan C.Y., Hewitt C.N., Gallagher M. (2001) Seasonal variations in VOC emission rates from gorse (*Ulex europaeus*). Atm.Env. (2001) 35:917-927.

Bolker B.M. & Romero C. (2008) Effects of stem anatomical and structural traits on responses to stem damage: an experimental study in the Bolivian Amazon. Can. J. For. Res.. 38.3 (Mar. 2008): p611.

Bond W.J. & van Wilgen B.W. (1996) Fire and Plants. Chapman and Hall, London. Volume 14 in the Population and Community biology series.

Bond W.J. & Midgley J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. Tr. Ecol. Evol., 16:45–51.

Bond W.J. & Midgley J.J. (2003) The evolutionary ecology of sprouting in woody plants. Int. J. Plant Sc., 164: 103–114.

Bond W.J., Dickinson K.J.M., Mark A.F. (2004) What limits the spread of fire-dependent vegetation? Evidence from geographic variation of serotiny in a New Zealand shrub. Gl. Ecol. Biogeogr., 2004, 13:115–127.

Bond W.J. (2008) What limits trees in C4 grasslands and savannas? Annu. Rev. Ecol. Evol. Syst. 39:641–59.

Bradshaw S.D., Dixon K.W., Hopper S.D., Lambers H, Turner R.S. (2010) Little evidence for fire-adapted plant traits in Mediterranean climate regions. Trends in Pl, Sc., 2011, 16:2.

Brando P.M., Nepstad D.C., Balch J.K., Bolker B., Christman M.C., Coe M., Putz F.E. (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. Gl. Ch. Bio., 2012, 18:630–641.

Briggs D.G. (1994) Forest products measurements and conversion factors: with special emphasis on the U.S. Pacific.

Brokaw N.V.L. (1985) Treefalls, Regrowth, and Community Structure in Tropical Forests in: White P.S. & Pickett S.T.A. (1985) Natural disturbance and patch dynamics: an introduction. The Ecology of Natural Disturbance and Patch Dynamics. Orlando FL, Academic Press. 3–13.

Burnham K.P. & Anderson D.R. (2001) Kullback–Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*, 2001, 28, 111–119

Burrows C. (1994) Do New Zealand Forest Trees Regenerate From Sprouts? J. Canterbury Bot. Soc., 28 – 1994.

Chatto K., Bell T., Kellas J. (2003) Effects of repeated low-intensity fire on tree growth and bark in a mixed eucalypt foothill forest in south-eastern Australia. Res. Rep. No. 66 December 2003.

Chave J. (2005) Measuring wood density for tropical forest trees - A field manual for the CTFS sites.

Clarke P.J., Knox K.J.E., Wills K.E., Campbell M. (2005) Landscape patterns of woody plant response to crown fire: disturbance and productivity influence sprouting ability. J. Ecol., 2005, 93:544 –555.

Clarke P. J., Lawes M. J., Midgley J. J., Lamont B. B., Ojeda F., Burrows G. E., Enright N. J., Knox K. J. E. (2012) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phyt. (2012).

Clearwater M.J. & Gould K.S. (1995) Leaf orientation and light interception by juvenile Pseudopanax crassifolius (Cunn.) C. Koch in a partially shaded forest environment. Oec., 1995, 104:363-371.

Collet C., Colin F., Bernier F. (1997) Height growth, shoot elongation and branch development of young Quercus petraea grown under different levels of resource availability. Ann. For. Sc. 54:65–81.

Cooney L.J. VanKlink J.W., Hughess N.M., Perry N.B., Schaefer M.H. Menzies I.J. Gould K.S. (2012) Red leaf margins indicate increased polygodial content and function as visual signals to reduce herbivory in Pseudowintera colorata. New Phyt., 2012, 194: 488–497.

Cornelissen J. H. C., Lavorel S., Garnier E. et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Austr. J. Bot. 51:335–80.

Crowe A. (1992) Which native tree? Penguin Books Ltd. Registred offices: Harmondsworth, Middlesex, England.

Crowe A. (1994) Which Native Forest Plant? Penguin Books Ltd., Registred offices: Harmondsworth. Middlesex, England.

Curran T.J., Brown R.L., Edwards E., Hopkins K., Kelley C., McCarthy E., Pounds E., Solan R., Wolf J. (2011) Plant functional traits explain interspecific differences in immediate cyclone damage to trees of an endangered rainforest community in north Queensland. Austr. Ecol., 2008, 33:451–461.

Dawson J. & Lucas R. (2000) New Zealand's Native Trees.

Del Tredici P. (2001) Sprouting in temperate trees: a morphological and ecological review. Bot Rev 67:121–140.

Duckworth J. C., Kent M. & Ramsay M. (2000) Plant functional types: an alternative to taxonomic plant community description in biogeography? Prog. Phys. Geogr. 24:515–42.

Ducrey M, Duhoux F., Huc R., Rigolot E (1995) The ecophysiological and growth responses of Aleppo pine to controlled heating applied to the base of the trunk. PIF1995-04; Can. J. For. 26:1366-1374.

Enright N.J. & Cameron E.K. (1988) The soil seed bank of a kauri (Agathis australis) forest remnant near Auckland, New Zealand. NZ J. Bot., 1988, 26:223-236.

Fernandes P. M., Vega J.A., Jiménez E., Rigolot E. (2008) Fire resistance of European pines. For. Ecol. & Mgmt. 256: 246 – 255.

Gould K.S. (1993) Leaf Heteroblasty in Pseudopanax crassifolius: Functional Significance of Leaf Morphology and Anatomy. Ann. Bot., 1993, 71:61-70.

Grime J (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. A. Nat., 111:1169–1194.

Groom P.K. & Lamont B.B (2011) Regional and local effects on reproductive allocation in epicormic and lignotuberous populations of Banksia menziesii. Plant Ecol., 2011, 212:2003–2011.

Gurvich D.E., Enrico L., Cingolani A.M. (2005) Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. Austr. Ecol., 2005, 30:868–875.

Gutsell S.L. & Johnson E.A. (1996) How fire scars are formed: coupling a disturbance process to its ecological effect. Can. J. For. Res., 1996, 26:166-174.

Harmer R. (1992) Do dominant oaks have few epicormic branches? For. Comm. Gr. Brit. Res. Div. For. Auth. Res. Inf. Note 223.

Harvey P.H. & Pagel M.D. (1998) The comparative method in evolutionary biology. Oxford University Press.

Hedge V., Chandran M.D.S., Gadgil M. (1998) Variation in bark thickness in a tropical community of Western Ghats in India. Funct. Ecol., 1998, 12:313-318.

Herman F.R. (1964) Epicormic branching of sitka spruce. USDA For. Serv. Res. Pap. PNW-18.

Hill R. L., Gourlay A.H., Barker R.J. (2001) Survival of Ulex europaeus seeds in the soil at three sites in New Zealand. NZ J. Bot., 2001, Vol. 39: 235-244.

Hodgkinson K. C. (1998) Sprouting success of shrubs after fire: height-dependent relationships for different strategies. Oec. 115:64–72.

Hoffmann W.A., Orthen B., Kielse P., DoNascimento V. (2003) Comparative fire ecology of tropical savanna and forest trees. Funct. Ecol., 2003, 17:720–726.

Hoffmann W.A. & Solbrig O.T. (2003) The role of topkill in the differential response of savanna woody species to fire. For. Ecol. & Mgmt. 180, 2003, 273–286.

Hoffmann W.A., Adasme R., Haridasan M., DeCarvalho M.T., Geiger E.L., Pereira M.A.B., Gotsch S.G., Franco A.C. (2009) Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. Ecol. 90(5), 2009, 1326–1337.

Hoffmann W.A., Geiger E.L., Gotsch S.G., Rossatto D.R., Silva L.C.R., Lau O.L., Haridasan M., Franco A.C. (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol. Let., 2012, 15:759–768.

Hood S. & Bentz B. (2007) Predicting post-fire Douglas-fir beetles attacks and tree mortality in the northern Rocky Mountains. Can. J. For. Res., 2007, 37:1058-1069.

Huffman E.L., MacDonald L.H, Stednick J.D. (2001) Strength and persistence of fire-induced soil hydrophobicity under ponderosa and lodgepole pine, Colorado Front Range. Hydrol. Pr., 2001, 15:2877-2892.

Hunt D. (2007) Department of Conservation fire research needs analysis: report on a project to implement Recommendation 7 of DOC's Fire Management Systems Audit. Department of Conservation, Wellington.

Ibanez T., Curt T., Hely C. (2012) Low tolerance of New Caledonian secondary forest species to savanna fires. J. Veg. Sc., 2012.

Iwasa Y. & Kubo T. (1997) Optimal size of storage for recovery after unpredictable disturbances. Evol. Ecol., 11:41–65.

Johnson P. N. (2001) Vegetation recovery after fire on a southern New Zealand peatland. NZ J. Bot., 2001, 39-2:251-267.

Keeley J.E. (2006) Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chapparal. Madrono, Vol. 53, No. 4, 373–379.

Keeley J.E., Brennan T., Pfaff A.H. (2008) Fire severity and ecosystem responses following crown fires in California shrublands. Ecol. App., 2008, 18(6):1530–1546.

Keeley J.E. (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage.

Keeley J.E., Pausas J.G., Rundel P.W., Bond W.J., Bradstock R.A. (2011) Fire as an evolutionary pressure shaping plant traits.

Kozlowski T.T. (1992) Carbohydrate sources and sinks in woody plants. Bot. Rev. 58: 107–222.

Kraft N.J.B, Metz M.R., Condit R.S., Chave J. (2010) The relationship between wood density and mortality in a global tropical forest data set. New Phyt., 2010, 188: 1124–1136.

Krivtsov V., Fernandes P., Higham B., Pezzatti G.B., Legg C. (2009) Release of prototype software for allometric modelling of fuel structure with provisional case studies. Deliverable D3.3-5 of the Integrated project “Fire Paradox”, Project no. FP6-018505, European Commission, 33 pp.

Kruger L.M., Midgley J.J. & Cowling R.M. (1997) Resprouters vs reseeders in South African forest trees; a model based on forest canopy height. Funct. Ecol. 11: 101–105.

Lamont B.B. & Wiens D. (2003) Are seed set and speciation rates always low among species that resprout after fire, and why? Evol. Ecol., 2003, 17: 277–292.

Lamont B.B, Wittkuhn R., Korczynskyj D. (2004) Ecology and ecophysiology of grasstrees. Austr. J. Bot. 52: 561–582.

Lamont B.B., Enright N.J., He T. (2011) Fitness and evolution of resprouters in relation to fire. Pl. Ecol., 2011, 212:1945–1957.

Lawes M.J. Adie H., Russel J., Murphy B., Midgley J.J. (2011) How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness.

Lawes M.J., Richards A., Dathe J., Midgley J.J (2011a) Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia.

Lawes M.J. & Clarke P.J. (2011) Ecology of plant resprouting: populations to community responses in fire-prone ecosystems.

Lawes M.J., Clarke P.J., Midgley J.J. (2012) Costs and benefits of relative bark thickness in relation to fire damage: a savanna/forest contrast. J. Ecol., 2012.

Leathwick J.R., Hay J.R, Fitzgerald A.E. (1983) The influence of browsing by introduced mammals on the decline of North Island Kokako. NZ J. Ecol. 6: 55-70.

Lloret F., Verdu M., Flores-Hernandes N., Valiente-Banuet N. (1999) Fire and resprouting in mediterranean ecosystems: Insights form an external biogeographic region, The Mexical shrubland. Am. J. Bot., 1999, 86(12): 1655–1661.

Madrigal J., Marino E., Guijarro M., Hernando C., Díez C. (2012) Evaluation of the flammability of gorse (Ulex europaeus L.) managed by prescribed burning. A. For. Sc., 2012, 69:387–397.

Martin, R. E. (1963) Thermal properties of bark. For. Prod. J., 13:419-426.

Meier A.R., Saunders M.R., Michler C.H. (2012) Epicormic buds in trees: a review of bud establishment, development and dormancy release. Tree Phys. 32:565–584.

Michaletz S.T. & Johnson E.A. (2007) How forest fires kill trees: A review of the fundamental biophysical processes. Sc. J. For. Res., 2007, 22:500-515.

Michaletz S.T., Johnson E.A., Tyree M.T. (2012) Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. New Phyt., 2012.

Midgley J.J., Kruger L.M., Skelton R. (2011) How does fire kill plants? The hydraulic death hypothesis and Cape Proteaceae “fire resisters”. S. Afr. J. Bot., 2011, 77:381–386.

Moreira B., Tormo J., Pausas J.G. (2012) To resprout or not to resprout: factors driving intraspecific variability in resprouting. Oikos, 2012, 000: 001–008.

Moreno J.M. & Oechl W.C. (1990) Fire intensity and herbivory effects on postfire resprouting of Adenostoma fasciculatum in southern California chapparal. Oec., 1991, 85:429-433.

Morisset J.B., Mothe F, Bock J., Breda N., Colin F. (2012) Epicormic ontogeny in Quercus petraea constrains the highly plausible control of epicormic sprouting by water and carbohydrates. Ann. Bot., 2012, 109:365–377.

Müller S.C, Overbeck G.E., Pfadenhauer J., Pillar V.D. (2007) Plant functional types of woody species related to fire disturbance in forest–grassland ecotones. Pl. Ecol., 2007, 189:1–14.

Nefabas L.L. & Gambiza J. (2007) Fire-tolerance mechanisms of common woody plant species in a semiarid savanna in south-western Zimbabwe. Afr. J. Ecol., 45:550–556.

Neke K.S., Owen-Smith N, Witkowski E.T.F. (2006) Comparative resprouting response of Savanna woody plant species following harvesting: the value of persistence. For. Ecol. & Mgmt., 2006, 232:114–123.

Nicolini E., Chanson B., Bonne F. (2001) Stem Growth and Epicormic Branch Formation in Understorey Beech Trees (Fagus sylvatica L.). Ann. Bot., 2001, 87:737-750.

Nobel P. S. (1974) Boundary layers of air adjacent to cylinders: Estimation of effective thickness and measurements on plant material. Pl. Phys.,54:177-181.

Nzunda E.F., Griffiths M.E., Lawes M.J. (2007) Resprouting enhances seedling persistence in a subtropical coastal dune forest. Afr. J. Ecol., 46:32–38.

Nzunda E.F. & Lawes M.J. (2011) Costs of resprouting are traded off against reproduction in subtropical coastal dune forest trees. Plant Ecol., 2011, 212:1991–2001.

O'Brien J.J., Hiers J.K., Mitchell R.J., Varner J.M. III, Mordecai K. (2010) Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. Fire Ecol. 6(2):1-12.

Ogawa K. (2006) Stem respiration is influenced by pruning and girdling in Pinus sylvestris. Sc. J. of For. Res., 2006, 21:293-298.

Ogden J., Basher L., McGlone M. (1998) Fire, Forest Regeneration and Links with Early Human Habitation: Evidence from New Zealand. Ann.Bot., 81: 687-696.

Ojeda F., Brun F.G., Vergara J.J. (2005) Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. New Phyt., 2005.

Paine C. E. T., Stahl C., Courtois E. A., Patiño S., Sarmiento C., Baraloto C. (2010) Functional explanations for variation in bark thickness in tropical rain forest trees. Funct. Ecol., 24:1202–1210.

Pausas J. (2001) Resprouting vs. seeding: a Mediterranean perspective. Oikos 94:193-194.

Pausas J.G. & Verdu M. (2005) Plant persistence traits in fire-prone ecosystems of the Mediterranean basin: a phylogenetic approach. Oikos, 2005, 109:196-202.

Pausas J.G. & Schwilk D. (2012) Fire and plant evolution. New Phyt., 2012, 193: 301–303.

Pausas J.G., Bradstock R.A., Keith D.A., Keeley J.E. (2004) Global change of terrestrial ecosystems fire network 2004: Plant functional traits in relation to fire in crown-fire ecosystems. Ecol. 85(4), 2004, 1085–1100.

Payton I.J., Allen R.B. (1984) A post-fire succession in the northern Urewera forests North Island, New Zealand. NZ J. Bot., 1984, 22:207-222.

Pekin B.K., Wittkuhn R.S., Boer M.M., Macfarlane C., Grierson P.F. (2011) Plant functional traits along environmental gradients in seasonally dry and fire-prone ecosystem. J. Veg. Sc., 2011, 22:1009–1020.

Perez B. & Moreno J.M. (1998) Methods for quantifying fire severity in shrubland-fires. Plant Ecol., 1998, 139:91-101.

Perry L.W.G., Enright N.J., Miller B.P., Lamont B.B. (2012) Do plant functional traits determine spatial pattern? A test on species-rich shrublands. W. Austr. J. Veg. Sc., 2012.

Pillar V.D.P. & Sosinski E.E.jr. (2003) An improved method for searching plant functional types by numerical analysis.

Pla L., Casanoves F., DiRienzo J. (2012) Quantifying Functional Biodiversity, Springer Briefs in Environmental Science.

Pratt R.B.,North G.B., Jacobsen A.L., Ewers F.W., Davis S.D. (2012) Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings. Funct. Ecol., 2010, 24:70–81.

Prior L.D., Williams R.J., Bowman D.M.J.S. (2010) Experimental evidence that fire causes a tree recruitment bottleneck in an Australian tropical savanna. Trop. Ecol. 26:595–603.

Quinn G.P. & Keough M.J. (2002) Experimental design and data analysis for biologists. Cambridge University Press.

Read J & Brown M. J. (1996) Ecology of Australian Nothofagus forests. – In: Veblen, T. T., Hill, R. S. and Read, J. (eds), The ecology and biogeography of Nothofagus Forests. Yale Univ. Press, 131–181.

Regelbrugge J.C. & Conard S.G. (1993) Modeling Tree Mortality Following Wildfire in Pinus ponderosa Forests in the Central Sierra Nevada of California. Int. J. W.Fire, 1993, 3(3):139-148.

Reyes O., Casal M., Rego C.F. (2009) Resprouting Ability of Six Atlantic Shrub Species. Folia Geobot, 2009, 44:19–29.

Runkle J.R. (1985) Disturbance Regimes in Temperate Forests in: White P.S. & Pickett S.T.A. (1985) Natural disturbance and patch dynamics: an introduction. The Ecology of Natural Disturbance and Patch Dynamics. Orlando FL, Academic Press. 3–13.

Russo S.E., Jenkins K.L., Wiser S.K., Uriarte M., Duncan R.P., Coomes D.A. (2010) Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand. Funct. Ecol., 2010, 24:253–262.

Ryan K.C. & Frandsen W.H. (1991) Basal Injury from Smoldering Fires in Mature Pinus Ponderosa Laws. Int. J. W. Fire, 1991, 2:107-118.

Salmon J.J. (1980) The trees of New Zealand. Reed Books, Birkenhead, Auckland.

Sterck F.J., Martınez-Vilalta J., Mencuccini M., Cochard H., Gerrits P., Zweifel R., Herrero A., Korhonen J.F.J, Llorens P., Nikinmaa E., Nole A., Poyatos R., Ripullone F., Sass-Klaassen U. (2012) Understanding trait interactions and their impacts on growth in Scots pine branches across Europe. Funct. Ecol., 2012, 26:541–549.

Sullivan J.J., Williams P.A., Timmins S.M. (2007) Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. NZ J. Ecol., 2007, 31(1):22-38.

Teskey R., Saveyn A., Steppe K., Mcguire M. (2007) Origin, fate and significance of CO_2 in tree stems. New Phyt., 177:17–32.

Timmins S.M. (1992) Wetland vegetation recovery after fire: Eweburn Bog, Te Anau, New Zealand. NZ J. Bot., 1992, 30:383-399.

Tyree M.T. & Sperry J.S (1989) Vulnerability of xylem cavitation and embolism Annu. Rev. Plant Phys. Mol. Bio., 1989, 40:19-38.

Uhl C. & Kauffmann J.B. (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. Ecol., 1990, 71(2):437-449.

Van Bloem S. J., Murphy P.G., Lugo A.E., Ostertag R., Costa M.R., Bernhard L.R., Colon S.M., Mora M.C. (2005) The influence of hurricane winds on caribbean dry forest structure and nutrient pools. Biotropica 37: 571–583.

VanderWeide B.L. & Hartnett D.C. (2011) Fire resistance of tree species explains historical gallery forest community composition. For. Ecol. & Mgmt., 2011, 261:1530–1538.

Van Nieuwstadt M.G.L. & Sheil D. (2005) Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. J. Ecol., 2005, 93:191–201.

Verdu M. (2000) Ecological and evolutionary differences between Mediterranean seeders and resprouters. J. Veg. Sc., 11:265-268.

Vesk P. A. & Westoby M. (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. J. Ecol., 92:310–20.

Vesk P.A. (2006) Plant size and resprouting ability: trading tolerance and avoidance of damage? J. Ecol., 2006. 94:1027–1034.

Vivian L. M., Doherty M. D., Cary G. J. (2010) Classifying the fire-response traits of plants: How reliable are species-level classifications? Austr. Ecol., 2010, 35: 264–273.

Waters D.A., Burrows G.E., Harper J.D.I. (2010) Eucalyptus Regnans (Myrtaceae): A fire-sensitive eucalypt with a resprouter epicormic structure. Am.J.Bot., 2010, 97(4): 545–556.

Weiner J., Campbell L.G., Pino J., Echarte L. (2009) The allometry of reproduction within plant populations. J. Ecol., 97:1220–1233.

Wells P.V. (1969) The relation between mode of reproduction and extent of speciation in woody genera of the California Chapparal. Evol. 23-2 (Jun1969): 264-267.

White P.S. & Pickett S.T.A. (1985) Natural disturbance and patch dynamics: an introduction. The Ecology of Natural Disturbance and Patch Dynamics. Orlando FL, Academic Press. 3–13.

Williams P.A. & Buxton R.P. (1989) Response to induced irradiance of 15 species of native and adventive shrub and tree sedlings from Eastern Canterburry. NZ J. Ecol. 12.

Wilson H. D. (1994) Regeneration of native forest on Hinewai Reserve, Banks Peninsula. The Royal Society of New Zealand 32:373-383.

Wilson B.G. & Witkowski E.T.F. (2003) Seed banks, bark thickness and change in age and size structure (1978-1999) of the African savanna tree, Burkea africana. Plant Ecol. 167:151–162.

Woolley L.P., Henkel T.W., Sillett S.C. (2008) Reiteration in the Monodominant Tropical Tree Dicymbe corymbosa (Caesalpiniaceae) and its Potential Adaptive Significance. Biotropica 40(1): 32–43 2008.

Zimmermann M.H. & Brown C.L. (1971) Tree structure and function. Springer, New York-Heidelberg-Berlin.

Zouhar K. (2005) Ulex europaeus. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2012, August 8].

APPENDIX

Plant Recording Form

Continuous number: ____________________ Tagging Nr.: _________________

Tagging Date: ___________ Position: ___________________________

GPS Position:________________ Species:__________________________ _____

Multistemmed: yes /no Nr. of stems: 1 2 3 4 >5

Height:_____________________________beneath/above/horizontal/telescopestack

Angles and distance: ________________________ Deciduous: O yes O no

[>2cm] d(30) / d (50) dbh(130):_______________________caliper/tape/diametertape
(to nearest mm) unit: cm / mm

BT(30) /BT(50)/BT(130): ____
(3x/at ridges) (<6cm 1/3 of the stem; >6cm at 1.3m)

Bark Texture: (1) smooth (2) very slight texture (0.5mm amplitude) (3) intermediate texture (0.5mm-2mm) (4) strong texture (2-5mm) (5) very coarse texture (>5mm amplitude)

Charheight: _________________________ (0) (1) <30cm (2) 30-130cm
(3) >130cm (50% blackening of the stem)

Burn Severity: (0) (1) (2) (3) (4) (5) Torch (black)
(brown) (green)

Topkill: (1) Topkilled – (2) not topkilled – (3) dead → Topkilled=no sprouting > 30cm

Resprout: yes / no Base <30 cm / Stem 30cm-1.3m / Canopy >1.3m

number of resprouts__________________ diameter__________ length__________

Leaf arrangement: opposite / alternate / clumped FI-Class: (u) (l) (m) (h)
Bark charring: (0) (1) (2) (3)

Charheight n-neighbors:____

Leaf length (cm):____

Leaf margin: entire – serrated – lobbed – undulate

Leaf hairs: yes / no many/some/ few underside Leave-venation:
pinn / palm

Photo Nr.:____